Outer Continental Shelf Environmental Assessment Program

Final Reports of Principal Investigators

Volume 43

June 1986

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Ocean Service
Office of Oceanography and Marine Assessment
Ocean Assessments Division
Alaska Office

U.S. DEPARTMENT OF THE INTERIOR
Minerals Management Service
OCS Study, MMS 86-0057

"Outer Continental Shelf Environmental Assessment Program Final Reports of Principal Investigators" ("OCSEAP Final Reports") continues the series entitled "Environmental Assessment of the Alaskan Continental Shelf Final Reports of Principal Investigators."

It is suggested that sections of this publication be cited as follows:

Johnson, K. W., C. H. Nelson, and H. L. Mitchell. 1983. Assessment of gray whale feeding grounds and sea floor interaction in the Northeastern Bering Sea. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):1-161

Nerini, M. K., L. Jones, and H. L. Braham. 1980. Feeding ecology of the gray whale in the northern Bering Sea. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):163-207

Thomson, D. H. (ed.). 1984. Feeding ecology of the gray whale (*Eschrichtius robustus*) in the Chirikof Basin, summer 1982. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):209-460

Individual sections of the above report may be cited as follows:

Thomson, D. H. 1984. Project rationale, design, and summary. *In*: D. H. Thomson (ed.), Feeding ecology of gray whales (*Eschrichtius robustus*)in the Chirikof Basin, summer 1982. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):209-460

Thomson, D. H. 1983. Distribution, production, and ecology of gray whale prey species. *In*: D. H. Thomson (ed.), Feeding ecology of gray whales (*Eschrichtius robustus*)in the Chirikof Basin, summer 1982. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):209-460

Miller, G. W. 1983. Distribution and abundance of gray whales. *In*: D. H. Thomson (ed.), Feeding ecology of gray whales (*Eschrichtius robustus*) in the Chirikof Basin, summer 1982. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):209-460

Würsig, B., D. A. Croll, and R. S. Wells. Assessment of gray whale feeding grounds and sea floor interaction in the northeastern Bering Sea. *In*: D. H. Thomson (ed.), Feeding ecology of gray whales (*Eschrichtius robustus*) in the Chirikof Basin, summer 1982. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):209-460

Thomson, D. H. and L. R. Martin. Feeding ecology of gray whales in the Chirikof Basin. *In*: D. H. Thomson (ed.), Feeding ecology of gray whales (*Eschrichtius robustus*) in the Chirikof Basin, summer 1982. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):209-460

Frost, K. J., L. F. Lowry, and R. R. Nelson. 1983. Investigations of Belukha whales in coastal waters of western and northern Alaska, 1982-1983: marking and tracking of whales in Bristol Bay. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):461-585

Stewart, B. S., F. T. Awbrey, and W. E. Evans. 1983. Belukha whale (*Delphinapterus leucas*) responses to industrial noise in Nushagak Bay, Alaska: 1983. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):587-616

Fishman, P. A., R. S. Caldwell, and A. H. Vogel. 1985. Lethal and sublethal effects of oil on food organisms (Euphausiid: *Thysandessa raschii*) of the bowhead whale. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 43(1986):617-702

OCSEAP Final Reports are published by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Office of Oceanography and Marine Assessment, Ocean Assessments Division, Alaska Office, Anchorage, and primarily funded by the Minerals Management Service, U.S. Department of the Interior, through interagency agreement.

Requests for receipt of OCSEAP Final Reports on a continuing basis should be addressed to:

NOAA-OMA-OAD
Alaska Office
701 C Street
P.O. Box 56
Anchorage, AK 99513

OUTER CONTINENTAL SHELF
ENVIRONMENTAL ASSESSMENT PROGRAM

FINAL REPORTS OF PRINCIPAL INVESTIGATORS

Volume 43

June 1986

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Ocean Service
Office of Oceanography and Marine Assessment
Alaska Office

U.S. DEPARTMENT OF THE INTERIOR
Minerals Management Service
Alaska OCS Region
OCS Study, MMS 86-0057

Anchorage, Alaska

The facts, conclusions, and issues appearing in these reports are based on research results of the Outer Continental Shelf Environmental Assessment Program (OCSEAP), which is managed by the National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and funded (wholly or in part) by the Minerals Management Service, U.S. Department of the Interior, through an Interagency Agreement.

Content of these reports has not been altered from that submitted by the Principal Investigators. In some instances, minor grammatical, spelling, and punctuation errors have been corrected to improve readability; some figures, charts, and tables have been enhanced to improve clarity in reproduction.

Outer Continental Shelf Environmental Assessment Program

Final Reports of Principal Investigators

VOLUME 43 JUNE 1986

CONTENTS

ASSESSMENT OF GRAY WHALE FEEDING GROUNDS AND SEA FLOOR INTERACTION IN THE NORTHEASTERN BERING SEA

by

Kirk R. Johnson, C. Hans Nelson, and
Heidi-Lynn Mitchell

U.S. Geological Survey

Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 634

July 1983

TABLE OF CONTENTS

LIST OF FIGURES

Figure 8. Histogram of Gray whale gape lengths compiled from Rice and Wolman (1971); Dale Rice, NMML, pers. comm., 1982; Steve Leatherwood, Hubbs-Seaworld Research Assoc., Pers. Comm. 1982. In cases in which only head length was known, gape length was computed as 75% of head length.

Figure 9. Water masses in the northeastern Bering Sea. The Alaskan Coastal Water (14-31.5 $^{o}/oo$, 8^{o} C) occupies the eastern portion of the map area, the Bering Shelf Water (sometimes called Modified Shelf Water, 31.5-33 $^{o}/oo$, $0\text{-}4^{o}$ C) covers the central area, and the Anadyr Water (33 $^{o}/oo$, $1\text{-}3^{o}$ C) occurs on the western portion of the map area. From Nelson et al., 1981.

Figure 10. Offshore water circulation and maximum bottom current velocities from available measurements in the northeastern Bering and sourthern Chukchi Sea. From Nelson et al., 1981.

Figure 11. (A) Histogram of bottom current speeds from long-term current meter, LD-3A. July-Sept., 1978. (B) Cumulative frequency graph of bottom current speeds from long-term current meter LD-3A. (C) Daily bottom current speeds from long-term current meter, LD-3A. Location of current meter shown in Figure 5.

Figure 12. Preliminary map of the northeastern Bering shelf surficial geology (modified from Nelson, 1982).

Figure 13. Mean grain size (Folk and Ward) for surface sediment in Norton Basin, northeastern Bering Sea.

Figure 14. Percent sand in surface sediment of Norton Basin, northeastern Bering Sea.

Figure 15. Sorting values (Folk and Ward) for surface sediment in Norton Basin, northeastern Bering Sea.

Figure 16. Potentially hazardous areas of the northeastern Bering Sea. Current scour depressions occur in the area of intense current activity off the Yukon Delta. From Thor and Nelson (1981).

Figure 17. 105 kHz sonograph of (A) ice scour from Norton Sound, (B) current scour depressions from the Yukon Delta front, (C) circular gas expulsion craters from Norton Sound. Arrows show location of features in B and C.

Figure 18. (A) Radiograph of a box core, showing the v-shaped burrows of the amphipod, Ampelisca macrocephala. The core was taken from the fine transgressive sand body in the center of Chirikov Basin at a water depth of 27 m. (B) Plan view photo of the box core top taken immediately after collection. Slit-like, mucus-lined burrows are typical of the amphipod Ampelisca macrocephala.

Figure 19. Distribution of ampeliscid amphipods in the northeastern Bering Sea. Compiled from USGS cruises 1960-1980, Stoker (1978), Nerini (1980), Feder and Jewett (1981), Thomson (1983).

Figure 20. (A) Distribution of gray whale sightings in the northeastern Bering Sea from June - August 1978 (From Consiglieri, Braham, and Jones, 1980). (B) Ship and aerial tracklines completed for whale observations during June - August 1978 (From Consiglieri, Braham, and Jones, 1980).

Figure 21. Sonograph of several long, narrow walrus feeding furrows, 100 kHz, eastern Chirikov Basin (see arrows).

Figure 22. Sonograph of a single walrus feeding furrow; note the large rocks on the record, northern Chirikov Basin (see arrows for furrow).

Figure 23. Sketches of three types of bottom pits, attributed to Gray whale feeding and subsequent current scour, based on observations from side scan sonar and by SCUBA divers in Chirikov basin and the nearshore areas of St. Lawrence Island. All drawings are to the scale shown for Type 1.

Figure 24. Sonograph of area near station Dog 7, 105 kHz, Type 1, close-up of a multiple suction feeding event (see arrow). Sonograph location is shown in Figure 7.

Figure 25. Sonograph of station Dog 8, 105 kHz, Type 1, current-scour enlarged and oriented pits with fresh multiple suction feeding events (see arrow). Sonograph location is shown in Figure 7.

Figure 26. Sonograph of station Dog 1, 105 kHz, Type 1, current-scour enlarged and oriented pits. Sonograph location is shown in Figure 7.

Figure 27. Sonograph of station Dog 14, 105 kHz, Type 1, current-scour enlarged pits. Sonograph location is shown in Figure 7.

LIST OF TABLES

ABSTRACT

A dense ampeliscid amphipod community in Chirikov Basin and around St. Lawrence Island in the northeastern Bering Sea has been outlined by summarizing biological studies, analyzing bioturbation in sediment samples, and examining sea floor photos and videotapes. The amphipod population is associated with a homogeneous, relict fine-grained sand body 0.10-1.5 m thick that was deposited during the marine transgression over the Bering land bridge 8,000-10,000 yr B.P. Modern current and water mass movements and perhaps whale feeding activity prevent modern deposition in this area.

The distribution of the transgressive sand sheet, associated amphipod community and feeding gray whales mapped by aerial survey correlate closely with three types of sea-floor pits observed on high (500 kHz) and low (105 kHz) resolution side-scan sonar; they are attributed to gray whale feeding traces and their subsequent current scour modification. The fresh and modified feeding pits are present in 22,000 km^2 of the basin and they cover a total of 2 - 18% of the sea floor in different areas of the feeding region. The smallest size class of pits approximates whale mouth gape size and is assumed to represent fresh whale feeding pits. Fresh feeding disturbance of the sea floor is estimated to average about 5.7% for a full feeding season. Combined with information that 34% of the measured benthic biomass is amphipod prey species, and calculating the number of gray whale feeding days in the Alaskan waters plus amount consumed per day, it can be estimated that Chirikov Basin supplies a minimum of 5.3% of the gray whale's food resource in the Bering Sea and Arctic Ocean. If 100% of the Chirikov biomass is assumed to be utilized as a whale food source and a maximum of 50% of the fresh feeding features are assumed to be missed because they parallel side-scan beam paths,then a maximum whale food resource of 32 - 42% is possible in northeastern Bering Sea. Because of side-scan techniques and higher biomass estimates, a reasonable minimum estimate of the total whale food resource in northeastern Bering Sea is 10%.

These data show that side-scan sonar is a powerful new technique for analyzing marine mammal benthic feeding grounds. Sonographs reveal that the gray whales profoundly disturb the substrate and initiate substantial further erosion by bottom currents, all of which enhances productivity of the prey species and results in a "farming of the sea floor". In turn, because of the high concentration of whale prey species in a prime feeding ground that is vulnerable to the development of petroleum and mining for sand, great care is required in the exploitation of these resources in the Chirikov Basin.

INTRODUCTION

The California Gray Whale (Eschrichtius robustus) is perhaps the most resilient and versatile of the great whales. Twice hunted to near-extinction levels (Gilmore, 1955), the gray whales have rebounded to near pre-exploitation levels. At present, approximately 18,000 gray whales exist in the eastern Pacific Ocean (Herzing and Mate, 1981; NMFS, 1981; Rugh, 1981; NMML, 1980; Reilly, Rice, and Wolman, 1980). An historic stock, the Korean Gray whales which inhabited the western Pacific Ocean are presumed extinct (Rice and Wolman, 1971) or at least highly depressed (Brownell, 1977). Subfossil remains and scanty whaling records verify the existence of an Atlantic stock which is also extinct (Mead and Mitchell, in press).

Each year the gray whales migrate from their winter breeding and calving lagoons in Baja California, Mexico to their summer feeding grounds in the Bering, Chukchi, and Beaufort Seas between Alaska and Siberia. For most of this 6000 km migration, the whales remain within sight of land. This coastal affinity, which at one time nearly spelled their doom by allowing easy access for whalers, now allows them to be thoroughly studied.

Approximately one million square kilometers in the Bering, Chukchi, and Beaufort Seas provide the major foraging grounds for the gray whales (Frost and Lowry, 1981; Votrogov and Bogoslavskaya, 1980; Rice and Wolman, 1971; Pike, 1962; Zenkovich, 1934; Scammon, 1874). Our study covers an important part of their summer feeding grounds, the Chirikov basin in the northeastern Bering Sea (Fig. 1).

The California Gray Whale is the only type of whale that relies predominantly on a benthic food source. Feeding on infaunal organisms, mainl

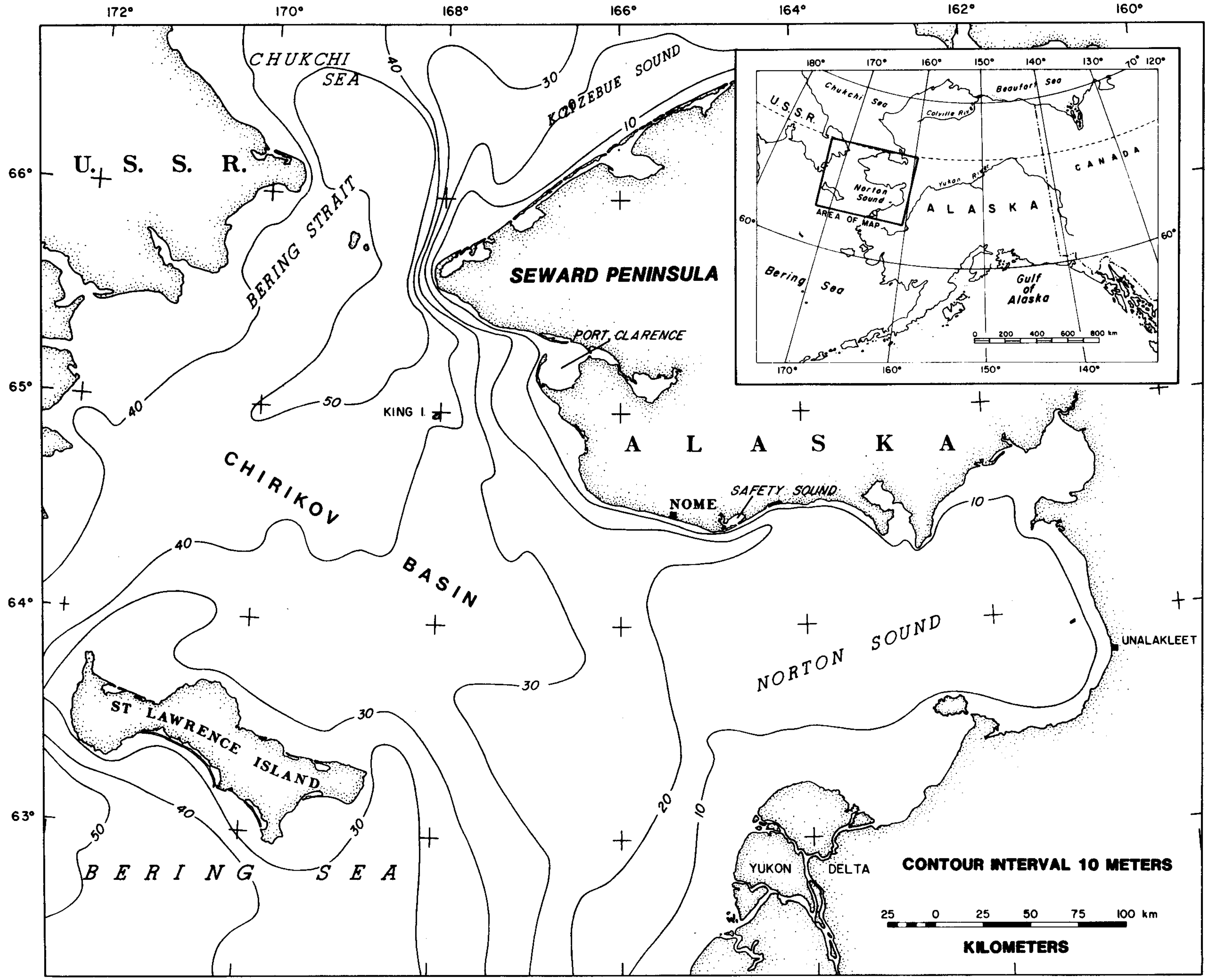


Figure 1 Generalized bathymetry of the northeastern Bering Sea in 10-m contour intervals.

Ampeliscid amphipods, disturbs the sediment surface and leaves a record preserved in the substrate. We use this record to map gray whale feeding grounds and understand the method of gray whale feeding.

To interpret this record we assess all of the main components of the system, including the distribution and feeding ecology of the gray whales, the distribution and ecology of the prey species, their oceanographic setting, the nature and extent of the surficial sediment types that are the habitat of the prey species, and, most importantly, the types and distribution of feeding traces left in the sea floor by foraging gray whales.

Physical processes also produce features on the sea floor such as ice gouges, current scour depressions, and biogenic gas expulsion craters (Larsen et al., 1979; Nelson et al., 1980; Thor and Nelson, 1981). These features have been mapped so they are not confused with whale feeding traces.

Both the physical features and the gray whale feeding traces have been inspected by underwater video, SCUBA divers, and side-scan sonar. The side-scan sonar is a planographic sea-floor mapping device which generates sonographs of the sea floor that are analogous to aerial photographs of land areas (Fig. 2). The side-scan sonar allows the size, density, distribution, and modification histories of the whale feeding traces to be approximated. These approximations can then be used to estimate the extent and degree of utilization of the gray whale feeding grounds in Chirikov basin.

Through a more complete knowledge of gray whale feeding and potential hazards in their northern feeding grounds, ecologically sound decisions can be made concerning the exploitation of resources on the Alaskan continental shelf.

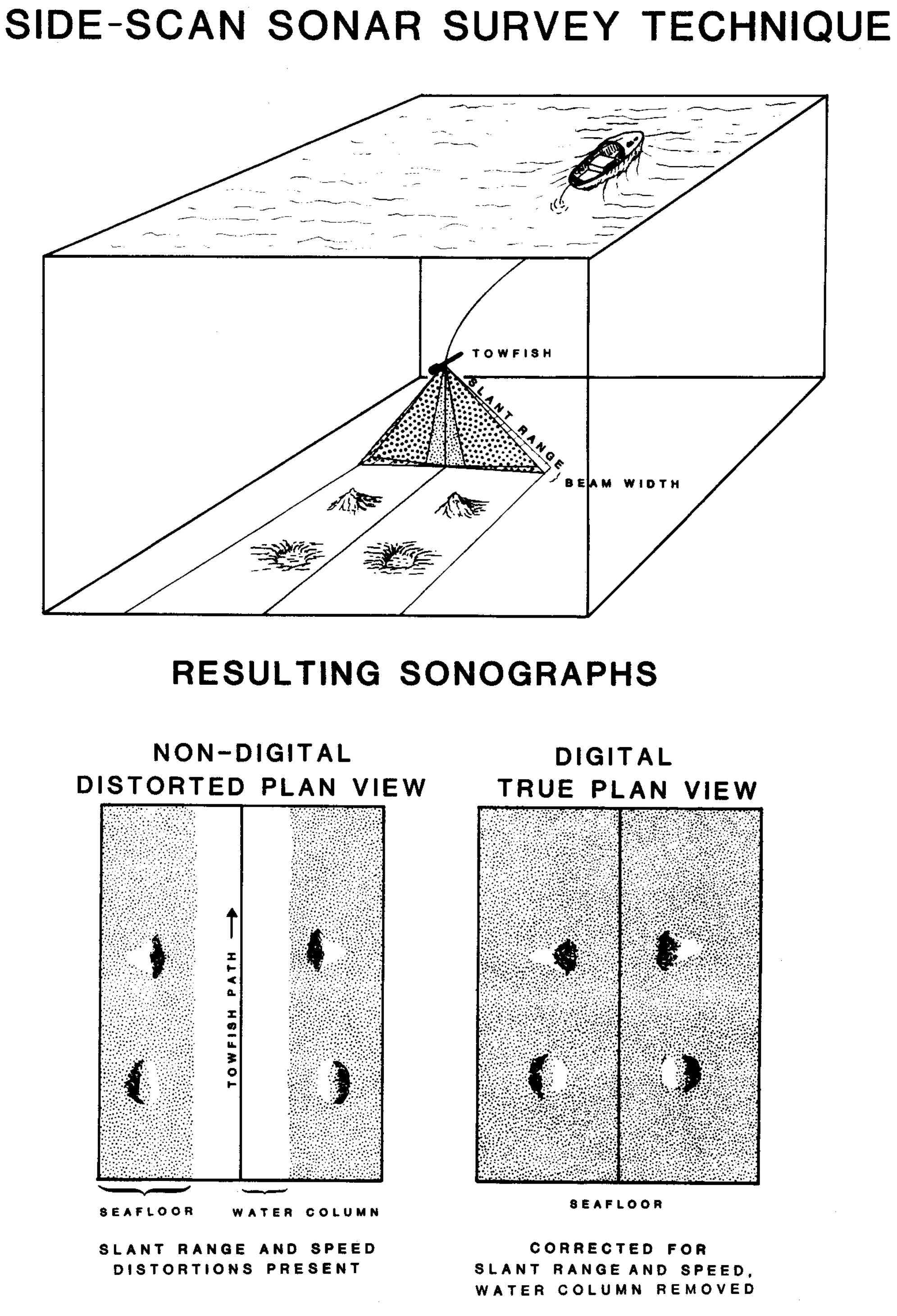


Figure 2 Schematic diagram of side-scan sonar survey technique.

TERMINOLOGY

A new terminology is required to define whale feeding features on the bottom. They may be called feeding features or feeding traces because these names have no implications as to the mechanism of their origin other than that they were caused by feeding. It is erroneous to call them feeding gouges or whale gouges for this implies direct scooping of sea-floor sediment. The term "whale bites" also suggests that the whales scoop up the sediment with their mouths, which is not likely. Also, it is erroneous to call them feeding furrows because this implies that the displaced sediment has been transferred to the side of the pit and not simply removed and dispersed in the water column as is the true case. The term "whale scour" implies some relationship to current or abrasive processes and does not accurately reflect the true process of sea-floor interaction by the whales. The terms "whale depressions", "bottom depressions", "sea-floor depressions", or "feeding depressions" all imply compaction of the sediment instead of its excavation. The word "depression" can be used, however, to describe places where whale flukes or bodies have made contact with the sea floor during the act of feeding.

Since benthic suction is the postulated mode of feeding, "multiple suction feeding events", "suction events" or "feeding pits" are all acceptable terms. For the description of these pits, the word "elongate" simply implies a length axis much greater than width axis. For specific definitions of shape, "wide elliptic" is used for pits whose L/W ratio is less than 2.3, "elliptic" for pits whose L/W ratio is between 2.3 and 3.0, and "narrow elliptic" for pits whose L/W ratio is greater than 3.0. These terms have been modified from Hickey (1973) who used them to describe leaf blade shape for dicotyledonous plants.

The large pits caused by scour enlargement of fresh feeding pits are known as "current-scour-enlarged pits", "current-enlarged pits", "scour pits", "current modified features", or "modified whale feeding pits" because their origin is both whale- and current-related.

The combination of fresh whale feeding pits, partially modified whale pits and current-scour-enlarged pits (considerably modified pits) is known as "total bottom disturbance". For the purposes of this paper, other bottom features, such as ice scour are not included in the calculation of total bottom disturbance. "Percent total bottom disturbance" is the percentage of sea floor affected by fresh feeding pits and current-scour-enlarged pits.

METHODS

Substrate

The data utilized in this study can be grouped into two categories. In the first are data derived from direct sampling or observation of the sea floor. These include box cores, grab samples, SCUBA diver observations, underwater still photographs and underwater television (Appendix A-1). The second group is remote sensing data gathered almost entirely by side-scan sonar (Figs. 2, 3).

Substrate parameters such as grain-size distribution and sorting were compiled from bottom samples collected by University of Washington and USGS cruises from 1960-1980 (Hess et al., 1981). Box core radiographs of amphipod bioturbation (Nelson, et al., 1981) combined with observations of

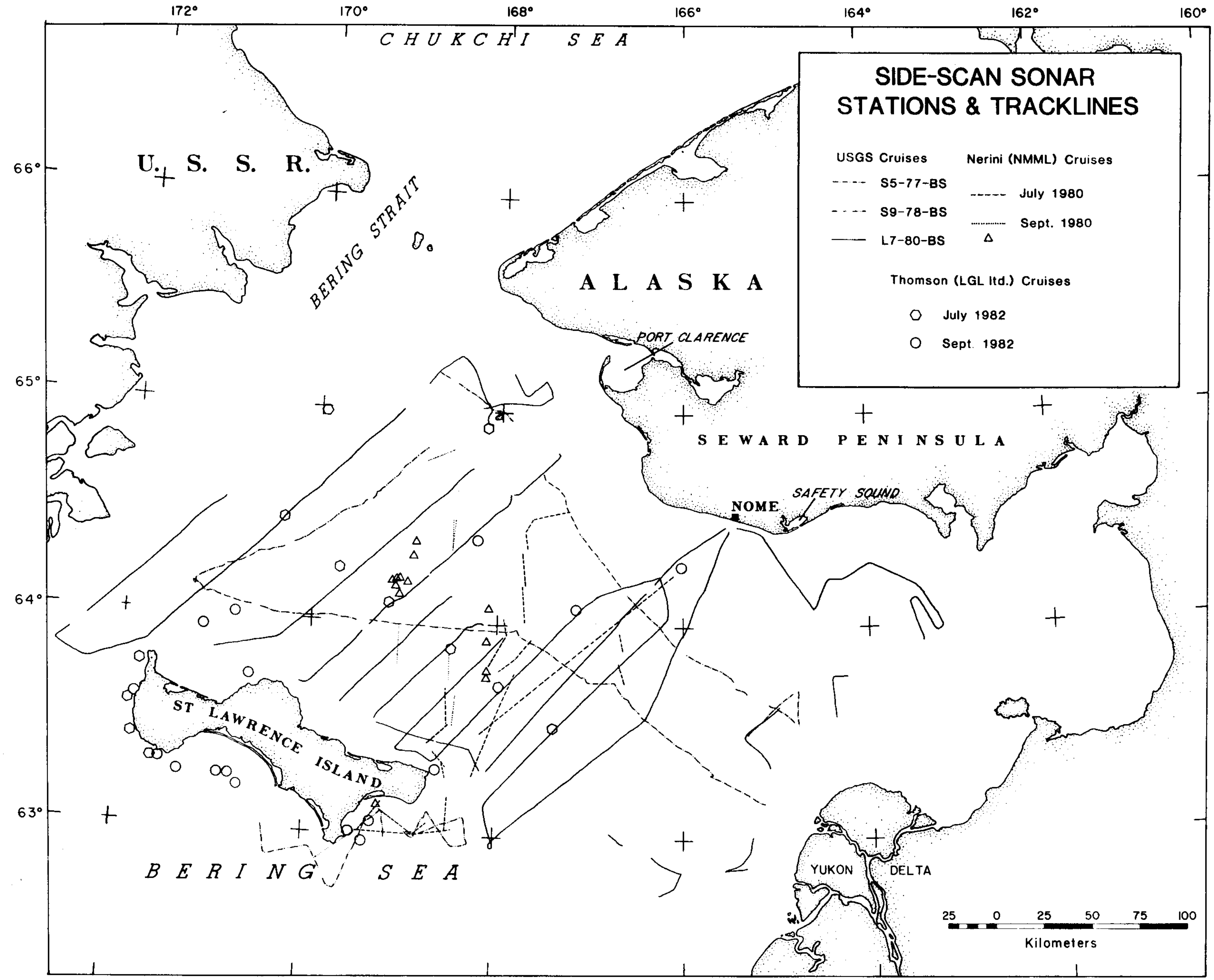


Figure 3 Location of 100, 105, and 500 kHz side-scan sonar tracklines and site survey stations from USGS cruises (S5-77-BS, S9-78-BS, L7-80-BS), NMML cruises (Mary Nerini, 2 cruises, 1980), LGL ltd. cruises (Denis Thomson, 2 cruises, 1982).

amphipods in bottom samples, sea-floor photographs, and underwater television qualitatively established the presence or absence of the amphipod community. Bottom samples with quantitative biological data available from Stoker (1978), Nerini et al. (1980), Feder and Jewett (1981), and Thomson (in press) were integrated with the USGS data base collected from 1968-1980. A total of 221 stations in Chirikov Basin were used in the assessment of the amphipod community, whereas 683 stations in Chirikov Basin and Norton Sound contributed to the substrate data base (Fig. 4) (Hess et al., 1981). Communication with divers from two cruises in 1980 led by Mary Nerini (NMML-NMFS-NOAA) and two cruises in 1982 led by Denis Thomson (L.G.L. Ltd.) provided insight as to the nature of the benthic biota and sea-floor depressions believed to be made by the gray whale.

Bottom current speed data from central Chirikov Basin were compiled from long-term current meters (Fig. 5) (J. Schummacher, NOAA-PMEL pers. comm., 1982; Cacchione and Drake, 1979) and bottom current measurements made during collection of substrate samples (Figs. 4, 5) (Larsen, Nelson, and Thor, 1979). These data were used to verify locations where current speeds are high enough to enlarge bottom features initiated by whale feeding.

Techniques and problems of side-scan analysis

The observation of whale feeding features on the sea floor of Chirikov Basin is best accomplished by SCUBA-diving. Unfortunately, harsh conditions, water depth, poor visibility (< 1 m), and size of the basin make it difficult for SCUBA divers to do extensive surveys. Though divers from the 1980 NMML cruise (Nerini et al., 1980) did dive in the central portion of the basin, most divers have kept to the shallower, inshore waters near St. Lawrence

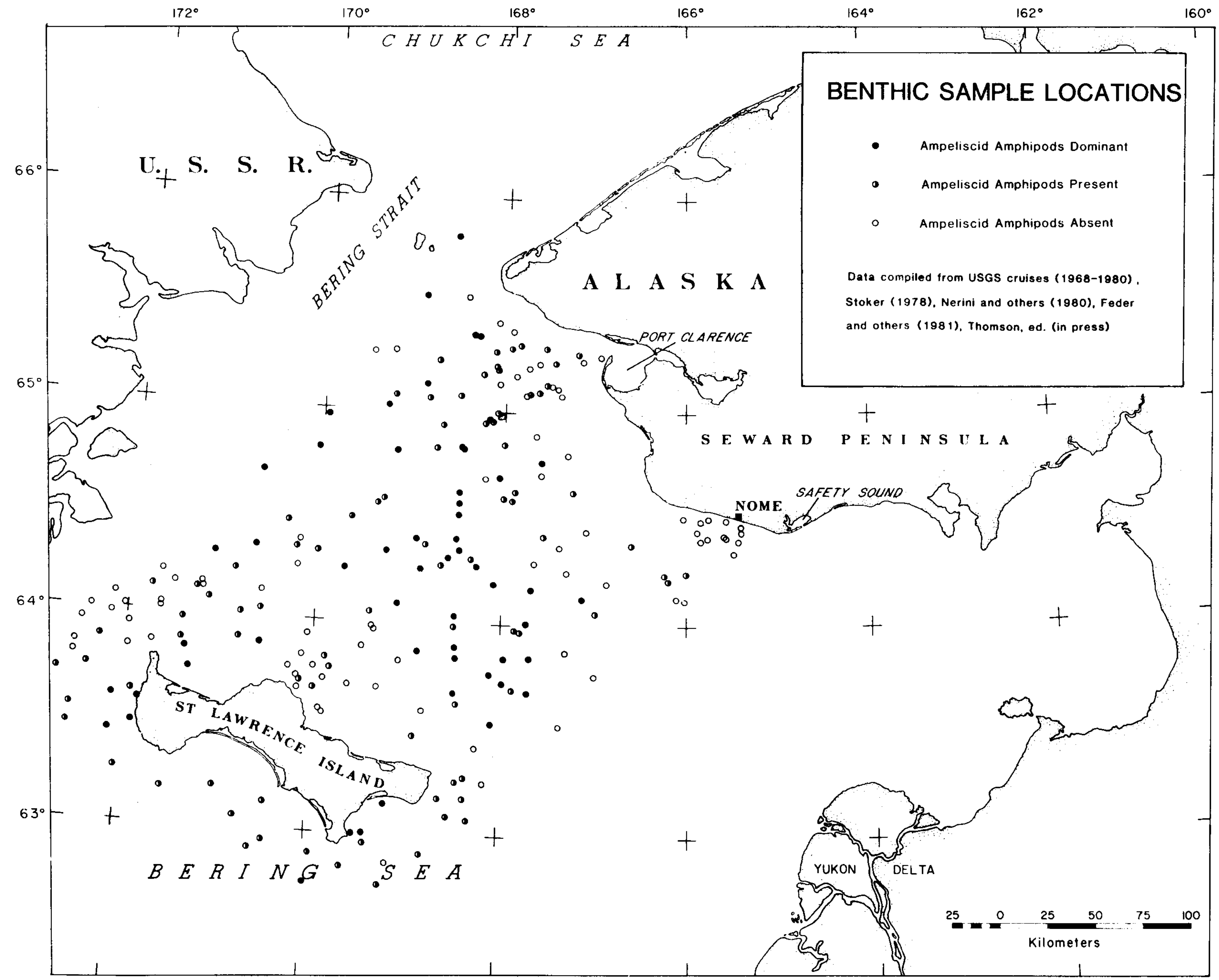


Figure 4 Location of benthic samples used to establish the extent of the Ampeliscid amphipod population in the northeastern Bering Sea.

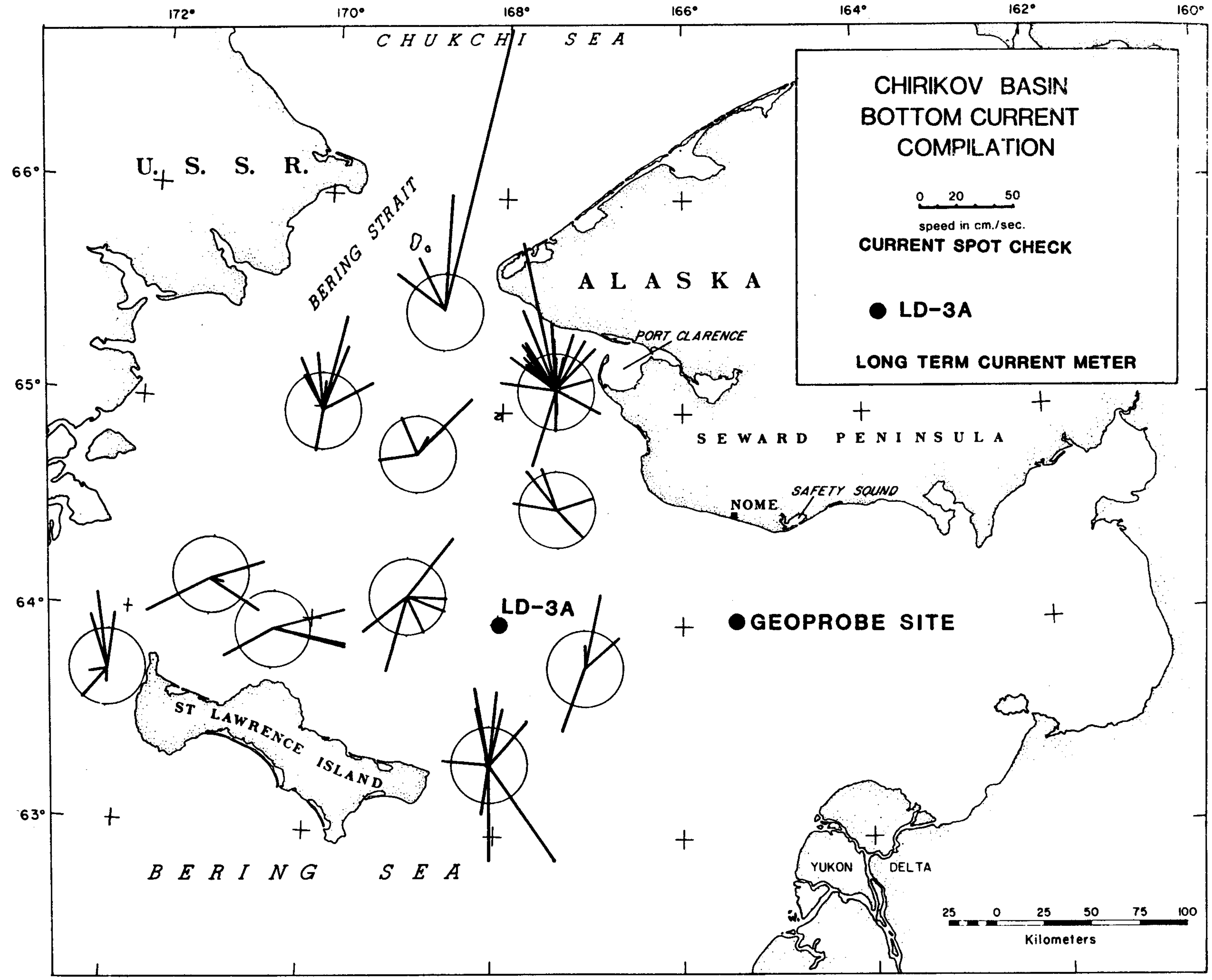


Figure 5 Compilation of spot check bottom current speeds in Chirikov Basin and location of long-term current meter, LD-3A. Each rose diagram has a radius of 20 cm/sec, the approximate current speed needed to initiate movement in a very fine sand. Compiled from USGS cruises, 1960-1980; Fleming and Heggarty, 1961; Husby, 1971; McManus and Smyth, 1970; Nelson and Hopkins, 1972; Nelson, Rowland, Stoker, and Larsen, 1981.

Island and Seward Peninsula (Oliver, Slattery, Silberstein and O'Connor, 1983; Thomson, in press; Nerini et. al., 1980; Nerini and Oliver, in press). It was this need for a regional but accurate bottom surveying device that suggested use of side-scan sonar. This study has placed an emphasis on the regional aspects of the whale feeding while interpreting the side-scan data. Site-specific work on pit morphology and the amount of prey consumed per pit has been undertaken by SCUBA divers who can directly measure and sample the pits (Oliver, Slattery, Silberstein and O'Connor, 1983, and writ. comm., 1983; Thomson, in press; Nerini, 1981; Nerini et al., 1980).

The possibility of side-scan sonar providing data on whale feeding traces was first noticed while Nelson was conducting OCSEAP geohazard surveys throughout Chirikov Basin. The appearance of long, sinuous furrows unlike any known physically created features suggested that marine mammal interaction with the sea floor was indeed discernible by side-scan sonar. Nerini (1980), cooperating with USGS scientists used side-scan sonar successfully on her two cruises studying gray whales. Since then, side-scan sonar has received more attention as a tool for the description and mapping of large-scale biological processes.

Three different degrees of resolution were utilized to obtain side-scan records. The vast majority of coverage was provided by the 105 kHz digital Seafloor Mapper produced by EG & G Environmental Equipment (Fig. 2). Additional 100 kHz non-digital data were gathered using a system manufactured by Klein Associates, Inc. Site-specific side-scans with a high-resolution (500 kHz) non-digital Klein system were undertaken by Nerini (NMML-NMFS-NOAA) on two cruises in 1980 and by Thomson (L.G.L. Ltd.) during two cruises in 1982. On the second Thomson cruise (September 1982), Kirk Johnson was aboard and involved in all side-scan data collection. Both of these data bases were made available to the USGS. In all, roughly 4500 line-km of side-scan data were collected from the Chirikov Basin and nearshore areas of St. Lawrence Island (Fig. 3).

The side-scan systems were calibrated during the second Thomson cruise, (Sept. 1982) on the NOAA R/V Discoverer by towing the high-resolution 500 kHz system simultaneously with the low-resolution 100 kHz system. The systems were towed off opposite sides of the ship's fantail so that their inner channels overlapped. In this way the same bottom features were obtained on each record and could be compared. A further calibration was performed by towing the 500 kHz side-scan system behind a small boat and past a buoy which marked areas previously inspected by SCUBA divers. Thus, direct diver observations could be compared with the records to establish their accuracy. The 500 kHz system also was used to scout potential dive sites. In this manner, the 100 and 105 kHz systems were linked with actual bottom observations. This is an important calibration because the majority of the continuous line side scan was collected with a 105 kHz system. A more thorough treatment of these side-scan operations can be found in Thomson (in press).

Side-scan sonar is a sonar device which produces a plan view of the sea floor by sending out a set of radiating sound beams which are gated to specify a certain lateral slant range (Fig. 2). The beams are sent out from a transducer known as the tow fish which is towed behind a ship. As the sound bounces off the sea floor it is picked up by the tow fish and transmitted up the tow cable to the recorder/printer aboard ship. A strong return signal caused by a strong reflector such as a rock or abrupt wall will be printed dark. A weak return from a weak reflector such as fine-grained sediment or an acoustic shadow behind a strong reflector will print light. Thus, a boulder on the sea floor would print with a dark return (from the direct reflection of the boulder) adjacent to a light patch (the acoustic shadow of the boulder), the dark return being nearer the center of the record (and the tow-fish trace) than the light patches. Conversely, a hole in the sea floor would print as a light patch (the acoustic shadow of the lip of the hole) nearer the center of the record and a dark patch (the strong reflection of the far wall of the hole) adjacent to it. The whale feeding traces show up as pits of varying sizes in the sea floor.

It is important to review the limitations of side-scan. The description of features from the side-scan record remains subjective and sensitive to weather and instrument conditions at the time of data collection. In addition to recording the surface of the sea floor, the side-scan system measures tow-fish height above the sea floor, tow-fish depth below the sea surface, as well as the sometimes erratic motion of the tow fish itself. In rough weather, the ship motion from swells is transmitted down the cable as a series of jerks and slacks and results in uneven accelerations of the tow fish. This distortion bends otherwise straight features into S-shaped folds (Fig. 6). Because of these factors, all measurements of whale-related features in this report were made from records taken during calm seas to minimize distortions. Distorted records are still valid for the qualitative mapping of general feature type and density.

The lateral resolution of the side-scan system is generally considered to be 1/400 of the lateral slant range (Klein Associates, Inc.,1982, EG & G Environmental Equipment, Inc.). Thus, with a slant range of 100 m, a feature

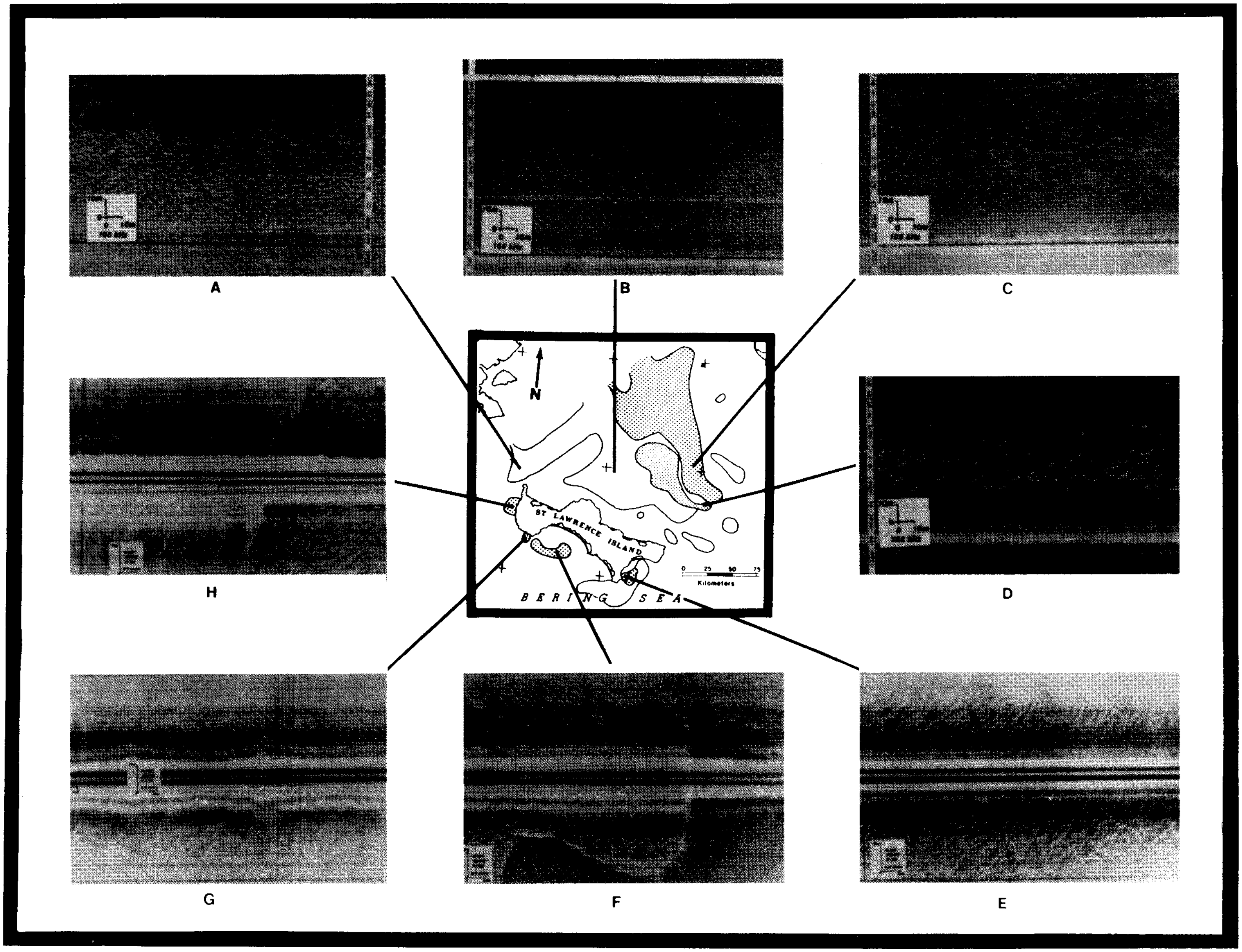


Figure 6 Locations and photographs of side-scan sonographs showing the three bottom pit types attributed to gray whale feeding and subsequent current scour. (A) 105 kHz, type 3, dense, wide elliptic pits (B) 105 kHz, type 3, sparse, wide elliptic pits (C) 105 kHz, type 2, dense, elongate (narrow elliptic) pits (D) 105 kHz, type 1, current enlarged pits showing regional lineation (E) 500 kHz, type 1, current enlarged pits showing regional lineation (F) 500 kHz, type 2, elongate (narrow elliptic) pits in inner shelf, fine-grained, transgressive sand adjacent to and overlying coarse basal transgressive sand which has been worked into sand waves. Note the sinuous distortion of sand waves and elongate pits due to wave swell effect on the side-scan sonar tow fish. (G) 500 kHz, type 1, current enlarged pits (H) 500 kHz, type 2, elongate (narrow elliptic) pits (left half of sonograph), fuzzy pit margin and lack of relief shadows indicate infilling by finer-grained sediment. Rock outcrop occupies the right half of the sonograph.

of 25 cm on an axis normal to the trackline can be discerned. The measurement of an object parallel to the trackline is subject to some distortion due to the width of the outgoing beam. On a high-resolution 500 kHz system operating at a lateral range of 37.5 m this beam error is approximately ± 10 cm. On a lower resolution 100 or 105 kHz system with a 100 m range, this error may grow to be substantial and though the system can discern objects to 0.5 m diameter which lie parallel to the trackline, these objects will probably be printed larger than they actually are. This applies mainly to features less than 1.7 m long (Jim Glynn, Klein Assoc., Inc.,Salem, N.H., pers. comm., 1982).

A result of these factors is the over-representation of features in the 1.5-2 m range. Thus, for all measurements made in the quantitative portion of this report, features less than 2.0 m in length have significant error bars and their primary value is obtained when they are used relative to one other and not on an absolute scale. Beam width error also may stretch some of the larger features but as the feature size increases and the range of error stays the same, the percent error decreases. Consequently, for features less than 5 m in length there may be noticeable error. Again the relative measurements are of more value than the absolute ones.

Another limitation of side-scan sonar is that it misses some of the objects whose strong reflecting portions are not parallel to the trackline. Thus, certain features such as furrows might not show up on the record if the beam was shot down the length of the furrow and not off one of the walls parallel to the tow path (Fig. 2). On the side-scan records, long narrow furrows and small (less than 5 m long) features show a marked trend of being oriented parallel or subparallel to the trackline. This parallel orientation is due to the stretching of small features by the beam width error and the over-representation of trackline parallel features. The result is an under-representation of features that are not parallel to the trackline. This causes estimates of apparent feature density which are smaller than the true density values. Up to 50% of the smaller features may be missed by this form of side-scan inaccuracy.

Though depth or height of features can be calculated from side-scan records (Flemming, 1976), the degree of accuracy in this calculation is too low to obtain depths on such shallow features as the whale feeding traces. Depths of feeding pits, when mentioned, are from SCUBA diver operations.

Discussion thus far has centered on the digitized side-scan systems from which all quantitative data were gathered. In a digital system, corrections are automatically made for the slant range distortion (relative to the tow-fish height above sea floor) and the trackline distortion (printer paper feed speed vs. ship speed). In a non-digital system, these corrections must be made by hand from the records. For consistency and convenience, all measurements used for quantitative purposes were taken from the 105 kHz digital system. Data from the non-digitized 100 kHz and 500 kHz systems were used for qualitative mapping and comparison with diver observations, and calibrations of larger scale features with those of the 105 kHz digital records.

Measurements and statistical techniques

The bottom features have been quantified from the EG & G 105 kHz digital sonographs in the following manner: 16 widely scattered areas of bottom features were selected in which the records were collected in calm seas and are of high quality (Fig. 7, Table 1). In each area a minimum of 50, but

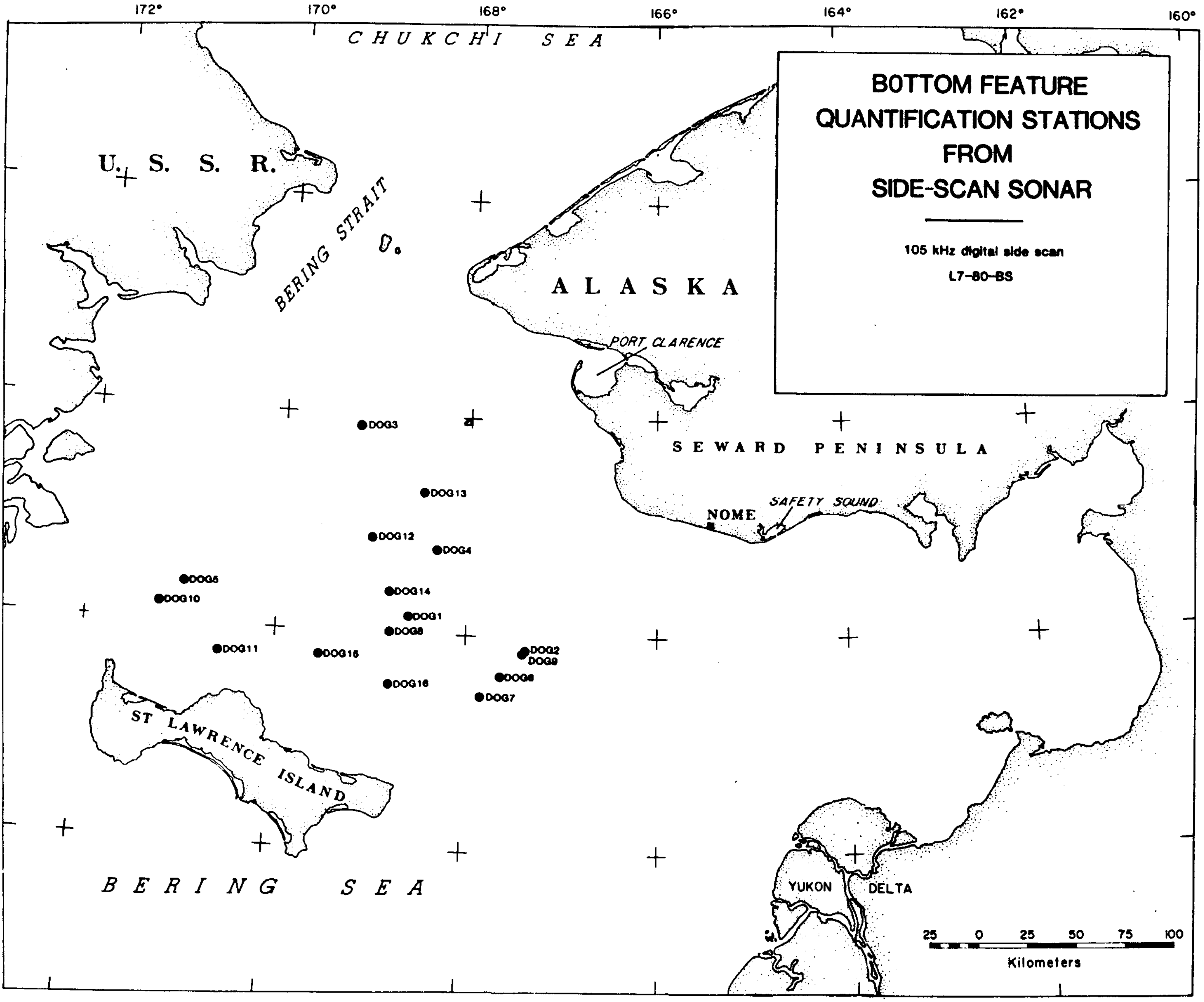


Figure 7 Location of bottom feature quantification stations from 105 kHz digital side-scan sonographs collected by USGS cruise. L7-80-BS

TABLE 1

LOCATION OF 105 kHz DIGITAL SIDE-SCAN QUANTIFICATION STATIONS

STATION	ROLL	DAY	TIME	LINE	BEARING IN DEGREES
DOG 1	42	JD238	00:30:06	55	45
DOG 2	18	223	08:50:00	35	--
DOG 3	26	229	01:15:00	49	229
DOG 4	34	233	10:35:00	49	228
DOG 5	28	229	14:26:17	47	236
DOG 6	19	223	11:21:00	35	240
DOG 7	19	223	12:35:40	35	233
DOG 8	41	237	22:54:39	55	40
DOG 9	18	223	09:04:52	35	240
DOG 10	29	229	15:50:14	47	229
DOG 11	38	234	21:42:00	51	50
DOG 12	39	235	04:56:55	51	48
DOG 13	40	235	08:01:32	51	47
DOG 14	40	233	18:30:35	49	232
DOG 15	36	234	03:18:52	49	228
DOG 16	43	238	11:38:00	58	233
TATE 1	01-B2-NC	Russian River sector			

All DOG stations are from USGS cruise L7-80-BS.
TATE 1 station is from S1-82-NC Cacchione N. California code 1 geology cruise.

usually 64 or more, features were measured. The measured parameters are length, width, density (of pits per 1875 m^2), and in some cases, orientation. From these numbers, area (area = length x width x 2/3) and length/width ratios were calculated. All parameters were plotted on frequency histograms (Appendix A). Maximum, minimum, mean, standard deviation, and median were calculated for each of the numbers except orientation and density (Table 2). Percent total disturbance was determined by multiplying average pit area (m^2) at a given station by pit density (number of pits per 1875 m^2, a 25 m x 75 m block) then dividing by 1875 and multiplying by 100% (Table 2).

The pits were broken into four size classes by area, 0-5.30 m^2, 5.31 m^2-10.00 m^2, 10.01 m^2-16.00 m^2, and those greater than 16.01 m^2. The reason for using these particular subdivisions in class size was to separate groups of pits which have a greater likelihood of being fresh whale feeding pits from those that show some modification. The assumption was that pits less than 4 m long and 2 m wide are more likely to be freshly made by whales. Given the size of whale gapes (Fig. 8), and what is known about whale feeding, this is valid. Thus, 5.3 m^2 is the area of a 4 m x 2 m feature (area = l x w x 2/3), 10 m^2 is the area of a 6 m x 2.5 m feature, and 16 m^2 is the area of an 8 m x 3 m feature.

This method of statistical analysis doesn't account for pit morphology, only pit area. The pits in the small size class are considered to be fresh whale feeding pits by size and shape criteria alone. The two intermediate size classes are considered to be intermediate stages between fresh and current-enlarged. These intermediate classes probably contain the largest fresh features as well as a whole range of modified features. The largest size class, containing features greater than 16 m^2 are most surely current-

TABLE 2

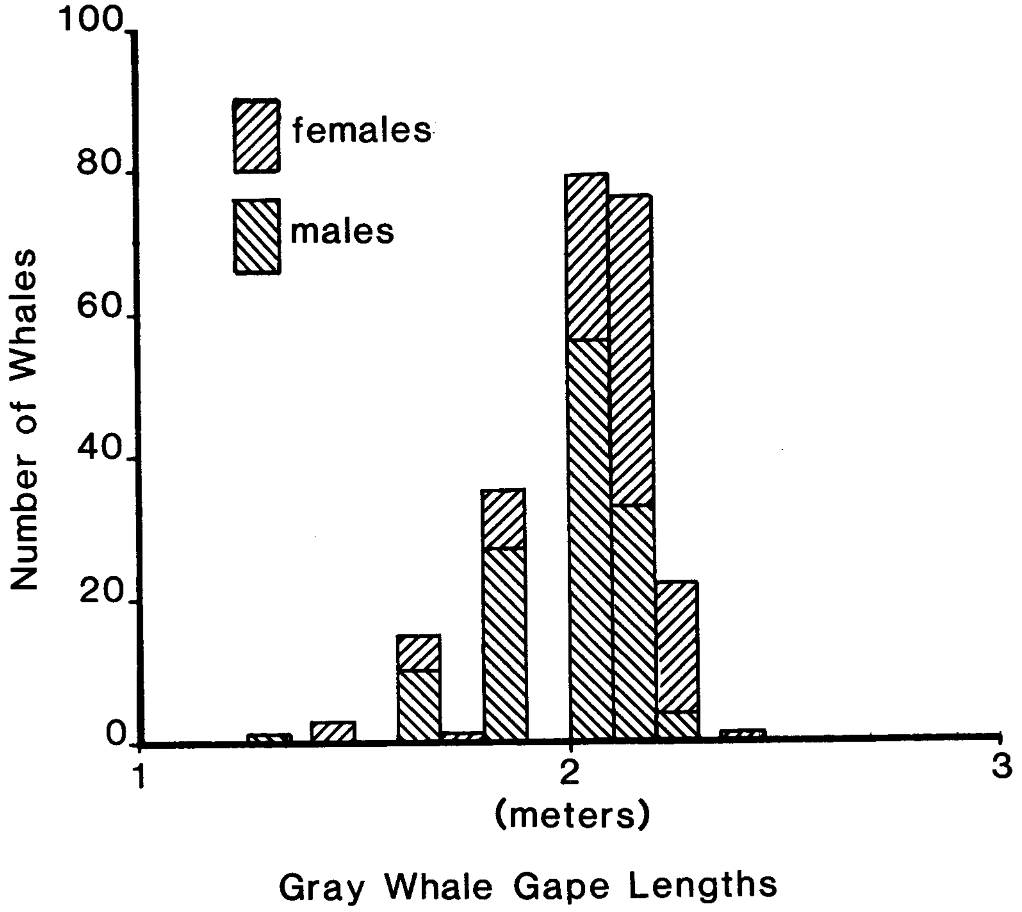
RESULTS OF BOTTOM FEATURE QUANTIFICATION FROM 105 kHz DIGITAL SIDE-SCAN SONAR

STATION	DOG 1	DOG 2	DOG 3	DOG 4	DOG 5	DOG 6	DOG 7	DOG 8	DOG 9	DOG 10	DOG 11	DOG 12	DOG 13	DOG 14	DOG 15	DOG 16	TATE 1
TYPE	1	3	2	2	3	2	1	1	3	3	3	2	2	1	3	3	1
n =	64	50	68	64	68	66	64	68	64	64	64	64	63	67	64	65	121
LENGTH																	
mean	6.1	3.1	4.7	5.1	2.4	3.9	2.8	5.9	2.7	2.6	1.6	3.1	3.9	3.4	2.3	1.8	4.6
med.	6.0	3.0	4.3	5.0	2.0	3.0	2.5	4.0	3.0	2.2	1.4	2.3	3.0	2.5	2.0	1.8	4.
st.dev.	4.0	0.94	2.3	3.0	1.2	2.1	1.48	4.6	0.8	1.5	0.68	2.0	3.4	2.4	0.95	0.67	1.7
max.	20.0	6.0	14.0	15.0	8.0	11.0	7.5	19.0	5.0	9.6	3.8	10.0	20.0	13.5	6.5	3.4	10.0
min.	2.0	2.0	2.0	2.0	1.0	0.75	1.0	1.0	1.0	0.6	0.75	0.8	1.0	0.8	1.0	0.5	2.0
WIDTH																	
mean	2.6	2.0	1.7	1.6	1.1	1.1	1.0	2.4	1.5	1.3	0.92	1.0	1.2	1.4	1.2	1.0	1.8
med.	3.0	2.0	1.8	1.5	1.0	1.0	1.0	1.5	1.5	1.3	1.0	1.0	1.0	1.0	1.0	1.0	2.0
st.dev.	1.4	0.6	0.56	0.59	0.31	0.27	0.28	1.9	0.6	0.48	0.27	0.44	0.63	0.97	0.32	0.32	0.49
max.	5.0	4.0	4.0	3.0	2.0	2.0	2.0	10.0	4.0	2.5	2.0	2.5	3.5	4.5	2.1	2.0	3.5
min.	1.0	1.0	1.0	1.0	0.5	0.5	0.5	0.5	0.8	0.4	0.4	0.4	0.5	0.5	0.8	0.5	1.0
AREA (Length x width x 2/3)																	
mean	13.0	4.4	5.4	6.0	1.8	3.0	2.0	14.0	2.9	2.5	1.0	2.4	3.7	4.0	1.8	1.3	5.8
med.	13.0	4.0	4.3	4.0	1.5	2.7	1.7	5.3	2.3	2.1	0.78	1.4	2.0	2.0	1.5	1.2	5.3
st.dev.	12.0	2.5	3.4	5.1	1.4	2.1	1.5	220.0	2.0	1.8	0.6	2.6	5.3	4.6	0.8	0.75	3.2
max.	53.0	12.0	19.0	26.0	11.0	9.3	10.0	113.0	13.0	8.3	2.8	120.0	35.0	18.0	4.3	4.3	20.0
min.	1.3	1.3	1.3	1.3	0.33	0.38	0.5	0.33	0.66	0.16	0.24	0.27	0.33	0.27	0.67	0.17	1.33
L/W ratio																	
mean	2.3	1.6	3.1	3.2	2.3	3.5	2.8	2.7	1.9	2.0	1.8	3.2	3.5	2.6	2.0	1.9	2.7
med.	2.0	1.5	2.5	2.8	2.0	3.0	2.5	2.3	2.0	2.7	1.5	2.8	2.5	2.3	2.8	1.7	2.8
st.dev.	0.95	0.49	1.7	1.6	1.1	1.8	1.4	1.6	0.67	0.96	0.91	1.5	3.2	1.4	1.0	0.72	1.1
Class.	E	WE	NE	NE	E	NE	E	E	WE	WE	NE	NE	E	WE	WE	E	E
Dens.	26	22	52	44	134	35	37	18	19	97	40	60	39	56	25	34	
%distur	18	5	15	14	13	5	4	14	3	13	2	8	8	12	2	2	

Med. = Median
Min. = Minimum
Max. = Maximum
St.dev. = Standard Deviation
Class. = Classification (Hickey, 1973)
E = Elliptical
WE = Wide Elliptical
NE = Narrow Elliptical

Dens.= Density of features per 1875 m^2

% distur = Percent of total bottom disturbance



Compiled from Rice and Wolman, 1971, Steve Leatherwood, oral commun., 1982, Dale Rice, oral commun., 1982.

Figure 8 Histogram of Gray whale gape lengths compiled from Rice and Wolman (1971); Dale Rice, NMML, pers. comm., 1982; Steve Leatherwood, Hubbs-Seaworld Research Assoc., pers. comm., 1982. In cases in which only head length was known, gape length was computed as 75% of head length.

scour-enlarged. This theory is reinforced by the fact that large features on the records often show a regional trend. Typically, as a feature increases in length, its width will also increase.

For each station, the relative percentage of area of the pit size class was calculated (Table 3). The relative percentages for each size were then multiplied by the percent total disturbance at each station to obtain the actual percent disturbance for each of the four size classes.

The drawbacks of quantifying the features from the side scan records need to be discussed. The nature of the pit margins and the line density on the side-scan records cause a fuzziness which makes the accurate measurement of feature size difficult. This fuzziness causes a margin of error of ±.25 m. As noted before, 105 kHz side-scan sonar has substantial accuracy problems in mapping features less than 1.7 m long and noticeable error in the measurement of features up to 5 m in length due to the beam width error. This error, coupled with the under-representation of small features that are not parallel or sub-parallel to the trackline, causes estimates of density and percent disturbance to be anomalously low. Thus, percentages for bottom disturbance, especially for the smaller pit size classes, should be considered minimum values.

OCEANOGRAPHIC SETTING

Water masses

Three water masses have been defined on the northeastern Bering shelf: the Alaskan Coastal Water, the Bering Shelf Water and the Anadyr Water (Coachman et al., 1976) (Fig. 9). The Alaskan Coastal Water is formed largely by river runoff from the area near Bristol Bay and the Yukon River and

TABLE 3

PERCENT OF BOTTOM DISTURBANCE

	CLASS				
STATION	0-5.3 m^2	5.31-10 m^2	10.01-16 m^2	16.01 m^2	TOTAL DISTURBANCE (sum of all classes)
DOG 1	0.94 %	0.81 %	2.56 %	12.78 %	18 %
DOG 2	2.4	1.77	0.54	0.0	5
DOG 3	4.92	6.72	2.58	0.76	15
DOG 4	3.98	4.2	2.67	3.05	14
DOG 5	11.86	0.0	1.14	0.0	13
DOG 6	3.4	1.5	0.0	0.0	5
DOG 7	3.52	0.17	0.3	0.0	4
DOG 8	0.96	1.16	0.74	11.14	14
DOG 9	2.2	0.57	0.22	0.0	3
DOG 10	10.24	2.75	0.0	0.0	13
DOG 11	2.0	0.0	0.0	0.0	2
DOG 12	4.42	2.44	0.6	0.52	8
DOG 13	3.55	1.11	1.12	2.2	8
DOG 14	4.45	3.35	2.55	2.28	12
DOG 15	2	0.0	0.0	0.0	2
DOG 16	2	0.0	0.0	0.0	2

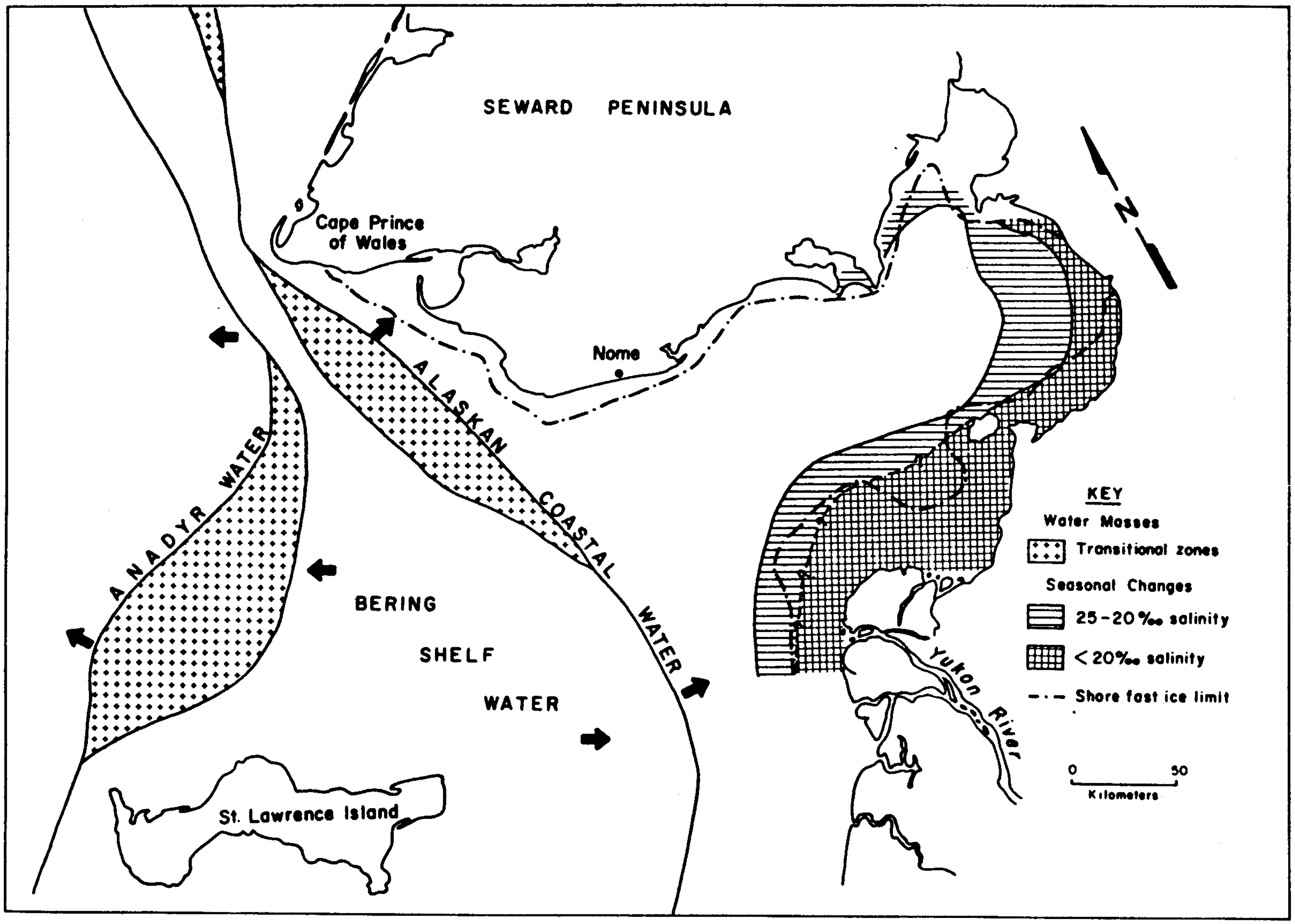


Figure 9 Water masses in the northeastern Bering Sea. The Alaskan Coastal Water (14-31.5 o/oo, 8° C) occupies the eastern portion of the map area, the Bering Shelf Water (sometimes called Modified Shelf Water, 31.5-33 o/oo, 0-4° C) covers the central area, and the Anadyr Water (33 o/oo, 1-3° C) occurs on the western portion of the map area. From Nelson et al., 1981.

moves along that coast: it fills Norton Sound and hugs the coast in a narrow band from Nome through the Bering Strait along the northern edge of Chirikov Basin. The Bering Shelf Water originates in the northeastern Bering Sea during winter ice formation and abuts the Alaskan Coastal Water in its net northward flow; it covers most of the central Chirikov Basin area. The Anadyr Water flows through the Anadyr Strait towards the Chukchi Sea.

The Alaskan Coastal Water is the warmest and the least saline of the three water masses (Coachman et al., 1976). It shows marked seasonal variations in salinity, particularly in Norton Sound where fluctuations in discharge from the Yukon River influence salinity. Temperature is greater than 8° C and salinity ranges from 20 to 30 $^{o}/oo$. The Bering Shelf water forms quite a sharp boundary with the Alaskan Coastal Water because is much colder, and more saline, ranging from 0° - 4° C and from 31.5 to 33 $^{o}/oo$.

Currents

The net northward flow of the entire water column has a direct effect on the Alaskan Coastal Water where westward-extending promontories deflect the flow (Fleming and Heggarty, 1966) (Figs. 9, 10). The less dense coastal water is piled up against the shore as a thickened section, and strong currents are produced to move the water. These currents reach a maximum of 180 cm/sec at a depth of 55 m in the most restricted region, the Bering Strait (Fleming and Heggarty, 1966): in the Chirikov Basin, velocities are as low as 5-15 cm/sec (Fleming and Heggarty, 1966; Husby and Hufford, 1971; and McManus et al., 1977). The current regime of central Chirikov Basin is not nearly as strong as at its margins near Bering, Anadyr, and Shpanberg straits: spot meter measurements in the Chirikov Basin are over 20 cm/sec. (Fig. 5). In the

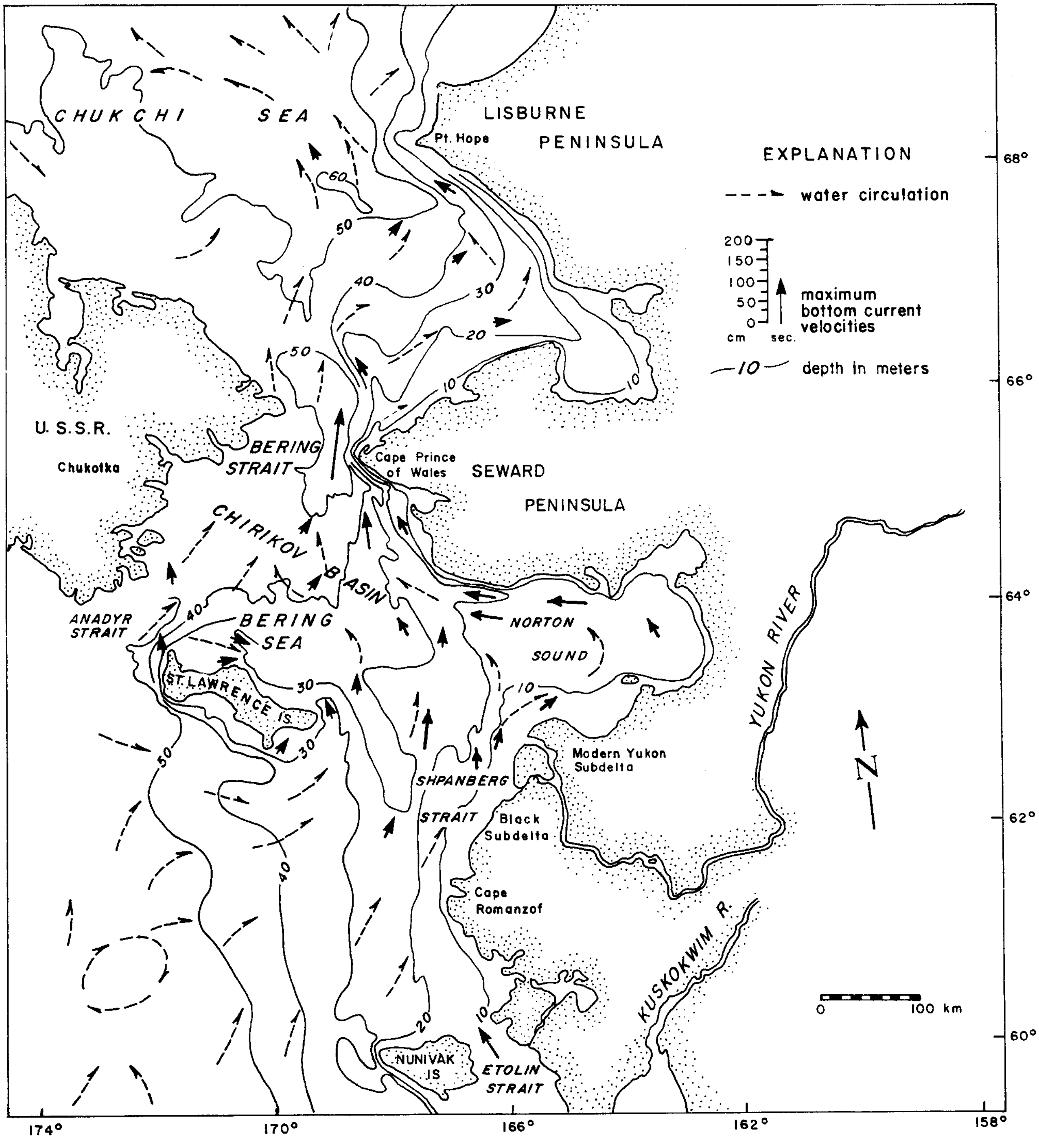


Figure 10 Offshore water circulation and maximum bottom current velocities from available measurements in the northeastern Bering and southern Chukchi Sea. From Nelson et al., 1981.

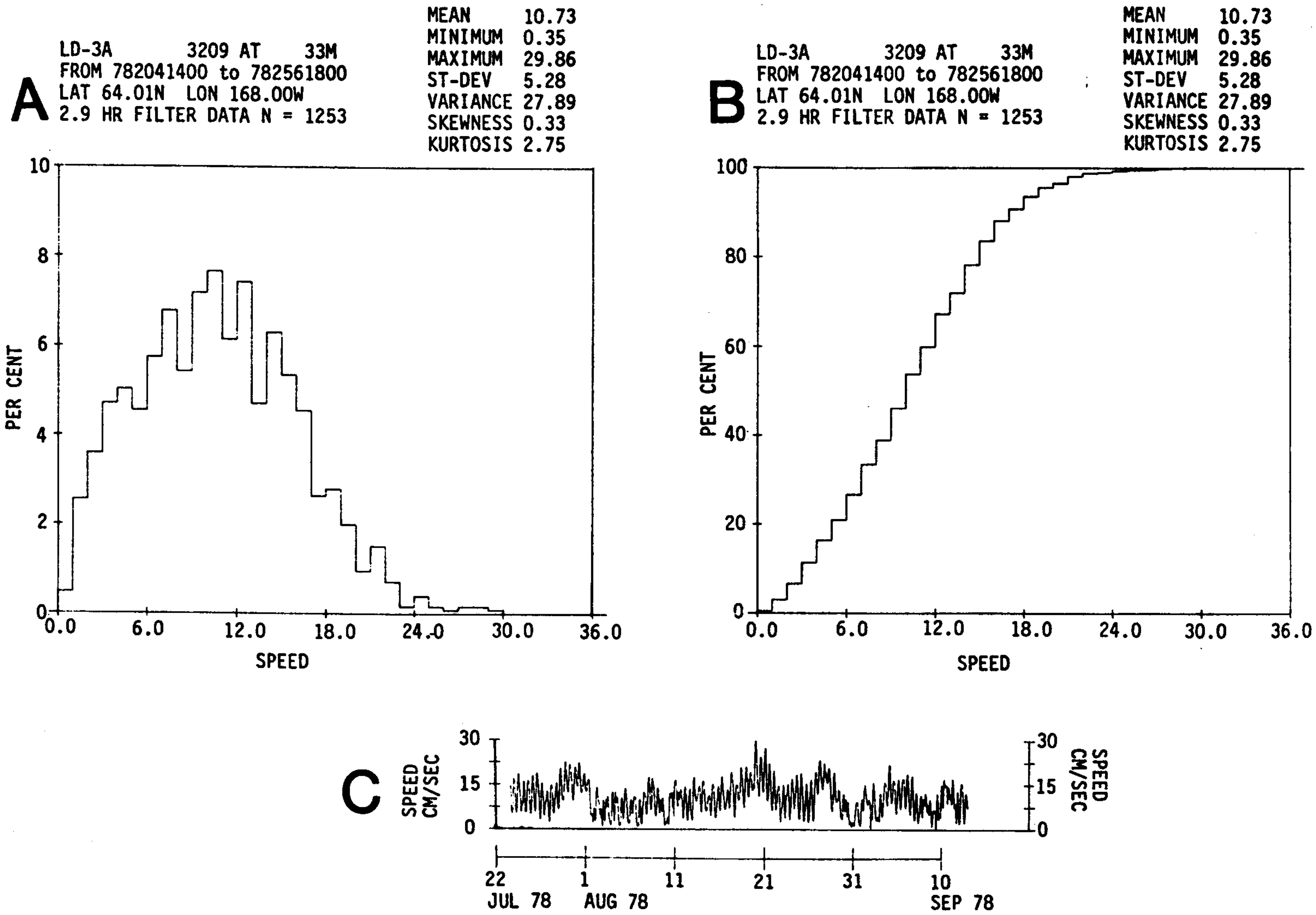


Figure 11 (A) Histogram of bottom current speeds from long term current meter, LD-3A. July-Sept., 1978. (B) Cumulative frequency graph of bottom current speeds for long term current meter LD-3A. (C) Daily bottom current speeds from long term current meter, LD-3A. Location of current meter shown in Figure 5.

northern half of the area and at its margins, current directions are generally northward; in the southern half, current directions are quite variable.

Long-term current meter moorings provide the best information on current parameters. Though moorings have not been placed at the center of Chirikov Basin, data are available from a mooring on the eastern margin of the basin from July-Sept., 1978 (Fig. 5). Mean current velocity of 10.7 cm/sec, speeds exceeding 18 cm/sec about 10% of the time, and maximum velocities of 30 cm/sec were measured (Fig. 11) (J. Schumacher and others, PMEL-NOAA, Seattle, pers. comm., 1982). The current velocity necessary to mobilize a 3 phi (.125 mm) sand on a flat bottom is approximately 30 cm/sec (Miller et al. 1977). On a rough bottom, threshold velocity of erosion becomes significantly less in this and other areas (Cacchione and Drake, 1982). With a known minimum bottom roughness of 10 cm and a grain size of .125 mm in whale feeding areas (Nerini et al., 1980), the velocities to erode sediment can be estimated at 18 cm/sec (Cacchione, U.S. Geological Survey, Menlo Park, pers. comm., 1983). Velocities greater than this were present about 10% of the time during normal weather in the summer of 1978.

Current speeds have not been measured during storms within Chirikov Basin, but in many northeastern Bering Sea areas surrounding it current velocity increases of 100% or more have been measured (Fleming and Heggarty, 1966; Coachman and Tripp, 1970; Coachman et al., 1976; Schumacher and Tripp, 1979; Cacchione and Drake, 1982). Even under moderate storm conditions, wave surge currents become important at the water depths of 20-40 m encountered in northeastern Bering Sea (Cacchione and Drake, 1982).

Storm surges

Moderate storms occur each fall in the northeastern Bering Sea resulting in changes in atmospheric pressure and wind velocity that can cause sea level set up of 1 meter and current speeds to fluctuate by as much as 100% over periods of a day or more (Coachman and Tripp, 1970; Tripp and Schumacher, 1979; Cacchione and Drake, 1982). At the northeastern edge of Chirikov Basin (Fig. 5), a GEOPROBE mooring measured a 100% increase in bottom current velocity (up to 72 cm/sec.) and a 1000% increase in suspended sediment transport during a moderate September storm (Cacchione and Drake, 1982). The GEOPROBE site has maximum spring tidal currents of 30 cm/sec. like those measured in Chirikov Basin (Fig. 9): this suggests that yearly storms can cause significant bottom erosion in Chirikov Basin. Six great storm surge events have occurred this century in the northeastern Bering Sea region and have caused sea-level set up of 4 m. (Fathauer, 1975); this suggests a potential for sea floor scour several orders of magnitude greater than yearly events just described.

Ice cover and seasonality of processes

The entire northeastern Bering Sea is covered by ice almost six months a year. For this reason the gray whale feeds in this region during the summer months only and storm activity which affects the sea floor bottom occurs mainly in the fall months.

Dupre (1982) recognizes three distinct seasons of coastal processes near the Yukon Delta in Norton Sound. The ice-dominated regime lasts from October or November to late May. The river-dominated regime, associated with the breakup of ice on the Yukon River, peaks rapidly in early summer and blends into the storm-dominated regime which grows through late summer and peaks in October or November. In the center of Chirikov basin, where whale features are being modified, the river-dominated regime is greatly reduced in importance and is usually replaced by a period of summer quiescence. Thus, in the basin there exist two seasons in which normal current regimes predominate and the bottom receives minimal disturbance, the ice-dominated regime and the summer quiescence, or, from November to August. The storm-dominated regime from August to November is the time period in which most of the sediment suspension and feature modification probably occurs.

Cacchione and Drake (1979, 1982), Drake et al. (1980), and Schumacher and Tripp (1979) document the importance of late summer/early fall storms to sediment movement. Their work with the GEOPROBE and long-term moorings of current meters found that even a moderate fall storm increased sediment transport by a factor of ten over normal transport rates (Cacchione and Drake, 1982). The inference is that a great deal and perhaps a majority of the sediment erosion, and thus fresh pit modification, is probably storm-related. Thus, bottom features may undergo very little modification during the winter, spring, and early summer and be rapidly modified during the late summer and early fall as the storms increase in strength and frequency.

GEOLOGIC SETTING

Quaternary history

The northeastern Bering Sea is a broad, shallow epicontinental shelf region covering approximately 100,000 km^2 of subarctic sea floor between

Seward Peninsula, Alaska and Chukotka Peninsula in the USSR (Fig. 1). The shelf can be divided into four general morphologic areas: 1) the western part, an area of undulating, hummocky relief formed by glacial gravel and transgressive-marine sand substrate (Nelson and Hopkins, 1972); 2) the central part, Chirikov Basin, a relatively flat featureless plain with a fine-grained transgressive sand substrate (McManus et al., 1977; Nelson, 19820; 30 the northeastern part, a complex system of sand ridges and shoals bordering the coastline with fine- to medium-grained transgressive sand substrate (Nelson et al., 1978); and 4) the eastern part, Norton Sound, a broad, flat marine reentrant covered by Holocene silt and very fine sand derived from the Yukon River (Nelson and Creager, 1977; McManus et al., 1977; Nelson, 1982).

During Pleistocene interglacial periods and the present Holocene high sea level stand, sediment eroded from Alaska and Siberia has been carried northward from the Bering Shelf through the Bering Strait into the Arctic Ocean (Nelson and Craeger, 1977). Under lowered sea level conditions, the Yukon and other rivers extended their courses across the continental shelf to the southern Bering Continental Margin where sediment was transported through major submarine canyons to be deposited on the abyssal plain (Nelson et al., 1974). As a result, the Quaternary sediment on the continental shelf is absent in some regions of strong bottom currents and rarely exceeds 100 m; the thickness of the Holocene sediment is only a few meters or less (Nelson, 1982).

During lowered sea level periods of the Pleistocene, the entire present-day northeastern Bering Sea region was emergent. Glacial moraines formed off Siberia, and St. Lawrence Island, and along the coast of what is now the Seward Peninsula (Nelson, 1982). The entire area was covered by tundra and deposits of freshwater peat and silt. As sea level began to rise, the freshwater silt and peat were covered by transgressive sand (Fig. 12). The moraines were winnowed, removing fine-grained sediment and leaving gravel lag deposits. As the sea transgressed, the basal, medium-coarse beach sand was overlain by an inner shelf fine-grained transgressive sand (Fig. 12). Between 5000 and 2500 years B.P., the Yukon Delta began to form and deposit coarse silt and very fine sand in Norton Sound (Nelson and Creager, 1977; Dupre, 1982).

Surface sediment distribution

The distribution of relict and modern surface sediment is patchy and dependent upon positions of bedrock and glacial debris outcrops on the sea floor, locations of river sediment inflow, and water current velocity and patterns. The gravel found in a 30 km wide belt along most of the coast from east of Nome to the Bering Strait and a 10 km belt along the north coast of St. Lawrence Island is relict and derived from glacial drift, outwash, alluvium, and bedrock in these areas (Fig. 12). Offshore from the bedrock gravel lag of Seward Peninsula, medium-grained sand fringes the northeastern edge of Chirikov Basin.

The southern margins of St. Lawrence Island and Central Chirikov Basin and southeastward into Spanberg Strait are covered by the fine-grained inner shelf transgressive sand; this sand is of particular interest because it is the Ampeliscid amphipod substrate of the gray whale feeding grounds. This sand body is quite thin and rarely is greater than one meter thick (Nelson, 1982). It is finer grained (.125 mm) than the underlying basal transgressive

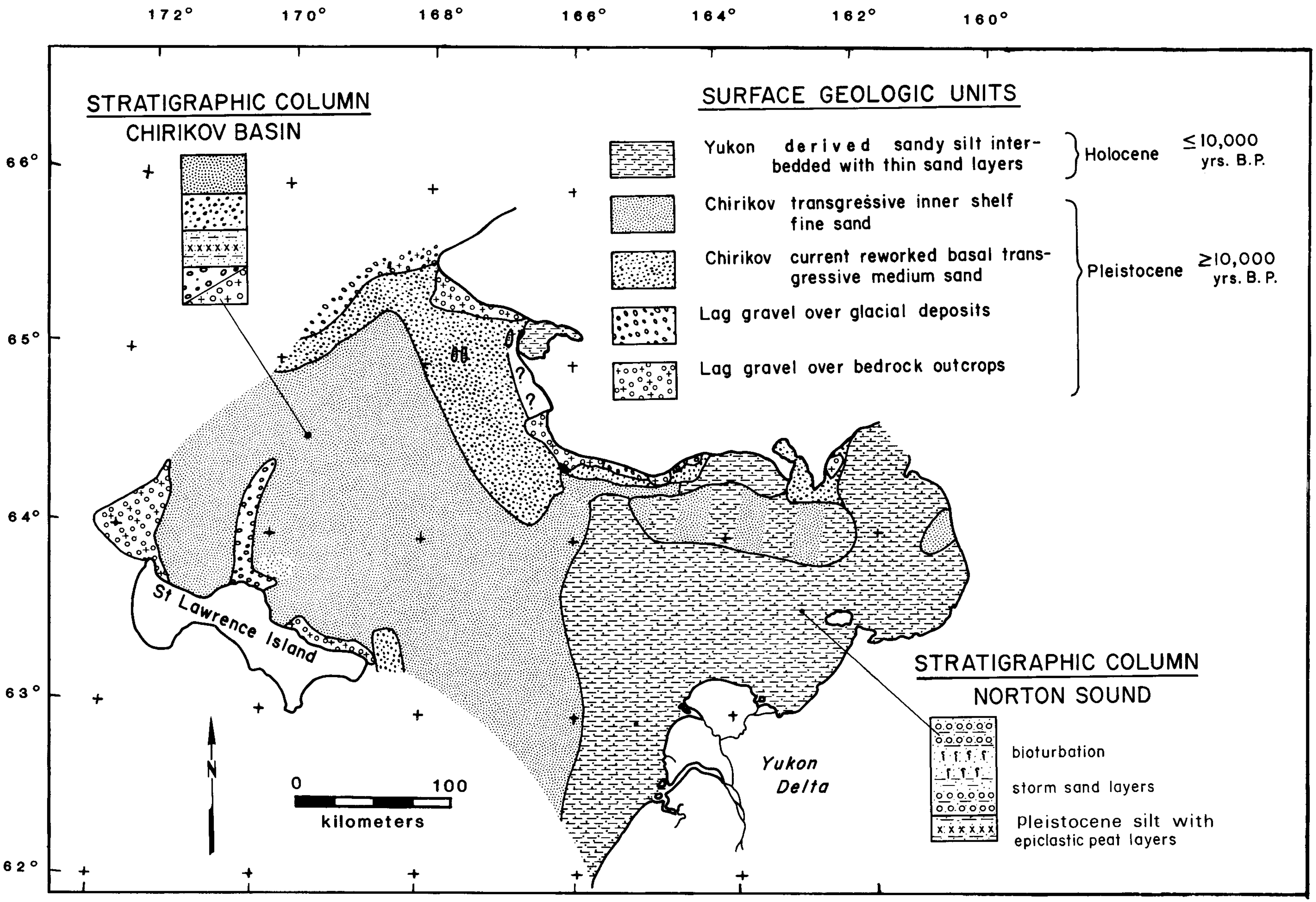


Figure 12 Preliminary map of the northeastern Bering shelf surficial geology (modified from Nelson, 1982)

sand that borders it and is exposed on the margins of Chirikov Basin (Fig. 13).

There are also subtle variations within the inner shelf sand sheet itself. For example, within the the Shpanberg Strait area, which has strong currents, the sand body has a slightly higher percentage of sand-sized particles and is better sorted (Figs. 14, 15). This combination of stronger currents and slightly cleaner or less muddy sand in the straits area results in a sand dollar benthic community compared to the amphipod-dominated community found in most other substrate areas of the inner shelf sand (Nelson et al., 1981).

Norton Sound to the east of the inner shelf sand sheet is covered by a modern very fine sand and coarse silt (.032-.062 mm) derived from the Yukon River (Figs. 12, 15) (McManus et al., 1977). Current and water mass movements prevent deposition of the modern Yukon sediment over the relict transgressive sediment of the Chirikov Basin area (Nelson, 1982).

Surficial geologic processes and bottom depressions

A number of surficial geologic processes produce different types of depressions on the sea floor that can be observed on side-scan records. Description of these physical features is important so that they can be distinguished from biologically produced bottom surface features. This separation is usually possible because most of the physical features require a very specific set of geologic conditions and only occur in certain areas (Fig. 16). Fortunately, even though some of the physical features closely resemble those of biological origin, they generally occur in different locations.

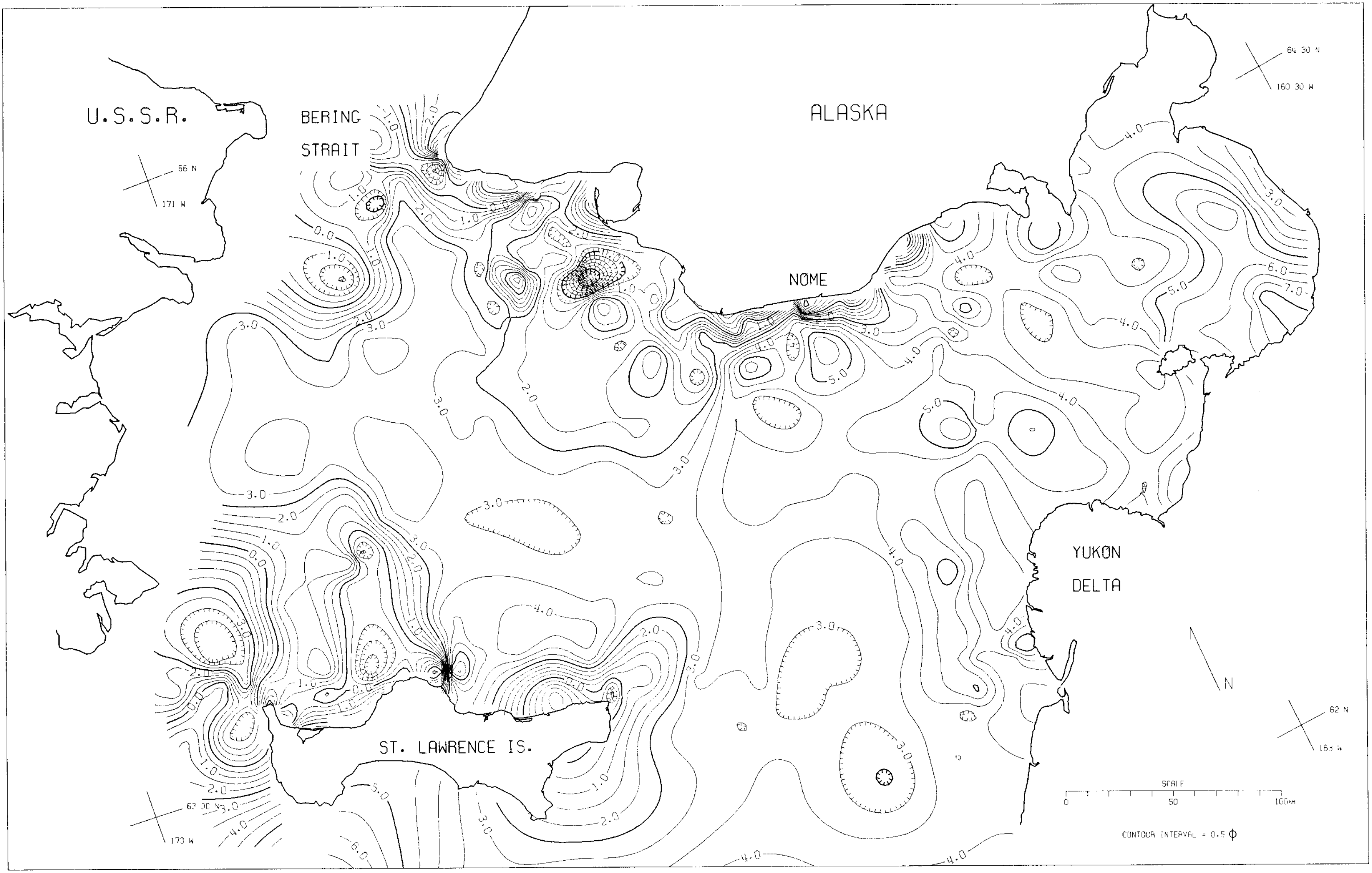


Figure 13 Mean grain size (Folk and Ward) for surface sediment in Norton Basin, northeastern Bering Sea.

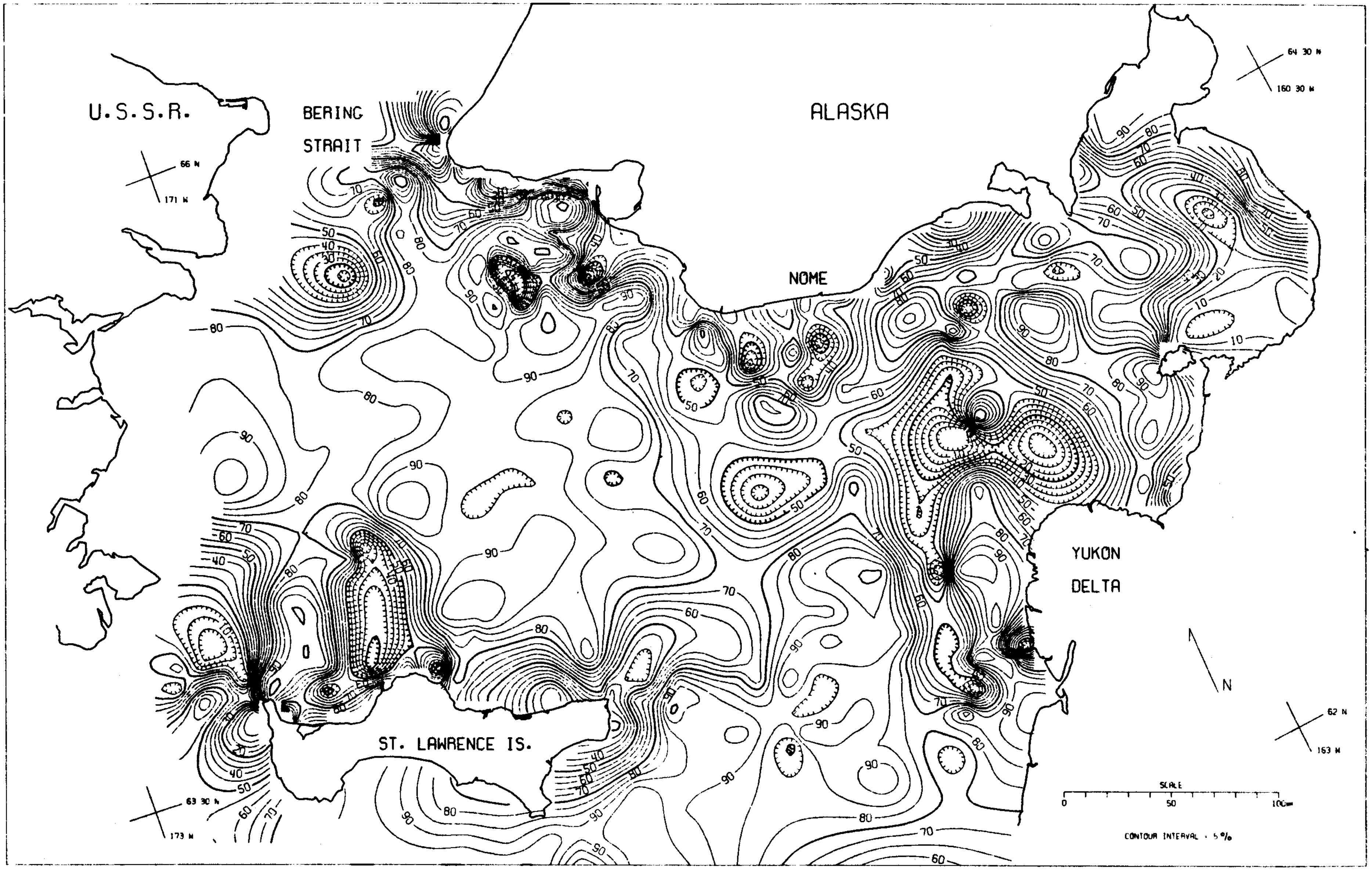


Figure 14 Percent sand in surface sediment of Norton Basin, northeastern Bering Sea.

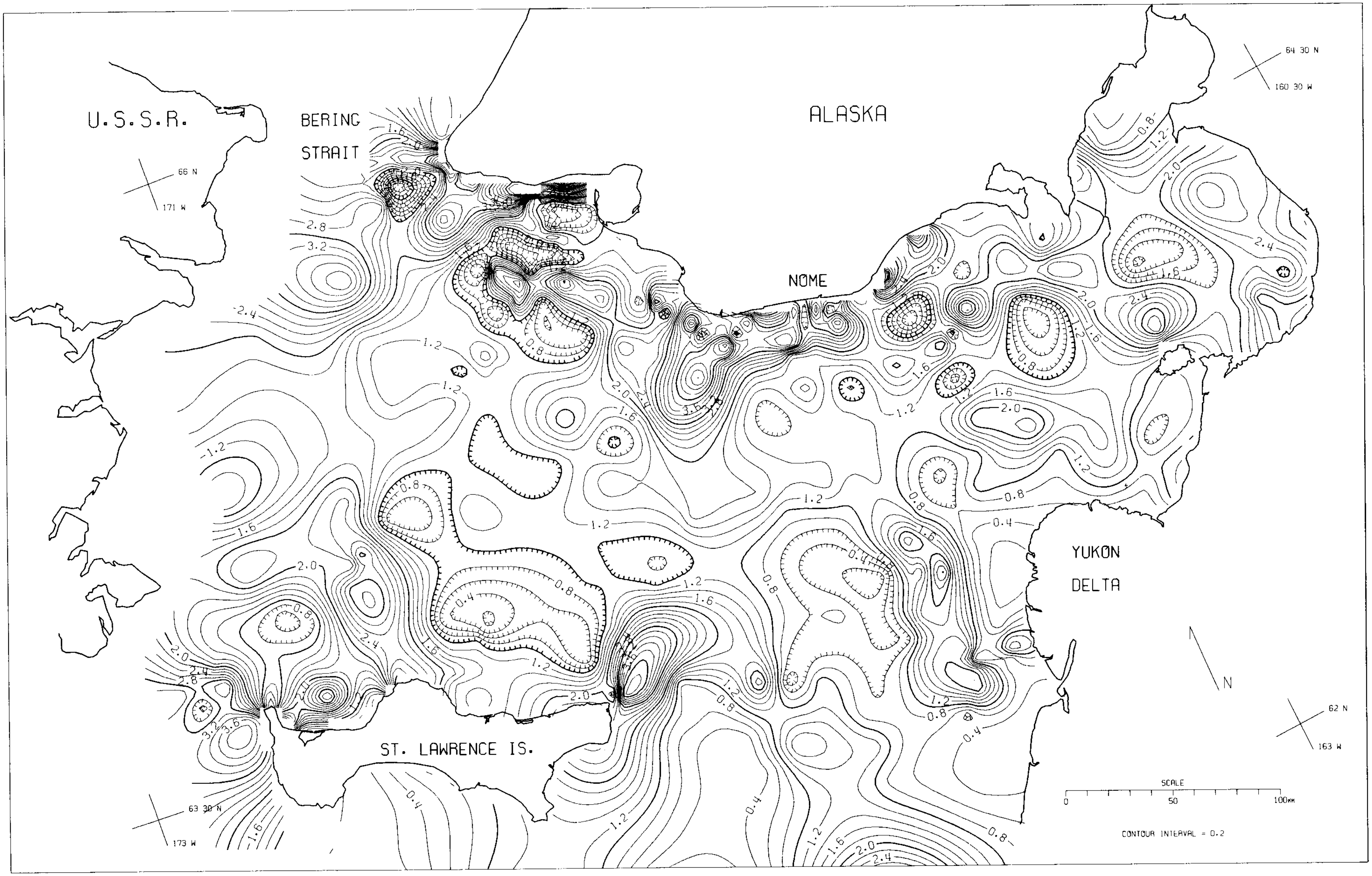


Figure 15 Sorting values (Folk and Ward) for surface sediment in Norton Basin, northeastern Bering Sea.

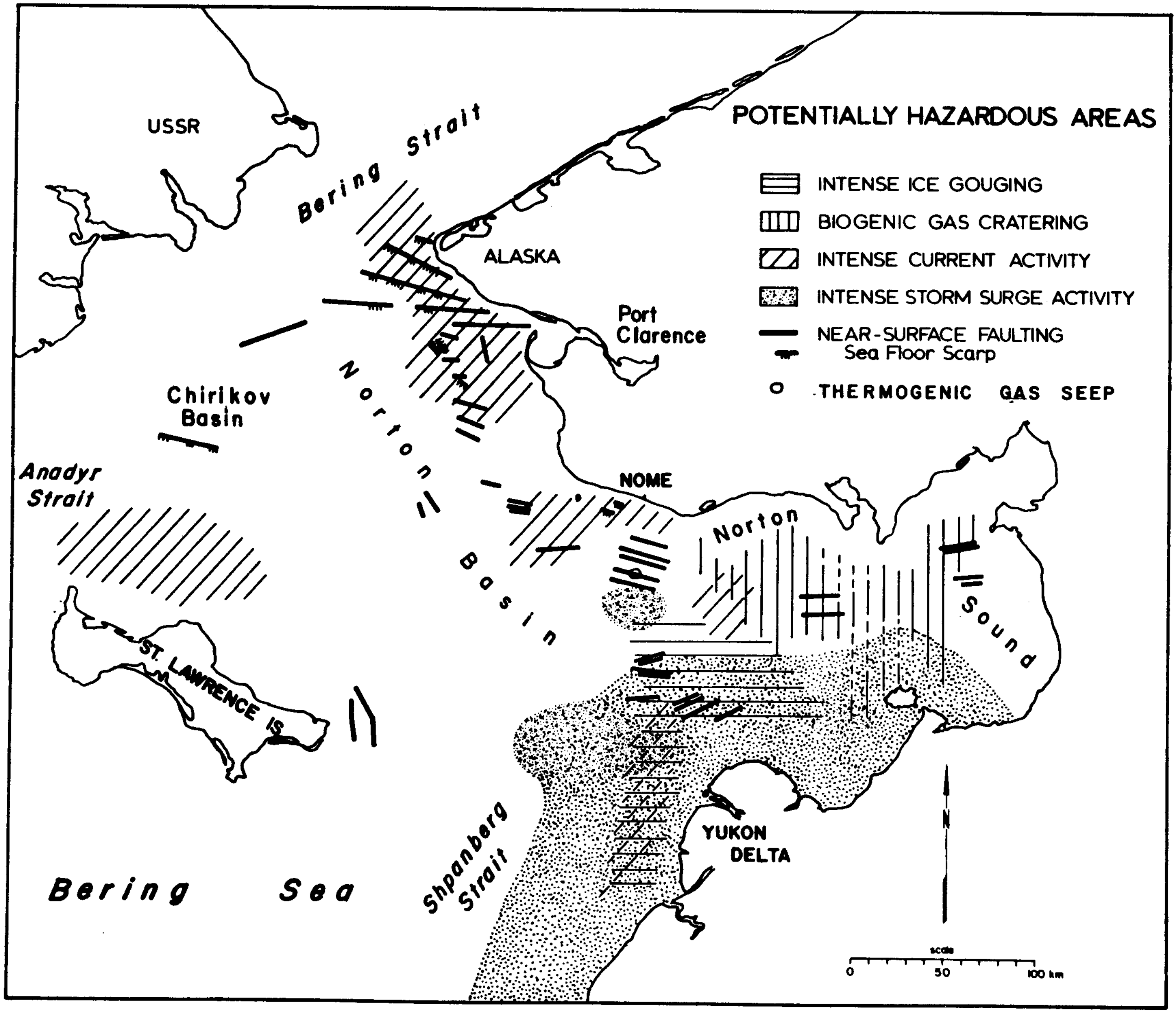


Figure 16 Potentially hazardous areas of the northeastern Bering Sea. Current scour depressions occur in the area of intense current activity off the Yukon Delta. From Thor and Nelson (1981).

Ice scour on the northeastern Bering Sea continental shelf has been identified on side-scan sonar and is classified into two types. The first is a single furrow (Fig. 17A) and the second is a series of multiple subparallel furrows (Thor and Nelson, 1981). The single scours are formed when single ice keels plow through the surficial sediment while multiple gouges are produced when multi-keeled floes rake the bottom. Ice scour occurs in water depths of 40 m or less, but it is most dense in water 10 to 20 m deep. In general, ice scour follows ice movement, parallel to isobaths and coastline configuration. Ice scour is concentrated in ice shear zones where the edge of shorefast ice meets offshore moving ice pans creating pressure ridges. This occurs most notably along the Yukon Delta margin (Fig. 16). Ice scour is rare in Chirikov Basin because of the increased depth of the water and the lack of extensive ice shear zones.

The second type of bottom depression that has been recognized in the northeastern Bering Sea is the current-induced scour depression (Fig. 17B). These irregular-shaped forms typically are 20-150 m in diameter and have a generally shallow (less than 1 m) depth of scour (Larsen et al., 1979). The depressions are found in areas where the grain size is very fine sand to coarse silt and where bottom current velocities are relatively high (greater than 20 cm/s mean speed) under non-storm conditions. These features typically occur where strong currents shear against margins of bathymetric constrictions or relief covered by very fine sand. Local topographic disruptions, such as ice scour help set off flow separation and greatly enhance this current-scour process. These scour depressions occur mainly along the Yukon Delta front and in northern Norton Sound (Fig. 16).

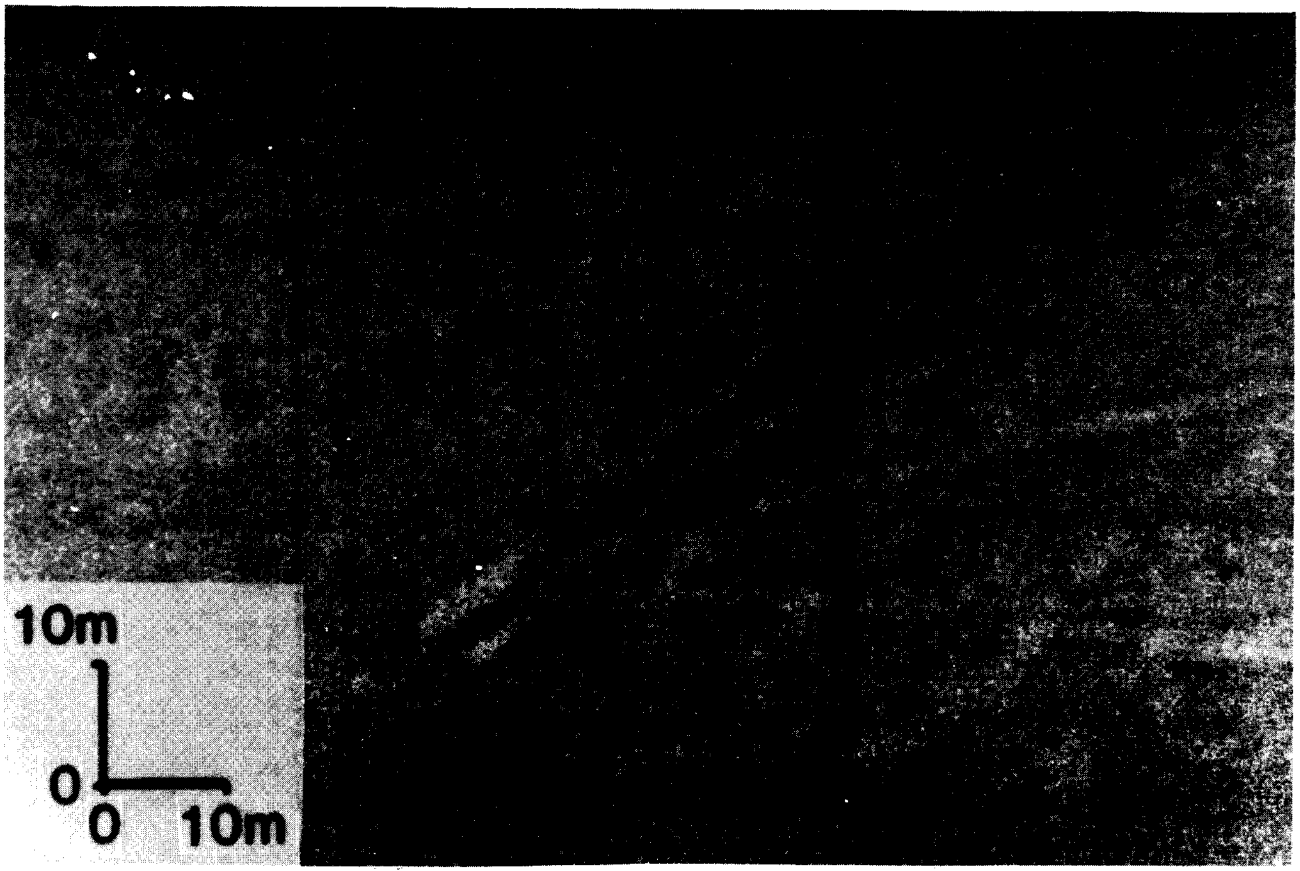


Figure 17A

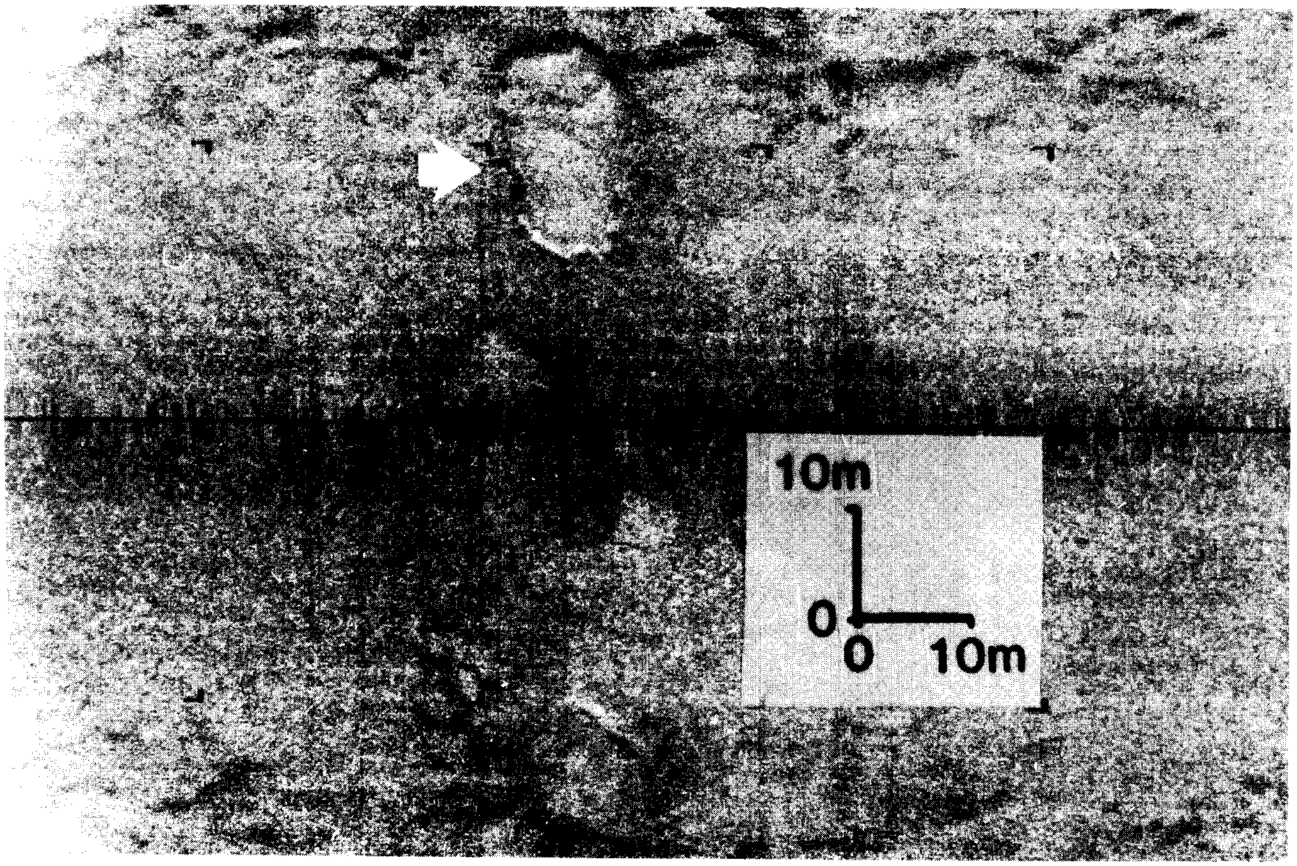


Figure 17B

Circular gas craters also form in regions of gas-charged sediment in Norton Sound (Fig. 17C) (Nelson et al., 1980). Biogenic gas formed by the decomposition of organic debris is trapped in the peaty mud in a saturated state by the overlying cover of Holocene mud. Periodically, during storms, the gas escapes through the thin Holocene mud blanket and forms craters. The craters are found predominately in Norton Sound and are circular, 1-10 m in diameter and are less than 1 m deep. Sea floor gas craters are typically associated with near-surface peaty mud, gas-charged sediment, and acoustic anomalies shown on seismic profiles; the latter occur because of gas saturation in the near-surface sediment. No craters of this type are found in the central Chirikov Basin, apparently because the sediment cover in this region is composed of fine sand that allows gas escape and prevents any near-surface gas saturation (Nelson et al., 1980). The lack of acoustic anomalies in Chirikov Basin to the west of Norton Sound indicates that sediment gas saturation does not exist in this area and that gas craters should not be present (Holmes and Thor, 1982).

BIOLOGICAL SETTING

The Bering Continental Shelf is an area of rich macrobenthic communities of low diversity but high density (Neiman, 1961; Filatova and Barsanova, 1964; Kuznetsov, 1964; Rowland, 1972; and Stoker, 1973). The major species show a preference for certain sediment types and grain sizes (Nelson et al., 1981; Stoker, 1978). In areas where the homogeneous sediment types are widespread, they form vast stable environments in which large numbers of individuals of these species can flourish.

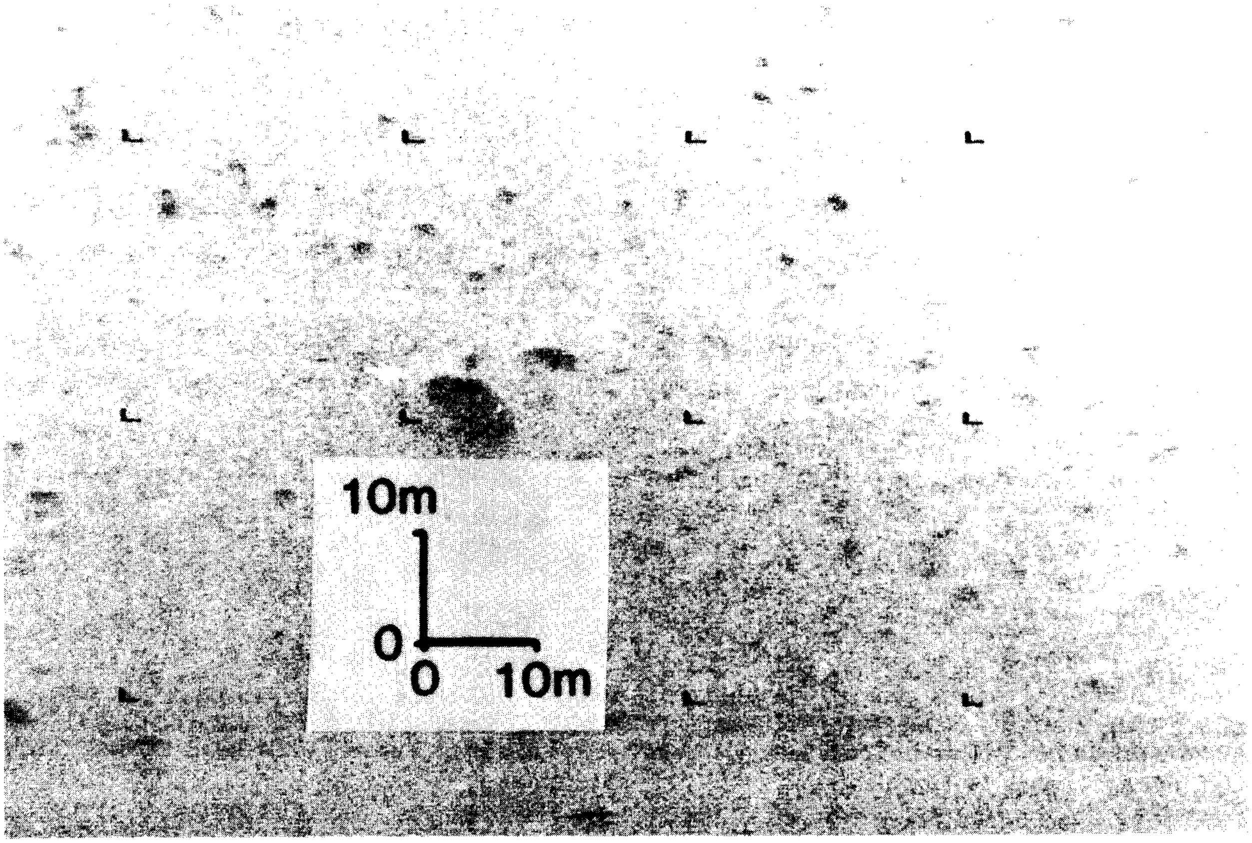


Figure 17C

Figure 17 105 kHz sonograph of (A) ice scour from Norton Sound, (B) current scour depressions from the Yukon Delta front, (C) circular gas expulsion craters from Norton Sound. Arrows show location of features in B and C.

In response to the rich benthic food resources, large populations of walrus, bearded seals, and gray whales inhabit the northeastern Bering Sea at least seasonally and, by their feeding, are likely to be responsible for considerable reworking of the shallow shelf sediment over much of this area.

The gravel lag layers are dominated by epifaunal species such as crabs and sea urchins which cause little disruption of physical sedimentary structures (Fig. 12) (Nelson et al., 1981). The medium and well-sorted sand bodies on the edges of the central Chirikov Basin show reworking by sand dollar and tellinid clam communities. The muddy, very fine sand and silt of Norton Sound are characterized by a deposit feeding community. The central Chirikov Basin is covered by an inner shelf fine-grained sand that shows intense bioturbation by ampeliscid amphipods. This intense bioturbation from the sediment surface to a depth of 10 cm is easily discernible in sediment radiographs from the central Chirikov Basin (Fig. 18) (Nelson et al., 1981).

The areas with a dominance of Ampeliscid amphipods show a definite association with the Chirikov fine sand sheet (Figs. 4, 12, 19) and with the Bering Shelf Water (Figs. 4,9,19) but presence of these amphipods is not exclusively limited to these environments. Water depth preferences range from 20 to 40 m and the amphipods are most common in the fine sand on the flat low-relief shelf area of Chirikov Basin. The optimum substrate habitat for the ampeliscid amphipods is a moderately sorted, slightly silty, very fine sand with 80-90% sand sized particles (Figs. 13, 14, 15); they are not found in the transgressive fine sand where it is well sorted and reworked by strong currents, an area occupied by the sand dollar community (Figs. 4,12) (Nelson et al., 1981). Ampeliscid amphipods are not common in Norton Sound due to

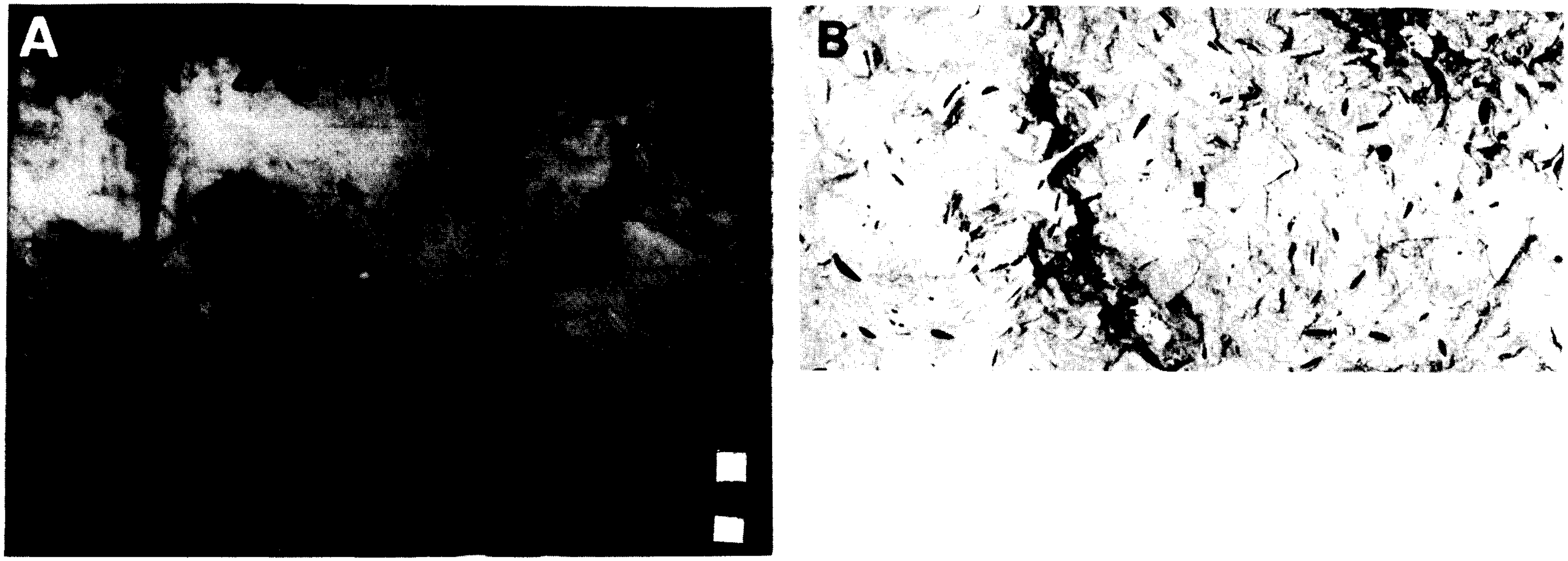


Figure 18 (A) Radiograph of a box core, showing the v-shaped burrows of the amphipod, *Ampelisca macrocephala*. The core was taken from the fine transgressive sand body in the center of Chirikov Basin at a water depth of 27 m. (B) Plan view photo of the box core top taken immediately after collection. Slit-like, mucus-lined burrows are typical of the amphipod *Ampelisca macrocephala*.

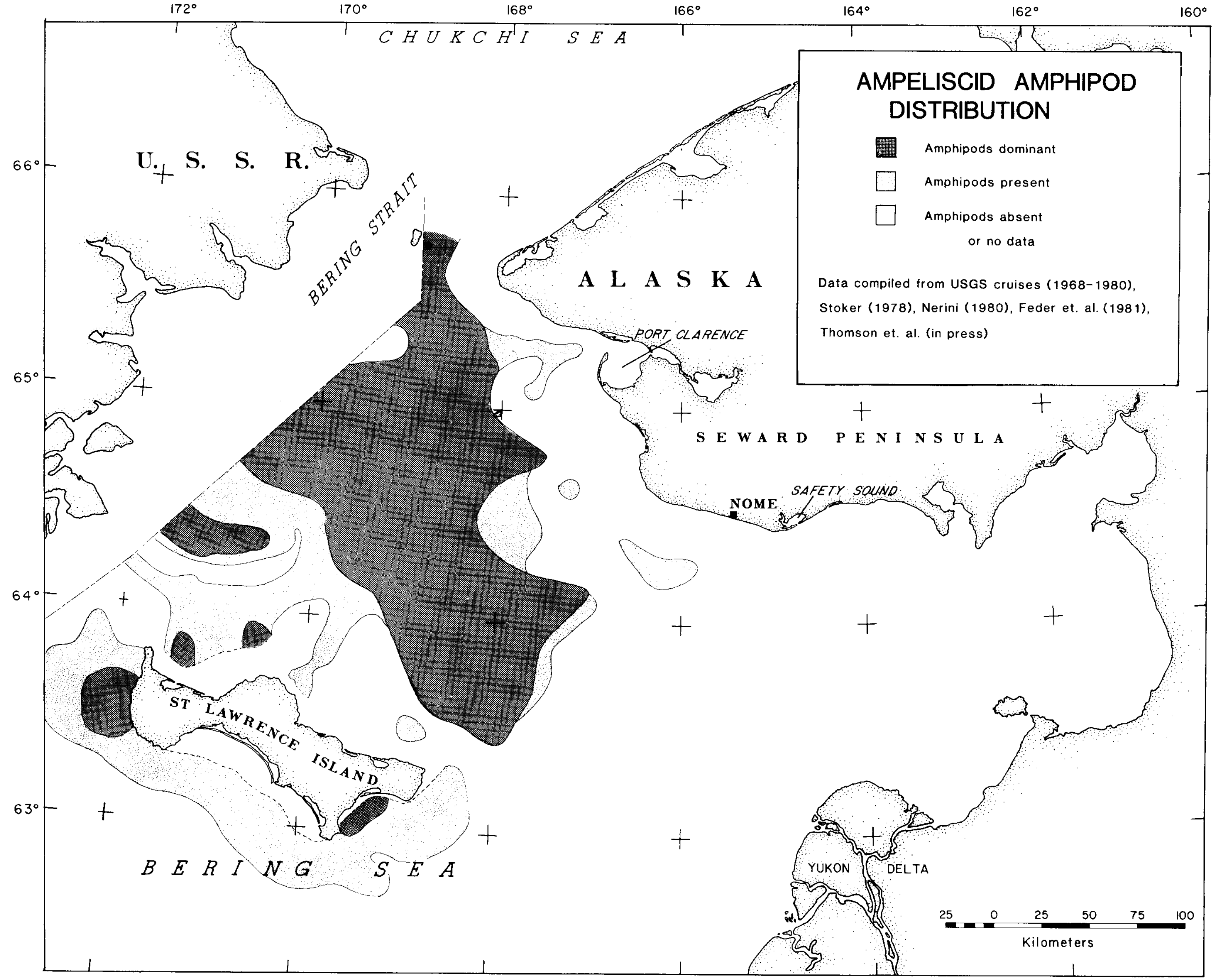


Figure 19 Distribution of Ampeliscid amphipods in the northeastern Bering Sea. Compiled from USGS cruises 1960-1980, Stoker (1978), Nerini (1980), Feder and Jewett (1981), Thomson (1983).

the decreased salinity (Ken Coyle, Institute of Marine Studies, Fairbanks, pers.comm., 1982) and grain size (Nelson et al., 1981).

The main prey species of the gray whale in Chirikov Basin is the Ampeliscid amphipod, *Ampelisca macrocephala* (Rice and Wolman, 1971). Ampeliscid amphipods are detritus feeders that build narrow V-shaped, mucus-lined tubes. When the population of amphipods becomes large, the densely packed tubes coalesce and create extensive mats that fix the surface of the sediment. Productivity and resultant biomass are very high in these areas. Stoker (1978, 1981) calculated an average total biomass of 533 g/m^2 (his group IA, dominated by ampeliscid amphipods) in central Chirikov Basin. Nerini (in press) calculated a total biomass of 483 g/m^2, with 34% of this biomass contributed by the amphipod community for the same area. The American section of Chirikov Basin contains nearly 30,800 km^2 of area with Ampeliscid amphipods present (Fig. 4). The southern nearshore area of St. Lawrence Island contains an additional 9,000 km^2 (Fig. 19).

GRAY WHALE FEEDING ECOLOGY

The gray whales feed mostly during the summer. The stomachs of migrating whales are generally empty (Rice and Wolman, 1971) as are those of the whales in the breeding lagoons (Scammon, 1874). Rice and Wolman (1971) reported that the southbound whales were 11 to 29% heavier than the northbound whales. The majority of evidence suggests that the whales feed only occasionally during migration, calving, and mating; they take most of their nourishment for the year during the summer on Alaskan shelves. Nerini (1981) cites numerous reports of whales actively feeding during migration; it is clear that they do feed sporadically and sometimes voraciously in migration to and from the southern waters, but the relative proportion of total yearly food intake this accounts for is unknown, although probably minor (Oliver, Slattery, Silberstein, and O'Connor, 1983; Swartz and Jones, 1982; Hudnall, 1981; Wellington and Anderson, 1978; Sund, 1975; and Howell and Huey, 1930).

The Bering Sea and Arctic Ocean undoubtedly are the main feeding areas of the gray whales. After their migration from the breeding and calving lagoons of Baja California, and once they are north of the Aleutian Islands, the whales move into various feeding grounds in these waters (Pike, 1962). The largest group feeds in the central Chirikov Basin and nearshore areas of St. Lawrence Island; it is the focus of this study (Fig. 20) (Braham, in press; Moor and Ljungblad, in press; Braham et al., 1977; Votrogov and Bogoslovskaya, 1980; S. Leatherwood, pers. comm., 1982; Consiglieri et al., 1980).

Ljungblad, in press), 85% were associated with sediment plumes, which is a sure indication of benthic feeding. Gray whales are not common in Norton Sound and this area seems to receive minimal feeding pressure (Nerini et al., 1980).

Another group of gray whales stays near the Alaskan peninsula and extends into Bristol Bay, where they are frequently spotted feeding in the surf or in very shallow water in Bristol Bay (Consiglieri et al., 1980; Braham et al., 1982; S. Leatherwood, pers. comm., 1982). Their main prey species in these areas are unknown.

Soviet whalers have been taking gray whales from the nearshore western side of Chirikov Basin and in the Gulf of Anadyr at least as far south as Cape Navarin (Zimushko and Lenskaya, 1977; Zimushko and Ivanshin, 1980, Zenkovich,

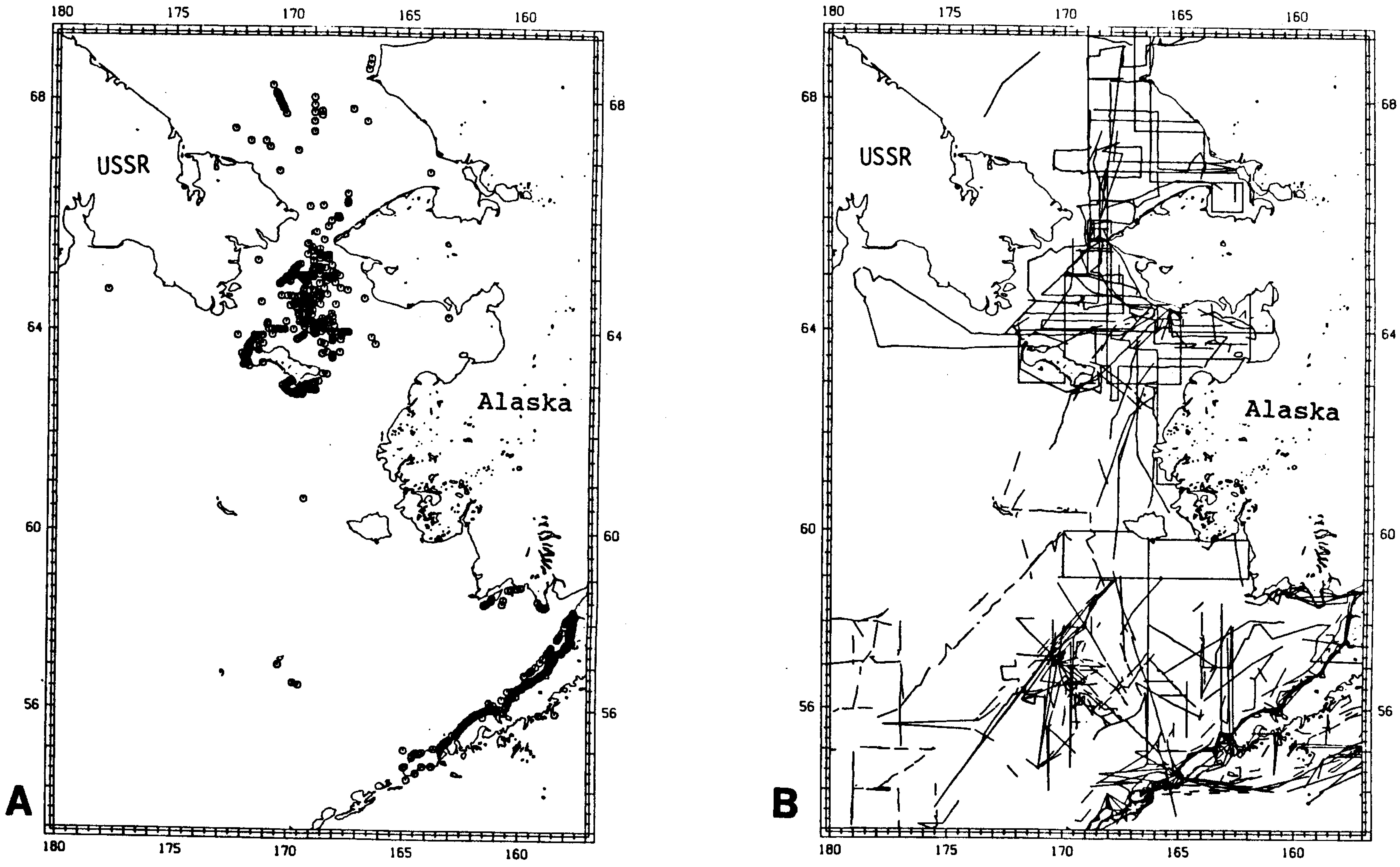


Figure 20 (A) Distribution of gray whale sightings in the northeastern Bering Sea from June-August 1978 (from Consiglieri, Braham, and Jones, 1980). (B) Ship and aerial tracklines completed for whale observations during June-August 1978 (from Consiglieri, Braham, and Jones, 1980).

1934, 1937, 1955). Zenkovich (1937) reported that feeding whales were apparently segregated by age. He noted the presence of a feeding ground near Cape Navarin in the Gulf of Anadyr used only by two-year-old male gray whales.

Another large group of feeding whales is found in the Chukchi Sea, along both the Alaskan and Siberian Coasts as well as in the central part of the Chukchi Sea and along the northern ice edge (Bogoslovskaya et al., 1981; Coyle, 1981; B. Nelson, Alaskan Dept. of Fish and Game, Nome, pers. comm., 1982). Gray whales have been spotted in the Beaufort Sea as far east as the MacKenzie River Delta, but this was probably an isolated occurrence (Rugh and Fraker, 1981).

A few, small isolated groups of gray whales do not go north to feed but instead shear off from the main population and spend the summer feeding at certain points along the migration route. One such group feeds in the outer Strait of Juan de Fuca and along the west coast of Vancouver Island, British Columbia (Hudnall, 1981; J. Oliver, Moss Landing Marine Station, pers. comm., 1982). A well-developed ampeliscid amphipod mat community exists in Pachena Bay, Vancouver Island and is being exploited by a small group of gray whales (J. Oliver, pers. comm., 1982). Even though the Chirikov Basin has historically been regarded as the main feeding area (Rice and Wolman, 1971), other areas certainly receive substantial feeding pressure. This pressure should increase as the gray whale population continues to rebound.

The feeding habits of the gray whale are diverse. As an omnivore, this whale feeds primarily by benthic suction, but also by engulfing and surface skimming (Nerini, 1981). This provides a high diversity of potential prey and a good survival potential for the whales. It also makes inaccurate the assessment of feeding resources by benthic means alone. Nevertheless, this inaccuracy is very small, as the vast majority of gray whale feeding is benthic in nature (Nerini, 1981; Rice and Wolman, 1971).

The grays are the only whales that regularly consume benthic infauna (Nemoto, 1970). Stomach contents of gray whales taken in the feeding grounds generally contain infaunal amphipods (Rice and Wolman, 1971; Pike, 1962; Zenkovich, 1934). Frequently the stomachs also contain quantities of sand, gravel, and cobbles (Zenkovich, 1937).

Other than the main prey species, the Ampeliscid amphipod, *Ampelisca macrocephala* (Coyle, 1981; Rice and Wolman, 1971; Pike, 1962; Zenkovich, 1934), other Ampeliscid amphipods such as *Ampelisca estrichii*, *Ampelisca birula*, *Byblis sp.*, and *Haploops sp.* are also heavily utilized by the whales. Closer to Siberia, the main prey species is the amphipod, *Pontoporeia femorata* (Bogoslovskaya et al., 1981; Zimushko and Ivashin, 1980; Zimushko and Lenskaya, 1970). In addition to *A. macrocephala* and *P. femorata*, a number of other amphipods, polycheate worms, incidental infauna, and nektonic forms such as mysids and bait fish are consumed (Nerini, 1981).

The manner in which the whales extract the amphipods from their sandy habitats has long been a subject of speculation. Scammon (1874) reported whales surfacing "besmeared with the dark ooze from the depths below" and indeed it is a common and almost invariable sight for benthic feeding grays to be associated with large sediment plumes in the water column. Plankton nets towed through these mud plumes have documented the presence of displaced infauna in the water column (Oliver et al., in press). Sea birds are frequently observed diving and apparently feeding in the mud plumes (Harrison, 1979). All these observations suggest that the whales are disturbing the sea floor.

From diving and behavior observations by Nerini (1982), J. Oliver (oral and writ. comm., 1982), S.J. Swartz (UCSC, oral comm., 1982), F.H. Fay (IMS, Fairbanks, oral comm., 1982), and Hudnall (1981) it is speculated that the grays roll to one side, mouth parallel to the bottom and use a suction formed by the retraction of the large muscular tongue in the mouth cavity to rip up patches of amphipod-rich sediment. The sediment is then expelled through the baleen on the opposite side of the mouth and the amphipods are retained on the hairy inner side of the baleen plates to be swallowed at a later time. This hypothesis is supported by the observed feeding behavior of the captive gray whale, Gigi (Ray and Schevill, 1974).

Though never seen directly in the wild, the suction feeding method is supported by whale behavior observed in shallow water by Steve Swartz (UCSC, pers. comm., 1982), John Oliver (Moss Landing, pers. comm., 1982), and Hudnall (1981). In all cases, the whales rolled on their sides, mouth parallel to the bottom, but further observation was impaired by the ensuing sediment plume.

before drawing the amphipod-rich sediment into their mouths.

Previous theories that grays actually came into contact with the sea floor and "bulldozed huge furrows" and "engulfed power-shovel helpings of crabs" (Walker, 1971) or "stirred up the bottom sediments with their snouts" (Rice and Wolman, 1971) seem unlikely as abrasion by bottom sediment would probably be much too severe for the relatively tender cetacean skin. It is untenable that gray whales plough the sea floor for the hundreds of kilometers necessary to filter sufficient amphipods to account for yearly and total gains of body weight.

Uneven wear on the inner side of the baleen plates of 31 whales studied by Kasuya and Rice (1970) shows that 27 of the whales fed predominately with the right side of their heads. Kasuya and Rice (1970) also showed a greater frequency of healed or open wounds and lesser numbers of parasitic barnacles on the right side of the rostrum. This suggests the idea of "right-handed" or "-mouthed" whales and implies that the whales do occasionally come into contact with the abrasive sea floor.

Benthic feeding produces a variety of pits and depressions in the sea floor. The feeding traces left by the whales are the main focus of this paper. Elongate furrows up to 10 m in length were discovered in areas of heavy whale feeding in the Bering Sea by Nerini and others (1980) and M. Larsen (USGS, Menlo Park, pers. comm., 1980). SCUBA divers measured pits ranging in length from 0.6 m to 3 m and attributed them to feeding gray whales (Nerini and Oliver, in press). S. Swartz (UCSC, pers. comm., 1982) has observed whales making pits, as long as their gape and up to a meter wide, in the highly mobile sands of the breeding lagoons in Baja California, Mexico. Core samples near these pits produced very little macroscopic fauna, so these pits are not technically feeding pits but might be attributed to "mock feeding", test feeding, or some other unexplained behavior. John Oliver (Moss Landing, pers. comm.) has observed oval pits up to 1.5 m long in ampeliscid amphipod-bearing sediment associated with an actively feeding juvenile gray whale in Pachena Bay, Vancouver Island. The oval pits often occur in groups as a multiple suction feeding event (Nerini, 1981, J. Oliver, pers. comm., 1983).

In order to determine the shape and size of features likely to be made by a whale foraging on the benthos, a histogram of gray whale gape (mouth) lengths based mainly on data from Rice and Wolman (1971) has been compiled (Fig. 8). Gape lengths were calculated by multiplying the head length by 0.75 (Dale Rice, NMML, Seattle, pers. comm., 1982). The average gape length for male gray whales was 2.0 m (n = 131) and for females, 2.1 m (n = 105). The average gray whale head, when viewed from above, is triangular and the line from the snout to the posterior end of the gape is straight. Thus, the majority of the mouth is parallel to the bottom and a large percentage of the gape may be utilized during feeding. Since the actual percentage of mouth area used is unknown, these measurements can only provide parameters for the maximum size of feature which a non-moving whale can produce.

If a whale were swimming or drifting in the current while sucking up the sediment, then the size of the resulting feature could be considerably larger. The length of feature made by a moving whale would be controlled by the duration of the suction event together with the speed of the whale and the effect of current movement on the whale. By coordinating its propulsion and suction, a whale could create an elongate pit of substantial length.

Observations of feeding whales show both stationary and mobile feeding modes. Bud Fay (Institute of Marine Sciences, Fairbanks, pers. comm., 1982) reported that whales feeding in the surf off the southern side of St. Lawrence Island remained stationary and head down with their flukes in the air. Norris et al. (1982) gave evidence that gray whales near the entrances to lagoons in Baja California made use of currents to sweep food into their mouths. Both of these observations apparently apply to whales feeding in the water column and not on the benthos.

Records of dive times and positions of diving and surfacing of bottom-feeding whales near St. Lawrence Island show that whales feed in rather small areas. They often surface near or behind where they dive implying minimal movement on the bottom (B. Wursig, Moss Landing Marine Lab, pers. comm., 1982). A juvenile gray whale at Pachena Bay, observed by SCUBA divers, was moving along the bottom while feeding. The resulting pits were up to 1.5 m in length, longer than the gape of the small whale (J. Oliver, pers. comm., 1983). Although the size of the pit left by a non-moving whale generally may be expected to be approximately the size and shape of the gape, there is considerable potential for smaller (suction out of only a portion of the mouth) or larger (suction while moving) pits.

The average depth of the pits is still an unresolved question but they are clearly less than 50 cm in depth because they are not observed in horizontal line bathymetry of the sonographs. SCUBA divers on the NMML cruises in 1980 (Nerini et al., 1980) found pits as deep as deep as 40 cm, although these may have been older features enlarged by current scour. Divers on the L.G.L. cruises in 1982 (Thomson, in press) found pits and furrows near St. Lawrence Island averaging 10 cm in depth. The ampeliscid tube matting which is the focus of the whales' feeding efforts is seldom deeper than 10 cm (Nelson et al., 1981). Thus, for the purpose of harvesting amphipods, excavations deeper than 15 cm appear unnecessary.

The gray whale is not the only marine mammal which feeds by excavating benthic infauna. The Pacific Walrus (Odobenus rosmarus) consumes a diet consisting almost exclusively of clams but not excluding certain epifauna such as crabs (Fay, 1982; Frost and Lowry, 1981). The walrus forage for their infaunal prey by hydraulically creating pits and furrows to excavate the clams. The walrus apparently excavate pits (up to 30 cm in diameter) when foraging in water of good visibility or when hunting for large, isolated deep-burrowing clams such as Mya sp. They create very long, narrow furrows when foraging in water of poor visibility or when searching for smaller, more numerous, near-surface clams such as Spisula sp. or Macoma sp. (Oliver, Slattery, O'Connor and Lowry, 1983). These furrows rarely exceed 40 cm in width but may be several tens of meters long and are distinguishable on the side-scan record due to their extensive length (Figs. 21, 22). Generally, the whale and walrus consume different prey species. This eliminates feeding competition between the two but does not always imply distinctly different feeding grounds.

epifauna but is also known to eat clams. The feeding excavations of the Bearded Seal are likely to be much smaller than those of the walrus simply because of the relative size of the two animals. Competition between the walrus and bearded seal, combined with a rapidly increasing walrus population, has caused the bearded seals to rely more on epifaunal prey and less on clams (Lowry et al., 1980).

Another possible creator of sea floor pits is the sculpin. Divers in the Bering Sea have reported that sculpins are frequently found in round, shallow depressions which are proportional to the size of the sculpin (Thomson, in press). There is some question as to whether the sculpins made the pits or are simply occupying natural depressions or mammal feeding pits. Even though sculpins may grow as large as .75 m, size would still be a limiting factor.

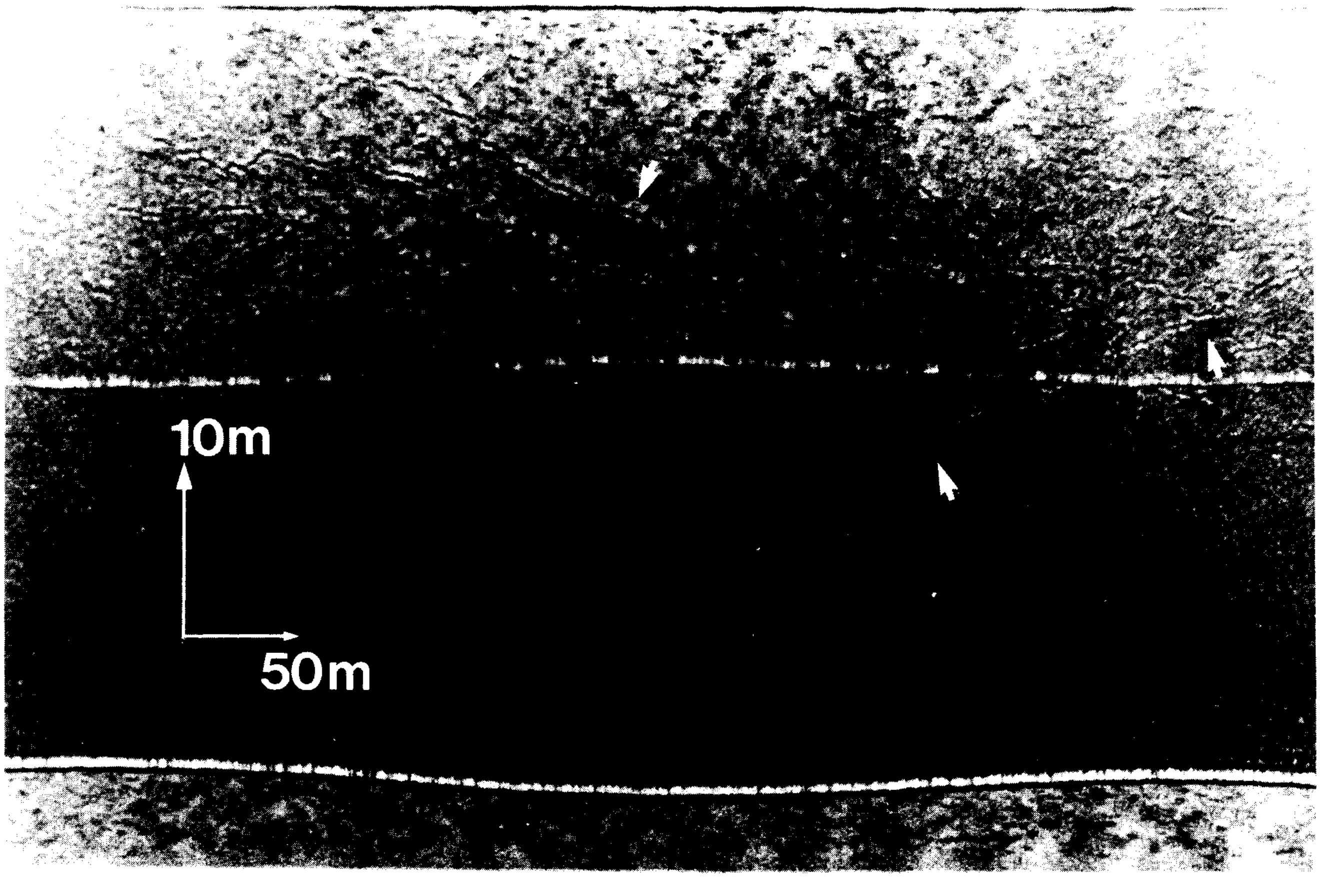


Figure 21 Sonograph of several long, narrow walrus feeding furrows, 100 kHz, eastern Chirikov Basin (see arrows).

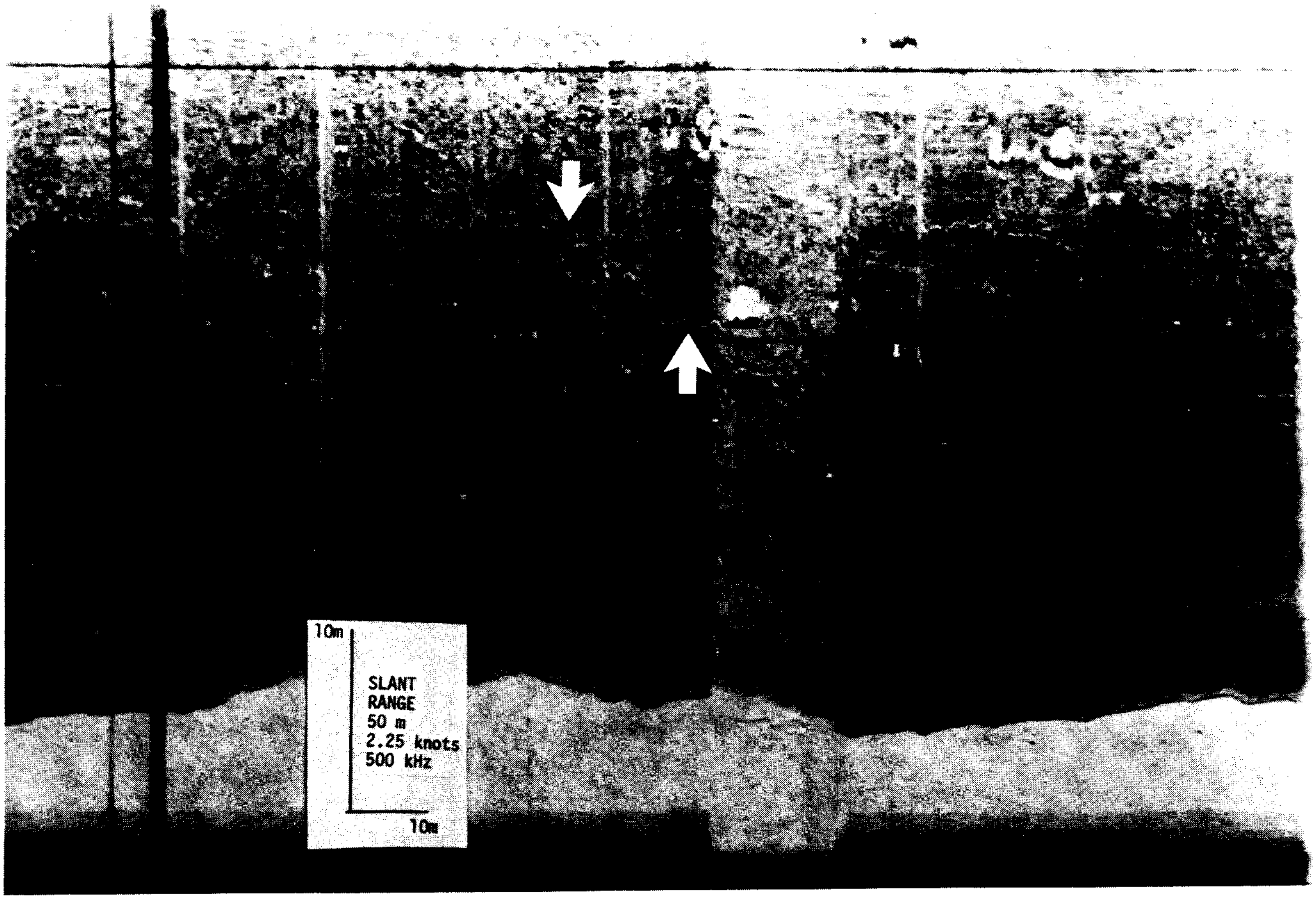


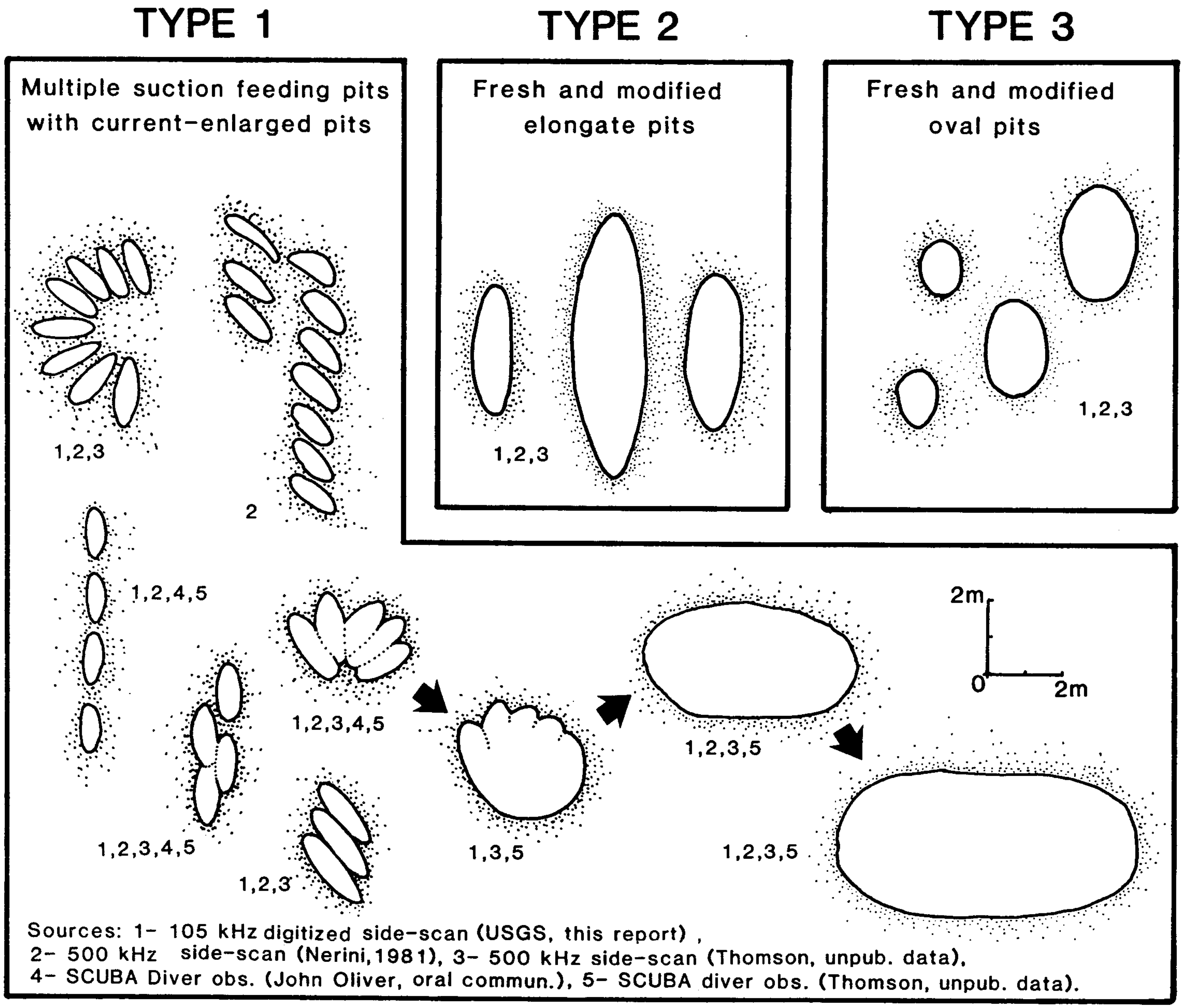
Figure 22 Sonograph of a single walrus feeding furrow, note the large rocks on the record, 500 kHz, northern Chirikov Basin (see arrows for furrow).

WHALE FEEDING PIT TYPES

Compilation of substrate types (Figs. 12-15), high concentrations of Ampeliscid amphipods (Figs. 4, 19), and the summer distribution of gray whales (Figs. 20) all show that the main feeding grounds of the gray whale occur in central Chirikov Basin and around the margins of St. Lawrence Island. Previous studies of physical surficial features on the sea floor (Fig. 16) reveal a general lack of these structures in areas of whale feeding. Consequently, the highly disturbed sea floor in the central Chirikov Basin and nearshore regions of St. Lawrence Island can be attributed to the feeding behavior of the gray whales and subsequent current scour activity triggered by the whales. Diver observations and calibration with high resolution side-scan sonographs show that a wide variety of feeding traces exists, but some basic patterns can be described and categorized.

Whale-created pits vary greatly in size but in general they are fairly shallow. Depending on age, the pits may have distinct or gently sloping edges. They may be partially infilled and appear only as a fine textured patch with no edges at all, or they may be greatly enlarged with very distinct edges.

We divide the features into three categories. Type 1 features are any combination of recognizable fresh feeding traces and current-scour-enlarged pits. A fresh feeding trace is defined as a series of oval pits ranging from 1 m to 3 m long and 0.5 m to 1.5 m wide, arranged in an organized pattern implying a multiple suction feeding event (Figs. 23, 24). These groupings of pits are discernable on 105 (Fig. 24) and 500 kHz sonographs (Thomson, in



Sources: 1- 105 kHz digitized side-scan (USGS, this report), 2- 500 kHz side-scan (Nerini, 1981), 3- 500 kHz side-scan (Thomson, unpub. data), 4- SCUBA Diver obs. (John Oliver, oral commun.), 5- SCUBA diver obs. (Thomson, unpub. data).

Figure 23 Sketches of three types of bottom pits, attributed to Gray Whale feeding and subsequent current scour, based on observations from side scan sonar and by SCUBA divers in Chirikov basin and the nearshore areas of St. Lawrence Island. All drawings are to the scale shown for Type 1.

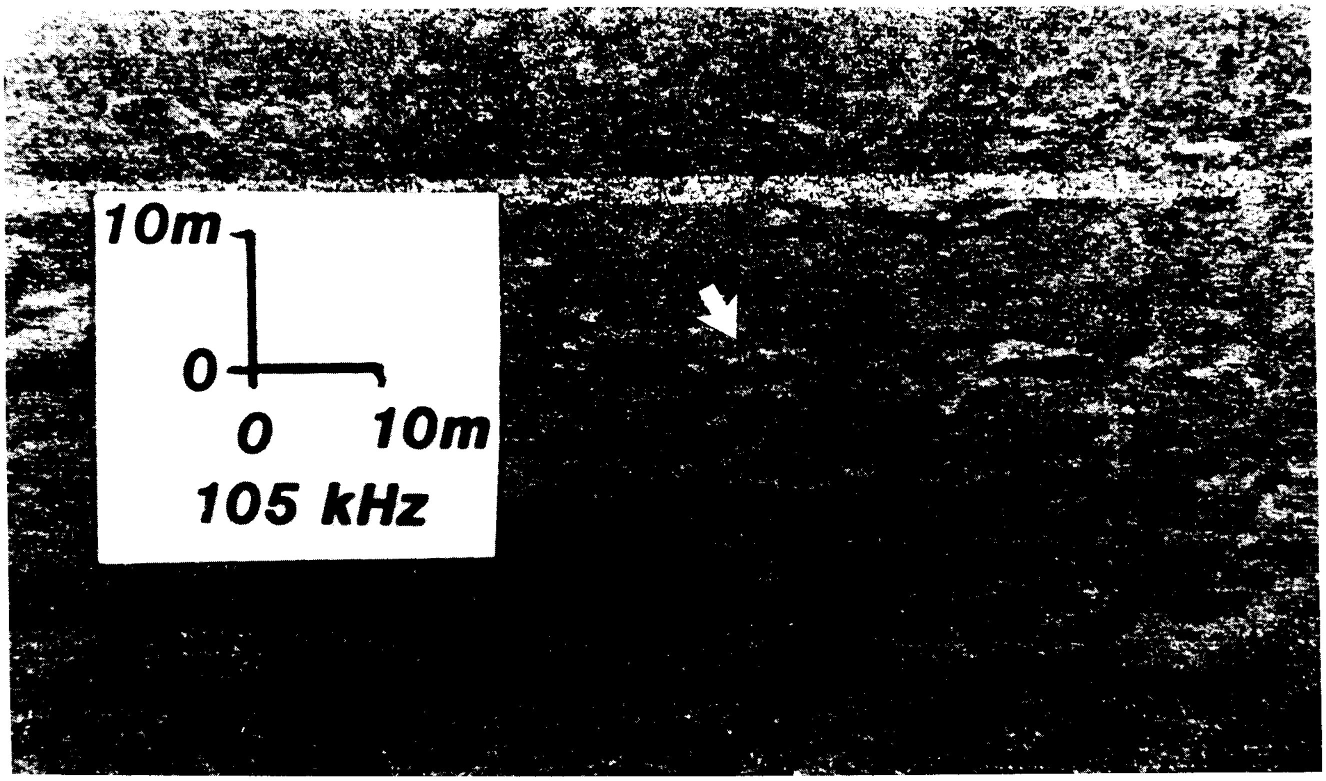


Figure 24 Sonograph of area near station Dog 7, 105 kHz, Type 1, close-up of a multiple suction feeding event (see arrow). Sonograph location is shown in Figure 7

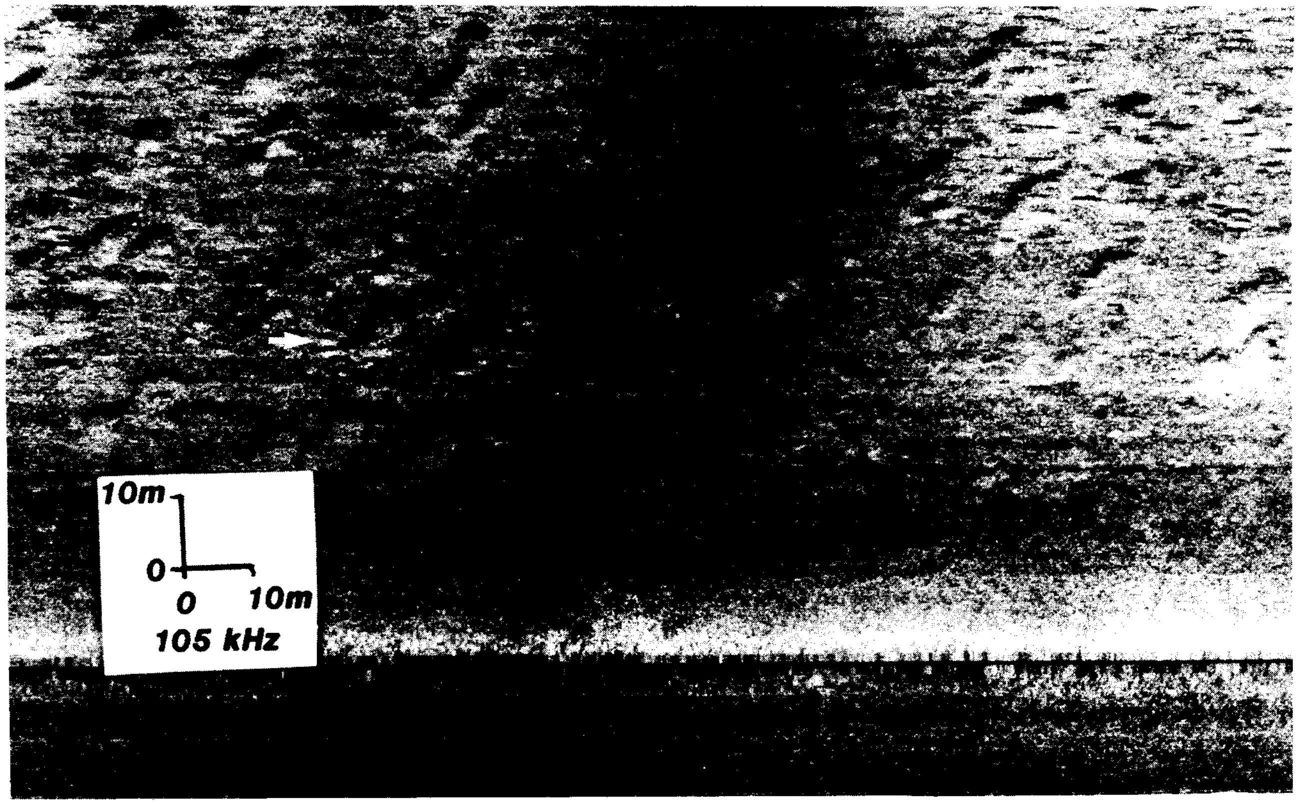


Figure 25 Sonograph of station Dog 8, 105 kHz, Type 1, current-scour enlarged and oriented pits with fresh multiple suction feeding events (see arrow). Sonograph location is shown in Figure 7.

press; Nerini et al., 1980), and have been observed by divers (John Oliver, pers. comm., 1983).

The arrangement of pits in a grouping is highly variable, but organized arrangements are seen frequently and these facilitate the recognition of a "fresh feeding area" or "multiple suction feeding event" (Fig. 23). The most common configurations are radiating pits resulting from a whale feeding while slowly turning, large U-shaped groups of pits caused by a whale turning on a larger radius, strings of several pits caused by whale feeding while moving in a straight line, and parallel adjacent pits caused by a whale feeding while moving laterally or drifting (Fig. 23).

Whale fluke marks and depressions made by the body bumping the bottom can be found associated with the multiple suction feeding events. Five hundred kHz side-scan records from the west side of St. Lawrence Island show frequent elongate depressions associated with multiple suction feeding events implying that certain feeding conditions might favor increased contact with the bottom. In general, recognizable fluke or body depressions are rare.

The current-scour-enlarged pits are large (up to 5 m x 20 m) and frequently have a distinct lineation that is parallel to predominant currents (see orientation histograms, Appendix A and Fig. 5). These pits apparently originate as fresh feeding traces. The whale feeding event removes the ampeliscid tube mats that bind the sediment and the exposed fine sand is then subject to erosion by current scour. Frequently, the scour-enlarged pits are seen with remnants of the fresh feeding pits still partially visible (Figs. 23, 25). Type 1 features can consist of fresh feeding traces and current-scour-enlarged pits together implying active feeding and active scour (Figs. 6D, 6E, 25-27); fresh feeding traces alone, suggesting active feeding but

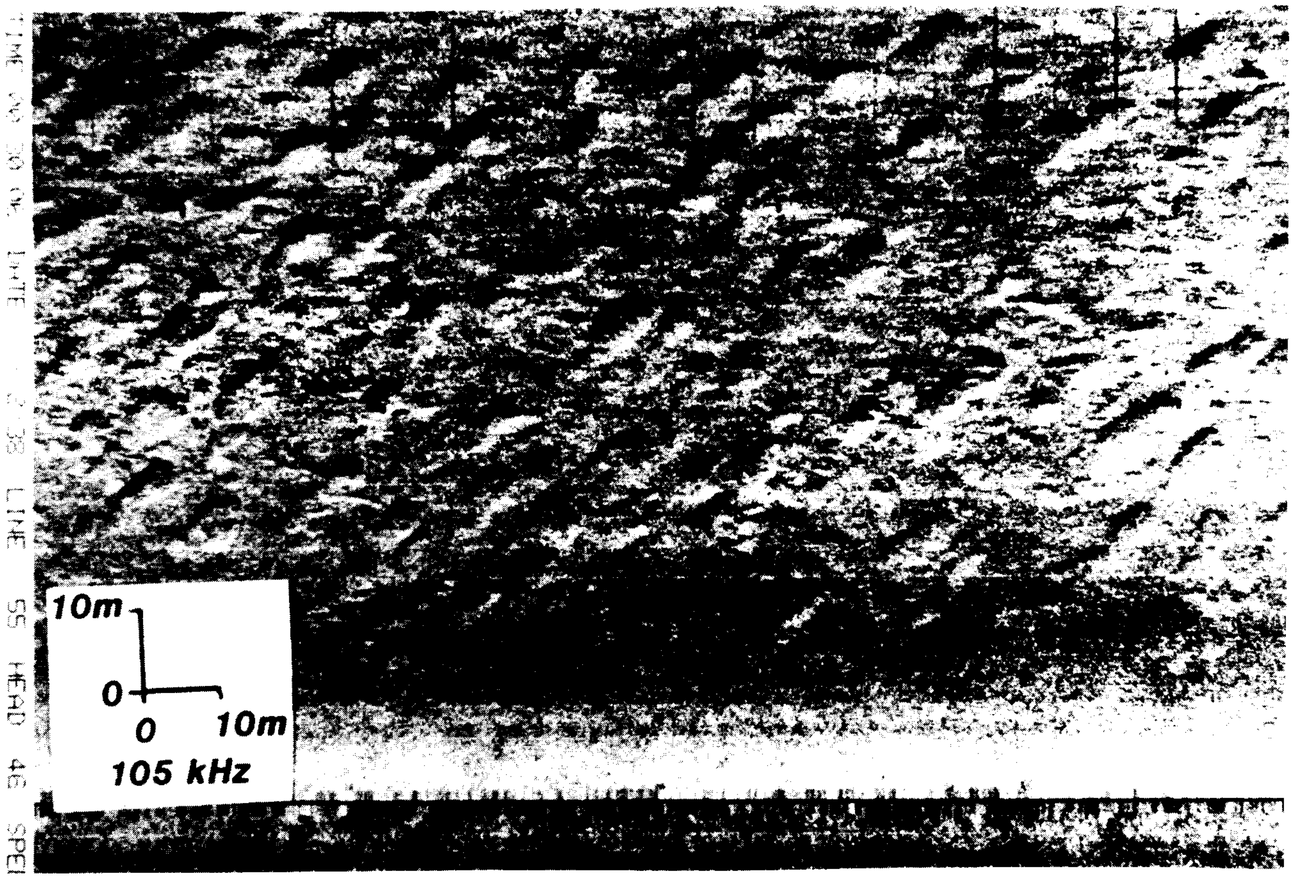


Figure 26 Sonograph of station Dog 1, 105 kHz, Type 1, current-scour enlarged and oriented pits. Sonograph location is shown in Figure 7.

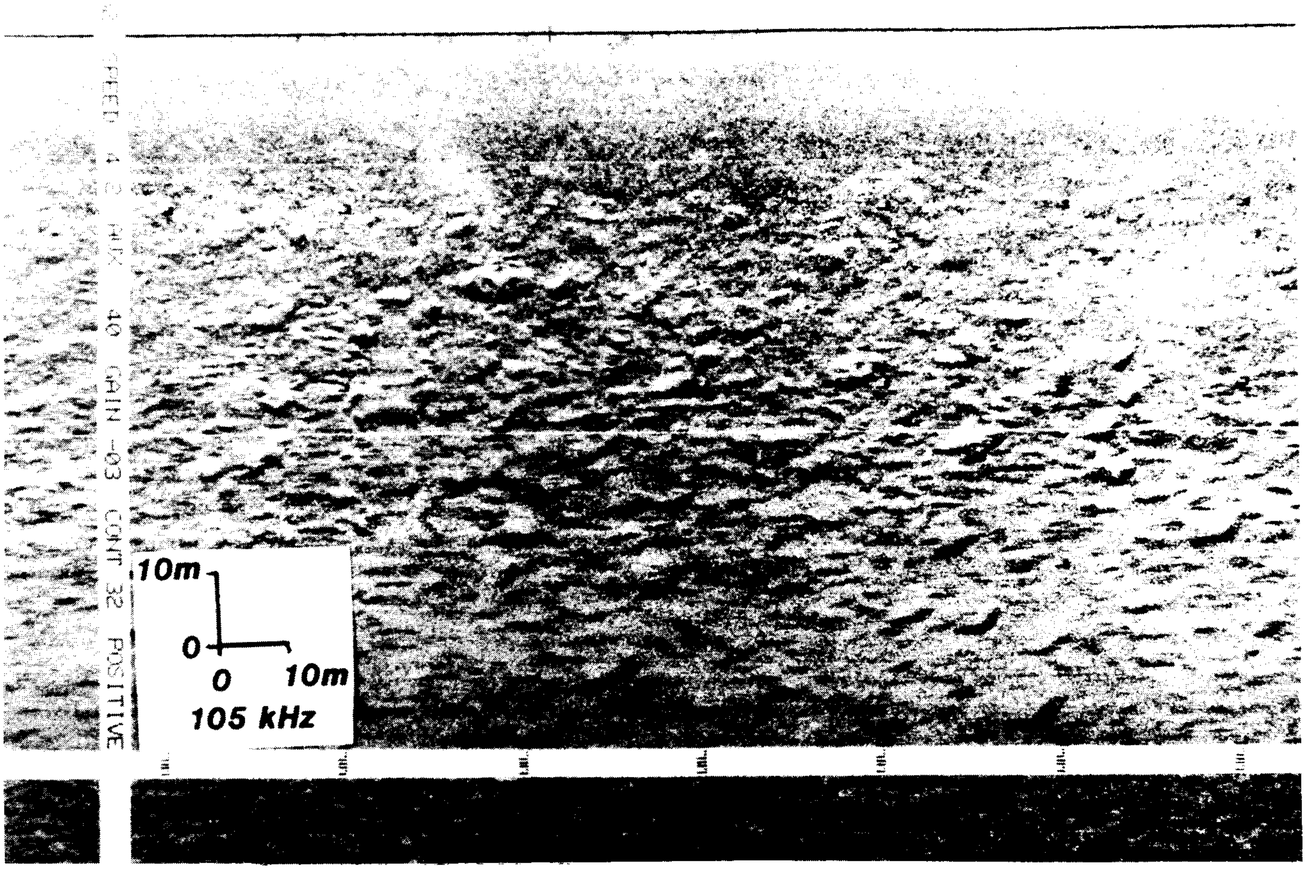


Figure 27 Sonograph of station Dog 14, 105 kHz, Type 1, current-scour enlarged pits. Sonograph location is shown in Figure 7.

insufficient current to initiate scour (Fig. 43); or current-scour-enlarged pits alone, indicating scour in an area where feeding has occurred but is not presently active (Fig. 6G).

Type 2 features are elongate pits measuring up to 20 m but averaging between 3 m and 5 m in length and 1 m to 2 m in width. They are discernible on 105 (Figs. 28-32) and 500 kHz sonographs (Figs. 6F, 6H) (Thomson, in press). SCUBA divers have not inspected these features yet. Their probable origin is either the feeding trace of a moving whale or a slightly modified set of fresh feeding pits. Occasional multiple suction feeding features are found in Type 2 areas (Fig. 31).

Type 3 features are oval pits averaging from 1.5 m to 3.1 m in length and 0.9 m to 2 m in width. They are discernible on 105 (Figs. 6A, 6B, 33-39) and 500 kHz sonographs (Thomson, in press) and have been observed by divers (Nerini et al., 1980; Thomson, in press). Generally, they occur in a fairly random scattering across the sea floor, but in some cases, they can be found in ordered groups, either as elongate strings of oval pits (Fig. 33) or in clover-shaped clusters of pits. With some notable exceptions (Figs. 6A, 34, 36), Type 3 features are of low density.

Types 1, 2, and 3 are distinguished by their average length vs. width ratios. Type 3 features have l/w less than 2.3, Type 1, l/w = 2.3-3.0, and Type 2, l/w greater than 3.0. Adopting Hickey's (1973) terminology to describe the shapes of dicotyledonous leaves by their length-width ratios, the Type 3 features are wide elliptic, the Type 1 features are elliptic, and the Type 2 features are narrow elliptic to very narrow elliptic.

Figures 6 and 40 show the distribution of Types 1, 2, and 3 in Chirikov Basin and the area immediately south of St. Lawrence Island. Type 1 features

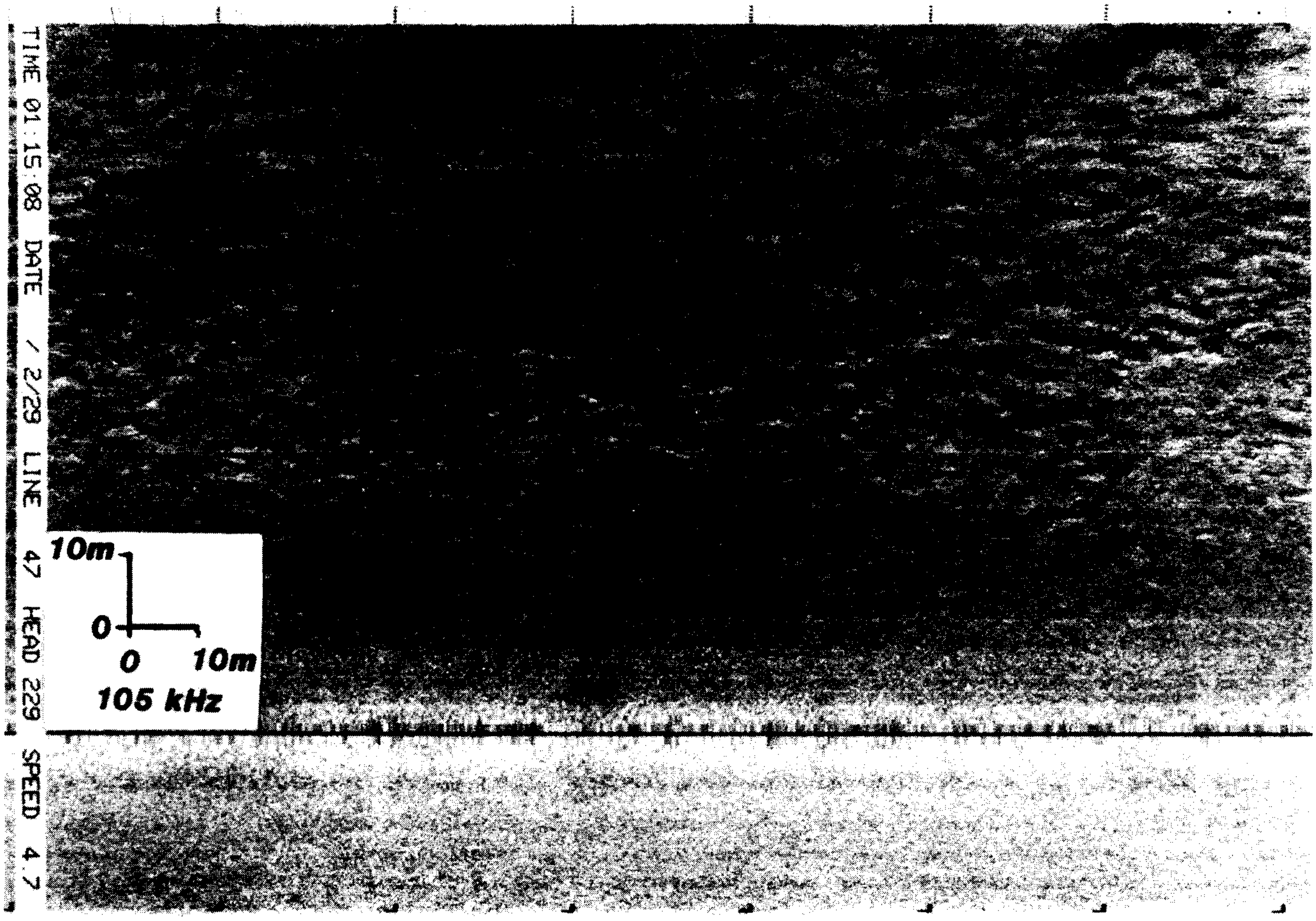


Figure 28 Sonograph of station Dog 3, 105 kHz, Type 2, elongate pits pervasive throughout the record. Sonograph location is shown in Figure 7.

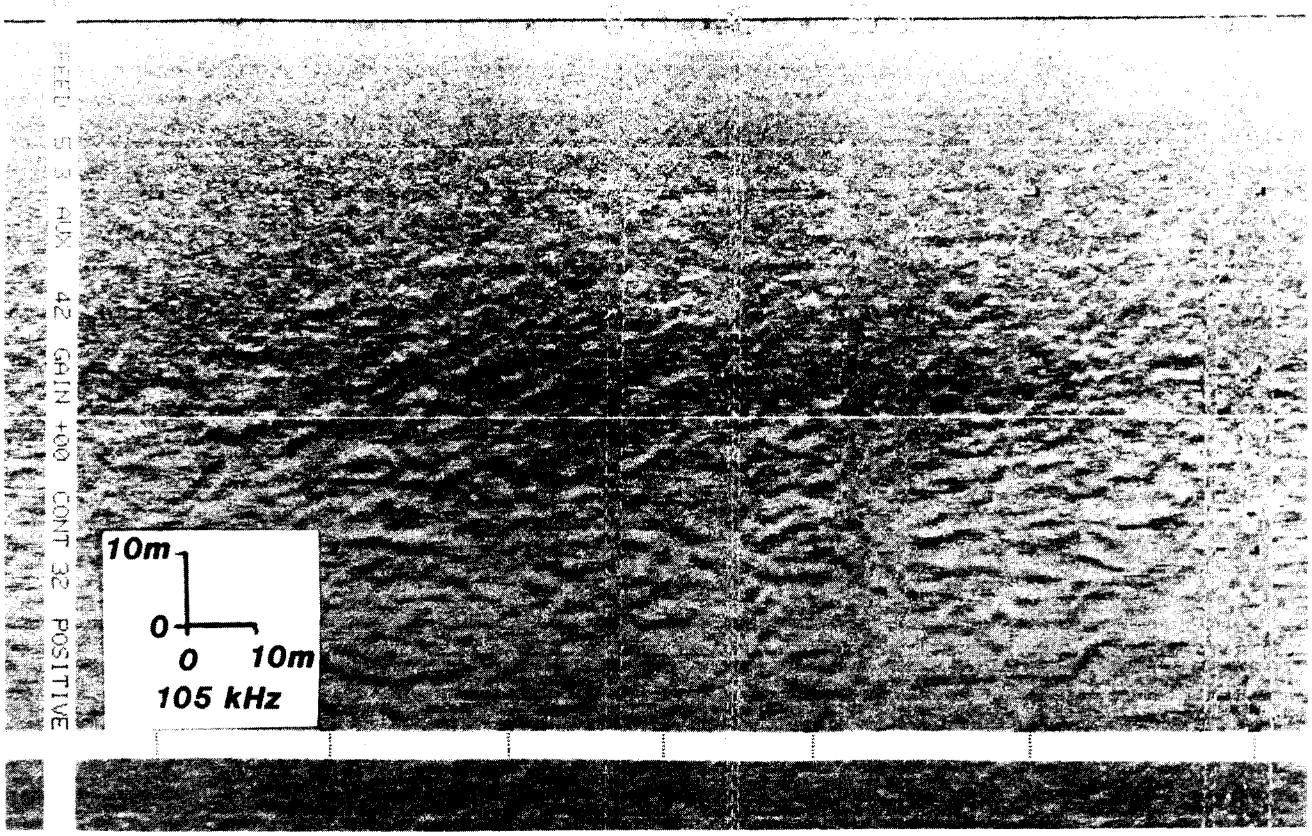


Figure 29 Sonograph of station Dog 4, 105 kHz, Type 2, elongate pits pervasive throughout the record. Sonograph location is shown in Figure 7.

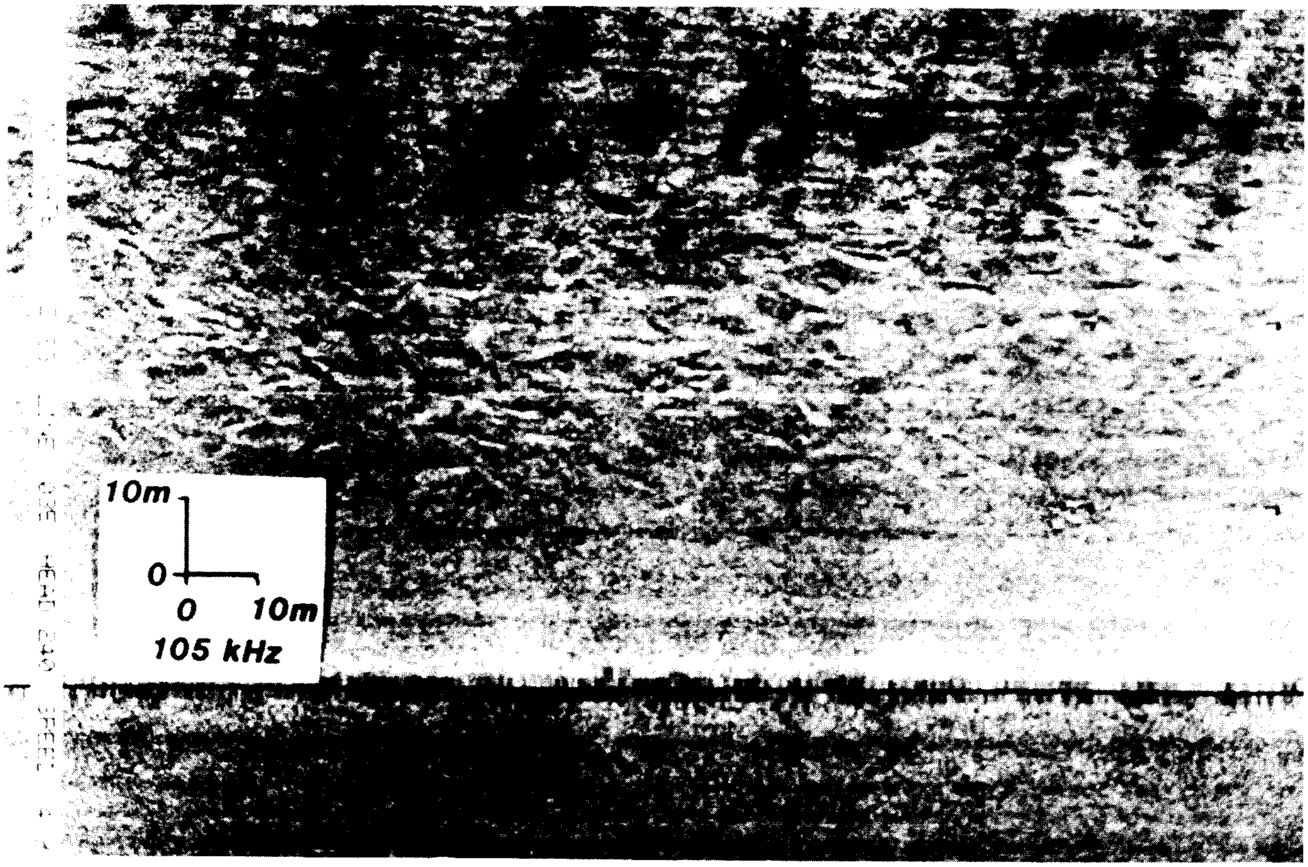


Figure 30 Sonograph of station Dog 6, 105 kHz, Type 2, elongate pits pervasive throughout the record. Sonograph location is shown in Figure 7.

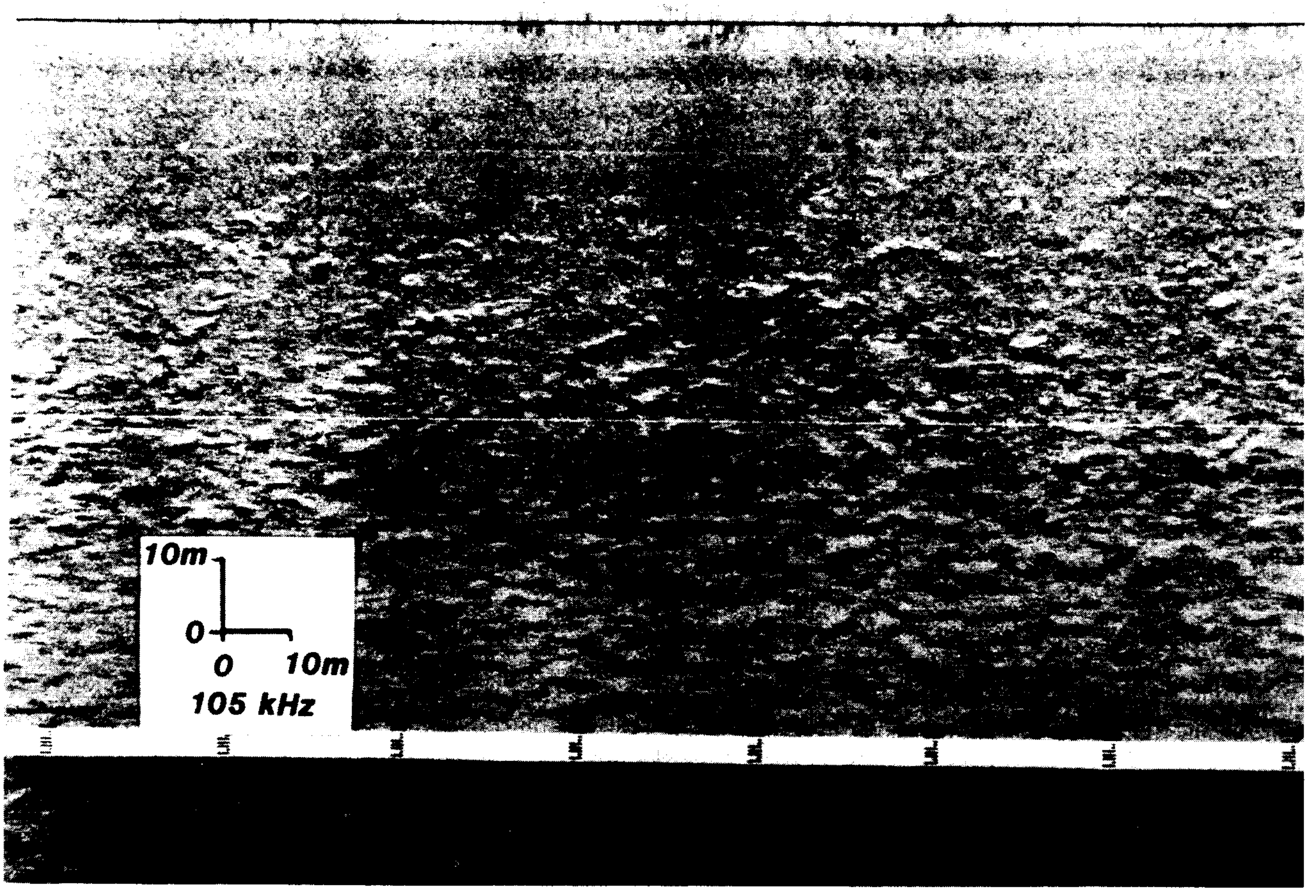


Figure 31- Sonograph of station Dog 12, 105 kHz, Type 2, dense fresh and partially modified pits. Sonograph location is shown in Figure 7.

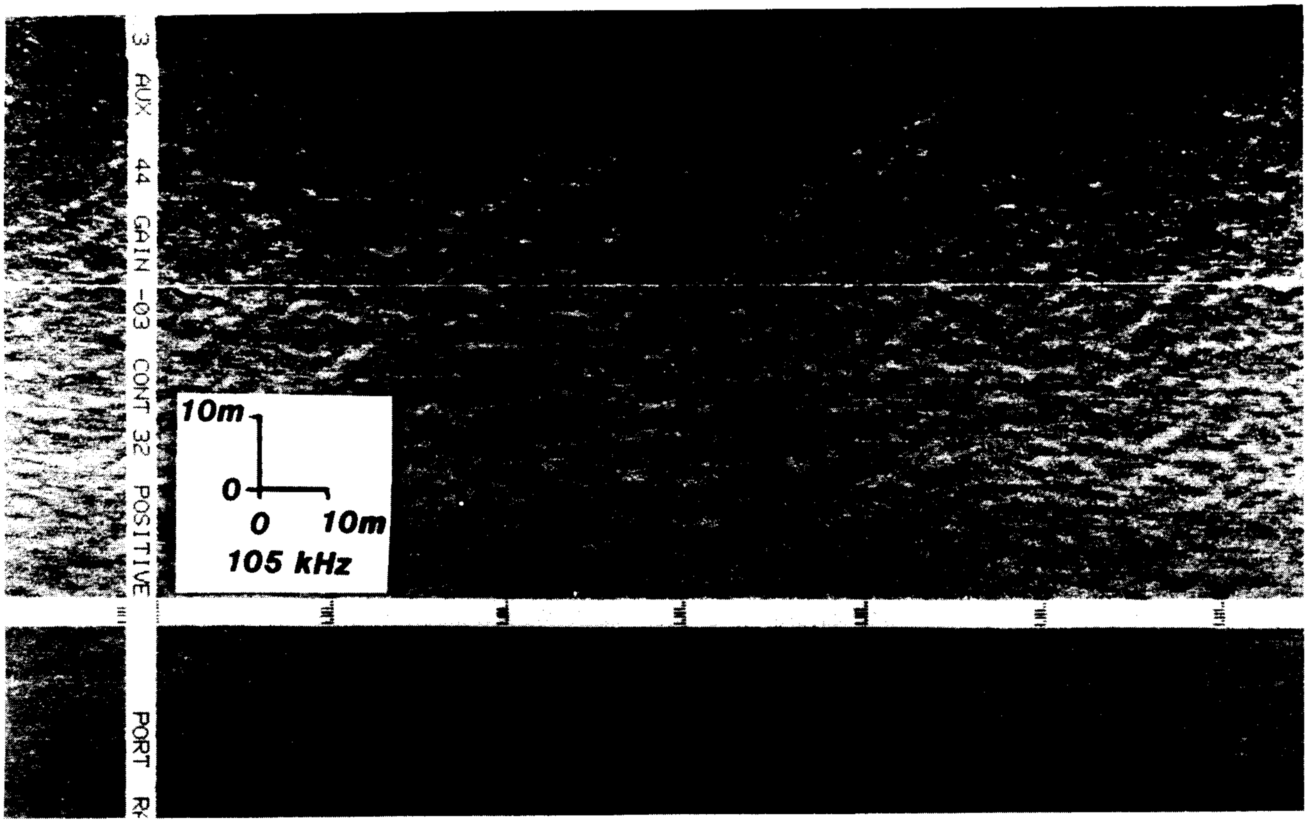


Figure 32 Sonograph of station Dog 13, 105 kHz, Type 2, common elongate pits. Sonograph location is shown in Figure 7.

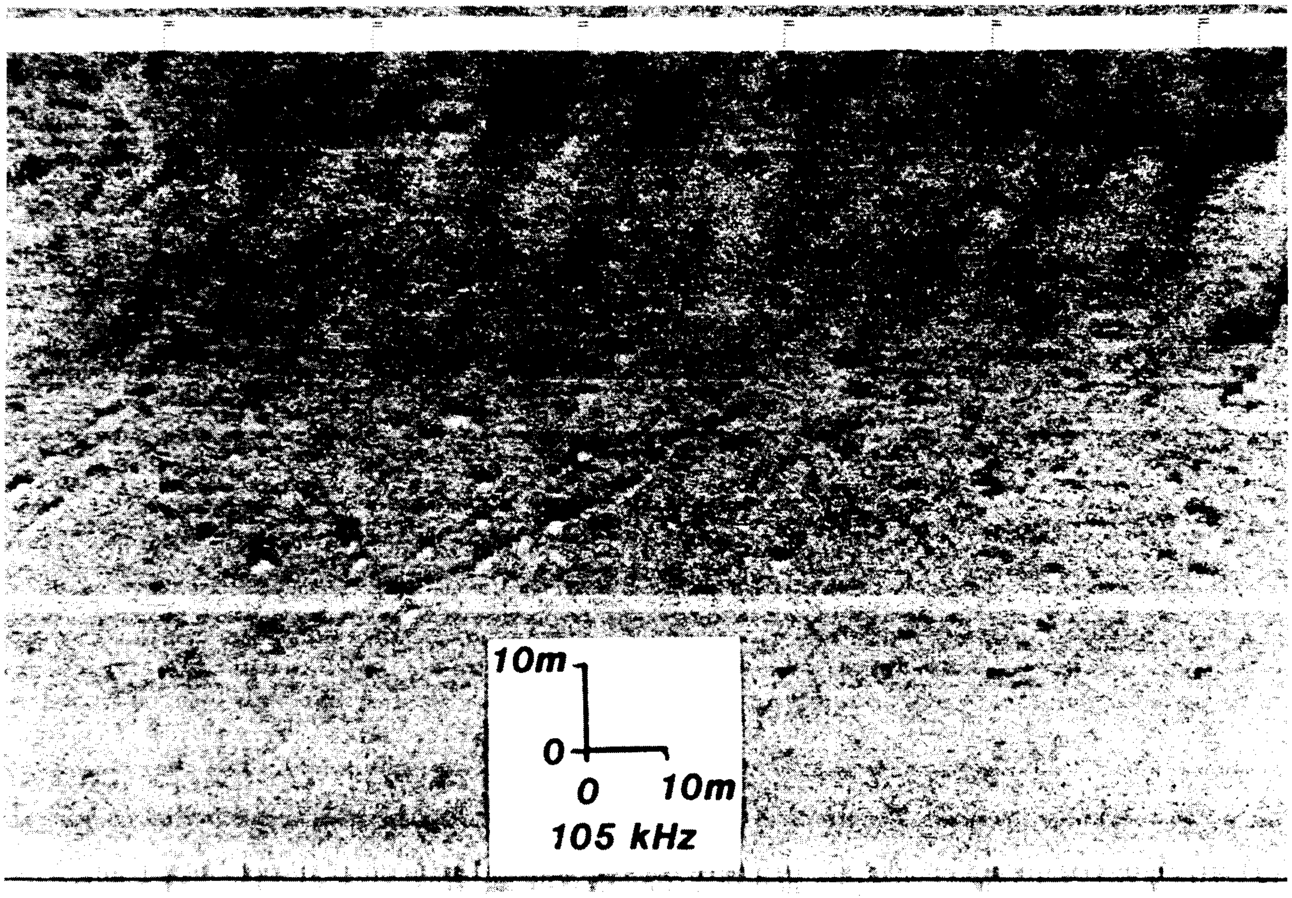


Figure 33 Sonograph of station Dog 2, 105 kHz, Type 3, scattered oval pits. Note elongate chain of pits in center of sonograph. Sonograph location is shown in Figure 7.

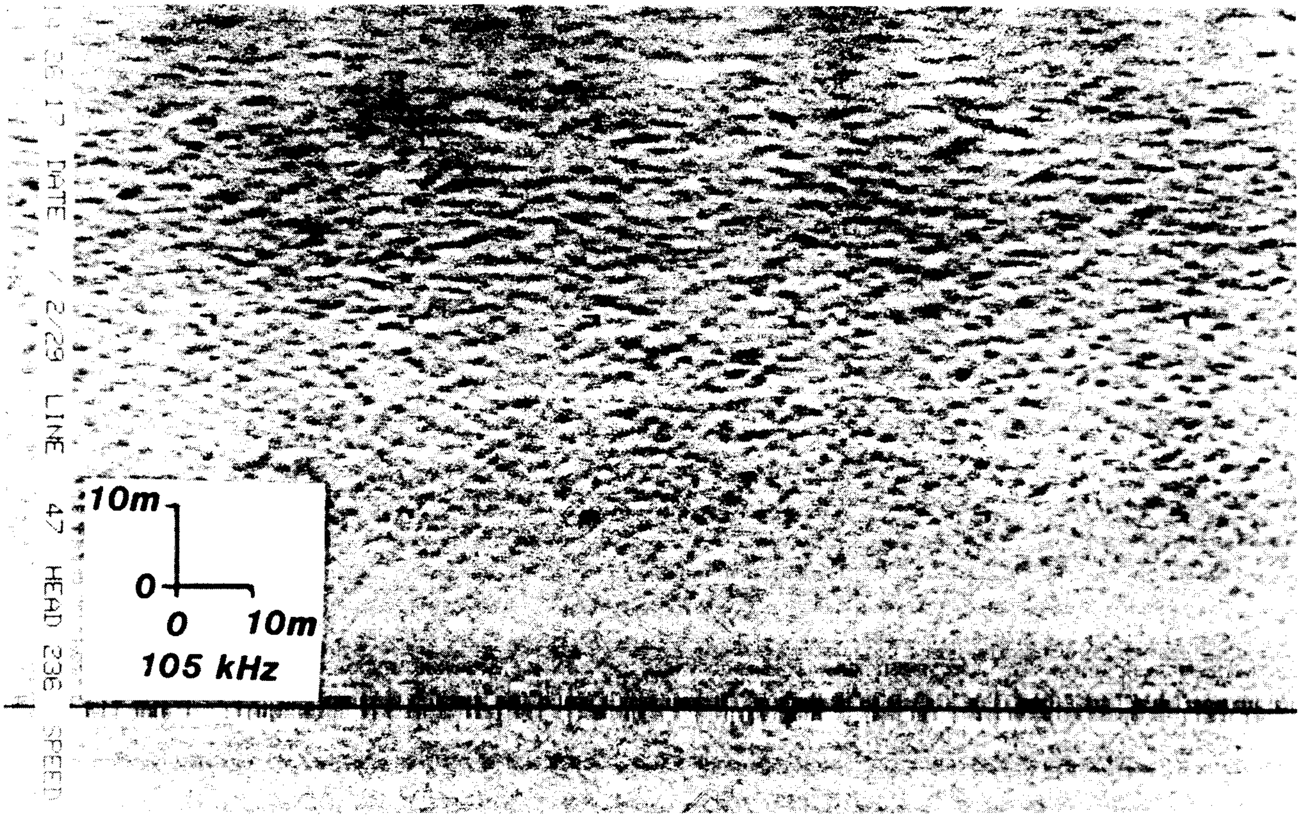


Figure 34 Sonograph of station Dog 5, 105 kHz, Type 3, dense oval pits. Note side-scan distortion which stretches pits that are near the margin of the record. Sonograph location is shown in Figure 7.

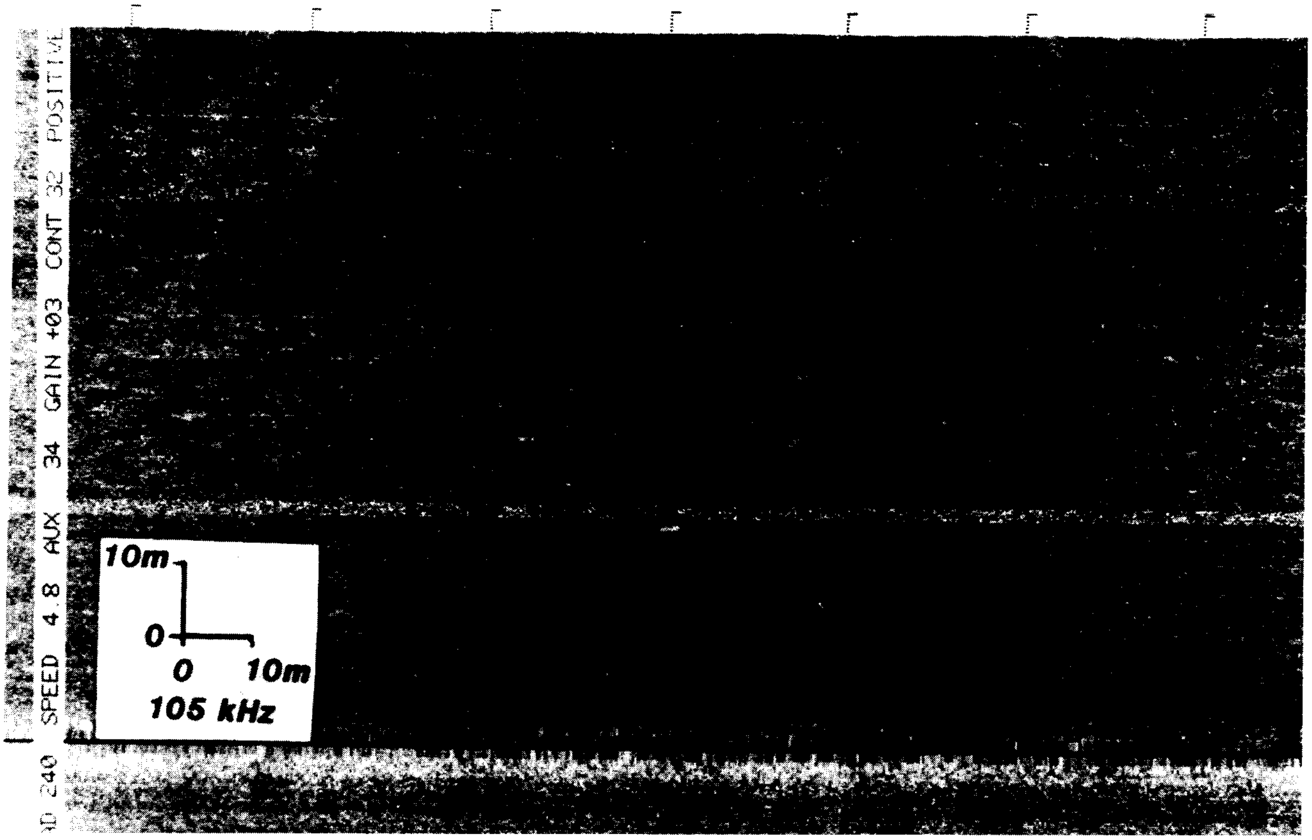


Figure 35 Sonograph of station Dog 9, 105 kHz, Type 3, scattered oval pits. Sonograph location is shown in Figure 7.

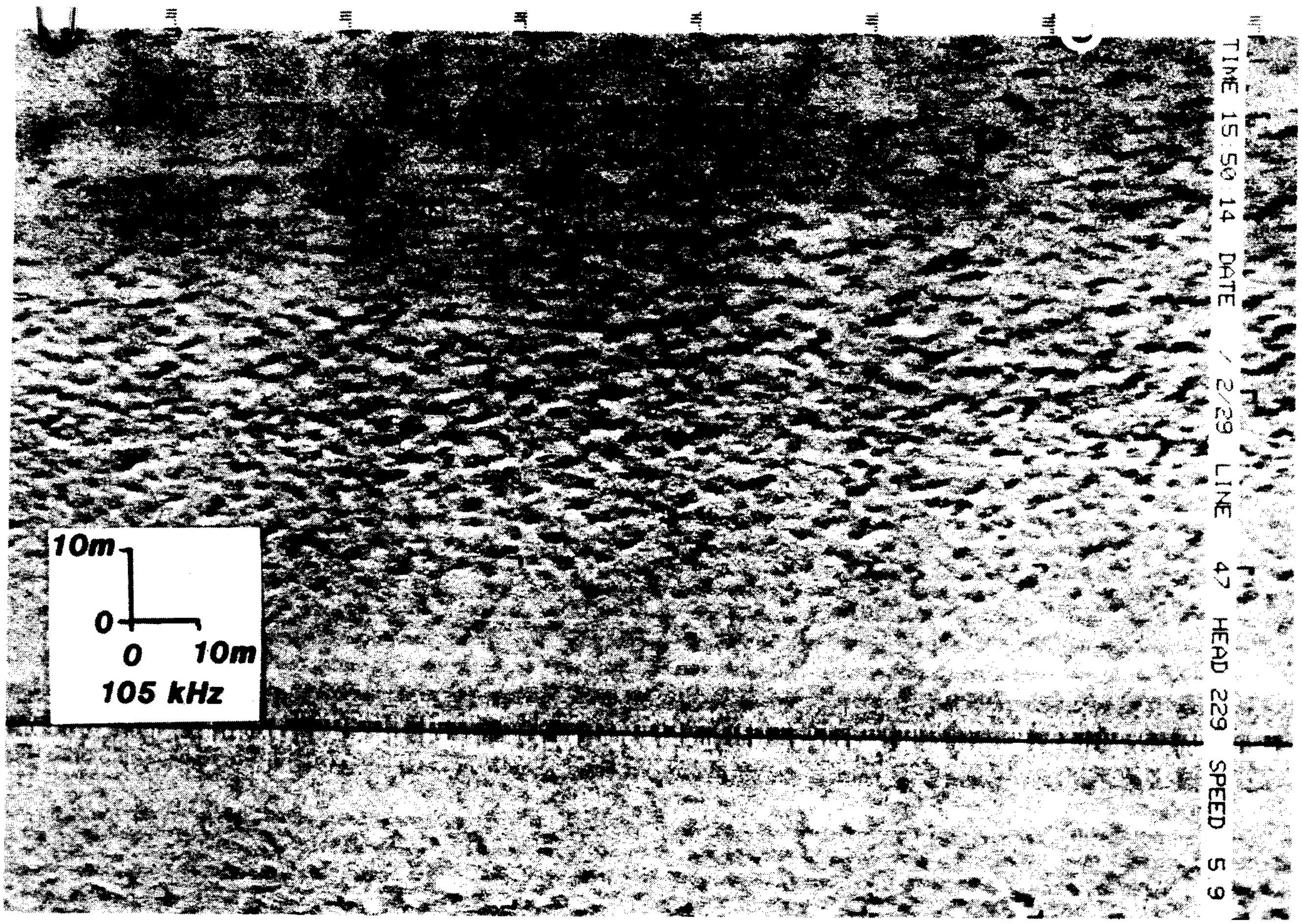


Figure 36 Sonograph of station Dog 10, 105 kHz, Type 3, dense oval pits. Sonograph location is shown in Figure 7.

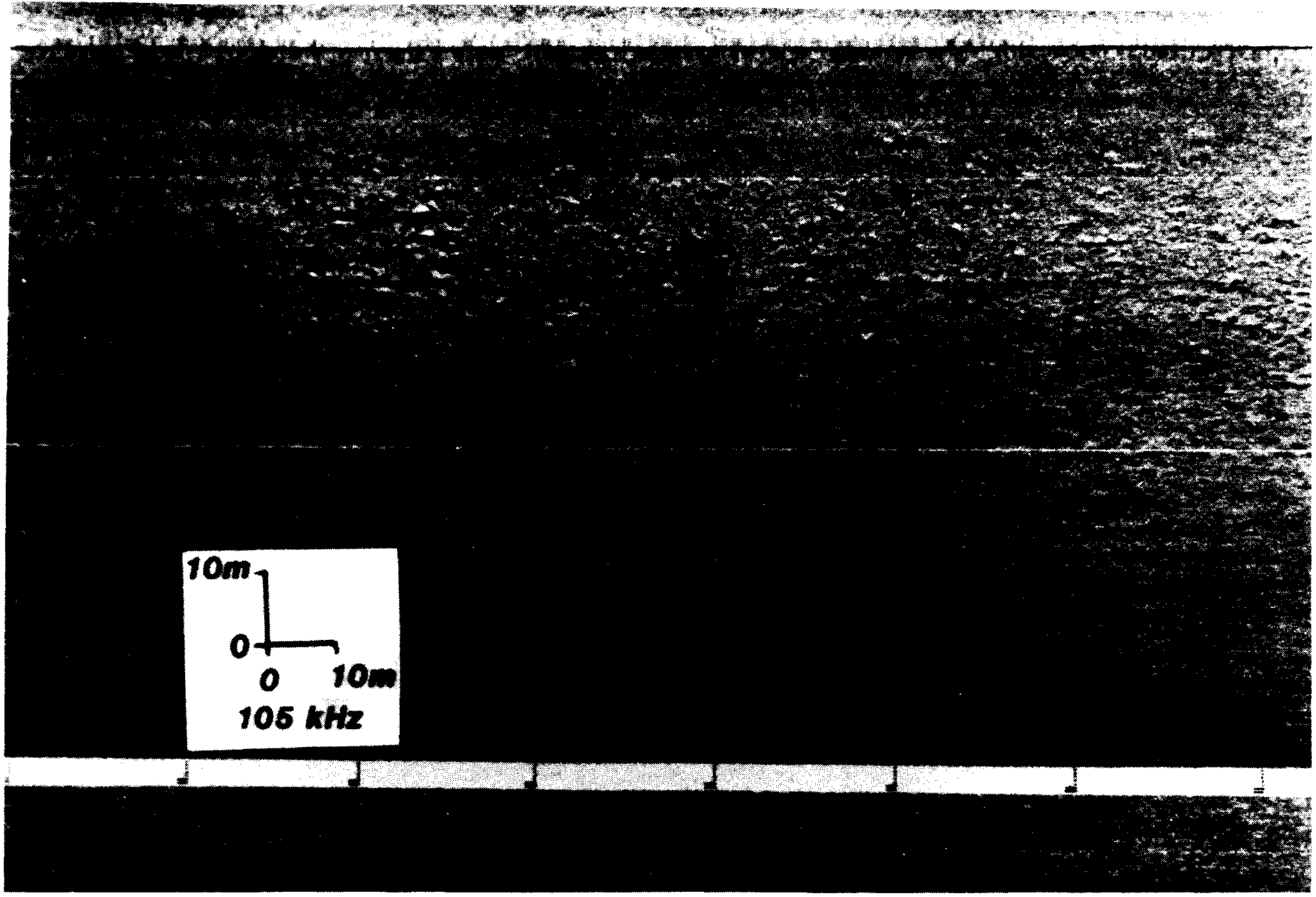


Figure 37 Sonograph of station Dog 11, 105 kHz, Type 3, sparse oval pits. Sonograph location is shown in Figure 7.

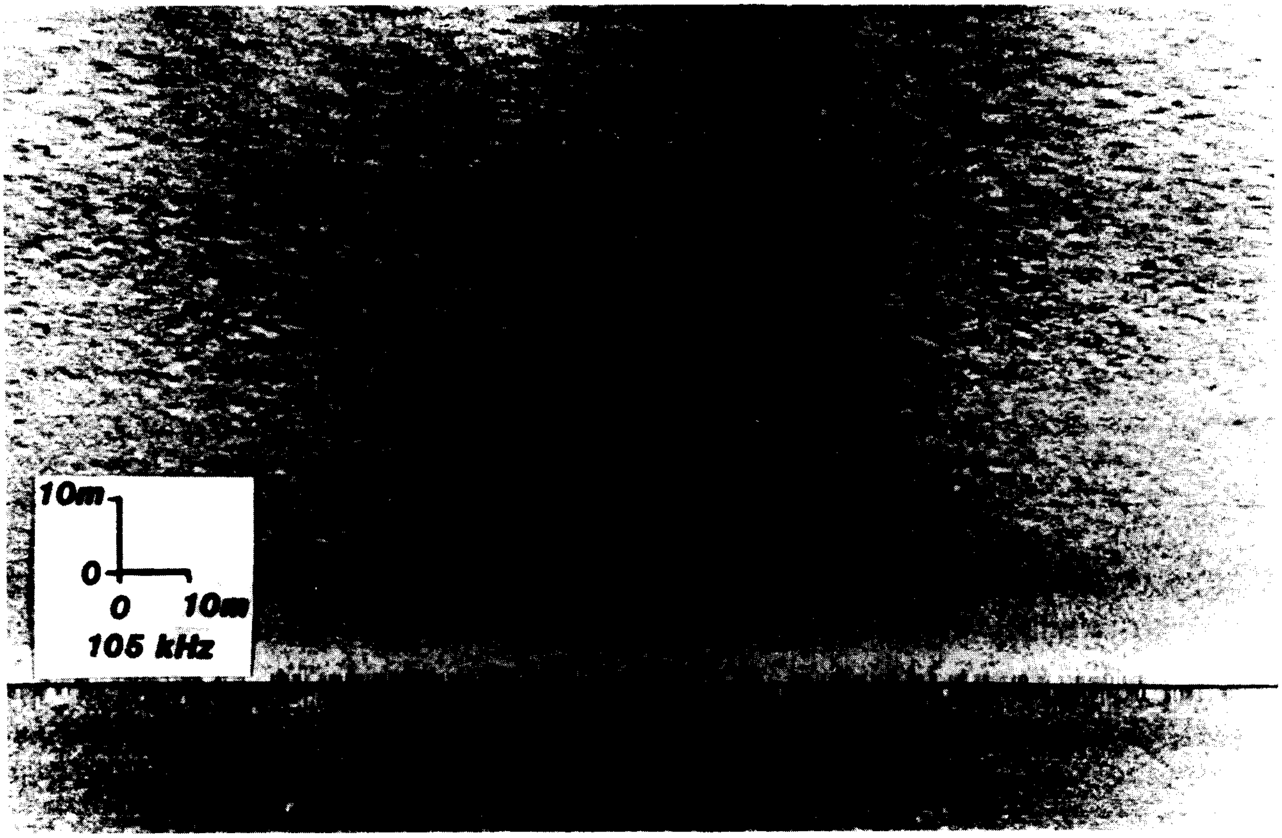


Figure 38 Sonograph of station Dog 15, 105 kHz, Type 3, sparse oval pits. Sonograph location is shown in Figure 7.

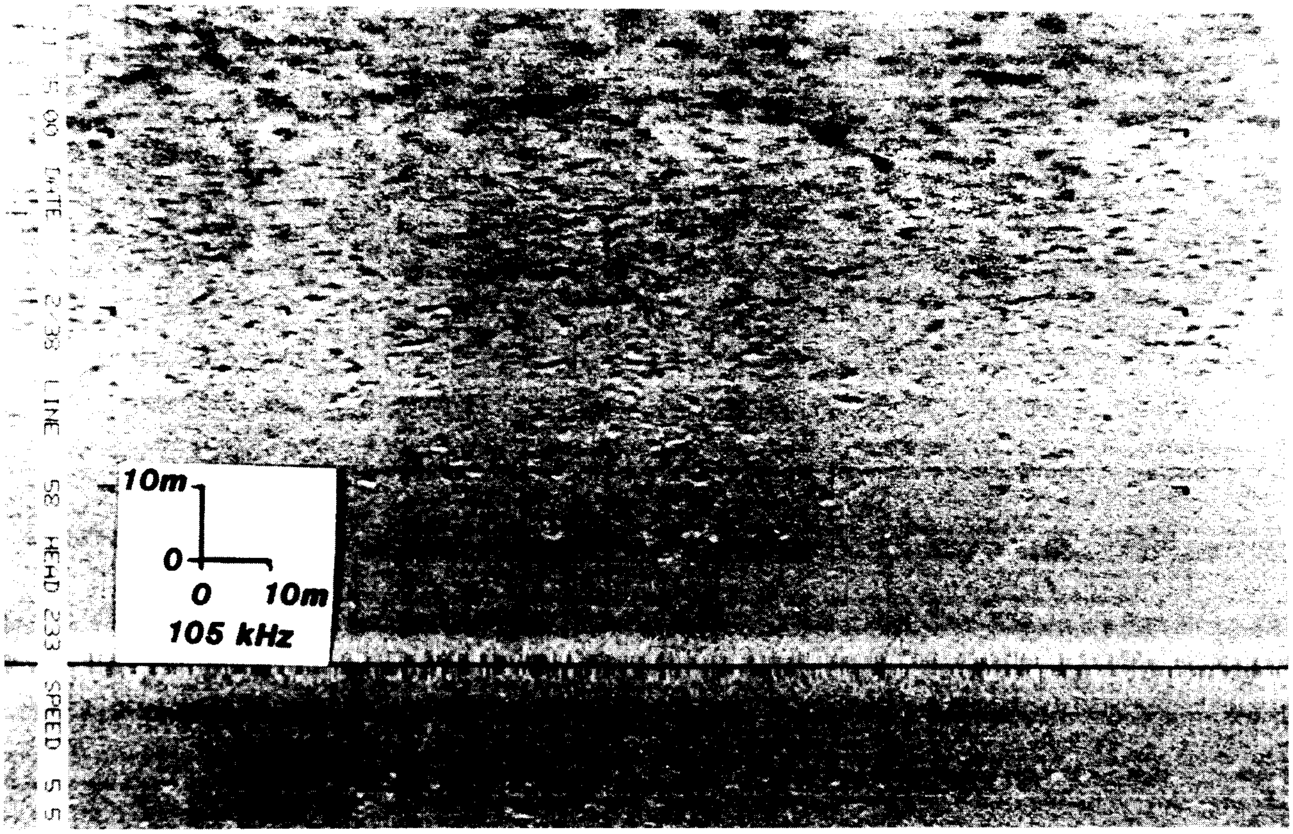


Figure 39 Sonograph of station Dog 16, 105 kHz, Type 3, sparse oval pits. Sonograph location is shown in Figure 7.

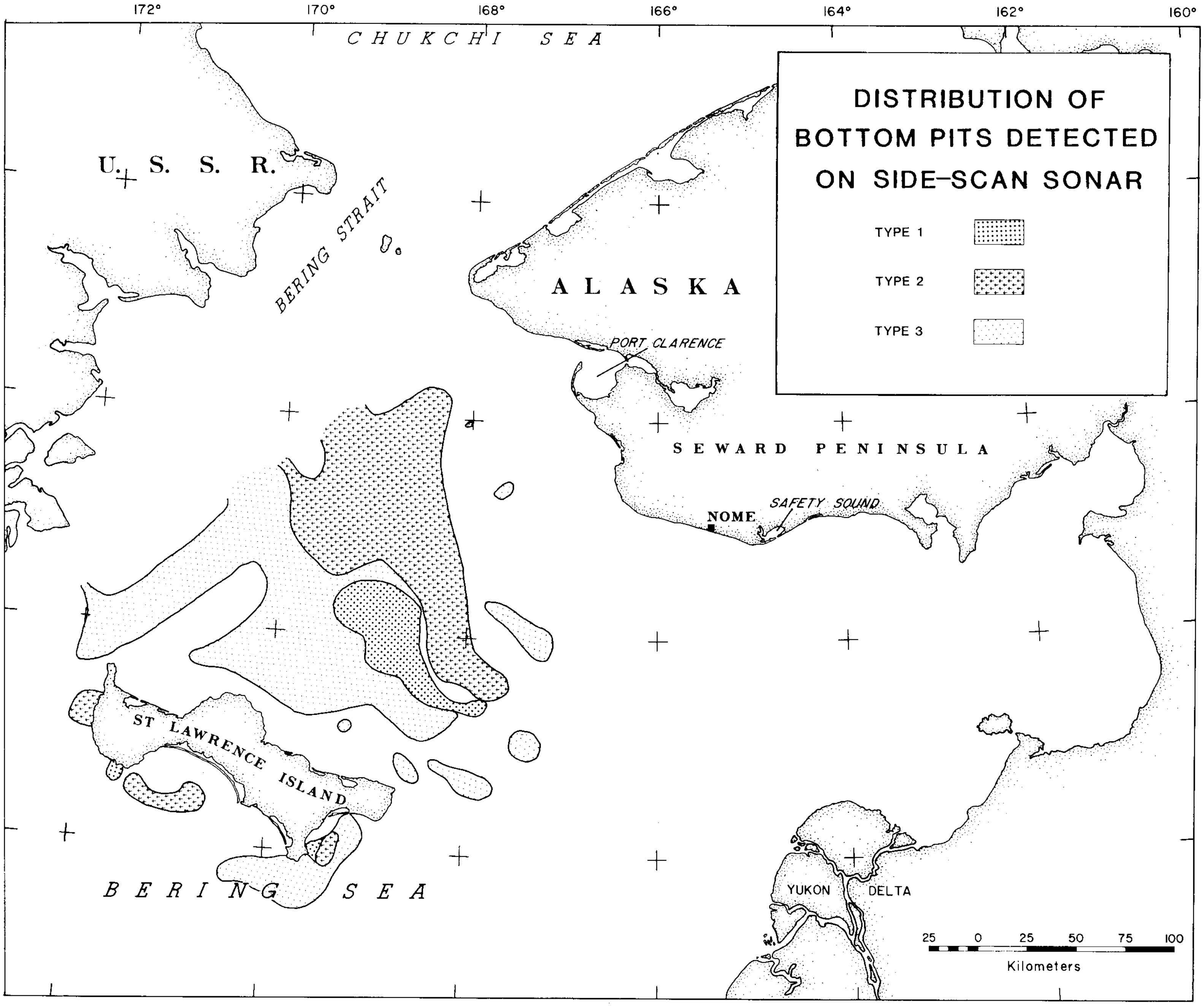


Figure 40 Distribution of three types of bottom pits, mapped by side-scan sonar and attributed to Gray Whale feeding on the seafloor of Chirikov basin, northeastern Bering Sea.

occur in the southeast portion of the center of the basin and in two isolated locations on the south side of St. Lawrence Island. Type 2 features are located in a large zone in the center of the basin and in three localities on the south side of the island. Type 3 features are found to the south of Type 1 and 2 zones in the center and south parts of the basin and to the south of these zones at the southeast cape of the island. Type 3 features occur as a halo around the other two types of features. In all, there exist 20,000 km^2 of sea floor in Chirikov Basin and 2,000 km^2 around St. Lawrence Island that bear evidence of gray whale feeding activity (Fig. 40).

The quantification of pit dimensions and area for stations Dog 1-Dog 16 (Fig. 7) and station Tate 1 are presented in Tables 2 & 3, Figures 41 and 42, and Appendix A. The range of total bottom disturbance in Type 1 areas is 4-18%, 5-15% in Type 2 areas, and 2-13% in Type 3 areas. Type 1 areas have high percentages of total disturbance, but a majority of this comes from the largest size class of pits. In general, the Type 2 areas are the most thoroughly reworked and uniformly disturbed areas of sea floor. The pitting occurs on an undulating bottom that bears evidence of much previous disturbance. The pit size distribution shows a fairly even representation of all four size classes (Table 3). Type 3 areas commonly contain pits of only the smallest size class and the density of pits is usually quite low. Exceptions to this are stations Dog 5 and Dog 10, which are close together and have high pit densities.

The smallest fresh feeding size class (0-5.3 m^2) is assumed to represent fresh feeding traces and this bottom disturbance ranges from 0.94-4.45% in Type 1 areas, 3.4-4.92% in Type 2 areas, and 2.0-11.86% in Type 3 areas. The average percent bottom disturbance by the fresh feeding pit size class (0-5.3

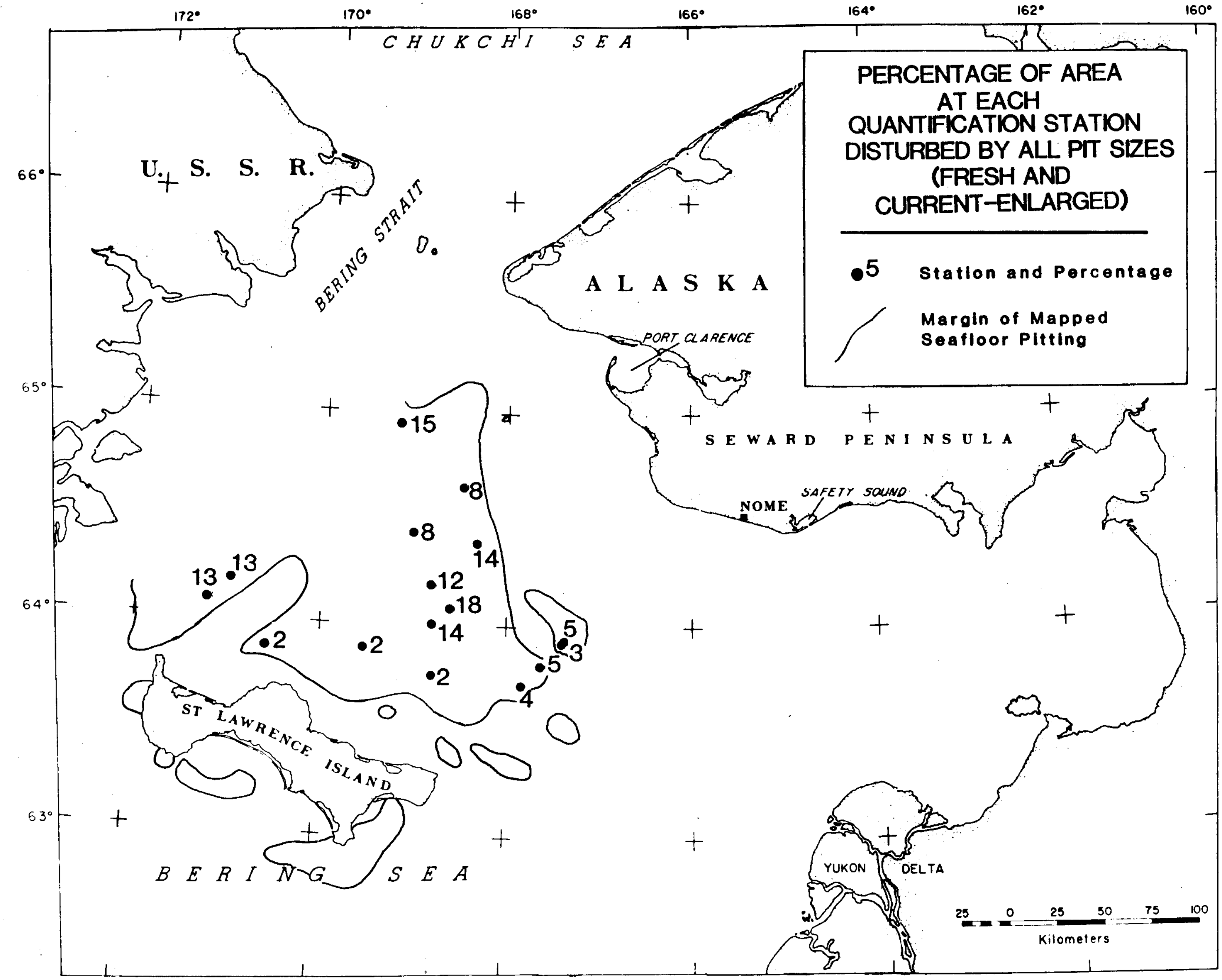


Figure 41 Total percentage of area at each side-scan quantification station disturbed by all fresh and current-enlarged feeding pits.

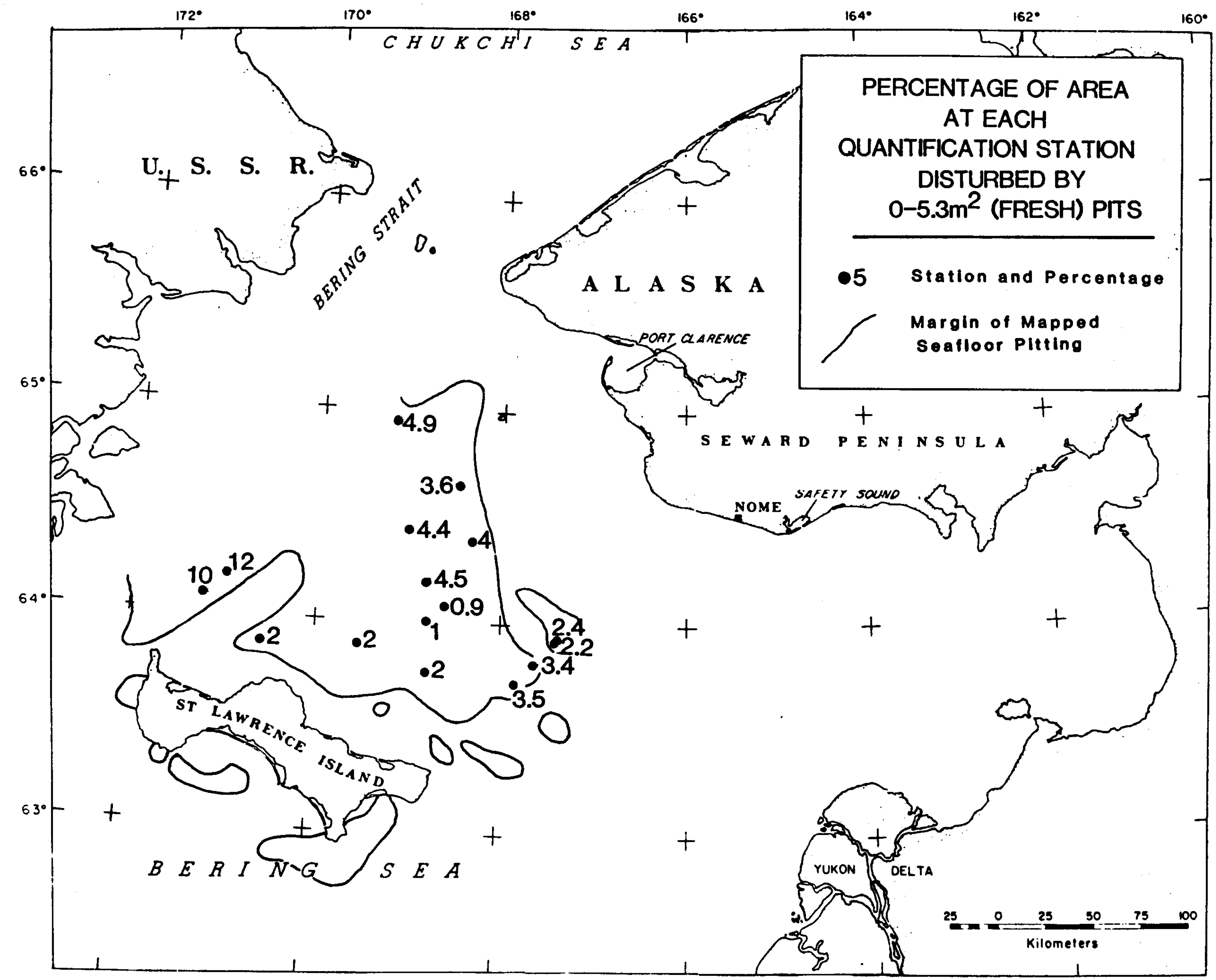


Figure 42 Percentage of area at each side-scan sonar quantification station disturbed only by fresh feeding pits in the smallest size class (0-5.3 m^2).

m^2) is 3.4% for the entire study area. It is important to remember that these percentages are taken from sonographs which underrepresent small features that are not parallel or sub-parallel to the trackline; consequently, these figures are low by an unknown amount that could be as large as 100% and the percentages given must be recognized as minima.

ORIGIN, MODIFICATION, AND DISTRIBUTION OF SEA FLOOR PITS

Type 1 features

Type 1 features are a combination of fresh whale feeding pits and current-scour-enlarged pits. The postulated mechanism of formation of the enlarged pits is as follows: whale feeding activity removes the amphipod mat which fixes the surface of the sediment. In areas or periods of strong bottom currents, the fine sand exposed under the mat is then subject to removal by current scour. The remaining mat around the margins of the pits is undercut and slumps into the pit. This continues until the pits are quite large. At a certain point, colonizing amphipods are able to re-establish a mat community in the center of the pit and restabilize the area.

The amount of time this process takes is not known. Divers from the L.G.L. 1982 cruises discovered amphipod tube mats slumping in on the pit margins as well as apparently new colonizations of the amphipod tube mat in the center of the larger pits. The divers also found that certain pits accumulated debris such as seaweed and appeared to have some infilling rather than enlarging. It is likely that the pits enlarge most readily during the storm season when bottom currents are greatly augmented by the effect of wave swell and sediment movement. Thus, the pits may be inactive or be gradually infilling during the long period of relative quiescence from November to September and receive most of their modification between September and November. This explains why the pits do not appear to be in the active process of modification during the summer months when they are inspected by divers.

The Type 1 area, then, is composed of a complex group of bottom features in different stages of modification. Certain Type 1 areas contain only fresh feeding pits (Fig. 43). This indicates that current velocities are not sufficient to enlarge these pits. Other Type 1 areas contain only current-enlarged pits suggesting that the whales have not actively fed in this area for some time. A less likely possibility is that they are feeding on the margins of the enlarged pits.

Frequently, Type 1 areas show distinct populations of fresh and enlarged pits supporting the theory that pit formation and enlargement are seasonal and not continuous activities. If either pit formation or modification were continuous throughout the year, one would expect to see a continuum of pit sizes ranging from fresh to greatly enlarged. Since both the times of feeding and of strong currents are seasonal, separate classes of pit sizes are expected in the Bering Sea setting. For example, two separate populations of pits can be seen in station Dog 1 (see Appendix A, Fig. 26). This separation is manifested in the pit length histogram, and in the length vs. width plot. Bimodality of the pit length histogram indicates two populations of pits whereas one population of gradually enlarging pits would be represented by a single curve skewed to the right. This situation also occurs in station Dog 8. In station Dog 14, the pit length histogram is a single curve skewed to the right but the area histogram is bimodal. The length vs. width plot also

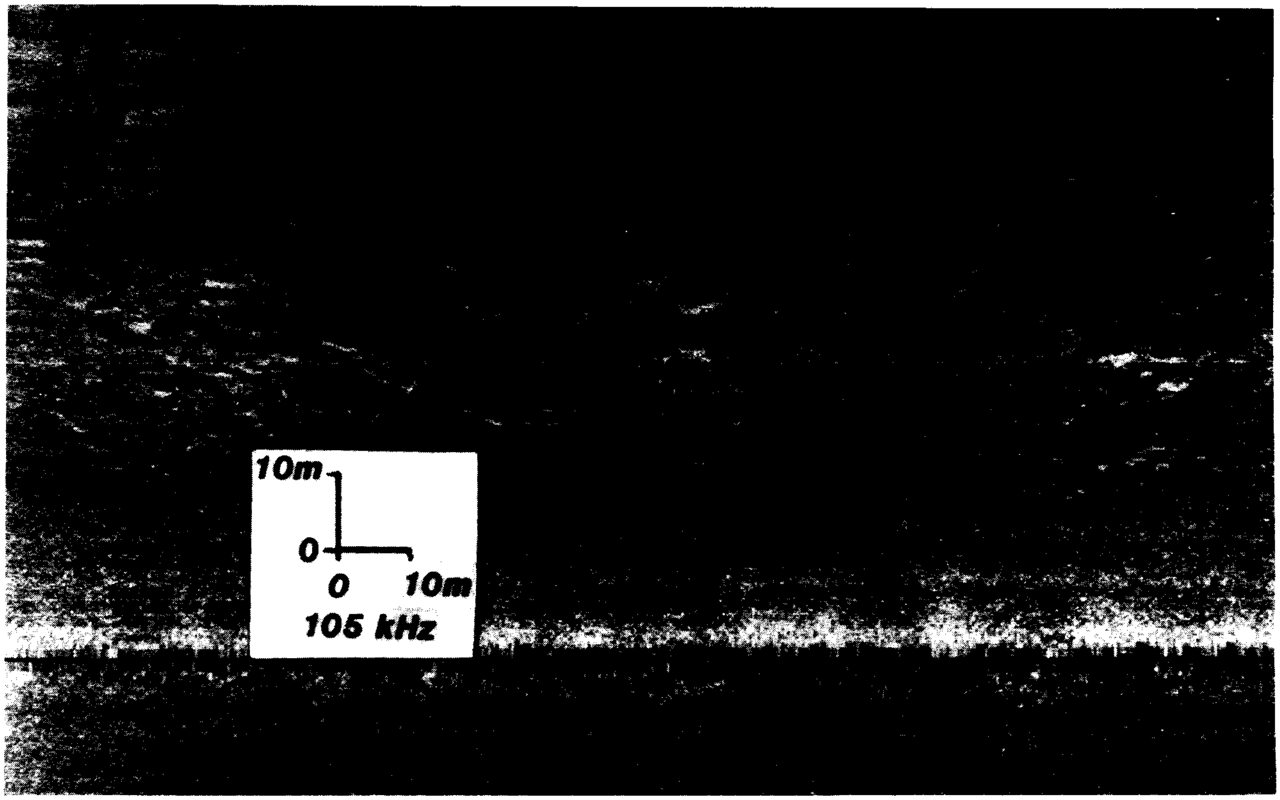


Figure 43 Sonograph of station Dog 7, 105 kHz, Type 1, multiple suction feeding events. Sonograph location is shown in Figure 7.

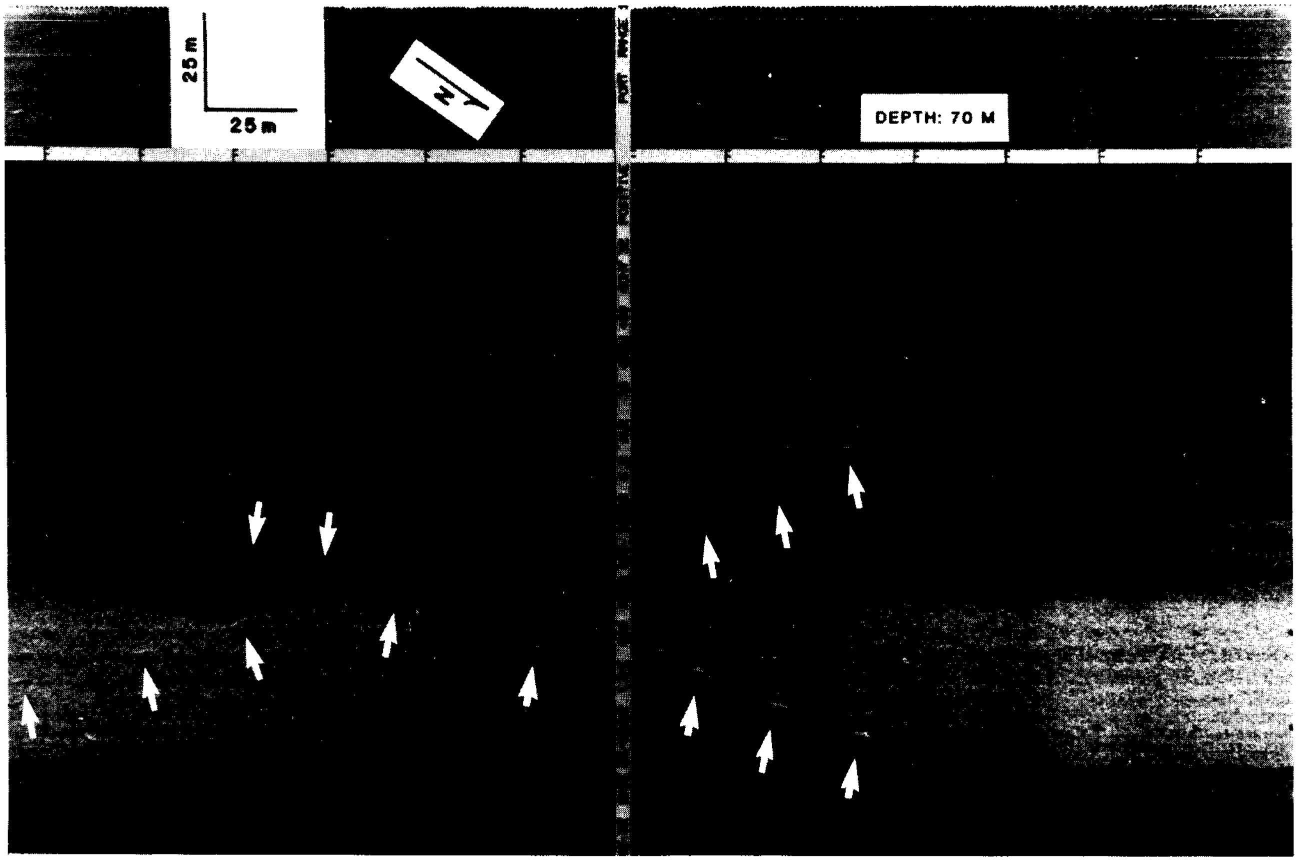


Figure 44 Sonograph of station Tate 1, 105 kHz, Type 1, distinct groups of fresh elongate feeding pits from the Russian River area of the California coast. Upper and lower sets of arrows point out pit groups in right half of sonograph.

shows separation between two populations. Thus, it is necessary to examine all measured parameters to establish the modification history of pits at a given site.

Type 2 features

Type 2 features are elongate pits whose average l/w ratio is greater than 3. These features occur mainly in the center of the basin in the area of most dense amphipod concentration and appear to result from the reworking of an already heavily worked area. Frequently, the margins of the Type 2 features are much less distinct than those of the Type 1 or Type 3 features. This and the even distribution of Type 2 pits through all size classes implies that the Type 2 features are undergoing continual rather than seasonal modification. The location of the Type 2 features in the central and northern portions of the basin where more consistent, stronger, northward-trending currents occur supports this possibility (Fig. 5). Also, the general bottom configuration in the Type 2 area is gently undulating, probably a result of heavy feeding pressure in the area leading to reworking of pitted areas. The area is underlain by old modified feeding pits which profoundly alter the bottom topography and attest to the intense feeding pressure in the area.

The predominance of elongate pits suggests an alternate current modification regime or an alternate feeding mode. The case for a different current regime has already been established. The same information may be used to explain an alternate feeding mode. Whales could create elongate pits as they are moved along by stronger currents while feeding. Though it is unlikely that whales would independently alter their feeding behavior from one area to the next, it seems feasible that local conditions may affect their actions. Type 2 features appear to have a random orientation that would not be expected from a current-influenced feeding activity. Therefore, we cannot eliminate the possibility that the whales are making these features by coordinating suction and propulsion.

The possibility that these features are made by self-propelled (not current-propelled) whales is reinforced by data collected off the coast of California during the northward migration of the gray whales. Cacchione (1983) reports:

> "The side-scan records taken on the central shelf in water depths of 70 to 120 meters are generally devoid of sea floor relief, as reported earlier, except for occasional elongate, coast-parallel depressions that probably are sea floor gouges caused by migratory gray whales. These features are usually linear gouges (infrequently "S" -shaped) about 2 to 8 meters long and 1 to 2 meters wide. They generally occur in groups of 3 to 8 arranged in a line oriented parallel to the bottom contours. The commonly measured spacing between multiple gouges is about 10 to 30 meters. In all of the records, the maximum density of whale gouges is about 10 to 20 gouges/0.1 km^2 and is located in water depths of 70 to 100 meters....During the L1-81-NC Code-1 cruise, we observed numerous gray whales at the ocean surface migrating along the shelf toward the north."

The presence of elongate features associated with migrating whales who are obviously moving while interacting with the sea floor verifies that this mode of bottom interaction is possible in Type 2 areas (Fig. 44). One hundred and twenty one of the California features were measured, their average length was 4.6 m and their average width was 1.8 m. These records were taken on 105 kHz digital Seafloor Mapper, the same side-scan system used in the Bering Sea for our measurements. Both length and width histograms (Appendix A, station Tate 1) plot as one population of pits, but the length vs. width plot shows that several features are much larger than the average (up to 10 m x 3 m). The presence of such large features, thought to be recent whale events, suggests that whales may be able to produce sea-floor pits on a scale much larger than the size of their gapes. In general, the individual pits in a given group are of similar size indicating that the group was made by a single whale. The size range between groups is very large indicating that both whale size and mode of bottom interaction have a high degree of effect on the size of features produced. The "S-shaped" linear gouges mentioned by Cacchione are probably straight features distorted by swell action on the towfish.

Extrapolating what we learned from the California features, the Type 2 area becomes more understandable. The length of Type 2 features in the Bering Sea averages from 3.1 to 4.7 m and the width ranges from 1 to 1.7 m. These values are like those of the California features and the two probably are made by similar whale behavior. The California features are in widely scattered but readily distinguishable groups implying that between 3 and 8 pits were made per dive. Pit density is much higher in the Bering Sea, and it is essentially impossible to distinguish discrete groups of pits. The Bering Sea features, also, are more modified and are superimposed on an undulating topography left by previous feeding seasons. Their margins are much less abrupt than those of the California features.

Length histograms of Type 2 features (Appendix A, stations Dog 3, Dog 12) show bimodality indicating modification of the long axis of the pits. Stations Dog 4 and Dog 13 exhibit length histograms with single populations skewed to the right; this suggests that either continual modification or very long fresh features are represented. It seems unlikely that a long feature could be further elongated without substantial widening, especially when the features are randomly oriented to begin with. Thus, the presence of very long (greater than 10 m) Type 2 pits is an enigma. In Type 2 station Dog 12 (Fig.

31) it appears that several of the longer features are created by closely adjacent multiple suction feeding events. This lends credence both to the theory of coordinated suction and propulsion by the whale and the theory of drifting with the current while feeding. With minimal current activity, the small elevated spots between the pits are easily smoothed out giving the impression of a single large elongate pit. Though present in Dog 12, this situation is not apparent at all Type 2 locations.

Total percent of bottom disturbed for Type 2 areas ranges from 5 to 15%. In the smallest size class, this translates to a 3.4 - 4.9% scour. Since the Type 2 features tend to be larger than Type 1 fresh feeding features, the second size class (5.3 m^2 - 10 m^2) may also represent fresh feeding in the Type 2 areas. The total scour for the two smallest size classes, the apparent fresh feeding classes, then ranges from 4.6 to 11.6%. This represents fairly heavy feeding pressure as would be expected in the area of highest amphipod density and most frequent whale sightings (Figs. 19, 20).

It is important to note that taking the side-scan towfish through rough water occasionally distorts Type 3 features so they resemble Type 2 features. This happens when slacking of the tow cable causes the towfish to decelerate thus stretching out features on the record. This artifact can be easily identified since the stretching of features occurs on a parallel band across the record. These bands reflect the periodicity of the waves and thus are regular and pervasive throughout the sonograph.

Type 3 features

In general, Type 3 features show much less size variability than the Type 1 and Type 2 features (Table 2). In almost all cases, the majority of Type 3 pits fall into the smallest size class. Apparently, there is very little enlargement and any modification probably occurs by marginal slumping or the silting-in of features. These shape discrepancies raise doubts as to the origin and modification history of these pits. Their oval to round shape does not allow accurate long axes orientations to be taken, so no inferences about regional trends can be drawn. Their relationship to prevailing currents also cannot be defined.

The distribution of the Type 3 pits is perhaps the key to their origin. Type 3 features occur around the margins of the Type 1 and Type 2 features with the largest zone of Type 3 features occurring in the southern central Chirikov Basin. This is a zone of low amphipod concentration (Fig. 19) and different substrate texture (Fig. 13). It is possible that the variable amphipod distribution causes scattered whale feeding behavior. However, in some areas of the southern Chirikov Basin containing high concentrations of feeding whales, the sea floor is very densely pitted with Type 3 features. This situation occurs above the northwest cape of St. Lawrence Island at stations Dog 5 and Dog 10. (Figs. 34, 36). The implication of this is that these areas are major feeding areas and the pit morphology is a function of the sediment type rather than whale feeding behavior. Surprisingly, the amphipod population is not extremely dense in this area. Perhaps the whales are exploiting an alternate food source. Percent total disturbance in these areas is high, ranging from 13 to 14%. The small size class accounts for nearly all of that scour and ranges from 10 to 12% of total bottom disturbance.

The coarser grain size in much of Type 3 areas compared to Type 1 and 2 areas may inhibit current scour modification and this may cause a lack of scour-enlarged pits. If feeding pits from older feeding seasons are not modified, the small size classes may over-represent fresh feeding which the high proportion of small pits to the total disturbance suggests. This too helps to explain high quantities of apparent fresh disturbance in low amphipod prey areas. It is possible that the increasing grain size of the substrate towards the southern margin of the basin (Fig. 13) may allow pit shape to tend towards ovalness. Also, the coarser sediment is less cohesive and therefore more subject to slumping around the pit margins, thus widening the pits.

Another possibility for the creation of round pits is the formation of gas expulsion craters or "sea floor pockmarks" (Nelson et al., 1980). Although all evidence suggests that the round pits of the Type 3 areas are created by feeding whales, the smaller gas expulsion craters would be very difficult to distinguish from the Type 3 features (compare Fig. 17C with Figs. 33, 35, 37). Even though methane-producing epiclastic peats underlie the sediment in Type 3 areas, the surficial fine-coarse sand and gravel in this area does not form an impermeable cap; this is a necessary condition to trap enough gas to allow expulsion and crater formation during storm surges. It is the paucity of gas-charged sediment in Type 3 areas, the lack of acoustic anomalies throughout Chirikov Basin showing no gas charging (Holmes and Thor, (1982), and the absence of any larger(10 m diameter) round pits (not recognizable as current scour pits) in the Chirikov basin that decreases the chance that small pits of Type 3 areas are gas expulsion craters. Although they are in areas that would probably be favorable to walrus feeding, these pits are of a much larger scale than could be produced by a walrus.

IMPLICATIONS FOR WHALE FEEDING ECOLOGY

Food resource

The distribution and density of the small-size class of pits, when assumed to represent fresh feeding, can be used to create a whale food resource budget for northeastern Bering Sea. A number of assumptions must be made before such a model can be created, and, of course, the value of such a model is thus based on the validity of these assumptions.

The northeastern Bering Sea contains approximately 22,000 km^2 of sea floor that bear evidence of gray whale feeding (Fig. 40). Assuming that a fresh pit is represented by the 0-5.3 m^2 pit size class, then the number of these pits represents a minimum feeding pressure in this area. Since little is known about the modification rates of these pits, great uncertainties exist. If, for example, modification rates were so high that pits only existed a few weeks before enlarging or filling-in, then several generations of pits could conceivably form during the span of one feeding season. Conversely, if modification rates were exceedingly slow, pits might last for several seasons before being altered. Both of these scenarios are unlikely since the current scour apparently occurs regularly in the fall storm season each year.

Surveys of the same areas at the beginning and at the end of the season could begin to explore this problem. Since the digital 105 kHz side-scan system was only used on the L7-80-BS cruise, no statistics comparing the features observed by the same system can be obtained. In areas of overlap with non-digital systems, some observations can be made. A Type 1 area showed examples of evolution from walrus furrow dominance to whale pit dominance over a period of one month. In several other cases, Type 1 and Type 2 areas remained more or less constant during that period, again negating ideas of rapid modification.

Type 1 areas are certainly those which show the most profound influence of currents and are the sites at which one would expect to find rapid modification. Unfortunately, low trackline overlap prohibits a detailed assessment of temporal changes of the bottom features. One must assume that since the percentage of disturbance by fresh pits (0-5.3 m^2) is relatively low (0.9 to 11.0%), they represent feeding for the present year only. Conversely, the larger size class pits are probably holdovers from previous feeding seasons. At this point in the research, we cannot determine how long the pits remain unmodified, but we speculate that most features probably are modified in the fall storm season and that fresh features last only one season before being enlarged or infilled.

Since the fresh pitting is probably not cumulative, the fresh pits can be taken as a measure of minimum yearly feeding pressure. Using the distribution of the three feature types (Fig. 40) and the percent area disturbed by fresh whale feeding pits (Table 3, Fig. 42), it is possible to calculate the total area of fresh pits in the northeastern Bering Sea feeding region. This value is 730 km^2, or an average of 3.4% disturbance due to fresh pits. Since the L7-80-BS data was collected during the second and third weeks of August, and the gray whale feeding season in northeastern Bering Sea lasts from June to late October (Pike, 1962), only 60% of the yearly feeding record was accumulated by the middle of August. Thus, we expect an average percent fresh bottom disturbance of 5.6% by the end of the season and a sum of areas of all the fresh pits at the end of the feeding season is estimated to be 1200 km^2 in northeastern Bering Sea.

The area of fresh feeding pits, combined with the biomass/unit area of the amphipod population may be used to approximate the total weight of amphipods consumed in one season in northeastern Bering Sea. Nerini (in press) recorded a mean amphipod biomass in the whale foraging area of 161 g/m^2 (161,000 kg/km^2). Mean amphipod biomass in the Nerini study accounted for 34% of the mean total biomass. Stoker (1978, 1981) shows an average total biomass of 533 gm/m^2 (533,000 kg/km^2). Using Nerini's figure of 34% as the amphipod fraction of the total biomass, then Stoker's figures represent a mean amphipod biomass of 181,000 kg/km^2. Using these figures, the consumption of benthic amphipod biomass in northeastern Bering Sea ranges from 117.53 million kg to 132.1 million kg for the season up until the third week of August; it is projected to range from 193.2 million kg to 217.2 million kg for the entire 1980 feeding season.

The amount of food that a mature gray whale consumes each day has been calculated by three groups of workers. Zimushko and Lenskaya (1970) calculated a rate of 1,200 kg/day. Both Rice and Wolman (1971) and Brodie (1975) calculated rates of 1,000 kg/day. Using this range of whale feeding rates and the range of amphipod biomass consumed in northeastern Bering Sea, we can estimate the number of whale feeding days (WFD) in these areas. This range is 97,942 - 132,100 WFD for the partial season and 161,000 - 217,200 WFD for the projected whole season.

The number of whale feeding days/season has significance in determining the relative importance of the northeastern Bering Sea as a gray whale feeding area. In order to do this, the total number of whale feeding days/season in

Alaskan waters must be calculated for the entire gray whale population for the duration of the feeding season. Assuming a population (in 1980) of 17,000 whales (Rugh, 1981) that spends at least 180 days a year feeding in the Bering and Chukchi Seas, this population accrues a total of 3,06,000 WFD/season. Thus, 22,000 km^2 of northeastern Bering Sea accounted for 5.3 - 7.1% (3.2 - 4.3% for the season until late August) of the entire gray whale feeding pressure for the 1980 season.

These estimates can be treated as minima for the following reasons. Only amphipod biomass was used in calculating food resource/unit area. In reality, the whales are utilizing much of the non-amphipod biomass as a food source. Also, side-scan sonar under-represents features that are not parallel to the trackline, and thus all whale feeding pits have not been accounted for in our calculations. Assuming that the whales utilized all of the total biomass (474 gm/m^2 of Nerini or 533 gm/m^2 of Stoker) and that the side-scan sonar missed the maximum possible 50% of the smaller features, then a total of 974,476 to 1,279,000 WFD, or 32 to 42% of the entire whale feeding pressure, would be accrued in the northeastern Bering Sea; this represents the maximum possible food resource utilized in this area. The northeastern Bering Sea region supplies at least 5.3% of the gray whale food resource and probably much less than the 32 to 42% maximum possible because whale stomach contents contain predominantly amphipods and not other biomass.

The summer feeding range of the gray whale occupies 1 million km^2 (Frost and Lowry, 1981). Thus 2% of the range in northeastern Bering Sea supplies a minimum of 5.3% of the food resource and very likely double this because side-scan sonar misses up to 50% of the feeding pits oriented transverse to the trackline. The northeastern Bering Sea therefore must be considered a major feeding ground for the gray whales. It is not however, the only major feeding ground. The Gulf of Anadyr, the Soviet side of Chirikov Basin, the northern side of the Alaskan Peninsula and all areas in the Chukchi Sea need to be studied to assess their respective contributions for gray whale food sources.

Food farming

Recent investigations show a unique relationship between the gray whales and their prey size. The size distribution of amphipods found in whale stomachs often shows a marked absence of small animals (less than 4-8 mm). Rice and Wolman (1971) examined the stomach of an immature female gray whale and found A. macrocephala ranging in size from less than 6 mm to more than 25 mm. Oliver, Slattery, Silberstein and O'Connor (1983) examined a gray whale fecal specimen and found amphipods as small as 4 mm. Coyle (1981) found no amphipods smaller than 8-10 mm in the stomach of a mature female gray whale. Nerini (1981) measured crab zoea as amall as 2 mm in the stomach of a migrating gray whale. Apparently, the baleen separation of the gray whales is of coarse enough mesh size to allow the smaller animals (less than 4 mm) to escape. The size bias for larger amphipods, however, may be an artifact of the whales' stomach acid consuming the smaller organisms first.

If the size separation of prey is real, then it has interesting implications for symbiotic relationships between ampeliscid amphipods and gray whales. Studies of ampeliscid amphipods in Barnstable Harbor on Cape Cod show that they are a tube-building, colonizing amphipod (Mills, 1967). The young thrive in areas of substrate disturbance. In Barnstable Harbor this disturbance exists from tidal scour; in the Bering Sea it is apparently caused by whale feeding disturbance combined with curren-scour modification of fresh feeding pits. Thus, the whales may be redistributing the young amphipods from mouth effluent feeding plumes into areas of fresh disturbance while at the same time consuming the mature amphipods or essentially "farming" the sea floor.

The possibility that the gray whales might be cultivating the sea floor by creating disturbances for the juvenile amphipods has been discussed previously (Frost and Lowry, 1981). New data presented in this report suggest that the current-scour modification triggered by whale foraging is producing in some areas much greater disturbance than the whales are capable of causing by themselves. For example, station Dog 1 shows 18% total bottom disturbance. Of this figure, only 0.94% is attributable to the smallest size class, the fresh feeding pits. This extreme situation also occurs in the Type 1 features at station Dog 8 (Table 2, Fig. 34). A more common occurrence is for the larger class of pits to constitute approximately half of the total disturbance. Still the increase in the disturbed area by current scour is considerable. This directly increases the area available for colonizing amphipods.

The reworking of the sediment could also be an effective vehicle for the more rapid recycling of nutrients through the system. Thus, the whales also contribute to the primary productivity of the area in two ways, by the addition of their feces as biological sedimentation and by the mixing of the nutrient-rich sediment into the water column and epifaunal environment.

IMPLICATIONS FOR GEOLOGIC PROCESSES

The gray whale feeding habits have a profound effect on the geology of their feeding areas because of the cumulative effect of reworking the sediment. The percentage of sea floor disturbance ranges from 0.9 to 11% for fresh feeding pits each year and the enhanced current scour often more than doubles the reworking by whales. Box cores from central Chirikov Basin show very few primary sedimentary structures. Years of whale feeding must effectively churn through and homogenize the sediment. This action also may lead to a winnowing of the fine particles and a better sorting of the fine sand. Whether the fine sediment suspended by whale feeding remains as part of the suspended sediment load or whether it settles back to the sea floor is a function of the local current regime. Certainly, the majority of sand- and coarse silt-sized particles expelled by the feeding whales will settle almost immediately to the bottom. This rain of expelled particles probably is an active agent in the eventual silting-in of the whale pits.

There is no doubt that the whales are a major force in initiating current scour of the bottom because they eliminate the biological binding of the sediment surface and cause large-scale biologically induced roughness of the sea floor. This is seen most clearly in Type 1 feature areas. The amphipod mat is a binding force that helps hold sediment particles together. When a whale sucks up a patch of the amphipod mat, it roughens the bottom and exposes the fine sand beneath. Current scour becomes active because sediment binding force is reduced and the increased roughness of the bottom greatly lowers threshold velocity required to erode sediment grains (Cacchione and Drake, 1982). In areas where currents are only strong enough to move unbound sediment, the whale activity provides the catalyst for erosion and scour.

The current-scour-enlarged pits can also be used to draw conclusions about current speed and direction. Regional lineation of large current-modified features imply a distinct prevailing current during feature modification.

Finally, the whale pits themselves are a type of megabioturbation and should be recognized as a biologic sedimentary structure. In their genesis they are not dissimilar to feeding pits made by walrus and, in their morphology, to sediment excavations made by rays. Ray pits have been described from modern and Cretaceous sediments (Howard and others, 1974). Whale pits can also provide a modern example of a feature that could be recognized in the rock record to establish the presence of prehistoric benthic-feeding whales. Given the geometry and size of the features, recognition of such large scale features may be difficult at rock outcrop scales.

HAZARDS SUSCEPTIBILITY

The susceptibility of the whale feeding ground to oil spills and oil development is a matter of no small concern. This area is complex due to the presence of sea ice for nearly half the year. All scenarios dealing with potential oil spill trajectories must account for both a winter and a summer situation. The ampeliscid amphipods are highly sensitive to oil spills (Sanders, 1977). Gray whales do not appear to be affected by minor amounts of oil (Braham et al., 1982). During the ice-free season, the current patterns around Chirikov Basin normally would deflect oil spills from Norton Sound into the Alaskan Coastal Water and around the northeastern margin of Chirikov basin up into the Chukchi Sea (Figs. 9, 10). Whale feeding grounds in the Chukchi Sea therefore might be more affected by an oil spill in Norton Basin than those in the adjacent Chirikov Basin.

During the ice-dominated portion of the year, however, oil spills from Norton Basin would be incorporated in the pack ice, and ice pan movement is highly susceptible to variable wind stress (Ray and Dupre', 1981). As a result, oil-bearing ice may eventually be carried over central Chirikov Basin. Under certain conditions of melting, oil could reach the substrate in this region and impact the amphipod population prior to its summer bloom. With the intense whale feeding in Chirikov Basin and the whales' limitation to a single yearly feeding season in the northeastern Bering Sea, the loss of feeding grounds for even part of a summer season could severely impact the minimum of 5 to 10% of the gray whale population supported by this amphipod stock.

Mining of the substrate in order to produce artificial drilling islands could be harmful to the whale population if portions of the relict inner shelf transgressive sand were utilized. Because the inner shelf sand body is less than 1 meter thick in most of Chirikov Basin and is a relict sediment that will not be replaced by modern processes, the loss of this substrate would permanently impact feeding grounds for a significant proportion of the whale population. More reasonable sand resources exist in other regions of the northeastern Bering Sea in the form of mobile sand bodies that are actively being replenished by Yukon sedimentation (Hess and Nelson, 1982).

POTENTIAL FUTURE STUDIES

The establishment of long-term current meters in the center of Chirikov Basin is essential to model the apparently significant circulation patterns previously considered weak and unimportant compared to the current patterns in the adjacent Bering Strait. Long-term current meter data is necessary to model oil spill trajectories and nutrient plume trajectories. Information should be obtained on the sources of productivity and the possible influence of an oil spill on each region of the whale feeding grounds in the Chirikov Basin. Another benefit from a long-term current study is the ability to quantify periods in which whale feeding features are modified and thus determine relative ages of the features. These data could be used to establish year-to-year fluctuations on the areal extent of the whale feeding grounds and thus determine more accurately the substrate carrying capacity of Chirikov Basin.

The modification rates of whale feeding pits and amphipod regeneration rates are both critical data necessary to understand the implications of gray whale interaction with the sea floor. Site-specific work in the Bering Sea involving the reoccupation of stations at different depths and in different current regimes could begin to quantify these variables.

Another method to approach the problem of feature modification is the sequential timing of side-scan surveys over the same sections of sea floor. It is possible, using shore-based navigational devices, to accurately re-survey an area with side-scan (Erk Reimnitz, USGS, Menlo Park, pers. comm., 1983). The areas of trackline overlap in this study were not adequate to approximate feature change through time because of the accuracy of the navigation, the use of different side-scan systems, and the temporal spacing of the different surveys. A thorough study should last at least two years and should have a minimum of two surveys a year, one as early as possible and one as late as possible. Ideally, a third survey should be made in the middle of each feeding season. Consistent side-scan techniques should be maintained throughout the study. A digital 500 kHz system would provide the best detail and ease of comparison of records.

A study similar to the present one that combines side-scan sonar surveys, substrate analyses and sediment history could be used to survey whale feeding grounds in the Chukchi Sea, the Beaufort Sea, the southern Gulf of Alaska, and Russian waters including the Gulf of Anadyr. With thorough knowledge of the sediment type and prey distribution throughout the entire feeding range of the gray whale, much more accurate estimates of feeding ground utilization can be obtained. Such a program would require the cooperation of Soviet scientists and should be coordinated with on-going studies of gray whale distribution.

Side-scan data collected on the L7-80-BS cruise was collected on magnetic tape as well as dry paper recorder. These tapes are suitable for computer enhancement. Future work involving enhancement of these data may provide more accurate estimates of figure size and density.

A thorough side-scan and sediment survey of some less remote gray whale summer grounds such as Pachena Bay, Vancouver Island, British Columbia might provide better data on whale feeding behavior and opportunity to correlate the side-scan record with SCUBA diver observations. Pachena Bay is an especially attractive area as the water visibility is very good and the bay supports an ampeliscid amphipod mat community which is actively being utilized by gray whales (Oliver, pers. comm., 1982). In addition, feeding traces on the sea floor can be accurately mapped by SCUBA divers and marked by side-scan sensitive pingers. Then, when the side-scan survey is conducted over the area, a very accurate determination of how much the features are distorted and how many features are missed can be calculated. These figures could then be extrapolated to the more remote feeding areas such as the Bering Sea that are less conducive to detailed site-specific research.

The question of where the gray whales fed during the Pleistocene might be addressed by deep-water side-scan surveys on the shelf break of the Bering continental shelf. When Beringia was emergent, this area contained the proper habitat depth ranges for the gray whales. Relict sedimentary features from the Pleistocene, namely large sediment waves, have been detected with sub-bottom profilers (Paul Carlson, USGS, Menlo Park, Cal., pers. comm., 1983) and the potential to detect relict whale feeding pits does exist.

The walrus feeding traces discovered in this study deserve further consideration. The walrus feeding furrows show up equally as well on 105 kHz as on the 500 kHz side-scan system but the smaller feeding pits have not yet been recognized on either system. The ability to recognize the smaller feeding pits exists as their size is larger than the minimum resolution claimed by the manufacturers of the 500 kHz system (John Oliver, pers. comm., 1982; Jim Glynn, Klein Assoc., Inc., Salem, New Hampshire, pers. comm., 1983). Also, the discarded bivalve shells around the pits might add to the overall seismic reflectivity of the surficial sediment. With proper diver calibration, it may well be possible to map walrus feeding grounds on side-scan sonar. In addition, the distribution and substrate affinities of the main prey species of the walrus can be mapped to some degree from data already in existence. Besides delineating the walrus feeding grounds, this type of study would further define the margins of the gray whale feeding areas.

CONCLUSIONS

1. Ampeliscid amphipods, the main prey species of the gray whale, have a high affinity for the widespread, homogeneous, relict, inner shelf transgressive sand body that blankets most of Chirikov Basin to a depth of no more than 1.5 meters. The amphipod community occupies nearly 40,000 km^2 in northeastern Bering Sea.

2. Gray whales feed on amphipods from this substrate by means of benthic suction, a process which produces a variety of feeding traces on the sea floor.

3. These traces can be accurately and regionally studied and quantified by means of the side-scan sonar, a planographic sea floor mapping device well suited to regional mapping.

4. Gray whale feeding trace distribution from side-scan sonar matches closely with the distribution of Bering Shelf Water, transgressive fine sand, high concentrations of Ampeliscid amphipods and the summer sighting of feeding gray whales from aerial surveys; this proves the validity of side-scan sonar as a biological mapping tool.

5. 22,000 km^2 in central Chirikov Basin and the nearshore areas of St. Lawrence Island show evidence of whale feeding as defined by side-scan sonar. Three types of whale feeding areas are recognized. Type 1 regions contain elliptic-shaped, recognizable fresh feeding traces. An older set of pits has been enlarged and regionally oriented by current-scour triggered by the whale feeding itself. Type 2 regions contain high concentrations of elongate (narrow elliptic) pits in areas with the most intense feeding pressure. Type 3 regions contain wide-elliptic-shaped feeding pits and occur in areas of decreasing amphipod density and increasing sediment grain size; they are found in locations with the least intense feeding pressure on the margins of Type 1 and 2 areas.

6. Different morphology of fresh feeding traces in various regions suggests that whale feeding behavior varies with changes in food amount and prey species, substrate type, and local current regimes. In areas of stronger current regimes or where whales are migrating or underway during feeding, original morphology of feeding pits may be more elongate with linear chains of fresh pits. Coarser substrates may result in more oval feeding traces.

7. There is minimal whale feeding pressure in Norton Sound because the Alaskan Coastal Water has low salinity and the substrate is a very fine-grained muddy sand. Both result from the high Yukon discharge and provide poor habitats for potential whale prey species.

8. Walrus feeding furrows can be readily identified on both 105 and 500 kHz side-scan systems and walrus feeding grounds seem to occur in areas of coarser substrate fringing the whale feeding grounds.

9. Total bottom disturbance from whale feeding pits and current scour enlargement of these ranges from 2% to 18% in different feeding areas of northeastern Bering Sea. The smallest size class of bottom pits approximates the size of whale-mouth gape size and is interpreted to represent fresh feeding pits; the larger size classes represent current-scour-enlarged pits with modification occurring mainly during the storm-prone months of the fall. This is substantiated by separate size classes of pits rather than a continual gradation of sizes indicating continual modification.

10. The percent bottom disturbance by the fresh feature size class (0-5.3 m^2) ranges from .9-11% and the average for the northeastern Bering Sea is 3.4%. These figures represent the feeding pressure at the time of data collection. Data for the whole season can be extrapolated from these figures to estimate a total seasonal average of 5.4% fresh disturbance.

11. Utilizing published biomass data, data on whole biomass feeding intake per day and counts of whale feeding days in Alaska, Chirikov Basin is estimated to account for a minimum of 5.3% and a maximum of 32-42% of the entire gray whale summer feeding resource for the Bering Sea and Arctic Ocean in only 2% of the total feeding region. Because side-scan sonar misses up to 50% of feeding traces transverse to the trackline, a minimum food resource estimate of 10% may be reasonable for northeastern Bering Sea.

12. Since the northeastern Bering Sea may provide 10-30% of the gray whale food resource and the amphipod population is susceptible both to oil spills plus any dredging or destruction of their substrate, exploitation affecting Chirikov Basin requires careful planning.

13. The whales may be farming their feeding grounds by (a) selectively capturing adult-sized amphipods, (b) seeding the juvenile amphipods, a pioneer species, into areas of freshly created and current-modified disturbance, and (c) mixing the nutrient-rich sediment into the water column thus boosting productivity.

14. The surficial sediment in Chirikov Basin is essentially devoid of primary sedimentary structures principally because of extensive sediment reworking by feeding whales. The roughening of the sea floor surface and exposure of biologically unbound fine sand caused by feeding, greatly enhances current scour in the central Chirikov Basin. Whale feeding also results in significant resuspension of fine-grained sediment and this combined with northward current advection may be a principal cause of non-deposition of modern sediment in this region.

15. Future studies should include (a) application of similar side-scan sonar reconnaissance in the main gray whale feeding regions of Alaska and the Soviet Union (b) periodic side-scan sonar monitoring of prime feeding grounds in central Chirikov Basis to outline different year classes and fresh feeding pits and refine food resource estimates and (c) utilization of existing USGS

side-scan records to outline areas and importance of walrus feeding habitats in northeastern Bering Sea to ascertain interplay with gray whale feeding grounds.

ACKNOWLEDGEMENTS

We thank Mary Nerini, John Oliver, Denis Thomson, Larry Martin, Kate Frost, Lloyd Lowry, Sam Stoker, Bud Fay, Ken Coyle, Steve Swartz, Mary Lou Jones, Steve Leatherwood, Jody Derman, Sue Moore, Marilyn Dalheim, Bob Nelson, Dale Rice, Gary Mauseth, Howard Braham, and Nora Foster for their willingness to share their knowledge of whale ecology and benthic biology. Jim Schumacher provided data from long-term current meters in the Bering Sea. Dave Cacchione and George Tate allowed us to use their side-scan data from the California coast. Both Mary Nerini and Denis Thomson were generous with their side-scan data from the Bering Sea. Discussions with Gordy Hess, Erk Reimnitz, Ralph Hunter, Jim Glynn, Chris Sherwood, and Jim Gardner added great depth to our understanding of the abilities and limitations of the side-scan sonar. Lavernne Hutchison helped type the manuscript. Russell Crane and John Barber Jr. aided in the preparation of the figures.

This study was funded by the Bureau of Land Management through interagency agreement with the National Oceanic and Atmospheric Administration as part of the Outer Continental Shelf Environmental Assessment Program.

REFERENCES CITED

Bogoslovskaya, L. S., L.M. Votrogov, and T.N. Semenova, 1981, Feeding habits of the gray whale off Chukotka: Report Int'l. Whaling Comm., vol. 31, p. 507-510, sc/32/ps 20.

Braham, H.W., 1983, Migration and feeding during migration by the Gray Whale (Eschrictius robustus) in: M.L. Jones et al. (eds.), The Gray Whale Eschrictius robustus: Academic Press, New York, 441p., in press.

Braham, H.W., R.D. Everitt, B.D. Krogman, D.J. Rugh, and D.E. Withrow, 1977, Marine Mammals of the Bering Sea: A Preliminary Report on Distribution and Abundance 1975-1976: NOAA-NMFS Northwest and Alaska Fisheries Center Processed Report.

Braham, H.W., G.W. Oliver, C. Fowler, K. Frost, F. Fay, C. Cowles, D. Costa, K. Schneider, D. Calkins, 1982, Marine Mammals, M.J. Hameedi (ed.), Proceedings of the Synthesis Meeting: St. George Environment and Possible Consequences of Planned Offshore Oil and Gas Development, 28-30 April, 1981, Anchorage, Alaska, Chap. 4, pg. 55-81.

Brodie, P. F., 1975, Cetacean energetics, an overview of intraspecific size variation: Ecology, vol. 56, p. 152-161.

Brownell, R. L., 1977, Current status of the gray whale: Report Int'l. Whaling Comm., vol. 27, p. 209-211, sc/28/Doc. 33.

Cacchione, D.A. and D.E. Drake, 1979, Sediment Transport in Norton Sound, Alaska, regional patterns and GEOPROBE system measurements: USGS Open-File Report 79-1555, 88 p.

Cacchione, D.A. and D.E. Drake, 1982, Measurements of Storm-Generated Bottom Stresses on the Continental Shelf. Jour. of Geophys. Res., vol. 87, no. C3, p. 1952-1960.

Cacchione, D.A., Drake, D.E., Grant, W.D., and Williams, III, A.J., Large and small scale morphology within the Coastal Ocan Dynamics Experiment (CODE) region, CODE Technical Report No. 17, Woods Hole Oceanographic Institution, in press, 45 p.

Coachman, L. K., K. Aagaard, and R.B. Tripp, 1976, Bering Strait: The regional physical oceanography: Univ. of Washington Press, Seattle.

Coachman, L. K., and R.B. Tripp, 1970, Currents north of Bering Strait in winter: Limnol. and Ocean., vol. 15, p. 625-632.

Consiglieri, L.D., H.W. Braham, L.L. Jones, 1980, Distribution and abundance of marine mammals in the Gulf of Alaska from the platform of opportunity programs, 1978-1979: Outer Continental Shelf Assessment Program Quarterly Report RU-68. 11 p.

Coyle, K. O., 1981, The oceanographic results of the cooperative Soviet and American cruise to the Chukchi and East Siberian seas aboard the Soviet whale hunting ship Razyashchii September-October 1980, Inst. Mar. Sci., Univ. Alaska, Fairbanks, 107 p.

Creager, J. S., M.L. Echols, M.L. Holmes, and D.A. McManus, 1970, Chukchi Sea continental shelf sedimentation (Abstract): American Association of Petroleum Geologists Bulletin, vol. 54, no. 12, p. 2475.

Drake, D.E., D.A. Cacchione, R.D. Muench, C.H. Nelson, 1980, Sediment Transport in Norton Sound, Alaska: Mar. Geol., 36: 97-126.

Dupre, W.R., 1982, Depositional environments of the Yukon Delta, northeastern Bering Sea, in: Geologie en Mijnbouw, vol. 61, p. 63-71.

EG & G Environmental Equipment, SMS 960 Seafloor Mapping System, Technical Presentation, 151 Bear Hill Road, Waltham, Mass. 02154.

Fathauer, T. F., 1975, The great Bering Sea storms of 9-12 November, 1974: Weatherwise Magazine of the American Meteorological Society, vol. 18, p. 76-83.

Fay, F.H., 1982, Ecology and Biology of the Pacific Walrus, Odobenus rosmarus divergens Illiger, Fish and Wildlife Service series, North American Fauna, no. 74.

Feder, H. M. and S.C. Jewett, 1981, Feeding interactions in the eastern Bering Sea with emphasis on the benthos, in: The eastern Bering Sea shelf: Oceanography and Resources, vol. 2, D. W. Hood and J. A. Calder, eds., Off. Marine Pollution Assessment, NOAA. Distrib. by Univ. Washington Press, Seattle.

Filatova, Z. A., and N.G. Barsanova, 1964, Communities of benthic fauna in the western Bering Sea: Trudy Inst. Okeanologiya, vol. 69, p. 6-97.

Fleming, R. H., and D. Heggarty, 1966, Oceanography of the southeastern Chukchi Sea, in: N. J. Wilimovsky and J. N. Wolfe, eds., Environment of the Cape Thompson region, Alaska, U.S. Atomic Energy Comm., p. 607-754.

Flemming, B.W., 1976, Side scan sonar: a practical guide. Technical report no. 7, Univ. of Capetown or Int. Hyd. Rev., vol. LIII #1.

Frost, K. J. and L.F. Lowry, 1981, Foods and trophic relationships of cetaceans in the Bering Sea, in: The eastern Bering Sea shelf: oceanography and resources, vol. 2, D. W. Hood and J. A. Calder, eds., Off. Marine Pollution Assessment, NOAA. Distrib. by Univ. Washington Press, Seattle.

Gilmore, R.M., 1955, The return of the Gray Whale, Sci. Amer., vol. 192, no. 1.

Harrison, C. S., 1979, The association of marine birds and feeding gray whales: Condor, vol. 81, p. 93-95.

Herzing, D. L. and B.R. Mate, 1981, California gray whale migration along the Oregon coast, in: 4th Biennial Conf. Biol. Mar. Mammals, 14-18 December 1981, San Francisco, p. 54.

Hess, G.R. and C.H. Nelson, 1982, Geology Report for Proposed Norton Sound OCS Sand and Gravel Lease Sale: USGS Open-File report no. 82-997.

Hess, G.R., B.R. Larsen, D. Klingman, and D. Moore, 1981, Marine Geologic Hazards in the Nortern Bering Sea, Final Report on data collected in FY 1980, RU429, Annual Report.

Hickey, L.J., 1973, Classification of the architecture of dicotyledonous leaves. Am. Jour. Bot. 60 (1): 17-33.

Holmes, M.L. and D.R. Thor, 1982, Distribution of gas-charged sediment in Norton Sound and Chirikov Basin, Geologie en Mijnbouw, vol. 61, p. 79-91.

Howard, J.D., T.V. Mayon, and R.W. Heard, 1977, Biogenic sedimentary structures formed by Rays: J. Sed. Pet., vol. 47, no. 1, p. 339-346.

Howell, A. B. and L.M. Huey, 1930, Food of the California gray and other whales: J. Mammal., vol. 2, p. 321-322.

Hudnall, J., 1981, Population estimate, feeding behavior and food source of the gray whales, Eschrichtius robustus, occupying the Strait of Juan de Fuca, British Columbia, in: 4th Biennial Conf. Biol. Mar. Mammals, 14-18 December, 1981, San Francisco, p. 58.

Husby, D. M., 1969, Report Oceanographic Cruise USCG Northwind, Northern Bering Sea-Bering Strait-Chukchi Sea, 1967: U. S. Coast Guard Oceanogr. Rep. 24, Washington, D. C., 75 p.

Husby, D. M. and G.L. Hufford, 1971, Oceanographic investigations in the northern Bering Sea and Bering Strait, 8-21 June, 1969: U.S. Coast Guard Oceanogr. Rep. No. 42.

Kasuya, T. and D.W. Rice, 1970, Notes on baleen plates and on arrangement of parasitic barnacles of gray whale: Sci. Report Whales Res. Inst., vol. 22, p. 39-43.

Klein Associates, Inc., 1982, Hydroscan, Klein Side Scan Sonar and Sub-bottom Profiling Systems, 47p.

Kuznetsov, A. A., 1964, Distribution of benthic fauna in western Bering Sea by trophic zone and some general problems of trophic zonation: Trudy Inst. Okean, vol. 69, p. 98-117 (Transl. Office of Naval Intelligence).

Larsen, M.L., C.H. Nelson, and D.R. Thor, 1979, Geologic implications and potential hazards of scour depression on Bering shelf, Alaska: Environmental Geology, vol. 3, p. 49-47.

Larsen, M.L., C.H. Nelson, and D.R. Thor, 1981, Sedimentary Processes and Potential Geologic Hazards on the Seafloor of the Northern Bering Sea, p. 247-267 <u>in</u>: The eastern Bering Sea Shelf: oceanography and resources, D.W. Hodd and J.A. Calder (eds.), OMPA, NOAA, Univ. of Wash. Press.

Inst. Okeanol. Akad. Nauk USSR, (Transl. by Israel Program for Scientific Translations), available from U.S. Dept. Commerce,Clearinghouse for Fed. Sci. and Tech. Infor., 1969, 614 p.

Lowry, L. F. and K.J. Frost, 1981, Feeding and trophic relationships of phocid seals and walruses in the eastern Bering Sea, in: The eastern Bering Sea shelf: oceanography and resources, D. W. Hood and J. A. Calder, eds., Office Marine Pollution Assessment, NOAA. Distrib. by Univ. Washington Press, Seattle, p. 813-824.

Lowry, L. F., K.J. Frost, and J.J. Burns, 1980, Feeding of bearded seals in the Bering and Chukchi seas and trophic interaction with Pacific walruses: Arctic, vol. 33, p. 330-342.

McManus, D. A., J.C. Kellery, and J.S. Creager, 1969, Continental shelf sedimentation in an arctic environment: Geological Society of America Bulletin, vol., 80, p. 1961-1984.

McManus, D.A. and C.S. Smyth, 1970, Turbid bottom water on the continental shelf of nothern Bering Sea: J. Sed. Pet., vol. 40, p. 869-877.

McManus, D. A., K. Venkataratham, D.M. Hopkins, and C.H. Nelson, 1977, Distribution of bottom sediments on the continental shelf, northern Bering Sea: U.S. Geol. Surv. Prof. Pap. 759-C.

Mead, J. G. and E.D. Mitchell, in press, The Atlantic Gray Whale in: The Gray Whale: Eschrichtius robustus, M.L. Jones et al. eds., Academic Press, 441p, in press.

Miller, M. C., I.N. McCave, and P.D. Komar, 1977, Threshold of sediment motion under unidirectional currents, Sedimentology, vol. 24, p. 507-527.

Mills, E. L., 1967, The biology of an Ampeliscid Amphipod Crustacean sibling species pair: Jour. Fish. Res. Bd. Canada, vol. 24, no. 2, p. 305-355.

Moore, S. and D. Ljungblad, 1983, The Gray Whale (Eschrichtius robustus) in the Bering, Beaufort and Chukchi Seas: Distribution and Sound production, in: M.L. Jones et al., eds., The Gray Whale: Eschrichtius robustus, Academic Press, N. Y., 441 p., in press.

Neiman, A. A., 1961, Nekotorye zakonomernosti kolishestvennogo raspredeleniya bentosa v Beringovom more (Certain regularities in the quantitative distribution of the benthos in the Bering Sea): Okeanologiya, vol. 1, p. 294-304.

Nelson, C. H., 1982, Holocene transgression in deltaic and non-deltaic areas of the Bering epicontinental shelf, in: The Northeastern Bering Shelf: New Perspectives of Epicontinental Shelf Processes and Depositional Products, Geologie en Mijnbouw, C. H. Nelson and S. D. Nio, eds., Geologie en Mijnbouw, vol. 61, p. 37-48.

Nelson, C. H. and J.S. Creager, 1977, Displacement of Yukon derived sediment from Bering Sea to Chukchi Sea during the Holocene: Geology, vol. 5, p. 141-146.

Nelson, C. H., W.R. Dupre, M.E. Field, and J.D. Howard, 1982, Linear sand bodies on the Bering epicontinental shelf, in: Nelson, C. H., and Nio, S. D., (eds.), The Northeastern Bering Shelf: New Perspectives of Epicontinental Shelf Processes and Depositional Products, Geologie en Mijnbouw, vol. 61, p. 37-48.

Nelson, C. H. and D. M. Hopkins, 1972, Sedimentary processes and distribution of particulate gold in northern Bering Sea: U.S. Geol. Surv. Prof. Pap. 689.

Nelson, C.H., D.M. Hopkins, and D.W. Scholl, 1974, Cenozoic sedimentary and tectonic history of the Bering Sea, in: Oceanography of the Bering Sea, D.W. Hood and E.J. Kelley, (Eds.), Univ. of Alaska, IMS, Occasional Pub. 2, p. 485-512.

Nelson, C.H., K.A. Kvenvolden, and E.C. Clukey, 1978, Thermogenic gas in sediment of Norton Sound, Alaska, Proceedings Offshore Technical Conference, Houston, Texas, Paper No. 3354, p. 1612-1633.

Nelson, C.H., R.W. Roland, S. Stoker, and B.R. Larsen, 1981, Interplay of physical and biological sedimentary structures of the Bering Sea epicontinental shelf, in: The eastern Bering Sea shelf: oceanography and Resources, D.W. Hood and J.A. Calder, eds. Office Marine Pollution Assessment, NOAA. Distrib. by Univ. Washington Press, Seattle.

Nelson, C.H., D.R. Thor, M.W. Sandstrom, and K.A. Kvenvolden, 1980, Modern biogenic gas-generated craters (sea floor "pockmarks") on the Bering shelf, Alaska: Geol. Soc. Amer. Bull., vol. 90, p. 1144-1152.

Nemoto, T., 1970, Feeding pattern of baleen whales in the ocean, in: Marine Food chains, J. H. Steele, ed., Univ. California Press, Berkeley, p. 241-252.

Nerini, M., 1981, Gray whales and the structure of the Bering Sea community, in: 4th Biennial Conf. Biol. Mar. Mammals, 14-18 December, San Francisco, p. 84.

Nerini, M., in press, The Feeding Ecology of the Gray Whale: A Review, in: The Gray Whale: *Eschrichtius robustus*, M.L. Jones et al., (eds.), Academic Press, N. Y., 441 p.

Nerini, M. K., L. Jones, and H.W. Braham, 1980, Gray whale feeding ecology. First Year Final Report, Mar.-Dec., 1980, OCSEAP, RU593, contract no. R7120828.

Nerini, M.K. and J.S. Oliver, in press, Gray whales and the structure of the Bering Sea benthos: Oecologia.

Norris, K.S. and B. Wursig, 1979, Gray whale lagoon entrance aggregations. pg. 44 in: Abstr. 3rd Biennnial Conf. Biol. Mar. Mammals, 7-11 October, 1979, Seattle.

Oliver, J.S., P.N. Slattery, M.A. Silberstein, E.F. O'Connor, 1983, A comparison of gray whale feeding in the Bering Sea and Baja California: Fish. Bull., vol. 81, in press.

Oliver, J.S., P.N. Slattery, E.F. O'Connor, and L.F. Lowry, 1983, Walrus Feeding in the Bering Sea: a benthic perspective: Fish. Bull., vol. 81, in press.

Oliver, J.S., P.N. Slattery, M.A. Silberstein, and E.F. O'Connor, in press, Gray Whale Feeding on Dense Ampeliscid amphipod communities near Bamfield, British Columbia: Can. Jour. of Zool.

Pike, G.C., 1962, Migration and feeding of the gray whale: J. Fish. Res. Board Can., vol. 19(5), p. 815-838.

Ray, G. C. and W.E. Schevill, 1974, Feeding of a captive gray whale: Mar. Fish. Rev., vol. 36, p. 31-37.

Ray, V. M. and W.R. Dupre, 1981, The Ice-Dominated Regimen of Norton Sound and Adjacent Areas of the Bering Sea. in: The eastern Bering Sea shelf: oceanography and resources, D.W. Hood and J.A. Calder, eds., OMPA, NOAA, Univ. of Wash. press.

Reilly, S., D. Rice, and A.A. Wolman, 1980, Preliminary population estimate for the California Gray Whale based upon Monterey shore censuses, 1967/68 to 1978/79: Report Int'l. Whaling Comm., vol. 30, p. 359-368.

Rice, D. W. and A.A. Wolman, 1971, The life history and ecology of the gray whale (Eschrichtius robustus): Am. Soc. Mammal. Spec. Publ. No. 3, 142 p.

Rowland, R. W., 1972, Ecology of the benthic fauna of the northern Bering Sea: Geological Society of America, Abstracts with Programs, vol. 4, p. 646.

Rugh, D., 1981, Fall gray whale census at Unimak Pass, Alaska 1977-79, in: 4th Biennial Conf. Biol. Mar. Mammals, 14-18 December 1981, San Francisco, p. 100.

Rugh, D. J. and M.A. Fraker, 1981, Gray whale (Eschrichtius robustus) sightings in the eastern Beaufort Sea: Arctic, vol. 34, p. 186-187.

Russell-Cargill, W.G.A., (ed.), 1982, Recent developments in side-scan sonar techniques, Cape Town, South Africa, 141p.

Sanders, H. L., 1977, The West Falmouth spill, Florida, 1969: Oceanus, vol. 20, no. 4, p. 15-24.

Scammon, C.M., 1874. The marine mammals of the northwestern coast of North America, Dover Publ., Inc., N.Y. 319 p.

Schumacher, J. D. and R.B. Tripp, 1979, Response of northeast Bering Sea shelf waters to storms: EOS, Trans. Amer. Geophys. Union, vol. 60, p. 856.

Sharma, G. D., 1970, Recent sedimentation on southern Bering shelf (Abstract): American Association of Petroleum Geologists Bulletin, vol. 54, no. 12, p. 2503.

Stoker, S. W., 1973, Winter studies of under-ice benthos on the continental shelf of the northeastern Bering Sea, Master's Thesis, Univ. of Alaska, unpublished.

Stoker, S.W., 1978, Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi Seas, Ph.D. Thesis, Univ. of Alaska, unpublished. 259 p.

Stoker, S.W., 1981, Benthic invertebrate microfauna of the eastern Bering/Chukchi continental shelf, in: The eastern Bering Sea shelf: oceanography and resources, vol. 1, D.W. Hood and J.A. Calder, eds., Off. Marine Pollution Assessment, NOAA. Distrib. by Univ. Washington Press, Seattle.

Sund, P.N., 1975, Evidence of feeding during migration and of an early birth of the California Gray Whale (Eschrichtius robustus): J. Mammal, vol. 56, p. 265-266.

Thomson, D.H., ed., 1983, Feeding Ecology of Gray Whales in the Chirikov Basin: in press, final report to OCSEAP-NOAA.

Thor, D.R. and C.H. Nelson, 1981, Sea ice as a geologic agent on the subarctic Bering shelf, in: The eastern Bering Sea shelf: oceanography and resources, vol. 1, D.W. Hood and J.A. Calder, eds., Off. Marine Pollution Assessment, NOAA, Distrib. by Univ. Washington Press, Seattle, p. 279-291.

Votrogov, L.M. and L.S. Bogoslovskaya, 1980, Gray whales off the Chukotka Peninsula: Report Int'l. Whaling Comm., vol. 30, p. 435-437, sc/31/Doc. 55.

Walker, T.J., 1971, The California Gray Whale comes back: Nat'l. Geogr., vol. 139, no. 3, p. 394-415.

Wellington, G.M. and S. Anderson, 1978, Surface feeding by a juvenile gray whale, Eschrichtius robustus: Fish. Bull., vol. 76, p. 290-293.

Zenkovich, B.A., 1934, (Research data on cetacea of far eastern seas): Bull. Far East Acad. Sci., USSR, No. 10. In Russian (Transl. by F. Essapian, Miami, Fl., 34 p.).

Zenkovich, B.A., 1937 [More on the gray California whale (Rhachianectes glaucus Cope, 1864]: Bull. Far East Acad. Sci. USSR 23. In Russian (Transl. by Bur. Commer. Fish., Off. Foreign Fish. Transl., Washington, D. C., 19 p.).

Zenkovich, B.A., 1955, O migratsiiakh kitov, promyslove raiony v dal'-nevostochnyk vodakh (The migration of whales, whale fishing in the waters of the Soviet Far East), in: Kitoiony Promysel Sovetskogo Soyuza, VNIRO, Part I, S. E. Kleinenberg and T. I. Makarova, eds. In Russian (Transl. by Israel Program Sci. Transl. for U.S. Dept. Interior and Nat'l. Sci. Found., 1968, 14 p.)

Zimushko, V.V. and M.V. Ivashin, 1980, Some results of Soviet investigations and whaling of gray whales (Eschrichtius robustus Lilljeborg, 1961): Report Int'l Whaling Comm., vol. 30, p. 237, sc/31/Doc. 19.

Zimushko, V.V. and S.A. Lenskaya, 1970, [Feeding of the gray whale (Eschrichtius gibbosus Erx.) at foraging grounds]: Ekologiya, vol. 1, p. 26-35. In Russian (Transl. by Consultant's Bur., Plenum Publ. Corp., NY, 1971, 8 p.).

APPENDIX A

SOURCES FOR THE DATA BASE

APPENDIX A-1 Sources for the Data Base.

DATA TYPE	DATE	COLLECTED BY	CRUISE NO.	LOCATION	MISC.
105 kHz digitized side-scan	1980	USGS-Nelson	L7-80-BS	Norton Sound Chirikov Basin	Rolls 1-49
105 kHz side-scan	1980	USGS-Nelson NMML-Nerini	S01-80-BS	Chirikov Basin	Rolls 1-21
105 kHz side-scan	1977	USGS-Nelson	S5-77-B5	Chirikov Basin	Rolls 30-59
105 kHz side-scan	1978	USGS-Nelson	S9-78-BS	Chirikov Basin	Rolls 34-38
105 kHz side-scan	6/23/80	NMML-Nerini	-----	Chirikov Basin	Rolls 1-21
500 kHz side-scan	7/17/80	NMML-Nerini	-----	St. Lawrence Is.	Rolls 1-21
500 kHz side-scan	7/82	L.G.L. Ltd.-Thomson	Leg 1	Chirikov Island St. Lawrence Is.	Transects 2-44
100 kHz side-scan	9/82	L.G.L. Ltd.-Thomson	Leg 2	Chirikov Basin	Transects 103-134
500 kHz side-scan	"	"	"	St. Lawrence Is.	
105 kHz digitized side-scan	1982	USGS-Cacchione Code Geology Rept.	S1-82-NC	No. Calif. Coast	
Vibracore radiographs and logs	1980	USGS-Nelson	L7-80-BS	Chirikov Basin Norton Sound	
Box cores	1968	USGS-Nelson	68-ANC-BS	"	
Box cores	1969	"	69-ANC-BS	"	
Box cores	1970	"	70-ANC-BS	"	
Underwater video	1980	"	L7-80-BS	"	
Underwater video	1978	"	S5-77-BS	"	
Underwater video	1977	"	S9-78-BS	"	

APPENDIX A-1 continued

Underwater still photos	1980	USGS-Nelson	L7-80-BS	Chirikov Basin and Norton Sound
Underwater still photos	1977	"	S5-77-BS	"
Box core radiographs	1976	"	S5-76-BS	"
Box core radiographs	1977	"	S5-77-BS	"
Box core radiographs	1978	"	S9-78-BS	"
Vibracore logs	1968	"	68-ANC-BS	"
Vibracore logs	1969	"	69-ANC-BS	"
Vibracore logs	1970	"	70-ANC-BS	"
Vibracore logs	1976	"	S5-76-BS	"
Vibracore logs	1977	"	S5-77-BS	"
Vibracore logs	1978	"	S9-78-BS	"
Grab samples	1978	S. Stoker, U. of Alaska	---	Bering and Chukchi Seas
Grab samples	1980	NMML-Nerini	SU1-80-BS	Chirikov Basin
Grab samples	1982	L.G.L. ltd.-Thomson	Legs 1&2	Chirikov Basin and St. Law. Is.
SCUBA diver observations	1980	NMML-Nerini	---	"
SCUBA diver observations	1980	J. Oliver, Moss Landing Marine Lab	---	"
SCUBA diver observations	1982	L.G.L. ltd.-Thomson	Legs 1&2	"
SCUBA diver observations	1982	J. Oliver	---	Pachena Bay, Vancouver Island, British Columbia
Current speed data current meters	1982	J. Schumacher NOAA-PMEL	---	Bering Sea
Current speed data spot checks	1960-80	USGS, Univ. of Wash.	all cruises	N. Bering Sea

APPENDIX B

RESULTS OF THE QUANTIFICATION OF 105 kHz DIGITAL SIDE-SCAN SONOGRAPHS

SIDE-SCAN QUANTIFICATION STATIONS:

Dog 1 through Dog 16

Tate 1

SIDE-SCAN STATION DOG 1

```
length

middle of   number of
interval    observations
   0.00       0
   1.00       0
   2.00      15     ***************
   3.00       8     ********
   4.00       4     ****
   5.00       4     ****
   6.00       3     ***
   7.00      11     ***********
   8.00       3     ***
   9.00       1     *
  10.00       9     *********
  11.00       1     *
  12.00       0
  13.00       2     **
  14.00       1     *
  15.00       0
  16.00       1     *
  17.00       0
  18.00       0
  19.00       0
  20.00       1     *

length in meters
```

```
width

middle of   number of
interval    observations
  0.000       0
  0.500       0
  1.000      17     *****************
  1.500       4     ****
  2.000       8     ********
  2.500       0
  3.000      16     ****************
  3.500       2     **
  4.000      10     **********
  4.500       0
  5.000       7     *******

width in meters
```

```
length
  20.0+            *
      -
      -
      -
      -
  16.0+          *
      -
      -            *
      -
      -          2
  12.0+
      -               *
      -       *  4*3
      -
      -            *
   8.0+          **   *
      -       *  5 *  4
      -          * *  *
      -
      -      **  * *
   4.0+       3    *
      -      *2  *
      -     +2
      -
      -
   0.0+
         +---------+---------+---------+---------+---------+width
        0.0       4.0       8.0  meters12.0      16.0      20.0

meters
```

```
area

 middle of   number of
 interval    observations
   0.00        19     *******************
   5.00         9     *********
  10.00         4     ****
  15.00         9     *********
  20.00         7     *******
  25.00        12     ************
  30.00         1     *
  35.00         2     **
  40.00         0
  45.00         0
  50.00         0
  55.00         1     *
```

area in square meters

```
orient.

 middle of   number of
 interval    observations
    0.0        12     ************
   10.0         9     *********
   20.0         4     ****
   30.0         5     *****
   40.0        17     *****************
   50.0         5     *****
   60.0         0
   70.0         0
   80.0         0
   90.0         0
  100.0         0
  110.0         0
  120.0         0
  130.0         0
  140.0         0
  150.0         0
  160.0         0
  170.0         0
  180.0         0
  190.0         0
  200.0         0
  210.0         0
  220.0         0
  230.0         0
  240.0         0
  250.0         0
  260.0         0
  270.0         1     *
  280.0         0
  290.0         0
  300.0         0
  310.0         0
  320.0         1     *
  330.0         0
  340.0         1     *
  350.0         7     *******
  360.0         2     **
```

degrees

SIDE-SCAN STATION DOG 2

```
length

 middle of    number of
 interval     observations
   0.000        0
   0.500        0
   1.000        0
   1.500        0
   2.000       13     *************
   2.500        5     *****
   3.000       17     *****************
   3.500        2     **
   4.000        8     ********
   4.500        2     **
   5.000        2     **
   5.500        0
   6.000        1     *
length in meters

width

 middle of    number of
 interval     observations
   0.000        0
   0.500        0
   1.000        4     ****
   1.500        9     *********
   2.000       26     **************************
   2.500        3     ***
   3.000        7     *******
   3.500        0
   4.000        1     *
width in meters

length
  20.0+
      -
      -
      -
      -
  16.0+
      -
      -
      -
      -
  12.0+
      -
      -
      -
meters
      -
   8.0+
      -
      -           *
      -
      -       ** * *
   4.0+        5  3
      -     2492 2
      -     25+*
      -
      -
   0.0+
        +---------+---------+---------+---------+---------+width
       0.0       4.0       8.0      12.0      16.0      20.0
                                meters

area

 middle of    number of
 interval     observations
   0.00         0
   1.00         2     **
   2.00         6     ******
   3.00        15     ***************
   4.00         9     *********
   5.00         8     ********
   6.00         1     *
   7.00         2     **
   8.00         4     ****
   9.00         0
  10.00         1     *
  11.00         0
  12.00         2     **
area in square meters
```

SIDE-SCAN STATION DOG 3

length in meters

```
length

 middle of    number of
 interval     observations
   0.000         0
   0.500         0
   1.000         0
   1.500         0
   2.000         8      ********
   2.500         4      ****
   3.000        14      **************
   3.500         3      ***
   4.000         5      *****
   4.500         1      *
   5.000        13      *************
   5.500         0
   6.000         6      ******
   6.500         1      *
   7.000         4      ****
   7.500         0
   8.000         6      ******
   8.500         0
   9.000         1      *
   9.500         0
  10.000         1      *
  10.500         0
  11.000         0
  11.500         0
  12.000         0
  12.500         0
  13.000         0
  13.500         0
  14.000         1      *
```

width in meters

```
width

 middle of    number of
 interval     observations
   0.000         0
   0.500         0
   1.000        20      ********************
   1.500        14      **************
   2.000        30      ******************************
   2.500         2      **
   3.000         1      *
   3.500         0
   4.000         1      *
```

SIDE-SCAN STATION DOG 3

```
 length
  20.0+
      -
      -
      -
      -
  16.0+
      -
      -      *
      -
      -
  12.0+
      -
      -      *
meters-
      -    *
   8.0+    *3**
      -    **2
      -    2*3   *
      -
      -    3*8*    *
   4.0+    3 2
      -    359
      -    633
      -
      -
   0.0+
        +---------+---------+---------+---------+---------+width
       0.0       4.0       8.0      12.0      16.0      20.0
                            meters
```

```
area

                     middle of    number of
                     interval     observations
                       0.00         0
                       1.00         4     ****
                       2.00         7     *******
                       3.00        14     **************
                       4.00         9     *********
                       5.00         8     ********
                       6.00         2     **
area in square meters  7.00         9     *********
                       8.00         7     *******
                       9.00         2     **
                      10.00         0
                      11.00         1     *
                      12.00         1     *
                      13.00         3     ***
                      14.00         0
                      15.00         0
                      16.00         0
                      17.00         0
                      18.00         0
                      19.00         1     *
```

```
orient.

 middle of   number of
 interval    observations
     0.0         2     **
    10.0         0
    20.0         0
    30.0         0
    40.0         0
    50.0         0
    60.0         0
    70.0         0
    80.0         0
    90.0         0
   100.0         0
   110.0         0
   120.0         0
   130.0         0
   140.0         0
   150.0         0
   160.0         0
   170.0         0
   180.0         2     **
   190.0         2     **
   200.0         3     ***
   210.0         5     *****
   220.0        18     ******************
   230.0        19     *******************
   240.0         4     ****
   250.0         7     *******
   260.0         3     ***
   270.0         2     **
   280.0         1     *
```

degrees

SIDE-SCAN STATION DOG 4

```
length

length in meters

 middle of   number of
 interval    observations
   0.000        0
   0.500        0
   1.000        0
   1.500        0
   2.000        6      ******
   2.500        7      *******
   3.000       10      **********
   3.500        3      ***
   4.000        5      *****
   4.500        0
   5.000       11      ***********
   5.500        0
   6.000        7      *******
   6.500        1      *
   7.000        5      *****
   7.500        0
   8.000        2      **
   8.500        1      *
   9.000        1      *
   9.500        0
  10.000        1      *
  10.500        0
  11.000        1      *
  11.500        0
  12.000        0
  12.500        0
  13.000        1      *
  13.500        0
  14.000        1      *
  14.500        0
  15.000        1      *
```

```
width

width in meters

 middle of   number of
 interval    observations
   0.000        0
   0.500        0
   1.000       24      ************************
   1.500        9      *********
   2.000       23      ***********************
   2.500        5      *****
   3.000        3      ***
```

```
meters

  length
    20.0+
        -
        -
        -
        -
    16.0+
        -      *
        -      *
        -
        -         *
    12.0+
        -      *
        -         *
        -
        -     **
     8.0+      **
        -    2***
        -    3 4  *
        -
        -    3233
     4.0+    *22
        -    623
        -    924
        -
        -
     0.0+
          +---------+---------+---------+---------+---------+width
         0.0       4.0       8.0      12.0      16.0      20.0
                                 meters
```

SIDE-SCAN STATION DOG 4

area in square meters

```
area

 middle of   number of
 interval    observations
   0.00        0
   1.00        2     **
   2.00       14     **************
   3.00        9     *********
   4.00       10     **********
   5.00        5     *****
   6.00        1     *
   7.00        4     ****
   8.00        7     *******
   9.00        2     **
  10.00        0
  11.00        2     **
  12.00        2     **
  13.00        1     *
  14.00        0
  15.00        1     *
  16.00        0
  17.00        0
  18.00        0
  19.00        1     *
  20.00        2     **
  21.00        0
  22.00        0
  23.00        0
  24.00        0
  25.00        0
  26.00        1     *
```

degrees

```
orient.

 middle of   number of
 interval    observations
    0.0        1     *
   10.0        0
   20.0        0
   30.0        0
   40.0        0
   50.0        0
   60.0        0
   70.0        0
   80.0        0
   90.0        0
  100.0        0
  110.0        0
  120.0        0
  130.0        0
  140.0        0
  150.0        0
  160.0        0
  170.0        0
  180.0        1     *
  190.0        5     *****
  200.0       16     ****************
  210.0       13     *************
  220.0       11     ***********
  230.0       10     **********
  240.0        3     ***
  250.0        1     *
  260.0        3     ***
```

SIDE-SCAN STATION DOG 5

```
length

 middle of   number of
 interval    observations
   0.000         0
   0.500         0
   1.000         5     *****
   1.500        11     ***********
   2.000        27     ***************************
   2.500        10     **********
   3.000         7     *******
   3.500         1     *
   4.000         0
   4.500         1     *
   5.000         5     *****
   5.500         0
   6.000         0
   6.500         0
   7.000         0
   7.500         0
   8.000         1     *
```

length in meters

```
width
 each * represents   2 observations

 middle of   number of
 interval    observations
   0.000         0
   0.500         3     **
   1.000        55     ****************************
   1.500         6     ***
   2.000         4     **
```

width in meters

```
 length
  20.0+
      -
      -
      -
      -
  16.0+
      -
      -
      -
      -
  12.0+
      -
      -
      -
      -
   8.0+      *
      -
      -
      -
      -   24
   4.0+
      -     6
      -   5+53
      -  **+
      -  2 3
   0.0+
        +---------+---------+---------+---------+---------+width
       0.0       4.0       8.0      12.0      16.0      20.0
                              meters
```

meters

area in square meters

```
area
 middle of   number of
 interval    observations
   0.00        2     **
   1.00       35     ***********************************
   2.00       17     *****************
   3.00       10     **********
   4.00        3     ***
   5.00        0
   6.00        0
   7.00        0
   8.00        0
   9.00        0
  10.00        0
  11.00        1     *
```

degrees

```
orint.
 middle of   number of
 interval    observations
    0.0        4     ****
   10.0        0
   20.0        0
   30.0        1     *
   40.0        7     *******
   50.0       14     **************
   60.0       14     **************
   70.0       15     ***************
   80.0       10     **********
   90.0        2     **
  100.0        1     *
```

```
length

 middle of    number of
 interval     observations
   0.000         0
   0.500         0
   1.000         3     ***
   1.500         3     ***
   2.000         9     *********
   2.500         6     ******
   3.000        15     ***************
   3.500         1     *
   4.000         8     ********
   4.500         2     **
   5.000         5     *****
   5.500         1     *
   6.000         5     *****
   6.500         1     *
   7.000         3     ***
   7.500         0
   8.000         1     *
   8.500         0
   9.000         2     **
   9.500         0
  10.000         0
  10.500         0
  11.000         1     *
```

length in meters

```
width
 each * represents   2 observations

 middle of    number of
 interval     observations
   0.000         0
   0.500         1     *
   1.000        54     ***************************
   1.500         8     ****
   2.000         3     **
```

width in meters

```
 length
  20.0+
      -
      -
      -
      -
  16.0+
      -
      -
      -
      -
  12.0+
      -    *
      -
      -
      -    **
   8.0+     *
      -    2 *
      -    5 *
      -    *
      -   *6
   4.0+    6**
      -  * +*
      -   2+2
      -    4
      -   2*
   0.0+
         +---------+---------+---------+---------+---------+width
        0.0       4.0       8.0      12.0      16.0      20.0
                              meters
```

meters

```
area

area_in square meters

 middle of   number of
 interval    observations
   0.000       0
   0.500       3      ***
   1.000       5      *****
   1.500      12      ************
   2.000      12      ************
   2.500       9      *********
   3.000       5      *****
   3.500       4      ****
   4.000       4      ****
   4.500       2      **
   5.000       2      **
   5.500       1      *
   6.000       1      *
   6.500       0
   7.000       1      *
   7.500       1      *
   8.000       1      *
   8.500       1      *
   9.000       1      *
   9.500       1      *
```

```
orient.

degrees

middle of   number of
interval    observations
   0.0        3      ***
  10.0        1      *
  20.0        2      **
  30.0        0
  40.0        5      *****
  50.0       12      ************
  60.0       12      ************
  70.0        9      *********
  80.0        9      *********
  90.0        9      *********
 100.0        2      **
 110.0        0
 120.0        0
 130.0        1      *
 140.0        1      *
```

```
length

 middle of   number of
 interval    observations
   0.000          0
   0.500          0
   1.000          8     ********
   1.500          3     ***
   2.000         17     *****************
   2.500          7     *******
   3.000         17     *****************
   3.500          0
   4.000          2     **
   4.500          2     **
   5.000          4     ****
   5.500          0
   6.000          1     *
   6.500          0
   7.000          2     **
   7.500          1     *
```

length in meters

```
width
 each * represents   2 observations

 middle of   number of
 interval    observations
   0.000          0
   0.500          3     **
   1.000         53     ***************************
   1.500          6     ***
   2.000          2     *
```

width in meters

```
    30 points out of bounds
-- plot c1 0 20 c2 0 20
          length
           20.0+
               -
               -
               -
               -
           16.0+
               -
               -
               -
               -
           12.0+
               -
               -
               -
               -
            8.0+
               -     2 *
               -     *
               -
               -    *32
            4.0+     * *
               -   *2+*
               -   23+3
               -    23
               -    43
            0.0+
                  +---------+---------+---------+---------+---------+width
                 0.0       4.0       8.0      12.0      16.0      20.0
```

meters

meters

SIDE-SCAN STATION DOG 7

```
area

 middle of   number of
 interval    observations
    0.00       0
    1.00      27     ***************************
    2.00      23     ***********************
    3.00       7     *******
    4.00       1     *
    5.00       5     *****
    6.00       0
    7.00       0
    8.00       0
    9.00       0
   10.00       1     *
```

area in square meters

```
orient.

 middle of   number of
 interval    observations
     0.0       4     ****
    10.0       2     **
    20.0       2     **
    30.0       5     *****
    40.0       9     *********
    50.0      14     **************
    60.0      11     ***********
    70.0       5     *****
    30.0       3     ***
    90.0       3     ***
   100.0       1     *
   110.0       0
   120.0       0
   130.0       1     *
   140.0       0
   150.0       0
   160.0       0
   170.0       3     ***
   130.0       1     *
```

degrees

SIDE-SCAN STATION DOG 8

```
length

 middle of   number of
 interval    observations
    0.00          0
    1.00          8     ********
    2.00          5     *****
    3.00         14     **************
    4.00          9     *********
    5.00          8     ********
    6.00          3     ***
    7.00          3     ***
    8.00          0
    9.00          1     *
   10.00          5     *****
   11.00          3     ***
   12.00          2     **
   13.00          1     *
   14.00          1     *
   15.00          2     **
   16.00          0
   17.00          1     *
   18.00          0
   19.00          2     **
```

length in meters

```
width

 middle of   number of
 interval    observations
    0.00          0
    1.00         28     ****************************
    2.00         15     ***************
    3.00          8     ********
    4.00          5     *****
    5.00          7     *******
    6.00          3     ***
    7.00          1     *
    8.00          0
    9.00          0
   10.00          1     *
```

width in meters

```
length
  20.0+
      -             *    *
      -
      -
      -                         *
  16.0+
      -             * *
      -              *
      -
      -               *
  12.0+             *
      -   *    *    2
      -   *    * 2  *
      -
      -      *
   8.0+
      -        * **
      -    *     *
      -    *
      -   *2*2 **
   4.0+   225
      -   6*2  *
      -   9
      -
      - 5 3
   0.0+
        +---------+---------+---------+---------+---------+width
       0.0       4.0       8.0      12.0      16.0      20.0
                                 meters
```

meters

area

```
middle of     number of
interval      observations
    0.0         31      *******************************
   10.0         18      ******************
   20.0          6      ******
   30.0          3      ***
   40.0          3      ***
   50.0          3      ***
   60.0          2      **
   70.0          0
   80.0          0
   90.0          1      *
  100.0          0
  110.0          1      *
```

area in square meters

orient.

```
middle of     number of
interval      observations
    0.0         11      ***********
   10.0          9      *********
   20.0          9      *********
   30.0          9      *********
   40.0         13      *************
   50.0          2      **
   60.0          1      *
   70.0          0
   80.0          0
   90.0          0
  100.0          0
  110.0          0
  120.0          0
  130.0          1      *
  140.0          0
  150.0          0
  160.0          2      **
  170.0          9      *********
  180.0          2      **
```

degrees

SIDE-SCAN STATION DOG 9

```
length

 middle of   number of
 interval    observations
   0.000          0
   0.500          0
   1.000          5     *****
   1.500          0
   2.000         17     *****************
   2.500          7     *******
   3.000         23     ***********************
   3.500          6     ******
   4.000          5     *****
   4.500          0
   5.000          1     *
```

length in meters

```
width

 middle of   number of
 interval    observations
   0.000          0
   0.500          0
   1.000         27     ***************************
   1.500         18     ******************
   2.000         15     ***************
   2.500          1     *
   3.000          2     **
   3.500          0
   4.000          1     *
```

width in meters

```
length
 20.0+
     -
     -
     -
     -
 16.0+
     -
     -
     -
     -
 12.0+
     -
     -
     -
     -
  8.0+
     -
     -
     -
     -            *
  4.0+       4  *
     -     ++6* *
     -    2+85
     -     *
     -     4
  0.0+
        +---------+---------+---------+---------+---------+width
       0.0       4.0       8.0      12.0      16.0      20.0
                              meters
```

meters

```
area

 middle of   number of
 interval    observations
    0.00        0
    1.00       14      **************
    2.00       19      *******************
    3.00       13      *************
    4.00        9      *********
    5.00        6      ******
    6.00        1      *
    7.00        0
    8.00        1      *
    9.00        0
   10.00        0
   11.00        0
   12.00        0
   13.00        1      *
```

area in square meters

```
length

 middle of    number of
 interval     observations
   0.000          0
   0.500          5      *****
   1.000          6      ******
   1.500          4      ****
   2.000         18      ******************
   2.500          7      *******
   3.000          8      ********
   3.500          6      ******
   4.000          5      *****
   4.500          1      *
   5.000          2      **
   5.500          0
   6.000          1      *
   6.500          0
   7.000          0
   7.500          0
   8.000          0
   8.500          0
   9.000          0
   9.500          1      *
length in meters


width

 middle of    number of
 interval     observations
   0.000          0
   0.500          6      ******
   1.000         25      *************************
   1.500         18      ******************
   2.000         14      **************
   2.500          1      *
width in meters

length
 20.0+
     -
     -
     -
     -
 16.0+
     -
     -
     -
     -
 12.0+
     -
     -
     -    *
     -
  8.0+
     -
     -      *
     -
     -    2 *
  4.0+    **3
     -    463*
     -   *756
     -   28
     -  542
  0.0+
       +---------+---------+---------+---------+---------+width
      0.0       4.0       8.0      12.0      16.0      20.0
                                 meters
meters
```

SIDE-SCAN STATION DOG 10

```
area

 middle of   number of
 interval    observations
    0.00        6     ******
    1.00       16     ****************
    2.00       13     *************
    3.00       14     **************
    4.00        8     ********
    5.00        3     ***
    6.00        2     **
    7.00        0
    8.00        2     **
```

area in square meters

SIDE-SCAN STATION DOG 11

```
length

 middle of   number of
 interval    observations
   0.000        0
   0.500        0
   1.000       31    *******************************
   1.500        8    ********
   2.000       18    ******************
   2.500        2    **
   3.000        3    ***
   3.500        1    *
   4.000        1    *
length in meters


width

 middle of   number of
 interval    observations
   0.000        0
   0.500       11    ***********
   1.000       48    ************************************************
   1.500        4    ****
   2.000        1    *
width in meters

 length
  20.0+
      -
      -
      -
      -
  16.0+
      -
      -
      -
      -
  12.0+
      -
      -
      -
      -
   8.0+
      -
      -
      -
      -
   4.0+    *
      -  2 2
      -    +**
      -   ++2
      -  3+7
   0.0+
meters
        +---------+---------+---------+---------+---------+width
       0.0       4.0       8.0      12.0      16.0      20.0
                           meters


area

 middle of   number of
 interval    observations
   0.000        1    *
   0.500       30    ******************************
   1.000       12    ************
   1.500       15    ***************
   2.000        2    **
   2.500        2    **
   3.000        2    **
area in square meters
```

length in meters

```
length

 middle of   number of
 interval    observations
  0.000        0
  0.500        0
  1.000        7      *******
  1.500        7      *******
  2.000       16      ****************
  2.500        8      ********
  3.000        8      ********
  3.500        2      **
  4.000        3      ***
  4.500        0
  5.000        6      ******
  5.500        0
  6.000        0
  6.500        0
  7.000        4      ****
  7.500        1      *
  8.000        0
  8.500        0
  9.000        1      *
  9.500        0
 10.000        1      *
```

width in meters

```
width

 middle of   number of
 interval    observations
  0.000        0
  0.500       15      ***************
  1.000       36      ************************************
  1.500        8      ********
  2.000        4      ****
  2.500        1      *
```

meters

```
length
  20.0+
      -
      -
      -
      -
  16.0+
      -
      -
      -
      -
  12.0+
      -
      -     *
      -
      -     *
   8.0+
      -    *2**
      -
      -
      -    4 2
   4.0+    3
      -  2332
      -  497**
      -  35*
      -  223
   0.0+
       +---------+---------+---------+---------+---------+width
      0.0       4.0       8.0       12.0      16.0      20.0
                            meters
```

```
area

 middle of   number of
 interval    observations
    0.00        3     ***
    1.00       30     ******************************
    2.00       12     ************
    3.00        9     *********
    4.00        1     *
    5.00        1     *
    6.00        0
    7.00        3     ***
    8.00        1     *
    9.00        1     *
   10.00        2     **
   11.00        0
   12.00        1     *
```

area in square meters

length in meters

```
length

 middle of    number of
 interval     observations
    0.00         0
    1.00        14      **************
    2.00         9      *********
    3.00        14      **************
    4.00         7      *******
    5.00         4      ****
    6.00         6      ******
    7.00         2      **
    8.00         3      ***
    9.00         1      *
   10.00         0
   11.00         1      *
   12.00         0
   13.00         0
   14.00         0
   15.00         1      *
   16.00         0
   17.00         0
   18.00         0
   19.00         0
   20.00         1      *
```

width in meters

```
width

 middle of    number of
 interval     observations
   0.000         0
   0.500        22      **********************
   1.000        20      ********************
   1.500         9      *********
   2.000         9      *********
   2.500         2      **
   3.000         0
   3.500         1      *
```

meters

```
lensth
 20.0+     *
     -
     -
     -
     -
 16.0+
     -          *
     -
     -
     -
 12.0+
     -  *
     -
     -
     -    *
  8.0+    * 2
     -      **
     -    ** *
     -  * 2
     -    *2*
  4.0+    2**
     -   *234
     -  258
     -  *
     -  86
  0.0+
       +---------+---------+---------+---------+---------+width
      0.0       4.0       8.0       12.0      16.0      20.0
                             meters
```

SIDE-SCAN STATION DOG 13

area in square meters

```
area

 middle of   number of
 interval    observations
    0.00       19     *******************
    2.00       17     *****************
    4.00       14     **************
    6.00        6     ******
    8.00        0
   10.00        4     ****
   12.00        1     *
   14.00        0
   16.00        0
   18.00        0
   20.00        1     *
   22.00        0
   24.00        0
   26.00        0
   28.00        0
   30.00        0
   32.00        0
   34.00        0
   36.00        1     *
```

```
length

 middle of    number of
 interval     observations
     1.          9     *********
     2.         22     **********************
     3.         10     **********
     4.          7     *******
     5.          6     ******
     6.          4     ****
     7.          4     ****
     8.          3     ***
     9.          1     *
    10.          0
    11.          0
    12.          0
    13.          0
    14.          1     *

length in meters
```

```
width

 middle of    number of
 interval     observations
    0.5          15    ***************
    1.0          24    ************************
    1.5           7    *******
    2.0          10    **********
    2.5           2    **
    3.0           6    ******
    3.5           0
    4.0           1    *
    4.5           2    **

width in meters
```

```
length
 20.0+
     -
     -
     -
     -
 16.0+
     -
     -
     -      *
     -
 12.0+
     -
     -
     -
     -         *
  8.0+    **
     -         2
     -     *3  * *
     -       *
     -    3*  *   *
  4.0+    *  *
     -   4322  *
     -  *2424
     -  735
     -  23        *
  0.0+
       +---------+---------+---------+---------+---------+width
      0.0       4.0       8.0      12.0      16.0      20.0
                              meters

meters
```

SIDE-SCAN STATION DOG 14

```
area

 middle of   number of
 interval    observations
     0.        16      ****************
     2.        24      ************************
     4.         9      *********
     6.         4      ****
     8.         6      ******
    10.         1      *
    12.         0
    14.         2      **
    16.         3      ***
    18.         2      **
```

area in square meters

length in meters

```
length

 middle of   number of
 interval    observations
     1.0         4      ****
     1.5        10      **********
     2.0        31      *******************************
     2.5         7      *******
     3.0         4      ****
     3.5         2      **
     4.0         4      ****
     4.5         0
     5.0         1      *
     5.5         0
     6.0         0
     6.5         1      *
```

width in meters

```
width

 middle of   number of
 interval    observations
     0.8         3      ***
     0.9         1      *
     1.0        33      *********************************
     1.1         4      ****
     1.2         4      ****
     1.3         2      **
     1.4         3      ***
     1.5         6      ******
     1.6         1      *
     1.7         0
     1.8         4       ****
     1.9         0
     2.0         2       **
     2.1         1       *
```

meters

```
length
  20.0+
      -
      -
      -
      -
  16.0+
      -
      -
      -
      -
  12.0+
      -
      -
      -
      -
   8.0+
      -
      -     *
      -
      -     *
   4.0+     3*
      -    *4*
      -    2+47
      -    *+4
      -     3
   0.0+
        +---------+---------+---------+---------+---------+width
       0.0       4.0       8.0      12.0      16.0      20.0
```

meters

```
area

 middle of   number of
 interval    observations
    0.5          2     **
    1.0         13     *************
    1.5         23     ***********************
    2.0          7     *******
    2.5         10     **********
    3.0          5     *****
    3.5          3     ***
    4.0          0
    4.5          1     *
```

area in square meters

```
length

 middle of   number of
 interval    observations
   0.000        0
   0.500        2     **
   1.000       15     ***************
   1.500        9     *********
   2.000       27     ***************************
   2.500        4     ****
   3.000        7     *******
   3.500        1     *
```

length in meters

```
width

 middle of   number of
 interval    observations
   0.000        0
   0.500       10     **********
   1.000       48     ************************************************
   1.500        3     ***
   2.000        4     ****
```

width in meters

```
 length
  20.0+
      -
      -
      -
      -
  16.0+
      -
      -
      -
      -
  12.0+
      -
      -
      -
      -
   8.0+
      -
      -
      -
      -
   4.0+
      -    24**
      -   *4+*3
      -    3+*
      -   544
   0.0+
        +---------+---------+---------+---------+---------+width
       0.0       4.0       8.0       12.0      16.0      20.0
```

meters

meters

```
area

 middle of   number of
 interval    observations
     0.0        1     *
     0.5       13     *************
     1.0       21     *********************
     1.5       18     ******************
     2.0        4     ****
     2.5        5     *****
     3.0        2     **
     3.5        0
     4.0        0
     4.5        1     *
```

area in square meters

SIDE-SCAN STATION TATE 1

```
length

length in meters

 middle of   number of
 interval    observations
   0.000         0
   0.500         0
   1.000         0
   1.500         0
   2.000         5      *****
   2.500         9      *********
   3.000        13      *************
   3.500         8      ********
   4.000        30      ******************************
   4.500         5      *****
   5.000        18      ******************
   5.500         2      **
   6.000        11      ***********
   6.500         3      ***
   7.000        10      **********
   7.500         2      **
   8.000         2      **
   8.500         1      *
   9.000         0
   9.500         0
  10.000         2      **
```

```
width

width in meters

 middle of   number of
 interval    observations
    2.          5      *****
    3.         23      ***********************
    4.         37      *************************************
    5.         24      ************************
    6.         12      ************
    7.         13      *************
    8.          4      ****
    9.          1      *
   10.          2      **
```

```
meters

length
20.0+
    -
    -
    -
    -
16.0+
    -
    -
    -
    -
12.0+
    -
    -      *  *
    -
    -        *
 8.0+     *  *
    -    225*2
    -    *272
    -      4*
    -    4593  *
 4.0+    54+***
    -    36+
    -    473
    -
    -
 0.0+
      +---------+---------+---------+---------+---------+width
     0.0       4.0       8.0      12.0      16.0      20.0
                           meters
```

SIDE-SCAN STATION TATE 1

```
orient.

 middle of   number of
 interval    observations
     0.0        0
    10.0        0
    20.0        0
    30.0        0
    40.0        0
    50.0        0
    60.0        7      *******
degrees 70.0    4      ****
    80.0        0
    90.0        0
   100.0        2      **
   110.0        2      **
   120.0       11      ***********
   130.0       20      ********************
   140.0       20      ********************
   150.0       33      *********************************
   160.0       15      ***************
   170.0        7      *******
```

GRAY WHALE FEEDING ECOLOGY

by

Mary K. Nerini, Linda Jones, and
Howard W. Braham

National Marine Mammal Laboratory
Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA

Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 593

December 1980

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

During three 1980 vessel cruises in the Northern Bering Sea, samples were taken to evaluate the feeding ecology of the gray whale. Side-scan sonar, close-circuit T.V., remote bottom samplers and SCUBA divers were employed to describe and quantify the infaunal community consumed by whales.

The summer distribution of whales is constrained by the distribution of prey items. The largest aggregations of whales were found in the central Chirikov Basin over dense beds of amphipods. Densities of *Ampelisca macrocephala*, the dominant species, alone reached 22,450 individuals/m^2. The bottom sediments from this region are deeply pitted possibly as a result of foraging whales. Long-term experiments on the turnover rates of the benthic community were begun in the first of a proposed three year study.

INTRODUCTION

Gray Whale Feeding

Gray whales, like other large animals which feed on relatively small prey, are best described as omnivores. As befits a true omnivore, the list of gray whale food items is extensive, including both pelagic and benthic fauna. However at least since 1874, gray whales have been recognized as primarily bottom feeders earning the name "mussel-digger", with the reports of surfacing whales "besmeared with the dark ooze from the depths below" (Scammon 1874).

Stomachs from almost all gray whales taken in the breeding lagoons or while migrating have been empty or contained small amounts of seaweed, pebbles, and a few miscellaneous items such as polychaete tubes, ascidian tunics, and bivalve shells (Scammon 1874; Andrews 1914; Pike 1962; Rice and Wolman 1971). The few cases of full stomachs reported taken from migrating and wintering whales include pelagic prey items of sardines (Walker 1949), crab zoea larvae (Rice and Wolman 1971) and smelt (K. Balcomb as reported in Ray and Schevill 1974). Records of whales apparently feeding on baitfish (Sund 1975), the euphasiid _Euphausia pacifica_ (Howell and Huey, 1930), and mysids in kelpbeds (Wellington and Anderson 1978) augment the list of possible prey items. Although the gray whale may not feed extensively during the winter, it probably consumes a variety of pelagic, swarming foods opportunistically on its southern range.

There is little doubt however, that most of the whale's energy stores are accumulated on the northern feeding grounds. Although only indirect evidence exists to suggest gray whales feed during their northward migration while in Alaska (Braham in prep.), stomach contents of gray whales from the northern Bering and Chukchi Seas are almost entirely comprised of benthic amphipods (genera: _Ampelisca_, _Lembos_, _Anonyx_, _Pontoporeia_, _Hippomedon_, _Paraphoxus_, _Pleuster_, _Atylus_, _Protomedia_, _Acanthostepheia_, _Ischyrocerus_, and _Dulichia_) with assorted other bottom living organisms (Zenkovich 1934; Tomilin 1957; Pike 1962; Zimushko and Lenskaya 1970; Rice and Wolman 1971; Zimushko and Ivashin 1979; Bogoslovskaya et. al. 1980.) Few gray whales harvested in the summer have empty stomachs (Votrogov and Bogoslovskaya 1979). This suggests that they are continously feeding or that they concentrate in areas of abundant food or both.

Gray Whale Distribution

Sightings of gray whales in the northern Bering and Chukchi Seas from aerial and vessel platforms are plotted by month in Figures 1-6. The areas where whales aggregate correspond to regions where high density benthic amphipod communities are located. Data from Stoker (1978), Makarov (1937), and our 1980 cruises have been combined to produce Figure 7, a composite chart delineating the dense amphipod communities in the Bering Sea.

Sightings of gray whales well inside Norton Sound are uncommon, although some enter the Sound on an annual basis. Probably because of the finer sediment in Norton Sound, there is not a dense amphipod community as is found in the Chirikov basin (Stoker 1978).

Stomach contents of whales taken by Soviet whalers appear to reflect the composition of the benthic community where the whales were taken. Animals taken in the nearshore areas were found to be smaller in size and had been feeding

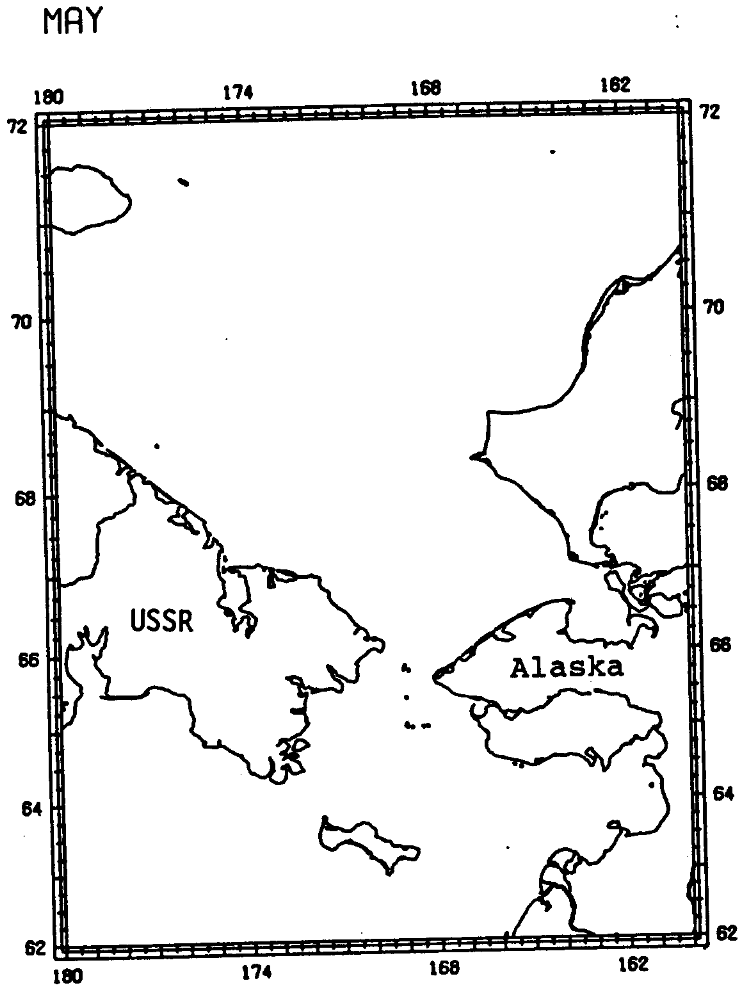


Figure 1. Gray whale distribution during May from N.M.F.S. aerial and vessel sightings 1975-1980 and B.L.M.-Project whales 1980 aerial data.

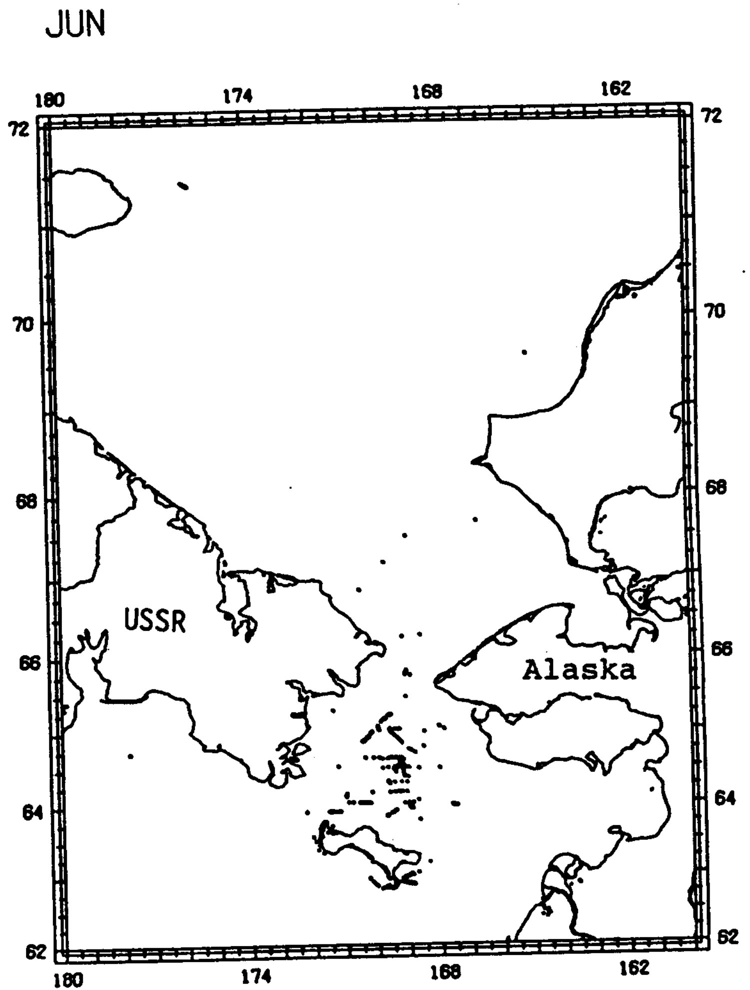


Figure 2. Gray whale distribution during June from N.M.F.S. aerial and vessel sightings 1975-1980.

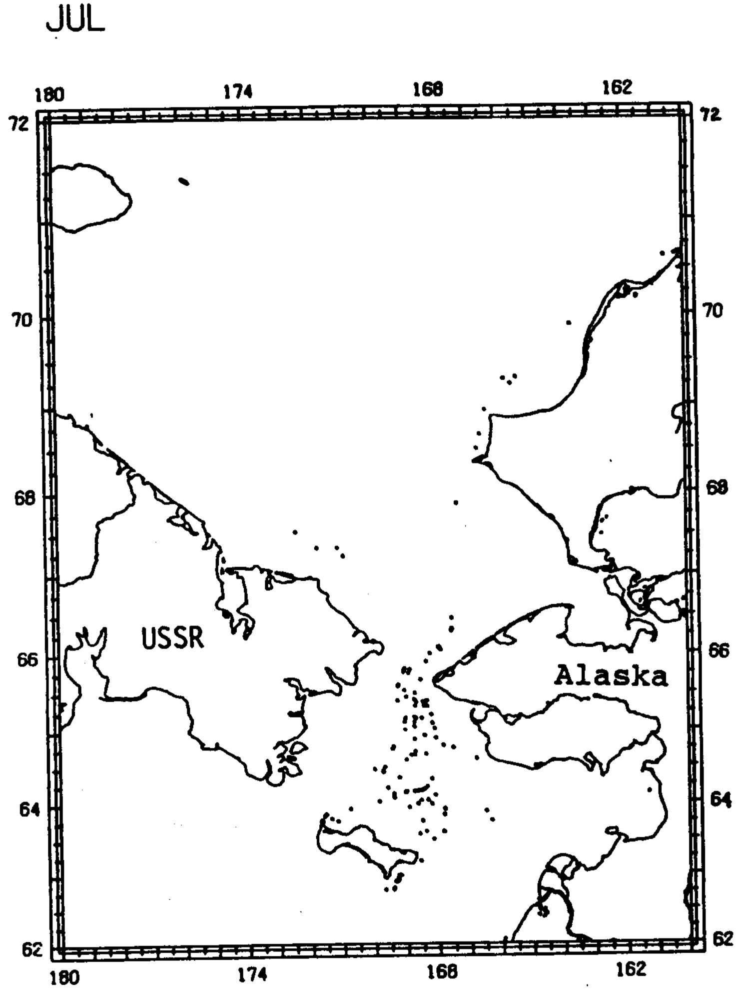


Figure 3. Gray whale distribution during July from N.M.F.S. aerial and vessel sightings 1975-1980.

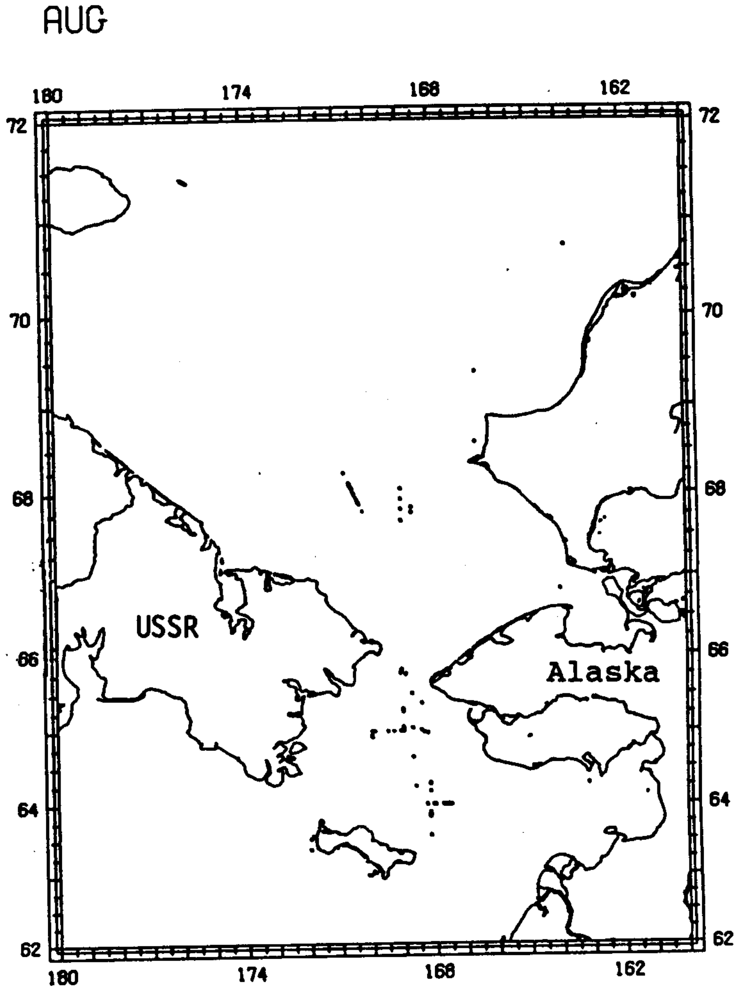


Figure 4. Gray whale distribution during August from N.M.F.S. aerial and vessel sightings 1975-1980.

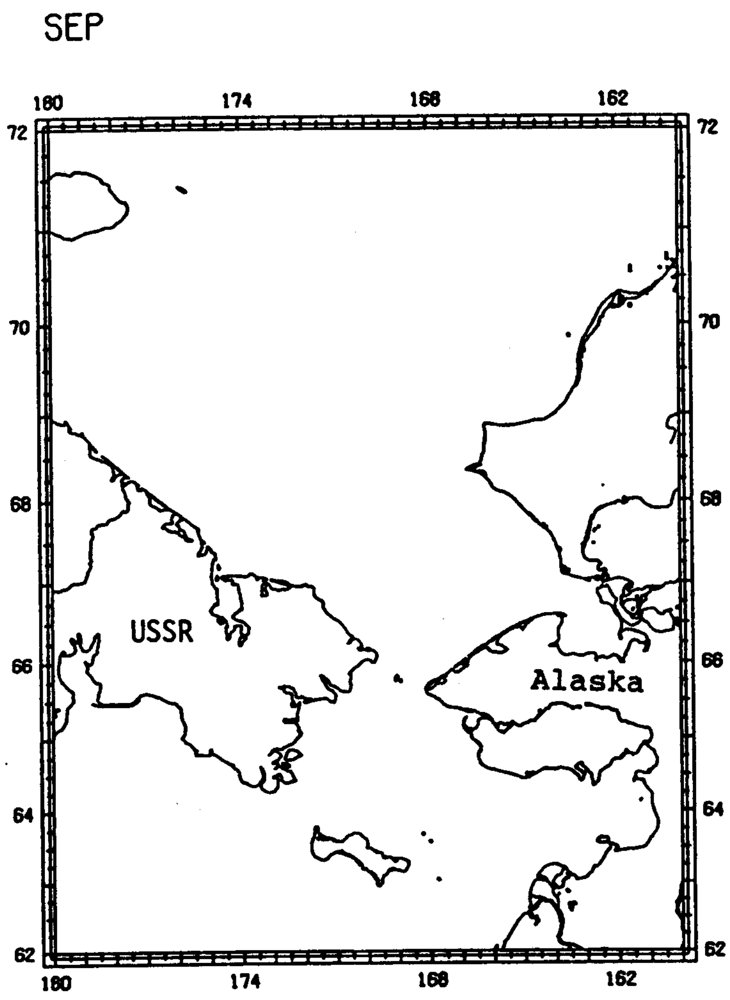


Figure 5. Gray whale distribution during September from N.M.F.S. aerial and vessel sightings 1975-1980.

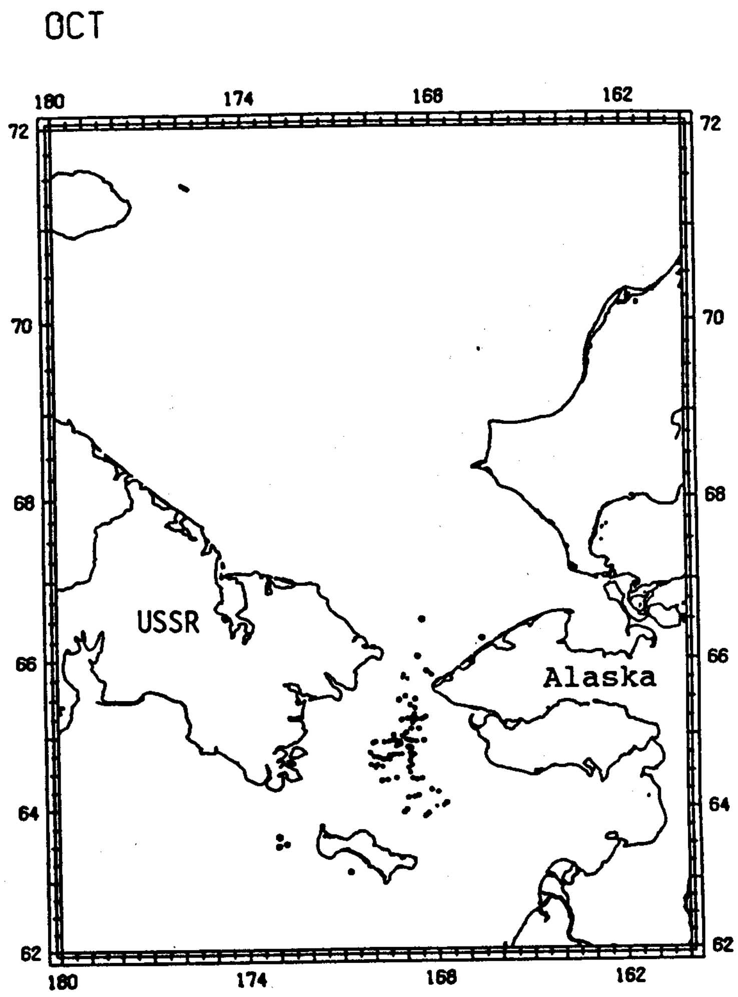


Figure 6. Gray whale distribution during October from N.M.F.S. aerial and vessel sightings 1975-1980 and B.L.M.-Project whales 1980 aerial data.

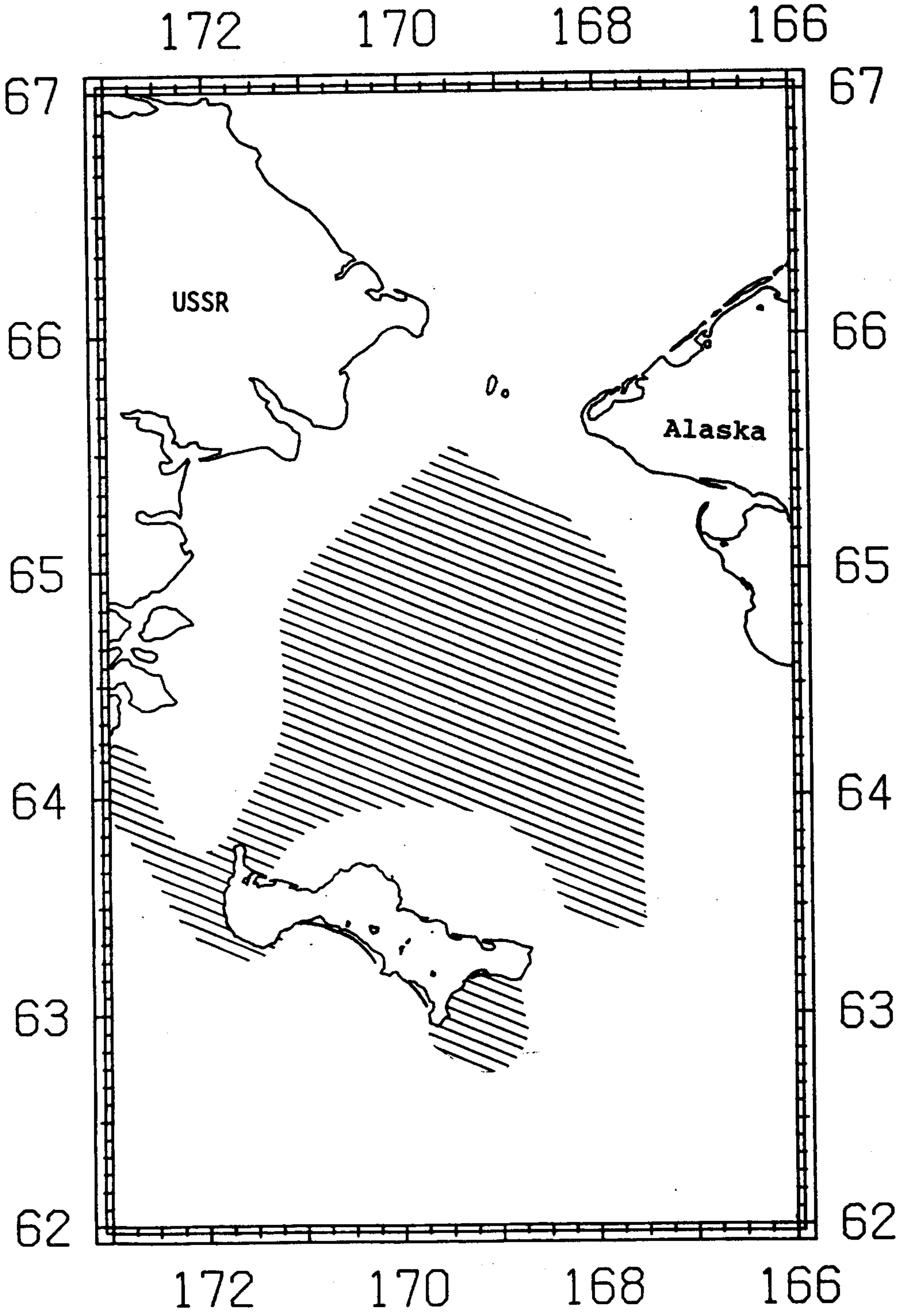


Figure 7. Schematic distribution of the dense benthic amphipod community in the northern Bering Sea.

mainly on the amphipod, Pontoporeia, in contrast to the large whales found further offshore which seem to exploit the vast Ampelisa amphipod concentrations (Zimushio and Ivashin 1979). It is noteworthy that the abundance of whales along the Soviet coast was annually more variable than the abundance in the north central Bering Sea. Areas where whales were found in dense aggregations for several consecutive years were often found to be barren of whales in subsequent years (Votrogov and Bogoslovskaya 1979). This change in summer distribution may reflect a cyclical food resource. Comparing the Soviet whaling data (Zimushko and Ivashin 1979, Votrogov and Bogoslovskaya 1979) with the benthic communities in the northwestern Bering Sea (Makarov, 1937; Belyayev, 1960) one might infer that gray whales predictably return to the regions of dense Ampelisca beds. Clearly, gray whale distribution in the Bering Sea, and probably in the Chukchi Sea, is inexorably linked to amphipod concentrations.

Objectives and Rationale

Information on the temporal and spatial patchiness of their food resource is integral to the understanding of gray whale feeding patterns. Thus, we have spent considerable effort to elucidate aspects of the benthic community dynamics in regions where gray whales feed. However, we approached the problem of cetacean feeding ecology[1] from several other aspects. Distributional data on summering whales was amalgamated from previous NMFS research (Wilke and Fiscus 1961; Braham et. al. 1977; Marquette and Braham 1980) and from 1980 BLM-Project Whales research to delineate areas that were frequently used by whales. Stomach contents of harvested whales were compared to the benthic community composition in the area where the whale was taken to validate the mechanism by which whales feed. We gathered data on gray whale dive times to determine activity budgets in foraging patterns. A side-scan sonar and an underwater video camera system were employed to evaluate the size and shape of whale-made disturbances as well as to evaluate how extensively a region of the ocean floor was used by whales. Infaunal data were collected to allow us to compare the communities consumed by whales and concommitently, to create a hierarchy of important feeding localities to the stock of whales.

The objectives of our study were:

1. Detailed observations of feeding behavior of gray whales in areas where whales concentrate such as St. Lawrence Island.
2. Determination of benthic community structure before, during and after feeding groups have entered a feeding area.
3. Quantitative and qualitative analysis of stomach contents of landed gray whales taken by Soviet whalers in cooperation with Soviet scientists.
Analysis of additional stomach samples from gray whales landed by St. Lawrence Island Eskimos.
4. Gross quantification of the benthic consumption by the gray whale population in the area north of St. Lawrence Island and, on this basis, evaluation of the importance of this community to the stock of whales.

---

[1] We note here that our research effort, designed to quantify and describe the relationship between a feeding whale and changes in its prey, is the first of its kind and thus is exploring untested theoretical and applied ecological questions.

5. Analysis of existing data on benthic community structure known to exist for areas near St. Lawrence Island.

METHODS AND MATERIALS

The Study Area

The area we defined as our study area is the Chirikov Basin, between St. Lawrence Island and the Bering Strait, and between the Straits of Anadyr and outer Norton Sound. The whales are also found in the southern Chukchi Sea which, because it has greater estimated oil and gas resources (Bureau of Land Management, undated), would be a suitable area to study the impacts of development on the community in question. However, there is far more background data on the Chirikov communities, the area is shallower (which provided us with the possibility of using SCUBA divers), and the logistics appeared more manageable. For these reasons we chose to study the benthic system in the northern Bering Sea. Elucidation of of community dynamics in the Chirikov Basin will be pertinent to the understanding of gray whale-benthic interactions in other areas as well.

All field research was conducted in the northern Bering Sea from the NOAA ship Surveyor during 3 legs of cruise RP-4-SU80A, the dates of which were:

Leg I	May 28-June 20, 1980 (Fig. 8)
Leg II	June 23-July 17, 1980 (Fig. 9)
Leg V	Sept 10-Sept 30, 1980 (Fig. 10)

Because of extensive travel time to the study site from Kodiak, the nearest port where the Surveyor could refuel, we spent only 34 of the 67 cruise days actually in the northern Bering Sea. We employed the video camera system and remote benthic samplers on all Legs, as well as recording all marine mammal sightings as part of the NMML's Platforms of Opportunity Program. A leased helicopter was aboard during Leg II and diving operations occurred during Legs II and V. Side-scan sonar records were collected during Legs I and II.

Vessel and Helicopter Operations

A Bell 206 helicopter was aboard the Surveyor from 13 June to 17 July, 1980. For navigation, it was equipped solely with a compass and radio direction finder. Aerial surveys were conducted with 2-3 observers and a recorder. We used systematic search patterns to locate whales, breaking the pattern only to circle over feeding whales when they were encountered. Transects and observations could only be made at altitudes greater than 500 feet. Lower altitudes disrupted feeding and caused the whales to submerge. During the 12 days the Surveyor was in the study area with the helicopter aboard, thirteen flights were initiated to gather data on location, distribution and behavior (primarily dive profiles) of gray whales. Six of these flights were aborted due to fog and cloud cover. Of the remaining seven, five were used to gather data on location and relative distribution of animals while the other two flights were used to gather data on feeding behavior.

Behavior Observations

The helicopter was helpful in finding different aggregations of gray whales and in determining the number of animals in the group. Behavioral observations

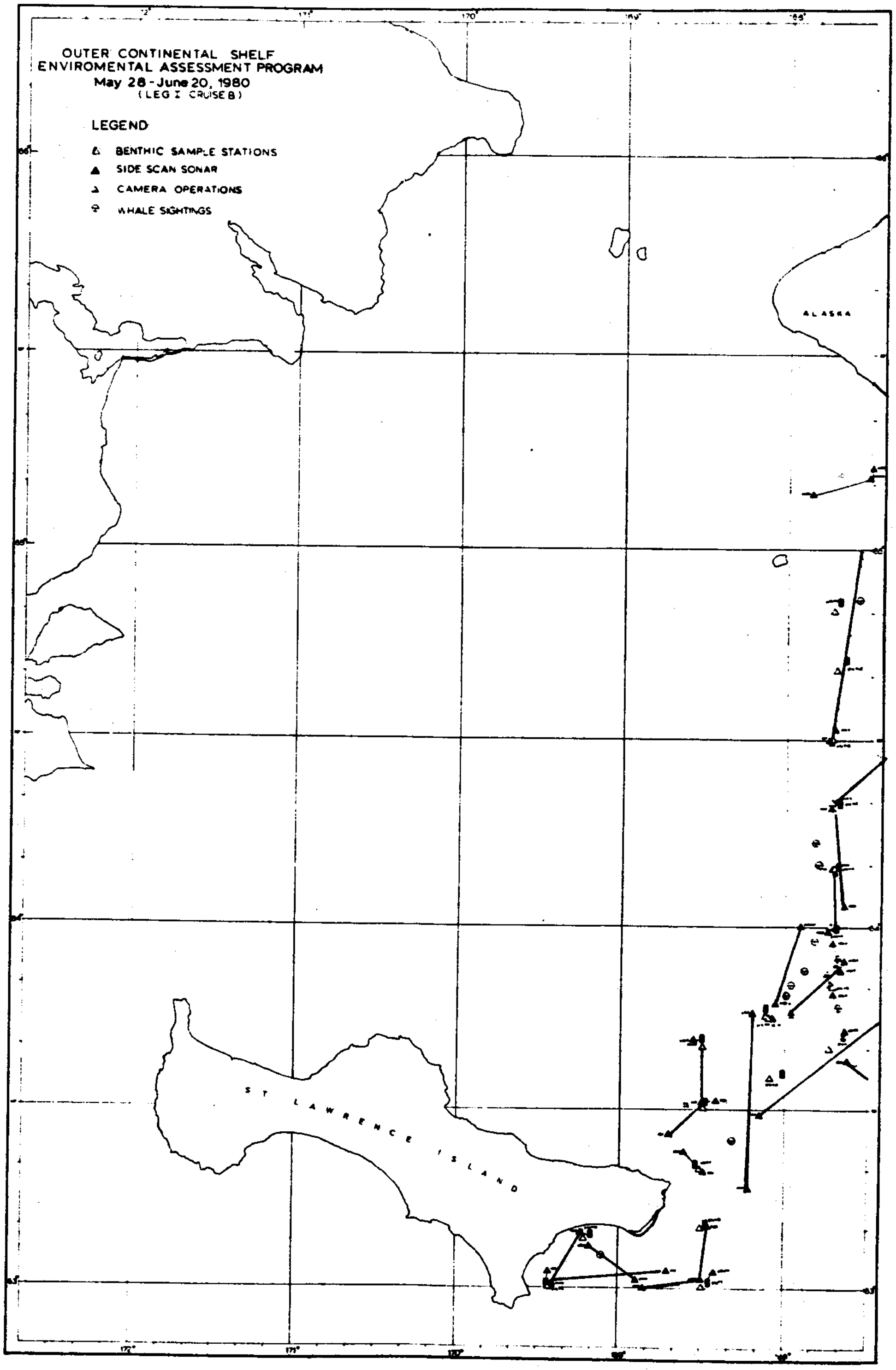


Figure 8. Gray whale sampling stations - leg I, May 28-June 20, 1980.

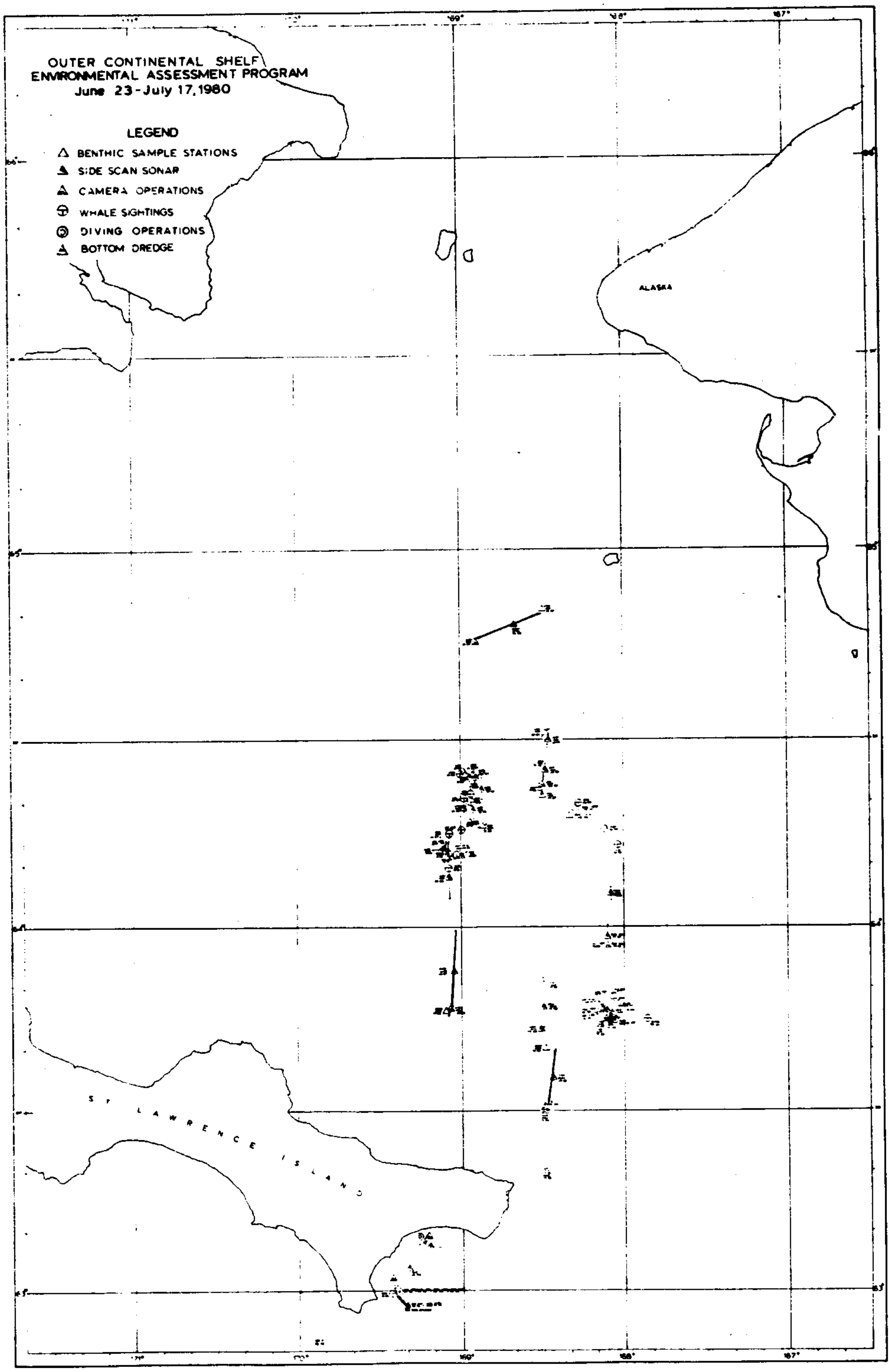


Figure 9. Gray whale sampling stations - Leg II, June 23-July 17, 1980.

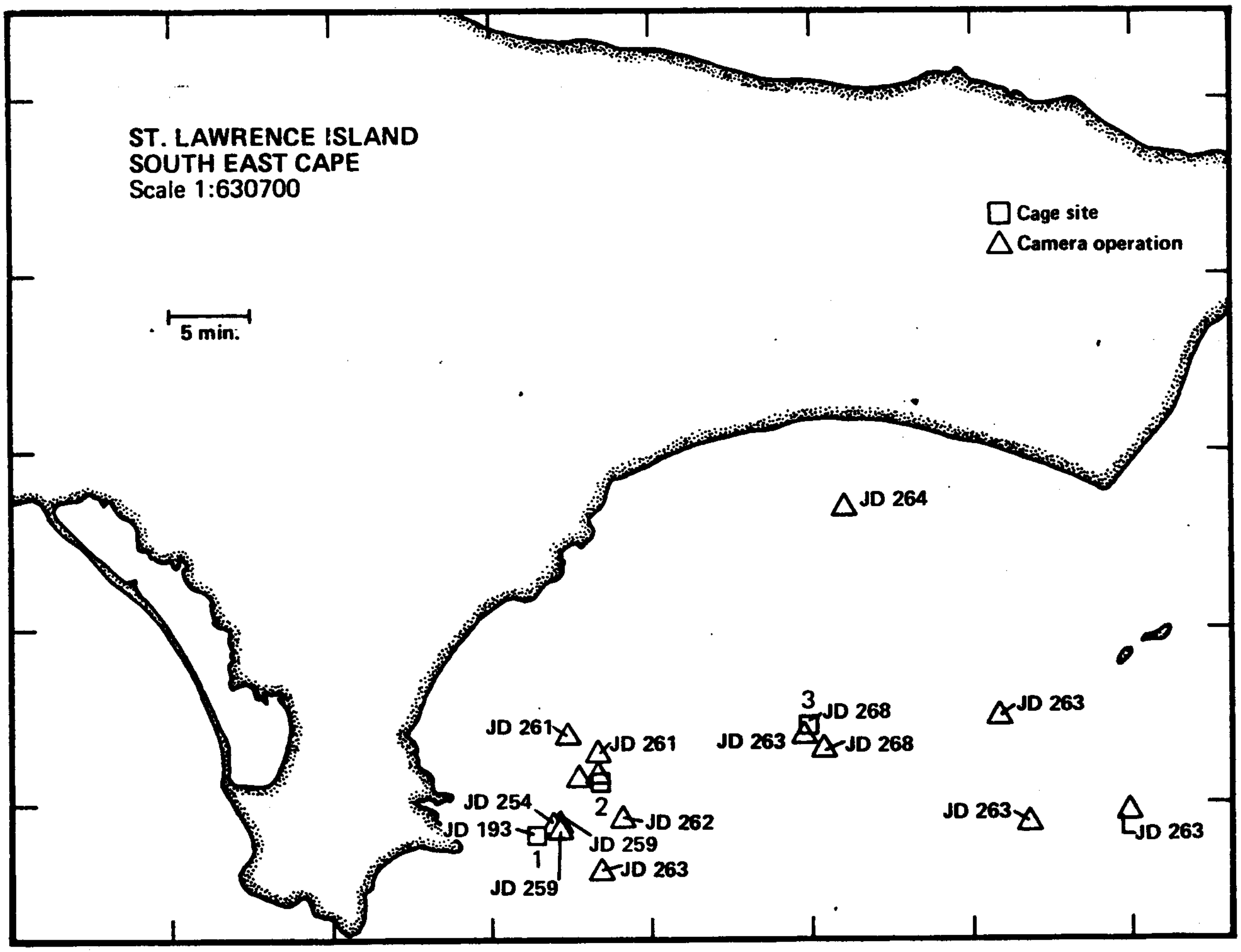


Figure 10. Gray whale sampling stations - Leg V, 10-30 September 1980.

of feeding gray whales were difficult because it was impossible to identify individuals. Dive times were obtained by spotting one animal, and circling it until the animal resurfaced. Observations were continued for half an hour and then the helicopter moved to another area. Unfortunately, there was no way of knowing whether two or more animals were surfacing in tandem. In six cases, we collected dive times on what we thought were solitary whales, and a second whale surfaced. In these cases, only respiration rates and not dive times were obtained from animals which had just surfaced after a feeding bout. Unless the animals are marked, it is very difficult to obtain meaningful diving data on feeding gray whales in offshore waters. One way to circumvent the difficulties of multiple feeding whales would be to attach a streamer tag to animals which would be visible to observers in the air, or to conduct observations from shore.

Side-scan Sonar

Side-scan sonar techniques have been successfully used in geological research to detect small topographic changes in the ocean bottom. We planned to use the same methods to detect and describe disturbances made by whales in the bottom sediments. Once the type of disturbance was identified, we planned to assess the impact made by whales on an area by quantifying the number of feeding scrapes.

Two separate systems were used in this endeavor. On leg II, an EG + G side-scan system[2] operated by the U.S. Geological survey was used. It was outfitted with a 105 khz transducer. These records belong to the U.S. Geological Survey, Menlo Park. On the second leg, we employed a Klein and Assoc. side-scan system operated by personnel from Jon B. Jolly Inc. and outfitted with a 500 khz or 100 khz fish. The recording track width was set at 50 m on both legs, towing speed was 5-7 kts. The side-scan sonar was towed a total of 787 km, covering our study site and the nearshore waters of St. Lawrence Island.

Underwater Video Camera

The video camera proved to be our most useful tool. We originally intended to use it solely to find whale-made disturbances but by the last cruise its function has expanded. We routinely towed the camera through a new area, which allowed us to plan our dives and choose our sampling sites. By routinely towing the camera through a new area, we were able to plan our dives and choose our sampling sites. By verifying what we observed on the camera with grab samples, we were able to categorize communities by sight. Most importantly, the video footage gave us insights into the variability in the community produced by the bottom depressions, and the importance of predators other than whales.

The camera was a Panasonic black and white newvicon camera in an underwater housing. It was equipped with a 16 mm lens and quartz halogen lights. The assembly was mounted on a towing frame which fixed the camera position approximately 30 cm above the substrate, with a field of view of 0.75 m by 1.2 m. We continually refined the system, and by the last cruise we had devised a method of releasing a float from the camera assembly to mark features we viewed on the video screen. This enabled the divers to investigate specific sites. The camera was on the bottom for a total of 34.4 hours at 43 locations.

---

[2] Reference to trade names does not necessarily imply endorsement by the National Marine Fisheries Service.

Benthic Sampling

A scuba diving operation was conducted to sample the benthic community inside and outside of targeted bottom disturbances which we believe to arise from foraging gray whales. The disturbances were separated into two conformations; those that were long, sinuous and narrow we termed furrows and those that were round or elliptical we designated pits. There were six divers on each of the legs. A total of 22 dives were made in water depths varying from 23-40 m (75-130 ft.). Diving conditions on leg II were superior to those on leg I. Visibility was generally poor but averaged 1.5m. The water was colder than predicted; on leg I, bottom temperatures hovered around -1° c.

The core samplers used by the divers to sample the infauna were #10 tin cans (0.188 m^2) with removable plastic lids. Samples were washed on 0.5 mm screens. In addition to collecting samples, divers removed the infauna from 1 m^2 plots for use in the re-colonization experiments, took photographs, and measured pit dimensions. The divers also helped deploy and anchor three 3.7 x 4.9 m structures, fabricated of 45.7 cm (1' 1/2") galvanized steel pipe, which we used to mark our study areas for long term studies of the benthic communities.

Both a $0.025m^2$ box corer and a 0.1 m^2 Smith-MacIntyre grab were used to sample the Chirikov bottom. In all, 130 samples representing 30 sites were collected. Samples were washed on 1 mm and 0.5 mm screens, relaxed in $MgCl_2$, fixed in a 5% formalin solution, and preserved in 70% alcohol. In addition to those collected on our own cruises, samples were collected from the more westerly portion of the study area by scientists on USCGS icebreaker Polar Star during June using a 0.1 m^2 Van Veen grab. Because of the difference in gear, these samples are not entirely compatible with our own data, but provide distribution information on community types. Taxonomic analysis of the Smith-McIntyre samples is underway and expected to be completed by the end of March. All the infaunal data provided in this report are from the cores collected by scuba divers.

RESULTS

Time Budgets: Gray Whale Dive Profiles

Table 1 provides time budget (dive profile) information gathered in 1977 by Braham and by Nerini during the summer 1980 study.

Feeding Furrows, Pits and Other Bottom Features

Side-scan records from leg I in areas where we sighted whales display series of irregular furrows. The furrows varied in length from 3 to 30 m and were 0.5-1 m wide. They were only present in areas where whales were sighted. Due to their irregular, twisting shape and their size, (Fig. 11) the origin of these bottom features is thought to be biogenic. Scientists at the U.S. Geological Survey suggested whales were the most likely cause of the furrows (H. Nelson, USGS, pers. comm.).

During the second leg, more varied furrow shapes were seen (Fig. 12) and we noted much of the Chirikov basin was pitted. The bottom appears to be pockmarked by shallow depressions varying in size from 2 to 10 m in diameter (Table

TABLE 1.--Dive profiles of foraging gray whales.

Whale ID#[1]	Surface time in seconds	Average time between breaths in seconds	Duration of dives	Average duration of dives
01	15	16.15		4 min. 38 sec.
	15			
	08			
	08			
	14			
	27			
	19		4 min. 58 sec.	
	06			
	12			
	14			
	25			
	22		1 min. 54 sec.	
	14			
	17			
	12			
	23			
	21		6 min. 14 sec.	
	11			
	33			
	27			
	13			
	09			
	08			
	17		4 min. 45 sec.	
	10			
	20			
02	15	18.25		
	15			
	18			
	25			
03	08	11.66		
	12			
	15			
04	12	19.8		
	14			
	15			
	38			
05	40	34.33		
	39			
	24			

TABLE 1.--Dive profiles of foraging gray whales--continued.

Whale ID#	Surface time in seconds	Average time between breaths in seconds	Duration of dives	Average duration of dives
06	14	26.25		
	18			
	38			
	35			
07	31	22.66		
	18			
	19			
29-1	90	88.8		
	147			
	60			
	86			
	68			
	129			
	33			
	128			
	22			
	125			
29-2	52	57.6		
	56			
	77			
	61			
	51			
	45			
	83			
	36			
30-3	19	58.5		3 min. 53 sec.
	37			
	13			
	127			
	93			
	70			
	86			
			3 min. 27 sec.	
			3 min. 36 sec.	
	23			

TABLE 1.--Dive profiles of foraging gray whales--continued.

Whale ID#	Surface time in seconds	Average time between breaths in seconds	Duration of dives	Average duration of dives
30-4	126	78.1		2 min. 43 sec
	127			
	134			
	91			
			2 min. 43 sec.	
	57			
	85			
	39			
	47			
	25			
	47			
	81			
30-5	63	83.66		
	150			
	135			
	45			
	110			
	50			
	95			
	65			
	40			
1-6	40	59.89		
	87			
	27			
	91			
	140			
	19			
	21			
	44			
	70			
2-7	31	34.29	3 min. 27 sec.	3 min. 56 sec.
			3 min. 38 sec.	
	18		3 min. 55 sec.	
	16			
			3 min. 15 sec.	
	20			
	110			
	10			
	35			

TABLE 1.-- Dive profiles of foraging gray whales--continued.

Whale ID#	Surface time in seconds	Average time between breaths in seconds	Duration of dives	Average duration of dives
2-8	11	17.33		4 min. 12 sec.
			3 min. 37 sec.	
	27			
	20			
			4 min. 55 sec.	
	12			
	14			
			3 min. 50 sec.	
	20			
2-9	18	26.6 sec.		3 min. 47 sec.
	87			
			3 min. 21 sec.	
	22			
	23			
			4 min. 51 sec.	
	15			
	25			
	23			
			2 min. 13 sec.	
	17			
	17			
	19			
2-10	24	47.53 sec.		2 min. 48 sec.
	52			
			2 min. 15 sec.	
	20			
	33			
	92			
	60			
	35			
			2 min. 42 sec.	
	23			
	18			
	104			
	15			
	66			
	63			
	27			
	81			

TABLE 1.--Dive profiles of foraging gray whales--continued.

Whale ID#	Surface time in seconds	Average time between breaths in seconds	Duration of dives	Average duration of dives
2-11	40	42.07		2 min. 44 sec.
			3 min. 03 sec.	
	82			
	11			
	23			
	39			
	151			
	22			
	12			
	36			
			2 min. 50 sec.	
	15			
	18			
	25			
	25			
	90			

---

[1] Numbers 01-07 collected May 28-July 17 1980 in the Chirikov Basin; #29-1 to 2-11 collected June 29-July 11, 1977, off SE Cape, St. Lawrence Island.

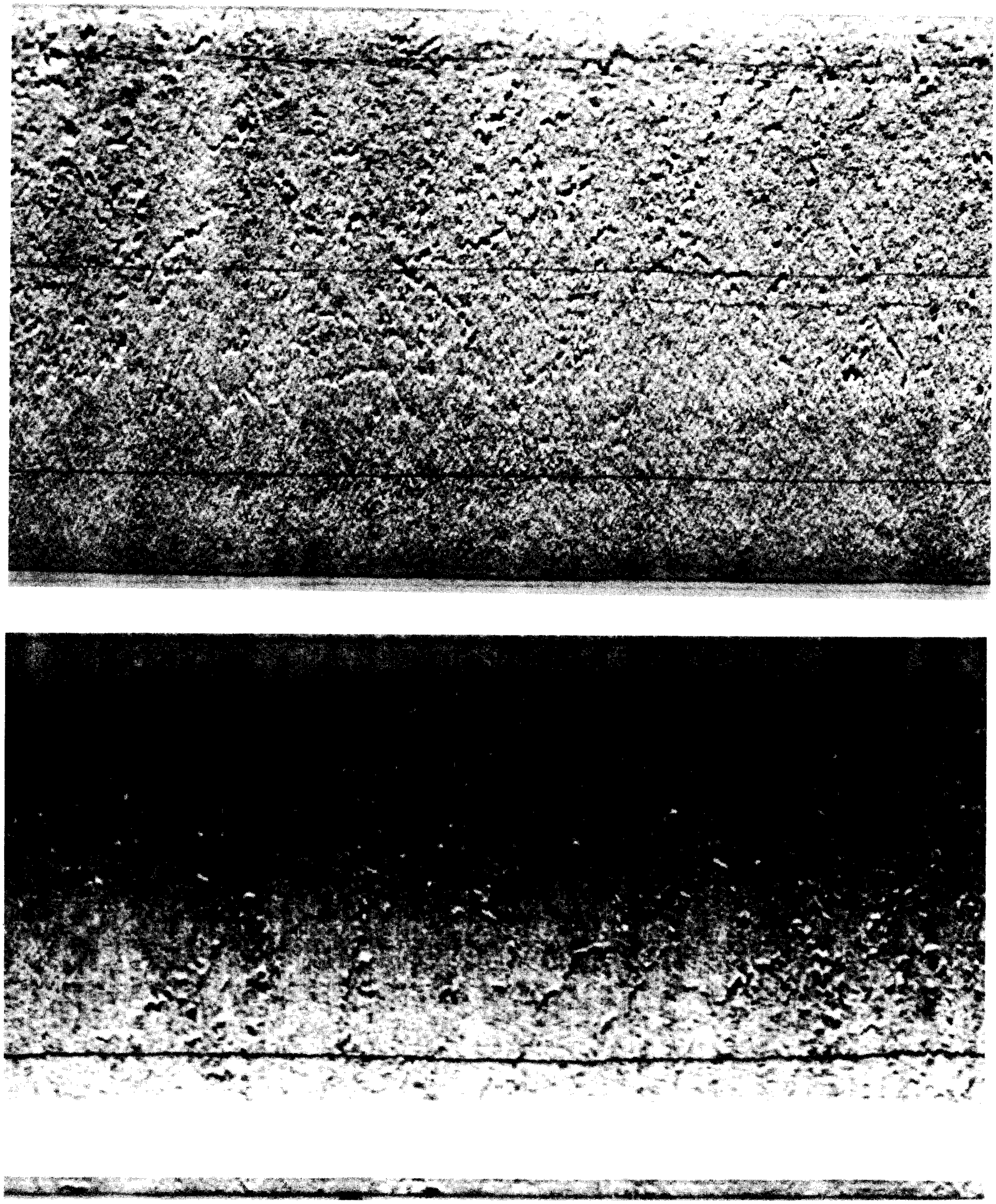


Figure 11. "Furrows" as depicted on 100 khz side-scan sonar records. Towing speed was 5.2 kts.

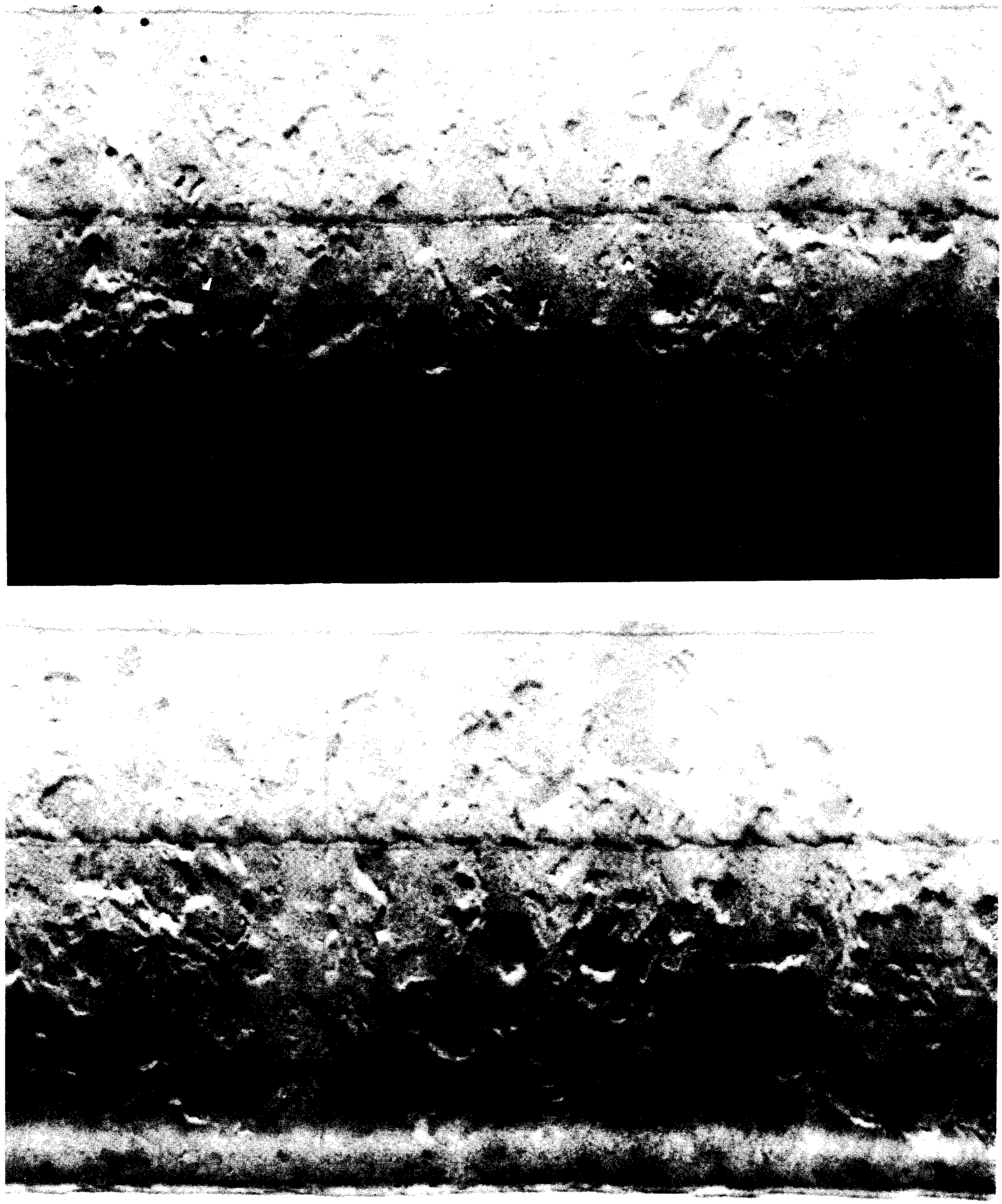


Figure 12. Bottom depressions depicted on 500 khz side-scan sonar records. Towing speed was 2.9 kts.

2). Although pits were evident over the entire northern Bering Sea, they appeared to be more pronounced, that is, both more abundant and larger, near the center of our study area.

The spatial distribution of the furrows is less clear than that of the pits. That is, there is no obvious area where furrows dominate the bottom features. Furrows appeared only in areas we presumed to be used by whales but whales were not always present. On one occasion, we made several passes through a small pod of feeding whales (~5 animals) while towing the side-scan transducer and saw no evidence of furrows with either the 100 or 500 khz fish.

Ice scour was found as expected near the northeast end of St. Lawrence Island. There was no evidence of scour from nearshore fast ice in the eastern bight of the island, nor in the central Chirikov Basin.

The bottom depressions are of interest because even slight topographic unevenesses in the sediments can create micro habitats into which organisms will distribute themselves non-randomly. Thus the pits almost certainly affect benthic community structure. We classified regions of the Bering Sea by the density and magnitude of the pits and by the visible infaunal organisms. We recorded general slope of the pit sides; epifaunal organisms and presence of dead shells which led us to subjective conclusions regarding the northern Bering Sea benthos. The most pronounced pits, that is, those which were deepest, had the steepest sides, and whose bottoms were strewn with shells, seem to be located in the central northern Bering Sea - the same region whales appear to be actively feeding.

Benthic Infauna

Species, Composition and Densities

The dominant (i.e. numerically and by biomass) organism in all but 3 of our samples was Ampelisca macrocephala. Densities ranged from 400-22,450 individuals/m^2 (Table 3). The higher values were in the area where we consistently saw feeding whales during leg II (near Station 21). The corresponding amphipod biomass was 94gm/m^2 to 500 gm/m^2. Because on the fall cruise we could not re-locate those sites we had marked in the spring, we cannot directly compare seasonal biomass levels.

The size structure of the amphipod population shifted only slightly with the season (Fig. 13). Gravid females were found in both seasons but recently hatched animals (0-3 mm) were found solely in the spring. The modal size class in all seasons was the 5-7 mm class although in the autumn, the distribution becomes bi-modal as the 9-11 mm class increases in frequency. Large individuals (>17 mm) were only found inside pits in the spring but this trend was not found in the autumn data. There is otherwise no significant difference between size classes inside or outside of the pits.

Ecological Attributes of the Bottom Features

We assume the topographical variation in the benthos may create differences in communities. If, as we thought, the pits were formed by foraging whales, then one might initially expect a depauperate infauna within the depression

TABLE 2.--Pit dimensions.

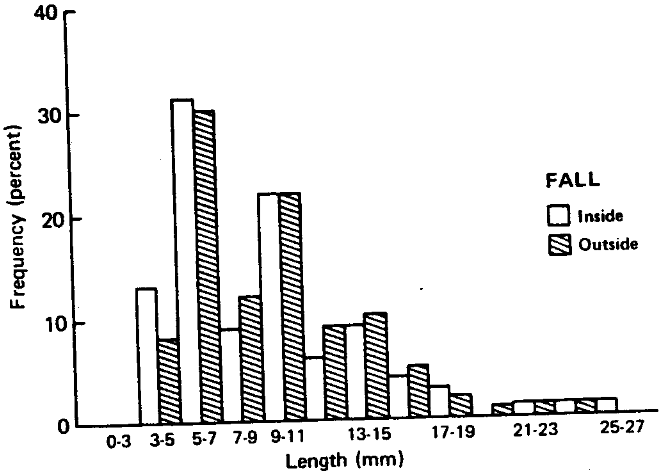
Axis 1 (m) A_1	Axis 2 (m) A_2	Depth (m)	Approx. area(m^2) $A = \frac{(A_1A_2)}{4}$	Index area x depth
.61	0.61	.13	0.30	0.039
* 1.0	1.5	.40	1.18	0.472
* 1.0	1.5	.40	1.18	0.472
* 1.0	1.5	.20	1.18	0.236
1.0	1.0	.10	0.8	0.08
2.3	0.9	.19	1.63	0.31
0.64	0.71	.08	0.36	0.03
2.2	0.9	.15	1.56	0.234
0.76	0.9	.20	0.54	0.11
* 1.2	0.76	.20	0.72	0.14
2.0	2.0		3.14	
* 2.0	3.0		4.71	
* 1.5	3.0	.10	3.53	0.34
1.7	1.7	.18	2.27	0.41

* Denotes $0.019m^2$ sample taken from within measured pit by divers.

Table. 3--Average amphipod abundances inside and outside of pits and partitioned by season.

Avg.# A. macrocephala/m²	(Spring)	5934.6	S.D. = 5000.2	n=40
	(Fall)	5025.4	S.D. = 2640.5	n=34
	(inside)	5557.6	S.D. = 4435.5	n=38
	(outside)	5694.8	S.D. = 3756.9	n=33
Avg. gms A. macrocephala/m²	(inside)	137.6	S.D. = 39.6	n=16
	(outside)	105.9	S.D. = 77.3	n=14
Avg. gms total Amphipods/m²	(inside)	190.9	S.D. = 59.2	n=16
	(outside)	199.5	S.D. = 94.5	n=14
Avg.# A. macrocephala/m²	Spring			
	(inside)	5165.4	S.D. = 5609.3	n=22
	(outside)	6874.7	S.D. = 3986.6	n=18
	Fall			
	(inside)	6097.0	S.D. = 1985.5	n=16
	(outside)	4278.9	S.D. = 3004.2	n=15

S.D. = standard deviation
n = number of observations



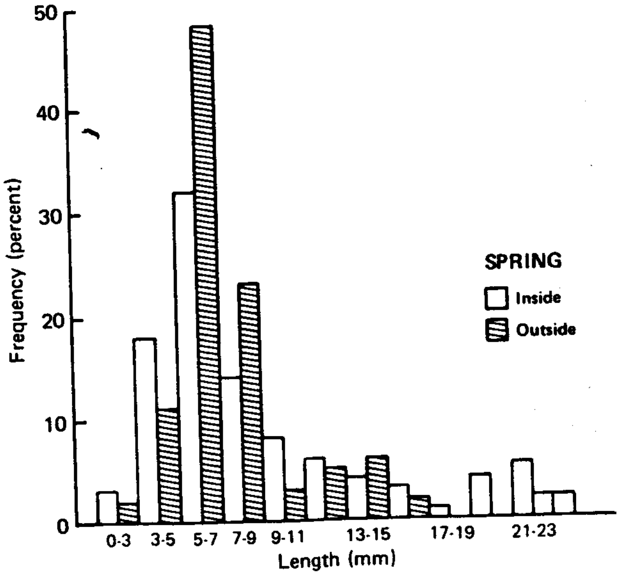


Figure 13. Length frequency histograms of *Ampelisca macrocephala*.

left by a feeding whale. Shortly after its creation, one might predict first an increase in scavenging organisms which subsist on detritus collecting in the pits, followed by the more sedentary tube-builders. This successional pattern is one commonly documented in disturbed areas (Pearson and Rosenberg, 1978; McCall, 1977; Oliver and Slattery, 1976). Since congeneric species may display similar colonizing and feeding strategies, we combined the species data and analyzed by genus using a Wilcoxon-Mann Whitney rank-sum test. There were only three instances where the abundance of genus inside a pit was significantly different from that found outside a pit (Table 4). All three genera were tube-building animals. The size (and inferred age) of the pit was not considered in this analysis due to small sample sizes with increased partitioning of the data.

In addition to species comparisons, we also measured the volume of tube material found in the sorted bottom samples inside and outside of pits (Fig. 14). Since we expect tube-dwelling organisms such as the Ampelisca species to be less adroit at colonizing an area, we expected tubal material to be less abundant inside the presumably defaunated pits. There was no significant difference (t-test, $P > .05$) in our data but again age of the pit was not considered.

To investigate temporal changes in the infaunal pit community corresponding to the time elapsed from the initial disturbance, we assigned relative ages to the sampled pits based on their area, estimated depth, slope of the sides and biological information such as the presence of dead shells or exposed worm tubes. By then, focusing on groups of organisms, i.e. representative families, we hoped to see successional trends in colonization of the pits. The families we chose to focus on were the Ampeliscidae (comprised of Ampelisca macrocephala, A. eschricti, A. birulai, and Byblis sp.); the Lysianassidae (Anonyx nugax and Orchomenella minuta); and the Corophiidae and their relatives (Protomedeia fasciata, Corophium sp., Photis sp.).

The Ampeliscidae are sedentary, tube-dwelling detritus feeders (Kanneworff 1965) as are the members of the Corophiidae we chose. Whereas the lysianassids are active, wide-ranging scavengers. Because of these attributes, we expected the three groups would dominate the pit community at different times relative to the age of the pit. That is, we predicted that in newly exposed sediments, the recent pits, there would be an increase in the lysianassids. Similarly, we reasoned that the less active tube-dwellers would be in low abundance in the recent pits but would subsequently increase in abundance until their densities inside the pits were indistinguishable from the densities outside of the old pits.

For this analysis, data from spring and autumn were pooled because of small sample sizes (Fig. 15). Only in the Lysiannasids were the means from the three ages of pits significantly different (one-way ANOVA $P < .05$). The plots presented include mean abundance and standard deviation. As the relatively sedentary tube-builders may be more active colonizers during the spring before their offspring hatch, we may have obscured trends in the paired samples by combining the seasonal data. In addition to unaccountable seasonal differences in dispersal strategies this test was based on inferred ages of pits which further complicates the interpretation.

Recolonization

As a controlled experiment, we created our own pits to document the benthic community change over time in a cleared area. By understanding this process,

TABLE 4.--Genera abundance inside + outside of pits (significant difference detected by Wilcoxon-Mann-Whitney rank-sum test).

Genus	# Species	Leg 2 (summer)	n	Leg 5 (fall)	n
Ampelisca	3	** outside	18	n.s.	15
Anonyx	2	n.s.	18	n.s.	15
Orchomene	2	n.s.	15	n.s.	9
Protomedeia	2	* outside	18	*** inside	15
Photis	1	n.s.	15	n.s.	11

*** denotes significant at .01 level
** denotes significant at .05 level
* denotes significant at .1 level
n.s. = not significant
n = number of (   )

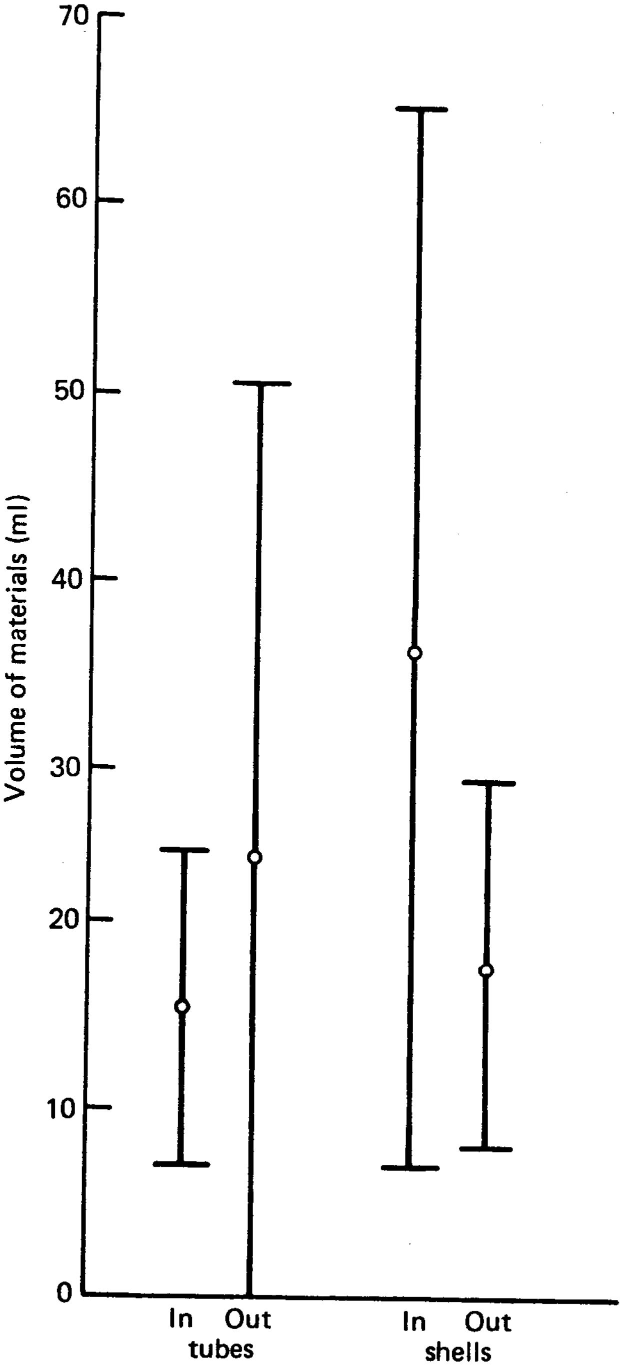


Figure 14. Volume of infaunal tubes and shell debris in 0.019 m^2 cores collected by divers inside and outside of bottom depressions. (N = 15 inside; N = 13 outside).

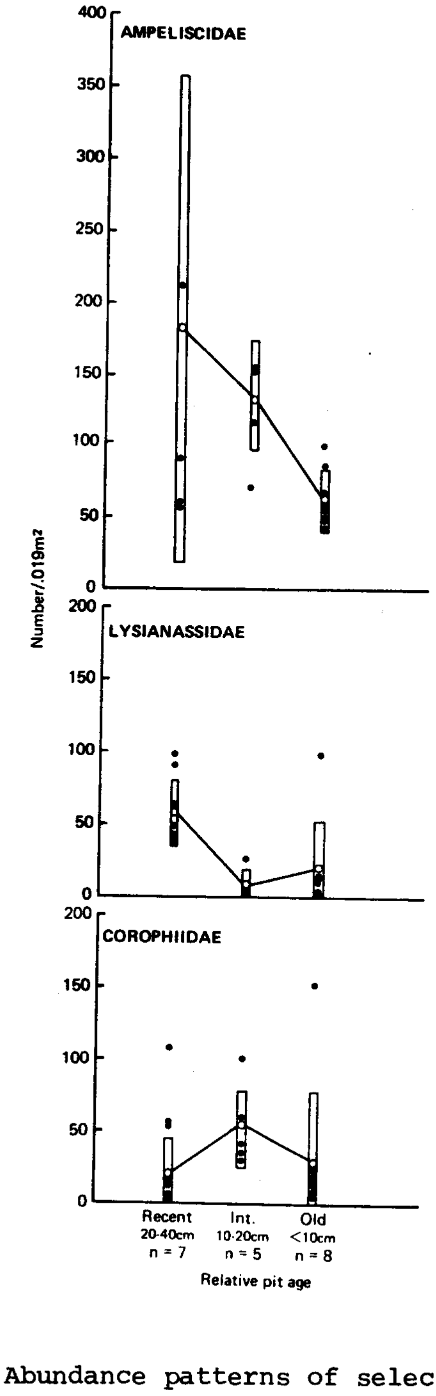


Figure 15. Abundance patterns of selected amphipod families inside pits. Pit "age" is subjectively assigned as indicated in the text.

we can better interpret data from our other samples. Two $1m^2$ patches were cleared of the top 10 cm of sediment using a pneumatic lift. Both patches were established near Southeast Cape St. Lawrence Island in September. The plots were sampled immediately after clearing the area, the following day, and six days later. Abundance of *Anonyx nugax*, *Orchomenella minuta*, *Ampelisca macrocephala* and *Protomedeia fasciata* are plotted in Fig. 16. As expected, there was a sharp increase in abundance of scavenging Lysiannasids (*Anonyx* and *Orchomenella*) by day 1 with a corresponding sharp drop in *Ampelisca*. This pattern corroborates the sequence we have tentatively documented in the natural system.

DISCUSSION

It became clear by leg II that we would be unlikely to see an actively foraging whale because of underwater visibility, dive time limitations and the paucity of whales on the study site during early July. Therefore we were unable to quantitatively describe how whales feed, how much they consume and where they chose to feed.

Our first goal, that of definitely establishing the mechanism by which whales feed, was patently impossible. However, for an animal the size of a whale to consume infaunal organisms without discriminating between prey, any feeding mechanism would entail a wholesale removal of sediment. Since sand and gravel are commonly found in gray whale stomachs, usually in small quantities, and because we see "mud" plumes emanating from foraging whales, we assume the feeding activities of the whales change the infaunal community by removing community dominants and by physically disturbing the substrate. Quantification of whale food consumption may only be possible by carefully monitoring the traces left in the bottom by foraging whales. Other investigators in soft-bottom systems have similarly examined the physical and community changes created by a benthic predator (VanBlairicom 1978).

Examining the small scale bathymetry of the northern Bering Sea both in areas where whales were present and where they were not, the ubiquitous features are the depressions or pits. The "furrows" mentioned earlier and apparent on the side-scan records were well correlated with the presence of whales but much rarer than the pits. In fact, we were unable to locate any "furrow" with divers. The cause of the furrows and pits is still unknown.

The furrows may represent a direct impingement of the whale on the bottom, whereas the pit may be shaped by several factors. Over most of the area which we sampled, the surface sediment was a cohesive muddy tube mat underlain by fine sand. Given such a structure one might expect to see wave and current scour only in those areas where there was a break in the surface tube mat. We postulate that a feeding whale must break up the tube mat, leaving the surrounding area vulnerable to wave scour. This may be analogous to the observations of Fager (1964) who noted that dense polychaete beds were susceptible to destruction by wave surge only after an initial intrusion through the cohesive sediments. Wave scour near objects protruding through the sediments is a well known geologic process (Larsen et. al. 1979) and scouring, added to the initial whale disturbance, would produce shallow symmetrical features such as the pits.

Subjectively, the abundance and the type of pits changed with the area. That is, in the central Chirikov basin at our deepest dive sites, we encountered

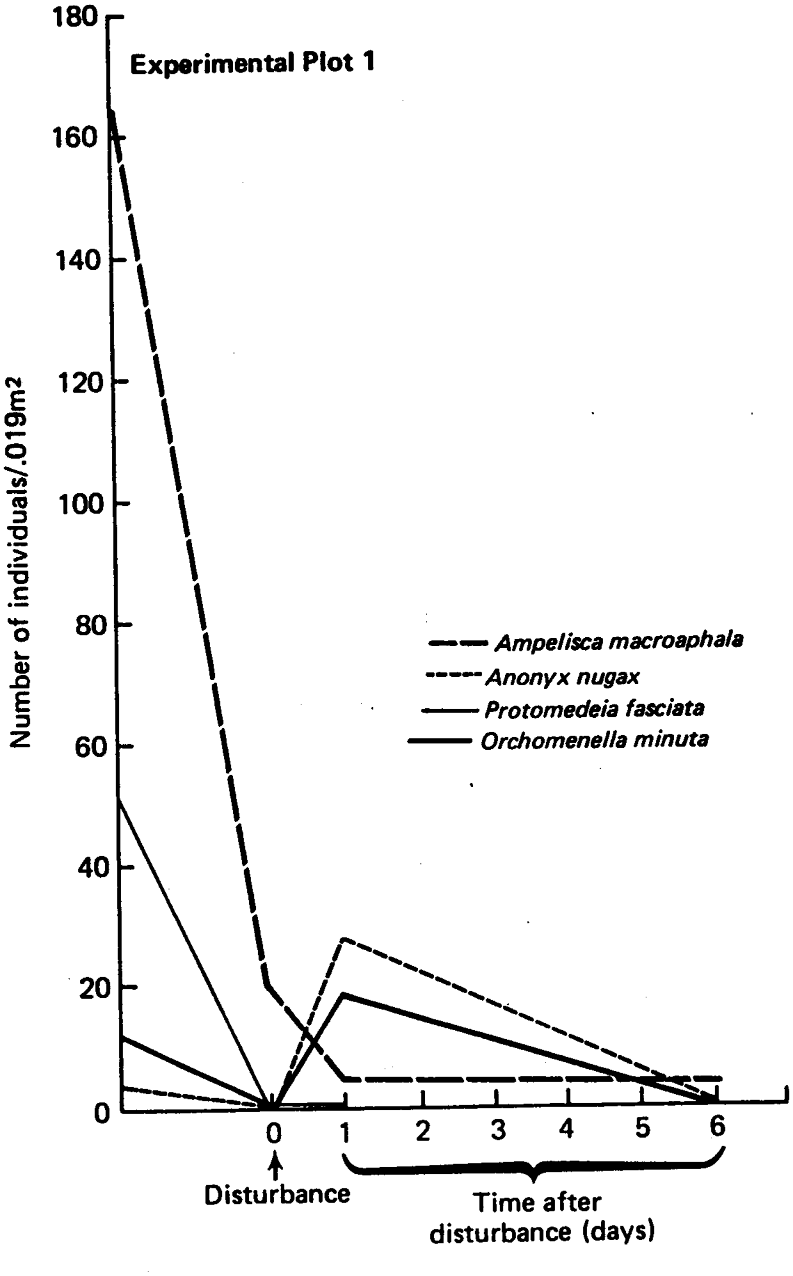


Figure 16. Species abundance over time in 1 m^2 plot after experimental defaunation. 0 indicates the day the plot was cleared of infaunal organisms and the top 10 cm of sediment.

the deepest and largest pits, the highest densities of amphipods and the greatest number of feeding whales. Admittedly, it is too early in the study to produce a concrete correlation between feeding whales and the appearance of pits but the hypothesis is appealing and reasonable. Since regions of abundant pits are patchy, we may also find that prime whale feeding habitat is correspondingly patchy.

The benthic infaunal data seem to support the hypothesis that pits are defaunated patches which are in various successional stages possibly returning to a high density, tube-building amphipod community. Our data (i.e. a six day time sequence) on the time required for a cleared patch to be recolonized is too scanty to predict how rapid the recovery is. However, the rate of return to original community state is undoubtedly heavily influenced by patch size and season of disburbance as it is in other bottom systems (McCall 1977; Holling 1973; Sutherland 1974; and Gray 1977) and these are factors we have not been able to test. Long-term experiments documenting changes in communities of various sized pits both in the Chirikov and off Southeast Cape should provide the necessary information on the regeneration time of the community.

Putting this preliminary information together in a rudimentary fashion, we can compute very gross estimates of gray whale consumption. We must caution that the assumptions behind the ensuing calculations are considerable at this stage of the research. However, one of our objectives was to estimate feeding rates of gray whales. In the most productive reaches of the northern Bering Sea the mean amphipod densities outside of pits are on the order of $9,600/m^2$ with a corresponding biomass of $400\ g/m^2$. Average area of a pit in this region was a minimum of $0.81/m^2$. By simply multiplying, we estimate 324 gms of amphipods may be removed per pit. Further field research is necessary to determine how accurate or meaningful this estimate is.

CONCLUSIONS

The data collected during this first year of research were less than hoped for and thus our conclusions are preliminary. The research has focused on processes that will take several years to understand. In addition, we feel that our initial year was in large part a feasibility study to determine which approaches were possible, what experiments could be attempted, and what questions could be addressed. In addition, and perhaps of greatest importance, this past year helped us determine which questions warrant further investigation.

We have reached the following conclusions regarding gray whale feeding ecology in the Bering Sea:

1. Whales seem to concentrate over areas of highest amphipod density, that is, in the Chirikov Basin. Their summer distribution is linked to the regions with dense prey assemblages.

2. Gray whales are omnivorous; their stomach contents appear to be random samples of the community upon which they feed.

3. There is large variation in the "quality" (as we assess it) of amphipod communities and in their corresponding usage by whales.

4. The bottom depressions seen across the Chirikov basin are possibly produced by foraging whales.

5. It will be possible to study regeneration time of a community by observing successional patterns in experimentally cleared areas and natural depressions.

Recommendations

1. A main question of our subsequent research is "do whales create the bottom depressions?". Since the characteristics of the bottom sediments are important to the evaluation and maintenance of the pits, investigation of sediment properties such as cohesiveness and resistance to scour will be helpful.

2. Without being able to see a whale foraging on the benthos, we need evidence that the production of bottom depressions is correlated with the presence of whales. By quantifying the number and size of pits present at the start of the summer and comparing that to what we see later in the season over precisely the same transect, we should be able to determine the magnitude of the gray whale impact on the sediments. This work would require a refined camera system which perhaps has a compass in the viewing screen and a mechanism to gauge depth and size of depressions.

3. We feel that any further work in this project should be conducted from a smaller vessel. A large vessel cannot maintain its steerage while moving at the slow speeds needed for the video camera operations. In order to quantify bottom features, it is essential to be able to run a charted course while towing the camera.

4. To further our understanding of the successional nature of the bottom depressions, we would continue the experiments involving cleared patches of sediment. Only by manipulation of this sort will we be able to arrive at estimates of community regeneration time. We would expand this research by varying the size of the original cleared area (from 1 m^2) and by establishing the patches in localities which may experience various current regimes.

5. A land-based study in an area used by whales (e.g. S.E. Cape St. Lawrence Island) may be necessary to assess feeding behavior. A fairly complete picture of foraging patterns (% of area used, length of dives) could be assembled from a nearshore area where whales forage. In addition a land-based camp would facilitate the recolonization experiments and the acquisition of stomach contents from stranded and harvested whales.

Acknowledgements

We thank L. Crew, S. Maupin and J. Rosapepe for their assistance in this project. In addition, this study could not have been done without the support of the NOAA Dive Office and a host of enthusiastic divers including: J. Blackwell, L. Consiglieri, S. DeBow, R. Moore, C. Newell, J. Oliver, D. Rutkowski, and M. Silverstein. We are also grateful for the stimulating discussions, suggestions and assistance K. Haflinger provided throughout the project. From J. Oliver we learned some valuable lessons relating to benthic ecology. P. Slattery generously helped with the taxonomy and discussed amphipod strategies, and D. Lungjblad kindly provided us the 1980 data on gray whale distributions in the Bering Sea. M. Larsen was instrumental in our understanding and interpretation of the bottom features recorded by side-scan sonar. H. Feder allowed access to bethnic samples previously collected from this region. Lastly, we thank the captain and crew of the NOAA ship *Surveyor* for their assistance during the field season and we thank M. Tillman and the NMML staff for their patience and unflagging support throughout this project.

REFERENCES

Andrews, R.C. 1914. Monographs of the Pacific Cetacea I. The California Gray Whale (Rhachianectes glaucus Cope). Mem. Amer. Mus. Nat. Hist. (New Series) 1:227-287.

Belyayev, G.M. 1960. Kolichestvennoye raspredeleniye donnoy fauny v severo-zapadnoy chasti Beringova Morya. (Quantitative distribution of bottom fauna in Northwestern part of the Bering Sea). Tr. Inst. Okeanologii 34:85-103. Trans. Nav. Oceanogr. Off. #337, 1968, 25 p.

Bogoslovskaya, L. S., L. M. Votrogov and T. N. Semenova. 1980. Feeding habits of the gray whales off the Chukotka peninsula. Paper submitted to the 32nd mtg. of the Int. Whaling Comm., Cambridge, 30 June-10 July 1980. SC/32/DOC. PS 20. 12 p.

Braham, H. 1978. Migration and feeding of gray whales Eschrictius robustus in Alaska. 24 p. (Unpubl. MS.)

Braham, H.W., R.D. Everitt, B.D. Krogman, D.J. Rugh and D.E. Withrow. 1977. Marine Mammals of the Bering Sea: A preliminary report on distribution and abundance, 1975-1976. NWAFC Proc. Rep., 90 p. U.S. Dep. Commer, NOAA,

Bureau of Land Management. (Undated). Draft environmental impact statement - proposed five year OCS Oil and Gas lease schedule, March 1980-February 1985. Bureau of Land Management, Washington, D.C.

Fager, E.W. 1964. Marine sediments: Effects of a tube-building polychaete. Science 143:356-359.

Gray, J.S. 1977. The stability of benthic ecosystems. Hegolander Meersunters. 32:427-444.

Holling, C.S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4:1-23.

Howell, A.B. and L. M. Huey. 1930. Food of the gray and other whales. J. Mammal. 11:321-322.

Kanneworff, E. 1965. Life cycle, food and growth of the amphipod Ampelisca macrocephala (Liljeborg) from the Øresund. Ophelia 2 (2):305-318.

Larsen, M.C., H. Nelson and D.R. Thor. 1979. Geological implications and potential hazards of scour depressions on Bering Shelf, Alaska. Environ. Geol. 3:39-47.

McCall, P.L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35:221-265.

Makarov, V.V. 1937. Materialy po kolichestvennomu uchetu donnoy fauny severnoy chasti Beringova Morya i Chukotskogo Morya (Data on quantitative calculations of the benthic fauna in the northern part of the Bering Sea and of the Chukchi Sea). Issled. Morey SSSR, Vol. 1, 1941.

Marquette, W.M. and H. Braham. 1980. The take and distribution of gray whales in northern Alaskan waters. Rep. Int. Whaling Comm. SC/32/PS12 15 p.

Oliver, J.S. and P.N. Slattery. 1976. Effects of dredging and disposal of some benthos at Monterey Bay, Calif. U.S. Army Corps of Engineers, Tech Pap. 76-15. 83 p. Avail. Natl. Tech. Inf. Serv., Springfield, Va.

Pearson, T.H. and R. Rosenberg. 1978. Macrobenthic sucession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16:229-311.

Pike, G.C. 1962. Migration and feeding of the gray whale (Eschrictius gibbosus) J. Fish. Res. Bd. Canada 19:815-838.

Ray, G.C. and W. E. Schevill. 1974. Feeding of captive gray whale, Eschrichtius robustus. Mar. Fish. Rev. 36(4):31-38.

Rice, D.W. and A.A. Wolman. 1971. The life history and ecology of the gray whale (Eschrictius robustus). Sp. Publ. 3. The Amer. Soc. Mammal. 142 p.

Scammon, C.M. 1874. The Marine Mammals of the Northwestern Coast of North America. John H. Carmany and Sons, San Francisco. Reprinted by Dover Publications, New York, 1968. 319 p.

Stoker, S.W. 1978. Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi Seas. PhD. Thesis, Univ. of Alaska, 259 p.

Sund, P.N. 1975. Evidence of feeding during migration and of an early birth of the California gray whale (Eschrichtius robustus). J. Mammal. 56(1):265-266.

Sutherland, J.P. 1974. Multiple stable points in natural communities. Amer. Natur. 108:859-873.

Tomilin, A.G. 1957. Zveri SSSR i prilezhaschikh stran-kitoobraznye (Mammals of the U.S.S.R. and adjacent countries - cetacea). Izd. Akad. Nauk SSSR, Moskva. (Transl. by Israel Prog. Sci. Transl. 1967, 717 p.)

VanBlaricom, G.R. 1978. Disturbance, predation and resource allocation in a high-energy sublittoral sand bottom ecosystem: experimental analyses of critical structuring processes for the infaunal community. PhD. Thesis, Univ. of Calif., San Diego. 328 p.

Votrogov, L.M. and L.S. Bogoslovskaya. 1979. Gray whale off the Chukotsk peninsula. Paper presented at the Int. Whaling Comm. Meeting, Cambridge, England. 22 June-3July 1979.

Walker, L.M. 1949. Nursery of the gray whales. Nat. Hist. 58(6):248-256.

Wellington, G.M. and S. Anderson. 1978. Surface feeding by a juvenile gray whale, Eschrichtius robustus. Fish. Bull. 76:290-293.

Wilke, F. and C.H. Fiscus. 1961. Gray whale observations. J. Mammal. 42:108-109

Zenkovich, B.A. 1934. Materialy k pozhaniyu kitoobraznykh dal'nevostochnykh morei (Seryi Kaliforniiski kit - *Rhachianectes glaucus* Cope) (Research data on Cetaceans of far eastern seas [the California gray whale - *Rhachianectes glaucus* Cope]). Vestnik Akad. Nauk SSSR, Dal'nevostochnyi Fil., 10:9-25.

Zimushko, V.V. and M.V. Ivashin. 1979. Some results of U.S.S.R. investigations and whaling of gray whales. (*Eschrichtius robustus*, Lilljeborg, 1961). Rep. Int. Whal. Comm. 31. Doc. 19.

Zimushko, V.V. and S.K. Lenskaya. 1970. O pitanii serogo kita (*Eschrichtius gibbosus* Erx.) na mestakh nagula (Feeding of the gray whale [*Eschrichtius gibbosus* Erx.] at foraging grounds). Ekologiya Akad. Nauk SSSR 1(3):26-35.

FEEDING ECOLOGY OF GRAY WHALES
(Eschrichtius robustus) IN THE CHIRIKOF BASIN,
SUMMER 1982

Edited by

Denis H. Thomson

LGL Alaska Research Associates, Inc.

Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 626

August 1984

TABLE OF CONTENTS

PROJECT RATIONALE, DESIGN, AND SUMMARY

PROJECT RATIONALE, DESIGN, AND SUMMARY

by

Denis H. Thomson

LGL, Ltd., Environmental Research Associates

1984

BACKGROUND

The Chirikof Basin is generally delineated by the Seward Peninsula and Norton Sound in the east, the Chukotka Peninsula and a shallow sill in the west, St. Lawrence Island and a sill in the south, and the Bering Strait sill in the north. Water depths in the central basin range from about 30 to 50 m. Sediments are silty sand over much of the basin, with gravely sand and sandy gravel predominating in the area off northwestern St. Lawrence Island (Sharma 1974).

The marine environment of much of the Chirikof Basin is classed as Pacific Subarctic (Dunbar 1968). Bottom temperatures are near 0°C (Takenouti and Ohtani 1974). Salinity is reduced through the influence of large rivers that empty into the Bering Sea (Stoker 1978). The general flow of water in the Chirikof Basin is northward to the Bering Strait (Takenouti and Ohtani 1974).

Large numbers of marine mammals inhabit the northern Bering Sea (see Braham et al. 1977). Some, like the bearded and ringed seal, are year-round residents, whereas others (bowhead whale, white whale) use it as wintering grounds. The gray whale (Eschrichtius robustus) frequents the northern Bering Sea in summer.

Gray whales calve and mate primarily in the lagoons of Baja California. Most have begun their northward migration along the North American west coast by early March (Rice et al. 1981), and they summer mainly in the northern Bering and southern Chukchi seas (Braham et al. 1977). One of the main areas of concentration in summer is the Chirikof Basin (Votrogov and Bogoslovskaya 1980; Zimushko and Ivashin 1980). Gray whales start to arrive in the St. Lawrence Island area in May (Pike 1962), and some remain there until October (Pike 1962, Votrogov and Bogoslovskaya 1980). Migration out of the Bering Sea summering areas is completed by mid December (Rugh and Braham 1979).

During migrations and in their summering range, gray whales are generally found in coastal areas or in shallow offshore areas (Pike 1962; Votrogov and Bogoslovskaya 1980; Zimushko and Ivashin 1980). In the summering areas, food consists almost entirely of the benthic amphipods Pontoporeia affinis, P. femorata, Anonyx nugax and particularly ampeliscids, especially Ampelisca macrocephala (Pike 1962; Zimushko and Ivashin 1980; Bogoslovskaya et al. 1981).

The present population of gray whales is approximately 17,600 (Reilly et al. 1983). It appears that most of the population utilizes the Bering Sea area at least as a migration route (Rugh and Braham 1979). However, it was not known what proportion of the animals summer in the area between St. Lawrence Island and the Bering Strait, or how many utilize the Chirikof Basin. Considerable numbers of gray whales occur along the Soviet coasts of the Bering and Chukchi seas (Zimushko and Ivashin 1980), and some move northeast along the Alaskan side of the Chukchi Sea. Many of these animals must move through the Chirikof Basin at least once or twice during the open-water season.

APPROACH USED IN THE STUDY

The present stock of gray whales is believed to be at or near its historic pre-exploitation level (Reilly et al. 1980). Reilly et al. (1983) have calculated that the population of gray whales showed a net increase of 2.5% per annum between 1967 and 1980. If the Russian catch is included, total net production was 3.8% (Reilly et al. 1983). Under these conditions natural factors may eventually act to regulate gray whale populations. One potentially important factor is the carrying capacity of the summer habitat. The general objective of this study was to determine the 'carrying capacity' of the Chirikof Basin for gray whales, in order to evaluate the importance of this area to gray whales and to estimate the effect on gray whales of any serious adverse impact on this habitat.

In order to address these objectives, information was obtained on (1) the numbers and distribution of gray whales utilizing the Chirikof Basin, (2) food consumption by gray whales in summer, (3) biomass and distribution of prey species, and (4) productivity of prey species.

The study encompassed four components:

1. Numbers and distribution of whales utilizing the Chirikof Basin were estimated based on the literature, and upon ship surveys and aerial surveys conducted during this project.
2. Food consumption by gray whales was estimated by two independent methods: a theoretical estimation based on energetic requirements, and an estimate based on direct observations of feeding behavior and observations of pits and furrows made by feeding gray whales.
3. Biomass and distribution of gray whale prey species in the Chirikof Basin were estimated through examination of samples collected by surface- and diver-operated gear, and video and still photography.
4. The productivity of the infaunal prey of the gray whale was estimated using commonly accepted methods (e.g., Wildish and Peer 1981). This required year-round sampling at a location chosen at the beginning of the field study.

Total food consumption by gray whales in the Chirikof Basin was estimated from our knowledge of the frequency of feeding dives, the amount of food removed per dive, and our estimate of the number of whales in the area. Food availability was determined by applying productivity to biomass ratios of prey species to the biomass of prey species in the area used by gray whales as foraging grounds.

STUDY DESIGN

Distribution and abundance of gray whales in the Chirikof Basin during the summer of 1982 were estimated from results of aerial surveys supplemented with information obtained from shipboard transect counts. Aerial surveys were flown along 10 transect lines across the Chirikof Basin. Additional lines to sample distribution of gray whales in coastal waters were also flown. Surveys were flown in mid July and early September.

Shipboard work was conducted from 16 stations in the central Chirikof Basin and 11 stations near St. Lawrence Island. An area off Southeast Cape, St. Lawrence Island, was studied intensively. At each station, we collected data needed to determine the extent of feeding by gray whales, kinds of potential prey organisms present, and nature of the substrate. This information, coupled with data on whale distribution as determined by aerial and shipboard surveys, enabled foraging grounds to be identified and characterized.

At each station a 500 kHz side-scan sonar was towed to detect the presence, number and outlines of feeding features made by foraging gray whales. These data were subsequently coded and/or digitized. The digitized records were corrected for ship speed and height of towfish. These data were used to produce corrected plots of the outlines of features, plus data on size of features and amount of sea floor covered by the features. The coded records were used to determine the density of feeding features in various parts of the study area.

Five Van Veen grab samples were taken at each station. Abundance, biomass and species composition of animals were recorded for each sample. Subsamples were analyzed for grain size, caloric content, and carbon and nitrogen content of the substrate. A video camera was used to typify the sea floor at each station and to provide data on homogeneity of bottom types in the vicinity of grab sampling locations.

Information about numbers of gray whales near sampling stations was obtained by 'station scans' while the ship was on station and transect counts while it was en route between stations.

Off Southeast Cape, St. Lawrence Island, divers investigated features in areas that had been marked by a boat towing the side-scan sonar, or marked by observers within a group of feeding whales. Airlift samples were taken inside and outside features made by feeding whales to determine the amount of food that had been removed. The size and shape of the features were measured and photographs were taken. A station for the estimation of amphipod productivity was established and sampled in August, September, January, March and May.

At each station where there were whales, and in the intensively studied nearshore area, we obtained observations and video recordings of the behavior of the whales. Observers recorded the breathing rate, durations of surfacings and dives, distance traveled, and whether or not dives were accompanied by evidence of feeding such as the presence of mud plumes and/or seabirds. These observations were made from small boats and from elevated positions on the ships and shore.

SUMMARY

Distribution, Abundance and Productivity of Amphipods

The areal extent of amphipod dominated benthic communities was as described by Stoker (1978). High biomass of amphipods was found in the central Chirikof Basin and off the south and west coasts and Southeast Cape, St. Lawrence Island. The ampeliscids Ampelisca macrocephala, A. eschrichti and Byblis gaimardi were the most abundant amphipods in three of four of the above areas. Photis fischmanni was dominant in areas off Southeast Cape.

Mean grain size and its square were significant predictors of the density of all three ampeliscid species in multiple regression analyses. The equations predicted maximum density of all three species at a mean grain size of between 2.9 and 3.1 Φ. Both Byblis gaimardi and Amplisca macrocephala were more abundant in sediments with a high caloric content. Niche separation between the three ampeliscid species with the same apparent grain size preference may be as follows. Ampelisca macrocephala was more abundant in poorly sorted substrates while A. eschrichti was more abundant in well sorted substrates. All three ampeliscid species ingested sediment, but Byblis gaimardi appeared to be the only species that ingested diatoms. Perhaps because of this preference for algal material it was the only one of the three species that was more abundant in shallow water than in deep water. Ampelisca eschrichti was most abundant in sediments with a high carbon content and low carbon/nitrogen ratio. The other two species exhibited no such relationship.

Photis fischmanni was the dominant benthic animal on the shallow shelf off Southeast Cape, St. Lawrence Island, where mean density was 95,000 indiv./m^2. Overall, its density was highest in shallow water in well sorted substrates with a high caloric content and a low carbon to nitrogen ratio.

Detailed analyses of seven other common species of amphipod also showed niche separation on the basis of depth, substrate, organic composition of the sediment and food habits.

Sampling was carried out off Southeast Cape, St. Lawrence Island, in July, September, January, March and May to determine productivity of Ampelisca macrocephala and Photis fischmanni, the two dominant species.

The life cycle of Ampelisca macrocephala appears complicated because individuals require two and a half years to reach maturity and young are released around January and around July. Young released in June-July at a length of 3 mm reach 5 mm in length by September, 10 mm by the following March and 11 mm one year later. The following July (two years after release) they would be about 18 mm in length, reach maturity that fall and release young in winter. The productivity to biomass ratio of both the January and July cohorts over one year was about 1.8.

Photis fischmanni also appears to release young in summer and winter, but this small amphipod (7 mm maximum length) appears to require only six months to reach maturity. Annual productivity to biomass ratio was 3.7.

The growth rates of these two species were comparable to those recorded for other arctic and northern amphipod species.

There appeared to be no difference in the length/weight relationship between specimens of Ampelisca macrocephala taken in July and January; however, specimens taken in January had a lower caloric content and higher percentage of ash than those taken in July.

Distribution and Abundance of Gray Whales

Aerial surveys in July and September (Miller, this report) showed that gray whales were concentrated in a broad band extending (roughly) from Cape Prince of Wales on the Seward Peninsula south to Northeast Cape on St. Lawrence Island. Few whales were observed within the American Chirikof Basin to the east or west of this band. Gray whales were also numerous along the east and west coasts of St. Lawrence Island. During the two surveys, 46% of whales sighted within 500 m of the aircraft's flight path were accompanied by feeding plumes.

The Fourier Series line transect method was used to estimate raw densities of gray whales. The resulting estimates were 0.0115 whales/km^2 in July and 0.0045 whales/km^2 in September. These raw estimates were then corrected for detectability of whales which is a function of the durations of surfacings and dives, and of the period of time during which each whale is potentially detectable from the passing aircraft. Separate correction factors were derived from behavioral data collected in July and September. Application of these correction factors to the raw density estimates for the 46,800 km^2 under consideration yielded abundance estimates of 1929 whales in July and 601 whales in September.

The distribution of whales observed during shipboard transects and scans was similar to distributions observed during aerial surveys. In addition, approximately 100 whales were observed across the international boundary in the west-central part of the Chirikof Basin and 35 whales were observed off the south coast of St. Lawrence Island. These two areas were not sampled by the aerial surveys.

Feeding Behavior

Blow intervals, number of blows per surfacing, durations of surfacings and durations of dives were recorded 3503, 1050, 1062 and 905 times, respectively (Würsig et al., this report). In July, most of the whales observed were solitary, while in September, the incidence of whales in social groups was higher and increased throughout the month. In July and September, whales spent an average of 20.8% and 23.2% of their time at the surface, respectively. Average blow rates were 0.997/min in July and 1.122/min in September.

Whale behavior was categorized as feeding, possibly feeding and not feeding. Blow rate did not vary with feeding category but was higher in September (1.186 and 1.288 blows/min for non-feeding and feeding whales, respectively) than in July (0.976 and 0.974 blows/min). In both months, number of blows per surfacing, durations of surfacings and durations of dives were greater for feeding than for non-feeding whales. Blow intervals and number of blows per surfacing were greater in September than in July. In

July, the feeding dive cycle (including the surface interval) lasted 4.61 min and the non-feeding dive cycle 2.92 min. In September, the feeding dive cycle lasted 4.88 min and the non-feeding dive cycle 2.74 min. In July, gray whales were estimated to spend 79% of their time feeding, making about 198 feeding dives per day. In September, whales spent about 69% of their time feeding, making about 164 feeding dives per day. Observations of behavior indicate that the whales spent more time socializing and traveling and less time feeding in September than in July.

While feeding, whales traveled a mean distance of 69 m during surfacings in July and 33 m in September. During dives, they traveled net horizontal distances of 100 m and 93 m below the surface in July and September, respectively. Speed of movement while feeding was about 1.7 km/h underwater and 3.4 km/h at the surface for an average of about 2 km/h.

In July, dive duration was similar for all depths where whales were feeding; however, duration of surfacing, number of blows per surfacing, and the blow rate all increased with increasing depth.

Feeding Ecology

In the Chirikof Basin and near St. Lawrence Island, gray whales feed in two different ways (Thomson and Martin, this report). Both methods are described in the literature (Ray and Schevill 1974; Nerini in press) and involve suction of the bottom while the whale is on its side. (1) **Furrows** are made while the whale is in motion. Side-scan sonar records showed that furrows extended for a mean distance of 46 m. Furrows observed by divers were 42.6 ± s.d. 34.1 cm wide, 1 to 2 cm deep, and were usually discontinuous. Gaps between furrows were 25 to 50 cm long and furrowed portions were 4 ± 4 m long. The mean length of furrows recorded on side-scan sonar, exclusive of gaps, was 41 ± 10 m and the mean furrowed area was 18 ± 5 m^2. (2) **Pits** are apparently made while the whale is nearly stationary. Individual suction 'bites' averaged 1.1 m^2 in area and were sometimes coalesced into large shallow pits. The mean area of pits, including the component 'bites', was 13 ± 3 m^2. Pits measured by divers were approximately 10 cm in depth.

In most areas there appeared to be a mixture of large and small pits and furrows. The side-scan sonar records indicated that the area around St. Lawrence Island and the central part of the Chirikof Basin were used extensively by feeding whales. The areas showing a high density of whale feeding features on the bottom had the following characteristics:

1. A high biomass of amphipods on the bottom.
2. A mean grain size of 3.1Φ (fine sand).
3. Sediment with very little gravel.
4. High densities of whales, as observed from the ship and during aerial surveys.
5. Presence of the ampeliscid amphipod community described by Stoker (1978).

Divers investigated five of the gray whales feeding features to examine the substrate communities. Animals other than amphipods appeared not to have been taken by the whales, most likely because they are deeper in the substrate, and the degree of recolonization, even in an apparently fresh feature, was considerable. Scavenging isopods, polychaetes and perhaps lyssianasid amphipods may move into denuded areas to take advantage of damaged animals. Amphipods appeared quick to respond to newly available substrate. Disruption of the 'mat', consisting mainly of animal tubes that give the surface layer of the bottom its cohesive nature, is not total and results in minimal changes to the grain size characteristics and organic makeup of sediments in feeding areas.

Analysis of the literature and aerial survey results indicates that annual utilization of the Chirikof Basin by whales migrating to and from the Siberian coast and Chukchi Sea may be about 100,000 whale-days. Utilization by the summer resident population may be about 265,000 whale-days.

Gray whale consumption was estimated using a mean of 198 feeding dives per day in July and 164 dives per day in September (Wursig et al., this report), a mean area cleared of 15.5 m^2 per dive, an average amphipod biomass in that portion of the Chirikof Basin used by feeding whales of 133 f/m^2, and a 95% baleen retention efficientcy for amphipods (calculated using data from

from plankton tows taken through mud plumes). The average amphipod consumption per whale based on these parameters is 321 kg/day. However, it would appear that gray whales select areas of high amphipod density in which to feed. If gray whales were to selectively feed in areas containing an amphipod biomass equivalent to that in the 25% of benthic samples with the highest biomass they would consume an average of 678 kg/day.

Energetic requirements for a male gray whale weighing 23,000 kg, 12.5 m in length, and spending 150 days on its northern feeding range, was estimated using Sumich's (1983) respiration method. Assuming that such a whale fed enough during migration to account for energy utilized during migration, then it would have to consume about 800 kg/day in summer in order to store sufficient energy for a 62-day period of fasting off Baja in winter. However, this estimate is high when compared to Lockyer's (1981) energetic computations for large whales. Using Lockyer's assumptions, the feeding rate would be 445 kg/day.

Based on analysis of speed of movement over various parts of the migration route and evidence of feeding while migrating, it would appear that gray whales may feed considerably during approximately half of their migration but not during the remainder of the migration. If energy intake balances energy expenditure during half of the migration and if the remainder of the energy needed for migration and winter is accumulated in summer, then the male gray whale would need to consume about 604 kg/day while in the Chirikof Basin (using Lockyer's (1981) assumptions). This value is higher than that derived through analysis of feeding behavior and furrows. However, it appears that gray whales selectively feed in areas with a standing crop of amphipods higher than average. There was a significant positive correlation between amount of feeding, as shown on side-scan sonar, and biomass of amphipods. Using our data on size of feeding structures (e.g., furrows and other indentations) and feeding dive rates, feeding at a rate of 604 kg/day requires the whales to feed in areas with a mean biomass of amphipods of 223 g/m^2. This value represents the mean biomass in the 35% of our samples that contained the highest biomass.

A comparison of (1) productivity and standing crop of the benthos with (2) consumption by gray whales shows that total consumption by gray whales utilizing the Chirikof Basin is roughly 7.5% of the standing crop and 4% of the annual productivity of amphipods in that part of the basin used as feeding grounds. These values are low. However, gray whales must feed in areas with a higher than average standing crop of amphipods. The extent of areas with a sufficient standing crop of amphipods to meet the requirements of gray whales is unknown.

LITERATURE CITED

Bogoslovskaya, L.S., L.M. Votrogov and T.N. Semenova. 1981. Feeding habits of the gray whale off Chukotka. Rep. Int. Whal. Comm. 31:507-510.

Braham, H.W., C.W. Fiscus and D.J. Rugh. 1977. Marine mammals of the Bering and southern Chukchi seas. p. 1-99. In: Envir. Assess. Alaskan Cont. Shelf, Annu. Rep. Prin. Invest., March 1977, Vol. 1. Receptors-Mammals. NOAA/BLM, OCSEAP, Boulder, CO.

Dunbar, M.J. 1968. Ecological development in polar regions. Prentice-Hall, Inc. Englewood Cliffs, N.J.

Lockyer, C. 1981. Estimates of growth and energy budget for the sperm whale, *Physeter catodon*. p. 489-504. In: Mammals in the seas. Vol. 3. General papers and large cetaceans. FAO and UNEP, Rome. 504 p.

Nerini, M. In press. A review of gray whale feeding ecology. In: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The Gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Pike, G.C. 1962. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). J. Fish Res. Board Can. 19:815-838.

Ray, G.C. and W.E. Schevill. 1974. Feeding of a captive gray whale *Eschrichtius robustus*. Mar. Fish. Rev. 36:31-38.

Reilly, S.B., D.W. Rice and A.A. Wolman. 1980. Preliminary population estimate for the California gray whale based upon Monterey shore censuses, 1967/68 to 1978/79. Rep. Int. Whal. Comm. 30:359-368.

Reilly, S.B., D.W. Rice and A.A. Wolman. 1983. Population assessment of the gray whale, *Eschrichtius robustus*, from California shore censuses, 1967-1980. Fish. Bull. 81:267-279.

Rice, D.W., A.A. Wolman and D.E. Withrow. 1981. Gray whales on the winter grounds in Baja California. Rep. Int. Whal. Comm. 31:477-493.

Rugh, D. and H.W. Braham. 1979. California gray (Eschrichtius robustus) fall migration through Unimak Pass, Alaska, 1977: A preliminary report. Rep. Int. Whal. Comm. 29:315-320.

Sharma, G.D. 1974. Contemporary depositional environment of the eastern Bering Sea. Part 1. Contemporary sedimentary regimes of the eastern Bering Sea. p. 517-540. In: D.W. Hood and E.J. Kelly (eds.), Oceanography of the Bering Sea. Univ. of Alaska, Fairbanks.

Stoker, S.W. 1978. Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi seas. Ph.D. thesis, Univ. of Alaska, Fairbanks. 259 p.

Sumich, J.L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, Eschrichtius robustus. Can. J. Zool. 61:647-652.

Takenouti, A.Y. and K. Ohtani. 1974. Currents and water masses in the Bering Sea: a review of Japanese work. p. 39-57. In: D.W. Hood and E.J. Kelly (eds.), Oceanography of the Bering Sea. Univ. Alaska, Fairbanks.

Votrogrov, L.M. and L.S. Bogoslovskaya. 1980. Gray whales off the Chukotka Peninsula. Rep. Int. Whal. Comm. 30:435-437.

Wildish, D.J. and D. Peer. 1981. Methods for estimating secondary production in marine amphipods. Can. J. Fish. Aquat. Sci. 38:1019-1026.

Zimushko, V.V. and M.V. Ivashin. 1980. Some results of Soviet investigations and whaling of gray whales. Rep. Int. Whal. Comm. 30:237-246.

DISTRIBUTION, PRODUCTION, AND ECOLOGY OF GRAY WHALE PREY SPECIES

by

Denis H. Thomson

LGL Ltd., Environmental Research Associates

1983

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Table 11.	Frequency of occurrence of food items found in the guts of 11 species of amphipods collected in the central Chirikof Basin in the summer of 1982. Samples are from areas 1B, 2A, 3B, 4A, 4B, 5A, and 7B.
Table 12.	Frequency of occurrence of food items found in the guts of 8 species of amphipods collected near St. Lawrence Island in the summer of 1982.
Table 13.	Mean biomass (g/m^2) of carbon in sediments and mean biomass according to major feeding mode of benthic animals taken in the Chirikof Basin and areas adjacent to St. Lawrence Island. Conversion of wet weight to carbon was accomplished using data provided by Stoker (1978).
Table 14.	Growth rates of arctic and temperate amphipods. All values in mm.
Table 15.	Computation of productivity estimate for *Ampelisca macrocephala* from Southeast Cape, St. Lawrence Island, by cohort summation of population growth. Biomass is expressed as dry weight.
Table 16.	Computation of productivity estimate for *Photis fischmanni* from Southeast Cape, St. Lawrence Island, by cohort summation of population growth. Biomass is expressed as dry weight.
Table 17.	Summary of habitat preferences and food habits of the 10 dominant amphipod species found in the Chirikof Basin and near St. Lawrence Island.
Table 18.	Percent of total amphipod density contributed by the dominant species at stations with a similar biomass of amphipods in the Chirikof Basin. Percentages are shown only where the indicated species are dominant.
Table 19.	Productivity of benthic amphipod species, the benthos as a whole, and the zooplankton from the temperate Atlantic and Bering Sea.
Table 20.	Mean biomass of amphipod species according to maximum size attained in that part of the Chirikof Basin dominated by amphipods.
Appendix Table 1.	Summary of samples collected and work performed in the Chirikof Basin near St. Lawrence Island in July and September 1982.
Appendix Table 2.	Level of effort and numbers of samples collected and analyzed from the Chirikof Basin and the vicinity of St. Lawrence Island in July and September 1982.

ABSTRACT

The productivity, ecology and distribution of ten amphipod species that form the principal prey of the gray whale were studied in the Chirikof Basin. Near St. Lawrence Island, a station for estimation of secondary productivity of amphipods was sampled by divers in July and September 1982 and with a grab through the ice in January, March and May 1983.

The benthos in most of the Chirikof Basin and all areas sampled near St. Lawrence Island was dominated by amphipods, especially the ampeliscid Ampelisca macrocephala in deep water, and the corophiid Photis fischmanni in shallow water. Ten amphipod species accounted for 95% of the density of all amphipod species collected. Multiple regression analyses on the densities of the species, using as predictor variables water depth, grain size, sorting coefficient, caloric content of the substrate, carbon content of the substrate, and carbon:nitrogen ratio of the substrate showed distinct niche separation in most species, as did analysis of gut contents. Where species showed similar habitat preferences, they were spatially separated.

Young of Ampelisca macrocephala are released in spring and fall at a length of about 3 mm, grow about 6 mm per year, may mature after 2 years, and live 2.5 years. Annual productivity to biomass ratio estimated by cohort summation was 1.8. Young of Photis fischmanni are released in fall and spring at a length of 1.4 mm; some may mature in 6 months, and they live 1 year. Growth is about 5.5 mm over the year. Annual productivity to biomass ratio was 3.7. Annual productivity to biomass ratio for the amphipods of the central Chirikof Basin as a whole was estimated at 1.9.

INTRODUCTION

The infaunal benthic communities of the Bering and Chukchi seas have been described in detail by Stoker (1978, 1981). Benthic samples collected during our study were taken in conjunction with observations of the behavior and distribution of gray whales and with observations of the bottom disruption caused by feeding gray whales. The objectives of the study as a whole were to characterize gray whale feeding areas, to assess food available to the whales, and to estimate the amount of food consumed by the whales.

In the northern part of the Bering Sea, gray whales feed on the upper strata of the benthos, primarily on amphipods (Nerini in press; Thomson and Martin, this report). This chapter discusses the ecology of the common amphipod species that appear to form the major part of the diet of gray whales in the Chirikof Basin and near St. Lawrence Island. Data on amphipod feeding habits and ecology, including relationships to the physical characteristics of their environment, can be used to assess food web relationships and energy flow along trophic pathways leading to gray whales.

As a part of this study, year-round sampling was conducted to determine the secondary productivity of the amphipods. These data were used to assess the total amount of gray whale food production in the area (see Thomson and Martin, this report).

MATERIALS AND METHODS

Studies were conducted in the central Chirikof Basin and off the east, west and south coasts of St. Lawrence Island (Fig. 1). The numbers and locations of samples collected are presented in Appendix Tables 1 and 2.

Sampling was conducted from the NOAA vessels MILLER FREEMAN (11-25 July 1982) and DISCOVERER (12-29 September 1982). Winter sampling was conducted from the ice near Southeast Cape, St. Lawrence Island, on 13 January, 5 March and 15 May 1983.

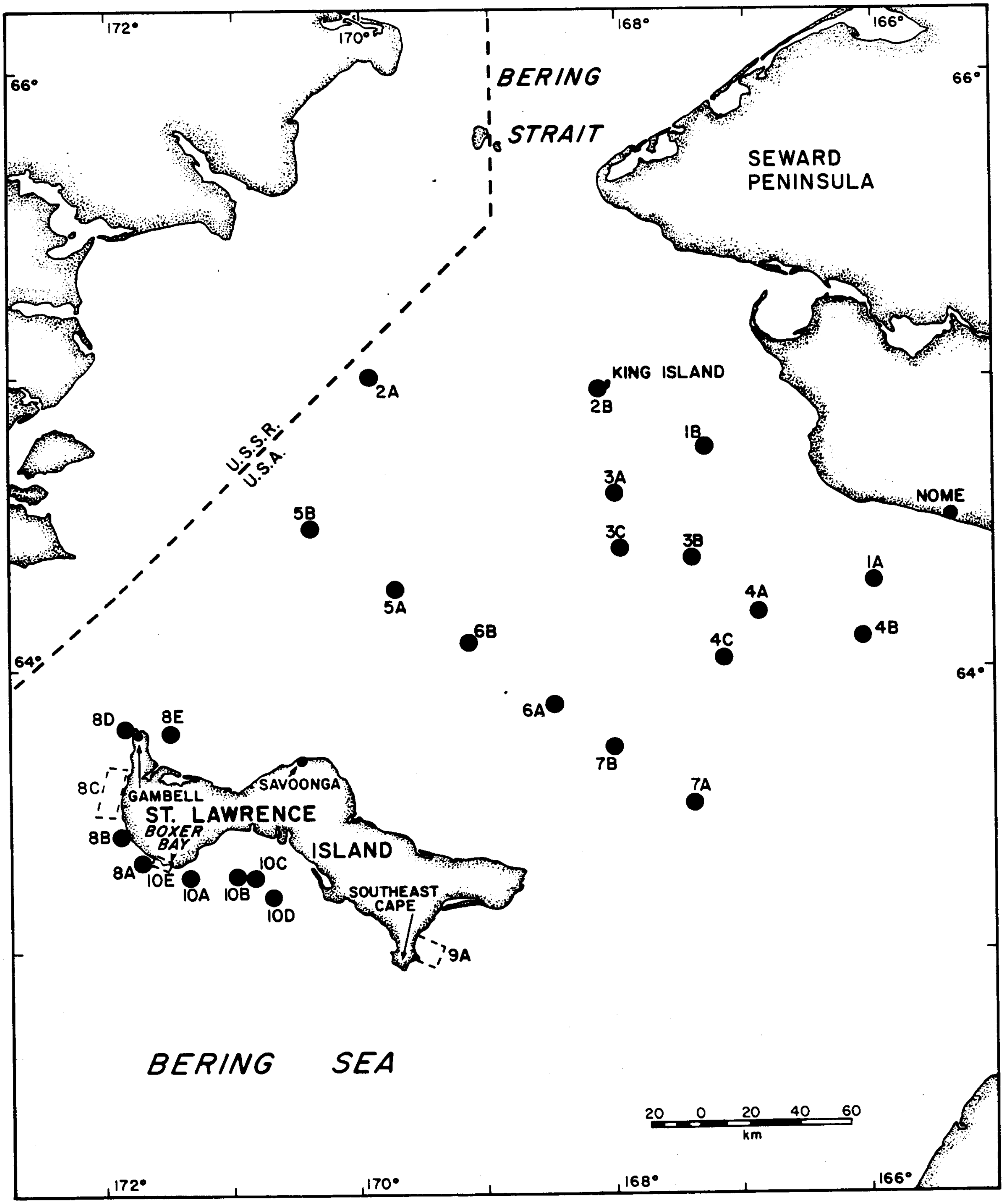


Figure 1. Sampling stations in the Chirikof Basin and near St. Lawrence Island occupied during July and September 1982.

Benthic Sampling

On board ship, benthic samples were taken with a 0.15 m^2 Van Veen grab. The volume of sediment in the grab was measured to the nearest 500 mL. A subsample of sediment was taken for grain size analysis and an additional subsample was frozen for later analysis of caloric content, carbon and nitrogen. A sample of surface detritus was retained and preserved in 10% formalin. On board ship the sample was washed through 5.6 and 1 mm nested sieves with seawater. With the exception of rocks, all material retained on the sieves was preserved in 10% formalin for later analysis in the laboratory.

In winter, samples were taken through the ice with a 0.05 m^2 Ponar grab and preserved whole for later processing in the laboratory.

Diver Sampling

Observations, photographs and samples were obtained by a team of 2 divers. All diving operations were carried out from small boats launched by the NOAA ships. Diving effort was restricted to shallow (<25 m) water in the vicinity of St. Lawrence Island.

Qualitative Sampling Procedure

Observations of the flora, fauna and the physical environment were recorded in waterproof notebooks during the dives and/or during a debriefing session immediately following the dive. Photographs were taken with a Nikonos or Olympus OM1 camera in an Ikelite housing, using color film and strobes.

Quantitative Sampling Procedure

A transect rope connected to an anchor was used to orient divers. Infauna was sampled by means of a self-contained diver-operated airlift. The airlift consisted of a weighted 2 m length of 8 cm diameter PVC pipe fitted at the top with a 1 mm mesh net which retained the sample and could be removed quickly and capped. Air was supplied from two 3000 psi SCUBA tanks fitted with the first stage of a diving regulator that reduced air pressure to 125 psi over ambient. Areas of substrate to be sampled were demarcated by a 0.1 m^2 round aluminum frame that was pushed into the soft substrate as far as possible. The airlift was operated until the upper 10 to 15 cm of substrate within the frame was removed. The net was then removed, capped and replaced. Airlift samples contained little mud and were not sieved further. They were preserved in 10% formalin.

Laboratory Analyses

Invertebrates

The preserved samples were washed on a 0.5 mm sieve. Subsequent analysis depended on the purpose for which the sample was collected and the nature of the sample. All animals were picked from samples that contained little detrital material. When samples contained over 100 g of detrital material, large (>9 mm) conspicuous organisms were picked from the whole sample. A subsample then was taken and all organisms were picked from the subsample.

In a few selected samples (45) all animals were identified to specific level. In remaining samples, all amphipods, bivalves and common conspicuous animals were identified to specific level while remaining animals were identified to familial level. Voucher specimens of each species that was identified were sent to appropriate authorities for verification.

Where required for productivity determinations, amphipods were measured to the nearest millimeter. Measurements were from the end of the telson to the tip of the rostrum on straightened animals.

Preserved animals were weighed wet, in groups, at the lowest taxonomic level to which they were identified; a Mettler electronic balance (accurate to 10 mg) was used.

Dry weights for amphipods used in productivity experiments were determined using a Sartorius substitution balance (0.1 mg) after drying overnight at 80°C. Amphipods for caloric determination were dried to a constant weight at 60°C in a vacuum oven. Triplicate observations were made for samples having enough material. Amphipods were pelletized for combustion and a Phillipson microbomb calorimeter was utilized to obtain calories per dry gram. Ash free dry weights were measured after drying at 450°C.

Feeding Habits of Amphipods

The length of each animal was measured, the gut was dissected out, and the contents mounted on a slide and examined under a compound microscope. In addition, maturity status, sex and presence of eggs or embryos in the brood pouches were noted where evident.

Subsamples of the surface detritus were examined to determine the flora and fauna available as potential food items. Subsamples were drawn with a Pasteur pipette and placed on a slide for examination under a compound microscope.

Sediment Analysis

Grain Size Analysis

The coarse fractions ($<4.0\ \Phi$) were separated by dry sieving and the fines by Day's (1965) hydrometer method.

Bomb Calorimetry

All samples were dried to a constant weight at 60°C in a vacuum oven. Triplicate observations were made for samples having enough material.

Sediments were sieved through a 0.5 mm screen using only the liquid present in the sample. Dry sediments were powdered and benzoic acid added to enhance combustion. Powdered samples, naturally difficult to combust (such as sediments), often are partially ejected from the crucible during combustion. This was a common occurrence with these samples and, to minimize the error caused by this methodological problem, only the closest two values, of three, were averaged to obtain the mean value. We did not attempt to obtain ash free dry weights of sediments because of the occurrence of carbonates in the samples. Even after sieving, sediments may have contained meiofauna or faunal parts.

Carbon and Nitrogen

Samples (approx. 50 g) were placed into beakers and weighed. The beakers were oven-dried at 60°C overnight and reweighed to determine water content (%). The dried samples were then acidified with 5 mL of 7% HCl to destroy carbonates. They were again oven-dried at 60°C for 12 h, powdered, and homogenized.

Approximately 30 mg of sample were used for analysis. The apparatus used for the CHN determinations was a Perkin-Elmer model 240C CHN elemental analyzer. The analytical precision, based on 3 replicate analyses, was better than 0.2%.

Chlorophyll a

Preweighed sediment samples were extracted for 1 h in 10 mL of 90% acetone at 4°C in darkness. Samples were centrifuged at 4000 rpm for 10 min. Then, the acetone solution was pipetted into a glass photometer cell with a 10 cm light path. Extinction of the solution was measured against 90% acetone at 6650, 6450 and 6300 nm in a spectrophotometer. After correction for the blank, the following equation was used to estimate mg Ca per g sediment wet weight (Strickland and Parsons 1972):

$$\text{mg Ca} = 11.6\ (E665) - 1.31\ (E645) - 0.14\ (E630)\ /\ \text{sediment weight g (cell path length)}$$

Observations were in triplicate. Small pieces of shell and animal parts were present in the samples and displaced sediment in samples. Organisms were removed from samples under a microscope, but it was impractical to remove all faunal parts and meiofauna.

Data Processing and Analysis

All data were coded and entered into Hewlett Packard HP9845B or AMDAHL 470 computers and later transfered to an IBM 3033 computer for analysis. Data tabulation was accomplished with programs developed by LGL, and additional analyses were performed using SAS (SAS 1982) and BMDP (Dixon 1981) statistical software.

RESULTS

Benthic Habitats

Mat Community

The shallow (10-15 m) shelf off Southeast Cape, St. Lawrence Island, was covered with a cohesive 'mat' that had a gelatinous texture. Presence of this 'mat' allowed bottom features made by feeding gray whales to be conspicuous and well defined.

Photis fischmanni was the dominant amphipod in samples from the shallow shelf off Southeast Cape, St. Lawrence Island. In this area its mean density was close to 100,000 indiv/m^2 and mean biomass was 125 g/m^2. This small (2-7 mm) amphipod inhabits a rather long soft tube, and it was the presence of these tubes that was the most conspicuous feature of the 'mat' layer in this area. Mean biomass of all tubes (not including sediment or animals) in airlift samples was 1470 ± s.d. 812 g/m^2 (n = 20) in July and 771 ± 395 g/m^2 (n = 20) in September. Sediments taken in 6 surface samples of this 'mat' were all very fine sand (range 3.47 to 4.03Φ) and were all poorly sorted (range 1.23 to 2.14 Φ).

Amphipods accounted for 98% of the total numbers of animals and 65% of biomass in airlift samples that penetrated to a sediment depth of 10 to 15 cm (the thickness of the mat). Cumaceans, isopods and other crustaceans contributed a further 0.5% to total numbers.

Ostracods, foraminifera and nematodes were conspicuous meiofaunal animals in the surficial sediments (Table 1).

Table 1. Total numbers of meiofauna counted in 3 subsamples from each of 5 samples of surficial sediments from the 'mat' layer in shallow water near Southeast Cape, St. Lawrence Island.

Ostracods	13	Foraminifera	18
Harpacticoid copepods	7	Nematodes	20
Crustacean larvae	1		

Large numbers of pennate and centric diatoms were also found in samples taken from the surface of the 'mat'. As a result, the chlorophyll _a_ content of these sediments was high, 11.8 ± s.d. 2.0 mg chl _a_/g sediment wet weight ($n = 5$) in July and 7.1 ± s.d. 2.3 mg/g ($n = 5$) in September.

A 'mat' may also be present in deeper waters of the Chirikof Basin. Density of animal tubes is high (Nelson et al. 1981; Johnson et al. 1983) but not as high as in shallow areas off Southeast Cape. Mean biomass of animal tubes, not including animals or sediment, in samples from that part of the Central Chirikof Basin dominated by amphipods was 344 ± 160 g/m^2 ($n = 25$). These tubes were similar in construction to the ampeliscid amphipod tubes found on Southeast Cape. Tubes were uncommon in areas not dominated by amphipods. Surficial sediments from this area also contained pennate and centric diatoms, nematodes and harpacticoid copepods.

Sediment Characteristics

Surface sediments in the Central Chirikof Basin are fine sand (Nelson 1982; Table 2). In the northeastern part of the basin, surface sediments are Yukon-derived sandy silt. Surface sediments south of the Seward Peninsula are coarser than those found in the central basin (Table 2). Fine sand substrates are also found in the study areas off the west, south and east coasts of St. Lawrence Island (Table 2). The total range of mean grain size

Table 2. Physical and chemical characteristics of sediments of the Chirikof Basin and nearshore areas of St. Lawrence Island in the summer of 1982. All values were measured and calculated on dry sediment.

Location	Mean grain size[1] Φ	Sorting Coefficient Φ	Caloric content cal/g	Organic carbon mg/g	Nitrogen mg/g	C/N ratio
Chirikof Basin						
South of Nome (Stn 1A, 4A, 4B; Fig. 1)	3.9 ± 0.1 (3)[2]	2.2 ± 0.4	266 ± 43 (3)[3]	4.6 ± 1.2	0.48 ± 0.07	9.6 ± 1.1
South of Seward Pen. (Stn 1B, 3B, 3A, 2B)	2.5 ± 0.3 (4)	2.1 ± 0.2	414 ± 349 (4)	2.7 ± 0.8	0.38 ± 0.13	8.5 ± 2.7
Central Basin (Stn 4C, 3C, 2A, 7A, 7B, 6A, 6B, 5A, 5B)	3.3 ± 0.3 (9)	1.8 ± 0.4	395 ± 193 (9)	2.8 ± 0.5	0.39 ± 0.06	7.3 ± 1.2
St. Lawrence Island						
West coast (Stn 8C)	3.2 ± 0.0 (2)	1.4 ± 0.0	444 ± 173 (2)	2.2 (1)	0.32 (1)	6.7 (1)
South coast (Stn 10C, 10D, 10E)	2.8 ± 0.2 (3)	1.4 ± 0.3	193 ± 91 (3)	3.0 ± 0.9	0.42 ± 0.07	6.7 ± 1.0
Southeast Cape - offshore (Stn 9A >20 m)	2.8 ± 0.3 (2)	1.6 ± 0.1	187 ± 182 (2)	4.1 ± 0.0	0.53 ± 0.08	7.8 ± 1.2
Southeast Cape - nearshore (Stn 9A <20 m)	3.7 ± 0.2 (6)	1.7 ± 0.3	382 ± 163 (7)	3.4 ± 2.1	0.40 ± 0.20	8.5 ± 2.2

---

[1] $\Phi = \frac{-\mathrm{Log}_{10}\ \mathrm{mm}}{\mathrm{Log}_{10} 2}$, 2-3 Φ = fine sand, 3-4 Φ = very fine sand, 4-5 Φ = coarse silt.

[2] Sample size for grain analysis.
[3] Sample size for caloric content and carbon and nitrogen determination.

for the sediments of the study area is very small (2.2-4.0 Φ) and is categorized as fine or very fine sand (4 Φ is the cutpoint between sand and silt).

The sorting coefficient indicates the amount of dispersion around the mean grain size. Large values (e.g. 1-4) indicate a heterogeneity of substrates in a sample. All areas show poorly (1-2 Φ) to very poorly sorted (2-4 Φ) substrates. Surface sediments from the nearshore waters of St. Lawrence Island showed less heterogeneity than those of the central basin.

Infaunal Benthos

One hundred and fifty benthic samples were taken in the Chirikof Basin and in nearshore waters of St. Lawrence Island. Standing stock biomass of all infauna was highest off Southeast Cape and the west coast of St. Lawrence Island (Table 3). The lowest infaunal biomass was found in the Chirikof Basin (Table 3). Overall, amphipods were the dominant taxa in terms of both density and biomass (Tables 3 and 4), followed by bivalves and polychaetes.

The benthic infaunal communities of the Bering Sea have been described by Stoker (1978, 1981). He found that a community dominated by ampeliscid amphipods occupied the central and western portions of the Chirikof Basin and the west and east coasts of St. Lawrence Island. The presence of this community is indicated by areas with a high biomass of amphipods and high density of the ampeliscid amphipod *Ampelisca macrocephala* (Figs. 2 and 3a). We found that stations off the south coast of St. Lawrence Island also showed high biomass of amphipods and a high density of *Ampelisca macrocephala*.

A community dominated by a sand dollar and a bivalve characterized the central-eastern portion of the Chirikof Basin (Stoker 1981). Farther east, the area south of Nome was characterized by a community dominated by the cockle *Serripes groenlandicus*, two polychaetes and two ophiuroids. The presence of these two communities is indicated by low biomass of amphipods and low density of *Ampelisca macrocephala* in Figures 2 and 3a. Station 5B (Fig. 1) falls within an area dominated by echinoderms (Stoker 1981) and also shows a low biomass of amphipods.

Table 3. Biomass (g/m^2 wet weight) of major taxa and dominant species in all samples taken in the Chirikof Basin and near St. Lawrence Island in the summer of 1982.

		St. Lawrence Island		Southeast Cape	
Location	Chirikof Basin	South Coast	West Coast	Depth 11-15 m	Depth 22-23 m
Stations[1]	1-7	10	8	9	9
Sample size	75	15	16	34	10
Total	210.8 ± 166.8	284.5 ± 99.5	327.1 ± 286.6	297.8 ± 144.9	353.1 ± 129.8
Amphipoda	69.3 ± 92.5	119.9 ± 48.7	129.6 ± 50.0	194.1 ± 77.8	139.3 ± 52.0
Polychaeta	26.8 ± 31.3	19.5 ± 13.2	51.2 ± 54.0	38.5 ± 56.6	25.4 ± 22.0
Bivalvia	64.4 ± 112.4	93.1 ± 65.1	118.1 ± 265.5	29.4 ± 63.5	142.8 ± 134.6
Isopoda	0	0	0	4.4 ± 7.5	1.9 ± 1.4
Echinodermata	27.1 ± 65.7	0.5 ± 1.9	0	9.0 ± 19.1	7.1 ± 8.8
Ascidiacea	2.8 ± 8.4	26.6 ± 26.2	24.9 ± 54.9	3.6 ± 11.0	14.6 ± 13.8
Ampelisca eschrichti (A)	7.5 ± 14.7	0.5 ± 1.3	0	0.8 ± 2.0	24.4 ± 41.0
Ampelisca macrocephala (A)	42.6 ± 61.4	67.5 ± 34.4	79.2 ± 43.5	10.9 ± 11.7	82.3 ± 29.6
Byblis gaimardi (A)	10.0 ± 22.4	0.7 ± 0.8	17.2 ± 25.7	5.2 ± 5.6	2.9 ± 5.4
Photis fischmanni (A)	0.2 ± 0.4	1.8 ± 3.4	0	124.5 ± 65.5	0.4 ± 0.6
Liocyma flexuosa (B)	1.8 ± 5.5	23.1 ± 46.2	6.8 ± 8.8	3.8 ± 6.8	0.4 ± 1.0
Liocyma viridis (B)	1.1 ± 9.7	6.6 ± 25.6	0.8 ± 3.1	0	14.7 ± 28.2
Macoma calcarea (B)	33.3 ± 69.8	47.4 ± 35.3	37.5 ± 54.6	14.3 ± 59.5	73.4 ± 102.1
Nephtyidae (P)	9.2 ± 21.8	3.3 ± 8.9	12.3 ± 26.1	15.6 ± 24.0	10.2 ± 13.1
Sabellidae (P)	0.7 ± 2.1	0	7.6 ± 13.1	0	0.1 ± 0.2
Travesia sp. (P)	0.0 ± 0.2	0.4 ± 1.7	15.4 ± 40.1	0.2 ± 0.8	0.2 ± 0.6
Dendraster extenuata (E)	16.0 ± 55.0	0	0	0.4 ± 2.2	0
Pelonaia corrugata (T)	2.6 ± 8.3	25.7 ± 26.2	6.9 ± 16.4	3.6 ± 11.0	14.4 ± 13.8

A = amphipod, B = bivalve, P = polychaete, E = echinoderm, T = tunicate

[1] See Figure 1 for locations.

Table 4. Mean density (no./m^2) of major taxa and dominant amphipod species in all samples taken in the Chirikof Basin and near St. Lawrence Island in the summer of 1982.

		St. Lawrence Island		Southeast Cape	
Location Sample size	Chirikof Basin 75	South Coast 15	West Coast 16	Depth 11-15 m 34	Depth 22-23 m 10
Total	6204 ± 6195	12918 ± 8515	10419 ± 5306	110262 ± 56084	9909 ± 4444
Amphipoda	5086 ± 5907	11056 ± 7790	9088 ± 4951	107873 ± 57192	8808 ± 4106
Polychaeta	651 ± 638	766 ± 787	740 ± 993	1256 ± 1943	704 ± 594
Bivalvia	150 ± 249	677 ± 522	251 ± 300	327 ± 490	162 ± 195
Cumacea	117 ± 248	140 ± 206	27 ± 48	406 ± 569	96 ± 75
Echinodermata	67 ± 136	1 ± 5	0	10 ± 21	16 ± 18
Ascidiacea	18 ± 63	46 ± 55	280 ± 740	6 ± 13	13 ± 17
Ampelisca eschrichti	74 ± 551	4 ± 8	0	31 ± 100	246 ± 286
Ampelisca macrocephala	2061 ± 3182	2582 ± 2391	2841 ± 2163	1080 ± 1278	5030 ± 2478
Byblis gaimardi	402 ± 865	74 ± 120	1573 ± 2652	952 ± 927	55 ± 82
Photis fischmanni	74 ± 143	1032 ± 2139	17 ± 36	95572 ± 54565	139 ± 164
Protomedia fasciata	607 ± 1795	191 ± 448	133 ± 264	50 ± 148	124 ± 148
Protomedia grandimana	872 ± 3446	5367 ± 5331	872 ± 1090	2800 ± 2997	1041 ± 1319
Grandiphoxus acanthinus	91 ± 213	205 ± 203	251 ± 368	153 ± 220	71 ± 144
Harpinia gurjanovae	113 ± 187	40 ± 79	70 ± 135	1439 ± 1130	187 ± 152
Pontoporeia femorata	65 ± 254	233 ± 377	34 ± 79	66 ± 134	500 ± 651
Orchomene lepidula	119 ± 269	198 ± 374	502 ± 659	2697 ± 1759	117 ± 180

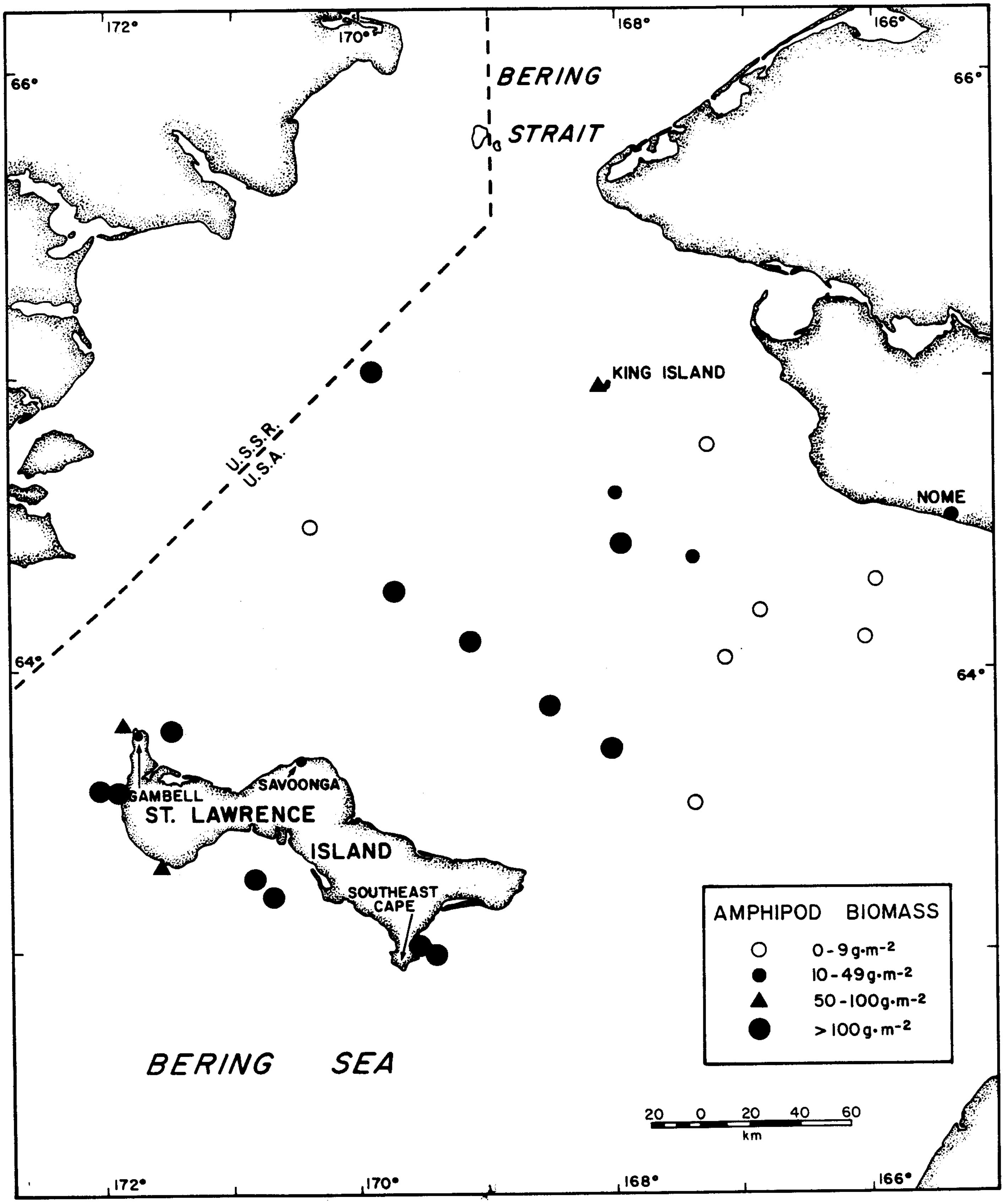


Figure 2. Amphipod biomass (wet weight) in the Chirikof Basin and near St. Lawrence Island in July and September 1982.

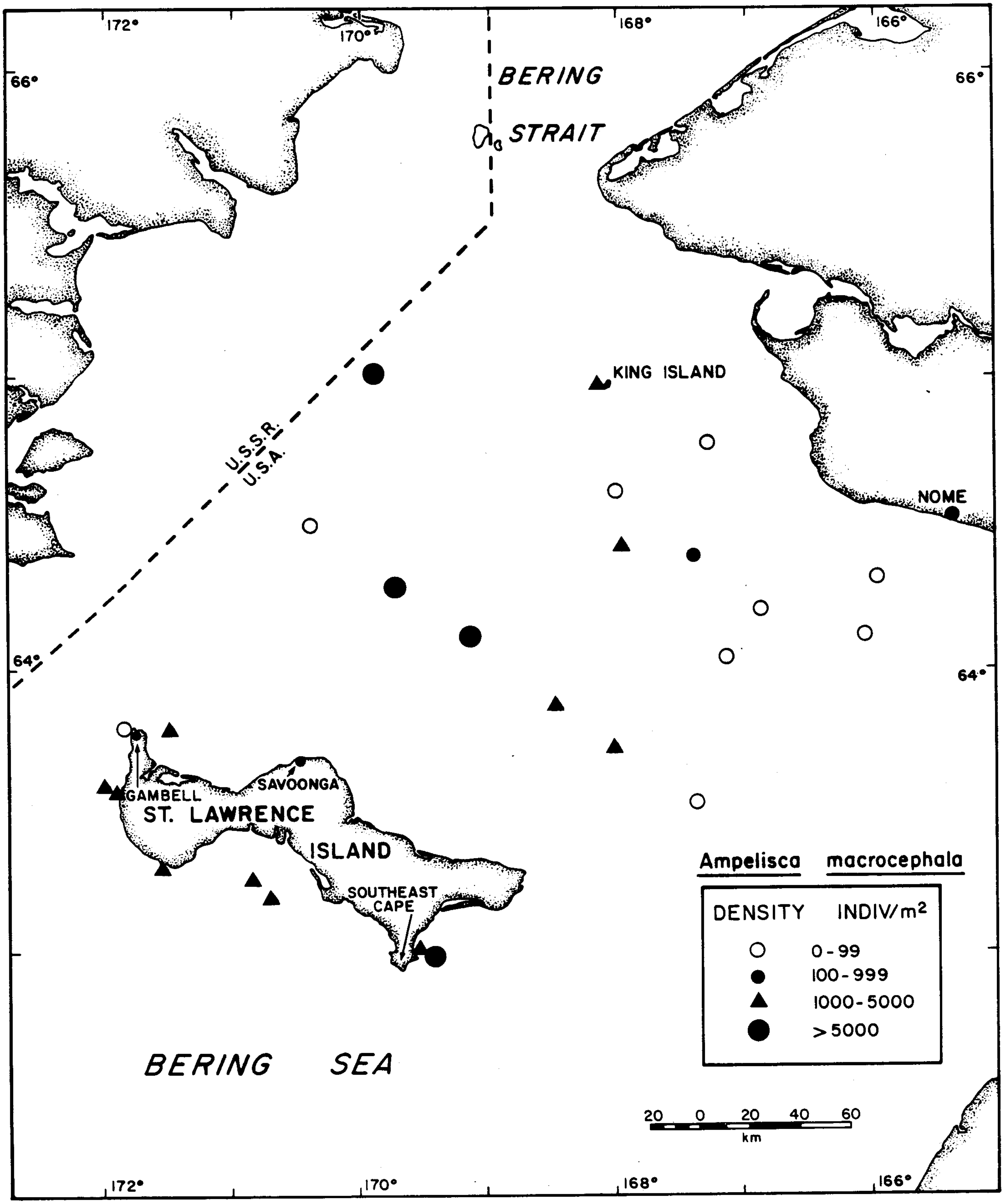


Figure 3a. Density of the common amphipod species collected in the Chiriko Basin and near St. Lawrence Island in July and September 1982.

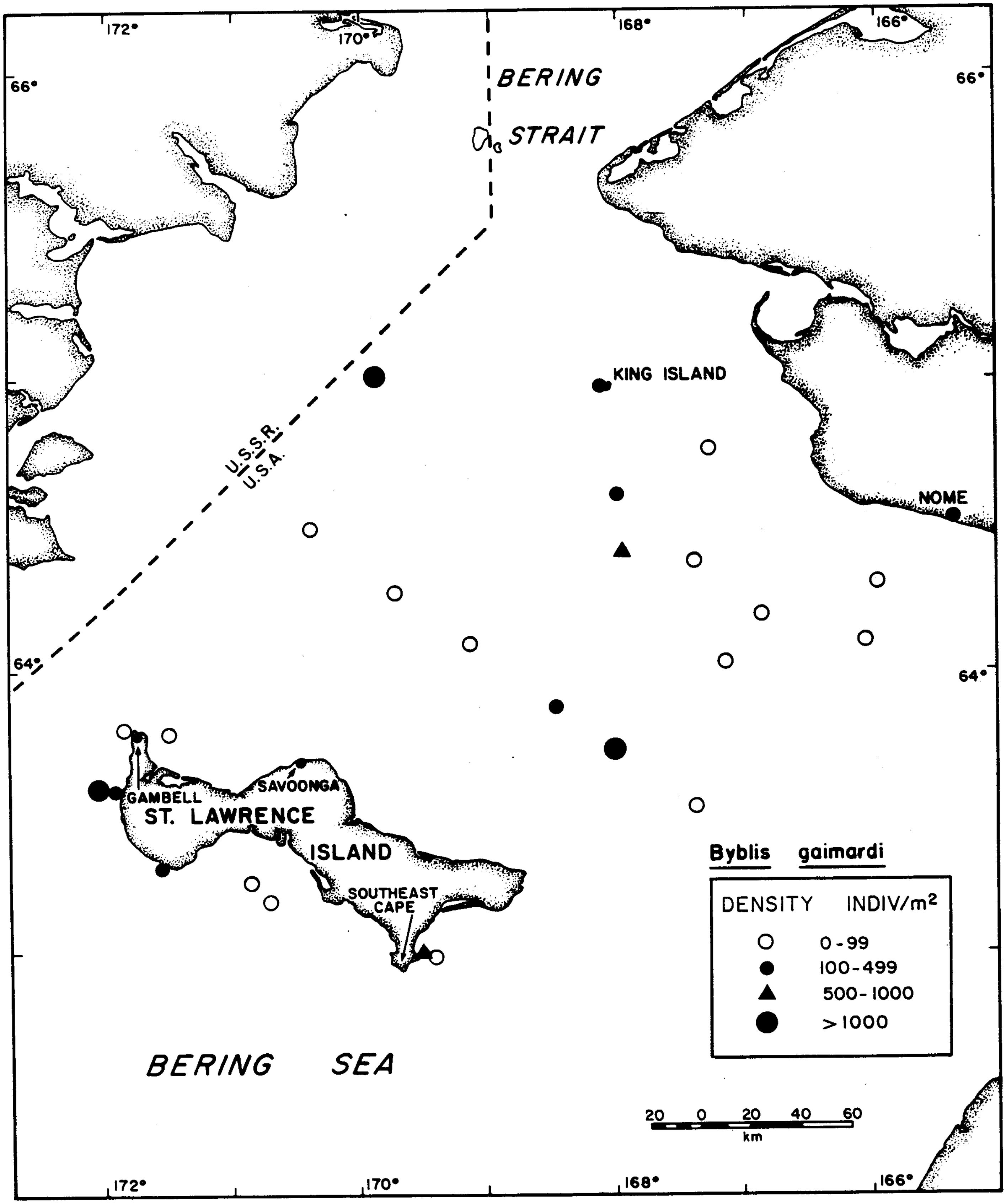

172°
170°
168°
166°
66°
64°
BERING
STRAIT
U.S.S.R.
U.S.A.
KING ISLAND
NOME
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST
CAPE
BERING SEA
Byblis gaimardi
DENSITY INDIV/m²
○ 0-99
● 100-499
▲ 500-1000
● >1000
20 0 20 40 60
km

Figure 3b.

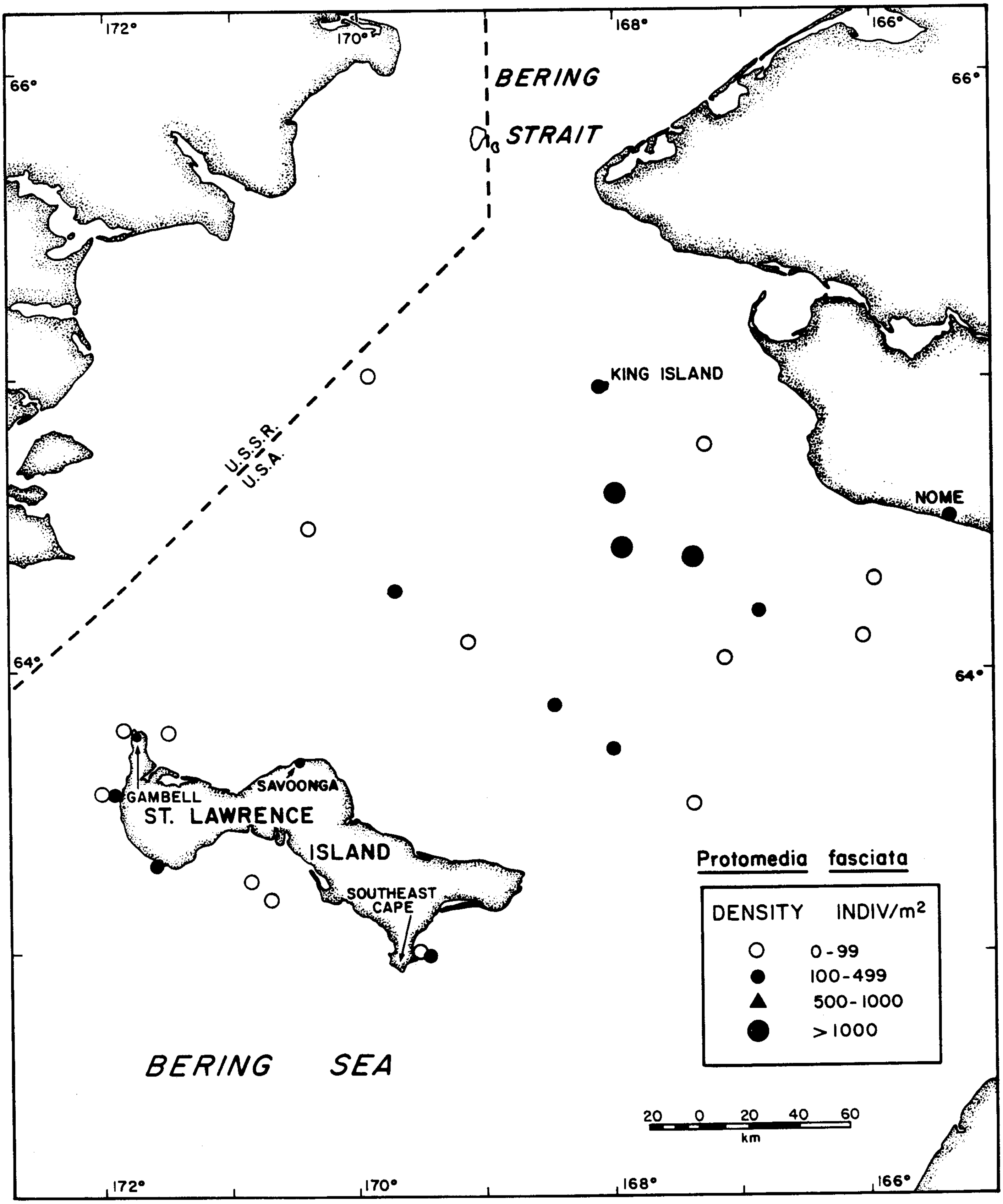

172°
170°
168°
166°
66°
64°
BERING
STRAIT
U.S.S.R.
U.S.A.
KING ISLAND
NOME
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST CAPE
BERING SEA
Protomedia fasciata
DENSITY INDIV/m²
○ 0-99
● 100-499
▲ 500-1000
● >1000
20 0 20 40 60
km

Figure 3c.

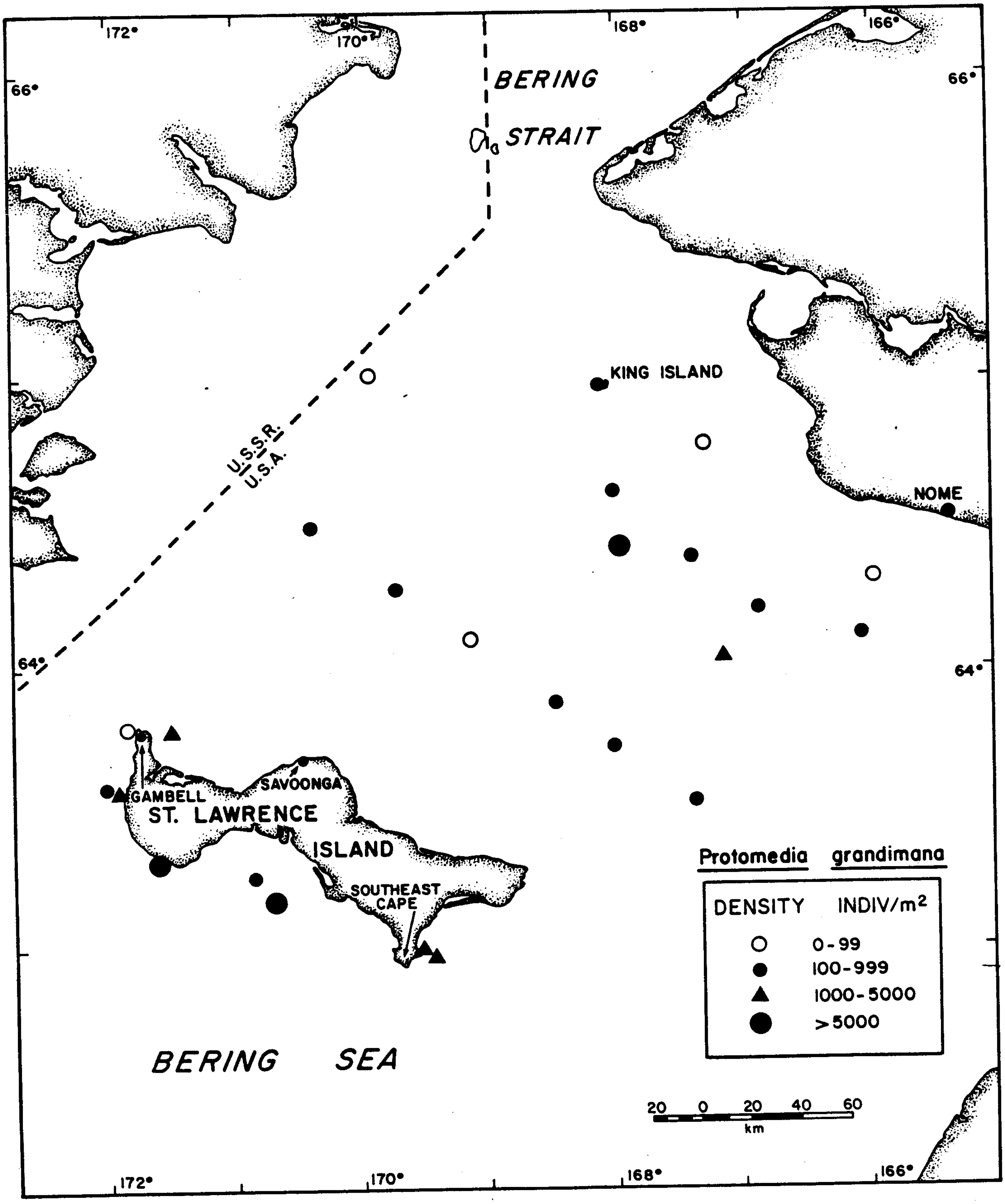

172°
170°
168°
166°
66°
64°
BERING
STRAIT
U.S.S.R.
U.S.A.
KING ISLAND
NOME
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST CAPE
BERING SEA
Protomedia grandimana
DENSITY INDIV/m2
○ 0-99
● 100-999
▲ 1000-5000
● >5000
20 0 20 40 60
km

Figure 3d.

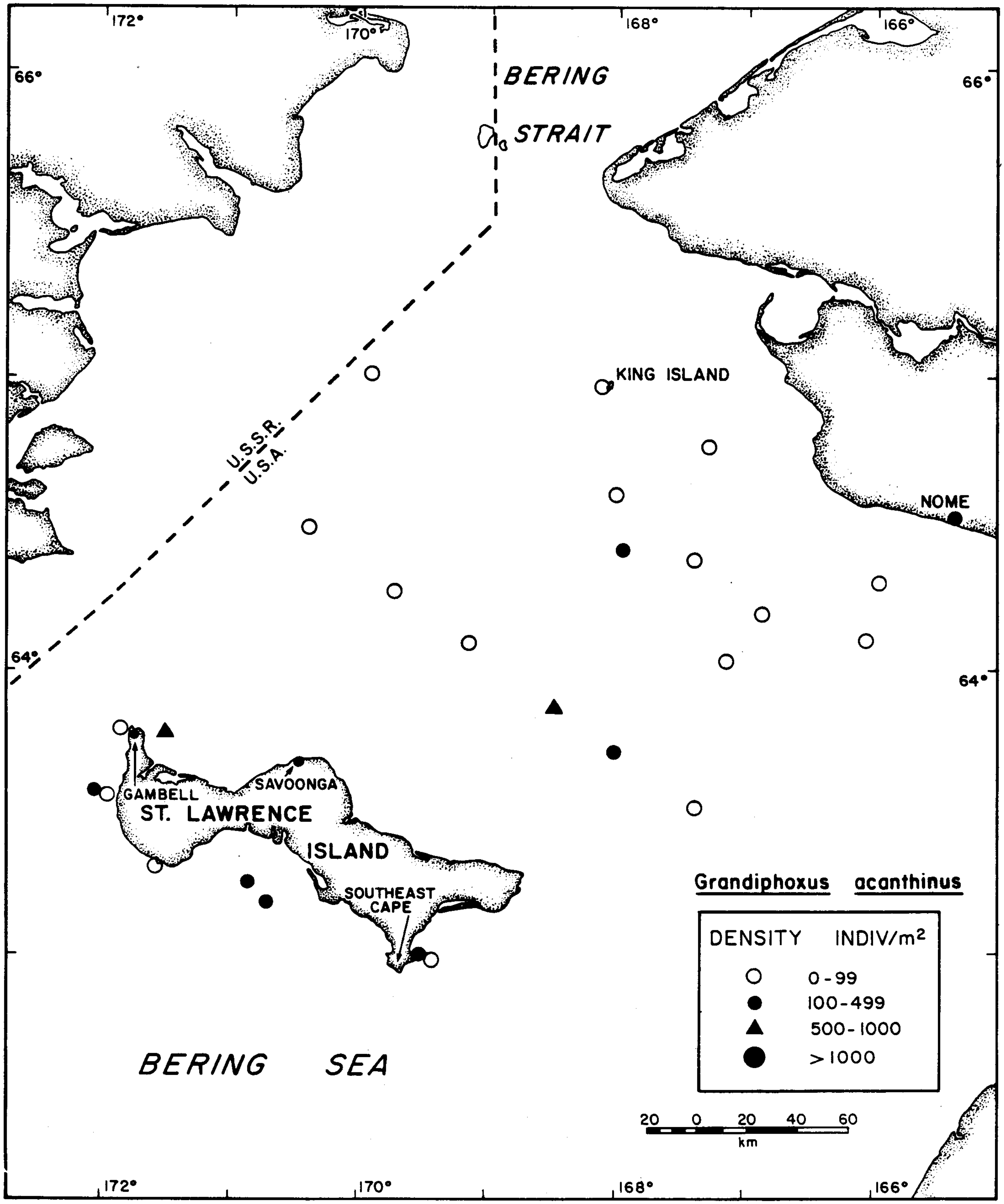

172°
170°
168°
166°
66°
64°
BERING
STRAIT
KING ISLAND
U.S.S.R.
U.S.A.
NOME
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST CAPE
BERING SEA
Grandiphoxus acanthinus
DENSITY INDIV/m2
○ 0-99
● 100-499
▲ 500-1000
● >1000
20 0 20 40 60
km

Figure 3e.

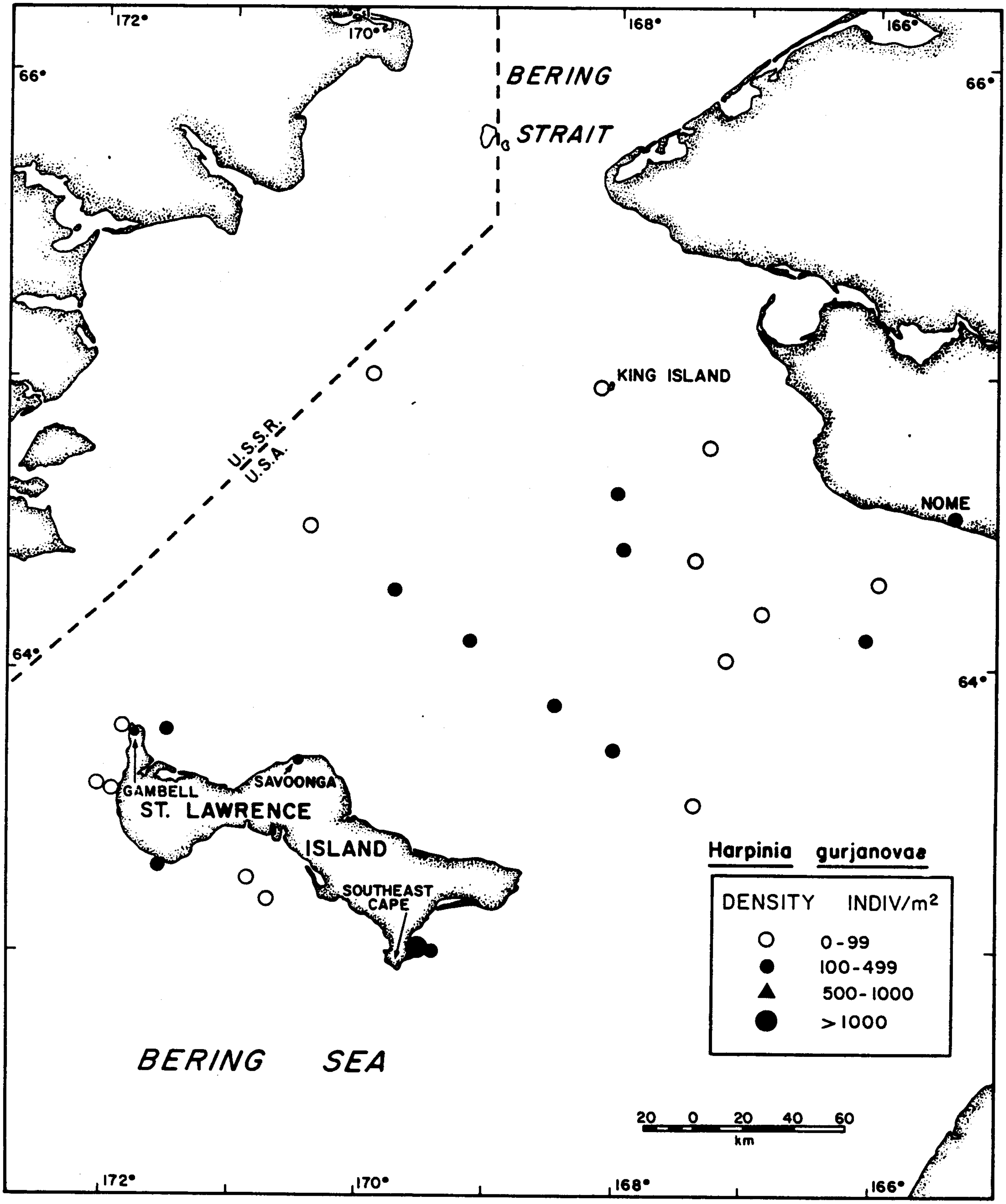

172°
170°
168°
166°
66°
66°
BERING
STRAIT
KING ISLAND
U.S.S.R.
U.S.A.
NOME
64°
64°
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST
CAPE
Harpinia gurjanovae
DENSITY INDIV/m²
○ 0-99
● 100-499
▲ 500-1000
● >1000
BERING SEA
20 0 20 40 60
km
172°
170°
168°
166°

Figure 3f.

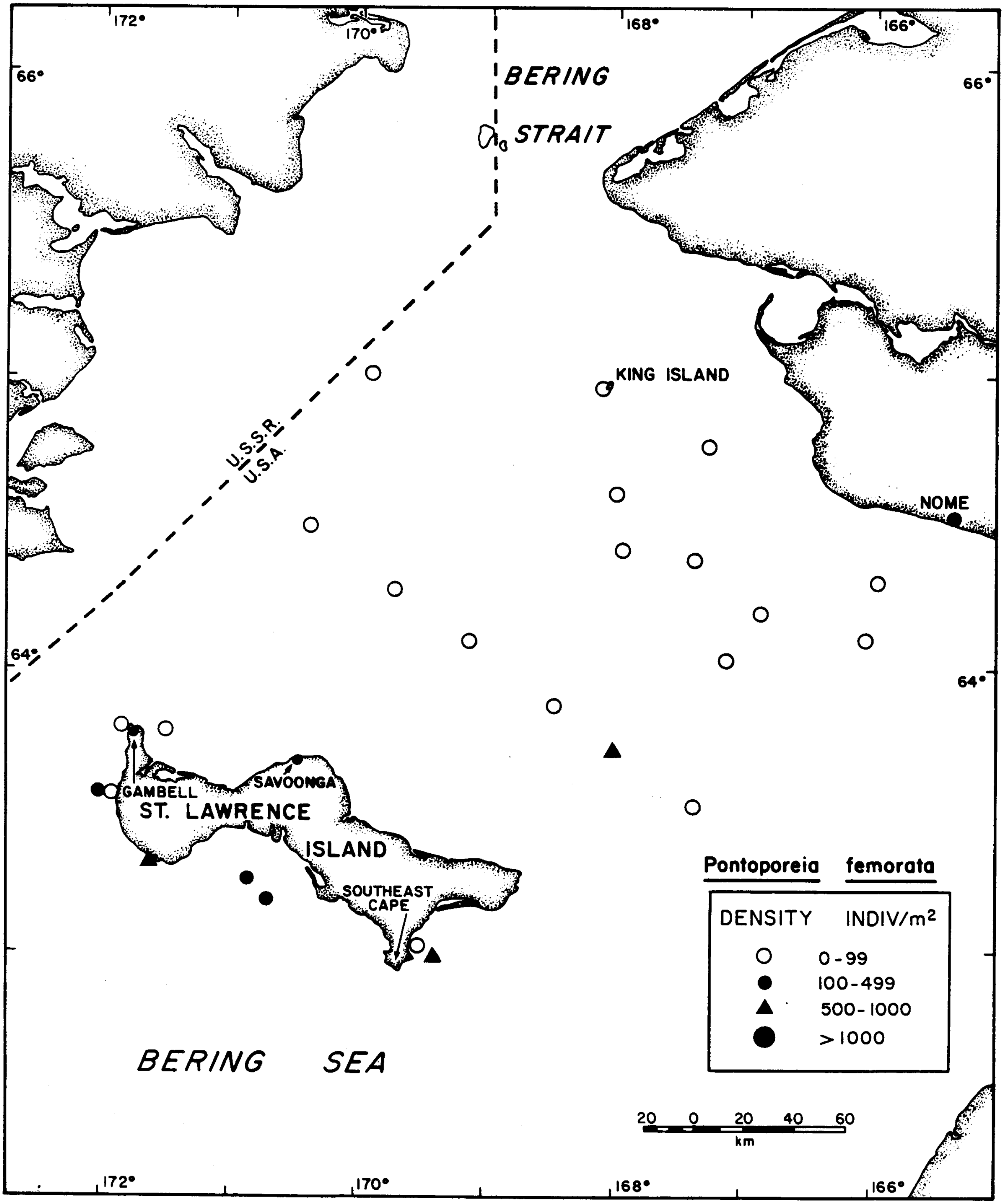

172°
170°
168°
166°
66°
64°
BERING
STRAIT
U.S.S.R.
U.S.A.
KING ISLAND
NOME
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST CAPE
BERING SEA
Pontoporeia femorata
DENSITY INDIV/m2
○ 0-99
● 100-499
▲ 500-1000
● >1000
20 0 20 40 60
km

Figure 3g.

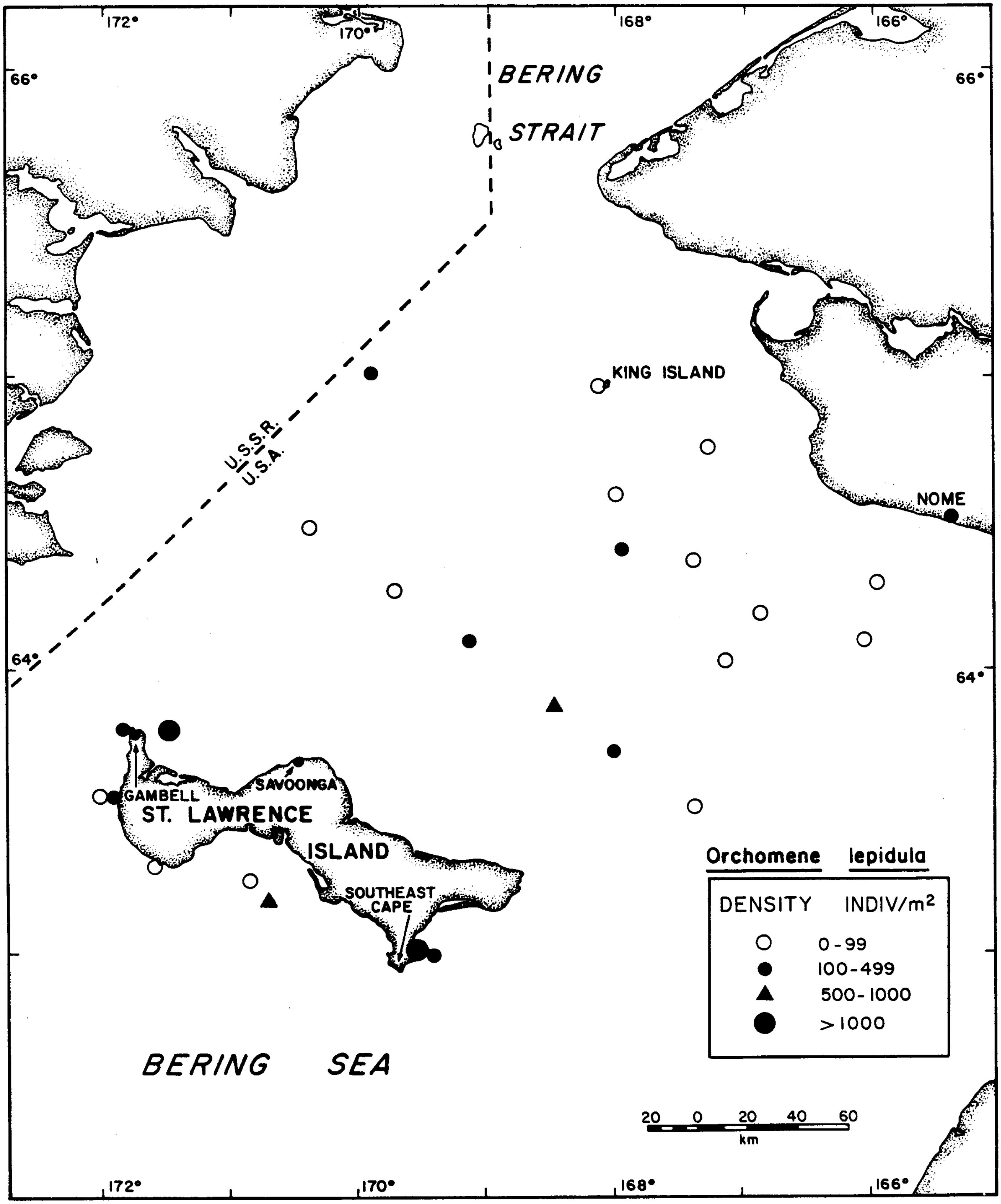

172°
170°
168°
166°
66°
64°
BERING
STRAIT
KING ISLAND
NOME
U.S.S.R.
U.S.A.
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST
CAPE
BERING SEA
Orchomene lepidula
DENSITY INDIV/m²
○ 0-99
● 100-499
▲ 500-1000
● >1000
20 0 20 40 60
km

Figure 3h.

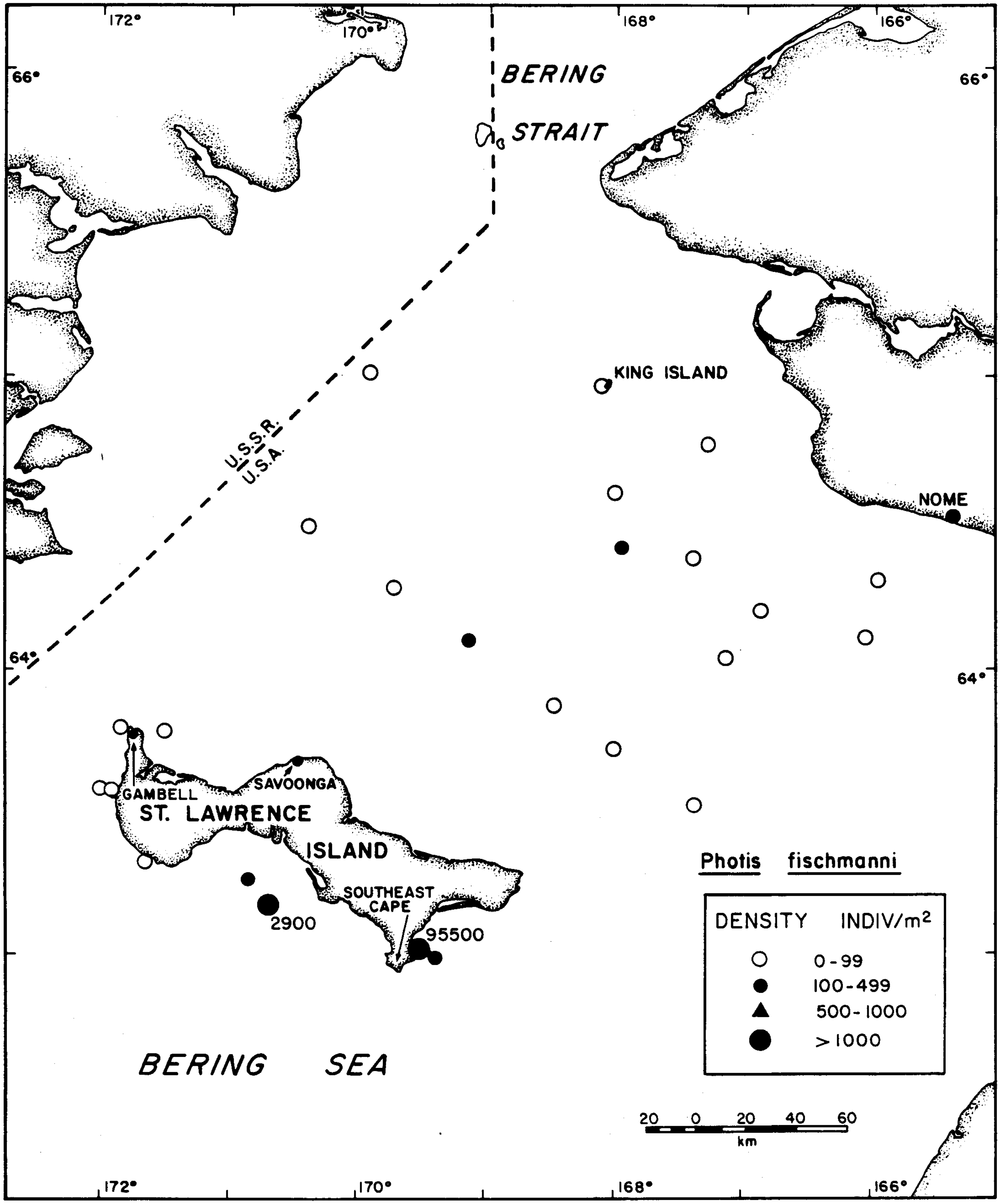

172°
170°
168°
166°
66°
64°
BERING
STRAIT
U.S.S.R.
U.S.A.
KING ISLAND
NOME
GAMBELL
SAVOONGA
ST. LAWRENCE
ISLAND
SOUTHEAST
CAPE
2900
95500
Photis fischmanni
DENSITY INDIV/m2
○ 0-99
● 100-499
▲ 500-1000
● >1000
BERING SEA
20 0 20 40 60
km

Figure 3i.

Mean total biomass of the 37 samples from the central Chirikof Basin that were dominated by amphipods (Fig. 2) was 298.1 g/m^2--lower than the 482 ± 286 g/m^2 reported by Stoker (1978) as the mean biomass of samples taken within the ampeliscid amphipod community. However, Stoker (1978) found the highest biomass values in the northwestern part of the Chirikof Basin, an area not sampled during this study. Mean biomass of 33 samples taken by us within the area dominated by the two 'non-amphipod' communities in the eastern Chirikof Basin was 289.5 g/m^2. Stoker (1978) found a mean biomass of 193 ± 111 to 265 ± 140 g/m^2 in this area.

Mean densities in our samples were higher than values reported by Stoker: 9317 ± 6897 indiv/m^2 vs. 3688 ± 823 indiv/m^2 for the amphipod community, and 2125 indiv/m^2 in our samples vs. 340 ± 103 to 702 ± 208 indiv/m^2 in Stoker's samples for other communities. Stoker's density and biomass estimates include samples from a much larger geographic area and as such are not directly comparable to values presented here.

There appeared to be considerable variation in the distribution of standing crop of the dominant amphipod species in the study area (Tables 3 and 4; Figs. 3a to 3h). One of the principal aims of the study was to define and characterize gray whale feeding areas. To this end, the following sections attempt to identify environmental conditions associated with the presence or absence of gray whale prey species.

The approach used was to quantify the abundance of the dominant amphipods in terms of various substrate conditions and depth regimes, and then use multiple regression analysis to determine if some of these environmental variables could be used as predictors of the standing crop of these animals.

All grab and airlift samples that were accompanied by measurements of the appropriate variables were used in the analyses. The environmental variables that were considered in the analysis were depth, mean grain size, sorting coefficient, organic carbon content of the sediment, caloric content of the sediment, and carbon to nitrogen ratio of the sediment. Inspection of scatter plots of the data indicated that, in some instances, a mean grain size squared term was necessary to account for non-linear relationships.

A stepwise multiple regression procedure (BMDP2R, Dixon 1981) was used to assess the relationships between the environmental variables and the standing crop of benthic animals. This technique added environmental variables to the regression equation one at a time beginning with the variable having the strongest simple correlation with animal abundance. Thereafter, environmental variables were added in decreasing order of partial correlation until no additional variable would, if included in the equation, significantly ($P<0.05$)* improve the equation's ability to predict standing crop.

Most of the environmental variables used in the analysis were correlated with one another (Table 5). Depth, the organic variables, sorting coefficient and mean grain size were all intercorrelated. The finest substrates tended to be associated with the shallowest depths, and finer substrates tended to have a higher carbon and caloric content than coarser substrates. In these circumstances it is usually impossible to determine which of the intercorrelated predictors is (or are) of direct importance to the animals.

Ampeliscid Amphipods

Ampelisca macrocephala was the dominant benthic animal in terms of both numbers and biomass in samples taken in the Chirikof Basin, off the west coast of St. Lawrence Island, and in the deeper waters near Southeast Cape (Tables 3 and 4; Fig. 3a). It was also the dominant species in terms of biomass in samples taken from the south coast of St. Lawrence Island.

The density of *Ampelisca macrocephala* varied greatly with mean grain size and sorting coefficient and less so with depth and organic composition of the substrate (Tables 6, 7 and 8). Because of an apparent non-linear relationship between mean grain size and the density of this species (Table 8), both mean grain size and its square were forced into the multiple regression equation. Both terms were significant predictors of the density

---

* Significance levels for individual variables in multiple regression equations in this report are the conventional ones derived directly from the F-to-delete values at the final step of the stepwise analysis. These levels generally overestimate the significance of each variable as a predictor (Hill 1979).

Table 5. Pearson product-moment correlation matrix of physical measurements taken with benthic samples from the Chirikof Basin and vicinity of St. Lawrence Island; n = 118.

	Depth (m)	Mean grain size (Φ)	Mean grain size squared (Φ^2)	Sorting coefficient	Caloric content Cal/g	Organic carbon mg/g
Mean grain size	-0.31**					
Mean grain size squared	-0.31**	1.00**				
Sorting coefficient	0.27**	0.09 NS	0.14 NS			
Caloric content	0.24*	0.23*	0.22*	0.34***		
Organic carbon	-0.41***	0.40***	0.41***	0.11 NS	0.10 NS	
Carbon/nitrogen	-.24*	0.04 NS	0.05 NS	0.19*	0.01 NS	0.33***

Significance (two-sided) shown by asterisks; NS means not significant, $p>0.05$; * means $0.05 \geq P > 0.01$, ** means $0.01 \geq P > 0.001$ and *** means $P \leq 0.001$.

Table 6. Mean density ± s.d. (no./m^2) of 10 dominant species of benthic amphipods in samples taken in the Chirikof Basin and vicinity of St. Lawrence Island in summer 1982.

	Depth Range (m)			
	12-19	20-29	30-39	40-50
Ampelisca macrocephala	946 ± 1243	2894 ± 2948	1939 ± 2249	4197 ± 4884
Byblis gaimardi	833 ± 920	90 ± 212	735 ± 1640	684 ± 1168
Ampelisca eschrichti	27 ± 94	67 ± 181	89 ± 170	34 ± 52
Harpinia gurjanovae	1282 ± 1732	84 ± 143	104 ± 190	112 ± 150
Grandiphoxus acanthinus	139 ± 209	155 ± 275	150 ± 252	7 ± 18
Protomedia fasciata	56 ± 148	104 ± 194	814 ± 2032	59 ± 134
Protomedia grandimana	2511 ± 2897	1882 ± 3582	1642 ± 4373	252 ± 340
Photis fischmanni	83319 ± 60276	437 ± 1426	107 ± 161	22 ± 39
Pontoporeia femorata	58 ± 127	152 ± 394	170 ± 356	5 ± 8
Orchomene lepidula	2351 ± 1876	319 ± 520	132 ± 218	104 ± 403
Sample size	39	37	57	17

Table 7. Mean density ± s.d. (no./m^2) of 10 dominant species of benthic amphipods in sediments of various organic characteristics. Samples were taken in the Chirikof Basin and vicinity of St. Lawrence Island during the summer of 1982.

	Caloric content (Cal/g)[1]			Organic carbon (mg/g^2)		Carbon/nitrogen (ratio)[1]	
Range of values	58-299	300-399	400-932	1.38-2.99	3.00-6.46	6.06-6.99	7.00-12.92
Species							
Ampelisca macrocephala	2299 ± 3131	2488 ± 2634	1698 ± 2241	2529 ± 2856	1635 ± 2561	3302 ± 3076	1284 ± 2129
Byblis gaimardi	315 ± 749	719 ± 1824	913 ± 1026	664 ± 1419	493 ± 811	684 ± 1557	526 ± 854
Ampelisca eschrichti	39 ± 134	129 ± 198	35 ± 93	63 ± 150	58 ± 148	96 ± 174	33 ± 119
Harpinia gurjanovae	232 ± 539	127 ± 199	920 ± 1130	511 ± 918	250 ± 502	360 ± 622	443 ± 897
Grandiphoxus acanthinus	158 ± 240	133 ± 278	91 ± 180	172 ± 273	72 ± 14	125 ± 235	138 ± 237
Protomedia fasciata	597 ± 1836	247 ± 742	86 ± 216	346 ± 1549	371 ± 817	78 ± 199	574 ± 1705
Protomedia grandimana	2193 ± 3433	1065 ± 4744	1750 ± 2415	1388 ± 2772	2343 ± 4508	1476 ± 3118	2000 ± 3917
Photis fischmanni	9927 ± 35821	152 ± 183	59115 ± 61727	22096 ± 44958	21392 ± 51684	17511 ± 41506	25195 ± 51875
Pontoporeia femorata	146 ± 333	143 ± 386	53 ± 120	94 ± 245	153 ± 377	167 ± 389	79 ± 212
Orchomene lepidula	379 ± 852	171 ± 256	1834 ± 1929	961 ± 1559	438 ± 995	763 ± 1262	743 ± 1477
Sample size	67	39	44	90	60	66	84

---

[1] Values expressed per unit dry sediment.

Table 8. Mean density ± s.d. (no./m^2) of 10 dominant species of benthic amphipods in various sediment types. Samples were taken in the Chirikof Basin and vicinity of St. Lawrence Island in the summer of 1982.

Species / Sorting Coefficient (Φ)	Mean grain size (Φ) 2.16-3.00	3.01-3.50	3.51-4.03
Ampelisca macrocephala			
1.10-1.75	2779 ± 2716	4226 ± 3436	212 ± 219
1.76-2.59	263 ± 495	3362 ± 2809	975 ± 1424
Ampelisca eschrichti			
1.10-1.75	41 ± 89	123 ± 245	0
1.76-2.59	29 ± 63	118 ± 173	36 ± 108
Byblis gaimardi			
1.10-1.75	128 ± 284	1113 ± 2055	1140 ± 1057
1.76-2.59	101 ± 126	1090 ± 1297	118 ± 313
Harpinia gurjanovae			
1.10-1.75	89 ± 131	423 ± 763	1182 ± 1306
1.76-2.59	44 ± 108	153 ± 259	619 ± 868
Grandiphoxus acanthinus			
1.10-1.75	241 ± 299	107 ± 159	190 ± 232
1.76-2.59	26 ± 51	187 ± 342	17 ± 34
Protomedia fasciata			
1.10-1.75	282 ± 800	102 ± 212	21 ± 63
1.76-2.59	2000 ± 3297	185 ± 423	96 ± 193
Protomedia grandimana			
1.10-1.75	2702 ± 6226	1692 ± 2461	3309 ± 2744
1.76-2.59	438 ± 669	2118 ± 3135	261 ± 348
Pontoporeia femorata			
1.10-1.75	191 ± 417	24 ± 62	13 ± 47
1.76-2.59	4 ± 16	371 ± 492	69 ± 141
Photis fischmanni			
1.10-1.75	585 ± 1506	22433 ± 52310	93419 ± 67718
1.76-2.59	62 ± 128	39 ± 81	25258 ± 36560
Orchomene lepidula			
1.10-1.75	364 ± 550	619 ± 1127	1972 ± 2086
1.76-2.59	33 ± 71	233 ± 392	1304 ± 1837
Sample size			
1.10-1.75	32	29	20
1.76-2.59	17	23	29

of Ampelisca macrocephala (Table 9) and defined maximum abundance (holding other factors constant) at a mean grain size of 2.9 Φ (the cutpoint between fine and very fine sand). Mean grain size in samples where abundance of A. macrocephala exceeded 1000 indiv/m^2 averaged 3.2 ± s.d. 0.4 Φ , (n = 16). The grain size terms in the equation appeared to be quite accurate in describing the relationship between grain size and density. The equation also predicted greater abundances in well sorted substrates than in poorly sorted substrates (Table 9). After allowances for mean grain size and sorting coefficient, high density of Ampelisca macrocephala was weakly related to high caloric content. Density of A. macrocephala was higher in sediments of low organic carbon content (Table 7) than those of high organic carbon content, but this variable was correlated with grain size and was not included in the equation after grain size was considered in the analysis.

Byblis gaimardi was a significant contributor to biomass, especially in samples from the Chirikof Basin, west coast of St. Lawrence Island, and shallow water off Southeast Cape (Table 3; Fig. 3b). Both mean grain size and its square were forced into the multiple regression equation and were significant predictors of the density of this species. Holding other terms constant, the equation predicts maximum density at a mean grain size of 3.1 Φ. Mean grain size in samples where abundance exceeded 1000 indiv/m^2 averaged 3.5 ± s.d. 0.2 Φ. Again the equation accurately predicted the preferred substrate. Shallow water and sediments containing a high caloric content were also significant predictors of a high density of Byblis gaimardi.

Ampelisca eschrichti was nowhere very abundant (Table 4) but is included in discussions that follow for comparison with the two common ampeliscid species. The multiple regression equation derived to explain variance in density of Ampelisca eschrichti placed much weight on the two mean grain size terms that were forced into the equation to account for an observed non-linear relationship. The equation (Table 9) predicts maximum densities of this species at a mean grain size of 2.9 Φ in poorly sorted substrates with a high carbon content and a low carbon to nitrogen ratio.

Table 9. Results of multiple regression analyses[1] of densities (no./m^2) of 10 dominant amphipod species, using as predictors the physical measurements associated with samples. All samples were taken in the Chirikof Basin and vicinity of St. Lawrence Island; n = 118.

	Ampelisca macrocephala	Byblis gaimardi	Ampelisca eschrichti	Harpinia gurjanovae	Grandiphoxus acanthinus	Protomedia fasciata	Protomedia grandimana	Photis fischmanni	Pontoporeia femorata	Orchomene lepidula
Constant (Y-intercept)	-6.6692	-9.3100	-12.8585	2.6919	2.6368	2.2533	5.2761	9.6869	-7.4828	5.1891
Depth	-	-0.0405***	-	-0.0342***	-	-	-0.0379***	-0.1176***	-	-0.0694***
Mean grain size	7.9337*	7.5308**	8.8900***	0.4780 NS	-	-0.6922***	-	-0.4487 NS	5.6445**^{2}	-
Mean grain size squared	-1.3815*^{2}	-1.1901**^{2}	-1.5102***^{2}	-^{3}	-^{3}	-^{3}	-^{3}	-^{3}	-0.9438 NS	-^{3}
Sorting coefficient	-1.4188***	-	0.7922***	-1.3050***	-1.6578**	0.8484*	-1.0073***	-2.2590***	-	-1.6915***
Caloric content	0.0017*	0.0033***	-	0.0016*	-	-0.0014**	-	0.0062***	-	0.0034***
Organic carbon	-	-	0.1532*	-	-	-	-	-	-	-0.2374**
Carbon/nitrogen	-	-	-0.1341***	-	1.1566***	-	-	-0.1417**	-	0.0959
Multiple *R*	0.61***	0.56***	0.52***	0.58***	0.59***	0.39***	0.50***	0.85***	0.27**	0.73***
% of variance explained	37.3	31.6	26.6	33.8	34.2	15.7	25.4	73.0	7.70	53.7
S.E. of estimate	1.15	1.10	0.78	1.06	0.91	1.20	1.11	1.04	1.00	1.00

---

[1] Regression coefficients of each variable that entered the equation are shown, along with the constant (Y-intercept) and statistics describing the fit of the equation. Significance levels of the regression equation and approximate significance levels of the regression coefficients are shown by asterisks; NS means not significant, $p>0.05$; * means $0.05 \geq P > 0.01$, ** means $0.01 \geq P > 0.001$ and *** means $P \leq 0.001$.

[2] In order to account for non linear relationships, both mean grain size and mean grain size squared were forced into the equation.

[3] Variable not considered for inclusion.

Phoxocephalids and Haustoriids

Harpinia gurjanovae was most abundant in shallow water off Southeast Cape, St. Lawrence Island, and moderately abundant in other areas (Fig. 3f). Maximum densities were found in shallow water in fine, well sorted substrates with a high caloric content (Tables 6, 7, and 8). All of these variables were significant predictors of the density of this species in multiple regression analysis (Table 9).

Grandiphoxus acanthinus was rare at the deepest depths sampled and was equally abundant over other depth ranges (Table 6). It was more abundant in well sorted substrates but density did not appear to vary with mean grain size (Table 8). Multiple regression analysis predicted maximum density in well sorted substrates with a high carbon to nitrogen ratio (Table 9).

Multiple regression analysis was not very successful in explaining densities of Pontoporeia femorata. None of the variables considered in the analysis was significantly correlated with the abundance of this species (Table 10). When mean grain size and its square were forced into the equation, only 8% of variance in the density of this species was explained (Table 9).

Corophiid Amphipods

The congeners Protomedia fasciata and P. grandimana differed in the habitats of maximum density. Multiple regression analysis predicted maximum densities of P. grandimana in shallow water and in well sorted substrates. In contrast, maximum densities of P. fasciata were predicted in poorly sorted coarse substrates with a low caloric content (Table 9).

Photis fischmanni was the dominant amphipod on the shallow shelf off Southeast Cape, St. Lawrence Island (Table 5). It was common in samples taken off the south coast and relatively rare in other areas. Multiple regression analysis predicted maximum densities of this species in shallow water, in substrates that were well sorted with a high caloric content and low carbon to nitrogen ratio (Table 9). Density of P. fischmanni was positively correlated with mean grain size (Table 10), indicating that highest densities were found in fine substrates. However, after all other variables had been considered by the analysis, high densities were predicted in coarse substrates.

Lysianassid Amphipods

Orchomene lepidula was most common in shallow water near St. Lawrence Island (Table 4; Fig. 3h). Multiple regression analysis predicted maximum densities of this species in shallow water, in well sorted substrates with a high caloric content, low organic carbon content, and high carbon to nitrogen ratio.

Trophic Relationships

Feeding Habits of Amphipods

The results of analysis of gut contents of 499 amphipods are shown in Tables 11 and 12. Three hundred and forty of these amphipods had been feeding on sediment. Fewer than 100 guts contained algal material and fewer than 60 contained animal material. The species represented in Tables 11 and 12 comprise the majority of amphipods collected during the study and are thus representative of the general feeding habits of the amphipods in the region.

Four species of ampeliscid amphipod dominated the benthos of the central Chirikof Basin and areas off the west and south coasts of St. Lawrence Island and deep water off Southeast Cape. All four species were deposit feeders. The three species of *Ampelisca* almost exclusively consumed sediment while *Byblis gaimardi* appeared to be a more selective feeder. Almost all of the guts of *Byblis gaimardi* contained diatoms in addition to sediment (Table 11).

Photis fischmanni, the dominant benthic animal in shallow water, and *Protomedia* spp., common amphipods in all areas, were also sediment feeders, as were *Pontoporeia femorata*, *Weycomedon similis* and all other amphipods examined except *Harpinia gurjanovae* and *Orchomene* sp. (Tables 11 and 12).

Table 10. Pearson product-moment correlation coefficients of the density (no./m^2) of dominant amphipod species with physical measurements associated with samples taken in the Chirikof Basin and vicinity of St. Lawrence Island; n = 118.

	Ampelisca macrocephala	*Byblis gaimardi*	*Ampelisca eschrichti*	*Harpinia gurjanovae*	*Grandiphoxus acanthinus*	*Protomedia fasciata*	*Protomedia grandimana*	*Photis fischmanni*	*Pontoporeia femorata*	*Orchomene lepidula*
Depth	0.03 NS	-0.21*	0.30**	-0.41**	-0.31**	0.13 NS	-0.42***	-0.59***	-0.09 NS	-0.56***
Mean grain size	-0.25*	0.17 NS	-0.24*	0.30**	-0.02 NS	-0.30**	0.10 NS	0.18*	-0.14 NS	0.08 NS
Mean grain size squared	-0.29**	0.15 NS	-0.26**	-[1]	-	-	-	-	-0.16 NS	-
Sorting coefficient	-0.46***	-0.13 NS	0.00 NS	-0.37***	-0.49***	0.15 NS	-0.38***	-0.46***	-0.16 NS	-0.44***
Caloric content	0.06 NS	0.40***	0.19*	0.07 NS	-0.29**	-0.18*	-0.22*	0.24*	0.03 NS	0.13 NS
Organic carbon	-0.22*	0.14 NS	-0.05 NS	0.19 NS	-0.09 NS	-0.09 NS	0.23*	0.16 NS	0.04 NS	0.06 NS
Carbon/nitrogen	-0.13 NS	0.01 NS	-0.25*	0.05 NS	0.22*	0.12 NS	0.10 NS	-0.08 NS	-0.07 NS	0.14 NS

[1] Variable not considered.

Significance (two-sided) shown by asterisks; NS means not significant, $p > 0.05$; * means $0.05 \geq P > 0.01$, ** means $0.01 \geq P > 0.001$ and *** means $P \leq 0.001$.

Table 11. Frequency of occurrence of food items found in the guts of 11 species of amphipods collected in the central Chirikof Basin in the summer of 1982. Samples are from areas 1B, 2A, 3B, 4A, 4B, 5A and 7B.

Species	*Protomedia* sp.[1]	*Ampelisca macrocephala*	*Ampelisca eschrichti*	*Ampelisca birulai*	*Byblis gaimardi*	*Harpinia gurjanovae*	*Bathymedon* sp.[2]	*Podoceropsis* sp.	*Ischyroceros* sp.[3]	*Photis fischmanni*	*Macharionyx mulleri*
Total no. examined	74	28	7	12	30	13	11	4	3	4	1
Sediment	66	28	7	8	29	4	8	3	3	3	1
Detritus	3										
Unidentified diatoms	26	3			27	1			1		
Chaetoceros sp.	1				2						
Filamentous diatoms	1										
Unidentified dinoflagellate	1										
Peridinium sp.		1									
Tintinids	1										
Foraminifera	1										1
Filamentous material	1										
Nematodes						2					
Polychaetes						1					
Sponge						1					
Unidentified animal tissue						1					
Empty	2			4	1	7	3	1		1	

---

[1] Includes *P. fasciata*, *P. dulkeiti*, *P. lindhlii* and *P. microdactyla*.
[2] Includes *B. nanseni*.
[3] Includes *I. angiupes*.

Table 12. Frequency of occurrence of food items found in the guts of 8 species of amphipods collected near St. Lawrence Island in the summer of 1982.

Area	Southeast Cape nearshore (11-14 m)				Southeast Cape offshore (22 m)				South coast (area 10D, 10E)			
Species	Photis fischmanni	Harpinia gurjanovae	Protomedia sp.^{1}	Orchomene sp.^{2}	Ampelisca macrocephala	Protomedia sp.^{3}	Weycomedon similis	Ampelisca eschrichti	Protomedia sp.^{4}	Ampelisca macrocephala	Pontoporeia femorata	Photis fischmanni
Total no. examined	40	31	25	28	13	15	5	2	30	30	15	10
Sediment	39	1	19	16	11	15	5	1	26	24	15	8
Detritus												
Unidentified diatoms	9	2	2	1								
Pennate diatoms		5										
Centric diatoms		1										
Naviculoid diatoms	1											
Chaetoceros sp.	1											
Peridinium sp.			1									
Dinophysis sp.												
Dinobryon sp.	1											
Foraminifera			1									
Unidentified protozoa											1	
Unidentified nauplii		4										
Harpacticoid nauplii		1										
Harpacticoid copepods		5										
Amphipod remains				9								
Crustacean remains	3	1		11								
Nematodes		7										
Unidentified animal tissue		1		6								
Empty	1	12	6	3	2			1	4	6		2

[1] Includes P. microdactyla.
[2] Includes O. lepidula.
[3] Includes P. microdactyla.
[4] Includes P. epimerata and possibly P. microdactyla.

The lysianassid Orchomene sp. fed on animal material in addition to sediment. Harpinia gurjanovae appeared to be a selective carnivore; few guts contained sediment or plant material (Tables 11 and 12).

Feeding Guilds

The trophic relationships among the various components of the benthos were identified and quantified in the following manner. Animals were assigned to a feeding guild according to the nomenclature of Fauchald and Jumars (1979), using information provided by them, Stoker (1978) and Tables 11 and 12.

Wet weight was converted to carbon using data provided by Stoker (1978). The carbon available to animals in the form of detritus, algae and meiofauna was estimated by applying the value of carbon content of sediment to the volume of sediment sampled by the grab or airlift.

A large amount of food in the form of meiofauna, algae and detritus appeared to be available to the benthic animals in all areas (Table 13). Surface deposit feeding appeared to be the most common feeding mode in all areas (Table 13). Surface deposit feeders included the ampeliscid amphipods, Photis fischmanni and the bivalve Macoma calcarea. In view of the total amount of food available in sediments, it is not surprising that biomass of this group was up to 3 times higher than that of the other primary consumers. In areas not dominated by amphipods, total biomass was lower due to the relative scarcity of surface deposit feeders.

Deposit feeders ingest substrate below the sediment surface and, in the areas studied, were represented mainly by polychaetes. This was the least common mode of feeding in all areas.

Carnivores included the isopod Tecticeps alascensis, polychaetes of the genus Nepthys and lysianassid amphipods. Some of these animals may also have been feeding on sediment; 16 of 28 specimens of Orchomene lepidula? had ingested sediment (Table 13).

Table 13. Mean biomass (g/m^2) of carbon in sediments and mean biomass according to major feeding mode of benthic animals taken in the Chirikof Basin and areas adjacent to St. Lawrence Island. Conversion of wet weight to carbon was accomplished using data provided by Stoker (1978).

	Chirikof Basin		Near St. Lawrence Island			
					Southeast Cape	
	Not dominated[1] by amphipods	Dominated by amphipods	West Coast	South Coast	Offshore	Nearshore
Carbon in sediments[2]	350	307	233	318	434	466
C/N ratio	9.0	7.0	6.7	6.7	7.8	8.5
Surface deposit feeders	2.2	11.3	11.5	10.2	13.2	10.1
Depost feeders	0.8	0.5	1.0	0.4	0.7	0.9
Filter feeders	1.2	0.7	2.7	3.0	1.9	1.0
Carnivores/scavengers	1.0	1.5	1.6	1.6	1.5	3.0
Not classified	1.5	1.0	1.6	0.7	1.2	0.9
Total	6.7	15.0	18.4	15.9	18.5	15.9
Sample size	38	37	11	15	10	55

[1] Less than 50 g/m^2 of amphipods

[2] Standardized to a sediment depth of 5 cm.

Filter feeders comprised only 5 to 19% of total biomass in various parts of the study area. In contrast, filter feeders generally dominate the benthos in other shallow areas (Jumars and Fauchald 1977). For example, in northwest Baffin Bay and Lancaster Sound in the eastern Canadian arctic, filter feeding was the dominant mode of feeding at depths <100 m (Thomson 1982); at Cape Hatt, northern Baffin Island, filter feeders, mainly bivalves, comprised 90% of standing crop at a depth of 7 m (Cross and Thomson 1981). Grain size and organic carbon content of sediments in Lancaster Sound and northern Baffin Bay were similar to those found in the Chirikof Basin.

Stoker (1978) believes that filter feeding bivalves were under-represented in his samples which, like many of ours, were taken with a Van Veen grab. However, we also obtained few bivalves when operating the airlift, and bivalve siphons were not conspicous when we were diving or observing the seafloor with the video camera. A heavy suspended sediment load was observed during all dives and video tows. It is possible that these massive amounts of sediment precluded filter feeding by bivalves. Another factor preventing the establishment of filter feeders may be competition for space. Brenchley (1982) has shown that animal tubes restrict burrowing activities of bivalves and polychaetes. The dominant surface deposit feeders were all tubicolous amphipods. Their prodigious numbers, closely packed tubes covering the entire seafloor, and apparent ability to recolonize quickly (Thomson and Martin, this report) may prevent other groups from establishing themselves.

Productivity of Amphipods

Samples for the estimation of secondary productivity were taken in 15 m depth off Southeast Cape, St. Lawrence Island, during July and September 1982 and during January, March and May 1983. Only *Photis fischmanni* and *Ampelisca macrocephala* were taken in sufficient quantities during all periods for the estimation of secondary productivity.

Ampelisca macrocephala

Ampelisca macrocephala is a large tubicolous ampeliscid amphipod that may reach 32 mm in total length. Ovigerous females were found in the Chirikof Basin in July and September. At this time, eggs were in early stages of development; those most developed showed only leg buds. These ovigerous females were 21 to 29 mm in length. Mean number of eggs per female was 18 ± 6 (n = 18). The eggs were large (1.2 x 1.5 mm) and weighed 1.2 to 1.3 mg wet weight (0.31-0.39 mg dry weight). Females with oostigites in formation were found off Southeast Cape in July. In September, large females were rare in samples taken off Southeast Cape. Ovigerous females were also taken in the March and May samples. In May, ovigerous females were 14 to 16 mm in length. The eggs were not well developed but had eye spots.

Examination of the length frequency histograms for Ampelisca macrocephala from Southeast Cape (Fig. 4) shows two periods of release of young. Individuals 3 mm in length were abundant in the samples taken in May but absent in March (Fig. 4). Individuals 2 to 4 mm in length were common in January and rare in September. The ovigerous females observed during summer apparently released young in fall.

The following interpretation has been placed on the life history of Ampelisca macrocephala at Southeast Cape. Young released in spring at a length of 3 mm were 4 to 5 mm in length by July and 5 mm in September. They reached 7 to 8 mm in January, 9 to 10 mm in March and May, and were 10 to 13 mm in length the following July. Some matured at 15 mm the following spring and may also have spawned in fall. The 7 and 8 mm individuals found in the July samples were hatched the previous fall, reach 9 mm in September, 10 mm in January, 12 mm in March, and 13 to 14 mm in May; they may have spawned in the fall at 15 mm and/or the following spring at 18 mm. Life span is about 2.5 years in this area.

The growth rate of Ampelisca macrocephala in the northern Bering Sea is similar to that of other northern and arctic amphipods (Table 14). Growth is about 6 mm per year.

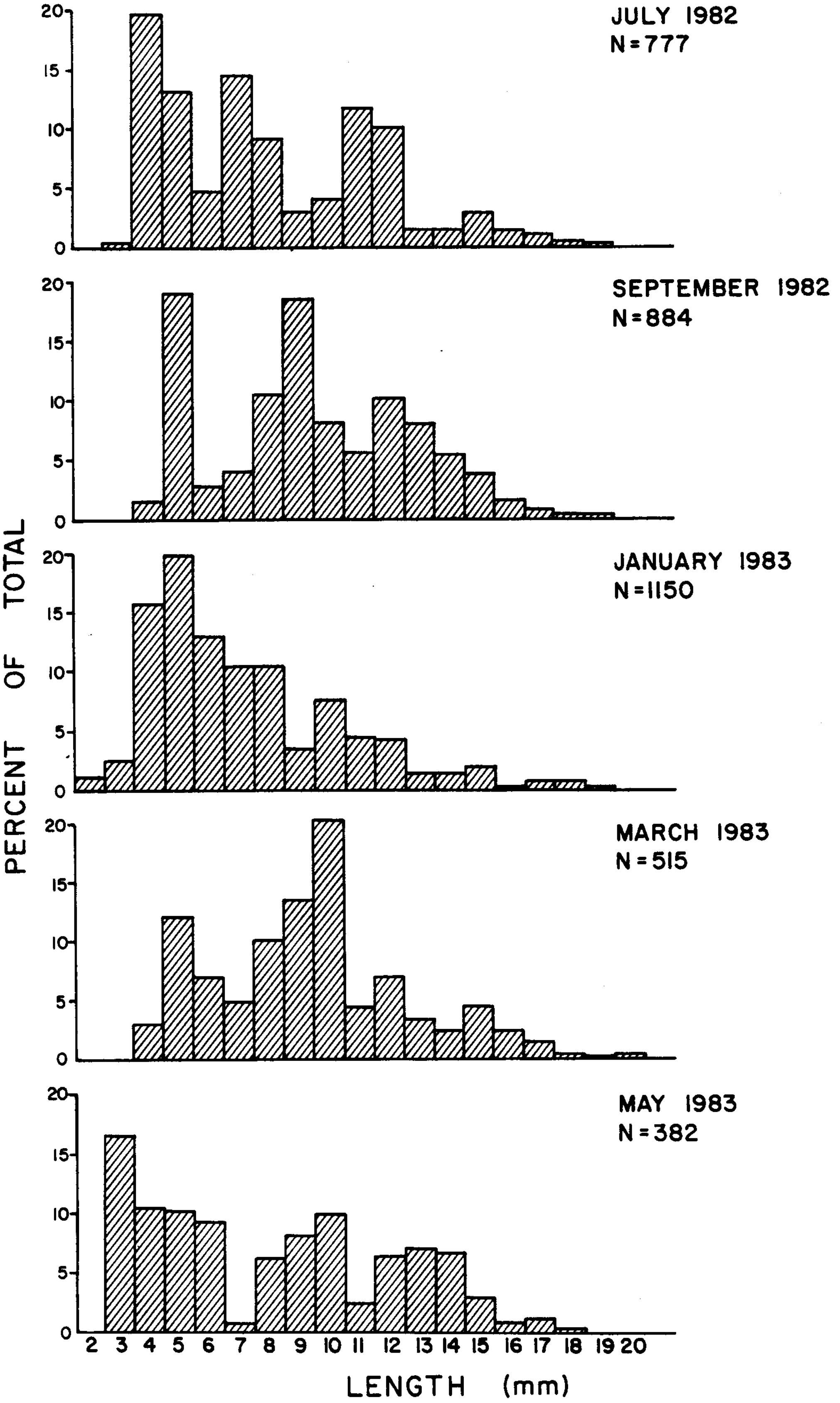


Figure 4. Length frequency histograms for Ampelisca macrocephala collected near Southeast Cape, St. Lawrence Island, in 1982 and 1983.

Table 14. Growth rates of arctic and temperate amphipods. All values in mm.

	Length at hatching	Growth over 1st year	Length at 1 year	Growth over 2nd year	Length at 2 years	Reference
Arctic Canada						
Gammarus setosus	3	4.5	7–8	7.5	14–16	Steele 1961; Cross 1982
Onisimus litoralis	3	9	12	6.5	16+	Steele 1961; Roy 1978; Cross 1982
Weyprechtia pinguis	3–4	9.5	11–14	12.5	19–24	Steele 1961; Cross 1982
Temperate Atlantic						
Ampelisca macrocephala	3	7.5	10–11	6	16.5	Kanneworff 1965
Ampelisca brevicornis	2	10	12			Klein et al. 1975
Bering Sea						
Photis fischmanni	1.4	5.5	6–7			This report
Ampelisca macrocephala	3	6	8–10	6	15	This report

Dry weight was regressed against length and used to compare condition of the animals in July and January, and to generate a length-weight equation for use in computation of productivity. Examination of the data and residuals showed that the length vs. dry weight relationship of Ampelisca macrocephala was well described by a power curve (length and weight were both log transformed). Analysis of covariance (Dixon 1981) showed that differences in slopes of the regression lines were nonsignificant for animals collected in summer and winter (F = 1.93, P = 0.17, df = 1, 62). After accounting for length, differences in mean weights of animals 4 to 18 mm in length taken in July and January were nonsignificant (F = 3.81, P = 0.056).

There was a difference in the caloric content of animals taken in winter and summer. Mean caloric content of animals was 3674 ± 436 cal/g dry weight in July and 2136 ± 584 cal/g in January. The mean difference was 1538 cal/g dry weight or about 0.16 g lipid/g dry weight (1 g lipid = 9540 cal) assuming that all of the loss was due to lipid utilization.

The regression of length on weight for all animals collected in July and January was highly significant (r = 0.98, P = 0.0000, n = 71). The equation dry weight = 0.00197 $(\text{length})^{3.02681}$ explained 96% of the variance of dry weight on length. This equation was used to estimate mean dry weight of the various categories of individuals listed in Table 15.

Productivity was estimated using the cohort summation method (Crisp 1971). Mean length was estimated for each cohort shown in Figure 4. Mean dry weight of individuals was estimated from length using the above equation. Several cohorts were present during each sampling period, and productivity was computed separately for each one (Table 15). The May to July productivity estimate is less precise because it necessitated comparing data from May 1983 with July 1982. Inter-year differences in growth rates could be substantial.

Total productivity of A. macrocephala for the ten month period between July 1982 and May 1983 was 3.8 g/m^2 dry weight and mean standing crop was 2.9 ± 1.0 g/m^2. Productivity to biomass ratio was 1.3. The May 1983 and July 1982 data were used to estimate productivity from May to July; this yielded a

Table 15. Computation of productivity estimate for *Ampelisca macrocephala* from Southeast Cape, St. Lawrence Island, by cohort summation of population growth. Biomass is expressed as dry weight.

Date	Spring Cohorts						Fall Cohorts				
	Mean length (mm)	Indiv. dry wt. (mg)	Mean density (no./m^2)	Standing crop (g/m^2)	Productivity[1] (g/m^2)		Mean length (mm)	Indiv. dry wt. (mg)	Mean density (no./m^2)	Standing crop (g/m^2)	Productivity[1] (g/m^2)
Hatched Spring 1982						Hatched Fall 1982					
July 1982	4.5	0.19	826	0.154	(0.157)[2]						
Sept 1982	5.0	0.26	239	0.061	0.037		3.0	0.05	Not sampled		
Jan 1983	7.3	0.81	775	0.626	0.279		4.6	0.20	1210	0.242	(0.182)[2]
March 1983	9.2	1.63	612	0.995	0.569		5.4	0.32	300	0.096	0.091
May 1983	9.1	1.58	201	0.318	-		5.7	0.38	115	0.044	0.012
Hatched Spring 1981						Hatched Fall 1981					
July 1982	11.2	2.95	664	1.959	(0.433)[3]		7.4	0.84	641	0.539	(0.174)[3]
Sept 1982	12.4	4.01	254	1.020	0.487		8.8	1.42	492	0.700	0.329
Jan 1983	14.4	6.31	114	0.720	0.423		10.7	2.57	464	1.192	0.320
March 1983	15.1	7.29	107	0.780	0.108		12.3	3.92	175	0.686	0.431
May 1983	16.7	9.89	20	0.198	0.165		13.1	4.74	193	0.915	0.151
Hatched Spring 1980						Hatched Fall 1980					
July 1982	18.3	13.05	18	0.235	(0.060)[3]		15.3	7.59	167	1.268	(0.513)[3]
Sept 1982			0				15.2	7.44	99	0.737	-
Jan 1983							18.2	12.84	47	0.603	0.394
March 1983							18.1	12.62	36	0.454	-
Hatched May 1983											
May 1983	3.6	0.10	251	0.024							

[1] Productivity = Weight increment per animal over the period x mean density over the period.

[2] Minimum estimate assuming no mortality between hatching and indicated time; weight of newly hatched individual estimated from extrapolation of length-weight regression.

[3] May to July productivity estimated from individual weight gain and standing crop difference between previous and following years' cohort (see text).

productivity estimate of 1.5 g/m^2 for a total annual productivity to biomass ratio of 1.8.

Photis fischmanni

Some females of Photis fischmanni 4 to 6 mm in length were ovigerous in January. Eggs were 0.3 mm in diameter with ill-formed embryos. In May 1983 females 2 to 7 mm in length were brooding and/or had just released young 1.3 to 1.5 mm in length.

Thus the 2 mm individuals that formed the greatest proportion of this species in samples taken in July 1983 (Fig. 5) had most likely been released in May. This cohort grew 1 mm in the period July to September and formed the spawning population for the fall. Ovigerous or brooding females were not taken in September; however, fall-winter spawning is indicated by the presence of 2 mm individuals in January samples and oostigite formation in July. Animals hatched in the fall reached 2 to 3 mm in length by January, at which time females were ovigerous, and reached 3 to 4 mm in May. The rate of growth proposed here of 0.5 mm/month is consistent with growth rates of other northern amphipod species (Table 14). Photis fischmanni appears to require six months to reach maturity, lives one year and may spawn twice.

Productivity was calculated by cohort summation (Table 16). Total productivity from July 1982 to May 1983 as estimated by this method was 24.97 g/m^2 and mean biomass was 8.158 g/m^2. Productivity to biomass ratio for the ten-month period was 3.1. Data from May 1983 and July 1982 yielded a productivity value of 5.42 g/m^2 for the period May to July. Total annual productivity was 30.39 g/m^2 and annual productivity to biomass ratio was 3.7.

DISCUSSION

Interrelationships Among Species

The ten amphipod species discussed in the preceding section accounted for 95% of the density of all amphipods taken in the study area. In most of the areas studied, amphipods were abundant and totally dominated the benthos. Within the narrow range of depths and bottom conditions that we

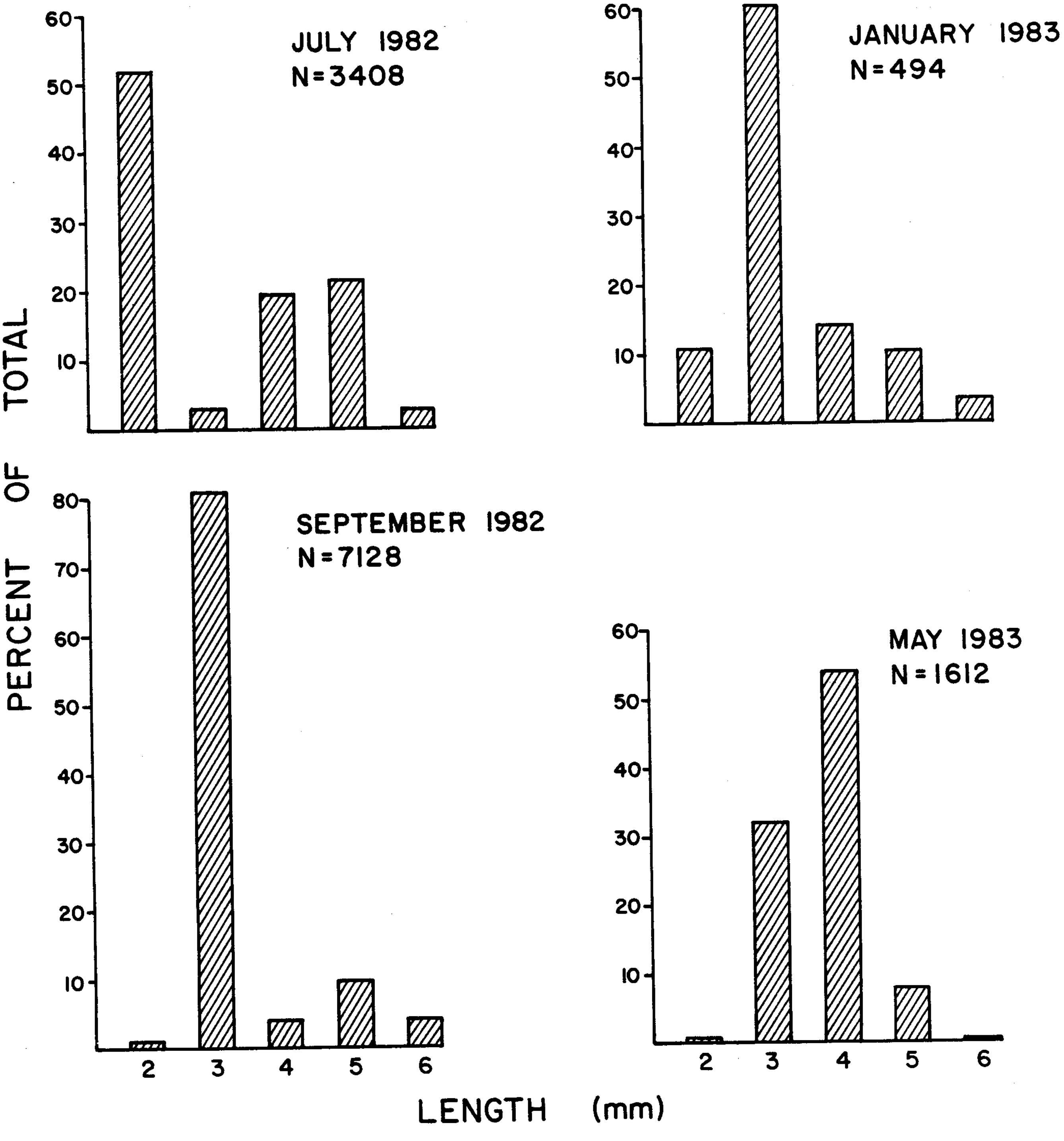


Figure 5. Length frequency histograms for *Photis fischmanni* collected near Southeast Cape, St. Lawrence Island, in 1982 and 1983.

Table 16. Computation of productivity estimate for Photis fischmanni from Southeast Cape, St. Lawrence Island, by cohort summation of population growth. Biomass is expressed as dry weight.

Date	Spring Cohorts						Fall Cohorts				
	Mean length (mm)	Indiv. dry wt. (mg)	Mean density (no./m^2)	Standing crop (g/m^2)	Productivity[1] (g/m^2)		Mean length (mm)	Indiv. dry wt. (mg)	Mean density (no./m^2)	Standing crop (g/m^2)	Productivity[1] (g/m^2)
Hatched Spring 1983											
May 1983	1.4	0.004	26020								
Hatched Spring 1982						Hatched Fall 1982					
July 1982	2.05	0.01	26797	0.268	(0.158)[2]						
Sept 1982	3.02	0.08	108635	8.691	4.740						
Jan 1983	4.64	0.37	609	0.225	15.840		1.4 2.85	0.004 0.06	Not sampled 3223	 0.193	 (0.180)[3]
May 1983	5.16	0.47	3360	1.579	0.198		3.62	0.17	30594	5.201	1.850
						Hatched Fall 1981					
July 1982							4.64	0.37	22035	8.153	(5.263)[2]
Sept 1982							5.28	0.48	17335	8.321	2.165

---

[1] Productivity = Mean density between sampling periods x weight increment per individual between sampling periods.

[2] Extrapolated between May 1983 and July 1982.

[3] Assumes no mortality between hatching and indicated period.

considered, each of these species appeared to differ from the others in terms of habitat selection and utilization. In cases where species showed somewhat similar habitat preferences, e.g. *Photis fischmanni* and *Protomedia grandimana*, there were spatial differences in location of maximum densities (Table 17). These spatial differences most likely reflect differences in environmental conditions that were not considered in the analyses.

Orchomene lepidula, *Harpinia gurjanovae*, *Protomedia grandimana*, *Byblis gaimardi* and *Photis fischmanni* were all abundant in shallow water. *Byblis gaimardi* appeared to be a selective deposit feeder, whereas *Photis fischmanni* was not. *Protomedia grandimana* was also a shallow water non-selective deposit feeder; however, it was most abundant off the south coast of St. Lawrence Island. The other shallow water species were relatively rare in this area. *Orchomene lepidula* fed on substrate and crustacea. *Harpinia gurjanovae* fed on crustacea and meiofauna.

Ampelisca macrocephala appeared to be the most successful amphipod species in the study area. Its habitat appeared to be only slightly different from that of its congener *A. eschrichti*. *A. eschrichti* was nowhere very abundant. *Protomedia fasciata* was also a non-selective deposit feeder, not apparently restricted to any particular depth. Unlike *Ampelisca macrocephala*, this species was most abundant in poorly sorted substrates having a low caloric content (Table 17).

There appears to be little niche overlap among the most common amphipod species in the study area.

In the Chirikof Basin, gray whales appear to feed only in areas with a high biomass of amphipods (Thomson and Martin, this report). Areas of the Chirikof Basin that had a high biomass of amphipods were dominated by large (lengths to 30 mm) ampeliscid amphipods (Table 18). Areas that had a low biomass of amphipods in samples were dominated by other taxa and the most abundant amphipods were smaller (to 15 mm) species such as *Protomedia* and *Ischyrocerus* (Table 18). Areas contiguous to St. Lawrence Island showed a high density of both ampeliscid amphipods and other amphipod species. Thus, gray whale feeding grounds in the Chirikof Basin are dominated by large

Table 17. Summary of habitat preferences and food habits of the 10 dominant amphipod species found in the Chirikof Basin and near St. Lawrence Island.

	Substrate							
	Grain size	Sorting	Caloric content	Carbon content	C/N ratio	Depth	Feeding	Location of maximum density
Ampelisca macrocephala	medium (2.9 Φ)	well sorted	high				sediment, non-selective	Least abundant SE Cape nearshore
Ampelisca eschrichti	medium (2.9 Φ)	poorly sorted		high	low		sediment, non-selective	SE Cape offshore
Byblis gaimardi	medium (3.1 Φ)		high			shallow	sediment, selective	West coast, St. Lawrence Island
Photis fischmanni	coarse	well sorted	high		low	shallow	sediment	SE Cape nearshore
Protomedia grandimana		well sorted				shallow	sediment	South coast, St. Lawrence Island
Protomedia fasciata	coarse	poorly sorted	low				sediment	Chirikof Basin
Harpinia gurjanovae	fine	well sorted	high			shallow	carnivorous	SE Cape nearshore
Grandiphoxus acanthinus		well sorted			high		not examined	None
Pontoporeia femorata	medium (3 Φ)						sediment	South coast, SE Cape offshore
Orchomene lepidula		well sorted	high	low	high	shallow	sediment/carnivorous	SE Cape nearshore

Table 18. Percent of total amphipod density contributed by the dominant species at stations with a similar biomass of amphipods in the Chirikof Basin. Percentages are shown only where the indicated species are dominant.

Range of Amphipod Biomass Station	*Ampelisca macrocephala*	*Ampelisca eschrichti*	*Ampelisca birulai*	*Byblis gaimardi*	*Protomedia fasciata*	*Protomedia grandimana*	*Ischyrocerus* sp.	*Photis fischmanni*	*Harpinia gurjanovae*
0–10 g/m^2									
1A				22	25	18			
1B	35						25	10	
4A					25	68			
4B						48			19
4C						91			
5B						43			
7A						55	15		
10–100 g/m^2									
3A					71	11			
3B					30	15	7		
2B	55			9	13	10			
3C	12				11	46			
>100 g/m^2									
2A	51		16	21					
5A	90								
6A	49					10			
6B	80	5							
7B	47			23					

amphipods. Smaller species appear to be excluded by habitat requirements and/or competition. Over most of their feeding range in the study area, gray whales are presented with a concentrated food source in the form of large amphipods.

Productivity

Differences in productivity among the species listed in Table 19 are due primarily to differences in life cycle. Generally, longer lived species will have a lower productivity than short lived species (Birklund 1977; Wildish and Peer 1981). The productivity of Photis fischmanni is similar to that of Ampelisca brevicornis and Pontoporeia femorata. All three species have a life span of one year. Corophium insidiosum produces 5-5.6 generations per year (Casabianca 1975) and has a very high productivity. The relatively low productivity of Ampelisca macrocephala in the Bering Sea is a reflection of its long life span.

One of the aims of this study was to determine the amount of food available to gray whales and food consumption by gray whales in relation to food availability. The mean biomass of amphipods in all areas utilized by gray whales in the Chirikof Basin was 132.8 ± 96.5 g/m^2 (n = 37, includes 0.3 g/m^2 of amphipod parts that could not be identified, Thomson and Martin, this report). Most of the biomass was accounted for by animals that reach a length of more than 20 mm (Table 20).

Application of the annual productivity to biomass ratio of 1.8 determined for Ampelisca macrocephala to the biomass of these large amphipods (124.9 g/m^2) yields a productivity of 224.8 g/m^2. Application of the productivity to biomass ratio of 3.7 determined for Photis fischmanni to the smallest class of amphipods yields a productivity of 7.4 g/m^2. Productivity of an intermediate-sized amphipod was not determined, so a productivity to biomass ratio intermediate between that of large and small amphipods (2.75) was used. In this manner, productivity of the intermediate size class of amphipods was estimated at 15.4 g/m^2. Total productivity of the 132.5 g/m^2 of amphipods listed above was thus estimated at 246.6 g/m^2. The annual productivity to biomass ratio of all amphipods in the Chirikof Basin was

Table 19. Productivity of benthic amphipod species, the benthos as a whole, and the zooplankton from the temperate Atlantic and Bering Sea.

Location/species	Productivity/ Biomass ratio	Time span considered	Reference
Temperate Atlantic			
Pontoporeia femorata	3.6-4.8	1 year	Wildish and Peer 1981
Corophium insidiosum	2-5	5 months	Birklund 1977
Corophium volutator	3-4	15 months	Birklund 1977
Corophium insidiosum	12-19.5	1 year	Casabianca 1975
Ampelisca brevicornis	3.4-4.4	1 year	Klein et al. 1975
Ampelisca sp.	5	1 year	Sanders 1956
Ampelisca brevicornis	3.4	1 year	Sheader 1977
Zooplankton (North Sea)	7	1 year	Crisp 1975
Benthos (North Sea)	3	1 year	Crisp 1975
Northern Bering Sea			
Photis fischmanni	3.7	1 year	This report
Ampelisca macrocephala	1.8	1 year	This report
Zooplankton	4.2	1 year	Ikeda and Motoda 1979
Macoma calcarea	0.3	1 year	Stoker 1978

Table 20. Mean biomass of amphipod species according to maximum size attained in that part of the Chirikof Basin dominated by amphipods.

Small <10 mm	g/m^2	Intermediate 10-20 mm	g/m^2	Large >20 mm	g/m^2
Phoxocephalids	1.3	*Boeckosimus plautus*	0.3	*Ampelisca birulai*	1.8
Ischyrocerus sp.	0.1	*Hippomedon granulosus*	0.2	*A. eschrichti*	14.4
Photis fischmanni	0.3	*Melita* spp.	0.1	*A. macrocephala*	85.5
Corophium sp.	0.3	*Orchomene lepidula*	0.7	*Byblis gaimardi*	19.7
		Pontoporeia femorata	1.3	*Anonyx nugax*	1.2
		Protomedia spp.	2.5	*Lembos arcticus*	1.9
		Others	0.5	*Wecomedon similis*	0.4
Total	2.0		5.6		124.9

estimated to be 1.9 in 1982. This estimate was used by Thomson and Martin (this report) to assess the food available to gray whales relative to their requirements in the Chirikof Basin.

ACKNOWLEDGMENTS

The gray whale feeding ecology project was funded by the Minerals Management Service through interagency agreement with the National Oceanic and Atmospheric Administration, as part of the Outer Continental Shelf Environmental Assessment Program. I wish to thank L. Jarvela and G. Oliver, contract monitors for this project, for their assistance.

Thanks are due to Cdr. E. Gelb, the officers and crew of the NOAA ship MILLER FREEMAN, and to Capt. R. Ganse, the officers and crew of the NOAA ship DISCOVERER for their able and enthusiastic assistance during all aspects of the field work. M. Kaiser and C. Newell of the NOAA diving office assisted with the planning and execution of diving operations. Ships divers L. Consiglieri, S. Christopherson, J. Rivera, F. Wood, J. Morris and M. White assisted with underwater sampling and collection. I especially wish to thank L. Martin and S. Viada of LGL for assistance with all aspects of the field work. L. Martin, D. Roseneau and D. Troy of LGL collected winter samples. I wish to thank the people of Savoonga, St. Lawrence Island, for their able and enthusiastic support and assistance with the winter work.

J. Cole of LGL and G. Lapiene and J. Talbot of NOAA provided valuable logistic support in Alaska.

R. Dillinger of LGL supervised sample analysis and identified most of the animals. K. Coyle of Univ. of Alaska verified the crustacean identifications, and K. Fitzhugh and H. Harry verified polychaetes and other taxa, respectively. S. Naidu and A.J. Paul of Univ. of Alaska performed carbon and nitrogen analysis and caloric analysis, respectively.

I wish to thank L. Maritzen, J.S. Baker and C. Holdsworth of LGL for assistance with data processing. B. De Long drafted the figures, B. Griffen and H. Hogarth typed the manuscript. I especially wish to thank W.J. Richardson of LGL for editorial assistance and for fruitful discussions on study design, data interpretation and analysis.

LITERATURE CITED

Birklund, J. 1977. Biomass, growth and production of the amphipod Corophium insidiosum Crawford, and preliminary notes on Corophium volutator (Pallas). Ophelia 16:187-203.

Brenchley, G.A. 1982. Mechanisms of spatial competition in marine soft-bottom communities. J. Exp. Mar. Biol. Ecol. 60:17-33.

Casabianca, M.-L. de. 1975. Méthode de calcul de la production par estimation de la mortalité. Application à une population à structure complex du crustace Corophium insidiosum Crawford. (Langune de Biguglia, Corse). C.R. Hebd. Seanc. Acad. Sci. Paris 280:1139-1142.

Crisp, D.J. 1971. Energy flow measurements. p. 197-279. In: N.A. Holme and A.D. McIntyre (eds.), Methods for the study of marine benthos. IBP Handbook no. 16. Blackwell Scientific Publications, Oxford.

Crisp, D.J. 1975. Secondary productivity in the sea. p. 71-89. In: Productivity of the world ecosystems. Proc. of a Symposium sponsored by U.S. National Committee for the IBP. NAS Washington, D.C.

Cross, W.E. 1982. In situ studies of effects of oil and dispersed oil on primary productivity of ice algae and on under-ice amphipod communities. In: Special studies - 1981 study results. (BIOS) Baffin Island Oil Spill Working Report 81-10. 61 p.

Cross, W.E. and D.H. Thomson. 1981. Macrobenthos-1980 study results. (BIOS) Baffin Island Oil Spill Working Report 80-3. 81 p.

Day, P.R. 1965. Particle fractionation and particle-size analysis. p. 562-566. *In*: C.A. Black et al. (ed.), Methods of soil analysis, Part 1. Am. Soc. of Agronomy, Monograph No. 9.

Dixon, W.J. (ed). 1981. BMDP statistical software. Univ. of California Press, Berkeley. 726 p.

Fauchald, K. and P.A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17:193-284.

Foy, M.G. 1978. Acute lethal toxicity of Prudhoe Bay crude oil and Corexit 9527 on four arctic marine invertebrates. Rep. by LGL Ltd. for Environmental Protection Service. 98 p.

Hill, M. 1979. Annotated computer output for regression analysis: a supplement to writeups for computer programs BMDP2R and BMDP9R. Health Sci. Comp. Facility, UCLA, Tech. Rep. No. 48. 74 p.

Ikeda, T. and S. Motoda. 1979. Zooplankton production in the Bering Sea calculated from 1956-1970 OSHORO MARU data. Mar. Sci. Comm. 4(4):329-346.

Johnson, K.R., C.H. Nelson and H.L. Mitchell. 1983. Assessment of gray whale feeding grounds and sea floor interaction in the northeastern Bering Sea. Final Report by U.S. Geological Survey, Menlo Park, CA to NOAA/OCSEAP, Juneau, AK. 78 p.

Jumars, P.A. and K. Fauchald. 1977. Between-community contrasts in successful polychaete feeding strategies. p. 1-21. *In*: B.C. Coull (ed.), Ecology of marine benthos. Univ. of S. Carolina Press, Columbia, S.C.

Jumars, P.A. and K. Fauchald. 1977. Between-community contrasts in successful polychaete feeding strategies. p. 1-21. *In*: B.C. Coul (ed.), Ecology of marine benthos. Univ. of S. Carolina Press, Columbia, S.C.

Kanneworff, E. 1965. Life cycle, food and growth of the amphipod *Ampelisca macrocephala* Liljeborg from the Øresund. Ophelia 2:305-318.

Klein, G., E. Rachor and S.A. Gerlach. 1975. Dynamics and productivity of two populations of the benthic tube-dwelling amphipod *Ampelisca brevicornis* (Costa) in Helgoland Bight. Ophelia 14:139-159.

Nelson, C.H. 1982. Late Pleistocene-Holocene transgressive sedimentation in deltaic and non-deltaic areas of the northeastern Bering epicontinental shelf. Geologie en Mijnbouw 61:5-18.

Nelson, H., R.W. Rowland, S.W. Stoker and B.R. Larsen. 1981. Interplay of physical and biological sedimentary structures of the Bering continental shelf. p. 1265-1296. *In*: D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea Shelf: oceanography and resources. Off. Mar. Poll. Assess., Natl. Ocean. Atmos. Admin., Washington.

Nerini, M. In press. A review of gray whale feeding ecology. In: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale *Eschrichtius robustus*. Academic Press, N.Y.

Sanders, H.L. 1956. Oceanography of Long Island Sound, 1952-1954. X. The biology of marine bottom communities. Bull. Bingham Oceanogr. Coll. 15:345-414.

SAS. 1982. SAS user's guide: basics. SAS Institute, Carey, N.C. 921 p.

Sheader, M. 1977. Production and population dynamics of *Ampelisca tenuicornis* (Amphipoda) with notes on the biology of its parasite *Sphaeronella longipes* (Copepoda). J. Mar. Biol. Assoc. U.K. 57:955-968.

Steele, D.H. 1961. Studies in the marine amphipods of eastern and north-eastern Canada. Ph.D. Thesis. McGill University, Montreal, P.Q. 350 p.

Stoker, S.W. 1978. Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi seas. Ph.D. thesis, Univ. of Alaska, Fairbanks. 259 p.

Stoker, S.W. 1981. Benthic invertebrate macrofauna of the eastern Bering/Chukchi continental shelf. p. 1069-1090. In: D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea Shelf: oceanography and resources. Off. Mar. Poll. Assess., Natl. Ocean. Atmos. Admin., Washington.

Strickland, J.D.H. and T.R. Parsons. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167. 310 p.

Thomson, D.H. 1982. Marine benthos in the eastern Canadian high arctic: multivariate analyses of standing crop and community structure. Arctic 35:61-74.

Wildish, D.J. and D. Peer. 1981. Methods for estimating secondary production in marine amphipods. Can. J. Fish. Aquat. Sci. 38:1019-1026.

Appendix Table 1. Summary of samples collected and work performed in the Chirikof Basin near St. Lawrence Island in July and September 1982.

Area	Benthic samples Station (no. samples)[1]	No. of sediment samples[4]	Amphipod feeding No. animals	Video tows Tow no. (h)
Central Basin				
1A	407(5)V	1		102(.5)
1B	263(5)V	1	17	37(1)
4A	283(5)V	1	27	43(1)
4B	292(5)V	1	15	45(1)
4C	417(3)V	1		104(.3)
3A	269(5)V	1		39(1)
3B	276(5)V	1	39	41(1)
3C	423(5)V	1		106(.5)
2A	246(5)V	1	36	33(1)
2B	257(2)V	1		35(1.2)
5A	232(5)V	1	15	29(1)
5B	240(5)V	1		31(1)
6A	219(5)V	1		25(1)
6B	225(5)V	1		26(1)
7A	199(5)V	1		21(1)
7B	207(5)V	1	43	23(1)
St. Lawrence Island				
South Coast				
10C	438(5)V	1		111(.75)
10D	446(5)V	1		113(.5)
Boxer Bay				
10E	455(5)V	1	45	115(.18)
West Coast				
8A				1(1)
8B				3(1.9)
8C nearshore	101(5)V	1		7(1)
offshore	92(5)V	1		11(1)
8D	113(4)V			14(1.9)
8E	125(5)A	1	45	
Southeast Cape				
9A offshore	136(5)V	2	46	16(1.7)
	179(5)V			19(2.1)
nearshore	152(8)[2]A	14	171	
	158(15)A			
	166(30)A			
	464(30)[2]A			
	475(10)[2]A			
	464(30)[3]P			

---

[1] V = Van Veen Grab, A = Diver-operated airlift, P = Ponar Grab.

[2] 50% of samples taken inside and 50% taken outside furrows.

[3] Winter sampling in January, March and May 1983.

[4] Grain size, caloric content, carbon and nitrogen content.

Appendix Table 2. Level of effort and numbers of samples collected and analyzed from the Chirikof Basin and the vicinity of St. Lawrence Island in July and September 1982.

Days on site		31
Days worked		24*
Video tows	No. tows	27
	Hours towed	26
Dives	No.	40
	Diver hours	39.5
Benthic Samples	Van Veen Grab	114
	Airlift Samples	98
	Ponar grab (winter)	30
	Total	242
Sediment samples	Grain size	38
	Caloric content	43
	Carbon nitrogen content	32
	Chlorophyll content	10
	Surface detritus	19
Amphipods	Stomach contents (no. animals)	499
	Caloric value	30

* 7 days were lost due to bad weather in September.

DISTRIBUTION AND ABUNDANCE OF GRAY WHALES

by

Gary W. Miller

LGL Ltd., Environmental Research Associates

1983

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Aerial surveys of the Chirikof Basin in mid July and early September 1982 showed that gray whales were concentrated in a north-south band across the center of the basin. Aerial and shipboard surveys also found concentrations along the west, south and east coasts of St. Lawrence Island. Many additional gray whales were present west of the U.S./U.S.S.R. Convention Line. These results are consistent with results from studies in previous years.

Raw line transect estimates of gray whale abundance in the Chirikof Basin (excluding the concentrations around St. Lawrence Island and in Soviet waters) were 540 in July and 215 in September. Our data on surfacing/dive cycles permitted us to correct these raw estimates to include whales that were below the surface and hence not visible when the survey aircraft flew over. The corrected estimates were 1929 for July and 601 for September. Similar values were obtained using sightings of mud plumes created by feeding gray whales to correct the raw survey results for whales below the surface.

INTRODUCTION

An understanding of the distribution and number of gray whales utilizing the Chirikof Basin in summer is a prerequisite for an analysis of the relationships between feeding gray whales and their prey. The most comprehensive previous information on distribution and numbers of gray whales in the study area has come from aerial surveys (e.g., Nerini 1980; Ljungblad et al. 1982). Additional information has come from shore-based and shipboard observers. A major limitation in most previous studies, particularly those based on aerial surveys, has been underestimation of numbers of whales present because of inability to detect whales that were below the surface.

In this study, we conducted both ship-based and aerial surveys to determine the distribution and numbers of gray whales in the study area in 1982. Aerial surveys were used because they offered the advantage of sampling large areas in a relatively short period of time, including areas where little or no ship-based work was planned. Ship-based observations both at benthic sampling stations and while steaming between stations provided additional information. Of major relevance to this study was the collection of data on the surfacing-dive cycle of the gray whale (Würsig et al., this report). Through use of those behavioral data and the analytical procedure of Davis et al. (1982), it was possible to estimate the proportion of the whales that were submerged (and, therefore, undetected) during the aerial surveys.

The distributional and abundance data presented here are used by Thomson and Martin (this report) to assess the interactions between gray whales and their prey organisms.

METHODS

Aerial Surveys

Approach

We conducted systematic aerial surveys to determine the distribution and estimate the abundance of gray whales in the study area. In order to sample the area in a systematic manner, we divided it into six bands of equal width by establishing seven lines (33.3 km apart) east of and parallel to the U.S.-U.S.S.R. Convention Line. These lines ran northeast from the St. Lawrence Island region to the Seward Peninsula. We randomly selected two sets of survey lines, each consisting of one line in each of the six bands we intended to sample. These two sets of survey lines, and additional lines designed to sample the distribution of gray whales in coastal waters off St. Lawrence Island, are shown in Figure 1. Lines flown to connect end and start points of successive lines (not shown in Fig. 1) were surveyed on an opportunistic basis to provide additional distribution data.

Timing and Number of Surveys

We originally planned to survey the study area during three different periods in 1982: mid July, late July to early August, and early September. Bad weather prevented us from conducting the second proposed survey; thus, surveys were conducted only during mid July and early September. During mid July, both sets of survey lines across the Chirikof Basin were surveyed. During early September only one set of lines could be completed. Additional surveys would have been desirable, but were impractical because of weather and logistical limitations.

Survey Aircraft

Two aircraft were used in these surveys. The first (mid July) survey was conducted from a Grumman Goose supplied by the Office of Aircraft Services, Anchorage, with the cooperation of the Naval Ocean Systems Center, San Diego. The second survey was conducted from a deHavilland Twin Otter

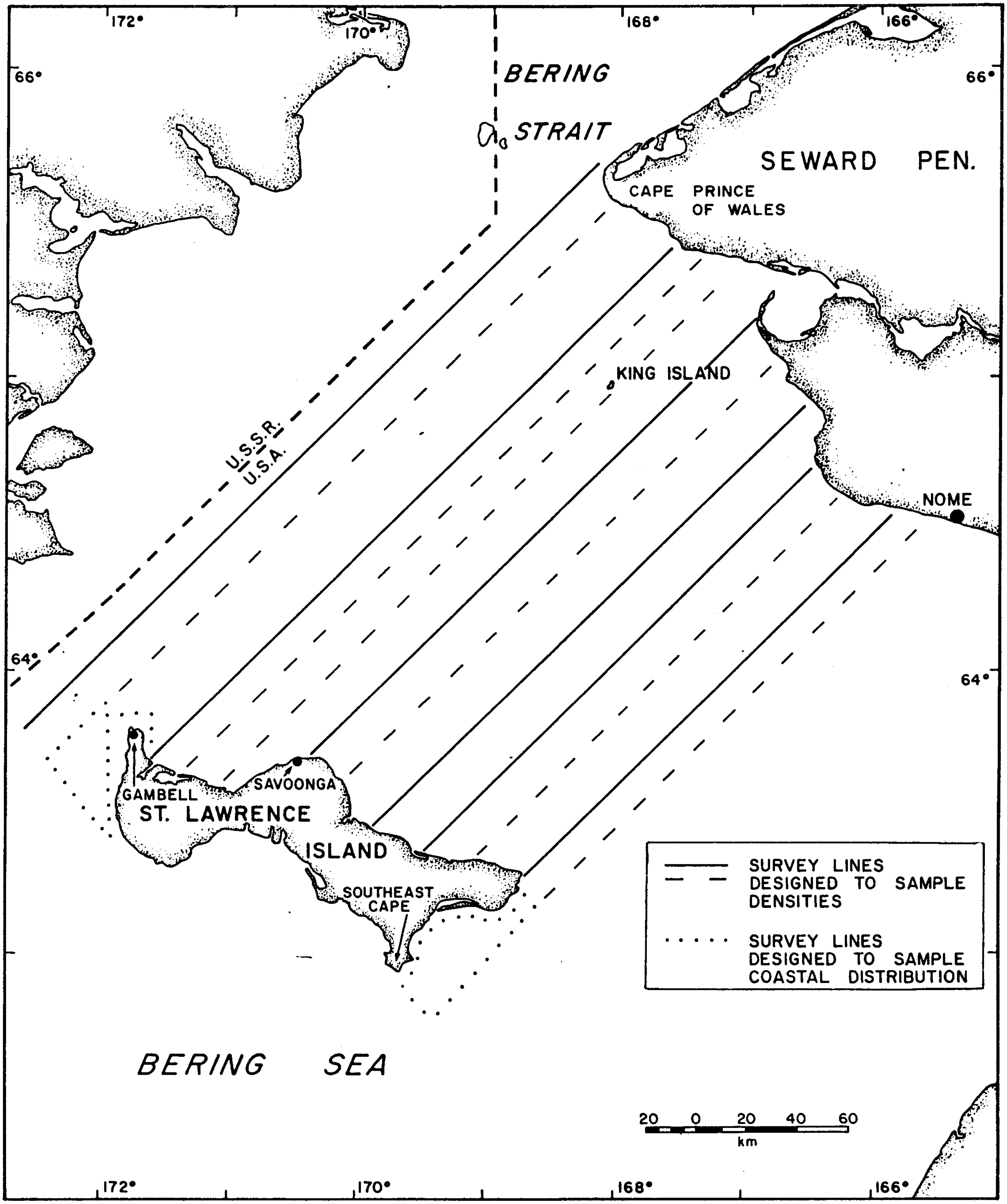


FIGURE 1. Planned transects for aerial surveys. Dashed and solid lines depict the two sets of six randomly-selected transects (see text).

operated by Evergreen Helicopters, Anchorage. Each aircraft was equipped with a VLF navigation system (GNS-500) for accurate offshore navigation, and a radar altimeter for accurate determination and maintenance of survey altitude.

Survey Procedure

Survey procedure was standardized to the extent possible; however, the use of two different aircraft required different survey speeds and different seating positions during the two surveys. We attempted to maintain a ground speed of 240 km/h when flying in the Grumman Goose. When surveying from the Twin Otter (second survey) it was practical to maintain a ground speed of about 205 km/h.

In the Grumman Goose the observers occupied seats opposite one another in the rear of the aircraft. The observers surveyed through a large window offering some forward and rearward visibility. Thus, the two observers had equal visibility when in the Goose. In the Twin Otter, one observer was seated in the front left (co-pilot's) seat. The second observer occupied a seat on the right side of the aircraft, two behind the pilot, and observed through a standard side window. During this survey the observer occupying the co-pilot's seat had better forward visibility than did the rear observer.

All surveys were flown at an altitude of 152 m. Fog caused occasional deviations from this altitude; however, when these deviations became prolonged the survey was terminated.

Surveyors recorded all observations onto audio tapes. Information for each sighting included species, number, group type, behavior (including description of activity, direction of movement), sighting cue, and presence or absence of feeding plumes and/or associated flocks of birds. An inclinometer (Suunto PM-S/360S) was used to determine the angle of depression of the line to the animal when it was directly to the side of the aircraft. Lateral distances of gray whales from the flight path were later calculated based on the sighting angle and aircraft elevation.

Position along the transect route was interpolated by the use of an interval timer system, digital watches, and the aircraft's VLF navigation system. The interval timer was reset to zero at the start of each transect and, thereafter, at 2-min intervals it produced a sound audible to all observers. This division of transects into 2-min transect segments permitted us to map gray whale sightings at intervals of approximately 6-8 km along each transect. During all surveys, weather (fog, rain, snow), sea state and sun glare intensity were recorded for each transect segment.

Ship-based Observations

During the gray whale benthic ecology and behavior cruises in July and September, 1982, a systematic watch for marine mammals was kept from the flying bridge of the MILLER FREEMAN (12 m above water), and from the flying bridge or "aloft conning tower" of the DISCOVERER (15 m and 23 m above water, respectively). One to three whale biologists scanned the sea with unaided eyes and with 9x30 binoculars. Distance of visibility varied with weather conditions and size of marine mammal, but the observers believed that they were usually able to sight blows of gray whales within five km of the vessel. Marine mammal sighting information included time, ship's position and heading, weather, species, number of animals, and distance of sighting from the ship.

When the ship was on station during benthic sampling, systematic binocular-aided scans were conducted for 10 min of every hour. In this way, estimates of number of whales within sight of the ship were made. These estimates, as well as the overall sighting effort, are presented in the Results.

RESULTS

Aerial Surveys

Distribution

We flew two sets of survey lines during the first survey period (10-17 July), totalling 3709 km. Coverage was virtually complete, except that Federal Aviation Administration regulations prevented us from flying lines we had laid out in the westernmost of the six survey bands. Seventy-six gray whales were sighted (20.5/1000 km of survey line) on the regular survey lines, and a total of 79 gray whales (21.3/1000 km) were seen. The survey lines flown and the distribution of all sightings recorded in July are shown in Figure 2. Sea states were generally good during the survey, ranging from Beaufort 2 to 4.

The distribution of sightings in July suggests that gray whales were concentrated in a broad swath extending (roughly) from Cape Prince of Wales on the Seward Peninsula south to Northeast Cape on St. Lawrence Island. Few gray whales were seen in offshore areas to the east or west of the swath. Gray whales were also found in substantial numbers in nearshore waters to the east and west of St. Lawrence Island.

Only one of the two sets of survey lines was flown during the second survey period (9-10 September) totalling 1933 km. Twenty-seven whales were recorded (14.0 whales/1000 km of survey line; Figure 3). Sea states were higher than observed in July, ranging from Beaufort 3 to 4 (average 3.5). The general distribution of whales appears to have been similar to that observed in July with the exception that no whales were seen north or west of King Island during the September survey. However, the lack of sightings in that area may be an artifact of the lower sampling effort during the second survey.

Feeding gray whales often bring considerable amounts of mud to the surface, which remains visible after the whale has dived. Thus, the distribution of mud plumes provides additional information about gray whale distribution beyond that provided by sightings of whales themselves. The distributions of all feeding plumes seen are plotted in Figures 4 and 5. These distributions correspond very closely to the distributions of whale sightings (Figs. 2 and 3). Thus, it appears that gray whales were feeding throughout all of the areas in which they were recorded. (For more details on the relationships between sightings, feeding plumes and gray whales see later section--Detectability of Feeding Plumes.)

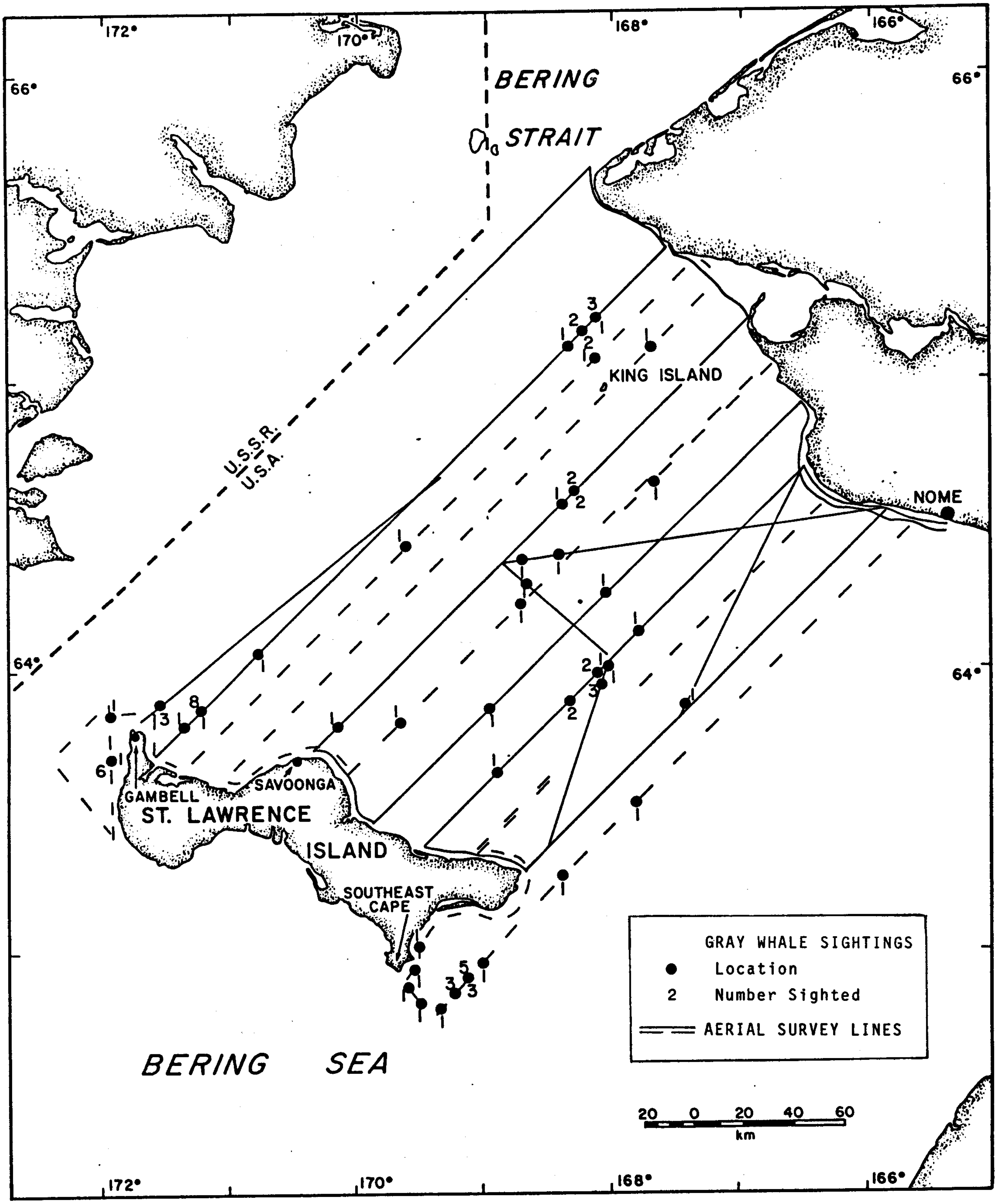


FIGURE 2. Survey lines and sightings of gray whales during aerial surveys on 10-17 July 1982.

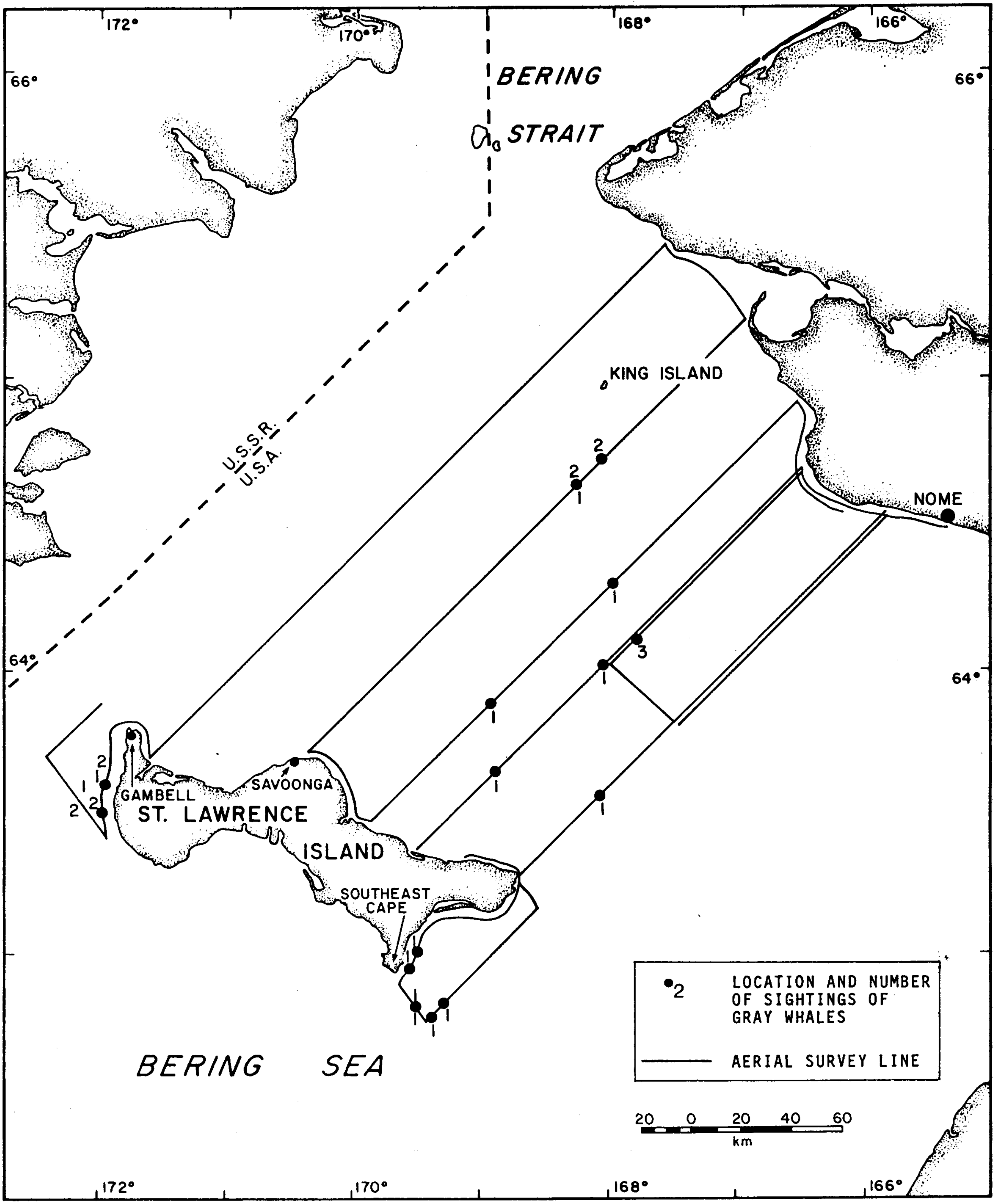


FIGURE 3. Survey lines and sightings of gray whales during aerial surveys on 9-10 September 1982.

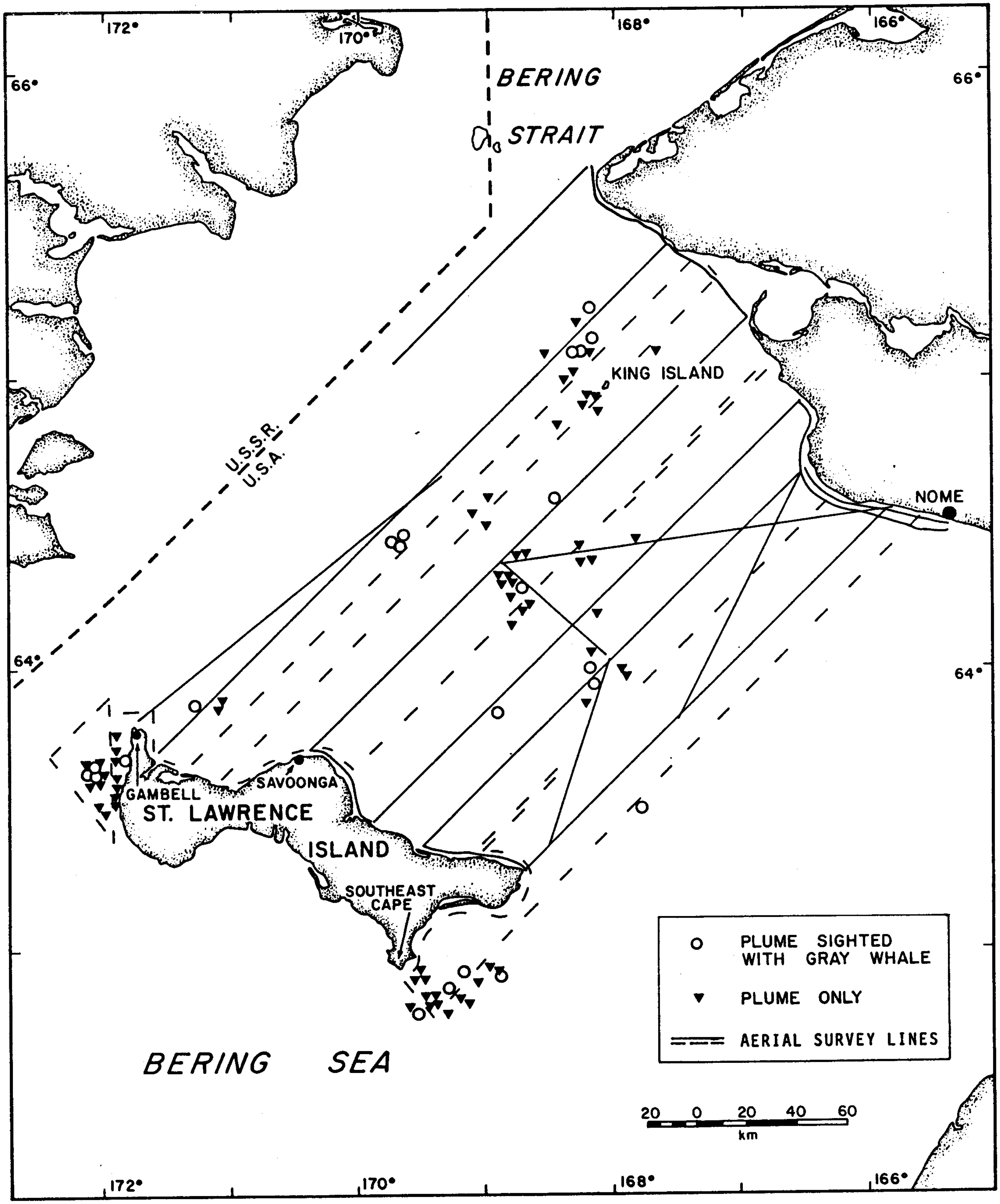


FIGURE 4. Aerial survey lines and sightings of mud plumes from feeding gray whales, 10-17 July 1982.

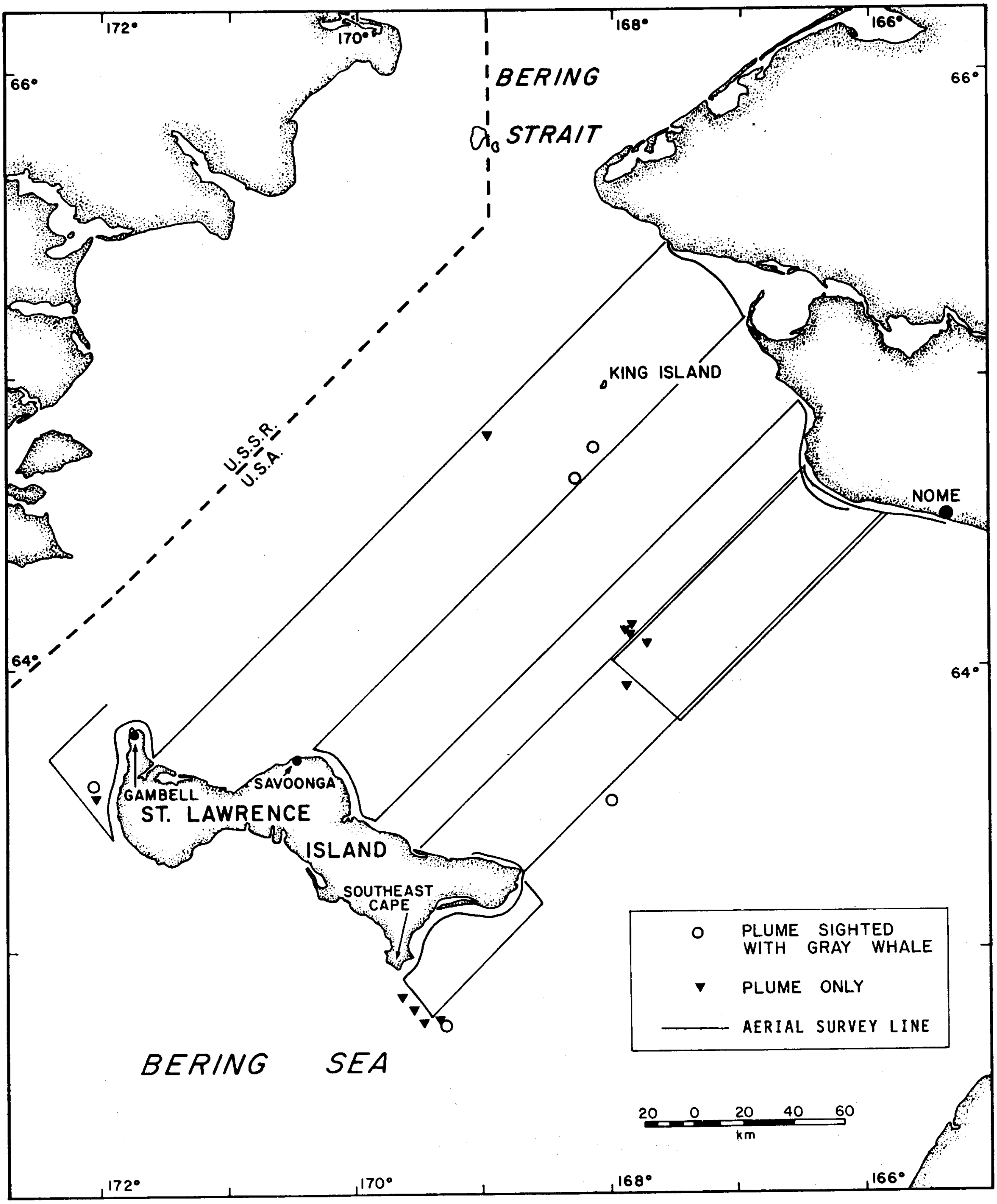


FIGURE 5. Aerial survey lines and sightings of mud plumes from feeding gray whales, 9-10 September 1982.

Population Estimation Procedures

In a later section we estimate the size of the gray whale population inhabiting the study area during the two surveys. The estimates are based on the gray whale sightings along the straight-line transects across the Chirikof Basin (see Figs. 6 and 7 for the July and September transects and sightings used in calculations). Line transect procedures were used to obtain 'raw' estimates of gray whale densities. In order to derive population estimates, we applied correction factors to the raw densities. These correction factors accounted for gray whales that were submerged and therefore not visible to the observers. The 'corrected' densities were applied to the area within the six survey bands (Fig. 1) to estimate the number of whales within those bands.

Survey Models

Use of inclinometers enabled us to estimate the perpendicular distance from the flight path to each whale we sighted. The availability of these estimates allows us to calculate gray whale densities according to either strip transect or line transect models, both of which are used commonly in aerial censuses of marine mammals (Eberhardt et al. 1979).

The choice of which of these two models to use depends on a number of factors, especially the distribution of lateral detection distances from the flight path. The lateral detection distances of gray whales sighted on the pre-established survey lines are plotted separately for July ($n = 41$) and September ($n = 13$) in Figure 8. We compared the lateral distances at which gray whales were observed during the two surveys, lumping sighting distances into categories of 0-500, 500-1000, 1000-1500 and 1500+ m from the flight path of the aircraft. No significant difference was found between the two surveys ($chi^2 = 3.40$, $df = 3$, $p>0.30$).

The median distances at which gray whales were sighted did differ considerably between July (470 m) and September (860 m), however, and some possible explanations for this difference are discussed below.

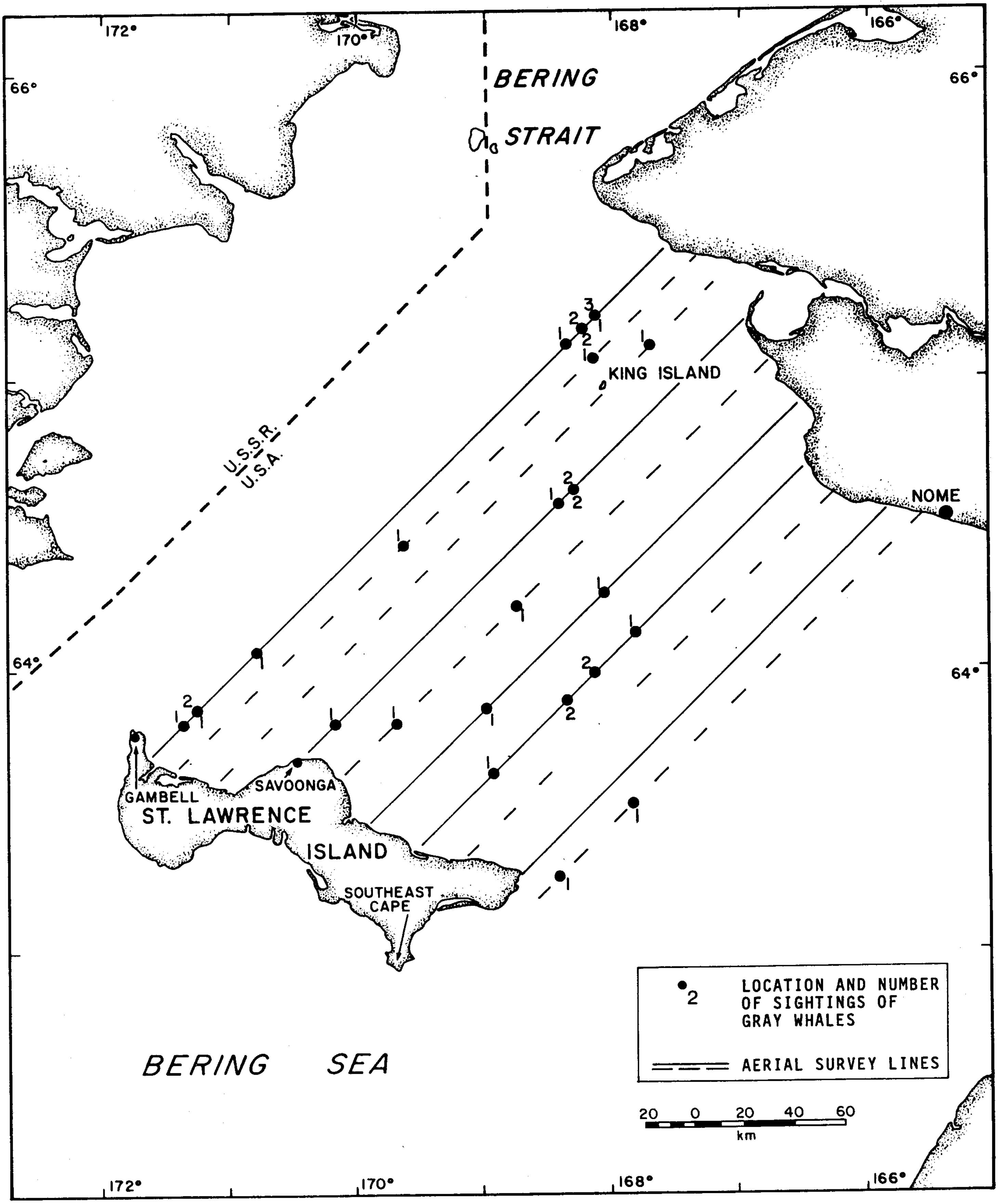


FIGURE 6. Aerial survey lines and whale sightings used to estimate gray whale abundance in July 1982. Sightings along opportunistic transects and at lateral distances <100 m or >2100 m are excluded (see text).

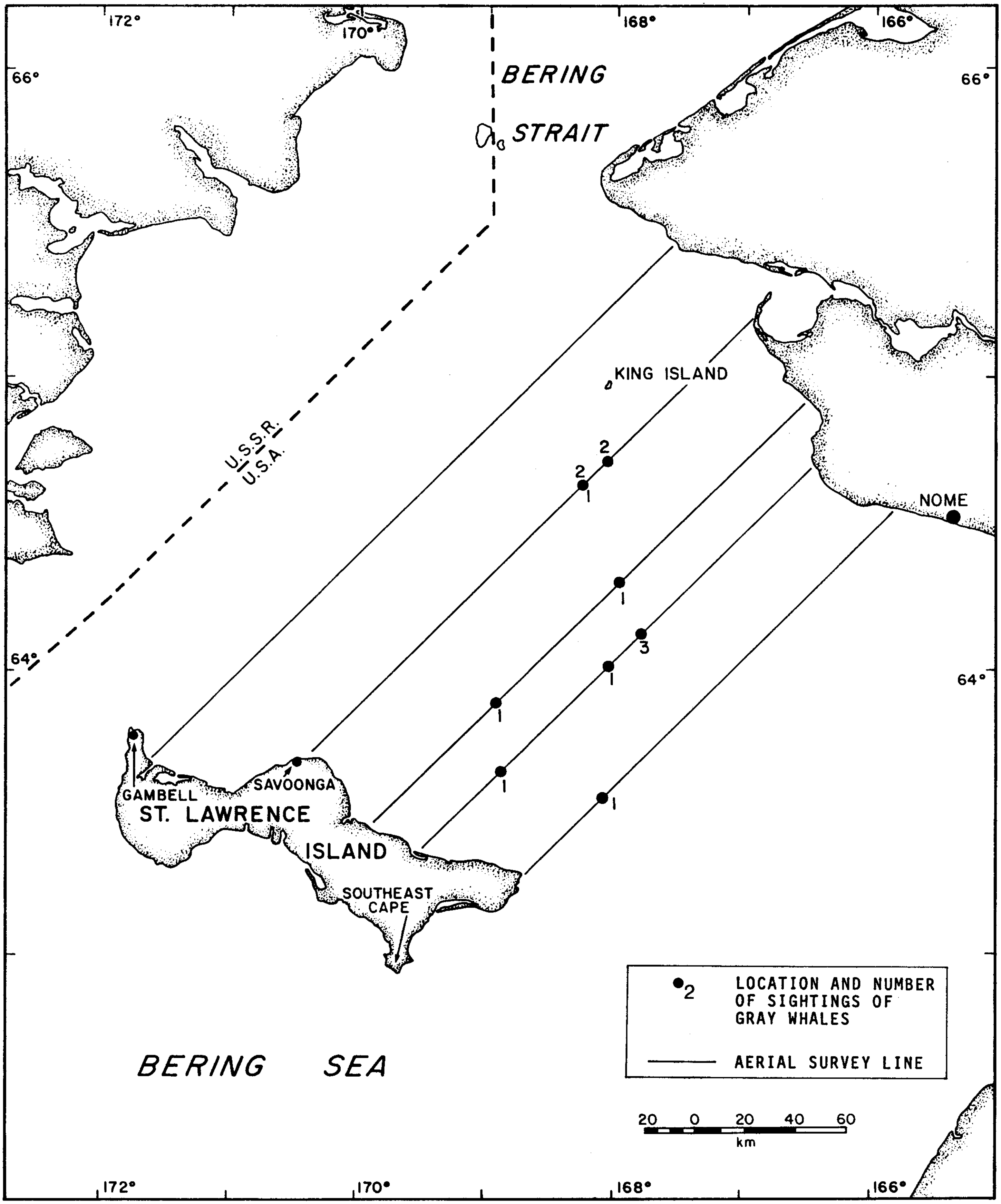


FIGURE 7. Aerial survey lines and whale sightings used to estimate gray whale abundance in September 1982.

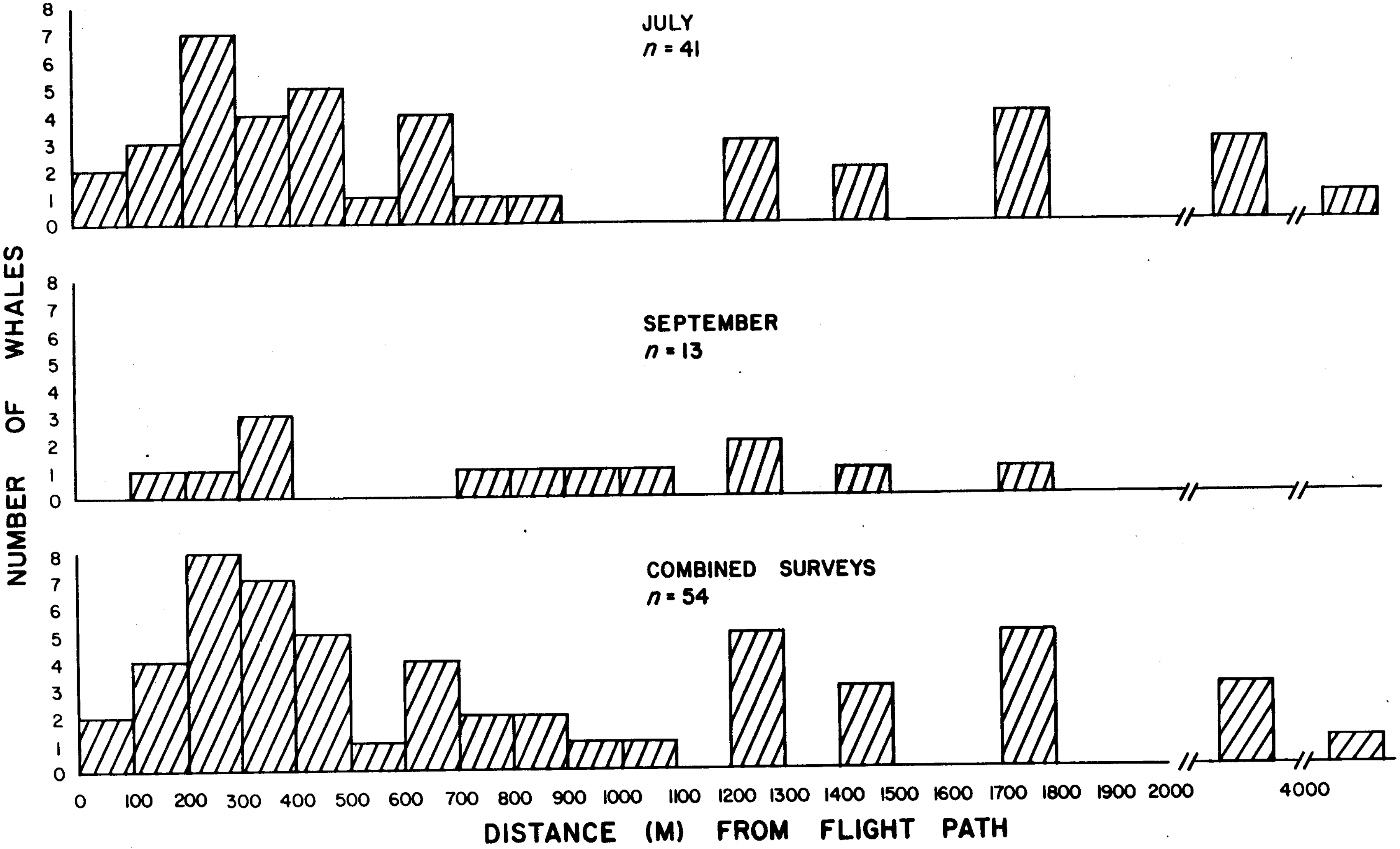


FIGURE 8. Distribution of lateral distances of gray whales sighted during aerial surveys.

The sample sizes for both the July and September surveys were small (41 and 13, respectively) and sampling error may account for some of the observed difference. Of the other variables that might conceivably account for differing lateral sighting distances (aircraft type, seating position, aircraft speed and weather and sea state conditions), sea state seems to be the most likely cause.

Sea states were generally higher in September than in July and this may have affected the sighting cues that the aerial observers relied on to spot and recognize gray whales. The aerial observers recorded, when possible, the sighting cues that first brought their attention to a gray whale. These cues included the whale itself (body, back, flukes), feeding plumes, aggregations of feeding birds, and blows (exhalation) from the whale. Blows tended to be visible at greater distances than other sighting cues. For example, in July the mean lateral distance of whales whose sighting cues were blows was 1803 m (n = 13) compared to 441 m for all other cue types (n = 20). In September, the comparable distances were 1223 m (n = 6) and 517 m (n = 6).

Although, intuitively, it may seem that higher sea states would decrease the likelihood of seeing whales at a distance, this may not be the case for whales that are sighted with a blow as the cue. Blows are conspicuous even in moderately high sea states. The probability of sighting a whale's back or body definitely deceases with increasing sea state because white caps, spray and swells tend to conceal such cues. The moderately higher sea states encountered in September may have decreased the sightability of whales near the aircraft, but left the sightability of whales farther from the aircraft, where blows are the most important sighting cue, relatively unchanged. In September, blows were the sighting cue for 50% (6 of 12) of the whales recorded compared to 29% (8 of 27) in July. Thus, in September, fewer whales may have been recorded and the distribution of lateral sighting distances may have been biased toward whales farther from the aircraft. This bias makes the estimating procedure more conservative and results in a lower population estimate for September.

A fundamental assumption underlying the strip transect model is that animals be equally detectable in all parts of the transect. To test this assumption we examined the combined (n = 54) distribution of lateral distances for surveys 1 and 2 (Fig. 8). Based on these data it would be difficult to choose a transect width that would satisfy the assumption of equal detectability. There appears to be a zone close to the aircraft (0-100 m from flight path) where few gray whales were detected. If we exclude this region and consider a hypothetical 1000 m transect width from 100 to 1100 m from the aircraft, we find that 71% (25) of the gray whales sighted were in the inner half (100-600 m) of the transect and only 29% (10) were in the outer half. This difference is statistically significant (binomial test, $p<0.05$). Thus, these data do not appear to be appropriate for strip transect analysis.

In the following section we use the line transect method to estimate the 'raw' density of gray whales in the survey area. The advantage of the line transect method is that animals in all parts of the transect need not be equally detectable. The line transect model assumes that all animals at the center of the transect (i.e. at zero distance from the survey line) are detected, and that the detectability of animals decreases with increasing distance from the line.

Uncorrected Estimates of Numbers Present in Study Area

We calculated uncorrected density estimates for each of the two surveys according to the line transect method of Burnham et al. (1980) using a computer program which they developed (TRANSECT version 1.1; Laake et al. 1979). The sightings used in the program are those shown in Figures 6 and 7. The line transect model assumes that all animals at zero lateral distance are recorded by the observers. Our data (Fig. 8) suggest that whales closest to the transect lines (0-100 m) were less likely to be seen than whales farther from the lines (100+ m). This is to be expected because it was impossible to detect whales directly below either of the survey aircraft that were used. To compensate for this, we eliminated two sightings of whales seen at distances of 90 m from the transect line and assumed that our transect began at 100 m from the aircraft flight path. All sighting distances were accordingly decreased by 100 m for the purpose of using the computer program. We truncated the sighting distances at 2100 m, eliminating a further four sightings beyond that distance. Two pairs of whales were treated as single sightings because the line transect method requires independent sightings. The resulting sample sizes used in the analysis were 33 and 13 sightings for the first and second surveys, respectively, based on a transect width of 0-2000 m (originally 100-2100 m).

The formula used to calculate the density of sightings is

$$D = \frac{N \cdot f(0)}{2L}$$

where N is the sample size of observations, L is the total line length and f(0) is the probability density function of the distribution of lateral distances at lateral distance 0. TRANSECT used the data to calculate probability density functions based on three different models

1. non-parametric linear (Fourier Series),
2. simple parametric (negative exponential),
3. generalized parametric (exponential power series).

Any of these models will provide a value of f(0) that can be used as an estimator in the above density formula. The values of f(0) determined from the above models are shown in Table 1. The f(0) values derived from the three models for the July survey were very similar, ranging from 1.511-1.587. The f(0) values calculated for the September survey were more variable, ranging from 0.667-1.033 (Table 1).

We used the f(0) values determined from the Fourier Series method for both the July and September surveys. The use of this estimator has been recommended by Burnham et al. (1980) on the basis of its robustness, shape criteria and its estimation efficiency for small samples. The fit of the Fourier Series probability density functions to our data (pooled into four lateral distance categories) is shown in Figure 9. Burnham et al.

Table 1. Line transect estimates of the abundance of gray whales in July and September 1982.

Survey	Model	f(0)	χ^2 probability	D*
July	Fourier Series	1.511	-**	0.01087
	Negative Exponential	1.534	0.474	0.01104
	Exponential Power Series	1.587	0.230	0.01142
Sept.	Fourier Series	0.813	0.953	0.00460
	Negative Exponential	1.033	0.767	0.00584
	Exponential Power Series	0.667	0.610	0.00377

* Raw sighting density (per km^2). July figures must be multiplied by 35/33 to convert to whale density, since two sightings involved pairs of whales.

** There were too few degrees of freedom to determine a chi^2 probability.

(1980) suggest that the Fourier Series performs well with samples as small as 30-40 sightings. Thus, the estimate for July based on 33 sightings may be considerably more reliable than the September estimate based on only 13 sightings.

Substitution of the f(0) values from the Fourier method into the aforementioned formula for density leads to raw density estimates of 0.0109 sightings/km^2 or 0.0115 whales/km^2 in July, and 0.0045 whales/km^2 in September. The difference between the two figures for July results from the fact that two of the 33 sightings involved two whales; the other 31 sightings in July and all 13 sightings in September were of single whales. These densities correspond to raw estimates of about 540 (July) and 215 (September) gray whales in the six survey bands, whose total area was 46,860 km^2.

Use of strip transect methods would have resulted in lower estimates. If we had chosen a 1000 m transect width (100-1100 m) on either side of the aircraft, the resulting raw density for July would have been 26 whales/4586 km^2, or 0.0057 whales/km^2. The September density would have been 9 whales/2300 km^2, or 0.0039 whales/km^2. Applying these densities to the 46,860 km^2 study area results in raw population estimates of 266 (July) and 183 (September) gray whales.

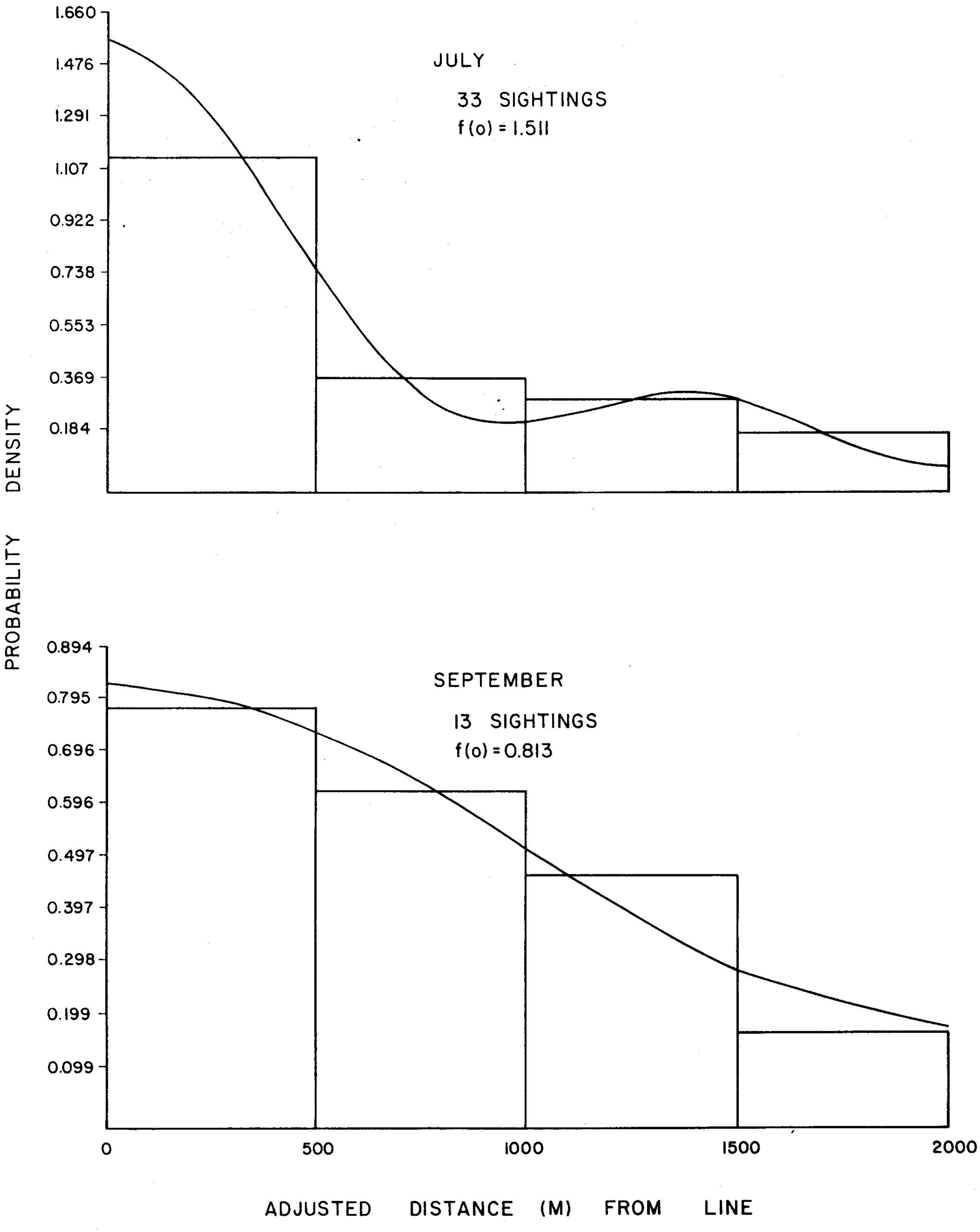


FIGURE 9. Fit of Fourier series probability density functions to lateral distances of gray whale sightings in July and September 1982.

Corrections for Submerged Gray Whales

Feeding gray whales spend large amounts of time below the surface of the water. Submerged whales are invisible to aerial surveyors and aerial survey results must be corrected to account for this if reliable population estimates are to be made. Information on the relative amounts of time gray whales are above and below the surface was obtained from ship-board observations during the present study (Würsig et al., this report).

Duration of Potential Detectability.--To correct the raw density estimates for submerged whales, it is necessary to estimate the parameter t, which is the period of time a whale at the surface is potentially detectable from the passing aircraft. The value of this parameter depends on the perpendicular distance between the flight track and the whale, the observer's horizontal field of view, and the aircraft's speed. We estimated two "average" values for t, one for the Grumman Goose (first survey), and one for the Twin Otter (second survey) according to the following formula

$$t = \frac{2 \tan \frac{\theta}{2} \cdot x}{v}$$

where θ is the field of view of the observer, x is the median sighting distance from the flight track, and v is the velocity of the aircraft. The parameters used to estimate t are shown in Table 2.

Table 2. Parameters used to estimate duration of potential detectability of a whale (t) for surveys 1 and 2.

Survey	Aircraft Type		x(km)	v(km/s)	t (s)
1	Grumman Goose	110°	0.47	0.067	20
2	Twin Otter	90°	0.86	0.057	30

The estimates of t (20 and 30 s for the Grumman Goose and Twin Otter, respectively) are approximations because of variation in survey speed and rather arbitrary estimates of the viewing angles from the two aircraft. We felt that windows in the Grumman Goose offered the observers a wider field of view than the narrower windows in the Twin Otter. This difference was probably offset to some extent, however, by the fact that one of the two observers in the Twin Otter occupied the co-pilot's seat and had improved forward visibility. The viewing angles we selected may be less than the maximum possible viewing angles: we attempted to estimate a "normal" field of view likely to be exercised by an observer.

Calculation of Correction Factors.--If all surface times are of length s, all dives are of length u and the duration of potential detectability is t, then probability that a whale will be at the surface (or will surface) while within the observer's field of view is

$$P = \frac{s}{s+u} + \frac{t}{s+u} = \frac{s+t}{s+u}$$

(Eberhardt 1978). In the above equation, s/(s + u) is the probability that the whale will be at the surface when its location first comes into visual range, and t/(s + u) is the probability that the whale will surface while its location is in visual range. The uncorrected estimate of the number of animals present should be divided by P to allow for animals that are undetectable because they are submerged when the aircraft passes over.

The above formula assumes that s and u are constant and that $t \leq u$. Conventionally, s and u are taken to be the mean duration of surfacings and dives. In fact, some dives may be short ($u<t$), and s and u are both highly variable and skewed.

Davis et al. (1982) developed a corrected version of the (s + t)/(s + u) formula that allows for dives that are short in duration ($u<t$). Their procedure also allows for the fact that s and u are variables that may have non-normal distributions. However, they found that this is not a critical factor provided that the cases with $u<t$ are treated separately.

We followed the approach of Davis et al. (1982), and calculated separate correction factors for July and September. The July correction factor was based on observations of 444 paired surfacings and dives during the 12-21 July period (data from Würsig et al., this report). All 444 of these dives were >20 s in duration. The September correction factor was based on observations of 376 paired surfacing/dive cycles in the 12-27 September period. Five of the 376 dives were <30 s in duration. The calculations from which the correction factors for July and September are derived are shown in Table 3. The correction factors by which raw abundance estimates should be divided are 0.280 for July and 0.358 for September.

Corrected Abundance Estimates

Dividing our raw population estimates (540 and 215) by the two correction factors derived above, we calculated corrected population estimates for the 46,860 km^2 survey area of 1929 (July) and 601 (September). Although these estimates allow for whales below as well as at the surface, they may be conservative because no attempt was made to correct for whales at the surface that might have been missed by the observers. Davis et al. (1982) developed such a correction factor for bowheads. They estimated that only 68.5% of the bowheads at the surface in their study were detected by the primary observers.

Had we used conventional strip transect methods, our 'corrected' estimates would have been 950 for July and 511 for September.

Detectability of Feeding Plumes

We examined the distribution of feeding plumes to determine whether they might be used as an index of gray whale abundance.

First, we looked at the limits of detectability of feeding plumes. The lateral detection distances were estimated for 99 of 101 sightings of plumes, separately for July and September surveys (Figure 10). There was a marked decrease in sightability at distances beyond 500 m from the flight path of the aircraft. Only five of 82 (6%) of the feeding plumes sighted

Table 3. Calculation of the probability that an average whale within the surveyed area will be at the surface while within an observer's field of view. All times are in seconds.

Observation period	Sum of dive durations	Sum of surface times	# dives and surfacings	Mean surface time (s)	Mean dive time (u)	$\frac{s+t}{s+u}$
12-21 July						
dives ≤20 s	-	-	0	-	-	-
dives >20 s	91,518	23,303	444	52.48	206.12	0.280
All dives	91,518	23,303	444	52.48	206.12	0.280
12-27 September						
dives ≤30 s	86	45	5	9.00	17.20	-
dives >30 s	66,765	19,716	371	53.14	179.96	0.357
All dives	66,851	19,761	376	52.56	177.80	0.358
					corrected*	0.358

* Following the method of Davis et al. (1982), the corrected (s + t)/(s + u) is calculated as

$$\frac{[(86 + 45) \times 1.0] + [(66{,}765 + 19{,}716) \times 0.357]}{(66{,}851 + 19{,}761)} = 0.358$$

Using three digits of precision, the corrected result is unchanged from the conventional result--a consequence of the very low percentage of surfacing/dive cycles for which u<t.

from the Goose and none of the 17 sightings from the Twin Otter were at distances >500 m from the flight path. As with whale sightings, few plumes were seen <100 m from the flight track.

We looked at the number of whales that were accompanied by at least one feeding plume, restricting the tabulation to whales sighted at distances between 100 and 500 m from the flight path (Table 4). The percentages of whales accompanied by at least one feeding plume were 42% (8 of 19) in the July survey, 60% (3 of 5) in the September survey, and averaged 46% (11 of 24) in the combined surveys.

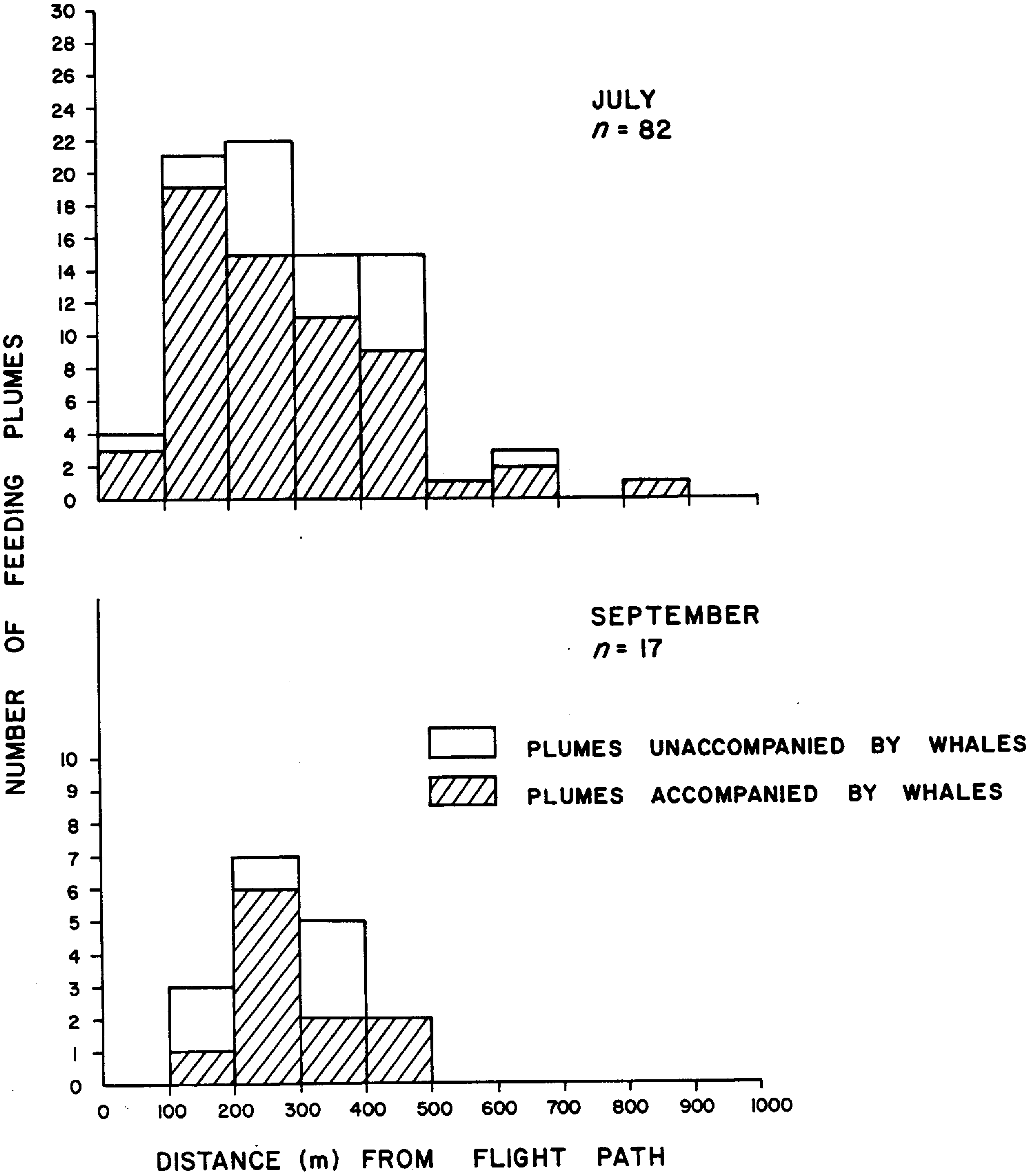


FIGURE 10. Distribution of lateral distances of mud plumes created by gray whales and sighted during aerial surveys.

Table 4. Sightings of gray whales and mud plumes during each aerial survey.

	Whales*			
Survey	Total	with plumes (%)**	without plumes (%)	Plumes without whales
1A	13	5 (38.5)	8 (61.5)	4
1B	6	3 (50.0)	3 (50.0)	11
Sub-total	19	8 (42.1)	11 (57.9)	15
2	5	3 (60)	2 (40)	2
Total	24	11 (45.8)	13 (54.2)	17

* Sighted between 100 and 500 m from the flight track.

** Closely grouped plumes that looked as though they might have been the result of a single whale's feeding activities were considered as one plume in this analysis.

Alternative Population Estimate Using Sightings of Mud Plumes

We used the mud plume data to obtain an entirely different estimate of abundance based on the strip transect method. Assuming a 400 m transect width on each side of the aircraft (lateral distance 100-500 m), we counted the number of whales sighted and used the number of unaccompanied plumes to correct for submerged whales.

In survey 1, eight of 19 whales sighted between 100 and 500 m from the flight path were accompanied by feeding plumes. If we assume that the same proportion of submerged whales would create plumes, then the number of submerged whales can be estimated by dividing the number of unaccompanied whale plumes by that proportion. In the first July survey, we saw 15 unaccompanied plumes at lateral distances of 100-500 m. Dividing that number by 8/19, we calculate that 35.6 additional submerged whales were present in the transect strip. Thus 54.6 whales (19 + 35.6) were present in the 2293 km of transect (width = 0.8 km) flown. This corresponds to a density of 54.6 whales/1834 km^2 or 0.0298 whales/km^2. Using the same approach for the second survey we calculated a density of 0.0123 whales/km^2. Applying those two densities to the sum of the areas in our six survey bands (46,860 km^2) results in population estimates of 1396 whales during the July survey and 576 whales during September. These estimates are reasonably close to our previously derived estimates of 1929 and 601 based on the line transect method with adjustment for submerged whales.

Shipboard Observations of Gray Whales

In July, approximately 291 gray whales were observed during station scans, transect counts and other shipboard operations in the nearshore waters of St. Lawrence Island (Table 5). Similarly, 116 gray whales were observed in September. In intensively worked areas and areas where whales were numerous, the same whales may have been counted several times. In these areas, the observers estimated the total number of whales present. These area estimates (Fig. 11) include whales observed along transects and during station scans.

High densities of whales were found off Southeast Cape, the south and west coasts of St. Lawrence Island, in the south central Chirikof Basin, and across the international boundary in the northwest part of the Chirikof Basin (observed from U.S. waters on a clear night; Fig. 11). No whales were observed along the north coast of St. Lawrence Island and only two whales were observed in the northern part of the study area between King Island and Nome.

The distribution of whales observed from the ship closely parallels that found during aerial surveys conducted during this study (Fig. 2-5).

DISCUSSION

Northward migrating gray whales arrive at St. Lawrence Island in May and June, and in summer are dispersed to the north and west (Braham in press). Approximately 17,000 whales enter the Bering Sea (Rugh in press). An estimated 7700 to 7800 are found in Russian waters (Zimushko and Ivashin 1980). Ljungblad et al. (1982, 1983) conducted aerial surveys throughout the Chukchi and northern Bering seas in 1981 and 1982 and computed densities of whales for these areas. The regions surveyed during the present study

Table 5. Level of effort and numbers of whales observed during shipboard observations in the Chirikof Basin and near St. Lawrence Island during the summer of 1982.

Day	Location	Type	Level of Effort	No. Whales Observed
July:				
10	Approaching southwest coast of St. Lawrence Island	Transect	13.0 h	0
11-14	West coast of St. Lawrence Island	Area estimate	4 d in area	65
15	North coast of St. Lawrence Island	Transect	5.5 h	0
16-21	Southeast Cape of St. Lawrence Island	Area estimate	6 d in area	40
22-23	Chirikof Basin, station 7A to Date Line	Transect	8.6 h	39
		Station scans	4.2 h	43
23	Across international boundary	Area estimate		100
24	King Island	Area estimate	4 h in area	4
25	King Island to Nome	Transect	8.1 h	0
		Station scans	2.8 h	0
27	South of Nome	Transect	3 h	0
September:				
12	Approaching Southeast Cape of St. Lawrence Island	Transect	6.8 h	21
13-15	Chirikof Basin	Transect	7.0 h	0
		Station scans	1.5 h	2
16	South coast of St. Lawrence Island	Transect	5.3 h	17
		Station scans	1.2 h	41
17	East coast of St. Lawrence Island	Station scans	0.5 h	0
18	Boxer Island	Area estimate	1 d in area	15
20-23	Southeast Cape of St. Lawrence Island	Area estimate	4 d in area	20
24	Gambell to Savoonga; north coast of St. Lawrence Island	Transect	2 h	0

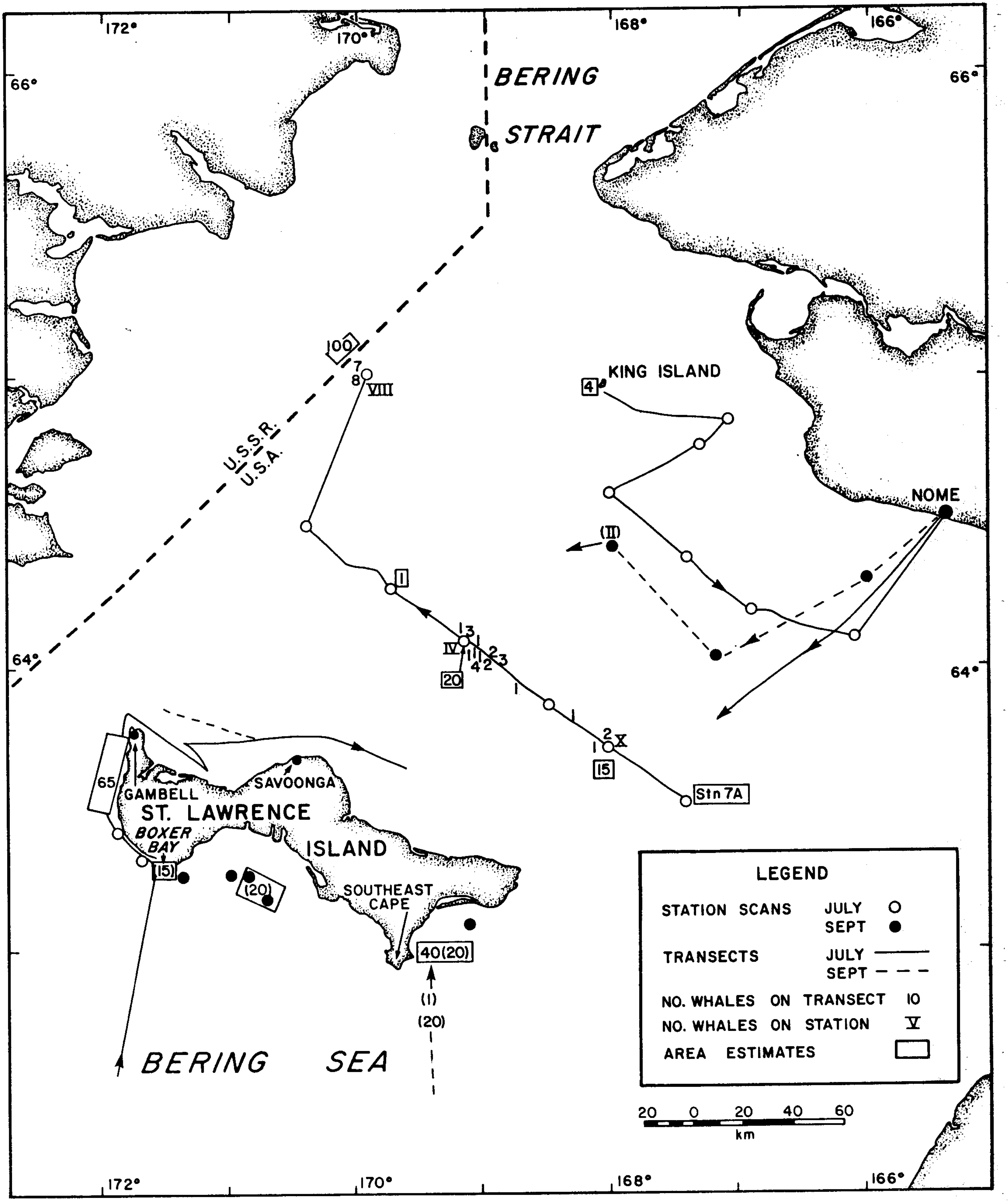


FIGURE 11. Gray whales observed during shipboard observations in the Chirikof Basin and near St. Lawrence Island during July and September 1982. Observations and estimates made in September are in parentheses. Area estimates in the Chirikof Basin include animals counted during nearby station scans and transect observations.

included some or all of blocks 5, 6, 7, 8, 10 and 11 surveyed by Ljungblad et al. (1983; Fig. B-26) in 1981 and 1982. Their mean raw density estimate for the whole area encompassed by these blocks between June and August 1981 was 0.0125 whales/km^2, and their raw mean density estimate for July 1982 was 0.0106 whales/km^2. Total area considered in their estimate was 62,848 km^2, including the Chirikof Basin and the west coast of St. Lawrence Island. Application of our July correction factor for whales below the surface to Ljungblad et al.'s data yields an estimated 2805 whales for 1981 and 2379 whales for 1982. Ljungblad et al.'s raw density estimates are close to the estimate of 0.0115 whales/km^2 found during the present survey. The total area of 46,860 km^2 surveyed during this study was smaller than the area surveyed by Ljungblad et al. and the estimate of 1929 whales/km^2 found during this study in July is correspondingly smaller.

In 1982, 105 gray whales were estimated to be in the areas observed from the ship off Southeast Cape and the west coast of St. Lawrence Island in July, and an estimated 76 whales were off the south coast and Southeast Cape in September. These results are also similar to estimates based on Ljungblad et al.'s (1982) data--193 gray whales in the St. Lawrence Island area in 1981. Densities were higher in 1982 (Ljungblad et al. 1983) and application of the correction factor yielded an estimate of 805 whales off Southeast Cape. Ljungblad et al.'s (1983) coverage of the southwest and south coasts in 1982 was insufficient for estimation.

The distribution of whales appears to have been similar in 1981 and 1982. Surveys conducted by Ljungblad et al. (1982: Fig. B-76 and 1983: Fig. B-64) also show high densities of whales off Southeast Cape of St. Lawrence Island, the west coast and in the south central basin, and no whales in the northeastern or southwestern part of the basin, or close to shore along the north coast of St. Lawrence Island.

The area across the international boundary where we estimated 100 whales to be present is part of an area referred to as the "large kitchen-garden" by Russian authors. In summer it may harbor up to 400 gray whales (Votrogov and Bogoslovskaya 1980).

Gray whales generally depart Russian waters in mid October to November, and passage out of the Bering Sea is between mid November and mid December (Rugh and Braham 1979; Yablokov and Bogoslovskaya in press). The decline in estimated whale numbers from 1929 in July 1982 to 601 in September 1982 is inexplicable in terms of what is known of their movements. It is not known whether these animals moved north, west or south between July and September.

ACKNOWLEDGMENTS

The gray whale feeding ecology project of which this distribution study was a part was funded by the Minerals Management Service through interagency agreement with the National Oceanic and Atmospheric Administration, as part of the Outer Continental Shelf Environmental Assessment Program. Aerial surveys in July were done with the cooperation of the Naval Oceans Systems Center, San Diego, whose personnel shared the use of the Office of Aircraft Services' Grumman Goose with us. I thank D.K. Ljungblad of NOSC, and S.E. Moore and E. Barrowclough of Hubbs Sea-World. We are grateful to Sitnasuak Native Corporation for logistic help and to pilot B. Jorgensen for his exceptional efforts during the September survey. C.R. Evans and M.S.W. Bradstreet of LGL participated in the surveys.

Shipboard observations and behavioral data were provided by B. Würsig, R. Wells, D. Croll, M. Newcomer and L. Spear of Moss Landing Marine Laboratories. I thank C. Holdsworth of LGL for implementing the TRANSECT program on our computer installation; J. Richardson, D. Thomson and B. Würsig for assistance with various parts of the report; B. DeLong for preparing the figures; and B. Griffen for typing the report.

LITERATURE CITED

Braham, H.W. In press. Migration and distribution of gray whales in Alaska. In: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Burnham, K.P., D.R. Anderson and J.L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. No. 72. 202 p.

Davis, R.A., W.R. Koski, W.J. Richardson, C.R. Evans and W.G. Alliston. 1982. Distribution, numbers and productivity of the Western Arctic stock of bowhead whales in the eastern Beaufort Sea and Amundsen Gulf, summer 1981. Rep. by LGL Ltd., Toronto, for Dome Petroleum Ltd., Calgary, and for Sohio Alaska Petroleum Co., Anchorage, AK. 134 p.

Eberhardt, L.L. 1978 Transect methods for population studies. J. Wildl. Manage. 42:1-31.

Eberhardt, L.L., D.G. Chapman and J.R. Gilbert. 1979. A review of marine mammal census methods. Wildl. Monogr. No. 63. 46 p.

Laake, J.L., K.P. Burnham and D.R. Anderson. 1979. User's manual for program TRANSECT. Utah State Univ. Press, Logan. 26 p.

Ljungblad, D.K., S.E. Moore and D.R. Van Schoik. 1983. Aerial surveys of endangered whales in the Beaufort, eastern Chukchi and northern Bering Seas, 1982. NOSC TD 605. Naval Ocean Systems Center, San Diego, CA. 382 p.

Ljungblad, D.K., S.E. Moore, D.R. Van Schoik and C.S. Winchell. 1982. Aerial surveys of endangered whales in the Beaufort, Chukchi, and northern Bering Seas. NOSC TD 486. Naval Ocean Systems Center, San Diego, CA. 406 p.

Nerini, M.K. 1980. Gray whale feeding ecology. Unpubl. rep. by Nat. Mar. Fish. Serv., Seattle, for Outer Cont. Shelf Envir. Assess. Prog., Nat. Oceanic & Atmos. Admin., Juneau, AK. 35 p.

Rugh, D. In press. Census of gray whales at Unimak Pass, Alaska, November-December 1977-9. *In*: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Rugh, D. and H.W. Braham. 1979. California gray whale (*Eschrichtius robustus*) fall migration through Unimak Pass, Alaska, 1977: A preliminary report. Rep. Int. Whal. Comm. 29:315-320.

Votrogov, L.M. and L.S. Bogoslovskaya. 1980. Gray whales off the Chukotka Peninsula. Rep. Int. Whal. Comm. 30:435-437.

Yablokov, A.V. and L.S. Bogoslovskaya. In press. Review of the Russian research on biology and commercial whaling of the gray whale. *In*: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Zimushko, V.V. and M. Ivashin. 1980. Some results of Soviet investigations and whaling of gray whales (*Eschrichtius robustus*, Lilljeborg, 1861). Rep. Int. Whal. Comm. 30:237-246.

BEHAVIOR OF SUMMERING GRAY WHALES

by

Bernd Würsig and Donald A. Croll

Moss Landing Marine Laboratories

Randall S. Wells

Joseph M. Long Marine Laboratory
University of California

1983

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

The behavior of gray whales was studied near St. Lawrence Island, Alaska, in July and September 1982. Most behavior involved apparent feeding near the bottom, as evidenced by mud plumes around surfacing whales, and kittiwakes landing near whales at the surface. There was little socializing by whales in July, but more toward the end of September.

Number of blows per surfacing, durations of surfacings, and durations of dives were all correlated. Whales spent about 21% of their time at the surface in July, and 23% of their time at the surface in September. There were fewer blows per surfacing, shorter surface times, and shorter dive times when whales were not feeding than when they were feeding. Intervals between successive blows were longer in non-feeding whales, but blow rate was not appreciably different with and without feeding.

Number of blows per surfacing and duration of surfacing increased with increasing water depth (from <20 to 80 m). However, dive duration did not change appreciably with depth in July. Blow rates by feeding whales increased in deeper water, indicating the need for whales to respire more as depth of dives increased. Time of day affected surfacing-dive-respiration characteristics differently in different months. Whales fed more from 18:00-21:00 than at other times of day in both months. There was a slight month to month variation in frequency of feeding: in July, about 79% of the time was spent feeding, whereas in September, only about 69% of the time involved apparent feeding. Calculations using estimates of feeding time and data on durations of surfacings and dives indicated that an average whale may have made about 198 feeding dives per 24-h period in July, and 164 feeding dives per 24-h period in September. During a surfacing, feeding whales moved about 50 m, and during a dive their net horizontal movement was about 90 to 100 m. Speed of movement averaged around 2 km/h, and was twice as fast at the surface (3.4 km/h) as underwater (1.7 km/h).

INTRODUCTION

The behavior of gray whales has been studied in Mexican calving lagoons (for example, Norris et al. 1977, in press; Swartz and Jones in press), and at points along the migration route near the North American coast (for example, Hatler and Darling 1974; Darling in press). Few long-term behavioral observations have been reported from the northern feeding areas, although Sauer (1963) described in detail the apparent courtship and copulations he witnessed off St. Lawrence Island, Bering Sea, Alaska.

As part of a study of the feeding ecology of gray whales, we spent parts of July and September 1982 observing behavior within 3 km of St. Lawrence Island (Fig. 1). Gray whales arrive at this island as early as May, and leave as late as November of most years (Pike 1962), although the main concentration of animals appears to be present from June through September (P. Gologergen, Savoonga, St. Lawrence Island, pers comm.). In order to help answer questions related to feeding ecology, we concentrated our effort on describing the surfacing, dive, and respiration patterns of whales. Surprisingly few data have been gathered on these aspects of behavior anywhere in the gray whales' range, although Sumich (1983) and Mate and Harvey (in press) gathered respiration information during northward migration; Murison et al. (in press) did similar work on gray whales summering off Vancouver Island, Canada. Nerini (1980) presents the only previous data on dive profiles of foraging gray whales off St. Lawrence Island.

The major intent of our behavioral investigations of gray whales was to determine amount of near-bottom feeding and associated respiration, surfacing and dive variables. We also investigated distance traveled at the surface and below the surface, and speed of travel. These data are being used by benthic ecologists to assess the importance of the northern Bering Sea as a primary summer feeding area of gray whales (Thomson and Martin, this report). Our data on durations of surfacings and dives are used to estimate the proportion of gray whales in the study area that were detected during aerial surveys conducted in July and September 1982 (Miller, this report).

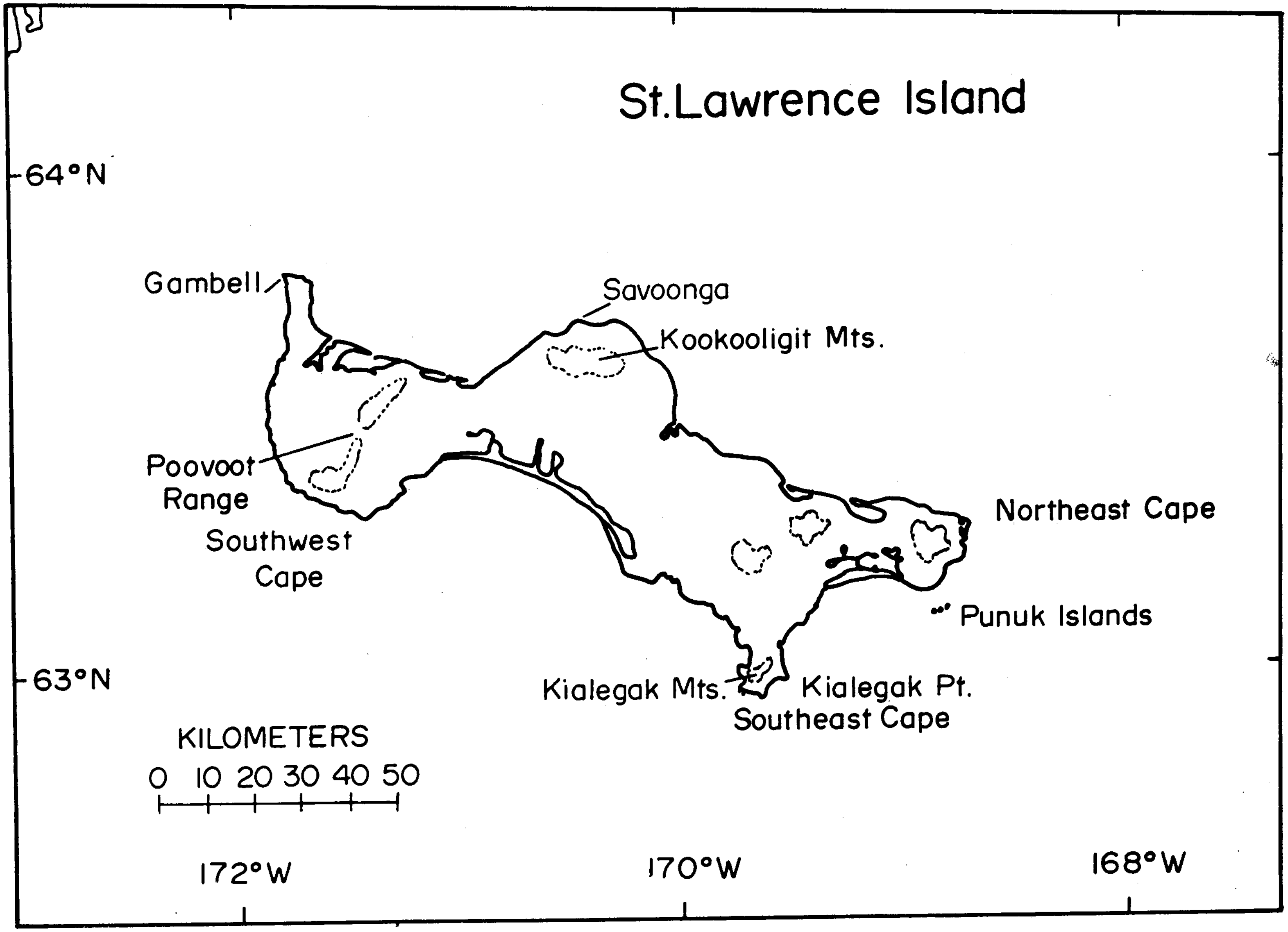


FIGURE 1. St. Lawrence Island, Bering Sea.

METHODS

In July and September 1982, the NOAA research vessels MILLER FREEMAN (length 65 m), and DISCOVERER (length 93 m), took us to the vicinity of St. Lawrence Island, Alaska, where most behavioral observations were carried out within 1 to 5 km of shore (Fig. 1). Although we watched whales from the flying bridge of MILLER FREEMAN (height above water 12 m), and the flying bridge and "aloft conning tower" of DISCOVERER (heights above water 15 m and 23 m, respectively), most observations were carried out from small vessels (4 to 8 m long) deployed from the research ships. We made detailed observations of behavior during 18 days: July 12-14, 16-21, and September 12, 16, 18-21, 23, 26, 27.

Behavioral observations were made from the large vessels while they were stationary and engaged in benthic ecology work (Thomson, this report), and from the small vessels while they were anchored, drifting, or slowly motoring within 300 m of whales. Three observers worked as a team (often with the casual help of a fourth observer); one to describe focal animals with the aid of binoculars; one to scan the surrounding area for number of whales, distances apart, direction of movement and general behavior; and one to record data and give feedback on what the other two observers might have forgotten to address. For focal animals, we systematically recorded durations of surfacings, all exhalations (termed blows), durations of dives, whether whales threw their tails out of the water upon diving, and our interpretation of general behavior.

Whales were often identified through distinctive pigment and other spot patterns and marks on their backs and/or tails. For such identified whales, we were able to determine dive durations. This technique of identification has been used successfully by Hatler and Darling (1974), Leatherwood (1974), and many other investigators.

We recorded a whale as feeding when it surfaced with mud coming off its body, or when birds landed at the surfacing site, and appeared to peck at substances in the water. The first characteristic was probably first described by Scammon (1869), and the latter in detail by Wilke and Fiscus

(1961) and Harrison (1979). In our experience, nearly all birds that landed at surfacing locations were black-legged kittiwakes (Rissa tridactyla). These were abundant off the cliffs on the west side of the island, but were seldom seen off Southeast Cape, where most of our observations were made. In the latter area, we had to rely mainly on presence of mud as evidence of feeding by the whales. Whales were scored as "possible feeding" if observed with mud at some point during the course of observation, but not upon each surfacing, as long as other aspects of their behavior pattern remained unchanged. Whales were assumed not feeding when we were close enough to be sure we could see mud if it were present and we did not see it, or when they were obviously socializing, traveling, or resting at the surface. Such negative data do not allow us to state for certain that feeding was not occurring, especially because feeding could have taken place in the water column without our knowledge.

Whales were considered socializing if they were within one-half body length of each other or were obviously interacting. We defined a group as whales within five body lengths of each other, but we realize that whales could be "grouping" by sound contact over longer distances. Resting whales were rarely seen, but when seen were quiescent at the surface for prolonged periods.

On 27 September, whales were observed from a 77-m high station near Kialegak Point, Southeast Cape (Fig. 1). Their positions and speeds of movement were plotted by the use of a Pentax TH 20D theodolite, or surveyor's transit, by a technique similar to descriptions of theodolite tracking by Würsig (1978) and Tyack (1981). These shore observations were coordinated by radio with those of observers in a small vessel.

All of the observations in this report are of "non-calf" whales. We did not obtain any data on whales that we could unequivocally call "young of the year". Our failure to recognize calves was probably because of (1) our usual low vantage point, (2) the frequent lack of any nearby whale for size reference, and (3) the fact that young are already quite large by late summer. We realize that we may have lumped data from young animals with our observations of non-calves.

Numerical data were analyzed with an Apple II+ home computer, a Hewlett-Packard 41 CV computer-calculator, and statistical techniques following mainly Sokal and Rohlf (1969) and Zar (1974).

RESULTS

General Description

Whales off St. Lawrence Island were generally alone, separated from their nearest neighbor by approximately 300 to 500 m. Most behavior appeared related to bottom feeding. We found in July that if we anchored near a feeding whale, it would stay near us, despite a current of 1 to 3 km/h. Thus, feeding whales apparently stay in roughly the same area for some time, possibly resisting current action. In July, we recognized two whales on subsequent days; one whale was sighted on 16 and 17 July and the other on 19 and 20 July. During each resighting, the whales were no more than 1000 m from the position where they fed on the previous day, and it is therefore likely that individual site tenacity during feeding is great. We have no such information for whales in September, when rough weather prevented us from anchoring or efficiently estimating distances covered by a particular whale. We also had no resightings of recognizable whales on different days in September.

In July, we obtained respiration and surfacing information on 158 whales, and only two were classified as socializing. In September, we obtained information on 53 whales, and nine of them were in social groupings. The difference between months in frequency of socializing was significant ($chi^2 = 19.84$ df = 1, $p<0.001$). Furthermore, whereas in July the two socializing whales were in groups of two, in September, five were in groups of two and four were in groups of three. In September, there were more incidences of socializing from 19-27 September (eight socializing whales among 25 whales) than during the early part of the month, 12-18 September (one socializing "focal" whale among 28 whales observed). Once again, the difference was significant ($chi^2 = 7.57$, df = 1, $p<0.025$), and the evidence appears strong that frequency of socializing increased toward the end of September. At the same time, feeding dives became shorter (to be detailed later), although feeding still took place. Ten of 158 focal whales observed in July were in groups of two (none in groups of three), while 15 of 53 whales in September were in groups of two (11 focal whales) or three (four focal whales). This difference was also significant ($chi^2 = 18.35$, df = 1, $p<0.001$). Overall, 14 of the 25 multi-whale groups were feeding, resting, or traveling rather than socializing.

Respiration and Surfacing Characteristics

The surfacing-dive cycle of the gray whale was quantified in terms of a period when the whale was below the surface, either swimming or feeding (duration of dive) and a period when the whale was at or near the surface (duration of surfacing). During each surfacing, we measured the frequency of exhalations (blows) and measured the interval between successive blows.

The blow interval, number of blows per surfacing, duration of surfacing, and duration of dive were measured 3503, 1050, 1062, and 905 times, respectively. Figure 2 presents the frequency distributions of these observations separated into the two months of field time. All variables approximated a normal distribution, and statistical comparisons with parametric tests were therefore possible.

The overall mean blow interval was 13.5 ± s.d. 7.27 s (n = 3503), and was significantly shorter in July (mean = 12.6 ± 6.45, n = 1947) than in September (mean = 14.7 ± 8.02, n = 1556) (t = 8.590, df = 3501, $p<0.001$). Number of blows per surfacing and duration of surfacing were remarkably similar in July and September (Table 1), and the combined values for the two months were 4.2 ± s.d. 2.23 blows/surfacing (n = 1050), and 0.89 ± s.d. 0.728 min surface time (n = 1062). The two values were also closely correlated, with greater numbers of blows per surfacing during longer surfacings (r = 0.636, df = 594, t = 20.08, $p<0.001$ in July; r = 0.851, df = 450, t = 34.44, $p<0.001$ in September). Durations of dives tended to be longer in July than in September (t = 4.406, df = 903, $p<0.001$). Dive duration was correlated with surfacing duration, both in July (r = 0.236, df = 441, t = 5.10, $p<0.001$), and in September (r = 0.374, df = 375, t = 7.83, $p<0.001$).

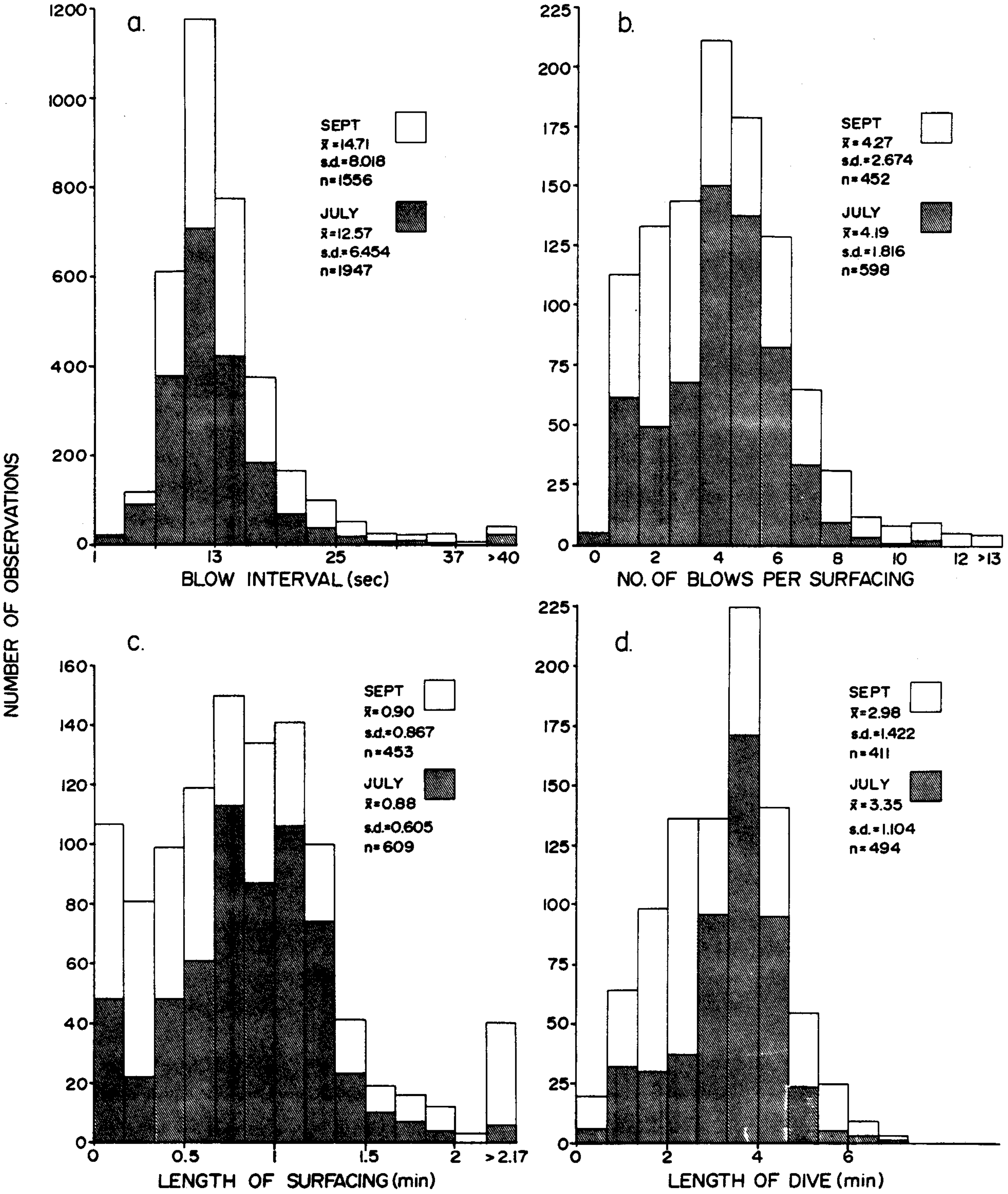


FIGURE 2. Frequency distributions of the four respiration, surfacing and dive variables.

Table 1. Summary statistics for the principal respiration, surfacing and dive variables.

	Blow interval (s)			Number of blows per surfacing			Duration of surfacing (min)			Duration of Dive (min)		
	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Overall:												
July	12.6	6.45	1947	4.2	1.82	598	0.88	0.604	609	3.35	1.104	494
September	14.7	8.02	1556	4.3	2.67	452	0.90	0.867	453	2.98	1.422	411
July-September	13.5	7.27	3503	4.2	2.23	1050	0.89	0.728	1062	3.18	1.271	905
July:												
Feeding	12.2	5.53	483	4.4	1.50	141	0.93	0.393	141	3.68	1.043	116
Possible feeding	12.6	4.74	859	4.5	1.75	247	0.91	0.429	260	3.42	0.976	239
Not feeding	15.2	12.58	110	3.0	2.37	51	0.49	0.561	56	2.43	1.236	46
September:												
Feeding	16.8	9.72	248	6.2	3.18	45	1.38	1.039	45	3.50	1.428	41
Possible feeding	13.8	6.78	877	4.0	2.48	276	0.80	0.737	277	3.01	1.337	264
Not feeding	18.0	9.85	152	3.3	2.76	64	0.83	1.220	64	1.91	1.120	64
July - Depth:												
1-20 m	13.3	9.72	243	3.1	1.52	116	0.72	0.853	118	3.22	1.102	95
21-40 m	12.6	5.16	1298	4.3	1.79	384	0.91	0.533	391	3.34	1.156	314
41-60 m	21.2	18.98	39	5.1	3.23	8	1.12	0.826	9	1.48	0.671	5
61-80 m	12.2	5.12	133	5.2	2.22	29	1.09	0.670	30	3.28	1.247	19

Continued...

Table 1. Concluded.

	Blow interval (s)			Number of blows per surfacing			Duration of surfacing (min)			Duration of Dive (min)		
	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
September - Depth:												
1-20 m	15.0	9.47	560	3.3	1.96	239	0.63	0.695	239	2.38	0.996	218
21-40 m	16.7	6.36	464	6.4	3.13	78	1.63	1.018	79	4.40	1.413	74
41-60 m	-	-	0	-	-	0	-	-	0	-	-	0
61-80 m	-	-	0	-	-	0	-	-	0	-	-	0
July - Time of Day:												
5-9	13.1	7.95	408	4.4	1.77	116	0.97	0.465	116	3.32	1.084	77
10-13	13.2	6.70	776	4.5	1.84	214	1.04	0.803	220	3.46	1.049	182
14-17	11.7	4.38	359	4.2	1.46	108	0.84	0.317	112	3.58	0.834	89
18-21	11.7	5.63	398	3.5	1.90	160	0.63	0.424	167	3.10	1.273	146
September - Time of Day:												
5-9	12.1	3.19	18	3.8	0.84	5	0.81	0.386	5	3.44	0.985	7
10-13	15.9	10.25	287	3.0	2.25	132	0.65	0.935	132	2.18	1.060	130
14-17	14.7	8.28	826	4.3	2.48	239	0.89	0.767	239	3.06	0.226	203
18-21	14.1	5.38	424	6.3	2.74	76	1.36	0.889	77	4.19	1.256	71

It is especially useful, when undertaking aerial surveys to determine numbers of whales, to know what proportion of time a whale spends at the surface, and is therefore visible. In July, average surface time divided by average duration of a surfacing-dive cycle (0.88/[0.88 + 3.35] min) yielded a surface time proportion of 0.208. In September, when dives were somewhat shorter, the average time at the surface (0.90/[0.90 + 2.98] min) yielded a surface time proportion of 0.232. These values give an indication of the probability of detecting a gray whale at a point in time along an aerial survey transect line, but the horizontal distance of the whale from the aircraft and the speed of the aircraft must also be taken into account (Miller, this report).

We calculated the number of blows per unit time, or blow rate, by analyzing the number of blows for surfacing-dive cycles when all blows were seen and total length of the surfacing and dive was known. In July, there were 1833 blows in the 1839.1 min total duration of 434 surfacing-dive cycles, for a blow rate of 0.997 blows/min. In September, there were 1612 blows in 1436.7 min of 377 surfacing-dive cycles, for a blow rate of 1.122 blows/min.

Relationships to Feeding

We divided our observations into (1) known feeding, (2) possible feeding, (3) not feeding, and (4) other behavior. Surfacing-dive characteristics of the first three categories of whales were summarized.

Blow intervals tended to be longer when whales were not feeding than when they were feeding or possibly feeding. This was so both in July ($F = 11.99$, $df = 2, 1449$, $p<0.001$) and in September ($F = 27.51$, $df = 2, 1274$, $p<0.001$) (Fig. 3a). Number of blows per surfacing also differed among the three feeding categories for July ($F = 16.80$, $df = 2, 382$, $p<0.001$), with fewer blows per surfacing while whales were not feeding, and more during possible and definite feeding (Fig. 3b). Duration of surfacings showed the same trend, which is not surprising because of the close relationship between duration of a surfacing and the number of blows during that surfacing (feeding characteristic comparisons: July $F = 23.58$, $df = 2, 454$, $p<0.001$;

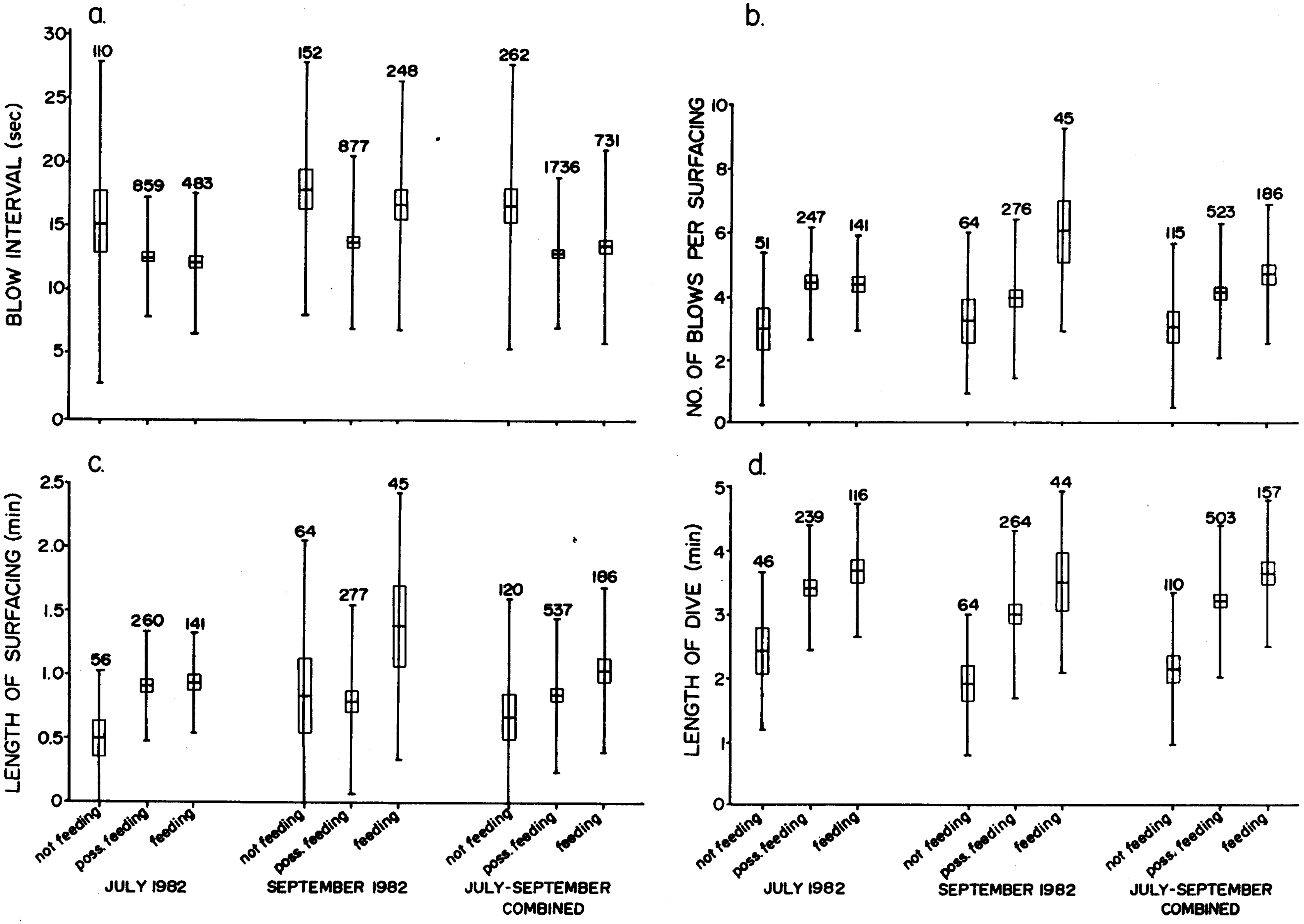


FIGURE 3. Respiration, surfacing and dive variables by feeding category. Bars represent 1 s.d. on each side of the mean, and boxes represent 95% confidence intervals.

September F = 8.85, df = 2, 383, p<0.001). Duration of dives was also lowest for non-feeding whales, and highest for feeding whales (Fig. 3d; July F = 24.84, df = 2, 398, p<0.001; September F = 23.29, df = 2, 366, p<0.001). Of the four variables, dive time was the one that differed most consistently between whales that were and were not feeding. Duration of dives may thus be a useful indicator of feeding. This concept will be explored further in the "Amount of Feeding" section.

Blow rates did not vary greatly with feeding category; in July, the blow rate for feeding whales was 0.974 blows/min (114 surfacing-dive cycles), and that for non-feeding whales was 0.976 blows/min (41 surfacing-dive cycles). In September, the feeding blow rate was 1.288 blows/min (41 surfacing-dive cycles), and the non-feeding blow rate was 1.186 blows/min (58 surfacing-dive cycles).

Relationships to Depth of Water

Whales were found around St. Lawrence Island in water depths ranging from 6 to 79 m. We divided this range into four depth categories as shown in Figure 4. Blow intervals were correlated with depth (Fig. 4a). Number of blows per surfacing and the correlated duration of surfacing increased with increasing depth, and the change was significant for both characteristics during both months (Number of blows: July F = 17.56, df = 3, 533, p<0.001; September t = 10.37, df = 315, p<0.001. Duration of surfacings: July F = 4.28, df = 3, 544, p<0.001; September t = 9.78, df = 316, p<0.001).

Duration of dives, on the other hand, did not show a consistent increase with increasing depth in July. The analysis of variance statistic is marginally significant only because of five short dives from one animal in 41-60 m water depth (Fig. 4d) (F = 4.475, df = 3, 429, p<0.05). According to the SNK multiple-comparison test, the value for 41-60 m is significantly lower than values from all other depth categories at p<0.01; values for all other pairs of depths were not significantly different. In September, durations of dives were determined only for the two shallower depth categories. Dives in 21-40 m depth were significantly longer than those in 1-20 m (t = 13.44, df = 290, p<0.001).

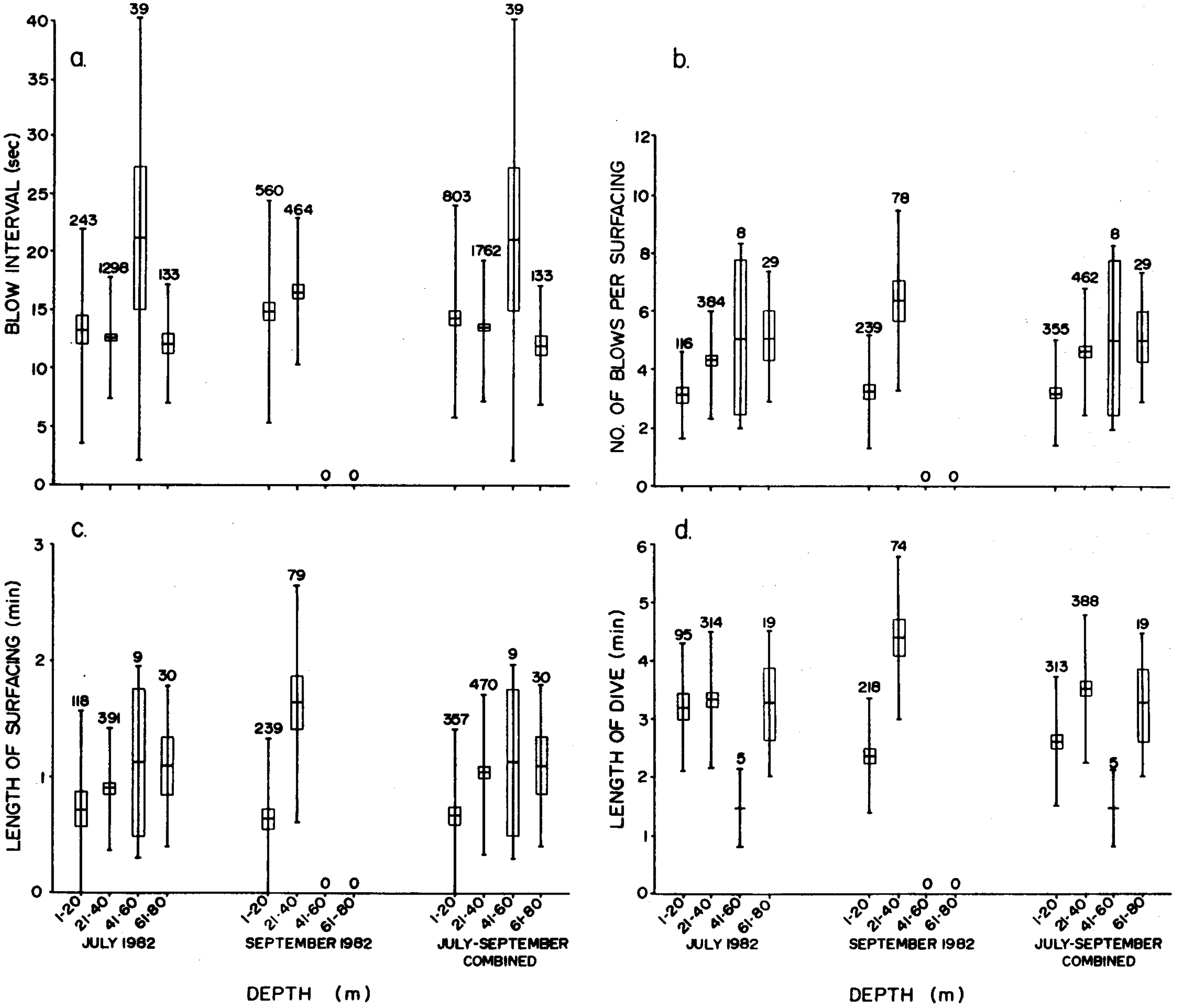


FIGURE 4. Respiration, surfacing and dive variables by depth of water. Statistics displayed as in Fig. 3.

To test whether the apparent relationship between durations of dives and depth may have been confounded by differences in feeding during the two months, we examined durations of definite feeding dives at various depths. In July, there was no longer a significant difference in durations of dives in waters of different depths, mainly because there were no feeding dives in the 41-60 m category (F = 0.176, df = 2, 107, ns). However, in September the difference in durations of feeding dives in waters 1-20 m and 21-40 m depth was again significant (t = 5.15, df = 36, p<0.001). Therefore, the month to month difference in depth effect does not appear to be due solely to differential amounts of feeding. In any case, the relationship between duration of dive and depth is not as linear or consistent as that between duration of surfacing and depth (compare Fig. 4c to Fig. 4d).

In July, with increasing depth there was a tendency for increased surface time and increased number of blows per surfacing, but little change in dive time. Thus, it is not surprising that the blow rate was higher in deeper water during that month. The July blow rates of feeding and possibly feeding whales were 0.794 blows/min (53 surfacing-dive cycles) in 1-20 m water depth, 1.043 blows/min (212 surfacing-dive cycles) in 21-40 m depth, and 1.190 blows/min (11 surfacing-dive cycles) in 61-80 m depth. In September, the increase was only slight: 1.085 blows/min (178 surfacing-dive cycles) in 1-20 m depth, and 1.116 blows/min (56 surfacing-dive cycles) in 21-40 m depth.

Our results of differential amounts of respiration in different water depths are particularly interesting, for we are reasonably certain that whales dove to the depths indicated while feeding. Therefore, the differential blow rates are apparently related to depth of dive.

Relationships to Time of Day

The four basic respiration and surfacing characteristics all differed significantly among the four 4-h categories that we compared (analysis of variance F>7.0, error df from 448 to 1937, p<0.001), but the trends were different for the two months, and for combined data, almost cancel each other (Fig. 5). In July, number of blows per surfacing, duration of surfacings,

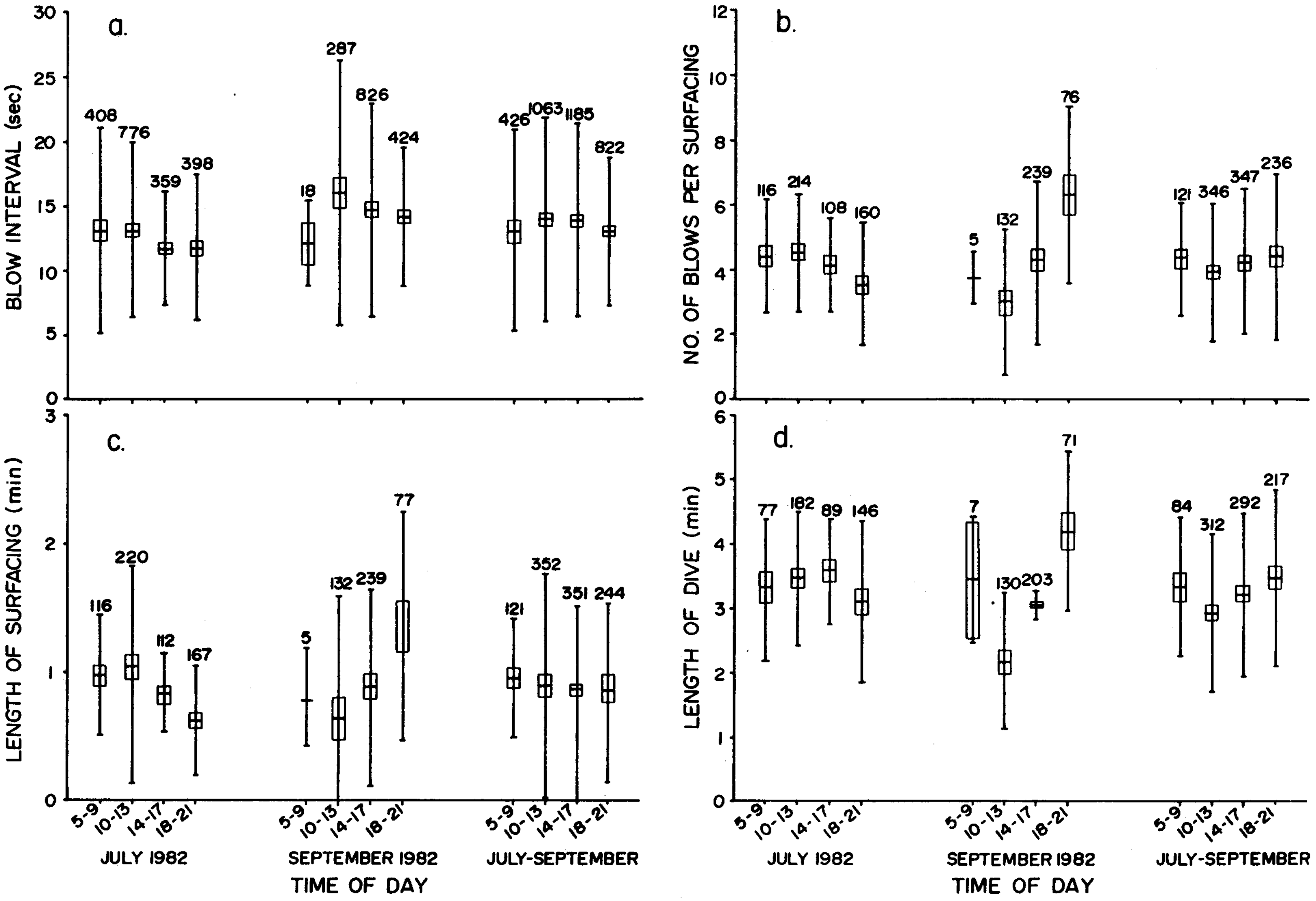


FIGURE 5. Respiration, surfacing and dive variables by time of day, divided into four 4-h categories. Time is Anchorage time, GMT-9 h. Statistics displayed as in Fig. 3.

and duration of dives were greater during midday, but in September, this trend was reversed. Other variables such as feeding behavior and depth of water probably were more important determinants of these characteristics.

To determine whether there was a relationship between amount of feeding and hour of day, we compared number of known feeding dives to total number of dives (Table 2). In both months, known feeding dives comprised a larger fraction of all dives during the evening (18:00-21:00) than earlier in the day. The ratios in Table 2 are intended only for comparative purposes between hours and months, because they grossly under-represent the actual frequency of feeding. The "No. of Dives" column only considers those whales that surfaced with mud, plus surfacings when kittiwakes landed behind the whale. The "possible feeding" category is not included.

Relationships to Time of Season

There was no consistent trend in amount of feeding across dates within either month, but there was much more known feeding in July than in September (Table 3). The duration of feeding dives was relatively stable from day to day in July, but in September, feeding dives became shorter at the end of the season (Fig. 6). Table 3 and Figure 6 do not represent all possible feeding dives because they consider known feeding only, as explained under "Time of Day". As mentioned previously, the frequency of socializing increased toward the end of September.

Amount of Feeding

With the available information on surfacing and dive characteristics, we can make reasonably good estimates of the proportion of time whales spend feeding. We make the assumption that we are just as likely to gather data on whales feeding as opposed to some other activity, and that our determination of feeding, possible feeding, and not feeding reflected actual behavior accurately.

Table 2. Relative frequency of feeding dives at different times of day in July and September.

Time	No. of Feeding Dives (1)	Total No. of Dives (2)	Ratio (1)/(2)
July:			
5-9	11	77	0.143
10-13	44	182	0.242
14-17	13	89	0.146
18-21	47	146	0.322
September:			
5-9	0	7	0
10-13	5	130	0.038
14-17	18	203	0.089
18-21	18	71	0.254
July and September:			
5-9	11	84	0.131
10-13	49	312	0.157
14-17	31	292	0.106
18-21	65	217	0.300

Table 3. Relative frequency of feeding dives on different dates.

Day	No. of Feeding Dives (1)	Total No. of Dives (2)	Ratio (1)/(2)
July:			
12	26	73	0.356
13	6	19	0.316
14	0	5	0
16	6	80	0.075
17	39	95	0.411
18	9	29	0.310
19	18	78	0.231
20	2	44	0.045
21	9	71	0.127
Total	115	494	0.233
September:			
12	1	26	0.038
16	1	7	0.143
18	14	46	0.304
19	0	62	0
20	0	4	0
21	11	73	0.151
23	4	13	0.308
26	2	28	0.071
27	8	152	0.053
Total	41	411	0.098

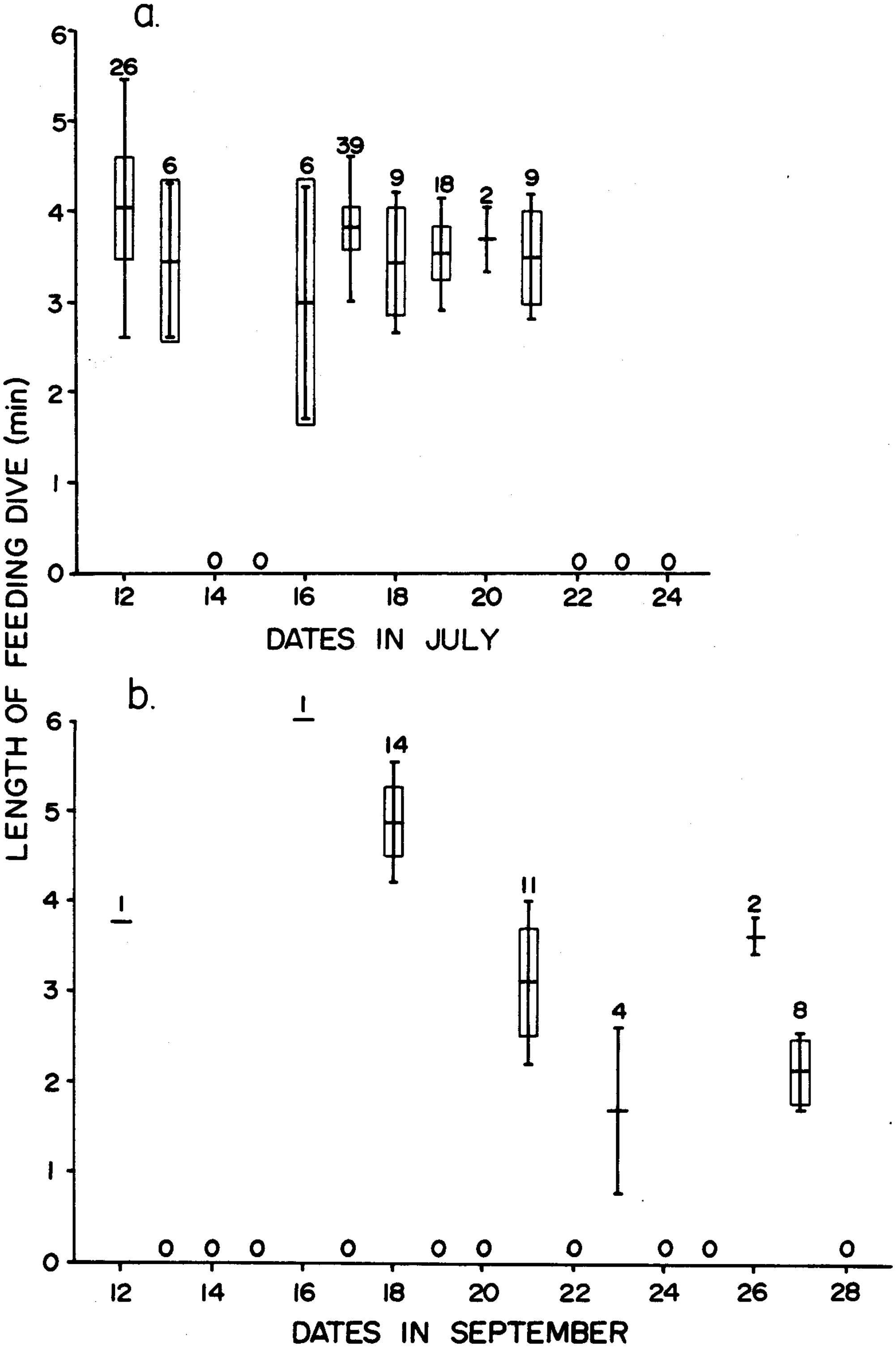


FIGURE 6. Duration of feeding dives during days with observations in July and September 1982. Statistics displayed as in Fig. 3.

In July, we watched whales for a total of 2190.82 min, and we watched whales definitely feeding for 558.01 min. This gives a feeding proportion of 0.255 total time, considering only definite feeding dives and associated surfacings. Many of the possible feeding observations also represent feeding. If we add this time (1053.98 min) to the definite feeding time, we have a total of 1611.99 min total possible feeding time. The possible feeding proportion is then 0.736 total time, and our range is from a low of 0.255 to a high of 0.736 total time spent feeding.

Similar calculations for September result in a range of 0.126 total time, considering only definite feeding, to 0.748 total time, considering both definite and possible feeding.

Although it is difficult to say how much feeding occurred within the "possible feeding" category, it was our subjective impression that in July, about three-quarters of the possible feeding time represented feeding, while in September, somewhat less than three-quarters represented feeding. The durations of dives appear to be a very good indicator of presence or absence of feeding. In July, the mean feeding dive was 3.68 min in duration, and in September, it was 3.50 min, with small standard deviations in both cases (± 1.043 and ± 1.428 min, n = 116 and 41, respectively). Non-feeding dives in July were 1.25 min shorter than feeding dives, and non-feeding dives in September were 1.59 min shorter than feeding dives. The mean durations of possible feeding dives were intermediate. We speculate that a ratio composed of the difference between the mean duration of non-feeding dives and of possible feeding dives divided by the difference between the mean duration of non-feeding dives and definite feeding dives represents the proportion of possible feeding dives than should actually be classified as feeding (here called "probable feeding"). For July, this value is 0.79 (proportion of possible feeding dives that are probable feeding dives), and for September, it is 0.69. These values are remarkably close to our subjective impression of the situation.

These calculated proportions may be used to adjust the possible feeding time to probable feeding time, and to add this new value to definite feeding time. The total probable feeding time for July is then 1390.65 min, and the proportion of time spent feeding is estimated to be 0.635 total time (total probable feeding time over overall time). For September, this value is 0.555 total time.

We observed feeding throughout the day from 05:00 to 21:00 h, but we have no detailed information on possible feeding or on surfacing-dive patterns during the night. If we assume that feeding dives continue at night, and that the average length of the surfacing-dive cycle is approximately the same as during the day, then approximately 312 feeding dives are possible in 24 h in July (4.61 min per feeding dive cycle, 1440 min per 24 h). Because the proportion of time spent feeding is approximately 0.635 total time, we may expect that one whale averaged about 198 (312 x 0.635) feeding dives per 24 h in July. In September, approximately 295 feeding dives were possible in 24 h, and the average number of feeding dives by one whale in 24 h was 164 (295 x 0.555). This is somewhat less than the amount of feeding seen in July, and agrees well with our impressions (before analysis of the data) concerning the relative amount of feeding in September vs. July. For a summary of the calculations, see Appendix I.

Our calculations are only as good as our assumptions. We are reasonably certain that we were not biased toward or away from gathering information on feeding whales. We also believe that duration of dive can be used as an indication of bottom feeding, and thus our correction factor to convert "possible dives" to "probable dives" is valid as a first approximation. We are less certain of the amount of feeding and the dive durations during the night, however, and therefore suggest that the final estimates of "number of feeding dives per 24 h" be treated with caution.

Distance Traveled and Speed of Travel

As an aid to describing the behavior of whales, we estimated distance traveled while whales were at the surface, and the net horizontal distance traveled during dives. These estimates were obtained on occasions when whales were within about 150 m of the boat and the boat was stationary.

In July, overall distance traveled during surfacing was 57 ± s.d. 55.0 m (n = 32), and minimum horizontal distance traveled during dives was 95 ± 82.9 m (n = 93). The difference between distance covered above and below the surface was significant (t = 2.42, df = 123, p<0.02). In September, surface distance was considerably shorter, at 30 ± 23.8 m (n = 25). Dive distance was comparable to the July value, 92 ± 88.1 m (n = 30), and the difference between surface and dive distance was again significant (t = 3.40, df = 53, p<0.002).

On 27 September, we obtained exact theodolite measurements of distances traveled at the surface five times, and minimum distance traveled below the surface eight times, all on one feeding whale in 6 m water depth. Distance at the surface was 36 ± 31.6 m (n = 5), and distance below the surface was 54 ± 22.3 m (n = 8). Estimates made at the time this whale was being observed agree with the calculated distances. It is therefore likely that this whale traveled especially small distances while diving. This may have been due to the exceptionally shallow water in which the whale was diving, although we have no proof for this assertion.

Table 4 summarizes distance traveled according to category of feeding. There are too few values for meaningful comparisons of distance traveled during feeding and during non-feeding dives. However, feeding whales surfaced an average of about 90 to 100 m from where they submerged. We do not know whether the whales' tracks underwater were in a straight line.

On 27 September, theodolite-generated tracks were obtained for three feeding whales (including the above-described whale). These three whales remained in an area 3700 m north-south, and 700 m east-west for the four hours of observation. This restricted movement was accomplished by whales moving northerly for about 60 min, then moving in a southerly direction for about 60 min, and then reversing direction again. This movement kept the whales close to 6 m depth at all times because the depth contour line ran north-south. The regular nature of feeding behavior is reflected in the similarity of the average speed of movement for each of the three whales: Whale A 2.3 ± s.d. 2.18 km/h, n = 77; Whale B 2.3 ± 1.75 km/h, n = 42; Whale C 2.8 ± 2.23 km/h, n = 34. For whale A, speeds were obtained separately for some surface and below-surface movements: 3.4 ± 2.14 km/h (n = 5) at the surface and 1.7 ± 0.66 km/h (n = 8) below the surface. It thus appears that net horizontal speed while diving was slower, but the result is a minimum

Table 4. Estimated distances traveled during surfacings and minimum distances traveled during dives, subdivided by feeding category and month.

	July			September		
	mean	s.d.	n	mean	s.d.	n
Surfacing Distance (m)						
Not feeding	150	-	1	17	28.9	3
Possible feeding	47	36.4	24	31	21.0	18
Feeding	69	79.8	9	33	41.6	3
Dive Distance (m)						
Not feeding	-	-	0	138	94.7	4
Possible feeding	83	45.0	62	68	55.9	21
Feeding	100	45.6	24	93	100.7	3

speed, because it assumes a straight line between the points of diving and surfacing, and ignores the vertical movement of the whale. The result appears reasonable, however, for we might expect whales to move forward slowly while feeding on benthic or epibenthic invertebrates.

DISCUSSION

Our observation that individual whales spent hours and, on at least two occasions, over a day feeding in a small area indicates some site tenacity. We do not know whether individual feeding ranges are actually well defined for most animals. The fact that feeding whales were generally far apart from each other hints at (but in no way proves) the possibility of feeding territories. Similar site tenacity has been observed for feeding gray whales off Vancouver Island, B.C., by Darling (in press) and Murison et al. (in press).

We encountered mainly what we judged to be "adult" whales, although some possible juveniles were perhaps four-fifths the size of most others. Zenkovitch (1937), Votrogov and Bogoslovskaya (1980), and Bogoslovskaya et al. (1981) provide data which show that young animals often forage in different areas than older ones, and this kind of size separation may be responsible for our apparent lack of sightings of young gray whales. It is also possible, as mentioned earlier, that we saw but failed to recognize some young.

Little socializing occurred in July, but more socializing was seen during the latter half of September. The two socializing incidences in July involved rolling at the surface and nudges and pushes. They appeared similar to (although not as boisterous as) the descriptions of apparent precopulatory activity witnessed along the west shore of St. Lawrence Island by Sauer (1963) and Fay (1963). Whales were more often in groups of two to three in September than in July. Zimushko and Ivashin (1980) also found that gray whales feeding along the Russian coast were generally alone, although groups of two to three occurred as well. They did not discriminate by time of season. We had the impression that behavior changed more often from feeding to socializing or traveling in September than in July. This heightened amount of change in general behavior may be part of a "migratory unrest" preceding the migration southwards.

Surface time, number of blows per surfacing, and dive time were all correlated. Similar results were obtained on bowhead whales, the only other baleen whale species for which detailed respiration and surfacing characteristics have been reported (Würsig et al. 1982, 1983). Surface time of gray whales in July was 21% of total time, and in September was 23% of total time. This is remarkably similar to the 24% surface time reported for mainly feeding bowhead whales in the Beaufort Sea in August (Würsig et al. 1983). These results are very different from the proportional surface times of gray whales near their wintering areas off Baja California and during migration; Harvey and Mate (in press) found that whales radio-tagged in Laguna San Ignacio, Mexico, were at the surface only 4.5% of the time. Detectability of gray whales during aerial surveys would clearly be very different in these two situations.

While feeding, gray whales had longer dives, longer surface times, and more blows per surfacing than while not feeding. However, the blow rate, or number of respirations per unit time, did not change appreciably. Number of blows per surfacing and duration of surfacings also increased in deeper water but--at least in July--duration of dives did not increase. Blow rates were higher in deeper water, which suggests that whales are more stressed physiologically during deep dives, even at depths only 20 m deeper than their shallowest dives (around 6 m depth, or one-half body length of a whale). This is a new and potentially important concept warranting further study. Sumich (1983) found a blow rate of 0.72 blows per minute in whales migrating south past California, and a blow rate of 0.5 blows per minute in essentially stationary whales in Laguna San Ignacio. These rates are appreciably lower than the blow rates of whales feeding in water >20 m deep (around 1 blow/min), but comparable to the blow rate of whales feeding in water <20 m during July (0.794 blows/min). Harvey and Mate (in press) calculated a blow rate of approximately 0.58 blows/min in stationary whales and 1.00 blows/min in a whale swimming at 4 km/h. The latter value is higher than the result for migrating whales observed by Sumich (1983). The difference may, in part, be due to methodology. Harvey and Mate used a radio transmitter and Sumich used visual observations. The blow rate of non-calf bowhead whales in the Beaufort Sea was approximately 0.70 blows/min (Würsig et al. 1983).

It is difficult to compare the individual surfacing, respiration, and dive variables of whales on the feeding grounds in summer with those in other areas at other times. Feeding whales generally dive for some time, and then surface for some time while blowing repeatedly. During migration and in winter, however, they only surface to breathe. This is well exemplified by data from Harvey and Mate (in press): surface time of whales in Laguna San Ignacio was only 0.07 ± 0.1 min (no sample size given), as opposed to 0.89 ± s.d. 0.728 min (n = 1062) during our study. However, only one blow occurred during each brief surfacing in the wintering area, whereas we observed an average of about 4 blows per surfacing.

Nerini (1980) published raw data concerning 20 dives of gray whales foraging near St. Lawrence Island. Our analysis of these data gives a mean dive time of 3.53 min (s.d. = 1.053 min, n = 20), close to our July and September combined mean of 3.63 ± 1.153 min (n = 157) for dives by feeding whale. Nerini also presented data on blow intervals and surface times, but the numbers were apparently not gathered systematically, and comparisons are not possible. Dive data in Nerini (1980) were gathered in 1977 and 1980, but there is no indication of time, depth of water, or other variables.

We calculated the frequency of feeding, as evidenced by gray whales surfacing with mud or by the presence of birds. Our corrected values (including estimates of feeding when mud could not be seen) indicate that whales fed about 79% and 69% of the time in July and September, respectively. This is less than the "total feeding" assumed by earlier researchers, but is reasonable in light of recent investigations on bowhead whales in which socializing and travel, apparently without feeding, occur on the feeding grounds in the Beaufort Sea (Würsig et al. 1982). Whales are social mammals with large behavioral repertoires, and they do not totally extinguish all other behaviors in favor of a single behavior.

During the present investigation, speed of travel of feeding whales was determined accurately on only one day. It was around 2 km/h for the three whales measured, and surface speeds were twice as high as apparent dive speeds. Mate and Harvey (in press) estimated speeds of 3 to 4 km/h for northward migrating gray whales, whereas Leatherwood (1974) obtained values of 2.6 to 2.9 km/h. The southward migration is generally thought to be faster; Sumich (1983) measured one whale's speed as 15.5 km/h, but this was probably during particularly rapid movement. Thus, the movements of whales in the feeding area around St. Lawrence Island generally appear to be more leisurely than those of migrating whales, and it is interesting that their blow rates are nevertheless higher; this is presumably related to diving deeper, as conjectured previously.

Whales moved a net distance of about 100 m below the surface while feeding, and moved about one-half that distance at the surface. Such data are fraught with uncertainty, however, for we do not know what the specific current regime was below the surface during these measurements, or whether whales below the surface traveled in a straight line. Thomson and Martin (this report) discuss the physical record of feeding in the St. Lawrence Island area, which consists of furrows and other indentations, and estimate how much biomass may be taken in by a foraging whale per dive.

ACKNOWLEDGMENTS

The gray whale feeding ecology project of which this behavioral work was a part was funded by the Minerals Management Service through interagency agreement with the National Oceanic and Atmospheric Administration, as part of the Outer Continental Shelf Environmental Assessment Program through a contract to LGL Alaska Research Associates, Inc. The behavioral research was carried out with the help of resources and facilities of Moss Landing Marine Laboratories, and the entire project was coordinated by LGL.

We are grateful to the officers and crew of the NOAA vessels MILLER FREEMAN and DISCOVERER, and we thank especially Lt. M. Eng, Technician R. Meyers, and fisherwoman D. Blum for conscientious help with gathering data from MILLER FREEMAN. M. Newcomer and L. Spear of Moss Landing Marine Laboratories helped with behavioral observations in July and September, respectively. D. Thomson (LGL) served as overall project leader and advisor, and M. Dahlheim (University of Washington) provided help in the field. W.J. Richardson (LGL) helped organize the project and edited this report, R. Stelow (NLML) and D. Tuel (NLML) typed drafts of the report, and L. McMasters (NLML) drew the figures. M. Würsig helped analyze data. We thank them all.

LITERATURE CITED

Bogoslovskaya, L.S., L.M. Votrogov, and T.N. Semenova. 1981. Feeding habits of the gray whale off Chukotka. Rep. Int. Whal. Comm. 31:507-510.

Darling, J.D. In press. Gray whales, *Eschrichtius robustus*, off Vancouver Island, British Columbia. *In*: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Fay, F.H. 1963. Unusual behavior of gray whales in summer. Psychol. Forsch. 27:175-176.

Harrison, C.S. 1979. The association of marine birds and feeding gray whales. Condor 81:93-95.

Harvey, J.T. and B.R. Mate. In press. Dive characteristics and movements of radio-tagged gray whales in San Ignacio Lagoon, Baja California, Mexico. *In*: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Hatler, D.F. and J.D. Darling. 1974. Recent observations of the gray whale in British Columbia. Can. Field-Nat. 88:449-459.

Leatherwood, J.S. 1974. Aerial observations of migrating gray whales, *Eschrichtius robustus*, off southern California, 1969-1972. Mar. Fish. Rev. 36:45-49.

Mate, B.R. and J.T. Harvey. In press. Ocean movements of radio-tagged gray whales. *In*: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Murison, L.D., D.J. Murie, K.R. Morin and J. da Silva Curiel. In press. Foraging of the gray whale (*Eschrichtius robustus* Lilljeborg) along the west coast of Vancouver Island, British Columbia. *In*: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Nerini, M.K. 1980. Gray whale feeding ecology. Unpubl. rep. by Nat. Mar. Fish. Serv., Seattle, for Outer Cont. Shelf Envir. Assess. Prog., Nat. Oceanic Atmospheric Admin., Juneau, AK 35 p.

Norris, K.S., R.M. Goodman, B. Villa-Ramires and L. Hobbs. 1977. Behavior of the California gray whale *Eschrichtius robustus* in southern Baja California, Mexico. Fish. Bull. U.S. 75:159-172.

Norris, K.S., B. Villa-Ramires, G. Nichols, B. Würsig and K. Miller. In press. Lagoon entrance and other aggregations of gray whales, *Eschrichtius robustus*. *In*: R. Payne (ed.), Behavior and communication of whales. AAAS Selected Symposia Series, Westview Press, Boulder, CO.

Pike, G.C. 1962. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). J. Fish. Res. Board Can. 19:815-838.

Sauer, E.G.F. 1963. Courtship and copulation of the gray whale in the Bering Sea at St. Lawrence Island, Alaska. Psychol. Forsch. 27:157-174.

Scammon, C.M. 1869. On the cetaceans of the western coast of North America. Proc. Acad. Nat. Sci. Philadelphia 21:40-49.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry. W.H. Freeman, San Francisco. 776 p.

Sumich, J.L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. Can. J. Zool. 61:647-652.

Swartz, S.L. and M.L. Jones. In press. Demography and phenology of gray whales, *Eschrichtius robustus* (Lilljeborg 1861) in Laguna San Ignacio, Baja California Sur, Mexico. *In*: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, *Eschrichtius robustus*. Academic Press, N.Y.

Tyack, P.T. 1981. Interactions between singing humpback whales and conspecifics nearby. Behav. Ecol. Sociobiol. 8:105-116.

Votrogov, L.M. and L.S. Bogoslovskaya. 1980. Gray whales off the Chukotka Peninsula. Rep. Int. Whal. Comm. 30:435-437.

Wilke, F. and C.H. Fiscus. 1961. Gray whale observations. J. Mammal. 42:108-109.

Würsig, B. 1978. On the behavior and ecology of bottlenose and dusky dolphins. Ph.D. Dissertation, State University of New York at Stony Brook. 326 p.

Würsig, B., C.W. Clark, E.M. Dorsey, M.A. Fraker and R.S. Payne. 1982. Normal behavior of bowheads. p. 33-143 *In*: W.J. Richardson (ed.), Behavior, disturbance responses and feeding of bowhead whales *Balaena mysticetus* in the Beaufort Sea, 1980-81. Unpubl. rep. by LGL Ecol. Res. Assoc., Inc., Bryan, TX, for U.S. Bureau of Land Management, Washington. 456 p.

Würsig, B., C.W. Clark, E.M. Dorsey, W.J. Richardson and R.S. Wells. 1983. Normal behavior of bowheads, 1982. In: W.J. Richardson (ed.), Behavior, disturbance responses and distribution of bowhead whales Balaena mysticetus in the eastern Beaufort Sea, 1982. Unpubl. rep. by LGL Ecol. Res. Assoc., Inc., Bryan, TX, for U.S. Minerals Management Service, Reston VA.

Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J.

Zenkovich, B.A. 1937. More on the gray California whale (Rhachianectes glaucus, Cope 1864). Bull. Far Eastern Branch Acad. Sci. U.S.S.R. 23:1-19.

Zimushko, V.V. and M.V. Ivashin. 1980. Some results of Soviet investigations and whaling of gray whales. Rep. Int. Whal. Comm. 30:237-246.

APPENDIX I. CALCULATIONS INVOLVED IN ESTIMATING THE NUMBER OF FEEDING DIVES OF AN AVERAGE GRAY WHALE AROUND ST. LAWRENCE ISLAND, ALASKA, IN JULY AND SEPTEMBER 1982.

July

Mean duration of feeding dive = 3.68 min

Mean duration of feeding surfacing = 0.93 min

4.61 min per feeding dive cycle.

There are 1440 min/24 h.

1440/4.61 = 312 feeding dives possible/24 h.

Mean duration of feeding dive = 3.68 min

1.25 min difference

Mean duration of non-feeding dive = 2.43 min

0.99 min difference

Mean duration of possible feeding dive = 3.42 min

.99/1.25 = 0.79; therefore, we speculate that 79% of possible feeding dives are actual feeding dives, and we call these "probable feeding dives".

Overall time observed = 2190.82 min

Feeding time observed = 558.01 min

Possible feeding time observed = 1053.98 min

x 0.79

= 832.64 probable feeding time

+ 558.01 definite feeding time

Total probable feeding time = 1390.65 min

1390.65/2190.82 = 0.635 proportion of time spent feeding.

Because 312 feeding dives are possible/24 h, 312 x 0.635 = 198 feeding dives for a whale/24 h.

(Or, 1440 min/24 h x .635 = 914.4 feeding min, ÷ 4.61 min per feeding cycle = 198 feeding dives/24 h.)

APPENDIX I. (continued)

September

Mean duration of feeding dive = 3.50 min

Mean duration of feeding surfacing = 1.38 min

4.88 min per feeding dive cycle.

There are 1440 min/24 h.

1440/4.88 = 295 feeding dives possible/24 h.

Mean duration of feeding dive = 3.50 min
1.59 min difference
Mean duration of non-feeding dive = 1.91 min
1.10 min difference
Mean duration of possible feeding dive = 3.01 min

1.10/1.59 = 0.69; therefore, we speculate that 69% of possible feeding dives are actual feeding dives, and we call these "probable feeding dives".

Overall time observed = 1631.53 min

Feeding time observed = 205.60 min

Possible feeding time observed = 1015.41 min

x 0.69

= 700.63 probable feeding time

\+ 205.60 definite feeding time

Total probable feeding time = 906.23 min

906/1631.53 = 0.555 proportion of time spent feeding.

Because 295 feeding dives are possible/24 h, 295 x 0.555 = 164 feeding dives for a whale/24 h.

FEEDING ECOLOGY OF GRAY WHALES IN THE CHIRIKOF BASIN

by

Denis H. Thomson
LGL Limited, Environmental Research Associates

and

Larry R. Martin
LGL Ecological Research Associates

1984

TABLE OF CONTENTS

LIST OF FIGURES

Figure 15. Density of individual identifiable bottom features attributed to feeding activities of gray whales, as recorded via side-scan sonar in the Chirikof Basin and near St. Lawrence Island in July and September 1982.

Figure 16. Length frequency distributions of *Ampelisca macrocephala* from airlift samples taken inside and outside a bottom feature attributed to feeding activities of a gray whale in shallow water off Southeast Cape, St. Lawrence Island, in September.

Figure 17. Length frequency distributions of *Ampelisca macrocephala* from (a) plankton tows taken in July through mud plumes emanating from feeding gray whales, and (b) benthic grab samples. Grab samples were taken off Southeast Cape, St. Lawrence Island, near the location of plankton tows.

Figure 18. Energy flow through the benthos of that part of the Chirikof Basin utilized by feeding gray whales. All values are expressed as g Carbon/m^2. Transfer of energy (g C/m^2/yr) is noted beside arrows. Standing crop and productivity (in parentheses) are shown within the blocks.

LIST OF TABLES

Table 11. Mean biomass ($g/m^2 \pm$ s.d.) of major taxa and dominant species from samples taken inside and outside bottom features attributed to the feeding activity of gray whales and from samples taken of the upper 2 cm and upper 10-15 cm of substrate. All samples were taken off Southeast Cape, St. Lawrence Island, by diver-operated airlift.

Table 12. Estimated relative ages of gray whale feeding features based on numbers of amphipods and biomass of amphpod tubes.

Table 13. Estimates of amphipod biomass in Chirikof Basin and the St. Lawrence Island areas.

Table 14. Frequency distribution (%) of amphipod biomass in 93 samples taken within that portion of the study area utilized by gray whales.

Table 15. Number of benthic animals found in eight surface plankton tows taken through mud plumes emanating from feeding gray whales off Southeast Cape, St. Lawrence Island, in July.

Table 16. Length to dry weight relationships for six size categories of amphipods.

Table 17. Estimated daily gray whale food consumption at three assumed above-mean levels of amphipod biomass.

Table 18. Breathing rates for gray whales in various locations and under various activity levels. Values are average for that activity.

Table 19. Annual food requirements of a 23 Mt male gray whale calculated from the breathing rate using Sumich's 1983 method.

Table 20. Daily food intake of gray whales while on their summer feeding grounds calculated by four different methods. Also shown is the standing crop of amphipods necessary to meet these requirements assuming 198 feeding dives/day in June, July, and August and 164/d in September and October, 15.5 m^2 cleared per dive, a retention efficiency of 95% and an assimilation efficiency of 80%.

Table 21. Comparison of estimates of energetic requirements of gray whales.

Table 22. Mean biomass ($g\ C/m^2$) and percent of total biomass according to major feeding mode of benthic animals taken in the Chirikof Basin and areas adjacent to St. Lawrence Island. Conversion of wet weight to carbon was accomplished using data provided by Stoker (1978).

ABSTRACT

In July and September 1982, morphology, size and distribution of bottom features made in the Chirikof Basin and near St. Lawrence Island by feeding gray whales were investigated with side-scan sonar and by divers. Distribution and abundance of gray whale prey species and physical characteristics of the substrate associated with the features were also investigated.

Within the American Chirikof Basin, gray whales fed extensively only in areas that had a high biomass of amphipods and a substrate composed of fine sand with little gravel. Within their foraging grounds, the percent of bottom disturbed and mean size of feeding features was higher in shallow water than in deeper water, and density of feeding features was positively correlated with biomass of amphipods.

Whales apparently fed either by suction furrowing of the bottom to a depth of 2 cm or stationary suctioning of shallow pits to a depth of 10 cm. These features encompassed mean areas of 18 m^2 and 13 m^2, respectively. The whales removed amphipods but little else. Amphipods 5 mm or less in length may not be retained by the baleen but these comprise less than 5% of biomass of amphipods.

Daily consumption of amphipods was estimated in two ways--from behavioral data and characteristics of feeding features, and on the basis of theoretical energy requirements. (1) Whales performing 198 feeding dives per

day in July and 164/d in September (Würsig et al., this report) would consume an average 321 kg/d wet weight if feeding on average densities of amphipods (133 g/m^2), and 678 kg/d if they selectively fed in areas containing 250 g/m^2 of amphipods. The latter biomass is equivalent to the mean biomass in the 25% of benthic samples containing the most benthos. Evidence is presented showing that gray whales may select areas with high amphipod biomass in which to feed. (2) Estimated energy requirements for active metabolism and food storage for winter are similar, ranging from 445 kg/d assuming no energy storage for migration to 763 kg/d assuming that all energy needed for migration is stored during summer. About 2500 gray whales are estimated to summer in the Chirikof Basin, and an additional 9000 may migrate through it. Assuming that consumption is 650 kg/d/whale, whales resident in and migrating through the Chirikof Basin would consume about 7.5% of the standing crop of benthic amphipods each year, or about 4% of their productivity. However, since the whales apparently select areas with a higher than average biomass of amphipods in which to feed and apparently must do so in order to meet energetic requirements, not all of the apparent feeding habitat in the Chirikof Basin is of use to the whales. The major consideration, with regards to industrial development, would be exclusion of whales from areas of prime feeding habitat.

INTRODUCTION

The present population of gray whales is estimated to be about 17,600 to 18,000 animals with most of these summering in the Bering Sea and areas to the north (Reilly 1981; Reilly et al. 1983; Rugh in press). During their stay on these summer foraging grounds, the whales must store enough energy to carry them through their stay on their winter grounds off Baja California and for all or at least part of their long southward and northward migrations.

The gray whale is the only baleen whale to feed primarily on benthic animals. In northern seas, benthic amphipods form the principal part of the diet of gray whales (see Nerini in press for a review of feeding ecology).

This chapter presents information on the amount of food consumed per dive by gray whales and integrates these results with observations of feeding behavior presented by Würsig et al. (this report) to estimate the daily rate of food consumption. This estimate is compared to estimates derived through consideration of the energetic requirements of gray whales. These estimates are, in turn, integrated with estimates of the abundance of whales (Miller, this report) and the abundance, distribution and productivity of principal prey species (Thomson, this report) to yield an estimate of the impact that these whales have on their food resources and to assess the carrying capacity of their summer habitat in the Chirikof Basin.

MATERIALS AND METHODS

Study Design

Sampling was conducted from the NOAA ships DISCOVERER (September) and MILLER FREEMAN (July). Sixteen stations were occupied in the Chirikof Basin and 12 stations in the vicinity of St. Lawrence Island (Figs. 1 to 4). At each station, side-scan sonar tows were made to detect the presence of bottom features made by feeding gray whales. Benthic samples were taken at each station to provide descriptions of the quantity and quality of benthic animals present, the mean grain size, and the caloric, carbon and nitrogen

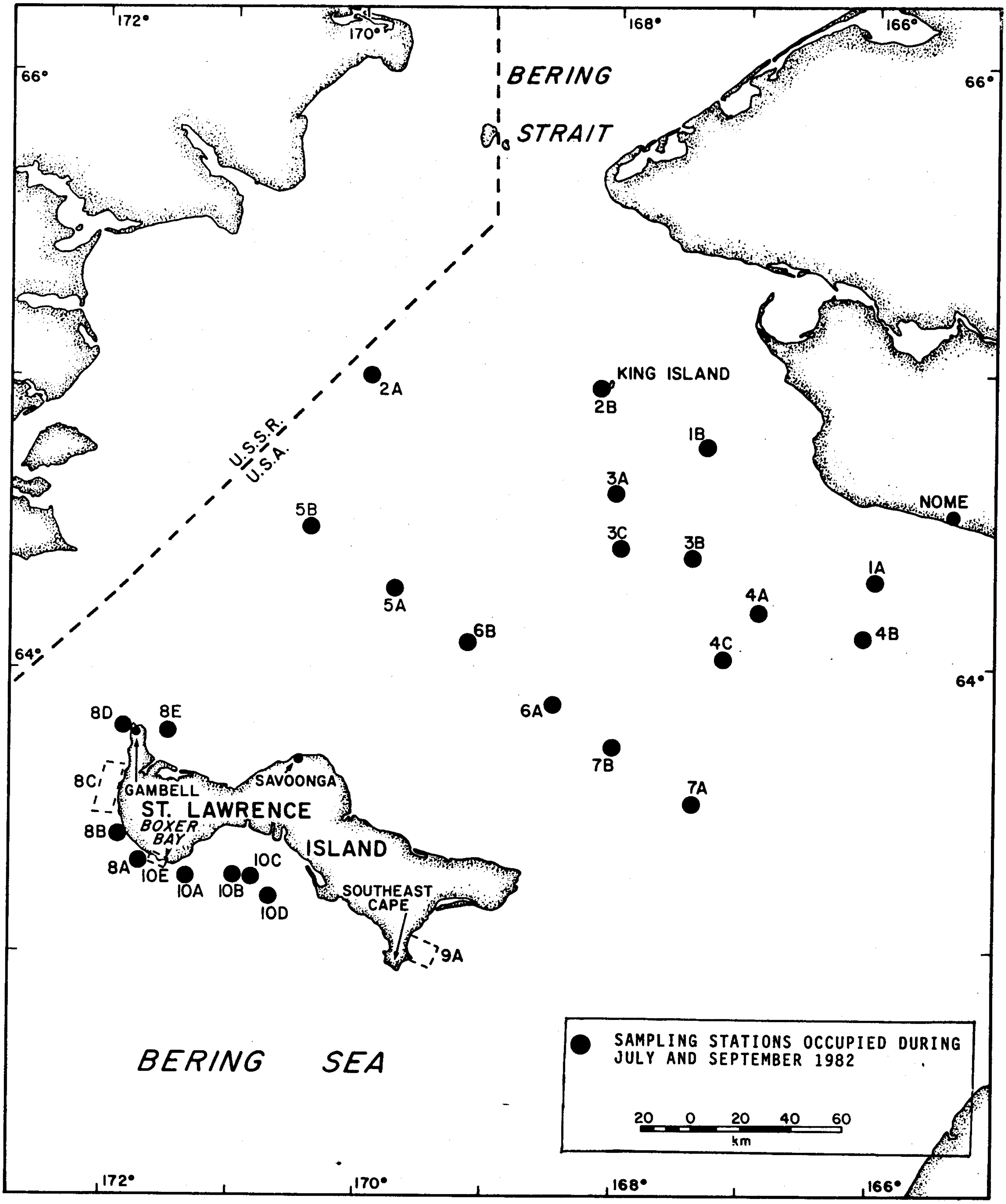


FIGURE 1. Sampling stations in the Chirikof Basin and off St. Lawrence Island occupied during July and September 1982.

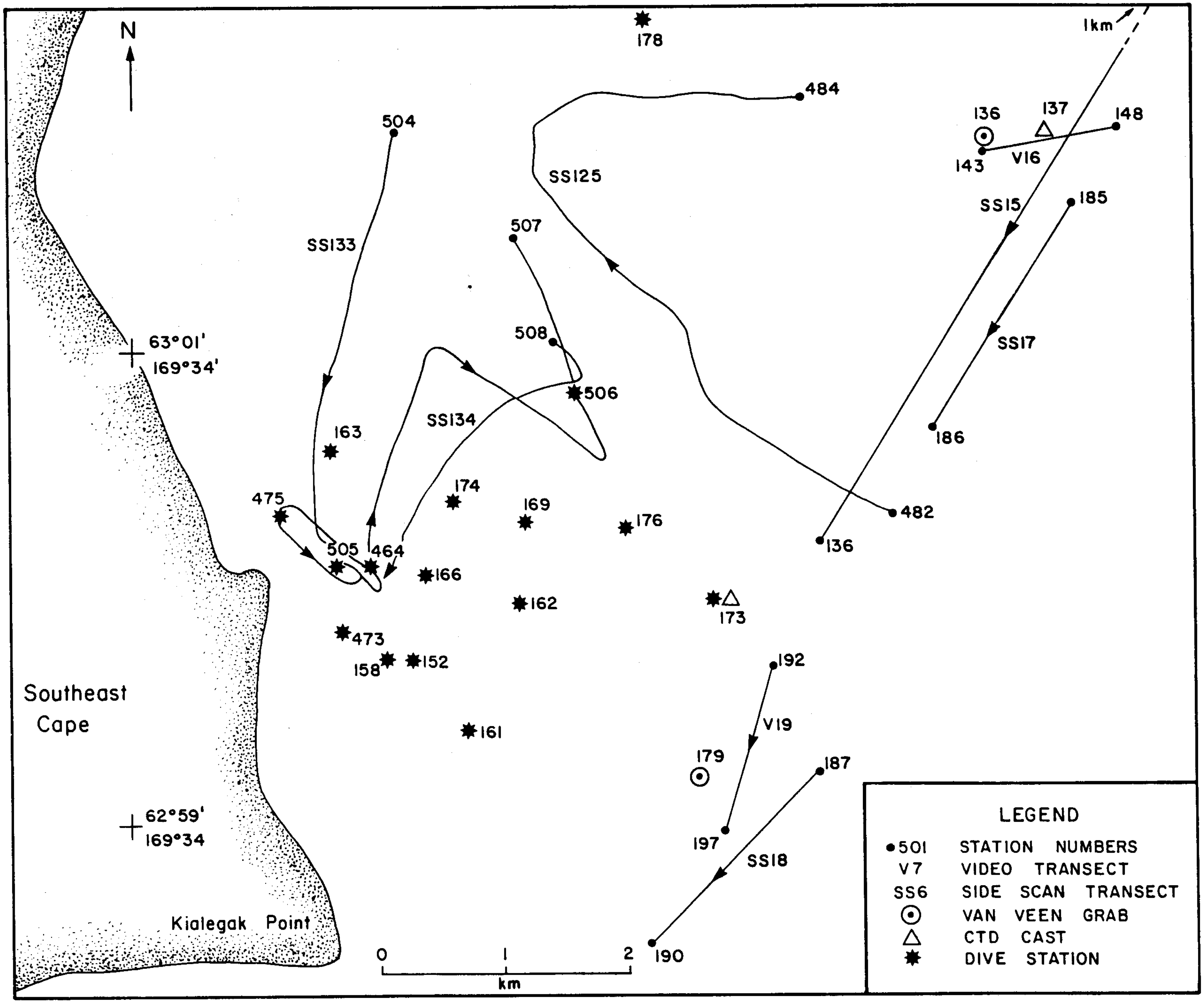


FIGURE 2. Sampling locations off Southeast Cape, St. Lawrence Island

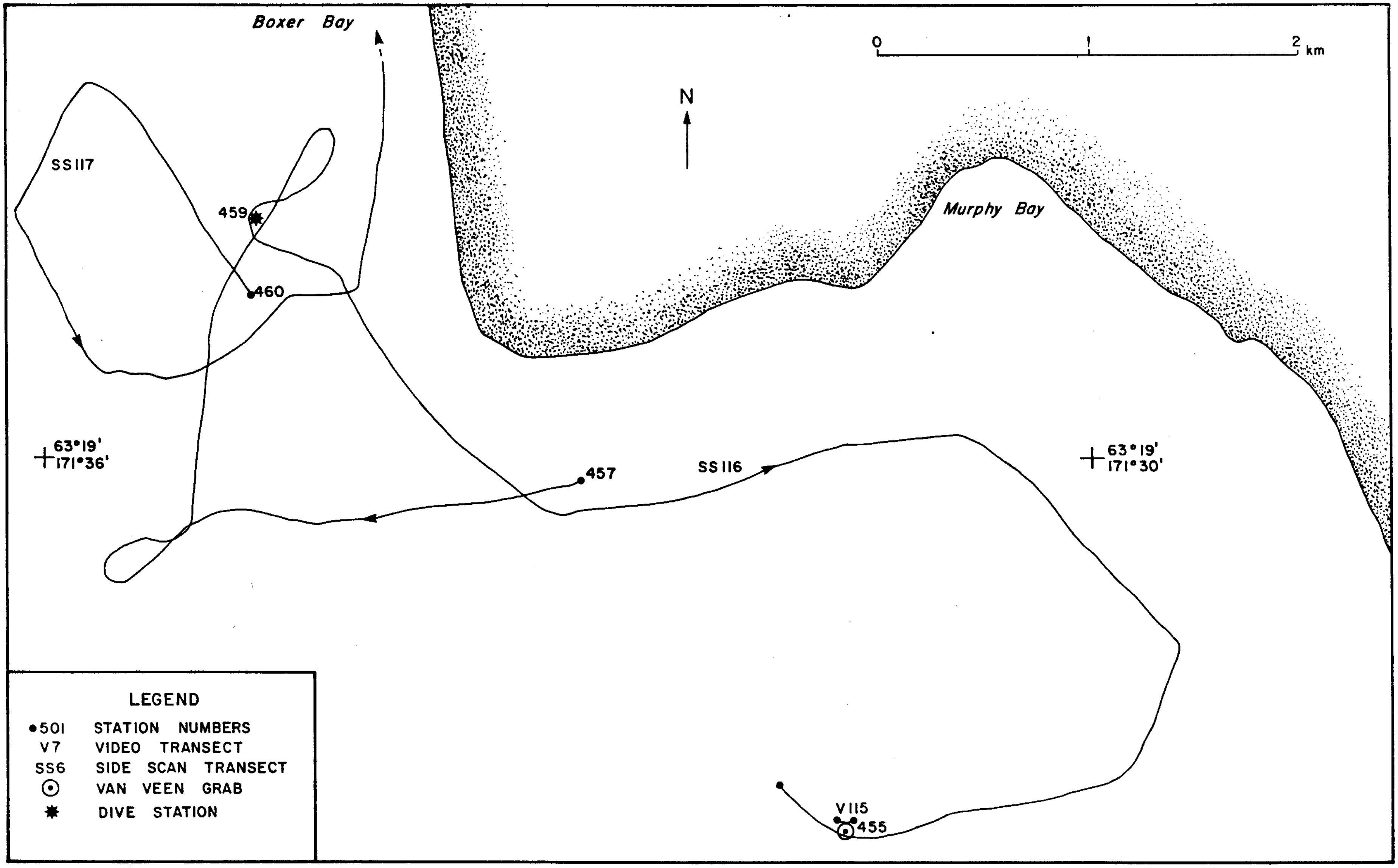


FIGURE 3. Sampling locations in Boxer Bay, St. Lawrence Island.

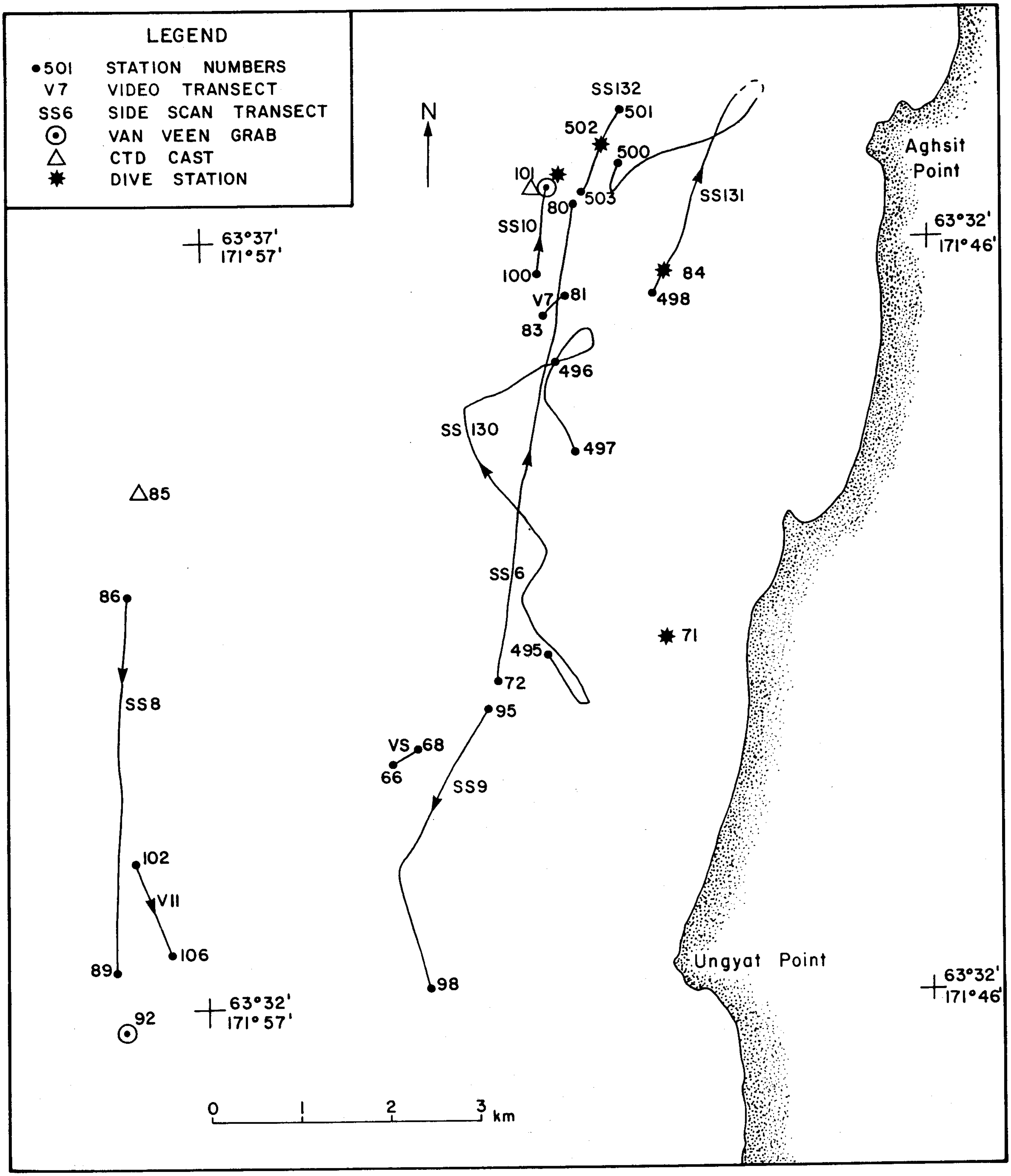


FIGURE 4. Sampling location in area 8C off the west coast of St. Lawrence Island.

content of the substrate. A video camera was also towed in an attempt to recognize bottom features indicative of feeding and provide greater coverage for descriptions of benthic habitat. Observations of the feeding behavior and distribution of whales were also made at each station (Würsig et al., Miller this report). In shallow water, divers investigated and sampled features made by feeding whales.

The types and amounts of work performed in each area are summarized in Table 1. Details of procedures and methods used in benthic sampling with grab, airlift and video camera are described by Thomson (this report).

Table 1. Level of effort and work performed in the Chirikof Basin and nearshore areas off St. Lawrence Island in July and September 1982.

			St. Lawrence Island			
		Chirikof Basin	West Coast	South Coast	Southeast Cape	Total
Stations Occupied		16	4	5	3	28
Side-Scan Sonar	- No. tows	16	9	6	8	39
	- km	37.1	30.7	29.7	66.9	164.4
Benthic Samples	- Van Veen grab samples	75	14	15	10	114
	- Airlift samples				93	93
	- Sediment samples	16	2	3	16	37
Diving Operations	- No. dives		7	1	32	40
	- Diver hours		4.8	1	33.7	39.5

Side-Scan Sonar

The side-scan sonar was generally towed from the ships. In shallow water it was deployed from a small boat. When towed from the small boat an anchor and float were used to mark areas showing evidence of feeding activity by gray whales. A Klein Associates 500 kHz side-scan sonar with a Model 521 two channel recorder was used routinely. At five stations an EG and G Model 259-4 100 kHz side-scan sonar unit was used instead of the 500 kHz unit.

Comparison of features observed on the bottom by divers and features detected by the side-scan sonar indicates that hard objects as thin as 2 cm (light anchor chain) were resolved, as were soft objects as small as 5 cm (mounds and depressions).

The side-scan unit routinely was towed for 30 min at each station. In shallow nearshore areas tows were of two or more hours duration. These long tows were used to look for and mark specific features and areas to be investigated by divers.

The ship's position, speed, heading, and water depth were recorded for each tow. The side-scan record was marked at 2-min intervals. Later, the total number of depressions in the bottom attributable to feeding activities of gray whales was recorded for 1 or 2-min segments, coded and entered into a computer.

From each of 18 transects, we digitized the feature boundaries from five 1- or 2-min segments of the side-scan chart record. Segments were 1-min long when many bottom features were evident, and 2-min long when few were evident. The digitized feature shapes were then corrected for ship speed and height of the sonar above bottom, and feature areas were computed. This was done with a Hewlett Packard HP9874A digitizer in conjunction with an HP9845B computer. Communication between machines was accomplished with a system 45 I/O ROM and an HP-IB interface. Digitizing and data management software was developed by LGL for this project. The area was calculated from the digitized data using a modified trapezoid rule (see Loomis 1975). The plotting was completed on a HP-9872A line plotter. Because of the irregularities of digitizing, a 3-point spatial smoothing filter was applied to the data (see Riply 1981). Only recordings made by the 500 kHz unit were digitized or used to estimate size of feeding features. Limitations of the side-scan sonar for this kind of work are discussed by Johnson et al. (1983).

Temperature

Temperature measurements were made with a Plessy Environmental Systems Model 9041 CTD.

Underwater Observations and Sampling

A team of two divers investigated bottom features in areas where whales were observed to be feeding and in areas marked by a small boat towing the side-scan sonar. Dimensions and morphology of features were measured and recorded in waterproof notebooks. Faunal observations were also made and recorded during a debriefing session after each dive. Features and the surrounding area were photographed with a Nikonos camera and strobe. Five diver-operated airlift samples were taken inside and five outside each of five features. Samples of the substrate were also taken for later analysis of grain size, caloric content, and carbon and nitrogen content. Details of airlift sampling, processing of benthic samples, and laboratory methods are described by Thomson (this report).

Plankton Tows

Eight horizontal plankton tows were made with a 1/2 m #6 mesh net deployed from the ship's launch. These tows were made through the mud plumes emanating from the mouths of feeding gray whales.

Data Processing and Analysis

All data were coded and entered into Hewlett Packard HP9845B or AMDAHL 470 computers and later transfered to an IBM 3033 computer for analysis. Data tabulation was accomplished with programs developed by LGL, and additional analyses were performed using SAS (SAS 1982) and BMDP (Dixon 1981) statistical software.

RESULTS AND DISCUSSION

Description and Distribution of Gray Whale Feeding Features

Morphology and Size of Bottom Features Made by a Feeding Whale

Nerini (in press) discussus the feeding mechanisms of gray whales. They apparently may feed in two different ways. Gigi, a captive gray whale, rolled on her side and--with her head 10-20 cm above the bottom--cleared a 30-50 cm wide swath through the squid lying on the bottom (Ray and Schevill 1974). Hudnall (1981 cited in Nerini in press) also describes a gray whale feeding on its side and sweeping along the bottom, in this case leaving depressions approximately the size of its head. Nerini (in press) believes that feeding whales suck up the surface layer of sediment leaving a series of oblong mouth-sized depressions. She describes these types of features from the Chirikof Basin.

In the following section we describe two different types of features resulting from gray whale feeding: pits and furrows. The pits were as described by Nerini (in press). Furrows were apparently made as described by Ray and Schevill (1974) with the whale sucking while in motion and leaving gaps when expelling sediment. A feeding event is defined as the disturbance made on the bottom by one whale on one dive, and usually consists of a series of features made on the bottom by the whale. As discussed below, a furrowing feeding event may be made up of a series of furrows.

Furrows.--In 13 m of water off Southeast Cape, St. Lawrence Island, a float and anchor marked a location where two whales had been feeding continuously for 2 h in July. In July, whales made approximately 198 feeding dives/day (Würsig et al., this report). This would represent approximately 33 dives in the small area investigated during the two hour period. The whales may also have been feeding before and after the period of observation. A dive was made 6 h after the float was dropped. The sea floor at this location was marred by long narrow furrows, often with short gaps between visible continuations of the feature. Although shallow, these furrows were easily recognized because of the disruption to the "mat" of amphipod tubes that covered the bottom. Density of furrows was so high that it was not possible to follow an individual feeding event composed of these furrows for any great distance. It was possible to isolate and measure 27 discrete portions of furrows but it was not possible to determine how many of these were made during one feeding dive. Discrete portions of the furrows (features) were separated from other furrows by short gaps. Mean length of all furrows measured, from one gap to the next, was 4.9 ± s.d. 3.7 m (n = 27). Mean width was 47.6 ± 34 cm. Depth of all features was 1 to 2 cm. It was possible to follow one feature (furrows and gaps) for 14 m and another for 13.5 m. None of the others could be followed this far, largely because of overlap between feeding features. Gaps between continuations of furrows were 25-50 cm wide.

The side-scan sonar records made in July did show what appeared to be complete furrows in areas not heavily utilized by whales. It was not possible to distinguish individual furrows in areas heavily utilized by whales. The furrows recorded by the side-scan sonar also showed gaps, and the furrows were between 25 and 50 cm in width (Fig. 5a).

The mean total length of the seven isolated furrows was 46 ± s.d 12 m (Table 2.) This distance is consistent with Wursig et al.'s (this volume) surface observations of mean horizontal distance traveled underwater by a feeding whale in July: 100 ± s.d. 46 m (n = 24). The mean furrow length not including gaps was 41 ± 10 m. Mead width of furrows measured by divers off Southeast Cape, St. Lawrence Island, in July (42.6 ± 34.1 cm) was used to calculate the mean area encompassed by these furrow. Mean area was 18 ± 5 m^2 for the seven furrows.

Table 2. Total length, total length of gaps and area encompassed by gray whales' feeding furrows recorded by side-scan sonar in the Chirikof Basin. Mean width of furrows recorded by divers was used to compute area.

Station	Total length (m)	Total length of gaps (m)	Furrow length (m)	Area (m^2)
2A	67	7	60	26
2A	54	15	39	17
2A	49	0	49	21
2A	38	4	34	14
2B	41	3	38	16
2B	37	0	37	16
2B	34	3	31	13

Pits.--Pits are defined here as shallow depressions in the sea floor. These were noted by divers and recorded by side-scan sonar in most areas investigated. Again, density of pits was so high in the shallow waters off Southeast Cape that isolation of single feeding events by divers was impossible. It was possible to measure individual features composed of a series of pits and individual pits.

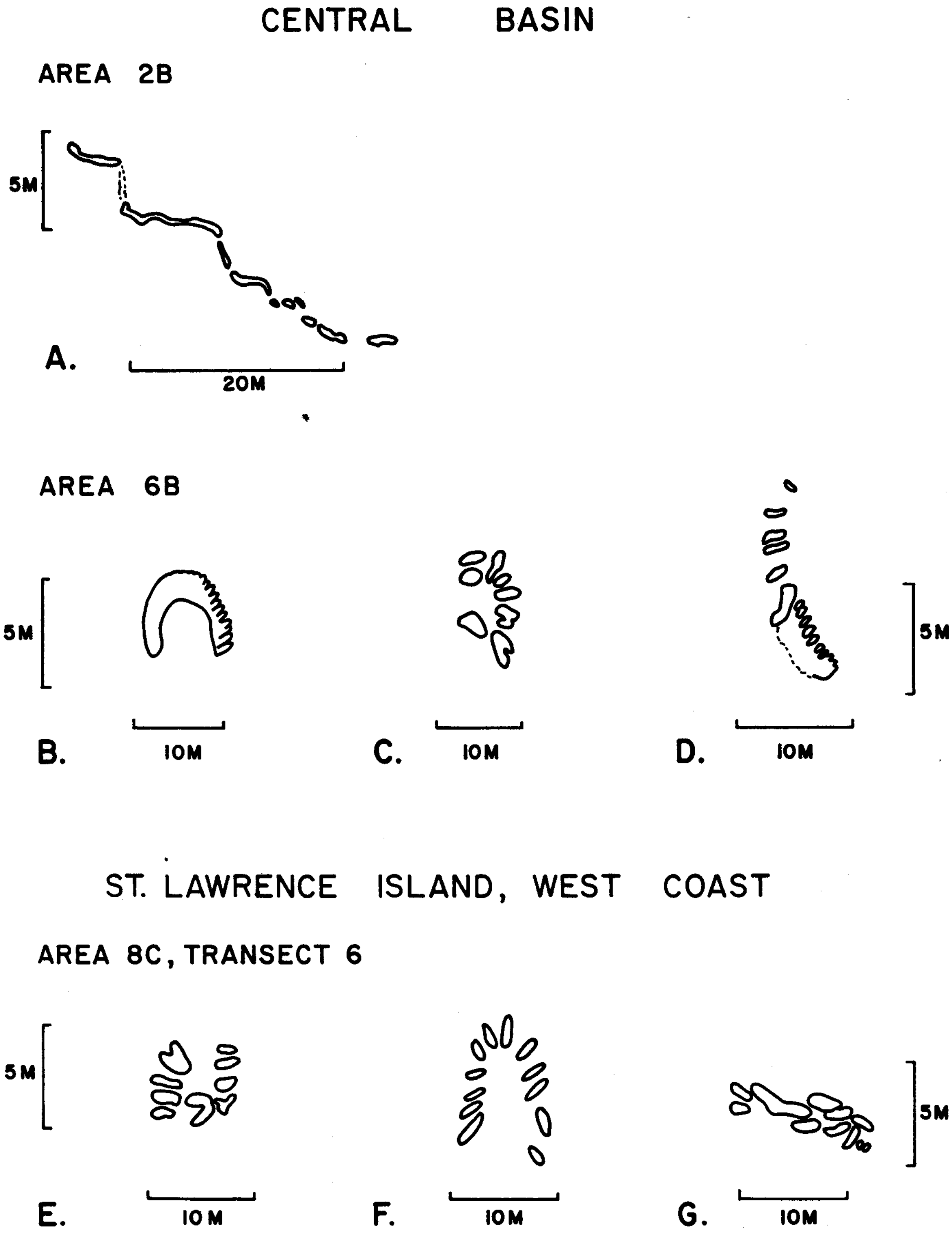


FIGURE 5. Individual bottom features recorded by 500 kHz side scan sonar and attributed to feeding activities of gray whales.

Individual isolated feeding events were recorded elsewhere by side-scan sonar (Figs. 5b to 5g). The whale's mode of feeding in this case was apparently as described by Nerini (in press). While on its side, the whale appears to have taken individual suction 'bites' of the substrate. These 'bites' may be regularly spaced in a semicircle, random in a small area, something between the previous two, or so close together that individual 'bites' are not recognizable (Figs. 5b to 5g). Mean total area of these is given in Table 3.

Table 3. **Mean area of gray whale 'bites' into substrate at six feeding-feature areas in the Central Basin and off the west coast of St. Lawrence Island (see Fig. 5).**

Feature No.[1]	Total Area (m^2)	No. 'Bites'	Mean Area of 'Bite' (m^2)
B	17.0		
C	11.0	9	1.2
D	10.2	5[2]	0.8
E	12.4	10	1.2
F	11.3	12	0.9
G	15.5	10[2]	1.2[1]

[1] See Figure 5.
[2] The largest pits are not included in the calculation.

Mean total area of individual feeding features was 12.9 + s.d. 2.7 m^2 (n = 6) and mean area of individual 'bites' that could be resolved was 1.08 m^2 (n = 46) with a range of 0.75 to 2 m^2.

In September, divers measured 49 features in the heavily pitted region off Southeast Cape (Fig. 6). Although features up to 28.5 m^2 in area were recorded, mean area of all features was 2.9 ± s.d. 5.5 m^2 (n = 49). At this time depth of all features was on the order of 10 cm. The features were close to each other, and often only a few centimetres separated them. Many features appeared to cross and merge with each other. The divers were unable to identify individual feeding events.

In September over the shallow waters off Southeast Cape, some features noted on the side-scan record could be identified as individual feeding events. Some showed elevations within the feature similar to 'coalesced bites' observed in deeper water. Mean area of eight of these features was

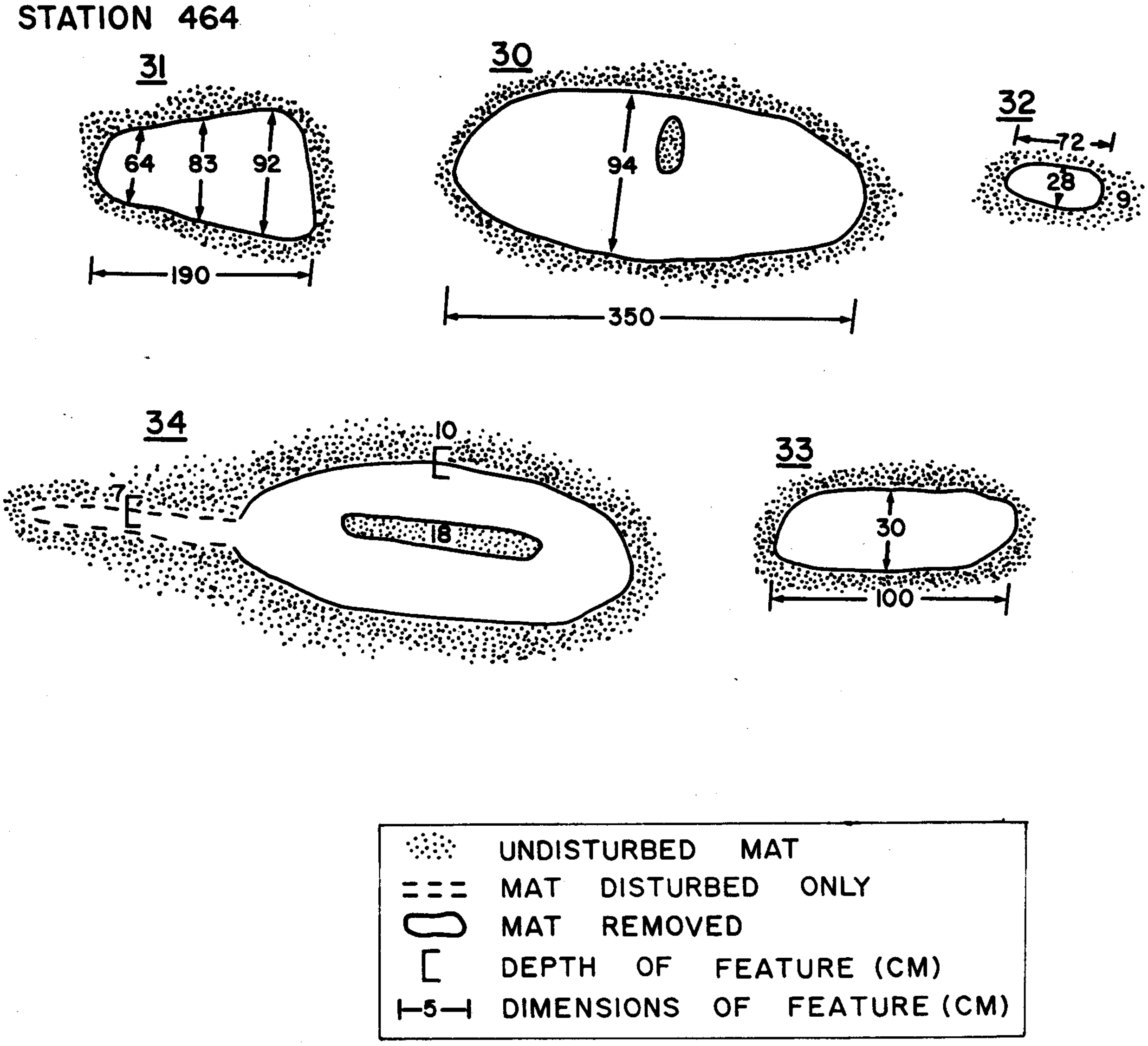


FIGURE 6. Features observed by divers off Southeast Cape, St. Lawrence Island, at depths 11 to 13 m in September 1982.

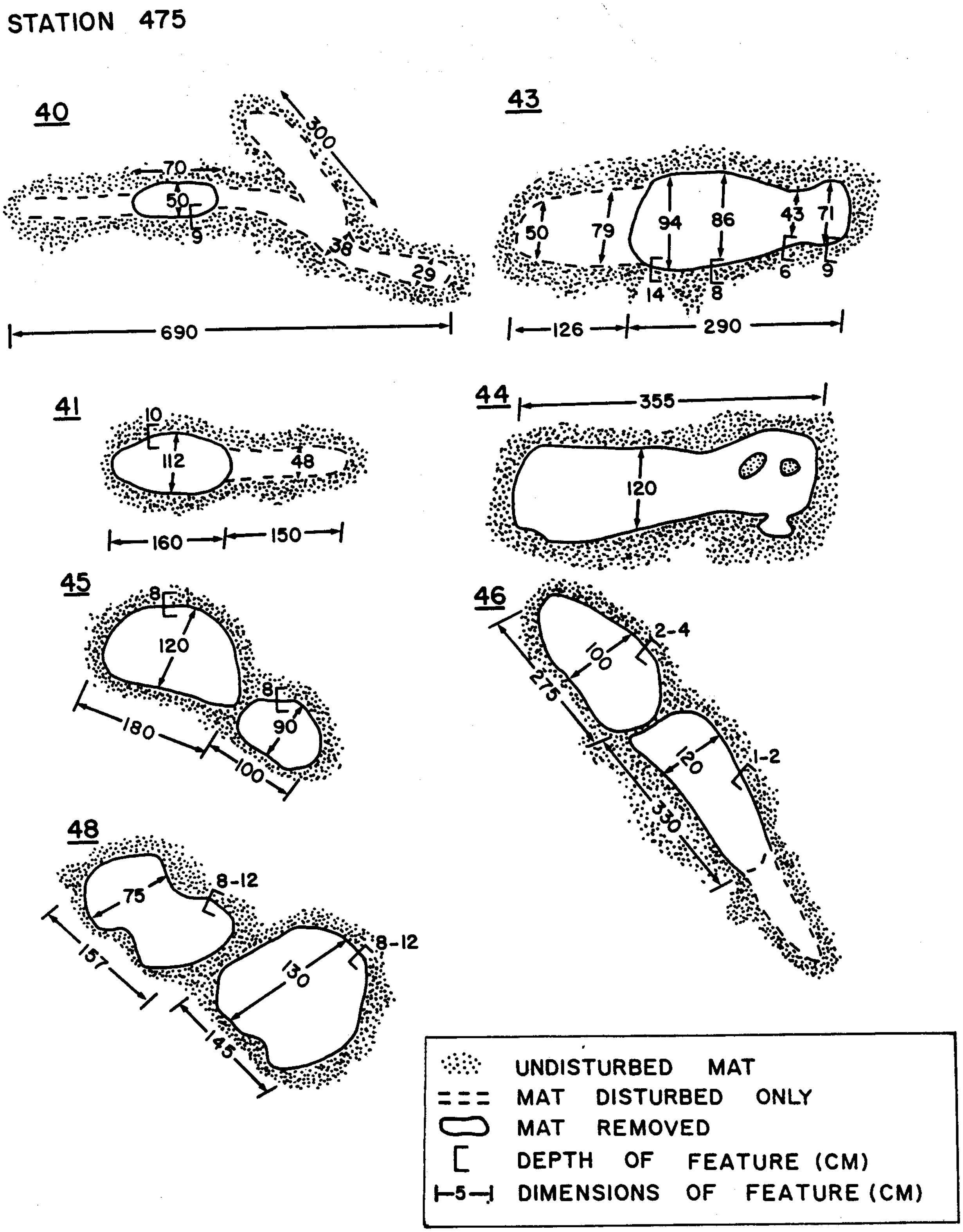


FIGURE 6. Continued

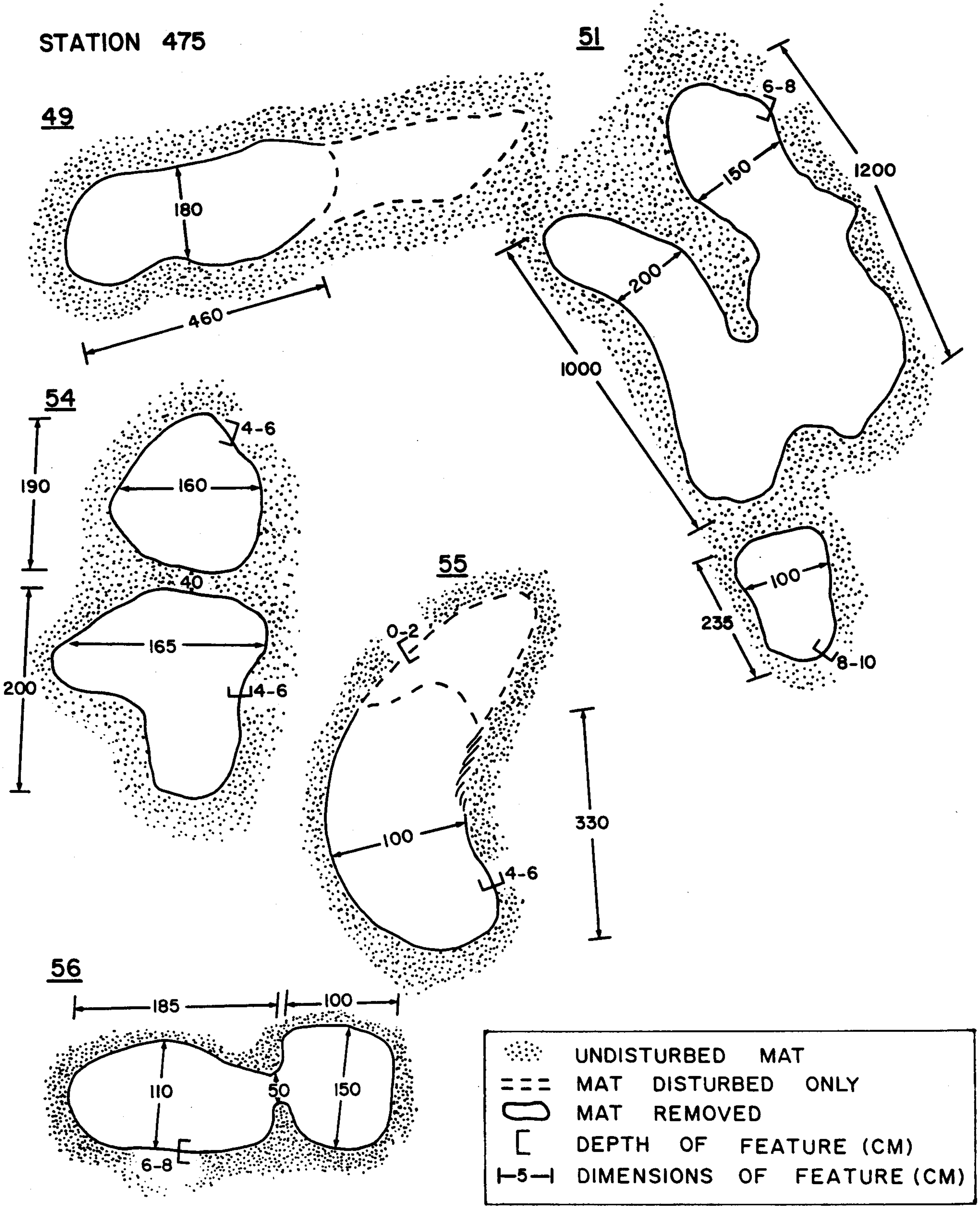


FIGURE 6. Continued

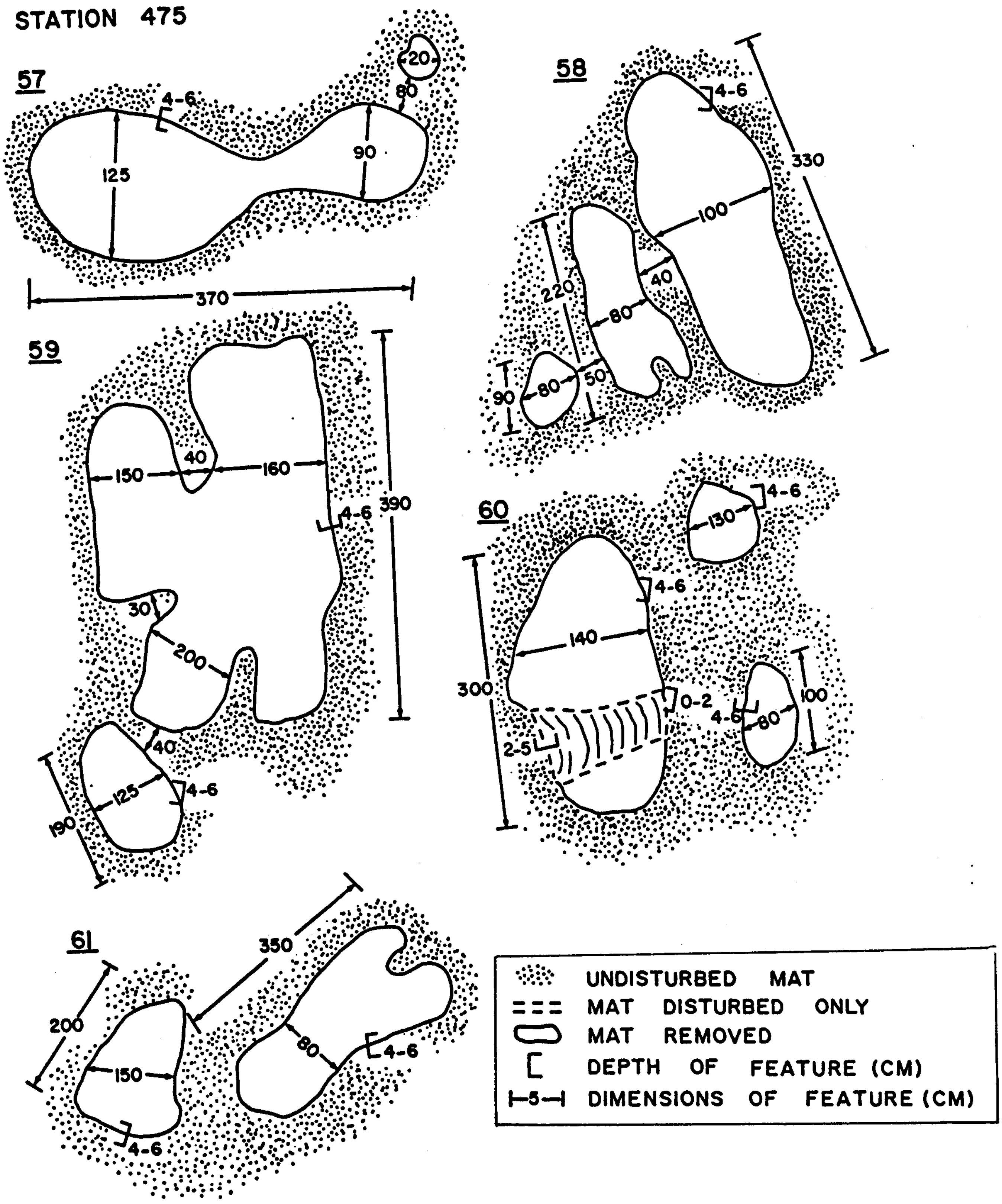


FIGURE 6. Continued

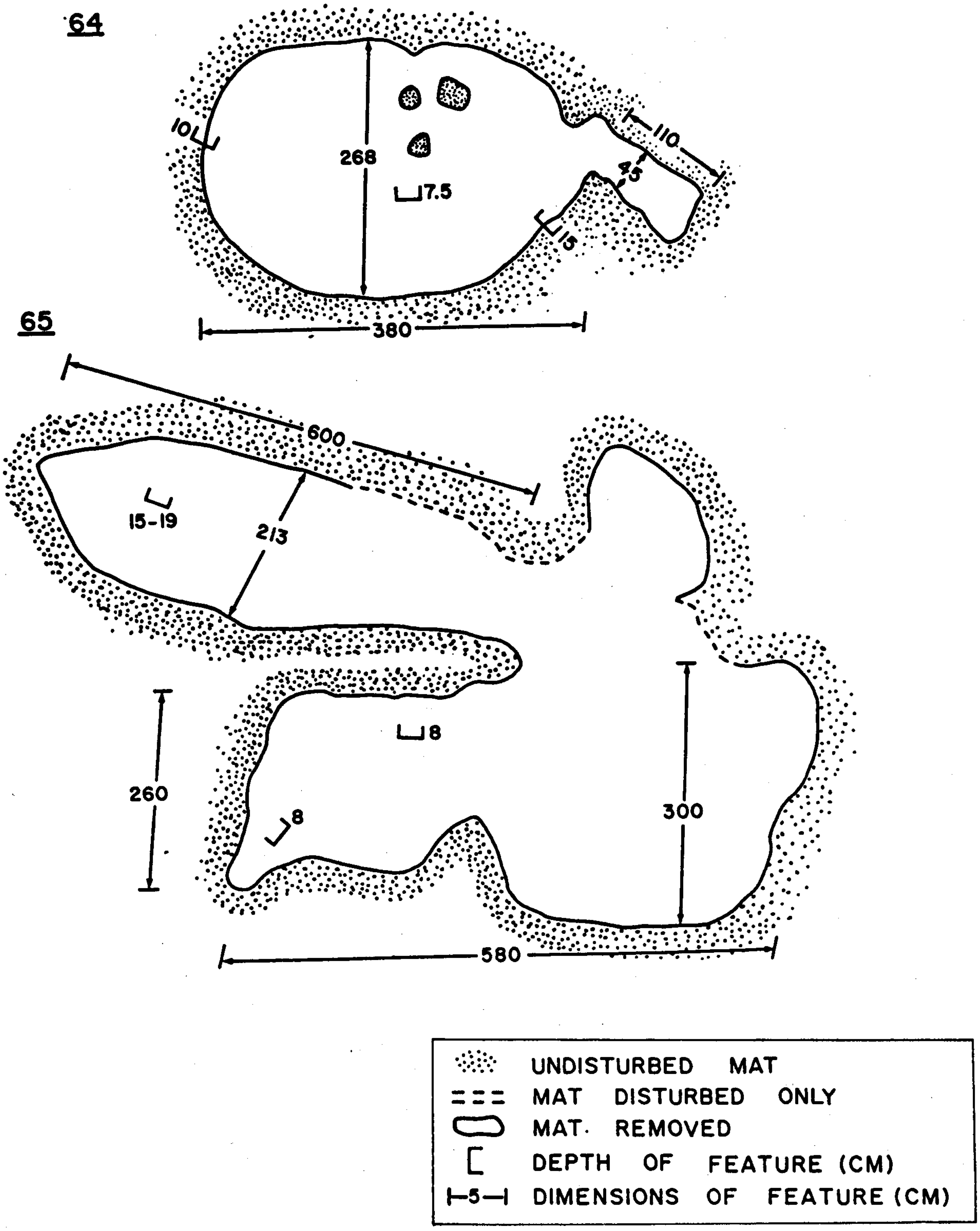


Figure 6. Continued

16.9 ± s.d. 3.3 m^2. At this time, however, most feeding features were so concentrated that individual feeding events were not discernible. This was especially evident on transect 133 made in 11 to 13 m off Southeast Cape in September (Fig. 7). As the area of intense pitting was approached, apparent size of features became larger (Table 4).

Table 4. **Mean size of whale 'bite' feeding-feature areas in relation to percent of bottom affected for five segments along transect 133 (see Fig. 7).**

Segment No.	% of Bottom Affected	Mean ± s.d. feature area (m^2)
A	2.2	4.3 ± 2.0
B	9.4	7.4 ± 3.6
C	36.4	20.7 ± 34.7
D	36.4	34.7 ± 38.3
E	26.9	15.5 ± 13.9

The large apparent size of some of the features in the heavily pitted areas was due to the difficulty in recognizing pit boundaries on the side-scan record. There was a large discrepancy between the size of features recorded by divers and by the side-scan sonar (Figs. 8 and 9). Inspection of the seabed by divers revealed that the feeding features made by the whales were convoluted, overlapped and resembled a maze. To further complicate the patterns, some whales had also been feeding within other features. Divers were able to determine feature boundaries and measure them. They were not able to identify the entire feeding event. Very poor visibility ensured random selection of transect line direction and features for measurement on the transect. During digitization, location of individual feature boundaries on the side-scan sonar record within these heavily pitted areas was extremely difficult and grossly overestimated mean feature size. Estimates of feature size made by divers were more realistic. Areas showing heavy feeding activity were easily recognizable and thus the estimate of percentage of bottom disturbed may be quite accurate.

Examination of the side-scan record indicated that the nearshore areas off Southeast Cape showing this heavy pitting encompassed about 12 km^2. Eighteen percent of the seabed was affected or about 2,300,000 m^2. If a whale cleared 15.5 m^2 per dive and made between 164 and 198 feeding dives

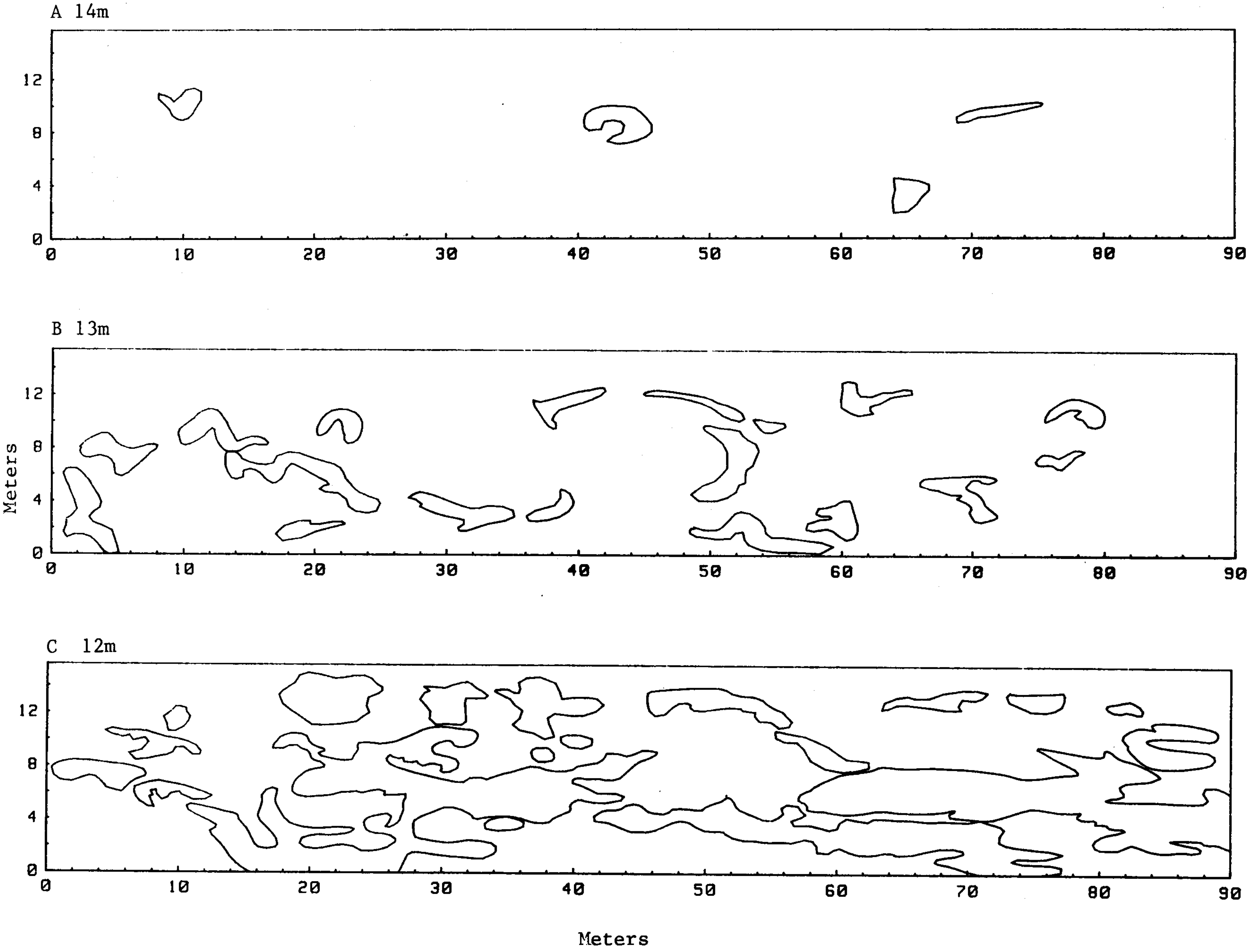


FIGURE 7. Corrected digitized side scan sonar records from transect 133 off Southeast Cape, St. Lawrence Island, in September 1982. The water depth is shown for each segment.

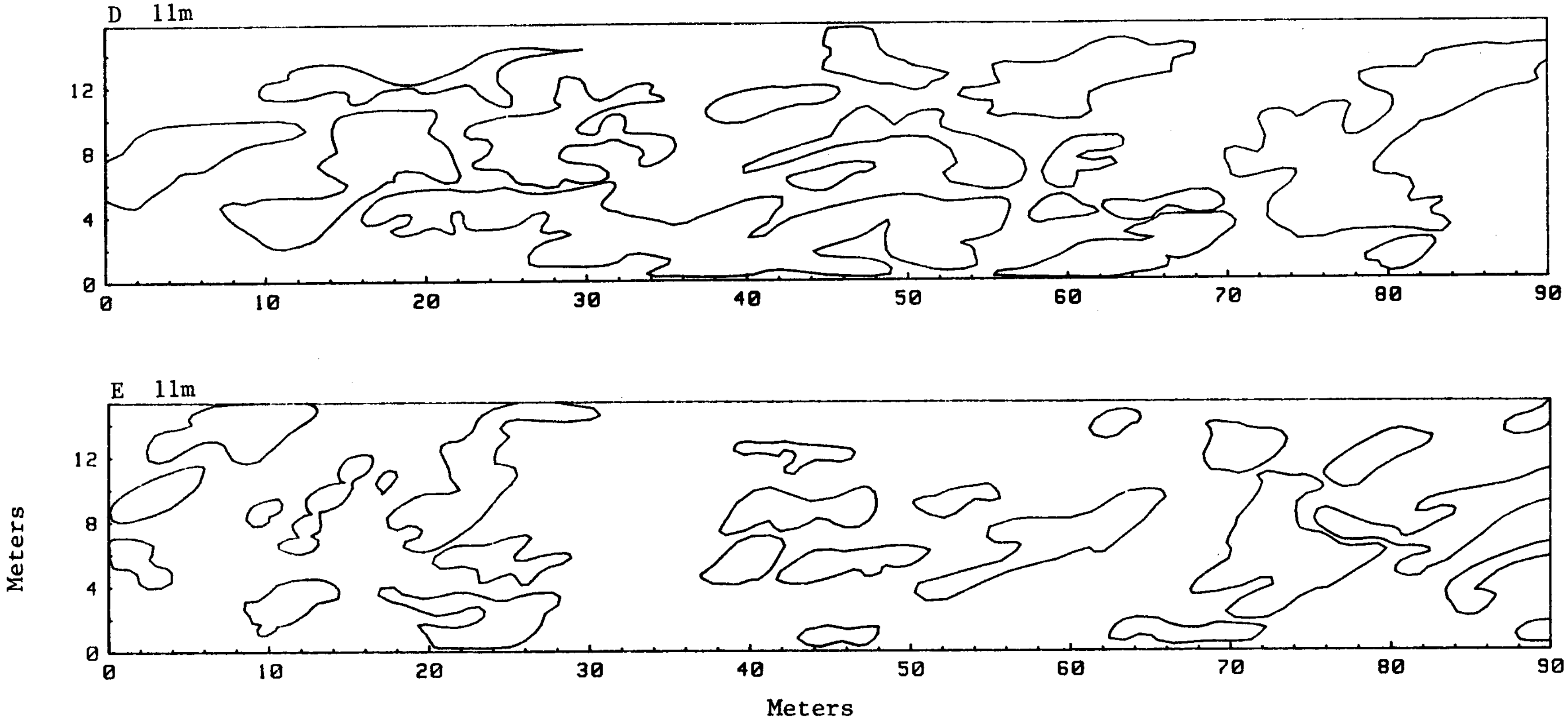


FIGURE 7. Continued

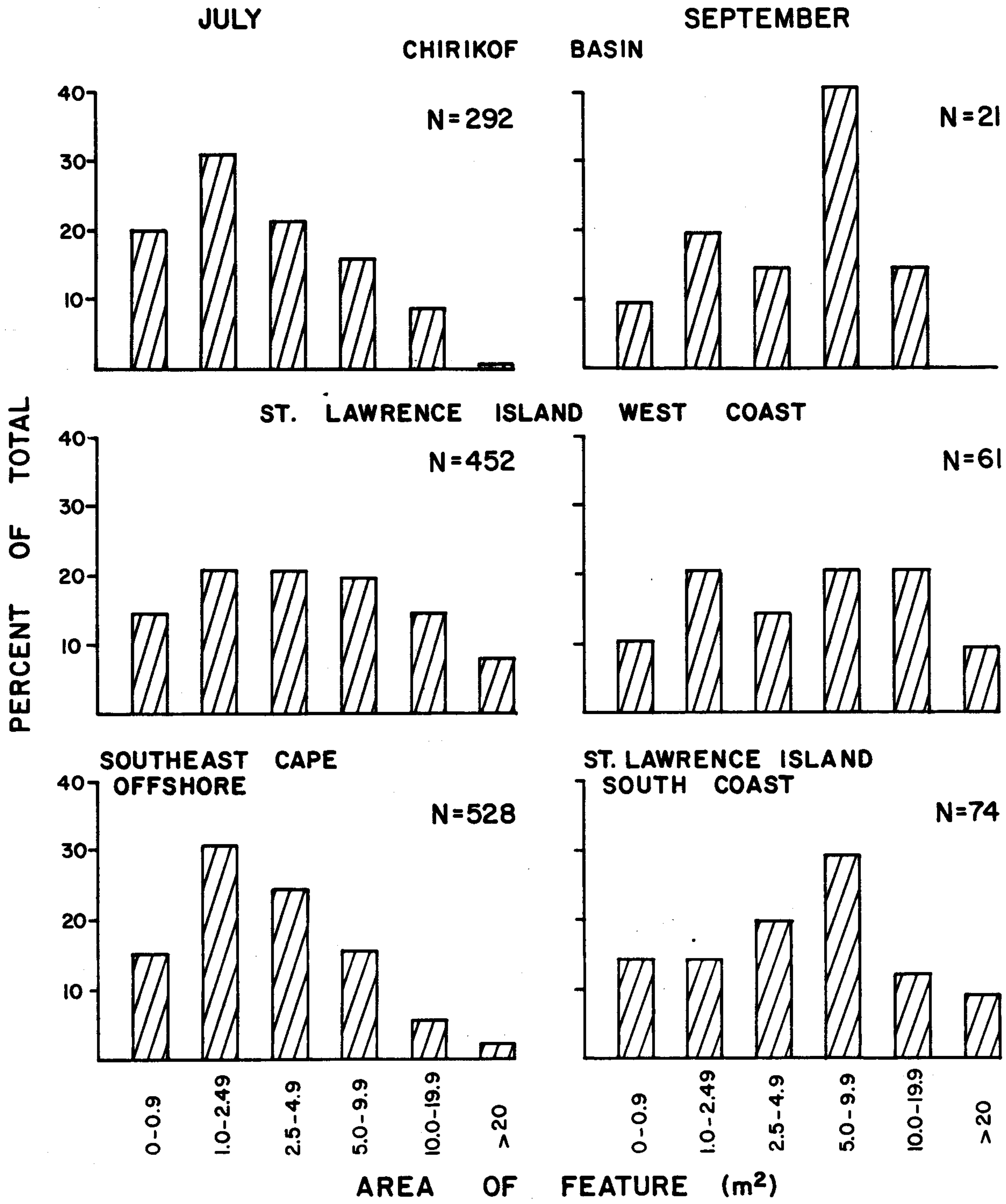


FIGURE 8. Size frequency distributions of the area of bottom features recorded by side-scan sonar and attributed to feeding activities of gray whales. Areas were calculated from digitized side scan records and were corrected for ship speed and height of tow fish above the bottom.

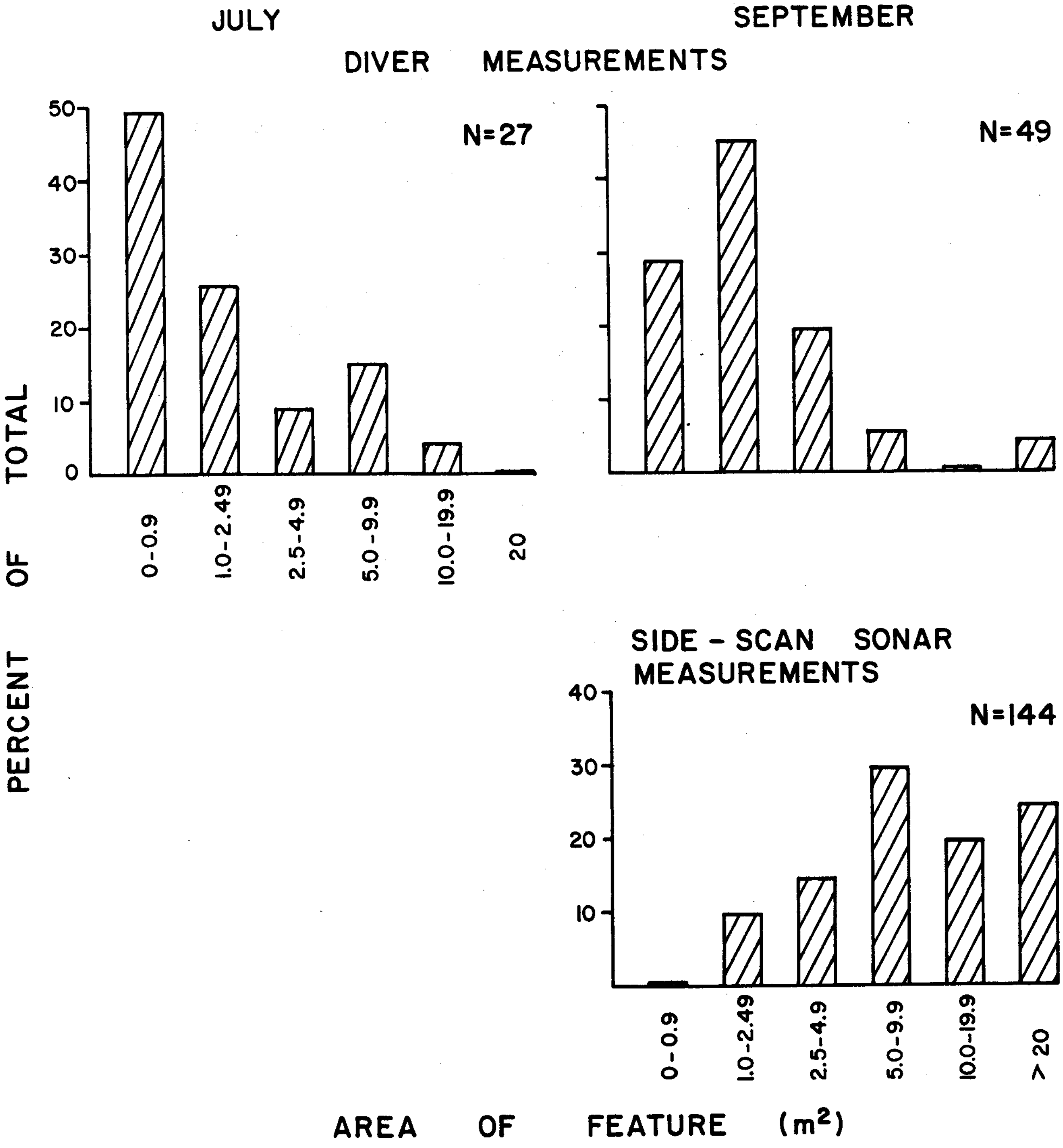


FIGURE 9. Size frequency distributions of the area of bottom features recorded by side-scan sonar or measured by divers and attributed to feeding activities of gray whales in nearshore waters off Southeast Cape, St. Lawrence Island. Measurements of features on side scan data were made on digitized corrected data.

per day (Würsig et al., this report), then only 820 whale-days or nine whales in the area from the beginning of July to the end of September were required to account for the disturbance to the seabed that was observed. About 40 whales were observed off Southeast Cape in July and twenty in September (Miller, this report).

In summary, mean area of furrows was 18 ± s.d. 5 m^2. Mean area of pit type feeding events in deep water was 13 ± s.d. 3 m^2 and mean area of pit type feeding events in shallow water may be on the order of 17 ± 3 m^2. In all areas examined, pits were slightly more numerous than furrows (8.0/1000 m^2 vs. 6.5/1000 m^2, n = 350). We do not know how many feeding events are represented by each of these types of features. A mean area of 15.5 m^2 (the mean of recognizable pits and furrows) will be used as the area of a feeding event in later computations.

The size frequency distribution of features recorded in July in deeper waters not investigated by divers was similar to that recorded off Southeast Cape by divers (Figs. 8 and 9). In the central basin and offshore waters off Southeast Cape approximately one-half of the features were less than 2.5 m^2 in area and as such were within the size range of individual 'bites'. The larger features could include coalesced 'bites' and long stretches of furrow that could not be resolved into smaller units.

Seasonal Comparisons.--Feeding feature size tended to increase in September (Fig. 8). In July, the modal size class in the Chirikof Basin and offshore from Southeast Cape was 1 to 2.5 m^2. In September, modal size in the Chirikof Basin and along the south coast of St. Lawrence Island was 5 to 10 m^2. This difference is also evident in the larger mean size of features recorded for September vs. July (Table 3).

Distribution of Features

In most areas, there appeared to be a mixture of small and large pits and furrows (Figs. 10 to 14). The distribution of bottom features recorded via side-scan sonar and attributed to the feeding activity of gray whales is shown on Figure 15, and their density and mean size in various areas are

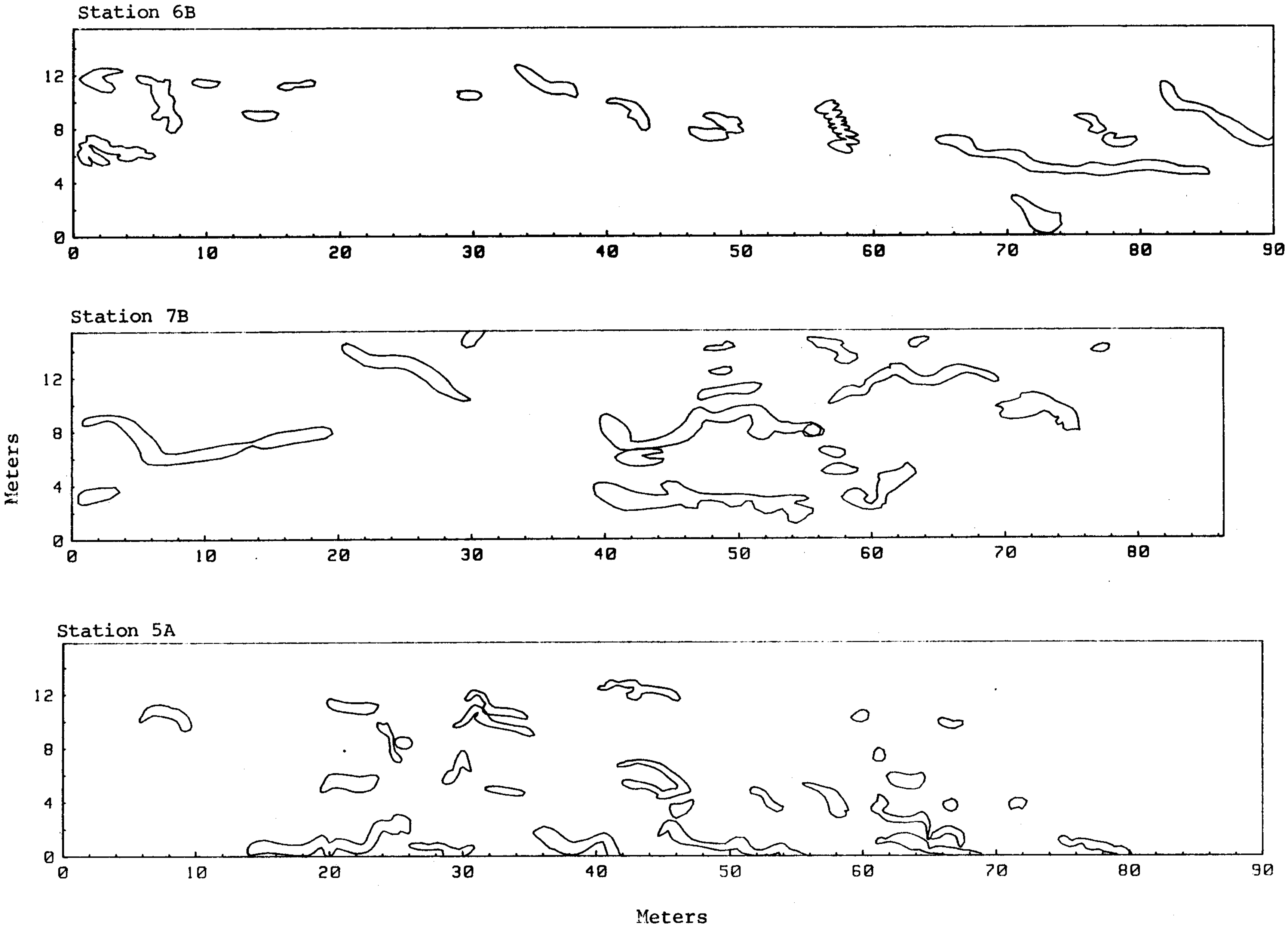


FIGURE 10. Corrected digitized side-scan sonar records from the Chirikof Basin taken in July 1982 at depths of 33 to 41 m.

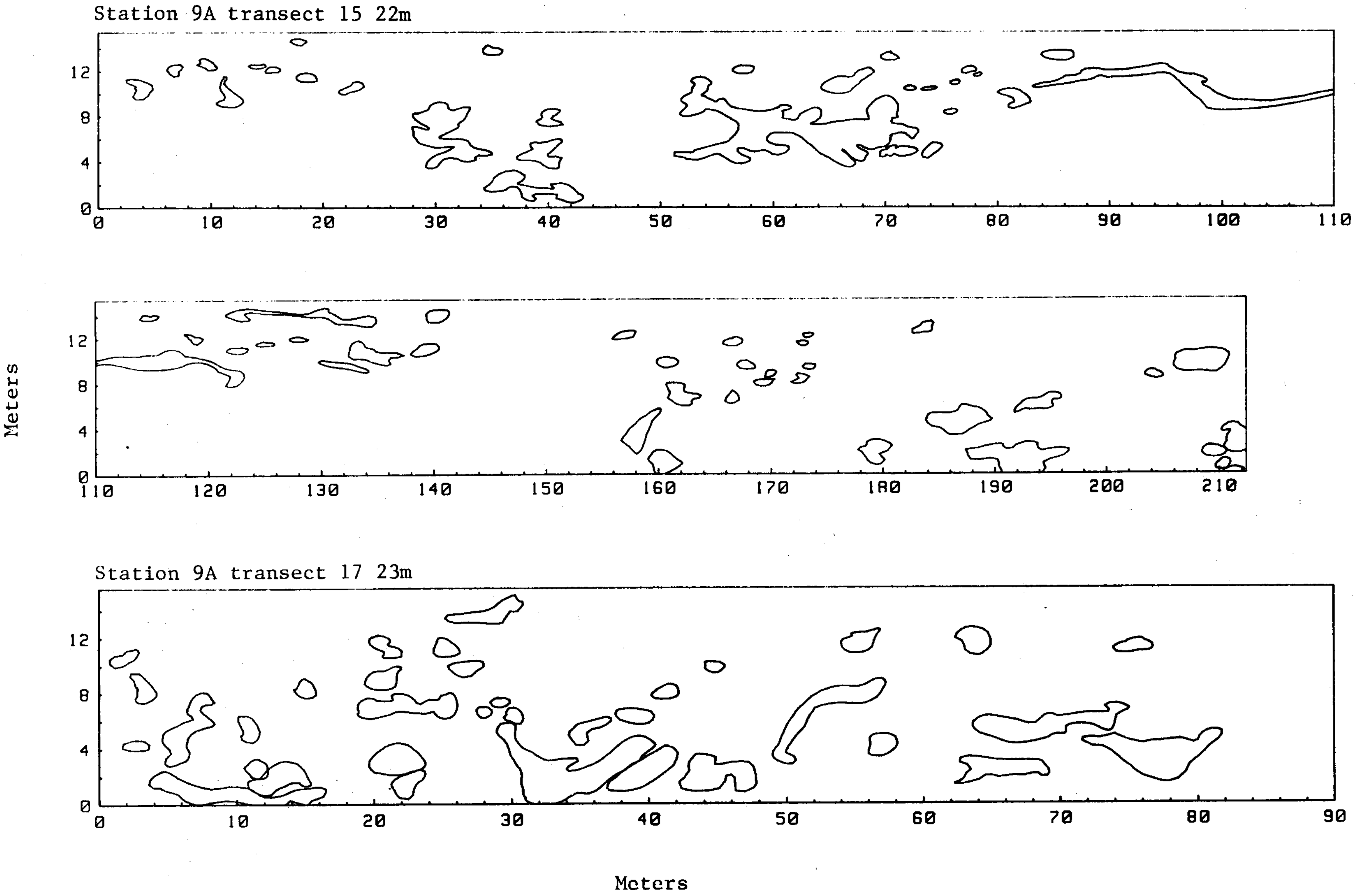


FIGURE 11. Corrected digitized side-scan sonar records from offshore waters off Southeast Cape, St. Lawrence Island taken in July 1982.

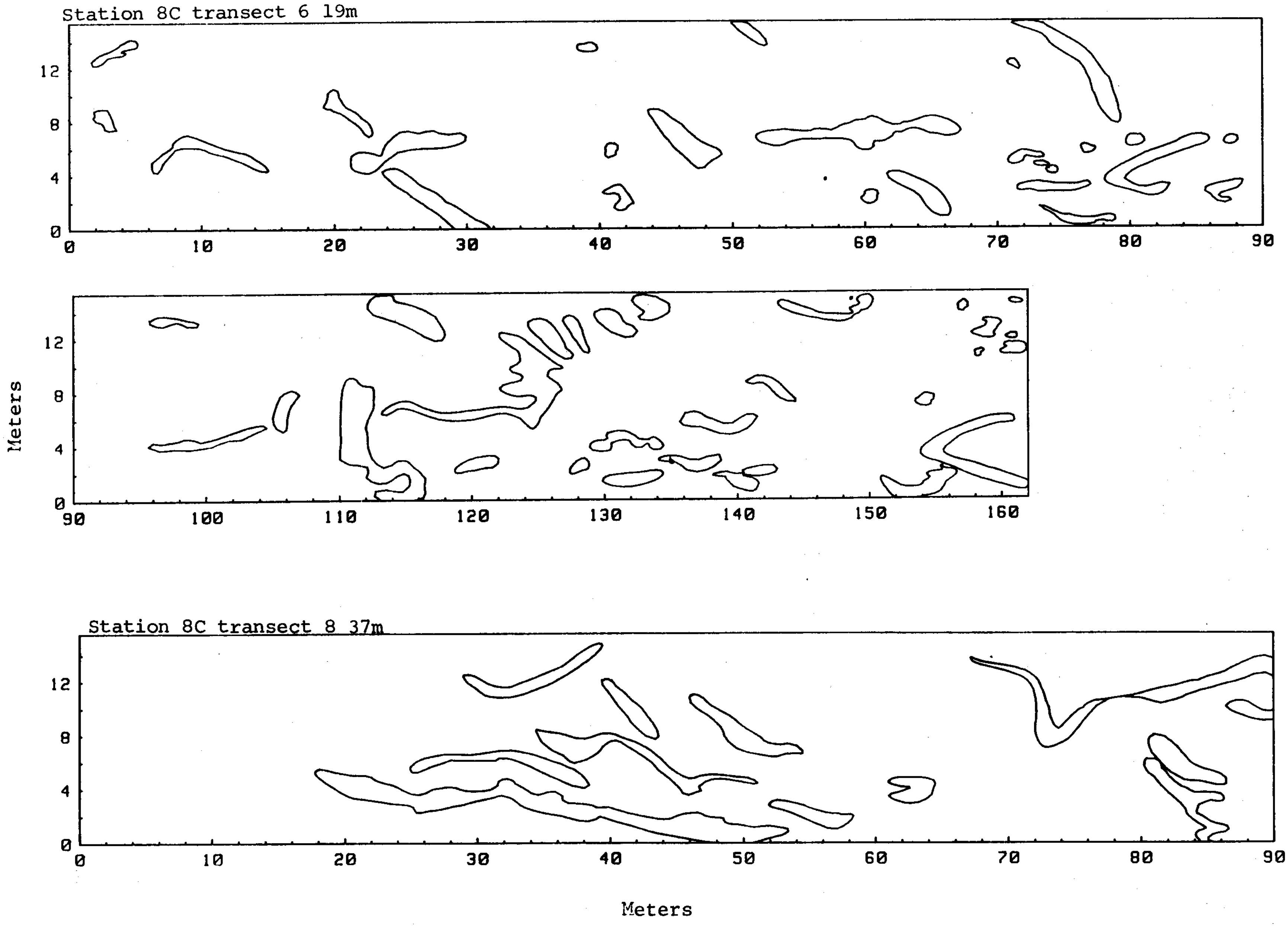
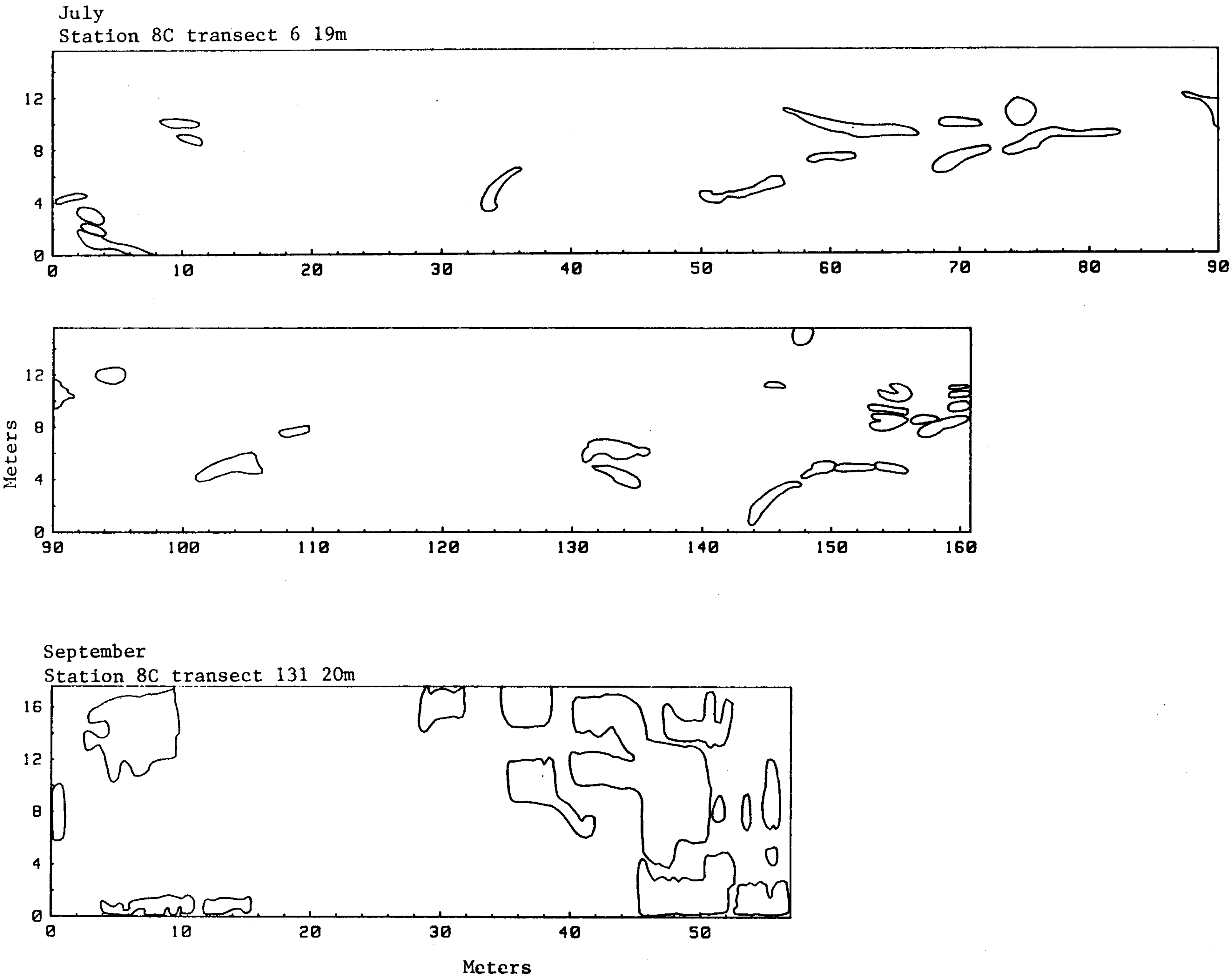


FIGURE 12. Corrected digitized side-scan sonar records from the west coast of St. Lawrence Island taken in July 1982.


July
Station 8C transect 6 19m

September
Station 8C transect 131 20m

FIGURE 13. Corrected digitized side-scan sonar records from the west coast of St. Lawrence Island taken in July and September 1982.

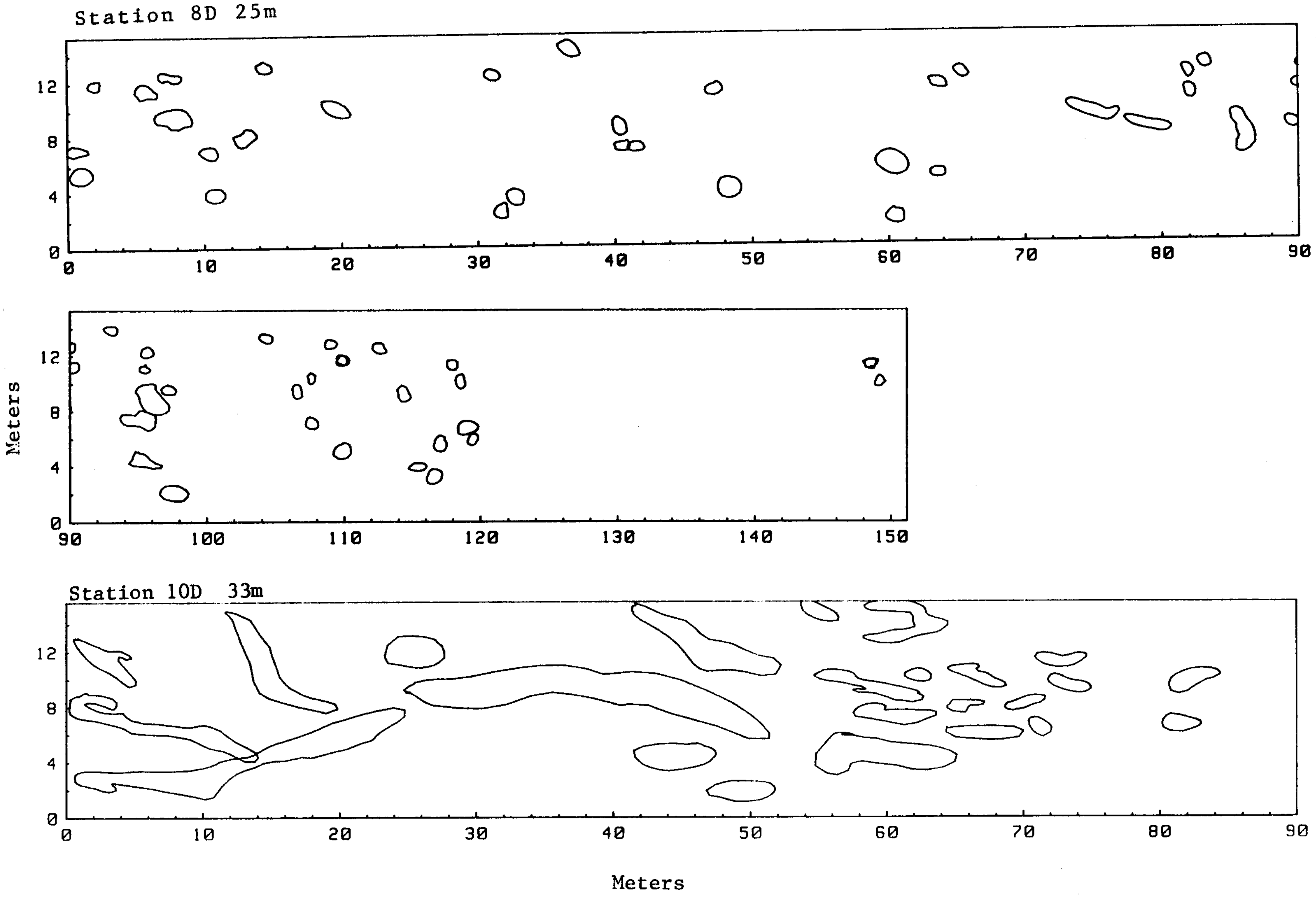


FIGURE 14. Corrected digitized side-scan sonar records from Station 8D off the west coast of St. Lawrence Island in July and from Station 10D off the south coast of St. Lawrence Island in September.

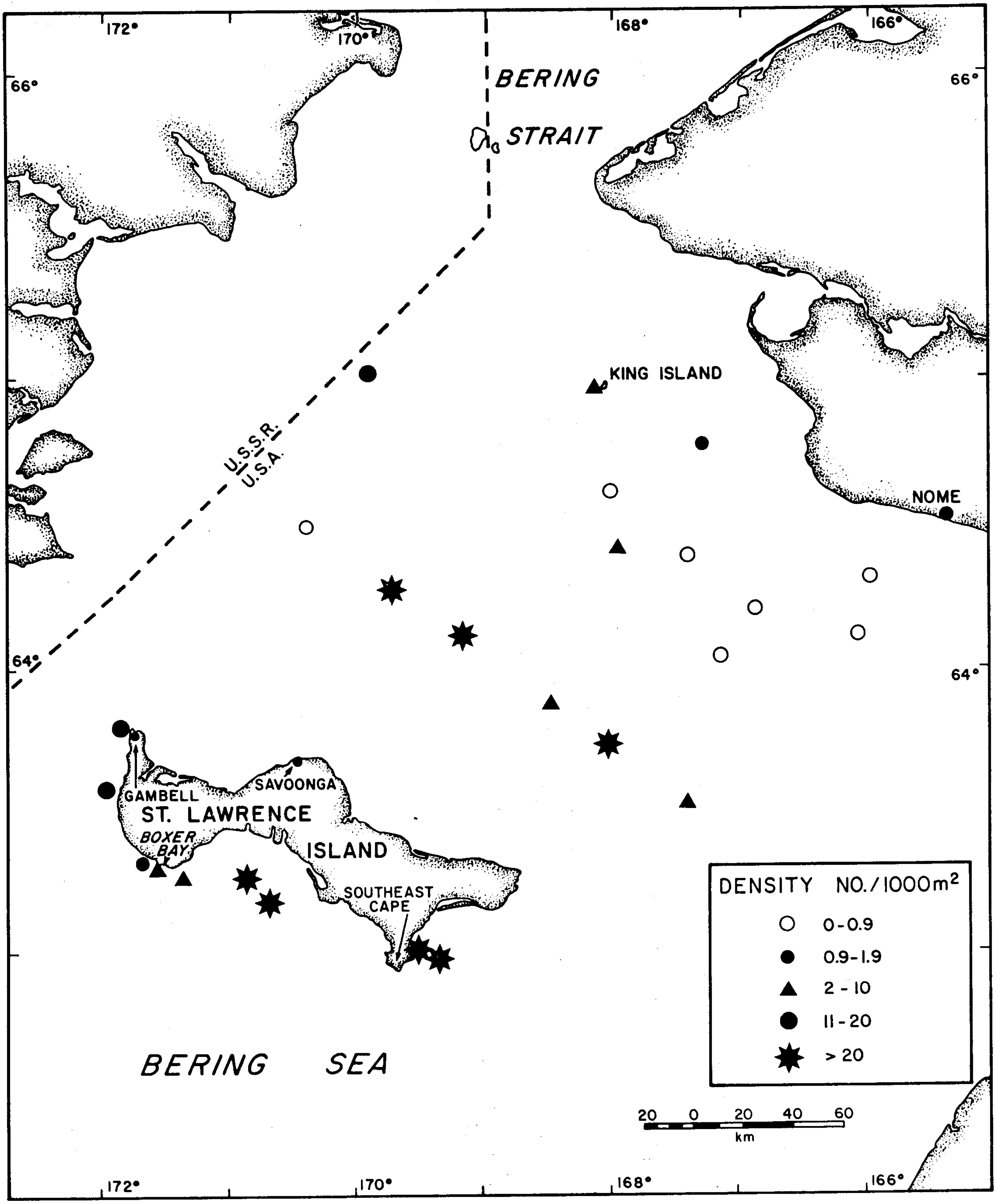


FIGURE 15. Density of individual identifiable bottom features attributed to feeding activities of gray whales, as recorded via side-scan sonar in the Chirikof Basin and near St. Lawrence Island in July and September 1982.

Table 5. Mean area (± s.d.) of features measured via corrected digitized side-scan sonar and by divers in July and September of 1982. Bottom features were atributed to the feeding activity of gray whales. The number of features measured is shown in parentheses.

Area	July	September
Chirikof Basin	3.9 ± 4.1 (292)	6.1 ± 4.5 (21)
St. Lawrence Island[1]		
west coast[1]	7.0 ± 9.0 (452)	8.8 ± 11.7 (61)
south coast[1]		8.3 ± 11.0 (74)
Southeast Cape (offshore)[1]	5.0 ± 8.3 (528)	
Southeast Cape (nearshore)[1]		17.8 ± 26.4 (144)
Southeast Cape (nearshore)[2]	2.3 ± 3.1 (27)	2.9 ± 5.5 (49)

[1] From side-scan sonar.
[2] Diver measurement.

shown in Table 6. It was possible to identify three categories of areas on the basis of the side-scan record:

1. The northeastern region and the west central region (Station 5B; Fig. 15) of the Chirikof Basin are used very little or not at all by gray whales. Mean density of features was only 0.01 ± s.d. 0.03/1000 m^2 in the 174,000 m^2 that were examined.
2. The north central region of the basin appears to be used only sparsely by the whales. Mean density of features was 0.60 ± 0.45/1000 m^2.
3. The central portion of the Chirikof Basin and all of the areas around St. Lawrence Island that were examined (Fig. 15) appear to be used extensively by gray whales. Mean density of features was greater than 10/1000 m^2 for all of these areas (Table 4).

Of the various category areas examined, the proportion of seabed affected by the whales was lowest in the deep waters of the central basin and highest in the shallow waters off Southeast Cape (Table 6.) This apparent inverse relationship between depth and percent of the seabed affected by whales was statistically significant ($r = -0.32$, $0.01>p>0.001$, $n = 82$).

Table 6. Mean density (no./m^2) of major taxa and dominant amphipod species in all samples taken in the Chirikof Basin and near St. Lawrence Island in the summer of 1982.

		St. Lawrence Island		Southeast Cape	
Location	Chirikof Basin	South Coast	West Coast	Depth 11-15 m	Depth 22-23 m
Sample size	75	15	16	34	10
Total	6204 ± 6195	12918 ± 8515	10419 ± 5306	110262 ± 56084	9909 ± 4444
Amphipoda	5086 ± 5907	11056 ± 7790	9088 ± 4951	107873 ± 57192	8808 ± 4106
Polychaeta	651 ± 638	766 ± 787	740 ± 993	1256 ± 1943	704 ± 594
Bivalvia	150 ± 249	677 ± 522	251 ± 300	327 ± 490	162 ± 195
Cumacea	117 ± 248	140 ± 206	27 ± 48	406 ± 569	96 ± 75
Echinodermata	67 ± 136	1 ± 5	0	10 ± 21	16 ± 18
Ascidiacea	18 ± 63	46 ± 55	280 ± 740	6 ± 13	13 ± 17
Ampelisca eschrichti	74 ± 551	4 ± 8	0	31 ± 100	246 ± 286
Ampelisca macrocephala	2061 ± 3182	2582 ± 2391	2841 ± 2163	1080 ± 1278	5030 ± 2478
Byblis gaimardi	402 ± 865	74 ± 120	1573 ± 2652	952 ± 927	55 ± 82
Photis fischmanni	74 ± 143	1032 ± 2139	17 ± 36	95572 ± 54565	139 ± 164
Protomedia fasciata	607 ± 1795	191 ± 448	133 ± 264	50 ± 148	124 ± 148
Protomedia grandimana	872 ± 3446	5367 ± 5331	872 ± 1090	2800 ± 2997	1041 ± 1319
Grandiphoxus acanthinus	91 ± 213	205 ± 203	251 ± 368	153 ± 220	71 ± 144
Harpinia gurjanovae	113 ± 187	40 ± 79	70 ± 135	1439 ± 1130	187 ± 152
Pontoporeia femorata	65 ± 254	233 ± 377	34 ± 79	66 ± 134	500 ± 651
Orchomene lepidula	119 ± 269	198 ± 374	502 ± 659	2697 ± 1759	117 ± 180

Mean area of the features was also greater in the shallow water off Southeast Cape than in deeper water (Table 6). The relationship of this variable to water depth was also statistically significant ($r = -0.32$, $0.01>p>0.001$, $n = 82$).

Comparison with Gray Whale Distribution

The distribution of feeding features on the sea floor as revealed by side-scan sonar closely parallels the distribution of whales as observed during shipboard transects (Table 7). A high density of feeding features on the bottom was generally accompanied by large numbers of whales sighted at the surface at or near side-scan sonar stations (Table 7). No whales were sighted at any of the stations where the sonar revealed one or fewer feeding features per 1000 m^2 on the bottom. Only at Station 7A were there a moderate number of feeding features but no observations of whales.

The correlation between number of feeding features on the sea floor and number of whales observed at the stations was significant ($r = 0.53$, $0.05>p>0.01$, $n = 20$).

Distribution of feeding features on the sea floor also parallels distribution of whales as shown by aerial surveys. Miller (this report) found high densities of whales off Southeast Cape and the west coast of St. Lawrence Island and in the central and northwestern portions of the Chirikof Basin. He observed few whales in areas that showed few or no feeding features on the sea floor. Aerial surveys conducted by Ljungblad et al. (1982, 1983) showed a similar distribution of whales.

Characteristics of Gray Whale Feeding Areas

There were striking biological and physical differences between areas that were heavily utilized as feeding grounds by gray whales and those that were only lightly utilized or not utilized at all (Table 8). The most obvious difference between the three types of areas was in the biomass of amphipods. Biomass of amphipods in areas where side-scan sonar showed many features attributable to feeding gray whales was an order of magnitude greater than in areas with a paucity of features, and almost two orders of

Table 7. Number of bottom features attributed to the feeding activities of gray whales as recorded via side scan sonar and numbers of whales observed via shipboard transects in 20 areas in the Chirikof Basin and near St. Lawrence Island.

	No. features/1000 m^2			
Area	mean ± s.d	(N)	No. Whales[1] Sighted at Station	Remarks
St. Lawrence Island				
West coast	14 ± 10	(66)	65	
South coast	24 ± 17	(36)	20	
Boxer Bay	10 ± 3	(5)[2]	15	
Southeast Cape	26 ± 16	(87)	40	
Chirikof Basin				
7A	8 ± 4	(10)	0	
7B	16 ± 10	(13)	10 (15)[3]	
6A	3 ± 1	(12)	0 (2)[3]	4 between 7B and 6A
6B	22 ± 4	(12)	4 (20)[3]	16 between 6A and B
5A	31 ± 8	(6)	1	
5B	0	(11)	0	
2A	13 ± 9	(8)	8	~100 across international boundary from 2A
2B	5 ± 10	(9)	4	
1B	1 ± 1	(5)	0	
3A	0.5 ± 0.5	(5)	0	
3B	0.1 ± 0.1	(5)	0	
3C	8 ± 5	(13)	2	
1A	0	(10)	0	
4A	0	(10)	0	
4B	0.1 ± 0.1	(4)	0	
4C	0	(19)	0	

---

[1] From Miller (this report).

[2] Includes only transects within Boxer Bay.

[3] Parenthetical values include whales sighted nearby.

Table 8. Physical and biological characteristics of stations where the side-scan sonar record showed no, few, and many features attributed to feeding activity of gray whales. The mean, standard deviation and sample size (in parentheses) are shown.

	Chirikof Basin			All Areas**
	No Features (0-0.08/1000 m^2)*	Few Features (0.14-1.23/1000 m^2)	Many Features (3.49-30.81/1000 m^2)	Many Features (3.49-40.62/1000 m^2)
Mean grain size (Φ)	3.82 ± 0.25 (4) 2.74 (1)	2.37 ± 0.23 (3)	3.23 ± 0.30 (8)	3.14 ± 0.32 (17)
Sorting coefficient (Φ)	2.19 ± 0.44 (5)	2.02 ± 0.11 (3)	1.79 ± 0.38 (8)	1.64 ± 0.32 (17)
Caloric content (cal/g)	328 ± 94 (5)	241 ± 60 (3)	464 ± 292 (7)	372 ± 237 (15)
Carbon/nitrogen ratio	9.2 ± 1.1 (5)	8.6 ± 3.3 (3)	7.0 ± 1.0 (8)	7.3 ± 1.0 (15)
Carbon content (mg/g)	3.9 ± 1.3 (5)	2.4 ± 0.8 (3)	2.9 ± 0.5 (7)	3.1 ± 0.8 (15)
Biomass of amphipods (g/m^2)	3.2 ± 4.0 (23)	13.7 ± 12.9 (15)	132.8 ± 96.5 (37)	148.3 ± 81.1 (93)
Total benthic biomass (g/m^2)	179.9 (23)	128.1 ± 131.2 (15)	262.8 ± 146.3 (37)	280.4 ± 131.9 (93)
Dominant species (% of total biomass)	*Macoma calcarea* (25)	*Macoma calcarea* (16)	*Ampelisca macrocephala* (33)	*Ampelisca macrocephala* (23)
	Serripes groenlandicus (15)	*Yoldia hyperborea* (7)	*Macoma calcarea* (12)	*Macoma calcarea* (14)
	Sand dollar (12)	*Astarte* spp. (7)	*Byblis gaimardi* (7)	*Photis fischmanni* (12)
	Chirodota (11)	*Nephtys* spp. (6)	Sand dollar (7)	*Byblis gaimardi* (5)
	Nephtys spp. (5)		*Ampelisca eschrichti* (5)	*Yoldia myalis* (4)
	Pelonaia corrugata (4)			*Nephtys* spp. (4)
				Ampelisca eschrichti (3)

* Range of mean no. features/1000 m^2 for stations in the category.

** Includes stations in the Central Basin as per Table 4 and stations near St. Lawrence Island.

magnitude greater than in areas showing no features. The correlation between log transformed biomass of amphipods in random samples taken in the vicinity of side scan tows and log transformed density of features attributable to feeding activities of gray whales was significant ($r = 0.75$, $p<0.001$, $n = 131$).

Bivalves, echinoderms, and polychaetes were the dominant benthic organisms in areas that showed few or no feeding features on the side-scan record. Ampeliscid amphipods and the corophiid amphipod Photis fischmanni accounted for 42 to 45% of the benthic biomass in samples taken from areas showing a large number of gray whale feeding features on the side-scan record (compare Figure 15, this chapter and Figures 2 and 3 in Thomson, this report).

The distribution of gray whales as shown by aerial surveys and shipboard observations (Miller, this report; Ljungblad et al. 1982, 1983) also corresponds closely to the area of the Chirikof Basin occupied by dense concentrations of ampeliscid amphipods (Stoker 1981: Fig. 62.2).

In all areas examined, the mean grain size of samples associated with side-scan records showing many gray whale feeding features was 3.1 ± s.d. 0.3 (Table 8). That value is within the range of mean grain sizes (2.9-3.5) preferred by the ampeliscid amphipods inhabiting the Chirikof Basin (Stoker 1978; Thomson, this report).

Areas with many whale feeding features also showed less heterogeneity of substrate than areas with few or no features on the side-scan record (the sorting coefficient was smaller, Table 8).

There was much less gravel (particle size >2.0 mm) in areas showing many features (0.2 ± s.d. 0.5% of dry sediment weight, n = 16) than in areas showing few or no gray whale feeding features (4.6 ± 6.8%, n = 8). Although gravel has been reported in the stomachs of gray whales (Zimushko and Ivashin 1980), it must interfere with feeding activities. A whale clearing 15 m^2 of sea bottom to a depth of 2 cm, given a mean gravel concentration of 4.6%, could ingest 37 kg of gravel at each feeding, as opposed to about 2 kg when mean gravel concentration is 0.2%. This difference in amount of gravel to be handled could be quite important, considering that the whales made between 164 and 198 feeding dives per day (Würsig et al., this report).

The mat community described by Thomson (this report) was characteristic of feeding areas on the shallow shelf off Southeast Cape, St. Lawrence Island. Presence of this cohesive layer allowed feeding whales to leave a long-lasting record of their feeding activities on the bottom. This mat layer may be characteristic of all portions of the study area utilized by foraging gray whales. As discussed by Thomson (this report), animal tubes were the most striking feature of this mat. Biomass of these tubes, less sediment and animals, was 1470 ± s.d. 812 g/m^2 (n = 14) in July and 771 ± 395 g/m^2 (n = 20) in September in the shallow waters off Southeast Cape. Along the south coast of St. Lawrence Island, biomass was 210 ± 103 g/m^2 (n = 15) and in the areas of the central basin utilized by whales it ranged between 242 ± 92 (n = 5) and 476 ± 217 (n = 5) g/m^2.

Food Removal by Gray Whales

Effects on Benthic Animals

In July and September, in the shallow waters off Southeast Cape, St. Lawrence Island, airlift samples were taken both inside and outside bottom features attributed to the feeding activities of gray whales.

At depths of 10-15 m on the shallow shelf off Southeast Cape, St. Lawrence Island, the bottom was covered by a 'mat' of animal tubes. This 'mat' consolidated the surface layer of sediment, imparting it with a cohesive gelatinous nature. Sediments were very fine sand. Amphipods accounted for 65% of the total biomass of 297.8 ± 144.9 g/m^2 (n = 34) and 98% of the total density (110,262 ± 56,084 $indiv./m^2$) of benthic animals in this area. Polychaetes and bivalves accounted for 13% and 10% of benthic biomass, respectively. The amphipod *Photis fischmanni* was the dominant benthic animal in terms of both biomass (42% of total) and density (87% of total). The ampeliscid amphipods *Ampelisca macrocephala* and *Byblis gaimardi* and the bivalve *Macoma calcarea* were also important contributors to biomass.

In July, a float and marker were placed within a group of two whales that were observed to be feeding for at least 2 h. The two whales, made at least 33 dives and showed concrete evidence of feeding (mud plumes, mud streaming from mouths). The bottom features were investigated 6 h after the float was dropped, but we have no way of knowing absolutely that the whales made the feature that was investigated or when the feature was made. Mean length of furrow determined above was 41 m. Over 1000 m of furrows could have been made in the 2 h of observation. In all, 27 features were measured and/or photographed and benthic sampling was carried out inside and outside one feature. Biomass of benthic animals inside the feature was 221 g/m^2, about 40 g/m^2 higher than outside. Yoldia myalis, a burrowing bivalve, was common (50 ± 21 g/m^2) in four samples taken within the feature and rare in four samples taken outside (<1 g/m^2) the feature. The furrow was likely over a high density patch of this species. If the bivalve Yoldia is excluded from consideration, the biomass within the feature was 171 g/m^2--equivalent to the biomass outside (182 g/m^2). It is not known how much of the biomass in the feature remained after the whale fed and how much immigrated subsequently.

The isopod Tecticeps alascensis was more abundant within the feature than outside. Analysis of stomach contents of this isopod showed that it had been feeding primarily on amphipods (Table 9). It seems likely that this isopod immigrated into the feature to take advantage of the sea bed that had been traumatized by a feeding gray whale. Carnivorous (Fauchald and Jumars 1979) nephtiid polychaetes were also more abundant within the feature (Table 11), and may also have quickly immigrated into it for the same reason.

The ampeliscid amphipod Ampelisca macrocephala was also more abundant within the feature than outside. In fact its biomass within the feature was higher than in other samples taken at similar depths away from areas that had been utilized by whales (Table 11). Photis fischmanni showed a markedly lower biomass within the feature (Table 11). Synidotea picta, another isopod, was more abundant within the feature than outside, as were the amphipods Protomedia grandimana and Dyopedes arcticus.

Table 9. Frequency of occurrence of food items found in the guts of 43 specimens of the isopod *Tecticeps alascensis* taken at depths of 10 to 15 m in the nearshore waters off the southeast cape of St. Lawrence Island in the summer of 1982.

Food Item	Frequency of Occurrence
Amphipods	
Unidentified amphipods	9
Ampeliscidae	3
Ampelisca eschrichti	1
Haustoriidae	1
Euhaustorius sp.	2
Lysianassidae	2
Orchomene sp.	1
Protomedeia sp.	10
Photis sp.[1]	7
Corophium sp.	3
Other taxa	
Foraminifera	1
Gastropoda	2
Animal tissue	2
Sediment	9
Empty	9

[1] Includes *P. fischmanni*.

In September, four features of indeterminate age were investigated; results were similar to those from July (Table 11). Within features, biomass of *Photis fischmanni* was lower than outside features, and biomass of *Ampelisca macrocephala*, isopods and nephtiid polychaetes was higher than outside features. Differences in mean individual weight for *Photis fischmanni* from samples taken inside and outside feeding features were negligible.

Table 10. Mean individual wet weight of the amphipod *Photis fischmanni* from samples taken inside and outside feeding features in the vicinity of Southeast Cape, St. Lawrence Island.

	Mean individual wet wt[1] (mg) ± s.d. (sample size)	
Month	**Inside feature**	**Outside feature**
July	**1.34 ± 0.80 (3)**	**1.72 ± 0.69 (4)**
August	**1.34 ± 0.76 (12)**	**1.16 ± 0.42 (15)**

[1] **Only samples containing more than 100 individuals were used. Values are biomass in sample/no. individuals in sample.**

Table 11. Mean biomass ($g/m^2 \pm s.d.$) of major taxa and dominant species from samples taken inside and outside bottom features attributed to the feeding activity of gray whales and from samples taken of the upper 2 cm and upper 10-15 cm of substrate. All samples were taken off Southeast Cape, St. Lawrence Island, by diver operated airlift.

Taxon	July		September		Surface 2 cm of mat	Samples taken to 10-15 cm into mud
	Inside	Outside	Inside	Outside		
n =	4	4	20	20	30	10
Total biomass	221 ± 69	182 ± 41	256 ± 131	263 ± 128	207 ± 102	412 ± 138
Amphipods	104 ± 62	159 ± 42	130 ± 70	206 ± 73	147 ± 77	184 ± 78
Polychaetes	12 ± 11	3 ± 2	46 ± 63	18 ± 25	7 ± 8	94 ± 73
Isopods	23 ± 12	3 ± 3	43 ± 29	5 ± 7	15 ± 18	3 ± 10
Bivalves	53 ± 19	6 ± 11	24 ± 67	26 ± 76	16 ± 38	44 ± 45
Amphipods						
Photis fischmanni	27 ± 27	106 ± 43	34 ± 42	150 ± 65	73 ± 69	81 ± 49
Protomedia grandimana	5 ± 5	1 ± 2	31 ± 28	19 ± 13	10 ± 11	7 ± 21
Ampelisca macrocephala	44 ± 27	12 ± 7	20 ± 20	6 ± 7	21 ± 16	21 ± 13
Byblis gaimardi	2 ± 2	4 ± 4	11 ± 10	8 ± 6	4 ± 5	<1
Anonyx nugax	8 ± 7	16 ± 9	12 ± 8	4 ± 3	8 ± 16	26 ± 9
Orchomene lepidula	4 ± 4	6 ± 4	5 ± 3	7 ± 6	6 ± 6	8 ± 6
Pyopedes arcticus	7 ± 10	2 ± 2	0 ± 0	0 ± 1	15 ± 14	33 ± 16
Some Other Taxa						
Tecticeps alascensis (I)	17 ± 7	0 ± 1	33 ± 28	4 ± 7	11 ± 15	<1
Synidotea picta (I)	5 ± 6	2 ± 3	8 ± 8	1 ± 2	3 ± 5	3 ± 10
Nephtys spp. (P)	8 ± 9	<1	39 ± 61	12 ± 21	2 ± 2	28 ± 29
Macoma calcarea (B)	1 ± 2	<1	15 ± 63	18 ± 77	1 ± 1	13 ± 18
Yoldia myalis (B)	50 ± 21	<1	6 ± 13	7 ± 12	4 ± 21	16 ± 38

I isopod, P polychaete, B bivalve.

Based on the length-weight relationship of P. fischmanni (Thomson, this report), all of the mean weights shown above correspond to a 4 mm individual. There were also no apparent differences in the size frequency distributions of Ampelisca macrocephala taken from inside and outside feeding features in September (Fig. 16). Recolonization by these species appears to involve the general population rather than specific size groups.

It is interesting that total biomass of polychaetes exclusive of Nephtys spp. was similar inside and outside the feeding features. Stomach contents of gray whales taken in Russian waters indicate that they feed almost exclusively on amphipods (Zimushko and Ivashin 1980; Bogoslovskaya et al. 1982; Blokhin and Pavlyuchkov 1983; Yablokov and Bogoslovskaya in press). Other animals are rare in stomach contents. It is also worth noting that amphipods accounted for 78 to 87% of total biomass in samples taken outside but immediately adjacent to furrows, but only 44% of total benthic biomass of samples taken 800 m from feeding features in July. Thus, the whales had been feeding in areas with a high biomass of amphipods and low biomass of other taxa. In July, whales were feeding on the top 2 cm of the 'mat' layer. Samples taken to a depth of 2 cm in the 'mat' layer contained a large biomass of amphipods and low biomass of other taxa (Table 11). The whales were selecting for amphipods both during selection of feeding sites and by processing only the top 2 cm of the substrate.

In these shallow waters off Southeast Cape, density of Photis fischmanni alone in areas where whales were feeding was over 100,000 animals/m^2. Density of Ampelisca macrocephala was only 1/5 of that in deeper (>20 m) water where density of all animals was only 10,000/m^2. There was a significant negative correlation between densities of A. macrocephala and P. fischmanni, considering all samples taken within, outside and away from the furrows found in shallow water off Southeast Cape ($r = -0.329$, $p<0.001$, $n = 86$). A high density of P. fischmanni was accompanied by a low density of A. macrocephala. Competition for space with P. fischmanni may be a factor that limits the abundance of A. macrocephala in this region.

In other regions, ampeliscid amphipods are opportunistic recolonizers of disturbed areas (Mills 1967). During this study, we observed that disturbance of the seabed by divers or the underwater video frame caused

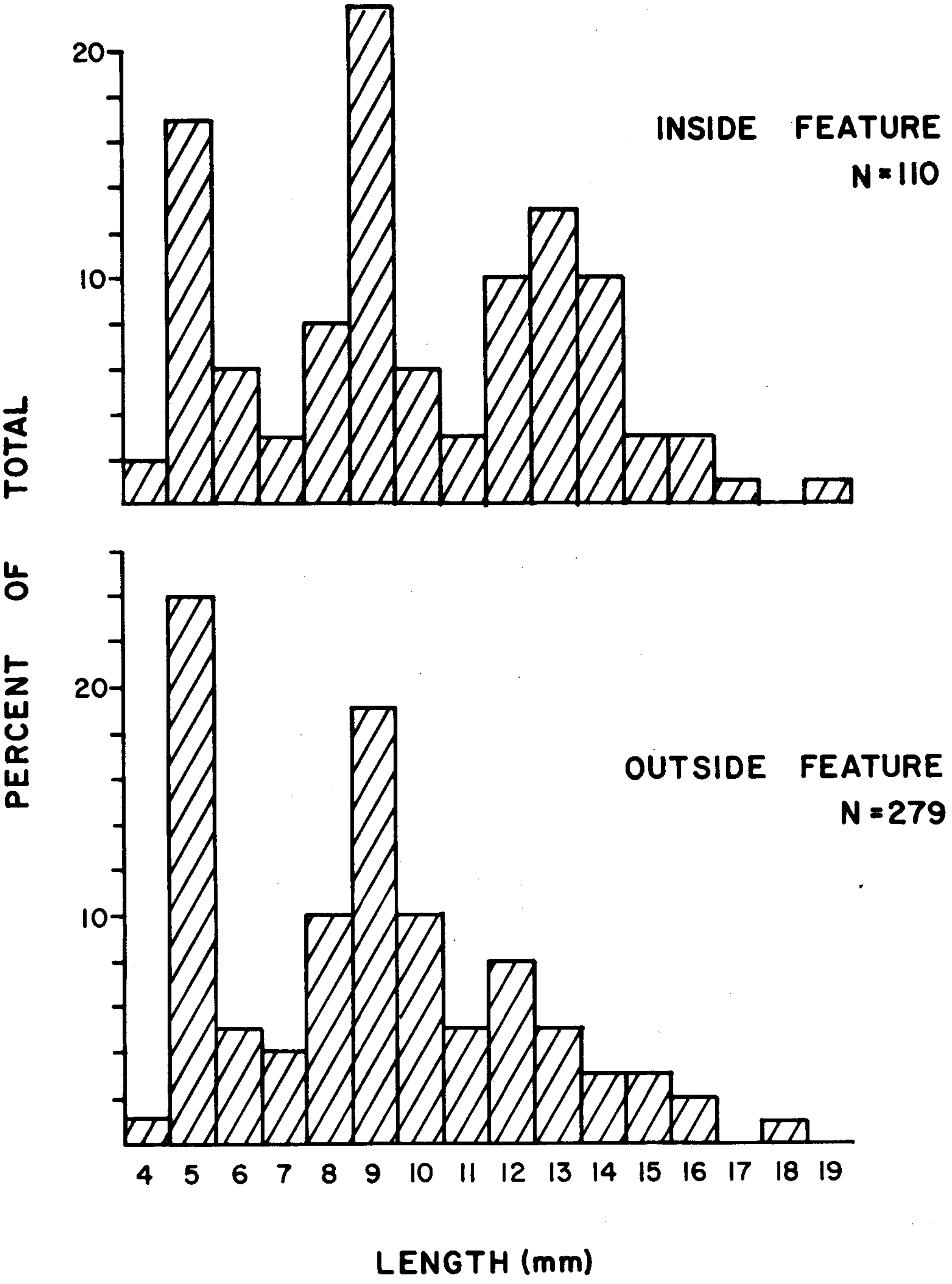


FIGURE 16. Length frequency distributions of Ampelisca macrocephala from airlift samples taken inside and outside a bottom feature attributed to feeding activities of a gray whale in shallow water off Southeast Cape, St. Lawrence Island, in September.

ampeliscids to leave their tubes and begin swimming about. Because of the high density of Photis tubes, ampeliscids disturbed by whales may not be able to settle again until they find a relatively depauperate substrate. Ampeliscids disturbed by a feeding whale would find a suitable habitat within the fresh furrow. When whales fed in these shallow areas they reduced the density of P. fischmanni within features and may have allowed Ampelisca macrocephala to recolonize the furrow.

Nerini et al. (1980) estimated relative ages of pits through examination of the densities of Ampelisca macrocephala and other species. In the following paragraph, we have used the same methodology to estimate relative furrow age. Twenty-four samples each were taken within and outside five furrows. The density of Photis fischmanni in all of these samples was negatively correlated with the density of both the isopod Tecticeps alaskiensis ($r = 0.416$, $0.01<p>0.001$, $n = 48$) and the ampeliscid amphipod A. macrocephala ($r = -0.446$, $p<0.001$, $n = 48$). There was no correlation between densities of A. macrocephala and T. alaskiensis ($r = 0.06$, $p<0.05$, $n = 48$).

We estimated the relative ages of furrows by comparing the numbers of animals and biomass of amphipod tubes found in samples taken inside as a percentage of those taken outside the furrows that were sampled.

In Table 12, we have estimated the relative ages of features by assuming that those with the lowest biomass of tubes and density of amphipods relative to biomass and density outside were the freshest features.

Table 12. Estimated relative ages of gray whale feeding features based on numbers of amphipods and biomass of amphpod tubes.

		No. Samples	Photis fischmanni	Ampelisca macrocephala	Tecticeps alaskiensis	Animal Tubes*
Age	Station	Inside/Outside	% in/out[1]	% in/out	% in/out	% in/out
Fresh	464a	5/5	5	83	1387	5
↓	464b	5/5	10	1168	0	43
	464c	5/5	22	2123	2909	54
	152	4/4	33	501	2900	49
Old	475	5/5	54	1	543	157

* Based on g/m^2.

[1] Mean density inside the feature expressed as percentage of mean density outside feature.

It would appear that when a furrow is first created it is denuded. The above table also shows that the scavenging amphipod Tecticeps alaskiensis is the first to colonize. Ampelisca macrocephala is relatively quick to colonize the area but its relative density decreases as Photis fischmanni re-establishes itself. If so, then the furrow at station 154, which was sampled in July in an area where whales had been observed to be feeding, was either an older furrow or reflected the effect of a different mode of feeding. As previously mentioned, in July the whales were apparently skimming the bottom and leaving furrows 2 cm deep while in September they were making pits 10 cm deep. Furrowing may be a less effective method of feeding.

There are some differences between these results and those of Nerini et al. (1980), Nerini and Oliver (1983), and Nerini (in press). Features we sampled off Southeast Cape were on average 2.9 m^2 in area and were 2-10 cm deep. Pits examined and sampled by Nerini were smaller (1.8 m^2) and deeper (19 cm). They found a reduction in density of Ampelisca macrocephala inside features. However, Nerini et al. (1980) were sampling in deeper water, where A. macrocephala was the dominant organism and Photis fischmanni was rare. Competition for space in the bottom may have been minimal as only a total 6000-12,000 animals/m^2 were present. Decreased competition for space in deeper water may have allowed ampeliscids to settle anywhere on the bottom. The smaller deeper pits found by Nerini et al. (1980) may, in fact, have been avoided by ampeliscids because they prefer areas with a substantial current (Sanders 1956). Length-frequencies of Ampelisca macrocephala sampled inside and outside furrows in September by ourselves are identical to Nerini et al.'s (1980; Fig. 13) results from the fall.

Feeding gray whales apparently have little effect on burrowing polychaetes and bivalves and a large effect on surface-dwelling forms such as amphipods and isopods. Recolonization by the latter groups is extremely rapid. Scavenging isopods, polychaetes and perhaps lysianassid amphipods may move into denuded areas to take advantage of damaged animals. Other species such as Ampelisca macrocephala and Photis fischmanni appear quick to respond to newly available substrate.

Effects on Physical Characteristics of the Substrate

Foraging gray whales cause a disruption of the surface 'mat' layer that overlays the sea bed in the shallow waters off Southeast Cape, St. Lawrence Island. This 'mat' is composed of dense concentrations of amphipod tubes and it is the presence of these tubes that give the surface layer its discrete and cohesive nature. Disruption of this 'mat' by feeding whales is not total. In July, biomass of the animal tubes and other organic matter not including animals was 937 ± s.d. 116 g/m^2 (n = 4) outside feeding features and 465 ± 315 (n = 4) g/m^2 inside features. In September biomass of this material was 795 ± 405 g/m^2 (n = 18) outside feeding features and 282 ± 256 g/m^2 (n = 18) inside. It should be noted that some of the tubes inside features may have been constructed by recently immigrated animals.

Mean grain size within the 'mat' layer averaged 3.4 ± s.d. 0.2 Φ (n = 4) outside of the features and 3.6 ± 0.1 Φ (n = 4) inside features. Mean sorting coefficient was 1.4 ± 0.3 Φ (n = 4) inside features and 1.5 ± 0.2 Φ (n = 4) outside features. The feeding activity of the whales or subsequent erosion (if any) of features does not appear to affect sediment characteristics. The presence of animal tubes within features may prevent or at least retard erosion of features.

Food Available to Gray Whales

In the shallow waters off Southeast Cape in July, gray whales were apparently feeding on the upper 2 cm of the 'mat' that covered the bottom. Airlift samples taken to a sediment depth of 2 cm indicated that a total biomass of 207 ± 102 g/m^2 wet weight was available to the whales. Amphipods, especially *Photis fischmanni* and *Ampelisca macrocephala*, accounted for 71% of this biomass. At the feeding feature sampled in July, 159 g/m^2 of amphipods were available to the whales.

Amphipod biomass estimates from deeper waters of the Chirikof Basin and areas adjacent to St. Lawrence Island are given in Table 13.

Table 13. Estimates of amphipod biomass in Chirikof Basin and the St. Lawrence Island areas.

	mean ± s.d.	(sample size)
Central Chirikof Basin[1]	133 ± 97	(37)
St. Lawrence Island		
south coast	120 ± 49	(15)
west coast	130 ± 50	(16)
Southeast Cape (offshore)	139 ± 52	
Southeast Cape (nearshore)	194 ± 78	(34)

[1] Only samples from areas utilized by gray whales are included.

Other baleen whales appear to seek out and feed in dense concentrations of zooplankton (e.g., Brodie et al. 1978; Griffiths and Buchanan 1982). As previously noted, over the study area as a whole there was a strong correlation between biomass of amphipods and number of feeding features. When all of the areas not used by whales are excluded from the computations, the correlation between log transformed percent of sea floor disturbed and log transformed mean biomass of amphipods was 0.69 ($0.01>p>0.001$, $n = 17$). This relationship would indicate that, within their feeding grounds, whales are selectively feeding in areas of high amphipod density. This relationship explains differences in gray whale feeding activities among stations that were 10's of km apart and we have no data on small scale distribution of feeding features in relation to biomass of amphipods.

Mean biomass of amphipods in all samples taken in areas utilized by feeding gray whales was 148 ± 81 g/m^2 ($n = 93$). The frequency distribution of biomass in the samples shows that 49% of samples contained a biomass of amphipods greater than the mean (Table 9).

Table 14. Frequency distribution (%) of amphipod biomass in 93 samples taken within that portion of the study area utilized by gray whales.

Range of Amphipod Biomass (g/m^2)							
0-49	50-99	100-149	150-199	200-249	250-299	300-349	>350
9%	20%	22%	24%	15%	6%	3%	1%

Food Retention Efficiency of Gray Whales

Not all animals may be retained by the baleen when the whale is feeding. Johnson et al. (1983) discuss the available conflicting evidence. Amphipods as small as 4 mm have been found in gray whale fecal material, but baleen separation of gray whales may allow animals of sizes less than 4 mm to escape.

Eight horizontal plankton tows were taken through mud plumes emanating from feeding gray whales. These tows were taken at a water depth of 20 m between grab stations 138 and 179 off Southeast Cape, St. Lawrence Island (Fig. 2). A control tow taken away from mud plumes contained no benthic animals. Species composition of the benthic amphipods recovered from tows through mud plumes (Table 10) reflects the species composition on the bottom at nearby grab stations. Ampelisca macrocephala was the dominant benthic species both in tows (Table 15) and in the grabs (Thomson, this report). Protomedia spp. were next in order of abundance both in tows and grabs. Unlike the situation on the shallow (10-15 m) shelf, Photis fischmanni and Byblis gaimardi were rare in these deeper water grab samples. These two species were also rare in the plankton tows through mud plumes.

A comparison of the sizes of Ampelisca macrocephala recovered from plankton tows through mud plumes with those taken in nearby benthic samples (Fig. 17) shows a preponderance of 4 and 5 mm individuals in the plankton tows (81%). These two size classes comprised 23% of the population on the bottom at Station 138 (Fig. 17). This evidence suggests that some individuals smaller than 6 mm are not retained by the whale. However, individuals less than 6 mm comprise only 3.2% of the wet weight biomass of A. macrocephala on the bottom. Ampelisca macrocephala, A. eschrichti and Byblis gaimardi, animals similar in size, were the dominant animals in areas heavily utilized by the whales (Table 8). Whales feeding on these species would retain most of the biomass, assuming that individuals greater or equal to 6 mm in length are retained. Protomedia spp. and Dyopedes arcticus were also abundant in plankton tows and may not have been retained by the whales. However, both of these animals are small, and together they comprised only

Table 15. Number of benthic animals found in eight surface plankton tows taken through mud plumes emanating from feeding gray whales off Southeast Cape, St. Lawrence Island, in July.

Taxon	Tow Number					Total
	1	2	3	4	5–8[a]	
Amphipods						
Ampelisca macrocephala	8	8	8	10	29	63
Byblis gaimardi	1				1	2
Photis fischmanni				1	3	4
Ischyrocerus sp.	1		1	1	3	6
Pontoporeia femorata	1	1	1		5	8
Protomedia sp.	6	2		3	13	24
Dyopedes arcticus	1		6	2	4	13
Atylis sp.	1					1
Orchomene sp.		1			2	3
Lembos arcticus		1				1
Grandiphoxus acanthinus					1	1
Boekosimus plautus			1			1
Podoceros sp.			4	1		5
Orchomene lepidula			1	1		2
Other Taxa						
Cumacea			1		1	2
Polychaeta			1			1

[a] Four tows combined.

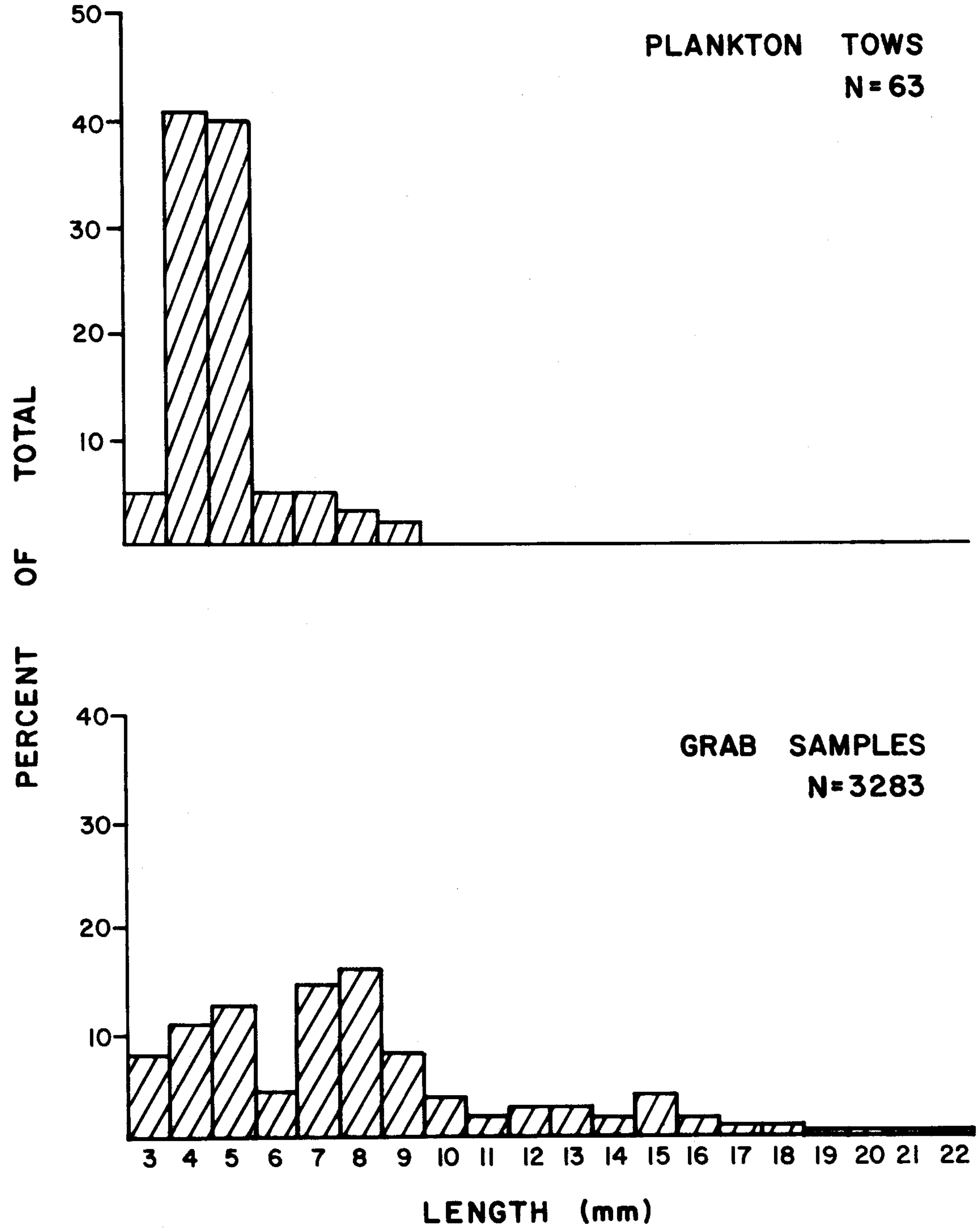


FIGURE 17. Length frequency distributions of Ampelisca macrocephala from (a) plankton tows taken in July through mud plumes emanating from feeding gray whales, and (b) benthic grab samples. Grab samples were taken off Southeast Cape, St. Lawrence Island, near the location of plankton tows.

6.5% of the biomass of amphipods found on the bottom in the area where the tows were made.

When all benthic species collected in the plankton tows are combined, individuals of 5 mm or less comprised 71% of the total number of animals collected in the tows. In benthic grab samples taken nearby, 39% of the 3744 amphipods taken were 5 mm or less in length. We estimated biomass of amphipods by length categories by applying the length vs. dry weight relationship developed for *Photis fischmanni* (Thomson, this report) to approximate the length weight relationship for small animals and that of *Ampelisca macrocephala* (Thomson, this report) to large animals. Animals of size 5 mm or less in these samples comprised only 4.3% of total amphipod biomass. The percent total amphipod biomasses contributed by six other size categories are shown in Table 16.

Table 16. Length to dry weight relationships for six size categories of amphipods.

	% of Total Dry Weight Biomass of Amphipods					
Size Range (mm)	2-5	6-10	11-15	16-20	21-25	26-29
% Total	4.4%	18.1	21.2	12.9	24.8	18.5

Thus, at water depths of more than 20 m, over 75% of the total amphipod biomass is contributed by amphipods greater than 10 mm in length. Even if none of the amphipods of size 5 mm or less are retained by the baleen, the loss would be less than 5% of total amphipod biomass.

The shallow water benthos off Southeast Cape was dominated by the small amphipod *Photis fischmanni*. In July and August 40-60% of the biomass was represented by amphipods less than 5 mm in length. Feeding efficiency may be lower in this region. However, we do not know what proportion of these small amphipods is retained by the whale. Oliver et al. (1983) found large numbers of amphipods less than 5 mm in length in gray whale feces collected in the vicinity of St. Lawrence Island.

Utilization of the Chirikof Basin By Gray Whales

Migration

The theoretical estimation of food consumption by gray whales while on their summer feeding grounds requires some knowledge of their migration patterns and food consumption while migrating. Migrating animals may consistently swim at a speed of 7.2 km/h (Sumich 1983). Other authors cited in Rugh and Braham (1979) have calculated travel rates of 7 to 10.2 km/h. Rugh and Braham estimated that gray whales travel at a mean speed of 4.3 km/h between Point Loma, California, and Unimak Pass in the Aleutian Islands. Würsig et al. (this report) calculated a mean forward speed of 2 km/h for feeding whales. It is not surprising that feeding whales move at a slower speed than traveling whales.

Oliver et al. (1984) and Darling (in press) found 'pockets' of suitable habitat along the Vancouver Island coast and Darling speculates that these may be found along migration routes between California and Alaska. If the whales feed while traveling through these 'pockets', or stop to feed there and then quickly traverse the regions between 'pockets' as they do off Vancouver Island and in Russian waters (see Darling in press), then mean speed of travel will be reduced.

Gray whales depart Russian waters in mid October to November, arriving at Unimak Pass during the last two weeks of November and the first three weeks of December (Rugh and Braham 1979; Yablokov and Bogoslovskaya (in press). If the whales depart the Siberian coast on the first of November and arrive at Unimak Pass on 22 November (the date of peak passage; Rugh and (in Braham (1979)) then a mean speed of 1.7 km/h is required to cover the 864 km coastal migration route outlined by Braham (in press) between the Bering Strait and Unimak Pass. This is less than the forward speed of a feeding whale.

Between Unimak Pass and Point Loma mean speed of migrating whales is 4.3 km/h (Rugh and Braham 1979), slow enough to allow feeding, given the traveling speeds cited above. The timing of movements past Vancouver Island

and Oregon (Herzing and Mate 1981; Darling in press) indicates that traveling speeds are similar between Unimak Pass and Vancouver Island and between Vancouver Island and California.

Northbound whales travel at a slower rate than southbound whales (Rugh and Braham 1979). The main pulse of northbound migrants passes California during the first week of March (Dohl et al. 1981). They reach Oregon by mid March and pass Vancouver Island during the last two weeks in March. Mean speed would have to be about 4 to 6 km/h during this time. By June animals are found between Unimak Pass and the Bering Strait. To arrive off St. Lawrence Island by the first of June, the whales traveling the coastal route would have to average only 2.2 km/h during this Bering Sea portion of their journey. Braham (in press) has observed these northbound whales to be feeding extensively in Bristol Bay and north of the Alaskan Peninsula. Migrating animals also feed sporadically off Vancouver Island in spring (Oliver et al. 1984; Darling in press).

Nerini (in press) has reviewed the question of feeding during the migrations and found some evidence for feeding all along the route, including feeding in offshore waters of Baja California. However, the only confirmed intensive feeding is from the northern part of the range, and the evidence suggests a lack of feeding activity off California (Nerini in press).

For the purposes of the following energetic computations, we consider a mature male gray whale that spends 62 days on its winter grounds (Rice and Wolman 1971). It departs on 12 March and arrives at Vancouver Island on 28 March. It passes through Unimak Pass on 19 May and arrives at St. Lawrence Island on 1 June. The whale spends 150 days on the summer feeding grounds in the Chirikof Basin, departing on 1 November. Unimak Pass is reached on 22 November and Point Loma, California, on 11 January. Alternative calculations will be made below assuming different rates of feeding while migrating.

Animals that summer in the American Chukchi Sea and off Siberia pass through the Chirikof Basin during migration. Information on the distribution of whales in Soviet waters is insufficient to determine what proportion of that population passes through the Chirikof Basin. Northward migrating whales appear to congregate near St. Lawrence Island before dispersing to their summering areas. Thus most of these whales must pass through the Chirikof Basin. An assumption will be made that all of the Soviet-summering animals and all animals that summer in the American Chukchi Sea (see below) do so. Mean traveling speed of migrating whales through the Bering Sea appears to be about 2 km/h and the distance across the Chirikof Basin is approximately 270 km. This journey would require six days and is performed twice. Following these assumptions, utilization of the Chirikof Basin by migrating whales would be on the order of 100,000 whale-days.

Resident Population

The total population of gray whales is estimated to be 17,600 (Reilly et al. 1983; Rugh in press). Most of these whales appear to summer in the Bering Sea and areas to the north (Rugh in press). Zimushko and Ivashin (1980) estimated that 7700 to 7800 gray whales summered off the coast of Siberia between Mys Olutorskiy and Wrangel Island. In July 1982, Ljungblad et al. (1983) found mean densities of 0.006 to 0.430 whales/n.mi.^{2} in their six survey areas in American Chukchi Sea in 1982. This represents an uncorrected total of 2550 whales. Application of our correction factor for whales below the surface (Würsig et al. and Miller, this report) yields a corrected estimate of 9109 whales.

Miller (this report) estimated that 1929 gray whales were found in the Chirikof Basin in July of 1982. Ljungblad et al.'s (1983) raw estimates for a larger area, including the west coast of St. Lawrence Island, for the period June to August 1981 and July 1982 were 743 and 666 whales, respectively. Application of Miller's (this report) correction for whales below the surface yields estimates of 2805 whales in 1981 and 2379 in 1982.

The estimates listed above for numbers of gray whales near St. Lawrence Island and in regions to the north in 1982 total 19,338, greater than the total number of whales that enter the Bering Sea. In July 1982, gray whales had apparently not yet completed their migration to Russian waters. Something on the order of 14% of the entire population of gray whales summered in the American Chirikof Basin and vicinity of St. Lawrence Island in 1982.

Whales arrive at St. Lawrence Island in May and June and depart in October and November (Pike 1962; Rugh and Braham 1979; Braham in press). If we assume that the Chirikof Basin fraction of the population is in residence from 1 June to 30 October and if we use the maximum population estimate of 2479 whales for June, July and August and the estimate of 701 whales for September and October (includes 100 whales in vicinity of St. Lawrence Island) (Miller this report), then utilization by these whales would be on the order of 265,170 whale-days. Total utilization of the Chirikof Basin would be on the order of 365,170 whale-days, 27% of which is by migrating whales.

Würsig et al. (this report) have estimated that gray whales made 198 feeding dives per day in July and 164 feeding dives per day in September. If we apply these estimates to the number of whale-days in the Chirikof Basin for summer residents, we obtain a total of 51.1 x 10^6 feeding dives for the entire resident population. We shall conservatively assume that whales en route to waters to the west and north make 164 feeding dives/day, the number of feeding dives recorded for whales in September by Würsig et al. (this report). Total number of feeding dives for whales migrating through the Chirikof Basin would be 16.4 x 10^6.

Total number of feeding dives made by gray whales in the Chirikof Basin during the course of a year would thus be on the order of 67.5 x 10^6. Mean area cleared during a feeding dive was estimated to be 15.5 m^2. Total area cleared would be 1046 x 10^6 m^2 (1046 km^2).

The total area of the American Chirikof Basin used as foraging grounds by gray whales is approximately 20,000 to 27,000 km^2. The area cleared by whales represents about 4.4% of their feeding habitat in the Chirikof Basin. The side scan records made during this study indicate that mean area of bottom disturbed in the areas of the Chirikof Basin used by whales was 3.9% in July and 6.1% in September. Johnson et al. (1983), based on many side-scan sonar records collected in 1980, have estimated that 1200 km^2

of seabed (5.6%) within the above mentioned foraging grounds were disturbed by the whales during that summer. Oliver et al. (1984) have shown through field experiments off Vancouver Island that feeding features made in an ampliscid mat by grey whales do not persist more than one year. The above estimate of bottom disturbance, therefore, represents annual feeding pressure.

Food Consumption by Gray Whales

Estimate from Behavior and Observations of Feeding Features

Most previous estimates of feeding intensity and food consumption by baleen whales have been made on the basis of assumed energy requirements (Brodie 1975, 1981; Gaskin 1982). The discussion that follows represents an attempt to estimate food consumption by a baleen whale in its natural habitat through observations of behavior and mode of feeding.

Gray whales made a mean 198 feeding dives per day in July and 164 feeding dives per day in September (Würsig et al., this report). Feeding dives lasted 3.7 ± s.d. 1.0 min in July and 3.5 ± 1.4 min in September (Wursig et al. this report). Two varieties of features made by feeding whales were noted on the sea floor. Furrows were a mean of 47 m long and encompassed a mean area of 18 m^2, and feeding events composed of pits made on one dive encompassed a mean area of 13 m^2.

Unfortunately, we were unable to determine directly whether gray whales create one or more than one bottom feature composed of several pits or furrows per dive. Oliver et al. (1984) have observed a small gray whale making five pits 0.72 m^2 in area on one dive of 3 to 4 min duration. It appears likely that gray whales can clear only one feeding feature per dive. They would have less than 4 min in which to clear over 800 kg of sediment from an area of 15.5 m^2. A great deal of water must be taken into the mouth while sucking mud off the bottom and this must also be processed through the baleen. In fact a large amount of water may be necessary to dilute the mud and keep it from consolidating on the baleen when expelling contents of the mouth.

Most of the food consumed consists of benthic amphipods, based on comparison of benthic animals found inside and outside of feeding features and the examination of literature on stomach contents of summering gray whales. Airlift sampling has shown that most of these amphipods are found in the upper few centimetres of the substrate. Some of these amphipods are too small to be retained by the baleen. However, as shown above, these small amphipods account for less than 5% of the total biomass of benthic amphipods over most of the feeding range. A food retention efficiency of 95% is assumed in the following calculations.

Assuming that the whales consume only amphipods and do so with a 95% retention efficiency, clear a mean area of 15.5 m^2 per dive, and feed on mean concentrations of amphipods (133 g/m^2), then the average whale in the Chirikof Basin will consume 388 kg/day in July and 321 kg/day in September or a mean of 361 kg/day over the 150 days in the Chirikof Basin.

As previously discussed, gray whales probably feed selectively in areas with a high biomass of amphipods. Twenty-five percent of samples contained a biomass of amphipods greater than 200 g/m^2 and 10% contained greater than 250 g/m^2. Table 17 gives estimates of daily food consumption (averaged over the summer) by a gray whale selectively feeding in areas with an amphipod biomass higher than the mean of 133 g/m^2.

Table 17. Estimated daily gray whale food consumption at three assumed above-mean levels of amphipod biomass.

Assumed mean biomass of amphipods at feeding locations (g/m^2)	200	250	300
Food consumption (kg/d)	542	678	813

Estimate from Energetic Requirements

Daily food intake of gray whales was estimated using data on daily requirements of an active whale provided by Rice and Wolman (1971) and Sumich (1983). These values were compared to standard metabolism calculated according to Brodie's (1975) method.

Computations were made for an adult male gray whale 12.5 m in length and weighing 23 metric tons. The average whale taken by Russian whalers in the northern areas weighs 23 metric tons (calculated from data provided by Zimushko and Ivashin 1980 and Blokhin and Vladimirov 1983). A male was used to avoid the problem of accounting for pregnancy and lactation. A male of this weight is approximately 12.5 m long (Rice and Wolman 1971).

Separate calculations were made assuming that (1) whales feed sufficiently during migration to offset energetic requirements during that time, (2) feeding during migration accounts for only 50% of energetic requirements at that time, the remainder coming from reserves stored during summer, and (3) feeding during migration provides a negligible proportion of a migrating whale's energetic requirements.

Standard Metabolism.--Standard metabolism of a cetacean includes basal metabolism and the energetic costs of buoyancy. This estimate of energetic requirements was calculated according to Brodie's (1975) method. Surface heat production was calculated from the following equation

$$H = k \frac{(36-Te)}{d}$$

where H is the surface heat produced in $Kcal/m^2$ of surface area, k is conductivity of blubber (Brodie's 1975 figure of 21.18 $Kcal/m^2/h$ per degree difference for 1 cm thickness was used), Te is the temperature of the environment, d the depth of blubber in cm (taken as 13 cm from Rice and Wolman 1971), and 36 is the body core temperature in °C.

Mean temperature at the bottom of the Chirikof Basin in July was 2.5° ± s.d. 1.4°C (n = 9) and temperature at the surface was 5.3 ± s.d. 2.7°C (n = 9). In July, gray whales made 198 feeding dives/day lasting an average of 3.68 min per dive (Würsig et al., this report), or 12 h of feeding dives. If the remaining 12 h were spent at or near the surface then the average temperature of the whales' environment was 3.9°C. Surface heat production was, therefore, calculated to be 52.2 $Kcal/m^2/h$.

Sumich (1983) estimates the metabolically active surface area of a gray whale at 0.33 x (length in m)^2 or in this case 51.5 m^2. Thus, total heat loss from the surface was estimated at 64.5 x 10^3 Kcal/d.

Heat is also lost through respiration and warming of food. Volume per breath of 644 liters was calculated from mean lung capacity 2.65% of body weight (in kg; see below) and a tidal volume of 80% of capacity (Rice and Wolman 1971). During the summer the whales breathe once a minute (Würsig et al., this report). Mean air temperature in the Chirikof Basin in July was 7°C. Warming this air to 36°C at a rate of 0.2 Kcal/°C/L (Brodie 1975) involves a heat loss of 5.1 x 10^3 Kcal/day. This figure must be doubled to account for heat loss through humidification of the air (Brodie 1975). A further 30 x 10^3 Kcal/day is lost through warming food that is ingested (Brodie 1981).

Considering surface heat loss, respiration and warming of food, total heat loss in July would be on the order of 1.0 x 10^5 Kcal/day. Basal metabolism may also be calculated from the formula (Lockyer 1981)

$$(Q = 70.5\ W^{0.7325})$$

where Q = basal metabolism in Kcal/d and W is the body weight in kg. For the 23 Mt gray whale under consideration basal metabolism would be 1.1 x10^5 Kcal/day. These figures represents standard and basal metabolism. If migrating and food gathering activities require energy expenditure above that allowed for by standard metabolism, then the additional energy expenditure must be added to these estimates (Brodie 1975).

Active Metabolism

Sumich (1983) estimated active metabolism of a gray whale through observations of the breathing rate of migrating animals. However, his estimate may be too high. He extrapolated tidal volume of a 6.2 Mt young gray whale with a total lung volume of 7% of body weight and a vital capacity of 50% of total lung capacity to an adult animal. The total lung capacity in large whales appears to be between 2.5 and 2.8% of body weight (Lockyer

1981). Vital capacity may be about 80% of total capacity, but appears to vary with activity levels. Lockyer, therefore, cautions about calculating metabolic rate from blow rate and swimming speed.

However, it is constructive to estimate metabolic rate from respiration rate using Sumich's (1983) method and different assumptions for comparison with other estimates. Breathing rates for gray whales are shown in Table 18. The following estimates for active metabolism assume a breathing rate of 1.1 blows/min while on the feeding grounds, and 0.72 blows/min while migrating and while on the winter grounds. Total annual energy expenditure and the food required to meet this expenditure for a 23 Mt gray whale are shown in Table 19.

Table 18. Breathing rates for gray whales in various locations and under various activity levels. Values are average for that activity.

Location/Activity	Speed (m/s)	Blow/min	Source
Winter Grounds			
Resting	-	0.5	Sumich (1983)
Resting	-	0.5	Harvey and Mate (in press)
Swimming	1.1	1.0	Harvey and Mate (in press)
California			
Migrating	1	0.52	Sumich (1983)
	2	0.69	Sumich (1983)
	3	1.14	Sumich (1983)
Average	1.97	0.72	Sumich (1983)
Feeding Grounds			
All activity, July		0.997	Würsig et al. (this report)
All activity, September		1.122	Würsig et al. (this report)
Shallow water feeding <20 m, July		0.794	Würsig et al. (this report)
Deep water feeding 20-40 m, July		1.043	Würsig et al. (this report)
60-80 m, July		1.190	Würsig et al. (this report)
Shallow water feeding <20 m, September		1.085	Würsig et al. (this report)
Deep water feeding 20-40 m, September		1.116	Würsig et al. (this report)

Table 19. Annual food requirements of a 23 Mt male gray whale calculated from the breathing rate using Sumich's 1983 method.

Area/ Activity	Days	Breathing rate (blows/min)	Oxygen Consumption[a] (litres x 10^6)	Energy Expended[b] (Kcal x 10^6)	Food Required[c] (kg)
Winter	62	0.72	3.13	15.12	25,511
Migration	153	0.72	7.73	37.32	62,956
Chirikof Basin	150	1.10	11.59	55.90	94,297
				108.34	182,765

---

[a] Assumes total lung volume of 2.65% body weight and that tidal volume is 80% of total (Lockyer 1981).

[b] Assumes that 1 litre of oxygen metabolizes 4.825 Kcal (Lockyer 1981).

[c] Assumes dry weight is 15% of wet weight, caloric value of amphipods is 5.2 Kcal/g dry weight, assimilation efficiency is 80%, and baleen retention efficiency is 95% (Stoker 1978; Lockyer 1981).

Daily ration calculated by the respiration method and averaged over the year would be 501 kg per day. Assuming no net gain or loss in energy stores during migration, a summering whale would have to collect 629 kg/d to meet its daily requirements while on the feeding grounds plus 170 kg/d to store energy for the 62 days it spends off the Baja. If the whales consume half their daily energetic requirements through feeding during the 152 days of migration, then a further 210 kg/d must be collected during summer to account for the other half of the energy needed for migration (i.e. a total of 1009 kg/d). If no feeding at all occurs during migration then whales feeding on the summer grounds must consume 1218 kg/d.

Averaged over the year, metabolic requirements calculated by this method would be almost 3.0×10^5 Kcal/d or about three times basal metabolism, and food consumption necessary to meet these requirements would be about 501 kg/d or about 2.2% of body weight per day (8 times body weight per year). In comparison, Hinga (1979) has collected data on the feeding rates of captive cetacea ranging in weight from 100 to 6000 kg and found energy usage between 1.5 and three times the basal rate. However, Gaskin (1982) cautions against using metabolic data from captive animals because many tend to be overfed and become obese.

Through an exhaustive study of food, feeding habits, feeding rates and energetic computations that allowed for growth, Lockyer (1981) concluded that blue and fin whales consume approximately five times their body weight in one year. Applying this value to the 23 Mt gray whale yields an average daily ration of 315 kg of amphipods. In order to store enough energy for the time spent on wintering grounds, the whale would have to consume a total of 445 kg/d while on the feeding grounds, according to this method of calculation. If energy must be stored for half the migration, then food consumption must be on the order of 604 kg/d for the 150 d spent on the summering grounds.

Comparison of Estimates

The eleven estimates of food consumption (Table 20) determined by four different methods represent a wide range of feeding rates. The greatest unknown in the calculations is the amount of feeding that occurs during migration. There is little evidence of benthic feeding while on the winter grounds (Oliver et al. 1983) but there is fairly strong evidence of pelagic feeding (Norris et al. 1983).

Available knowledge about gray whale behavior during migration makes it unrealistic to accept either that whales feed throughout the migration or not at all. Food consumption during migration was estimated as follows. South of Vancouver Island, mean traveling speed is over 4 km/h during both the northward and southward migrations and feeding is negligible (see Migration). North of the Aleutians, traveling speed is 2 km/h and feeding activity is extensive in the whole area. Therefore, we shall assume that on those portions of the route that involve travelling at 2 km/h, whales feed sufficiently to offset the energetic cost of migration. This would occur over all of the route north of Vancouver Island for northbound whales (70 days) and north of the Aleutians for southbound whales (22 days, see Migration). Sixty-one days are spent feeding only sporadically along the migration route and 62 days are spent on the winter grounds.

Energetic requirements based on our calculations from respiration rate data required the whale to consume 799 to 1218 kg/day while on their summer foraging grounds (Table 20). This is greater than the range of values

Table 20. Daily food intake of gray whales while on their summer feeding grounds calculated by four different methods. Also shown is the standing crop of amphipods necessary to meet these requirements assuming 198 feeding dives/day in June, July and August and 164/d in September and October, 15.5 m^2 cleared per dive, a retention efficiency of 95% and an assimilation efficiency of 80%.

Methods and Assumptions	Daily Food Intake kg (wet weight)	Biomass of Amphipods[1] (g/m^2)
1. Behavior, analysis of furrows		
(a) feeding on mean amphipod density	361	133
(b) feeding on 200 g/m^2 of amphipods	542	200
(c) feeding on 250 g/m^2 of amphipods	678	250
(d) feeding on 300 g/m^2 of amphipods	813	300
2. Energetic, daily ration + storage for winter		
Respiration		
(a) no storage for migration	799	280
(b) storage for 1/2 migration	1009	356
(c) storage for all migration	1218	427
Using Lockyer's assumptions		
(a) no storage for migration	445	164
(b) storage for 1/2 migration	604	223
(c) storage for all migration	763	281
3. Analysis of stomach contents[2]	1200	443

[1] Biomass of amphipods that whales must feed on to meet the daily intake shown.

[2] Zimushko and Lenskaya (1970).

derived from examination of behavior and food removal. A feeding rate of 1009 kg/day determined by the respiration method allows for storage of energy required for one half of the migration and requires a standing stock of 356 g of amphipods/m^2. Only a few of our samples contained a biomass of amphipods greater than 350 g/m^2.

Based on Lockyer's (1981) assumptions, a feeding rate of 604 kg/d would store energy for about half the migration and for winter. Based on our data concerning behavior and size of feeding events, this feeding rate would require feeding on concentrations of amphipods of about 223 g/m^2. This value represents the mean biomass in the 35% of our samples that contained the highest biomass.

The estimate of energy intake based on observations of whale behavior and furrow characteristics may be 678 kg/whale/day (estimate 1c in Table 20). As previously mentioned, gray whales preferentially feed in areas with a higher than average standing crop of amphipods and this feeding rate requires whales to seek out areas with a mean amphipod biomass of 250 g/m^2. Using Sumich's (1983) method based on respiration, feeding at a rate of 678 kg/d would not allow sufficient energy storage to meet the requirements of migration or the 62 days spent wintering off Baja California. In order to balance the annual energy budget using Sumich's method, the whale would have to feed at an average daily rate of 678 kg/d for the entire 150 days spent on the northern feeding grounds and during the 92 days of migration when whales travel at speeds of 2 km/h; furthermore, the whales would have to meet 40% of the daily requirements (271 kg wet weight of food/d) on the remainder of the migration route and while on their wintering grounds off Baja. In contrast, the 678 kg/d estimate from food removal and behavior does meet energetic requirements as computed using Lockyer's (1981) assumptions, provided that some feeding occurs during migration (Table 20).

A comparison of five estimates of gray whale energetics is presented in Table 21. The estimates based on food removal and energetics using Lockyer's assumptions and our calculations of respiration all fall within the envelope of acceptable values developed for feeding rates of captive cetaceans by Hinga (1979) which, as previously mentioned, may be too high. The active metabolic rate for a gray whale calculated by Sumich (1983) may also be too high. It is 3.8 times basal metabolism and as such is higher than Hinga's 1979 envelope of values. It is also worth noting that the metabolic rate computed from observations of behavior and furrows would fall below this envelope if whales fed on mean concentrations of amphipods.

Our best estimate of the feeding rate while on the summer grounds would be between 600 and 700 kg/d (650 kg/d will be used in following computations). Using Lockyer's assumptions this would allow for storage for all the

Table 21. Comparison of estimates of energetic requirements of gray whales.

		Daily Energy Expenditure		Food Required to Meet Requirements		
Method	Weight (kg)	Kcal/d	as a multiple of basal metabolism	kg/d[1]	% Body wt per day	as a multiple of body wt/yr
Theoretical/BMR	23,000	1.1×10^5	-	186	0.8	3.0
Respiration[2]	23,000	3.0×10^5	2.7	501	2.2	7.9
Food removal[3]	23,000	2.5×10^5	2.3	420	1.8	6.7
Energetics[4]	23,000	1.9×10^5	1.7	315	1.4	5.0
Respiration[5]	23,000	4.2×10^5	3.8	708	3.0	11.2
Weight Loss						

[1] Averaged over the year.

[2] Calculated using Sumich's (1983) method and Lockyer's data on lung volume and vital capacity.

[3] Assumes feeding at 678 kg/d for 1/2 the migration period and all of the time on the summer grounds. See text.

[4] Using Lockyer's assumptions.

[5] As presented by Sumich (1983) converted to 23,000 kg whale.

time spent off Baja California and for 1/2 the migration period. This would necessitate that the whales feed on a mean biomass of about 220 to 260 g/m^2. Based on the total number of whale days in the Chirikof Basin as determined above (365,000), total food removed by the whales would be about 10 g/m^2 for the 23,500 km^2 of the Chirikof Basin used by gray whales.

Mean biomass of amphipods in the area of the Chirikof Basin utilized by gray whales is 133 g/m^2. The productivity to biomass ratio for amphipods in the area was 1.9 (Thomson, this report). The above value for food removed represents about 7.5% of standing stock and 4% of productivity of the amphipods.

Trophic Interactions Between Gray Whales and Benthic Animals

In the following discussion, we attempt to trace the flow of energy through the benthic food web of that portion of the Chirikof Basin utilized by feeding gray whales. This type of exercise is useful in that it identifies major energy pathways and key components in the food web. In this case, the purpose is to compare the food removal by gray whales with food availability and removal by other components in the benthic food web.

Animals taken in grab and airlift samples were assigned to feeding guilds according to the nomenclature and definitions of Fauchald and Jumars (1979). Information on the trophic position of each species was taken from Fauchald and Jumars (1979), Stoker (1978) and Thomson (this report).

Filter feeders include bivalves of the genera Liocyma, Serripes, Astarte, Hiatella, sabellid polychaetes, tunicates, and some phoxocephalid and haustoriid amphipods. These animals filter the water, extracting phytoplankton, small zooplankton and detritus.

Surface deposit feeders feed at the water/substrate interface and include ampeliscid amphipods, cumaceans, and bivalves of the genera Macoma and Yoldia.

Deposit feeders often burrow through the mud and ingest it to extract nutritive value. This group included many polychaetes and some holothurians. Carnivores and scavengers included polychaetes of the genus Nephtys, lysianassid amphipods, starfish, and some isopods.

Surface deposit feeders, mainly amphipods, comprised 63 to 75% of standing crop within those portions of the study area utilized by gray whales (Table 22). Filter feeders were next in order of importance, comprising 5 to 19% of standing crop. Carnivores and scavengers comprised between 9 and 19% of standing crop. The guild whose abundance differed most between areas that were and were not used as foraging grounds by gray whales was the surface deposit feeding guild (Table 22).

In the central Chirikof Basin, grab samples contained a mean of 6.05 liters of substrate with a carbon content of 2.9 g/kg. Assuming a water content of 10% and a specific gravity of 2.7, the mud associated with the animals taken in the grab contained a mean of 252.9 g C/m^2. Some of this carbon was in the form of bacteria, meiofauna and nutritive detritus directly utilizable by animals. Some of it was refractory and of little nutritive value. The low carbon to nitrogen ratio found in this region (7.0 ± s.d 1.0,

Table 22. Mean biomass (g C/m^2) and percent of total biomass according to major feeding mode of benthic animals taken in the Chirikof Basin and areas adjacent to St. Lawrence Island. Conversion of wet weight to carbon was accomplished using data provided by Stoker (1978).

Area	No. samples	Surface deposit feeders		Deposit feeders		Filter feeders		Carnivores, scavengers		Not classified	Total
		g C/m^2	%	g C/m^2	%	g C/m^2	%	g C/m^2	%	%	g C/m^2
Chirikof Basin											
Area not used by whales	38	2.2	33	0.8	12	1.2	18	1.0	15	22	6.7
Area used by whales	37	11.3	75	0.5	3	0.7	5	1.5	10	7	15.0
St. Lawrence Island											
West coast	11	11.5	63	1.0	10	2.7	15	1.6	9	4	18.4
South coast	15	10.2	64	0.4	3	3.0	19	1.6	10	4	15.9
Southeast cape (offshore)	10	13.2	71	0.7	4	1.9	10	1.5	8	6	18.5
(nearshore)	55	10.1	64	0.9	6	1.0	6	3.0	19	6	15.9

n = 8) indicates that much of this organic matter may have been of direct use to the animals.

To estimate total productivity of the benthos, we multiplied measured biomass by assumed production to biomass ratios. Most of the surface deposit feeders were amphipods. Thomson (this report) determined a productivity to biomass ratio of 1.9 for the dominant amphipods in this region. Polychaetes in west Greenland have a productivity-to-biomass ratio approaching unity (Curtis 1977) and this value was used to approximate productivity of polychaetes. Stoker (1978) found a productivity-to-biomass ratio of 0.32 for Macoma calcarea. Stoker claimed, however, that this estimate is too low. In the following computations we have conservatively estimated a productivity to biomass ratio of one for bivalves. A productivity to biomass ratio of one was also applied to all other groups. A gross production to consumption efficiency of 0.15 was assumed for all groups. Values for productivity of zooplankton in the area north of St. Lawrence Island were taken from Ikeda and Motoda (1979).

Consumption by whales was calculated as follows. The previously derived estimate of 650 kg per whale per day was assumed for the previously determined 365,000 whale-days in the 23,500 km^2 of the Chirikof Basin utilized by gray whales. Wet weight was converted to carbon using data provided by Stoker (1978). Total consumption by whales in the Chirikof Basin would be on the order of 237×10^6kg/yr or 10 g/m^2 wet weight (0.7 g C/m^2).

Figure 18 summarizes these estimates of standing crop, productivity and energy flow between the various components of the benthic ecosystem of the central Chirikof Basin. Benthic deposit feeders consume more than one half of the available carbon in sediments. Filter feeders, on the other hand, appear to consume only a small fraction of primary productivity. Productivity of the benthic filter and deposit feeders as a whole may approach 23 g $C/m^2/yr$ and as such appears larger than the estimated productivity of zooplankton. Infaunal benthic carnivores consume approximately one half of the productivity of filter and deposit feeders. Gray whales, on the other hand, consume about 5% of total benthic standing crop and 3% of

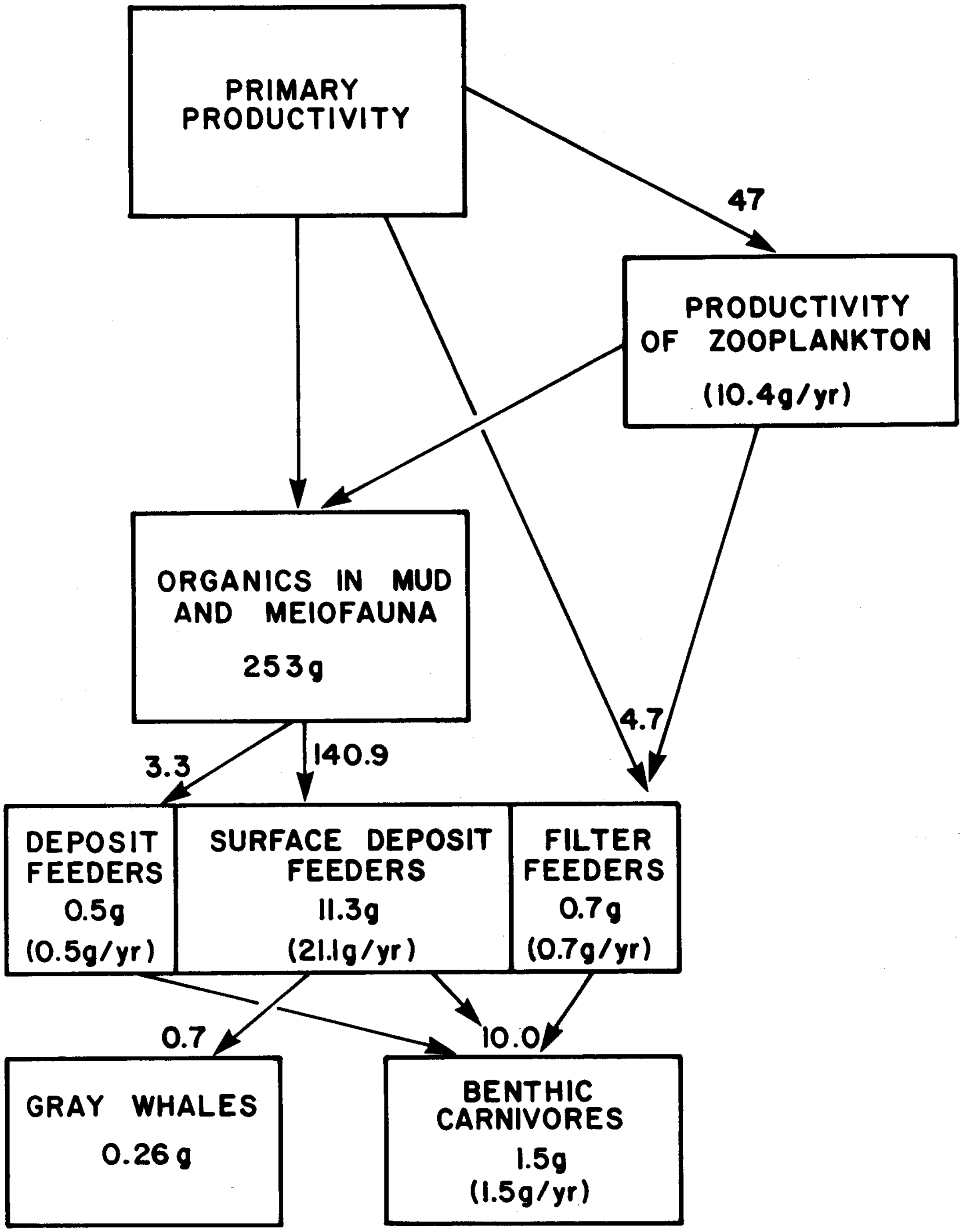


FIGURE 18. Energy flow through the benthos of that part of the Chirikof Basin utilized by feeding gray whales. All values are expressed as g Carbon/m^2. Transfer of energy (g C/m^2/yr) is noted beside arrows. Standing crop and productivity (in parentheses) are shown within the blocks.

productivity. They consume approximately 7.5% of the standing crop of amphipods, their primary food source, and approximately 4% of amphipod productivity. The remaining 23 g C/m^2 annual benthic productivity is available to walrus, bearded seal, ringed seal, fish and large epibenthic animals.

Overall, gray whale food requirements do not appear to be as close to the carrying capacity of their environment as are the food requirements of some other consumers. The Pacific walrus is believed to be near the carrying capacity of its environment in that its annual consumption of the bivalves that form its major food resource approaches the annual productivity (Fay et al. 1977). In the North Sea, demersal fish consume approximately 60% of the annual productivity of the benthos (Crisp 1975). In contrast, gray whales in the Chirikof Basin consume approximately 4% of the productivity of the benthic amphipods. However, as previously mentioned, gray whales appear to selectively feed in areas with a higher than average standing crop of benthic animals and energetic computations show that they may, in fact, have to do so in order to survive. The areal extent of areas with a sufficient standing crop of amphipods usable as a food resource for the gray whales within 23,500 km^2 identified as suitable feeding habitat is unknown. About 30% of our samples contained a mean biomass of amphipods sufficient to meet the needs of the whales.

IMPLICATIONS FOR DEVELOPMENT

The Chirikof Basin appears to be a major migration corridor for gray whales and is the foraging grounds for at least 14% of the population over the summer. Feeding pressure by migrating and resident whales appears to be low when compared to the overall food resource in the area. However, gray whales appear to feed selectively in areas with a high biomass of amphipods. As shown by the uneven distributions of feeding features and of whales, some areas are heavily utilized and some are not.

Darling (in press) has theorized on the basis of his own work and information presented in the Russian literature that gray whales occupy 'pockets' of suitable habitat and move quickly between these. In order to meet the requirements of food storage for migration and the stay off the Baja, it appears that gray whales may have to feed in areas with an extremely high biomass of amphipods. These prime areas may represent only a small fraction of apparently suitable habitat in the Chirikof Basin. Several heavily utilized areas are evident in Figure 15. Our survey of the Chirikof Basin was by no means comprehensive and we cannot identify all of the areas that are more important than others within the 23,500 km^2 of suitable habitat defined by us, Johnson et al. (1983), Nerini (in press), and Ljungblad et al. (1982).

The primary concern with regard to potential development would be disruption or denial to the whales of 'pockets' of prime feeding habitat. This might have an effect on the whales out of proportion to the area affected.

LIMITATIONS, DATA GAPS AND RECOMMENDED STUDIES

Our estimates of food consumption and utilization of the American Chirikof Basin by gray whales are based on several major kinds of data of varying precision. In the following section, we identify those data in which we lack a reasonable degree of confidence and outline the kinds of studies needed to strengthen the estimates.

1. **Migration:** A great deal is known about migration routes and timing for gray whales in the vicinity of Unimak Pass and south of Vancouver Island. However, the nature and extent of use of the Chirikof Basin by whales en route to and from Siberia and the Chukchi Sea are poorly known. Systematic surveys would have to be conducted at monthly or shorter intervals from May through November to determine numbers, movements and frequency of feeding for gray whales in the Chirikof Basin. Some of the requisite data have been collected by Ljungblad et al. (1982, pers. comm.) but not yet reported in detail. The amount of feeding that occurs along the migration route is also unknown. This information is required for more precise energetic computations.

2. **Behavior:** Our estimates of feeding dive duration, blow rates and surface times are based on large data sets from July and September of one year. Our estimates of the percentage of time that a whale spends feeding are rough and should be refined by prolonged observations of individual whales. It is possible that some whales travel between 'pockets' of concentrated food. These whales should be distinguished from whales feeding in 'pockets'. The apparent tenacity of individual gray whales with respect to particular feeding locations requires further study, as does the possibility that specific feeding territories may exist.

Movements and behavior of whales resident in the study area should be studied along the lines of the work performed by Darling (in press) off Vancouver Island. Shore-based work at St. Lawrence Island could provide much additional information on the behavior of summering gray whales.

3. **Food removal:** Our estimate of the amount of food removed during an average dive is weak, mainly because we obtained no direct underwater observations of feeding whales. Single bottom features made by one whale during one dive should be isolated by divers, the area determined, and the standing crop of potential prey organisms immediately adjacent to the feature determined. This sampling should be conducted over the season to determine changes (if any) in mode of feeding. A large number of features would have to be sampled to determine the extent of small scale selectivity of feeding sites by the whales.

4. Studies of the gray whale may offer the only opportunity to obtain detailed and precise data concerning the **energy budget** of a large cetacean. The gray whale's mode of feeding lends itself to the determination of food consumption in nature. An energy budget incorporating accurate estimates of food consumption in nature would provide valuable insight into the energetic requirements of large cetaceans that migrate and store food for a period of relative food scarcity.

   The present procedure for estimating energetic requirements is based on assumed lung capacity, assumed oxygen utilization, and estimated weight loss during winter. Estimates of weight loss while in Baja are useful but must be used with caution. It is uncertain whether all of the weight loss by non-pregnant females in winter is due to metabolic requirements. Whales may be overinsulated for tropical waters (Gaskin 1982) and some weight loss may represent adaptation to warm water.

   High technology telemetric techniques may offer an opportunity to refine some of the data used in energetic computations. Measurements of CO_2 content of expelled air and temperature at various depths in the blubber of active animals would be helpful. Positional and movement data obtainable via telemetry (especially satellite telemetry) would also assist in characterizing behavior during the parts of the migrations that have not been studied in detail.

ACKNOWLEDGMENTS

The gray whale feeding ecology project was funded by the Minerals Management Service through interagency agreement with the National Oceanic and Atmospheric Administration, as part of the Outer Continental Shelf Environmental Assessment Program. We wish to thank L. Jarvela and G. Oliver, contract monitors for this project, for their assistance.

Thanks are due to Cdr. E. Gelb, the officers and crew of the NOAA ship MILLER FREEMAN; and Capt. R. Ganse, the officers and crew of the NOAA ship DISCOVERER for their able and enthusiastic assistance during all aspects of the field work. M. Kaiser and C. Newell of the NOAA diving office assisted with the planning and execution of diving operations. Ships' divers L. Consiglieri, S. Christopherson, J. Rivera, F. Wood, J. Morris and M. White assisted with underwater sampling and collection. C. Sherwood of NORTEC and K. Johnson of USGS operated the side scan sonar in September. We also wish to thank M. Dahlheim of Univ. of British Columbia, B. Würsig, D. Croll, M. Newcomer and L. Spear of Moss Landing Marine Laboratories, and R. Wells of Univ. of California Santa Cruz for their assistance with field work. We especially wish to thank S. Viada of LGL for his assistance with all aspects of the field work.

J. Cole of LGL and G. Lapiene and J. Talbot of NOAA provided valuable logistic support in Alaska.

R. Dillinger of LGL supervised sample analysis and identified most of the animals. K. Coyle of Univ. of Alaska verified the crustacean identifications, and K. Fitzhugh and H. Harry verified polychaetes and other taxa, respectively. S. Naidu and A.J. Paul of Univ. of Alaska performed carbon and nitrogen analysis and caloric analysis, respectively.

L. Maritzen and J.S. Baker of LGL wrote the programs for digitizing the side scan sonar records. We wish to thank C. Holdsworth of LGL for his assistance with data processing. B. DeLong drafted the figures, and B. Griffen and H. Hogarth typed the manuscript. We especially wish to thank W.J. Richardson of LGL for editorial assistance and for fruitful discussions on study design, data interpretation and analysis.

LITERATURE CITED

Blokhin, S.A. and V.A. Pavlyuchkov. 1983. Feeding of gray whales off Chukotka. Rep. Int. Whal. Comm. 33:549-552.

Blokhin, S.A. and V.L. Vladimirov. 1983. Investigations of gray whales taken off Chukotka in 1981. Rep. Int. Whal. Comm. 33:553-555.

Bogoslovskaya, L.S., L.M. Votrogov and T.N. Semenova. 1982. Feeding habits of the gray whale off Chukotka. Rep. Int. Whal. Comm. 32:507-510.

Braham, H.W. In press. Migration and distribution of gray whales in Alaska. In: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, Eschrichtius robustus. Academic Press, N.Y.

Brodie, P.F. 1975. Cetacean energetics, an overview of intraspecific size variation. Ecology 56:152-161.

Brodie, P.F. 1981. A preliminary investigation of the energetics of the bowhead whale (Balaena mysticetus L.). Rep. Int. Whal. Comm. 31:501-502.

Brodie, P.F., D.D. Sameoto and R.W. Sheldon. 1978. Population densities of euphausiids off Nova Scotia as indicated by net samples, whale stomach contents and sonar. Limnol. Oceanogr. 23:1264-1267.

Crisp, D.J. 1975. Secondary productivity in the sea. p. 71-89. In: productivity of world ecosystems. Proc. of a Symposium sponsored by U.S. National Committee for the IBP. NAS Washington, D.C.

Curtis, M.A. 1977. Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of west Greenland. Ophelia 16:9-58.

Darling, J.D. In press. Gray whales, Eschrichtius robustus, off Vancouver Island, British Columbia. In: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, Eschrichtius robustus. Academic Press, N.Y.

Dixon, W.J. (ed.). 1981. BMDP statistical software. Univ. of California Press, Berkeley. 726 p.

Dohl, T.P., M.L. Duman and R.C. Helm. 1981. Distribution and movement of migratory and resident gray whales along the California coastline. In: Fourth Biennial Conference on the Biology of Marine Mammals, Dec. 14-18, 1981. San Francisco (abstract only).

Fauchald, K. and P.A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17:193-284.

Fay, F.H., H.M. Feder and S.W. Stoker. 1977. An estimation of the impact of the Pacific walrus population on its food resources in the Bering Sea. U.S. Marine Mammal Comm. Rep. No. MMC-75/06 and MMC-74/03. U.S. Nat. Tech. Inform. Serv. Cat. No. PB-273505. 38 p.

Gaskin, D.E. 1982. The ecology of whales and dolphins. Heineman, London. 459 p.

Griffiths, W.B. and R.A. Buchanan. 1982. Characteristics of bowhead feeding areas. In: W.J. Richardson (ed.), Behavior, disturbance responses and feeding of bowhead whales Balaena mysticetus in the Beaufort Sea, 1980-81. Rep. by LGL Ecol. Res. Assoc., Inc., Bryan TX, for U.S. Bureau of Land Management, Washington. 456 p.

Herzing, D.L. and B.R. Mate. 1981. California gray whale migration along the Oregon coast. In: Fourth Biennial Conference on the Biology of Marine Mammals, Dec. 14-18, 1981, San Francisco (abstract only).

Hinga, K.R. 1979. The food requirements of whales in the southern hemisphere. Deep Sea Res. 26:569-577.

Ikeda, T. and S. Motoda. 1979. Zooplankton production in the Bering Sea calculated from 1956-1970 OSHORO MARU data. Mar. Sci. Comm. 4(4):329-346.

Johnson, K.R., C.H. Nelson and H.L. Mitchell. 1983. Assessment of gray whale feeding grounds and sea floor interaction in the northeastern Bering Sea. Final Report by U.S. Geological Survey for National Oceanic and Atmospheric Administration, Juneau, AK.

Ljungblad, D.K., S.E. Moore and D.R. Van Schoik. 1983. Aerial surveys of endangered whales in the Beaufort, eastern Chukchi and northern Bering Seas, 1982. NOSC TD 605. Naval Ocean Systems Centre, San Diego, CA. 382 p.

Ljungblad, D.K., S.E. Moore, D.R. Van Schoik and C.S. Winchell. 1982. Aerial surveys of endangered whales in the Beaufort, Chukchi, and northern Bering seas. NOSC TD 486. Naval Ocean Systems Center, San Diego, CA. 406 p.

Lockyer, C. 1981. Growth and energy budgets of large baleen whales from the southern hemisphere. F.A.O. Fisheries Series No. 5, Vol. 3:379-484.

Loomis, L.H. 1975. Introduction to calculus. Addison-Wesley, Reading, Mass.

Mills, E.L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. J. Fish. Res. Board Can. 24:305-355.

Nerini, M. In press. A review of gray whale feeding ecology. In: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The Gray Whale, Eschrichtius robustus. Academic Press, N.Y.

Nerini, M.K. and J.S. Oliver. 1983. Gray whales and the structure of the Bering Sea benthos. Oecologia 59:224-225.

Norris, K.R., B. Villa-Ramirez, G. Nichols, B. Würsig and K. Miller. 1983. Lagoon entrance and other aggregations of gray whales (Eschrichtius robustus). p. 259-293. In: R. Payne (ed.), Communication and behavior of whales AAAS Selected Symposium 76, Washington, D.C.

Oliver, J.S., P.N. Slattery, M.A. Silberstein and E.F. O'Connor. 1983. A comparison of gray whale, Eschrichtius robustus feeding in the Bering Sea and Baja California. Fish. Bull. 81:513-522.

Oliver, J.S., P.N. Slattery, M.A. Silberstein and E.F. O'Connor. 1984. Gray whale feeding on dense amphiscid amphipod communities near Bamfield, British Columbia. Can. J. Zool. 62:41-49.

Pike, G.C. 1962. Migration and feeding of the gray whale (Eschrichtius gibbosus). J. Fish Res. Board Can. 19:815-838.

Ray, G.C. and W.E. Schevill. 1974. Feeding of a captive gray whale Eschrichtius robustus. Mar. Fish. Rev. 36:31-38.

Reilly, S.B. 1981. Population assessment and population dynamics of the California gray whale (Eschrichtius robustus). Ph.D. Thesis, Univ. of Washington, Seattle. 265 p. (cited in Nerini in press).

Reilly, S.B., D.W. Rice and A.A. Wolman. 1983. Population assessment of the gray whale, Eschrichtius robustus, from California shore census, 1967-80. Fish. Bull. 81:267-279.

Rice, D.W. and A.R. Wolman. 1971. The life history and ecology of the gray whale (Eschrichtius robustus). Amer. Soc. Mammalogists Spec. Publ. No. 3. 142 pp.

Ripley, B.D. 1981. Spatial statistics. J. Wiley and Sons, New York.

Rugh, D.J. 1981. Fall gray whale census at Unimak Pass, Alaska, 1977-79. In: Fourth Biennial Conference on the Biology of Marine Mammals, Dec. 14-18, 1981. San Francisco (abstract only).

Rugh, D.J. In press. Census of gray whales at Unimak Pass, Alaska, November-December 1977-9. In: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, Eschrichtius robustus. Academic Press, N.Y.

Rugh, D. and H.W. Braham. 1979. California gray (Eschrichtius robustus) fall migration through Unimak Pass, Alaska, 1977: A preliminary report. Rep. Int. Whal. Comm. 29:315-320.

SAS. 1982. SAS user's guide.: basics. SAS Institute, Carey, N.C. 921 p.

Stoker, S.W. 1978. Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi seas. Ph.D. thesis, Univ. of Alaska, Fairbanks. 259 p.

Stoker, S.W. 1981. Benthic invertebrate macrofauna of the eastern Bering/Chukchi continental shelf. p. 1069-1090 In: D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea Shelf: oceanography and resources. Off. Mar. Poll. Assess., Natl. Ocean. Atmos. Admin., Washington.

Sumich, J.L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, Eschrichtius robustus. Can. J. Zool. 61:647-652.

Yablokov, A.V. and L.S. Bogoslovskaya. In press. Review of the Russian research on biology and commercial whaling of the gray whale. In: M.L. Jones, J.S. Leatherwood and S.L. Swartz (eds.), The gray whale, Eschrichtius robustus. Academic Press, N.Y.

Zimushko, V.V. and M.V. Ivashin. 1980. Some results of Soviet investigations and whaling of gray whales. Rep. Int. Whal. Comm. 30:237-246.

Zimushko, V.V. and S.K. Lenskaya. 1970. Feeding of the gray whale (Eschrichtius gibbosus Erx.) at foraging grounds. Ekologia Akad. NAUK SSSR 1:26-35.

INVESTIGATIONS OF BELUKHA WHALES IN COASTAL WATERS OF WESTERN AND NORTHERN ALASKA, 1982-1983: MARKING AND TRACKING OF WHALES IN BRISTOL BAY

by

Kathryn J. Frost, Lloyd F. Lowry,
and Robert R. Nelson

Alaska Department of Fish and Game

Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 612

December 1983

TABLE OF CONTENTS

LIST OF FIGURES

Figure 22. Locations of beach-cast belukha carcasses found in Nushagak Kvichak bays, May - July 1983.

Figure 23. Length distribution of 21 beach-cast carcasses from Nushagak and Kvichak bays, summer 1983.

Figure 24. Respiration patterns of five species of cetaceans.

LIST OF TABLES

I. Summary

A 2-year study was conducted in Bristol Bay, Alaska, to develop and test techniques for marking belukha whales with visual and radio tags. Information was also gathered on belukha distribution and abundance, foods and feeding, and rates and causes of mortality.

Two types of radio packages were developed: an OAR "backpack" designed to be bolted through the dorsal ridge, and a Telonics "barnacle" tag with an umbrella-stake attachment. Testing of tags and attachments revealed that the more powerful OAR radio could be received at longer distances and lower antenna heights, and that the umbrella-stake attachment penetrated too deeply for reliable use on belukhas. Visual streamer tags were fabricated which were designed to be sewn through the dorsal ridge.

In 1982, one whale was caught in Nushagak Bay, tagged with visual streamer tags, and released. In 1983 in Kvichak Bay, two whales were tagged with OAR transmitters and visual tags. The radio-tagged whales each retained the radio for about 2 weeks. The packages were shed due to migration of the attaching bolts through the tissue.

During the time that they were monitored, movements of the radio-tagged whales were restricted to Kvichak Bay and the lower Kvichak River. Recordings of the pattern of surfacings and dives revealed the three following basic types: rolls that did not occur during restricted ventilation periods, rolls that were distinctly grouped into ventilation periods separated by soundings, and a pattern in which long to very long surfacings alternated with short to very short dives. These patterns were interpreted as representing traveling, feeding, and feeding or resting in very shallow water. For the first two respiration pattern types, the percentage of total time spent at the surface ranged from 2.6 to 7.2.

Observations of distribution indicate that although belukhas are widespread in both Nushagak and Kvichak bays, whales concentrate in certain areas at certain times. In Nushagak Bay, the largest concentration (400-600) occurs near the Snake River mouth in early July. In Kvichak Bay, the areas used most commonly are off the Naknek River mouth, the Halfmoon Bay area, and the lower portion of the Kvichak River. Tidally induced currents affected belukha movements in Kvichak Bay, but such effects were not evident in Nushagak Bay. Availability of prey appears to be the major factor influencing belukha distribution. Calves are born in both bays, principally in June and July.

Counts of belukha whales from aerial surveys ranged from 86 to 334. Correction factors were developed based on surface- and dive-time data and comparisons of counts from the air and small boats. Applying the correction factor to data from the most complete aerial survey yielded an estimate of 919 belukhas in the two bays on 29 June 1983. Correction for neonates and yearlings, which are dark colored and difficult to

count from the air, raises this estimate to 1,100, which is comparable to estimates made in the 1950's.

Stomach contents of five beach-cast belukhas were examined. Contents were remains of shrimp, isopods, mussels, and fishes, including flatfishes, smelt, sculpins, and red salmon. Data from earlier studies and observations of groups of feeding whales indicate that red salmon smolt are major prey from late May to early June, while adult salmon are the primary foods from mid-June to mid-August. Calculations based on belukha abundance and food requirements indicate that in Kvichak Bay in 1983 they consumed about 6 million smolt and 280,000 adult salmon. This was about 5% of the average smolt run, 1% of the commercial red salmon catch, and 9% of the catch of other salmon species.

During 1982, six belukha carcasses were found in Nushagak Bay. In 1983, 27-31 carcasses were located or reported in Nushagak and Kvichak bays. Most of the animals for which cause of death was determined were entangled in fishing gear. Seven of the dead whales were neonates. The incidence of entanglement has increased substantially since the 1950's.

This study has demonstrated the feasibility of attaching radios to belukha whales. Further work is required to develop long-lasting attachments. Techniques developed in this study should be applied to belukhas in other areas such as Kasegaluk Lagoon.

II. Introduction

Since 1980 the Alaska Department of Fish and Game (ADF&G), with support from the Outer Continental Shelf Environmental Assessment Program, has been conducting a program of research on belukha whales (Delphinapterus leucas) in coastal waters of western and northern Alaska. Major components of this program have been studies of distribution, reproductive biology, age and growth, food habits, and characteristics of the subsistence harvest. Results of parts of these studies have been published (Seaman and Burns 1981; Seaman et al. 1982), and a comprehensive final report covering all biological studies is in preparation.

In 1982, an additional objective was added to the belukha research program which was to initiate marking efforts using both visual and radio tags in order to determine daily and short-term movements of belukhas. Initiation of such a study was deemed necessary for several reasons. Belukhas are a very important subsistence resource to Alaskan coastal residents. In recent years, the total harvest in Alaska has ranged from 138 to 247 animals (Seaman and Burns 1981). During summer months, belukhas are very common in portions of the coastal zone (Frost et al. 1982), and their distribution in those areas appears to be affected to varying degrees by human activities (Burns et al., in prep.). Virtually the entire range of the Bering-Chukchi-Beaufort Sea population of belukha whales may be leased for oil and gas exploration and development, in spite of the fact that the effect of those activities, and others such as commercial fishing and sub-sea mineral extraction, cannot be assessed.

Marking of animals with visual and telemetric tags is essential in order to address many important aspects of belukha biology and ecology. Significant research problems that can only be addressed through tagging include:

1. The interrelationships of the groups of belukhas that summer along the Alaskan coast. What degree of intermingling occurs during other times of the year, and what fidelity do individuals have to summering areas?

2. The sorts of small-scale movements that occur in local areas such as Bristol Bay. Are animals that occur in the various river systems discrete groups, or do they intermingle freely? Are local movements related to physical factors or biological circumstances such as food availability?

3. The normal behavior of belukhas in terms of the amount of time spent feeding, resting, socializing, etc. What are normal rates of movement, respiration patterns, surface and dive times, and dive depths?

4. The effects of disturbance on normal behavior patterns, and the nature and magnitude of the response.

Unfortunately, in spite of decades of research and development, standardized, "off-the-shelf" techniques for marking of cetaceans are not available (Leatherwood and Evans 1979; White et al. 1981). Cetaceans have proven difficult to work with for a number of reasons, including the difficulty of capture, instrument packaging and attachment, signal transmission as affected by water, and tracking as complicated by large-scale movements of whales and the relatively short duration of time spent at the sea surface. Therefore, the principal objective during the 2 years of this research project was the development of methods for live capture of belukhas in Alaskan waters and for the attachment of visual and radio tags. Efforts by Sergeant and Brodie (1969) had shown that, in favorable geographic settings, belukhas could be marked after live capture by stranding in shallow water or by using tags delivered with a harpoon-type instrument. Lensink (1961) successfully applied dart tags to belukhas in Kvichak Bay. Field trials of methods and equipment done by this project in Nushagak Bay during June and July 1982 (Lowry et al. 1982) demonstrated the feasibility of capturing belukhas in Bristol Bay by herding them into shallow water and catching and restraining them during the attachment of tags. In that year, one belukha whale was captured and marked with visual streamer tags. Extensive testing was also done of transmitter-receiver systems and attachments for radio packages. Prior to the 1983 field season, minor modifications were made to capture and tagging techniques which later resulted in successful application of radio packages to two whales.

The river systems of Bristol Bay support the largest single-species salmon fishery in the world. In 1983 the catch of red salmon (Oncorhynchus nerka) was over 35 million fish, and the total run exceeded 45 million fish (C. P. Meacham, ADF&G, pers. comm.). Fishermen there have long considered belukha whales to be serious predators of salmon and in years of poor salmon returns have urged action to control the depredation of salmon. In response to that concern, in the mid-1950's the Alaska Department of Fisheries undertook studies of the natural history and ecology of belukhas, including detailed analyses of stomach contents (Brooks 1954, 1955). Those studies concluded that belukha predation on outmigrating red salmon smolt was a serious mortality factor which retarded the restoration of depleted salmon stocks and was costly to the greatly depleted fishery. Off and on from 1956 until 1978, various nonlethal harassment activities were conducted to displace whales from the Kvichak River during May and June. The "belukha spooker" program was discontinued after 1978, and organized attempts to displace whales no longer occur. In 1982, we began to consider the interaction of salmon fisheries and belukhas as part of our belukha whale studies.

In 1954 and 1955, it was estimated that about 1,000-1,500 belukhas spent the summer in inner Bristol Bay, with considerable annual variation in numbers (Brooks 1954, 1955). Since those early estimates, which were based mostly on observations from boats, airplanes, and talks with fishermen, no progress had been made in further refining estimates of the numbers of whales or annual variations in numbers until initiation of this project in 1982. In that year, regular observations were made of belukhas in Nushagak Bay only, and the peak number using that area in late June-early July was estimated at approximately 400-600. In 1983, a systematic effort was made to estimate the total number of belukhas in both Nushagak and Kvichak bays.

III. Current State of Knowledge

The distribution of belukha whales is generally circumpolar in arctic and subarctic waters. In Alaska they occur in two discrete groups. A small group numbering 300-500 ranges principally in Cook Inlet, although they are occasionally seen elsewhere in the Gulf of Alaska (Klinkhart 1966; Harrison and Hall 1978; U.S. Department Commerce 1979). The majority of belukhas occurs in the Bering and Chukchi seas and ranges seasonally into the Beaufort and East Siberian seas (Seaman and Burns 1981).

Belukha whales in western Alaska are often associated with sea ice, and their movements are affected by the seasonal cycle of ice distribution. During winter they are excluded from most of the coastal zone by the formation of shorefast ice. Most sightings of whales during this season have been in the moving ice of the Bering and southern Chukchi seas, and it is presumed that the majority of the population winters in those areas (Seaman and Burns 1981). Some animals migrate northward in spring through leads in the pack ice, passing Point Barrow in April and May, then moving eastward to the Mackenzie River delta and Amundsen Gulf (Seaman and Burns 1981; Braham et al. 1982). Other whales move into nearshore waters of the Bering and Chukchi seas shortly after ice breakup and concentrate in locations such as Bristol Bay, Norton Sound, Kotzebue Sound, and Kasegaluk Lagoon (Lensink 1961; Seaman and Burns 1981). Similarly, they move along the Siberian coast, although little data about these whales in western Bering and Chukchi seas are available. Although the relationships among groups summering in various locations are poorly known, the Bering-Chukchi-Beaufort population of belukhas is presently considered a single stock since the animals are thought to mingle during the breeding season in February-April (Burns et al., in prep.).

Due to their possible interactions with the commercial fishery for red salmon, belukhas summering in Bristol Bay have been comparatively well studied with respect to their use of river systems and predation on salmon (summarized by Lensink 1961). Investigations of the abundance of whales and their foods indicated that belukha predation could significantly impact red salmon stocks, primarily through consumption of smolt during their seaward migration in late May and early June. To reduce predation on smolts, attempts were made to displace belukhas from the Kvichak River, initially by harassing them using boats and small explosive charges (Lensink 1961). This method was later replaced by acoustic harassment devices which transmitted vocalizations of killer whales (Orcinus orca) (Fish and Vania 1971). Use of the acoustic system was discontinued after 1978, and organized attempts to displace the whales no longer occur. However, some consideration has recently been given to the possible effects of belukha predation on red salmon stock-enhancement efforts in the Snake River (Fried et al. 1979).

It has been estimated that 1,000-1,500 belukhas are present in Bristol Bay during summer months (Lensink 1961). They are seldom seen anywhere except in Kvichak Bay and Nushagak Bay, and their associated river systems (Frost et al. 1982). Belukhas occur in the Kvichak River and Kvichak Bay from at least April to September (Frost et al. 1982), where they ascend 26-55 km up the river on flood tides and return to the bay on the ebbing tide (Lensink 1961). They are seen off the mouth of the Naknek River in April and May and sometimes move as much as 27 km upstream, past the town of King Salmon (Frost et al. 1982). They stop entering the Naknek in late May when boat traffic on the river becomes extensive (Lensink 1961). The distribution and movements of whales in Nushagak Bay appear more complex and are less well studied. Belukhas occur in the Bay and its estuaries from at least April to early October, with numerous sightings occurring near the mouths of the Snake River and Wood River (Frost et al. 1982). Fried et al. (1979) conducted a series of 11 surveys of the region from 28 May to 28 June 1979. In total, they sighted 280 whales; most of those were seen near the Snake River and in northern Nushagak Bay near the junction of the Wood, Little Muklung, and Nushagak rivers. Some animals were also seen in the Igushik River and along the shores of Grassy Island. Fried et al. observed no significant relationship between whale movements and tides or between whale abundance and numbers of outmigrating red salmon smolt.

The only censuses of whales in the Kvichak-Nushagak area were conducted in 1954 and 1955 (Brooks 1955). Results indicated an increase in abundance from May to August and considerably more whales in the area in 1954 (approximately 1,000) than in 1955 (approximately 525). The relationship among groups of belukhas in the Kvichak and Nushagak systems is unclear, although Brooks (1955) postulated a seasonal movement from the Kvichak to the Nushagak caused by changing abundances of prey (salmon). Lensink (1961) in 1959-1960 applied visual tags to 46 belukhas in Kvichak Bay in an attempt to address this question. One tagged animal was recovered 1 month later from a gillnet near the mouth of the Naknek River, not far from where it was tagged.

To visually identify individual cetaceans, it is generally necessary to mark the animal with some sort of brand, tattoo, or tag. Marking and tagging of cetaceans have met with very variable success (White et al. 1981). Many of the tags that have been tried are designed for attachment through the dorsal fin and are therefore not applicable to belukhas. Lensink (1961) applied dart tags with heads similar to those made by Floy Tag and Manufacturing, Inc. to 46 belukhas in Kvichak Bay. Two resightings were made: one on the animal noted above and a second which was seen on a live animal at least 3 months after tagging. Sergeant and Brodie (1969) attached over 800 tags to belukhas in Hudson Bay. They attached 700 harpoon tags (Floy type FH-67) to the dorsal part of the body and 188 Petersen disc tags through the dorsal ridge. The only resightings were of animals tagged with harpoon tags. Two were caught

5-7 weeks after tagging, 300-800 km from the point of tagging. A third was seen on a live stranded whale 1 year later near the location of where it was tagged. The skin around the tag had completely healed, and the tag was in "excellent structural condition." Tests on captive animals confirmed the durability and safety of spaghetti-type tags attached with stainless-steel darts which toggle in the blubber or fascia (White et al. 1981).

The use of radio tags is considerably more complicated than visual tags. Successful radio tagging and tracking of cetaceans involves two relatively discrete components. First is the selection or development of appropriate electronic systems (telemetry) for transmitting and receiving signals. Second is the design of appropriate packaging for transmitters and mechanisms with which to attach them to and have them retained on the animal being tagged.

There are presently three general classes of telemetry equipment that are potentially suitable for tagging and tracking of cetaceans: HF (high frequency), VHF (very high frequency), and satellite-linked. Each system has its advantages and drawbacks (Hobbs and Goebel 1982). HF transmitters have long theoretical tracking distances but are comparatively large (due to battery requirements), have problems with antenna configuration, and are expensive. VHF transmitters are compact and inexpensive but provide poor surface reception due to line-of-sight transmission characteristics. Satellite-linked systems offer great potential for tracking but to date have had limited application for cetaceans due to size and configuration of transmitters and signal requirements of satellite receivers. In addition to appropriate antennas and logistics platforms, efficient tracking of cetaceans requires automatic direction finding (ADF) equipment to rapidly localize brief, infrequent signals, and scanners to monitor multiple frequencies if more than one animal is tagged in a particular area. At present, most development and testing of ADF systems has been done with HF transmitters, while VHF transmitters have well-developed scanning and data-processing systems available (Hobbs and Goebel 1982). Butler and Jennings (1980) did comparative tests of VHF and HF systems on free-ranging dolphins and concluded that the VHF system was the more reliable.

A number of techniques have been tried for attachment of telemetry packages to cetaceans. With the exception of the implanted Woods Hole Oceanographic Institute/Ocean Applied Research (WHOI/OAR) tag developed by Watkins (Watkins 1981; Watkins et al. 1981), all packages have been attached to the surface of the animal. Attachments have been made using belly bands, bolts which usually pass through the dorsal fin, sutures, or curved metal tines (umbrella stakes) (Leatherwood and Evans 1979; Mate and Harvey 1981; Hobbs and Goebel 1982). Important considerations in design and selection of attachments are whether the attachment will be "permanent" or incorporate a timed release, and whether it will be applied to animals that are in-hand and restrained, or remotely to free-swimming individuals.

Radio packages have been attached to a number of species of porpoises and whales in the wild. Bolted-on backpack-type transmitters have generally remained attached for 1 to 30 days and have proven useful for short-term observations of movements and behavior (Irvine et al. 1979; Leatherwood and Evans 1979). A common problem has been movement of the bolt(s) through the tissue at the point of attachment. Watkins et al. (1981) have tracked finback (Balaenoptera physalus) and humpback (Megaptera novaeangliae) whales tagged with the implanted WHOI/OAR tag in Prince William Sound, Alaska. They demonstrated minimum retention times of 16-17 days. Mate and Harvey (1981), using umbrella-stake attachments, applied tags to 19 gray whales (Eschrichtius robustus) in San Ignacio Lagoon, Baja California. Maximum documented retention time was 50 days. None of the gray whales showed any noticeable response to the tag attachment procedure. Similarly, Watkins (1981) observed little visible response to implantation of the WHOI/OAR tag in three species of large whales.

IV. Study Area

Field work during 1982 and 1983 was conducted in Nushagak and Kvichak bays, Alaska (Fig. 1). Both are large embayments in northcentral Bristol Bay. Nushagak Bay is approximately 65 km long and tapers from approximately 30 km across in the outer portion to 3-6 km across at its upper end. Four major rivers flow into Nushagak Bay: the Igushik and Snake rivers on the west side and the Wood and Nushagak rivers in the north. The major human habitations in the area are the city of Dillingham (1980 population 1,563) at the north end of Nushagak Bay and a small village at Etolin Point near the southeast portion of the entrance to the bay. Several canneries are located on the east side of the bay, particularly near Clarks Point.

Kvichak Bay is approximately 60 km long and tapers from 40 km across the outer portion to approximately 4 km across at its upper end. Two major rivers flow into Kvichak Bay: the Naknek River on the east side and the Kvichak River to the north. The major human habitations are the towns of Naknek (1980 population 318) and King Salmon (population 545) approximately 20 km upriver from Naknek. There are several large canneries at and near the mouth of the Naknek River. Fishing camps line the shores of most of the bay in June and July during the red salmon fishery.

Both bays are generally shallow, with water depths (at low tide) seldom exceeding 15 m. The area is characterized by numerous sand and mud flats which are exposed during low tides. During June and July, daily tidal ranges vary from 4.8 to 8.6 m. River outflow and tides combine to produce strong currents throughout both bays. Water in the bays is very muddy. In and near major rivers, visibility in the water is effectively zero.

During June and July, one of the world's largest salmon fisheries occurs in Bristol Bay. Fishing is done with gillnets, both from shore

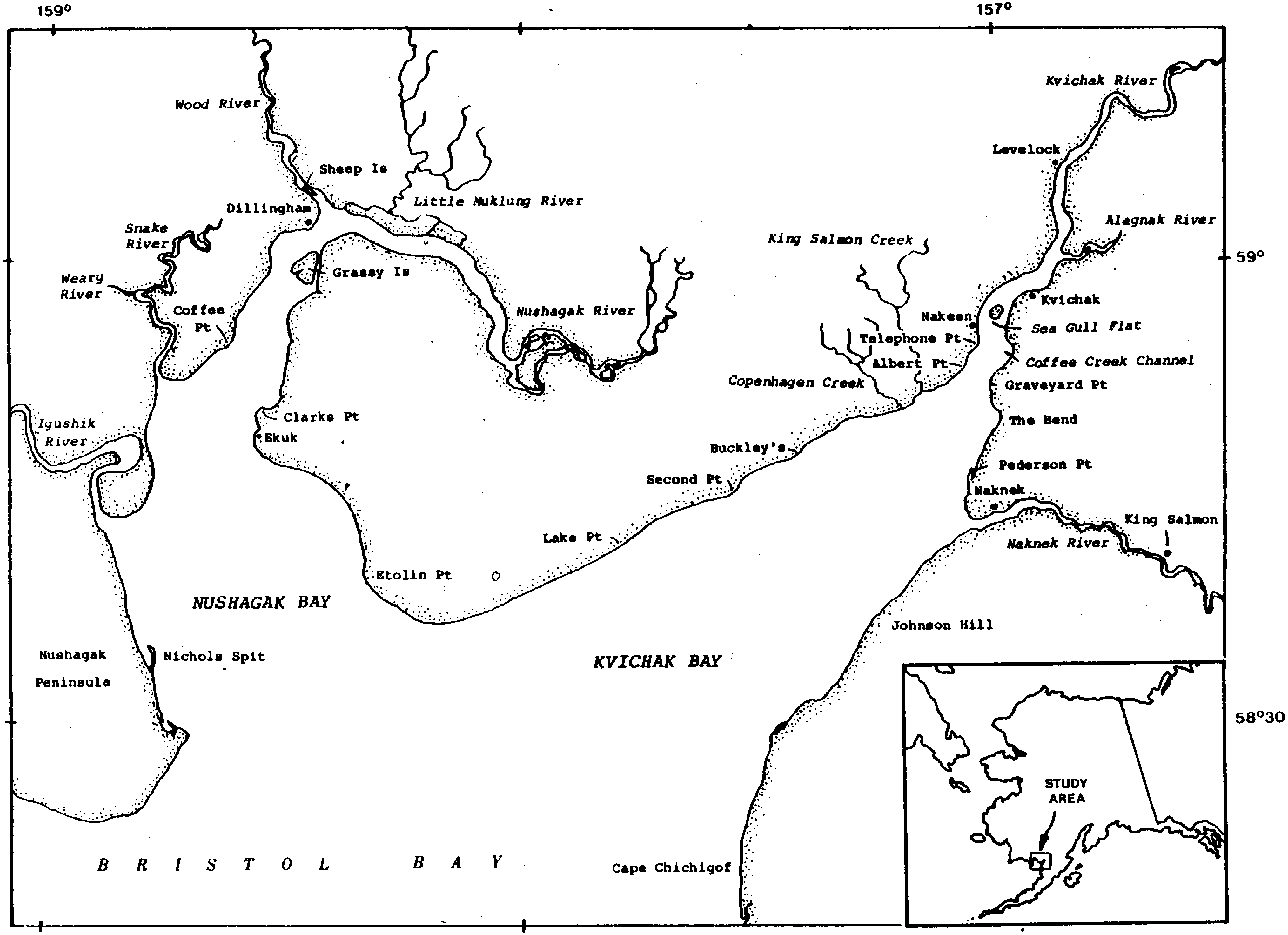


Figure 1. Map of Nushagak and Kvichak bays showing major locations mentioned in text.

(setnet) and boats (drift gillnet). During the peak fishing period in 1983, an estimated 1,000 drift-net boats and 344 setnet sites were fished in Kvichak Bay, and an additional 300-600 drift netters and up to 230 set-netters were in Nushagak Bay (ADF&G, unpubl.). Collectively, over 450 km of gillnet were fished in the two bays. The fishermen are supported by a fleet of tenders, processors, freighters, and air transports. The principal species harvested is red salmon, although chum salmon (Oncorhynchus keta), pink salmon (O. gorbuscha), king salmon (O. tshawytscha), and silver salmon (O. kisutch) are also taken. Red salmon runs in Bristol Bay have fluctuated greatly in strength during past years. The catch in Kvichak and Nushagak bays combined in 1983 was approximately 27 million fish; 10 years earlier, in 1974, the catch was approximately 1.5 million fish.

V. Methods

Field work was conducted in Kvichak and Nushagak bays from 9 May through 15 July 1983. We used the ADF&G vessel Iliaska, a 32-ft (9.8-m) gillnet boat, as a base of operations. During most of the project, the Iliaska was anchored either off Naknek or in the Kvichak River off the abandoned Diamond J cannery. Project personnel lived aboard, and Iliaska was sometimes used for tracking radioed whales. The NOAA Bell 204 helicopter (57 RF) operated out of King Salmon from 24 May through 29 June and was used to transport personnel and supplies, conduct aerial surveys of whales, track radioed whales, locate beached carcasses, and coordinate whale-capture attempts.

Eleven people were primarily involved in the whale capture and tagging operations (Table 1). ADF&G contributed the time of eight of those at no cost to the project.

Table 1. Personnel directly involved in belukha whale capture, tagging, and tracking operations, Kvichak Bay, 1983.

Name	Dates	Affiliation
Lloyd Lowry	9 May-15 Jul	ADF&G, Fairbanks
Bob Nelson	9 May-28 Jun	ADF&G, Nome
Dick Tremaine	23 May-19 Jun	ADF&G, Fairbanks
Don Calkins	23 May-6 Jun	ADF&G, Anchorage
Kathy Frost	29 May-15 Jul	ADF&G, Fairbanks
Warren Ballard	29 May-11 Jun	ADF&G, Glennallen
Wayne Regelin	10 Jun-16 Jun	ADF&G, Fairbanks
Jack Whitman	11 Jun-24 Jun	ADF&G, Glennallen
Ken Taylor	May-Jun, intermittent	ADF&G, Dillingham
Dick Sellers	May-Jun, intermittent	ADF&G, King Salmon
Mark McNay	May-Jun, intermittent	ADF&G, King Salmon

In 1983, as in 1982 (see Lowry et al. 1982), we planned to catch whales by driving them with small boats until they stranded themselves in shallow water. This technique, in combination with the use of nets, can be very effective for catching belukha whales (e.g., Ray 1962; Sergeant and Brodie 1969). Our fleet of small boats included two Zodiac rafts (one 3.7-m and one 4.3-m) with 35-hp motors, one 6.4-m Boston whaler with 140-hp motor, and one 4.9-m aluminum riverboat with 35-hp motor. Other equipment included a 25-fathom (45.7 m) net which was 1.5 fathoms (2.8 m) deep, constructed of 6-inch (15.2-cm) stretch-mesh No. 48 thread nylon, and hung like a gillnet with net floats and lead line. The net was intended to be detectable (acoustically and perhaps visually) by the whales so that they would not become entangled and was to be used as a fence to direct or contain the animals. A stretcher 3.0 m by 1.5 m was constructed of sturdy nylon fabric with several rope hand-holds and was to be used to transport stranded animals into the water after tagging. A head net was constructed of 6-inch (15.2-cm) stretch-mesh webbing and was used to restrain the animal during tagging.

Visual tags and radiotelemetry packages were attached to two whales in 1983 (Fig. 2). Visual tags were constructed of brightly colored polyvinyl chloride fabric and measured 3.8 cm wide and 32.0 cm long. Each was numbered and preprinted with the words "RTN TO ADFG FAIRBANKS." Two pairs of visual tags were attached to each whale. They were applied by sewing a piece of plastic-coated stainless steel wire, to which one tag was attached, through the dorsal ridge and crimping the second tag onto the other side (see also Lowry et al. 1982).

The radio package (Fig. 2) consisted of an OAR (Ocean Applied Research Corp., San Diego, California) AB340 transmitter with 250-milliwatt power output, 100-millisecond pulse width, and a pulse rate of 120 per minute. Transmitter crystals were in the 164 MHz range. The transmitter was constructed as a pair of tubes, each 1.9 by 14.7 cm, with electronic components on one side and batteries on the other. A semi-rigid whip antenna 47.5 cm long was attached to the tubing which connected battery tube to electronics. Each radio operated with a saltwater switch located in the antenna and therefore transmitted only when the antenna broke the surface. The transmitter was attached to a fiberglass saddle, measuring 24 cm long by 11 cm wide by 7 cm high, and weighing approximately 575 g. The saddle was constructed by Dr. John D. Hall of Anchorage, Alaska, from a cast of a belukha dorsal ridge provided to us by Dr. Lanny Cornell, Sea World, Inc. The inner surface of the saddle was lined with 4-mm open-cell foam. Closed-cell foam was added to the top of the package to make the transmitter float with the antenna out of the water. The completed backpack transmitter was similar to that described and used by Gaskin et al. (1975) and Butler and Jennings (1980).

Packages were attached by means of a nylon rod inserted into a hole cored through the skin and blubber of each whale in the anterior portion of the dorsal ridge. Corrodible magnesium screws which were designed to release the package in approximately 6 weeks were passed through holes in the leading edge of the packages and threaded into the nylon rod.

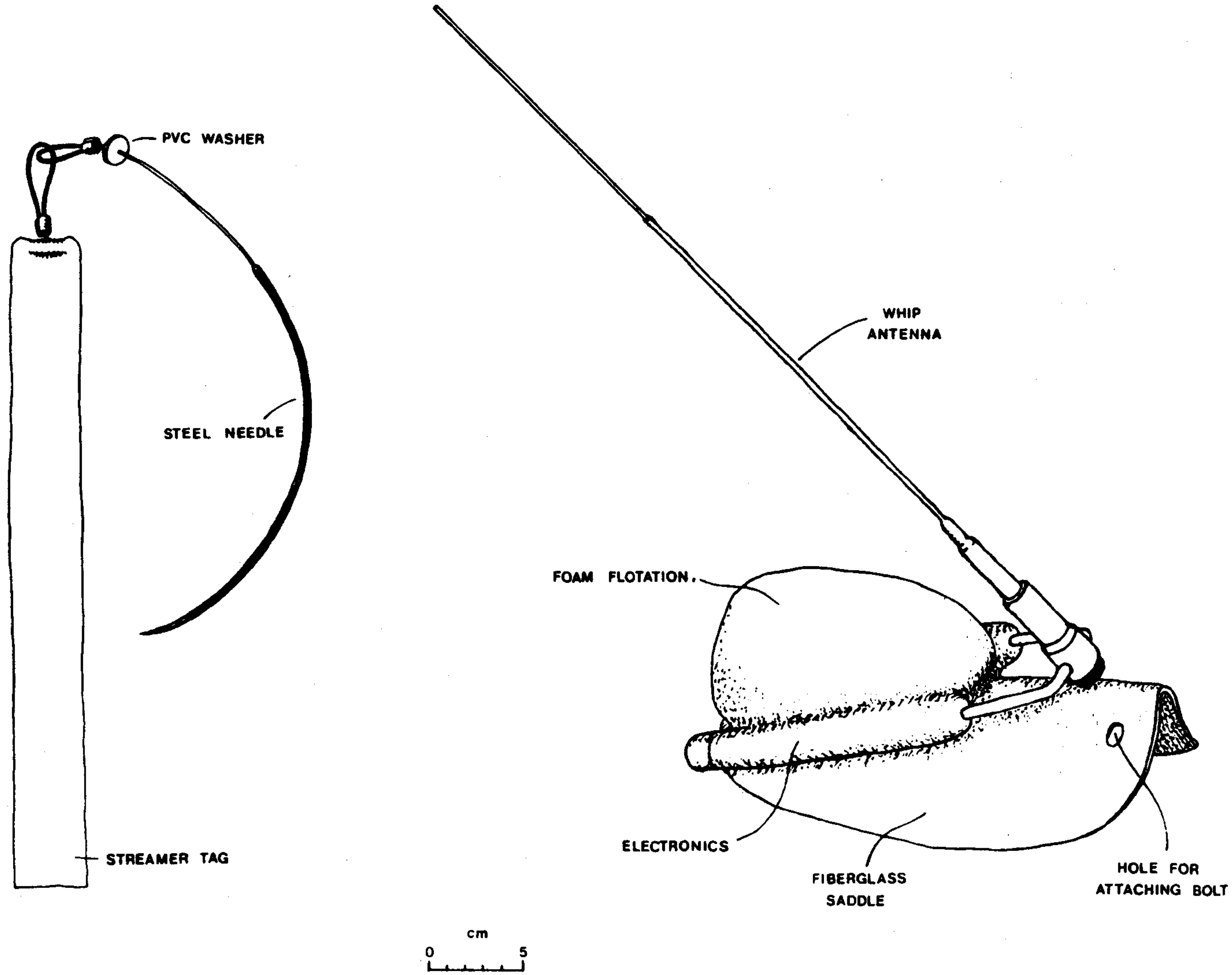


Figure 2. Illustration of visual streamer tag and OAR "backpack" radio tag.

Telonics barnacle tags as described by Mate and Harvey (1981) and Lowry et al. (1982) were taken into the field for additional testing. As a result of recalculations by the manufacturer on the frequency characteristics of the radios, antennas were cut 5 cm shorter in 1983 than they had been in 1982. It was anticipated that this would increase the effective range of the radios. The attachment tines were shortened to a length of 5.4 cm to decrease the depth of penetration. However, no Telonics radios were attached to whales.

Our primary receiving system consisted of a Telonics TR-2 receiver with automatic scanner which was connected to a two-element YAGI antenna. Antennas were either hand held (on land or in small boats), mounted at the end of a 3.7-m mast (in the Boston whaler), or mounted on the helicopter. When a helicopter was used to track, two antennas were used to more easily determine directionality of the signal. The antennas were affixed to either end of a 3-m piece of conduit secured horizontally to the nose of the aircraft. In addition to the Telonics system, we tested our ability to track radios using an OAR automatic direction finder (model ADFS-320) with an Adcock antenna. Although the ADF worked quite well at short range, it was only useful at distances of less than 1 km. In essence, by the time we were close enough to use the ADF, we already knew where the whales were and could track them more easily with hand-held YAGIs. We also attempted to use a Telonics digital data processor (model TDP-2) in combination with a two-channel strip chart recorder (American Analog Co.) as a remote data-acquisition station. We had hoped to acquire dive time:surface time data on a 24-hour basis through the use of this setup. However, due to a built-in 5-second lag in the response time of the recorder, this system proved unsuitable to the task at hand. The surfacings of the whales were closer together than the lag time of the equipment.

Dive times and surface times of the radio-tagged whales were recorded manually using digital stopwatches. Observers measured the length of all dives and recorded the number of signals per surfacing. Surface intervals were calculated by multiplying the number of signals received per surfacing by the pulse interval (0.5 sec).

Aerial surveys of Kvichak and Nushagak bays were conducted from fixed-wing aircraft or helicopter at approximately 2-week intervals from 15 April through 15 August (Table 2). Surveys were flown along the coastline approximately 0.5-0.9 km offshore at an altitude of 305 m and speeds of 183-274 km/hr. Observers did not survey a specified transect width but instead counted all of the whales they could see on their respective sides of the aircraft. When large groups of whales were encountered and a single observer was present, the aircraft sometimes circled the groups to obtain the best possible estimate. The single exception to this method was a line-transect survey on 29 July, when a predetermined grid of both bays was flown and observations were confined to a 0.9-km strip on either side of the aircraft.

Table 2. Aerial surveys of Kvichak and Nushagak bays, 15 April-14 August 1983.

Date	Time	Tide	Platform	Observer(s)
15 Apr	0912-1239	low - 1012	C-185	K. Taylor
2 May	1550-1628	low - 1357	C-185	K. Taylor
5 May	0925-1407	low - 1614	C-180	K. Taylor
17 May	0921-1204	low - 1329	C-185	L. Lowry/R. Nelson
31 May	1100-1400	low - 1332	helo	K. Frost/D. Calkins/ R. Tremaine
14 Jun	1535-1822	low - 1214	helo	K. Frost/W. Regelin
24 Jun	1318-1609	high - 1411 low - 2045	helo	K. Frost/L. Lowry
29 Jun	1034-1146 1340-1558	low - 1303	helo	K. Frost/L. Lowry
14 Jul	1206-1539	low - 1241	C-185	K. Frost/L. Lowry
14 Aug	1420-1642	low - 1402	C-185	K. Taylor

Beach-cast and floating dead belukhas were located from aircraft and boats. During 1982, most observations of beach-cast belukhas in Nushagak Bay were made on an opportunistic basis (Lowry et al. 1982). In 1983, systematic surveys were conducted in June and July. Aerial surveys were flown along the beach at altitudes of 25-50 m. Boat surveys were conducted by motoring along the shore, scanning the beach both visually and with the aid of binoculars. When a carcass was located, the animal was examined for cause of death and measured, its sex was determined, the lower jaw or several teeth were taken for age determination, and if condition permitted the stomach was examined for food remains. Additional information was obtained from ADF&G biologists in King Salmon and Dillingham and from salmon fishermen.

Fish remains in stomach contents were usually identified by their otoliths or characteristic bones. Information on probable foods was also obtained by observing feeding whales and by examining salmon caught in nets for the presence of belukha toothmarks.

VI. Results

A. Capture, Tagging, and Tracking of Whales

We conducted two field tests of the OAR and Telonics transmitters to determine the effect of partial submersion of the antennas on reception range, to compare different antenna lengths on Telonics transmitters, and to compare the range of the OAR and short-antenna Telonics transmitters. On 15 June, from 0900-1000 hours, testing was conducted from the Iliaska, which was anchored near the mouth of the Naknek River. The receiving system consisted of a Telonics receiver with a two-element YAGI antenna at approximately 5 m above sea level (ASL). A Boston whaler was used to take transmitters out to various distances. Positions were fixed by triangulation of sighting compass bearings to recognizable landmarks, and all test locations were in line of sight of the receiving antenna. One at a time at each test location, the transmitters were hand held in the water with 5 cm, half, or all of the antennas out of the water, and comparative signal strength was noted. Results (Table 3) indicated that the OAR transmitter emitted the strongest signals and was audible to 9 km with only half of its antenna emergent. The Telonics receiver had very limited range when the antennas were partly submerged. None of the transmitters emitted audible signals with 5 cm of the antenna exposed. In the case of the OAR, this was because the saltwater switch is activated at a point 16.5 cm down from the tip of the antenna.

On 5 July, testing was done in the lower Kvichak River at slack low water (Table 4). Sea state was flat calm. The short-antenna Telonics transmitter was mounted on a small board and floated in the river. The OAR package was floated approximately 6 m away to prevent interference between the two transmitters. A Boston whaler was used to transport the Telonics receiver various distances from the floating transmitters. Positions were fixed by triangulation of sighting compass bearings to prominent landmarks. Antennas were either handheld at approximately 1.5 m ASL or mounted on a mast 3.7 m ASL with the elements in vertical orientation. The OAR transmitter could be heard at all test locations; the maximum test distance was 20.1 km. The Telonics transmitter could be heard only at the 6.4- and 8.2-km locations. There was no detectable difference in signal strength between the two receiving antenna heights. The major factor affecting signal strength, other than distance, was orientation of the antenna. Maximum reception was obtained with the antenna elements vertical rather than horizontal.

We attempted to capture whales on 16 days between 27 May and 19 June (Table 5). Five of those attempts were made in the Kvichak River, four in inner Kvichak Bay on Salmon Flats, five in eastern Kvichak Bay on the flats south of the Naknek River mouth, and two in Halfmoon Bay (Fig. 3). Whales were usually located from the helicopter. The four small boats, were then used to form a line behind the whales in an attempt to drive them, under direction of personnel in the helicopter, into shallow water over tidal flats. In most instances, the whales were difficult or impossible to drive for the distances required to reach adequately shallow water. On several days individual whales were herded for up to 90 minutes but could not be moved into water shallower than about 1.5 m. On two occasions, single whales swam into the net that was trailed behind the Boston whaler to act as a fence and close off one avenue of escape. However, in both instances the water was too deep for would-be capturers to jump in, and before the whales could be otherwise restrained they

Table 3. Comparative tests of OAR and Telonics transmitters, 15 June 1983.

Transmitter	Portion of antenna out of water	Distance from radio to receiver (km) 1.6	3.3	5.7	9.3
OAR 164.585	5 cm	no signal	no signal	no signal	no signal
	1/2	yes	yes	yes	faint
	all	strong	strong	strong	yes
Telonics 165.458 (18-cm antenna)	5 cm	no signal	no signal	no signal	no signal
	1/2	no or very faint	no signal	no signal	no signal
	all	yes	yes	yes	yes
Telonics 165.257 (23-cm antenna)	5 cm	no signal	no signal	no signal	no signal
	1/2	faint	faint	no signal	no signal
	all	strong	strong	yes	yes

Table 4. Comparative tests of OAR and Telonics transmitters, 5 July 1983.

Transmitter	Antenna height (m)	Distance from radio to receiver (km) 6.4	8.2	11.0	11.9	20.1
OAR 164.535	1.5	strong	strong	moderate	moderate	faint
	3.7	strong	strong	moderate	moderate	faint
Telonics 165.857 (18-cm antenna)	1.5	moderate	moderate-weak	no signal	no signal	no signal
	3.7	moderate	moderate-weak	no signal	no signal	no signal

Table 5. Dates and locations at which we attempted to catch whales in Bristol Bay during May-June 1983.

Date	Location	Comments
27 May	Alagnak R. mouth	20-25 whales in several small groups; chased 2 groups of 2 into shallow water, but they escaped downriver.
28 May	Sea Gull Flat	Chased 2 or 3 into shallow water but couldn't hold them there.
30 May	Telephone Pt.	20+ whales; 2 or 3 whales temporarily stuck on sandbar but got off. Too much deep water nearby.
31 May	S. Alagnak R. mouth	Moved 2 different gray animals into shallow water; worked for a while but couldn't catch them.
1 Jun	King Salmon Creek/ Copenhagen Creek	Followed/pushed group downstream; set net off spit but whales broke out and headed offshore; followed another group but they broke out between the boats to deep water.
2 Jun	Nakeen	Whales disappeared as soon as boats lined up.
3 Jun	Salmon Flats	Came really close; had 3 or 4 whales right along bar, tide dropping; wind came up quickly just as whales reached bottleneck in spit; lost whales because we couldn't see them.
4 Jun	Salmon Flats	10-15 whales in this area; moved 1 white animal up against bar, but it was a cut bank, water too deep, whale got away.
6 Jun	Salmon Flats	Tried to drive but water too rough.
8 Jun	Big Flat	70+ whales feeding; worked 1 large white animal for over 1-1/2 hr; it hit net, thrashed around, then swam under it; we kept it from going offshore, but couldn't move it into less than 1 m water; finally, helo ran low on fuel and tide was coming in, wind picked up.

Table 5. Continued.

Date	Location	Comments
11 Jun	Big Flat	Most whales offshore and moving upriver in deep water; we were unable to move them into shallower water.
14 Jun	Big Flat	Worked a big white animal until it turned offshore and ran hard upriver to the channel.
15 Jun	Big Flat	Whales in tight group; cut out a young 1- or 2-yr-old and worked it for >1 hr; pushed it into net but it got out; helo ran low on fuel, wind picked up, had to give up.
16 Jun	Big Flat	Whales very difficult to drive; would not be moved near to shore; water muddy, windy, too foggy to spot from helo.
18 Jun	Halfmoon Bay	SUCCESS! Tagged adult white female. Tide low and falling during capture; extensive flats in area, including long bars with no channels or breaks to allow escape; whale became disoriented, swam along a bar and was surrounded and captured.
19 Jun	Halfmoon Bay	Attempted to drive, futile; rain, wind, waves; no whales.

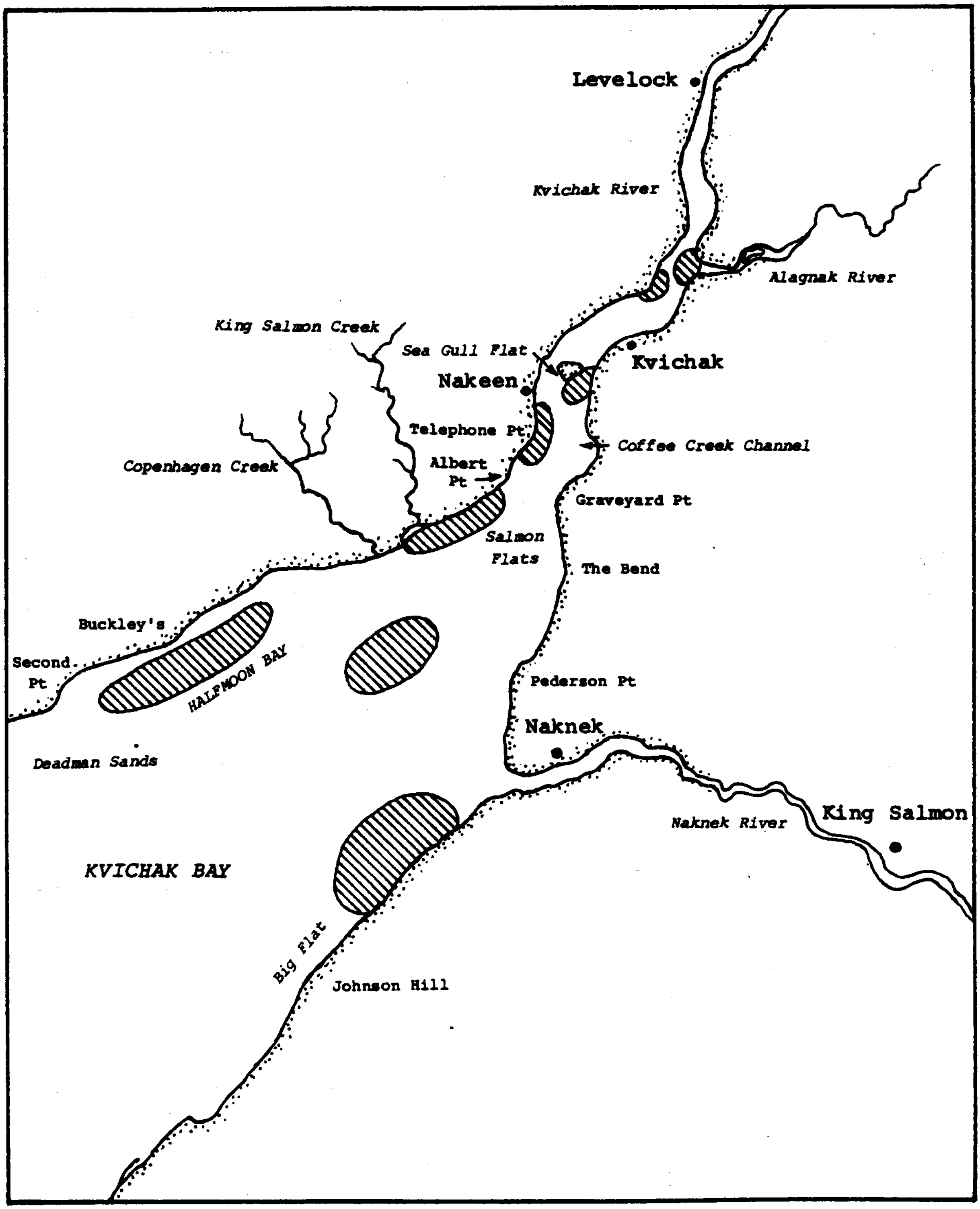


Figure 3. Map showing locations at which whale catching was attempted in May-June 1983.

swam under the net and escaped. Subsequent conversations with local Eskimo residents indicated that whales were sometimes driven for 2-3 hours or more before becoming sufficiently exhausted to catch.

Despite the difficulty in capturing, we successfully attached visual tags and radio transmitters to two whales (Table 6). The first whale to be tagged (later referred to as "BB") was caught between 1530 and 1930 hours on 9 June in a salmon setnet about 7 km south of the Naknek River mouth. Two employees of the Bumblebee Cannery disentangled this small belukha from the net and transported him by truck to the cannery, where he was covered with canvas and kept wet until our tagging crew was notified and arrived by helicopter. The whale had superficial net marks on the caudal peduncle and flukes but did not appear badly hurt. When we arrived, the whale was respiring regularly and lying quietly in the truck bed. It was transported by truck to the beach at the south side of the Naknek River mouth, where it was measured, tagged, and released at about 2145, using a stretcher and help from cannery workers to carry it into the water. As soon as the whale touched the water, it began to move and upon release swam away to the west in an apparently normal manner. The whale was monitored for 30 minutes after release to ensure proper functioning of the radio.

Table 6. Belukha whales captured and tagged in Kvichak Bay, June 1983.

Whale	Transmitter	Visual tags	Color	Std. length (cm)	Comments
"BB"	OAR 164.535	Red 11, 12 Blue 01, 02	dark gray	230	Caught in salmon setnet on 9 Jun
"Mama"	OAR 164.585	Red 13, 14 Blue 03, 04	white	370	Caught in Halfmoon Bay on 18 Jun

On 18 July, a second whale (later referred to as "Mama") was tagged. At approximately 1500 hours, approximately 1 hour before a +6-cm low tide, our four small boats assembled near Copenhagen Creek and moved south into central Halfmoon Bay where the helicopter had located 20-30 dispersed whales in very shallow water. Almost immediately upon arrival of the boats, the whales scattered and disappeared in the muddy water. However, one large white animal swam directly toward a long, shoaling sandbar. When the boats surrounded it and nets were set on one side, the whale submerged and laid on the bottom, invisible from either the boats or helicopter, for 5-10 minutes. Shortly thereafter, the wake of the whale appeared running offshore along the sandbar. Two boats blocked its retreat, and at approximately 1615 hours, when the other two boats arrived, the whale was physically captured. She struggled very little, and after a head net was put on she lay quietly, lifting her head to breathe every minute or so. The whale was restrained for 10-15 minutes while tags

were applied, after which the head net was removed and the whale swam away toward deeper water. As with the first whale, the radio was monitored for approximately 30 minutes after the release to ensure that it functioned properly.

Each of the whales to which we attached radio packages retained the radios for approximately 2 weeks. BB was last located with the radio attached on the 13th day after tagging. On the 14th day, the radio was discovered floating free, antenna upright, and emitting a constant signal approximately 3 km northwest of BB's last known location. Mama's radio remained on for 12-14 days. She was last located on the 11th day after tagging. On the 12th day, we did not attempt to locate her, and on the 13th and 14th days we were unable to locate her in the customary areas. On the 15th day, the radio was recovered approximately 20 km southwest of the last known location. The radio was lying on its side at the high-tide line with the antenna partially buried in the gravel. Both radios came off by working their way out of the tissue through which they were bolted. The magnesium screws, designed to last 4-6 weeks, were partially corroded but intact and were still in place in the nylon rod.

Determining the location of tagged whales was usually quite easy. The OAR radio worn by BB (frequency 164.535) emitted a very strong, clear signal that could be received over substantial distances (Table 7). With two YAGI antennas mounted on the front of a helicopter flying at 305 m, we routinely picked up moderate to strong signals over 30 km distant. On one occasion, a signal was received at 59 km. This signal was "moderate" in strength and could have been heard from considerably farther away. Using hand-held or mast-mounted YAGI antennas in a Boston whaler or on the Iliaska, we were able to receive and track BB from 20-30 km distant. As previously discussed and shown in Table 4, there was little apparent difference in reception between antennas hand held at 1.5-2.0 m and those mast mounted at 3-4 m.

The OAR radio worn by Mama (frequency 164.585), although supposedly identical to the one worn by BB, was considerably more difficult to track. The maximum reception distance from the helicopter (305 m antenna height) was 42 km, with a signal that was considered weak. Maximum recorded reception for Mama's radio from the Boston whaler (antenna height 2-3 m) was 23 km (signal strength moderate), and on at least several occasions we could not receive signals at a distance of 30 km.

During the 14 days that BB was radio-tagged, his position was determined on 16 occasions (Appendix I, Fig. 4). For the first 26+ hours after tagging, he remained in the Naknek River mouth area near where he was released. On the morning of 11 June, approximately 36 hours after his release and 9 hours after he was known to be off the Naknek River mouth, BB was visually relocated by an ADF&G fixed-wing pilot in the area of the Bend about 14 km to the north. Later that same day, he moved down the west side of Kvichak Bay against a flooding tide to near Second Point, a distance of about 30 km in approximately 6 hours.

Table 7. Distances at which signals were received from OAR radio 164.535 ("BB").

Date	Time	Antenna height (m)	Distance (km) to whale	Signal strength
10 Jun	1340	305	18	strong
	1706	2-4	7-8	weak
11 Jun	1250	2	20+	weak
12 Jun	1100	4	27	moderate
	2350	4	22+	weak
13 Jun	1100	2-4	31	moderate
14 Jun	1000	305	35	strong
	1725	305	37	moderate
	1800	305	59	moderate
15 Jun	1030	305	35+	strong
	1640	6-7	35+	weak
16 Jun	1510-1550	2	20	strong
21 Jun	1430	100	18+	moderate
22 Jun	1045	2-3	18+	moderate
23 Jun	1210	2-3	30+	weak
	1328	305	43	moderate-strong

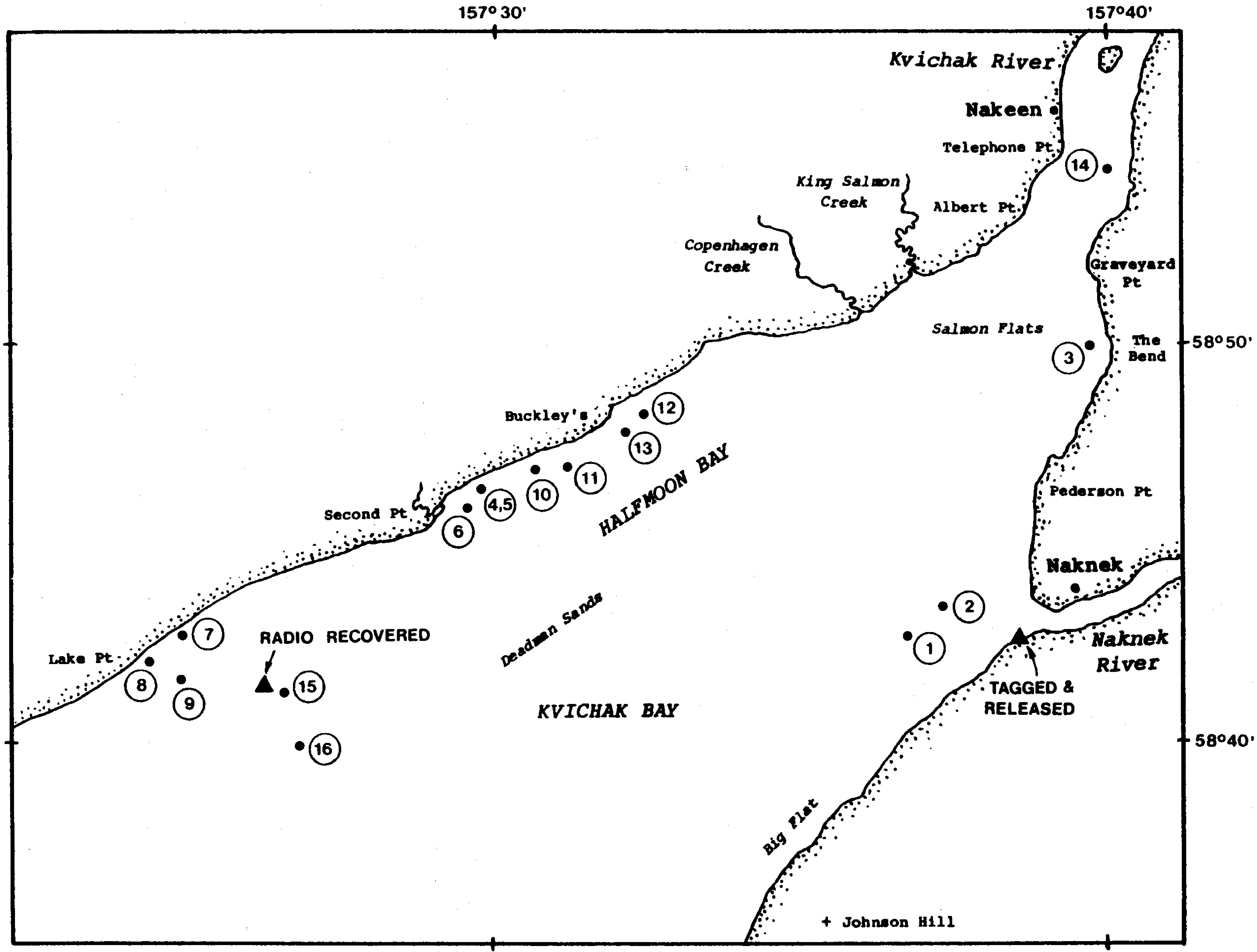


Figure 4. Relocations of the whale "BB" (frequency 164.535) from the time of tagging on 9 June at 2145 until recovery of the radio on 23 June 1983 at 1410. 1-10 June, 1630; 2-10 June, 2215; 3-11 June, 0830; 4-11 June, 1500; 5-12 June, 1150; 6-12 June, 1530; 7-13 June, 1200; 8-13 June, 1625; 9-14 June, 1600, 1745; 10-16 June, 1640; 11-18 June, 1000; 12-30 June, 1314; 13-20 June, 1730; 14-21 June, 1157; 15-22 June, 1319; 16-22 Jun, 1737.

During the subsequent 11 days, BB's location was determined on 12 occasions. Eleven of those positions were either in Halfmoon Bay or the Lake Point area and were within 30 km of each other. Between sometime before midnight on 20 June and about noon on the 21st, BB moved 25 km from mid-Halfmoon Bay to Graveyard Point and by later that afternoon back to Halfmoon Bay. On at least two other occasions, he moved to the northeast toward Graveyard Point and back to Halfmoon Bay in a 12- to 24-hour period. By noon on 22 June, he was 45 km from his location at noon the day before. Several times relocations were within 1-2 km of each other over 24- to 32-hour periods. It is unknown whether BB had remained in the same area for this duration or had moved from that area and returned.

During the 15 days from Mama's capture to the recovery of her radio, her position was determined on 14 occasions (Appendix II, Fig. 5). Within the first 25 hours after capture and release, she swam a minimum of 60 km and perhaps considerably more (based on a 20-km maximum range of her radio, which is probably quite conservative). On 20 June, she moved at least 20 km and probably over 30 km to the northeast in about 3 hours. One day later she was back again near her original position. Although fixes of her position are not frequent enough to determine daily movement patterns, they do demonstrate that substantial movements can and do occur over relatively short time periods. During most of the time Mama was radioed, she moved between the west side of Kvichak Bay and the mouth of the river near Graveyard. On several occasions, her signal was heard from the direction of the Naknek River mouth/Big Flat, but the position was not fixed.

The effect of tides on movements of radioed whales is unclear (Table 8). On seven occasions, BB's direction of movement over a period of several hours was known and could be compared to tidal stage. In five instances, he moved against either falling or flooding tides, while in two instances he moved with the tide. Mama's direction of movement in relation to the tide was also known for seven time periods. She moved with the tide three times, against it twice, and remained essentially stationary twice.

Prior to describing the respiration patterns of telemetered belukhas, some definition of terms is required. The terminology that we will use, which is similar to that of Watson and Gaskin (1983), is as follows:

roll - a single surfacing of a whale

surface period - the length of time a whale is visible above the air-water interface during a single roll

ventilation period - the total time from the beginning to the end of a series of rolls, with less than 30 seconds separating rolls within the series

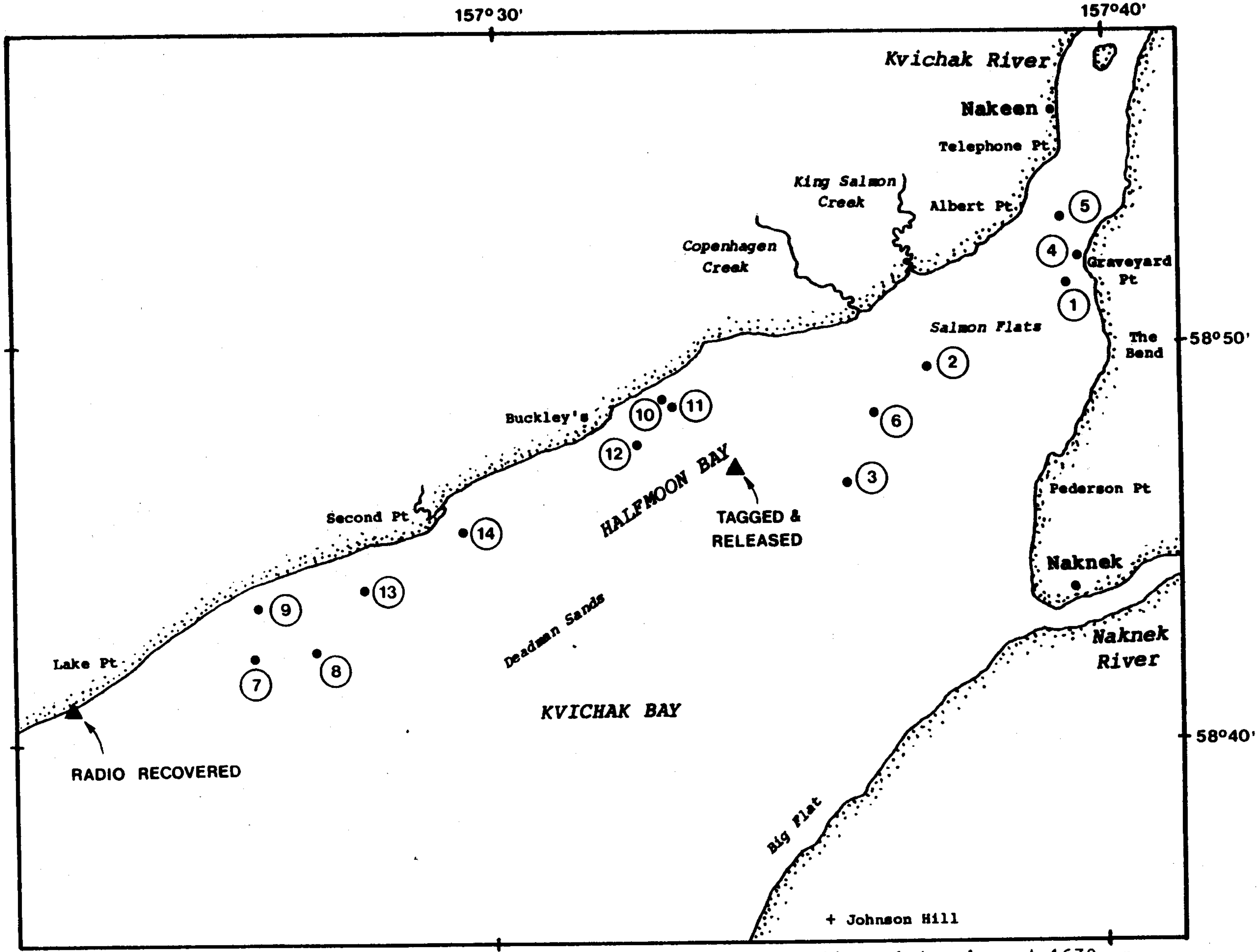


Figure 5. Relocations of the whale "Mama" (frequency 164.585) from the time of tagging at 1630 on 18 June until recovery of the radio at 1500 on 3 July. 1-19 June, 1800; 2-20 June, 1351; 3-20 June, 1730; 4-21 June, 1157; 5-21 June, 1232; 6-22 June, 1805; 7-23 June, 1405; 8-23 June, 1425; 9-23 June, 1648; 10-24 June, 1339; 11-27 June, 1255; 12-27 June, 1502; 13-28 June, 1110; 14-29 June, 1410.

Table 8. Movements of two radio-tagged whales in relation to tidal stage.

Date	Time	Tidal stage	Direction of whale	Relation to tide
"BB"				
11 Jun	1015-1530	flooding	out	against
13 Jun	1200-1625	flooding	out	against
17 Jun	1500-1900	flooding	in	with
	2200-2400	falling	in	against
18 Jun	0700-1000	flooding	out	against/slack
19 Jun	0400-1000	flooding	out	against
21 Jun	1200-1430	falling	out	with
"Mama"				
20 Jun	1350-1730	falling	out	with
21 Jun	1157-1430	high/falling	stationary	
22 Jun	1455-1805	falling	in	against
23 Jun	1405-1648	high/falling	stationary	
24 Jun	1230-1340	flooding	in	with
27 Jun	1255-1500	flooding	out (slightly)	against (slightly)
28 Jun	1110-1430	flooding	in	with

dive - a single submersion of a whale, either between rolls or between ventilation periods

sounding period - dives between sequences of rolls, almost always lasting greater than 30 seconds

In the following presentation of results we have assumed that the length of time during which a signal was received from the transmitter is equivalent to the surface period and, correspondingly, the dive period equals the length of time during which no signal was heard. Based on the placement of radio packages on the whales and our observations of swimming and diving patterns, we think this assumption is basically correct, with one exception that will be discussed.

We took respiration pattern data for the whale BB for a total of 726 minutes. Of that, 38 minutes of data taken on the day after capture were not used in the analysis, leaving 688 minutes of usable data which included 1,327 surfacings and 1,325 dives. All data were plotted graphically then grouped into similar patterns (Figs. 6-9). Following Watson and Gaskin (1983), we divided our data into two basic patterns: type A in which rolls did not occur during restricted ventilation periods, and type B in which rolls were distinctly grouped into ventilation periods separated by soundings. Each major type of pattern was further subdivided as follows: type A1 - surfacings irregular and often widely spaced; type A2 - surfacings irregular and frequent with few long dives; type B1 - surfacings clumped into a very regular series of ventilation periods; type B2 - surfacings generally clumped into ventilation periods but with some irregularities. For Mama we recorded respiration data for a total of 224 minutes, of which 64 were taken on the evening of capture and 18 were taken when signals were weak and not considered reliable, yielding 142 minutes of usable data. This included 325 surfacings and 323 dives. Two patterns were recognizable (Figs. 10 and 11): one corresponded to type A1, and the second, which we designated type C, consisted of long to very long surfacings alternated with short to very short dives.

The type C pattern observed for the whale Mama was unlike anything we expected. When we first recorded signals of this type, i.e., long periods of continuous signals with irregular short-to-moderate interruptions, we were concerned that either the radio package had been released from the whale or that Mama was somehow incapacitated. Therefore, immediately subsequent to recording the data of 23 June (Fig. 11), we followed the signal to its origin. After tracking shoreward from our data-recording position for about 10 minutes, the signal stopped and we saw four large wakes caused by whales passing by our boat to seaward. Water depth in that location was 1.3 m. We therefore interpret the type C pattern as indicative of feeding (or perhaps resting or socializing) in very shallow water where the antenna of the transmitter seldom goes below the surface. We did not actually see the whales when we located them, indicating that their backs were not necessarily above the surface for the entire time we recorded type C signals.

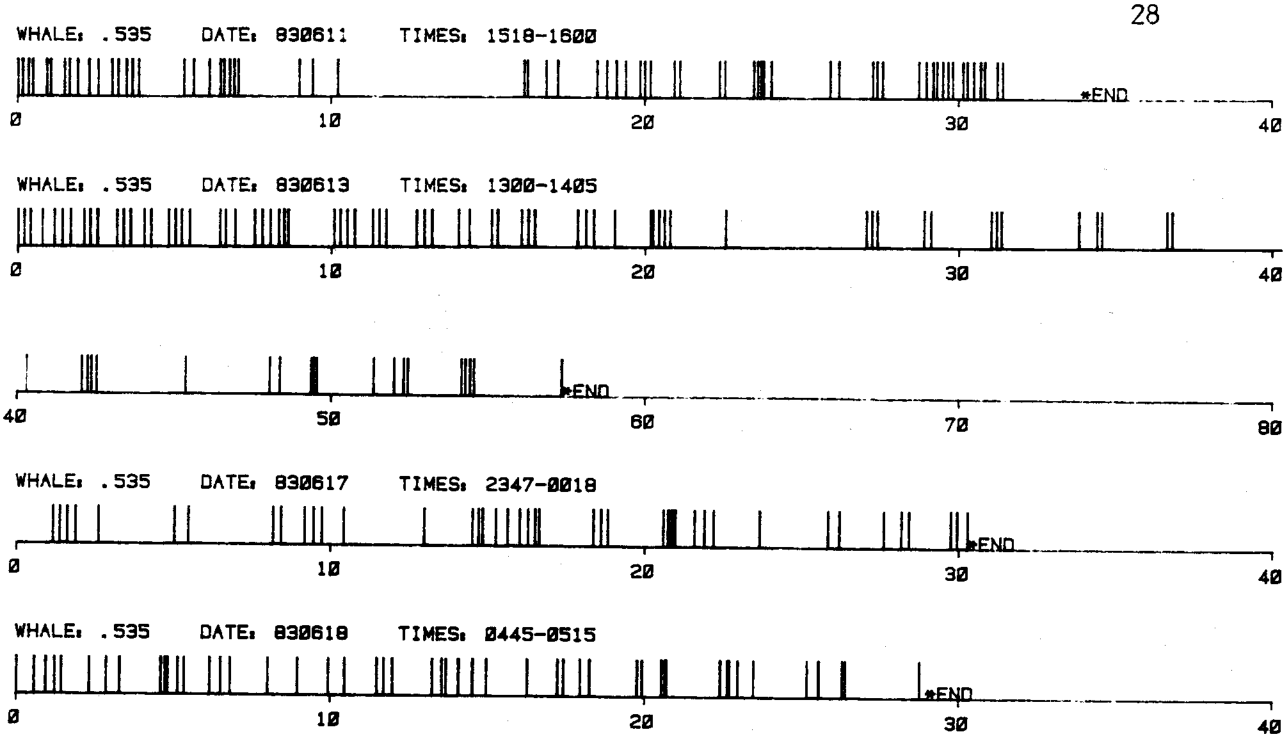


Figure 6. Type A1 respiration pattern for the whale BB.

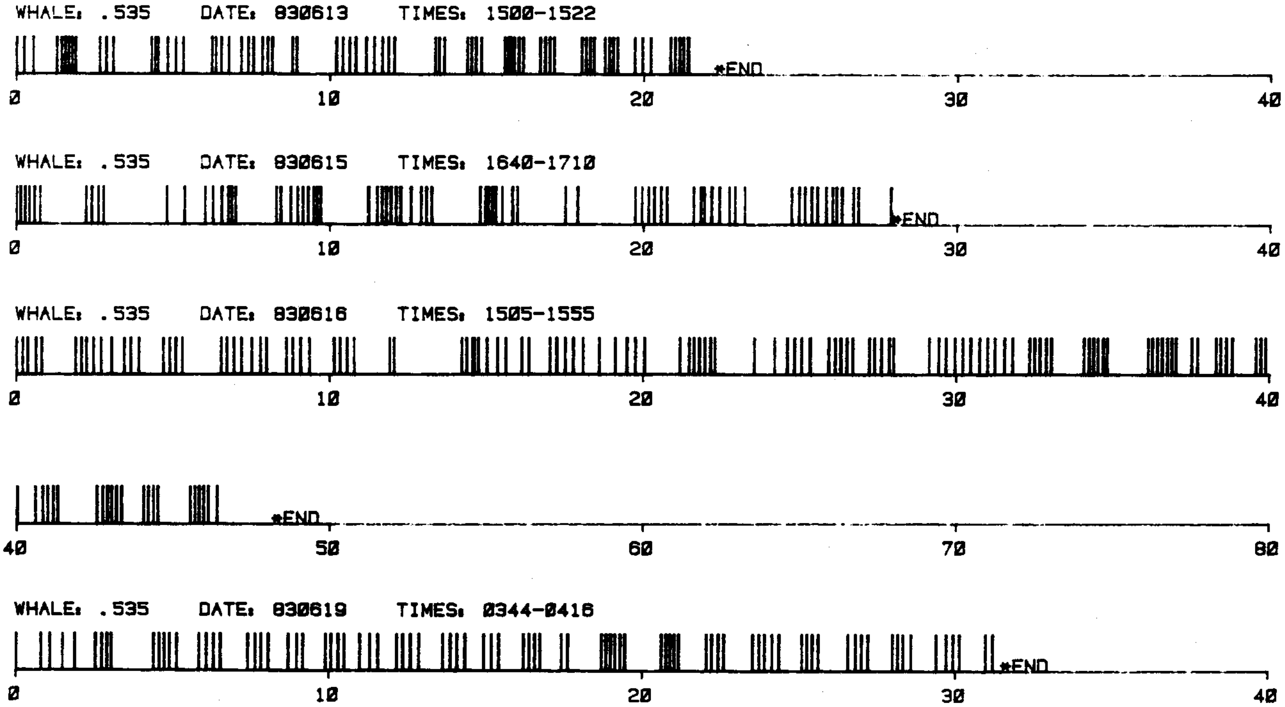


Figure 7. Type A2 respiration pattern for the whale BB.

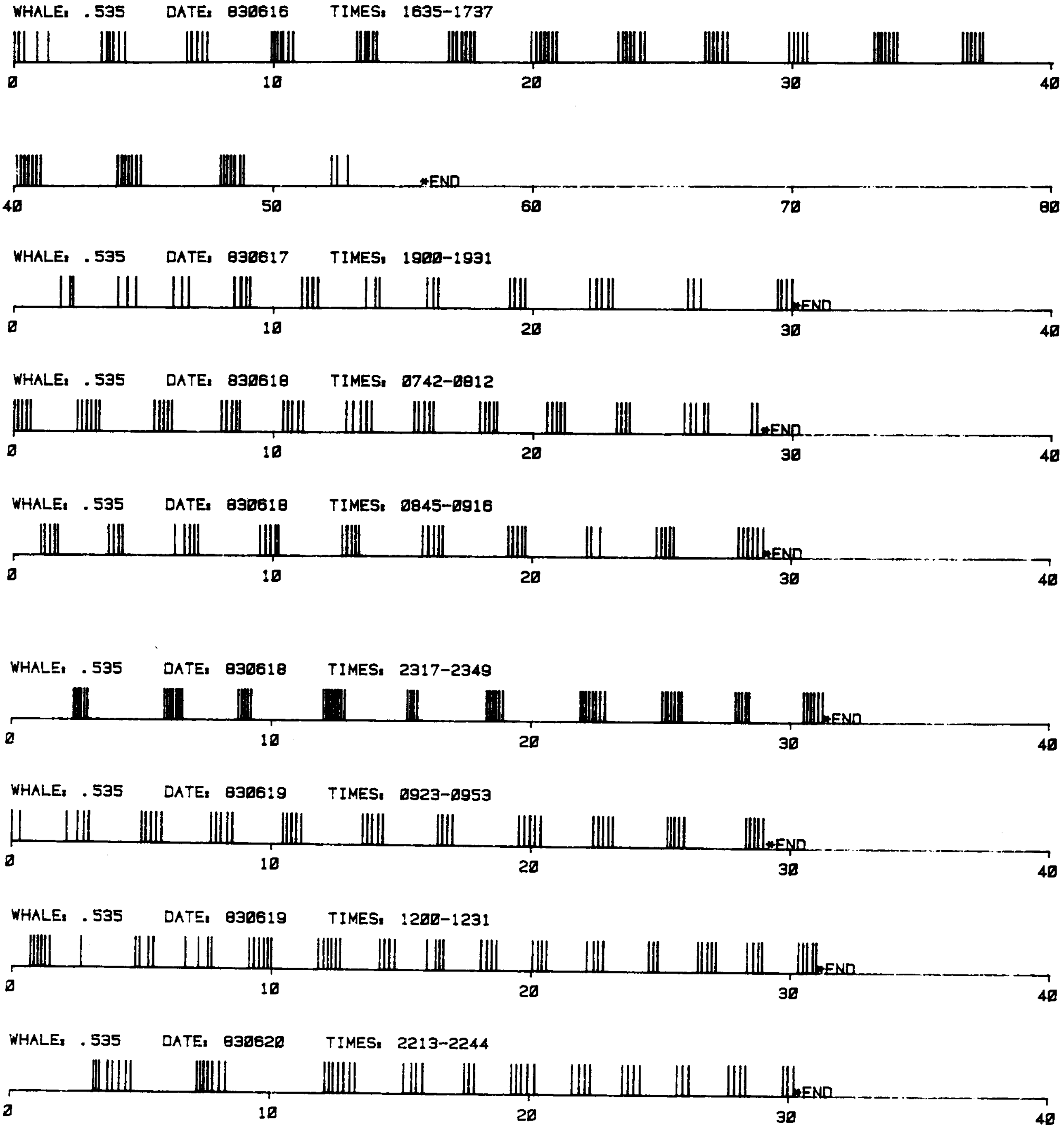


Figure 8. Type B1 respiration pattern for the whale BB.

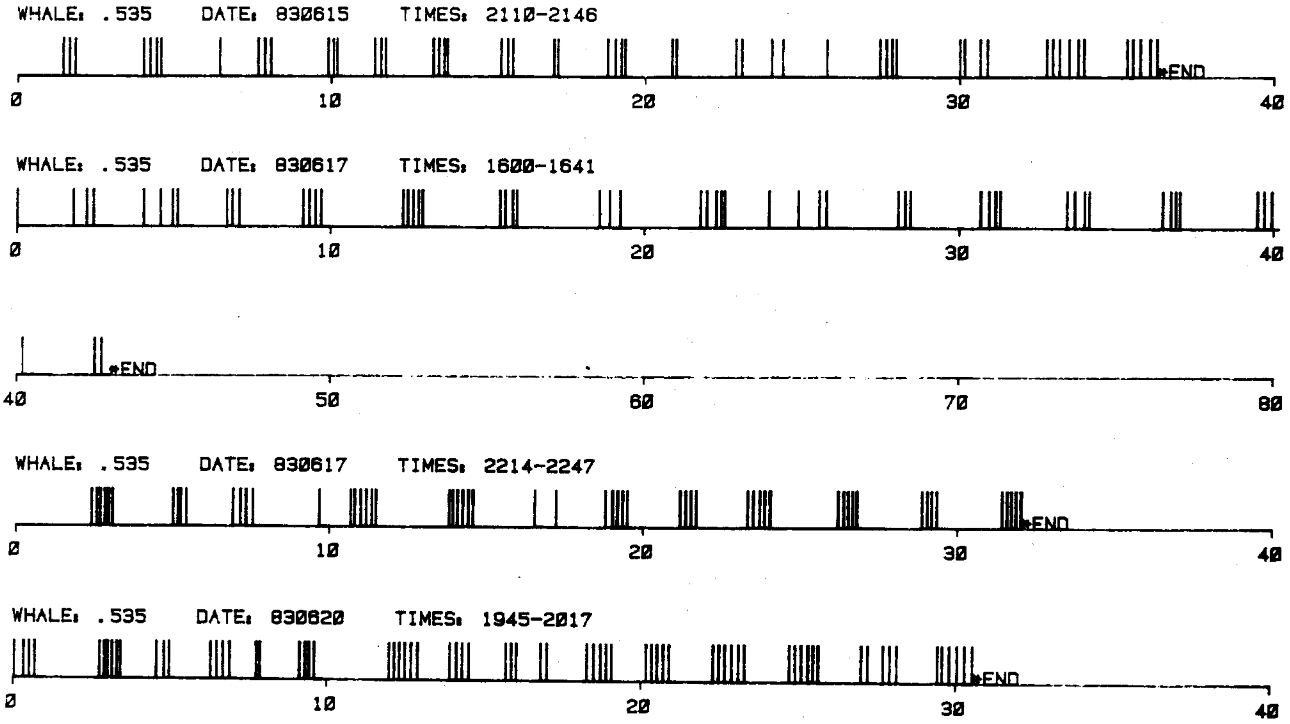


Figure 9. Type B2 respiration pattern for the whale BB.

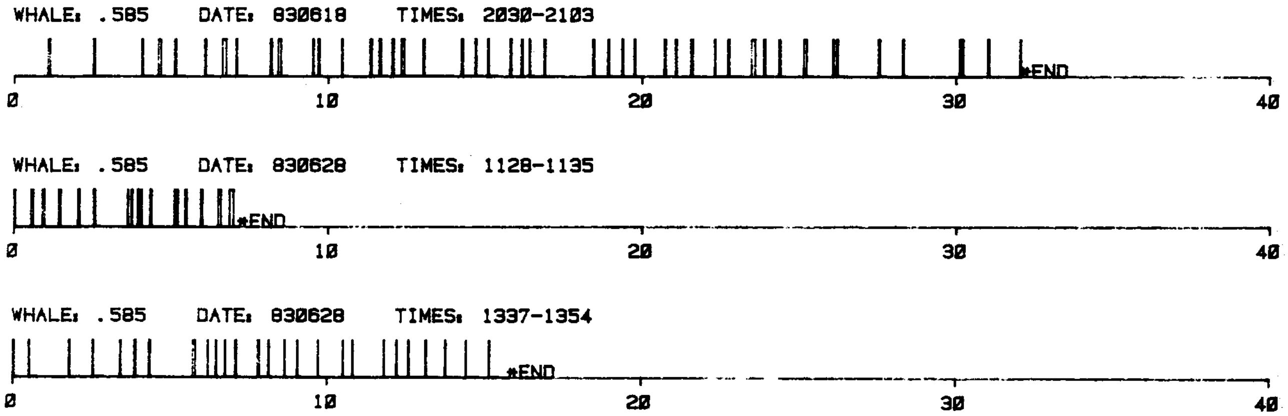


Figure 10. Type A1 respiration pattern for the whale Mama.

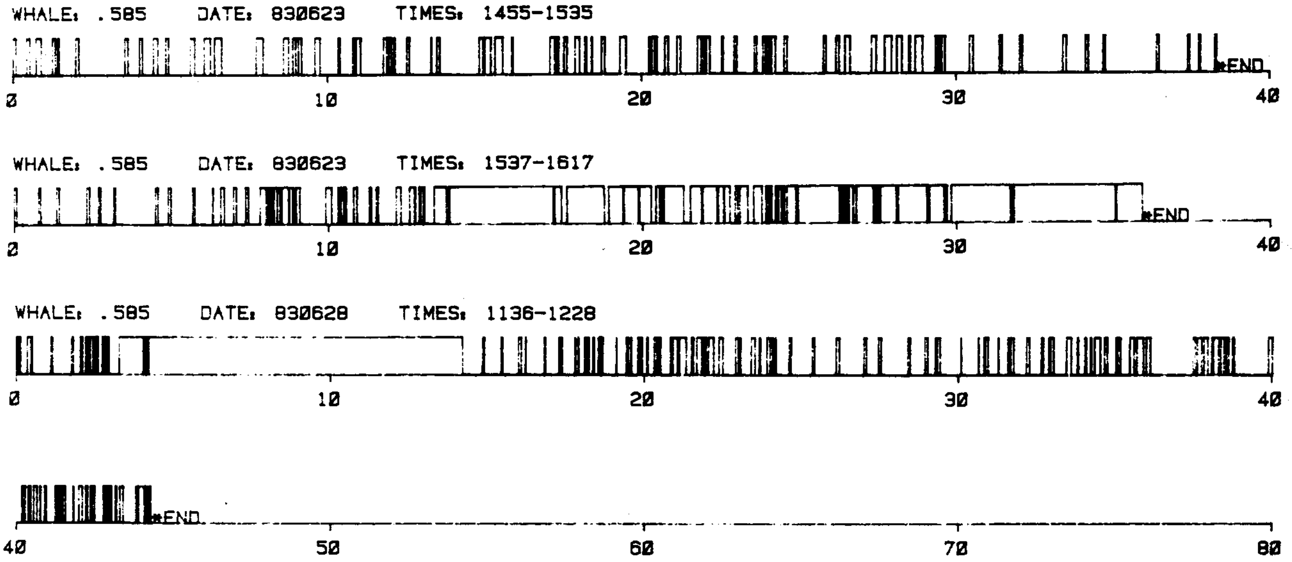


Figure 11. Type C respiration pattern for the whale Mama.

Characteristics of the respiration patterns of telemetered whales are shown in Table 9. Pattern A was recorded for 41% of the total observation time of BB. Types A1 and A2 differed in terms of the surfacing rate and the relative amounts of time spent above and below the surface. This is not surprising since differences in those characteristics were used to select the data sets. In pattern A1, the mean surface interval (0.94 sec) was significantly shorter than in type A2 (1.50 sec; $t = 15.06$, $p < 0.01$), and the mean length of dive was significantly longer (36.07 vs. 19.55 sec; $t = 5.59$, $p < 0.01$), which suggests that these two patterns are actually discrete. Due to the greater frequency of surfacings, the proportion of time spent at the surface was almost three times as great in pattern A2 as in A1. For BB, pattern B occurred during 59% of the data collection periods. Types B1 and B2 were very similar except for the higher incidence of single rolls during type B2 (Figs. 8 and 9). There was no significant difference in the mean length of surfacings (1.150 vs. 1.151 sec; $t = 0.03$, $p > 0.90$) or of dives (32.68 vs. 34.16 sec; $t = 0.41$, $p > 0.50$), and the surfacing rates and proportions of time spent above and below the surface were virtually identical. In pattern B1, the respiration sequence consisted of a ventilation period averaging 4.9 rolls (range 1-8), separated by dives lasting about 10 seconds, followed by a sounding which lasted an average of 2 minutes and 5 seconds (range 1 min 3 sec to 3 min 48 sec).

Pattern A1 for Mama was recorded during 16% of the usable data. Although the surfacing rate was similar to type A1 for BB, the proportion of time spent at the surface was considerably greater due to a significantly greater average surface interval (2.22 vs. 0.94 sec; $t = 10.62$, $p < 0.01$). The average length of dives of BB (36.07 sec) and Mama (29.78 sec) was not significantly different ($t = 0.89$, $p > 0.30$). Pattern type C for Mama was unlike all others and differed most notably in that signals were received during 40% of the monitoring periods. The longest recorded dive for BB was 5 minutes 56 seconds, which was over twice as long as for Mama (2 min 8 sec).

B. Distribution, Abundance, and Movements

Observations of the distribution and movements of belukha whales in Nushagak and Kvichak bays were made during systematic aerial surveys flown at approximately 2-week intervals, in the course of whale capture attempts, and on an opportunistic basis from locations onshore, from the Iliaska while anchored in Kvichak River, and during transit in the helicopter and small boats.

All observations from Nushagak Bay are listed in Appendix III and summarized in Table 10. In summarizing those observations, we divided the bay into six geographical subareas: Igushik and Snake rivers, Snake River mouth - Clarks Point, Wood River, and central part and outer Nushagak Bay (Fig. 12). Belukhas were seen in the Nushagak on all aerial surveys except the last in mid-August (Table 10). Maximum numbers were observed in late June and mid-July. Most sightings in Nushagak Bay were

Table 9. Characteristics of the respiration patterns of telemetered whales.

Whale	Pattern type	Mean no. of surfacings per min	% time at surface	% time diving	No. rolls per ventilation period	Mean length of vent. period (min)	Mean length of sounding period (min)	% of total observation time
BB	A1	1.63	2.6	97.4	4.9	0.73	2.09	22
BB	A2	2.86	7.2	92.8				19
BB	B1	1.77	3.4	96.6				38
BB	B2	1.70	3.3	96.7				21
BB	overall	1.91	3.8	96.2				
Mama	A1	1.88	6.9	93.1				16
Mama	C	2.38	40.5	59.5				84
Mama	overall	2.31	34.7	65.3				

Table 10. Summary of whale observations in Nushagak Bay, April-August 1983.

Date	Number of whales sighted: Igushik River	Snake River	Snake R. mouth-Clarks Point	Central Nushagak	Wood River	Outer bay
15 Apr	37	3	14	0	0	5
2 May	0	7	5	0	--	0
5 May	--	--	--	0	0	6
17 May	12	11	0	0	0	0
31 May	0	0	0	2	8	0
3 Jun	--	--	20+	--	0	--
14 Jun	10	2	4	0	2	0
24 Jun	0	0	50	3	12	1
27 Jun	15	--	54	0	24+	--
29 Jun	17	0	107	2	0	0
12 Jul	--	--	90+	--	--	0
13 Jul	--	25+	87+	--	--	--
14 Jul	0	15	119	0	0	0
14 Aug	0	0	0	0	--	0

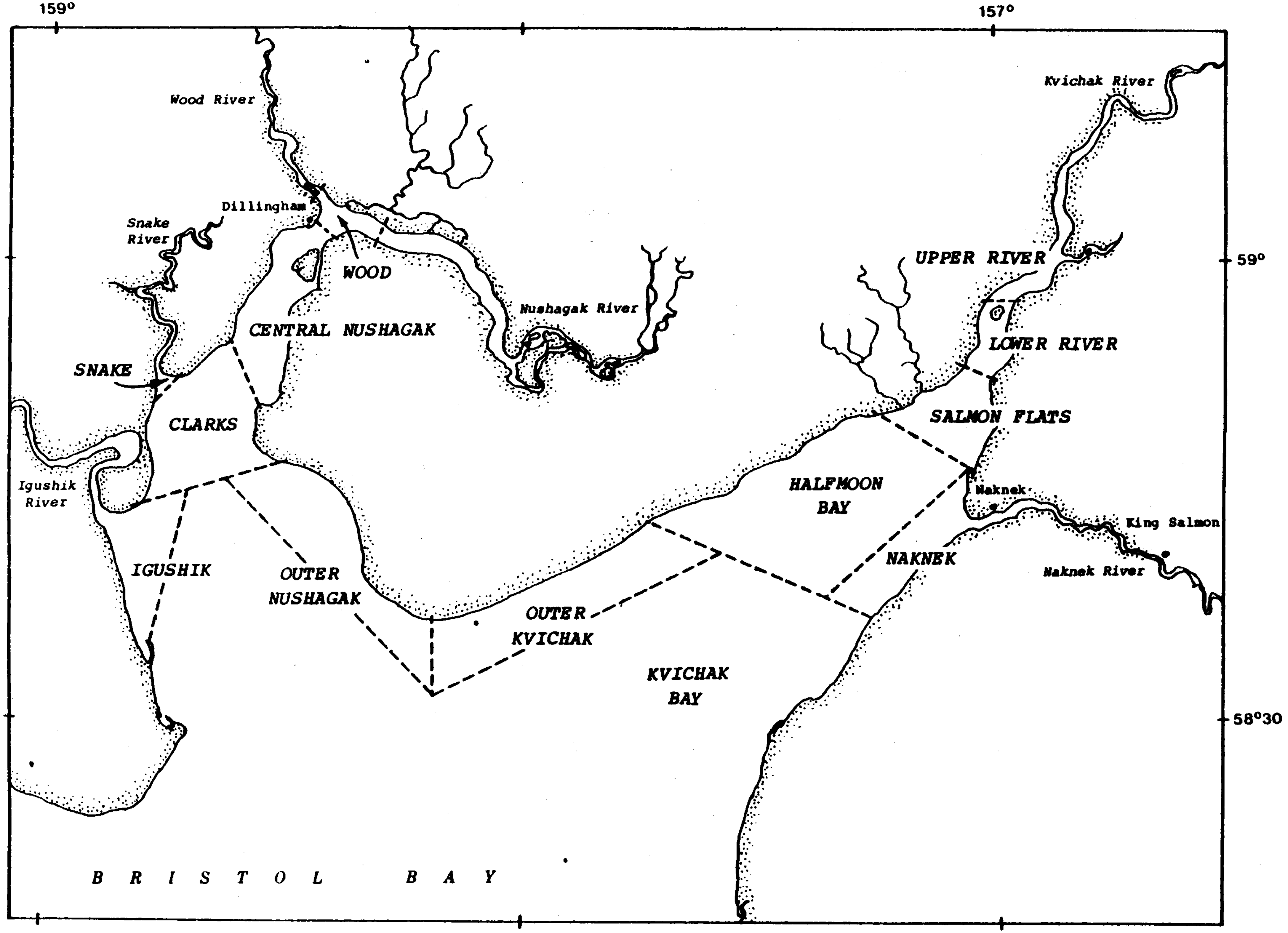


Figure 12. Map of the study area showing geographical subareas referred to in summarizing information on distribution of belukha whales.

near the Snake River mouth or between the Snake River mouth and Clarks Point. From mid-April to mid-June, sightings were of fewer than 20 whales. In late June to mid-July, 50-120 were counted. Whales were regularly seen in the Snake River and on two occasions in May were found approximately 12 km upstream at the confluence of the Snake and Weary rivers.

Small numbers of whales, usually fewer than 20, were present in the Igushik River on four occasions in April-June. In only one instance in mid-May were they seen above the first large bend in the river, approximately 18 km from the river mouth.

Belukhas were sighted near the mouth of the Wood River and the Little Muklung or in the central Nushagak area once in late May and three times in mid- to late June. The largest number counted was 24 on 27 June between Sheep Island and the bar at the mouth of the Little Muklung. In three instances, one to four whales were sighted in outer Nushagak Bay near Etolin Point.

Since Kvichak Bay was our base of operations for tagging whales in 1983, observations there were more extensive than those in Nushagak Bay. From mid-May through mid-July, we made over 150 sightings of whales in Kvichak Bay and the Kvichak River (Appendix III). Figure 12 shows the geographical subareas used in summarizing that distributional information (Table 11). The use of the six areas changed markedly during the study period.

During surveys conducted from mid-April to mid-May, belukhas were present in Halfmoon Bay and outer Kvichak Bay, Salmon Flats, and near the mouth of the Naknek River. The group at the mouth of the Naknek consisted of 70 or more whales on five occasions. After 19 May, belukhas were not seen again near the mouth of the Naknek for over 2 weeks. Between 25 May and 4 June, up to 225 whales were seen in the upper Kvichak River each day. Twice daily, groups of whales moved upriver on the flooding tides, usually traveling at least to the mouth of the Alagnak River (18 km upstream), and downriver on ebbing tides. They were usually seen traveling in mid-river or feeding in rips or current eddies, probably on the smelt (<u>Osmerus mordax</u>) and salmon smolt present in the river during this period.

Prior to 25 May, we did not make regular observations in the Kvichak River and thus were unable to determine when regular use of the river began. During the same 2-week period that belukhas used the upper Kvichak River on high tides, they were common in the lower river, Salmon Flats, and Halfmoon Bay. After 6 June, the whales were not again seen in large numbers in the Kvichak River. When they were seen, it was in small groups of fewer than 10 whales. These whales were usually swimming close to the riverbank and appeared to be feeding on adult salmon. From 6-16 June, belukhas were present off the mouth of the Naknek and southward toward Johnson Hill. Over 100 were present on several days, feeding at low tide over Big Flat. At high tide they moved upriver toward Salmon Flats, and at least some were present in Halfmoon Bay. After about

Table 11. Summary of whale observations in Kvichak Bay, April-August 1983.

	Number of whales sighted					
Date	Upper river	Lower river	Salmon Flats	Naknek River	Halfmoon Bay	Outer Kvichak
15 Apr			14	60-70	3	43
5 May			31	2	88	37
17 May			4	70		
19 May				many		
25 May	75-80	60			16	
26 May	40+	6				
27 May	20-25					
28 May	45	38	150-200	0	150-200	
29 May	150+	50-100				
30 May	80-100	100-150				
31 May	223	12	29		1	
1 Jun	104		20+			
2 Jun	10-15	few	± 20		100+	
3 Jun	120+	10-20	30-50			
4 Jun	200+	16	10-15			
6 Jun	few			30-50	12+	
7 Jun		100+				
8 Jun		3		75+	few	
9 Jun				± 10	10-15	
10 Jun			10+	2-3		
11 Jun			some.	50-100+	10-20+	
12 Jun					50-100	
13 Jun				1	few	20+
14 Jun		20-30		100+	22	40+
15 Jun				125-200+		
16 Jun		3+		100+	100's	
17 Jun		23+				
18 Jun	6	30-50	86+		30-50	
19 Jun	1	1			few	
20 Jun	few					
21 Jun		50+	20+	present		
22 Jun	several	1			few	
23 Jun	several		20+			many
24 Jun		few			many	2
27 Jun			few 35+		present	
28 Jun			57		124	
29 Jun					202	6
30 Jun		25+				
2 Jul		present				
3 Jul			100+			20+
4 Jul		100+	30+			

Table 11. Continued.

Date	Number of whales sighted					
	Upper river	Lower river	Salmon Flats	Naknek River	Halfmoon Bay	Outer Kvichak
5 Jul		10-20	80-100			
6 Jul			few			
7 Jul			400+			
12 Jul		200+	present			
14 Jul			50+			
14 Aug				3	179	127

16 June, belukhas were no longer seen in the Naknek River-Big Flat area. Instead, from then until our studies terminated in mid-July, they apparently moved between the lower Kvichak River-Salmon Flats area, mostly at high tide, and Halfmoon Bay, or in some instances outer Kvichak Bay at low tide.

For all observations (n = 73) in which the whales' direction of movement was known, we compared the tidal stage and direction of flow with the direction the whales were moving (Table 12). In 77% of the observed cases, the whales were found to move with the direction of the tide ($chi^2 = 20.84$; $p < 0.01$). The number of observations of whales moving with the flood (37%) versus with the ebb (63%) is in proportion to the total amount of time the tide was flooding (35%) and ebbing (65%). Of the whales that moved against the tide, only 18% of those moved against a flooding tide, whereas 82% moved against an ebbing tide ($chi^2 = 12.6$; $p < 0.01$). All movements against the tide occurred within 2 hours of a tidal change, and 85% were within 1.5 hours of a change. Movements with the tides occurred throughout the tidal cycle.

Our best information on abundance of whales came from systematic aerial surveys in which we attempted to cover all areas of Kvichak and Nushagak bays where whales regularly occurred (Table 13, Figs. 13-21). However, when counting from the air, not all whales are at the surface where they can be enumerated during the passage of the aircraft. Consequently, a correction factor (CF) was developed and applied to the counts in order to estimate actual abundance. We have used two independent methods to derive correction factors to apply to our surveys.

During early June, large numbers of belukhas were predictably moving up and down the Kvichak River. The river was generally less than 2 km across in this area and the surface conditions were usually calm. On 4 June, three observers in two Zodiac rafts counted 201 belukhas passing downstream in the vicinity of the Alagnak River mouth from 1105-1155 hours. Since the whales were moving rapidly downstream with the ebbing tide, it was easy to track individuals and avoid duplicate counts. It is, however, likely that some whales passed unseen downriver past the rafts. From 1032-1034, prior to the downstream movement, two observers in the helicopter counted 85 whales in the region upstream from the rafts, using standard aerial-survey techniques. If all whales were seen and counted by the observers in the rafts, the correction factor derived from these data is 2.4 (i.e., total whales = whales counted from the air X 2.4). If, as was estimated at the time, observers missed 20% of the whales passing by the boats, the total number of whales in the group was about 241, and the actual correction factor would be 2.8.

A second method for correcting aerial survey counts involves estimating the probability that a given whale will be at the surface where it can be seen at the time an observer scans the area, based on the length of surfacings and dives, and the length of time a particular spot is in the field of view. This method has been applied to surveys of bowhead whales (Balaena mysticetus) (Davis et al. 1982) and gray whales

Table 12. Movement of belukha whales in Kvichak Bay, summer 1983, in relation to tidal stage. Numbers represent the number of observations of one or a group of whales.

Direction of movement (n = 73)	Hours after change in tide								
	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	>4.0
with flood (n = 20)	1	6	4	6	1	2			
with ebb (n = 36)	1	10	7	2	6	4	2	3	1
against flood (n = 3)	1	1		1					
against ebb (n = 14)	6	1	4	3					

Table 13. Aerial survey counts of belukha whales in Nushagak and Kvichak bays, April -August 1983.

Date	Wood River	Central Nushagak	Clarks Point	Snake River	Igushik River	Outer Nushagak	Total Nushagak	Outer Kvichak	Halfmoon Bay	Naknek River	Salmon Flats	Lower river	Upper river	Total Kvichak	TOTAL
15 Apr	0	0	14	3	37	5	59	43	3	68	14	fog	fog	128	187
2/5 May	0	0	5	7	0	6	18	37	88	2	31	--	--	158	176
17 May	0	0	0	11	12	0	23	0	0	70	4	0	0	74	97
31 May	8	2	0	0	0	0	10	0	1	0	29	12	35	77	87
4 Jun	--	--	--	--	--	--	--	--	1	0		15	85	101	--
14 Jun	2	0	4	2	10	0	18	29	31	0	3	31	0	94	112
18 Jun	--	--	--	--	--	--	--	0	32	0	86+	0	8	126	--
24 Jun	12	3	50	0	0	1	66	5	11	0	0	4	--	20	86
27 Jun	24+	0	54	--	15	--	93	--	--	--	--	--	--	--	--
29 Jun	0	2	107	0	17	0	126	6	202	0	0	0	0	208	334
14 Jul	0	0	119	15	0	0	134	0	0	0	49	0	--	49	183
14 Aug	--	0	0	0	0	0	0	127	179	3	0	--	--	309	309

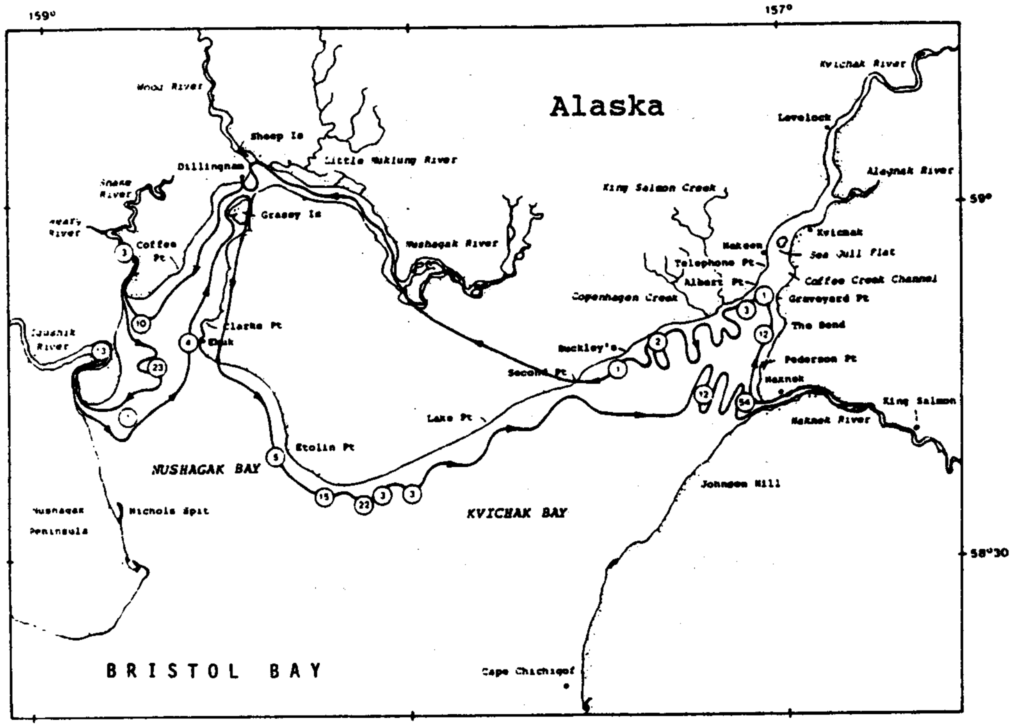


Figure 13. Aerial survey of Nushagak and Kvichak bays, 15 April 1983. Numbers along survey track lines indicate the number of belukhas counted.

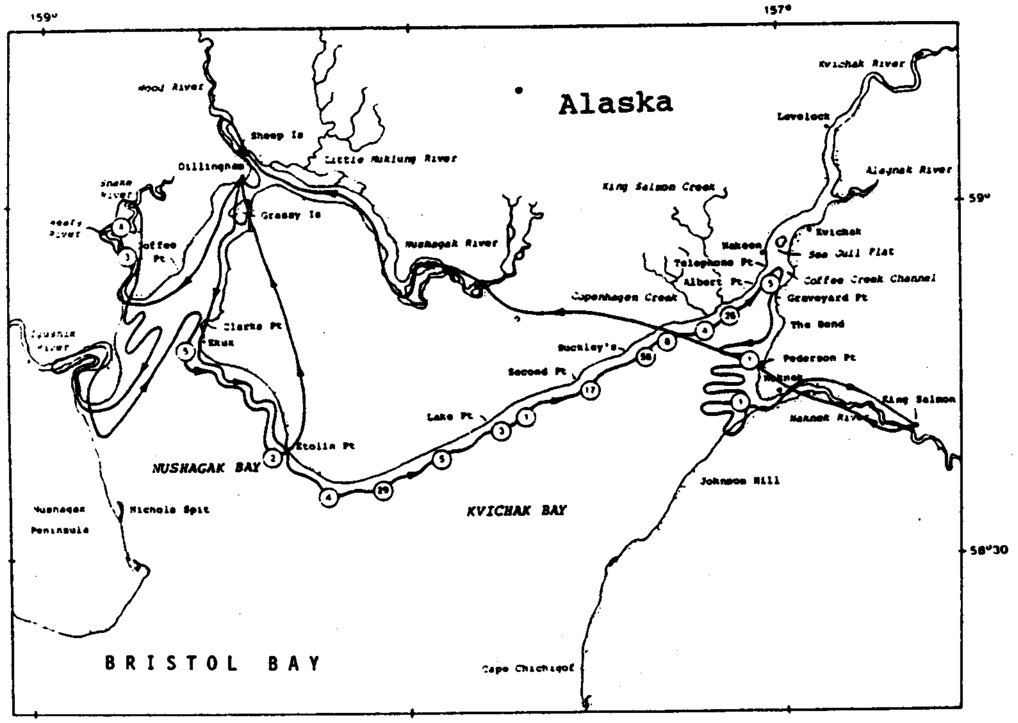


Figure 14. Aerial survey of Nushagak and Kvichak bays, 2 and 5 May 1983. Numbers along survey track lines indicate the number of belukhas counted.

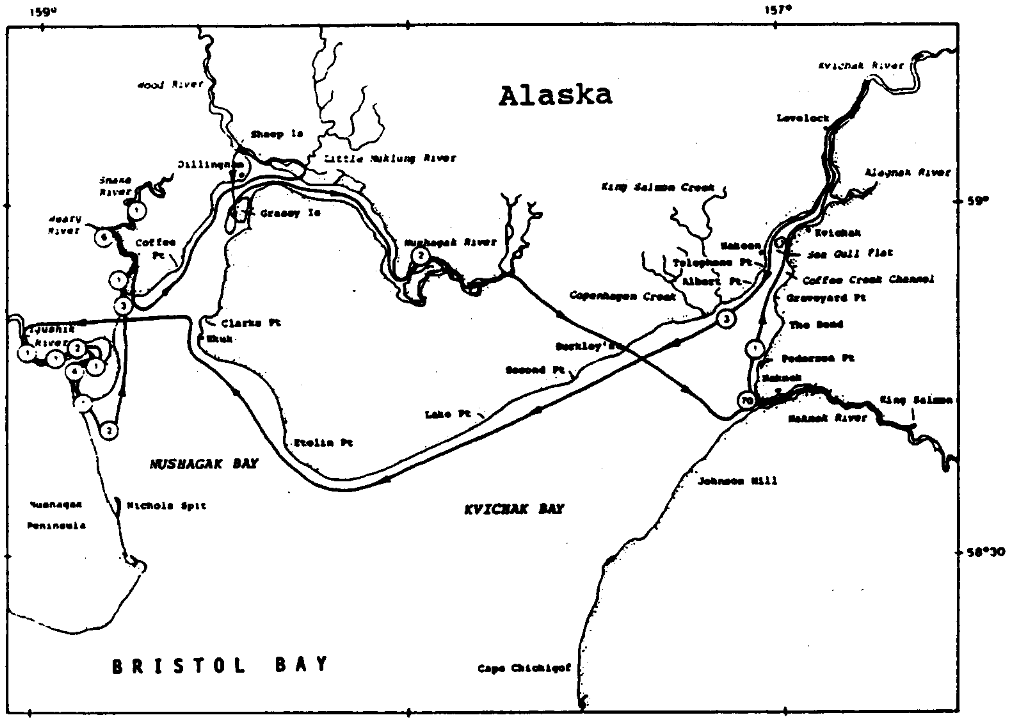


Figure 15. Aerial survey of Nushagak and Kvichak bays, 17 May 1983.

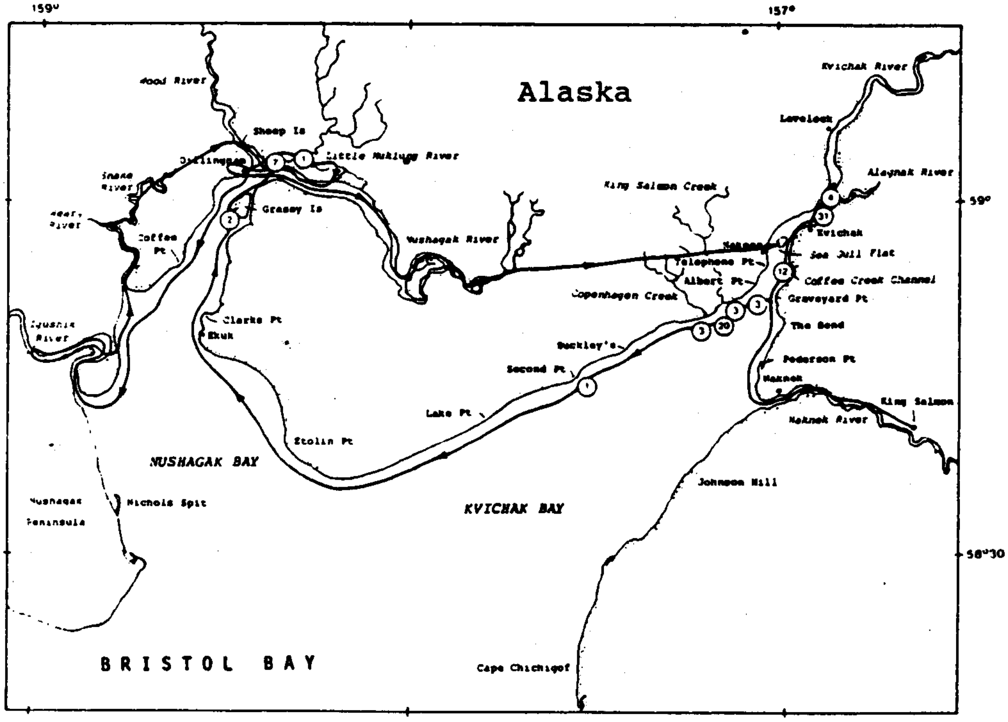


Figure 16. Aerial survey of Nushagak and Kvichak bays, 31 May 1983.

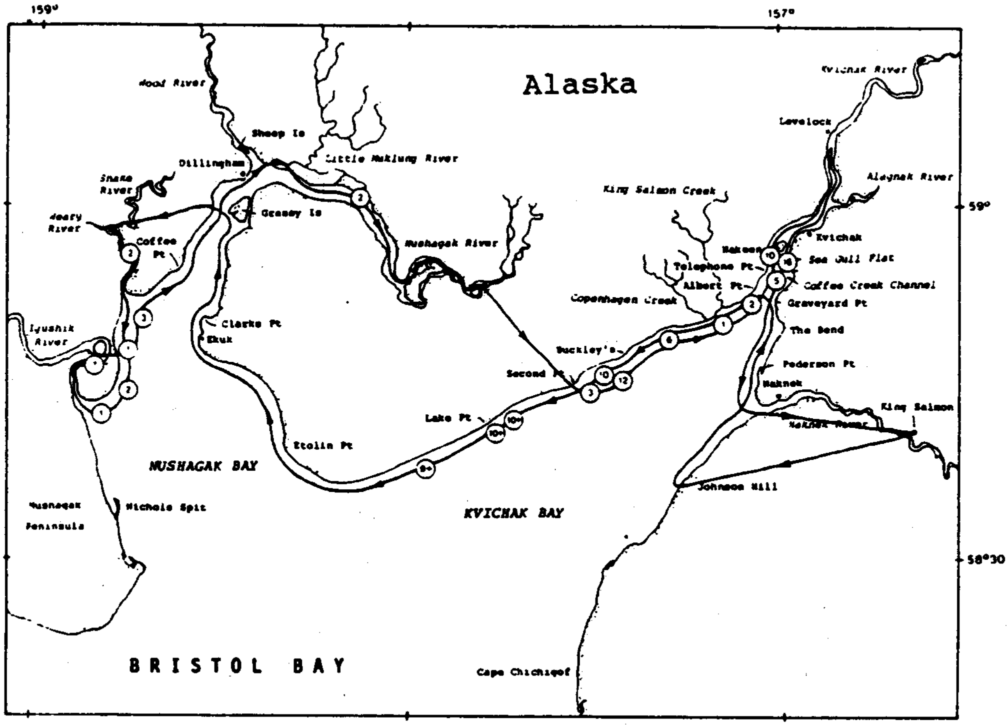


Figure 17. Aerial survey of Nushagak and Kvichak bays, 14 June 1983.

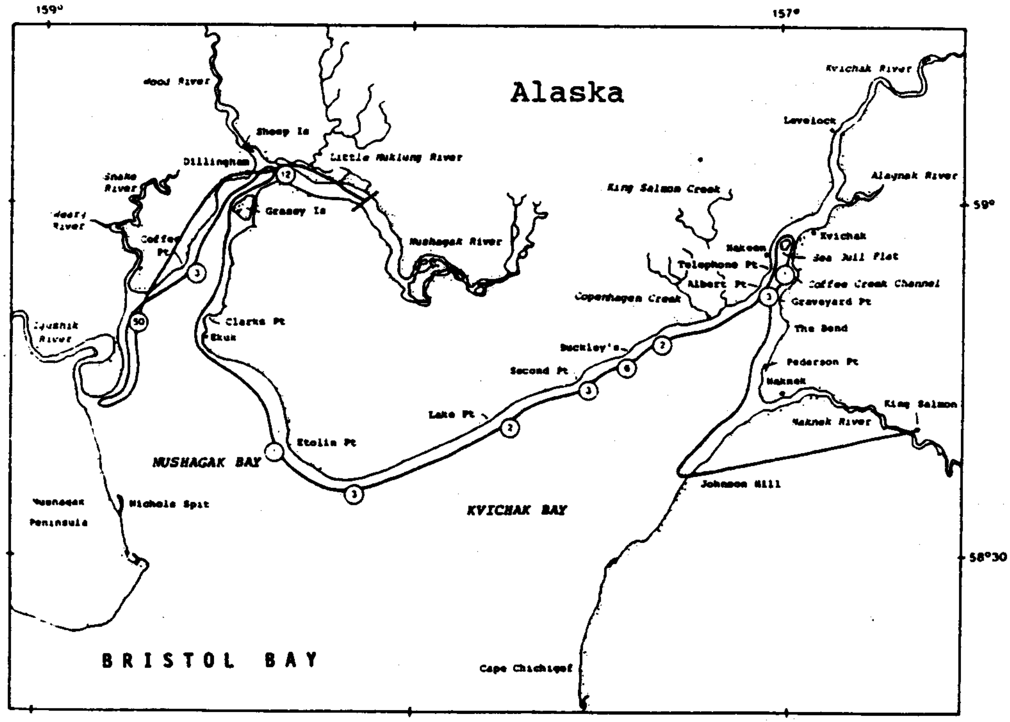


Figure 18. Aerial survey of Nushagak and Kvichak bays, 24 June 1983.

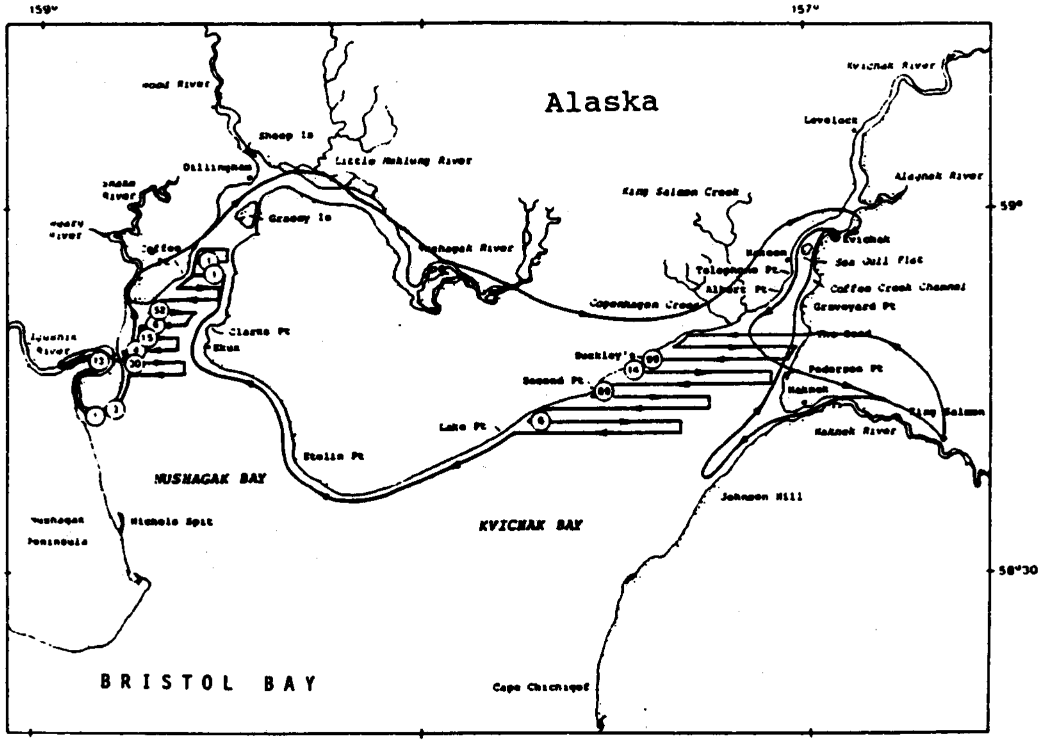


Figure 19. Aerial survey of Nushagak and Kvichak bays, 29 June 1983.

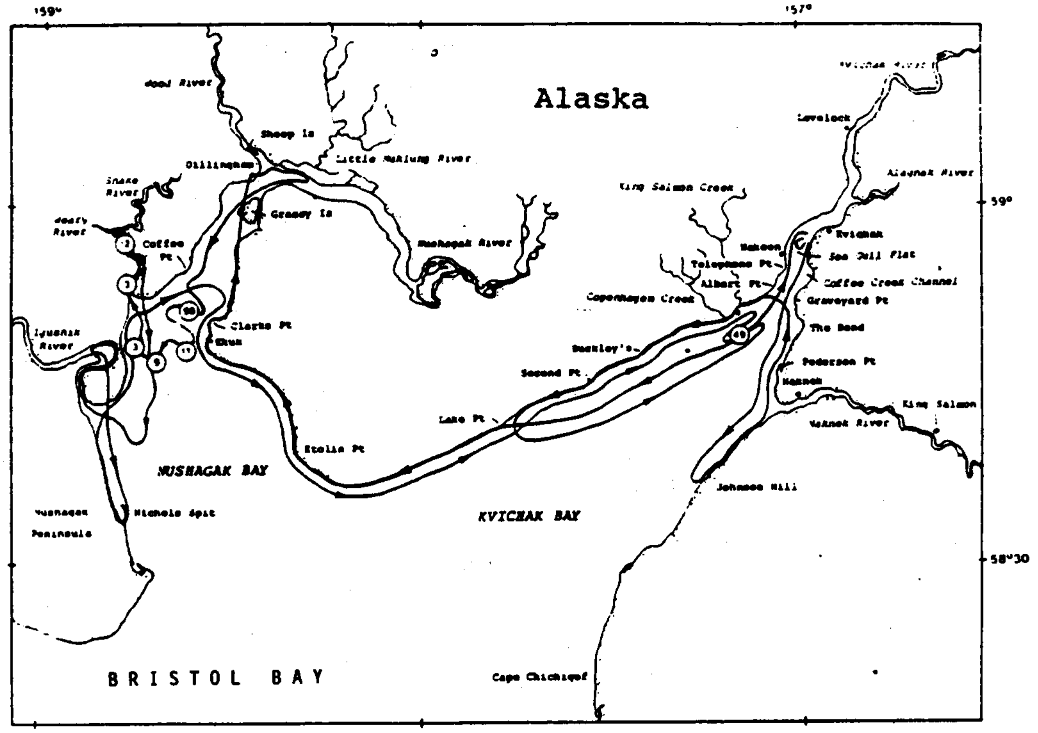


Figure 20. Aerial survey of Nushagak and Kvichak bays, 14 July 1983.

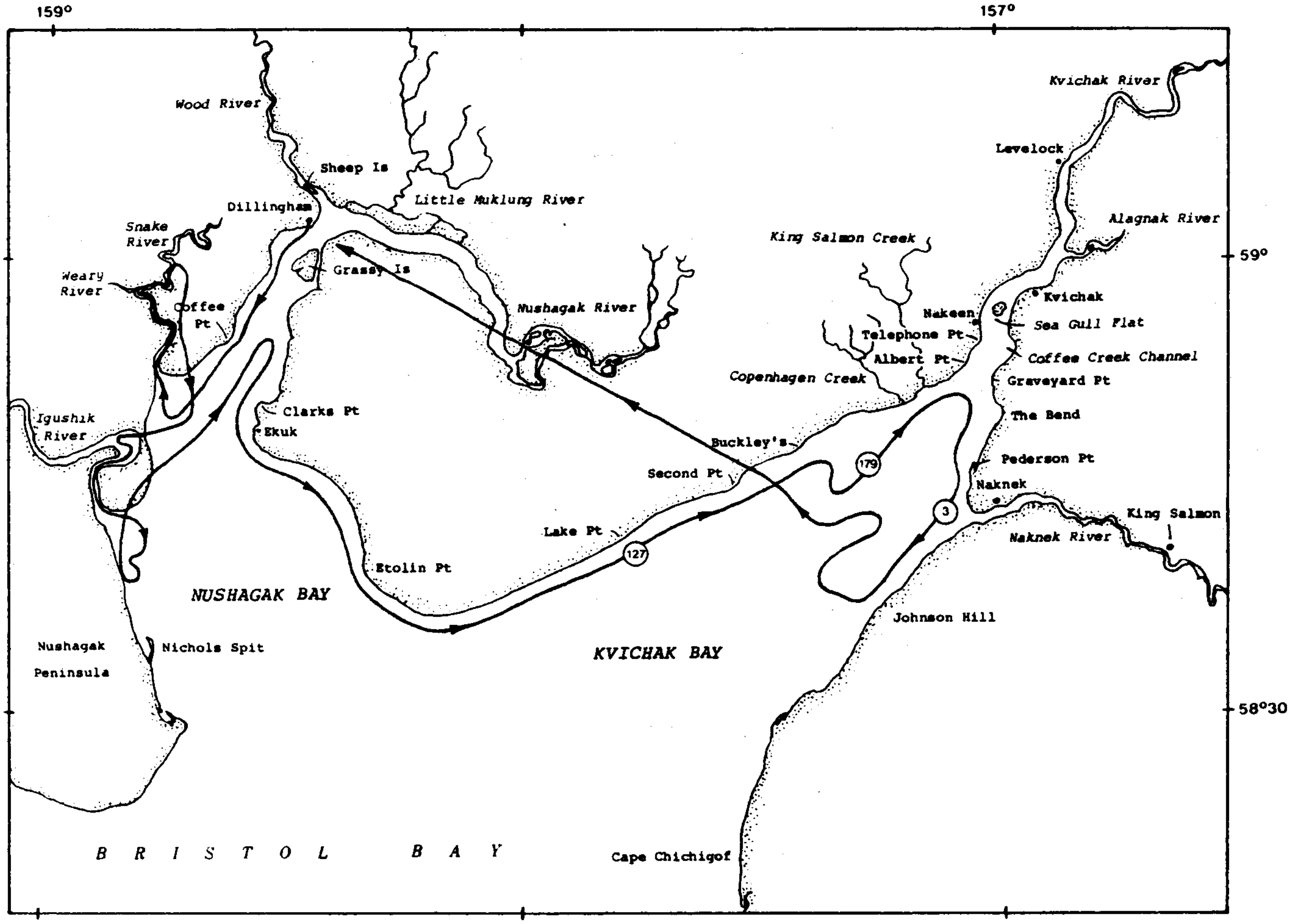


Figure 21. Aerial survey of Nushagak and Kvichak bays, 14 August 1983.

(Miller 1983). The formula for calculating the probability that a whale will be at the surface where it can be seen is:

$$P = \frac{S + t}{S + u}$$

where S = the mean surface interval, u is the mean dive interval, and t is the length of time an area is within the field of view of an observer. The correction factor by which aerial counts can be multiplied to derive the actual abundance of whales is the reciprocal of this probability (i.e., CF = 1/P).

The value of t can be determined based on the angular field of view of the observer (ϕ), the median distance from the flight track to sighted whales (X), and the velocity of the aircraft (v), using the following formula (Miller 1983):

$$t = \frac{2 \tan \frac{\phi}{2} \cdot X}{v}$$

We have assumed that the median sighting distance occurred at a point halfway across the strip transect (i.e., 457 m). The angular field of view is difficult to determine accurately since it does not equate to the maximum angle that can be seen from inside the aircraft, but rather to the angle that is included in the normal scan of the observer. We estimate that angle to be approximately 60°. Parameters used to estimate t for the two survey aircraft used are given in Table 14.

Table 14. Parameters used to estimate the period of detectability (t).

Aircraft type	ϕ	x(m)	v(m/sec)	t(sec)
Bell 204 helicopter	60°	457	50.8	10.4
Cessna 185	60°	457	76.2	6.9

We also determined the value of t empirically by timing the period during which floating objects passed through the normal field of observation during surveys from the helicopter. Objects from 228 to 457 m from the trackline passed by in 4.5-6.2 seconds with an average time of 5.8 seconds (N = 15). Corrected to a median sighting distance of 457 m, this indicates a value of t of 7.3 sec. Although this empirically derived value may be the most realistic, we will use the values of t in Table 14 since, being larger, they will underestimate the correction factor and result in a population estimate that is conservative (i.e., smaller than the true population).

The values for S and u which are needed for calculations are measurements of the time during which a whale is visible from the air and the time during which it cannot be seen, which, depending on the turbidity of the water, may or may not be equivalent to actual surfacing and dive times. In the muddy waters of Kvichak and Nushagak bays where we surveyed, whales were invisible unless their bodies were actually breaking the surface. Therefore, our telemetry data on lengths of surfacings and dives can be used to approximate S and u. Type C data from Mama was not included since during those periods she was in shallow water with the antenna, but not her body, breaking the surface. An exception occurred off and to the south of the Naknek River mouth. On several occasions whales were seen there in clear, shallow water, and, since our counts probably included all individuals, no correction factor was applied to them.

As noted by Davis et al. (1982) and Miller (1983), calculations of probability of detection must treat instances where the dive time is less than the detection time separately from those where u > t. Taking that factor into account, and using all data for BB and type A1 data for Mama, the appropriate correction factors for each survey aircraft are shown in Table 15.

Table 15. Correction factors for aerial counts based on surface times, dive times, and the duration of potential detectability.

Aircraft type	BB	Mama	Mean
Bell 204 helicopter	2.9	2.6	2.75
Cessna 185	3.8	3.6	3.7

These correction factors were applied to aerial survey counts to estimate the number of belukhas present in Nushagak and Kvichak bays during spring and summer 1983 (Table 16). The most complete survey was flown on 29 June from a helicopter and was an aerial strip-transect survey of known concentration areas combined with a coastal survey of other areas (Fig. 19). On that day we counted 126 belukhas in Nushagak Bay and 208 in Kvichak Bay, for a total of 334 whales. When the mean CF for BB and Mama of 2.75 is applied to those counts, it yields estimates of 347 whales in the Nushagak and 572 in the Kvichak, for a total of 919 whales. Total counts on all other days were lower and yielded corrected estimates of 237-692 whales. In Nushagak Bay, the highest estimated number of whales, 496, occurred on 14 July in the Snake River mouth-Clarks Point area. Numbers increased steadily between mid-June and mid-July. In Kvichak Bay, there was no clear trend in abundance. Maximum corrected counts occurred on 5 May and 29 June.

Table 16. Aerial survey counts and corrected estimates of abundance for belukha whales in Nushagak and Kvichak bays, April-August 1983. Dashes indicate no or incomplete aerial survey coverage.

	Nushagak Bay		Kvichak Bay		Total	
Date	Counted	Corrected estimate	Counted	Corrected estimate	Counted	Corrected estimate
15 Apr	59	218	128	474	187	692
5 May	11	41	158	584	169	625
17 May	23	85	74	274	97	359
31 May	10	27	77	212	87	239
4 Jun	--	--	101	278	--	--
14 Jun	18	49	94	259	112	308
18 Jun	--	--	126	347	--	--
24 Jun	66	182	20	55	86	237
27 Jun	93	256	--	--	--	--
29 Jun	126	347	208	572	334	919
14 Jul	134	496	49	181	183	677
14 Aug	0	0	309	n/a	309*	n/a

* CF not considered applicable to these counts as whales were in very shallow water and the observer considered that more than the usual proportion was counted.

C. Foods and Feeding

Information on belukha whale feeding was obtained in three ways: through analysis of stomach contents of beach-cast whales, observations of apparent feeding behavior, and examination of net-caught salmon. During our 1982 and 1983 field seasons, we examined five whales in which the stomachs were suitably fresh for examination and contained food (Table 17). The three 1983 whales had all died in May. Two had mostly flatfish remains in their stomachs, while the third contained primarily rainbow smelt with lesser amounts of flatfish and shrimp. The shrimp may have been from the stomachs of the flatfish that were eaten. None of the stomachs were full; the largest volume of contents was 163 ml. Of the 1982 whales, one had probably died in late May or early June; its stomach contained otoliths from smelt and a few from sculpins (F. Cottidae). The other whale died in late June and had eaten entirely red salmon. Its stomach was the fullest of the five and contained 415 ml.

During 1983, apparent feeding behavior was observed throughout the study period (Table 18). From mid-May until early June, whales were regularly seen 10-25 km up the Kvichak River, often accompanied by flocks of feeding birds (seagulls, Larus spp., and kittiwakes, Rissa tridactyla) in areas where many small fish dimpled the surface. In general, the whales moved upriver on rising tides and back down on falling tides. In some instances, they worked localized areas (such as tide rips at Nakeen or the Alagnak River mouth), remaining in those areas for some time. Their activity consisted of many short dives with lots of turning; in blowing, they exposed only their heads. While in the rivers during this early period, they were also observed to swim fairly rapidly upstream or downstream (with the tide) until they found a concentration of fish (smelt or smolt), then drift along in that concentration with the current and feed. During feeding, it was more typical for whales to blow by raising their heads up, or by exposing only their blowholes, than by rolling and raising their backs out of the water. Consequently, it was often possible to hear whales in an area where they were feeding but to see them only occasionally through very careful observation and under ideal viewing conditions (calm water).

After the first week in June, large groups of belukhas were no longer seen moving up and down the Kvichak River. From about 6 June until 18 June, they moved at least once and perhaps twice (one tide was during the night when observation was precluded) daily on the ebbing tide to the Big Flat area south of the Naknek River mouth to feed. Compact groups (within a 0.5- to 1.0-km^2 area) of up to 100 whales were seen on several occasions. About 2-3 hours before low tide, the whales could be seen moving toward Big Flat from the Kvichak River mouth area. At that time they were quite widely dispersed. As slack tide approached, the whales began to concentrate in large groups (100+) containing smaller groups of 30 or more. Within these smaller groups, clusters of usually four to eight individuals (both gray and white) lined up parallel and so close they appeared to be almost touching. The whales within the clusters would simultaneously dive to the bottom and stir up clouds and trails of mud. In several

Table 17. Stomach contents of belukha whales collected in Bristol Bay in June-July 1982 and May 1983.

SPECIMEN #	BBD-1-82		BBD-3-82		BBD-1-83		BBD-2-83		BBD-3-83	
DATE WHALE DIED	29 Jun		early Jun?		11 May		11 May		26 May	
PREY ITEM	% Vol.	% No.	% Vol.	% No.	% Vol.	% No.	% Vol.	% No.	% Vol.	% No.
Shrimp	0	-	*	-	4	-	11	-	0	-
Isopod	0	-	0	-	1	-	1	-	0	-
Mussel	0	-	0	-	1	-	0	-	0	-
TOTAL INVERTEBRATE	0	-	*	-	6	-	12	-	0	-
Rocks and Pebbles	0	-	0	-	1	-	0	-	100	-
TOTAL FISHES	100	-	*	-	92	-	88	-	*	-
Flatfishes	-	0	-	1	-	90	-	13	-	100
Rainbow smelt	-	0	-	87	-	0	-	83	-	0
Salmon	-	100	-	0	-	0	-	0	-	0
Sculpins	-	0	-	9	-	0	-	0	-	0
Other fish	-	0	-	3	-	10	-	4	-	0
VOLUME OF CONTENTS (ml)	415		*		163		142		20	
NUMBER OF IDENTIFIED FISHES	4		78		20		71		4	

* Trace (< 1 ml).

Table 18. Observations of feeding whales made in May-July 1983.

Date	Location	Time	Number of whales	Comments
5 May	Copenhagen Cr.	1020	32	feeding
17 May	just N of Naknek R. mouth	1109	70	milling/feeding; many gulls feeding nearby
25 May	Branch R. - Levelock	1119-1123	75-80	some feeding at river mouth
25 May	Nakeen	1209-1330	± 60	working the tide rip; obviously feeding; short dives; lots of turning and blowing by exposing only heads
26 May	Nakeen	1355	6	"
26 May	Coffee Cr. - Kvichak	1320-1351	41-43	some feeding
27 May	Kvichak	2000	12 +	50 gulls with them; big group of smolt at surface
27 May	Branch R.	1200	20-25	feeding
31 May	Kvichak	1807-1916	223 +	milling/feeding in river
4 Jun	Kvichak	0700-0800	± 30	lots of smolt at the surface
6 Jun	Naknek R. mouth	1630	30 +	feeding
8 Jun	Big Flat	2000-2200	75 +	milling and feeding
14 Jun	Big Flat	1000-1200	100 +	feeding; diving to bottom; stirring up mud clouds
15 Jun	Big Flat	1230-1330	125 +	"
16 Jun	Big Flat	1230-1330	100 +	"
18 Jun	Graveyard Pt.	1043	86 +	feeding
23 Jun	Halfmoon Bay	1400-1420	many	milling

Table 18. Continued.

Date	Location	Time	Number of whales	Comments
24 Jun	Halfmoon Bay	± 1200	many	feeding
29 Jun	Lake Pt.	1430	6	feeding
30 Jun	Nakeen/ Sea Gull Flat	0400-0700	25 +	feeding; some moving against floodtide
3 Jul	Sea Gull Flat to Telephone Pt.	1115-1125	100 +	feeding/milling
3 Jul	Lake Pt. area	1620	20 +	feeding on salmon on flats
4 Jul	Copenhagen Cr.	1015	30 +	feeding; in among nets
7 Jul	Copenhagen Cr.	1320-1350	400 +	most traveling; some stopped to feed on salmon

instances, groups of 30 or more whales would be diving together in a very small area, sometimes with eight to 12 in "rosette" formation (forming a circle with heads pointed inward). Sometimes a single whale could be seen swimming round and round in tight circles, stirring up mud in the midst of the others. They may have been feeding on flatfishes or some other demersal prey.

After about 18 June, we no longer saw large groups of whales on Big Flat. Instead of making twice-daily movements between the Kvichak River mouth and Big Flat, they began moving en masse between the river mouth at high tide and Halfmoon Bay or Deadman Sands at low tide. This change coincided with the arrival of adult red salmon in the Bay. (A few reds were caught in setnets in Halfmoon Bay on 18 June; drift netters had been catching a few earlier that week.) The whales were often seen in very shallow water within 10 m of the shoreline or over the extensive tidal flats but seldom in deeper, offshore waters. They could be seen chasing fish, making rapid turns, and lunging through the water. When feeding on salmon, they swam into the current (against the tide) more often than they did at other times. Although most feeding on salmon took place in the lower river or in the Bay, some whales did move upriver to feed. In contrast to earlier in the season during the smelt and smolt runs when they were common in mid-river, they worked close to the riverbank. They often breathed by lifting only the tops of their heads and blowholes out of the water and were frequently audible but not visible.

On several instances we examined salmon caught in gillnets for signs of belukha tooth marks. Although not all catches contained marked fish, one catch of seven fish had two with tooth scrapings across the posterior third of the body, and another catch of 11 had three marked fish. Most fishermen we talked to were familiar with the marks we described, although some thought they were seal bites. The incidence of such marks was apparently not high enough to cause many complaints, nor were the fish usually scraped very deeply. The tooth marks look as if someone had raked the fingernails of one hand across the tail end of the fish. The scales were removed and the flesh bruised, but the skin was rarely broken. If there was ever any doubt about the identity of these marks, it was dispelled when a belukha bit one of us and the tooth marks left on a hipboot matched those on the fish.

D. Mortality

During June and July 1983, we conducted 856 km of systematic aerial or boat surveys for beach-cast, dead belukhas (Table 19). During these surveys we located 25 carcasses, of which 19 were original sightings and six were resightings. Of the 19, 15 were recently dead (within the past 2-3 months) and four probably had been dead for over 6 months. Six additional dead belukhas were located in the course of other activities. Most carcasses were found along the high-tide line of gently sloping beaches. Very old, highly decomposed carcasses were usually located at the extreme high-tide line and often were partially covered by sand.

Table 19. Surveys for beach-cast, dead belukha whales conducted in Kvichak and Nushagak bays, May-July 1983.

Date	Area surveyed	Platform	Observer(s)	km	Number of beach-cast belukhas	Other
3 Jun	Telephone Pt. to Etolin Pt. to Ekuk; Igushik to Dillingham	helicopter	Frost; Ballard	161	1	
4 Jun	Johnson Hill to Naknek R. mouth	helicopter	Frost; Calkins	18	0	
18 Jun	Johnson Hill to Egegik	helicopter	Lowry; Frost	46	0	1 walrus, 1 seal
21 Jun	Johnson Hill to Naknek R. mouth; Telephone Pt. to Grassy Is.; Bradford Pt. to Nichols Spit	helicopter	Frost; Nelson; Whitman	210	6[*]	1 minke whale, 1 harbor porpoise
28 Jun	Telephone Pt. to Etolin Pt.; Naknek to Graveyard	helicopter	Lowry; Nelson	82	3	
4 Jul	Telephone Pt. to Second Pt.	whaler	Lowry; Frost	33	2	
5 Jul	Telephone Pt. to Lake Pt.	whaler	Frost; Lowry	46	0	
7 Jul	Copenhagen Cr. to Second Pt.	whaler	Lowry; Frost	22	0	
14 Jul	Nichols Spit to Snake R. mouth; Clark's Pt. to Telephone Pt.; Naknek R. to Johnson Hill	fixed-wing	Frost; Lowry	156	6[a]	1 gray whale
15 Jul	Clark's Pt. to mid-Halfmoon Bay	fixed-wing	Lowry; Frost	82	7[b]	1 walrus
			TOTAL	856	25	

---

[*] Four of these very old (probably greater than 1 year).

[a] One was a duplicate of a 28 June sighting.

[b] Four of these were duplicates of 14 July sightings; 1 was a duplicate of a 4 July sighting.

Fresher carcasses were sometimes found farther down the beach, depending on the height of the most recent high tides. One animal was found floating dead about 7 km up the Kvichak River. Another was found in the marsh grass in an area flooded only by exceptionally high tides. Two were caught by setnet fishermen and reported to the local ADF&G office.

Carcasses were found in both Kvichak and Nushagak bays, with the greatest number on the exposed beaches of Etolin Point, Halfmoon Bay, and near the Igushik River mouth (Fig. 22). It is probable that most carcasses flushed out with the tide, then washed back onshore with incoming tides and onshore winds.

Measurements were taken and sex was determined for 21 carcasses (Appendix IV). Of those, one was probably an abortus and seven were recently born calves. Standard length for the seven neonates ranged from 137 cm to 150 cm, with a mean of 141 cm. The remaining animals ranged from 192 cm to 410 cm standard length (Fig. 23). All of those shorter than 300 cm were gray in color, and those longer than 350 cm were white. One 320-cm individual was gray; color was indeterminable for the other three carcasses between 300 and 350 cm.

Sex ratio for all 21 carcasses was 13 males:7 females (1 unknown). Of the eight neonates (including the abortus), six were males and two females. Of those 1 year or older, seven were males and five were females.

In addition to conducting aerial and boat surveys, we interviewed fishermen and fisheries biologists to gather information on belukha whale mortality in Kvichak and Nushagak bays during spring and summer (Appendix V). By combining information from all sources, we compiled an estimate of the rates and causes of mortality (Table 20). In general, it was difficult to ascertain cause of death of beach-cast carcasses unless fishermen were present nearby to tell us whether or not the whales had been caught in nets. In some instances net marks in the form of superficial cuts around the caudal peduncle and flukes were obvious. The flukes had been cut off of one large whale and a pectoral flipper from each of two neonates, presumably in order to disentangle carcasses from nets. However, in at least two instances when whales were known to have been killed in setnets within the previous few days, no net marks or other indications of cause of mortality were obvious. Rapid degradation of the skin upon exposure to wind and sun aggravated this problem.

Hunting mortality was determined through interviews with ADF&G biologists and with local residents. One of the deaths attributed to hunting in Table 20 was a beach-cast carcass with obvious bullet wounds in the mid-body region. It could have been a hunting loss or possibly an animal shot at for some other reason.

One of the remaining carcasses was probably an abortus. The others had no obvious marks, bullet holes, or wounds indicating cause of death.

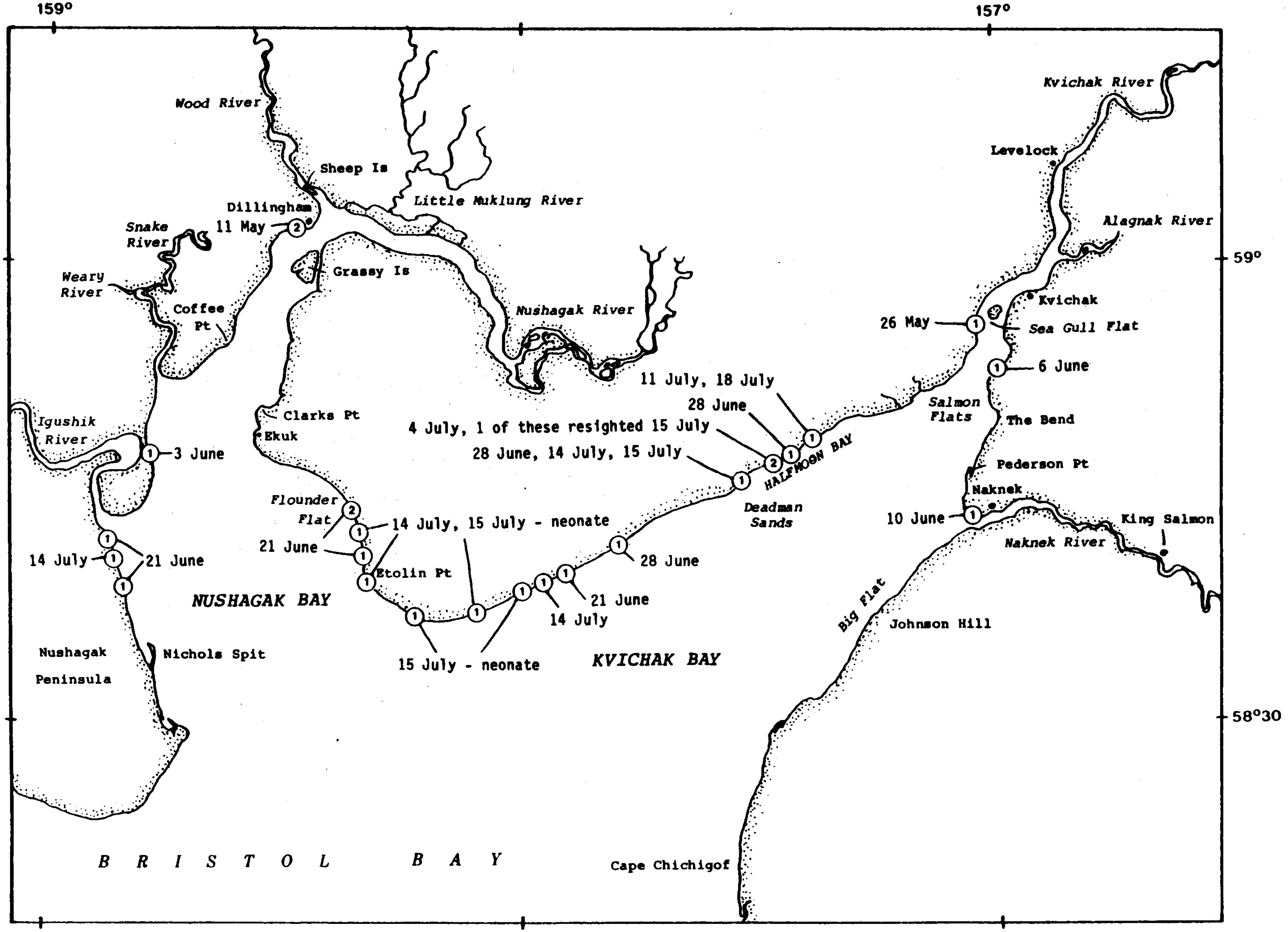


Figure 22. Locations of beach-cast belukha carcasses found in Nushagak and Kvichak bays, May-July 1983.

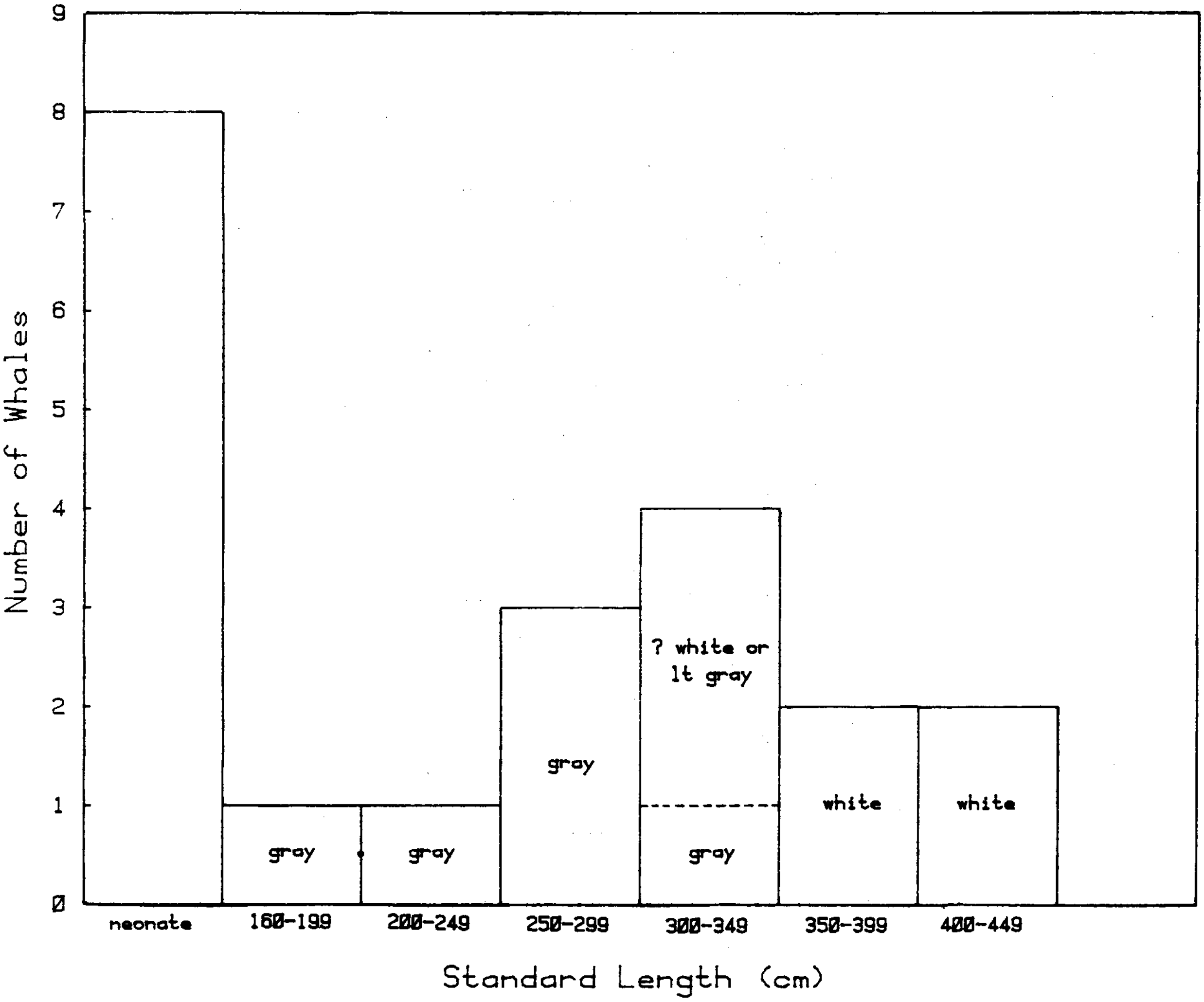


Figure 23. Length distribution of 21 beach-cast carcasses from Nushagak and Kvichak bays, summer 1983.

Table 20. Known mortality of belukha whales in Nushagak and Kvichak bays, May-July 1983.

Date	Comments	Cause of death			
		Fishing	Hunting	Unknown	Possible duplicate
4-8 May	Whale shot at Black Pt. - Nushagak R.		1		
11 May	Whales caught in king salmon setnets - Nushagak Bay	2			
11-20 May	Whales hunted at Levelock - Kvichak R.		2		
26 May	Floating dead whale - Nakeen, Kvichak R.			1	
1 Jun	Dead whale reported by F/V Pluto - Kvichak Bay				1
1-6 Jun	Whales caught in king salmon drift nets - Nushagak Bay	4			
3 Jun	Beach-cast whale S of Snake R. mouth - Nushagak Bay				1
6 Jun	Beach-cast whale - near Kvichak R. mouth			1	
17 Jun	Dead whale reported by set-netter S of Johnson Hill - Kvichak Bay			1	
21 Jun	Beach-cast whales - Nushagak Bay		1	1	
28 Jun	Beach-cast whales - W side of Kvichak Bay	1		2	
4 Jul	Whales caught in setnets, W side of Kvichak Bay	2			
6 Jul	Report of dead whale in Kvichak Bay, W side				1
11 Jul	Whale drowned in drift net - Kvichak Bay	1			
14 Jul	Beach-cast whale near Igushik Beach - Nushagak Bay			1	
14 Jul	Beach-cast whales - Etolin Pt.			3	
14 Jul	Beach-cast whale - W side Kvichak Bay			1	
15 Jul	Beach-cast whales - Etolin Pt.	2			
18 Jul	Beach-cast whale - W side Kvichak Bay				1
	TOTAL	12	4	11	4

There were four instances in which it was not possible to positively correlate carcasses found with reports of dead whales. In Nushagak Bay, four whales were reported as taken in drift nets from 1-6 June. On 3 June, a large, fresh carcass which may have been one of those four was found on the west side of that bay. Dead whales were reported by setnet fishermen in Kvichak Bay on two occasions, but we did not find the carcasses when we searched for them in the specified areas. It is possible that the animals washed off the beach with a high tide or in stormy weather and came onshore at another location, to be discovered on later surveys. On 11 July, the crew of a drift-net boat in Kvichak Bay told us about a white or very light gray whale that became entangled and drowned in their net a few days earlier. To disentangle it, they cut off the tail flukes. On 18 July, a large whale with the tail flukes missing washed up on the beach in Halfmoon Bay. It was estimated to have been dead a week or more and was probably the same whale.

When belukhas are caught in nets, they become entangled in two ways. Some, especially neonates and juveniles because of their small size, become tangled in the web of the net, catching pectoral flippers or tail flukes. In at least some instances, fishermen are able to disentangle and release these individuals before they drown. The small male animal that we tagged on 9 June had been caught in a net. He had superficial cuts in the skin and blubber and slightly dry skin but apparently suffered no long-term damage when set free. Several days later he was over 20 km from the release site and swimming with other whales. Larger individuals are able to break through net webbing but sometimes become entangled in the lead and cork lines. They roll and thrash when hitting the net, wrapping themselves so tightly that they have to be cut out. The tail flukes may be cut off in the process.

Approximate time of entanglement was known for six whales, five of which were caught by set-netters and one by a drift-netter. All but one (the small whale that was rescued and radio-tagged) were caught at night or on early-morning tides.

VII. Discussion and Conclusions

A. Capture, Tagging, and Tracking

The choice of radio transmitters for application to marine mammals requires consideration of multiple factors, including signal strength and therefore range, battery life, package size and design, attachment mechanism, cost, and availability. One of the aims of this project was to compare two types of transmitters, the OAR model AB340 backpack-style radio, and the Telonics barnacle-type tag. During both years of our study, we conducted comparative field tests of signal strength and range. Signals from the more powerful OAR radios (250 vs. 40 milliwatts) were consistently received at distances up to four times greater than the Telonics radios. Maximum range for a Telonics transmitter emitting a constant signal from a known direction was approximately 9 km when the receiving antenna was hand held at ground or water level. In contrast, signals from OAR radios attached to whales and transmitting intermittently were received at distances of 20-35 km. From aircraft, the range of the Telonics transmitter increased to over 40 km but was highly dependent on altitude, whereas signals from OAR radios had greater range and could be heard at low altitudes. The extra power output of the OAR produces a greater drain on the battery, but this is compensated for by a switching mechanism which causes the radio to transmit only while the whale is at the surface. Although the OAR radios were six times more powerful than the Telonics radios, they probably transmitted for less than one-tenth of the time they were on the instrumented whales.

Because of range limitations and concern over penetration depth of the tines, Telonics barnacle tags were not applied to the two captured whales. The OAR package was successfully attached by bolting through the dorsal ridge. The whales showed no apparent reaction to being tagged in this manner and subsequently appeared to behave normally. The packages came off the whales after approximately 2 weeks, in contrast to the desired 6-week duration. When recovered, neither of the radio packages or antennas showed any signs of damage that would indicate attempts at removal by the whales. We assume that hydrodynamic drag on the package caused the bolt to migrate through the hide and blubber. Irvine et al. (1982) applied similar radio packages to dorsal fins of bottlenose dolphins, Tursiops truncatus, and noted problems with migration of bolts through the tissue which resulted in a maximum tracking period of 22 days. The amount of tissue above the nylon sleeve was a triangle about 4.5 cm across the base and 1.5 cm high on the belukhas we tagged. In spite of the fact that belukhas are thicker skinned than true porpoises and dolphins (Sergeant and Brodie 1969), the radio packages were shed quite quickly. There appeared to be no difference in duration of attachment between the subadult (BB) and adult (Mama) belukha.

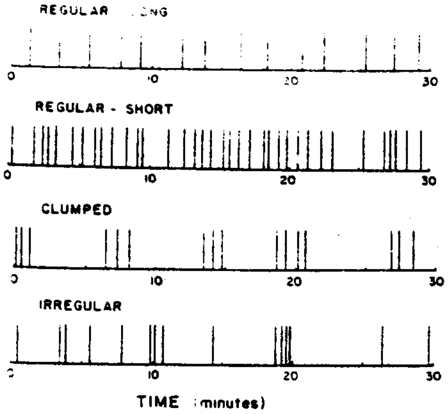
Two modifications to radio packages would be likely to substantially increase the retention time. First and simplest would be to reduce the amount of drag exerted by the package. At least half of the cross-sectional area of the OAR package we used was the result of foam flotation. If it was not necessary or desirable to recover radios, the flotation could be eliminated. Alternately, the smaller Telonics transmitter could be installed on a backpack and would exert correspondingly less drag. Secondly, different or additional methods could be used to attach the radio packages to the whales. The dorsal ridge attachment we used appeared very good in terms of production of signals and effects on the whales. Elimination of flotation from the package and use of two bolts could perhaps increase attachment duration to 2 or 3 months. Mate et al. (1983) have used an attachment consisting of two sets of umbrella stakes on gray whales. They received signals from whales 50 days after tagging (Mate and Harvey 1981) and recorded a sighting of a whale with at least part of the package still attached at least 27 months after tagging (Mate et al. 1983). We think the umbrella-stake attachment has great promise for use on belukhas but requires modification so that the depth of penetration can be reliably controlled.

Clearly, in terms of signal strength, the OAR is the preferred radio. However, the model AB340 transmitter is no longer being manufactured, and considerable development and modification would be required to adapt currently produced OAR transmitters for application to belukhas. The resulting radios would probably cost approximately $2,000 each (A. Wiggins, OAR, pers. comm.), which does not include the cost of construction of the backpack. The Telonics transmitters use currently produced, standard components and were purchased (packaged and ready to apply) for $800 each. If reacquisition of signals is to be done principally from aircraft, the Telonics radios should be adequate; however, the OAR transmitters are far more preferable if animals are to be detected and tracked principally from boats or shore.

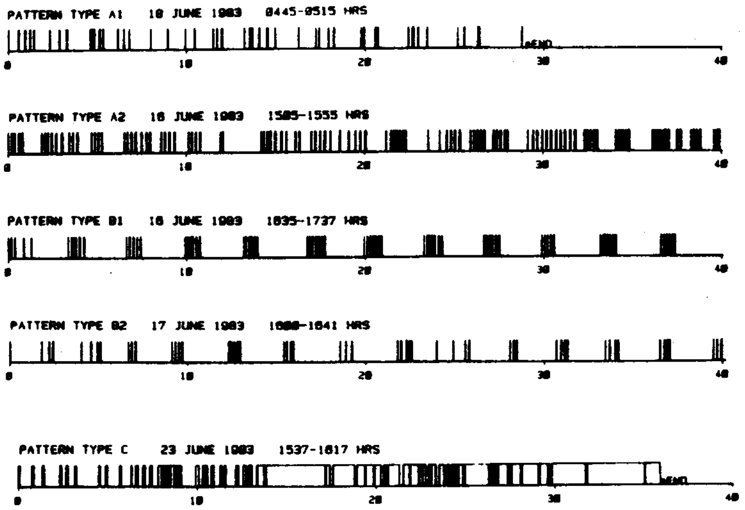
Three main respiration patterns were identified from the surface and dive-time data collected from the two telemetered belukhas. Similar respiration patterns have been described for other cetaceans (Fig. 24). Each of the species shown in Figure 24 exhibits a pattern of clumped ventilations separated by short dives, resembling what we termed pattern type B. Similarly, all five species show a variation of pattern type A where ventilations do not occur in clumped ventilation periods but are more widely spaced with short dive intervals between. Since we seldom visually resighted tagged whales, it was difficult to correlate those respiration patterns with behavior and activity. Pattern type B, with rolls clumped into discrete ventilation periods, has been interpreted to represent feeding in harbor porpoises, <u>Phocoena phocoena</u> (Watson and Gaskin 1983), and in spotted dolphins, <u>Stenella attenuata</u> (Leatherwood and Ljungblad 1979).

Pattern type A for belukhas resembles patterns associated with traveling in <u>Phocoena</u> and <u>Stenella</u>. The significance of the different surfacing frequency in types A1 and A2 is unclear. Leatherwood and Ljungblad (1979) associated frequent surfacings in <u>Stenella</u> with "running" and periods of less frequent surfacings with "traveling or exploratory diving." Watson and Gaskin (1983) reported a higher surfacing frequency in harbor porpoises trapped in weirs or carrying radio transmitters as compared to other free-ranging animals. Mate and Harvey (1981) suggested that surfacing frequency increased for gray whales holding their position against a strong current. We speculate that patterns A1 and A2 for belukhas may represent traveling with versus against the current, although it is equally possible that they may represent different behaviors such as resting and traveling.

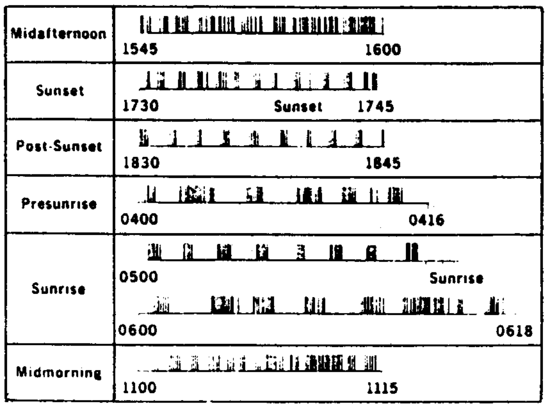
The respiration pattern for Mama which we called type C was characterized by very long periods of continous signals with irregular interruptions. When we first received these continuous signals, we thought that the radio had come off or some other malfunction had occurred. However, when we tracked the signal to its source, we located a group of whales in water slightly more than a meter deep, and the signals stopped as the whales moved rapidly to deeper water. We interpret this pattern as indicative of whales feeding or resting in very shallow water.



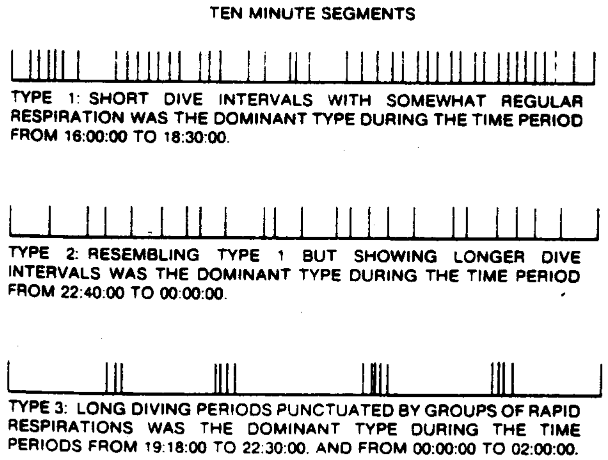
Examples of dive patterns of gray whales (from Mate and Harvey 1981).



Examples of respiration patterns of belukha whales (this report).



Respiration patterns of <u>Delphinus delphis</u> (from Evans 1971).

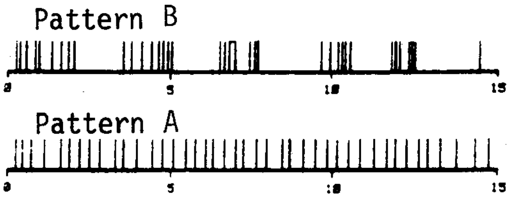


TYPE 1: SHORT DIVE INTERVALS WITH SOMEWHAT REGULAR RESPIRATION WAS THE DOMINANT TYPE DURING THE TIME PERIOD FROM 16:00:00 TO 18:30:00.

TYPE 2: RESEMBLING TYPE 1 BUT SHOWING LONGER DIVE INTERVALS WAS THE DOMINANT TYPE DURING THE TIME PERIOD FROM 22:40:00 TO 00:00:00.

TYPE 3: LONG DIVING PERIODS PUNCTUATED BY GROUPS OF RAPID RESPIRATIONS WAS THE DOMINANT TYPE DURING THE TIME PERIODS FROM 19:18:00 TO 22:30:00. AND FROM 00:00:00 TO 02:00:00.

Examples of 3 diving patterns of a spotted dolphin, <u>Stenella attenuata</u> (from Leatherwood and Ljungblad 1979).



Respiration patterns of harbor porpoises, <u>Phocoena phocoena</u> (after Watson and Gaskin 1983).

Figure 24. Respiration patterns of five species of cetaceans.

Near-continuous signals were also reported for harbor porpoises traveling or feeding very near the surface (Watson and Gaskin 1983).

Caution should be used in assigning behaviors to respiration patterns. In gray whales, Mate and Harvey (1981) noted that patterns are not exclusive to a particular behavior but include a variety of activities. For example, in gray whales, clumped respirations occur during migration and probably also during feeding and milling in moderate currents. Although Watson and Gaskin (1983) assigned traveling and foraging behavior to pattern types A and B, Read and Gaskin (1983 and pers. comm.) have subsequently cautioned that harbor porpoise behavior is highly variable and cannot always be clearly assigned to a particular pattern.

Characteristics of the ventilation and sounding periods for belukhas were very similar to those for harbor porpoises, with the exception of a longer mean sounding period in the former (2.09 vs. 1.44 min). The average ventilation period of belukhas was about one-third the length of the sounding period, which suggests they may be somewhat better divers than harbor porpoises in which ventilations were one-half as long as soundings (Watson and Gaskin 1983). The longest dive we recorded was almost 2 minutes longer than that reported for harbor porpoises. Watson and Gaskin suggested the possibility of a common maximum-to-mean dive ratio for all odontocetes, based on killer whales and harbor porpoises with ratios of 2.7 and 2.8. Dive data for BB give a maximum-to-mean ratio of 2.8 and thus support that suggestion.

B. Distribution, Abundance, and Movements

The distribution of belukha whales in Nushagak Bay was similar in 1982 and 1983. Most whales were seen in four areas: the Igushik River, the Snake River, between the Snake River mouth and Clarks Point, and near the junction of the Wood, Little Muklung, and Nushagak rivers (Fig. 12). Small numbers of whales, usually fewer than 20, were present in the lower Igushik River during June 1982 and from April-June 1983. Belukhas were not sighted in the Igushik in July of either year, although surveys were flown there on several occasions.

Whales were regularly seen in the Snake River and in both 1982 and 1983 were seen upriver as far as the junction of the Snake and Weary rivers, approximately 12 km from the river mouth. The largest sightings were of 15-25 whales on 13 and 14 July 1983. All others were of fewer than 10 individuals. No whales were seen in the Weary River.

The largest observed concentration of belukhas in Nushagak Bay occurred between the Snake River mouth and Clarks Point. Although the number seen there varied considerably, there was a clear trend of increasing abundance from late June to mid-July. From mid-April to mid-June, sightings were of fewer than 20 whales. In late June to mid-July, the number estimated to be in this area ranged from 30 or 40 to 400 to 600 in 1982 and from 150 to over 400 in 1983. In 1979, belukhas were also reported to be concentrated near the Snake River mouth in late June (Fried et al. 1979). Fried et al. and others have suggested that whales may gather near the Snake River to avoid boat activity since that area is closed to commercial fishing. Indeed, there was very little boat activity there in June and July 1982-83. However, that same group of whales apparently moves regularly between the Snake River mouth and the east side of the bay near Clarks Point, where there is constant boat activity and where most of the processing fleet is anchored. On several occasions, we observed a large group of whales swimming among the boats at Clarks Point. Local ADF&G biologists also have reported that belukhas are frequently numerous around Clarks Point (K. Taylor, pers. commun.). Thus, it seems unlikely that the absence of boat activity entirely explains the whales' preference for the Snake River mouth. Topography may be one of the factors affecting the suitability of the area. Although several rivers flow into Nushagak Bay, the most extensive mud flats occur at the mouth of the Snake River and extend south to the mouth of the Igushik River. The red salmon run in the Snake River is smaller than that in any of the three other major rivers, but the extensive shallows may make those salmon easier to catch.

Belukhas were sighted near the mouth of the Wood River and the Little Muklung River during May through early July. The number seen there varied considerably but was usually fewer than 50 in 1982, and in 1983 it was never more than 24. In both years we received reports of belukhas at Portage Creek, approximately 50 km up the Nushagak River from the Wood-Little Muklung area. Fried et al. (1979) also reported that belukhas regularly occurred off the mouth of the Little Muklung.

Observations on the distribution of belukha whales in Kvichak Bay were made only in 1983. The use of different areas within the bay changed markedly from April through August. From mid-April to mid-May, belukhas were present along the west side of the bay and near Salmon Flats, and large groups were sometimes seen near the mouth of the Naknek River. Frost et al. (1982) also listed sightings near the mouth of as well as in the Naknek River in April and May. The whales are thought to be feeding on smelt in the river at this time. In late May through the first week in June, up to several hundred whales were seen in the upper Kvichak River each day. Twice daily, groups of whales moved upriver on the flooding tides and returned downriver on ebbing tides. Brooks (1954, 1955) and Lensink (1961) also reported that from early May until mid-June, belukhas swam up the Kvichak on each incoming tide and returned to the bay on ebbing tides. Brooks estimated that about 250 whales used the river in 1954 and about 100 in 1955. Fish and Vania (1971) reported that 50-500 moved daily up and down the Kvichak.

The period during which belukhas make daily movements up and down the Kvichak River coincides with the seaward migration of post-spawning smelt and with the peak outmigration of red salmon smolt. Smelt spawn in the rivers of Kvichak Bay from late March to early May and then return to the bay. Red salmon smolt migrate from Lake Iliamna and Naknek Lake to the sea during the last 2 weeks in May and the first 2 weeks in June, with the peak migration occurring from about 22 May to 3 June (Meacham 1981; Huttenen 1982). In 1983, belukhas were last seen in large numbers in the Kvichak River on 6 June. By that date, approximately 90% of the smolt outmigration had occurred. Between 21 May and 3 June, from 1 to 14 million smolt moved down the river each day, with the number dropping rapidly after 3 June.

Between the end of the smolt outmigration and the beginning of the red salmon run, belukhas moved twice daily between the western or upper part of Kvichak Bay at high tide and the Big Flat area south of the Naknek River mouth at low tide. The whales were almost certainly feeding over Big Flat, but we were unable to determine what they were eating. Possibilities include flatfish, smelt, smolt, or shrimp.

After 16-18 June, distribution shifted away from the Big Flat area. From then until our study terminated in mid-July, the whales moved between the west side of Kvichak Bay and the mouth of the river between Sea Gull Flat, Nakeen, and Graveyard. They were particularly numerous there after 28 June. This change coincided with the beginning of the red salmon run. Red salmon were first caught in numbers during the week of 13-18 June, and between the 23rd and the 28th the catch increased from 170,000/day to 1.8 million/day. Escapement of fish upriver past the open fishing area increased 50 fold between the 27th and the 28th.

In the Kvichak in 1983, we observed a strong correlation between tidal stage and the direction of movement of the whales. Other studies have reported variable results when comparing tide and whale movements. Brooks (1954) and Lensink (1961) found, as we did, that belukhas generally swam up the Kvichak on flooding tides and down on the ebb. In Nushagak Bay, Fried et al. (1979) found that belukha movement patterns were independent of tide stage. Our observations in the Nushagak in 1982 and 1983 were too few to test for significance, but we also noted that whales moved with and against the tide with about the same frequency. We have no explanation for the apparently different behavior in the two areas.

Our telemetered whales showed substantial movements up and down the bay but were also sometimes relocated in particular areas over periods of several days. Because relocations were often almost a day apart, it was not possible to determine whether the radioed whales had moved to other areas and returned, or remained in the same area for the entire time. Based on our observations of other whales, which appeared to move between the inner bay and outer bay on a fairly regular twice-daily basis, it is likely that the radioed whales did the same. Large tides in the area result in currents of several km/hour flowing both up and down the bay. Because of river influence, the tide ebbs about 65% of the time so the net movement of a passive floating object would be out to the ocean. Although in most of the observed instances whales were moving with the direction of the tide, occasional movements against the tide, which were predominantly up the bay against ebbing tides, serve to maintain their relative position from day to day. The overall pattern of movements and utilization of various areas appears to be influenced largely by the distribution and movements of prey.

Although it has been assumed by previous investigators that belukhas move back and forth between Nushagak and Kvichak bays, we are unable to confirm such movements based on observations of radio-tagged whales or from aerial surveys. The two whales we radioed and tracked appeared to remain in Kvichak Bay throughout the 2 weeks during which they were tagged. We regularly observed whales moving between the Kvichak River mouth and Lake Point on the west side but seldom saw them along the coast between Nushagak and Kvichak bays. The two surveys in which they were seen in substantial numbers along the outer coast, and perhaps moving between areas, were on 15 April and 5 May. Lensink (1961) put visual tags on 46 belukhas in Kvichak Bay in 1959 and 1960. Only two tags were recovered or resighted: the first 1 month after tagging and the other approximately 3 months after tagging, both in Kvichak Bay. Brooks (1955) stated that there was some movement between Kvichak and Nushagak bays but presented no evidence to that effect. We consider it highly likely that such movements do indeed occur, but further radio-tagging studies are required to delineate their frequency and timing.

Fried et al. (1979) noted that local residents reported belukhas calving in the Snake River area. However, they did not observe any neonates during their surveys (26 May-28 June). In 1982, we observed very small calves from boats and the helicopter, found two dead neonates near the Snake River mouth during the 1st week in July, and received a report of four floating belukha placentas there on 9 July. In 1983, in the Nushagak, we found a single dead neonate, with an estimated birth date of about 10 June. We observed a substantial increase in the number of belukhas using the Snake River mouth area in late June-early July 1982 and 1983, with an estimated 400+ whales present in mid-July of both years. We conclude that the area near the mouth of the Snake River is a calving area and that most calving occurs in late June or early July. In 1983, similar observations were made in the Kvichak. One of us (LFL) observed what was thought to be a birth of a belukha on 31 May in the Kvichak River. A local setnet fisherman found a placenta on 28 June in Halfmoon Bay. Six beachcast neonates were found between Halfmoon Bay and Etolin Point from 3 to 15 July, and an abortus was found on 28 June. We noticed a group of 20-30 or more females with new calves on 7 July in the inner bay. It is obvious from this summer's observations that calving also occurs in Kvichak Bay, probably with a peak in late June and early July. Lensink (1961) reported that near-term fetuses were collected on 11 and 17 June and that in 1958 the first newborn calves were seen on 14 June.

A recurrent problem in the enumeration of cetaceans which spend a considerable portion of time under water, and therefore are not visible, has been how to estimate the total number of animals present based on the number observed at any one time. Consequently, one of the primary applications of radiotelemetry has been to provide quantitative data with which to interpret and extrapolate aerial survey counts. In this project, surface-time to dive-time information obtained from radioed whales was used to calculate an average correction factor of 2.75 by which to multiply our aerial survey counts. A comparison of simultaneous aerial and boat counts also suggested a multiplier of 2.4-2.8. Similar correction factors have been used by others. Sergeant (1973) observed that ventilation periods during which the whales were visible lasted 20-30 seconds and dives during which they were not visible lasted 60-100 seconds, therefore indicating a correction factor of 3. Fraker (1977, 1980) suggested a correction factor of 2 rather than 3 since an aerial surveyor's view is not instantaneous. He also believed that neonates and yearlings were for the most part not visible at altitudes of 300 m and more, and further stressed that it was unknown at what age juveniles became light enough to count. Brodie (1971) used a correction factor of 1.4 for belukhas in Cumberland Sound; however, the water there is clear, and the whales were visible for a greater proportion of the time. He added 18% to the corrected estimate to account for neonates (10%) and yearlings (8%).

Multiplication of our aerial survey counts by a correction factor of 2.75 yielded an estimate of 919 belukhas in Nushagak and Kvichak bays in late June 1983. If we correct that estimate by 18%, as Brodie did, to account for neonates and yearlings, the total estimated number of whales would be 1,100. We believe that is a minimum estimate, as the number of gray animals other than neonates and yearlings was probably also somewhat underestimated, and survey coverage was not complete, although it did include known concentration areas. A similar estimate of 1,000-1,500 was made by Brooks (1955). Thus, it appears that the number of whales using Nushagak and Kvichak bays is approximately the same now as 30 years ago.

C. Foods and Feeding

Stomachs examined in 1982-83 and observations of whales that appeared to be feeding on salmon smolt and adult salmon agreed well with the more extensive data collected in the 1950's and 1960's (Brooks 1954, 1955; Lensink 1961; ADF&G 1969). Those studies found that during May and early June, belukhas fed in the rivers, particularly the Kvichak, on smelt and red salmon smolt (Table 21). Smelt were eaten in the greatest numbers in the earliest May samples from a given year, followed later by red salmon smolt. The whales congregate in the rivers and at river mouths to feed on smelt during and after they spawn. In mid- to late May, the red salmon smolt outmigration begins, and almost immediately the diet of belukhas switches to primarily smolt. Brooks (1955) proposed that smolt, which travel downstream in large, dense schools, moving within about a meter of the surface, are more easily caught than smelt, which also may be abundant but swim closer to the bottom.

The first adult red salmon appear in Kvichak and Nushagak bays around mid-June, with peak numbers usually present from the last week in June through the first 2 weeks in July. A few king salmon are present in early June. After mid-July, the red salmon run tapers off and other species of salmon (chums, pinks, and silvers) are present, although

Table 21. Stomach contents of belukha whales from the Kvichak River and its estuary, May and June 1954, 1955, 1965, and 1966. (Brooks 1955; ADF&G 1969).

	Mean number per stomach			
Date	Smelt	Salmon smolt	Shrimp	Other fish
26-28 May 1954 n = 3	501	*		
22-24 May 1955 n = 2	548	73		
20-22 May 1966 n = 3	62	0	2	*
31 May-6 Jun 1954 n = 5	17	983	*	
26-31 May 1955 n = 8	29	607	6	*
29-31 May 1965 n = 3	0	283		
1-7 Jun 1955 n = 9	20	873		*
11-17 Jun 1954 n = 4	3	399	*	7
8-14 Jun 1955 n = 6	90	201	4	*
11-12 Jun 1965 n = 4	0	125	*	

* Trace (average of < 1 per stomach).

their runs are much smaller than that of the red salmon (Nelson 1981). Brooks (1954, 1955) collected no belukhas between mid-June and 1 July. By 1 July, smelt and red salmon smolt had disappeared entirely from the whales' diet and had been replaced by adult salmon, which composed the bulk of the diet for the subsequent 7 weeks (Table 22). During the first 3 weeks of July, reds were the predominant species of salmon eaten. After that, chums, pinks, and silvers became relatively more important. Chums first showed up in the diet during the 2nd week of July, pinks in the 3rd week, and silvers in the 4th week. Only a very few kings were eaten. After the 15th of August, stomachs contained very few salmon. Some had small quantities of shrimp or other fish such as sculpins, flounder, or lampreys (Lampetra japonica), as did stomachs of eight belukhas taken in September 1959 and 1960 (Lensink 1961).

Table 22. The occurrence of adult salmon in belukha stomachs on a weekly basis from 1 July-18 August 1954-55 (Brooks 1955).

Date	No. of belukhas (excl. calves)	No. of salmon		Average/belukha	
		red	all species	red	all species
1-7 Jul	6	32	34	5.3	5.7
8-14 Jul	10	33	45	3.3	4.5
15-21 Jul	14	41	74	3.0	5.3
22-28 Jul	5	5	50	1.0	10.0
29 Jul-4 Aug	10	8	31	0.8	3.1
5-11 Aug	15	10	59	0.7	4.0
12-18 Aug	10	8	21	0.8	2.1

In 1955, Brooks estimated the consumption of red salmon smolt in the Kvichak River using the following assumptions, which were based on his 1954-55 field studies: an average meal consisted of 685 smolt; each whale averaged 1.5 meals/day and fed on smolt for 19 days; and 150 belukhas fed in the river each day during the smolt run. Based on these assumptions, he calculated that belukhas ate approximately 3 million salmon smolt per season.

The consumption of smolt by belukhas in 1983 was estimated in the following manner. During late May and early June, the number of whales estimated to be in Kvichak Bay ranged from 210 to 280. We regularly counted groups of 75-225 in the river and consider 200 to be a reasonable estimate of the average number feeding there during this time. The large groups of whales were in the river for 14 days from 25 May through 7 June, after which we did not see them there. We made no observations in the Kvichak prior to 25 May. In recent years, the smolt run in the Kvichak has lasted for about 30 days from approximately mid-May to mid-June (Meacham 1981). Since whales clearly did not use the river after mid-June, and since they probably did use it before 25 May, 19 days seems a reasonable approximation of the period spent feeding on smolt.

Daily ration can be calculated as a product of predator size and consumption rate. Brooks (1954, 1955) and Lensink (1961) collected and measured 82 belukhas of all ages from Nushagak and Kvichak bays. Mean length of those animals, excluding calves, was 326 cm. Similar mean lengths were reported by Nelson (1887), who found that the average adult in the Yukon-Kuskokwim area was 305-366 cm long, and by Doan and Douglas (1953), who found that the average length of 1,077 belukhas from Churchill, Northwest Territories, was 308-325 cm. Weight data are not available for belukhas from Bristol Bay. However, Sergeant and Brodie (1975) plotted a length-weight regression for belukhas from Churchill, which are similar in size to those from Bristol Bay. On the basis of Sergeant's and Brodie's data, a whale averaging 326 cm in length will weigh about 350 kg.

Sergeant (1969) summarized data on the daily ration of six captive belukhas and found that they consumed 4-7% of their body weight per day. The average for four of those measuring 300-400 cm in length was 5.1% per day; therefore, a 350-kg whale will consume about 18 kg per day. Based on estimated weight of prey items, we calculated that the stomach of an average whale collected during the smolt run in 1954-55 contained 7-8 kg. Estimated numbers of smolt, and therefore weight of food per stomach, are almost certainly low due to the difficulty of counting partially digested fishes. During the peak of the adult salmon runs, that average was 15 kg per stomach and, later in the season, 6-11 kg. Assuming two meals per day, daily consumption (based on stomach contents) would therefore be about 15 kg of smolt or 12-30 kg of adult salmon, which is very close to the calculated consumption of 18 kg. Using data on the number of fishes eaten, and information on the average size of fishes, it was estimated that smolt composed 73% of the diet during the 19 days when the whales ate them, or approximately 13 kg (of a total 18 kg) eaten per whale per day. That number can then be divided by the average weight per smolt (± 8 g, taking into account the ratio of age I and II smolt and their mean sizes based on the 20-year average provided in Meacham 1981) to estimate the number of smolt eaten per whale per day. Using the above assumptions, the consumption of red salmon smolt can be calculated as follows:

200 belukhas X 1625 smolt/day X 19 days = 6,175,000 salmon smolt

The average annual smolt run in the Kvichak from 1971-1980 was approximately 122 million (Meacham 1981). Consumption by belukhas represents about 5% of that average. If no predation had occurred and 10% of these smolt survived to spawn (Huttenen 1982), they would number about 618,000, or approximately 3% of the 1983 commercial salmon catch in Kvichak Bay. Belukha predation on salmon smolt undoubtedly also occurs in the Nushagak, but we do not have the information necessary to make calculations for that area.

Brooks (1955) calculated the predation on adult salmon based on the average number of salmon per stomach for the whales he collected (2.1 reds, 5 total), a 49-day period of eating salmon, and an estimated 800 whales in 1954 and 450 in 1955. In 1954, estimated consumption was 196,000 (82,320 reds), and in 1955 it was 99,225 (41,674 reds).

Based on observations of feeding and data on the duration of salmon runs in 1983 (ADF&G, unpubl.), we consider 70 days as a more realistic estimate of the period during which belukhas prey on adult salmon. Brooks's data indicate that fewer salmon are taken in August than in July and that even during the peak salmon run other prey are eaten. By multiplying data on the number and kinds of salmon and other species eaten per day over a 7-week period by average fish size, and assuming a total daily consumption of 18 kg per whale, the average daily consumption of salmon from 17 June through 25 August was estimated as 13 kg. Based on our most complete aerial survey in late June 1983, we consider 920 whales to be a reasonable estimate of the number of belukhas (older than calves and yearlings which do not eat adult salmon) present during the adult salmon runs. Using these assumptions, then, the estimated 1983 consumption of adult salmon by belukhas is:

920 whales X 70 days X 13 kg salmon/whale/day = 837,200 kg adult salmon

If the total amount of salmon is allocated by species according to Brooks's data, excluding pinks since there were essentially none present in 1983, then the 837,200 kg represents approximately 182,000 red salmon and 101,000 salmon of other species. The catch of red salmon in Kvichak and Nushagak bays in 1983 was close to 27 million, out of a run of slightly over 33 million, so that belukha predation was the equivalent of less than 1% of the commercial catch and just over 0.5% of the total run. Catch of other species was approximately 1.1 million, with belukha consumption equaling about 9% of that number.

D. Mortality

From May-July 1983, 27-31 dead belukha whales were located or reported in Nushagak and Kvichak bays. In 1982, only six belukha carcasses were found; however, search effort was much less systematic and was confined to the Nushagak area (Lowry et al. 1982). Of the 27-31 whales found in 1983, at least 12 and perhaps several more were fishing-related mortalities. One of the six 1982 carcasses was definitely a fishing-related death. This represents an apparent change in the incidence of entanglement of whales in nets over the last 3 decades. In the 1950's, Brooks observed no net-caused mortality (J. Brooks, National Marine Fisheries Service, Juneau, pers. commun.). Since then, some mortality has been known to occur in conjunction with the king salmon fishery but not, generally, with the red salmon fishery (J. J. Burns, ADF&G, pers. comm.). Of the 12 known fishing-related mortalities in 1983, six were killed in king salmon nets, four in red salmon nets, and two in nets of unknown type.

The cause of this apparent increase in entanglement warrants further study. Possible factors could include changes in gear type, particularly the switch from cotton to nylon webbing; the increase in the number of setnets in areas such as western Kvichak Bay, where many whales concentrate to feed; and the increased amount of time gear is in the water.

If the number of belukhas present in Nushagak and Kvichak bays in summer 1983 (including neonates and yearlings) is estimated at 1,100, the number extrapolated from maximum aerial survey counts on 29 June, then the 27-31 dead animals located in May-July represent 2.5-2.8% of that total group of whales. Gross productivity for belukhas has been estimated at 10% (Brodie 1971), which means in a group of 1,100 whales, 110 would be calves. The seven dead neonates located by us in summer 1983 would represent 6% of that year's calf production. Actual mortality is undoubtedly greater as our mortality figures are based only on carcasses we personally located or happened to hear about. We did not systematically interview fishermen, yet heard of at least four dead belukhas through casual conversation. Although aerial survey efforts were considerably more extensive in 1983 than in 1982, carcasses were probably missed in the Nushagak system which we surveyed less frequently and less intensively. In 1982, three of the six carcasses we found were located up the Snake River in the grass along the riverbank. Such carcasses are extremely difficult to see from the air and probably would not have been noticed on the 1983 aerial surveys.

VIII. Needs for Further Study

This project was initially designed as a 3-year study, the first 1-2 to be spent developing and testing tags and techniques in Bristol Bay, after which techniques were to be used in other areas such as Norton Sound, Kotzebue Sound, and Kasegaluk Lagoon. For a number of reasons, the first field season was not productive in terms of capturing and tagging whales. In the second year, although we did not attach radios to as many whales as we intended, our results were comparable to other successful studies involving radiotelemetry of free-ranging cetaceans.

With respect to belukhas in Bristol Bay, our study has resulted in a reasonably comprehensive description of distribution, abundance, and movements. The issue in this area that merits further investigation is the present level of interaction between belukhas and the commercial fishery for red salmon. Although we have estimated the consumption of salmon by belukhas, our estimates are extrapolations based on old data and numerous assumptions. In truth, we have only a general idea of the predator-prey interactions between belukhas and salmon, and it would be difficult, for example, to suggest means by which to reduce the effects of belukha predation. Of particular interest is the present level of entanglement of belukhas in fishing gear. The reason for the increase in entanglement since the 1950's is unknown, and therefore it would be impossible to suggest means by which to reduce the present level. The actual amount of mortality caused by entanglement is not known nor are the costs to fishermen in terms of damaged gear and lost fishing time.

Our intentions were to develop telemetry as a tool which could be used for studies of belukha movements and behavior. As demonstrated in this report, the OAR backpack radios we used are adequate for short-term studies of that nature. Long-term studies will require development and modification of transmitter packages and attachment mechanisms. Such development should be continued and telemetry applied to whales in other areas in order to describe habitat use, respiration patterns, movements, abundance, and interrelationships among groups of whales. A description of these aspects of belukha whale biology is needed prior to proceeding with oil and gas exploration and other such activities in important parts of their range.

IX. Literature Cited

ADF&G. 1969. A report on beluga whales in Alaska. Unpubl. ms. prepared for the Board of Fish and Game meeting, Anchorage, AK, 1969. 12pp.

Braham, H. W., B. D. Krogman, and G. M. Carroll. 1982. Bowhead whale (Balaena mysticetus) migration, distribution, and abundance in the Bering, Chukchi, and Beaufort seas, 1975-1978, with notes on the distribution and life history of white whales (Delphinapterus leucas). NOAA Tech. Memo. NMFS SSRF-000. In press.

Brodie, P. F. 1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale (Delphinapterus leucas) with reference to the Cumberland Sound, Baffin Island, population. J. Fish. Res. Board Can. 28:1309-1318.

Brooks, J. W. 1954. Beluga. Pages 51-57 in Annual Report for 1954. Alaska Dep. Fish., Juneau.

Brooks, J. W. 1955. Beluga investigation. Pages 98-106 in Annual Report for 1955. Alaska Dep. Fish., Juneau.

Burns, J. J., K. J. Frost, G. A. Seaman, and L. F. Lowry. In prep. Biological investigations of belukha whales in waters of western and northern Alaska. Final Rep. Contract NA 81 RAC 00049, NOAA, Outer Continental Shelf Environmental Assessment Program.

Butler, R. W., and J. G. Jennings. 1980. Radiotracking of dolphins in the eastern tropical Pacific using VHF and HF equipment. Pages 757-759 in C. J. Amlaner, Jr. and D. W. MacDonald, eds. A Handbook on Biotelemetry and Radio-Tracking. Pergamon Press, New York.

Davis, R. A., W. R. Koski, W. J. Richardson, C. R. Evans, and W. G. Alliston. 1982. Distribution, numbers and productivity of the western arctic stock of bowhead whales in the eastern Beaufort Sea and Amundsen Gulf, summer 1981. Unpubl. rep. by LGL Ltd., Toronto, for SOHIO Alaska Petroleum Co., Anchorage, and Dome Petroleum Ltd., Calgary. 134pp.

Doan, K. H., and C. W. Douglas. 1953. Beluga of the Churchill region of Hudson Bay. Fish. Res. Board Can. Bull. 98. 27pp.

Evans, W. E. 1971. Orientation behavior of delphinids: radio telemetric studies. Ann. N.Y. Acad. Sci. 188:142-160.

Fish, J. F., and J. S. Vania. 1971. Killer whale, Orcinus orca, sounds repel white whales, Delphinapterus leucas. Fish. Bull. 69:531-535.

Fried, S. M., J. J. Laner, and S. C. Weston. 1979. Investigation of white whale (Delphinapterus leucas) predation upon sockeye salmon (Oncorhynchus nerka) smolts in Nushagak Bay and associated rivers:

1979 aerial reconnaissance surveys. Unpublished rep. Project 11-41-6-340, Alaska Dep. Fish and Game, Dillingham. 15pp.

Frost, K. J., L. F. Lowry, and J. J. Burns. 1982. Distribution of marine mammals in the coastal zone of the Bering Sea during summer and autumn. Final Rep. Contract NA 81 RAC 00050 submitted to NOAA, Outer Continental Shelf Environmental Assessment Program. 166pp.

Gaskin, D. E., G. J. D. Smith, and A. P. Watson. 1975. Preliminary study of movements of harbor porpoises (Phocoena phocoena) in the Bay of Fundy using radio telemetry. Can. J. Zool. 53:1466-1471.

Harrison, C. S., and J. D. Hall. 1978. Alaskan distribution of the beluga whale, Delphinapterus leucas. Can. Field-Nat. 92:235-241.

Hobbs, L. J., and M. E. Goebel. 1982. Bowhead whale radio tagging feasibility study and review of large cetacean tagging. NOAA Tech. Memo. NMFS F/NWC-21. 68pp.

Huttenen, D. C. 1982. 1981 Bristol Bay sockeye salmon smolt studies. Alaska Dep. Fish and Game Tech. Data Rep. No. 73. 63 pp.

Irvine, A. B., J. H. Kaufmann, M. D. Scott, R. S. Wells, and W. E. Evans. 1979. A study of the activities and movements of the Atlantic bottlenosed dolphin, Tursiops truncatus. Final Rep. U.S. Mar. Mammal Comm., Contract Nos. MM4AC004 and MM5AC0018. 34pp.

Irvine, A. B., R. S. Wells, and D. M. Scott. 1982. An evaluation of techniques for tagging small odontocete cetaceans. Fish. Bull. 80: 135-143.

Klinkhart, E. G. 1966. The beluga whale in Alaska. Fed. Aid Wildl. Rest. Proj. Rep., Vol. VII: Proj. W-6-R and W-14-R, Alaska Dep. Fish and Game, Juneau. 11pp.

Leatherwood, S., and W. E. Evans. 1979. Some recent uses and potentials of radiotelemetry in field studies of cetaceans. Pages 1-31 in H. E. Winn and B. L. Olla, eds. Behavior of Marine Mammals, Vol. 3. Plenum Publ. Corp.

Leatherwood, S., and D. K. Ljungblad. 1979. Nighttime swimming and diving behavior of a radio-tagged spotted dolphin, Stenella attenuata. Cetology 34:1-6.

Lensink, C. J. 1961. Status report: beluga studies. Unpubl. ms., Div. Biol. Res., Alaska Dep. Fish and Game, Juneau. 20pp.

Lowry, L. F., K. J. Frost, and R. R. Nelson. 1982. Investigations of belukha whales in coastal waters of western and northern Alaska: marking and tracking of whales in Bristol Bay. Annu. Rep. Contract

NA 81 RAC 00049, NOAA, Outer Continental Shelf Environmental Assessment Program. 43pp.

Mate, B. R., and J. T. Harvey. 1981. An evaluation of three radio tags applied to gray whales and their utility in assessing whale movements and dive characteristics. Final Rep. Contract AA 730 794120 0109 submitted to BLM, Anchorage, Alaska. 68pp.

Mate, B. R., J. T. Harvey, L. Hobbs, and R. Maiefski. 1983. A new attachment device for radio-tagging large whales. J. Wildl. Manage. 47:868-872.

Meacham, C. P., ed. 1981. 1980 Bristol Bay sockeye salmon smolt studies. Alaska Dep. Fish and Game Tech. Data Rep. No. 73. 63pp.

Miller, G. W. 1983. Distribution and abundance of gray whales. Pages 13-45 in D. H. Thomson, ed. Feeding ecology of gray whales (Eschrichtius robustus) in the Chirikof Basin, summer 1982. Unpubl. rep. by LGL Alaska Res. Assoc., Inc., Anchorage, for NOAA, Juneau, AK.

Nelson, E. W. 1887. Report upon natural history collections made in Alaska between the years 1877 and 1881. H. W. Henshaw, ed. Congressional Ser., U.S. Public Doc. No. 2349, U.S. Gov. Printing Off., Washington, DC.

Nelson, M. L. 1981. Annual management report 1981 - Bristol Bay area 1981. Unpubl. rep., Alaska Dep. Fish and Game, Anchorage. 175pp.

Ray, C. 1962. Three whales that flew. Natl. Geogr. 121(3):346-359.

Read, A. J., and D. E. Gaskin. 1983. The application of radio tracking techniques to the study of harbour porpoises (Phocoena phocoena) in the Bay of Fundy. Pages 346-352 in D. G. Pincock, ed. Proc. Fourth Int. Conf. Wildl. Biotelemetry, Halifax, Nova Scotia.

Seaman, G. A., and J. J. Burns. 1981. Preliminary results of recent studies of belukhas in Alaskan waters. Rep. Int. Whaling Comm. 31:567-574, SC/32/SM 13.

Seaman, G. A., L. F. Lowry, and K. J. Frost. 1982. Foods of belukha whales (Delphinapterus leucas) in western Alaska. Cetology 44: 1-19.

Sergeant, D. E. 1969. Feeding rates of Cetacea. Fisk. Dir. Skr. Ser. Hav Unders. 15:246-258.

Sergeant, D. E. 1973. Biology of white whales (Delphinapterus leucas) in western Hudson Bay. J. Fish. Res. Board Can. 30:1065-1090.

Sergeant, D. E., and P. F. Brodie. 1969. Tagging white whales in the Canadian Arctic. J. Fish. Res. Board Can. 25:2201-2205.

Sergeant, D. E., and P. F. Brodie. 1975. Identity, abundance, and present status of white whales, *Delphinapterus leucas*, in North America. J. Fish. Res. Board Can. 32:1047-1054.

U.S. Department of Commerce. 1979. Taking of certain Alaska marine mammals: waiver of the moratorium, final rule. Pages 2539-2554 *in* Federal Register, Vol. 44, No. 8.

Watkins, W. A. 1981. Reaction of three species of whales *Balaenoptera physalus*, *Megaptera novaeangliae* and *Balaenoptera edeni* to implanted radio tags. Deep-Sea Res. 28A:589-599.

Watkins, W. A., K. E. Moore, D. Wartzok, and J. H. Johnson. 1981. Radio tracking of finback (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales in Prince William Sound, Alaska. Deep-Sea Res. 28A:577-588.

Watson, A. P., and D. E. Gaskin. 1983. Observations on the ventilation period of the harbour porpoise *Phocoena phocoena* (L.) in coastal waters of the Bay of Fundy. Can. J. Zool. 61:126-132.

White, M. J. Jr., J. G. Jennings, W. F. Gandy, and L. H. Cornell. 1981. An evaluation of tagging, marking, and tattooing techniques for small delphinids. NOAA Tech. Memo. NMFS-SWFC-16. 142pp.

APPENDIX I

RADIO-TRACKING RECORD FOR THE WHALE "BB"

Appendix I. Radio-tracking record for the whale "BB," frequency 164.535, 9 June-23 June 1983. Numbers in circles correspond to those in Figure 4.

Date	Time	Listening location		Signal received	Comments
9 Jun	2145-2215	Naknek R. mouth		strong	whale released after tagging
	2330-2345	Kvichak		no	from *Iliaska*
10 Jun	0800	Kvichak		no	from *Iliaska*
	1000	Nakeen		no	from whaler
	1015	S end Albert Channel		no	"
	1021	mid-Salmon Flats		no	"
	1255	Kvichak		no	from *Iliaska*
	1340	Halfmoon Bay		strong	from helo at 305 m; BB probably near Naknek R. mouth
	1355	S of Naknek R.		strong	from helo at 152 m; BB between Naknek R. and Johnson Hill
	1556-1647	3.7 km S Naknek R.	①	strong	from whaler; 3-6 signals per surfacing; BB here
	1706-2200	Naknek R. mouth		weak	from whaler and *Iliaska*
	2215-2315	off Naknek R. mouth	②	strong	from whaler; BB 4-5 km W of Naknek R. mouth

Appendix I. Continued.

Date	Time	Listening location		Signal received	Comments
11 Jun	0830	off the Bend	③	visual	seen by fixed-wing aircraft
	1015	Naknek R. mouth		weak	from whaler; BB toward Copenhagen Cr.
	1250	1.8 km W Naknek R.		weak	from whaler; BB toward Halfmoon Bay
	1444-1500	S Halfmoon Bay	④	strong	from whaler and helo; BB very close but no visual
12 Jun	1100	Naknek R. mouth		moderate	from *Iliaska*; BB in Halfmoon Bay
	1150	S Halfmoon Bay	⑤	strong	from whaler and *Iliaska*; BB in area; same location as yesterday
	1530	"	⑥	strong	whale very close; with other whales
	2350	Naknek R. mouth		weak	from *Iliaska*; signal from across bay
13 Jun	± 1030	Naknek R. mouth		no	from *Iliaska* and whaler
	± 1100	mid-Kvichak Bay		yes	from *Iliaska* and whaler; BB in Lake Pt. area
	1200	Lake Pt. area	⑦	strong	from *Iliaska* and whaler; BB here
	1625	"	⑧	strong	BB sighted visually nearshore
14 Jun	1000-1200	Naknek R. mouth		strong	from helo; BB on W side of bay

Appendix I. Continued.

Date	Time	Listening location	Signal received	Comments
14 Jun, cont.	1600/1745	near Lake Pt. ⑨	strong	from helo; BB here
	1725	Lewis Pt.	moderate	from helo; BB near Lake Pt.
	1800	Alagnak R. mouth	moderate	"
15 Jun	1030	Naknek R. mouth	strong	from helo; BB on W side of bay
	1640-1710	S side Naknek R. mouth	weak	from bluff; BB on W side
16 Jun	1000	Naknek R. mouth		from *Iliaska*; BB on W side
	1510-1550	3.7 km W Naknek R. mouth	strong	from W side of bay
	1640-1700	S Halfmoon Bay ⑩	strong	from helo; BB here (circled and located)
17 Jun	1200-1500	Buckley's	no	BB out of range to the SW
	1600-1630	"	mod-strong	from bluff
	1900-1931	"	strong	from bluff; whale nearby
	2214-2247	Buckley's	mod-strong	from bluff; whale to NE toward Graveyard
	2347-0018	"	weak-mod	"

Appendix I. Continued.

Date	Time	Listening location	Signal received	Comments
18 Jun	0445-1515	Buckley's	strong	from bluff
	0742-0815	"	strong	from bluff; signal from the E
	0845-0916	"	mod-strong	from bluff
	1000	" ⑪	strong	from helo; BB here
	1323	Graveyard	weak	from helo; BB to S
	2030-2103	Buckley's	strong	from bluff
	2317-2349	"	moderate	"
19 Jun	0344-0415	Buckley's	weak	from bluff; signal from E
	0923-0953	"	moderate	"
	1105-1115	Kvichak	no	from Iliaska
	1200-1231	Buckley's	weak	from bluff
	1230-1330	Kvichak to Copenhagen Cr.	no	from whaler
	1800	mid-Halfmoon Bay	weak	from whaler; signals to the SW
	1900	4 km SE Copenhagen Cr.	no	from whaler
	2020	Sea Gull Flat	no	"

Appendix I. Continued.

Date	Time	Listening location	Signal received	Comments
19 Jun, cont.	2130-2140	Kvichak	no	from Iliaska
	2240-2245	"	no	"
20 Jun	1300-1400	Halfmoon Bay ⑫	strong	from helo; BB here
	1310-1320	Kvichak	no	from Iliaska
	1730	Halfmoon Bay ⑬	strong	from helo; BB here
	1945-2017	Buckley's	strong	from shore
	2213-2244	"	strong	"
21 Jun	1157	S Coffee Cr. channel ⑭	strong	from helo; BB here
	1430	Naknek R. mouth	moderate	from helo; BB in Halfmoon Bay area
	2300	Graveyard	no	from whaler
22 Jun	1045	N of Graveyard	no	from whaler
	1108	3 km W Graveyard	no	"
	1129	3-4 km E Copenhagen Cr.	no	from whaler
	1150	3-4 km S Copenhagen Cr.	no	"
	1217	2-3 km off Buckley's	moderate	from whaler; BB to S

Appendix I. Continued.

Date	Time	Listening location	Signal received	Comments
22 Jun, cont.	1237	4 km ESE Second Pt.	moderate	from whaler; BB to S
	1307	5 km SW Second Pt.	mod-strong	from whaler; BB to S toward Lake Pt.
	1319	11 km SW Second Pt. ⑮	strong	from whaler; BB in Lake Pt. area
	1737	12 km SW Second Pt. ⑯	strong	from helo; whales seen in area
23 Jun	1131	1 km S Graveyard	no	from whaler
	1150	5-6 km WNW Bristol Bay cannery	no	"
	1210	mid-Kvichak Bay off Naknek R.	weak	from whaler; BB to SW
	1230	7-8 km E Buckley's	moderate	from whaler; signals steady
	1328	Graveyard	mod-strong	from helo; signal continuous, BB's radio near Lake Pt.
	1410	E Lake Pt.	mod-strong	radio recovered by whaler-floating

APPENDIX II

RADIO-TRACKING RECORD FOR THE WHALE "MAMA"

Appendix II. Radio-tracking record for the whale "Mama," frequency 164.585, 18 June-3 July 1983. Numbers in circles correspond to those in Figure 5.

Date	Time	Listening location	Signal received	Comments
18 Jun	1630	N Halfmoon Bay	strong	whale released; headed to the S
	1852-1945	Buckley's	strong	from bluff; whale at surface for ± 40 min
	2030-2103	"	strong	from bluff; whale to S
	2242-2315	"	very strong	"
19 Jun	0341-0953	Buckley's	no	whale out of range to S
	1105-1115	Kvichak	no	from *Iliaska*
	1240	Sea Gull Flat	no	from whaler
	1310-1320	Kvichak	no	from *Iliaska*
	1330	Copenhagen Cr.	no	from whaler
	1800	Graveyard ①	strong	from helo; Mama here
	1800	mid-Halfmoon Bay	moderate	from whaler; Mama toward Graveyard
	1900	3-4 km SE Copenhagen Cr.	moderate	"
	2020	Sea Gull Flat	no	from whaler
	2130-2140	Kvichak	no	from *Iliaska*
	2240-2245	"	no	"

Appendix II. Continued.

Date	Time	Listening location	Signal received	Comments
20 Jun	1351	4 km SE Copenhagen Cr. ②	strong	from helo; Mama here; 3 whales seen in area
	1730	8 km S Copenhagen Cr. ③	strong	from helo; Mama here
	1945/2020	Buckley's	no	from bluff
	2210/2245	"	no	"
21 Jun	1157	1.8 km W Graveyard ④	strong	from helo; Mama here; whales seen in area
	1232	⑤	strong	from helo; Mama here
	1430	Naknek R. mouth	strong	from helo; Mama in Graveyard area
	2310	W of Graveyard	weak	from whaler; Mama toward Johnson Hill/Naknek R.
22 Jun	1045	N of Graveyard	no	from whaler
	1108	3 km W Graveyard	no	"
	1129	3-4 km E Copenhagen Cr.	no	"
	1150	3-4 km S Copenhagen Cr.	no	from whaler
	1217	2-3 km off Buckley's	weak	from whaler; Mama to S toward Johnson Hill

Appendix II. Continued.

Date	Time	Listening location	Signal received	Comments
22 Jun, cont.	1237	4 km ESE Second Pt.	no	from whaler
	1307	5 km SW Second Pt.	no	"
	1319	11 km SW Second Pt.	no	"
	1455	3-4 km W Naknek R.	weak	from whaler; Mama on W side somewhere
	1523	5-6 km SSW Graveyard	weak	from whaler; Mama on W side toward Copenhagen Cr.
	1805	4-5 km S Copenhagen Cr. ⑥	strong	from helo; Mama here
23 Jun	1131	1 km S Graveyard	no	from whaler
	1150	5-6 km WNW Bristol Bay cannery	no	"
	1210	mid-Kvichak Bay off Naknek R.	no	"
	1230	7-8 km E Buckley's	no	"
	1328	S Graveyard	weak	from helo; Mama to SW
	1405	6 km E Lake Pt. ⑦	strong	from helo; Mama here
	1425	9 km E Lake Pt. ⑧	strong	"

Appendix II. Continued.

Date	Time	Listening location		Signal received	Comments
23 Jun, cont.	1648	halfway Lake Pt. to Second Pt.	⑨	strong	from whaler; Mama here
24 Jun	1230	Buckley's		moderate	from whaler; Mama to S
	1339	N Halfmoon Bay	⑩	strong	from helo; Mama here
27 Jun	1255	N Halfmoon Bay	⑪	strong	from helo; Mama here
	1502	mid-Halfmoon Bay	⑫	strong	"
28 Jun	1110	4-5 km SW Second Pt.	⑬	strong	from helo; Mama here
	1345	4 km W Second Pt.		moderate	from bluff; Mama to NE toward Graveyard
	1430	4 km W Second Pt.		no	from bluff; Mama out of range to N
29 Jun	1143	King Salmon Cr.		moderate	from helo; Mama to SW
	1410	S Halfmoon Bay	⑭	strong	from helo; Mama here
1 Jul	1200-1300	Naknek R. mouth		no	from bluff
2 Jul	1200-1600	Buckley's to Lake Pt.		no	from whaler; listened every 1/2 hr down and back
3 Jul	1037-1400	Telephone Pt. to Lake Pt.		no	from whaler; listened every 1/2 hr

Appendix II. Continued.

Date	Time	Location	Signal received	Comments
3 Jul, cont.	1410	2 km S Lake Pt.	mod-weak	from whaler; radio to W
	1500	4.6 km SW Lake Pt.	mod-strong	radio recovered on beach with antenna partially buried

APPENDIX III

LISTING OF BELUKHA SIGHTINGS AND OBSERVATIONS IN BRISTOL BAY, MAY - JULY 1983

Appendix III. Listing of belukha sightings and observations in Bristol Bay, May-July 1983.

				Whales		
Date	Time	Location	Tide	No.	Dir.	Comments
KVICHAK BAY						
6 Apr	1215	King Salmon-Naknek R.	ebb	2	down	seen by King Salmon residents
5 May	1000-1015	Halfmoon Bay	ebb/H 0945	83	up	traveling
	1020-1025	Copenhagen Cr.	ebb/H 0945	32		feeding
	1158	Naknek R. mouth	ebb/H 0945	1		feeding
17 May	1043	Copenhagen Cr.	ebb/H 0703	3		
	1109	Naknek R. mouth	ebb/L 1330	70		feeding
19 May	±1230-1300	Naknek R. mouth	ebb/L 1513	many	down out	traveling
25 May	1119-1123	Branch R. to Levelock	ebb/L ±1145	75-80	up	some feeding at river mouth
	1230	Nakeen - off dock	flood/H 1315	50		feeding
	1352-1356	Halfmoon Bay	H 1351	16		
	1404	Albert Pt.	slack or just ebb/ H 1351	6	down	
26 May	1320-1351	Coffee Cr. to N of Kvichak	flood/H 1515	41-43		some feeding
	1400	Nakeen	flood/H 1440	6		feeding
27 May	±0900	Branch R.	ebb/H ±0500	present		
	± 1200	Branch R.	ebb/L ±1340	20-25	down	feeding
	2000	Kvichak	ebb/H ±1600	12+	down	many gulls and 3-4" fishes (smolt) at surface
28 May	0630-0800	Kvichak	ebb/H ±0530	25	down	
	0800-1000	Kvichak	ebb/H ±0530	20		
	±0900	Branch R. mouth	ebb/H ±0600	20-25		
	±1030	Coffee Cr. channel	ebb/H ±0500	38		
	1045	Graveyard to Deadman Sands	ebb-slack/ L 1107	150-200		none Naknek-Graveyard
	±1200	S Sea Gull Flat	slack-flood/ L 1107	some		
29 May	0730-1100	Kvichak	ebb/H 0615	150+	down	calm
	±0830	Coffee Cr. channel	ebb/H ±0600	50-100		
	1630-1730	Kvichak	flood/H 1740	8-10	up	choppy

Appendix III. Continued.

Date	Time	Location	Tide	Whales No.	Dir.	Comments
29 May, cont.	1730-1830	Kvichak	ebb/H 1740	4	up	choppy
	± 1900	Kvichak	ebb/H 1740	± 2	up	choppy
30 May	1030-1045	Kvichak	ebb/H 0700	8-10	down	choppy
	±1000	Salmon Flats to Branch R.	ebb	present		
	±1400	Telephone Pt. area	flood/L 1248	30-50		choppy
	1500-1600	off & N of Graveyard	flood/L 1248	100-150		from helo
	1655-1740	Kvichak	flood/L 1600	80-100	up	calm
	1740	Kvichak	flood/L 1600	8	down	
	2033	Kvichak	ebb/H 1830	2	up	
31 May	0620	Kvichak	flood/H 0740	2	up	calm
	0915-1020	Kvichak	ebb/H 0740	40-60	down	rough
	±0900	Coffee Cr. channel	ebb/H ±0710	12	up	
	±0900	Kvichak to Branch R.	ebb/H ±0800	35	up	
	1101-1104	Graveyard-Copenhagen Cr.	ebb/H 0710	29		
	1112	S end Halfmoon Bay	ebb/L 1330	1		
	1807-1916	Kvichak	flood/H 1915	223	up	calm; at end milling/feeding
	2045-2055	Branch R. mouth	ebb/H 1940	20-25	down	choppy
	2140	Coffee Cr. channel	ebb/H 1840	8	down	choppy
1 Jun	0930-1050	Kvichak	ebb/H 0815	104	down	mod. calm; 1 side of boat only
	1300-1400	Albert Pt.-Copenhagen Cr.	ebb/L 1416	20+	down	
	1925-1945	Kvichak	flood/H ±2000	14	up	
2 Jun	0725	Kvichak	flood/H 0900	1 or 2	up	choppy
	1310-1345	Kvichak	ebb/H 0940	few (10-15)	down	calm
	±1330	Coffee Cr. channel	ebb/L ±1500	few	down	
	±1400	Albert Pt.	ebb/L ±1500	few		
	1430-1500	Copenhagen Cr. area	ebb-slack/ L 1500	±20	up	
	1430-1500	Halfmoon Bay	ebb-slack/ L 1500	100+	up	about 2 mi out

Appendix III. Continued.

				Whales		
Date	Time	Location	Tide	No.	Dir.	Comments
3 Jun	0728	Kvichak	flood/H 0935	2	up	choppy
	1055	Copenhagen Cr.	ebb/H 0902	12+		
	1046-1111	Branch R. mouth + 1 mi	ebb/H 1010	96+	down	
	1230	Branch R. mouth	ebb/H 1010	6	down	
	1140-1225	Kvichak	ebb/H 0940	86	down	to W of *Iliaska* only
	1305-1340	Kvichak	ebb/H 0940	34	down	to W of *Iliaska* only
	1352-1355	Copenhagen Cr.-Nakeen	ebb/L 1540	19-21	down	
	2015	Kvichak	flood/H 2140	5	up	
	1430-1630	Salmon Flats	ebb/L 1540	30-50	down	
4 Jun	0720-0805	Kvichak	flood/L 0600	30+	up	smolt activity at surface; feeding
	1032-1034	Branch R. & above	ebb/H ±1030	85	down	helo count
	1105-1155	Branch R. mouth area	ebb/H ±1030	201	down	boat count (both sides)
	1054-1057	Nakeen-Albert Pt.	ebb/H 0940	16	down	
	1142-1144	Graveyard	ebb/H 0940	12		
	1145-1149	Kvichak to Branch R.	ebb/H ±1000	22		helo
	±1400	King Salmon Cr.-Copenhagen Cr.	ebb/L 1620	10-15+		
	±1600	Telephone Pt.	ebb-slack/ L 1620	few		
5 Jun	1410	1/2-3/4 mi off Peterson Pt. area	ebb/H 1050	30-50	down	
	1515	Halfmoon Bay	ebb/L 1740	12+		
	1630	Naknek R. mouth	ebb/L 1740	30+		feeding
	1700	4 mi off Halfmoon Bay	ebb/L 1740	8		choppy
	2330-0000	Kvichak	flood/H ±0025	some		heard but didn't see
7 Jun	2205-2235	Graveyard	flood/H 0045	100+	up	
	2235-2330	Nakeen	flood/H 0045	5-10+ some	up	same ones seen 1 hr earlier at Graveyard
8 Jun	0905-0930	Telephone Pt.-Graveyard	flood/L 0640	3		conditions poor
	1830-1900	Halfmoon Bay	ebb-slack/ L 1900	few		light chop

Appendix III. Continued.

				Whales		
Date	Time	Location	Tide	No.	Dir.	Comments
8 Jun, cont.	2000-2200	Big Flat - 1-2 mi S of Naknek R.	flood/L 1900	75+ (prob. 100-200)		milling/feeding
9 Jun	1920	mid-Halfmoon Bay	ebb-slack/ L 1940	3-5		choppy
	1925	mid-Kvichak Bay	ebb-slack/ L 1940	10-15		
	1940	Naknek R. mouth	slack/L 1940	±10		milling; choppy
10 Jun	1337	Copenhagen Cr. to King Salmon	slack/H 1330	10+		
	2000	Naknek R. mouth	slack/L 2020	2-3		poor conditions; milling
11 Jun	0830	The Bend	ebb/L 0930	present		
	1030-1130	Big Flat/Naknek R.	flood/L 0930	50+ (prob. 100+)	up	in deep water
	1400-1600	central Halfmoon Bay	slack-ebb/ H 1430	10-20+ present		
12 Jun	1630-1700	mid-Halfmoon Bay	ebb/H 1520	50-100; many	up	light chop
13 Jun	1035	Naknek R. - 1 mi W	ebb/L 1120	1		choppy; milling
	1140	mid-Halfmoon Bay	slack/L 1120	few		
	1630-1650	Lake Pt. area	slack-ebb/ H 1615	20+	up	calm
14 Jun	1000-1200	Big Flat	ebb/L 1214	100+		milling/feeding
	1607-1617	Halfmoon Bay-Lake Pt.	flood/H 1720	40+	up	traveling very close to shore
	1745-1748	Halfmoon Bay	ebb/H 1720	22	up	
	1758-1759	Nakeen-Sea Gull Flat	ebb/H 1720	10+		
	1812-1814	Sea Gull Flat-Graveyard	ebb/H 1720	21	down	
15 Jun	1030-1330	Big Flat	ebb/L 1310	>125 (prob. ± 200)	down	swimming here from E; feeding toward end
	1640-1710	Big Flat	flood/H 1823	present		chop
16 Jun	1200	Naknek R. mouth	ebb/L 1400	10-20	down	
	1230-1330	Big Flat	ebb/L 1400	100+		milling/feeding
	± 1500	Halfmoon Bay	flood/L 1400	several 100's		

Appendix III. Continued.

Date	Time	Location	Tide	Whales		Comments
				No.	Dir.	
16 Jun, cont.	1630-1700	Halfmoon Bay	flood/L 1400	70+	up	chop; some milling
	1833	Graveyard	flood/H 1930	3+	up	
17 Jun	A.M.	Leader Cr.	H 0830	6 or 7		in river; report by fisherman
	1911-1918	Graveyard/Coffee Cr. channel	flood/H 2040	23+	up	
	2130	Nakeen-Sea Gull Flat	ebb/H 2040	20-25	down	
18 Jun	0943-0944	Branch R.	slack-flood/ H 1010	6	down	
	0948-0956	Nakeen - Graveyard - Sea Gull Flat	H 0910	30-50	down	
	0958	King Salmon Cr.	ebb/H 0910	1		
	1004-1033	Halfmoon Bay	ebb/H 0910	30+	down	some milling
	1043-1046	Graveyard-Libbeyville	ebb/H 0910	86+	down	feeding
	1530	Halfmoon Bay	ebb-slack/ L 1550	30-50+		
19 Jun	1252	Telephone Pt.	ebb/H 1003	1	down	
	1430-1530	Halfmoon Bay	ebb/L 1640	few		
	2150	Kvichak	flood/H 2330	1	up	
20 Jun	1310	Kvichak	ebb/H 1130	1	down	
	evening	Kvichak dock	flood/L 2020	few		reported by Commercial Fish Div.
21 Jun	1000	Coffee Cr. channel	flood/H 1140.	1		
	1115-1200	Nakeen - Sea Gull Flat - Graveyard	flood-slack/ H 1140	50+	up	
	1232	W of Graveyard	ebb/H 1140	20+	down	
	2255	Telephone Pt.	flood/H 0108	2		
	2300	Naknek R. area	flood/H 0108	present		
22 Jun	1045	Graveyard	flood/L 0700	1 or 2		choppy
	1730	Deadman Sands	ebb/L 1910	small group		
	2214	Coffee Cr. channel	flood/L 1910	1	up	
	2330	Kvichak	flood/L 2200	several		

Appendix III. Continued.

				Whales		
Date	Time	Location	Tide	No.	Dir.	Comments
23 Jun	0010	Kvichak	flood/L 2200	several	up	
	1320-1330	Graveyard-Bend	slack-ebb/ H 1320	20+	down	
	1400-1420	Halfmoon Bay-Lake Pt.	ebb/H 1330	many		milling
24 Jun	± 1200	Halfmoon Bay	flood/H 1410	many		feeding
	1330-1331	Graveyard	flood/H 1410	2		
	1336	Albert Pt.	flood/H 1410	2+		
	1339-1343	Halfmoon Bay	flood/H 1410	11+		
	1347	Lake Pt., N of	flood/H 1410	2		
27 Jun	1250	Copenhagen Cr.	flood/L 1135	few present		
	1255	Halfmoon Bay	flood/L 1135	present		none on E side of Bay
	1505	King Salmon Cr.	flood/H 1630	35+		
28 Jun	1057	Copenhagen Cr.	ebb/L 1221	57		
	1100-1146	Halfmoon Bay	ebb/L 1221	124	up	feeding
	±1900	Halfmoon Bay	ebb/H 1720	±60	up	300 m offshore
29 Jun	A.M.	E side Graveyard & Kvichak R.	ebb/H 0637	0		surveyed
	1353-1410	Halfmoon Bay	flood/L 1303	202	up-113 down-89	
	1429	Lake Pt. area	flood/L 1303	6		feeding
30 Jun	0400-0700	Nakeen/Sea Gull Flat	flood/H 0713	25+		feeding
2 Jul	A.M.	Sea Gull Flat		present		
3 Jul	1115-1125	below Graveyard	ebb/H 0852	100+		milling/feeding
	1620	S of Lake Pt.	flood/L 1540	20+		feeding
	1820	Copenhagen Cr.	flood/L 1540	5+		
	1830-1900	S of Graveyard	flood/L 1540	present		
4 Jul	0945	Nakeen-Sea Gull Flat	slack-ebb/ H 0930	100+		
	1015	N Copenhagen Cr.	ebb/H 0930	30+	down	feeding; in among nets
	2100	Coffee Cr. channel	flood/H 2230	5-10		

Appendix III. Continued.

				Whales		
Date	Time	Location	Tide	No.	Dir.	Comments
5 Jul	1005	Nakeen- Sea Gull Flat	slack/H 1000	10-20		
	1300	King Salmon Cr.	ebb/H 1000	80-100	down	
6 Jul	±1145	S of Graveyard	ebb/H 1040	few		
7 Jul	1320-1350	King Salmon-Copenhagen Cr.	ebb/H 1120	400+	down	some stopped to feed
12 Jul	±0100-0200	Graveyard	flood/H 0434	present		
	0558	S Nakeen	ebb/H 0434	2		
	0615	N Graveyard	ebb/H 0434	200+	up	
14 Jul	1345-1450	King Salmon-Copenhagen Cr.	flood/L 1240	50+		milling
14 Aug	1525	SW of Halfmoon Bay	flood/L 1401	127		in very shallow water
	1546	Halfmoon Bay	flood/L 1401	179		resting or feeding
	1557	Naknek R. mouth	flood	3	up	traveling
NUSHAGAK BAY						
15 Apr	0923	Snake R. mouth	ebb/L 1012	10	down	all adults
	0932	Snake R., near Weary R.	ebb/L 1012	3		feeding, up as far as ice permitted
	0945	Igushik R. mouth, N of	ebb/L 1012	24	N	feeding in very shallow water
	0956	Igushik R., big bend	ebb/L 1012	13		feeding in shallows
	1004	Clarks Pt.	ebb/L 1012	4		
	1012	Etolin Pt.	ebb or slack/ L 1012	5		feeding
2 May	1601-1605	Snake R.	flood/L 1357	7	up	
5 May	0932	Ekuk	flood/H 0945	5		traveling
	0939-0944	Etolin Pt. area	flood-slack/ H 0945	2		traveling
15 May		Nushagak R., Black Pt.		present		from Doug McCart of Armstrong Air
17 May	0935-0937	Snake R., near mouth	ebb/H 0703	4	down	
	±0940	Snake R., near Weary R.	ebb/H 0703	7		
	0951	Igushik R. mouth	ebb/H 0703	2		

Appendix III. Continued.

				Whales		
Date	Time	Location	Tide	No.	Dir.	Comments
17 May, cont.	0952-1005	Igushik R., in river	ebb/H 0703	10		
31 May	1141	Grassy Is.	ebb/L 1332	2		
	1146-1250	Little Muklung R. mouth	ebb/L 1332	8		
3 Jun	1310	mid-Bay, Igushik to Ekuk	ebb/L 1538	20-30	NW	grays and whites
14 Jun	1647	Snake R.; in river	flood/H 1719	2		
	1650-1710	Snake R. mouth & S	flood/H 1719	6		
	1655	Igushik R. mouth	flood/H 1719	?		
	1700	Igushik R., near big bend	flood/H 1719	7		
	1724	Nushagak R., Lewis Pt.	slack/H 1719	2		
24 Jun	1359	Etolin Pt.	flood/H 1411	1		very close to shore
	1422-1423	Coffee Pt.	slack or ebb/ H 1411	3		
	1426-1433	Snake R. mouth	ebb/H 1411	50+		feeding/milling
	1602	Little Muklung R. mouth	ebb/H 1411	12		
27 Jun	1320	Little Muklung R. mouth	flood/L 1135	24+		milling, very close to shore
	1330-1400	Snake R. mouth to Coffee Pt.	flood/L 1135	54		
	1337-1338	Igushik R. mouth, N of	flood/L 1135	15		
29 Jun	1503-1510	Coffee Pt.	flood/L 1303	2		
	1520-1530	Snake R. mouth	flood/L 1303	107		
	1540	Igushik R. mouth	flood/L 1303	4		
	1546	Igushik R., near big bend	flood/L 1303	13		
12 Jul	1440-1450	Clarks Pt.-Ekuk	flood/H 1559	90+	down	among and W of processor fleet
13 Jul	1145-1255	Snake R., in river	slack-flood/ L 1148	25+	up	very close to bank
	1400	Snake R. mouth, E of bar toward Clarks Pt.	flood/L 1148	87+		conditions poor for counting
	1445	Grassy Is.	flood/H 1705	1		
14 Jul	1226	Snake R. mouth	ebb-slack/ L 1241	12		

Appendix III. Continued.

				Whales		
Date	Time	Location	Tide	No.	Dir.	Comments
14 Jul, cont.	1230	in Snake R.	ebb-slack/ L 1241	15	up	
	1315	Clarks Pt.	flood/L 1241	96		
	1321	Ekuk	flood/L 1241	11		

APPENDIX IV

BECAH-CAST BELUKHA CARCASSES FOUND IN NUSHAGAK AND KVICHAK BAYS, MAY - JULY 1983

Appendix IV. Beach-cast belukha carcasses found in Nushagak and Kvichak bays, May-July 1983.

Specimen number	Location	Date	Sex	Std. length	Girth	Fluke width	Comments
BBD-1-83	Scandinavian Landing, Nushagak Bay	11 May	F	259.1	157.5	55.9	caught in king salmon net; color-gray; saved skull, stomach, repro; hide and blubber at sternum-5.1 cm
BBD-2-83	"	11 May	F	280.7	156.2	66.0	caught in king salmon net; color-gray; saved skull, stomach, repro; hide and blubber at sternum-7.9 cm
BBD-3-83	Nakeen Cannery, Kvichak River	26 May	F	320	173	65.0	found floating; dead for several days; no obvious cause of death; color-gray; saved skull, stomach, repro
BBD-4-83	Between mouths of Snake and Igushik rivers	3 Jun	M	310	-	-	recently dead; stomach empty; no obvious cause of death; saved skull
BBD-5-83	1-2 km below S end of Coffee Cr. channel	6 Jun	M	380	-	-	found high up in grass; estimated dead 3+ weeks; saved skull
BBD-6-83	near Etolin Point village	21 Jun	M	410	-	-	very old carcass, probably >1 year; upper jaw missing, lower one broken (saved)

Appendix IV. Continued.

Specimen number	Location	Date	Sex	Std. length	Girth	Fluke width	Comments
BBD-7-83	Flounder Flat, about halfway between Etolin Pt. and Ekuk	21 Jun	M	230	-	-	bullet holes mid-body; dead several weeks; saved lower jaw
BBD-8-83	"	21 Jun	U	-	-	-	very old carcass, probably >1 year; posterior 1/3 to 1/2 gone; very large
BBD-9-83	Igushik Beach camp	21 Jun	M	139	-	-	estimated 30 kg; 3" umbilicus; on beach about 1-1/2 weeks
BBD-10-83	1-2 km S of Igushik Beach camp	21 Jun	M	± 360	-	-	old carcass, on beach last year
BBD-11-83	mid-Halfmoon Bay	28 Jun	M	343	-	-	old carcass; jawbone exposed; skin dried; skull saved
BBD-12-83	near Lake Point	28 Jun	M	127.3	-	-	fetus or premature calf, too small for normal newborn; carcass 1-2 weeks old
BBD-13-83	southern Halfmoon Bay	28 Jun	F	192	-	-	yearling, no erupted teeth; caught 23 Jun by set-netter Jim McDade; gray

Appendix IV. Continued.

Specimen number	Location	Date	Sex	Std. Length	Girth	Fluke width	Comments
BBD-14-83	mid-Halfmoon Bay	4 Jul	F	250	-	-	caught in setnet by Jim McDade on night of 2 Jul; gray; stomach empty; teeth erupted
BBD-15-83	"	4 Jul	M	150	94.5	31.5	washed up on beach 3 Jul, fresh; neonate; caught near flukes in net
BBD-16-83	southern Flounder Flat	15 Jul	F	137.2	-	25.1	neonate with umbilicus
BBD-17-83	near Etolin Point village	15 Jul	M	139.1	-	26.7	neonate without umbilicus
BBD-18-83	Etolin Point	15 Jul	M	138.4	-	-	neonate; missing right pectoral; maggots
BBD-19-83	"	15 Jul	M	139.4	-	29.8	neonate; umbilicus rotted out; no obvious cause of death
BBD-20-83	halfway between Lake Pt. and Etolin Pt.	15 Jul	F	143.5	-	-	umbilical scar not healed; missing left pectoral
BBD-21-83	mid-Halfmoon Bay	18 Jul	M	est. 335	-	-	probably dead ≥ 1 week; flukes cut off; tooth taken from lower jaw; possibly the whale reported by the *Silver Surfer* on 11 Jul

APPENDIX V

INFORMATION ON BELUKHA WHALE MORTALITY IN BRISTOL BAY, MAY - JULY 1983

Appendix V. Information on belukha whale mortality in Bristol Bay, May-July 1983.

4-8 May	One belukha taken, probably by shooting, near Black Point, Nushagak River. The carcass was given to Stepan Pat in Dillingham.
11 May	Two small gray female belukhas (BBD-1-83; BBD-2-83) caught and drowned in king salmon setnets at Scandinavian Landing, Nushagak Bay.
10-20 May	Two belukhas taken (hunted) by people at Levelock, according to Dick Russell of Commercial Fisheries Division, King Salmon.
	According to John Wright of Subsistence Division, Dillingham, the villages of Clark's Point and Manokotuk each take about 2 belukhas per year.
26 May	Dead gray female belukha (BBD-3-83) found floating near Nakeen. Dead for several days, no obvious cause of death.
1 June	Report received by ADF&G from Bumblebee Cannery that the fishing vessel *Pluto* had a dead belukha. No further details available. We were unable to contact the *Pluto*.
1-6 June	Four belukhas caught in commercial king-salmon drift nets in Nushagak Bay, according to Ken Taylor, Game Division, Dillingham.
3 June	On a survey of Kvichak and Nushagak bays for beach-cast carcasses, one white male belukha (BBD-4-83) was found on the beach between the Snake and Igushik rivers. The carcass was fresh, cause of death was not obvious.
6 June	Dead male belukha (BBD-5-83) found on tundra north of Graveyard Point. Whale had been dead for quite a while (3+ weeks), bear tracks all around it.
9 June	Small male belukha caught in king-salmon setnet about 7 km south of Naknek River mouth at 1530-1930. This whale (BB) was rescued and subsequently tagged and tracked for 2 weeks until the radio came off.
10 June	A small (2.5-2.75 m) dead belukha was found on the beach near the north point at the entrance to the Naknek River. This was a very old, long-dead carcass, badly decomposed and beaten up. The lower jaw was missing.

Appendix V. Continued.

17 June	Employee at Bumblebee Cannery reported a dead belukha on the beach about 18 km south of Johnson Hill. We surveyed this area on 18 June and did not find it.
21 June	Aerial survey flown of Kvichak and Nushagak bays for beach-cast carcasses. Six belukha carcasses were found, 4 of which may have been dead for over (or up to) 1 year. One was located about 5 km southwest of Lake Point. The skull was smashed and mostly gone; probably dead over a year; no specimens taken. Two other very old carcasses were found near Etolin Point and Flounder Flat (BBD-6-83; BBD-8-83) and another (BBD-10-83) about 2 km south of Igushik Beach. This one was known to be dead over 1 year (local set-netters had seen it last year). A gray juvenile male (BBD-7-83) dead several weeks, with bullet holes in the mid-body region, was found about halfway from Ekuk to Etolin Point village. A male neonate (BBD-9-83), umbilicus attached, was found at Igushik Beach. Local residents said it had been there about 1-1/2 weeks.
28 June	Aerial survey for beach-cast carcasses was flown of Kvichak Bay. Three dead belukhas were found on the west side. One (BBD-11-83) was a very old carcass of a male, lower jaw exposed and skin very dry. One was a premature male calf (BBD-12-83), dead at least 1-2 weeks, and the third (BBD-13-83) was a yearling female. We subsequently found out this one was caught at night on 23 June by a set-netter (Jim McDade) on the west side. It was covered with sand by the local folks on 3 July. On 15 July it had washed out of the sand and moved north about 1-2 km, where we located it on an aerial survey.
4 July	Two carcasses were found on the west side of Kvichak Bay in central Halfmoon Bay. One (BBD-14-83) was a subadult female that had been caught in a setnet the night of 2 July by Jim McDade. The other was a neonate (BBD-15-83) with umibilicus that washed up on the beach on 3 July. Both of these carcasses were towed offshore into deep water after examination.
6 July	Dick Russell received a call about another dead belukha on the west side of Kvichak Bay. We looked for it on the 7th but did not find it.
11 July	Crew of the *Silver Surfer* told us they caught a 3.4-3.7-m belukha sometime the previous week. The whale was caught at night, in the distal 2-3 m of their drift net. It was tangled in the web and float and lead lines. They cut the flukes off to get it out of the net and threw it overboard. It was white when it came aboard but later turned gray.

Appendix V. Continued

14 July	An aerial survey for beach-cast carcasses was flown of Kvichak and Nushagak bays. Six belukha carcasses were located: 1 small ($\leq$ 3 m) animal about 2 km south of Igushik Beach; 3 neonates around Etolin Point; and 2 subadults, 1 in mid-Halfmoon Bay and 1 south of Lake Point.
15 July	An aerial survey was flown from Clark's Point to northern Halfmoon Bay to relocate and take specimens from belukha carcasses seen on 14 July. Five neonates (BBD-16 to 20-83), 3 presumably the same as the 3 seen on the 14th, were located between Flounder Flat and Lake Point. In addition, 1 juvenile without a head was seen south of Buckley's (probably BBD-14-83), and the carcass we examined on 28 June (BBD-13-83) was seen about 1 km north of Buckley's.
18 July	An adult male, estimated 335 cm, was found in mid-Halfmoon Bay. It had been dead a week or so; the flukes were missing. This may have been the dead whale caught by the *Silver Surfer* and reported to us on 11 July.

BELUKHA WHALE (Delphinapterus leucas) RESPONSES TO INDUSTRIAL NOISE IN NUSHAGAK BAY, ALASKA: 1983

by

Brent S. Stewart, Frank T. Awbrey, and
William E. Evans

Hubbs-Sea World Research Institute

Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 629

1983

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Stewart et al. (1982) reported that belukha whales in Snake River, Alaska did not appear to react strongly to playbacks of oil industry-related noise at levels up to 60 dB above ambient, and they suggested that sound quality is more important than sound quantity in eliciting responses. Noise from outboard motors, for example, seemed to cause aversion even when it was barely perceptible. Playback experiments with captive belukhas indicated that whales acclimate more quickly to some sounds than to others (Thomas and Kastelein 1983, Awbrey et al. 1984). Observations of free-ranging and captive belukha whales also suggested that responses of belukhas to sounds are affected strongly by habitat and by the whales' activity (Stewart et al. 1982).

Between 15 June and 14 July 1983 we conducted playback experiments with belukha whales in the Snake River, Alaska, using sounds recorded near an operating oil drilling rig. The objectives of these experiments were to quantify behavioral responses of belukha whales to oil drilling noise in an area where foreign acoustic stimuli were absent, and to test the hypothesis that belukha whales would not approach a source of loud sound.

Observations made in 1982 showed that belukhas would leave an area when outboard motor noise was present, regardless of their previous activity, swim direction, or tide conditions. We hypothesized that their response to oil rig noise would be similar. If whales did remain in the river during playback, we hypothesized that they would neither approach nor pass through the area of the playback sound source.

METHODS

Research in the Snake River, Alaska, was conducted from 15 June to 14 July 1983. Observations were made from a 32' motor vessel anchored about 30m off the east bank near "Belukha Point" (Figure 1). The boat's engines were run infrequently (only to reset the anchor) to prevent that noise source from affecting normal behavior of whales or from interfering with playback experiments.

Collection of Behavioral Data

Data on whale presence, swim direction, group size and composition, distance from shore, spacing between individuals (in body lengths), respiration rates, intervals between blows, general activity and response to disturbances were collected daily between 15 and 21 June and 4 and 13 July (Table I). Data were collected using focal animal and focal group sampling techniques (Altman 1974) similar to those used by Stewart et al. (1982). Observations, including group size and composition, swim direction and timing of respirations, were recorded on cassette tapes. For groups of less than three whales, focal animal sampling was used to record all respirations of each whale. For groups of more than three, the number of whales in the group was first determined and the total number of respirations for the group was recorded for the observation period. Blow interval is defined as the elapsed time between each blow or surfacing; these data were obtained for focal animals only. Respiration rate is defined as the number of respirations per whale per minute; these data were obtained for both focal animals and focal groups.

Intervals and rates were determined for the following treatments:

1) Whales moving down river/tide falling/undisturbed
2) Whales moving down river/tide falling/disturbed
3) Whales moving down river/tide falling/after disturbance
4) Whales milling/undisturbed
5) Whales milling/disturbed

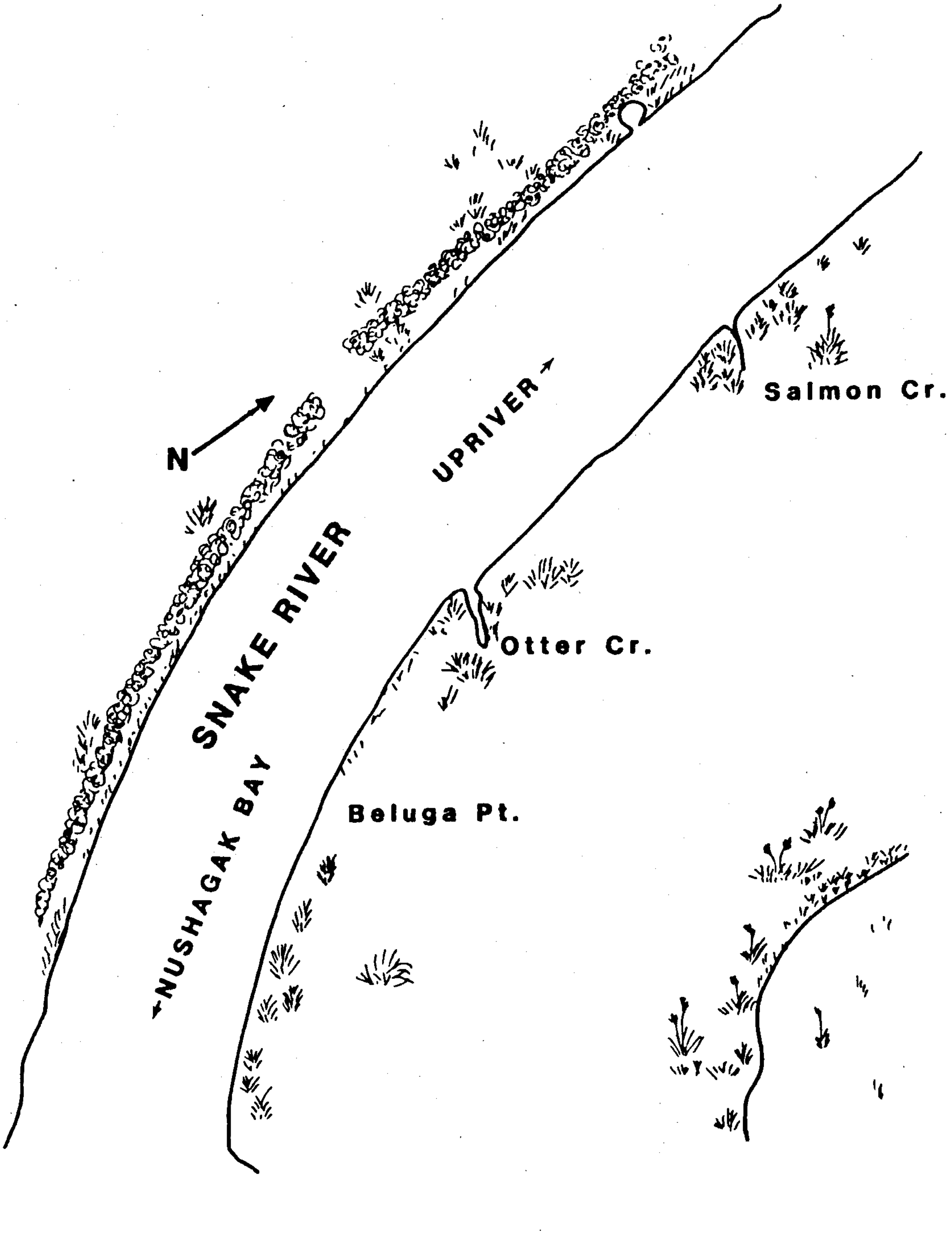


Fig. 1. Map of belukha whale study area on the Snake River during June-July 1982 and 1983

Table I. Effort summary of Belukha whale observations in Snake River, Nushagak Bay, Alaska; 15 June - 13 July 1983.

Date	Begin observations	End observations	Hrs. observations
15 June	0900	1800	9.0
15 June	1900	2100	2.0
16 June	0700	1400	7.0
16 June	1600	2200	6.0
17 June	0700	2230	15.5
18 June	0830	2300	14.5
19 June	0800	1200	4.0
19 June	1400	1500	1.0
19 June	1645	2300	6.25
20 June	0800	1400	6.0
20 June	1830	2100	2.5
21 June	0900	2300	15.0
4 July	1900	2230	3.5
5 July	0700	2200	15.0
6 July	0730	2230	15.0
7 July	0730	2230	15.0
8 July	0730	2300	15.5
9 July	0730	2300	15.5
10 July	0630	2330	17.0
11 July	0500	2230	17.5
12 July	0500	2330	18.5
13 July	0500	0800	3.0
		Total	224.25

6) Whales milling/after disturbance

7) Whales moving upriver/tide falling/undisturbed

8) Whales moving upriver/tide falling/disturbed

9) Whales moving upriver/tide falling/after disturbance

A t-test was used to test for differences among 'disturbed', 'undisturbed' and 'post-disturbed' treatments.

Acoustic Data Collection and Analysis

The system used to collect and record sound pressure level and spectral data consisted of a calibrated ITC 6050C hydrophone (sensitivity 11.75mv/Pa; frequency response 30 Hz to 50 kHz ± 3 dB) and a Nagra IV SJS tape recorder (frequency response 20 Hz to 35 kHz ± 2 dB at 38.1 cm/s). The hydrophone was suspended from the boat by an elastic band to reduce acceleration noise. The recorder has precision 1 dB step attenuators and is designed to be used for making sound level measurements. Its meter reads "peak" (5 ms time constant) sound level (SL). Insert calibration voltages corresponding to known underwater SL's were recorded on each tape and used to set the engineering units scale of a Spectral Dynamics model 345 FFT spectrum analyzer to read directly in decibels re 1 Pa or re 1 Pa^2/Hz, as appropriate, when the tapes were analyzed. Ambient sound pressure and spectral levels were measured and recorded at various sites in the river. Results were the same as reported in the Year I report.

Playback Experiments

All playback experiments used an Acoustic Systems, Inc. TS107A underwater sound projector (a specially modified battery-operated 100 watt per channel 2-channel amplifier driving a LuBell Labs model 98 underwater loudspeaker), which can produce SL's as high as 180 dB re 1 Pa at 1m. Recordings of the sounds from SEDCO 708 semi-submersible drilling platform recorded at 0.1nmi, hydrophone depth 30m, were supplied by Polar Research Labs (PRL). The source level of this sound computed by PRL is 154dB re 1 Pa. The actual average levels on the tape vary about 5dB. The tape segment recorded at this distance and hydrophone depth on the cassette supplied to us was about 7 min. long. It contained numerous signal dropouts where high voltages generated by acceleration of the hydrophone as it was moved by wave action caused the preamplifier to block. This problem was surmounted by copying the cassette onto reel-to-reel tape at 38 cm/sec, cutting out the segments with no signal, and then splicing together the taped segments containing good signals. This procedure yielded a 4 minutes long tape with no obvious splice noise or signal dropouts. Eight duplicates of this tape were spliced together to make a 32 minute submaster for making playback cassettes. These cassettes were recorded on the same Sony TCD5 used for field playback. A spectrum analyzer was used to compare the signal on the final cassette with that on the Polar Research Labs cassette to ascertain that signal degradation was acceptably low. Belukha whale vocalizations were analyzed with the FFT spectrum analyzer and a Kay Elemetrics Model 6061B sonagraph.

Playback Experiment Design

Two kinds of playback experiments were conducted. Both used a 30 minute cassette of SEDCO 708 semi-submersible drilling platform as the noise source. Eleven of 13 playbacks involved whales first seen approaching within 1.5km or less of the boat. With the amplifier's level control set at minimum, the playback system was turned on, the tape started and then the level control was advanced smoothly within about 5 seconds to a preset point. At this setting the playback level measured with the hydrophone 1 m from the projector ranged between 158 and 163 dB re 1 μPa. Any effects on the whales' behavior were noted. Playback was stopped when no whales had been seen for at least one minute.

The second type of experiment tested the hypothesis that the whales would not approach and pass the sound source. In these two sessions, playback was started as soon as possible after the whales came into view around a river bend 4.6km upstream. It continued until (i) the cassette ended, (ii) the whales passed the boat or (iii) turned back.

Aerial Surveys

Number and distribution of belukha whales in Nushagak Bay and its estuaries was documented from six aerial surveys (Table II). Surveys were flown in a single engine, high wing, Cessna 185 (bubble windows) or a Cessna 210 Station Air at altitudes of 150m to 300m. Survey routes were parallel to the coastline (.5km offshore or along one bank when rivers were surveyed) and were essentially identical on all flights (Fig. 2). Survey teams consisted of a senior observer, pilot (who also spotted whales), and occasionally a third observer. Both sides of the track line were monitored on all flights. The track line itself was monitored when surveys were flown in the Cessna 185. A specified transect width was not surveyed but, instead, observers recorded all whales observed at the surface. Position, size and composition of whale groups, and direction of whale movement were recorded on maps and cassette tapes for all sightings.

Table II. Distribution and abundance of Belukha whales in Nushagak Bay, Alaska; June-July 1983.

Date	Lat./Long	Total No. whales	No. groups
4 June	58°47'N/158°34'W	24	3
4 June	59°01'N/158°41'W	9	2
11 June	58°43'N/158°42'W	5	1
11 June	59°03'N/158°23'W	15	1
11 June	58°47'N/158°45'W	13	1
11 June	58°52'N/158°45°W	2	1
11 June	58°47'N/158°53'W	5	1
23 June	58°49'N/158°39'W	3	1
23 June	58°52'N/158°36'W	20	1
23 June	58°53'N/158°37'W	3	1
23 June	59°02'N/158°24'W	3	1
23 June	59°02'N/158°21'W	10	1
23 June	58°45'N/158°46'W	22	1
23 June	58°49'N/158°45'W	9	1
23 June	58°50'N/158°45'W	13	1
23 June	58°50'N/158°45'W	12	1
23 June	58°54'N/158°46'W	1	1
23 June	58°56'N/158°45'W	4	1
23 June	58°57'N/158°48'W	1	1
23 June	58°58'N/158°47'W	3	1
23 June	58°47'N/158°51'W	1	1
23 June	58°48'N/158°49'W	2	1
23 June	58°48'N/158°50'W	4	1

23 June	58°48'N/158°52'W	5	1
23 June	58°48'N/158°52'W	4	1
30 June	59°42'N/158°42'W	60-70	1
30 June	58°47'N/158°41'W	40	1
30 June	58°51'N/158°33'W	1	1
30 June	58°50'N/158°40'N	4	1
30 June	58°52'N/158°38'W	2	1
30 June	58°53'N/158°37'W	1	1
30 June	59°03'N/158°23'W	7	1
30 June	59°04'N/158°22'W	2	1
30 June	58°47'N/158°53'W	8	1
30 June	58°48'N/158°50'W	12	1
30 June	58°57'N/158°48'W	1	1
30 June	58°56'N/158°46'W	1	1
14 July	58°48'N/158°35'W	3	1
14 July	58°53'N/158°33'W	70	1
14 July	58°55'N/158°34'W	15	1
14 July	58°56'N 158°32'W	200	1
14 July	59°01'N/158°27'W	40-50	1
14 July	58°49'N/158°44'W	25-30	1
14 July	58°56'N/158°45'W	2	1
14 July	58°58'N/158°46'W	10	1
14 July	58°47'N/158°51'W	2	1
18 July	58°44'N/158°38'W	400	1
18 July	58°47'N/158°34'W	40	1
18 July	59°03'N/158°23'W	12-15	1

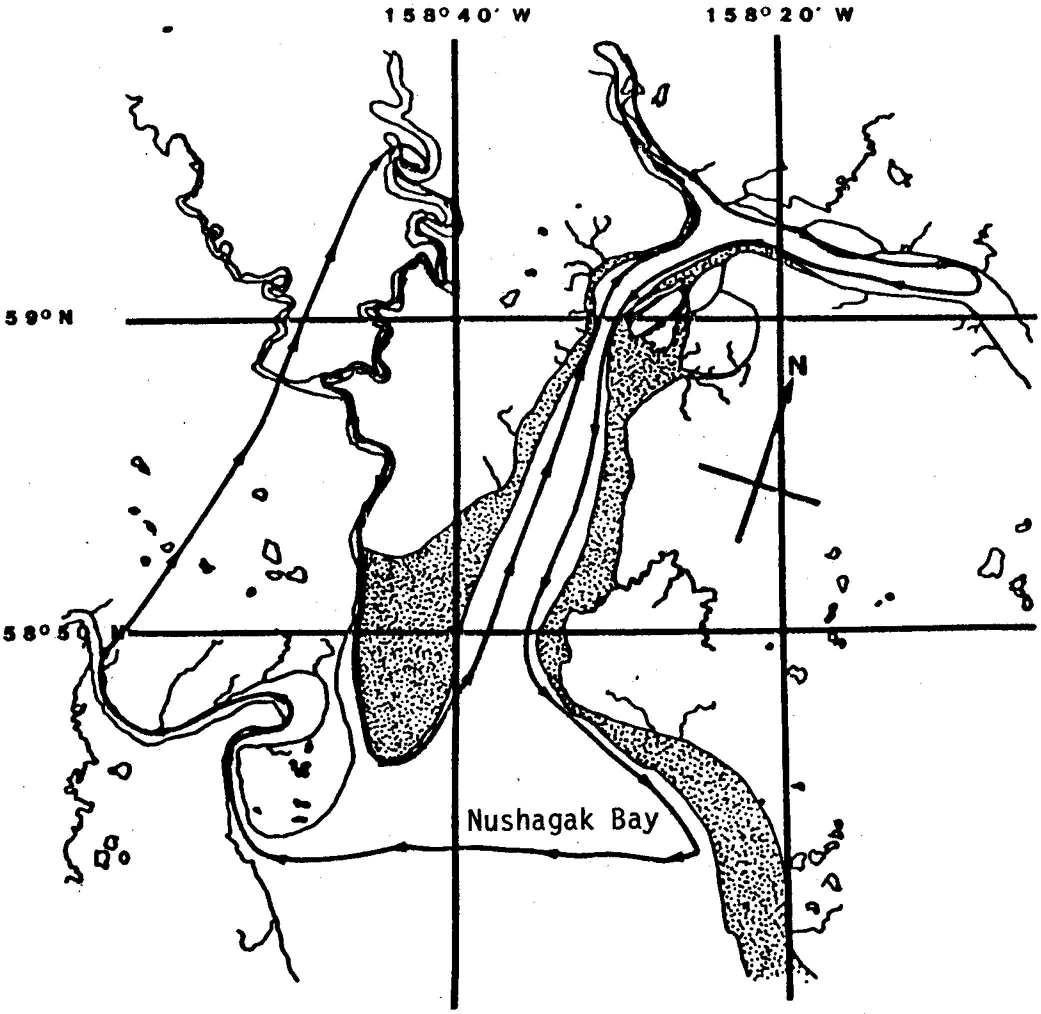


Fig. 2. Route flown on six aerial surveys in Nushagak Bay and its tributaries between 4 June and 13 July 1983.

RESULTS

Distribution and relative abundance of belukha whales in Nushagak Bay; 4 June to 18 July 1983.

Few whales were seen in Nushagak Bay in early June (Table VI). Abundance apparently increased steadily through mid-July when about 454 whales were seen, most just outside the mouths of the Snake and Igushik Rivers (Table VI, Fig. 3). Throughout the study period most whales were seen outside the mouth of the Snake River and near Clark's Point. Smaller numbers, however, were seen regularly near the mouth of the little Muklung River, at the confluence of Wood and Nushagak Rivers. The largest number of groups were seen between 23 June and 14 July, when whales were the most dispersed. Belukha whales prey on adult salmon beginning mid June (Brooks 1954, 1955, 1956; Lensink 1961; Seaman et al. 1982; Frost et al. 1984, Stewart and Awbrey, unpublish. data) and their presence and relative abundance in Nushagak Bay and its tributaries is apparently related to salmon abundance. Our observations in 1982 and 1983 indicate that calves are born in early to mid June. The presence of whales in the Snake and Igushik Rivers at this time may be related to calving.

Effects of sound playback (SEDCO 708) on the Behavior of Belukha Whales in Snake River, AK.

Thirteen playback experiments (using recorded noise from the drilling Rig SEDCO 708) were conducted from 19 June to 13 July (Table III). Data were sufficient only for comparisons of whales milling or moving upriver or downriver on falling tides before, during, or after disturbances (Table IV).

Table VI. Approximate seasonal abundance of Belukha whales in Nushagak Bay; June to July 1983.

Survey Date	Time	Total No. whales	Total No. groups	Average group size
4 June	1340-1540	33	5	7 ± 3
11 June	1435-1556	40	5	8 ± 6
23 June	1410-1604	120	18	7 ± 6
30 June	1355-1530	144	12	12 ± 19
14 July	1500-1627	375	9	42 ± 63
18 July	1401-1550	454	3	151 ± 215

Table V. Summary of Belukha presence in Snake River observation and direction of whale movement.

Date	Hours whales present	Direction of movement		
		Upriver	Downriver	Milling
15 June	No whales seen			
16 June	0930-1030		x	
	1800-1830	x		
17 June	No whales seen			
18 June	1000-1030		x	
19 June	1920-2130		x	
	2215-2230		x	
20 June	1300-1330		x	
	2100-2130			x
21 June	2015-2350	x		
	2245-2300			x
4 July	No whales seen			
5 July	0915-0930	x		
	1945-2015			x
6 July	0750-0800	x		
	0830-0835		x	
	0850-0900	x		
	1100-1115			x
7 July	0830-1030			x
	1630-1640		x	
	2100-2130	x		x
8 July	0930-0950		x	x
	1140-1200		x	
	2200-2230		x	x

9 July	1830-1850	x		
	1920-1950	x		
	2110-2130	x		
	2220-2230	x		
10 July	0650-0720	x		
	1020-1030	x		x
11 July	0520-0550		x	
	0830-0930	x		
12 July	0515-0600		x	
	0620-0650		x	
13 July	0520-0630	x	x	
	0750-0820		x	

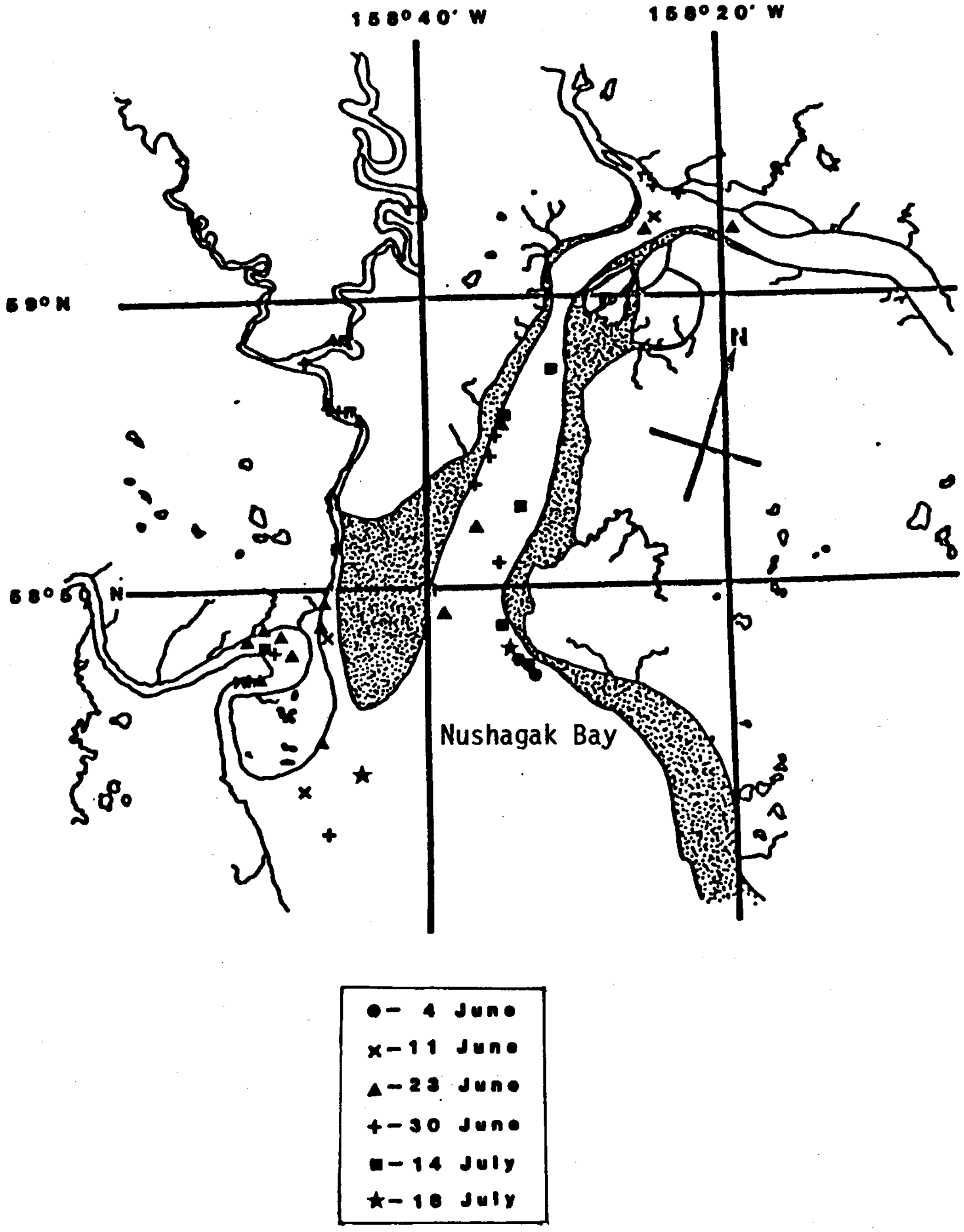


Fig. 3. Location of belukha whale individuals and groups seen in aerial surveys of Nushagak Bay and its tributaries.

Table III. Schedule of playback (SEDCO 708) experiments.

Date	Begin	End	Tide stage	Number of whales exposed to playback	Before experiment	After and during experiment
19 June	2048	2118	Rising	9-11	Downriver	Downriver
6 July	0856	0910	Rising	10	Upriver	Upriver
7 July	1032	1042	Slack	13	Milling	Milling
7 July	2134	2141	Rising	12-15	Upriver	Upriver
9 July	1840	1844	Falling	4-6	Upriver	Upriver
9 July	1930	1933	Slack	3	Upriver	Upriver
9 July	2217	2220	Rising	7	Upriver	Upriver
11 July	0545	0549	Falling	8-10	Downriver	Downriver
11 July	0838	0841	Slack	6-8	Upriver	Upriver
11 July	0911	0945	Slack	6-7	Upriver	Upriver
12 July	0554	0557	Falling	16-18	Downriver	Downriver
12 July	0620	0650	Falling	10-13	Downriver	Downriver
13 July	0759	0822	Falling	14-16	Downriver	Downriver/upriver

Table IV. Mean respiration rates (blows/min) and respiration intervals (secs) of belukha whales in Snake River, Alaska in different environmental and experimental conditions. (Values in parentheses are standard deviations).

	Undisturbed		Disturbed		Post disturbed	
	Resp. Rate	Resp. intervals	Resp. Rate	Resp. intervals	Resp. Rate	Resp. intervals
Moving downriver on a falling tide	1.4 (.7)	45 (30)	2.9 (.8)	29 (9)	2.6 (.8)	24 (10)
Moving upriver on a falling tide	2.6 (.6)	25 (23)	3.8 (2.2)	33 (26)	2.2 (.6)	18 (14)
Milling	1.5 (.5)	21 (14)	2.7 (.6)	16 (7)	2.5 (.4)	24 (6)

Activity, respiration rates and respiration intervals were moderately affected by sound playback. At the onset of playback, whales within 1.5 km usually swam faster in the direction they had been drifting or moving before the noise began. In only one case (discussed below) did whales change swim direction in response to playback sound (Table III). Whales apparently did not leave the river in response to playback noise during any experiment.

Only when playback started while whales were moving downriver on a falling tide (Table IV) did the whales' respiration rate and respiration interval appear to change significantly. Respiration rate was faster ($p<0.05$) and respiration interval shorter ($p<0.05$) during than before the disturbance. After the playback, respiration rate was slightly greater than before the disturbance and slightly less than during the disturbance, but neither difference was significant ($p>0.1$). Respiration interval was significantly shorter ($p<0.05$) after playback. The same trend occurred when the whales were milling and when they were moving upriver on a falling tide, but differences were not significant.

To test the whales' response to a constant sound source, we started playback when a group of whales came into view 4.6km upstream on 12 July, at 0650. Belukhas' hearing threshold at 1 and 2kHz is about 100dB (White, et al. 1978, Awbrey, et al. 1984). The sound level 3.5 to 4.5km away would be above the whales' threshold assuming cylindical spreading loss, but below it assuming spherical spreading loss. Given the complex effects of the river's configuration and tidal flow on sound attenuation and the unknown effects of water flow on the swimming whales' auditory sensitivity, we cannot say for certain that they could or could not hear the sound when it came on. We know only that the whales showed no overt response. They continued to move steadily downriver until they were within 50 to 75m of the boat. They then submerged, swam rapidly between the boat and the bank within 15-20m of the sound source, and surfaced about 50-75m downstream from the boat. The next day, playback was started when approaching whales were about 3.5km upstream. Eleven whales were strung out in groups of 2 to 4 over about 1/2km. Most of these whales turned around after approaching within 300 to 500m of the boat, but one group of 3 approached to within 300m, submerged, and swam past within 15m of the sound source.

Discussion

Our observations of belukha whale responses to playbacks of oil drilling sounds indicates that direction of whale movement and general activity (feeding, travelling) was not greatly affected by these sounds, especially if the sound source was constant. Whales continued to move in the direction they were travelling before playbacks began. On several occasions, whales within 2 km of the sound source appeared to feed during playback experiments. Whales also approached and quickly passed closely by the underwater speaker while sounds were being projected. By contrast, Stewart et al. (1982) found that whales responded to outboard motor noise by immediately swimming downriver, regardless of their behavior before the outboard motor noise began.

Whales did not abandon the river in response to playbacks of oil drilling noise in 1983, but their behavior did appear to change somewhat. Whales breathed more often and intervals between blows were shorter on average when these sounds started while the whales were nearby. The data on respiration rates, primarily, suggest that whales usually resumed normal behavior shortly after the termination of sound playbacks.

Our qualitative observations of belukha whales in Nushagak Bay, where whales are frequently exposed to fishing and processing boats with diesel engines, suggest that their behavior there differs from that in rivers and estuaries. In the open waters of the bay, whales appeared to remain much longer at the surface between blows and also to rise much higher out of the water. Reactions to outboard motors, however, seemed to be similar in both situations, perhaps because outboard powered boats are used to hunt belukhas.

Experiments exposing captive belukha whales to the same Sedco 708 sounds (Thomas and Kastelein 1983, Awbrey et al. 1984) indicated that belukha whales can acclimate quickly to oil-drilling sounds at typical sound levels. This agrees with McCarty's (1981) observations. He reported that belukha whales (including mother-calf pairs) regularly approached oil production platforms in Cook Inlet to within 10 m. He also reported that as long as noise from these platforms was constant it did not seem to affect whales, but that a sudden change in noise levels elicited a temporary avoidance reaction. Our observations also indicate that whales usually respond to sudden acoustic disturbance but are less likely to avoid a constant sound source.

REFERENCES

Altman, J. 1974. Observational study of behavior sampling methods. Behaviour. 49: 227-265.

Awbrey, F. T., J. A. Thomas, W. E. Evans, and R. A. Kastelein. 1984. Behavioral and physiological responses of Belukha whales to oil-related noise as determined by Playbacks of Underwater drilling noise and hearing threshold tests. HSWRI Technical Report. March 1984.

Brooks, J. W. 1954. Beluga. Annual Report for 1954. Alaska Department Fisheries, pp. 51-57.

__________ 1955. Beluga investigation. Annual Report for 1955. Alaska Department Fisheries. pp. 98-106.

__________ 1956. Marine predator control and investigation. Annual Report for 1956. Alaska Dept. Fisheries. pp. 50-59.

Frost, K. J., L. F. Lowry, and R. R. Nelson. 1984. Belukha whale studies in Bristol Bay Alaska. pp. 187-200. In: Proceedings of the workshop on biological interations among marine mammals and commercial fisheries in the Southeastern Bering Sea. Alaska Sea-Grant Report 84-1. University of Alaska.

Lensink, C. J. 1961. Status Report: beluga studies, unpubl. manuscripts. Division of Biological Research, Alaska Dept. Fish and Game, Juneau, AK. 20 p.

McCarty, S. 1981. Survey of effects of Outer Continental Shelf Platforms on Cetacean Behavior. Appendix C. Vol. II in: Gales, R. S. Effects of noise of offshore oil and gas operations on marine mammals. An introductory assessment. NOSC Tech. Rept. 844.

Seaman, G. A., L. F. Lowry , and K.J. Frost. 1982. Foods of Belukha whales (Delphinapterus leucas) in Western Alaska. Cetology 44: 1-19.

Stewart, B. S., F. T. Awbrey, and W. E. Evans. 1982. Effects of man-made waterborne noise on behavior of belukha whales (Delphinapterus leucas) in Bristol Bay, Alaska. HSWRI Tech. Rept. No. 82-145.

Thomas, J. T. and R. Kastelein. 1983. Behavioral and physiological responses of captive beluga whales to playbacks of drilling noise. J. Acoust. Soc. Amer. Suppl. 74(S1): S54(A).

LETHAL AND SUBLETHAL EFFECTS OF OIL ON FOOD ORGANISMS (EUPHAUSIID: *Thysandessa raschii*) OF THE BOWHEAD WHALE

by

Paul A. Fishman

Fishman Environmental Services

with

Richard S. Caldwell

Northwestern Aquatic Sciences, Inc.

and

Allan H. Vogel

ZP's Taxonomic Services

Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 662

December 1985

TABLE OF CONTENTS

List of Figures

List of Tables

1 SUMMARY OF OBJECTIVES, CONCLUSIONS, AND IMPLICATIONS WITH RESPECT TO OCS OIL AND GAS DEVELOPMENT

This study was contracted for the purpose of investigating the sensitivity of Arctic krill, namely the euphausiid *Thysanoessa raschii*(M. Sars, 1864), to the water soluble fraction (WSF) of Prudhoe Bay crude oil. The study had two primary objectives: (1) determine, through laboratory bioassays, the 96-hr LC_{50} of Prudhoe Bay crude oil WSF for *T. raschii*; and (2) estimate the losses to populations of *T. raschii* and the potential recovery rates resulting from hypothetical oil spills in the Beaufort Sea. The major concern prompting this study is the fact that euphausiids are a major food source for the endangered bowhead whale in the western Beaufort Sea.

The experimental results indicate that *T. raschii* sensitivities to Prudhoe Bay WSF are within the range expected, based on previous tests using Alaskan marine crustacea. No data could be found for this or similar species; thus, this study provides an important data point in the oil effects literature. Unlike other marine crustacea tested, *T. raschii* larvae appear to be less sensitive to oil WSF than older life stages. Gravid females were found to be the most sensitive life stage. The concentrations of WSF that resulted in euphausiid mortalities were fairly high, relative to results of studies with other species. These higher levels also produced changes in molt frequency, resulting in longer intermolt periods for adult animals.

The population loss and recovery estimates were based on scenarios supplied by NOAA, information from literature review, and several assumptions. A major impediment to estimation was a lack of distribution and abundance data for *T. raschii* in the Beaufort Sea, and a lack of life history information for this species in the Alaskan Arctic. A "worst case" situation was assumed, using distribution data for known euphausiid predators, to select an area of potential great risk. Conclusions for both spill scenarios were that NEGLIGIBLE to MINOR effects would result from the spills. The dissolution concentrations of oil in seawater, known vertical distribution of euphausiids, and derived LC_{50}'s for *T. raschii* contributed to the conclusions reached. The fact that local euphausiid populations are replenished through reproduction in other locations contributed to the conclusion that recovery of a localized population was dependent on factors other than losses due to a spill event.

A number of important data points were missing in the analyses described above. These are primarily related to the distributions, abundance, population structure and life history of *T. raschii* in the Beaufort Sea. As these data gaps are filled, our ability to assess impacts to natural populations of euphausiids resulting from OCS oil and gas development will improve. This study concluded that euphausiid mortalities resulting from the oil spill scenarios would be minimal; thus, bowhead whale food supplies would not be severely impacted. Other investigators have noted, however, that the predator-prey balance in Alaskan Arctic waters is delicate, and a poor year for zooplankton may increase competition between predators for this resource. An oil spill event during such a year may have more severe implications for bowheads.

2 INTRODUCTION

This project was funded through the Outer Continental Shelf Environmental Assessment Program. The purpose of the Program is the filling of information gaps in knowledge of Alaskan marine organisms and the ecological impacts of oil and gas development. Objectives of this study included the laboratory determination of effects from various levels of the sea-water soluble fraction of Prudhoe Bay crude oil on the euphausiid *Thysanoessa raschii*, and estimation of population losses and probable recovery potential following hypothetical oil spills in the Alaskan Beaufort Sea.

3 CURRENT STATE OF KNOWLEDGE

The euphausiid *Thysanoessa raschii* is a major food item in the diets of a variety of marine fish, birds and mammals in the Beaufort Sea. *T. raschii* is important in the diets of Arctic cod, terns, gulls, jaegers, ringed seal and bowhead whale (U.S. Army COE 1984; USDI,MMS 1984). The effects of oil spills on *T. raschii* populations are of particular interest in relation to food resources for the bowhead whale, an endangered species.

The effects of petroleum hydrocarbons have been tested on a variety of Alaskan marine organisms. Lethal and sublethal effects have been investigated; however, the majority of organisms tested have been benthic or demersal invertebrates and fish (Craddock 1977; Malins et al. 1985; Rice et al. 1985). Few pelagic invertebrates have been the subject of oil-effect studies due to the difficulty of capturing and/or culturing healthy organisms; *T. raschii* has not been tested previously. Published study results indicate that pelagic organisms are more sensitive than either benthic or intertidal organisms (Rice et al. 1985); this difference is attributed to the relatively more uniform pelagic environment.

The importance of *T. raschii* in pelagic ecosystems of northern waters is well known; the bulk of studies, however, concerning distribution, abundance and other ecological characteristics of populations is for the North Atlantic and contiguous waters. The importance of this species as a food supply for key Arctic marine fish, bird and mammal species underscores the importance of increasing the knowledge of this organism's natural ecology, and the effects of oil/gas development related perturbations on local populations. The current state of knowledge concerning *T. raschii* ecology is summarized as part of Section 6, Discussion.

4 METHODS

4.1 Collection and Transportation

Study objectives included the testing of adult, gravid female, egg and larval *T. raschii*. Three sampling periods were therefore planned in order to obtain various life stages of this species from waters near Juneau, Alaska. A late winter (March) collection was scheduled to obtain non-reproductive adults; a spring (May) collection was planned to obtain gravid females; and a late-summer (late-August) collection was designed to obtain juvenile and adult animals. The spring collection plan was designed to obtain sufficient numbers of gravid females to supply eggs and larvae for tests.

Euphausiids were collected from Auke Bay, near Juneau, Alaska, and shipped to the laboratory in Newport, Oregon. Towed bongo nets and vertically-hauled plankton nets, both with modified collection buckets, were used to capture euphausiids. Samples were sorted and maintained alive in a laboratory of the University of Alaska, Juneau. Animals were shipped via commercial air freight from Juneau to Portland, Oregon in 5-gallon plastic containers packed inside camp-type coolers with frozen "blue ice". Containers were transported from Portland to Newport by small airplane or automobile. Shipping time ranged from 7 to 10 hours.

Details of the sampling schedule are presented in Table 4-1.

TABLE 4-1

COLLECTION DATA FOR EUPHAUSIID SAMPLING

Date	Vessel[a]	Gear[b]	Target Depth (m)	Envir. Conditions			Shipping		
				Depth (m)	Temp. (C)	Sal. (ppt)	Date	No.	Sex
9MAR85	Maybeso	RN/O	80-90	0	2.9	31.3	3/11	300	M+F
2MAY85	Maybeso	RN/O	70	0	6.0	30.0	5/11	600	F
				20	4.2	31.0			
				40	3.9	31.6			
7-8MAY85	Maybeso	RN/O	45-90	0	8.2	25.2	same as 5/11		
				50*	4.9	31.5			
21JUN85	Searcher	RN/O	45	0	9.2	23.5	6/23	6	F
				45*	6.0	31.5			
9SEP85	Maybeso	RN/V	50-70	0	9.0	22.4	9/11	300	Juv
				50*	5.9	31.5			

(a) *Maybeso*, research vessel of University of Alaska, Juneau, School of Fisheries and Natural Sciences

Searcher, research vessel of Auke Bay Laboratory, National Marine Fisheries Service

(b) Sampling gear: RN/O = ring net (1 meter, 560u mesh)/oblique tow
RN/V = ring net (as above)/vertical tow

* Temperature and salinity values estimated from Bruce, McLain and Wing (1977)

TABLE 4-1 (continued)

Sampling Notes:

9MAR85 collection:
- sampling location,SE of Coughlan Island
- 650 *T. raschii* collected, low mortality during sorting, maintenance and shipping

2MAY85 collection:
- sampling location, middle of Auke Bay, SE of Coughlin Is., and Stephens Passage
- females sorted from samples
- very high percentage of males and copepods (*Metridia sp.*)
- Approx. 500 *T. raschii* collected, 25% were females, very high mortality during sorting and maintenance, mostly females, probably from low DO due to copepod numbers

7-8MAY85 collection:
- sampling location, middle of Auke Bay, SE of Coughlin Is., Fritz Cove,Stephens Passage
- approx. 4,000 *T. raschii* collected, 30 - 35% females
- high mortality of females during sorting

21JUN85 collection:
- sampling location, SE of Coughlin Is.
- greater ratio of females than May collections

9SEP85 collection:
- sampling location, same as May
- 65% of euphausiids in sample were *T.longipes*
- approx. 750 juvenile *T. raschii* collected
- high mortality of smaller juveniles during sorting, 300 shipped

---

4.2 Laboratory Acclimation and Culture

Euphausiids from the first shipment were initially cultured in seven-gallon glass aquaria. Observation and handling of the animals proved to be difficult with this system, however, and the euphausiids were transferred into one-gallon glass jars containing 2 liters of culture water for the final 11 days of acclimation. Subsequent shipments of euphausiids were cultured in 3.5 gal. plastic pails (27 cm diameter X 25 cm deep) containing approximately 7 liters of culture water. Euphausiids, along with the water used in shipment, were transferred into the culture vessels which were then immersed in a refrigerated water bath for temperature control and supplied with gentle aeration through 1 ml disposable glass pipets.

The shipping water was gradually replaced over a two to three day period with filtered Yaquina Bay (Oregon) water supplied to the laboratory through all PVC pipe from a 6000 gal fiberglass storage tank. Euphausiids were held at a density of approximately 10 per liter in the acclimation vessels. One- to three-day old brine shrimp (*Artemia salina*) nauplii were supplied as a source of food three times per week at a density of approximately 2000 per liter. In addition, animals in the first shipment were fed sea urchin (*Strongylocentrotus purpuratus*) plutei at a density of approximately 800 per liter on two occasions. Uneaten brine shrimp and fecal material were periodically removed by suction from the acclimation containers. Euphausiids were acclimated to a photoperiod of 16 hours light and 8 hours darkness.

4.3 Bioassay Tests

4.3.1 Flow-Through Toxicity Test System

The flow-through toxicity test system consisted of three principal components; a device to prepare the stock water-soluble fraction (WSF) in a continuous-flow mode, a toxicant diluter, and exposure aquaria or containers.

The crude oil WSF was prepared on a continuous basis using the apparatus described by Nunes and Benville (1978). The apparatus (saturator) consisted of a 2.5 liter pyrex bottle, the top of which was removed and fitted with a stainless steel plate perforated with 1 mm diameter holes. The bottom portion of the bottle was fitted near the bottom with a constant level siphon arm for outflow of prepared WSF, and with entry and overflow ports near the top for introduction and overflow of crude oil. The cut surfaces of the top and bottom halves of the bottle were ground, and, in operation, held together with stainless steel springs.

During each dilution cycle, seawater was introduced into the top of the saturator at a rate of about 1 liter per minute. Droplets of seawater, formed by passing through the perforated stainless steel plate, subsequently passed through a 4-6 cm layer of crude oil floating on the surface of a pool of seawater in the bottom half of the saturator. The oil layer was replenished at an average rate of approximately 1 ml/min to maintain a constant composition throughout the exposure period. The more soluble components of the oil were dissolved in the seawater droplets on passage through the oil layer.

A barrel of Prudhoe Bay crude oil was supplied by NOAA. Five concentrations of the WSF and a dilution water control were prepared using an effluent type Mount-Brungs diluter (Peltier 1978) calibrated for a dilution factor of 0.60. No predilution of the stock WSF was performed. Each 30-minute cycle of the diluter delivered 500 ml of solution per test concentration to a four-way flow splitter chamber resulting in a flow of approximately 125 ml to each of four replicate aquaria per test concentration per cycle.

Small glass aquaria, 27 cm long X 12 cm wide X 15 cm high were filled to a depth of 10.5 cm and contained 3.4 liters of test solution each. In the tests of adult (Test I) and juvenile (Test IV) euphausiids, animals were allowed to move unimpeded in the test aquaria. The overflow tubes were fitted with 1 mm plastic mesh screen to prevent the loss of animals. Aquaria were partially immersed in a water bath for temperature control.

The same test chambers were employed in tests of gravid females (Test II) and larvae (Test III), but aquaria were compartmentalized to permit testing of both stages simultaneously and to provide a mechanism for collecting and enumerating any eggs released by females during the test. Gravid females, initially eight per replicate, were confined in 8.0 cm diameter polyvinylchloride (PVC) cylinders 10.8 cm deep fitted with 1 mm mesh plastic window screen on the bottom. The cylinders were placed into pyrex dishes (11.2 cm diameter) and were supported above the bottom of the dishes by four legs 0.9 cm high. The cylinder/dish assemblies were placed at the influent ends of the rectangular test aquaria. Eggs released by the females passed through the 1 mm screen mesh and were collected in the pyrex dish. Adequate circulation in the PVC confinement chamber was accomplished by placing the chambers directly under the test solution splitter, causing the test solution to pass first through the chamber, then over the lip of the pyrex dishes and into the main compartment of the test aquaria. The rate of flow was sufficiently low that eggs were not flushed out of the pyrex dishes.

Test cages for the larval stages were constructed of 3.0 cm diameter PVC cylinders 3.6 cm deep fitted with a 210 µm Nitex screen on the bottom and a plastic hook cemented near the top on the outside. The larval test chambers were suspended, using the plastic hooks, in the rectangular aquaria and in operation contained test solution to a depth of approximately 1 cm.

4.3.2 Toxicity Test Procedures

The experimental design employed in tests of all life stages consisted of exposure of the euphausiids to five WSF concentrations in a logarithmic series and a control. Four replicate aquaria or animal exposure chambers were used at each treatment level. Because the number of euphausiids available for testing was limited, the total number of animals per treatment replicate varied from six to eight in the several tests performed with adults or juveniles. In the tests of larval *T. raschii* only five individuals were used per replicate. Although more first naupliar stage larvae were available at the time this test was begun, the use of more than five organisms per replicate was not considered practical due to the extreme difficulty of observing and counting this life stage without risk of losing or damaging the test specimens.

Toxicity tests with postlarval forms of *T. raschii* were begun by addition of euphausiids, one at a time, to each test container until all available animals were distributed to the containers. This method reduces or eliminates the "hard-to-catch" vs. "easy-to-catch" bias in toxicity testing. Prior to addition of the animals, the flow-through test system was operated for a 24-hr period to ensure the equilibration of all test parameters.

Observations on the survival, number of molts, gross behavior, and, in the tests with gravid females, numbers of eggs released, were performed daily for up to seven days in tests with postlarval individuals. After day 8 in Test I and day 7 in Test IV, observations were made every second day. Dead animals were removed when observed and preserved in buffered 5% formalin in seawater. The absence of visible appendage movement during a 15 second observation period under a dissecting microscope was used as the criterion of death.

In tests of the larvae, eggs that were released by several females were transferred, using a Pasteur pipet, to beakers of control seawater at the approximate test temperature and salinity. Four days after isolation of the eggs, most had hatched and free-swimming first nauplii were observed to be actively swimming near the water surface. Swimming nauplii were captured under a dissecting microscope using a Pastuer pipet and transferred into the larval test chambers. The latter, resting on the floor of a 10.0 cm diameter crystallizing dish containing test water, were approximately half full, and nauplii were released under the water surface.

Daily observation of the larvae under a dissecting microscope was accomplished by carefully removing the larval test cages in a small (10.0 cm diameter) pyrex crystallizing dish. The dish was carefully moved into position under the suspended larval test cage, and both the cage and dish were removed from the aquarium in a manner that prevented water from draining out of the test container. The test chamber and dish were then placed onto the stage of the dissecting microscope for observation of the larvae. After observation, the larvae were returned to the test aquarium by reversing the above procedure.

The number of surviving larvae was the primary observation performed. If the number of surviving larvae was less than on the previous day, this usually correlated with the presence of a dead organism which was then removed. Occasionally, however, an organism was missing, i.e. could not be found either in the water or on the wall of the test vessel. Entrapment of larvae on the vessel wall was thought to occur occasionally as a result of changing water level in the cage as it was handled for observation. Larvae trapped at the time of beginning the observation could be flushed back into the water without apparent ill effects, but animals trapped while returning the cage to the test aquarium after making an observation may have remained on the wall and become dessicated. This may account for the occasional missing larva. In addition to survival, observations on the stage of development of larvae and on gross behavior were also noted.

The water quality parameters, temperature, dissolved oxygen, and pH, were recorded daily or on alternate days at the same time that biological observations were made. Measurements were made on one replicate aquarium at each treatment level. Temperature was measured using a calibrated mercury thermometer with 0.1 °C scale divisions. Dissolved oxygen was determined with a YSI Model 51B polarographic oxygen meter and probe with temperature and salinity correction. A Chemtrix Model 40E pH meter with divisions of 0.1 pH units was used for pH measurement.

In Test I, measurement of salinity was also performed in one replicate of each treatment level, but in the remaining tests only the salinity of the dilution water was determined at each observation period. In the initial test, salinity was determined by measuring the conductivity of a diluted 5 ml test water sample and obtaining the salinity from a calibration curve. In the latter tests, salinity of the dilution water was measured using specific gravity hydrometers and conversion from density to salinity by reference to U.S. Coast and Geodetic Survey conversion tables. At each time that water quality parameters were measured, a 500 ml sample of test solution frôm one replicate at each treatment level was also taken for petroleum hydrocarbons analysis.

4.3.3 Chemical Analyses

The concentrations of individual aromatic hydrocarbons in the test solutions were measured by capillary column gas chromatography (GC) after solvent extraction with methylene chloride. Test solution samples of 500 ml were siphoned from test aquaria into 500 ml brown glass bottles, sealed with teflon lined caps, and stored under refrigeration (5° C) until extraction within 7 days. Samples were extracted three times by shaking with 30 ml volumes of methylene chloride in 1000 ml separatory funnels. The methylene chloride extracts were pooled in 125 ml erlenmeyer flasks and dried by the addition of anhydrous sodium sulfate. Dried extracts were transferred to 250 ml Kadura-Danish evaporator flasks fitted with 25 ml concentrator tubes and concentrated on a steam bath to 5 ml. After cooling, the concentrator tubes were fitted with micro-Snyder columns and were further concentrated to 0.8 ml. The concentrated extracts were quantitatively transferred to 1 ml GC autosampler vials, spiked with exactly 15.90 ng of hexamethylbenzene internal standard (I.S.) in 10 µl of methylene chloride solvent, and immediately capped with teflon lined seals.

Analyses were performed using a Hewlett-Packard 5840A gas chromatograph equipped with auto-sample injection, a flame ionization detector, and integration and methods calculation capability. A 30 meter Supelco SBP-5 fused silica capillary column was employed at an initial oven temperature of 30 °C held for 4 minutes, followed by temperature programming at 4 °C per minute to a final temperature of 280 °C which was held for 4 minutes. The injection temperature was 280 °C and the detector temperature was 300 °C. Analyses were performed in the splitless injection mode. The injection volume was 1 µl.

Qualitative and quantitative analyses of most major aromatic hydrocarbons in the WSF were performed by comparison with authentic reference standards using the internal standard calculation method. Response factors for each compound and the internal standard were individually determined from the analyses of standards and used to calibrate the chromatograph. An average calibration factor was calculated from the standards and used to determine the approximate concentration of prominent unidentified peaks which were assumed also to be hydrocarbons. A quantitative standard containihg all of the reference standards in the approximate concentration ratios actually observed in the WSF was prepared and used to spike representative seawater samples in order to establish the recovery and precision of analysis of individual compounds. Analysis of spiked seawater samples demonstrated that the recovery of most aromatic hydrocarbons was in the range of 92-98% (Table 4-2). The average recovery of benzene was 54%; that of toluene 86%. Lower recovery of these latter compounds is to be expected because of volatilization loss during concentration steps in the analysis. Precision of the analyses, indicated by the percent relative standard deviation, ranged from 0.6% to 2.1% for all compounds analyzed except benzene. The percent relative standard deviation for benzene was 5.9%. The results of analyses of hydrocarbons in bioassay test water were not corrected for recovery.

4.4 Data Analysis

All tests of significance between treatment means in the toxicity tests were performed using one-way analysis of variance (ANOVA). An arcaine transformation was employed with percent data (survival) and untransformed data were employed in comparisons of molt frequency. When the ANOVA test indicated differences between treatment means, the "least significant difference" multiple range test (Snedecor and Cochran 1967) was used to determine when treatments differed significantly (P=).05) from the controls. Calculation of LC_{50} concentrations of the WSF were performed using the probit method (Finney 1971), or by the binomial procedure (Stephan 1977) when the use of the probit analysis was not permitted by the data.

TABLE 4-2

ACCURACY AND PRECISION OF ANALYSIS OF AROMATIC HYDROCARBONS IN SEAWATER

Compound	Average Percent Recovery	Standard Deviation	Percent Relative S.D.
Benzene	54.0	3.2	5.9
Toluene	86.3	1.7	1.9
Ethylbenzene	95.1	2.0	2.1
p-Xylene	91.7	1.6	1.7
o-Xylene	97.8	2.1	2.1
Isopropylbenzene	92.4	1.8	2.0
n-Propylbenzene	92.6	1.3	1.4
1,3,5-Trimethylbenzene	92.6	2.0	2.1
1,2,4-Trimethylbenzene	92.6	1.6	1.7
1,2,3,4-Tetramethylbenzene	93.7	0.8	0.9
DI-Isopropylbenzene	92.9	1.5	1.6
Naphthalene	94.7	2.0	2.1
2-Methylnaphthalene	95.4	0.6	0.6
1-Methylnaphthalene	95.0	0.5	0.6

Based on analysis of 5 spiked seawater samples.

5 RESULTS

5.1 Collection and Transportation

The numbers of euphausiids collected and shipped during each collection period were presented in Table 4-1. Sufficient numbers of animals were collected for each of the tests; mortalities during shipment were fairly low. The highest mortalities experienced during handling and shipment occurred with the gravid females. Water temperatures during shipment increased generally 1 or 2^{o} C.

Each of the shipments of animals was received at the toxicology laboratory in apparantly satisfactory condition. The temperature of several representative containers in the initial shipment was found to be about 6°C, an increase of 2° over the initial shipping temperature. Gravid females received in the second shipment were in water at 4.7°C; temperature on arrival for the last shipment was 6°C. The transport water was oxygen saturated in all shipments, and the salinity was between 31 and 32 o/oo. Dead animals were found in most shipping containers upon receipt in the laboratory.

5.2 Laboratory Acclimation and Culture

A summary of water quality conditions employed during acclimation of each tested group of euphausiids is presented in Table 5-1. Holding times for postlarval animals (Tests I, II and IV) varied from 9 to 17 days. All water quality conditions were relatively constant during acclimation of Test I and Test IV animals. Test II animals experienced greater fluctuation of temperature and dissolved oxygen. Temperature for this group, which for most of the acclimation period averaged less than 6.0°C, was elevated to the range of 6.5 to 9.4°C during two days of unusually warm weather which caused the cooling capacity of the water bath refrigeration system to be exceeded. Dissolved oxygen levels remained essentially at saturation, but the concentrations fluctuated with temperature.

TABLE 5-1

WATER QUALITY CONDITIONS DURING ACCLIMATION OF EUPHAUSIIDS

Test No.	Days held prior to testing	Temperature (°C)	Dissolved oxygen (mg/l)	pH	Salinity (o/oo)
I	17	4.4 ± 0.4	8.8 ± 0.8	7.3 ± 0.2	33.1 ± 0.8
II	9	6.0 ± 1.4	9.2 ± 1.5	7.6 ± 0.1	31.9 ± 0.4
III	4	6.8	9.3	7.7	32.1
IV	12	6.5 ± 0.1	9.2 ± 0.3	7.6 ± 0.1	32.2 ± 0.3

Eggs released by gravid females were held in 250 ml beakers in a temperature controlled water bath for four days prior to use in the larval test (Test III). Hatching occurred during that period, resulting in swimming first stage nauplii. Water quality conditions were measured only at the time that larvae were removed for use in the test, but were assumed to be unchanged during the 4 day development period.

Records of mortalities for adult euphausiids received in the first shipment were not available for the first six days because counts could not readily be made in the large holding aquaria. During the last 11 days of acclimation, however, an average of 5.7 animals, representing about 2% of the culture, died per day. This is in contrast to the low mortality observed in the control (0%) and low test concentration groups (3-10%) during the subsequent 16-day test period.

For the second and third groups of acclimating postlarval euphausiids, highest mortalities occurred during the initial few days after arrival at the laboratory, but daily mortalities substantially declined thereafter. For example, of the gravid females received on May 10, 78 dead or dying animals were removed on the day of receipt. Two days later, 98 dead animals were removed; on subsequent days the numbers of dead animals found were 39, 10, 5, 3, 6, 10, and 2. The same pattern was found with the juvenile and young adult animals received in September, but the numbers of dying animals were much fewer. The daily number of dead animals removed from the culture from September 17 through September 23 were 9, 6, 2, 1, 0, 1, and 1.

5.3 Bioassay Tests

5.3.1 Test Conditions

Four tests were conducted during three time periods, or series, with Tests II and III conducted simultaneously. Water quality conditions during each of the three test series are summarized in Table 5-2. In the first test, with adult *T. raschii*, mean temperatures ranged from 5.3 to 6.0 °C. Tests with gravid females and larvae (Tests II and III, respectively) had mean water temperatures ranging from 6.8 to 7.5 °C. Test IV, with juveniles, had mean temperatures ranging from 7.2 to 7.4 °C. Mean dissolved oxygen concentrations ranged from a low of 6.8 mg/l in one treatment in the second test series to a high of 9.3 mg/l in

TABLE 5-2

HYDROCARBON CONCENTRATIONS AND WATER QUALITY CONDITIONS DURING EUPHAUSIID BIOASSAYS

Test No. (a)	Total Measured Hydrocarbon (mg/l)	Temp. (°C)	Dissolved Oxygen (mg/l)	pH	Salinity (o/oo)
I	0 (control)	5.8±0.5	9.3±0.8	7.5±0.1	30.6±2.3
	0.301±0.051	5.9±0.4	9.2±0.9	7.5±0.1	30.9±2.2
	0.543±0.072	5.8±0.4	9.2±1.0	7.4±0.2	31.1±2.0
	0.897±0.093	5.9±0.3	9.2±1.0	7.4±0.2	31.0±2.3
	1.413±0.113	5.3±0.4	9.0±1.0	7.5±0.1	30.9±2.1
	2.062±0.288	6.0±0.4	8.7±1.1	7.5±0.1	30.6±2.4
II & III	0(control)	7.2±0.8	7.5±0.5	7.4±0.0	30.8±0.6 *
	0.054±0.043	7.5±0.8	7.1±0.5	7.4±0.0	
	0.142±0.104	7.1±0.9	7.3±0.6	7.4±0.0	
	0.620±0.176	7.0±0.9	6.8±0.5	7.4±0.0	
	1.329±0.138	6.8±0.7	7.2±0.6	7.4±0.0	
	1.956±0.301	7.4±1.0	6.9±0.5	7.4±0.0	
IV	0(control)	7.3±0.3	8.1±0.2	7.4±0.1	32.8±0.4 *
	0.191±0.126	7.3±0.4	7.9±0.4	7.4±0.1	
	0.497±0.225	7.3±0.3	7.7±0.6	7.4±0.1	
	0.742±0.332	7.4±0.3	7.5±0.8	7.4±0.1	
	1.627±0.206	7.2±0.3	7.6±0.8	7.4±0.1	
	2.184±0.308	7.4±0.3	7.6±0.7	7.4±0.1	

(a) Test I: *T. raschii* adults, test begun on March 29, 1985
Test II: *T. raschii* gravid females, test begun on May 19, 1985
Test III: *T. raschii* larvae, test begun on May 19, 1985
Test IV: *T. raschii* juveniles, test begun on September 24, 1985

* Salinity measured only at the seawater source.

the control treatment of the first test series. None of the temperature or dissolved oxygen differences were significant within a test series.

The mean pH in all tests was within the range of 7.4 to 7.5. Mean salinities in Test I, for individual test concentrations ranged from 30.6 0/00 to 31.1 0/00. In Tests II, III, and IV, salinity was measured only at the seawater source; the average salinity in the second test series was 30.8 0/00, that of Test IV was 32.8 0/00.

5.3.2 Concentration and Composition of Prudhoe Bay WSF

The mean of total measured hydrocarbons at each treatment level in each of the three test series is also shown in Table 5-2. The highest levels in the three test series were similar; 2.06 mg/l in Test I, 1.96 mg/l in Tests II and III, and 2.18 mg/l in Test IV. Lowest test concentrations ranged from 0.054 mg/l (Tests II and III) to 0.301 mg/l (Test I). The average concentrations of the principal components of the Prudhoe Bay water soluble fractions found in each of the three test series are shown in Table 5-3. Benzene and toluene together accounted for roughly 75% of the measured compounds.

Ethylbenzene and the three xylene isomers account for an additional 13% of the measured compounds. The remainder of the measured peaks consisted of more highly subatituted benzenes, naphthalene, methyl naphthalenes, and eight unidentified peaks.

TABLE 5-3

AVERAGE CONCENTRATIONS OF AROMATIC HYDROCARBONS IN UNDILUTED WATER SOLUBLE FRACTIONS OF PRUDHOE BAY CRUDE OIL USED FOR EUPHAUSIID BIOASSAYS

Compound	Concentration (mg/l)		
	Test I	Tests II & III	Test IV
Benzene	0.789 ± 0.134	0.757 ± 0.119	0.823 ± 0.126
Toluene	0.757 ± 0.128	0.698 ± 0.123	0.819 ± 0.137
Ethylbenzene	0.046 ± 0.014	0.029 ± 0.011	0.044 ± 0.013
m-,p-xylene	0.141 ± 0.030	0.129 ± 0.023	0.149 ± 0.028
o-xylene	0.073 ± 0.008	0.068 ± 0.010	0.081 ± 0.013
Isopropylbenzene	0.004 ± 0.001	0.003 ± 0.001	0.004 ± 0.001
n-Propylbenzene	0.004 ± 0.002	0.002 ± 0.001	0.004 ± 0.002
unidentified	0.016 ± 0.003	0.014 ± 0.003	0.016 ± 0.003
1,3,5-Trimethylbenzene	0.006 ± 0.001	0.005 ± 0.001	0.006 ± 0.002
unidentified	0.008 ± 0.001	0.007 ± 0.001	0.009 ± 0.002
1,2,4-Trimethylbenzene	0.017 ± 0.004	0.016 ± 0.003	0.018 ± 0.005
p-Cymene	0.012 ± 0.001	0.011 ± 0.001	0.013 ± 0.002
unidentified	0.022 ± 0.012	0.030 ± 0.009	0.027 ± 0.006
unidentified	0.014 ± 0.007	0.012 ± 0.005	0.014 ± 0.005
unidentified	0.018 ± 0.006	0.024 ± 0.004	0.023 ± 0.004
1,2,3,4-Tetramethylbenzene	0.008 ± 0.002	0.013 ± 0.003	0.004 ± 0.003
Di-isopropylbenzene + unidentified	0.055 ± 0.022	0.076 ± 0.020	0.060 ± 0.014
Naphthalene	0.021 ± 0.009	0.011 ± 0.003	0.020 ± 0.009
unidentified	0.018 ± 0.004	0.024 ± 0.002	0.027 ± 0.004
unidentified	0.008 ± 0.002	0.011 ± 0.002	0.004 ± 0.002
2-Methylnaphthalene	0.012 ± 0.002	0.012 ± 0.003	0.014 ± 0.004
1-Methylnaphthalene	0.013 ± 0.001	0.013 ± 0.002	0.014 ± 0.002

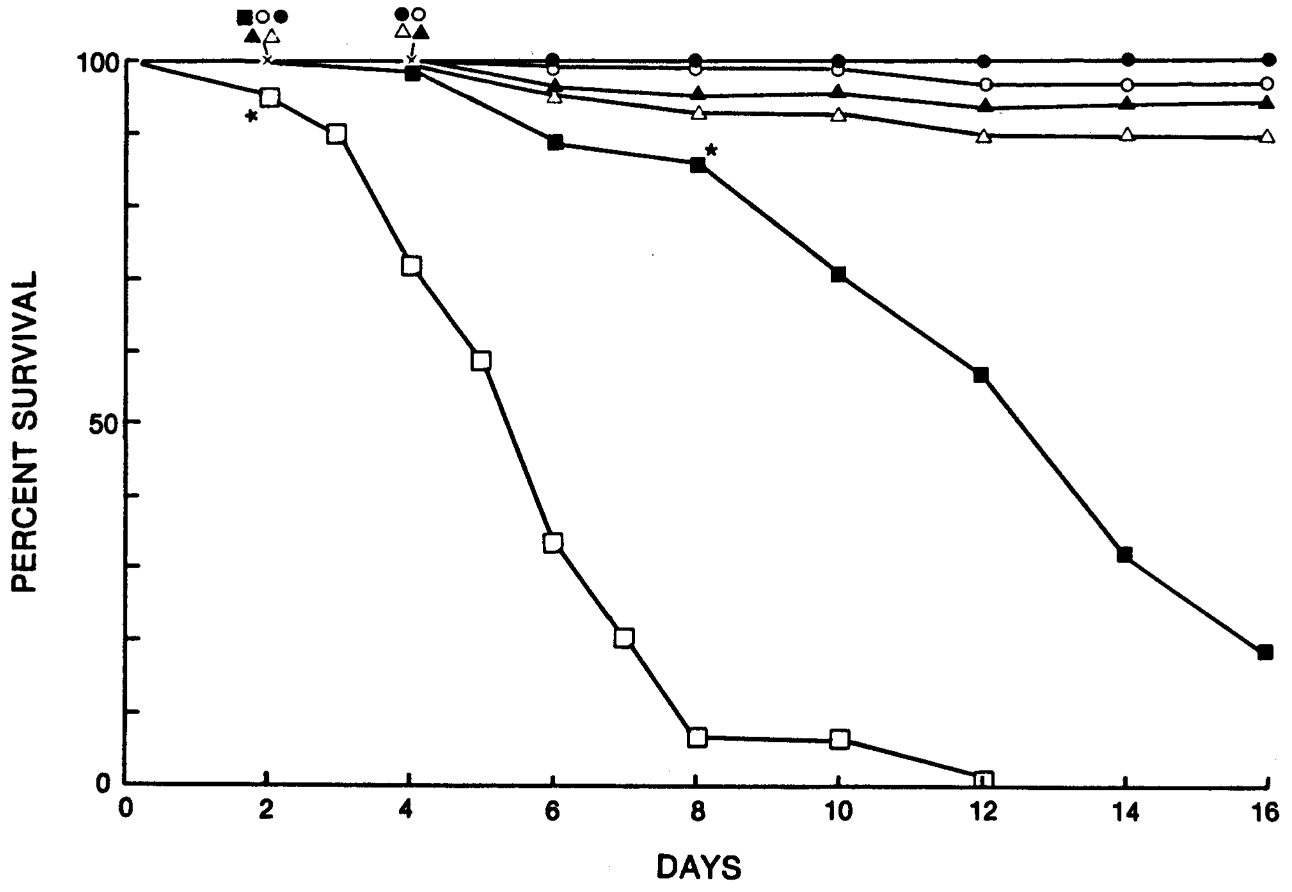
5.3.3 Effects of WSF on Euphausiid Survival

In Test I, using adult *T. raschii*, animals exposed to the highest test concentration, 2.06 mg/l TMH (total measured hydrocarbons), were severely narcotized within the initial 24-hr period, but deaths occurred gradually over a period of eight days (Figure 5-1). Survival in this group was significantly less than in controls' by day 2. Euphausiids exposed to 1.41 mg/l TMH were also slightly to moderately narcotized within the initial 24 hours and generally throughout the remainder of the test. Survival in this group was significantly less than in controls on day 8, and survival continued to decrease until the end of the test on day 16, by which time only 18% of the initial number of animals had survived. Euphausiids exposed to 0.897 mg/l TMH did not experience significantly poorer survival than control animals and those at lower test concentrations and did not appear to be behaviorally affected.

In the second test, with gravid females, reduced survival occurred at the highest (1.96 mg/l) and second highest (1.33 mg/l) test concentrations as in the first test, but the effect occurred much more rapidly (Figure 5-2). Survival was significantly less than controls by day 2 at 1.96 mg/l and complete mortality was noted within 3 days. At 1.33 mg/l, survival was significantly less than in controls by day 3 and 75% mortality occurred within 5 days. Euphausiids at the third highest test level (0.62 mg/l) also experienced significantly higher mortality than controls by day 6.

Figure 5-3 presents the results of WSF toxicity testing on *T. raschii* nauplii. Survival was not significantly lower at either 1.96 mg/l or 1.33 mg/l TMH compared with the controls at any time during the six day exposure period. During the naupliar test, animals were observed to progress from first to second nauplius and then to first calyptosis stage. On day 6 virtually all larvae were in the calyptosis stage. During the test, larvae were occasionally damaged or lost by adhering to the sides of the test cages, a circumstance contributing to the steady decrease in apparent survival of the nauplii at all test levels, including the controls, during the six day test period.

A final test (Test IV) was performed using juvenile (Age 0+) *T. raschii*. The results of this last test were very similar to the initial test with adults (Test I). Euphausiids exposed to 2.18 mg/l, the highest test level, experienced a steady decrease in percent survival over the ten day period (Figure 5-4). The percent survival was first significantly less than that of the controls on day 4 of the



TOTAL MEASURED HYDROCARBONS

● CONTROL
○ 0.3101 mg/l
▲ 0.543 mg/l
△ 0.897 mg/l
■ 1.413 mg/l
□ 2.062 mg/l

*Significant difference from control group (5% level)

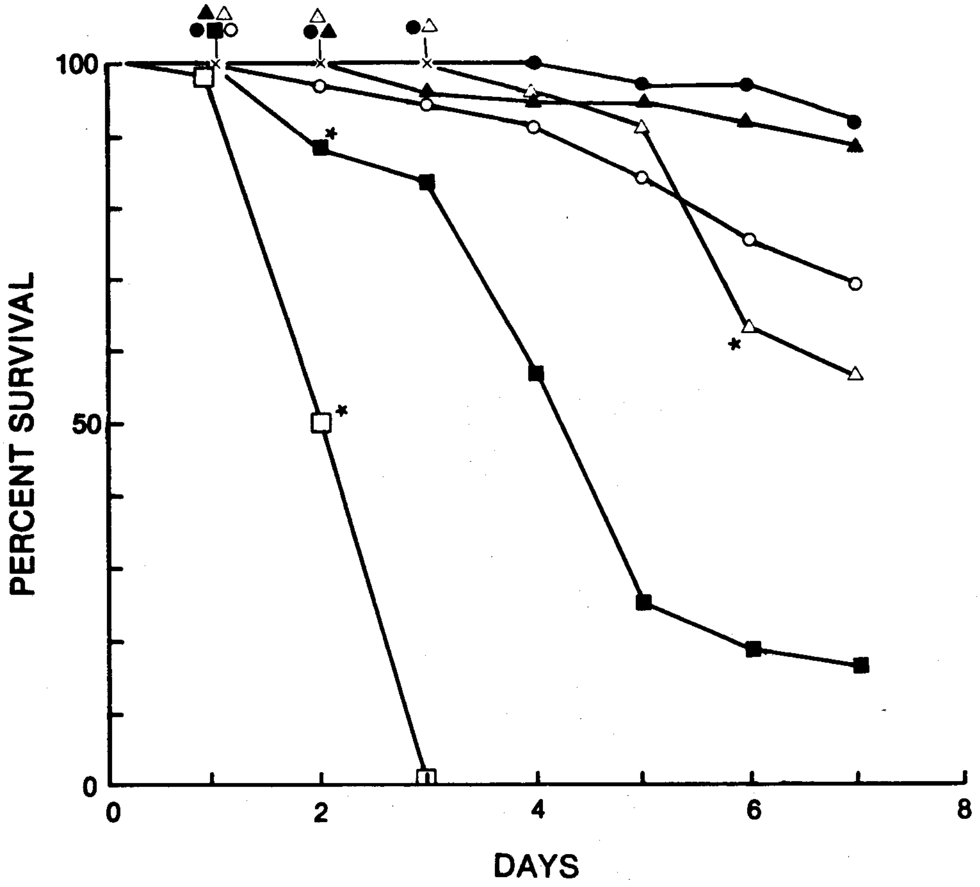
EFFECTS OF OIL ON FOOD ORGANISMS OF THE BOWHEAD WHALE
NOAA/OCSEAP RU 662

EUPHAUSIID SURVIVAL AT EXPERIMENTAL LEVELS OF PRUDHOE BAY CRUDE OIL WSF

TEST I: ADULTS

1985

FIGURE 5-1



TOTAL MEASURED HYDROCARBONS

● CONTROL △ 0.620 mg/l
○ 0.054 mg/l ■ 1.329 mg/l
▲ 0.142 mg/l □ 1.956 mg/l

*Significant difference from control group (5% level)

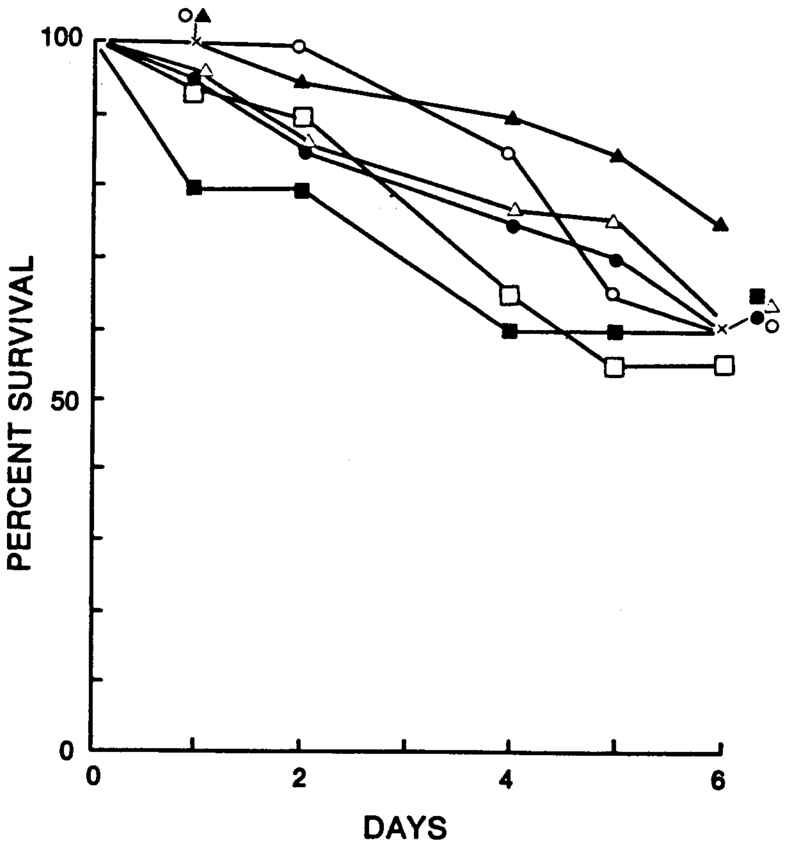
EFFECTS OF OIL ON FOOD
ORGANISMS OF THE BOWHEAD WHALE
NOAA/OCSEAP RU 662

EUPHAUSIID SURVIVAL AT
EXPERIMENTAL LEVELS OF PRUDHOE
BAY CRUDE OIL WSF

TEST II: GRAVID FEMALES

1985

FIGURE 5-2



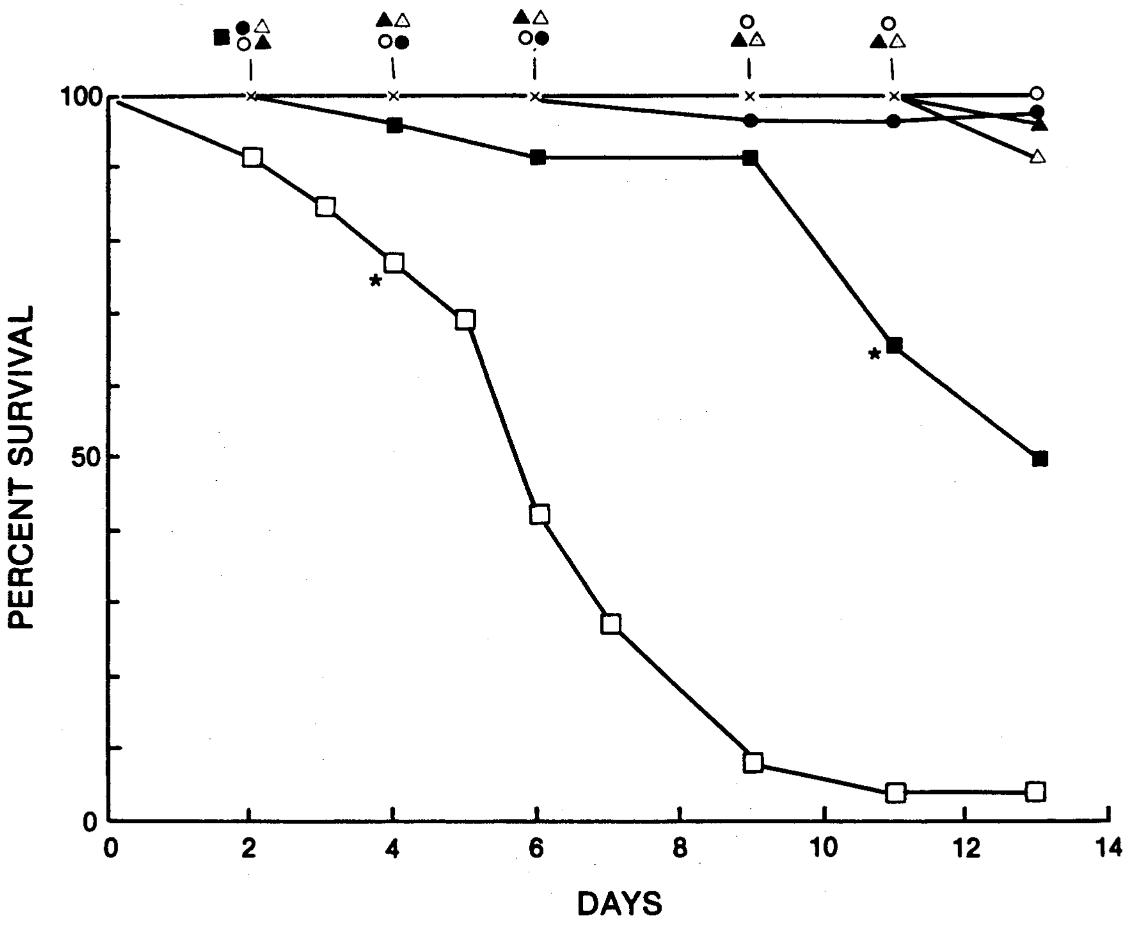
TOTAL MEASURED HYDROCARBONS
- ● CONTROL
- ○ 0.054 mg/l
- ▲ 0.142 mg/l
- △ 0.620 mg/l
- ■ 1.329 mg/l
- □ 1.956 mg/l

EFFECTS OF OIL ON FOOD ORGANISMS OF THE BOWHEAD WHALE
NOAA/OCSEAP RU 662

EUPHAUSIID SURVIVAL AT EXPERIMENTAL LEVELS OF PRUDHOE BAY CRUDE OIL WSF

TEST III: LARVAE

1985 **FIGURE 5-3**



TOTAL MEASURED HYDROCARBONS

● CONTROL	△ 0.742 mg/l
○ 0.191 mg/l	■ 1.627 mg/l
▲ 0.497 mg/l	□ 2.184 mg/l

*Significant difference from control group (5% level)

EFFECTS OF OIL ON FOOD ORGANISMS OF THE BOWHEAD WHALE
NOAA/OCSEAP RU 662

EUPHAUSIID SURVIVAL AT
EXPERIMENTAL LEVELS OF PRUDHOE
BAY CRUDE OIL WSF

TEST IV: JUVENILES

FISHMAN ENVIRONMENTAL SERVICES

1985

FIGURE 5-4

test, more than 50% mortality was recorded by day 6, and only one of 26 initial animals in this group survived to the end of the test on day 13. Animals exposed to 1.63 mg/l, the next highest test level, exhibited significantly reduced survival compared with controls by day 11 and 50% mortality at the end of the test on day 13. Euphausiids exposed to 0.742 mg/l did not experience reduced survival compared with controls.

LC_{50} concentrations for approximately 4, 7 and 10-day intervals in tests of all four life stages are presented in Table 5-4. Gravid females had the lowest LC_{50}'s of any stage tested, 1.37 and 0.69 mg/l for days 4 and 7, respectively. Adults and juveniles were approximately equal in sensitivity; adult LC_{50}'s ranged from 1.58 mg/l at day 10 to >2.06 mg/l at day 4, and juvenile LC_{50}'s ranged from 1.72 mg/l at day 11 to >2.18 mg/l at day 4. Larvae were the least sensitive stage; LC_{50}'s were >1.96 on both days 4 and 7.

5.3.4 Sublethal Effects of WSF on Euphausiids

A sublethal effect that could be evaluated in the adult organisms was the frequency of molting. On each day that test animals were examined for survival, the number of molts that had occurred during the previous 24 hours was recorded. After day 8 in Test I and day 7 in Test IV, aquaria were examined only every second day and the number of molts recorded, thereafter, was for a 48-hr period. At the end of the tests, the numbers of surviving adults in each test concentration each day was summed to provide a total number of animal days. Dividing this by the total number of molts found yields a molt frequency value (animal days per molt).

In Test I, euphausiids exposed to 1.41 and 2.06 mg/l had significantly longer periods between molts, 17.33 and 20.29 days/molt, respectively, compared with from 8.24 to 9.30 days/molt for controls and euphausiids exposed to 0.897 mg/l TMH and less (Table 5-5). The interval between molts of gravid female euphausiids was significantly longer than found in the controls at 1.96 mg/l TMH, but not at 1.33 mg/l TMH or at lower test concentrations (Table 5-6).

Juvenile euphausiids experienced the least sensitivity of WSF exposure on molting frequency. The interval between molts at 2.18 mg/l TMH at 27.80 days was significantly longer than at lower test levels and in controls, but the molt interval, 8.23 days, for the next highest test level, 1.63 mg/l, was not significantly different than the interval found for controls (Table 5-7).

TABLE 5-4

LC_{50} CONCENTRATIONS FOR *T. RASCHII* DEVELOPMENTAL STAGES

	LC_{50} in mg/l (95% Confidence Interval)		
Test Number/ Life Stage	**4-day**	**7-day**	**10-day**
I / Adults	> 2.06	1.76 (1.41-2.06)	1.58 (1.41-2.06)
II/ Gravid Females	1.37 (1.33-1.96)	0.69 (0.62-1.33)	--------
III/ Larvae	> 1.96	>1.96 *	--------
IV/ Juveniles	> 2.18	2.00 (1.87-2.14)	1.72 (1.60-1.83) **

* Day 6

** Day 11

TABLE 5-5

EFFECT OF OIL WSF ON ADULT T. RASCHII MOLT FREQUENCY DETERMINED DURING TEST I

Total measured hydrocarbons (mg/l)	Test Day *												Total molts	Total animal days	Days per molt
	1	2	3	4	5	6	7	8	10	12	14	16			
Control	7	4	3	3	2	2	5	1	14	2	7	3	53	480	9.06
0.301	5	6	5	3	1	0	1	5	12	7	7	1	54	474	8.78
0.543	5	10	0	1	4	3	1	2	11	5	6	5	53	463	8.24
0.897	6	3	3	1	1	3	1	3	8	6	6	6	47	437	9.30
1.413	3	5	2	4	0	0	1	0	2	0	1	0	18	312	17.33
2.062	6	0	1	0	0	0	0	0	0	0	-	-	7	142	20.29

TABLE 5-6

EFFECT OF OIL WSF ON GRAVID FEMALE T. RASCHII MOLT FREQUENCY DETERMINED DURING TEST II

Total measured hydrocarbons (mg/l)	Test Day *							Total molts	Total animal days	Days per molt
	1	2	3	4	5	6	7			
Control	2	1	2	1	5	12	3	26	219	8.42
0.054	2	3	0	7	1	10	2	25	195	7.80
0.142	2	2	3	6	6	7	2	28	210	7.50
0.620	1	1	7	3	3	6	3	24	193	8.04
1.329	3	2	1	2	1	0	2	11	116	10.6
1.956	1	0	0	-	-	-	-	1	48	48.0

TABLE 5-7

EFFECT OF OIL WSF ON JUVENILE T. RASCHII MOLT FREQUENCY DETERMINED DURING TEST IV

Total measured hydrocarbons (mg/l)	Test Day *										Total molts	Total animal days	Days per molt
	1	2	3	4	5	6	7	9	11	13			
Control	4	1	8	3	2	5	3	6	10	8	50	333	6.66
0.191	1	5	7	2	2	7	0	11	7	8	50	338	6.76
0.497	5	4	0	3	5	3	6	7	7	13	53	333	6.28
0.742	4	1	3	3	3	6	6	5	8	11	50	336	6.72
1.627	2	3	6	4	2	3	3	3	7	2	35	288	8.23
2.184	1	2	1	0	0	0	0	0	1	0	5	139	27.80

* Numbers in Test Day columns = number of molts.

Molt frequencies were not compared between life stages because of differences inherent in each stage, and some differences in test temperatures.

No attempt was made to quantitatively evaluate swimming, activity level or other gross behavior during the tests of WSF toxicity. It was readily apparent, however, that euphausiids exposed to the highest test levels in each of the three tests of postlarval animals were highly narcotized during the initial 24 hours of exposure. To a lesser extent, euphausiids exposed to the second highest levels in all three postlarval tests were similarly affected. As the tests progressed, some of the narcotized animals at this test level became progressively more affected and eventually died, but others appeared to recover. At all lower test levels, the postlarval animals generally appeared to be unaffected behaviorally in comparison to controls. Nevertheless, it seemed to the observer that control euphausiids and those at the lowest test levels (e.g. < 0.5 mg/l TMH) were more robust and healthy appearing at times, and were more successful in consuming available food organisms (based on the amount of food remaining in test chambers by the next feeding time), than animals exposed at the middle test concentrations of WSF (e.g. in the range of 0.5 to 0.9 mg/l TMH).

6 DISCUSSION

6.1 Ecology of *Thysanoessa raschii*

6.1.1 Ecological Importance of *T. raschii*

Euphausiids comprise up to one-third of the zooplankton biomass in boreal waters (Mauchline and Fisher 1969). *T. raschii* averages over 30% of the total number of individual euphausiids in the northern seas (Hopkins, et al. 1978; Rogers, et al. 1979). Thus, this species represents at least one tenth of the total zooplankton biomass in these areas and more in neritic waters where it is more common (Mauchline and Fisher 1969). As a consequence, the ecological interactions of this species are of considerable importance in Arctic and subarctic coastal marine environments.

Early growth stages of euphausiids apparently feed upon phytoplankton, (primarily, but not exclusively diatoms) (Mauchline and Fisher 1969; Mauchline 1980). As they mature, *T. raschii* individuals become more omnivorous; but remain primarily herbivorous as adults (Mauchline 1966). The combination of the large biomass, herbivorous nature, and vertical migration of *T. raschii* means that this species is a major route of energy and materials transfer from the epipelagic region to the mesopelagic habitat in Arctic and subarctic waters. Its fecal pellets and moults can further transfer material to the ocean floor as well. For example, forty percent of the zinc-65 discharged by the Columbia River in the Pacific is incorporated into the exoskelton of *Euphausia pacifica* individuals, then molted off into deeper waters (Fowler and Small 1967; Pearcy and Osterberg 1967).

Other significant ecological interactions include the synthesis of vitamin A. Euphausiids are the only group of organisms in which all members synthesize vitamin A and they have greater concentrations than all other invertebrates (Mauchline and Fisher 1969). It has been suggested that they are responsible for the bulk of naturally-synthesized vitamin A.

The key ecological significance of *T. raschii* and other euphausiid species, however, lies in the fact that they are a major source of food for marine animals higher in the food web, transforming energy and materials synthesized by its food supply, the phytoplankton, into a more utilizable form for marine fish, birds, and mammals (Table 6-1).

The importance of euphausiids in diets of subarctic Alaskan fish species is fairly well documented. Euphausiids have been found important in diets of juvenile salmon (Gosho 1977; Harris and Hartt 1977; Rogers et al. 1979), capelin (Harris and Hartt 1977; Rogers et al. 1979), sand lance (Rogers et al. 1979), walleye pollock (Rogers et al. 1979; VTN 1980), and other species. Studies in Balsfjorden, Norway found capelin, herring, and Atlantic cod feeding extensively on *Thysanoessa* euphausiids (Pearcy et al. 1979).

The role of euphausiids in Alaskan Arctic fish diets has not been well documented. Fish collected in nearshore waters of the northeastern Chukchi Sea during 1983 were found to eat a variety of items, but only one species of eight examined had eaten euphausiids. Pink salmon (*Oncorhynchus gorbuscha*) stomach contents were less than 1% euphausiids (2 of 12 fish). The other species examined, which did not have euphausiids in their stomachs, were Arctic cod (*Boreogadus saida*), fourhorn sculpin (*Myoxicephalus quadricornis*), capelin (*Mallotus villosus*), saffron cod (*Eleginus navaga*), Pacific herring (*Clupea harengus palasii*), boreal smelt (*Osmerus mordax*), and Arctic flounder (*Liopsetta glacialis*). Lowry and Frost (1981) found euphausiids of minor importance in diets of Arctic cod in the Bering, Chukchi and Beaufort Seas.

Euphausiids are utilized by pelagic and nearshore birds in the Beaufort Sea (Divoky 1984; Frost and Lowry 1984). Species feeding on euphausiids include glaucous gull (*Larus hyperboreus*), ivory gull (*Pagophila eburnea*), Ross' gull (*Rhodostethia rosea*), Sabine's gull (*Xema sabini*), Arctic tern (*Sterna paradisaea*), black-legged kittiwake (*Rissa tridactyla*), thick-billed murre (*Uria lomvia*), red phalarope (*Phalaropus fulicarius*), and oldsquaw (*Clangula hyemalis*). Arctic tern and several of the gull species were the greatest euphausiid feeders.

Six of the seven species of baleen whales known to occur off Alaska live on euphausiids and copepods (Nemato 1970; Nishiwaki 1972). Sei, blue and bowhead whales live almost entirely on these organisms, while minke, fin, and humpback whales add small, gregarious fish, such as the euphausiid-eating capelin, other smelt, herring and sand lance, to their diets as well.

TABLE 6-1

EUPHAUSIIDS AS FOOD ITEMS OF ALASKAN ARCTIC MARINE VERTEBRATES

PREDATOR SPECIES	EUPHAUSIID REPRESENTATION IN STOMACH CONTENTS (reference)
MAMMALS	
Bowhead whale	37% (n=5). Whales taken during Autumn, 1979 near Kaktovik. (A)
	92% (n=2). Whales taken during Autumn, 1976 near Barrow. (A)
Ringed seal	90% (vol., n=3). Spring (May), 1976, near Barrow. (A)
	99% (vol., n=2). Summer (Aug-Sep), 1976, Barrow (A)
	44% (n=16).Summer, 1980 Beaufort Lagoon(A)
	<1% (n=8). Summer, 1980, Pingok. (A)
	0 (n=13). Summer, 1977, Prudhoe. (A)
	0 (n=73). Autumn (Nov),1977 and 1978, Barrow and Prudhoe. (A)
	2% (vol., n=24). Winter (Feb-Apr), 1979, Prudhoe. (A)
	0 (n=34). Winter (Feb-Apr), 1978 and 1979, Barrow. (A)
BIRDS	
Black-legged kittiwake	2% (A)
Glaucous gull	9% (A)
	0 (n=9). Pelagic region. (B)
	13% (wt.); 33% (freq.), (n=9). Nearshore region. (B)

TABLE 6-1 (continued)

Ivory gull	10%	(A)
Ross' gull	40%	(A)
Sabine's gull	10%	(A)
	13% (wt.); 17% (freq.), (n=6) Pelagic region.	(B)
	4% (wt.); 3% (freq.), (n=32) Nearshore region.	(B)
Arctic tern	18%	(A)
	35% (wt.); 22% (freq.), (n=6) Pelagic region.	(B)
	23% (wt.); 23% (freq.), (n=48) Nearshore region.	(B)
Thick-billed murre	2%	(A)
Red phalarope	5% (freq.) (n=76). Pelagic and nearshore regions combined.	(B)
Oldsquaw	17% (wt.); 13% (freq.), (n=93) Nearshore region.	(B)
Fish		
Arctic cod	5%	(A)
Pink salmon	<1% (wt.); 17% (freq.), (n=12). Pt. Lay, Chukchi Sea.	(C)

References: (A) = Frost and Lowry (1984), Beaufort Sea.
(B) = Divoky (1984), Beaufort Sea.
(C) = Fechhelm et al. (1985), Chukchi Sea.

In the Beaufort Sea, bowhead whales (*Balaena mysticetus*) and ringed seals (*Phoca largha*) are major consumers of euphausiids. Stomachs of bowhead whales have been found to contain 5-98% euphausiids, depending on location and season of capture (Frost and Lowry 1984). Whales taken near Kaktovik (5 animals) in 1979 had a mean composition of 37% euphausiids in their stomachs; 2 whales taken near Barrow in 1976 averaged 92% euphausiids in their stomachs. (Referenced locations are shown in Figure 6-1.) Ringed seals examined had 2-99% stomach content composition represented by euphausiids (Frost and Lowry 1984).

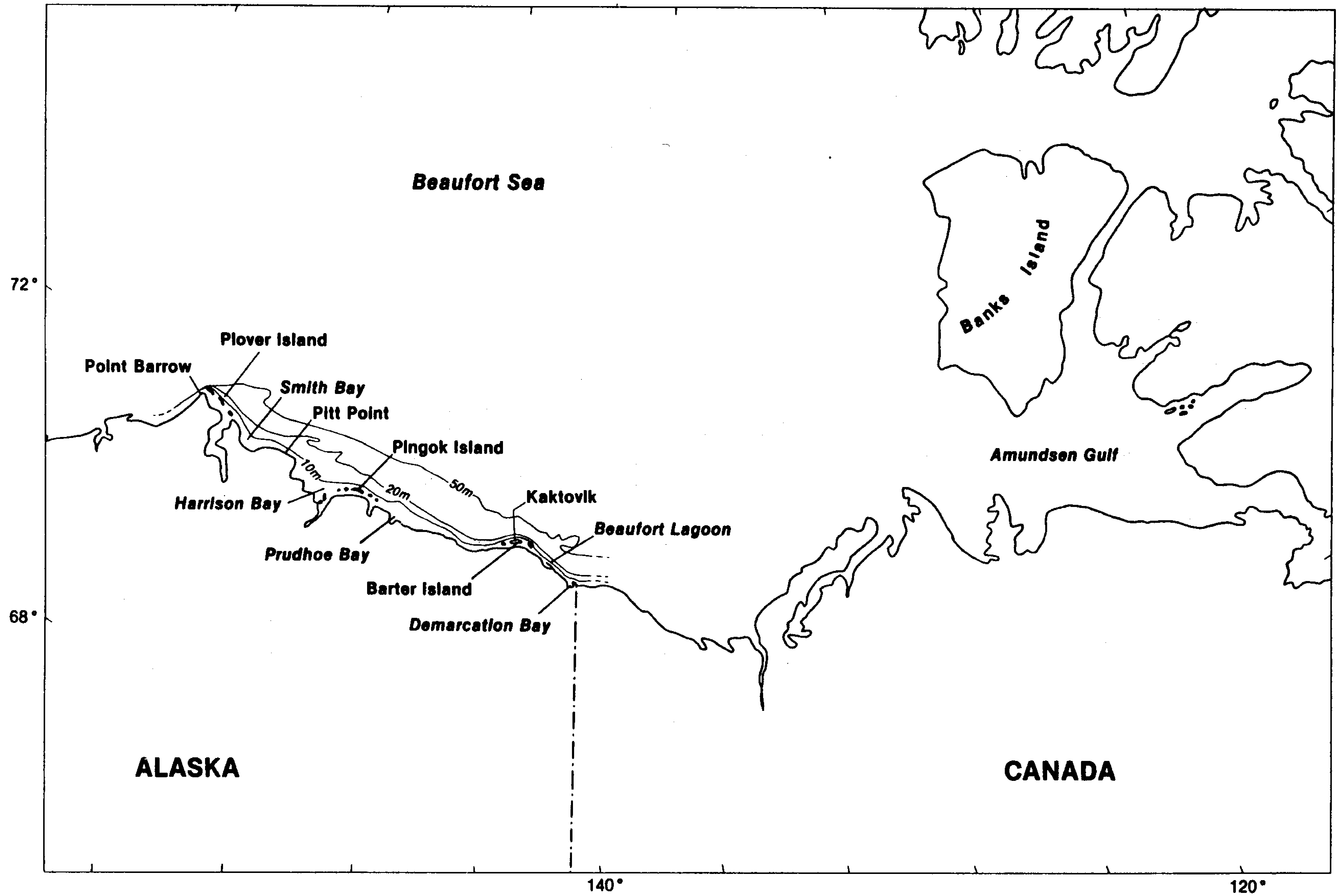
Data concerning trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea were recently synthesized and summarized by Frost and Lowry (1984).These authors estimated the total quantities of food consumed annually by the major vertebrate consumers. Euphausiids represented 7%, by weight, of the 2+ million tons of estimated food consumption; copepods, Arctic cod, hyperiid amphipods and "others" represented 48%, 6%, 1% and 37%, respectively. The estimated 143,000 tons of euphausiids consumed annually are eaten by Arctic cod (65.8%), bowhead whales (31.5%), ringed seals (2.6%) and birds (less than 0.1%). Euphausiids represented 65% of annual consumption by bowhead whales, 9.7% of consumption by ringed seals, 2.5% of consumption by all marine birds, and 5% of consumption by Arctic cod.

6.1.2 Distribution of *T. raschii* within the Arctic Ocean

T. raschii is found throughout the boreal coastal waters of the world's oceans. It occurs in the North Atlantic between 40 and 70 degrees north off West Greenland to the Gulf of Maine, around Iceland, around Scotland, in the North Sea, and off Norway (Mauchline and Fisher 1969). In the Pacific it is present along the coastlines of Asia and North America, and north into the Bering and Beaufort Seas at the same latitudes (Brinton 1962; Mauchline and Fisher 1969). *T. raschii* is seldom found in oceanic waters.

Thysanoessa raschii and *T. inermis* are the only two species of euphausiids common in the Arctic Ocean (Mauchline 1980). *T. raschii* is abundant in the Barents and White Seas (Zelikman, et al. 1978; 1979; 1980), in the Sea of Okhotsk (Zhuravlev 1977), in the Bering Sea (Cooney 1977) and in the Chukchi and Beaufort Seas (Carey 1978; Horner 1981).

Typical daytime densities reported off Alaska for *Thysanoessa raschii* were 16 individuals per 1000 cubic meters in southeastern fjords (VTN 1982), 100 per 1000 cubic meters in Kodiak bays (Kendall et al. 1980; Rogers, et al.



EFFECTS OF OIL ON FOOD
ORGANISMS OF THE BOWHEAD WHALE
NOAA/OCSEAP RU 662

THE BEAUFORT SEA

FISHMAN ENVIRONMENTAL SERVICES

1985

FIGURE 6-1

1979; Vogel and McMurray 1982) and up to 510 per 1000 cubic meters in the Beaufort Sea (Horner 1981). The average density of adult *T. raschii* in the Beaufort was between 50 to 200 individuals per 1000 cubic meters (Carey 1978). During August and early September, 1977 densities in excess of 100 animals per 1000 cubic meters occurred all along the Beaufort Sea coastline in waters of 20 to 80 m depth, approximately 15 to 100 km offshore (Carey 1978). Pack ice apparently inhibited collections farther offshore, thus, the offshore distribution of this species in the Beaufort Sea is unknown.

The lack of abundance and distribution data for *T. raschii* in the Alaskan Beaufort necessitates consideration of indirect evidence: bird and mammal feeding behavior and distribution. Bowhead whales are reported to feed extensively on euphausiids (primarily *T. raschii*), particularly in the western Beaufort (L. Lowry 1985, personal communication). Bowheads are found in nearshore waters along the western Beaufort during their fall westward migration. The inshore waters between Pt. Barrow and Smith Bay are utilized annually between August and November, with most sightings (>90%) during September (Braham et al. 1983). Whales were observed feeding in these waters during September of 1974, 1975, 1976 and 1978; whales were observed feeding near the surface during a swarming and onshore movement of euphausiids during September, 1976 (Braham et al. 1983). Bodfish (1936) reported bowheads consistently in water less than 40 m, Braham et al. (1983) observed whales in water 3 to 12 m deep, with 172 of 234 sightings during August-November, 1974-78 near Pt. Barrow in water less than 12 m. Braham et al. (1983) concluded that nearshore waters are more important for feeding whales than offshore waters in the area of the Plover Islands.

The area near the Plover Islands appears to be important in terms of primary and secondary productivity, and feeding for marine birds and mammals. Divoky (1984) discussed the apparent importance of this area to marine birds. Warmer northeastward-flowing water from the Bering Sea (Bering Sea Intrusion) is a major oceanographic feature found off Pt. Barrow. Divoky attributed higher bird densities in the western Beaufort to higher prey densities associated with this warm, subarctic water. Bering Sea water meets the westward-moving Beaufort Gyre and nearshore waters, resulting in the formation of eddies in the Plover Islands and Pitt Point region. While zooplankton samples in an intrusion area produced inconclusive results related to abundance/density differences compared with nearby areas, stomach samples of Arctic terns captured while feeding at a convergence line off the Plover Islands contained mostly euphausiids (Divoky 1984). Also, major wash-ups of dead and dying *T. raschii* have been documented about once every 2 years during late August - early September (Divoky 1985, personal communication). The observed 2-3 inch deep windrows of beached euphausiids fed major concentrations of sea birds (mixed species flocks of about 10,000 birds). Based on bird feeding data, Divoky (September 24, 1985, personal comm. by telephone) found euphausiids distributed farther offshore (20 m and deeper) in the western Beaufort than the eastern Beaufort.

Feeding data for ringed seals (Frost and Lowry 1984) provide evidence of euphausiid distribution, and, perhaps, seasonality. Stomach contents of seals captured near Barrow were 90% euphausiids during spring (May), 1976, and 99% euphausiids during summer (Aug-Sep), 1976; no euphausiids were in stomachs of seals captured during autumn (November), 1977 and 1978, and winter (Feb-Apr), 1978 and 1979. The stomach contents of seals captured in Prudhoe Bay were 0% euphausiids during spring, 1979, summer, 1977, autumn, 1977 and 1978; and 2% during winter,1979. Stomach contents of seals taken in Beaufort lagoon during summer, 1980 were 44% euphausiids.

Most collection programs in nearshore waters and coastal lagoons of the Beaufort and Chukchi Seas have found few or no euphausiids either in the water column or in fish stomachs (Craig and McCart 1976; Griffiths 1984; Craig et al. 1982; Craig 1984). Exceptions include euphausiids reported in stomachs of Arctic cod taken in Beaufort Sea shallow water (5 m; Lowry, Alaska Dept. Fish and Game, October 7, 1985, personal comm. by telephone, and pink salmon in the Chukchi (Fechhelm et al. 1985).

The data summarized above suggest several points concerning *T. raschii* distribution in the Beaufort Sea:

1. Euphausiids are found in nearshore waters as well as deeper offshore areas.

2. The area around Pt. Barrow and the Plover Islands appears to support a major concentration of euphausiids, particularly during August - September.

3. The Bering Sea Intrusion appears to be a major factor in assumed euphausiid distribution and density. (Euphausiids associated with the intrusion, however, may represent transported Bering Sea populations [Divoky 1984]).

6.1.3 Vertical distribution patterns of *T. raschii*

In areas where this species has been studied, adults typically live at 200 m or less during the day and migrate toward the surface at night, while earlier life history stages are collected in the surface 25 m (Mauchline and Fisher 1969). As adults, *Thysanoessa raschii* migrate vertically about 100 m (Mauchline and Fisher 1969; Mauchline 1980). Light intensity apparently is the key physical parameter causing vertical migration. Clarke (1971) found that the optimal light intensities for adult euphausiids off California were 10^{-3} to 10^{-4} W/cm^2 (micro-watts). Disruption of *T. raschii* vertical migration may occur during mid-summer in the Beaufort Sea due to the continuous light conditions at that time of year. While this phenomenon was not observed for euphausiids in Balsfjorden by Hopkins, et al. (1978) or Pearcy, et al. (1979), neither study was performed during the period of continuous light (Eilertsen, et al. 1981). Wiborg (1954) found, however, that vertically migrating zooplankton species appear to stop migrating during the High Arctic summer.

The association of euphausiids with isolumes results in their tendency to live within a restricted vertical layer of the water column during daylight hours. Extensive information is now available suggesting that euphausiids are sometimes responsible for the deep scattering layers (DSL) recorded by echo sounders (Farquhar 1971). *T. raschii* causes sound scattering at 100 to 200 kHz (kilohertz) (Farquhar 1977) and several studies have tracked vertical distribution of this species using 120 kHz echo sounders (Hopkins, et al. 1978; Sameoto 1976a, 1980b).

High light levels have been found to reduce the lifespan of euphausiids (Mauchline and Fisher 1969). Despite their preference for a low optimal light level, some populations of euphausiids have biochemically adapted to higher light intensities. *Euphausia pacifica* in Saanich Inlet, British Columbia migrates only 85 m due to the presence of an anoxic layer below (Bary, et al. 1962). This population lives in light two to three orders of magnitude greater than other populations of the same species. Boden and Kampa (1965) determined that individuals of the Saanich Inlet population have differentially deposited a screening pigment which allows them to survive the higher light levels, suggesting that some euphausiid species may possess significant amounts of genetic variability between different populations.

Obviously, *T. raschii* living in shallow (less than 20 m) nearshore waters will not exhibit large-scale vertical migrations. The occurence of large numbers of euphausiids in nearshore waters, such as described off the Plover Islands, may be related to reproductive swarming. Another factor in this apparent concentration of euphausiids could be the Bering Sea Intrusion. Aagaard (1984) describes cross-shelf flow, or exchange between the Beaufort Undercurrent and inshore waters over distances of 13 km. The Barrow Sea Valley, running just east of Pt. Barrow, has depths of 150+ m within 5 km of water <10 m deep off Pt. Barrow. Cross-shelf flow and localized upwelling events might provide a transport mechanism for euphausiids into shallow, nearshore waters.

6.1.4 Life history and fertility of *T. raschii*

In Balsfjorden, Norway, (approx. 69.5° N latitude) *T. raschii* lives for two years, three months (Falk-Petersen and Hopkins 1981). Similar periods of longevity have been found for this species in the Clyde Sea area off southwest Scotland (Mauchline 1966), in the Gulf of St. Lawrence (Berkes 1976), in the Gulf of Maine and in the central North Sea (Lindley 1980).

Spawning typically takes place in the spring at water temperatures of 0 to 7° C. Surface (0 to 25 m) breeding swarms of *T. raschii* have been collected in several locations, including Alaska, during this spawning period. The duration of spawning is from two to three weeks, usually with a peak period in April or May, coinciding with the spring diatom bloom. Berkes (1976), however, found some evidence for a low level of spawning activity throughout the spring and summer, and Mauchline (1980) suggested that there might be a second spawning period in the fall in a few, favored locations. *T. raschii* have been reported to breed in the Beaufort Sea during the fall and early winter (Carey 1978). Falk-Petersen and Hopkins (1981) regard phytoplankton production as being more important than temperature in controlling spawning. This correlates well with the observed 1977 Beaufort Sea euphausiid densities. Distribution of *T. raschii* densities in excess of 100 animals per 1000 cubic meters match the areas in the Beaufort with high chlorophyll *a* concentrations and C^{14} uptake rates (Carey 1978).

The estimated fecundity per *T. raschii* female during a breeding season is 300 t0 400 eggs (Mauchline 1980); the eggs, however, are shed freely into the sea after fertilization and direct counts have not been made. The number of eggs produced is a function of the size of the female (Mauchline 1980). The eggs sink, then hatch, and the larvae migrate toward the surface. Larval euphausiids are mainly found in the top 15 to 25 m of water (Mauchline and Fisher 1969); however, as they mature, fewer and fewer are found there during daylight hours. The mortality of the egg and larval stages (nauplius, calyptopis, and furcilia) is calculated to be 98.2% (Lindley 1980).

Larvae in the Clyde Sea area become juveniles after three to four months (Mauchline 1966) and reproduction occurs the following spring. In Balsfjorden, on the other hand, the animals usually become sexually mature two years after birth, although a few mature one-year-old females have been found (Falk-Petersen and Hopkins 1981). Some Clyde Sea females reproduce in their second year as well. *Thysanoessa* populations from fjords in southeast Alaska have a similar lifecycle to the Balsfjorden population (Vogel, unpublished data). Beaufort Sea populations are likely to be similar to those of Balsfjorden, although life history information for Beaufort Sea *T. raschii* is not available.

6.1.5 Feeding patterns and productivity of *T. raschii*

Thysanoessa raschii is almost exclusively an herbivore (Mauchline and Fisher 1969; Mauchline 1980). The growth of *Thysanoessa* in Balsfjorden, in terms of changes in carapace length, is closely related to primary productivity (Falk-Petersen 1981; Falk-Petersen and Hopkins 1981). Likewise, over 80% of the annual increase in individual size for Clyde Sea populations occurs between March and June during the spring diatom bloom (Mauchline 1966).

A second line of evidence for the herbivory of *T. raschii* has recently been developed. Euphausiids store excess consumed food in the form of lipids. These lipids can be characterized by their source population and origin. As a consequence, the food habits by season for four euphausiid species, including *T. raschii* , have been described (Henderson, et al. 1982). During mid-winter *T. raschii* individuals in Balsfjorden lacked 20:1 and 22:1 fatty acids and wax esters (indicative of feeding upon calanoid copepods) while they were rich in 16:0 and 18:1 fatty acids and phytol, which are characteristic of phytoplankton (Sargent and Falk-Petersen 1981). It is believed that the presence of phytol is indicative of detrital feeding during this period (Falk-Petersen, et al. 1982; Sargent and Falk-Petersen 1981). Apparently, neither *T. raschii* nor *T. inermis* fed upon *Phaeocystis pouchetti*, a major spring phytoplankton species in Balsfjorden, as their fatty acid composition was entirely different from this alga's (Falk-Petersen, et al. 1982).

Stomach content analyses of *T. raschii* indicate that this species eats detritus, phytoplankton (mainly diatoms and dinoflagellates) tintinnids and radiolarians (both microzooplankton) and that larger individuals include *Sagitta* and small crustaceans in their diet (Mauchline 1980; Mauchline and Fisher 1969). Recently, Sameoto (1980a) found that *T. raschii* from the Gulf of St. Lawrence preferred to feed upon phytoplankton (except *Chaetoceros atlanticum*, a large, spiny diatom) and at night in the top 75 m of water. They also occasionally ate microzooplankton. Only 5% of the stomachs had copepod remains in them (as opposed to 90% of those of *Meganyctiphanes norvegica*, known to be carnivorous, and 22% of the stomachs of *T. inermis*). The highest frequency of copepod remains in the stomachs of *T. raschii* was during September when phytoplankton densities are low in boreal waters. Sameoto further reported that none of the stomachs of any of the three species he studied had bottom mud in them, unlike results from previous studies. Sameoto concluded that all three species preferred to feed in the water column when food was available. Daily calorie consumption in the Gulf of St. Lawrence by the average individual *T. raschii* was 3.1 calories during June, and 2.2 calories during December (Sameoto 1976b); this represented 1.5% of the daily phytoplankton production in June, and 60% in December.

Annual production of *T. raschii* is relatively uniform in the subarctic Atlantic. Lindley (1980) found that annual production for this species equalled 1.54 mg dry weight (DW) per cubic meter off the Gulf of St. Lawrence, in the Bay of Fundy and in the Gulf of Maine, but only 1.02 mg DW m^{-3} in the central North Sea. In the Gulf of St. Lawrence proper, production of this species was 1.8 mg DW m^{-3} per year (Berkes 1977), while in Balsfjorden it was estimated to be about 1.9 mg m^{-3} yr^{-1} (Falk-Petersen 1981; Hopkins, et. al. 1978). Annual production measurements have not been made for this species in either the boreal North Pacific or the Arctic.

Individual specimens of *T. raschii* (Average dry weight = 10 mg) consume 1.8 µl of oxygen per hour per mg DW at 0 to 2 degrees C (Sameoto 1976b). Oxygen consumption per mg DW doubles between 5 and 15° C for *T. inermis* according to this study. As respiration rates for *Thysanoessa raschii* and *T. inermis* are not significantly different (Sameoto 1976b), a similar increase in metabolic rate should occur in *T. raschii*. Respiration rates also change with age of the animal due to the change in the surface area to body weight ratio (Harding 1977). About 6% of the total energy needs of this species is required for molting (Sameoto 1976b), much lower than the 38% necessary for molting by *Euphausia superba* (Ikeda 1984) or the 34% required by *E. pacifica* (Paranjape 1967).

6.1.6 Comparison of *T. raschii* and *Euphausia superba*

Euphausia superba is probably the single most abundant euphausiid in the world's oceans, and has been the subject of a large number of ecological studies. Comparisons of *E. superba* to *T. raschii* can increase our understanding of *T. raschii* biology and ecology.

E. superba occupies the same ecological niche as *T. raschii* . It is primarily an herbivore feeding on similarly sized particles (Boyde, et al. 1984) with similar lipid composition to *T. raschii* (Clarke 1984; Falk-Petersen 1981). *E. superba*, however, does not change to detritus feeding during the winter as do the *Thysanoessa* species, but rather the animals overwinter on their stored reserves, losing weight and literally shrinking throughout the winter (Ikeda 1984). Nor are its lipid reserves especially large for an animal of its size; shrinkage is the primary overwintering survival mechanism. The ecological similarity in these two animals' niches also extends to their importance as major food organisms for the pelagic food web in the region of the world's oceans where they occur (Laws 1985; Mauchline and Fisher 1966; Mauchline 1980).

Another similarity is schooling by the two species. Both species, like all euphausiids studied to date, form breeding swarms, and all species of euphausiids aggregate vertically to some extent (Mauchline 1980). Only eight or nine species, however, including both *T. raschii* and *E. superba* live in large, hollow feeding swarms outside of the breeding season (Brinton and Antezana 1984; Mauchline and Fisher 1966; Mauchline 1980). Behavior of *E. superba* feeding schools has now been directly observed by divers (Hamner 1984). *T. raschii* probably behaves similarly.

E. superba is a much larger animal than *T. raschii* (Average total length, or TL, of *E. superba* = 34 to 35 mm, Fevolden and George 1984; average TL of *T. raschii* = 22 to 25 mm, Mauchline and Fisher 1966). It also lives for up to 5 years (Ettershank 1984; Ikeda 1984; Marr 1962) instead of the two and a quarter of *T. raschii* . Annual growth and respiration rates are thus quite different for the two species. During the second year of life juvenile *E. superba* increase, on the average, from 2.3 mg DW to 30 mg DW (Ikeda 1984); by contrast, juvenile *T. raschii* in Balsfjorden grow from 1.0 mg DW to 9.3 mg DW (Falk-Petersen 1981). Growth rates in both species, however, are controlled by phytoplankton production (Falk-Petersen and Hopkins 1981;

Holm-Hansen and Huntley 1984). Juvenile *E. superba* (Average DW = 10 mg have a respiration rate of 0.7 µl of oxygen hr^{-1}p mg^{-1} DW at -1 to +1° C (Ikeda 1984), not the 1.8 l per hr found by Sameoto (1976b) for *T. raschii* specimens of the same size and maturity.

Another difference between these two organisms is in their development. Due to the great depth from which the newly hatched *E. superba* nauplii must ascend (1200 to 2000 m, George 1984; Marr 1962), this species does not begin to feed until the first calyptopis stage (Brinton and Townsend 1984; George 1984; Ikeda 1984; Marr 1962; Mauchline and Fisher 1969). The first stage nauplius of *T. raschii* is an active phytoplanktivore by comparison. Since the larvae of both species are phytoplanktivorous, yet enter the surface waters after differing lengths of time for development, reproduction must be timed differently, possibly using different environmental cues.

6.1.7 Sensitivity of *T. raschii* to organic pollutants

Euphausiids have not been extensively used as bioassay organisms. Lee (1975), in a study of the effects of petroleum hydrocarbons upon marine zooplankton, included two euphausiids, *Euphausia pacifica* and *Thysanoessa raschii* , in his comparisons to two calanoid copepods, *Calanus plumchrus* and *C. hyperborealis* . Unfortunately, no specific values were given for the reactions of the two euphausiids. It may safely be inferred, however, that the euphausiids reacted similarly to the copepods when exposed to different hydrocarbons because, first, Lee commented on various differences he found using a hyperiid amphipod, *Parathemisto pacifica* , and second, Harding and Vass (1979) found similar uptake rates on a per mg DW basis by *T. raschii* and *Calanus finmarchicus* for DDT ingestion and clearance. According to Lee, most of the uptake by the copepods was within the first 24 hours and most of the clearance occurred within three days, although some remained after 28 days. Naphthalene, benzpyrene, and octadecane were successfully metabolized by the copepods. However, 500 ppb of Fuel Oil #2 caused copepod mortality and paralysis occurred at 200 to 500 ppb. Survival of copepod eggs was reduced from 75% to 40% in the presence of 80 ppb of either 1-methyl naphthalene or 1,2-dimethyl naphthalene, but not in the presence of either naphthalene or mineral oil.

6.2 Effects of Crude Oil WSF on T. raschii.

6.2.1 Limitations of Experimental Data

Interpretation and discussion of the results from the tests described in this report must be carefully qualified. First, the euphausiids used for the tests were from a southeast Alaskan population of T. raschii; second, experimental temperatures were generally several degrees C higher than summer temperatures of water over the Alaskan Beaufort continental shelf; and, third, as explained in Section 6.3, the experimental concentrations of crude oil WSF and individual components may be quite different from those experienced in a real oil spill.

6.2.2 Laboratory Test Results

No test reports of the effects of crude oil WSF on euphausiids could be found in the scientific literature; the present study, therefore, represents an important contribution to the body of knowledge concerning oil fate and effects. The sensitivities of T. raschii life stages to oil WSF concentrations can be presented in terms of the highest "no effect" concentrations (Table 6-2). From this table, it is clear that larvae were the least sensitive, and gravid females were the most sensitive stage tested (gravid females were also the most sensitive to handling and shipping).[1] Juveniles seemed more resistant to effects of oil WSF than adults. The highest concentrations producing "no effect" on molt frequency were lowest for non-reproductive adults and highest for juveniles.

---

[1] No data were obtained, however, for larval molt frequency.

TABLE 6-2

HIGHEST "NO EFFECT" WSF CONCENTRATIONS FOR T. RASCHII LIFE STAGES BASED ON SURVIVAL AND MOLT FREQUENCY

Test	Highest "no effect" concentration (mg/l)			
	Survival			Molt Frequency
	Day 4	Day 7	Day 10	End of Test
I. Adults	1.42	1.42	0.90	0.90
II. Gravid females	0.62	0.14	----	1.33
III. Larvae	>1.96	>1.96*	----	----
IV. Juveniles	1.63	1.63	0.74**	1.63

* Day 6
** Day 11

6.3 Comparison with Toxicity Data for other Marine Crustacea

A variety of marine crustaceans have been the subjects of laboratory bioassay tests using hydrocarbons. This discussion is focused on Alaskan species of crustacea.

6.3.1 General Considerations

Direct comparison of data generated from different tests, even of the same species, is difficult due to variation in experimental parameters. Static and flow-through tests yield different results because the hydrocarbon concentrations decrease with time during the static tests, and mixing methods may differ greatly. Exposure methods, chemical analyses, life stage and condition of test animals, and temperature are factors that can lead to differences in results and misinterpretation of data. In addressing these concerns, Rice et al. (1979, p. 552) concluded:

> "Consequently, there is little point in comparing animal sensitivities derived from experiments of different investigators, although the comparisons and conclusions within a study are usually valid."

We strongly agree with Rice et al. on the validity of comparisons between studies. It is obvious from Table 6-3 that the concentrations of aromatic hydrocarbons in undiluted WSF's of Prudhoe Bay crude oil used in this study were different from those measured by Rice et al. (1985) in their studies; concentrations in our study were lower for all aromatics reported. The relative proportions of the mono-aromatics (benzene, toluene, O-xylene) to total aromatics were similar between the studies: proportions of di-aromatics (naphthalenes) were lower in our study. Thus, even though the source of crude oil was the same (Prudhoe Bay), either the oil samples themselves, or the preparation of WSF's differed between studies.

The lack of oil WSF data for euphausiids, or any pelagic crustacean for that matter, forces us to use comparisons with other studies, using other species, for points of reference. With the preceding discussion in mind, these comparisons are not directly usable, but serve as general guidelines in the application of the T. raschii bioassay data to real-world estimations. The published results of toxicity tests using Alaskan marine crustaceans and two types of Alaskan crude oil are presented in Table 6-4.

TABLE 6-3

BETWEEN-STUDY COMPARISON OF AROMATIC HYDROCARBON CONCENTRATIONS

Component	Aromatic Hydrocarbon Concentrations (mg/l)			
	PBCO-WSF (a)	PBCO-WSF (b)	CICO-WSF (b)	Fuel Oil WSF (b)
Benzene	0.757 - 0.823	1.8	3.2	0.11
Toluene	0.698 - 0.819	2.0	2.5	0.17
o-xylene	0.068 - 0.081	0.28	0.35	0.12
m-p-xylene	0.129 - 0.149	0.58	0.78	0.17
Naphthalene	0.011 - 0.021	0.084	0.15	0.15
1-Methylnaphthalene	0.013 - 0.014	0.032	0.066	0.13
2-Methylnaphthalene	0.012 - 0.014	0.048	0.088	0.25
Ratio of all mono-aromatic to di-aromatic hydrocarbons	26.7 : 1 (b)	19.3:1	15.7:1	1.1:1

PBCO = Prudhoe Bay crude oil
CICO = Cook Inlet crude oil

(a) From this study, Test Series 2 (Tests II and III)

(b) From Rice et al. 1985; Table 2

TABLE 6-4

OIL SENSITIVITY DATA FOR ALASKAN MARINE CRUSTACEA

SPECIES (a)	OIL USED(b)	LC50 (ppm)(b)	REFERENCE	REMARKS
coonstripe shrimp, egg	CICO	>1.4(GC)	Rice, et al. 1985	96hr, flow-through
larva	PBCO	8.53(IR)	Rice et al. 1975	96hr, static
larva	CICO	1.0(GC)	" "	" "
stage I larva	CICO	1.7(IR)	Brodersen, et al. 1977	96hr, static
adult	PBCO	1.96(IR)	Rice, et al. 1975	"
adult	CICO	2.72(IR)	Rice, et al. 1976	96hr, static
adult	CICO	1.4(GC)	" "	" "
adult	CICO	2.7(IR)	Brodersen, et al. 1977	96hr, static
gravid female	CICO	1.4(GC)	Broderson and Carls, in prep.	96hr, flow-through
humpy shrimp, adult	PBCO	1.26(IR)	Rice et al. 1975	96hr, static
adult	CICO	4.94(GC)	Rice et al. 1979	96hr, static
adult	CICO	2.0(IR)	Brodersen, et al. 1977	96hr, static
stage I larva	CICO	1.7(IR)	" " "	" "
pink shrimp, adult	PBCO	2.11(IR)	Rice, et al. 1975	" "
adult	CICO	2.43(IR)	Rice, et al. 1976	96hr, static
adult	CICO	4.94(GC)	Rice et al. 1979	96hr, static
dock shrimp, adult	CICO	0.81(IR)	Rice, et al. 1975	96hr, static
kelp shrimp, adult	CICO	1.4(GC)	Rice, et al. 1985	96hr, flow-through
adult	CICO	1.86(GC)	Rice, et al. 1979	96hr, static
adult	CICO	0.95(IR)	Brodersen, et al. 1977	96hr, static
stage I larva	CICO	1.1(IR)	Brodersen, et al. 1977	96hr, static
scooter shrimp, adult	PBCO	1.94(IR)	" "	"
larva	PBCO	6.36(IR)		
adult	CICO	1.46(IR)	Rice, et al. 1976	" "
adult	CICO	4.3(IR)	Brodersen, et al. 1977	96hr, static
stage I larva	CICO	0.95(IR)	" " "	" "
grass shrimp, adult	CICO	0.87(GC)	Rice, et al. 1979	96hr, static
shrimp	CICO	0.87-1.86 (GC)	Rice, et al. 1985	96hr, flow-through
pelagic crab and shrimp	CICO	1-5(GC)	Rice, et al. 1985	96hr, flow-through

TABLE 6-4 (continued)

crab	CICO	3.6-)10 (GC)	Rice, et al. 1985	96hr, flow-through
king crab	PBCO	2.35(IR)	Rice, et al. 1975	96hr, static
larva	PBCO	)6.4(IR)	" "	"
adult	CICO	3.69(GC)	Rice, et al. 1979	96hr, static
adult	CICO	4.2(IR)	Brodersen, et al. 1977	96hr, static
stage I larva	CICO	0.96(IR)	" "	" "
Tanner crab, larva	CICO	1.7(IR)	" "	" "
purple shore crab	CICO	8.45(GC)	Rice, et al. 1979	96hr, static
hairy hermit crab	CICO	)10.58(GC)	" "	" "
amphipod	CICO	)7.98(GC)	" "	" "
mysid	CICO	)9.02(GC)	" "	" "

(a): coonstripe shrimp (Pandalus hypsinotus)
humpy shrimp (Pandalus goniurus)
pink shrimp (Pandalus borealis)
dock shrimp (Pandalus danae)
kelp shrimp (Eualus suckleyi)
scooter shrimp (Eualus fabricii)
grass shrimp (Crangon alaskensis)
king crab (Paralithodes camtschatica)
Tanner crab (Chionoecetes bairdii)
purple shore crab (Hemigrapsis nudus)
hairy hermit crab (Pagurus hirsuiticulus)
amphipod (Orchomene pinguis)
mysid (Acanthomysis pseudomacropsis)

(b): GC = gas chromatography
IR = infrared spectrophotometry

All of the studies represented in the table used seawater soluble fractions of either Cook Inlet or Prudhoe Bay crude oil, and were either static or flow-through 96 hr tests. The concentrations of hydrocarbons were measured by either infrared spectrophotometry (IR) or gas chromatography (GC). IR analysis is more sensitive to paraffinic hydrocarbons than to aromatics; the aromatic components are generally agreed to be more toxic (Rice et al. 1977). Rice et al. (1979) discuss comparisons of IR and GC analyses, and conclude that comparisons cannot be made.

Hydrocarbon toxicity data for euphausiids are not available in the literature, so only comparisons with other crustaceans are possible. Shrimps and crabs, which comprise the bulk of data in the table, are in the order Decapoda, which, like the Euphausiacea, is a subgroup of the Superorder Eucarida. This taxonomic relationship somewhat validates comparisons betweeen the euphausiid T. raschii and various shrimps and crabs. The ecology of these species is also important to consider. Pelagic species tend to be more sensitive to hydrocarbons than benthic species, which in turn are more sensitive than intertidal species (Rice et al. 1985). Data for pelagic decapod larvae might be similar to data for euphausiid larvae.

6.3.2 Life Stage Sensitivities

The 96 hr LC_{50} data presented in Table 6-3 for shrimp species have the following ranges for life stages:

adults:	1.4 - 4.94 ppm (GC);	0.81 - 2.72 ppm (IR)
eggs:	>1.4 ppm (GC) (one value only)	
larvae:	1.0 ppm (GC) (one value only) ;	0.95 - 8.53 ppm (IR)

Values for adults of the crabs tested tended to be higher than the LC_{50}'s reported for adult shrimp; shore crab, hermit crab, mysid and amphipod LC_{50}'s were also generally higher than for adult shrimp.

The 96 hr LC_{50} values presented in this report for T. raschii were:

adults:	> 2.06 ppm (GC)
gravid females:	1.33 - 1.96 ppm (GC)

larvae: > 1.96 ppm (GC)

juveniles: > 2.18 ppm (GC)

Several investigators have examined the sensitivities of shrimp life stages to oil WSF levels. Broderson and Carls (in preparation) found that eggs of coonstripe shrimp (Pandalus hypsinotus) and kelp shrimp (Eualus suckleyi) survived exposure to oil WSF if the females carrying them survived; further, larvae hatched from these eggs were physiologically more resistant to the WSF than females. Eggs from weak and dying females hatched into swimming larvae, leading the authors to conclude that the shrimp eggs were more tolerant to WSF than adult females. Since eggs of these species are carried by the female until hatching, the LC_{50}'s of the females were considered to be the important values in a real-world situation. Eggs of T. raschii, on the other hand, are shed into the water before hatching, and, if more resistant to oil WSF than females, may have better survival than the adults in a spill situation.

Larval shrimp and crabs are generally considered more sensitive to oil WSF than adults. First stage larvae of four shrimp species were "somewhat more sensitive" than adults in tests conducted by Broderson et al. (1977). Each of several coonstripe shrimp larval stages (I - VI) tested by these investigators had a different sensitivity to oil WSF, ranging from 0.24 ppm for Stage VI, to 1.9 ppm for Stage IV larvae. Larvae were considered more vulnerable perhaps due to their rapid growth and frequent molting. Mecklenberg et al. (1977) found that molting larvae of king crab (Paralithodes camtschatica) and coonstripe shrimp were 4 to 8 times more sensitive to oil WSF than intermolt larvae. Exposure of molting larvae to 1.15 - 1.87 ppm WSF (IR) for as little as 6 hours reduced molt success by 10-30%, with some mortality resulting; while exposure for 24 hours or longer reduced molting success by 90-100%, with death usually resulting. The lowest WSF test concentrations (0.15-0.55 ppm) resulted in no reduction of molting; however, many exposed larvae died after molting.

The results of tests with T. raschii, presented in this report, provide important information not previously available in the scientific literature. Larval T. raschii were found less sensitive to oil WSF than adult or juvenile animals. Gravid female T. raschii appeared to be the most sensitive of life stages tested. Unfortunately, most gravid females held in the laboratory re-absorbed their eggs before or during the bioassay tests, so data were not generated for the effects of WSF on egg survival or hatching success. The LC_{50}'s for T. raschii are within the range of GC-derived LC_{50}'s for shrimp species presented in Table 6-3 (1.4 - 4.94

ppm) and pelagic crabs and shrimp (1-5 ppm); however, these cited values are from tests using Cook Inlet crude oil, and most were static bioassays.

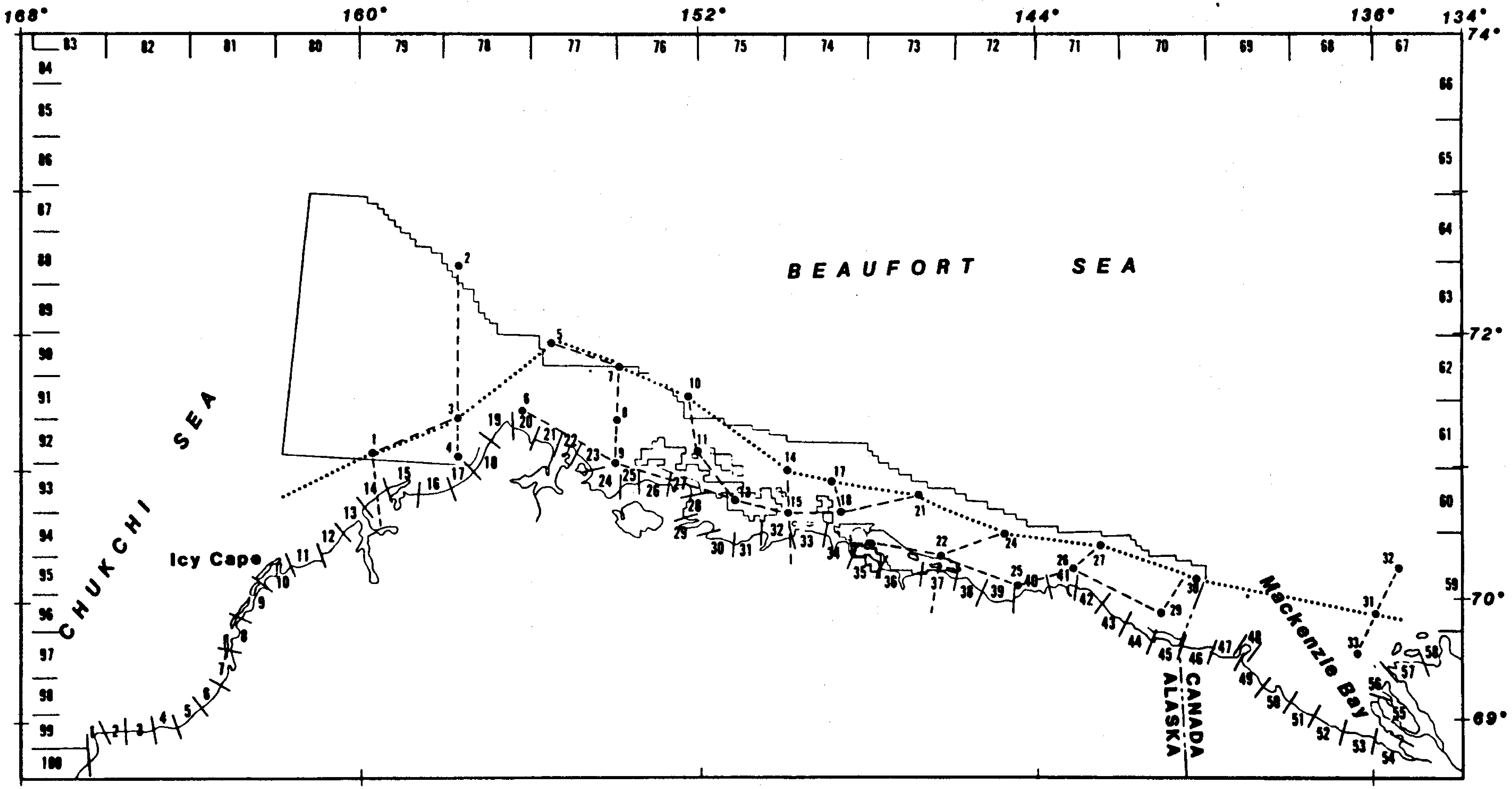
6.4 Estimates of Oil Spill Impacts to *T. raschii* Populations

6.4.1 Oil Spill Risk Analysis

An oil spill risk analysis was prepared for the southern Alaskan Beaufort Sea as part of the Environmental Impact Statement for the Diapir Field Lease Offering (MMS 1984). Review of this analysis is instructive in relation to the potential effects of oil spills on euphausiid populations. Primarily, the analysis was helpful in determining areas of high vulnerability to oil spill effects, and seasonal considerations.

Figure 6-2 shows the oil transportation routes and spill launch points used in the risk analysis. Probability estimates resulted in a total expected number of spills of 29.3 over the 40 year life of the Diapir Field; this total includes 7.8 spills expected from the proposed developments, 8.9 spills from existing leases, and 12.6 spills from production and transportation of Canadian oil in the eastern Beaufort. A 99+% chance of one or more spills of 1,000 barrels (bbl) or greater and of 10,000 bbl or greater was predicted.

Oil spill trajectory simulations were run for both the ice covered (winter) and open water (summer) seasons. The assessment of impacts to sea bird habitats included open water areas used for feeding. As seen from Figure 6-3, the area identified as the Bering Sea Intrusion has the highest probability (40+%) of oil spill contact when compared with other seabird areas. This probability approaches 60% when spills from existing leases are included. Winter spills contribute a significant amount to these probabilities. Oil spilled beneath ice cover will essentially become encapsulated in the ice, and oil trajectories thus become ice trajectories. Breakup and thaw of ice cover will release essentially fresh oil to the water. Because of the net westward flow of ice and surface currents in the nearshore Alaskan Beaufort, oil spills during winter east of Barrow become factors in spill contact risk probabilities for the Barrow area, including the Bering Sea Intrusion. The Bering Sea Intrusion area is important seabird feeding habitat as well as bowhead whale migration (and seasonal feeding) area (Figure 6-4).



Source: MMS (1984). Diapir Field Lease Offering FEIS   Figure IV-1

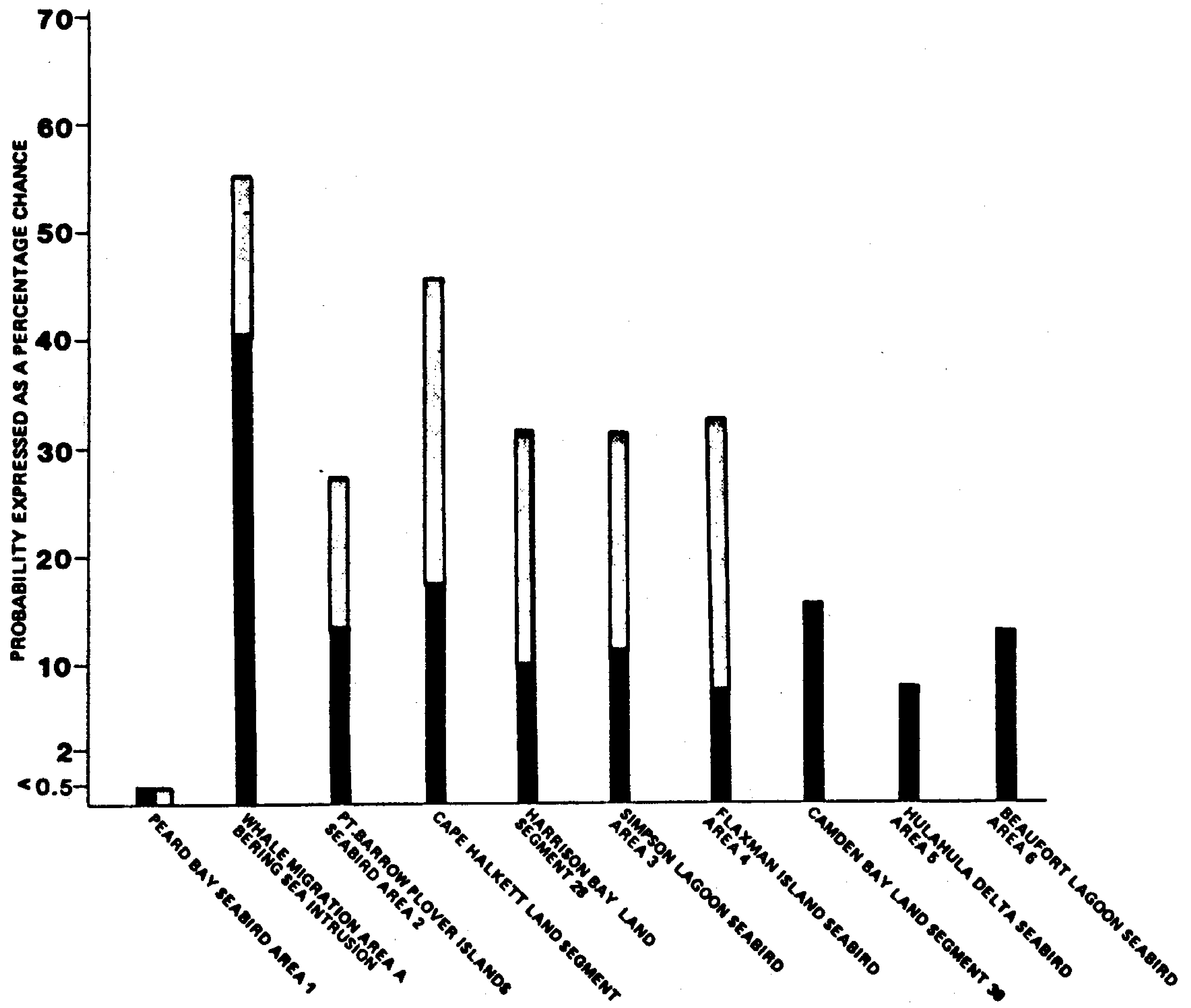
EFFECTS OF OIL ON FOOD ORGANISMS OF THE BOWHEAD WHALE
NOAA/OCSEAP   RU 662

STUDY AREA, LAND AND BOUNDARY SEGMENTS, TRANSPORTATION ROUTES AND SPILL LAUNCH POINTS HYPOTHESIZED IN OILSPILL RISK ANALYSIS

FISHMAN ENVIRONMENTAL SERVICES

1985

FIGURE 6-2



■ Proposal

☐ Proposal plus existing leasing

PROBABILITY WITHIN 10 DAYS FOR OPEN-WATER SEASON OVER THE EXPECTED PRODUCTION LIFE OF THE LEASE AREA

Source: MMS (1984). Diapir Field Lease Offering FEIS Figure IV-7

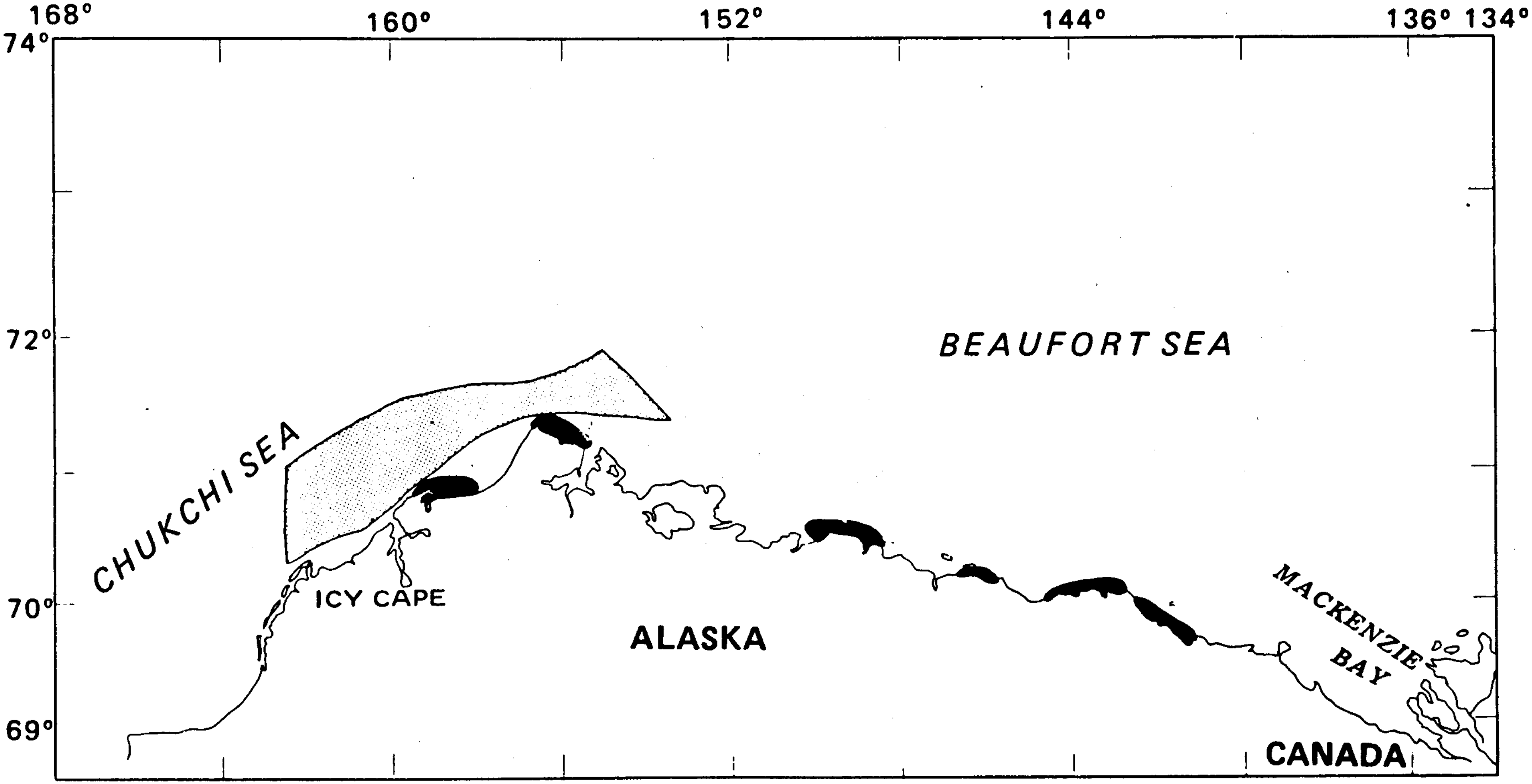
EFFECTS OF OIL ON FOOD ORGANISMS OF THE BOWHEAD WHALE
NOAA/OCSEAP RU 662

PERCENTAGE PROBABILITY OF ONE OR MORE SPILLS OF 1,000 BARRELS AND GREATER OCCURRING AND CONTACTING BIRD HABITATS

FISHMAN ENVIRONMENTAL SERVICES

1985

FIGURE 6-3



░ WHALE MIGRATION AREA **(Bird Offshore Feeding Area)**

■ SEABIRD FEEDING AND CONCENTRATION AREAS

Source: MMS (1984). Diapir Field Lease Offering FEIS Figure IV-9 .

EFFECTS OF OIL ON FOOD ORGANISMS OF THE BOWHEAD WHALE
NOAA/OCSEAP RU 662

WHALE MIGRATION AND SEABIRD FEEDING AND CONCENTRATION AREAS

FISHMAN ENVIRONMENTAL SERVICES

1985

FIGURE 6-4

The Diapir Field EIS regarded the effect of oilspills on plankton communities to be MINOR in all cases except uncontrolled blowouts, in which case effects could be MODERATE. [2] The FEIS also concluded that contamination or loss of seasonally abundant crustaceans in the Bering Sea intrusion due to an oilspill could substantially increase sea bird mortality during the fall migration due to reduction in food resource. It was also concluded that detrimental changes in zooplankton biomass relative to bowhead whale feeding requirements would be unlikely even from a major oil spill; primarily because of plankton patchiness and rapid repopulation of plankton communities. During heavy ice years, however, when food could be limiting to vertebrate consumers, increased competition among vertebrates for reduced zooplankton populations could force bowhead whales to rapidly leave the Alaskan Beaufort and rely on stored nutrients (MMS 1984).

6.4.2 Selection of Worst Case Parameters

The use of a "worst case" situation requires some qualification. Estimation of worst case conditions relies heavily on the use of assumptions, particularly in the present study where important data are non-existent. A number of oil spills have been thoroughly documented in the past, and data are available describing the spread of oil and effects to biological units. Each spill is different, however, beginning with the characteristics of the oil involved, the general oceanographic patterns in the spill area, the population structures of biological components, and such fine-scale particulars as the weather on the day of the spill.

The attempt in the following sections is to build "worst case" situations that are based on reality: the realitiy of the Beaufort Sea and our knowledge of its environmental and biological variables. Thus, while WSF concentrations, for example, recorded during historical spills may have reached 10 or 20 ppm, the potential levels estimated for the Beaufort Sea scenarios are much less, based on experimental models.

---

[2] MINOR impact: A specific group of individuals of a population in a localized area and over a short time period (one generation) is affected. MODERATE impact: A portion of a regional population changes in abundance and/or distribution over more than one generation, but is unlikely to affect the regional population.

and modeling work for the Bering Sea.

Two oil spill scenarios were provided by NOAA for this assessment, with instructions to consider a "worst case" situation. The provided scenarios defined the type, duration and coverage of spills, but not the location or season. A worst case location and season therefore needed to be selected.

As indicated previously, distribution and abundance data for *T. raschii* are relatively non-existent for the Beaufort Sea. The evidence provided from bird and mammal studies, however, points to the area of the Bering Sea Intrusion, off Barrow, as a major feeding area for birds and mammals that are known to consume euphausiids. Work in the Canadian Beaufort indicates that zooplankton are more abundant in nearshore areas, especially areas of mixing between coastal and offshore waters (ESL 1982). In discussing the Beaufort Undercurrent (= Bering Sea Intrusion), Aagaard (1984) concluded that cross shelf flow is frequent, and links the Beaufort Undercurrent with the nearshore. For these reasons, and the results of spill contact probability presented above, the Bering Sea Intrusion area off the Plover Islands was selected as the location for a worst case spill event.

Consideration of seasons indicated that August-September would be a worst case time for a spill event. Zooplankton abundance is likely to be at its peak during this time, following the open water phytoplankton maximum. Again, bird and mammal studies indicate that large concentrations of sea birds and bowhead whales utilize the Bering Sea Intrusion area and nearshore waters east of Barrow during this time period. The observed die-off of euphausiids subsequently washed up on the Plover Islands was also during this period.

6.4.3 Oil Spill Scenarios and Impact Estimates

The information and integrations required for estimation of oil spill impacts to *T. raschii* are outlined below:

1. Hypothetical Oil Spill Parameters
    1. Time of year
    2. Location
    3. Quantity

    4. Duration

2. Literature Review Data
    1. Hydrographic/oceanographic characteristics
    2. Behavior of hydrocarbons in seawater
    3. Biology of target species
    4. Distribution/abundance of target species

3. Experimental Results
    1. Lethal effects of WSF on target species
    2. Sublethal effects of WSF on target species

4. First Level Estimates
    1. Oil spill transport
    2. WSF distribution/concentration in water column

5. Second Level Estimates
    1. Estimate of direct mortality to target species life stages
    2. Estimate of changes in fertility/fecundity of target species population

6. Third Level Estimates
    1. Estimate of target species population losses and probable recovery potential

Two oil spill scenarios were presented for this analysis. Each scenario is detailed below in the format presented in the previous outline.

Scenario 1

Oil Spill Parameters

Time of year: late August - early September

Location: Bering Sea Intrusion off Plover Islands

Quantity: 200,000 bbl Prudhoe Bay crude oil

Duration: Instantaneous; area covered and concentrations maximum for 96 hours

Literature Review Data

Hydrographic/oceanographic characteristics: open water; nearshore wind-driven westerly currents (MMS 1984); exchange with Bering Sea Intrusion water possible (Aagaard 1984).

Hydrocarbon behavior in seawater: maximum concentrations in water column from dissolution = 0.6 ppm at 0-2 m depth, 0.2 ppm at 2-7 m depth, 0.1-0.01 ppm at >7 m depth (Thorsteinson 1984).

Water column dynamics: stratified, thermo-haline (assumed)

Distribution/abundance of *T. raschii*: unknown; maximum recorded density in Beaufort Sea = 510/1000 cu m; high seasonal densities assumed from bird and mammal research.

Biology of *T. raschii*: time of spawning unknown; fecundity = 300-400 eggs/female; eggs shed into water, sink, larvae ascend toward surface; natural mortality of eggs and larvae estimated at 98.2%; sexual maturity at age 2 (some at age 1) in Balsfjorden, Norway; euphausiids very motile, fast; form large breeding swarms, and possibly large feeding swarms (as in *Euphausea superba*).

Experimental Results

Lethal effects of WSF: 96 hr LC_{50}'s = adults: >2.06 ppm; gravid females: 1.37 ppm; larvae: >1.96 ppm; juveniles: >2.18 ppm.

Sublethal effects of WSF: longer intermolt period for adults: ≥1.41 ppm; gravid females: >1.96 ppm; juveniles: ≥2.18 ppm. Observations suggested that animals exposed to >0.5 ppm were less healthy.

First Level Estimates

The scenario parameters provided by NOAA included the maxima of sea surface areal coverage by the slick and concentrations in the water column remaining steady over a 96 hr period. Maximum spill areal coverage is assumed to be 168 sq km, with WSF concentrations greater than 0.01 ppm in an area of 407 sq km. These scenario parameters were developed and presented in the North Aleutian Shelf Synthesis report (Thorsteinson 1984). The highest concentration of WSF observed in experimental situations or predicted by spill dissolution models was 0.6 ppm. Therefore, for the First Level Estimate, an instantaneous spill of 200,000 bbl (perhaps from a tanker accident) covers 168 sq km in the area of the Bering Sea Intrusion off Plover Islands, with WSF concentrations reaching a maximum of 0.6 ppm in the top few meters of the water column.

Second Level Estimates

Direct mortality of eggs, larvae or adult *T. raschii* is not expected as a result of this hypothetical spill. Although LC_{50} values are not available for eggs, they would likely not be exposed to hydrocarbons due to their sinking. Larval stages would probably be at the greatest risk of maximum exposure due to their ascent toward surface water; however, our tests indicate that the larvae are least sensitive to WSF of life stages tested. Adult euphausiids could certainly avoid contaminated waters if, in fact, they can detect and are repulsed by hydrocarbons. Adults, however, are not expected to be in the surface layers except, perhaps, when in breeding swarms. (Adult *T. raschii* in subarctic waters and in Arctic fjords of Norway are known to be vertical migrators, having little if any contact with surface waters. The behavior of Beaufort populations, however, especially in nearshore waters, is unknown, and may prove very different.) The group at highest risk, in terms of direct mortality, is gravid females, with the highest "no effect" WSF concentration for survival (Table 6-2) being at the same level as maximum WSF concentration expected during the spill scenario. Mortalities could be experienced in this group if individuals were in the surface 2 m of water for 96 hours; however, the expected concentrations are the bottom threshold for mortality. Mortality to gravid females would potentially decrease the fecundity of the local population; however, this impact is considered very minor in terms of impacts to future populations due to the high natural mortality rate of euphausiid eggs and larvae (98+%) and the mobility of local populations. The success of any particular euphausiid year class in a specific locality is more dependent on transport of individuals into the area from outside.

Indirect mortalities are quite likely as a result of increased predation on narcotized or weakened animals if they are exposed to near-surface concentrations of hydrocarbons. Interruption of molt frequency was noted at high WSF concentrations, some animals may experience this effect near the surface. The extent of these indirect mortalities and sublethal effects is impossible to estimate. estimate.

Third Level Estimates

The impact of this hypothetical oil spill would be NEGLIGIBLE to MINOR; that is, the greatest impact would be that a specific group of individuals of a population in a localized area over a short period of time would be affected. Population losses would likely be minimal, if any. Any effects would not be carried through to the next generation due to the replenishment of localized populations from surrounding areas. The Bering Sea Intrusion might act as a dispersal pathway for Bering Sea populations, which would seed the populations in the Beaufort Sea; euphausiid populations east of Barrow would also be dispersed into the spill area.

Scenario 2

Oil Spill Parameters

Time of year: late August - early September

Location: East of Bering Sea Intrusion off Plover Islands

Quantity: 2,000 bbl/day Prudhoe Bay crude oil

Duration: Continuous; 5 days

Literature Review Data

Hydrographic/oceanographic characteristics: open water; nearshore wind-driven westerly currents (MMS 1984); exchange with Bering Sea Intrusion water possible (Aagaard 1984).

Hydrocarbon behavior in seawater: maximum concentrations in water column from dissolution = 0.6 ppm at 0-2 m depth, 0.2 ppm at 2-7 m depth, 0.1-0.01 ppm at >7 m depth; maximum concentration under slick from source to 2 km downwind = 0.65 ppm (Thorsteinson 1984).

Water column dynamics: stratified, thermo-haline (assumed); wind-driven westerly surface current.

Distribution/abundance of *T. raschii*: unknown; maximum recorded density in Beaufort Sea = 510/1000 cu m; high seasonal densities assumed from bird and mammal research.

Biology of *T. raschii*: time of spawning unknown; fecundity = 300-400 eggs/female; eggs shed into water, sink, larvae ascend toward surface; natural mortality of eggs and larvae estimated at 98.2%; sexual maturity at age 2 (some at age 1) in Balsfjorden, Norway; euphausiids very motile, fast; form large breeding swarms, and possibly large feeding swarms (as in *Euphausea superba*).

Experimental Results

Lethal effects of WSF: 96 hr LC_{50}'s = adults: >2.06 ppm; gravid females: 1.37 ppm; larvae: >1.96 ppm; juveniles: >2.18 ppm.

Sublethal effects of WSF: longer intermolt period for adults: ≥1.41 ppm; gravid females: >1.96 ppm; juveniles: ≥2.18 ppm. Observations suggested that animals exposed to >0.5 ppm were less healthy.

First Level Estimates

The scenario parameters provided by NOAA indicate a slick size of 100 sq km, and an area of 0.8 sq km with WSF concentrations greater than 0.01 ppm. These scenario parameters were developed and presented in the North Aleutian Shelf Synthesis report (Thorsteinson 1984). The highest concentration of WSF observed in experimental situations or predicted by spill dissolution models was 0.6 ppm. Therefore, for the First Level Estimate, a continuous spill of 2,000 bbl/day (perhaps from a well blowout) covers 100 sq km in the area of the Bering Sea Intrusion off Plover Islands, with WSF concentrations reaching a maximum of 0.65 ppm in the top few meters of the water column.

Second Level Estimates

The Second Level Estimate for this scenario is the same as for Scenario 1. Direct mortalities to *T. raschii* are not anticipated, or are very minor (NEGLIGIBLE).

Third Level Estimates

The Third Level Estimate for this spill scenario is the same as for Scenario 1.

7 RECOMMENDATIONS FOR FURTHER STUDIES

Several studies are recommended to further the knowledge of *T. raschii* ecology, interactions with the Arctic environment, and responses to hydrocarbons in the environment.

7.1 Ecology of *T. raschii* in the Alaskan Beaufort Sea

7.1.1 Distribution of *T. raschii* in the Alaskan Beaufort Sea

Objective. This study would describe the spatial and temporal distributions of *T. raschii* in the Alaskan Beaufort Sea, with an emphasis on nearshore and offshore waters proposed for oil and gas development. Few data presently exist concerning the distribution of this species, thus, predictions of effects of development are speculative. Diel vertical distribution is also included in the scope of this study.

Proposed Methods. Data collection should consist of acoustical surveys and net samples in specific areas during open water seasons. Attempts should be made to obtain acoustic data from the U.S. Navy for ice-covered seasons. The study design should also include following large euphausiid swarms over a several day period to describe daily distributions. Data would be analyzed and summarized to show diel and seasonal distribution.

Schedule. The study should be conducted over a period of 2 to 3 years to determine year-to-year variability.

7.1.2 Relative Abundance of *T. raschii* in the Alaskan Beaufort Sea

Objectives. The relative abundance of *T. raschii* is little known for the Beaufort Sea. Standard plankton sampling methods usually underestimate euphausiid abundance due to the inefficiency of sampling equipment. The lack of abundance data restricts the ability of investigators to estimate regional biomass, and thus, the role of euphausiids in Arctic trophic dynamics. Abundance relative to other zooplankters is also important in studies of vertebrate consumer feeding; for example, bowhead whales are thought to consume more copepods in the eastern Beaufort and more euphausiids in the western Beaufort.

Proposed Methods. Techniques for estimating density and biomass of euphausiid swarms have been developed and used in the Antarctic. Acoustics and net samples are used in this work.

Schedule. The study should be conducted during open water. Euphausiid swarms should be sampled opportunistically when they are encountered.

7.1.3 Life History Studies of Beaufort Sea Euphausiids

Objectives. No data exist describing the life history of *T. raschii* in the Alaskan Beaufort. Data collected should include: distribution (spatial and temporal) of eggs and larvae; timing of larval development; growth rates, including over winter; sex ratios of local populations or swarms; timing of spawning, and annual productivity. These data are needed in order to understand and predict the distribution, abundance and behavior of euphausiids, especially in relation to vertebrate consumer distributions, and potential oil development impacts.

Proposed Methods. Plankton sampling should be scheduled once or twice per month in specific areas in order to track the development of life stages. Samples should also be obtained from past or present feeding studies of fish, birds and marine mammals known to eat euphausiids. Major wash-ups, such as those described on the Plover Islands, should be sampled to determine age and reproductive condition of beached euphausiids.

Schedule. The study should be conducted through two consecutive open water seasons.

7.2 Study of the Bering Sea Intrusion Near Pt. Barrow

Objectives. The Bering Sea Intrusion may be an important feature of the western Beaufort Sea related to biological productivity. Seasonal concentrations of bowhead whales, sea birds, and other vertebrates have been described in the area. Oceanographic conditions in the area may be related to swarms of euphausiids and other plankters. The importance of this area, and its vulnerability to oil spill effects, needs to be assessed. The study would examine oceanographic conditions and related biological events in the area of the Bering Sea Intrusion.

Proposed Methods. CTD casts would be made along transects in order to describe the characteristics and distribution of intrusion water and other masses. Concurrent samples of chlorophyll, phytoplankton and zooplankton would be collected. Data would be synthesized to determine relationships between water masses and productivity, species composition and diversity.

Schedule. The study should be conducted over a period of several years in order to assess year-to-year variability.

7.3 Detection of and Reaction to Hydrocarbon WSF by *T. raschii*

Objectives. Many oil effects estimates involving marine animals assume that the organism in question will be exposed to hydrocarbons if they co-occur in the water column. Few studies have examined the physiological and behavioral responses of organisms to oil in water. This study would examine the ability of *T. raschii* to detect crude oil WSF at various concentrations, and the behavioral responses to these levels. Results will add important information for future assessments of oil spill effects on euphausiid populations.

Proposed Methods. Laboratory experiments will be designed to test the detection ability of euphausiids for crude oil WSF. Once detection levels are established, additional experiments will be conducted to determine the behavioral responses of euphausids to these WSF concentrations. Possible behavioral indices might include: repulsion and flight, attraction, changes in feeding behavior, changes in locomotory behavior, changes in responses to environmental stimuli such as light, pressure and temperature.

Schedule. No specific schedule is proposed.

7.4 Additional Oil WSF Bioassays with *T. raschii*

Objectives. Additional bioassay experiments are proposed for *T. raschii* to complement the results of the present study. Important data not obtained from the present study included some longer-term effects of oil WSF. The reproductive success of adults exposed for 96 hours was not determined. It was concluded that adults (except gravid females) were fairly tolerant to all but the highest concentrations of

WSF; however, the subsequent reproductive success of these animals was not determined. Another long-term effect might be the survival of animals exposed to WSF for 96 hours as larvae. Larvae were found to be highly tolerant to WSF, but subsequent survival might be affected. Larval molt frequency and egg survival also need testing.

Proposed Methods. Experiments will be designed in which larval and adult *T. raschii* will be exposed to various levels of crude oil WSF for 96 hours. Test animals will then be cultured in clean water and survival compared with control groups. The reproductive success of females will also be determined relative to control animals (assuming females will breed in the laboratory situation).

Schedule. A specific schedule is not proposed for this study.

8_LITERATURE_CITED

Aagaard, K. 1984. The Beaufort undercurrent. In: P.W. Barnes, D.M. Schell and E. Reimnitz (eds.). The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press, Inc. Orlando.

Bary, B. Mck., W.E. Barraclough and R. Herlinveaux. 1962. Scattering of underwater sound in Saanich Inlet, British Columbia. Nature 194: 36-37.

Berkes, F. 1976. Ecology of euphausiids in the Gulf of St. Lawrence. J. Fish. Res. Bd. Canada 33: 1894-1905.

_____. 1977. Production of the euphausiid crustacean *Thysanoessa raschii* in the Gulf of St. Lawrence. J. Fish. Res. Bd. Canada 34: 443-446.

Boden, B.P. and E.M. Kampa. 1964 An aspect of euphausiid ecology revealed by echo-sounding in a fjord. Crustaceana 9: 155-173.

Bodfish, H.H. 1936. Chasing the bowhead. Harvard Univ. Press, Cambridge, Mass.

Boyde, C.M., M. Heyraud and C.N. Boyd. 1984. Feeding of the Antarctic krill *Euphausia superba*. J. Crust. Biol. 4(Sp.No.1): 123-141.

Braham, H.W., B.D. Krogman, and G. Carroll. 1983. Bowhead whale (*Balaena mysticetus*) migration, distribution,and abundance in the Bering, Chukchi, and Beaufort Seas, 1975-1978, with notes on the distribution and life history of white whales (*Delphinapterus leucas*). U.S. Dept. Commer., NOAA, OCSEAP. Final Rep. 20: 75-170.

Brinton, E. 1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr. 8: 51-270.

_____ and T. Antezana. 1984. Structures of swarming and dispersed populations of krill (*Euphausia superba*) in Scotia Sea and South Shetland waters during January-March 1981, determined by bongo nets. J. Crust. Biol. 4(Sp. No.1): 45-66.

_____ and A.W. Townsend. 1984. Regional relationships between development and growth in larvae of Antarctic krill, *Euphausia superba*, from field samples. J. Crust. Biol. 4(Sp.No.1): 244-246.

Brodersen, C.C., S.D. Rice, J.W. Short, T.A. Mecklenburg, and J.F. Karinen. 1977. Sensitivity of larval and adult Alaskan shrimp and crabs to acute exposures of the water-soluble fraction of Cook Inlet crude oil. Pp. 575-578 in: API, EPA, and USCG, *1977 Oil Spill Conference (Prevention, Behavior, Control, Cleanup)*, Proceedings. American Petroleum Institute. Washington, D.C.

Broderson, C.C. and M.G. Carls. In preparation. Sensitivity of egg, larval and adult coonstripe shrimp (*Pandalus hypsinotus*) to long-term exposure to the water-soluble fraction of Cook Inlet crude oil. Abstracted in: Rice et al. 1985.

Bruce, H.E., McLain, D.R., and B.L. Wing. 1977. Annual Physical and Chemical Oceanographic Cycles of Auke Bay, Southeastern Alaska.NOAA Tech. Rept. NMFS SSRF-712.

Carls, M.G. and S.D. Rice. 1980. Toxicity of oil-well drilling muds to Alaskan larval shrimp and crabs. NOAA/OCSEAP RU 72, Final Report, 18 Dec. 1980.

Carey, A.G., Jr. (ed.) 1978. Environmental Assessment of the Alaskan Continental Shelf, Beaufort/Chukchi Interim Synthesis Report, NOAA/OCSEAP.

Clarke, A. 1984. Lipid content and composition of Antarctic krill, *Euphausia superba* Dana. J. Crust. Biol. 4(Sp.No.1): 285-294.

Clarke, W.D. 1971. Comparison of different investigative techniques for studying the deep scattering layers. In: G.B. Farquhar (ed.). Biological Sound Scattering in the Ocean, pp. 550-562.

Cooney, R.T. 1977. Zooplankton and micronekton studies in the Bering-Chukchi/Beaufort Seas. NOAA/OCSEAP RU 426, Annual Report.

Craddock, D.R. 1977. Acute toxic effects of petroleum on Arctic and Subarctic marine organisms. In: D.C. Malins (ed). Effects of Petroleum on Arctic and Subarctic Marine Environments and Organisms. Vol. II: Biological Effects. Academic Press, New York.

Craig, P.C. 1984. Fish use of coastal waters of the Alaskan Beaufort Sea: A review. Trans. Amer. Fish. Soc. 113: 265-282.

Craig, P.C. and P. McCart. 1976. Fish use of nearshore coastal waters in the western Arctic: emphasis on anadromous species. In: D.W. Hood and D.C. Burrell (eds.). Assessment of the Arctic Marine Environment: Selected Topics. Univ. of Alaska. Institute of Marine Science. Occas. Publ. No. 4. Fairbanks, AK.

Craig, P.C., W.B. Griffiths, L. Haldorson, and H. McElderry. 1982. Ecological studies of Arctic Cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Can. J. Fish. Aquat. Sci. 39: 395-406.

Divoky, G.J. 1984. The pelagic and nearshore birds of the Alaskan Beaufort Sea: biomass and trophics. In: P.W. Barnes, D.M. Schell and E. Reimnitz (eds.). The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press, Inc.

Eilertsen, H.C., S. Falk-Petersen, C.C.E. Hopkins and K. Tande. 1981. Ecological investigations on the plankton community of Balsfjorden, northern Norway. Program for the project, study area, topography, and physical environment. Sarsia 66: 25-34.

ESL Environmental Sciences, Ltd. 1982. Biological impacts of three oil spill scenarios in the Beaufort Sea. Pallister Resource Management, Ltd. Ontario.

Ettershank, G. 1984. A new approach to the assessment of longevity in the Antarctic krill *Euphausia superba*. J. Crus. Biol. 4(Sp.No.1): 295-305.

Falk-Petersen, S. 1981. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: seasonal changes in body weight and the main biochemical compostion of *Thysanoessa inermis* (Kroyer), *T. raschii* (M. Sars), and *Meganyctiphanes norvegica* (M. Sars) in relation to environmental factors. J. Exp. Marine Biol. Ecol. 49: 103-120.

_____ and C.C.E. Hopkins. 1981. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: population dynamics of the euphausiids *Thysanoessa inermis* (Kroyer), *T. raschii* (M. Sars) and *Meganyctiphanes norvegica* (M. Sars) in 1976 and 1977. J. Plankton Res. 3: 177-192.

_____, J.R. Sargent, C.C.E. Hopkins, and B. Vaja. 1982. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: lipids in the euphausiids *Thysanoessa raschii* and *T. inermis* during spring. Mar. Biol. 68: 97-102.

Farquhar, G.B. (ed.). 1971. Biological Sound Scattering inthe Ocean. Mawry Center for Ocean Science, U.S. Dept. of the Navy.

_________. 1977. Biological sound scattering in the ocenas: a review. *In*: N.R. Andersen and B.J. Zahuranec (eds). Oceanic Sound Scattering Prediction. Marine Science, Vol. 5: 493-527. Plenum Press.

Fechhelm, R.G., P.C. Craig, J.S. Baker, and B.J. Gallaway. 1985. Fish distribution and use of nearshore waters in the northeastern Chukchi Sea. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 32: 121-298.

Fevolden, S.E. and R.Y. George. 1984. Size frequency pattern of *Euphausia superba* in the Antarctic Peninsula waters in the austral summer of 1982. J. Crust. Biol. 4(Sp.No.1): 107-122.

Finney, D.J. 1971. Probit analysis. 3rd ed., Cambridge Univ. Press. London.

Fowler, S.W. and L.F. Small. 1967. Sinking rates of euphausiid fecal pellets. Limnol. Oceanogr. 17: 293-296.

Frost, K.J. and L.F. Lowry. 1984. Trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea. In: P.W. Barnes, D.M. Schell and E. Reimnitz (eds.). The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press, Inc.

George, R.Y. 1984. Ontogenetic adaptations in growth and respiration of *Euphausia superba* in relation to temperature and pressure. J. Crust. Biol. 4(Sp.No.1): 252-262.

Gosho, M.E. 1977. The food and feeding habits of juvenile pink salmon in the estuaries of Kodiak Island, Alaska. M.S. Thesis, Univ. of Washington.

Griffiths, W.B. 1984. Fish. In: J.C. Truett (ed.). Environmental characterization and biological use of lagoons in the eastern Beaufort Sea. U.S. Dept. Commer. NOAA. OCSEAP Final Rep. 24: 325-368.

Hamner, W.M. 1984. Aspects of schooling in Eupausia superba. J. Crust. Biol. 4(Sp. No.1): 67-74.

Harding, G.C.H. 1977. Surface area of the euphausiid Thysanoessa raschii and its relation to body length, weight, and respiration. J. Fish. Res. Bd. Canada 34: 255-231.

_____ and W.P. Vass. 1979. Uptake from seawater and clearance of p,p'-DDT by marine planktonic crustacea. J. Fish. Res. Bd. Canada 36: 247-254.

Harris, C.K. and A.C. Hartt. 1977. Assessment of pelagic and nearshore fish in three bays on the east and south coasts of Kodiak Island, Alaska. NOAA/OCSEAP RU 485, Final Report.

Henderson, R.J., S. Falk-Petersen and J.R. Sargent. 1982. The composition and biosyntheais of lipids in Thysanoessa raschii from the Clyde estuary, Scotland. Mar. Biol. 70: 7-12.

Holm-Hansen, O. and M. Huntley. 1984. Feeding requirements of krill in relation to food sources. J. Crust. Biol. 4(Sp. No.1): 156-173.

Hopkins, C.C.E., S. Falk-Petersen, K. Tande and H.C. Eilertsen. 1978. A preliminary study of zooplankton sound scattering layers in Balsfjorden: structure, energetics and migrations. Sarsia 63: 255-264.

Horner, R. 1981. Beaufort Sea plankton studies. In: U.S. Dept. Commer., NOAA, OCSEAP Final Rept. 13.

Ikeda, T. 1972. Chemical composition and nutrition of zooplankton in the Bering Sea. In: A.Y. Takeouti (ed.) Biological Oceanography of the Northern North Pacific. P. 433-442.

_____. 1984. Sequences in metabolic rates and elemental composition (C,N,P) during the development of Euphausia superba Dana and estimated food requirements during its life span. J. Crust. Biol. 4(Sp.No.1): 273-284.

Kendall, A.W., Jr., J.R. Dunn, R.J. Wolotira, Jr., J.H. Bowerman, Jr., D.B. Dey, A.C. Matarese and J.E. Munk. 1980. Zooplanton, including ichthyoplankton and decapod larvae, of the Kodiak Shelf. Northwest Fisheries Center, Nat. Marine Fisheries Serv., NWAFC Processed Rept. 80-8.

Laws, R.M. 1985. The Ecology of the Southern Ocean. Amer. Sci. 73(1): 26-40.

Lee, R.F. 1975. The fate of petroleum hydrocarbons in marine zooplankton. In: Proceedings of the 1975 Conference on Prevention and Control of Oil Pollution, March 25-27, American Petroleum Inst., pp. 549-553.

Lindley, J.A. 1980. Population dynamics and production of euphausiids. II. Thysanoessa inermis and T. raschii in the North Sea and American coastal waters. Mar. Biol. 59: 225-233.

Lowry, L. 1985. Telephone conversation. October 7, 1985. Alaska Department of Fish & Game.

Lowry, L.F. and K.J. Frost. 1981. Distribution, growth, and foods of Arctic Cod (Boreogadus saida) in the Bering, Chukchi, and Beaufort Seas. Canadian Field-Naturalist 95(2): 186-191.

Malins, D. C., H. O. Hodgins, U. Varanasi, S.-L. Chan, B. B. McCain, D. D. Weber, and D. W. Brown. 1985. Sublethal effects of petroleum hydrocarbons and trace metals, including biotransformations, as reflected by morphological, chemical, physiological, and behavioral indices. U.S. Dept. Commer., NOAA, OCSEAP Final Rep. 29: 1-229.

Marr, J.W.S. 1962. The natural history and geography of the Antarctic krill (Euphausia superba Dana). Discovery Rept. 32: 33-464.

Mauchline, J. 1966. The biology of Thysanoessa Raschii (M. Sars), with a comparison of its diet with that of Meganyctiphanes norvegica (M. Sars). In: H. Barnes (ed.). Some Contemporary Studies in Marine Sciences. pp. 493-510.

_____. 1980. The biology of Mysids and Euphausiids. Adv. In Marine Biology, Academic Press.

_____ and L.R. Fisher. 1969. The Biology of Euphausiids. Adv. in Marine Biology. Academic Press.

Mecklenburg, T.A., S.D. Rice, J.F. Karinen. 1977. Molting and survival of king crab (*Paralithodes camtschatica*) and coonstripe shrimp (*Pandalus hypsinotus*) larvae exposed to Cook Inlet crude oil water-soluble fraction. Pp. 221-228. In: D.A. Wolfe (ed.). Fate and Effects of Petroleum in Marine Organisms and Ecosystems, Proceedings. Permagon Press. New York.

Minerals Management Service, Alaska OCS Region. 1984. Diapir field lease offering (June 1984) Final Environmental Impact Statement,Vol. 1. U.S. Dept. Interior.

Nemato, T. 1970. Feeding patterns of baleen whales in the ocean. *In*: J.H. Steele (ed.). Marine Food Chains, Univ. of California, Berkeley, pp. 241-252.

Nishiwaki, M. 1972. General biology. *In*: S.H. Ridgway, (ed.). Mammals of the Sea: Biology and Medicine. C.C. Thomas, pp. 3-204.

Nunes, P. and P.E. Benville. 1978. Acute toxicity of the water soluble fraction of Cook Inlet crude oil to the manila clam. Mar. Pollut. Bull. 9:324-331.

Paranjape, M.A. 1967. Molting and repiration of euphausiids. J. Fish. Res. Bd. Canada 24: 1229-1240.

Pearcy, W.G., C.C.E. Hopkins, S. Gronvik and R.A. Evans. 1979. Feeding habits of cod, capelin and herring in Balsfjorden, northern Norway, July-August 1978: The importance of euphausiids. Sarsia 64: 269-277.

_____ and C.L. Osterberg. 1967. Depth, diel, seasonal and geographic variations in zinc-65 of midwater animals off Oregon. Int. J. Oceanol. Limnol. 1: 103-116.

Peltier, W. 1978. Methods for measuring the acute toxicity of effluents to aquatic organisms. U.S. Environmental Protection Agency, Cincinnati. Publ. No. EPA-600/4-78-012. 52 pp.

Percy, J.A. and F.J. Fife. 1981. The biochemical composition and energy content of Arctic marine macrozooplankton. Arctic 34: 307-313.

Rice, S.D., J.W. Short, C.C. Broderson, T.A. Mecklenburg, D.A. Moles, C.J. Misch, D.L. Cheatham,and J.F. Karinen. 1975. Acute toxicity and uptake-depuration studies with Cook Inlet crude oil, Prudhoe Bay crude oil, No. 2 fuel oil and several subarctic marine organisms. N.W. Alaska Fisheries Center, NMFS, NOAA, U.S. Dept. of Commerce, Auke Bay Fisheries Laboratory. Processed Report, 144p.

Rice, S.D., J.W. Short, and J.F. Karinen. 1976. Toxicity of Cook Inlet crude oil and No. 2 fuel oil to several Alaskan marine fishes and invertebrates. In: Sources, effects and sinks of hydrocarbons in the aquatic environment. The American Institute of Biological Sciences, Washington, D.C. Pp. 395-406.

Rice, S.D., J.W. Short, and J.F. Karinen. 1977. Comparative oil toxicity and comparative animal sensitivity. In: D.A. Wolfe, (ed.), Fate and Effects of Petroleum Hydrocarbons in Marine Organisms and Ecosystems. Pp. 78-94. Permagon Press. N.Y.

Rice, S.D., D.A. Moles, T.L. Taylor,and J.F. Karinen. 1979. Sensitivity of 39 Alaskan marine species to Cook Inlet crude oil and No. 2 fuel oil. Pp. 549-554 in: API, EPA, and USCG, *1979 Oil Spill Conference (Prevention, Behavior, Control, Cleanup)*, Proceedings. Washington, D.C., American Petroleum Institute. 728 p.

Rice, S.D., D.A. Moles, J.F. Karinen, S. Korn, M.G. Carls, C.C. Brodersen, J.A. Gharrett, and M.M. Babcock. 1985. Effects of petroleum hydrocarbons on Alaskan aquatic organisms: a comprehensive review of all oil-effects research on Alaskan fish and invertebrates conducted by the Auke Bay Laboratory, 1970-81. U.S. Dept. Commer., NOAA, OCSEAP Final Rep. 29: 311-427.

Rogers, D.E., D.J. Rabin, B.J. Rogers, K. Garrison and M.E. Wangerin. 1979. Seasonal composition and food web relationships of marine organisms in the nearshore zone off Kodiak Island - including ichthyoplankton, meroplankton (shellfish), zooplankton and fish. NOAA/OCSEAP RU 553, Annual Report, 30 Sept. 1979.

Sameoto, D.D. 1976a. Distribution of sound scattering layers caused by euphausiids and their relationship to chlorophyll *a* concentrations in the Gulf of St. Lawrence estuary. J. Fish. Res. Bd. Canada 33: 681-687.

_____. 1976b. Respiration rates, energy budgets, and molting frequencies of three species of euphausiids found in the Gulf of St. Lawrence. J. Fish. Res. Bd. Canada 33: 2568-2576.

_____. 1980a. Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschii*, and *T. inermis* (Crustacea Euphausiacea). J. Plankton Res. 2: 129-143.

_____. 1980b. Quantitative measurements of euphausiids using a 120 kHz sounder and their *in situ* orientation. Can. J. Fish. Aquat. Sci. 37: 693-702.

Sargent, J.R. and S. Falk-Petersen. 1981. Ecological investigations on the zooplankton community in Balsfjorden, northern Norway: lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschii*, and *T. inermis* during mid-winter. Mar. Biol. 62: 131-137.

Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods. 6th ed. Iowa State Univ. Press. Ames, Iowa.

Stephan, C.W. 1977. Methods for calculating an LC50. pp. 65-84, In: F.L. Mayer and J.L. Hamelink (eds.). Aquatic toxicology and hazard evaluation. Am. Soc. Testing Mater., Philadelphia.

Thorsteinson, L.K. (ed.) 1984. The North Aleutian Shelf Environment and Possible Consequences of Offshore Oil and Gas Development: Proceedings of a Synthesis Meeting. U.S. Dept. Commer. NOAA/OAD.

U.S. Army Corps of Engineers, Alaska District. 1984. Endicott development project. Final Environmental Impact Statement,Vol. 1.

Vogel, A.H. and G. McMurray. 1982. Seasonal population density distribution of copepods, euphausiids, amphipods, and other holoplankton on the Kodiak Shelf. NOAA/OCSEAP RU 608, Final Report.

VTN. 1980. Boca de Quadra baseline report, Quartz Hill Molybdenum Project, Southeast Alaska. U.S. Borax & Chemical Corp. Los Angeles, CA.

VTN. 1982. Boca de Quadra and Wilson Arm/Smeaton Bay Monitoring Study, Quartz Hill Molybdenum Project. Southeast Alaska. U.S. Borax & Chemical Corporation.

Wiborg, K.F. 1954. Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway. Rept. Norwegian Fish. Marine Invest. 11: 1-246.

Zelikman, E.A., I.P. Lukashevich and S.S. Drobysheva. 1978. Aggregative distribution of *Thysanoessa inermis* (Kroyer) and *T. raschii* (M. Sars) (Euphausiacea) in the Barents Sea. Oceanology 18: 709-713.

_____, _____ and _____. 1979. Year-round diurnal vertical migrations of the euphausiids *Thysanoessa inermis* and *T. raschii* in the Barents Sea. Oceanology 19: 82-85.

_____, _____, _____ and A.A. Degtereva. 1980. Fluctuations in the number of eggs of the Barents Sea crustaceans *Thysanoessa inermis* Kr. and *T. raschii* (M. Sars) (Euphausiacea). Oceanology 20: 716-721.

Zhuravlev, V.M. 1977. Species composition and character of distribution of euphausiids in the Sea of Okhotsk. Oceanology 17: 81-83.

ACKNOWLEDGEMENTS

This study was funded, wholly, by the Minerals Management Service, Department of the Interior through an Interagency Agreement with the National Oceanic and Atmospheric Administration, Department of Commerce, as part of the Alaska Outer Continental Shelf Environmental Assessment Program.

Dr. Carol-Ann Manen was the Contracting Officer's Technical Representative for this project; her support and assistance are gratefully acknowledged. The untiring efforts of Mr. Yoji Endo, Juneau, Alaska, provided live, sorted euphausiids for the project. The cooperation and efforts of University of Alaska, Juneau staff and the skipper of the *Maybeso* enabled collection of live euphausiids. The cooperation of Dr. Bruce Wing, National Marine Fisheries Service, Auke Bay Laboratory, is also acknowledged for collection time during a sampling cruise.