Environmental Assessment of the Alaskan Continental Shelf

Final Reports of Principal Investigators

Volume 8. Biological Studies

U.S. DEPARTMENT OF COMMERCE
National Oceanic & Atmospheric Administration
Office of Marine Pollution Assessment

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The facts, conclusions and issues appearing in these reports are based on interim results of an Alaskan environmental studies program managed by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) of the National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce, and primarily funded by the Bureau of Land Management (BLM), U.S. Department of Interior, through interagency agreement.

DISCLAIMER

Volume 8 Biological Studies

This is the second of a two volume final report for:

RU#	INVESTIGATOR(S)	AGENCY	TOPIC
467	Steven R. Johnson J.W. Richardson	LGL Ecological Research Associates, Incorporated	Beaufort Sea-Barrier Island-Lagoon Ecological Processes Studies: Final Report, Simpson Lagoon

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BEAUFORT SEA BARRIER ISLAND-LAGOON ECOLOGICAL PROCESS STUDIES: FINAL REPORT, SIMPSON LAGOON

RESEARCH UNIT 467

By

LGL Ecological Research Associates, Inc.

and

LGL Ltd.
Environmental Research Associates

To

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March 1980

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SUMMARY

Invertebrate investigations were conducted in the Simpson Lagoon area on the Alaskan Beaufort Sea coast during the open-water seasons of 1977 and 1978 and during the winter of 1978-1979. The research concentrated on those organisms identified as important food items for animals at higher trophic levels (fish and birds). The main objective of the research was to study the seasonal and habitat distributions, abundances and biomasses, and life histories of these important invertebrates.

Results of these studies showed that mysids and amphipods were among the most abundant invertebrates in Simpson Lagoon in summer, in terms of numbers and biomass, and also were the most common foods of key species of birds and fish that used the lagoon in summer. Divers observed that most of the amphipods and mysids were on or near the bottom, and were frequently associated with the detritus layer that covered most of the bottom of the lagoon. Portions of this detritus may have provided these organisms with a direct or indirect source of food.

In both 1977 and 1978, amphipod and mysid densities and biomasses varied widely in time and space during the open-water season. The total biomass of these invertebrates was an order of magnitude lower in 1978 than it was in 1977. Extensive current-assisted movements of amphipods and mysids into, out of, and within the lagoon appeared to occur during the open-water season.

Mysids appeared to leave the lagoon in winter, but amphipods overwintered there. For example, in November 1978 both amphipods and mysids were found under the ice in the lagoon, in abundances similar to those of summer. By February 1979, mysid densities in the lagoon were greatly reduced but amphipod densities remained high. Amphipods, but not mysids, were found in April 1978 in high-salinity waters under the ice. This suggests that mysids either die or leave the lagoon in winter. Mysids apparently recolonized the lagoon each spring during and immediately after breakup by moving in from the adjacent sea and along the shallow leads next to the mainland and island beaches.

Mysis litoralis and *Mysis relicta* grew at a rate of about 2.4 mm/30 days during the open-water season, but the only abundant amphipod (*Onisimus glacialis*) grew much more slowly, about 0.8 mm/30 days. All

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three species grew less rapidly during the winter; however, it is important to note that for all three species growth continued in winter.

Results showed that some *M. litoralis*, *M. relicta* and *O. glacialis* lived for three years, but most appeared to have two-year life cycles. Breeding was generally restricted to second and third year individuals. The major breeding season for these species was late fall and early winter. Young of the two mysid species were released from brood pouches in late spring (June-July), whereas those of *O. glacialis* were apparently released by April.

Two potential sources of adverse impacts are causeway construction and contamination by oil. Construction of causeways or other structures that would block important movements of these invertebrates, particularly those movements between the lagoon and offshore areas, are likely to be detrimental. Likewise, invertebrates could be adversely affected by oil in the water-column or (probably more critical to epibenthos) by oil on and in bottom substrates. Previous investigations have shown that responses of epibenthic invertebrates to oil are highly variable, but that adverse effects occur under some circumstances. Adverse impacts of blockage of critical migration routes or of oil on invertebrates might indirectly affect the fish and birds that depend on those invertebrates for food.

ACKNOWLEDGEMENTS

We would like to take this opportunity to mention the unique contribution of Howard McElderry, who played an especially active and interested role in modifying and carrying out the field program. Ken Coyle of the University of Alaska and Hal Koch of Western Washington State University provided prompt assistance in confirming the identification of the epibenthic invertebrates. Benny Gallaway and Joe Margraf of LGL Ecological Research Associates, Inc. contributed fresh ideas and insight concerning the sampling design and the analysis of results. Joe Truett and John Richardson of LGL Ltd. provided helpful criticism of the manuscript and editorial comments.

INTRODUCTION

The apparent inevitability of petroleum exploration and development activities along the Alaskan Beaufort continental shelf has heightened concern regarding the effects of these activities on the nearshore marine environment. The interdisciplinary study of which this report is a part (Beaufort Sea Barrier Island-Lagoon Ecological Process Studies, RU 467) was initiated to examine nearshore trophic relationships and to define important biological processes in a barrier island-lagoon system as a strategy to assess the potential impacts of these activities. The first year of field research (1977) emphasized higher trophic levels (fish and birds), with the view that it would thereafter be possible to progress down the food web to develop an understanding of processes that supported the key vertebrates. Consequently our first Annual Report of research (LGL 1978) described the importance of nearshore barrier island-lagoon systems along the Alaskan Beaufort Sea coast (and especially Simpson Lagoon) as summer breeding, rearing and feeding areas for birds, and as feeding and rearing areas for anadromous and marine fishes. That report showed that epibenthic invertebrates were the primary source of food for the important vertebrate species in the barrier island-lagoon system, and indicated that these invertebrates were present in sufficient quantities to supply the energy needed by the birds and fish utilizing the system. The objectives of the 1977-1978 open-water studies and the 1978-1979 winter programs were to provide more detailed information on the biology and trophic relationships of the important invertebrate species.

Objectives

The specific objectives for the invertebrate investigations during the Simpson Lagoon study in 1977-1979 were

1. to determine the importance of infaunal and epibenthic organisms to the higher trophic levels (fish and birds) in Simpson Lagoon;
2. to determine temporal and spatial variations in the abundances and biomasses of important invertebrate groups;

3. to determine how biomass and productivity of important invertebrates are related to energetic needs of their consumers in Simpson Lagoon;
4. to gather seasonal life-history and growth information (length, weight, sex, breeding condition) for the important species of invertebrates;
5. to investigate the immigration and emigration of key invertebrates in Simpson Lagoon during the open-water season; and
6. to determine the winter utilization of Simpson Lagoon by invertebrates.

In 1977, the first objective was addressed and preliminary data on the second objective were collected. Objectives two through five were met in 1978, and objective six was addressed in the winter of 1978-1979.

Relevance to Problems of Development

Oil contamination of the Jones Islands-Simpson Lagoon barrier island-lagoon system might have serious effects, either direct or indirect, on the epibenthic community. If organisms came into physical contact with oil in the water, indications from previous studies are that they might succumb (e.g., Percy 1976; Busdosh and Atlas 1977; Foy 1978, 1979). Oil entering a shallow lagoon would also become mixed with bottom sediments and organic debris. Benthic invertebrates inhabiting or repopulating lagoons after water-column contamination had diminished, would have to contend with oil-contamination of habitats and possibly of food sources. These effects of oil could reduce densities of epibenthic organisms, which in turn might affect organisms at higher trophic levels.

Alteration of land masses through development activities (e.g., causeway construction, building of artificial islands) are likely to accompany development. Such alterations could affect circulation patterns and thus disrupt the normal patterns of transport of invertebrates. The results of this study showed transport of epibenthic invertebrates by currents to be important in maintaining the standing crop of invertebrates in the lagoon. Moreover, maintenance of these standing crops appeared to be important in sustaining food supplies for fish and birds that used the lagoon in summer.

CURRENT STATE OF KNOWLEDGE

Prior to oil and gas development on the Alaskan coast of the Beaufort Sea, most arctic studies of benthic invertebrates were qualitative in nature and, because of logistics difficulties, were conducted primarily near the Naval Arctic Research Laboratory at Point Barrow. MacGinitie (1955) conducted extensive survey work in this area from 1948 to 1950, and documented the species composition of the invertebrate community. Taxonomic studies of a variety of benthic organisms have been conducted near Point Barrow: sponges (De Laubenfels 1953), polychaetes (Pettibone 1954), amphipods (Shoemaker 1955), molluscs (MacGinitie 1959), mysids (Holmquist 1963), and cumaceans (Given 1965). These taxonomic studies are relevant to this study since several of the species of invertebrates are common along the Alaskan Beaufort Sea coast east to Demarcation Point. An extensive review of existing literature and unpublished data on the distributions, abundances and life-histories of benthic organisms, with emphasis on the Alaskan arctic coast, has been compiled by Carey (1977). In addition, Feder et al. (1976a) have published an annotated literature review of benthic invertebrates of arctic regions in Canada and Alaska.

With the discovery and development of oil and gas in or near both the Canadian and Alaskan parts of the Beaufort Sea, several quantitative studies of infaunal and epibenthic invertebrates were initiated. (Infaunal organisms live in bottom substrates, whereas epibenthic organisms live in or near the bottom.) Crane and Cooney (1974) investigated the invertebrate fauna of Simpson Lagoon during late summer. They found that crustaceans, molluscs and polychaetes were the dominant members of the nearshore invertebrate community, that biomass increased seaward of the lagoon, and that the seasonal distribution of infauna was strongly influenced by bottom-fast ice. However, as Feder et al. (1976a) point out, the study was conducted over a short time period in August and it lacked information on seasonal variations of invertebrate distribution and biomass.

More extensive work by Feder and Schamel (1976) in the nearshore areas of Prudhoe Bay indicated that benthic biomass was low in that area, although the number and diversity of organisms increased with increasing distance from shore. This seaward increase suggests the existence of a marine stock of invertebrates that is available to repopulate nearshore ice-stressed areas each spring (Feder and Schamel 1976; Feder et al. 1976; Broad 1978). Broad (1977; Broad et al. 1979), in a comprehensive study of the littoral region (2-10 m depth) along the Alaskan Beaufort Sea coast, found that the infauna was comprised predominantly of polychaete and oligochaete worms and bivalve molluscs, and that the epibenthos was made up primarily of motile crustaceans (amphipods, mysids and isopods). The littoral region is poor in species and biomass, probably because it is annually depopulated by shore-fast ice. They found no detectable variation in the composition of the fauna with depth over the 2-10 m range, or with the presence or absence of peat.

Carey et al. (1974) and Carey (1977, 1978) sampled benthos across the Alaskan Beaufort Sea continental shelf in depths ranging from 20 to >2,000 m. The results of these studies indicated that, generally, species diversity and biomass increase with depth and distance from shore, at least from the 20-m depth contour to the edge of the continental shelf (2,000 m). Wacasey (1975) also reported diversity and biomass to increase with depth and distance from shore in the Canadian Beaufort Sea between Herschel Island and Cape Dalhousie; his study was centered principally in nearshore waters of the Mackenzie Delta. He found low diversity (<20 species per station) and low biomass (2 g/m^2) in most nearshore areas, but found biomasses as high as 5 g/m^2 in protected bays and lagoons.

Awareness that specific groups of invertebrates are important to higher trophic levels has been steadily building. Numerous studies have shown that arctic epibenthic and pelagic invertebrates, principally mysids, amphipods, isopods and copepods, comprise major components of the diets of fish, birds and mammals (Griffiths et al. 1975, 1977; Kendel et al. 1975; Stirling et al. 1975; Bradstreet 1977, 1979; Bendock 1977; Fraker et al. 1977; Bain and Sekerak 1978; Divoky 1978; Lowry et al. 1978).

Schneider and Koch (1979) studied the diets of epibenthic organisms at Point Barrow, Alaska and found none of the species to be trophic specialists. They concluded that primary production (particularly benthic diatoms) was the main source of energy for the nearshore marine ecosystem; however, some species (e.g., the amphipod *Gammarus setosus*) were able to assimilate detrital material, which is largely of terrestrial origin.

STUDY AREA

A description of the topography of and the annual climatic cycle in Simpson Lagoon is provided in Craig and Haldorson (1980). Figures 1 and 2 show the locations of the principal sampling stations in the Simpson Lagoon study area for 1977 through 1979. The water depths and substrate characteristics at the 1977 and 1978 stations are shown in Table 1 and Fig. 3.

Simpson Lagoon has an average depth of 2.0 m and a maximum of 3.0 m. On the ocean side of the barrier islands, depths increase to 2.0 m within 50 m of the shoreline and to 10-15 m within 1 km.

The lagoon floor is uniformly flat and almost featureless (Table 1, Fig. 3). In the nearshore areas of the mainland and on both shores of the barrier islands (Stations 78-1, 5 and 6), the substrate is composed primarily of sand, with occasional soft sediments overlaying the sand. Some exceptions to this are shallow embayments which have a soft mud-clay substrate and are, in some cases, covered by a thick mat of detritus. The deeper central portions (Stations 78-2, 3 and 4) are uniformly composed of mud and detritus. The detrital layer, which varies in thickness up to 2 cm, consists of a flocculent, amorphous mass. In the deeper offshore waters (Station 78-7), the substrate is composed of mud overlaid by a very light flocculent detritus.

Some topographic relief on the lagoon floor is provided by shallow (3-5-cm deep) ice gouge marks in the central portion of the lagoon and occasional tundra clumps and piles of small stones (~2.5 cm in diameter).

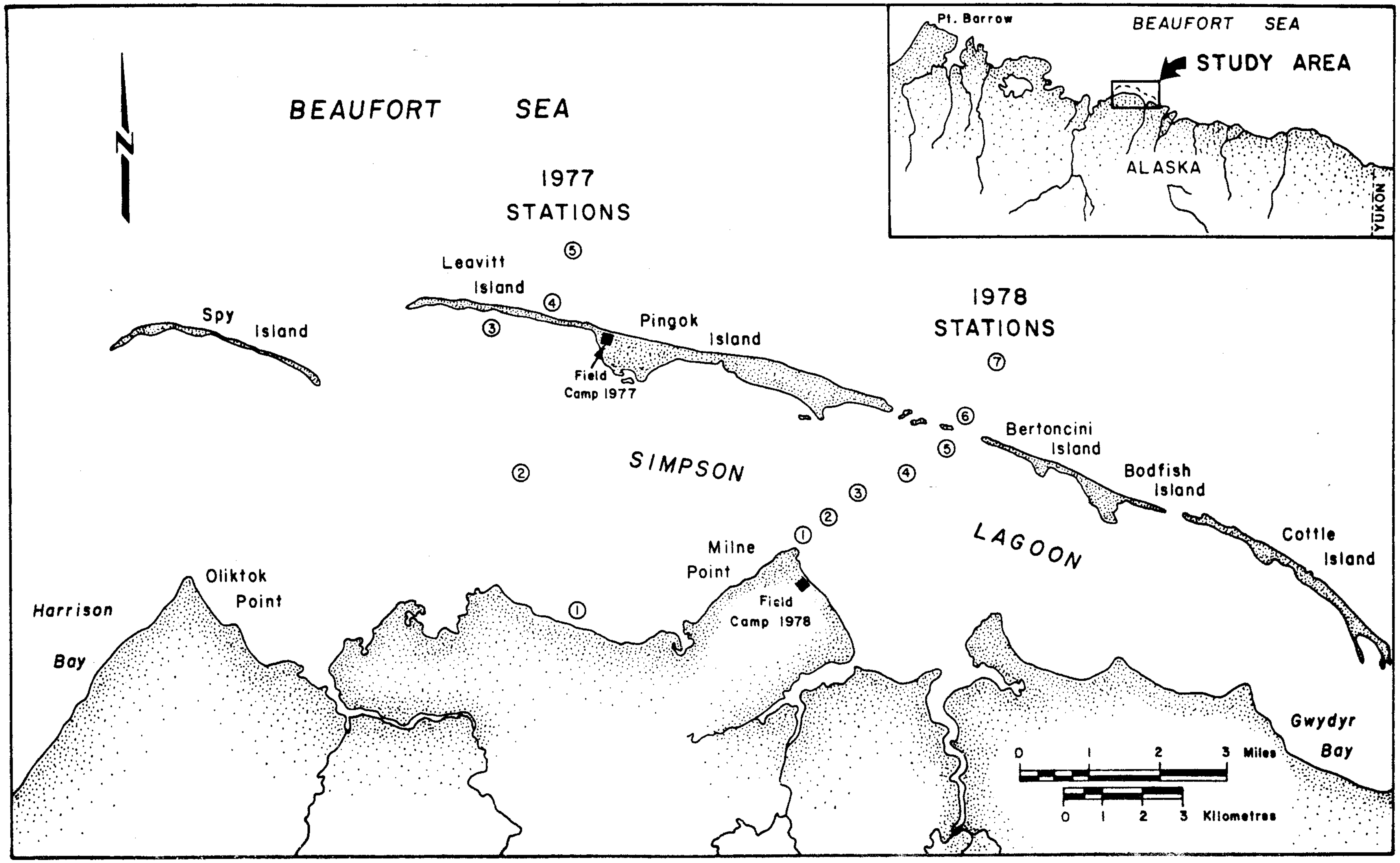

Figure 1. Principal invertebrate sampling stations in Simpson Lagoon during the open water seasons of 1977 and 1978.

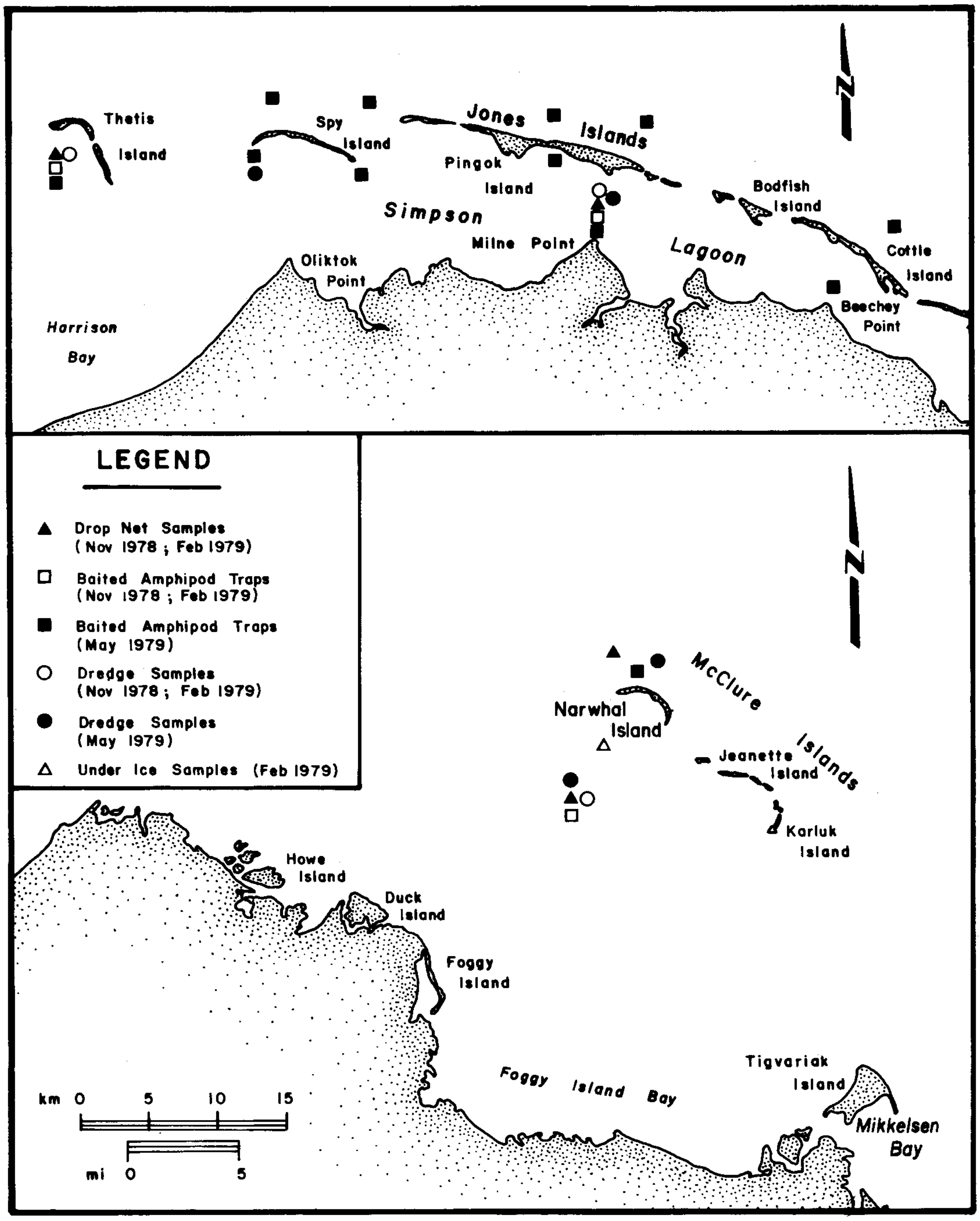

Figure 2. Invertebrate sampling stations during the winter program, November 1978-May 1979.

Table 1. Water depth, bottom type and sampling dates at principal sampling stations in the Simpson Lagoon area 1977 and 1978.

Sampling Period	Date		Stations		Approximate Water Depth (m)	Bottom Type
	1977	1978	1977	1978		
I	11-15 July	8-12 July	77-1	78-1	1.8	-Sand; occasionally covered by soft sediment
II	23-30 July	18-20 July		78-2	2.5	-Mud/detritus
III	31 July-7 Aug.	3-5 Aug.	77-2	78-3	2.5	-Mud/detritus
IV	14-20 Aug.	17-19 Aug.		78-4	2.5	-Mud/detritus
V	23 Aug.-2 Sept.	20-31 Aug.	77-3	78-5	1.0	-Sand ridges; detritus between ridges
VI	4-9 Sept.	14 Sept.		78-6	1.5	-Sand ridges; detritus between ridges
VII	14-20 Sept.	23 Sept.	77-5	78-7	7.5	-Very light flocculent mud/ detritus

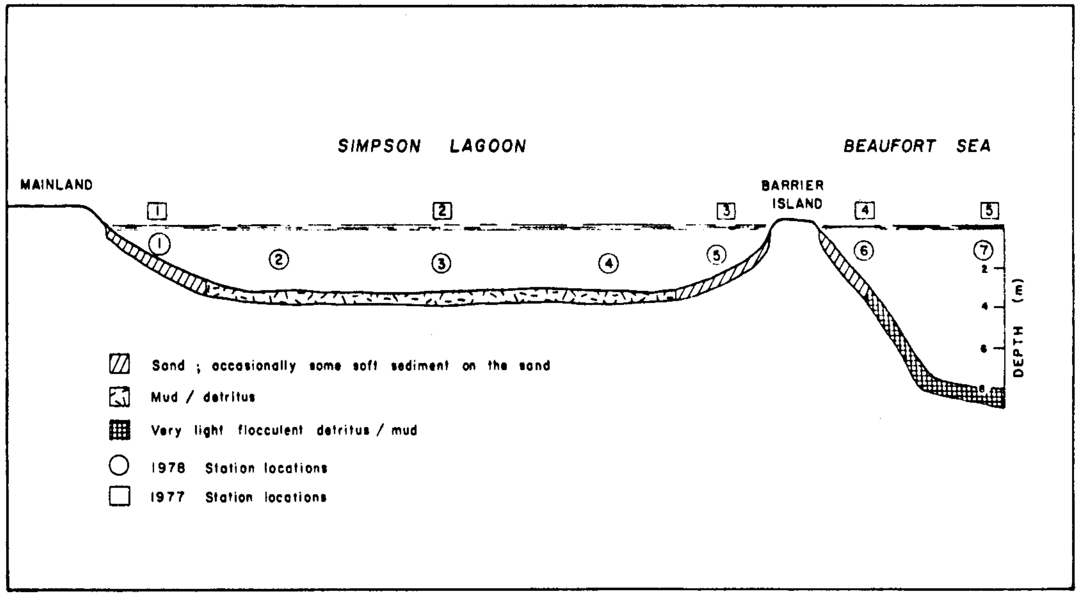

Figure 3. Schematic cross-section of Simpson Lagoon showing invertebrate sampling stations for the open-water seasons of 1977 and 1978 and substrate types.

METHODS AND RATIONALE OF DATA COLLECTION

Results from the first year of study (1977) showed that epibenthic mysids and amphipods and, to a lesser degree, infaunal molluscs were the predominant food items of birds and fish. Therefore, these organisms were selected as the focal point of the 1978 summer invertebrate program. In addition, a winter sampling program was conducted between November 1978 and May 1979 to determine epibenthic invertebrate use of the nearshore areas during the period of ice cover. This period is particularly important for these organisms; results from both 1977 and 1978 indicated that epibenthic invertebrates breed and brood their young at this time.

Open-Water Season, 1977

Epibenthic invertebrates were sampled by otter trawl, Faber net and zooplankton net. Samples of all three types were collected at stations 77-1 through 77-5 (Fig. 1) during each of seven sampling periods (Table 1), ice and weather conditions permitting.

Otter Trawl

A small otter trawl was used to sample epibenthic invertebrates on and near the lagoon bottom. The trawl measured 4.9 m wide and 4.0 m long with 16-mm bar mesh nylon marquisette with a 6.5 mm bar mesh cod end. It was towed directly behind a boat for 3 min at a constant speed of 1.1 m/s. Time was measured using a stopwatch, and the boat's speed using a Gurley current meter (direct readout model No. 665). Tow rope length varied from a ratio (length:depth) of 10:1 to 5:1 depending on water depth.

Faber Net

A 0.5 m diameter modified Faber net (Faber 1968) was used to sample ichthyoplankton and pelagic amphipods and mysids in surface waters of Simpson Lagoon. The 1.024 mm mesh net was towed 30 m directly astern of the boat for 5 min at a constant speed of 1.4 m/s.

Zooplankton Net

A 0.25 m diameter zooplankton net (mesh size 0.239 mm) was used to sample zooplankton in surface waters of Simpson Lagoon. The net was towed at a constant speed of 1.1 m/s beside the boat for 5 min.

Epibenthic Shore Transects

Prior to spring breakup, a hand-pulled 14x10 cm neuston net (mesh size 0.079 mm) was used to sample epibenthic invertebrates on 10 m transects parallel to the shoreline at seven sites in open leads around Pingok Island.

Diver Transects

Diver transects, generally 25 m in length, were surveyed only on relatively calm, clear days when water turbidity was minimal and visibility was optimal. Along each of 12 transects, the diver made five estimates of the densities of mysids and amphipods in a 10 cm^2 area. The mean of these estimates was then extrapolated to 1 m^2.

An analysis of the 1977 sampling techniques illustrated that traditional invertebrate sampling methods (trawls and nets) did not collect reliable quantitative data about the epibenthos (Table 2). Estimates based on diver observations were over 100 times those from traditional sampling gear. It is believed that many epibenthic invertebrates move to avoid approaching trawls and nets (Clutter 1965). Consequently, in 1978, invertebrates were sampled using a variety of improved techniques (Table 3; see Limitations and Biases section).

Open-Water Season, 1978

Faber Net

A modified Faber net (0.5 m diameter; 1.024 mm mesh) (Faber 1968) was used to collect samples of invertebrates and ichthyoplankton in the water-column in Simpson Lagoon. The net was towed 30 m directly astern a Boston whaler for 5 min. The volume of water filtered was calculated

Table 2. Comparison of densities (No/m) of mysids, amphipods, and isopods collected in trawl samples and observed during diver transects from three studies on the Alaskan Beaufort Sea Coast.

Study	Location	Mysid No/m^2	Amphipod No/m^2	Isopod No/m^2
Simpson Lagoon	Deep Lagoon (>2m)	1.0	NT	0.002
Crane, 1971[1]	Shallow Lagoon (<2m)	1.8	NT	0.060
	Offshore Ocean	22.7	NT	NT
Kaktovik Lagoon	Deep Lagoon (>2m)	17.9	2.0	0.7
Griffiths et al. 1977[2]	Shallow Lagoon (<2m)	1.6	0.8	0.2
Simpson Lagoon	Deep Lagoon (>2m)	0.2	0.2	0.002
Griffiths and Craig, 1978[3]	Shallow Lagoon (<2m)	2.2	0.3	0.007
Simpson Lagoon	Deep Lagoon (>2m)	700	188	only 3 seen on all dives combined
Griffiths and Craig, 1978[4]	Shallow Lagoon (<2m)	532	188	

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[1] 2.0 m benthic trawl, 2.8 mm stretch mesh; approx. 900 m^2 sampled.

[2] 4.88 m otter trawl; 16 mm bar mesh; 6.5 bar mesh cod end; approx. 940 m^2 sampled.

[3] 1.0 m benthic trawl; 6.5 stretch mesh; 3 mm stretch mesh cod end; approx. 100 m^2sampled.

[4] Diver transects; 5 estimates/transect of numbers in a 10 cm^2 area extrapolated to 1 m^2.

NT Data not taken.

Table 3. Invertebrate sampling schedules and methodologies followed in Simpson Lagoon during the open-water season of 1978.

Sampling Technique	Stations Sampled	Approximate Sampling Periodicity	No. of Samples/Station	Data Acquired
Faber net	2,3,4,6,7†	14 days	3	Density estimates of invertebrates in the water column.
Drop net	1-7	14 days	5	Density estimates of epibenthic invertebrates.
Drift net	Gaps in islands	Weekly	2-10	Movements into and out of the lagoon by epibenthic invertebrates.
Under-ice baited amphipod traps	1-7	Daily from 4-7 June	1	Early season presence of invertebrates in the lagoon.
Observations by divers	1-7	Five dates (see text)	10	Density estimates of epibenthic invertebrates.
Air lift	1-7	Three dates (see text)	2	Bivalve biomass estimates.
Photographic quadrats	1-7	Five dates (see text)	6	Density estimates of epibenthic invertebrates; evaluation of substrate characteristics.

†Ice prevented sampling at Station 7 early in the season.

using time and a digital readout flowmeter (General Oceanics, Inc., model 2030). Triplicate Faber net samples were obtained at Stations 2, 3, 4 and 7 (the water at other stations was too shallow to sample with this technique).

Drop Net

Two models of a central pursing drop net (Fig. 4) were designed specifically for this project by modifying an epibenthic sampler developed by Clutter (1965).

1. A shallow-water version equipped with a pole handle.
2. A deep-water version with a heavy (10 kg) metal frame.

All net screening was 1.0 mm nitex, and the purse collar was nylon ballistics cloth with 0.65 cm^2 atlas netting around the margin. Five drop net samples were obtained at each of seven stations in each sampling period, weather and ice conditions permitting.

The drop net used in shallow water was operated by first folding the purse collar back over the metal frame so that the metal rings on the collar encircled the bottom edge of the frame. With both the top and bottom of the net open, it was thrust to the bottom and held in place by the pole. Both purse lines were immediately pulled to enclose the sample in the net. The sample was then washed down the sleeve into a collecting bucket and the net was inspected to insure that all organisms had been removed.

The drop net used in deep water was prepared and operated as above, except that the net was dropped rather than thrust to the bottom. The heavy weight of the frame caused the net to drop rapidly, and then held the net on bottom substrates while the pursing lines were drawn.

Drift Net

A 2.8 m long tapering drift net (1.024 mm mesh size) was used to collect current-borne invertebrates moving into and out of the lagoon

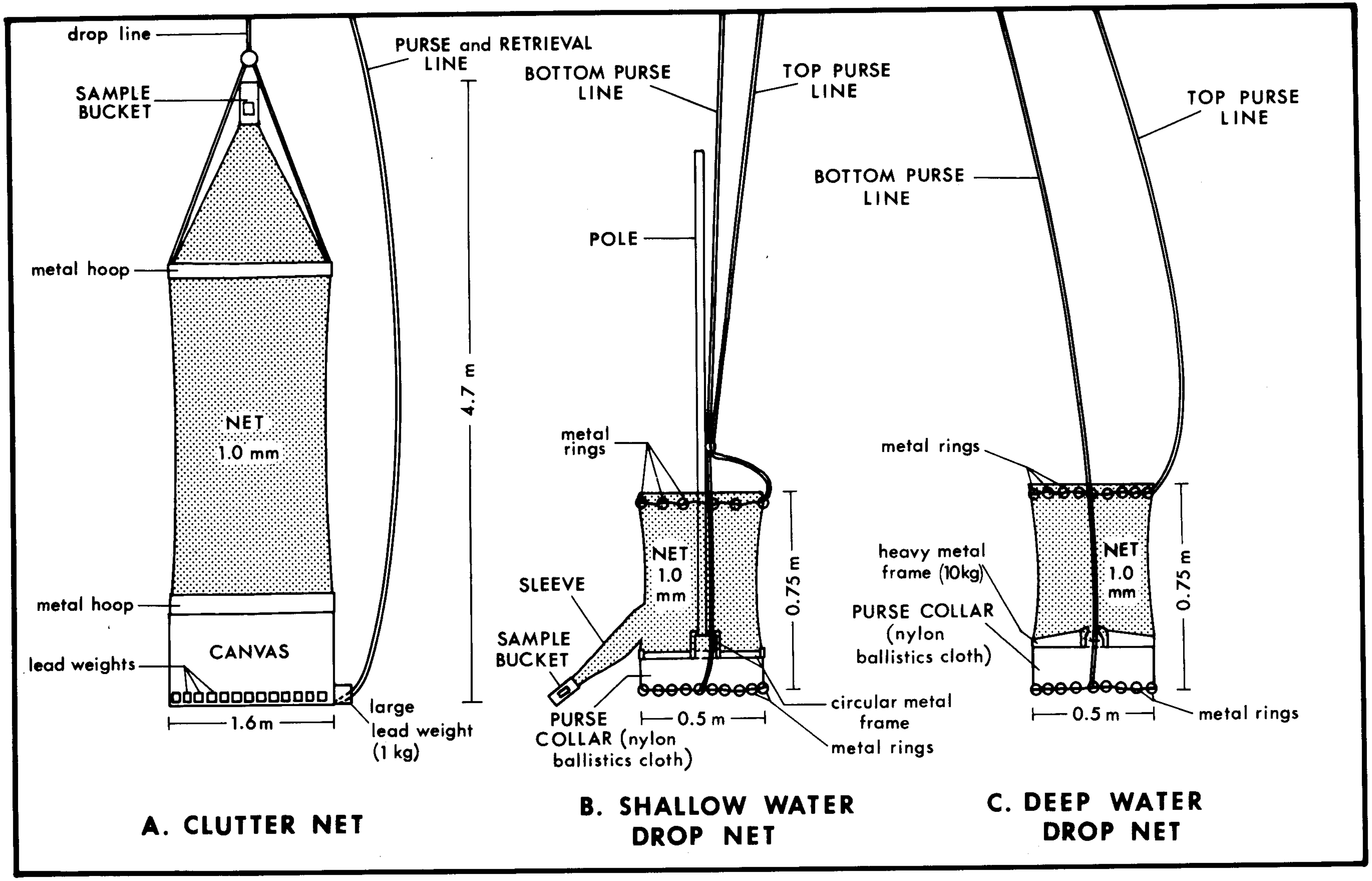

Figure 4. Two models of a central-pursing drop net (modified from the Clutter net) used for collecting epibenthic invertebrates in Simpson Lagoon in 1978.

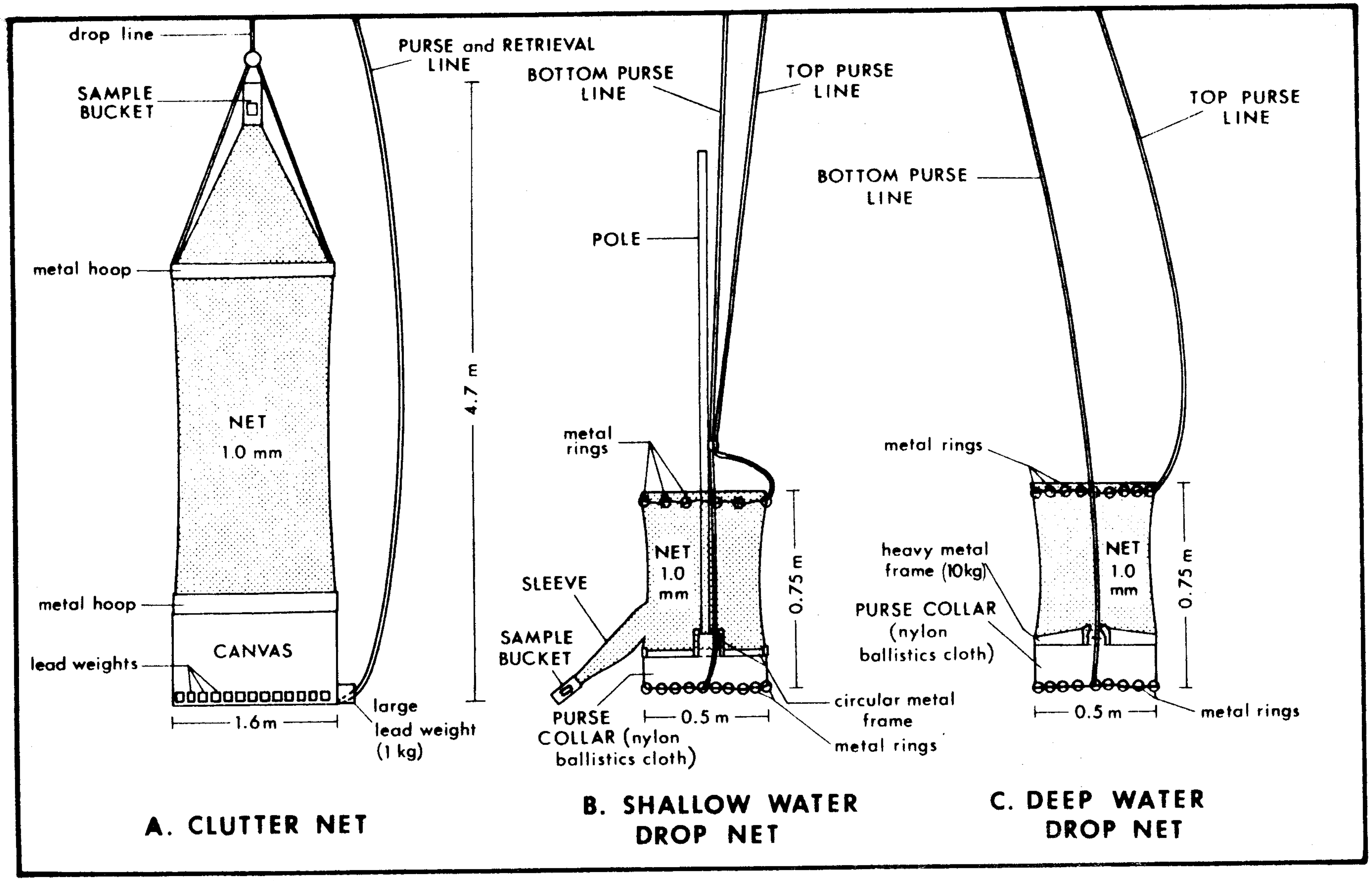

Figure 4. Two models of a central-pursing drop net (modified from the Clutter net) used for collecting epibenthic invertebrates in Simpson Lagoon in 1978.

through the gaps between the barrier islands. The net was attached to a 1.0 m x 0.2 m metal frame and was set with its long axis vertical in water about 1 m deep. Thus the net extended from the bottom to the top of the water-column. The sample trap attached to the net was emptied every hour and replaced by a new trap. The volume of water filtered was calculated using time and a digital readout flowmeter (General Oceanics, Inc., model 2030).

Amphipod Trap

During the preliminary stages of spring breakup in 1978 (5-7 June) traps for amphipods were baited with meat and placed on bottom substrates under the ice at six locations (See RESULTS section for locations) across the lagoon and at one site on the ocean side of the barrier islands. The traps were cylindrical with a funnel shaped entrance and measured 25 cm in length, 7 cm in diameter and were constructed of 1 mm wire mesh.

Diver Operations

SCUBA dives were conducted in Simpson Lagoon on five dates during the open-water season: 21, 25 and 31 July; 19 and 29 August. Stations 1-5 were sampled on all these dates; stations 6 and 7 were sampled on the last two dates only. Three divers were used on each occasion; two conducted the sampling and the third acted as a safety diver. Divers used the following sampling techniques.

Visual Estimates of Epibenthic Invertebrates. Each diver carried a 20 x 20 cm (0.04 m^2) quadrat frame and on five occasions during each dive held the frame approximately 10 cm off the bottom and estimated the number of organisms encompassed by the quadrat. This method was soon discontinued for amphipods and used only for mysids because divers noted that many amphipods burrowed into bottom substrates and could not be counted.

Airlift Samples. Two airlift samples were collected from each station during each of the last three dives. Divers implanted a plastic tapered cylinder (15 cm in height and 40 cm in diameter = 0.125 m^2 area at the bottom) into the substrate and vaccuumed out all material to a depth of about 2 cm. The airlift itself was a 1.5 m length of PVC pipe (10 cm in diameter) with a net (mesh size = 1.0 mm) on the top. When the compressed air inlet near the bottom of the pipe was activated, material was drawn up the pipe and filtered through the net. Samples were later sieved (0.5 mm mesh size).

Photographic Quadrats. Divers attempted to take color photographs of benthic invertebrates by using a Nikonos camera equipped with a wide angle lens and a strobe light system. An area of 50 x 25 cm (0.125 m^2) was photographed using a fixed-focus frame that ideally would allow measurements and counts to be made from the photographs. Six photographs of the bottom were taken at each station during each dive period. However, because of the turbidity of the water and back-scattering of light, mysids and amphipods were not visible in the photographs.

Winter Season, 1978-1979

Samples of overwintering invertebrates were collected during three periods (November 1978, February and May 1979) in Harrison Bay, in Simpson Lagoon, and near the 'Boulder Patch' in Stefansson Sound (Table 4, Fig. 2). Where possible, the procedures used during the open-water season were followed; however, when ice and weather conditions made collections difficult, some modifications were necessary.

Drop Net

The deep-water drop net was used during November and February; however, this device was not used in May, when ice thickness made operation of the net impractical. Samples were collected by first cutting a hole in the ice (of adequate size to accommodate the net) and then operating the drop net as described for the open-water season. The holes were cut in approximately 10-15 min, using a power auger, and one sample per hole was collected 15-30 min after the hole had been completed. All drop net samples were taken during daylight hours.

Table 4. Invertebrate sampling schedule and methodologies, winter sampling period, November 1978-May 1979. The number of each type of sample collected is indicated.

Sampling Technique	November 1978			February 1979			May 1979		
	Harrison Bay	Simpson Lagoon	Stefansson Sound	Harrison Bay	Simpson Lagoon	Steffanson Sound	Harrison Bay	Simpson Lagoon	Stefansson Sound
Drop Net	5	5	5	-	5	8[†]	-	-	-
Large baited amphipod trap	1	4	-	-	2	5[†]	-	-	-
Small baited amphipod trap	-	-	-	-	-	-	7*	13**	8
Wildco dredge	1	2	2	-	2	3[†]	3	1	3
Air lifts	-	-	-	-	-	4	-	-	-
Under ice dip net	-	-	-	-	-	9	-	-	-

[†] 3 of these samples collected from ocean side of Narwhal Islands.

* 2 of these samples collected from ocean side of Thetis Island.

** 4 of these samples collected from ocean side of the Jones Islands.

Amphipod Trap

Small amphipod traps used in May were identical in size to, and were operated in a similar fashion as, those described for the open-water season. The larger traps (1.0 m in length and 0.4 m in diameter, mesh size 1.0 mm) used in November and February were baited with meat and light (light sticks) simultaneously. The nets were lowered through holes in the ice to the bottom; they were lifted and cleared after 24 h.

Wildco Dredge

Epibenthos was qualitatively sampled at each location using a Wildco scrape/skid dredge (61 cm long, 36 cm wide, 36 cm in height, with a 1.05 mm mesh). The dredge was towed 50 m along the bottom between two holes in the ice.

Dip Net

Hand-held dip nets were used by divers to sample invertebrates on the underside of the ice in Stefansson Sound during the February sampling period. The nets were flat top (40 cm wide at the top of the net) and were made of 1.0 mm mesh. To obtain one sample the net was pushed in front of the diver along the undersurface of the ice for a distance of 10 m (area sampled = 4 m^2). To reduce potential bias induced by the presence of the dive-hole, the area within 5 m of the hole was not sampled.

Airlift Samples

The airlift used in winter to collect epifauna and infauna differed from the one used during the open-water season. It consisted of a weighted length of PVC pipe 8 cm in diameter fitted at the top with a 1 mm mesh net that retained the sample and could be removed quickly and capped. Areas to be sampled were circumscribed by an aluminum ring containing an area of 0.15 m^2. Motile epifauna within the 0.15 m^2 area was contained, and those outside were excluded, by 1 mm mesh netting covering the top of the ring. The airlift frame was placed on the bottom and pushed as far as possible into the substrate to insure collection of shallow infauna. The netting over the ring contained a capped central receptacle to receive the 'mouth' of the airlift. The airlift was attached to the net, the air was turned on, and the mouth of the airlift was moved around to cover thoroughly the area within the ring. The air was turned off when reasonable (2-5 cm) penetration had been achieved and all visible organisms had been collected, and the net on the airlift was then removed, capped and replaced. The depth of penetration of the airlift was variable, and was apparently inversely related to the degree of consolidation and the particle size of the substrate.

Miscellaneous Collections

All invertebrates collected incidentally in gillnets, fyke nets, trammel nets and minnow traps (see Craig and Haldorson 1980) were preserved and returned to the laboratory.

Laboratory Techniques, 1977-1979

All samples were preserved in 10% formalin and shipped to the laboratory for analyses.

Sorting

Samples were sieved through a 1.024 mm mesh nylon screen, washed with water, and examined under a low-power binocular microscope. All whole or partial organisms were separated into major taxonomic groups (amphipods, mysids, etc.) and counted. Techniques for counting fragmented organisms were as follows:

1. Copepods: The total number of copepods was assumed to be the number of whole organisms plus the number of separate cephalothoraxes present.
2. Amphipods: Amphipod specimens were often in two parts (head plus peraeon, abdomen plus telson) or three parts (head, peraeon, abdomen plus telson). The sum of the numbers of whole amphipods and separate 'abdomens plus telsons' constituted the total number.
3. Mysids: The total number of mysids equalled the number of whole organisms plus the number of separate telsons.

4. Polychaetes: Polychaetes were generally broken in half. The total number present was assumed to be the number of whole polychaetes plus the number of anterior parts.
5. Medusae: The number of whole medusae plus the number of bells constituted the total number in the sample; fragmented bells were counted if over one-half the bell was present.
6. Bivalves: Similarly, the number of whole bivalves plus the number of partial shells (>½ of whole shell) constitued the total number of bivalves in the sample. Half shells were presumed to be from non-living individuals and were not counted.

If large numbers of individuals were present, the sample was first scanned for large or rare organisms, and was then sub-sampled with a Folsom Plankton Splitter (following the methods of McEwen et al. 1954). We found no significant difference between the number of specimens when pairs of chambers were compared (Wilcoxon matched-pairs signed-ranks test: $n = 10$ pairs, $P < 0.05$).

In 1977 all amphipods and mysids were identified to species if possible; however, in 1978 and 1979 only those taxonomic groups that comprised significant portions of the drop net samples or the diets of vertebrates were identified to species.

Measuring

Two techniques were used to obtain total lengths of dominant invertebrate species.

1. Because broken organisms sometimes precluded measurements of total lengths of organisms (especially those in fish and bird stomachs) specific anatomical structures (referred to as "partial lengths") were measured (Table 5 and Fig. 5). These measurements were converted to total lengths by using best-fit equations for the relationship between the partial length and total length. These equations are presented in Appendices 1 to 8. Because partial lengths were easy to measure, all samples were analyzed in this fashion and later converted to total lengths. On the basis of total lengths, organisms were assigned to 2-mm length intervals.
2. Bivalve and copepod total lengths were measured directly because it was difficult to establish precise relationships between partial and total lengths.

Table 5. Equations and comparisons used to determine energy (Kcal) available to birds and fish in Simpson Lagoon, 1978.

Organism	Partial Length:Total Length Conversion	Total Length:Wet Weight Conversion	Ash-Free Dry Weight as % of Wet Wt	Kcal/g Ash-Free Dry Wt. N	Kcal/g Ash-Free Dry Wt. $\bar{X}$	S.E.
Mysis litoralis	Total Length = 6.47 (Partial length) + 0.844	Wet Weight = 0.029 (Total length)$^{2.45}$	11.5[1]	3	5.47	0.03
Mysis relicta	Total Length = 6.60 (Partial length) + 0.651	Wet Weight = 0.044 (Total length)$^{2.31}$	11.5[1]	3	5.47	0.03
Onisimus glacialis	Total Length = 2.23 (Partial length) + 0.600	Wet Weight = 0.054 (Total length)$^{2.56}$	19.7[1]	3	5.07	0.03
Pontoporeia affinis	Total Length = 2.67 (Partial length) + 0.265	Wet Weight = 0.640 (Total length)$^{1.27}$	17.8[2]	-[2]	5.39	-[2]
Apherusa glacialis *Haliragès mixtus*	Total Length = 5.067(Partial length) - 0.093	Wet Weight = 0.083 (Total length)$^{2.11}$	13.7[3]	7	6.80	0.18
Gammarus setosus	Total Length = 5.10 (Partial length) + 0.608	Wet Weight = 0.050 (Total length)$^{2.50}$	11.1[3]	1	5.17	-
Parathemisto spp.	Total Length = 3.75 (Partial length) + 0.177	Wet Weight = 0.056 (Total length)$^{2.44}$	14.9[3]	3	6.30	0.10
Mysid spp.	-[4]	-[4]	11.5[1]	3	5.47	0.03
Amphipod spp.	-[4]	-[4]	15.1[1]	3	5.37	0.12
Cyrtodaria kurriana	-	Body Weight = 0.0194(Total length)$^{3.30}$	74.3(Dry Weight)[1]	1	5.20	-
Calanoid copepods	-	Dry Weight = 0.0016 (length)$^{2.89}$	76.3(Dry Weight)[1]	3	6.17	0.10

[1] Determined from bomb calorimetry results by Dr. D. Pattie, Northern Alberta Inst. Technology.

[2] Determined from data of Sars (1953).

[3] Determined for corresponding length intervals by Bradstreet (1977).

[4] Organisms in these groups were counted and wet weighed.

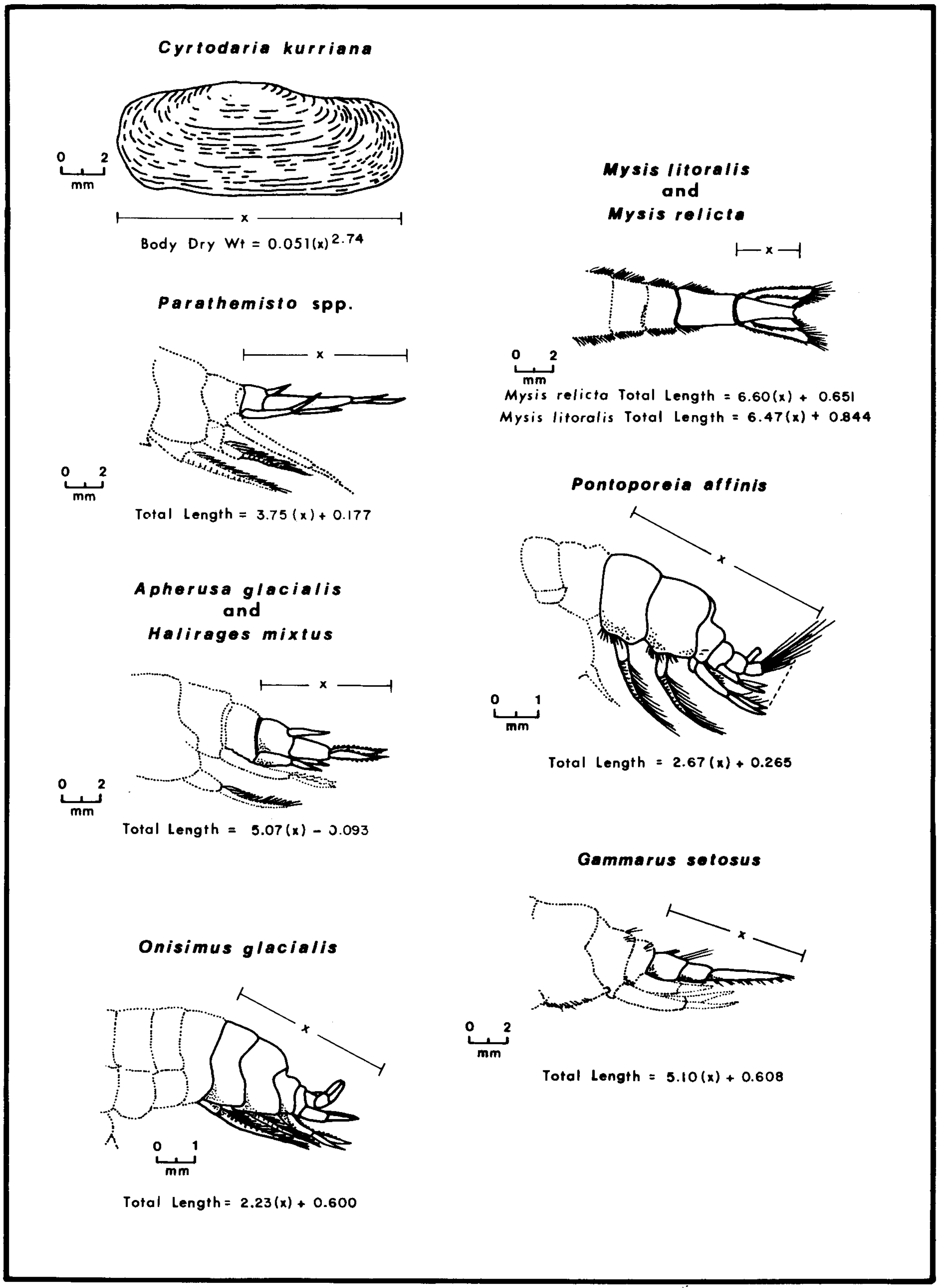

Figure 5. Anatomical features of invertebrates that were measured for later conversion (by equations) to total lengths.

3. For the winter collections, technique 1 was altered so that, where possible, total lengths of the organisms were measured. In cases of broken organisms, the method outlined in 1 was used.

Biomass

For each important invertebrate species, we measured and weighed approximately 50 organisms from each 2 mm length interval and developed best-fit equations for the relationship between total length and wet weight (Appendices 1 to 8).

Wet weight was converted to ash-free dry weight and then to Kcal energy content by using data from microbomb calorimeter studies carried out by Dr. Donald Pattie of the Northern Alberta Institute of Technology (Table 5). These data were used to calculate the amount of energy available (per m^2) to consumers in Simpson Lagoon.

Limitations and Biases

Any method that involves the capture of mobile organisms with trawls or nets contains inherent errors that should be taken into account. One source of error results from the natural avoidance behavior of the organisms. Swift-moving epibenthic invertebrates (e.g., amphipods and mysids) are able to avoid nets and trawls, but slow-moving or sessile organisms (e.g., isopods and tunicates) are not. Consequently, densities of the swifter organisms can be underestimated but estimates of the slower moving ones are relatively accurate. As an example of the extent to which swift organisms may avoid nets and trawls, estimates made of amphipod and mysid densities in this study by divers are two to three orders of magnitude greater than are estimates based on trawl data (Table 2).

Differences in mesh size also introduce a source of error since small organisms may escape from large-mesh trawls and nets. Density estimates resulting from standard trawl and net sampling techniques may, therefore, be low, particularly for swift-moving and/or small organisms.

Limitations and biases of new techniques that were utilized in 1978 and 1979 are discussed below.

Drop Net

This net proved to be an excellent sampling device for epibenthic invertebrates, which were usually within 10 cm of the lagoon bottom. Diver observations of the operation of the drop net indicated that the move-and-freeze evasive behavior of mysids did not prevent their capture. The drop net was at maximum velocity just before it struck the bottom and sealed against the substrate. No animals were seen to avoid the descending net. Moreover, pursing of the net's bottom would be expected to cause the mysids and amphipods to move upward and into the bag. The drop net did not effectively sample infaunal organisms because the pursing operation only scraped the substrate.

Several factors may have combined to make the use of this net less efficient under ice. By cutting holes in the ice, workers exposed the areas to be sampled to more light than illuminated the surrounding areas; whether this attracted or repelled epibenthic invertebrates is not known. When operated in shallow water (1.0 m of water between the bottom of the ice and the substrate), the movements of the net prior to the drop may have caused some invertebrates to leave the area to be sampled.

Visual Estimates by Divers

This method provided densities that were, for several reasons, biased downward.

1. As the number of organisms increased, the ability of divers to count accurately the number within the quadrat decreased.
2. Early in the season, organisms were small, almost transparent, and therefore difficult to see and count.
3. Many of the epibenthic organisms moved in and out of the detritus, and some thereby escaped observation.

Diver observations also provided only limited taxonomic differentiation of mysid and amphipod species, since diagnostic characters are often observable only under a dissecting microscope.

Airlift Samples

Airlifts appear to be effective in sampling infaunal organisms to a depth of 2 cm; however, epibenthic animals are able to escape the airlift during the placement of the circular frame and prior to activation of the lift. This method is most effective when used for sampling soft bottom substrates.

Photographic Quadrats

This technique was used to acquire permanent records of benthic organisms and substrates at particular points in space and time. Its recording capabilities were limited because of the evasive behavior of the motile organisms (amphipods and mysids), the periodic turbidity of the water, and the presence of highly effective cryptic coloration in some of the benthic organisms. The positioning of the strobe lights on the photographic frame was critical to the acquisition of good quality photographs, since animals were obscured by improperly reflected light. Partly because the strobe lights were improperly positioned, most of the photographs were not sufficiently distinct to use for estimating numbers of invertebrates.

Amphipod Trap

This technique is obviously biased, since some species of epibenthic invertebrate (i.e., planktivores, filter feeders) would not be attracted by the bait and others might avoid light rather than be attracted to it.

Wildco Dredge

This sampler suffers from the same limitations as other dredges and trawls; namely, motile epibenthic organisms (mysids and amphipods) can easily avoid capture by taking evasive action as the dredge approaches (Table 2).

Laboratory Techniques

Wet weights used in this study are from formalin-preserved samples. These wet weights must be considered approximate, since actual wet weights of crustaceans and some other invertebrates are significantly altered by preservation in 10% formalin (Conover and Lalli 1972; Bradstreet 1977; LGL Ltd. unpubl. data). The degree of weight alteration depends on the species; for example, various amphipods may show changes of ±5-20% in weight.

Comparison of Sampling Techniques

The 1977 results indicated that traditional invertebrate sampling methodology caused underestimation of the actual densities of mobile epibenthic organisms by two to three orders of magnitude; diver estimates appeared to provide more reliable values (Griffiths and Craig 1978). However, comprehensive sampling coverage by divers is limited by expense, periodically adverse weather, ice conditions and high turbidity. In 1978, an effort was made to develop a sampling device that could be used to sample epibenthic organisms quantitatively from a small boat in most weather conditions. Clutter (1965) developed a large drop net to collect epibenthic invertebrates; this design was modified to produce two types of drop net (see 'Open-Water Season, 1978'), which were used in addition to diver observations and diver-operated sampling devices (airlift). In this report, drop net results are used in most analyses, since this method was applied more widely in time and space than were other methods, and appeared to provide relatively realistic estimates of the abundance of epibenthos, as discussed below.

Statistical comparisons of the density estimates obtained by the various sampling techniques used in 1978 are shown in Table 6. The comparisons are based on occasions when two or three methods were employed at the same place and time. Mysid and amphipod density estimates did not differ significantly between the two types of drop net. Density estimates for amphipods did not differ significantly between airlift and drop net samples.

Table 6. Statistical comparisons of density estimates of mysids and amphipods obtained with various sampling techniques in Simpson Lagoon, 1978.

Sampling Techniques	Organisms Compared	Statistical Test	Results	Comments
Shallow vs Deep Water[†] Drop Net	Mysids Amphipods	Paired t-test Paired t-test	$t=0.068$, $P>0.20$, d.f.$=4$ $t=1.661$, $P>0.10$, d.f.$=4$	No significant difference between nets for either organism
Shallow Water Drop Net vs Airlift	Amphipods Amphipods	t-test Mann-Whitney u	$t=0.0496$, $P>0.20$, d.f.$=12$ $u=13$, $P>0.10$, $N_1=4$, $N_2=10$	No significant difference with either test
Shallow Water Drop Net[††] vs Estimate by Diver 1 vs Estimate by Diver 2	Mysids	Friedman Test	$\chi^2=9.4$, $P<0.01$ $K=3$, $N=10$	Significant differences among methods
Shallow Water Drop Net vs Diver 1	Mysids	Multiple comparisons of Friedman rank sums[‡]	Rank sum diff.[‡]$=1$ $K=3$, $N=10$	No significant difference between shallow drop net vs diver 1 $P>0.05$
Shallow Water Drop Net vs Diver 2	Mysids	Multiple comparisons of Friedman rank sums	Rank sum diff.$=11$ $K=3$, $N=10$	Diver 2 estimate significantly higher than shallow drop net $P=0.037$
Diver 1 vs Diver 2	Mysids	Multiple comparisons of Friedman rank sums	Rank sum diff.$=9$ $K=3$, $N=10$	No significant difference between diver 1 and diver 2 $P>0.05$

[†] Data collected in a pair-wise fashion.

[††] Only two divers were in the water at a time, so diver 3 could not be used in the comparison.

[‡] See Hollander and Wolfe (1973, p. 151).

There was a significant difference among mysid density estimates by drop net, diver 1 and diver 2; the drop net gave significantly lower estimates than diver 2 (Table 6). No direct comparisons among all three divers were possible since only two divers were in the water at any one time. However, three independent paired t-tests of estimates by divers showed the following:

Diver 1 vs Diver 2 $t = 3.8753$ d.f. = 28 $P < 0.01$
Diver 1 vs Diver 3 $t = 0.5333$ d.f. = 28 NS $P > 0.50$
Diver 2 vs Diver 3 $t = 1.3858$ d.f. = 28 NS $P > 0.10$

Divers 1 and 3 were the most experienced in estimating densities of epibenthic invertebrates and the agreement between them was the closest. Diver 2 tended to give higher estimates in the early part of the season, possibly because of his inexperience.

RESULTS

Under-Ice Distribution of Epibenthic Invertebrates

Shallow nearshore areas of the Beaufort Sea, including Simpson Lagoon, remain ice-covered for approximately nine months of the year. Organisms inhabiting these areas during this period are subjected to low temperatures (-1.5 to -2.0°C) and high salinities (>40 ppt). Prior to this study, data on the winter utilization of Simpson Lagoon and other nearshore areas by invertebrates were sparse. This deficiency was partially addressed by (1) limited sampling conducted on the bottom under the ice in Simpsom Lagoon in April-May 1978, (2) a more routine sampling program carried out in the lagoon on 5-7 June 1978 prior to inundation of the lagoon by river discharge, and (3) collections made under the ice in November 1978, February 1979 and May 1979 in Simpson Lagoon and adjacent areas. These collections completed the year-round sampling of epibenthic invertebrates in Simpson Lagoon. A further sampling effort will be conducted in the winter of 1979-1980 to further delineate important processes (growth, reproduction) of epibenthic invertebrates in shallow nearshore waters.

The results of the under-ice sampling have been organized seasonally:

1. Early Winter, 1978
2. Mid-Winter, 1979
3. Late Winter and Spring, 1977-1979

Early Winter, 1978

In November 1978, invertebrates were sampled at various locations along the Beaufort Sea coast using baited traps, drop nets and a Wildco dredge (Fig. 2). A total of 21 species or groups were collected at this time and catches varied considerably among sampling methods and sites (Table 7). In Simpson Lagoon (2 m deep), *Onisimus glacialis* (6-12 mm) was by far the most common amphipod collected by three sampling techniques. At Harrison Bay (4 m deep), *Boeckosimus affinis* (7-15 mm) predominated in the one amphipod trap collection but was absent from the Wildco

Table 7. Percent composition of invertebrates collected at various locations along the Beaufort Sea coast during early winter (November 1978).

Group or Species	Amphipod Traps		Wildco Dredge			Drop Net		
	Simpson Lagoon	Harrison Bay	Simpson Lagoon	Harrison Bay	Stefansson Sound	Simpson Lagoon	Harrison Bay	Stefansson Sound
AMPHIPODS								
Onisimus glacialis	95	*	73	1	3	33	*	9
Boeckosimus affinis	1	99	3		9			
Gammarus setosus	*		*				*	
Apherusa megalops					6			2
Haliragea quardridentatus					1			
Pontogeneia inermis				1				1
Pontoporeia affinis							5	
Orchomene sp.					2			
Oedicerotids			*	48	1	16	15	
Calliopiids					1			1
Amphipod sp.								3
MYSIDS								
Mysis litoralis			19	39	9	12	9	27
Mysis relicta				*		3	*	2
Mysis sp.			4	10	1	*	*	7
HYDROIDS						14		2
ISOPODS								
Saduria entomon	4	1	1			5		
CUMACEANS						8	37	1
POLYCHAETE LARVAE					1	6	33	8
COPEPODS					63		1	37
CHITONS					1			
†Total %	100	100	100	99	98	97	100	99
No. of Samples	4	1	2	1	2	5	5	5
Total No. of Organisms	8,176	2,370	242	348	95	274	335	101

*Indicates <1%.

†Percentages do not always total exactly 100 because of rounding-off.

dredge sample and the drop net samples (possibly indicating avoidance behavior) (Table 7). The Wildco dredge and drop net tended to collect a more diverse array of organisms (7 and 9 species or groups, respectively vs 3 for amphipod traps in Simpson Lagoon) and proved much more effective in capturing mysids (Table 7). The Wildco samples and the drop net samples from Stefansson Sound (5 m deep) contained a wider variety of organisms than did samples from either Simpson Lagoon or Harrison Bay. This greater diversity may be a reflection of the unique habitat associated with the kelp community in the Stefansson Sound (for a description of this community see Dunton and Schonberg 1979).

Most samples collected in each area contained gravid females of both mysid and most amphipod species; this indicates that most of the pelagic and epibenthic invertebrates in the near-shore area of the Beaufort Sea breed after ice formation. (For a more detailed discussion of the reproductive process see 'Biology of Key Invertebrates Species' section.)

Mid-Winter, 1979

In February 1979, invertebrate samples were collected from Simpson Lagoon and Stefansson Sound, again using a variety of techniques (amphipod traps, Wildco dredge and drop nets) (Table 8 and Fig. 2). Due to the presumed ecological importance of Stefansson Sound (notably, the presence of the kelp community), additional samples were collected (1) from the undersurface of the ice by divers using hand-held dip nets and (2) from the bottom with a diver-operated airlift (Table 8 and Fig. 2).

In Simpson Lagoon, *O. glacialis* was the dominant organism collected; however, several other species of amphipods, both species of mysids, and isopods were also present in the lagoon (Table 8). Females of both mysid species and *O. glacialis* were brooding young developing at this time (see 'Biology of Key Invertebrate Species' section). Collections from Stefansson Sound contained a more diverse fauna than was found in Simpson Lagoon (Table 8). *Onisimus litoralis*, which was not found in November 1978 samples, was the dominant amphipod species in the February collections, particularly on the ocean side; this species was found to be much more abundant in deeper (9-11.5 m) offshore waters than in inshore areas (2-3.5 m) during the 1978 open-water season (Broad et al. 1979).

Table 8. Percent composition of invertebrates collected at various locations along the Beaufort Sea coast during mid-winter (February 1979).

Group or Species	Amphipod Trap			Wildco Dredge		Dip Net (4 m²)	Airlift (0-15 m²)	Drop Net	
	Simpson Lagoon	Stefansson Sound Lagoon	Stefansson Sound Ocean	Simpson Lagoon	Stefansson Sound Ocean	Under Surface of Ice Stefansson Sound	Stefansson Sound	Simpson Lagoon	Stefansson Sound
AMPHIPODS									
Onisimus glacialis	47		*	64	6	3		36	
Onisimus litoralis		10	91		56		1		
Boeckosimus affinis	35	71	*	1			4		16
Boeckosimus plautus			1		6		24		3
Apherusa glacialis						3			
Apherusa megalops						3			35
Atylus carinata		*		1					
Pontogeneia inermis			*			11			3
Gammarus setosus		*				3			
Gammaracanthus loricatus		1				22			
Weyprechitia heuglini		1				5			
Weyprechtia pinguis		*	*			8	6		
Paroediceros lycaneus							1		
Anonyx sp.		17	7		6				6
Orchomene sp.			*		6				
Oedicerotids				26		19	7	19	26
Calliopiids						3	1		
Amphipod spp.			*			14	1		3
MYSIDS									
Mysis litoralis	3	*		2	6		1	1	3
Mysis relicta	7		*	1				7	
Mysis spp.					6			3	
EUPHAUSIIDS							1		
COPEPODS					6	3			
ISOPODS	8			4				22	
CUMACEANS				1			11	10	
POLYCHAETE LARVAE						5	10		3
ECHINODERMS		*					4		
CHITONS							1		
PRIAPULIDS				1					
HYDROIDS								1	
BIVALVES									
Musculus niger							1		
Axinopsida orbiculata							1		
Astarte borealis							1		
Astarte sp.							7		
GASTROPODS									
Plicifusus kroyeri							1		
Neptunea heros							1		
Boreotrophon sp.							1		
Buccinum sp.							1		
Colus sp.							10		
PTEROPODS							1		
DECAPODS			*		6				
†Total %	100	100	99	101	104	102	100	99	100
No. of Samples	2	2	3	2	3	9	4	5	5
Total No. of Organisms	1,753	1,089	31,003	180	18	37	84	73	31

*Indicates <1%.

†Percentages do not always total exactly 100 because of rounding-off.

It appears that, as winter progressed, several species of amphipods (e.g., *O. litoralis*, *Anonyx* sp.) moved into the Stefansson Sound area from deeper offshore waters. The reason for this shoreward movement is not known.

Samples from the undersurface of the ice indicate that the epontic community is well developed by February; at this time amphipods comprise the major portion of the community (Table 8). Similar amphipod-dominated communities of ice fauna have been reported to occur later in the season (May-June) in the Canadian High Arctic (Buchanan et al. 1977--Bridport Inlet, Melville, Island, N.W.T.; Thomson et al. 1978--Brentford Bay, Boothia Peninsula, N.W.T.). Several amphipod species were common to the under-ice surfaces in the three areas; these included *O. glacialis*, *Gammarus setosus*, *Gammaracanthus loricatus* and *Apherusa glacialis*. It is interesting to note that in Stefansson Sound *O. glacialis* also occurred on the lagoon bottom at this time. *Gammaracanthus loricatus* was the most abundant ($2/m^2$) amphipod collected from the under-ice surface; this species also has been found associated with ice in Resolute Bay, N.W.T., by Green and Steele (1975).

The density and species composition of amphipods on the bottom of Stefansson Sound in February 1979 (collected by airlift) were substantially different than were those recorded at the same time on the undersurface of the ice. Densities were higher on the bottom than the undersurface of the ice ($560/m^2$ vs $9.3/m^2$). *Boeckosimus plautus* ($134.4/m^2$) was the dominant species collected from the bottom, whereas *Gammaracanthus loricatus* dominated on the undersurface of the ice (Table 8). Numerous bivalves ($56/m^2$) and gastropods ($78/m^2$) were also collected in the four airlift samples (Table 8); however, *Cyrtodaria kurriana*, the dominant bivalve in Simpson Lagoon during the open-water season, was absent from the collections. Most of the species of bivalves and gastropods collected were the same as those reported during the summer of 1978 for the same area by Dunton and Schonberg (1979).

In summary, the February results indicated that the species composition of epibenthic invertebrates in Simpson Lagoon was similar to that reported for November. However, in Stefansson Sound a much greater diversity of organisms (particularly amphipods) was found in February than in November using the same sampling techniques. This increased diversity appears to be caused by an onshore movement of more marine species of amphipods (Table 8). Under-ice sampling showed a well-developed ice fauna community already formed by this time.

Late Winter and Spring (April-May 1978-1979, June 1977-1978)

During the periods 12-15 April 1978 and 22-25 May 1978, four baited amphipod traps were set beneath the ice off Milne and Oliktok Points (Fig. 6). All traps, with the exception of one set in May near Oliktok Point, were recovered after 24 h and all contained amphipods. On both occasions at the site north of Milne Point in the central portion of the lagoon, *Onisimus glacialis* was the dominant amphipod collected (Table 9). In the April sample near Oliktok Point, *Boeckosimus affinis* was the principal amphipod (total numbers in each trap are not available, because only representative qualitative subsamples were returned to the laboratory for analysis). In May 1979, a series of amphipod traps were set along the length of Simpson Lagoon and on the ocean side of the barrier islands. As was the case in 1978, *Onisimus glacialis* (6-12 mm) was by far the dominant amphipod in the eastern portion of Simpson Lagoon during late winter and spring, but *Boeckosimus affinis* (7-15 mm) predominated both in the western portion of the lagoon (i.e., on the lagoon side of Leavitt and Spy Islands) and on the ocean side of the barrier islands. These results were consistent between years and suggest that conditions in the western part of the lagoon and seaward of the islands may be similar at this time of year (Table 9, Fig. 6). Except for the absence of *B. affinis*, Wildco trawl samples collected in the Simpson Lagoon area during this same period showed a similar distribution pattern for amphipods, but tended to collect a more diverse array of organisms (Table 9). Figure 7 shows a schematic representation of late winter (April-May) distribution of amphipods in the Simpson Lagoon area in 1979.

Stefansson Sound samples from May 1979 showed a greater diversity than those collected in Simpson Lagoon. The species composition of samples from Stefansson Sound was most similar to that of samples taken

Table 9. Percent composition of invertebrates collected at various locations along the Beaufort Sea coast during late winter and spring (April-May 1978-1979, June 1977-1978).

	Amphipod Traps							Wildco Dredge		
	Simpson Lagoon Area				Leavitt and Spy Islands		Stefansson Sound	Simpson Lagoon Area	Spy Island	Stefansson Sound
	Lagoon Habitat		Ocean Habitat		Lagoon Habitat	Ocean Habitat	Lagoon Habitat	Lagoon Habitat	Lagoon Habitat	Lagoon Habitat
Group or Species	June 78	May 79	June 78	May 79	May 79	May 79	May 79	May 79	May 79	May 79
AMPHIPODS										
Onisimus glacialis	99	99	16	*			1	90	32	
Boeckosimus affinis	*	*	82	75	99	100	23	2		
Boeckosimus plautus							35			
Apherusa megalops										62
Atylus carinatus							*			
Gammarus setosus		*			*		*	4	4	
Gammaracanthus loricatus							*			
Anonyx sp.					*		8			
Orchomene sp.				3	*		32			
Oedicerotids				22					54	15
MYSIDS										
Mysis relicta		*								8
Mysis spp.								4		
ISOPODS	*		2				*			
CUMACEANS									11	
POLYCHAETE LARVAE							*			15
ECHINODERMS							*			
Total %	99	99	100	100	99	100	99	100	101	100
No. of Samples	12	9	3	4	5	2	8	1	1	3
Total No. of Organisms	16,548	25,358	542	1,246	3,684	3,029	879	53	28	13

*Indicates <1%

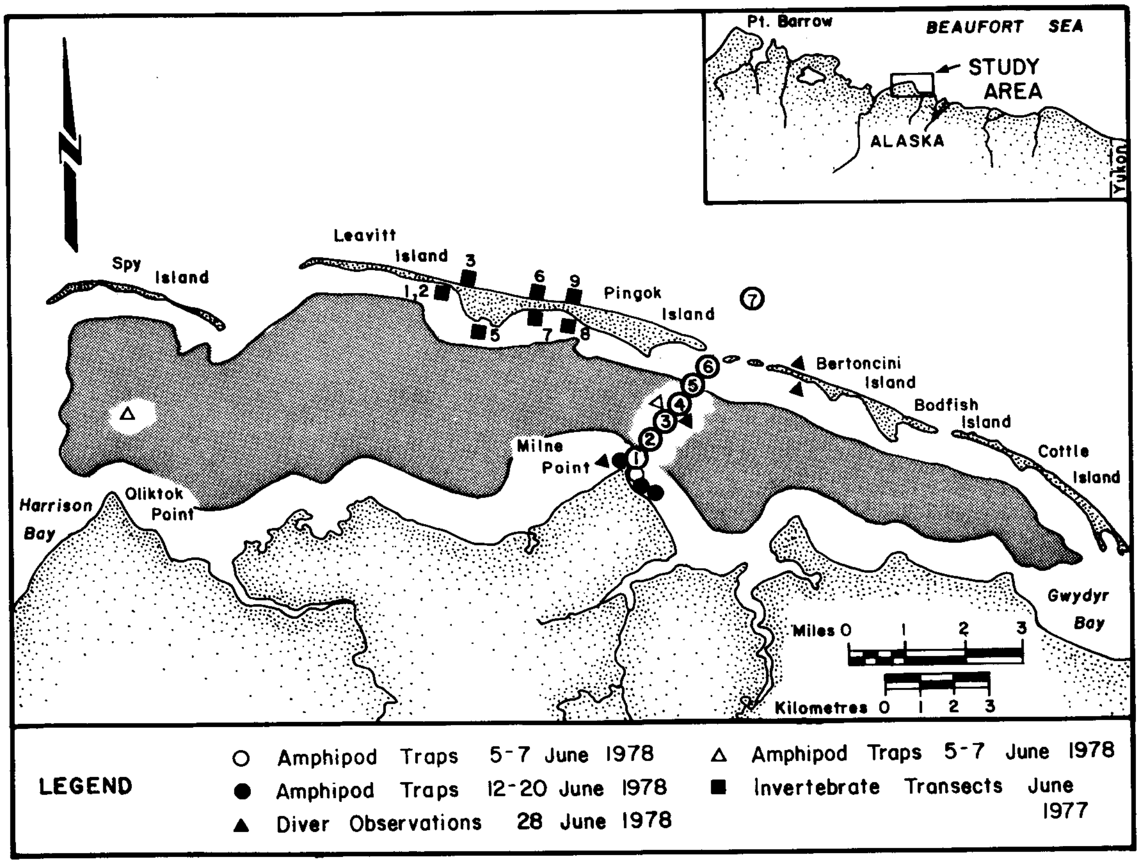

Figure 6. Early season invertebrate sampling sites in Simpson Lagoon June 1977 and April-June 1978. Shaded area approximates overwintering habitat available to invertebrates.

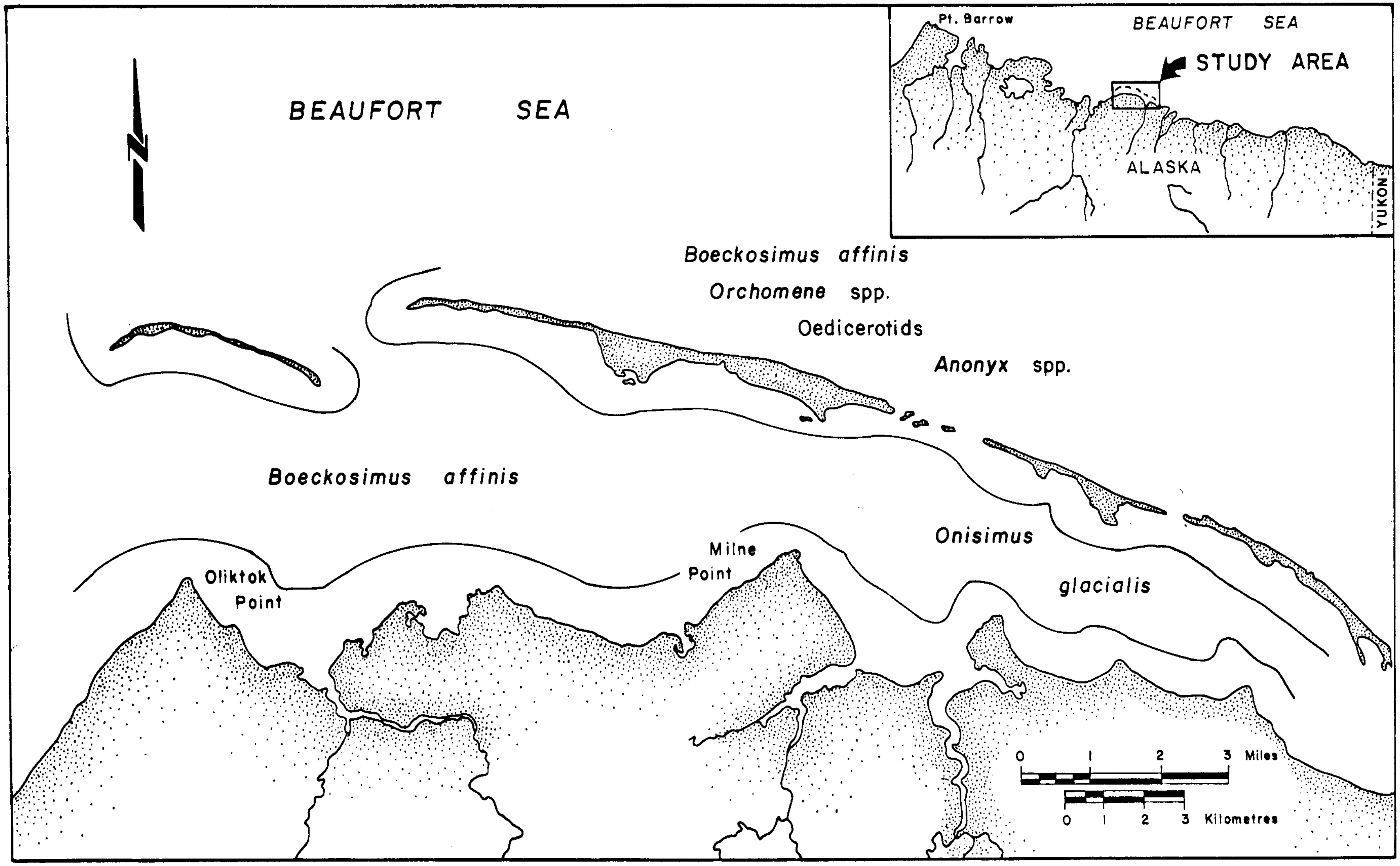

Figure 7. Schematic representation of late April-May distribution of major amphipod species in Simpson Lagoon and surrounding areas, 1979. Winter habitat is illustrated in Figure 6.

on the ocean side of the barrier islands and in the western portion of Simpson Lagoon (Table 9).

Between 5 and 7 June 1978, before river discharge reached the coast, baited amphipod traps were set under the ice at six sites in Simpson Lagoon and at one site offshore of the barrier islands (Fig. 6). Large *Onisimus glacialis* (8-10 mm) were the most abundant amphipods in collections from the lagoon, but on the ocean side of the barrier islands *Boeckosimus affinis* (8-10 mm) was the most abundant species (Table 9). The absence of newly-released young (2-4 mm) of these species is not fully understood; young may have different feeding habits than adults (i.e., plankton feeders vs scavengers) and thus are not attracted to meat-baited traps, or they may occupy a different habitat. Buchanan et al. (1977) reported large numbers of *Onisimus glacialis* and *O. litoralis* in the layer of soft ice on the ice undersurface in Bridport Inlet, Melville Island, N.W.T., in June. Similar observations of *Onisimus glacialis* were reported during May in Brentford Bay, Boothia Peninsula, N.W.T., by Thomson et al. (1978).

On 12 June 1978, after the peak of over-ice river runoff but before the nearshore fast ice lifted from the bottom, four baited amphipod traps were set in the shallow lead next to the mainland shore at Milne Point (Fig. 6). The intention was to determine the rate at which amphipods colonized previously frozen shoreline habitats. The traps were checked twice daily. No organisms were captured until 19 June, approximately 12 h after the land-fast ice had lifted from the bottom between the shore lead and the lagoon center. By 20 June, all four traps contained numerous large *Onisimus glacialis* (8-10 mm) but no small individuals; in addition, one *Mysis litoralis* (7.0 mm in length) was collected.

On 28 June 1978, divers observed that small mysids and amphipods (both 2-4 mm long) were abundant in the leads next to the mainland and on the lagoon and ocean sides of the barrier islands (Table 10). A few large mysids and amphipods were also observed near Milne Point at this time. On 7 July, four female mysids (1 *Mysis litoralis*, 3 *M. relicta*) that ranged from 11 to 16 mm in length and still brooding young (4-16 individuals per female; 2-4 mm in length) were collected just north of Milne Point in shore leads. In the central portions of the lagoon at

Table 10. Diver observations in leads inside and outside Simpson Lagoon on 28 June 1978.

Location	Substrate	Water Depth (m)	Visibility (m)	Observations
Milne Point	Tundra clumps sand and gravel	0.5	0.5	1 large mysid (1 cm), many small mysids (2 mm), many small amphipods (2-4 mm), a few large amphipods of several genera (*Onisimus*, *Pontoporeia*, *Gammarus*)
0.5 km lagoonward[†] from Milne Point	Soft sediments and sand	2.5	1.0	A few amphipods and some polychaetes
Mid-lagoon[†]	Soft sediments and sand	3.0	1.0	Many polychaete worms, many *Onisimus* amphipods, only one mysid, 3 tunicates, 3 isopods
Lagoon side of Bertoncini Island	Mostly sand	0.5	1.0	Numerous small mysids and amphipods. Most mysids were moving passively westward with the current (≈3 cm/s); those not moving were close to the substrate
Ocean side of Bertoncini Island	Fine sand, cobble bottom rippled with detritus in troughs	1.0	0.5	Amphipods of various sizes in water column; numerous small ones about 3 cm off bottom. Few large mysids but many small ones (2-4 mm) on the substrate

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[†] Dives were conducted through large holes in the ice.

this time, numerous small and large amphipods were seen, but only one large mysid (12-14 mm) and no small mysids were seen by divers. In 1977, from 17 June to 3 July, small (<5 mm) mysids and amphipods were noted in all the open leads around Pingok Island; however, no adults of either group were collected (Table 11 and Fig. 8).

In summary, the winter and spring results show that the nearshore areas of the Beaufort Sea are heavily utilized by a variety of mysid and amphipod species during the period of ice-cover. In the Simpson Lagoon area, *O. glacialis* was the primary species found in the shallow under-ice waters of the lagoon, whereas *B. affinis* was most abundant in deeper water on the ocean side of the barrier islands and in samples taken in the Harrison Bay region. It is uncertain whether this differential distribution is the result of preference or requirements. Several species of amphipod appear to utilize the nearshore areas through the entire ice-covered period, but both *Mysis litoralis* and *M. relicta* decreased in abundance as winter progressed. This decrease in mysid abundance may be due to one or a combination of emigration, out of the system, predation, or mortality (see below).

Samples collected in Simpson Lagoon during June of 1977 and 1978 and diver observations indicate that mysids recolonize the lagoon each spring during and immediately after breakup, apparently by moving in from the adjacent ocean along shallow shore leads next to the mainland and island beaches.

Winter Abundance and Biomass of Key Epibenthic Species

The winter abundance and biomass of important species of epibenthic invertebrates in Simpson Lagoon, Harrison Bay and Stefansson Sound are shown in Table 12. In November 1978, *M. litoralis* and *M. relicta* appeared to be distributed along the nearshore Beaufort Sea from Harrison Bay to Stefansson Sound (125 km) although *M. litoralis* was present in larger numbers than *M. relicta* (Table 12). By February 1979, the abundance and biomass of *M. litoralis* had decreased substantially in both Simpson Lagoon and Stefansson Sound (Harrison Bay was not sampled). By February the abundance and biomass of *M. relicta* in Simpson Lagoon had

Table 11. Numbers of mysids and amphipods collected in epibenthic trawl samples in nearshore leads around Pingok Island 17 June-3 July 1977.

	Site 1, 2		Site 3		Site 5		Site 6		Site 7		Site 8		Site 9	
	No/m^2		No/m^2		No/m^2		No/m^2		No/m^2		No/m^2		No/m^2	
Date	Amph.	Mysid	Amph.	Mysid	Amph.	Mysid	Amph.	Mysid	Amph.	Mysid	Amph.	Mysid	Amph.	Mysid
17/06/77	400	0	NA	NA	NA	NA	5	0	NA	NA	0	0	NA	NA
19/06/77	171	0	26	214	19	1	21	70	0	0	0	7	13	9
21/06/77	321	1	2	2	0	17	50	143	43	0	1	0	9	10
24/06/77	59	153	ice over	ice over	50	1414	ice over	ice over	9	68	NA	NA	ice over	ice over
26/06/77	221	1150	ice over	ice over	14	1571	ice over	ice over	100	7243	NA	NA	ice over	ice over
03/07/77	250	2985	50	6	129	1407	ice over	ice over	NA	NA	NA	NA	ice over	ice over

NA Data not available.

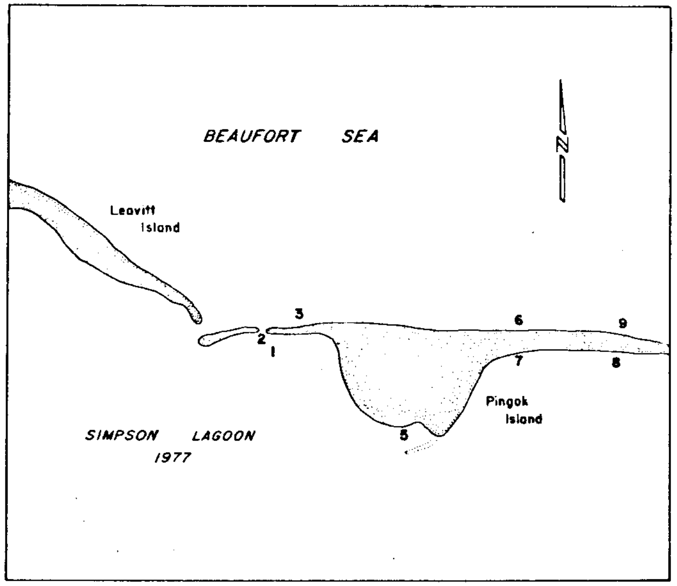

Figure 8. Epibenthic trawl sites in nearshore leads around Pingok Island 17 June-3 July 1977.

Table 12. Abundance (No. m^{-2}) and biomass (mg ash free dry weight m^{-2}) of important species of epibenthic invertebrates, 1978-1979. Based on 5 drop-net samples taken through 5 different holes at each sampling station on each date (Fig. 2). Holes were 100 ft apart.

		SIMPSON LAGOON				HARRISON BAY		STEFANSSON SOUND			
		November		February		November		November		February	
Species		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Mysis litoralis	$\bar{x}$	33.0	43.0	0.2	1.4	28.0	47.5	27.0	46.1	1.0	0.2
	SD	12.5	24.3	0.4	3.2	15.2	18.4	24.5	49.3	2.2	0.5
Mysis relicta	$\bar{x}$	10.0	14.5	5.0	4.0	2.0	8.1	2.0	0.3	0.0*	0.0*
	SD	8.7	9.4	3.5	5.6	2.7	11.2	4.5	0.6	0.0	0.0
Onisimus glacialis	$\bar{x}$	99.0	137.9	26.0	34.0	2.0	1.3	9.0	15.7	0.0	0.0
	SD	156.8	283.2	13.4	21.2	2.7	2.0	10.0	25.6	0.0	0.0

*Some present in amphipod traps, but none caught in drop-nets.

decreased, but not significantly (Mann Whitney U = 8, P = 0.210); no *M. relicta* were collected by drop net in Stefansson Sound in February, but some *M. relicta* were still present because some were captured in amphipod traps. Thus, as winter progressed, the density of *M. litoralis* declined in the nearshore shallow waters of the Beaufort Sea, while that of *M. relicta* declined in at least Stefansson Sound. The reasons for these reductions are not clear but may be related to one or more of the following:

1. emigration out of these areas triggered by changes in temperature and salinity, or by changing current patterns resulting from ice formation,
2. predation by marine species of fish (arctic cod, snailfish, etc.), and
3. mortality due to changing physical characteristics in the nearshore system.

In both November 1978 and February 1979 the amphipod *O. glacialis* was more abundant in Simpson Lagoon than in any of the other areas sampled (Table 12). This distributional trend is similar to the one reported above for the late winter samples of 1978 and the open-water season of 1978 (i.e., *O. glacialis* is most abundant in Simpson Lagoon). Although the abundance and biomass declined between November 1978 and February 1979, qualitative samples collected in May 1979 showed this species to be very abundant in Simpson Lagoon during late winter, particularly in the eastern section (Table 9, Fig. 7). During late winter the highest salinities (46-54%) occurred in areas of high *O. glacialis* abundance; salinities were more marine (30-35%) in areas of *B. affinis* abundance.

Open-Water Season Movements, Distributions and Abundances of Epibenthic Invertebrates

Drop net and Faber net samples were collected in a systematic temporal and spatial pattern during the open-water season of 1978 to determine movements, distributions and abundances of the key invertebrate species. The drop net was used to sample invertebrates near or on the bottom, and the Faber net sampled invertebrates higher in the water column. Results of both sampling methods are presented in Appendices 9 and 10. The results are expressed in terms of biomass (ash-free dry weight per m^2 for bottom samples or per m^3 for samples in the water column), since this measure, of the several available, most accurately describes the energy available to higher trophic levels (birds and fish) utilizing the system. By this measure, the two dominant groups of invertebrates, both in the water-column and associated with the bottom, were mysids and amphipods. However, it should be noted that if a smaller (0.240 mm) mesh size had been used, copepods would probably have comprised a larger portion of the collections.

General Distribution and Behavior of Epibenthic Invertebrates

Diver observations, both in 1977 and particularly in 1978, have produced an overall picture of the distributions and behavior of invertebrate organisms in Simpson Lagoon. Generally, divers have found that epibenthic invertebrates (mysids and amphipods) are concentrated on or within 0.5 m (usually within 10-20 cm) of the bottom even during calm conditions (Fig. 9). A comparison of drop net (No/m^2) and Faber net results (converted to No/m^2) showed that the key invertebrate species were generally at least an order, and at times two to three orders, of magnitude more abundant on the bottom than in the water-column (Fig. 10).

In the lagoon, mysids rested on and within the detrital layer and seemed closely associated with the bottom. In areas swept by more rapid currents (Stations 5 and 6), mysids tended to concentrate behind bottom irregularities or in depressions where water velocities were reduced. When startled, mysids moved rapidly in a horizontal direction from the disturbance. They appeared to respond more to mechanical stimuli (i.e., water motion) than to visual clues.

Amphipods were more commonly associated with detrital material and soft sediments than with sand substrate. Generally, amphipods were observed to crawl or burrow into soft detrital material; if the detritus were disturbed, larger numbers of amphipods became visible. In swift currents, amphipods tended to collect in depressions and behind ridges and, if disturbed, they showed the same escape response exhibited by mysids.

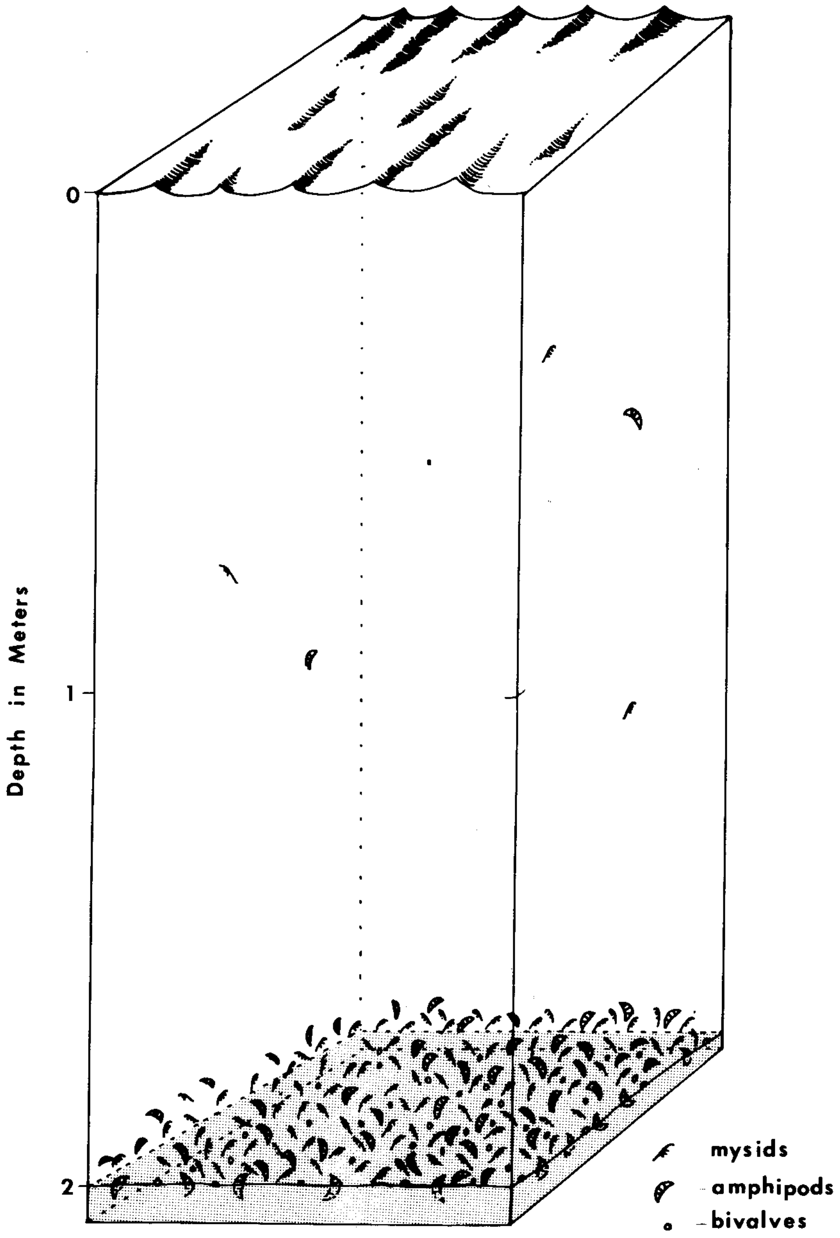

Figure 9. Schematic diagram showing relative abundances of invertebrates on or near the bottom and in the water column.

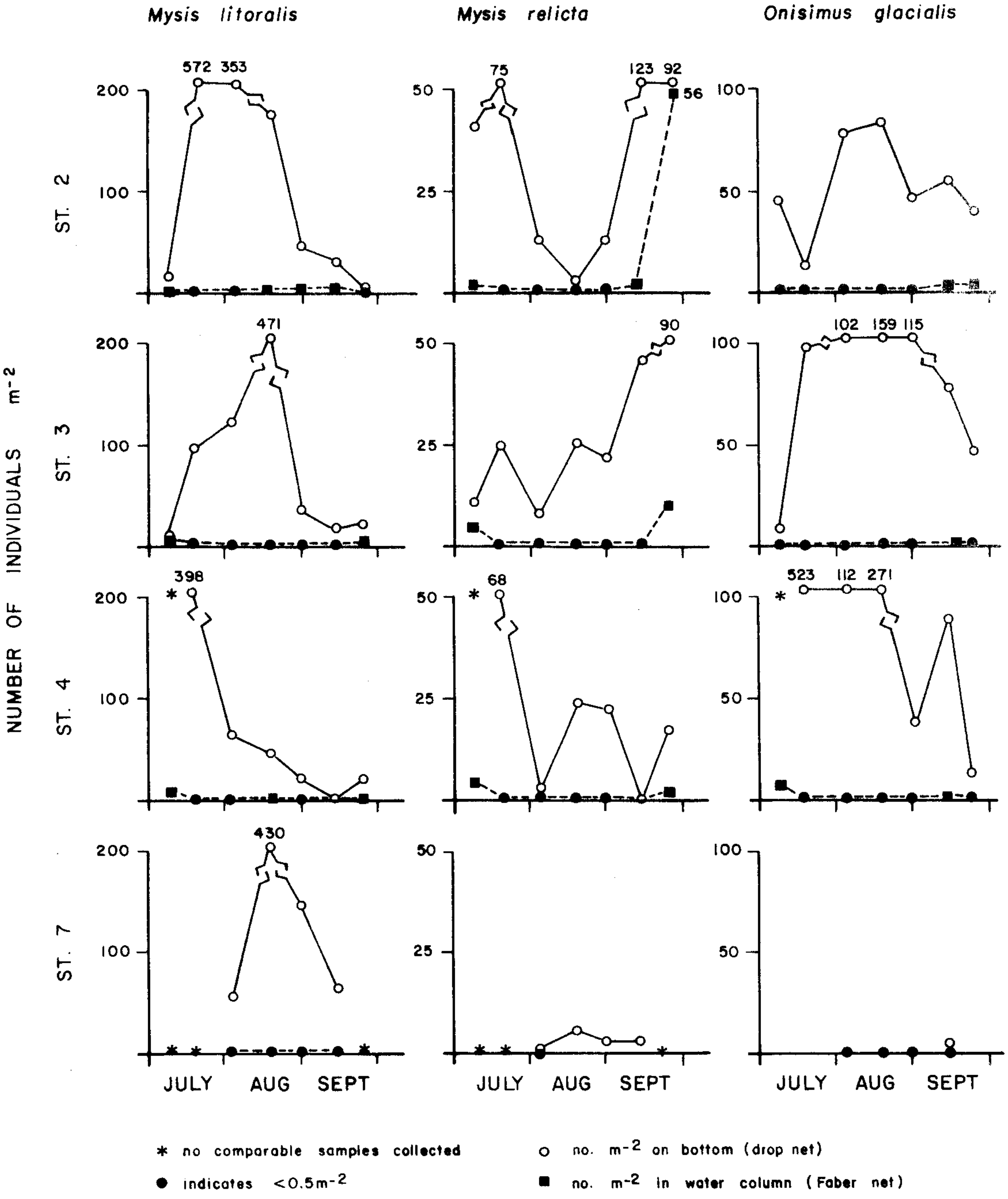

Figure 10. Comparison of numbers m^{-2} near the bottom and in the water-column for key invertebrate species in the Simpson Lagoon area, 1978. Water column values are no. m^{-3} from Faber net multiplied by water depth.

In the following analyses, the biomasses estimated in 1978 were transformed to natural logarithms and the data were analyzed using two-way analyses of variance for unequal sample sizes; collection period and location were the two factors. Specific comparisons among and between stations were done using orthogonal comparisons. However, in the case of sampling periods, specific comparisons were based on Duncan's multiple range test as planned orthogonal comparisons were not feasible. Results based on these methods are, for the most part, similar to those based on non-parametric analyses of the same data after pooling of replicates (Griffiths and Dillinger 1979). Emphasis is placed on the 1978 data because these were more reliable than 1977 data (see 'Limitations and Biases'). However, the 1977 results are mentioned below where relevant.

Mysids

Mysids were very abundant in the study area and were the major food item of vertebrate consumers in the system. Two species, *Mysis litoralis* and *M. relicta*, were identified in 1978 samples. Other preserved specimens, identifiable only as *Mysis* sp. because of the absence of diagnostic characteristics, were most likely one or the other of the identified species.

Mysids Near the Bottom. Mysid biomasses near the bottom at the seven standard stations during seven 1978 sampling periods are shown in Appendix 10 and Figs. 11-13 and compared in Tables 13 and 14. When all stations (1-7) and sampling periods are considered, the biomasses of both species of mysid and total mysid biomass showed significant differences among stations, and among sampling periods (Table 13 and Fig. 11). A comparison of lagoon vs ocean stations showed no significant differences for *M. litoralis* or total mysid biomasses, but the biomass of *M. relicta* (a brackish water species) was significantly higher at lagoon stations (Table 14, Fig. 12). At Station 7 (deep ocean), the biomasses of *M. litoralis*, *M. relicta* and total mysids were significantly higher than those at Station 6 (nearshore shallow ocean), possibly due to the unstable nature of the habitat at Station 6 (i.e., frozen during winter and ice-scoured in summer).

DROP NET

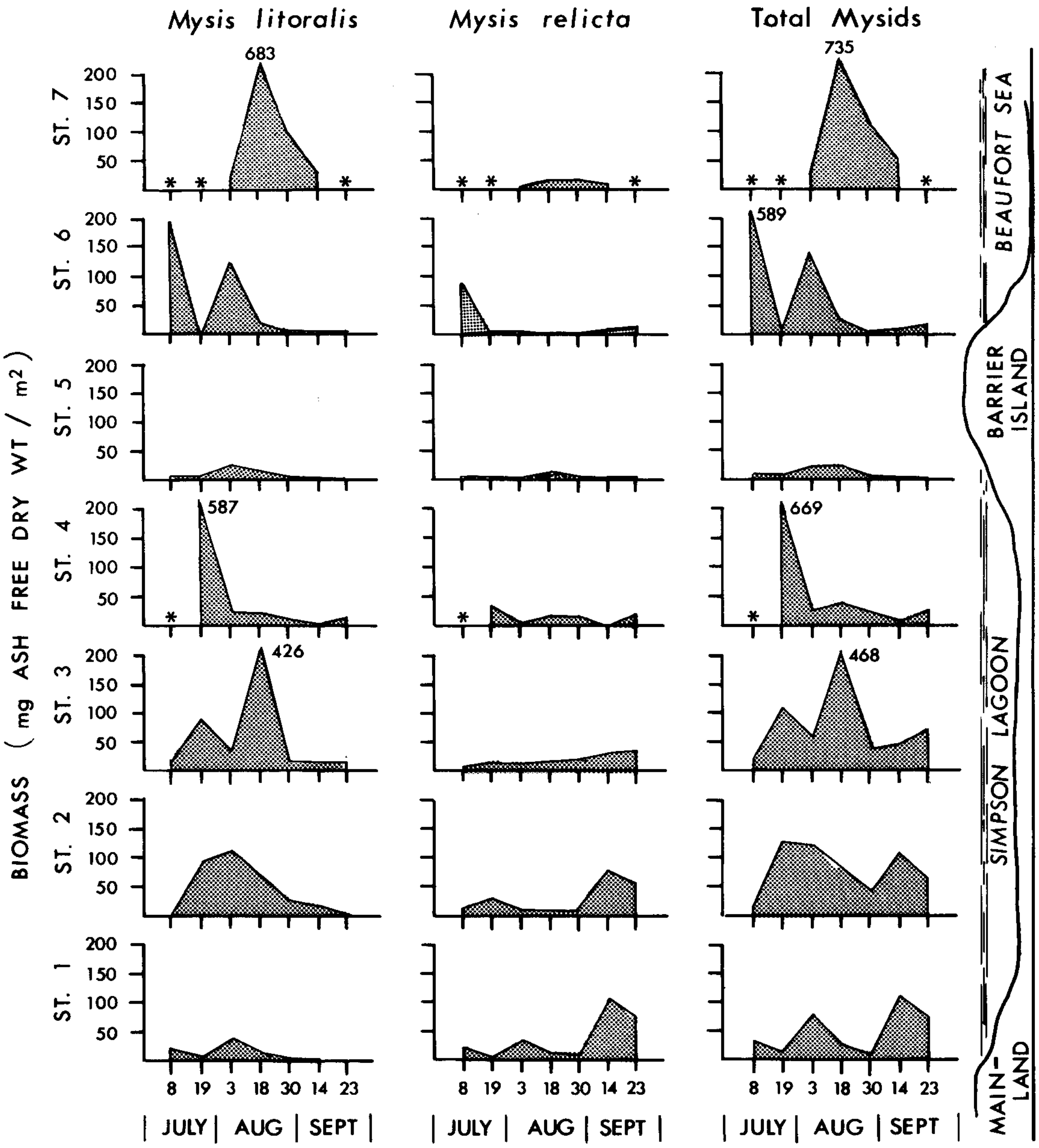

Figure 11. Biomass of mysids near the bottom in relation to date and sampling station. Each data point is a mean of five drop-net samples collected in or near Simpson Lagoon during 1978. * indicates no samples collected.

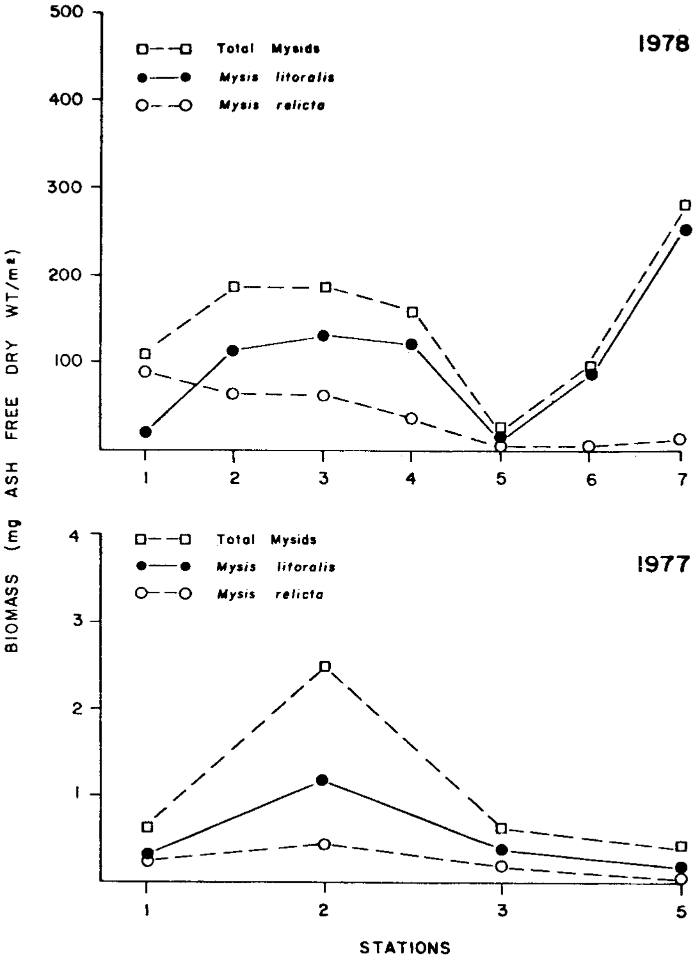

Figure 12. Biomass of mysids near the bottom of various sampling stations in and near Simpson Lagoon in 1977 and 1978. Each 1978 data point is a mean of five drop-net samples for each sampling date. Station 78 1-5 based on seven sampling periods (8 July-23 September), Stations 78-6 and 7 based on four sampling periods (3 August-14 September). The 1977 data are recalculated from Griffiths and Craig (1978). Because different sampling techniques were used in the two years, only general trends can be compared.

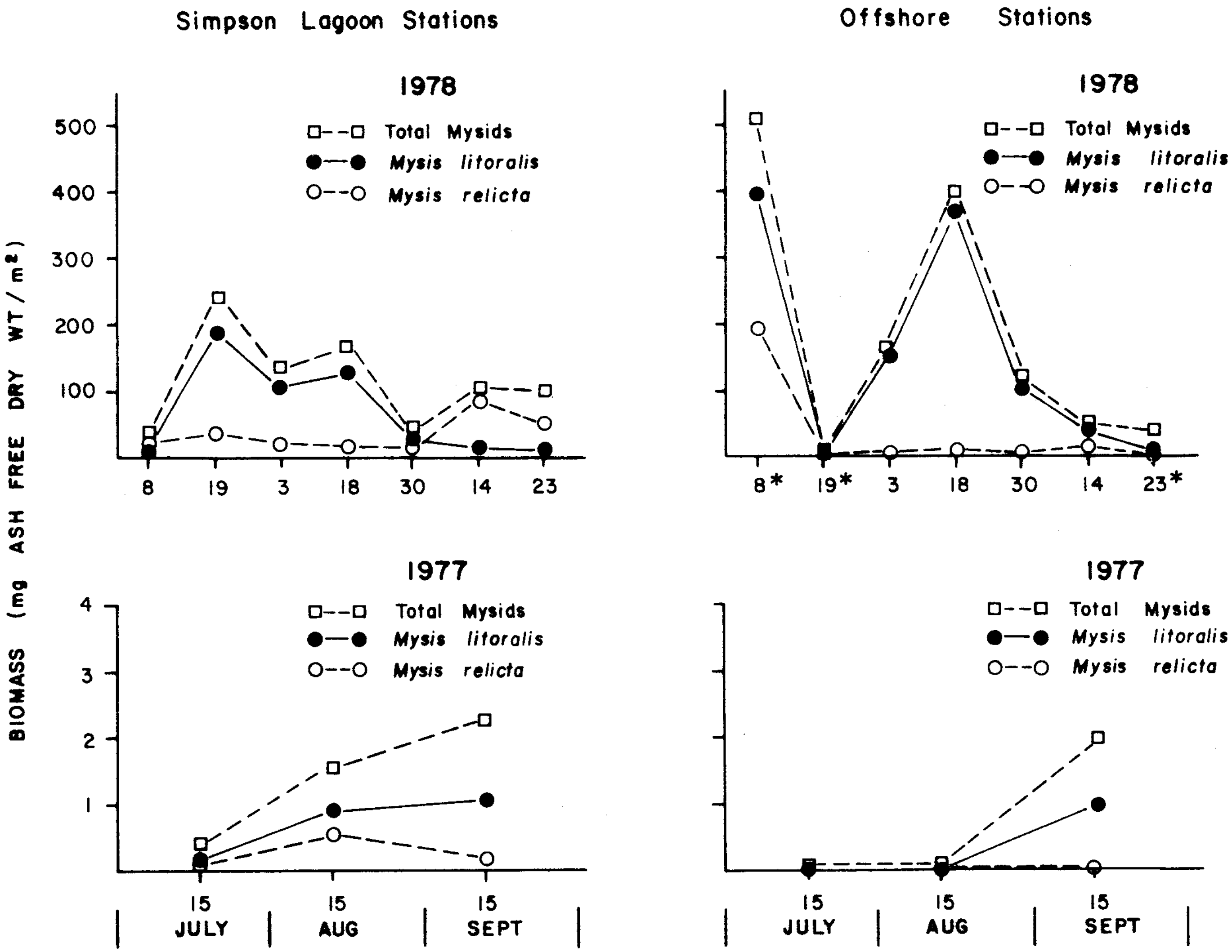

Figure 13. Biomass of mysids near the bottom of lagoon and offshore stations in relation to date 1977 and 1978. Each 1978 data point is a mean of five drop-net samples from each station on each date. The 1977 data are recalculated from Griffiths and Craig (1978). Because of different sampling techniques used in the two years, only general trends can be compared. * indicates no samples collected at 1978 station 7 on these dates.

Table 13. Comparisons of mysid biomass near the bottom (ln mg ash-free dry weight m^{-2}), all stations (1978 1 through 7) and all sampling periods (8 July-23 September) considered. Data analyzed using two-way analysis of variance for unequal sample size.

Species	Among Stations F value (d.f.=6,32)	Among Stations P	Among Sampling Periods F value (d.f.=6,32)	Among Sampling Periods P
Mysis litoralis	11.14	<<0.001	21.47	<<0.001
Mysis relicta	18.02	<<0.001	3.98	<0.01
Total mysids	19.36	<<0.001	10.01	<<0.001

Table 14. Planned orthogonal comparisons for mysid biomass (ln mg ash-free dry weight m^{-2}) near the bottom using 1978 stations.

Stations Compared	Habitat Types	All Stations (1-7)[+] F values d.f.=1,112 *Mysis litoralis*	All Stations (1-7)[+] F values d.f.=1,112 *Mysis relicta*	All Stations (1-7)[+] F values d.f.=1,112 Total Mysid	Lagoon Stations (1-5)[++] F values d.f.=1,143 *Mysis litoralis*	Lagoon Stations (1-5)[++] F values d.f.=1,143 *Mysis relicta*	Lagoon Stations (1-5)[++] F values d.f.=1,143 Total Mysid
6,7 vs 1-5	Ocean vs Lagoon	0.11 P=0.74	52.84 P<<0.001	0.83 P=0.36	-	-	-
6 vs 7	Nearshore Ocean vs Offshore Ocean	22.50 P<<0.001	7.18 P<0.001	52.24 P<<0.001	-	-	-
1,5,vs 2, 3,4	Shallow Nearshore vs Central Lagoon	-	-	-	74.31 P<<0.001	19.23 P<<0.001	94.95 P<<0.001
1 vs 5	Mainland Nearshore vs Barrier Is. Nearshore	-	-	-	1.64 P=0.20	46.38 P<<0.001	76.17 P<<0.001
3 vs 2,4	Central Lagoon vs Intermediate Depths	-	-	-	1.97 P=0.16	1.08 P=0.30	2.68 P=0.10

[+] Only sampling periods 3 August through 14 September used in comparisons.

[++] Only sampling periods 19 July through 23 September used in comparisons.

Within the lagoon, the biomasses of *M. litoralis*, *M. relicta* and total mysids were significantly higher at mid-lagoon stations (2, 3 and 4) than at the shallow nearshore stations (1 and 5), indicating that all species of mysid preferred the deeper (>1.2 m) central portion of the lagoon (Table 14, Fig. 12). The biomasses of *M. relicta* and total mysids were significantly higher at Station 1 (nearshore mainland) than at Station 5 (nearshore barrier island) (Table 14, Fig. 12). This trend, and the relatively low biomass of *M. relicta* at the ocean stations (6 and 7), indicate that this species prefers the lagoon habitat, possibly due to its warmer temperatures and lower salinities. There were no significant differences among mysid biomasses at any of the central lagoon stations (2, 3 and 4).

When all sampling periods (19 July-23 September) are considered, the biomasses of both species of mysid and also of total mysids differed significantly among periods (Table 13). *Mysis litoralis* biomass decreased sharply (particularly after 18 August 1978) at both offshore and lagoon stations (Fig. 13), possibly due to a combination of predation and a net emigration from the lagoon (see later sections). Overall *Mysis relicta* biomass was highest on 19 July (mainly due to Station 6) and 23 September (due to lagoon Stations 1-5) but showed no differences* among the other sampling dates (19 July through 14 September) (Fig. 13). The reasons for these early and late peaks are not clearly understood at present. Total mysid biomass was highest from early to mid-season (19 July to 18 August) and lowest near the end of the season (30 August and 14 September) (Fig. 13). In general total mysid biomass followed the pattern of *M. litoralis* biomass, since the latter was the dominant mysid in the system; however, on 23 September *M. litoralis* biomass was at its lowest value during the open-water season but total mysid biomass did not show as sharp a decline because *M. relicta* biomass reached a late season peak (Fig. 13).

Although direct comparisons between 1978 and 1977 results are not possible, since different collection techniques were used, general trends can be compared (Figs. 12 and 13). For lagoon stations, the

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*Comparisons among sampling periods were done using Duncan's multiple range test, where $\alpha = 0.05$.

biomasses of *M. litoralis* and of total mysids followed similar patterns. In both years, both of the biomasses were highest in the deep central lagoon. *Mysis relicta* biomass tended to be highest near the mainland in 1978, but not in 1977. *Mysis relicta* biomass was low at offshore stations (Station 77-5 and 78-7) in both years (Fig. 12). However, *M. litoralis* (and consequently total mysid) biomass tended to be higher at offshore stations, in relation to the lagoon, in 1978 than in 1977 (Fig. 12).

A comparison of biomasses among dates shows marked differences in trends between the two years for *M. litoralis*, *M. relicta* and total mysids at both lagoon and offshore stations (Fig. 13). In 1977, *M. litoralis* biomass and total mysid biomass within the lagoon increased as the season progressed. However, at the offshore stations the increase was noted only at the end of the season. In contrast, during 1978, these biomasses showed significant decreases at both lagoon and offshore stations late in the open-water season. *Mysis relicta* biomass, which was almost always low at offshore stations, decreased in the lagoon toward the end of the 1977 season, but increased in the lagoon late in the 1978 season. The reasons for these different trends are unclear, but could represent between-year variations.

In summary, in 1978 there appeared to be a marked reduction in *M. litoralis* biomass near the end of the open-water season; however, the biomass of *M. relicta* showed an increase at lagoon stations during the same period. Thus, emigration, rather than predation appeared to be the main cause for the decrease in *M. litoralis* biomass, since it seems unlikely that predators would select between these two similar species. Mysid distribution within the lagoon was similar in both years but markedly higher *M. litoralis* biomass was found at offshore stations in 1978 than in 1977.

Mysids in the Water-Column. Mysid biomasses in the water-column at the four stations sampled by Faber net during seven 1978 sampling periods are shown in Appendix 9 and Figs. 14-17 and are compared in Table 15. The 1978 biomass estimates of *M. litoralis*, *M. relicta* and total mysids varied widely among stations and dates throughout the open-water period. Neither the differences among lagoon stations nor among

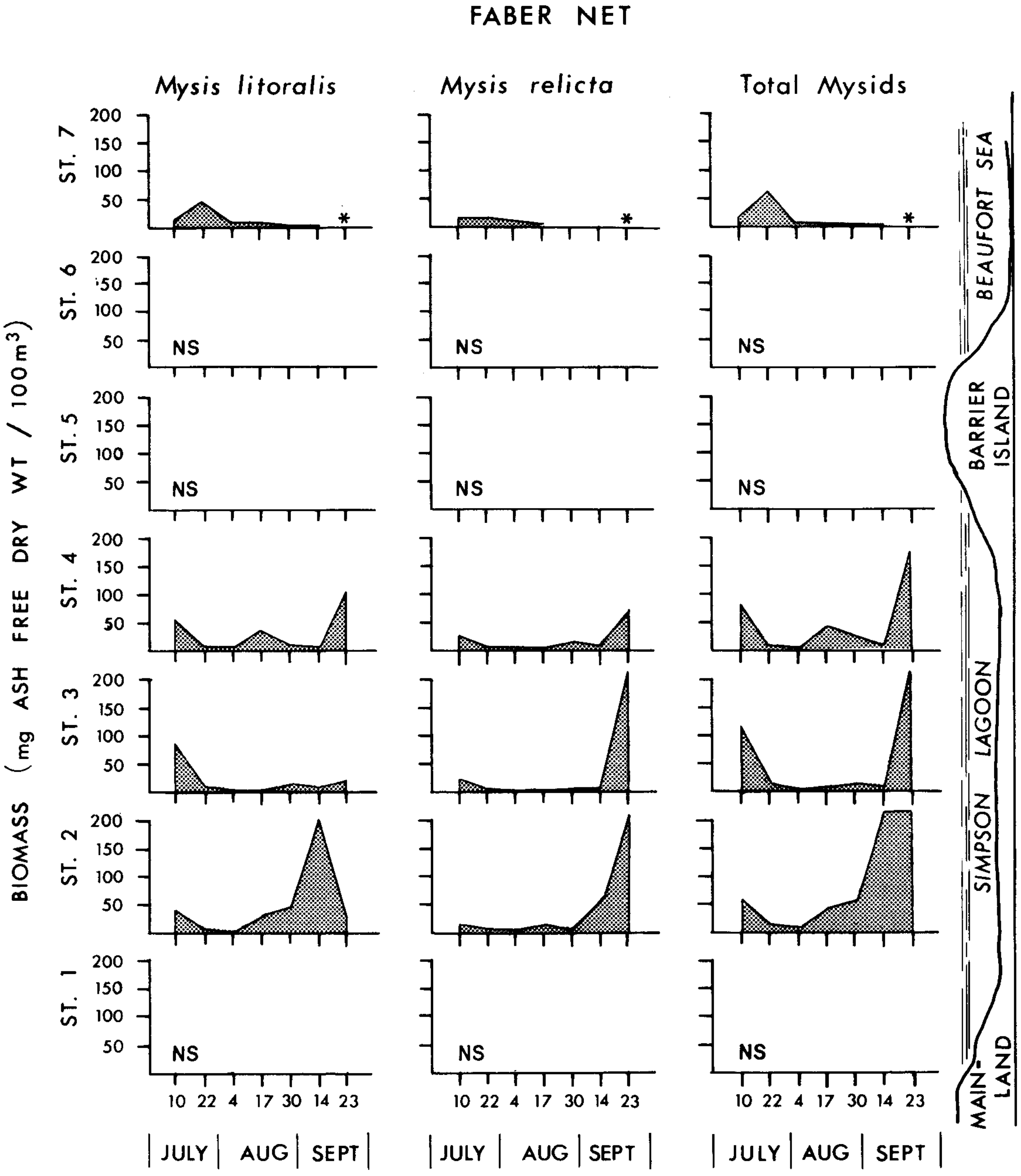

Figure 14. Biomass of mysids in the water-column in relation to date and sampling station. Each data point is a mean of three Faber net samples collected in and near Simpson Lagoon during 1978. * indicates no samples collected. NS indicates these stations not sampled due to shallowness of the water.

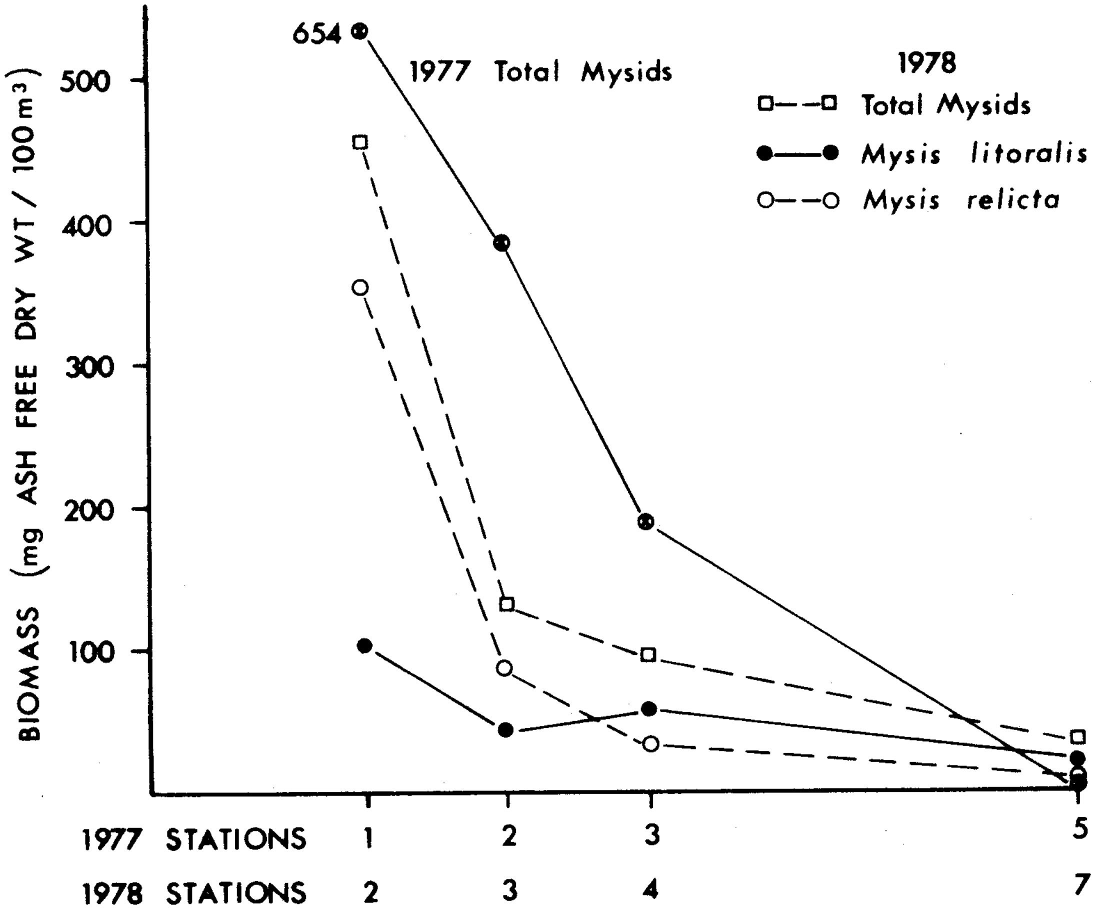

Figure 15. Biomass of mysids in the water-column at various sampling stations in and near Simpson Lagoon in 1977 and 1978. Each 1978 data point is the mean from three Faber net samples for each of seven collection periods. The 1977 data are recalculated from Griffiths and Craig (1978). In 1977 only total mysid biomass was available.

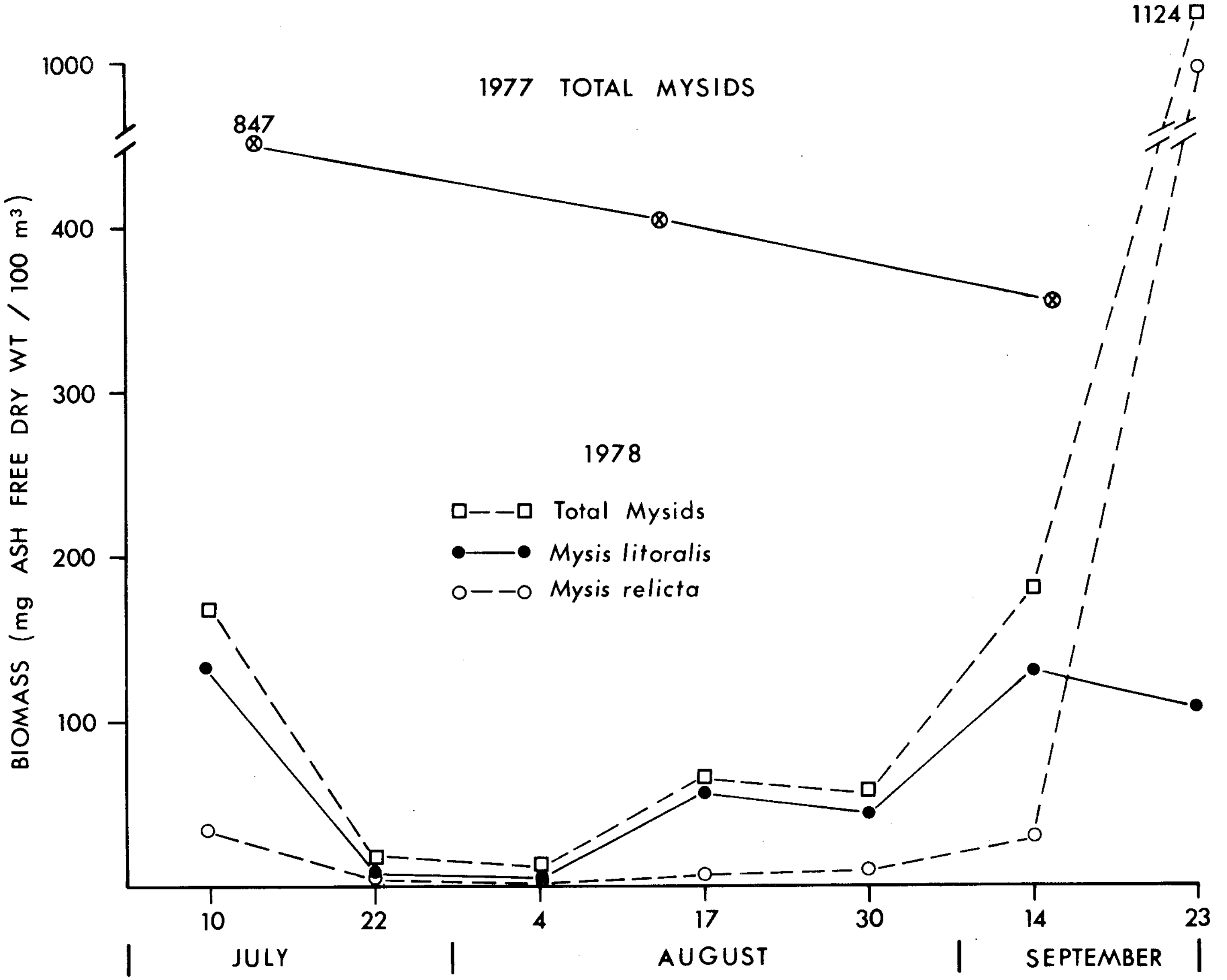

Figure 16. Biomass of mysids in the water-column at lagoon stations in Simpson Lagoon in relation to date in 1977 and 1978. Each 1978 data point is the mean from three Faber net samples for each station on each date. The 1977 data are recalculated from Griffiths and Craig (1978). In 1977 only total mysid biomass was available.

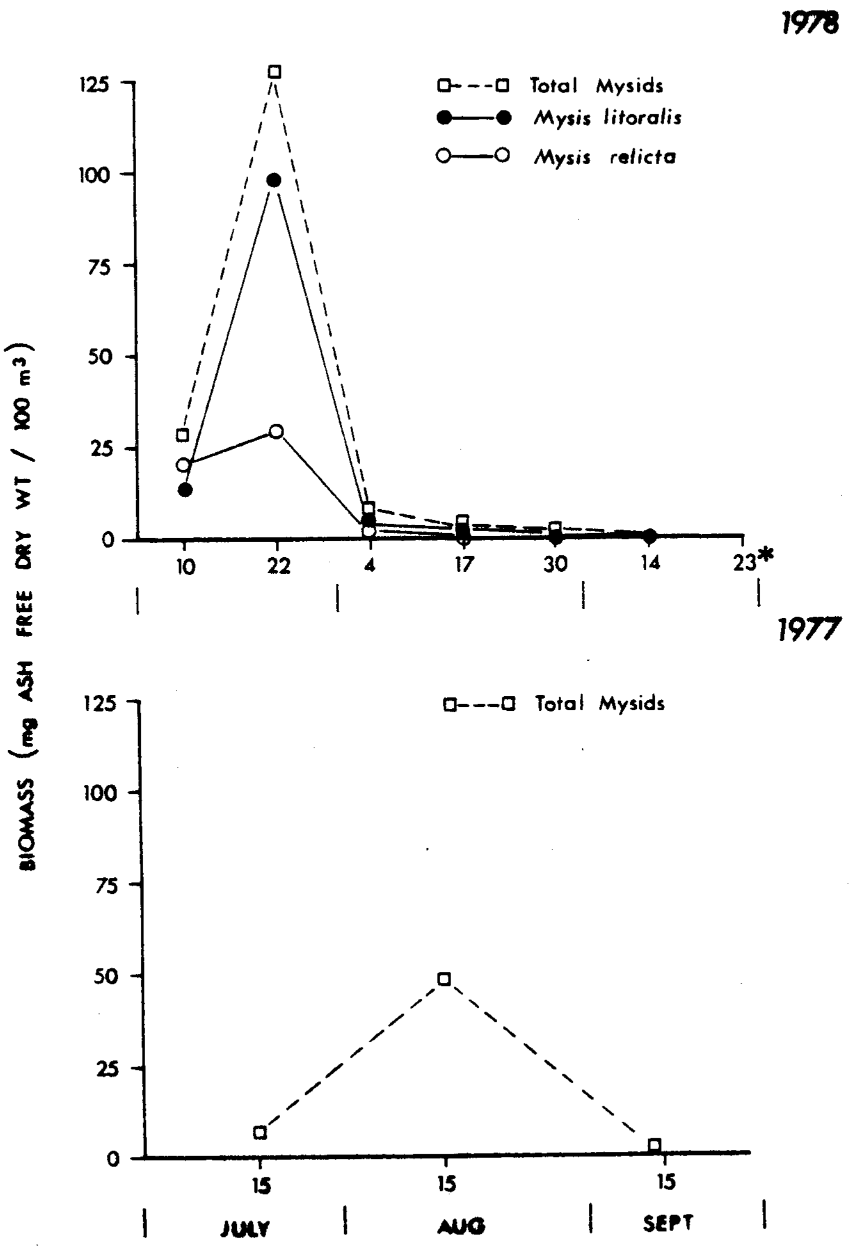

Figure 17. Biomass of mysids in the water column at offshore stations in Simpson Lagoon in relation to date in 1977 and 1978. Each 1978 data point is a mean of three Faber samples from each station on each date. The 1977 data are recalculated from Griffiths and Craig (1978). In 1977 only total mysid biomass was available. * indicates that no samples were collected on this date at Station 7.

Table 15. Comparisons of 1978 mysid biomass in the water column (ln mg ash-free dry wt. 100 m^{-3}), in relation to station and sampling period 1978. Data analyzed using two-way analysis of variance. Each station/date value was the mean of three Faber net hauls at the station during the sampling period.

	All Stations (2,3,4,7)		Lagoon Stations (2,3,4)	
Species	F value Among Stations (d.f.=3,15)	F value Among Periods[+] (d.f.=5,15)	F value Among Stations (d.f.=2,12)	F value Among Periods[++] (d.f.=6,12)
Mysis litoralis	1.77 $P>0.05$	2.14 $P>0.05$	1.94 $P>0.05$	5.12 $P<0.01$
Mysis relicta	1.10 $P>0.05$	2.29 $P>0.05$	2.53 $P>0.05$	9.54 $P<0.01$
Total mysids	1.82 $P>0.05$	2.41 $P>0.05$	3.51 $P>0.05$	10.79 $P<0.01$

[+] Only sampling periods 10 July-14 September 1978 used in comparisons.

[++] All sampling periods 10 July-23 September 1978 used in comparisons.

the combined lagoon and offshore stations were statistically significant (Table 15, Figs. 14 and 15). However, *M. relicta* was most common at lagoon Stations 2 and 3, and it was rare at Station 7 seaward of the barrier islands (Fig. 15). No *M. relicta* were found in offshore samples taken after 17 August (the offshore marine station was not sampled on 23 September), but during this same late-season period *M. relicta* biomass increased markedly at the lagoon stations (Fig. 16).

When all stations were considered together, mysid biomasses in the water-column did not differ significantly among sampling periods (Table 15). However, when only the lagoon stations (2, 3 and 4) were considered, there were significant differences among collection periods (Table 15, Fig. 16). *Mysis litoralis* biomass was greater in the lagoon on 10 July than on 4 August ($P < 0.05$, Duncan's multiple range test), and *M. relicta* and total mysid biomasses were markedly higher on 23 September than on 4 August ($P < 0.05$). Although there were insufficient data to statistically compare biomasses during various sampling periods at the one offshore station, from Fig. 17 it appears that the biomass for all mysids was high early in the season and then declined dramatically to negligible levels after 4 August. These results are generally consistent with the concept that, at least in the lagoon, mysids are most abundant in the water-column during the periods soon after breakup and just before freeze-up.

Comparisons of these data with 1977 results are limited to total mysid biomass, not biomasses of individual species because mysids collected in the water-column by Faber net in 1977 were not identified to species. Offshore biomass was lower than nearshore biomass in both years (Fig. 15); the differences among stations were significant in 1977 (Friedman $\chi^2 = 6.49$, $P < 0.05$, $k = 3$) but not in 1978. In 1977, total mysid biomass generally decreased during the course of the season at lagoon stations but showed a mid-season peak at the offshore station (Figs. 16 and 17). In 1978, it generally increased at lagoon stations and decreased markedly at offshore stations as the season progressed (Figs. 16 and 17). The pronounced increase in total mysid biomass at lagoon stations during the last collection period of 1978 occurred largely because of the increase of *M. relicta* biomass (Fig. 16).

In summary, mysids were much more abundant near the bottom than in the water-column at both lagoon and offshore stations (Fig. 10). The wide variations in mysid biomass among stations and collection periods in both water-column and benthic habitats (in 1977 and 1978) suggests that there may be both uneven distribution and rapid rates of movement of these organisms within the nearshore system. The occurrence of rapid movements is further indicated by the apparent immigrations of mysids into the lagoon during early summer (see 'Transport of Invertebrates' and 'Late Winter and Spring').

Amphipods

The amphipod species collected in 1977 and 1978 were known from previous studies to occur along the Alaskan Beaufort Sea coast (MacGinitie 1955; Crane 1974; Feder and Schamel 1976; Feder et al. 1976b). In 1977, all amphipods collected both near the bottom and in the water-column were identified to species (Griffiths and Craig 1978). In 1978, only those amphipods that comprised a significant portion of the samples or contributed significantly to the stomach contents of birds and fish were analyzed to the species level.

Amphipods Near the Bottom. Amphipods near the bottom were collected by drop nets at the seven standard stations during each sampling period of 1978, weather and ice conditions permitting. The results are shown in Appendix 10 and Figs. 18-21 and are compared in Tables 16 and 17. It is apparent from these figures that *O. glacialis* was by far the most important amphipod in the lagoon on a biomass basis; it was also one of the most important species to birds and fish (Johnson and Richardson 1980; Craig and Haldorson 1980). Only *O. glacialis* and *Gammarus setosus* were collected in sufficient numbers to allow for statistical analyses. However, the seasonal trends of three other amphipod species (*Halirages mixtus*, *Pontoporeia affinis* and *Parathemisto* sp.) are of sufficient interest to deserve comment.

Two-way analyses of variance for unequal sample size, for all seven stations and sampling periods showed significant among-station differences in biomasses of total amphipods and the two amphipod species

DROP NET

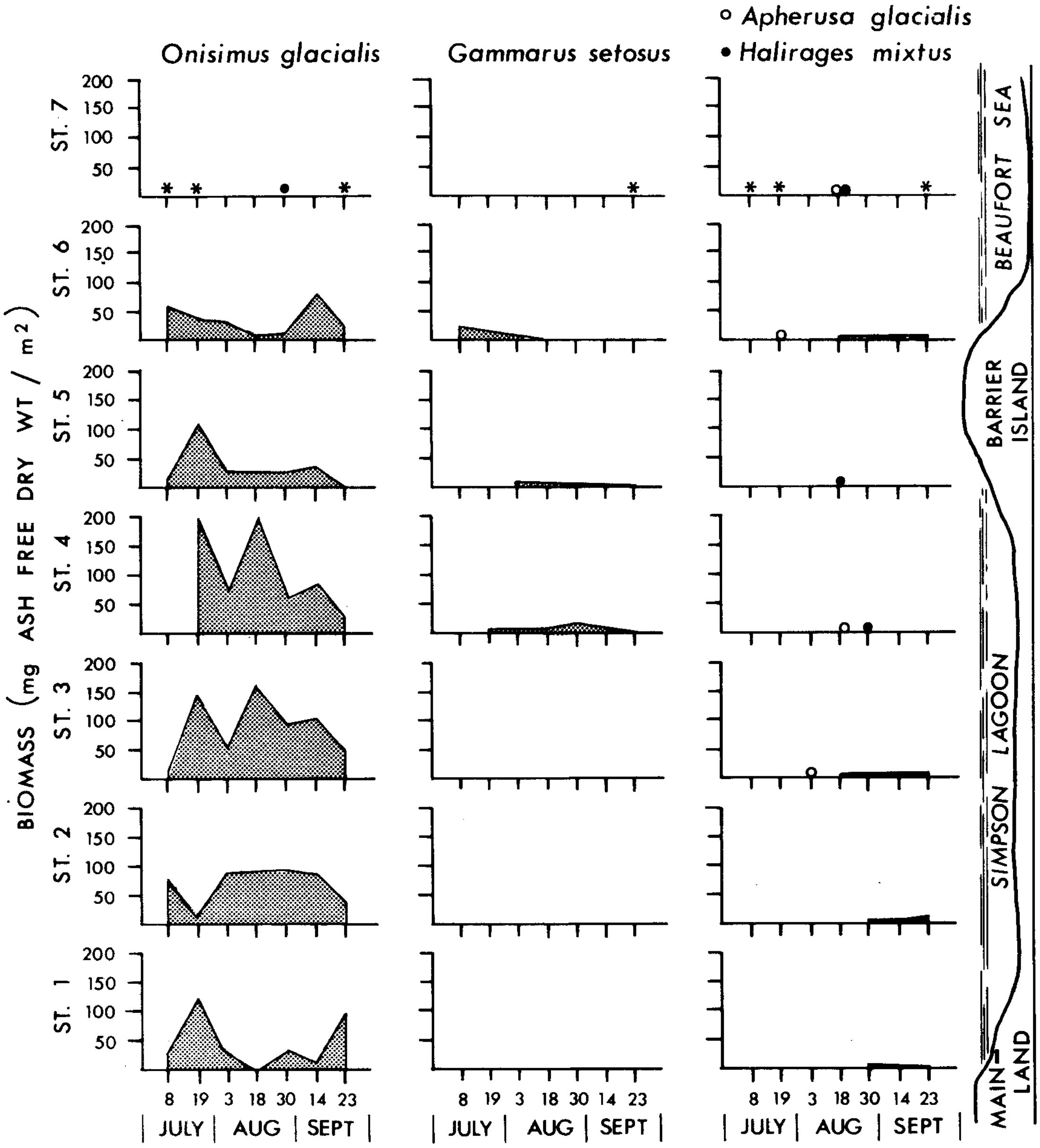

Figure 18. Biomass of amphipods near the bottom in relation to date and sampling station. Each data point is a mean of five drop-net samples collected in or near Simpson Lagoon, 1978. * indicates no samples collected.

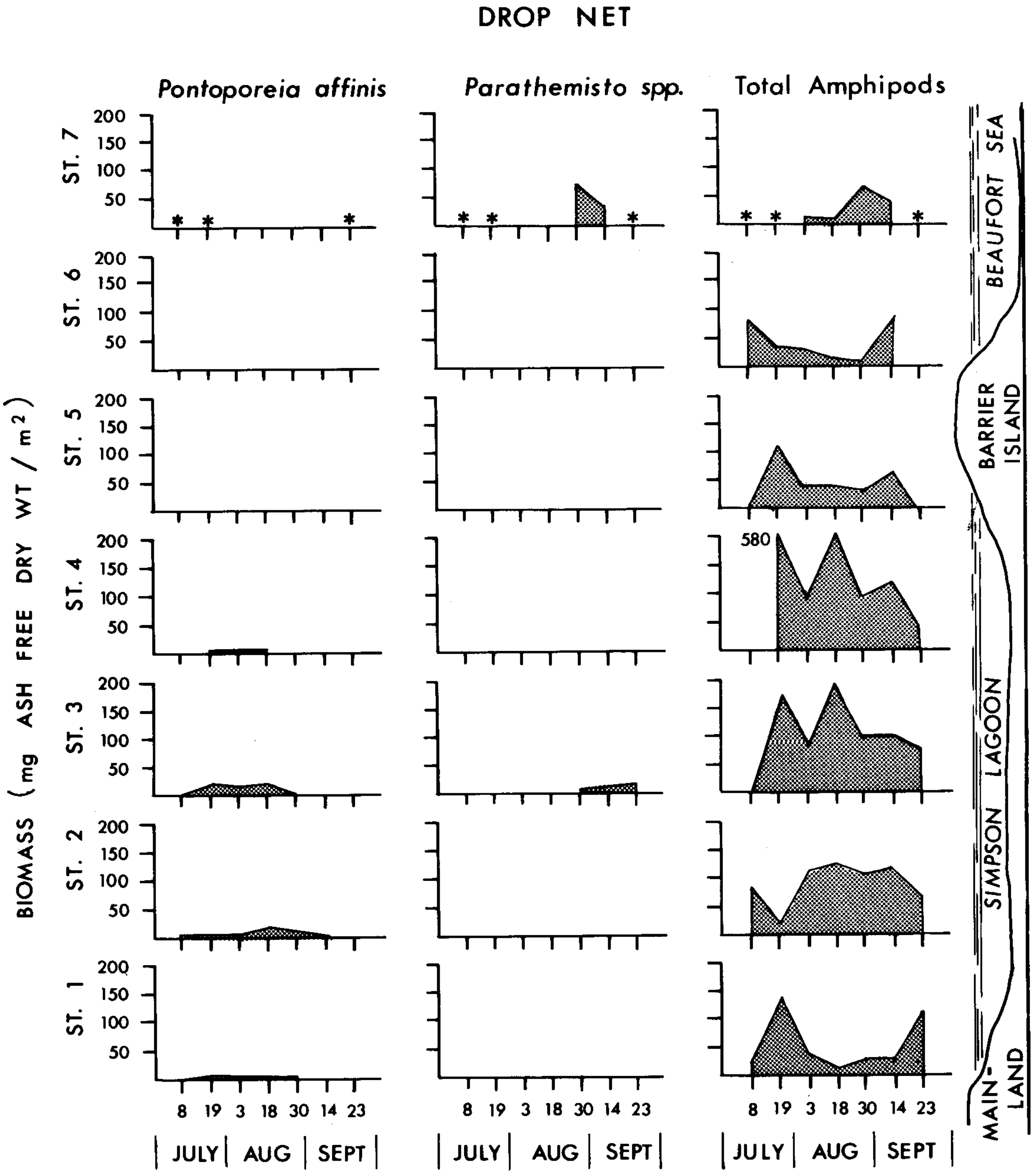

Figure 18 (continued).

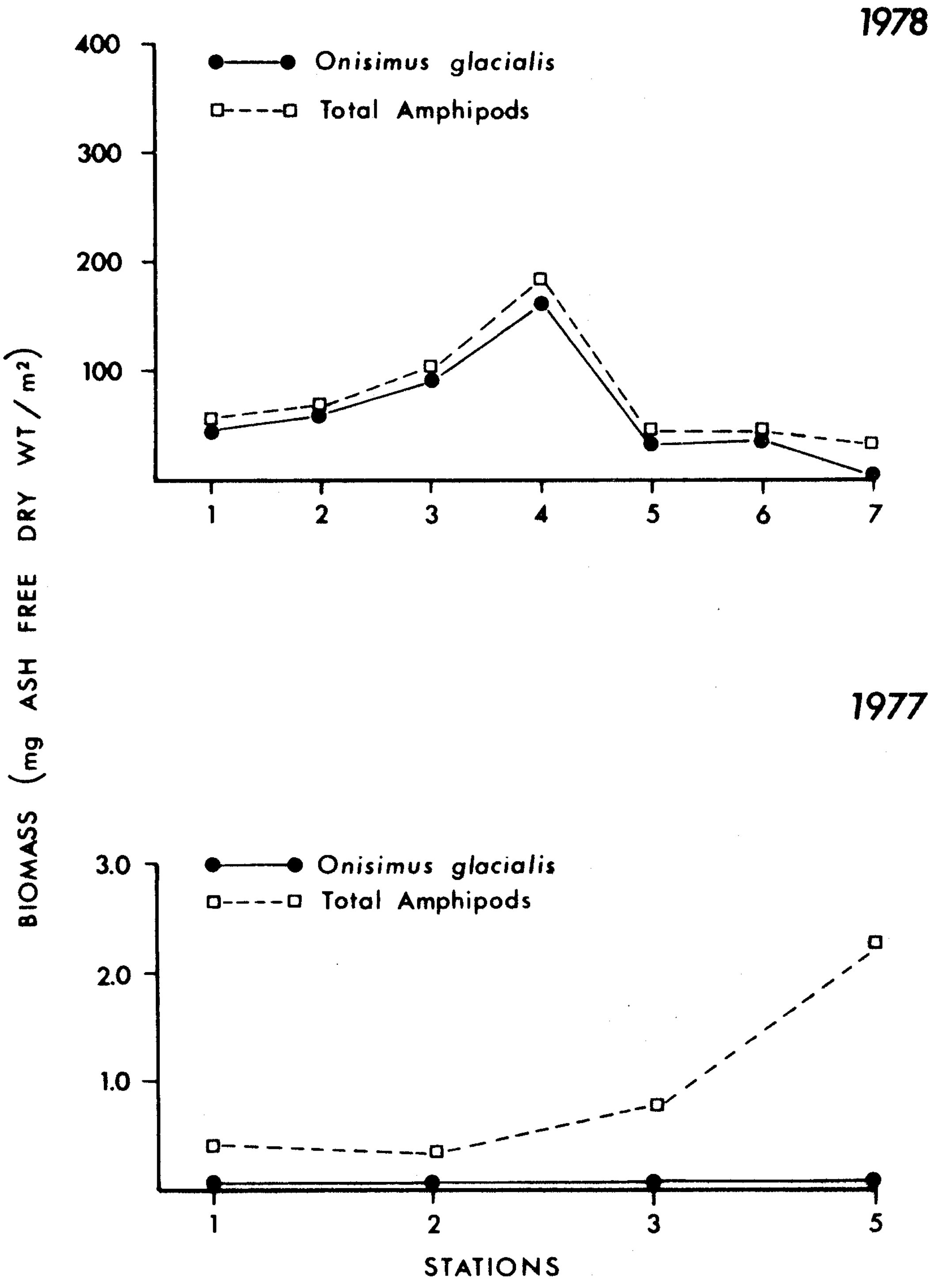

Figure 19. Biomass of amphipods near the bottom at various sampling stations in 1977 and 1978. Each 1978 data point is a mean of five drop-net samples for each sampling date Stations 78 1-5 based on seven sampling periods (8 July to 23 September), Stations 78-6 and 7 based on four sampling periods (3 August-14 September). The 1977 data are recalculated from Griffiths and Craig (1978). Because different sampling techniques were used in the two years, only the general trends can be compared.

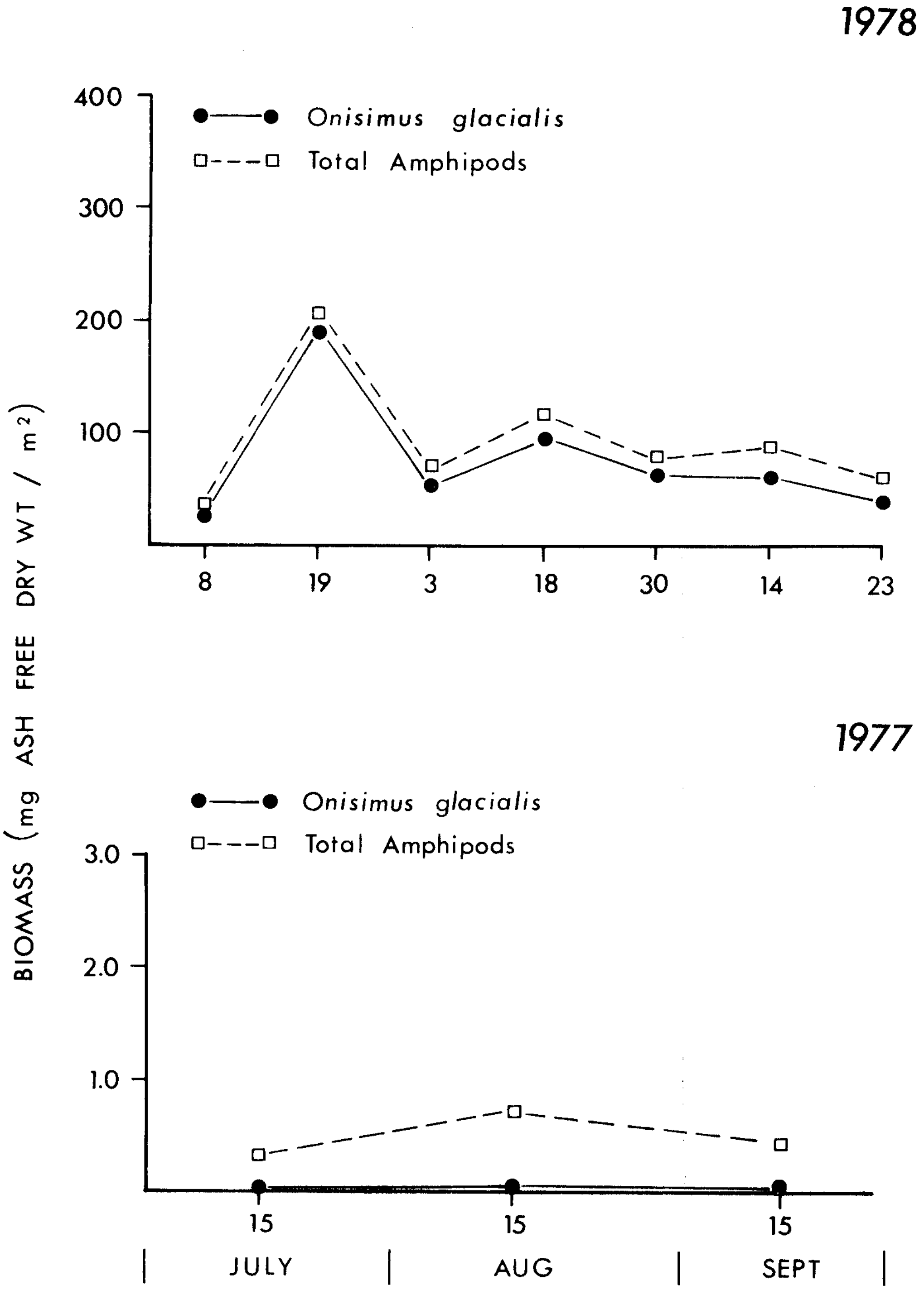

Figure 20. Biomass of amphipods near the bottom at lagoon stations in Simpson Lagoon in relation to date in 1977 and 1978. Each 1978 data point is a mean of five drop-net samples from each station on each date. The 1977 data are recalculated from Griffiths and Craig (1978). Because different sampling techniques were used in the two years, only general trends can be compared.

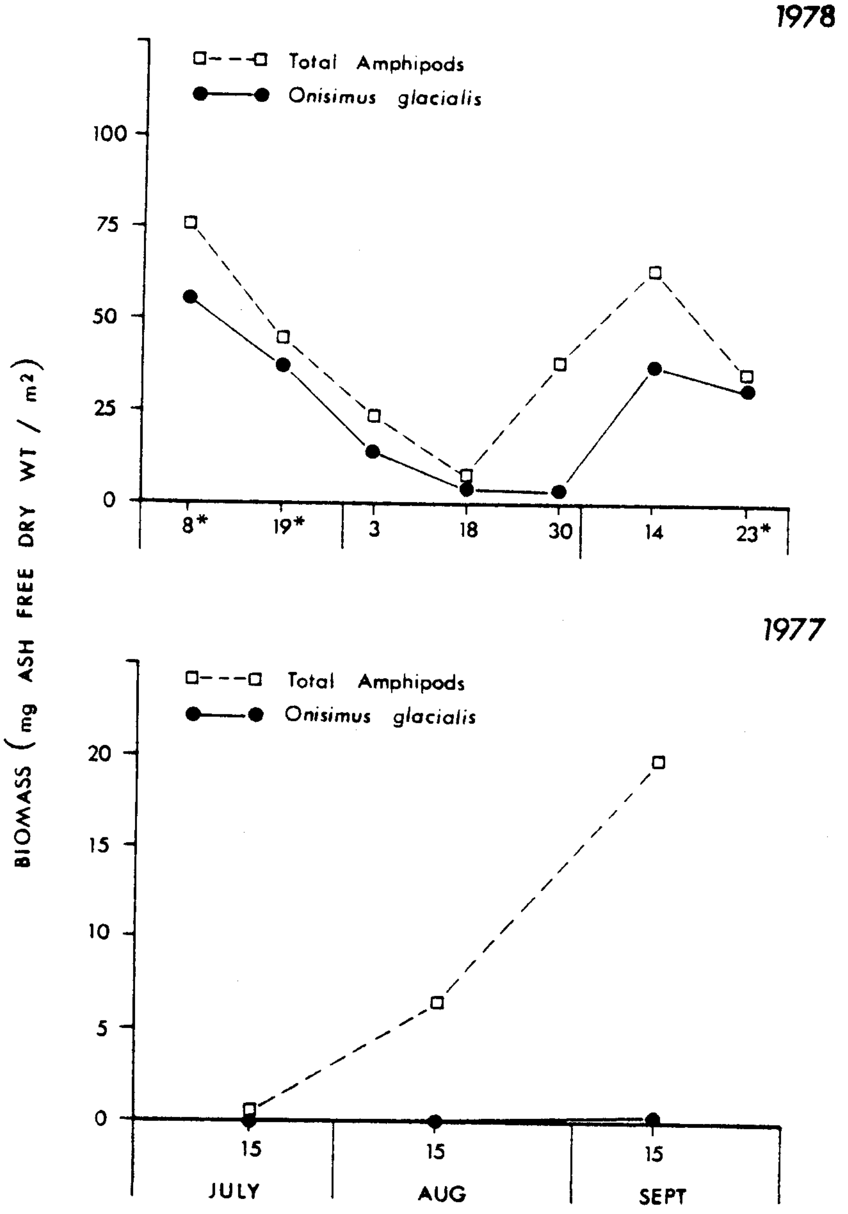

Figure 21. Biomass of amphipods near the bottom at offshore stations in Simpson Lagoon in relation to date in 1977 and 1978. Each 1978 data point is a mean of five drop-net samples from each station on each date. The 1977 data are recalculated from Griffiths and Craig (1978). Because different sampling techniques were used in the two years, only general trends can be compared. * indicates that no samples were collected on these dates at Station 7.

Table 16. Comparisons of amphipod biomass near the bottom (ln mg ash-free dry wt. m^{-2}), all stations (1-7) and sampling periods considered. Data analyzed using two-way analysis of variance for unequal sample size.

Species	Among Stations		Among Periods	
	F Value (d.f.=6,32)	P	F Value (d.f.=6,32)	P
Onisimus glacialis	27.49	<<0.001	3.39	<0.01
Gammarus setosus	4.77	<0.001	0.56	0.78
Total amphipods	11.26	<<0.001	4.55	<0.001

Table 17. Orthogonal comparisons of amphipod biomass on the bottom at various stations and groups of stations.

Stations Compared	Habitat Type	F values for *Onisimus glacialis*	F values for *Gammarus setosus*	Total Amphipods
6,7 vs 1-5[+]	Ocean vs Lagoon	107.21 P<<0.001	6.34 P<0.001	61.50 P<<0.001
6 vs 7[+]	Nearshore Ocean vs Offshore Ocean	30.62 P<<0.001	0.01 P=0.91	0.71 P=0.40
1,5 vs 2,3,4[++]	Shallow Nearshore vs Central Lagoon	13.15 P<<0.001	5.35 P<0.001	28.11 P<<0.001
1 vs 5[++]	Mainland Nearshore vs Barrier Is. Nearshore	1.15 P=0.29	0.07 P=0.79	0.17 P=0.68
3 vs 2,4[++]	Center of Lagoon vs Intermediate Depths	1.95 P=0.16	9.39 P<<0.001	2.61 P=0.11

[+] Only sampling periods 3 August-14 September considered.

[++] Only sampling periods 19 July-23 September considered.

considered, and significant among-period differences for *O. glacialis* and total amphipods, but not for *G. setosus* (Table 16 and Fig. 18). Biomasses of the two amphipod species considered individually and also total amphipod biomass were higher in the shallower lagoon waters than in the deeper ocean waters (Table 17, Figs. 18-19). *Onisimus glacialis* biomass was also greater in the lagoon than at the offshore station in under-ice collections during early June 1978. Only *O. glacialis* differed significantly in biomass at offshore Stations 6 and 7; its biomass was significantly higher at Station 6 (ocean side of barrier islands) than at Station 7 (offshore ocean) (Table 17, Figs. 18-19).

Biomasses of *O. glacialis*, *G. setosus* and total amphipods were all significantly higher in the central lagoon (Stations 2, 3 and 4) than near the edges of the lagoon (Stations 1 and 5; Table 17, Figs. 18-19). Thus, amphipods appeared to show a preference for the deeper (> 2.0 m) waters of the lagoon. There were no significant differences in biomasses for the two individual species or total amphipods between Station 1 (nearshore mainland) and Station 5 (nearshore barrier island) (Table 17, Figs. 18-19). A comparison of the central lagoon stations (3 vs 2 and 4) showed no significant differences in the biomasses of *O. glacialis*, and total amphipods; however, the biomass of *G. setosus* was significantly higher at Stations 2 and 4 than at Station 3 (Table 17, Figs. 18-19). Reasons for the differences in this last comparison are unknown; physical conditions and habitat types are similar at all three stations.

Gammarus setosus biomass did not differ significantly among sampling periods (Table 16 and Fig. 18), but the biomass of *O. glacialis* was significantly higher on 19 July than on any other sampling date* (Table 16, Figs. 18 and 20). *Halirages mixtus* biomass tended to be higher later in the season; it did not appear in samples until 18 August 1978 and reached a maximum on 14 September 1978 (Fig. 18). This marine pelagic species appears to move into the system from offshore waters late in the open-water season. *Pontoporeia affinis* biomass showed a reversed

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*Comparisons among sampling periods were done using Duncan's multiple range test, where $\alpha = 0.05$.

pattern; it was higher in the early samples (10 July-18 August 1978) than in the later ones (30 August-23 September 1978) (Fig. 18). The reasons for this decrease in biomass as the open-water season progressed are not known. Total amphipod biomass followed a seasonal trend similar to that of *O. glacialis*, the most abundant species in the system; total amphipod biomass was significantly higher on 19 July 1978 than in any other sampling period (Figs. 18 and 20).

Although other amphipod species did not comprise a major component of the total amphipod biomass in the system in 1978, the distributional trends of these species are of note, especially in relation to 1977 results. For example, the large increase in total amphipod biomass at offshore Station 7 late in the 1978 season (Fig. 18) was the result of an influx of *Parathemisto* sp., a genus of pelagic marine amphipod. A larger influx of *Parathemisto libellula* was noted in 1977 at offshore Station 77-5. That year, large numbers of this amphipod were washed-up in windrows on the ocean side of the barrier islands.

In 1978, *Onisimus glacialis* was the dominant bottom-dwelling amphipod in Simpson Lagoon in terms of biomass, but in 1977 trawl samples had showed this species to be only a minor component of the amphipod fauna (Figs. 19, 20 and 21). *Gammaracanthus loricatus* and *Gammarus setosus* were the most abundant amphipods in 1977 samples. However, their apparent importance that year was likely an artifact of the sampling technique--the large mesh size of the trawl used in 1977 selected against the relatively small *O. glacialis*. In 1978, the apparent importance of other smaller amphipod species (e.g., *Halirages mixtus* and *Pontoporeia affinis*) also increased relative to that of the larger amphipods *G. loricatus* and *G. setosus*; this may have been caused by the same sampling artifact. Consequently, any between-year comparisons of amphipod biomasses or trends are confounded by this problem.

Amphipods in the Water-Column. Amphipods were collected in the water-column regularly over the open-water season of 1978. The results for all collections are shown in Appendix 9, Figs. 22-25 and are compared in Table 18.

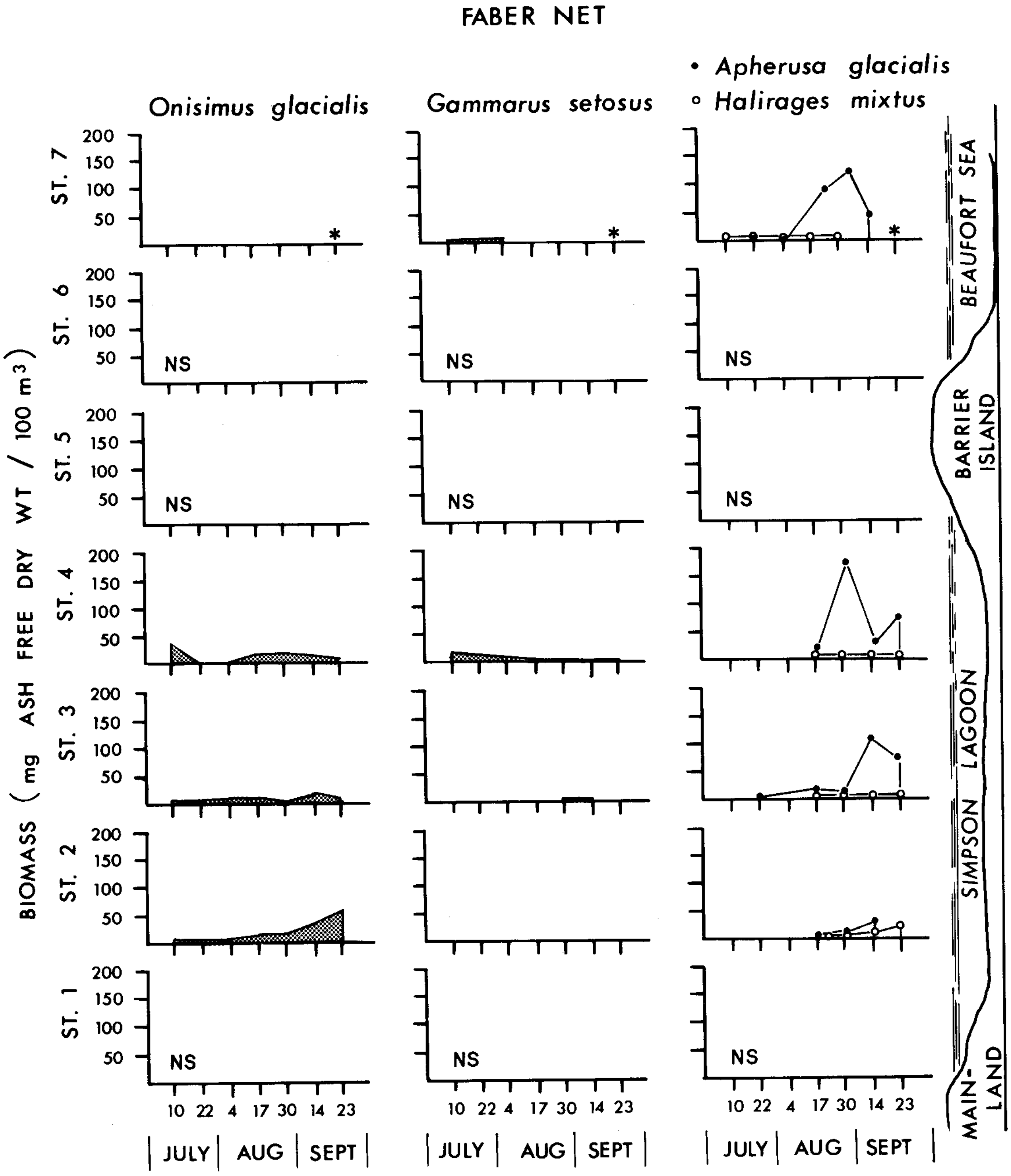
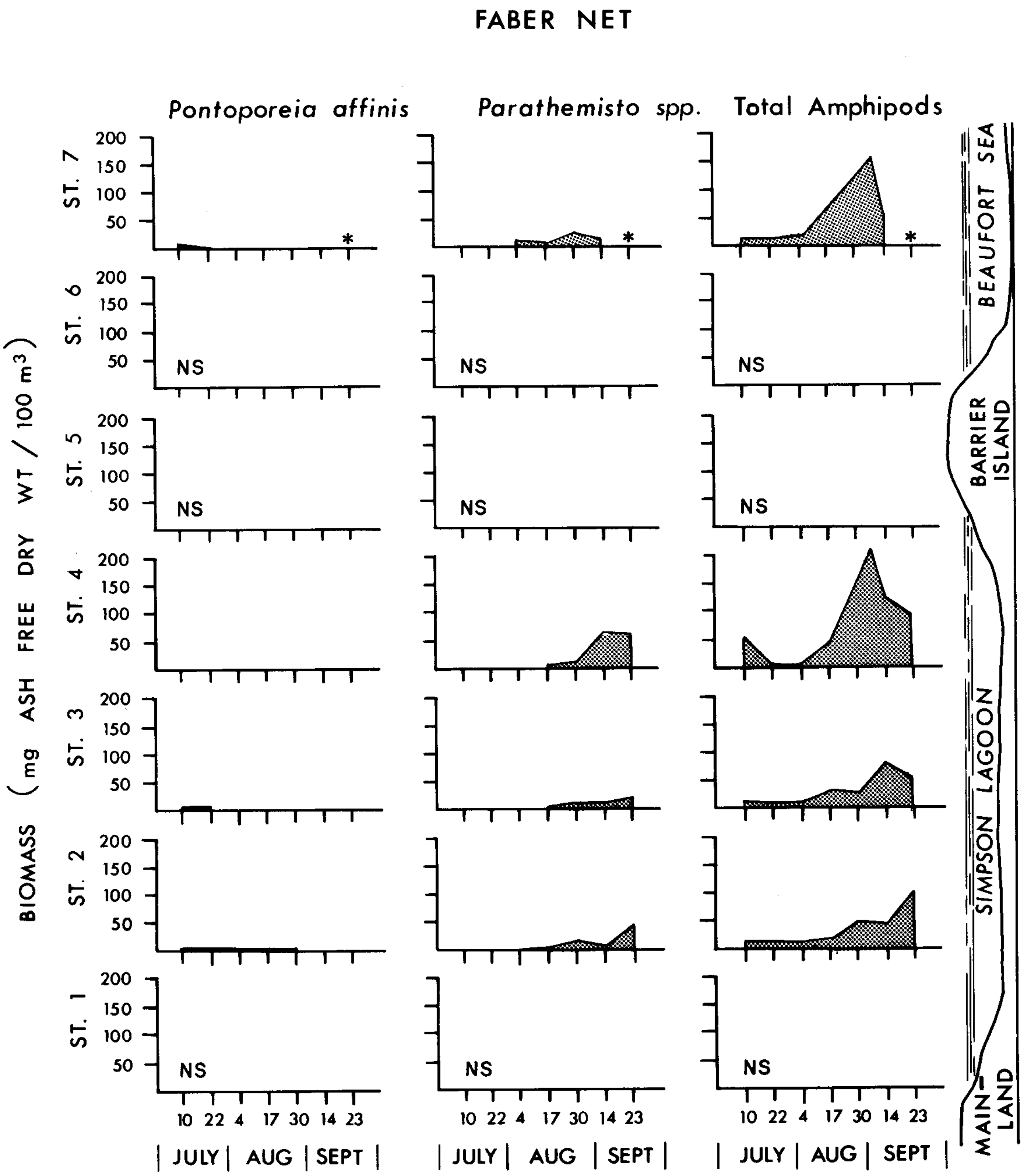


Figure 22. Biomass of amphipods in the water-column in relation to date and sampling period. Each data point is a mean of three Faber net samples collected in and near Simpson Lagoon in 1978. * indicates no samples collected. NS indicates these stations not sampled due to shallowness of the water.



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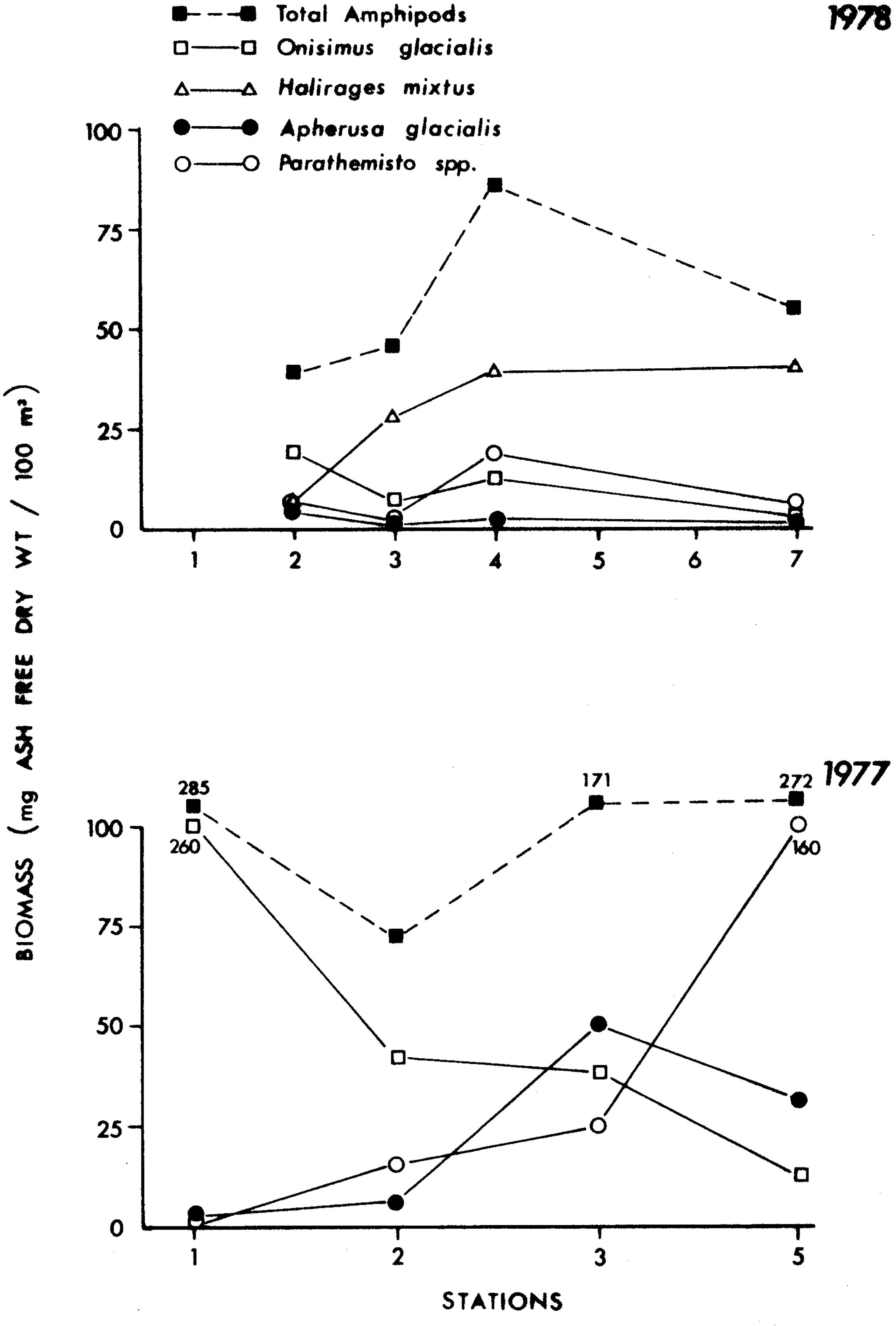


Figure 23. Biomass of amphipods in the water-column at various stations in Simpson Lagoon in 1977 and 1978. Each 1978 data point is a mean of three Faber net samples from each station on each sampling date. The 1977 data are recalculated from Griffiths and Craig (1978).

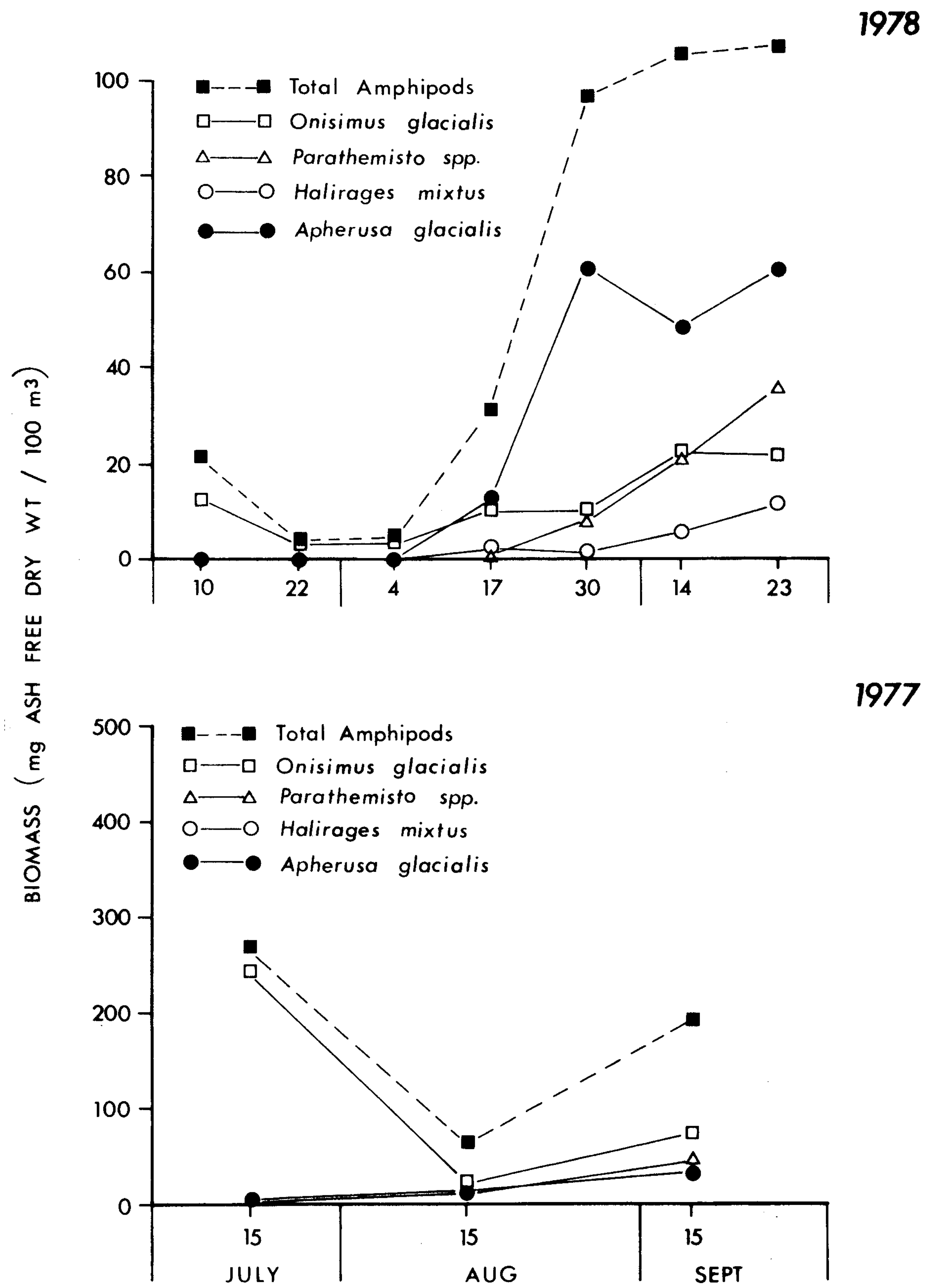


Figure 24. Biomass of amphipods in the water-column at lagoon stations in Simpson Lagoon in relation to date in 1977 and 1978. Each 1978 data point is the mean of three Faber net samples from each station on each date. The 1977 data are recalculated from Griffiths and Craig (1978).

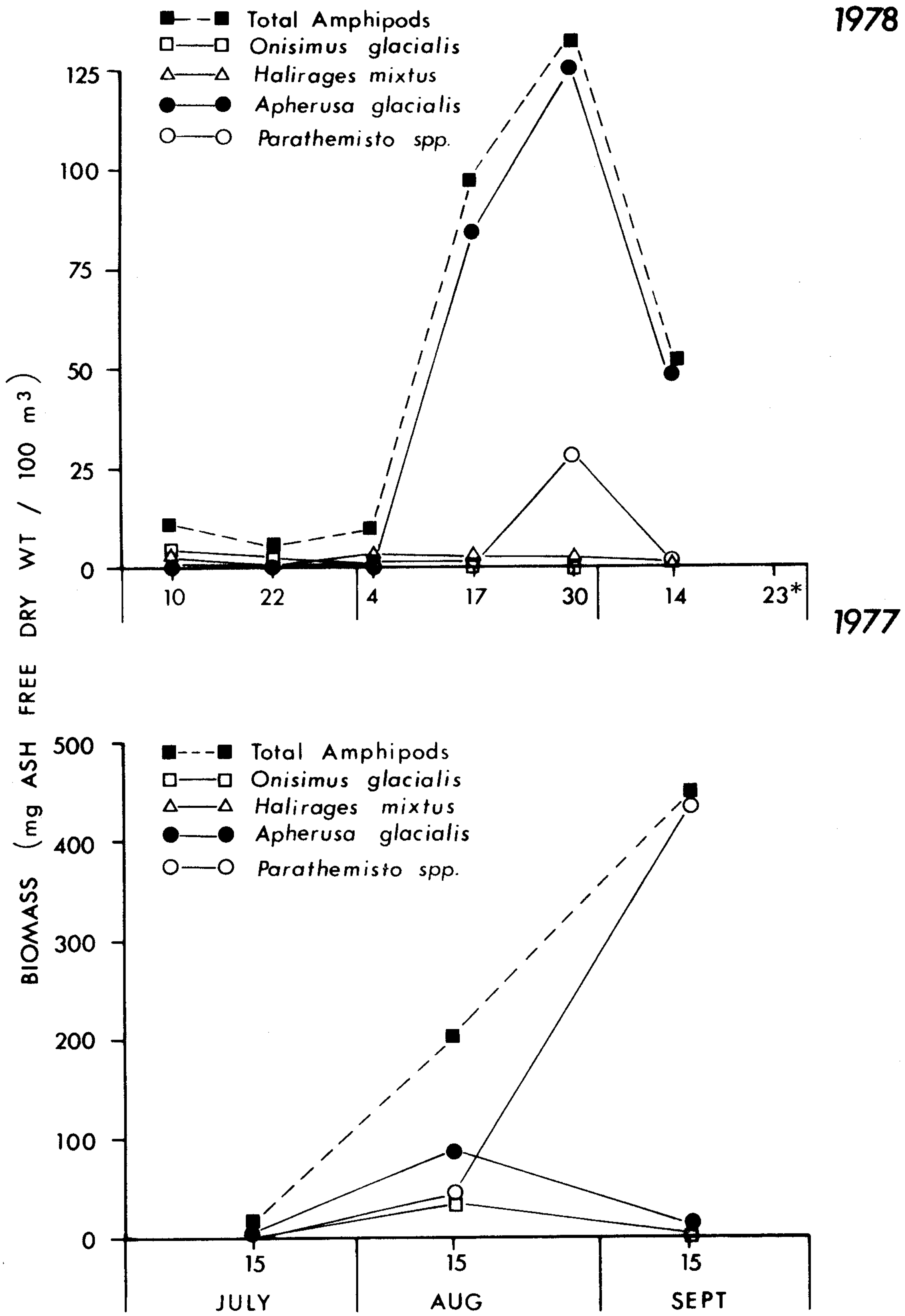


Figure 25. Biomass of amphipods in the water-column at offshore stations in Simpson Lagoon in relation to date in 1977 and 1978. Each 1978 data point is a mean of three Faber net samples from each station on each date. The 1977 data are recalculated from Griffiths and Craig (1978). * indicates no samples collected.

Table 18. Comparisons of amphipod biomass in the water column (ln mg ash-free dry wt. per 100 m^{-3}) within lagoon stations (2,3,4) and all stations (2,3,4,7) combined, and among respective sampling periods. Data analyzed using two-way analysis of variance. Each station/date value was a mean of three Faber net hauls at the station during the sampling period.

	All Stations (2,3,4,7)		Lagoon Stations (2,3,4)	
Species	F value Among Stations (d.f.=3,15)	F value Among Periods[+] (d.f.=5,15)	F value Among Stations (d.f.=2,12)	F value Among Periods[++] (d.f.=6,12)
Onisimus glacialis	3.54 0.05>P>0.01	1.34 P>0.05	2.73 P>0.05	3.34 0.05>P>0.01
Gammarus setosus	1.01 P>0.05	0.61 P>0.05	1.37 P>0.05	0.97 P>0.05
Apherusa glacialis	3.13 P>0.05	11.51 P<0.01	2.93 P>0.05	8.33 P<0.01
Halirages mixtus	0.31 P>0.05	3.41 0.05>P>0.01	1.82 P>0.05	27.57 P<0.01
Pontoporeia affinis	4.02 0.05>P>0.01	3.21 0.05>P>0.01	1.99 P>0.05	0.99 P>0.05
Parathemisto spp.	1.36 P>0.05	4.49 0.05>P>0.01	1.95 P>0.05	7.80 P<0.01
Total amphipods	2.14 P>0.05	16.46 P<0.01	2.82 P>0.05	15.36 P<0.01

[+] Only sampling periods 10 July-14 September 1978 used in comparisons.

[++] Only sampling periods 10 July-23 September 1978 used in comparisons.

The total biomass of amphipods, and the biomasses of the six individual species considered, did not differ significantly among deep (> 2.0 m) lagoon stations (2, 3 and 4) (Table 18, Figs. 22 and 23). However, there were spatial differences in biomasses of *Onisimus glacialis* and *Pontoporeia affinis* when the ocean Station 7 was included in the comparisons. *O. glacialis* biomass was higher in the lagoon (Stations 2, 3 and 4) than in the ocean (Station 7) (orthogonal comparison, $0.05 > P > 0.01$; Fig. 23). (Similarly, *O. glacialis* biomass in the under-ice samples, and on the bottom during the summer, was higher in the lagoon.) The differences (orthogonal comparisons) in biomass of *P. affinis* among lagoon and ocean stations (7, 2, 3 and 4) lies in a combination of stations not predicted and not tested due to lack of degrees of freedom for additional orthogonal comparisons.

Within the lagoon (Stations 2, 3 and 4), the biomasses of *O. glacialis*, *Apherusa glacialis*, *H. mixtus*, *Parathemisto* spp., and total amphipods differed significantly among sampling periods (Table 18, Figs. 22 and 24). In all cases, the biomasses increased markedly during August 1978 (Fig. 24). (*Apherusa glacialis*, *H. mixtus* and *Parathemisto* sp., are all pelagic marine species and apparently move into Simpson Lagoon during August from deeper offshore areas.) When lagoon and offshore stations (2, 3 4 and 7) were considered together, biomasses of *A. glacialis*, *H. mixtus*, *P. affinis*, *Parathemisto* sp., and total amphipods showed significant differences among sampling dates (Table 18, Figs. 23 and 24); the seasonal patterns were similar to those within the lagoon. Except for *P. affinis*, which was not collected in the system after 30 August 1978, biomass of all these species increased significantly in mid- to late August and remained high until the termination of sampling in late September (Figs. 22, 24 and 25).

Early in the open-water season of 1978 (10 July-4 August), *O. glacialis* comprised most of the amphipod biomass in the water-column at both lagoon and offshore stations (Figs. 24 and 25). As the season progressed (4 August-23 September), no one species of amphipod dominated the amphipod biomass at lagoon stations, but several species (*Apherusa glacialis*, *Parathemisto* sp., *Onisimus glacialis* and *Halirages mixtus*) were common (Fig. 24). At offshore stations during August and September, *Apherusa glacialis* and *Parathemisto* spp. formed the largest portion of the amphipod biomass in the water-column (Fig. 25).

The total amphipod biomass in the water-column at both lagoon and offshore stations increased markedly late in the season in 1978. In 1977, the total amphipod biomass at lagoon stations was high early in the season, declined at mid-August and then increased into September, while at offshore stations it increased dramatically as the season progressed (Figs. 24 and 25). In the water-column of the lagoon relative abundances of different species of amphipods were similar in the two years (except for *Halirages mixtus* which was not recorded in 1977). At the offshore stations, *Parathemisto libellula* was the most abundant species in the water-column after mid-August 1977 and *Apherusa glacialis* was the second most common; this was the reverse of the situation in 1978. The abundance of *Parathemisto* sp. offshore in late summer of 1977 paralleled the increase of this species in near-bottom habitats (see previous section).

In summary, all sampling methods (drop and Faber nets and diver observations) showed seasonal and among-station variations in biomasses of amphipods and mysids, and in species composition of amphipods, both in the water-column and near the bottom. This suggests an uneven distribution and rapid movements of epibenthic and pelagic amphipods and mysids within the Simpson Lagoon and nearshore system. Similar uneven distribution patterns of epibenthic invertebrates have been noted in arctic waters by numerous authors (MacGinitie 1955; Crane 1974; Feder et al. 1976a; Griffiths et al. 1977). The occurrence of rapid movement is also suggested by analysis of drift net data in this study (see following section) and by the apparent immigration of mysids into the lagoon during early summer (see 'Under-Ice Distribution of Epibenthic Invertebrates')

Transport of Invertebrates

Periodically during the open-water season, plumes of water from offshore areas were observed moving into the lagoon through entrances between the barrier islands. Our studies showed that amphipods and mysids are carried into the lagoon entrained in this water, suggesting that movements of invertebrates were likely to be facilitated by wind-driven water exchange, which may provide a means of dispersal for amphipods and mysids. The high flushing rate of the lagoon (0.2 times/day on the average and as much as once per day during winds greater than 40 km/h, Mungall 1978) could in theory result in the rapid movement of amphipods and mysids into and out of Simpson Lagoon at various times throughout the season. Data collected by Feder and Schamel (1976) suggested the onshore movement throughout the open-water season of marine epibenthic invertebrates from offshore populations.

Basically, two types of movements of amphipods and mysids into and out of the lagoon were postulated:

1. <u>Movements parallel to the shore</u>. Longshore movements might be a consequence of, or at least assisted by, wind-generated currents which typically move in an east-west direction during the open-water season, and
2. <u>Movements between shallow estuarine and deeper marine waters</u>. During the open-water period these movements may depend on wind and current action, perhaps during storms. The organisms may respond particularly to water motion near the bottom, where they exist in greatest abundance.

Drift net samples were collected in the gap between Pingok and Peat Islands on an intermittent basis throughout the 1978 open-water season in order to estimate the transfer rates of epibenthic invertebrates between the ocean and the lagoon. Mysids, the dominant food item in the diets of both fish and birds (Craig and Haldorson 1980; Johnson and Richardson 1980), were the dominant component of the biomass in the drift net samples. The biomass of *M. litoralis* in these samples exceeded that of *M. relicta* by a ratio of 24:1; consequently, in the analysis, only *M. litoralis* was considered. The data are presented as the biomass of *M. litoralis* passing through a square meter vertical plane in one hour.

Too few samples were collected at locations and times when water was entering the lagoon (6 of 40) to provide a reliable estimate of the immigration rate of organisms into the lagoon. The results from the 34 samples collected at locations and times when water was leaving Simpson

Lagoon are presented in Table 19 and Fig. 26. The data were separated into two groups; those collected when *M. litoralis* biomass was high near the bottom of the lagoon (20 July-23 August) and those collected after it had declined significantly (29 August-16 September) (Figs. 10 and 12). Our intention was to determine if, under conditions of high *M. litoralis* biomass, the current speed required to initiate transport out of the lagoon was lower than that required when the biomass was lower. Biomass data were transformed to natural logarithms before carrying out the analysis.

There was a positive but not statistically significant correlation between current speed and *M. litoralis* biomass transported out of the lagoon during the period of high *M. litoralis* biomass (r = 0.362, d.f. = 14, $P > 0.10$) (Fig. 26). The lack of significant correlation may be a reflection of the limited range of current speeds in which these samples were collected; 12 of the 16 samples were collected in currents of 29-36 cm/s ($\bar{x}$ = 33.6, S.D. = 2.6). During the subsequent period of low *M. litoralis* biomass, the variation in current speeds was much greater ($\bar{x}$ = 47.8 cm/s, S.D. = 20.0) and there was a significant positive correlation between current speed and biomass transported (r = 0.800, d.f. = 16, $P < 0.001$) (Fig. 26). The slopes of the 'biomass transported vs current speed' lines during the two periods were not significantly different (P = 0.685), whereas the intercepts were ($P < 0.05$). The results suggest that the rate of transport depends on *M. litoralis* biomass; a lower current speed was required to initiate transport when the biomass was higher (Fig. 26).

Although *M. litoralis* biomass near the bottom of the lagoon was measured on only a few dates, estimates for other dates were made by interpolation between values measured at Station 5 (station nearest site of drift net sampling where drop net samples were taken; Table 18). The results of a 3-variable multiple regression analysis of emigration rate, expressed on a logarithmic scale, vs (1) the date of the collection, (2) current speed and (3) estimated biomass of *M. litoralis* on the lagoon bottom are summarized below:

Table 19. *Mysis litoralis* biomass transported out of Simpson Lagoon through the pass between Pingok and Peat Islands, 20 July-23 September 1978.

Mysis litoralis
Biomass High*

Date	Current Speed (cm/s)	*Mysis litoralis* Transported (mg ash-free dry wt. m^{-2} h^{-1})	Estimate of *M. litoralis* Biomass at Station 5 on Given Date (mg ash-free dry wt. m^{-2})
20/07/78	36	7.24	0.014
	34	5.43	
	36	10.68	
	36	8.08	
	34	6.15	
	29	18.22	
25/07/78	32	49.53	0.0268
	35	55.48	
02/08/78	30	0.60	0.048
	30	0.72	
	35	0.40	
	36	0.45	
06/08/78	8	0.04	0.036
	5	0.54	
23/08/78	17	5.98	0.022
	22	13.88	
Mysis litoralis Biomass Low*			
29/08/78	48	6.94	0.007
	35	3.05	
	48	5.55	
	28	2.68	
	52	8.77	
	36	3.25	
	38	2.76	
	26	0.76	
	47	3.89	
	33	1.68	
05/09/78	25	0.50	0.004
	22	0.63	
	59	0.38	
	47	0.89	
/09/78	76	46.68	0.0005
	85	34.13	
	78	7.38	
	78	72.72	

*For definition of high and low *M. litoralis* biomass, see text.

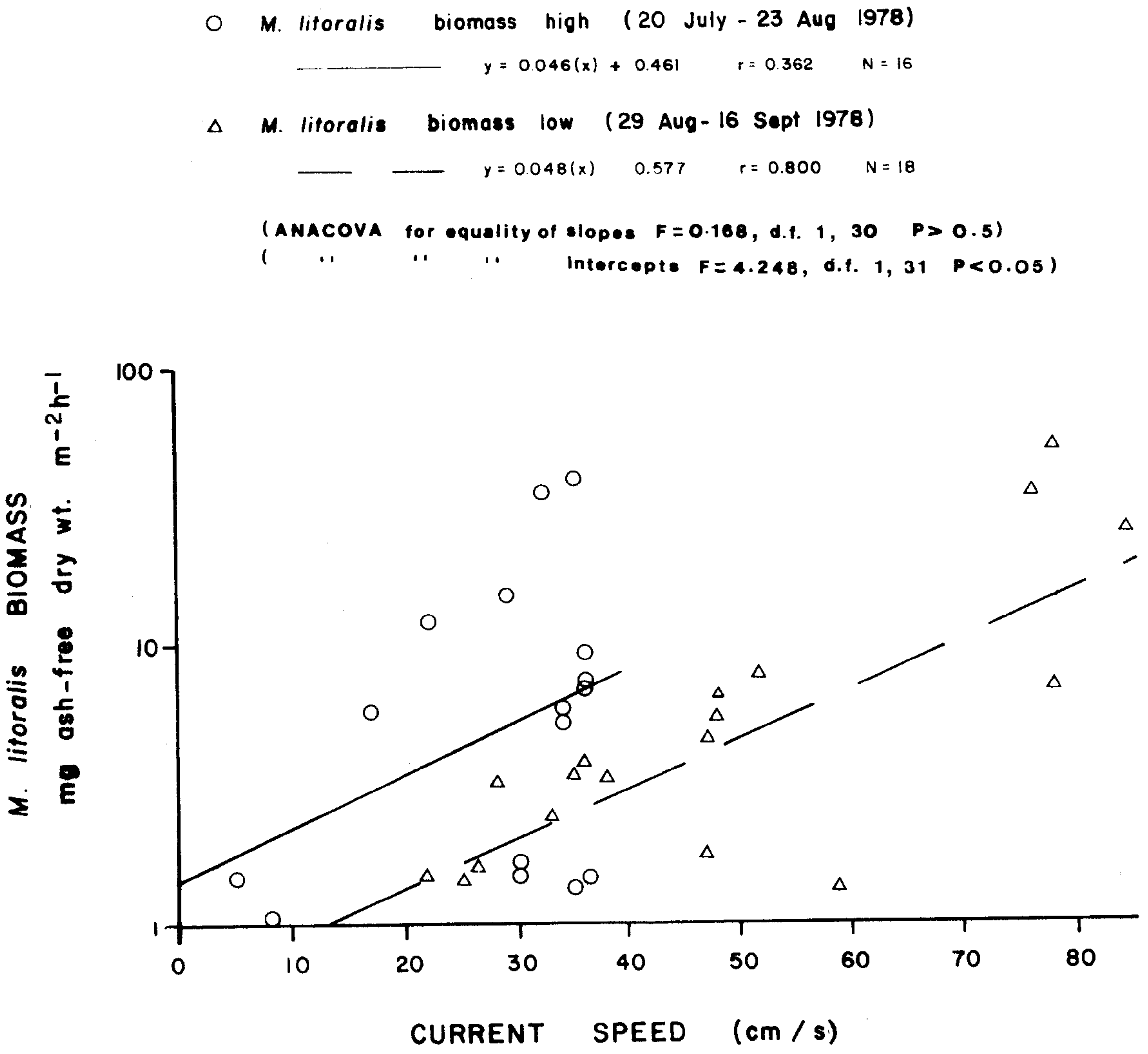


Figure 26. Relationship between current speed and *Mysis litoralis* biomass (mg ash-free dry wt. $m^{-2}h^{-2}$) transported through a vertical meter^2 plane in one hour in 1978. Relationship shown for high (O) and low (Δ) *M. litoralis* biomass.

	F Value	d.f.	Standardized Regr. Coeff.	P
Date	11.28	1,30	-0.575	<0.01
Current	11.17	1,30	0.542	<0.01
Biomass	6.56	1,30	-0.448	<0.05

These results indicate that the biomass of *M. litoralis* transported out of the lagoon decreases as the season progresses, presumably reflecting the seasonal decrease in *M. litoralis* biomass in the lagoon; and that the rate of emigration is positively correlated with current speed. More surprisingly, the negative partial correlation of transport rate with biomass suggests that, even after allowing for the date and current effects, the transport rate increased as biomass in the lagoon decreased. Furthermore, on 14-16 September 1978, the biomass of *M. litoralis* in the water-column showed a late season peak at Station 4, the station nearest the site of drift net collections where densities in the water-column were measured (Figs. 14 and 16). This may have been due to high current speed on 14 September (Table 19). However, it is also possible that the decrease in *M. litoralis* biomass on the bottom of the lagoon recorded at the end of the open-water season (Figs. 11 and 13) may be partially due to an active movement--the organisms may move up from the bottom into the water-column in order to facilitate emigration. This postulated movement up into the water-column may be in response to an external stimulus such as photoperiod, temperature, salinity.

Trophic Relationships

The most important food sources for both fish and birds in Simpson Lagoon during summer are mysids (*Mysis litoralis*, *M. relicta*) and amphipods (especially *Onisimus glacialis*) (Craig and Haldorson 1980; Johnson and Richardson 1980). This section compares the daily food requirements of fish and birds to the availability of food (mysids and amphipods) during the open-water season. Since the fish and birds selectively utilize the lagoon in preference to the ocean, only the feeding interactions within the lagoon were evaluated. However, as will be noted later, food appeared to be equally abundant in the marine water habitats beyond the barrier island.

Daily food requirements of the key vertebrates (fish and birds) in the study area during both 1977 and 1978 were estimated using fish and bird densities estimated by Craig and Haldorson (1980) and Johnson and Richardson (1980) (Tables 20 and 21). Bird densities were available for both years. Oldsquaw ducks were the prime avian consumers, and were the only birds considered in this analysis. The 1977 and 1978 energy requirements for birds have been computed using the following equation from Kendeigh et al. (1977:201): at 0°C, $M = 4.142\ W^{0.5444}$, where M = daily existence energy requirements during the molting period (Kcal) and W = weight of bird (g). A digestive efficiency of approximately 70% (Owen 1970) has been used in converting daily existence energy requirements to intake requirements. Fish densities for 1977 were assumed to be the same as those estimated for 1978 by Craig and Haldorson (1980), with the exception that the run of arctic cod encountered on 11-20 August 1978 did not occur. Fish species considered were arctic char, arctic cisco, least cisco, arctic cod and fourhorn sculpin. Energy requirements of fish are assumed to correspond to an intake of 6% of body weight per day for small fish, and 5% per day for large fish. The 6% figure was derived by Craig and Haldorson (1980); the 5% figure is arbitrary but based on the general principle that energy requirements do not increase linearly with body weight.

In 1977 the amount of food (mysids and amphipods) available was calculated using diver estimates of densities of mysids and amphipods. The diver estimates in August 1977 at lagoon Stations 1, 2 and 3 were converted to estimated biomasses of epibenthic invertebrates, by using the 1978 ash-free dry weight (Table 5) for the predominant size classes of mysids and *Onisimus* amphipods observed by the diver in 1977.

For July 1977 and September 1977, the only available data concerning epibenthos were the otter trawl samples. The following procedure was used to correct these results for underestimations of the biomass present. For each of mysids and amphipods, and separately for each of the stations 1-3, the July:August and September:August ratios of wet weights in trawl samples were multiplied by the August estimate of grams ash-free dry weight/m^2 previously mentioned. A weighted mean for the

Table 20. Estimates of daily food requirements (g ash-free dry wt*/m^2) of small and large fish in Simpson Lagoon in 1977** and 1978.

	Lagoon Edge (6.9 km^2)				Lagoon Center (153.1 km^2)				
	Small Fish (=15 g)		Large Fish (=470 g)		Small Fish (=15 g)		Large Fish (= 470 g)		Daily Ration (Weighted Mean)
Date	Density† No./m^{2}x10^{-4}	Ration†† g/m^{2}x10^{-4}	Density No./m^{2}x10^{-4}	Ration g/m^{2}x10^{-4}	Density No./m^{2}x10^{-4}	Ration g/m^{2}x10^{-4}	Density No./m^{2}x10^{-4}	Ration g/m^{2}x10^{-4}	g/m^{2}x10^{-4}
Jul 01-10	5	0.5	5	14.1	0.5	0.1	0.5	1.4	2.1
11-20	20	2.2	20	56.4	2	0.2	1.5	4.2	6.7
21-31	50	5.4	40	112.8	5	0.5	4	11.3	16.4
Aug 01-10	50	5.4	40	112.8	5	0.5	4	11.3	16.4
11-20	1250†††	72.0	40	112.8	1200†††	69.1	4	11.3	84.9
21-31	70	7.6	40	112.8	7	0.8	4	11.3	16.8
Sep 01-10	100	10.8	40	112.8	10	1.1	4	11.3	17.2
11-20	100	10.8	10	28.2	10	1.1	1	2.8	5.4
20-30	100	10.8	5	14.1	10	1.1	0.5	1.4	3.5

*Ash-free weight calculated by taking 12% (mean of mysids and amphipods) of wet weight.

**Density estimates for 1977 are assumed to be the same as 1978 less the arctic cod run 18-20 August.

†Density estimates from Craig and Haldorson (1980).

††Daily food rations (wet weight) are assumed to be 6% of body weight for small fish (Craig and Haldorson 1980) and 5% of body weight for large fish.

Food ration for this period is based on small fish approximately 8 g in weight (arctic cod).

Table 21. Estimated daily food requirements (mg ash-free dry wt./m^2) of oldsquaw ducks in Simpson Lagoon in 1977 and 1978.

	1977		1978	
	no./km^2 †	mg/m^2 ††	no./km^2	mg/m^2
5 June	0.0	0.0	---	---
20 June	0.2	0.009	---	---
23 June	---	---	0.1	0.004
5 July	6.0	0.26	15.5	0.68
15 July	---	---	183.2	7.99
25 July	---	---	79.8	3.48
28-29 July	321.1	14.01	---	---
5 August	---	---	75.4	3.29
15 August	261.0	11.39	100.7	4.39
25 August	---	---	58.2	2.54
30 August	137.1	5.98	---	---
5 September	---	---	23.2	1.01
15 September	---	---	26.3	1.15
22 September	666.3	29.07	---	---
23 September	---	---	199.2	8.69

†Densities are based on the results of aerial surveys and are weighted means for the lagoon (Johnson and Richardson 1980).

††Food requirements were calculated assuming 240 Kcal/bird-day as the gross energy needs of oldsquaw ducks (Johnson and Richardson 1980). This was converted to mg ash-free dry weight by assuming that 5.5 Kcal is equivalent to 1.0 g ash-free dry weight.

whole lagoon was then determined for each sampling period (15 July, 15 August and 15 September) (Table 22). The estimate for Station 3 on 15 September 1977 was not used as it appeared unrealistically high (68.7 g ash-free dry weight/m^2), possibly due to a sampling artifact; only one otter trawl sample was collected at this station and date. In this case, the weighted means for Stations 1 and 2 was assumed to apply to the entire lagoon.

For 1978, available biomass was determined using results from the drop net samples. For each sampling date, the five lagoon stations were combined to produce a weighted mean for the entire lagoon (Table 22).

Comparisons of food (mysids and amphipods) available in the lagoon during 1977 and 1978 with the daily food requirements of the oldsquaw ducks and the major fish species using the lagoon are shown in Fig. 27. The energy available showed different trends in the two years. In 1977, it exceeded the daily requirements of consumers by 1½ or 2 orders of magnitude and apparently increased in availability as the season progressed; this suggests that food was not a limiting factor for the fish and birds in the lagoon during the summer of 1977. Also, diver estimates of densities of epibenthic invertebrates, the basis for the 1977 'Food Available' line in Fig. 27, are biased downwards (see 'Sampling Limitations and Biases'). Thus, the difference between food available and daily food requirements were, for 1977, probably somewhat larger than shown in Fig. 27. In 1978, the available supply of food apparently was an order of magnitude less than in 1977 by the end of the open-water season. The number of oldsquaw ducks present during late summer of 1978 was approximately half of that in 1977, and their energy demand was correspondingly reduced. However, fish densities and energy needs were greater in 1978 because of a large influx of arctic cod in mid-August of 1978 (Table 20). Whether the year-to-year variations in numbers of consumers are related to differences in the energy available is not known. The interpretation problem is compounded by imprecise estimates of both vertebrate densities and food availability and by natural variations in the densities of all the organisms involved

Table 22. Estimates of food available (mysids and amphipods) (g ash-free dry weight/m^2) in Simpson Lagoon in 1977 and 1978. Recalculated from Griffiths and Craig (1978).

Station	Approximate Lagoon Area Represented (km^2)	1977 (g AFDW m^{-2})* 15 Jul	15 Aug	15 Sep
1	36	0.12	0.33	0.24
2	102	0.15	0.76	1.16
3	22	0.30	0.93	†
Total	160			
Weighted Means		0.16	0.69	0.92

Station	Approximate Lagoon Area Represented (km^2)	1978 (g AFDW m^{-2})* 8 Jul	19 Jul	03 Aug	18 Aug	30 Aug	14 Sep	23 Sep
1	36	0.11	0.16	0.22	0.068	0.06	0.27	0.25
2	34	0.12	0.23	0.37	0.30	0.20	0.33	0.18
3	34	0.04	0.39	0.19	0.66	0.18	0.20	0.23
4	34	**	1.25	0.14	0.30	0.14	0.12	0.11
5	22	0.029	0.12	0.10	0.09	0.04	0.06	0.01
Total	160							
Weighted Means		0.079	0.45	0.22	0.30	0.12	0.21	0.17

* Biomass is the sum of all mysids and amphipods in g ash-free dry weight/m^2.

** Value at Station 4 assumed to be a mean of values at Stations 2 and 3.

† Estimates for Station 3 on this date not used as they appeared unrealistically high (68.7 g/m^2).

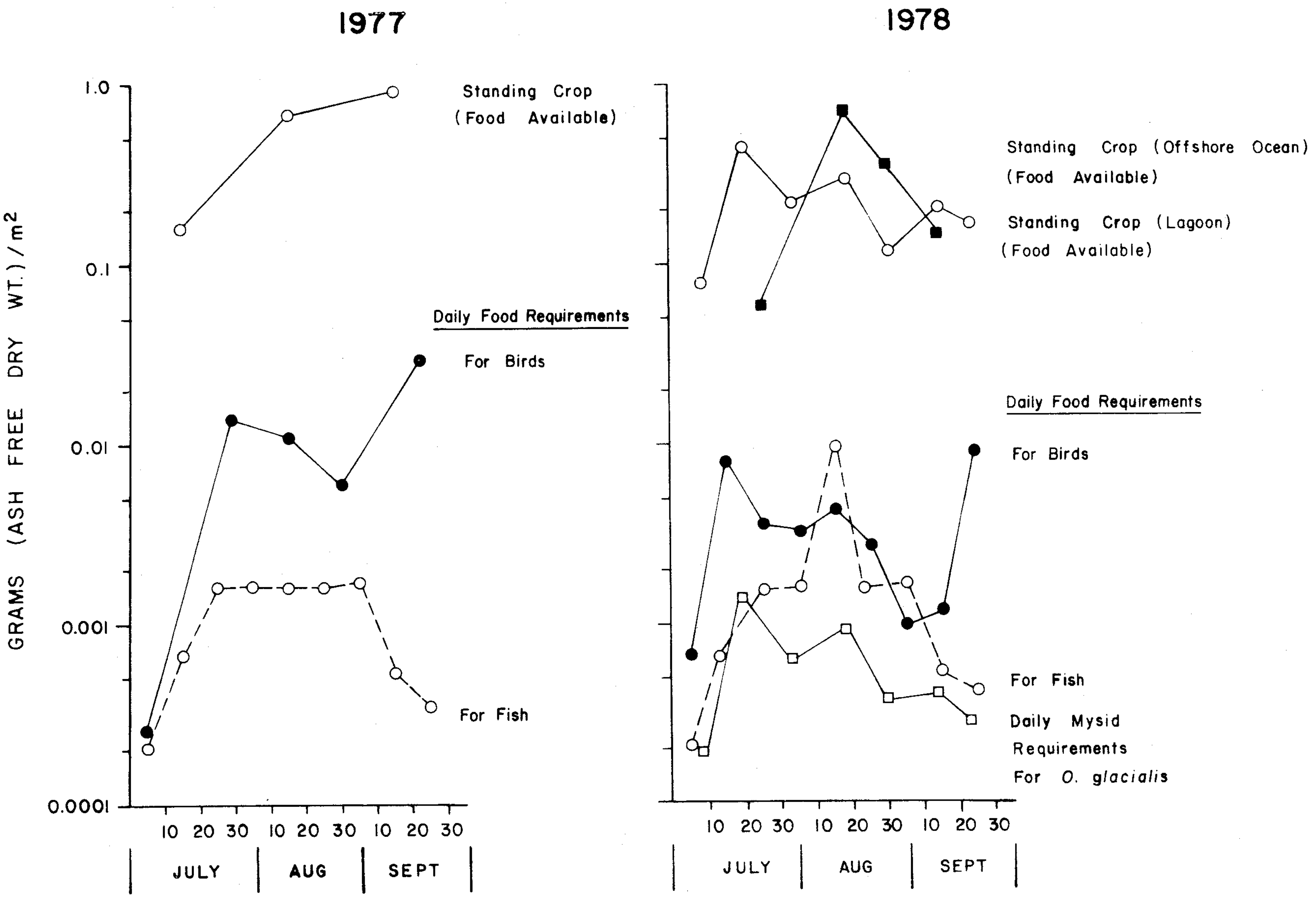


Figure 27. Comparison of food available (mysids and amphipods) and the daily food requirements of birds, fish and *Onisimus glacialis* in relation to time in Simpson Lagoon, 1977 and 1978.

caused, in part, by the responses of the organisms to various physical conditions (wind, temperature, salinity, ice, etc.).

The biomass of mysids and amphipods was apparently similar in mid-July of the two years. In 1977 it increased thereafter until the end of the open-water period, but in 1978 it tended to decrease during the same period. The drop net results of 1978 showed that the biomasses of *M. relicta* and *O. glacialis* did not decrease significantly in the lagoon as the season progressed, but that the general biomass decrease was caused by a decrease in the biomass of *M. litoralis*. In order to support the vertebrate consumers during the 80-day open-water period in 1978, and at the same time maintain the standing stock, the invertebrate biomass would have had to be replenished through growth of individuals and/or a net immigration of organisms into the lagoon from other locations (i.e., offshore and/or other nearshore areas) (Fig. 27). In 1977, when the invertebrate standing stock was higher relative to requirements of vertebrates, it is not as clear that growth or replenishment of the epibenthos was necessary to support the vertebrates. But growth and/or replenishment must have also occurred in 1977 because the biomass present increased with time.

The importance of invertebrate (particularly mysid) growth and/or immigration in 1978 became even more apparent when the energy requirements and food habits of *O. glacialis* were considered. A large portion of the diet of this omnivorous amphipod consists of crustacean parts (Broad 1977; Broad et al. 1979). Observations of feeding *O. glacialis* in aquaria and in the field indicated that they readily consumed mysids. An estimate of the daily ration of mysids for *O. glacialis* was calculated using the following findings and assumptions:

1. An average daily increase in weight of 0.04 mg wet weight was determined for first year class individuals, the dominant size class in the lagoon (see 'Biology of Key Species').
2. If we assume that this growth represents 10% of the food consumed (Parsons et al. 1977:143), the daily food ration of *O. glacialis* is about 0.4 mg wet weight or approximately 0.08 mg ash-free dry weight.
3. It is also assumed for the sake of argument that only 10% of the diet of *O. glacialis* is comprised of mysids.

Using these estimates in conjunction with the weighted mean density of *O. glacialis* in the lagoon we calculated the food requirements for this species in summer (Table 23 and Fig. 27). Even if only 10% of the diet of *O. glacialis* is composed of mysids, this predation represents a significant demand on the food resource when compared to the demands by birds and fish.

The question now arises as to whether the initial early summer immigration of mysids coupled with growth during the summer was sufficient to provide an adequate food supply for the consumers present (birds, fish and amphipods) or whether additional immigration was required throughout the open-water season to replenish the food supply. Weighted mean density estimates of mysids in the lagoon are used since no recruitment through reproduction occurs during the open-water season. Therefore, any variations observed during the summer in weighted densities must have been caused by a combination of immigration, emigration and/or cropping by predators. The number of mysids consumed by predators was calculated using the following assumptions:

1. The mysid component of the diets of consumers was

   80% for fish (Craig and Haldorson 1980)
   69% for birds (Johnson and Richardson 1980)
   10% for *O. glacialis* (see above)

2. Fish and *O. glacialis* consumed size ranges of mysids in approximately the same ratios that existed in the environment at any given time; oldsquaw ducks consistently selected the larger (~ 10 mm) mysids.

3. For the consumers, the ash-free dry weight (AFDW) of mysids required during each interval between sampling periods was determined using the relationship:

$$\text{Required AFDW} = \frac{(Y_1+Y_2)}{2}(\Delta x)(\text{\% of mysids in the diet})$$

where Y_1 = AFDW required at start of sampling period interval
Y_2 = AFDW required at the end of sampling period interval
Δx = number of days in the interval between sampling period

Table 23. Estimated total daily food ration (mg ash-free dry wt. m^{-2}) for *Onisimus glacialis* in Simpson Lagoon 8 July-23 September 1978.

Station	Approximate Lagoon Area Represented (km^2)	Estimated Total Food Requirements (mg ash-free dry wt. m^{-2})						
		8 July	19 July	3 August	18 August	30 August	14 September	23 September
1	36	0.5	1.3	0.8	0.1	0.5	0.1	1.2
2	34	1.1	0.2	1.3	1.4	0.8	1.0	0.6
3	34	0.2	1.7	1.7	2.7	1.9	1.3	0.8
4	34	†	8.8	1.9	4.6	0.6	1.5	0.2
5	22	0.1	1.8	0.8	0.5	0.1	0.3	0.1
Weighted Means		1.9	13.9	6.5	9.3	3.9	4.2	2.9
Assuming Diet 10% Mysids Daily Ration of Mysids		0.19	1.39	0.65	0.93	0.39	0.42	0.29

†Value at Station 4 assumed to be mean of values at Stations 2 and 3.

4. For oldsquaw ducks, the required AFDW of mysids was converted to number of mysids by dividing by the AFDW of a 10.5 mm mysid. For fish and *O. glacialis* the numbers were obtained by dividing by the AFDW of an average mysid during each time period.

The expected and observed mysid density at the end of each time period are shown in Table 24. The generally greater observed densities suggest that net immigration of mysids continues intermittently and replenishes the lagoon supply throughout the open-water season; without this immigration mysid populations would presumably be rapidly depleted by the predators (Fig. 28). The expected depletion rate of mysid populations for each time period (Fig. 28) suggests that even as late as 3 August the density of mysids was insufficient to last the predators until the end of the open-water season without new immigration. Obviously disruption of these mysid immigrations could have adverse effects on their consumers, the fish and birds.

The food preferences of some of the epibenthic invertebrates themselves is at present being studied under a separate contract (Schneider and Koch 1979). Generally, these authors have found that most species of epibenthic invertebrates in the study area were not trophic specialists.

Major species of epibenthic invertebrates and their principal foods.*

Species	Principal Foods
Onisimus glacialis	Crustacean parts, Diatoms
Mysis relicta	Peat, Diatoms, Crustacean parts
Mysis litoralis	Diatoms, Peat, Crustacean parts
Onisimus litoralis	Diatoms, Crustacean parts
Gammarus setosus	Peat, Diatoms, Crustacean parts
Apherusa glacialis	Diatoms, Dinoflagellates, Peat, Crustacean parts
Saduria entomon	Diatoms, Polychaetes, Peat

*Adapted from Schneider and Koch (1979).

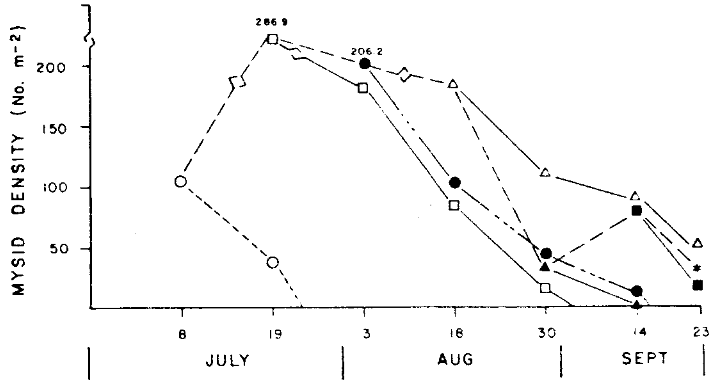
Similarly other investigators have found arctic epibenthic invertebrates to be omnivorous: *Gammarus setosus*, Steele and Steele (1970) and Broad (1977); *Onisimus glacialis*, Broad (1977); *Parathemisto libellula*, Dunbar

Table 24. Comparison of expected mysid densities† (No./m^2) after predation and observed mysid densities in Simpson Lagoon during the open water season 1978.

	Requirements of Consumers				
Time Period	Daily	For Sampling Period	Observed at Start of Each Time Period	Predicted at End of Each Time Period (After Predation)	Observed at Start of Successive Time Period
8-18 July	7.3	73.5	106.8	33.3	286.9
19 Jul - 2 Aug	6.8	102.4	286.9	184.5	206.2
3 Aug - 17 Aug	6.7	100.2	206.2	106.0	185.4
18 Aug - 29 Aug	5.3	63.5	185.4	121.9	39.9
30 Aug - 13 Sep	2.1	30.8	39.9	9.1	78.6
14 Sep - 23 Sep	3.5	34.5	78.6	44.1	55.8

† All densities are weighted means for the lagoon.

Figure 28. Seasonal densities (---) of mysids observed in Simpson Lagoon and expected rates of depletion assuming only cropping by predators and no new immigration.



1946), Wing (1976); *Parathemisto pacifica*, Wing (1976); *Pontoporeia affinis*, Segerstrale (1973). Although peat is abundant in the lagoon system, Schneider and Koch (1979) reported that, of all the epibenthic organisms tested, only the amphipod *Gammarus setosus* could directly assimilate it; some of the other amphipods (e.g., *Onisimus* spp.) could utilize it with the aid of a microbial intermediate and *Mysis litoralis* did not appear to derive any of its carbon from peat.

The ultimate sources of carbon for the epibenthic organisms in the nearshore system are also being studied (Schell 1979). The age (i.e., 'old' [peat] or 'modern'*) of the carbon comprising the tissues of the organisms was used to determine its source. Old carbon in tissues indicated that its source was terrestrial detritus (peat). Old carbon from peat could be assimilated either directly as detritus or indirectly in the form of microfauna living on the detritus; in either case, detrital peat would be the main food source for the lagoon epibenthos. However, if the carbon was modern, then recent primary production must have been the main food source for the epibenthic invertebrates. Recent production could be marine production (phytoplankton and ice algae) or recent terrestrial production (modern detritus) carried to the lagoon by runoff.

Schell (1979) reports the depressions in C-14 activity in epibenthic invertebrates from Simpson Lagoon indicate that peat (i.e., old) carbon appears to account for approximately 10 percent of the carbon in the organisms. Total terrestrial carbon (i.e., peat carbon plus river-transported modern carbon) may account for as much as 30-40 percent of the carbon comprising the organisms in the lagoon (Schell 1979). If this is the case, then the largest (60-70%) portion of the carbon utilized by invertebrates in Simpson Lagoon comes from marine primary production.

In summary, it appears that primary production in the ocean is the main supplier of carbon for the nearshore epibenthos. Each spring, a major portion of these epibenthic invertebrates (which comprise most of the diets of fish and birds) repopulate the shallow nearshore areas.

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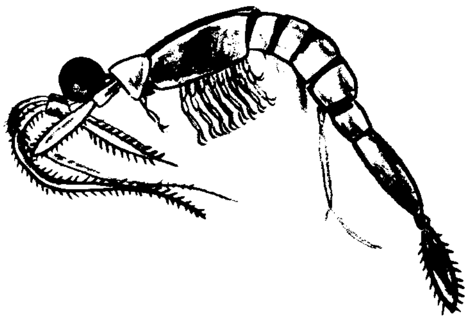
*See Schell (1979) for a discussion of 'old' and 'modern' carbon, methods used for aging, and use of the techniques.

Any disruption of either the migration of these invertebrates or of the food used by the invertebrates could have repercussions that would be felt to the top of the food chain (e.g., by fish and birds).

Biology of Key Invertebrate Species

The three most important invertebrate species in diets of birds and fish in Simpson Lagoon are *Mysis litoralis*, *Mysis relicta* and *Onisimus glacialis* (Johnson and Richardson 1980; Craig and Haldorson 1980). This section discusses selected aspects of the life histories of these key species and presents brief outlines of the life histories of other invertebrates that are present in the nearshore environment.

The biology of arctic marine epibenthic invertebrates is poorly known because most previous studies have been conducted over short periods of time during the open-water season or have been mainly concerned with the species composition of the invertebrate community. The kinds of information acquired in this study permit a more detailed description of the biology of the three most important species.



Distribution of *Mysis litoralis* and *Mysis relicta*

The reported geographical distributions of *Mysis relicta* and *M. litoralis* are somewhat confusing because of taxonomic disagreements. *Mysis relicta* was formerly described as a subspecies of *M. oculata* (*M. oculata* var. *relicta*) and there is still considerable disagreement as to its taxonomic status in relationship to *M. oculata* and *M. litoralis*. *M. relicta* can be found in freshwater lakes and the brackish coastal zones of both Europe and North America. In North America *M. relicta* ranges as far south as the Great Lakes and the Upper Lakes in New York and Wisconsin (Tattersall 1951; Holmquist 1958; 1963; Johnson 1964). *Mysis litoralis* is a recently described species. Banner (1948) described a new genus and species of mysid found in Puget Sound, *Pugetomysis litoralis*, which he redescribed in 1954 as *Mysis oculata*. Holmquist (1958) separated *M. oculata* into *M. litoralis* and *M. oculata*, further confusing distribution records for *M. litoralis*. She also defined the distribution of *M. litoralis* as circumpolar; it is found in Spitsbergen, Nobaya Zemlya, the Bering Strait, Baffin Island and Greenland. The distribution of *M. oculata* was described by Tattersall (1951) as circumpolar in the arctic regions (south to Labrador in the Atlantic and to the Gulf of Alaska in the Pacific); Banner (1948) extended that range to the Northwestern coast of the United States. *M. oculata* has also been found in algal beds in Greenland (Holmquist 1963) and in the Arctic Ocean where it is considered an under-ice dweller (Geiger 1969). In general, *M. oculata* is considered to be a marine species not commonly found in coastal waters (Holmquist 1963, Geiger 1969).

The differences in the habitat preferences of the arctic species of mysids are unclear, but there is some evidence that *M. relicta* prefers less saline waters than does *M. litoralis*. (Holmquist (1963) concluded that both are coastal and euryhaline, but that *M. relicta* prefers nearshore brackish waters, whereas *M. litoralis* avoids freshwater and ranges into the marine environment. Geiger (1969) collected both *M. litoralis* and *M. oculata* in the Arctic Ocean off the coast of Siberia but did not find *M. relicta*. We found that *M. relicta* and *M. litoralis* are both common in Simpson Lagoon but *M. oculata* was collected in offshore waters (Station 77-5) only in September of 1977.

Mysis litoralis

In temporate areas, mysids generally have a one-year life cycle (Wigley and Burns 1971; Morgan and Beeton 1978). *Mysis litoralis* collected in Simpson Lagoon and surrounding areas between 8 July 1978 and 15 May 1979 were separated into three year-classes on the basis of length-frequency distributions (Table 25, Fig. 29). However, both sexes of the larger (30-35 mm) third-year *M. litoralis* were only found in significant numbers in otter trawl samples taken seaward (1-5 km) of Pingok Island in 1978.

The size used for a division point between first- and second-year individuals increased throughout the year because growth continued for these organisms (Fig. 29). In most cases the division point was readily apparent; on dates when this was not the case (19 July, 18-30 August) the point was estimated. By 15 May 1979, the first-year individuals had reached the size that the second-year individuals were on 8 July 1978 (Fig. 29).

It is evident from Fig. 29 that second-year individuals were not always represented in the collections (e.g., 3 August, 14 and 23 September 1978), indicating that these animals possibly move about more than first-year individuals or that they occupy different habitats during certain portions of the year. First-year individuals (i.e., those individuals released in the spring of 1978) reached 10-12 mm in length by the end of the open-water season, second-year animals are 16-18 mm long at this time and third-year animals range from 25 mm to 35 mm. The Simpson Lagoon population consists predominantly of first-year animals and some two-year-old individuals.

Growth Rate. *Mysis litoralis* collected between 8 July 1979 and 15 May 1979 were used to determine growth rates (i.e., rates of increase in both total length and wet weight) for this species at various times in its life cycle (Table 25, Fig. 30). In these analyses, the mean length and weight of mysids on each collection data (not each individual mysid) constituted a unit of observation, and data were transformed to natural logarithms because growth was non-linear. The sexes have been combined in these analyses as there were no significant differences in the growth rates of males and females for either first-year (ANACOVA F for equality of exponents = 0.380 d.f. = 1, 13, $P > 0.25$) or second-year individuals (ANACOVA F for equality of exponents = 0.400, d.f. = 1, 10 $P > 0.25$). The relationships between time and both total length (mm) and wet weight (mg) are summarized below:

Table 25. Growth rate (total length and wet weight) for *Mysis litoralis* collected in Simpson Lagoon and surrounding areas, 8 July 1978-15 May 1979.

			All Individuals Combined				Male				Female			
				Length (mm)				Length (mm)				Length (mm)		
Year Class	Date	Day Number	n	$\bar{x}$	S.D.	wet weight* (mg)	n	$\bar{x}$	S.D.	wet weight (mg)	n	$\bar{x}$	S.D.	wet weight (mg)
First Year	8 July	1†	137	5.0	0.7	1.5	---	---	---	---	3	6.5	0.4	2.8
	19 July	11	864	6.5	1.2	2.8	---	---	---	---	442	7.2	1.3	3.7
	3 August	26	735	8.8	0.9	6.0	188	9.0	0.8	6.3	533	8.7	0.8	5.8
	18 August	41	681	9.7	1.0	7.6	270	9.9	0.9	8.0	411	9.6	1.0	7.4
	30 August	53	114	9.9	2.4	8.0	54	9.5	1.8	7.2	54	10.8	2.2	9.8
	14 September	68	57	10.9	0.9	10.1	28	10.9	0.9	10.1	28	10.9	0.7	10.1
	23 September	77	48	11.7	1.6	12.0	21	11.2	1.2	10.8	27	12.1	1.8	13.0
	15 November	130	182	12.7	1.5	14.6	104	12.6	1.6	14.3	78	12.7	1.2	14.6
	15 February	222	14	14.2	1.7	19.2	7	14.3	2.2	19.5	7	14.1	1.1	18.9
	15 May	311	1	15.0	---	22.0	1	15.0	---	22.0	---	---	---	---
Second Year	8 July	366**	7	16.5	1.3	27.7	3	15.7	1.9	24.5	4	17.2	0.1	30.7
	19 July	377	172	16.3	2.1	27.0	23	16.7	2.1	28.5	149	16.3	2.1	27.0
	3 August	392	---	---	---	---	---	---	---	---	---	---	---	---
	18 August	407	9	18.4	2.3	36.2	4	17.3	2.1	31.1	5	19.3	2.3	40.6
	30 August	419	9	17.2	0.8	30.7	5	17.5	0.7	32.0	4	17.0	1.0	29.8
	14 September	434	---	---	---	---	---	---	---	---	---	---	---	---
	23 September	443	1	17.0	---	29.8	1	17.0	---	28.8	---	---	---	---
	15 November	496	17	22.2	2.9	57.2	11	22.5	1.1	59.1	6	21.5	4.8	52.9
	15 February	588	11	23.7	3.0	67.1	2	23.6	0.8	66.4	9	23.7	3.3	67.1
	15 May	677	1	27.2	---	94.0	---	---	---	---	1	27.2	---	94.0
Third Year	8 July	731††	---	---	---	---	---	---	---	---	---	---	---	---
	19 July	742	5	23.1	2.4	63.0	1	22.2	---	57.2	4	23.1	2.2	63.0
	3 August	757	---	---	---	---	---	---	---	---	---	---	---	---
	18 August	772	2	25.8	2.3	82.6	2	25.8	2.3	82.6	---	---	---	---
	30 August	784	---	---	---	---	---	---	---	---	---	---	---	---
	14 September	799	---	---	---	---	---	---	---	---	---	---	---	---
	23 September	808	---	---	---	---	---	---	---	---	---	---	---	---
	15 November	861	---	---	---	---	---	---	---	---	---	---	---	---
	15 February	953	---	---	---	---	---	---	---	---	---	---	---	---
	15 May	1042	---	---	---	---	---	---	---	---	---	---	---	---

* Wet weight was calculated using total length-wet weight relationship shown in Appendix 1.

† Day 1 corresponds to the first collection date (8 July 1978).

** Day 386 assumes these *M. litoralis* are one year older than day 1 individuals.

†† Day 731 assumes these *M. litoralis* are two years older than day 1 individuals.

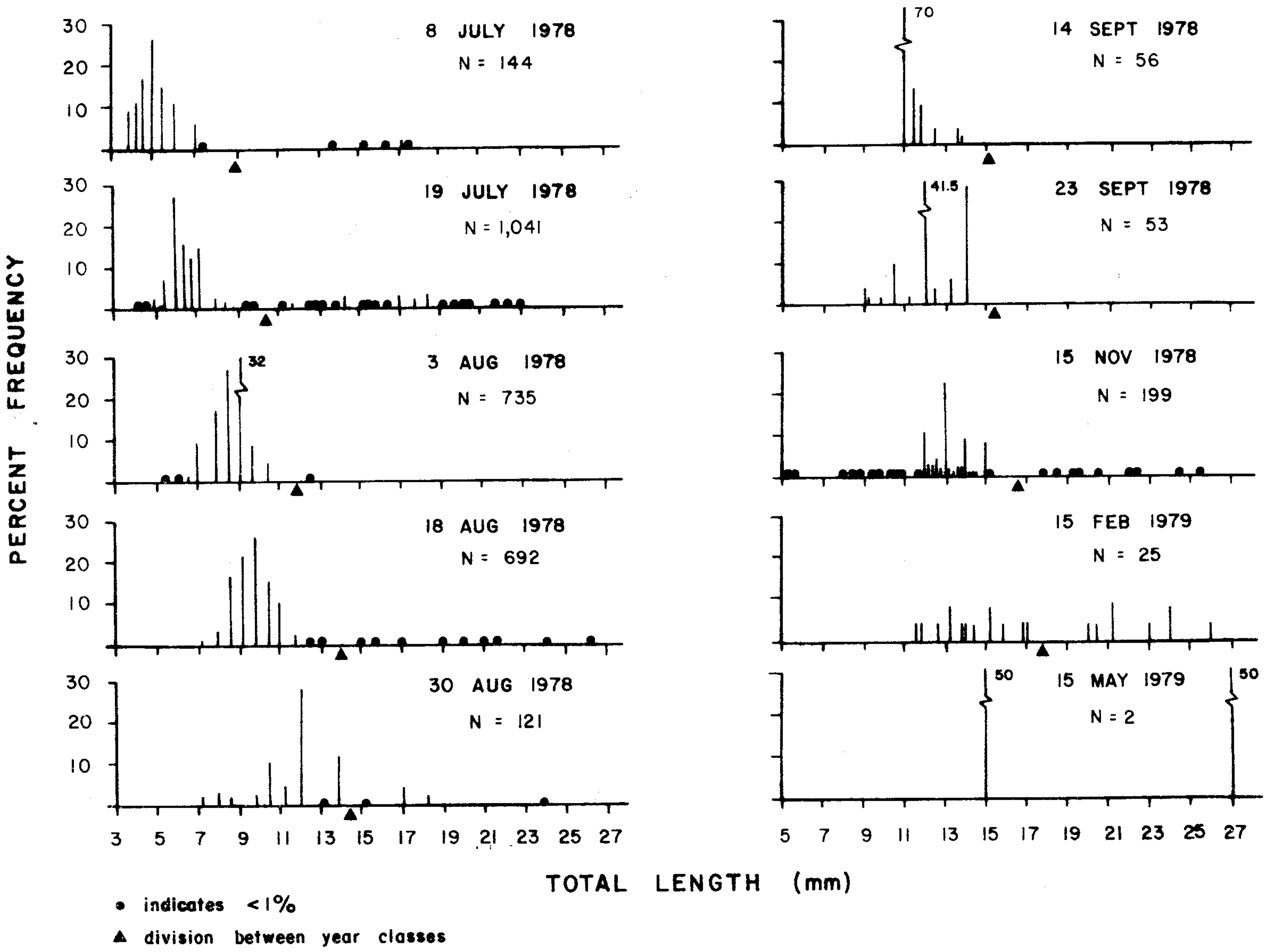


Figure 29. Length frequency of *Mysis litoralis* collected in Simpson Lagoon and adjacent waters 8 July 1978-15 May 1979.

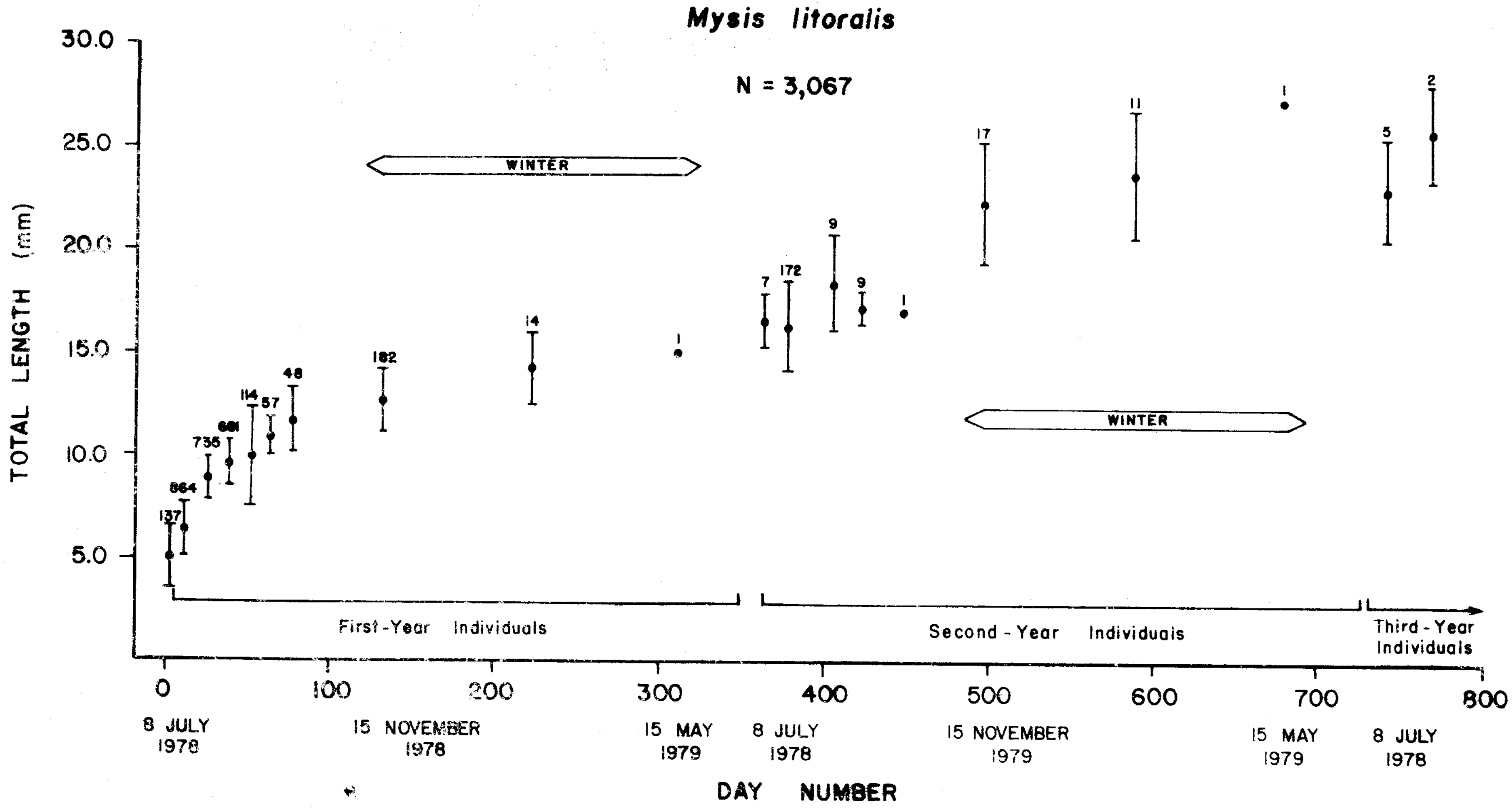


Figure 30. Increase in total length for first- and second-year *Mysis litoralis* in Simpson Lagoon and surrounding areas, July 1978-May 1979. Bars indicate ± SD.

First-Year Class	Total Length	$= 4.591(\text{day})^{0.203}$ $P < 0.001$	$r = 0.984$
	Wet Weight	$= 1.213(\text{day})^{0.499}$ $P < 0.001$	$r = 0.983$
Second-Year Class*	Total Length	$= 0.102(\text{day})^{0.855}$ $P < 0.001$	$r = 0.960$
	Wet Weight	$= 0.00011(\text{day})^{2.087}$ $P < 0.001$	$r = 0.960$
Third-Year Class	Insufficient data to determine significant relationships.		

Although sample sizes and numbers of individuals were insufficient during the under-ice period to allow for a statistical comparison of growth rates between summer and winter, some trends are obvious from Fig. 30. First-year individuals grew more rapidly in July and August of the open-water season; the rate then slowed after late August but continued through the under-ice period suggesting an active life style during this period (Fig. 30). A somewhat similar pattern appears to hold for the second-year class; however, the small number of individuals of this year class collected tends to confound the picture to some degree (Table 25, Fig. 30). The different growth rates exhibited by this species in summer and winter may be related to temperature and/or food availability (i.e., colder temperatures and/or less food available during the winter months causing decreased growth rates).

Reproduction. The sexes of mysids can be distinguished when mysids are ~6 mm in length on the basis of sexual characteristics described by Tattersall (1951) and Tattersall and Tattersall (1951). Male and female *M. litoralis* appeared to reach sexual maturity at different ages; sexually mature first-year males (10-12 mm in length) with elongated fourth pleopods (a breeding characteristic) were collected in Simpson Lagoon by the end of September, but no first-year females showing secondary breeding characteristics were found in these collections. Of the 19 female *M. litoralis* in breeding condition (carrying eggs or with brood pouches) collected during November from Harrison Bay to Stefansson Sound, none were first-year individuals (see Table below; also cf. Table 25). We concluded that breeding was apparently confined to second- and

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*For second-year class equations, only days 366-677 are valid.

third-year males and females with a possible contribution from first-year males. Differences in secondary sexual development have also been reported for other mysid species (Mauchline 1967, 1968, 1969, 1970 Wigley and Burns 1971).

Number of Females in Breeding Condition	Total Length (mm)	Number of Eggs/Brood Pouch	Diameter of Eggs (mm)	Comments
19	$\bar{x} = 24.2$ SD = 2.8 range 18-29	$\bar{x} = 48.9$ SD = 14.8 range 28-81	0.7-0.8	Only 10 females with intact brood pouches were considered in egg analysis

Most spawning appeared to occur in late September or early October; gravid *M. litoralis* were collected in November 1978 in Simpson Lagoon, Stefansson Sound and Harrison Bay. However, there may be a minor amount of spawning during the open-water season; three immature individuals with lengths typical of newly released young-of-the-year mean length 3.8 mm (range 3.5-4.1 mm) were found in Stefansson Sound in November 1978. The young are apparently brooded over winter and released the following spring, by which time they are 2-4 mm in length. In February 1979, a single *M. litoralis* (21.1 mm in length) collected in Simpson Lagoon was carrying 38 developing young mean length 2.2 mm, (range 2.0-2.3 mm), and in May 1978 another *M. litoralis* found in Stefansson Sound was carrying 61 young mean length 3.1 mm (range 2.7-3.8 mm) (Table 25). In both cases the brood pouch was intact. The exact time of release of young probably depends on conditions (perhaps temperature, food supply, etc.) immediately surrounding the female; because the coastal environment is spatially variable, release of necessary young by the population as a whole probably occurs over a long period.

Fecundity. Of the 19 female *M. litoralis* collected in breeding condition, only 10 had intact brood pouches. The spawning females averaged 24.2 mm in length and carried a mean of 48.9 eggs, 0.7-0.8 mm.

Fecundity was significantly related to total length ($r = 0.62$, d.f. = 10, $0.05 > P > 0.01$) (Fig. 31) indicating that the larger the female, the greater the number of offspring produced.

Mysis relicta

Mysis relicta collected in Simpson Lagoon and surrounding areas between 8 July 1978 and 15 May 1979 were grouped into two year-classes on the basis of length-frequency distribution data (Table 26, Fig. 32). As with *M. litoralis*, the size used for a division point between first- and second-year individuals increased over the year as growth continued (Fig. 32). In most cases the division point was clear; however, on dates when this was not the case (14 September, 23 September) the point was estimated. By 15 May 1979 the first-year individuals had reached the size that the second-year individuals were on 8 July 1978 (Fig. 32).

First-year individuals (released in the spring of 1978) reached a mean length of 8-10 mm (range 4-11 mm) by 23 September, and second-year individuals had reached a mean length of 14-16 mm (range 13-20 mm). A few larger *M. relicta* (23-28 mm) of both sexes were collected in otter trawls both inside and outside the lagoon, suggesting that some portion of the population lives at least three years. Insufficient numbers of these larger *M. relicta* have been collected to permit their inclusion in the following analysis.

In temperate lakes, *M. relicta* has essentially a one-year life-cycle, although in some cases a few females live an additional three months and produce a second brood (Tattersall 1951; Lasenby and Langford 1972; Morgan and Beeton 1978). McWilliams (1970) found that in Lake Michigan the life span of this species varied with depth and that individuals in shallow water lived only seven months but those in deep water lived for as long as 20 months. Larkin (1948) found *M. relicta* to live slightly longer than two years in Great Slave Lake; and a similar life span was reported for this species in Char Lake in the High Arctic (Lasenby and Langford 1972). It appears that the life span of *M. relicta* increases with latitude and water depth.

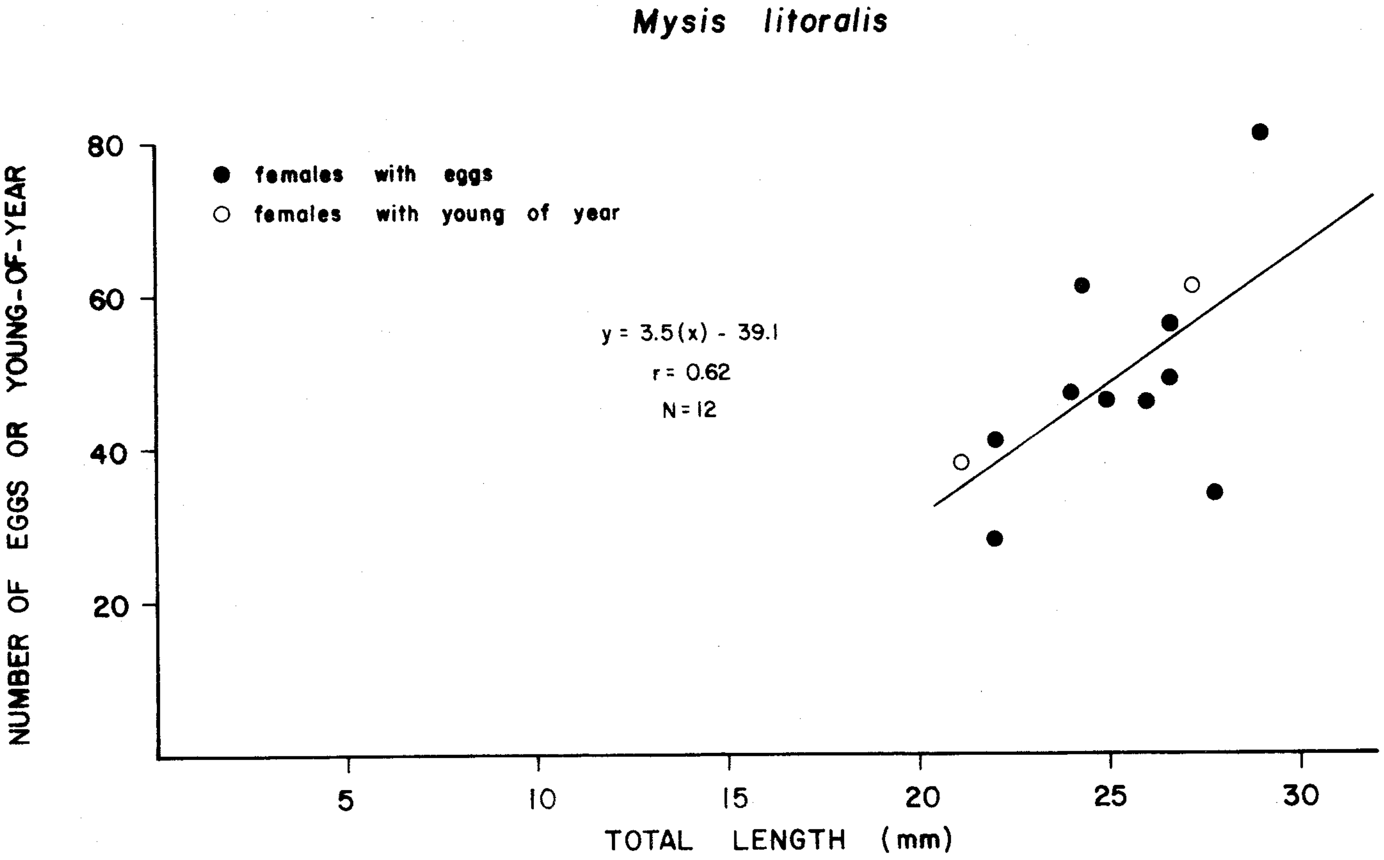

Figure 31. Relation between total length and fecundity for *Mysis litoralis*. Only individuals with intact brood pouches used.

Table 26. Growth rate (total length and wet weight) of *Mysis relicta* collected in Simpson Lagoon and surrounding areas, 8 July 1978-15 May 1979.

Year Class	Date	Day Number	All Individuals Combined				Male				Female			
				Length (mm)		wet weight*		Length (mm)		wet weight		Length (mm)		wet weight
			n	$\bar{x}$	S.D.	(mg)	n	$\bar{x}$	S.D.	(mg)	n	$\bar{x}$	S.D.	(mg)
First Year	8 July	1[†]	80	4.8	1.1	1.6	---	---	---	---	---	---	---	---
	19 July	11	177	6.1	0.8	2.8	2	6.9	0.5	3.8	88	6.3	0.7	3.1
	3 August	26	162	8.2	0.9	5.6	66	8.3	0.8	5.8	93	8.2	0.8	5.6
	18 August	41	82	9.1	1.0	7.2	48	9.2	0.8	7.4	34	9.0	1.3	7.0
	30 August	53	54	10.0	2.2	8.9	29	10.0	2.4	8.9	25	10.0	1.9	8.9
	14 September	68	313	10.4	0.9	9.8	146	10.3	0.8	9.6	166	10.5	0.9	10.0
	23 September	77	289	10.5	1.0	10.0	151	10.6	0.9	10.2	138	10.4	1.1	9.8
	15 November	130	---	---	---	---	---	---	---	---	---	---	---	---
	15 February	222	5	11.8	1.0	13.1	1	11.0	---	11.1	4	12.0	1.0	13.6
	15 May	311	24	13.3	1.1	17.3	15	13.2	0.9	17.0	9	13.6	1.4	18.2
Second Year	8 July	366**	17	14.0	1.8	20.6	6	14.5	2.0	21.2	11	13.7	1.8	18.6
	19 July	377	46	15.3	1.9	24.0	12	16.4	1.3	28.2	34	15.0	2.0	22.9
	3 August	392	7	16.1	2.2	27.0	3	14.9	1.5	22.5	4	17.0	2.3	30.6
	18 August	407	13	17.0	1.3	30.6	8	17.0	1.2	30.6	5	17.0	1.6	30.6
	30 August	419	10	16.3	0.9	27.8	3	16.5	1.1	28.6	7	16.2	0.9	27.4
	14 September	434	25	16.6	1.2	30.0	12	16.3	1.0	27.8	13	16.9	1.3	30.2
	23 September	443	14	17.9	1.2	34.5	5	17.5	0.6	32.8	9	18.2	1.4	35.9
	15 November	496	6	19.2	1.1	40.6	---	---	---	---	6	19.2	1.1	40.6
	15 February	588	9	20.5	0.7	47.3	---	---	---	---	9	20.5	0.7	47.3
	15 May	677	8	18.6	1.4	37.7	3	17.6	0.6	33.2	5	19.2	1.5	40.6

* Wet weight was calculated using total length-wet weight relationship shown in Appendix 2.

[†] Day 1 corresponds to the first collection date (8 July 1978).

[††] Day 366 assumes these *M. relicta* are one year older than day 1 individuals.

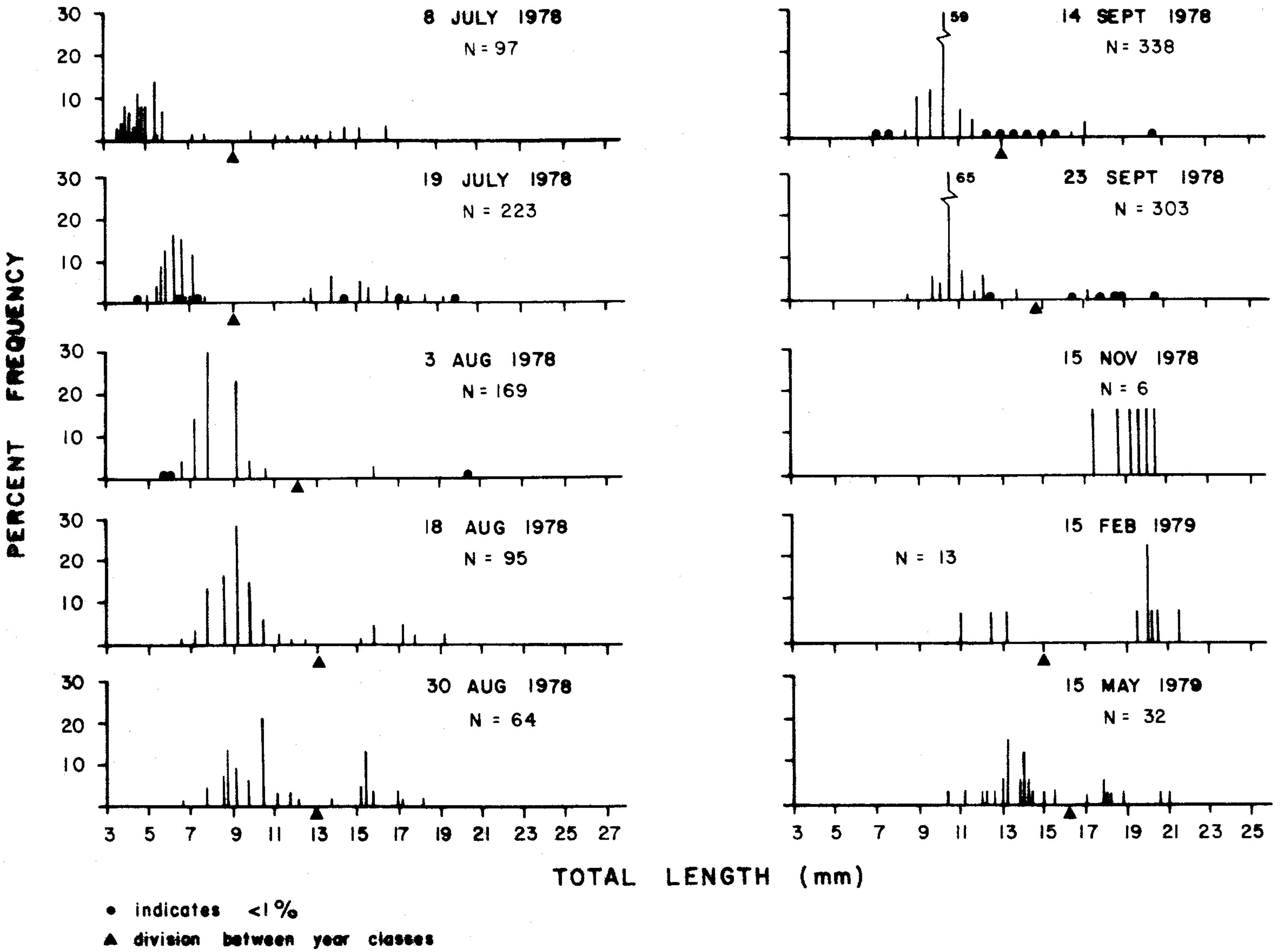

Figure 32. Length frequency of *Mysis relicta* collected in Simpson Lagoon and surrounding areas 8 July 1978-15 May 1979.

Growth Rate. For the subsequent analyses, the data were transformed to natural logarithms, and the mean for each collection date constituted a unit of observation. Growth rates for *M. relicta* collected in Simpson Lagoon and nearshore areas between 8 July 1978 and 15 May 1979 are shown, separately for each year-class and by sex, in Table 26 and Fig. 33. There were no significant between-sex differences in the growth rates for either first-year individuals (ANACOVA F for equality of exponents = 2.318, d.f. 1,12; $P > 0.10$) or second-year individuals (ANACOVA F for equality of exponents = 2.93, d.f. 1,14; $P > 0.10$), so that males and females of a given year-class were grouped for subsequent analyses.

The relationships between date and both length and weight are summarized below for each year-class. The year classes were separated to give a clear picture of growth during the first year; first-year individuals comprise the dominant group in the lagoon.

First-Year Class $\quad \text{Total Length} = 4.541(\text{day})^{0.185} \quad r = 0.98$
$\text{Wet Weight} = 1.408(\text{day})^{0.433} \quad r = 0.98$

Second-Year Class* $\quad \text{Total Length} = 0.967(\text{day})^{0.470} \quad r = 0.83$
$\text{Wet Weight} = 0.050(\text{day})^{1.053} \quad r = 0.84$

It is clear that individuals of both year classes grow rapidly until late August when the growth rate slows, but growth does continue through the winter (Fig. 33). However, insufficient numbers of *M. relicta* were collected in under-ice samples to allow for a statistical comparison of summer vs winter growth rates. The relative roles of reduced mean temperature, reduced food levels and other factors potentially causing this decrease in growth rate during winter are not known. Morgan and Beeton (1978) found young-of-the-year *M. relicta* in Lake Michigan to grow at a rate of 0.7 mm/30 days between March and September. Similar findings were reported for *M. relicta* by Lasenby and Langford (1972). This rate was slower than that of our first-year individuals during the 1978 open-water season; however, it should be noted that after 365 days young-of-the-year *M. relicta* had reached 14.0 mm length in both Lake Michigan and in Simpson Lagoon. Thus, the overall growth rate of *M. relicta* in the

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*These equations are only valid for day numbers 366-677.

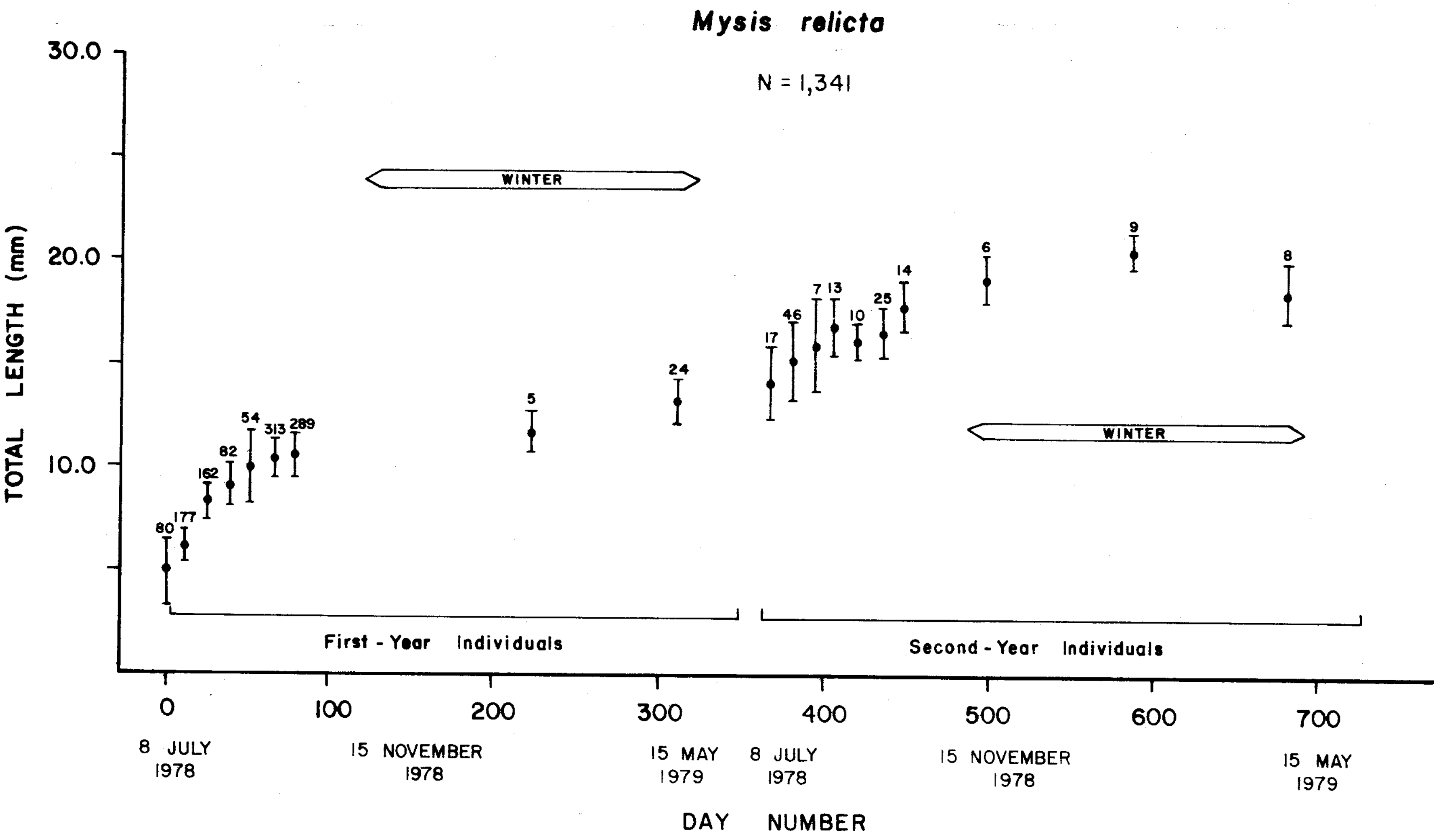


Figure 33. Increase in total length for first- and second-year *Mysis relicta* samples collected between 8 July 1978 and 15 May 1979 in Simpson Lagoon and surrounding areas. Bars indicate ± SD.

first year was similar in both areas. Growth, relative to that in temperate waters, appears to be faster in the summer in the Arctic, but slower in the winter.

Growth rates of *M. litoralis* and *M. relicta* were similar for first-year individuals (ANACOVA F for equality of exponents = 0.978, d.f. = 1,15, $P > 0.50$); however, second-year *M. litoralis* grew more rapidly than did second-year *M. relicta* (ANACOVA F for equality of exponents = 6.355, d.f. = 1,14, $P < 0.025$) (Fig. 34).

Reproduction. The sexes of *M. relicta* can be distinguished when they reach 6 mm in total length, although the animals are not sexually mature until they are 11-12 mm in length (Tattersall 1951). Large numbers of 8-10 mm (first-year) *M. relicta* were collected on 23 September; these animals included males with breeding characteristics (elongated fourth pleopod). However, no females in this size class showed evidence of sexual maturity (i.e., no brood pouch). Samples collected in November 1978 included gravid second-year *M. relicta* of mean length 19.2 mm (range 17.3-21.0 mm); these females contained a mean of 33 eggs, 0.7-0.8 mm in diameter. No first-year females (8-10 mm) were found in gravid condition in the November samples (Table 27). This indicates that first-year female *M. relicta*, like first-year female *M. litoralis*, do not breed; however, some first-year males may. McWilliams (1970) reported size differences between breeding male and breeding female *M. relicta* in Lake Michigan (mean lengths 14.5 and 17.8 mm, respectively).

Breeding appears to take place in late September or early October in the Simpson Lagoon area; in temperate zones *M. relicta* breeds from October to May (Juday and Birge 1927; Tattersall 1951). In our study area, the young are brooded until sometime in early spring; then they are released at about 2-4 mm in length. Samples collected in February 1979 contained 11 *M. relicta* that were brooding young. The mean length of these females was 20.4 mm (range 19.1-21.5 mm), and the mean length of their young was 2.4 mm, range 1.7-3.1 mm) (Table 27). None of the brooding females collected had an intact brood pouch, so no estimate of brood size was possible. No *M. relicta* brooding young were collected in April-May 1979, and in 1978 small free-swimming individuals (2-4 mm)

Table 27. Fecundity estimates of *Mysis relicta* collected during November 1978. Female *M. relicta* collected during February 1979 carrying young are also shown.

Number of Females in Breeding Condition November	Total Length (mm)	Number of Eggs/Brood Pouch	Diameter of Eggs	Comments
	$\bar{x}$=19.2	$\bar{x}$=33.0		Only three females with intact
11	S.D.=1.2	S.D.=2.6	0.7-0.8	brood pouches considered in
	Range=17.3-21.0	Range=30-35		egg analysis.

Number of females Carrying Young February	Total Length (mm)	Number of Young/Brood Pouch	Total Length of Young	Comments
	$\bar{x}$=20.4	---	$\bar{x}$=2.4	No intact brood pouches
11	S.D.=0.8	---	S.D.=0.3	found.
	Range=19.1-21.5	---	Range=1.7-3.1	

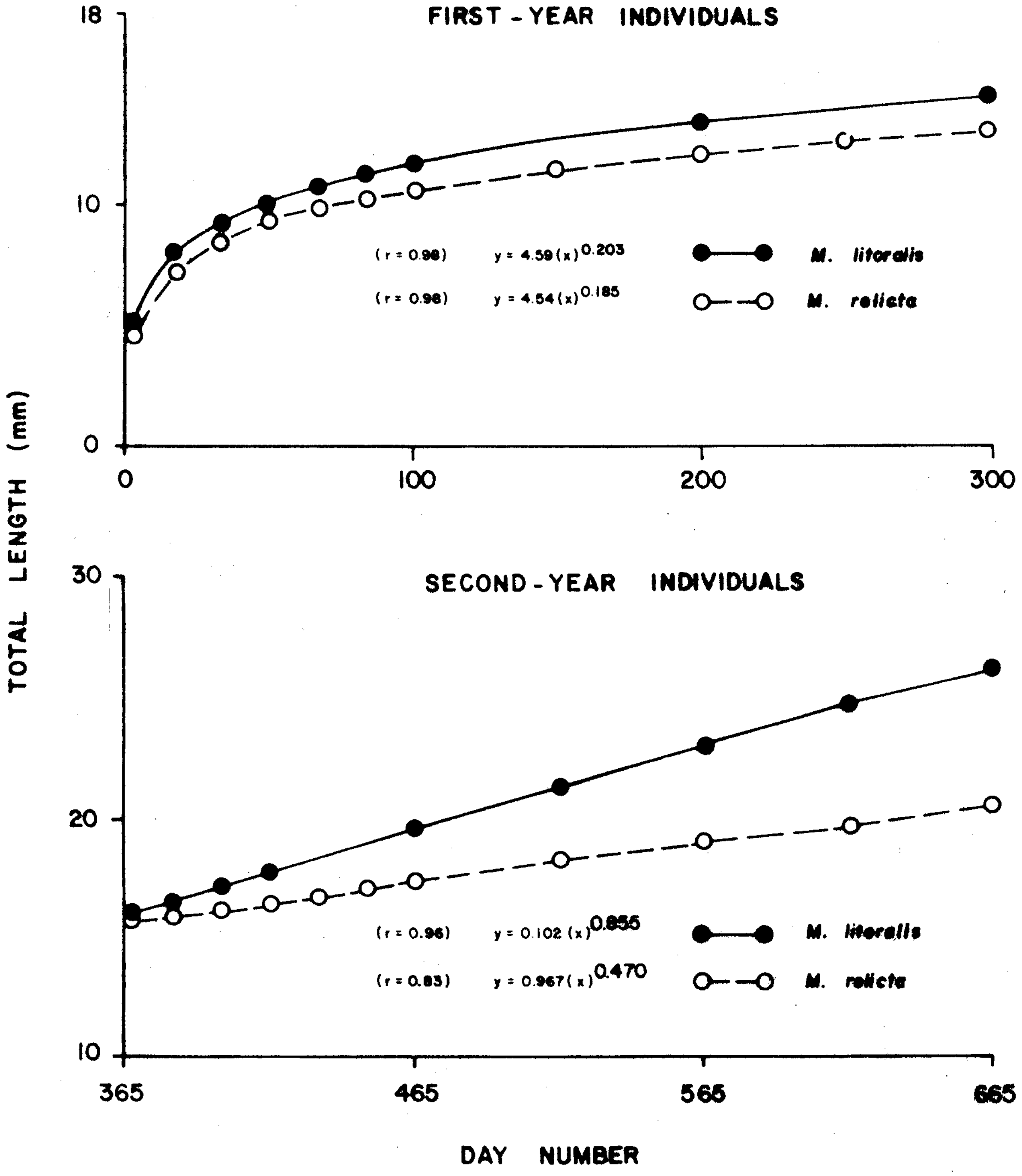
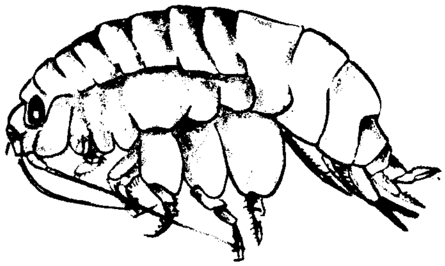


Figure 34. Comparison of increases in total length of *M. litoralis* and *M. relicta*. Lines represent best-fit equations.

were found in the lagoon in late June and early July. However, three female *M. relicta* with ruptured brood pouches containing several juveniles (2-4 mm) were also found, suggesting that all the young had not been released as of early July.

The main spawning period of *M. relicta* in Simpson Lagoon is in September and October, but some spawning occurred earlier during the open-water season. Drift net samples collected between the barrier islands from late July to late September contained male and female *M. relicta* (10-12 mm) with secondary breeding characteristics. No newly-released *M. relicta* or gravid females were captured during the summer; however, five juveniles of mean length 4.5 mm (range 3.7-5.5 mm) were collected in November 1978; they must have been released sometime after 23 September. Two individuals 4.2 and 4.3 mm in length were found in February 1979 in Simpson Lagoon.

Fecundity. Only three gravid *M. relicta* with intact brood pouches were collected during the winter sampling, so that an analysis of the relationship between total length and brood size was not feasible. The mean number of eggs in these three females was 33 (range 30-35), and egg diameters were 0.7 and 0.8 mm.



Onisimus glacialis

Our understanding of the biology of *Onisimus glacialis* is confused by uncertainty about its taxonomy. Whether *O. glacialis* and *O. birulai* should be grouped together as *O. glacialis* has been the subject of a great deal of taxonomic dispute. *O. birulai* has been described only for Arctic Russia, and is thought to replace *O. glacialis* and *O. litoralis* in that region. It is probable that *O. birulai* is a form of *O. glacialis*; considered together, the two forms range south as far as Kotzebue, Alaska, and the Strait of Belle Isle in North America, and occur off Iceland, Northern Norway, and the Russian Bering Sea in Europe and Asia (Shoemaker 1955; Holmquist 1965). Thus, the distribution of *Onisimus glacialis* is circumpolar subarctic to arctic.

Onisimus glacialis inhabits the nearshore, brackish water zone of Simpson Lagoon and is the dominant species of amphipod found there. Outside the barrier islands it is replaced by *O. litoralis* and *Boeckosimus affinis*, which in turn are replaced farther offshore by *Anonyx* spp. and possibly *B. plautus* (Dunbar 1954; Feder and Schamel 1976; Feder et al. 1976a and b; Griffiths and Dillinger 1979; H. Koch pers. comm.).

Specimens of *Onisimus glacialis* collected in drop net samples and amphipod traps during the 1978 open-water season and through the winter of 1978-1979 were separated into two year-classes on the basis of their size frequency distributions and the state of maturity of individuals (Table 28 and Fig. 35). From Fig. 35 it is evident that on 8 July 1978 the population of *O. glacialis* consisted of two distinct groups--(1) immature, first-year animals of mean length 3.8 mm (range 1.5-6.5 mm) and (2) sexually mature, second-year individuals of mean length 9.0 mm (range 7.5-11.6 mm). The size used for a division point between the two year-classes was $\leq$ 7.0 mm (i.e., immature vs mature) for the open-water period (8 July-23 September). For November and February the separation was estimated, and in May only one year-class was collected. If group (1), the immature first-year animals, is followed through subsequent samples, it can be seen that by the following spring (15 May 1979) these animals were approximately the same size as group (2), the sexually mature second-year individuals, had been on 8 July 1978 (Fig. 35). Animals belonging to group (2) on 8 July 1978 also increased in size in subsequent samples, but were entirely absent from the last sampling collections on 15 May 1979 (see 'Reproduction' below).

First-year immature animals released in spring 1978, the dominant group in the lagoon, averaged 5.3 mm in length by the end of the open-water season (23 September) and 8.0 mm by the spring of 1979 (15 May). Second-year individuals (released in spring 1977) averaged 10.2 mm by 23 September 1978 and 11.9 mm by 15 May 1979 (Table 28). Steele (1961) has postulated a similar two-year life cycle for *O. glacialis* in the eastern Arctic. However, several large (15-16 mm) individuals of both sexes were collected during the winter of 1978; this suggests that some small portion of the population lives beyond two years. Too few of

Table 28. Growth rate (total length and wet weight) for *Onisimus glacialis* collected in Simpson Lagoon 8 July 1978-15 May 1979.

			Sexes Combined				Male				Female			
				Length (mm)		wet† weight (mg)		Length (mm)		wet weight (mg)		Length (mm)		wet weight (mg)
Year Class	Date	Day Number	n	$\bar{x}$	S.D.		n	$\bar{x}$	S.D.		n	$\bar{x}$	S.D.	
First Year	8 July	1**	120	3.8	0.8	1.7	Individuals too small to be sexed.							
	19 July	11	711	4.0	0.7	1.9								
	3 August	26	366	4.1	0.8	2.0								
	18 August	41	483	4.4	0.7	2.4								
	30 August	53	187	4.8	1.1	3.0								
	14 September	68	172	5.6	0.7	4.5								
	23 September	77	134	5.3	0.6	3.9								
	15 November	130	129	6.7	0.8	7.1								
	15 February	222	184	7.6	1.3	9.8								
	15 May	311	527	8.0	1.0	11.1	17	9.8	0.9	18.7	252	8.6	0.6	13.4
Second Year	8 July	366††	40	9.0	1.0	15.1	10	9.9	1.2	19.3	30	8.6	0.8	13.4
	19 July	377	221	8.9	1.0	14.7	81	9.3	1.1	16.4	140	8.7	0.8	13.8
	3 August	392	67	8.2	1.0	11.9	31	8.6	1.2	13.4	36	7.9	0.6	10.8
	18 August	407	85	8.6	1.0	13.4	35	9.4	0.8	16.9	50	8.1	0.8	11.5
	30 August	419	48	9.4	1.4	16.9	14	9.8	1.1	18.8	29	9.4	1.5	16.9
	14 September	434	40	10.8	1.6	24.1	17	11.0	1.0	25.2	20	10.9	1.9	24.6
	23 September	443	50	10.2	1.5	20.8	29	10.7	1.3	23.5	17	9.8	1.2	18.8
	15 November	496	400	11.6	1.5	28.9	38	12.3	2.1	33.6	362	11.5	1.4	28.2
	15 February	588	24	12.3	1.4	33.5	4	13.3	1.0	41.0	20	12.1	1.5	32.2
	15 May	677	---	---	---	---	---	---	---	---	---	---	---	---

First Year Class: n=10	Total Length=0.015(day)+4.06 r=0.96 P<0.01 Wet Weight=0.034(day)+1.585 r=0.98 P<0.01		
***Second Year Class: n=9	Total Length=0.018(day)+1.79 r=0.90 P<0.01 Wet Weight=0.100(day)-23.873 r=0.93 P<0.01	Total Length=0.020(day)+1.65 r=0.92 P<0.01 Wet Weight=0.123(day)-30.380 r=0.94 P<0.01	Total Length=0.019(day)+1.25 r=0.88 P<0.01 Wet Weight=0.101(day)-25.101 r=0.90 P<0.01
First and Second Year Class: n=19	Total Length=0.014(day)+4.10 r=0.98 P<0.01 Wet Weight=0.046(day)+0.129 r=0.94 P<0.01		

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†Wet weight was calculated using total length-wet weight relationship shown in Appendix 3.

**Day 1 corresponds to the first collection date (8 July).

††Day 336 assumes these *O. glacialis* are one year older than day 1 individuals.

***For second year-class equations are only valid for day 366 to 588.

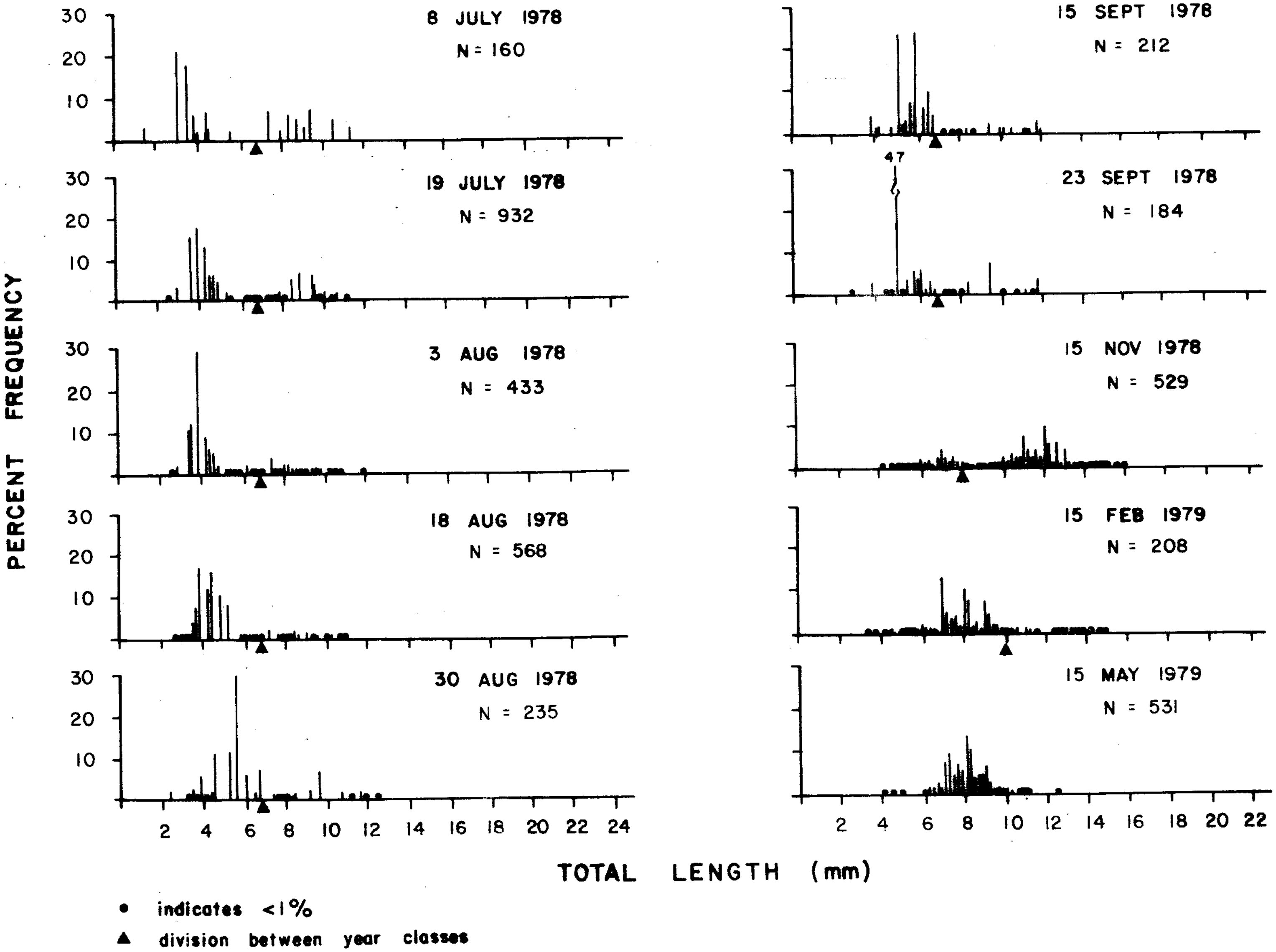

Figure 35. Length frequency of *Onisimus glacialis* collected in Simpson Lagoon 8 July 1978-15 May 1979.

these large *O. glacialis* were collected to permit their inclusion in subsequent analyses.

Growth Rate. Samples of *O. glacialis* collected between 8 July 1978 and 15 May 1979 were analyzed to determine increase in total length and wet weight in relation to time for both year-classes; this was done for the population as a whole and, where data permitted, separately for the different sexes (Table 28). These relationships were approximately linear and are summarized below.

	Daily Increase in Length (mm)	Daily Increase in Weight (mg)
First-year class	0.015 $(r = 0.96)$	0.034 $(r = 0.99)$
Second-year class	0.018 $(r = 0.90)$	0.100 $(r = 0.93$
Second-year males	0.020 $(r = 0.92)$	0.123 $(r = 0.94)$
Second-year females	0.019 $(r = 0.88)$	0.101 $(r = 0.90)$
Population as a whole	0.014 $(r = 0.98)$	0.046 $(r = 0.94)$

To statistically compare summer vs winter growth rates for both groups, each sample collected during the under-ice period was used as a unit of observation, but for the open-water season each unit of observation was the mean on each collection date. This was necessary because of the limited number of sampling periods during the winter.

For first-year individuals growth rates during the open-water and winter seasons differed significantly suggesting that growth decreased during winter (ANACOVA F for equality of slopes = 5.491, d.f. = 1,23, $0.05 > P > 0.01$) (Fig. 36). However, the winter slope for growth was significantly > 0 ($F = 35.115$, d.f. = 1, 19 $P < 0.01$), and suggests that growth is maintained during winter for this group, indicating that an active life style (i.e., feeding) persists during periods of low temperature (-1.5 to -2.0°C). Field observations during winter showed *O. glacialis* actively swam in holes that were cut through the ice.

The results of a similar analysis for second-year individuals were somewhat confused by the absence of this group after February. Growth rates during the open-water and winter seasons did not differ significantly (ANACOVA F for equality of slopes = 4.587, d.f. = 1, 14 $P > 0.05$) and the winter slope for growth was not significantly > 0 ($F = 3.087$, d.f. = 1, 10 $P > 0.10$). This suggests that second-year individuals stop growing during their second winter after breeding has occurred (see below).

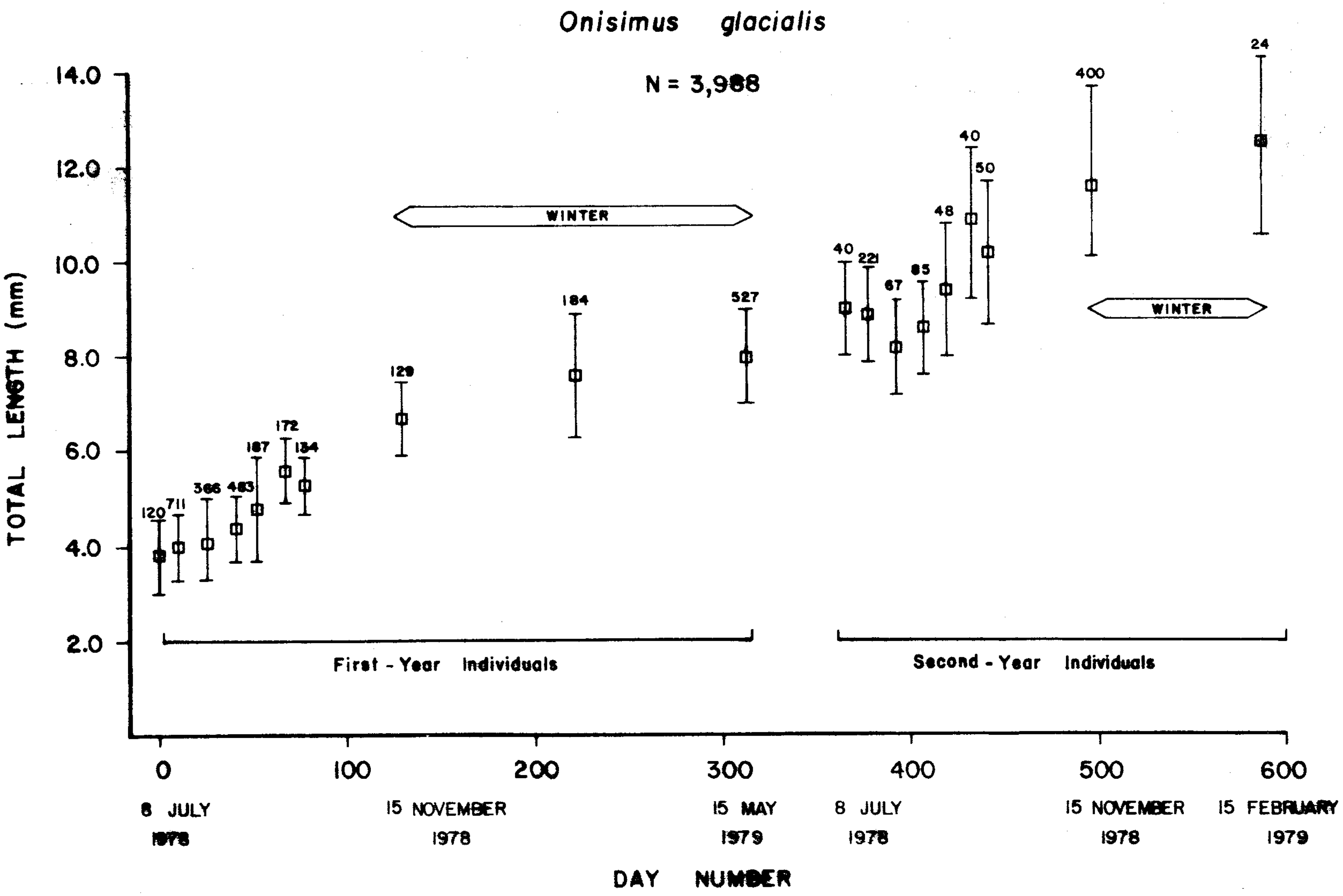

Figure 36. Increase in total length of first- and second-year *Onisimus glacialis*. Samples collected between 8 July 1978 and 15 May 1979 in Simpson Lagoon. Bars indicate ± SD.

There was no significant difference in the growth rate between the sexes (only second-year individuals are large enough to determine sex) (ANACOVA F for equality of slopes = 0.034, d.f. = 1, 14, $P > 0.75$). However, on each sampling date, second-year males were consistently larger than second-year females (Paired t-test = 5.874, d.f. = 8, $P < 0.001$) (Table 28), suggesting that male *O. glacialis* are larger at the start of their second year than corresponding females.

Reproduction. The majority of the *O. glacialis* found in the lagoon during the open-water season were juveniles (< 7.0 mm long). These had not attained sufficient size (8-10 mm) by 23 September, when open-water sampling was terminated, to permit us to distinguish gender.

Second-year males collected in Simpson Lagoon during September showed some lengthening of antennae, a breeding characteristic of *Onisimus* amphipods. However, second-year females collected at this time showed no brood pouch development or egg production.

Breeding times of *Onisimus* amphipods are not well-defined, but some breeding is known to occur in September or October in other arctic areas; several researchers have found male *O. glacialis* in varying stages of breeding condition at this time (Dunbar 1942, 1954; Steel 1961).

Samples collected in Simpson Lagoon during November 1978 contained 343 gravid *O. glacialis* of mean length 11.6 mm (range 9.5-15.0 mm). Thus, *O. glacialis* breed between September and November (Table 29). It appears that only second-year individuals (i.e., those released in the spring of 1977) contributed to the 1978 breeding population. The eggs produced in late fall are brooded during the winter. In February 1979, five female ($\bar{x}$ length 11.5 mm, range 10.5-14.2 mm) *O. glacialis*, brooding young ($\bar{x}$ number 11.5, range 9-14) were collected in Simpson Lagoon. The young ($\bar{x}$ length 2.1 mm, range 1.1-2.9 mm) were more advanced in their development (i.e., all appendages present) by this time, compared to *M. litoralis* or *M. relicta*.

By May 1979, our collections contained no males or females large enough to be second-year individuals. The female *O. glacialis* collected in May averaged 8.6 mm long (range 8.0-11.0 mm). This was significantly shorter than animals collected during November ($\bar{x}$ = 11.6 mm) and February ($\bar{x}$ = 12.1 mm). The males showed a similar trend; their average lengths were 9.8 mm in May but 12.3 mm in November and 13.3 mm in February. Second-year animals were also absent from March and April 1978 collections. Apparently the young had already been released by this time and the larger individuals had either died or moved to some other area. Small individuals (2.1-3.2 mm) were collected in Stefansson Sound and in Harrison Bay during the May 1979 sampling effort, but none were found in Simpson Lagoon.

Although most spawning by the Simpson Lagoon population appeared to occur in the fall, some breeding must also occur in the summer. Small individuals (2-3 mm), the size of recently-released *O. glacialis*, were collected during November 1978 in both Simpson Lagoon and in Stefansson Sound. In August, Feder and Schamel (1976) found *O. glacialis* with empty brood pouches in Prudhoe Bay; these animals had apparently released young recently, and thus must have bred in early spring. This wide range of breeding times has been reported for other arctic amphipods (*Stegocephalus inflatus*, *Pontoporeia femorata* and *Anonyx nugax*) by Steele (1961). *Onisimus litoralis* has been found to spawn in winter and spring in the eastern Arctic, and *Anonyx nugax* was found to have an extremely long breeding period (December to August) in Barrow Strait, N.W.T. (Foy 1978).

Fecundity. Eighty-seven gravid *O. glacialis* carrying a mean number of 11.2 eggs (range 9-15) of 0.7-0.8 mm diameter were collected in Simpson Lagoon in November 1979 (Table 29). There was no correlation between size of female and number of eggs (Fig. 37).

Other Species of Amphipods

A brief discussion of the other amphipod species collected in trawl samples, Faber hauls, drop net samples and fish and bird stomachs in Simpson Lagoon during 1977 and 1978 follows. The relative biomasses of all species of amphipods collected in the water-column and on the bottom in 1977, when all amphipods were identified, are shown in Fig. 38 and 39. As discussed in the 'Limitations and Biases' section, the trawl data in Fig. 37 are biased in that many individuals of the smaller species probably escaped through the coarse mesh used in the trawl.

Apherusa glacialis (Hansen). This pelagic amphipod is circumpolar, arctic-subarctic; it usually occurs in the upper portions of the water-column (Dunbar 1957) and under-ice (Barnard 1959; Buchanan et al. 1977;

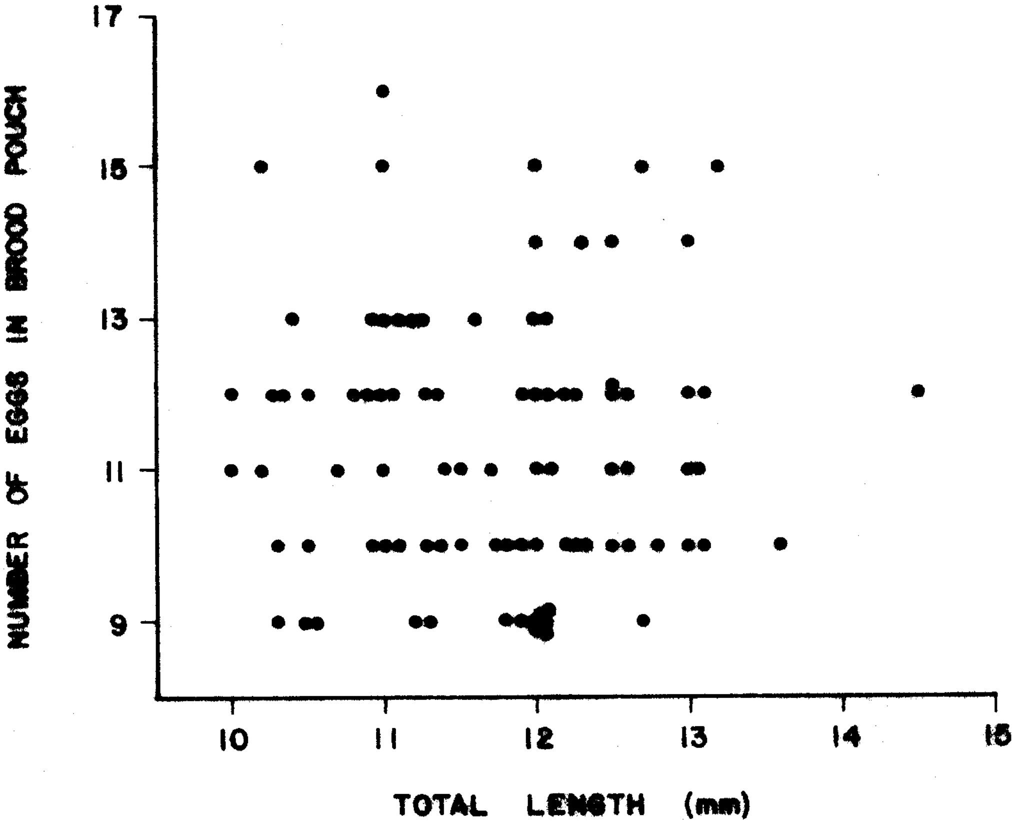

Figure 37. Relation between total length of *O. glacialis* and fecundity. Only individuals with intact brood pouches were used.

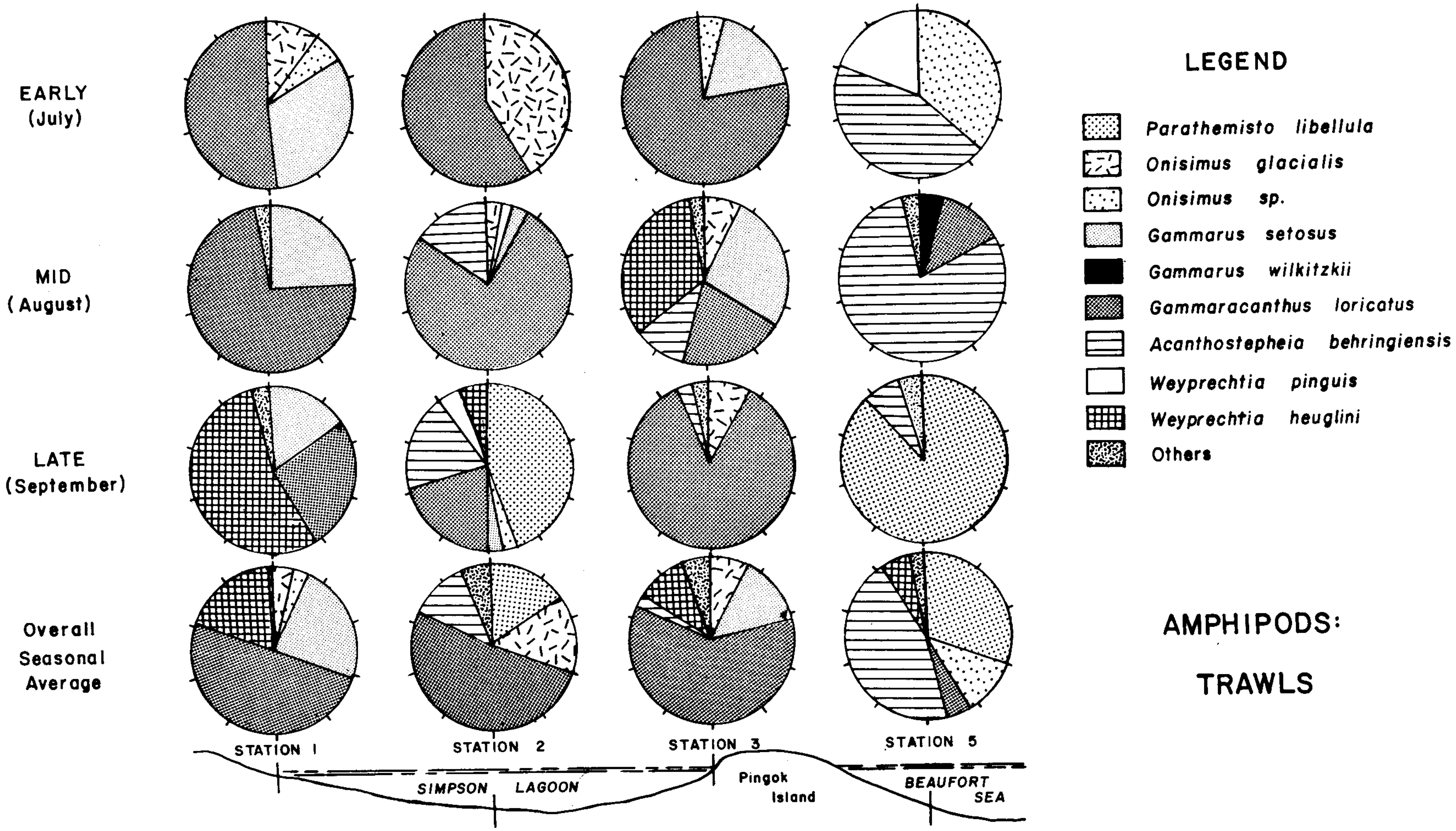

Figure 38. Relation biomass (g wet weight) of amphipods collected in trawl samples, Simpson Lagoon, 1977. Numerical details in Appendix 11.

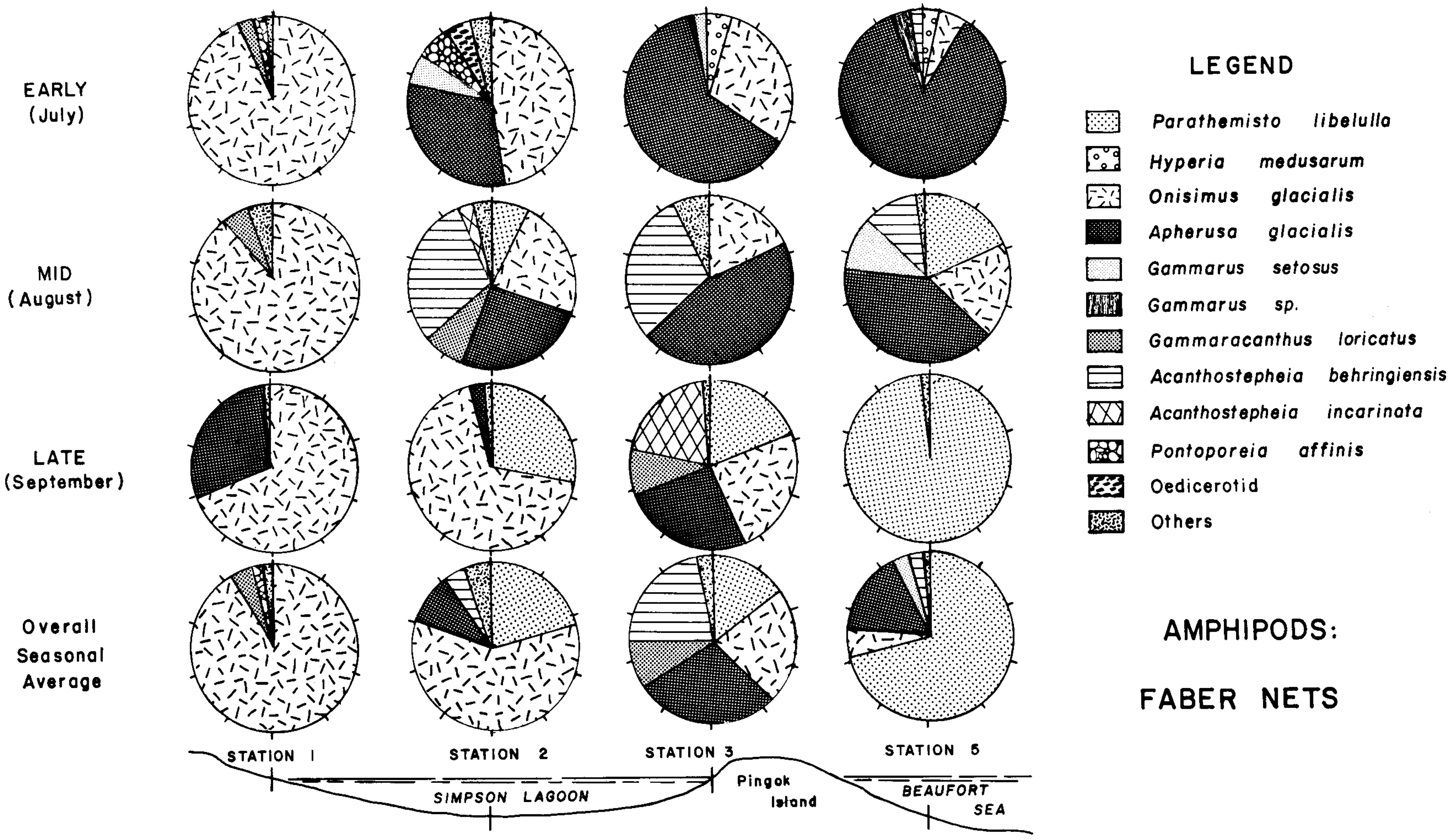

Figure 39. Relative biomass (g wet weight) of amphipods collected in Faber net samples, Simpson Lagoon, 1977.

Thomson et al. 1978). It is considered to be a member of the ice-associated amphipod community in the Alaska and Soviet Arctic and the Canadian High Arctic (Sekerak et al. 1976; Golikov and Averincev 1977; Divoky 1978). During summer it occurs in large numbers on the undersurface of ice pans, but it also occurs in the water-column in nearshore and offshore areas (Shoemaker 1955). Sekerak et al. (1979) sampled the entire water-column in northwest Baffin Bay during summer and found *A. glacialis* occurred at all depths (surface to > 1200 m), but was most abundant between 250-1200 m. In 1977, four oldsquaws collected on the ocean side of Pingok Island among many small ice pans had consumed large numbers of *A. glacialis*; inspection of the undersurface of these small pans revealed swarms of *A. glacialis*. Arctic cisco also fed on *A. glacialis* throughout the season.

In 1977 *A. glacialis* was not collected from the bottom in trawl samples (probably because of its small size); however, it formed a major component of the amphipod community in the water-column (Fig. 38). Generally, it was most abundant early in the season in offshore waters (Station 77-5) and on the lagoon side of the barrier islands (Station 77-3) (Fig. 38). The 1978 seasonal distribution of *A. glacialis* is presented in the 'Open-Water Season' section.

Pontoporeia affinis (Lindstrøm). *Pontoporeia affinis* is a widespread northern species, although it is not circumpolar in distribution. It is found in shallow brackish estuarine habitats and freshwater lakes in Europe and North America. In 1978 in our area, *P. affinis* showed a preference for warmer, less saline water (see 'Open-Water Season'). In 1977 it was not found in trawl samples, and only occasionally in the water-column.

In northern marine waters, individuals do not breed until the winter of their second year, and young are released in the following spring. In other areas, such as the Baltic Sea, a one-year life-cycle has been recorded; the shorter cycle is presumed to have been a consequence of the higher environmental temperature (Segerstrale 1967).

Pontoporeia affinis is considered by Segerstrale (1973) to be a deposit feeder; he recorded it feeding heavily on bivalve sprat in the

Baltic Sea. In our study this species was not an important food item for fish or birds except for arctic and least cisco collected in the Colville Delta, in the spring of 1978.

Halirages mixtus (Stephenson). This species was first described from water off eastern greenland by Stephenson (1931). Dunbar (1954) found *H. mixtus* in Ungava Bay and it was also captured in plankton samples taken in Frobisher Bay (Steele 1961). The species appears to have an Arctic distribution although there are relatively few distribution records. It was not recorded in our study area in 1977; however, in 1978, *H. mixtus* was collected both near the bottom and in the water-column (see 'Open-Water Season').

Gammarus setosus (Dementieva). This circumpolar species generally inhabits intertidal zones and shallow water (Ellis and Wilce 1961). It has been reported to be ice-associated in several locations in the eastern Canadian Arctic (Green and Steele 1975; Buchanan et al. 1977; Thomson et al. 1978). It is euryhaline and can survive in low-salinity waters (Steele and Steele 1970). In 1977 and 1978, *G. setosus* was collected intermittently near the bottom during the open-water season in Simpson Lagoon, but was rarely found in the water-column (Figs. 37 and 38; see 'Open-Water Season').

Only one brood is produced each year, and young are released in early spring when plant production begins (Steele and Steele 1970). Thomson et al. (1978) recorded 25 female brooding young in Brentford Bay, N.W.T., in May.

Steele and Steele (1970) found *G. setosus* to be predominantly carnivorous; however, Schneider and Koch (1979) found it to be able to assimilate organic detritus.

On a seasonal basis, *G. setosus* was not a major food item for oldsquaw (0.8-1.7% wet weight) ducks or fish (3.6% wet weight) in Simpson Lagoon in either 1977 or 1978 (Craig and Haldorson 1980; Johnson and Richardson 1980). However, in Creswell Bay, Sommerset Island, N.W.T. this species comprised 36.9% (wet weight) of the diet of oldsquaw ducks (Alliston et al. 1976).

Parathemisto libellula (Lichtenstein). In the Arctic this species is circumpolar in distribution; it is found in the Pacific Ocean and in the Bering and Okhotsk seas as well. The near-bottom and water-column distribution of *P. libellula* in 1977 and of *Parathemisto* sp. in 1978 are presented in the 'Open-Water Season' section and in Figs. 37 and 38. *Parathemisto libellula* is the largest member of the genus (up to 60 mm long) and is found in waters as deep as 2500 m (Shoemaker 1955). It has a two-year life-cycle in arctic waters and spawns from September to May or June (Dunbar 1957). The young are brooded in the female's marsupium and are released when they reach a length of 2-3 mm. In southeastern Alaska, *P. libellula* has a one-year life-cycle. Broods are released in early May. Juveniles initially live in the surface 50 m, but by late June (at a size of 10 mm) they migrate vertically. By late October, they have a daytime depth of 200-300 m. Males mature in late winter at 19-21 mm and females at 21-25 mm (Wing 1976).

The species is predominantly carnivorous but also ingests some vegetable matter (Dunbar 1946). *Parathemisto libellula* and *Parathemisto* sp. have been shown to be important food items for a variety of Arctic birds and mammals from the Chuckchi Sea, Alaska to northwest Baffin Bay, N.W.T. (Alliston et al. 1976; Divoky 1978; Lowry et al. 1978; Bradstreet 1977, 1979). In our area, *Parathemisto* sp. was found in oldsquaw stomachs only in September collections during both 1977 and 1978 (Johnson and Richardson 1980). In September 1977, glaucous gulls were observed feeding on windrows of *P. libellula* that had been stranded on the seaward side of Pingok, Island. However, these amphipods were never a major component of the fish diets (Craig and Haldorson 1980).

Parathemisto abyssorum (Boeck). This arctic species also occurs in deep waters of subarctic regions (Ekman 1953). Bowman (1960) found that *P. abyssorum* avoided shallow coastal waters and was generally found throughout the water-column over deep areas. In Lancaster Sound, N.W.T., during the summer of 1976, this species was more abundant in deeper water (150 m) than in shallow water (<50 m) (Sekerak et al. 1976). However, Sekerak et al. (1979) found that this species was most abundant in the top 150 m of the water-column in the Baffin Bay area.

In the Barents Sea, *P. abyssorum* requires two years to reach maturity, breeds once, and then dies (Bogorov 1940, in Bowman 1960). The breeding season in the Arctic extends from February to August (Bowman 1960).

Gammaracanthus loricatus (Sabine). This circumpolar amphipod was found in shallow water and depths of 35 m at Point Barrow (MacGinitie 1955; Shoemaker 1955). Ellis and Wilce (1961) found *G. loricatus* in Admiralty Inlet (Baffin Island) under boulders and among rockweeds. This species is at times pelagic and is found on the underside of permanent ice in the Arctic Basin (Barnard 1959). In 1977, *G. loricatus* was the most abundant amphipod in trawl samples, within Simpson Lagoon, possibly due to its large size (Fig. 37) (see 'Limitations and Biases'). In 1978, this species was rarely collected by the sampling technique used. *Gammaracanthus loricatus* is a hardy species and can tolerate great changes in salinity (MacGinitie 1955). Broad (1977) found this species to be omnivorous in feeding habit. In 1977, this species appeared only incidentally in the diets of oldsquaw ducks and arctic cisco.

Acanthostepheia behringiensis (Lockington). This amphipod is a widely-distributed arctic species and reaches lengths up to 37 mm (Shoemaker 1955). MacGinitie (1955) collected *A. behringiensis* at Point Barrow in water 3-4½ m deep. In 1977, trawl samples showed *A. behringiensis* to be most abundant in offshore waters (Station 77-5) during July and August (Fig. 37). This species feeds mainly on diatoms but is probably omnivorous (Broad 1977). *Acanthostepheia behringiensis* was not an important food item in the diets of either oldsquaw ducks or fish.

Bivalves

Bird feeding ecology studies conducted in 1977 and 1978 showed that bivalves, particularly *Cyrtodaria kurriana*, periodically comprised a portion of oldsquaw diets during the open-water season (Johnson and Richardson 1980). Airlift samples were collected at all stations during diving operations in 1978 to determine the distribution and biomass of this bivalve species. Data from lagoon Stations 78-1 and 78-5 (<2 m depth) were not included in the analyses because *C. kurriana* was found infrequently in samples at these sites, probably because the ice annually froze to the bottom there. Crane (1974) also reported few *C. kurriana* in shallow water (<2 m) during his survey in Simpson Lagoon. *Cyrtodaria kurriana* was only a minor component of the bivalve community at 1978 Stations 6 and 7 (ocean side of the barrier islands); there the bivalve *Portlandia arctica* was dominant. Carey (1977) reported a similar distribution for *C. kurriana* in that it was found alive only inshore of the barrier islands.

Results of all dates at deeper (>2 m depth) lagoon stations (78-2, 3 and 4) were combined to produce a seasonal mean density and biomass for *Cyrtodaria kurriana*.

No. of Airlifts	no./m^2	S.D.	mg ash-free* dry weight/m^2	S.D.
17	366.6	282.3	639.9	700.6

*Dry weight refers to body dry weight only, shell removed.

Crane (1974), using a grab sampler, found lower densities (112 ± 167 individuals/m^2) but higher biomasses (9.61 ± 13.69 g dry weight/m^2) in deeper (>2 m) portions of Simpson Lagoon. His dry weights included shells, and corresponds to approximately 1268.8 mg ash-free dry weight with shell removed. These results indicate that, on the average, his collections contained larger individuals than ours; however, Crane presented no specific information about size distribution. The apparent difference in size distribution between 1974 and 1978 may have been due to physical forces, as postulated by Feder and Schamel (1976). These authors found that size distribution and abundance of *C. kurriana* increased significantly between 1974 and 1975 in Prudhoe Bay (45 km east of Simpson Lagoon)(Fig. 40), and suggested that these increases in density and size were due to storm waters moving individuals of the species towards shore. MacGinitie (1955) also reported that storms moved bivalves toward shore at Point Barrow, Alaska.

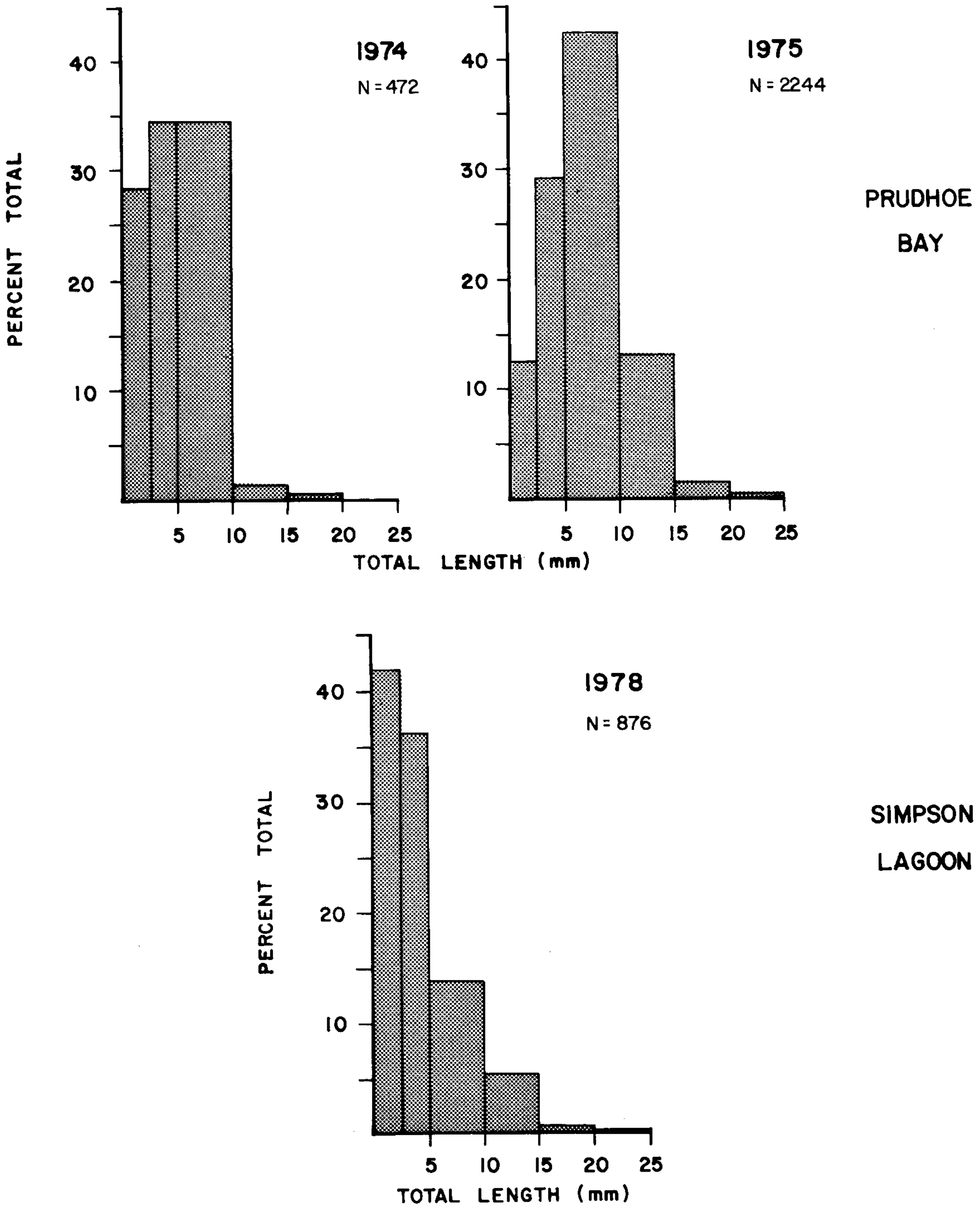

Figure 40. Length frequency of *Cyrtodaria kurriana* from air-lift samples collected in Prudhoe Bay (1974, 1975) and in Simpson Lagoon 1978.

Isopods

The isopod *Saduria entomon* was collected in all habitat types (i.e., shallow and deep water) in Simpson Lagoon and in the deep offshore waters during the open-water seasons of 1977 and 1978, and in under-ice samples during the winter of 1978-1979. Densities of this species were similar to those reported in other studies along the Beaufort Sea coast (range $1.0 \times 10^{-3}/m^2$ to $110 \times 10^{-3}/m^2$) (Crane 1974; Griffiths et al. 1977). In Simpson Lagoon, densities were highest ($110 \times 10^{-3}/m^2$) in waters more than 2 m deep.

Crane (1974) provides a detailed account of this species in Simpson Lagoon. He speculated that isopods in Simpson Lagoon emigrate as freeze-up progresses, perhaps in response to increases in salinity below the ice, and reoccupy the lagoon each spring from offshore areas. However, our winter collections showed that at least some small (<50 mm) *S. entomon* remain in Simpson Lagoon the entire winter.

Isopods were found in the diets of fish (particularly fourhorn sculpins) and birds during this study but not in significant numbers.

Tunicates

Tunicates were sampled during the 1977 open-water season. The presence of this sessile group at all lagoon stations indicates that they overwintered in the lagoon. The tunicate biomasses at Station 77-1 (nearshore mainland) early in the season and at Station 77-3 (nearshore barrier island) late in the season suggest that these animals may be able to withstand freezing, since the water freezes to the bottom at these shallow (<2 m) stations during the winter. Many of these tunicates were large (2.0 cm diameter), and had apparently been present for a considerable period. It is unlikely that they could have moved either out of the deep central portion of the lagoon earlier in the year or back into deeper waters late in the season. However, some redistribution of tunicates from the central lagoon may have occurred as a result of storm-generated turbulence.

Tunicates were not eaten by fish and were found in only one bird stomach during the two summers.

DISCUSSION

The results of the present study have been combined with the pertinent literature to assess the potential vulnerability of population regulating processes (e.g., breeding, growth, feeding), of key epibenthic invertebrates in the nearshore waters of the Alaskan Beaufort Sea, to development-related perturbations. These regulating processes can be affected either directly or indirectly. Direct effects could result from contamination by oil and refined petroleum products, natural gas, drilling muds and formation water. Indirect effects could be caused by changing patterns of temperature, salinity, tides, currents and migration; these changes might occur because of the construction of causeways or artificial islands, or through shoreline stabilization, barrier island removal and dredging. Where possible, factors affecting these processes have been treated separately in the following sections.

Temperature

The biology of estuarine epibenthic invertebrates is temperature-dependent (Kinne 1964; Vernberg and Vernberg 1972; Golikov and Scarlato 1973). However, the effects of temperature are variable and are often difficult to isolate from the effects of other environmental factors. For example, salinity tolerances decreased with increasing temperature for *Mysis relicta* and *M. stenolepis* (Dormaar and Corey 1973, 1978), but increased with temperature for *Neomysis vulgaris*, *Mysidopsis almyra*, and *M. bahia* (Vorstmann 1951; Conte and Parker 1971; Price 1976). In the case of two arctic amphipods, *Boeckosimus* (*Onisimus*) *affinis* and *Gammarus zaddachi*, salinity tolerances were inversely related to temperature (Busdosh and Atlas 1975; Percy 1975). In European estuaries, salinity tolerance also decreased with increasing temperature for *Gammarus* amphipods (Dorgelo 1974). Conversely, *G. palustris* (a salt marsh gammarid amphipod found on the east coast of the United States) was stressed by low salinities when temperatures were low (Van Dolah 1978). With these limitations in mind, the effects of temperature on mysids and amphipods in estuarine regions are discussed below.

Mysids

Although no temperature tolerance or preference tests were conducted during this study, the year-round (1978-1979) sampling in our study area suggested that both mysid species not only tolerated but thrived within a wide range of temperatures during the open-water season (0.2 to 13.5°C) and in winter (-0.5 to -2.0°C).

Holmquist (1959), cited in Fass (1974), found arctic mysids to be eurythermal, in that they survived both low (-2°C) and constantly high (17-18°C) temperatures. Gunter (1975) found that cold-water organisms appeared to have the ability to maintain a high metabolic rate at low temperatures. Our field observations tend to confirm this because mysids appeared to be equally active in summer and winter.

Temperature affects several aspects of mysid biology (e.g., breeding and brooding time, incubation, growth, migration). In temperate regions, breeding of some mysids is initiated by increasing temperature (Muus 1967; Rasmussen 1973; Pezzack and Corey 1979). In our study area, both *Mysis litoralis* and *M. relicta* bred in early winter (October to November), when water temperature in Simpson Lagoon fell below freezing for the first time since spring (early July). However, winter results showed that breeding occurred simultaneously in the lagoon and in deeper offshore waters, where the bottom temperatures remain constantly near or below freezing year-round. This suggests that breeding may perhaps be stimulated by a more consistent factor (e.g., photoperiod).

Incubation in *Neomysis americana* and *Mysis stenolepis* is temperature-dependent; growth of brooded young slows or stops during winter enabling them to be held until spring, a more favorable period for rapid growth (Amaratunga and Corey 1975; Pezzack and Corey 1979). In Simpson Lagoon, *M. litoralis* and *M. relicta* both follow a similar strategy; the young grow and develop slowly through the winter and are released in the spring (Table 25 and 27).

No obvious effects of temperature on molting frequency and growth rates of *Metamysidopsis* sp. in California were observed by Clutter and Theilaker (1971). Faas (1974) stated that the metabolic rates of temperate mysids were greatly reduced in winter. Most species consumed less or stopped feeding entirely, and *Neomysis integer* nearly ceased growing at -2°C (Faas 1974). The winter growth rate for *M. relicta* appears to be variable. In Lake Michigan, its most rapid growth was in January-April (Reynolds and DeGraeve 1972); in Stony Lake, Ontario, and Char Lake, N.W.T., the winter rate decreased (Lasenby and Langford 1972); while in Paajarvi Lake in Finland growth ceased (Hakala 1978). In Simpson Lagoon *M. litoralis* and *M. relicta* continued to grow during the winter months, although at a reduced rate, and thus presumably continued feeding (Tables 24 and 26, Figs. 30 and 33). This reduced growth rate may be either temperature-dependent or the result of a reduction in available food or both.

Migratory behavior in mysids has been related to temperature. In the Indian River inlet, Delaware, decreased winter temperatures cause *Neomysis americana* to move to deeper water (Hopkins 1965). A similar phenomenon has been reported in Denmark and Sweden for *N. vulgaris* (Muus 1967; Rasmussen 1973). Although *Mysis litoralis* appeared to emigrate out of Simpson Lagoon in late fall and early winter and reoccupy it in the following spring (Tables 8, 9 and 12), there are no data to show whether these movements are temperature-dependent.

Amphipods

Although no temperature tolerance or preference tests were conducted during this study on *Onisimus glacialis*, the principal amphipod in Simpson Lagoon, this eurythermal organism was collected and apparently thrived in a wide range of temperatures (-2.0 to 13.5°C) during 1978-79.

Temperature-associated breeding in amphipods has been documented by several authors. Kine (1963) found reproduction in amphipods to be primarily temperature-dependent, and for intertidal, burrowing and subtidal tubicolous amphipods, increased spring temperatures initiated breeding (Nagle 1968; Parker 1969; Fincham 1970; Coker et al. 1975). Autumn breeding in *Onisimus* (*Pseudalibrotus*) and other arctic amphipods provides for release of the young in the spring when temperature and food supply are most favorable (Steele 1961). In Simpson Lagoon, *O. glacialis* breeds in early winter, but whether this breeding is induced by temperature, photoperiod or other factors is uncertain.

Most temperate amphipods reduce or cease feeding during winter months (Faas 1974), and in the case of *Gammarus duebeni* growth ceased at -2°C (Kinne 1963). In contrast, first-year *O. glacialis* in Simpson Lagoon continue to grow and presumably feed through the winter months (-2°C), although at a rate slightly reduced from that of the open-water period (Table 28, Fig. 36). The brooded young of *O. glacialis* also grow and develop during the winter months and are released in late winter (i.e., prior to April).

The distribution of amphipods may also be temperature related. In a study at Cape Cod, Sameoto (1969a, b) found haustoriid amphipods to be distributed vertically through the water column according to temperature tolerance. Intertidal species, *Haustorius canadensis* and *Neohaustorius biarticulatus*, tolerated temperatures of up to 41°C; the subtidal species *Acanthohaustorius millsi*, *Protohaustorius deichmannae* and *P. longimerus* succumbed at 39°C.

Amphipods may migrate in response to temperature changes. Decreased winter temperatures initiated a seaward migration in *Gammarus palustris* (Van Dolah 1978) and *Bathyporeia* spp. and in haustoriid amphipods (Fincham 1969; Coker et al. 1975). However, Moore (1978), found no temperature-induced migration patterns in haustoriid amphipods in the Mersey estuary, although such had been documented earlier by Fincham (1970). In our study, *Onisimus glacialis* appeared to utilize Simpson Lagoon year-round, suggesting that no temperature-induced migration occurred (Tables 7, 8 and 9).

Other Crustaceans

Most temperature related research on invertebrates has dealt with the economically important groups (e.g., shrimp, crabs).

Population success of brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, is affected by temperature. For example, laboratory experiments by Zein-Eldin and Aldrich (1965) suggest that low winter temperatures in brackish bay systems are unfavorable for survival and growth of brown shrimp postlarvae.

In Barataria Bay, Louisiana, growth rates of brown shrimp range from 20-45 mm per month in summer, and increase with temperature above 20°C and salinities below 22 ppt (Jacob and Loesch 1971). Juvenile white and brown shrimp found in Mobile Bay, Alabama, grow more rapidly in summer (June to September) than in winter (Loesch 1965). Growth and reproduction of the grass shrimp, *Palaemonetes pugio*, are temperature-dependent; growth was most rapid at high temperatures (30°C), and a minimum temperature of 18-20°C was required for reproduction (Wood 1967).

Movements of penaeid shrimp appear to be strongly temperature-dependent. For example, in the Gulf of Mexico, these shrimp move onshore in the spring and offshore in the fall. Gunter et al. (1964) felt these movements were due to changes in salinity; however, a number of authors found temperature to be a major factor (Gunter 1950; Williams 1959; Hoese 1960; Gunter 1961a; Barrett and Gillespie 1973; Gaidry 1974; Barrett and Ralph 1976).

Holland et al. (1971) found that the survival of blue crab larvae (*Callinectes sapidus*) increased with increasing temperature, but decreased with a combination of high salinities and lower temperatures. Costlow (1967) suggests that blue crabs required both high salinity and high temperature for successful metamorphosis and increased survival.

In summary, while eurythermal nearshore arctic organisms can tolerate and survive well in a wide temperature range, some biological processes (breeding and growth) may occur at optimal levels only within a relatively narrow band of temperatures. For example, in Simpson Lagoon, both species of mysid and the amphipod *O. glacialis* grow more rapidly during the warmer open-water periods than in the winter months. Breeding and the brooding of young occur during the winter months, so that the young are ready for release during the spring--the most opportune time for rapid growth. Although no single pattern of response to temperature variations will hold for all epibenthic species in arctic estuaries, the wide range of tolerance exhibited by most species suggests that a shift in these patterns, of a few degrees centigrade, will not adversely affect the organisms involved.

Salinity

Marine epibenthic invertebrates can be divided into two groups: stenohaline, those tolerating only a narrow salinity range, and euryhaline, those able to adjust to a broad salinity range (Kinne 1964). Typically, stenohaline organisms dwell in the open ocean and appear in estuaries only as migrants brought in by the tides or currents; euryhaline animals are typically estuarine in distribution for at least part of their life cycle (Day et al. 1952; Scott et al. 1952; Doreglo 1974).

Mysids

Although *Mysis relicta* and *M. litoralis* are both considered euryhaline, their salinity preferences differ. *Mysis relicta* is a euryhaline species found in all waters from fresh to marine (Tattersall 1954; Dormaar and Corey 1978). In the present study, *M. relicta* was significantly more abundant along the mainland shore where the water was more brackish than along the lagoon shore of the barrier islands where the water was usually marine (Fig. 11). Typically, this species was not abundant at the more marine ocean stations during the study (Fig. 10), suggesting that *M. relicta*, in our system, prefers brackish rather than marine waters. *Mysis litoralis* has not been found in fresh water, but it has been collected in a wide variety of brackish and marine habitats (Holmquist 1958, 1963). Holmquist (1963) estimated that both *M. litoralis* and *M. relicta* can tolerate a salinity range of 0-60‰. Faas (1974) reported that *M. relicta* survived salinities ranging from 1 to 65‰. Broad et al. (1979) found that *M. litoralis* collected at Point Barrow, Alaska, tolerated acute salinity changes (range 5-70‰) and gradual salinity changes (5‰ increments every 2 days) from 0.25 to 65‰, and thrived at salinities ranging from about 5 to 45‰. In the Simpson Lagoon area, both *M. litoralis* and *M. relicta* were collected in a wide range of salinities (1-36‰), suggesting that these species are well adapted to the estuarine environment.

Holmquist (1963) reported that mysids, amphipods and other estuarine organisms, in Northern Alaska, apparently preferred the hypersaline (40-60‰) unfrozen bottom waters during the winter months and did not hibernate as resting stages, although the survival mechanisms are unknown. However, in Simpson Lagoon, winter results suggested that densities and biomasses of both mysids decreased (possibly due to a combination of mortality and emigration) as winter progressed (Table 12). By late winter, salinities in the lagoon had reached 50-60‰ and, although both species of mysid can tolerate these high salinities, they seem to prefer the more marine offshore waters or deeper (≈5 m) but less saline (30-35‰)nearshore waters (e.g., Stefansson Sound; Tables 7, 8, 9 and 12). It is evident that both mysid species have adapted physiologically to the harsh winter conditions, as both continue to grow and reproduce.

In other estuarine areas, including the Atlantic and Pacific Oceans, the Gulf of Mexico and the coastal waters of Britain, euryhaline mysids are common; tolerance of high rather than low salinity is usually the rule. Salinity tolerances ranged from 0 to 35‰ for *Mysis stenolepis* (Dormaar and Corey 1973), *Neomysis americana* (Hurburt 1957), *Mysis oculata* (Remane and Schlieper 1958), and *Mysidopsis almyra* and *Taphromysis louisiana* (Conte and Parker 1971; Odum 1971; Price 1976), and from 10 to 35‰ for *Gastrosaccus dissimilis* and *Mysidopsis bahia* (Odum 1971), *Neomysis vulgaris* (Percival 1929; Vorstman 1951; Wittman 1978) and *Neomysis* (*awatschensis*) *mercedis* (Turner and Heubach 1969).

Amphipods

Most estuarine gammarid amphipods are euryhaline (Day et al. 1952; Saunders et al. 1965; Odum 1971; Larson 1976; Thomas 1976). Although salinity tolerance vs preference experiments were not conducted, *Onisimus glacialis* were collected and appeared to thrive in a wide range of salinities (1-54‰) during this study. Salinity changes in the Simpson Lagoon area can be very dramatic (e.g., from > 35‰ to 0‰) in less than 24 h during inundation of the lagoon by the Kuparuk River 7-8 June 1978, Matthews 1979). Similar rapid osmotic adjustments appeared necessary for amphipods in hypersaline under-ice communities; these amphipods tolerated the rapid salinity shifts typical during spring runoff (Mohr and Tibbs 1973, cited in Faas 1974).

Busdosh and Atlas (1975) and Percy (1975) found that an amphipod of a closely related genus, *Boeckosimus affinis*, was able to tolerate acute salinity changes (4-50‰) over a range of temperatures (5-15°C), to tolerate an even wider range of salinities (4-63‰) if the changes were gradual, and to tolerate higher salinities if temperatures were lower (5-15°C vs 25°C).

In the arctic coastal zone, Carey (1978) found fewer species of epibenthic gammarid amphipods than in deep offshore waters. He attributed this to the extreme variations in salinity and to habitat disturbance by sea ice. Gammarid amphipods collected in Simpson Lagoon (e.g., *Gammaracanthus loricatus*, *Gammarus setosus*, *G. wilkitzkii*, *Weyprechtia heugleni* and *W. pinguis*) are euryhaline estuarine species able to tolerate salinities from 1 to 50‰. They appear to utilize the shallow nearshore areas year-round (Tables 7, 8 and 9). Van Dolah (1978) found *Gammarus palustris*, a tidal salt marsh amphipod, to be more affected by low salinity at low temperatures. Generally, species affected by low salinities are able to migrate vertically or horizontally to regions of favorable salinity (Brattegard 1966).

Amphipods of the Baltic Sea display a range of salinity tolerances. For example, *Gammarus* spp. and *Calliopus laevisculus* are considered euryhaline (Dahl 1973; Jazdzewski 1973); however, the two species of *Pontoporeia* show niche differentiation with respect to salinity. *P. affinis* ranges from fresh to brackish water but is absent from truly marine habitats, while *P. femorata* is typically marine (Dahl 1973). In Simpson Lagoon *P. affinis* was most abundant along the shore, a region of lower salinities (range 2-24‰) than at other lagoon stations (salinity range 14-30‰) while *P. femorata* was usually found only at the offshore marine station.

Gammarid amphipods in other estuarine areas also show salinity related niche determination; some authors feel that salinity is the main limitation on amphipod distribution (Goodhart 1941; Reid 1941; Bassindale 1942).

In the deltas of the Rhine, Meuse and Scheldt rivers, gammarid amphipods are distributed according to salinity tolerances. *Marinogrammus marinus* is intertidal (salinity range 10-25‰, *M. obtusatus* is more marine (salinities > 28‰),*Gammarus duebeni* and *G. locusta* are generally estuarine in habitat (salinity range 5-35 , and *G. zaddachi* is tolerant of low salinities (range 2-15‰)but is unable to penetrate fresh water (Den Hartog 1964).

Other Crustaceans

Shrimp production in the Gulf of Mexico is related to salinity; however, the range of salinities suitable for growth and survival increases with increasing water temperature (Zein-Eldin and Aldrich 1965).

Freshwater input from rainfall and river discharge reduces estuarine salinities and can affect shrimp production (Barrett and Gillespie 1973). In Louisiana estuaries, production for both white (*P. setiferus*) and brown (*P. aztecus*) shrimp was better when river discharges were low, while the poorest production occurred during years of high river discharges (Barrett and Gillespie 1973; Barrett and Ralph 1976). However, white shrimp appear to have greater tolerance of low salinities than brown shrimp (Gunter 1961b), and studies in Texas estuaries (which receive a much lower average freshwater discharge than Louisiana) suggest that higher rainfall and runoff lowers the salinity to optimum values for white shrimp (Gunter and Hildebrand 1954; Gunter 1961b).

In summary, estuarine epibenthic invertebrates in Simpson Lagoon are able to tolerate and thrive in wide ranges of salinities and consequently, shifts of a few ppt in the salinity patterns would not be expected to have noticeable effects on the organisms. However, since no studies have been conducted on the salinity preferences or on the optimal salinities for major biological processes (e.g., growth and breeding) of the major individual species, the effects of long-term large changes in the salinity patterns of Simpson Lagoon cannot be predicted with accuracy.

Tides and Currents

The effects of tides and current-caused water movements through an estuary are variable. The water movements can be either beneficial, by replenishing and turning over food supplies, or detrimental, by moving organisms into less desirable environments.

Mysids

Holmquist (1963) found *M. relicta* in isolated coastal arctic ponds and speculated that they had been carried in from the sea by the high tides or storm surges. In laboratory studies, Holmquist (1959), cited in Ricker (1959), found *M. relicta* able to turn against a gentle current and take refuge in the bottom detrital layers; however, a strong current would wash them away. Although Ricker (1959) did not observe *M. relicta* to swim against the current during his field observations, in Simpson Lagoon, a concentration of *M. litoralis* and *M. relicta* (1.3 m in width ; estimated densities of 10,000-50,000 mysids/m^2) was observed in water (0.2 m deep) next to shore on 2 August 1978. The mysids were moving with the current (approximately 5 cm s^{-1}) but were oriented into it and easily swam against it when startled. Other authors have found that mysids are capable of holding their position or even advancing against tides and currents. Clutter (1967) found that the *Metamysidopsis* species in California headed upstream into currents and advanced against water speeds of up to 10 cm^{-1}. In eastern Canada, *Acanthomysis sculpta* was able to maintain both horizontal and vertical positions in surge channels with a 1-2 m swell (Green 1970). Colman and Segrove (1955), working in Yorkshire, U.K., felt that, although mysids (even those species that normally sought the water's edge) could be passive drifters, they could also swim well enough to avoid being cast onto the shore during rough weather.

Several authors have observed mysids being passively carried by tides and currents. For example, in the estuary of the Rivers Tamar and Lynher in Britain, mysids were carried about by the tides, and tended to concentrate at the eddies (Percival 1929; Mauchline 1971d). In the Delaware River estuary, *Neomysis americana* was more abundant than in the nearby sea and appeared to collect there by avoiding out-flowing surface waters and by taking advantage of landward flowing bottom waters (Hurlburt 1957). In spring, *N. americana* reproduces in both the sea and the estuary, but most young and adults are carried into the estuary and collect there (Hurlburt 1957). In the present study, both species of mysid appear to reoccupy the shallow water of the lagoon from deeper offshore waters each spring (late June-July) by moving in with the prevailing currents and then dropping to the bottom where divers noted that currents were almost nil. Most of the mysids moving into the region in spring are young-of-the-year (i.e., released in May-June). Drift net samples collected between the barrier islands during the open-water season (Table 18) showed that there was continuous movement of mysids into and out of the lagoon; this movement was directly dependent on current.

The significant decrease in abundance of *M. litoralis* recorded in Simpson Lagoon during the latter part of the open-water season (Fig. 12) may have been due to active migration accomplished by moving up into the water-column (where currents are much stronger than on the bottom) and being transported out of the lagoon by the prevailing currents (see 'Transport of Invertebrates').

Amphipods

Currents and tides appear to have primarily indirect effects on epibenthic or benthic amphipods, since current patterns influence the distributions of sediments and organic matter, which then determine the zonation and distribution of filter-feeding and detritus-feeding amphipods (Sanders 1958; Nagle 1968; Parker 1969). In Simpson Lagoon, the dominant amphipod species (*O. glacialis*), unlike either of the mysids, is a year-round resident. It apparently completes its two-year life cycle within the lagoon. This species is most abundant on the bottom where currents are the least strong. In contrast, other more pelagic species (e.g., *Parathemisto* spp., *Apherusa glacialis* and *Halirages mixtus*) moved into the nearshore area and the lagoon as the season progressed (August-September) in 1977 and 1978, possibly under the influence of onshore currents. In 1977, large numbers of *Parathemisto libellula* were stranded on the ocean side of the barrier islands after a period of storms in late September. These species either died or left the lagoon during winter, since none were collected with any sampling device in the spring of 1977 or 1978.

Nuttall (1975) found that *Gammarus duebeni* gathered and began migrating in anticipation of tidal currents. Fincham (1969, 1970) documented the nocturnal presence of benthic amphipod species in the surf zone of British beaches and concluded that these amphipods were actively migrating rather than being passively transported, since breeding coincides with the spring tides.

Other Crustaceans

Penaeid shrimp larvae utilize the flood tides to move into estuarine nursery areas (Copeland 1962; Cook and Linner 1970 and others). Rekas (1973) found that flood tides were responsible for 99% of the migration of *Penaeis aztecus* and *P. setiferus* into the Airplane Lake (Louisiana) nursery area. The larvae were caught near the surface both day and night (more post-larvae were caught at night) except during full or new moons when increased numbers of post-larvae were caught at all depths.

In the Alaskan Beaufort Sea, astronomical tides are small (15-20 cm), and the main agents of transport are wind tides (up to 1.5 m) and prevailing wind-generated currents. This transport is particularly important for mysids that reoccupy the nearshore areas from offshore refugia each spring. This method of transport also appears to be important in maintaining the standing crop available to the higher trophic levels (fish and birds) utilizing the lagoon, by constantly replenishing the lagoon with mysids from offshore and/or adjacent alongshore areas. Any alteration of this transport by shifts in existing current patterns through development (e.g., causeways or artificial island construction) could affect the food available to birds and fish utilizing the lagoon.

Migration

A pronounced seasonal migratory cycle appears to exist among most crustaceans in estuarine regions. Typically, these migrations are of two types: (1) spawning migrations, photoperiod being the major factor in the synchronization of the breeding cycle, and (2) seasonal migrations to and from summer and wintering habitats, possibly under the influence of temperature (Vernberg and Vernberg 1972).

Mysids

Many mysid species appear to follow seasonal migratory patterns, moving into bays, lagoons and estuaries in spring or summer and returning to deeper waters in fall or winter.

The mysid populations in Simpson Lagoon appear to be seasonal; they reoccupy the lagoon in late June and emigrate during the early winter months (see 'Under-Ice Distribution of Epibenthic Invertebrates'). However, it should be noted that some mysids of both species are present through the winter until May, but late winter densities are greatly reduced compared to those in summer. Alexander et al. (1973) found evidence of small-scale seasonal migrations of *Mysis oculata* from offshore areas into shallow lagoons along the Beaufort Sea coast. As pointed out in the 'Tides and Currents' section, *M. litoralis* appears to emigrate actively from the lagoon at the end of the open-water season, presumably to deeper offshore waters. The stimulative clue used by the mysids is uncertain; however, photoperiod seems the most likely (i.e., dependable), because temperatures in these shallow waters are extremely variable (0-13°C) during the open-water season.

Similarly, *Mysis stenolepis* in eastern Canada moved from shallow water in summer and fall to deeper offshore water in winter (Amaratunga and Corey 1975). The same behavior has been observed for *Neomys americana* in Delaware coastal waters, Delaware Bay and Chesapeake Bay (Hurlburt 1957; Hopkins 1965). In his comprehensive study on Danish lagoons and estuaries, Muus (1967) noted that larger crustaceans, including mysids, made seasonal migrations to deeper water in the winter, and returned to the shallows in spring.

In Britain, several species of mysids (e.g., *Schistomysis ornata*, *S. kervillea* and *Paramysis arenosa*) show a similar pattern that is not only seasonal but also related to breeding. Several species migrate to and from well-defined breeding and spawning grounds (Mauchline 1967, 1968, 1969, 1970, 1971 a-d and f).

Amphipods

Less evidence of seasonal migrations exist for amphipods. There is no evidence of a seasonal migration to and from Simpson Lagoon by *Onisimus glacialis* or by the common species of gammarid amphipods. However, this type of migration has been reported to occur in nearby Prudhoe Bay for the closely-related *Boeckosimus affinis* (Feder and Schamel 1976; Feder et al. 1976 a, b). During our winter sampling (November 1978-May 1979) it was noted that the species composition of amphipods on the ocean side of the barrier islands changed as winter progressed (Tables 7, 8 and 9). It appears that some marine species of amphipod (e.g., *O. litoralis*, *Anonyx* sp.) move into shallower nearshore areas from deeper offshore waters. The reasons for these movements are not clear but may be related to breeding, as some gravid females were collected during February 1979.

Seasonal migratory behavior also occurs among the amphipods *Bathyporeia*, *Acanthohaustorius* and *Haustorius* on the coasts of the U.K. and the U.S. (Coker 1967a, b; Fincham 1969, 1970; Coker et al. 1975) and among *Microdentopus* in the Gulf of Mexico (Nagle 1968; Parker 1969).

Other Crustaceans

Seasonal migratory behavior is common among other crustaceans.

In Texas, brown and white shrimp have similar life histories. Adult shrimp spawn in the open Gulf waters where their larvae also hatch. After hatching, tides and currents transport the young into estuaries which serve as nursery areas for these post-larval shrimp. These shrimp grow quickly and return to the sea in fall when they have matured (Loesch 1965; Zein-Eldin and Aldrich 1965; Moffett 1967; Wilson 1969; Clark 1977).

In the Gulf of Mexico, pink shrimp (*Penaeus duorarum*) spawn offshore, and currents carry their larvae toward the mainland. During this period (3-5 weeks) the larvae pass through several developmental stages and reach approximately 1.25 cm in length. After entering inlets and estuaries, their growth accelerates and within 2 to 4 months they return to the sea as adults to complete their life cycle (Clark 1977).

The larval migrations of shrimp (*Penaeus setiferus*, *P. duorarum* and *P. aztecus*) into the estuaries of North Carolina are to some extent circulation-dependent; however, some migration may occur independently: shrimp feed and grow rapidly and then move toward the sea as they mature (Williams 1955).

Blue crabs, *Callinectes sapidus*, also migrate as larvae and postlarvae into estuaries along the East and Gulf coasts of the United States; they return to deeper water again in the fall as they mature (Saila 1973).

The spring (June-July) migration of mysids into Simpson Lagoon is extremely important, as these organisms comprise the largest portion of the diets of birds and fish (Fig. 27). This net immigration into the lagoon appears to continue intermittently throughout the open-water season and maintains an adequate level of food for consumers (see 'Transport of Invertebrates'). A disruption of their migration patterns could alter the trophic balance in the lagoon to the extent that food for fish and birds might become limited.

Feeding Ecology

Mysids

Numerous studies conducted in various locations throughout the world have found that mysids utilize a wide variety of foods. Members of the genus *Mysis* are thought to be omnivorous, generally feeding on plant material (detritus and diatoms) and occasionally capturing copepods and other small crustaceans (Tattersall and Tattersall 1951; Lasenby and Langford 1973; Bowers and Grossnickle 1978; Foulds and Mann 1978; Morgan and Beeton 1978). Other mysid genera are also omnivorous (Mauchline 1967, 1968, 1969, 1970, 1971 a, b, c, d; Odum 1971; Kost and Knight 1975; Price 1976; Chadwick et al. 1972) with some evidence of cannibalism (Wittman 1978).

Segerstrale (1967) believed that the presence of *Mysis relicta* and *Limnocalanus grimaldi* in the Gulf of Bothnia (Baltic Sea) was attributable to their ability to utilize the loose layers of humus (i.e., detritus) that collected on the bottom in the deep waters of the Gulf. This material originated in peat bogs and was carried in great quantities into the Gulf by surface waters.

In Simpson Lagoon, both *M. litoralis* and *M. relicta* are omnivorous; Schneider and Koch (1979) found principal food items to include diatoms, peat and crustacean parts. They concluded that primary production (particularly diatoms) was the main source of energy. A study complementary to ours suggests that 60-70% of the carbon utilized by these mysids is derived from new marine primary production, while the remainder is from terrestrial sources (i.e., carbon from peat or from recent terrestrial production transported to the lagoon by river runoff) (Schell 1979).

Amphipods

Few estuarine amphipods appear to be trophic specialists and most species ingest detrital material and assimilate the microfauna found on it (Heald 1971; Odum 1971; Harrison 1977; Livingston et al. 1977; Van Dolah 1978). Schneider and Koch (1979) found that, of all arctic nearshore amphipod species they tested, only *Gammarus setosus* was able to assimilate the peat itself. They suspected that the other species (e.g., *O. litoralis*) probably utilized the microfauna that derive their energy from the peat.

Members of the amphipod family Lysianassidae (e.g., *O. glacialis*) are reported to be omnivorous (Enequist 1949). Holmquist (1965) reported that *Onisimus* amphipods feed not only on injured or dead animals but also attack mysids held in sampling jars with them. Similar observations were made in Simpson Lagoon during the present study. In addition *O. glacialis* kept in aquaria were observed to feed actively on mysids. Marine primary production appears to be the most important source of energy for *O. glacialis* in Simpson Lagoon.

An epontic community study near Pond Inlet, N.W.T., conducted through May-July 1978, showed *O. glacialis* to feed mainly on ice-associated pennate diatoms, while *O. glacialis*, *Apherusa glacialis*, *Gammarus wilkitzkii*, *Parathemisto libellula* consumed ice-associated pennate diatoms and crustacean appendages (W. Cross, LGL Ltd., pers. comm.). Buchanan et al. (1977) found *O. litoralis* grazing on pennate diatoms on the under-surface of the ice in Bridport Inlet, N.W.T.

Other Crustaceans

Clark (1977) found that the penaeid shrimps (i.e., brown, pink and white) of the southeastern U.S. and Gulf coasts subsist on plant detritus, small crustaceans, worms and various larvae and, thus, they served as important converters of energy (Idyll et al. 1968). Studies of the grass shrimp, *Palaemonetes pugio*, found that it not only satisfied its own feeding requirements but in doing so played an important part in the food web by accelerating the process of detritus breakdown. *Palaemonetes pugio* actually created a steadier flow of detrital energy through its breakdown of detritus into feces, heterogeneous fragments and shrimp biomass. This reduced the accumulations of detritus from emergent grass and macroalgae that otherwise might have occurred (Welsh 1975). Although epibenthic invertebrates in Simpson Lagoon appear to utilize little of the peat in the lagoon for nourishment, they probably play a similar role in accelerating the process of peat breakdown. The most important source of carbon for the invertebrates of Simpson Lagoon appears to be marine primary production, so the continuous replacement of lagoon water provides a constant source of nourishment for the invertebrates. A disruption of the water movement through the lagoon could reduce the amount of carbon available to the epibenthic invertebrates, which could ultimately mean less food for the birds and fish.

Habitat Utilization

Mysids

Estuarine areas throughout the world have long been known to be highly productive (Hedgpeth 1966; and others). Many studies have shown estuaries to be used as nursery grounds by both marine fishes and invertebrates (Gunter 1960, 1961a; Skud and Wilson 1960; Chin 1961; Livingston et al. 1977). Mauchline (1970) found that young of the mysid *Schistomysis ornata* in the U.K. migrate to shallow, brackish waters to grow. Whether *Mysis relicta* and *M. litoralis* utilize Simpson Lagoon as a nursery ground is not clear. First-year individuals were the dominant group of both species of mysid collected during this study (Figs. 29, 32). The low proportion of larger second-year animals in the lagoon and offshore (Station 78-7) may reflect an increased predation pressure (i.e., being larger, they are more easily seen and captured by predators) or the utilization of an alternate habitat or some combination of these. There was no obvious difference in the seasonal size distribution of either mysid species between samples from the lagoon and samples from the ocean. This suggests that the growth rate was similar in the two areas (Fig. 41). The mysid populations residing in the lagoon on any given date are probably transient in nature, since drift-net data show a continuous flux of mysids in and out of the lagoon, and since prevailing currents would carry new individuals in and resident ones out. It appears, then, that the entire nearshore area within several km of shore, and not just lagoons and bays is important, since several key biological processes (growth, breeding) for these species may occur throughout this zone and not just in specific areas like Simpson Lagoon.

Within Simpson Lagoon, both species of mysid showed a preference for the mid-lagoon area (Fig. 11). Whether this was due to the deeper water (i.e., less turbulence) or the presence of large amounts of detritus is not clear, although divers noted that mysids appeared to collect on the detrital mat and dive into it when startled.

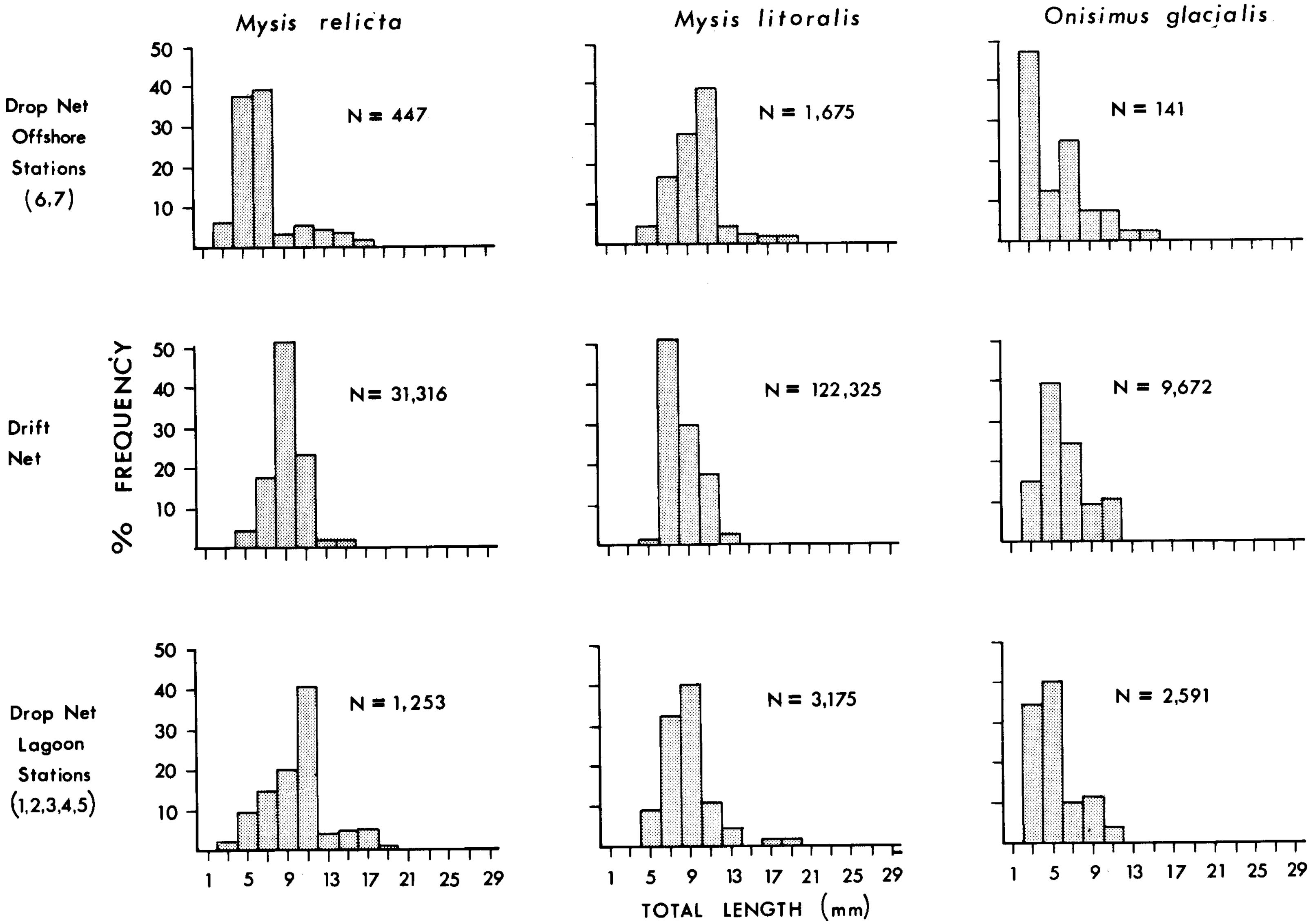

Figure 41. Length frequency for key epibenthic invertebrates collected inside, outside and between gaps of the barrier islands in the Simpson Lagoon area, 1978.

Amphipods

Non-burrowing members of the *Onisimus* family (Lysianassidae) are thought to dwell in or around bottom detritus layers (Enequist 1949). However, the newly-released young may utilize different habitats; Thomson et al. (1978) and Buchanan et al. (1977) found young (2 mm) *Onisimus* spp. on the ice undersurface community in the Canadian High Arctic. *Atylus* sp., *Gammarus tigrinus* and *Melita nitidae* all dwell on or near the detrital layer in Barataria Bay, Louisiana, as do similar species in South Florida estuaries (Odum 1971; Thomas 1976; Livingston et al. 1977).

Division of habitat among amphipods according to sediment type was found by Jones (1948) on the Isle of Man. Burrowing species (Lysianassidae, Haustoriidae, Ampeliscidae, Corophiidae) preferred fine sand and silty sand, and most non-burrowing Lysianassids preferred coarse sand or gravel, while Oedicerotids preferred mud. Thomson et al. (1979) found *Onisimus litoralis* associated with sand and small pebbles (< 1 cm) and *Gammarus setosus* with large cobbles (> 5 cm) in the intertidal zone near Pond Inlet, N.W.T.

Since *O. glacialis* appears to be a year-round resident of Simpson Lagoon and was only rarely collected at offshore marine stations, its microhabitat requirements in the lagoon are of the greatest interest. As was the case with the mysids, *O. glacialis* appears to prefer the deeper mid-lagoon stations (Fig. 19). Divers noted that this species moved about in large numbers on the surface of the detritus layer and also lived within the layer (i.e., numerous individuals of this species were observed rising up from within the mat when it was disturbed). *Onisimus glacialis* also dived into the detrital layer when startled.

Other Crustaceans

Estuaries serve as nursery areas for many species, including shrimp (Rounsefell 1963). Sand shrimp (*Crangon franciscorum*) use the upper Columbia River estuary as a nursery ground (Haertel and Osterberg 1967). Caillouet (1970) felt that commercially important shrimp depend on estuaries to serve as their nursery areas, and occasionally to support adult populations. Some ecologists believe it is critical for early stages of ocean-spawning shrimp to reach bay waters in order to survive (McHugh 1976).

Although several authors agree that estuarine waters are necessary for penaeid shrimp to complete their life cycle, there is a great deal of discussion as to whether temperature or salinity is the key parameter (Gunter 1950, 1961a; Williams 1959; Barrett and Gillespie 1973; Gaidry and White 1973; Barrett and Ralph 1976).

Some authors believe that residence in estuaries serves a dual purpose for young shrimp: (1) estuaries provide rich feeding grounds for shrimp, with an abundance of detrital and microfloral material sufficient to meet the food requirements of shrimp during their rapid physical growth in the period before they assume their oceanic residence as adults (Idyll et al. 1968; Jones 1973; Clark 1977; Livingston et al. 1977); (2) estuaries provide protection from predators and competitors (Hoese 1960; Idyll et al. 1968; Wilson 1969; Clark 1977).

In Simpson Lagoon, both amphipods and mysids obtained 60-70% of their carbon from marine primary productivity, and use the detrital layer as a habitat rather than as a main source of food. This layer may afford protection from predators by providing a place to hide.

Influence of Predators

Mysids and amphipods appear to form important links in many estuarine and marine food webs. The predator-prey relationships for important mysids and amphipods are detailed below.

Mysids

Mysis litoralis and *M. relicta* are the major food items for anadromous and marine fish and oldsquaw ducks in the Simpson Lagoon area (Craig and Haldorson 1980; Johnson and Richardson 1980). Competition appears to be relatively minor for this plentiful food supply, as there is much overlap among the diets of predators (Craig and Haldorson 1980) and the food supply remains large relative to the daily requirements of the predators. However, the continued abundance of these important food items in the nearshore environment appears to depend on uninterrupted immigration or dispersal of these mysid species into shallow water (see 'Transport of Invertebrates').

Craig and Haldorson (1980) found that arctic cod in nearshore zones feed heavily on mysids and gammarid amphipods; similar results were reported for offshore waters (Frost et al. 1978). This feeding pressure can be significant, as was the case during August of 1978, when a large school (estimated in the millions) of arctic cod moved through Simpson Lagoon and, through predation, may have been at least partly responsible for the decline in *M. litoralis* biomass recorded in the latter part of August.

It should be noted that, during the open-water season, predation is much heavier in Simpson Lagoon than on the ocean side of the barrier islands. The difference is due primarily to the absence of oldsquaw ducks in the marine environment, except under special circumstances (e.g., the presence of large amounts of floe ice).

In other areas, mysids also form an important part of the diet of predators. *Mysis stenolepis* is an important food item for cottids, gadids and rajiids on the east coast of Canada (Amaratunga and Corey 1975) and, in the Baltic Sea, *Gastrosaccus spinifer* is a preferred food of cod (Arnte 1978). Striped bass on the east coast of the U.S. prey heavily on *Neomysis americana* (Markle and Grant 1970), while striped bass on the west coast prey almost exclusively on *N.* (*awatchensi*) *mercedis* (Heubach 1969; Turner and Heubach 1969). According to Turner (1972), when striped bass larvae reach approximately 0.6 inches in length they begin to feed heavily on *Neomysis* (*awatchensi*) *mercedis*. Although the bass prey increasingly on other fish after one year of age, *Neomysis* remains an important food source. Adult shad of the Sacramento-San Joaquin estuary consume primarily *Neomysis*, and all sizes of catfish and black crappie fed on *Corophium* and *Neomysis* (Stevens et al. 1972). In South Florida, Odum (1971) found *Mysidopsis almyra*, *M. bahia* and *Gastrosaccus dissimilis* to be major food items for fishes. The eight major species of mysids found in Galveston Bay serve as important food items for six species of fish and two species of penaeid shrimp (Price 1976), and Clutter (1967) found similar predation on mysids in

California coastal waters. *Mysis relicta* is also an important component in freshwater fish diets in some northern lakes (Juday and Birge 1927; Larkin 1948; Morgan and Beeton 1978).

Amphipods

Next to mysids, amphipods, particularly *Onisimus glacialis*, were the most important prey item found in the stomachs of anadromous fishes and birds in Simpson Lagoon in 1977 and 1978 (Johnson and Richardson 1980; Craig and Haldorson 1980). Competition among these groups apparently was relatively minor for this abundant food supply; the index of overlap among consumers was high (Craig and Haldorson 1980). *Onisimus* amphipods are also important food items of birds and fish in nearshore waters in the eastern Arctic (Alliston et al. 1976; Bain and Sekerak 1978). Barnard (1959) found *Onisimus* amphipods in the stomachs of arctic cod captured in traps at Ice Island T3 in the Arctic Ocean.

Other amphipods also serve as food items in various estuarine systems. Fish in a South Florida estuary were heavy predators on three species of amphipods--*Melita nitida*, *Grandidirella bonnieri* and *Corophium lacustre* (Odum 1971). The salt marsh gammarid amphipod, *Gammarus palustris*, is also heavily preyed upon--most particularly the adults as a result of their size (Van Dolah 1978). Amphipods in Barataria Bay, Louisiana, were a major food item of the sheepshead (Thomas 1976).

Any perturbation that reduces the biomasses of these key epibenthic invertebrates in shallow waters could have serious effects on the higher trophic levels, as the largest concentrations of predators occur in these areas rather than in the offshore marine environment (Divoky 1978; Johnson and Richardson 1980; Craig and Haldorson 1980).

Effects of Contaminants

Several studies of the effects of oil contamination on arctic marine and littoral invertebrates have been conducted (Percy and Mullin 1975; Percy 1976, 1977; Busdosh and Atlas 1977; Johnson 1977; Atlas et al. 1978; Foy 1978, 1979). However, comparisons of relative sensitivities of different species to various toxicants are difficult due to differences in the methodology of the various studies, the variety of species tested, and the variable chemical composition of the oil. The sensitivity of littoral and sublittoral invertebrates to oil contamination can also vary significantly depending on species, habitat, life stage, time of year and even the time of day (Swedmark et al. 1973; Foy 1978, 1979). In spite of these limitations, certain generalizations concerning the effects of a major oil blow-out or spill in a shallow nearshore zone are possible. The contamination of a barrier island-lagoon system might have serious effects on the epibenthic community. These effects could be either direct or indirect. If organisms came into physical contact with the oil, the indications are that they could succumb. Effects on invertebrates of water-soluble and suspended components of oil in the water-column would depend on the concentration and chemical composition of these components. On the other hand, epibenthic invertebrates might actively move out of the lagoon as a result of avoidance behavior.

Oil entering a shallow lagoon would become mixed with bottom sediments and organic debris. Any repopulation of the lagoon from stocks of marine invertebrates offshore (Feder et al. 1976; this study) would have to contend with an oil-contaminated substrate and food source. The species composition can be significantly different after oil-contamination of the sediments. For example, Atlas et al. (1978) found more bivalves and polychaetes and fewer amphipods after contamination by oil. This could result in drastically reduced densities of epibenthic organisms, the effects of which might be felt to the top of the food web. The rate of recovery of oil-contaminated benthic communities varies with substrate (i.e., a few weeks for rocky shorelines; up to five years in soft bottom areas) (Boesch et al. 1974). In arctic nearshore areas, Atlas et al. (1978) found the rates of biodegration to be limited by temperature and availability of nutrients; consequently petroleum hydrocarbons may remain in arctic ecosystems for prolonged periods after oil contamination. This may be particularly true for nearshore zones like Simpson Lagoon, which has a soft-bottom substrate overlaid by an unconsoliated flocculent amorphous detrital layer.

Large scale blow-outs and accidental spills of oil account for only a small portion of the total amount of oil entering the marine environment. Small spills, losses during offshore production, natural seeps, and pumping of ballast tanks and bilge water account for most of the oil entering the sea (NAS 1975). In the Beaufort Sea, the amount of oil likely to enter the marine environment through the above routes has been estimated to be about 200 barrels of every million produced, or about 0.02% (Mackay 1977). This chronic oil contamination may have long-term sublethal effects on the biology of nearshore marine invertebrates. Johnson (1977) has compiled an extensive literature review on the sublethal effects of petroleum hydrocarbon exposures on the physiology, behavior, growth, development and reproduction of arctic and subarctic marine invertebrates. He found that, for crustaceans (e.g., mysids and amphipods), each of these processes was adversely affected by sublethal levels of hydrocarbons; which could result in a reduction in biomass or density of the affected organism.

In the Simpson Lagoon barrier island-lagoon system, the high flushing rate of the lagoon (0.2 times/day on the average and as much as once per day during winds greater than 40 km/h, Mungall 1978) could result in a rapid turnover of mysids and some species of amphipod (e.g., marine pelagic species). This rapid replacement rate, and the enormous reservoir of these organisms in the large offshore area in relation to numbers in restricted lagoon areas, indicate that the availability of these important food organisms in lagoons would not be appreciably altered. However, a low level chronic oil spill might have more serious effects on the less mobile amphipods like *O. glacialis*. It might cause the higher trophic levels (birds and fish) to become tainted and thus unsuitable for human consumption since a wide variety of marine organisms are able to accumulate polycyclic aromatic hydrocarbons present at low concentrations in food or sediments (Neff 1979).

CONCLUSIONS

1. Invertebrate Use of Simpson Lagoon in Winter

In late winter (March-June 1978) when ice was 2 m thick, amphipods (particularly *Onisimus glacialis*) and isopods were common in Simpson Lagoon. Mysids, in contrast, were not found in the lagoon at this time but appeared to repopulate the lagoon during spring breakup, presumably from offshore marine waters. However, mysids of both species are present at least until February but in reduced numbers. The winter period seems especially important for epibenthic invertebrates in general, as breeding and the brooding of young occur at this time.

2. Trophic Relationships and Summer Use of Simpson Lagoon

In 1977 and 1978, the biomass of mysids and amphipods (g/m^2) available to key vertebrate consumers remained 1-2 orders of magnitude greater than daily demand over the open-water period. However, in 1978 food availability was approximately ½-1 order of magnitude less than in 1977. In 1978, the total biomass of these key invertebrates reached a peak in July and then slowly declined during late summer. In 1977, the biomass generally increased throughout the open-water period. Growth and predation could not account for the fluctuations in biomass recorded during the open-water season. Net immigration plays an important role in keeping the mysid biomass in the lagoon at high levels.

Marine primary production accounts for 60-70% of the carbon utilized by key epibenthic invertebrates (mysids and amphipods).

3. Life History Information

Mysids grew rapidly during the open-water period: *M. litoralis* (2.5 mm/30 days) and *M. relicta* (2.2 mm/30 days), while *Onisimus glacialis* (0.7 mm/30 days) grew more slowly. The growth rates of *M. litoralis*, *M. relicta* and first-year *O. glacialis* decreased during winter, but it is important to note that some growth continued even in winter. *M. litoralis*, *M. relicta* and *O. glacialis* appeared to have two-year life cycles with some individuals living as long as three years. Breeding (limited to second- and third-year individuals) appears to occur in late fall and early winter; young are brooded until the following spring.

First-year individuals formed the dominant groups for all three species in the lagoon during the open-water season.

RECOMMENDED FURTHER RESEARCH

1. Immigration of epibenthic invertebrates into the lagoon has been shown to be of great importance in maintaining the levels of food available to higher consumers (fish and birds), and emigration in late summer may be important in maintaining a breeding stock of mysids. More refined estimates of the rates of these movements in relation to currents, date, temperature and salinity would enhance our ability to determine the effects of particular types of development (i.e., causeway and artificial island construction).
2. Laboratory investigations on the salinity-temperature preferences and requirements of *Mysis litoralis*, *M. relicta* and *Onisimus glacialis*, and the effects of temperature on the rapid growth of the two mysid species reported during the open-water season, would help to determine if the warmer brackish waters of barrier island-lagoon systems are critical habitats for these organisms.
3. A comparison of invertebrate populations along lagoons and seaward of them with those along and seaward of exposed coasts would help determine the importance of lagoon habitats vs exposed coasts.

SUMMARY OF 4TH QUARTER OPERATIONS

Fourth quarter operations consisted of data analysis and the preparation of this annual report.

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APPENDICES

Appendix 1. Estimates of total length and wet weight[1] for *Mysis litoralis* for different length intervals.

Length Interval mm	mid-point	Number of Individuals	Partial Length mm Mean	SD	Estimated Total Length[2] mm	Wet Weight[1] mg Mean	SD	Estimated Wet Weight[2] mg
0-2	1	-	-	-	-	-	-	0.3
2-4	3	50	0.3	0.0	2.8	0.8	0.1	0.4
4-6	5	50	0.5	0.0	4.1	1.0	0.2	1.5
6-8	7	66	1.0	0.1	7.3	3.4	0.8	3.4
8-10	9	50	1.2	0.2	8.6	5.1	0.9	6.3
10-12	11	50	1.5	0.2	10.6	7.2	1.2	10.3
12-14	13	10	2.1	0.3	14.4	13.6	3.0	15.5
14-16	15	32	2.3	0.4	15.7	23.6	5.4	22.0
16-18	17	30	2.5	0.4	17.0	29.9	5.0	29.8
18-20	19	48	2.9	0.3	19.6	33.2	4.5	39.1
20-22	21	51	3.2	0.3	21.6	49.4	3.2	49.9
22-24	23	50	3.3	0.4	22.2	69.9	3.2	62.4
24-26	25	46	4.0	0.2	26.7	80.9	2.6	76.5
26-28	27	48	4.0	0.3	26.7	106.0	2.5	92.3
28-30	29	21	4.2	0.4	28.0	128.5	0.5	109.9
30-32	31	8	4.4	0.5	29.3	143.0	0.0	129.3
32-34	33	2	5.0	0.0	33.2	154.0	0.0	150.6

Best-fit Equations	Estimated Total Length=6.4739 (Partial Length)+0.8442	Estimated Wet Weight=0.0294 (Total Length)$^{2.4426}$
	r=0.9955 P<0.001	r=0.9905 P<0.001

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[1] Wet weights used in calculations are formalin preserved wet weights.

[2] Estimated values determined using best-fit equations and mid-point of length interval.

Appendix 2. Estimates of total length and wet weight[1] for *Mysis relicta* for different length intervals.

Length Interval mm	mid-point	Number of Individuals	Partial Length mm Mean	SD	Estimated Total Length[2] mm	Wet Weight[1] mg Mean	SD	Estimated Wet Weight[1,2] mg
0-2	1	-	-	-	-	-	-	0.04
2-4	3	33	0.3	0.0	2.6	0.8	0.3	0.5
4-6	5	42	0.9	0.1	6.6	1.5	0.6	1.8
6-8	7	50	1.0	0.0	7.2	3.6	0.2	3.9
8-10	9	51	1.3	1.0	9.2	5.3	0.8	7.0
10-12	11	47	1.5	0.1	10.5	8.5	1.7	11.1
12-14	13	43	1.8	0.3	12.5	16.2	2.6	16.4
14-16	15	50	2.0	0.1	13.8	21.1	0.6	22.9
16-18	17	49	2.3	0.2	15.8	33.1	6.7	30.6
18-20	19	50	3.0	0.2	20.4	49.4	3.5	39.6
20-22	21	50	3.1	0.4	21.1	62.2	5.9	50.0
Best-fit Equations			Estimated Total Length=6.5982 (Partial Length)+0.6512 $r=0.9878$ $P<0.001$			Estimated Wet Weight=0.0426 (Total Length)$^{2.3219}$ $r=0.9886$ $P<0.001$		

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[1] Wet weights used in calculations are formalin preserved wet weights.

[2] Estimated values determined using best-fit equations and mid-point of length interval.

Appendix 3. Estimates of total length and wet weight[1] for *Onisimus glacialis* for different length intervals.

Length mm	Interval mid-point	Number of Individuals	Partial Length mm Mean	Partial Length mm SD	Estimated Total Length[2] mm	Wet Weight[1] mg Mean	Wet Weight[1] mg SD	Estimated Wet Weight[2] mg
0-2	1	-	-	-	-	-	-	
2-4	3	50	1.4	0.2	3.7	1.2	0.1	0.9
4-6	5	50	1.8	0.5	4.6	1.7	0.4	3.4
6-8	7	50	2.6	0.5	6.4	11.5	1.0	7.9
8-10	9	50	3.8	0.4	9.1	15.2	2.0	15.1
10-12	11	50	4.7	0.4	11.1	25.7	2.5	25.2
12-14	13	56	5.6	0.5	13.1	38.6	2.9	38.7
Best-fit Equations			Estimated Total Length=2.2313 (Partial Length)+0.5995 $r=0.9925$ $P<0.001$			Estimated Wet Weight=0.0544 $(\text{Total Length})^{2.5597}$ $r=0.9667$ $P<0.01$		

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[1] Wet weights used in calculations are formalin preserved wet weights.

[2] Estimated values determined using best-fit equations and mid-point of length interval.

Appendix 4. Estimates of total length and wet weight[1] for *Pontoporeia affinis* for different length intervals.

Length Interval mm	mid-point	Number of Individuals	Partial Length mm Mean	SD	Estimated Total Length[2] mm	Wet Weight[1] mg Mean	SD	Estimated Wet Weight[2] mg
0-2	1	1	0.5	0.0	1.6	1.0	0.0	0.6
2-4	3	31	0.7	0.3	2.1	1.2	0.5	2.6
4-6	5	44	1.9	0.5	5.3	4.5	2.0	4.9
6-8	7	27	2.5	0.6	6.9	6.7	3.5	7.5
8-10	9	29	3.4	0.6	9.3	13.1	4.5	10.4
10-12	11	5	3.9	0.7	10.7	18.0	4.4	13.4
Best-fit Equations			Estimated Total Length=2.6674 (Partial Length)+0.2652 $r=0.9896$ $P<0.001$			Estimated Wet Weight=0.6395 (Total Length)$^{1.2687}$ $r=0.9322$ $P<0.01$		

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[1] Wet weights used in calculations are formalin preserved wet weights.

[2] Estimated values determined using best-fit equations and mid-point of length interval.

Appendix 5. Estimates of total length and wet weights[3] for *Apherusa-glacialis* and *Halirages mixtus* for different length intervals.

Length Interval		Number of Individuals	Partial Length mm		Estimated Total Length mm[2]	Wet Weight mg[1]		Estimated Wet Weight mg[2]
mm	Mid-point		Mean	SD		Mean	SD	
0-2	1	-	-	-	-	-	-	0.8
2-4	3	9	0.7	0.2	3.5	1.0	0.0	0.8
4-6	5	12	1.0	0.2	5.0	1.8	0.8	2.5
6-8	7	50	1.4	0.3	7.0	5.4	1.8	5.0
8-10	9	46	1.6	0.3	8.0	8.2	1.4	8.5
10-12	11	4	2.3	0.3	11.6	14.5	4.4	13.0
Best fit Equations		Estimated Total Length=5.0667(Partial length)$^{-0.0933}$ $r = 0.9812$ $p < 0.01$				Estimated Wet Weight=0.0832(Total length)$^{2.1070}$ $r = 0.9845$ $p < 0.01$		

[1] Wet Weights used in calculations are formalin preserved wet weights.

[2] Estimated values determined using best-fit equations and mid-point of length interval.

[3] The same relationships are used for *Apherusa glacialis* and *Halirages mixtus* as the two species have identical length-weight relationships and data insufficient to treat each separately.

Appendix 6. Estimates of total length and wet weights[1] for *Gammarus setosus* for different length intervals.

Length Interval mm	mid-point	Number of Individuals	Partial Length mm		Estimated Total Length[2] mm	Wet Weight[1] mg		Estimated Wet Weight[1,2] mg
			$\bar{x}$	SD		$\bar{x}$	SD	
0-2	1	-	-	-	-	-	-	0.05
2-4	3	21	0.5	0.1	3.2	1.2	0.5	0.8
4-6	5	53	0.9	0.2	5.2	1.5	0.6	2.8
6-8	7	16	1.4	0.3	7.8	7.0	5.1	6.5
8-10	9	26	1.7	0.3	9.3	12.8	4.6	12.2
10-12	11	15	1.8	0.3	9.8	17.9	6.8	20.1
12-14	13	7	2.5	0.2	13.4	29.4	4.8	30.6
14-16	15	10	2.6	0.5	13.8	41.3	8.6	43.8
16-18	17	1	3.4	0.0	18.0	73.0	0.0	59.9
18-20	19	24	3.5	0.4	18.4	84.7	31.9	79.2
20-22	21	-	-	-	-	-	-	101.7
22-24	23	3	4.7	0.8	24.6	118.7	9.6	127.7
24-26	25	2	4.5	0.0	23.6	172.0	17.0	157.4

Best-Fit Equations

Estimated Total Length = 5.1022 (Partial length) + 0.6080

$r = 0.9910$ $p < 0.001$

Estimated Wet Weight = 0.0497 (Total length)$^{2.5045}$

$r = 0.9882$ $p < 0.001$

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[1] Wet weights used in calculations are formalin preserved wet weights.

[2] Estimated values determined using best-fit equations and mid-point of length interval.

Appendix 7. Estimated total length and wet weight[1] for *Parathemisto*[2] sp. for different length intervals.

Length Interval mm	mid-point	Number of Individuals	Partial Length mm x	SD	Estimated Total Length[3] mm	Wet Weight[1] mg	SD	Estimated Wet Weight[3] mg
0-2	1	-	-	-	-	-	-	0.1
2-4	3	5	0.9	0.2	3.6	1.0	0.0	0.8
4-6	5	48	1.3	0.2	5.1	3.7	4.3	2.9
6-8	7	65	1.7	0.2	6.6	5.1	2.0	6.5
8-10	9	30	2.3	0.3	8.8	8.7	2.9	12.1
10-12	11	29	2.8	0.2	10.7	14.6	5.3	19.8
12-14	13	6	3.4	0.5	12.9	26.5	3.8	29.7
14-16	15	3	4.0	0.3	15.2	47.0	8.9	42.2
16-18	17	4	4.5	0.5	17.1	60.3	16.7	57.3
18-20	19	2	5.1	0.6	19.3	97.0	14.1	75.1
20-22	21	5	5.5	0.3	20.8	110.4	20.0	96.0

Best-fit Equations	Estimated Total Length = 3.7535 (Partial length) + 0.1765 $r = 0.9988$ $p < 0.001$
	Estimated Wet Weight = 0.0564 (Total length)$^{2.4436}$ $r = 0.9890$ $p < 0.001$

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[1] Wet weights used in calculations are formalin preserved wet weights.

[2] Mostly *Parathemisto libellula* plus a few *P. abyssorum*.

[3] Estimated values determined using best-fit equations and mid-point of length interval.

Appendix 8. Relationship of total length to body wet weight[1] and body dry weight[2] for *Cyrtodaria kurriana* of different length intervals.

Total Length Interval mm	Mid-point	Number of Individuals	Total length mm $\bar{x}$	Total length mm SD	Body Wet Weight mg $\bar{x}$	Body Wet Weight mg SD	Body Dry Weight mg $\bar{x}$	Body Dry Weight mg SD
0-2	1	-	-	-	-	-	-	0.02
2-4	3	5	4.0	0.0	2.2	1.1	1.2	0.4
4-6	5	12	5.2	0.7	3.8	2.1	1.3	0.7
6-8	7	24	7.1	0.7	10.8	5.2	2.3	1.5
8-10	9	11	9.1	0.7	30.7	12.2	4.3	2.0
10-12	11	17	11.4	0.5	61.9	17.9	9.3	3.8
12-14	13	22	13.5	0.4	97.6	22.1	13.8	6.8
14-16	15	12	15.8	0.4	159.9	41.7	34.2	16.3
16-18	17	6	17.3	0.5	266.2	37.6	61.8	17.3
18-20	19	3	19.7	0.6	345.0	75.1	62.0	14.0

Best-fit Equations

Body Wet Weight = 0.0194 (Total length)$^{3.2930}$

$r = 0.9980 \quad p < 0.001$

Body Dry Weight = 0.0152 (Total Length)$^{2.7387}$

$r = 0.9721 \quad p < 0.001$

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[1] Wet weight and dry weight determined from fresh (frozen) and formalin preserved material.

Appendix 9. Abundance (No./100m³) and biomass (mg ash free dry weight/100m³) of important species of epibenthic invertebrates collected in the water column in Faber net samples in Simpson Lagoon and nearshore areas, 10 July-23 September 1978. (N=3 for each station-day).

		10 July		22 July		4 August		17 August		30 August		14 September		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 2 Water Column															
Mysis litoralis	$\bar{x}$	305.3	93.9	25.2	9.4	1.4	0.8	95.8	71.0	96.0	99.5	317.9	403.8	48.8	56.0
	sd	156.9	62.9	25.6	9.7	1.4	1.0	44.8	30.0	31.3	34.7	120.1	170.9	27.7	54.6
Mysis relicta	$\bar{x}$	56.4	13.0	32.2	9.6	0.8	0.5	21.5	13.0	8.0	7.2	89.7	110.4	2242.8	2324.1
	sd	41.3	10.7	7.1	1.5	0.7	0.5	7.6	6.1	5.8	5.8	25.4	42.6	705.1	714.8
Mysid spp.	$\bar{x}$	25.8	1.1	26.8	3.9	-	-	2.0	0.4	0.5	0.4	7.5	5.2	34.6	37.8
	sd	13.2	0.5	3.8	1.1	-	-	2.0	0.3	0.9	0.7	6.5	5.5	40.5	34.7
Onisimus glacialis	$\bar{x}$	18.5	3.0	13.4	3.7	11.9	5.3	28.2	15.0	36.2	16.3	140.0	34.0	141.6	33.1
	sd	1.6	0.6	2.2	1.5	5.5	3.2	3.4	4.9	32.0	14.6	47.8	6.6	54.5	15.0
Gammarus setosus	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	2.2	3.1	-	-
	sd	-	-	-	-	-	-	-	-	-	-	3.8	5.4	-	-
Apherusa glacialis	$\bar{x}$	-	-	-	-	-	-	6.0	2.3	9.5	9.6	-	-	38.1	34.5
	sd	-	-	-	-	-	-	3.6	1.7	5.1	4.8	-	-	12.0	25.7
Halirages mixtus	$\bar{x}$	-	-	-	-	-	-	1.9	1.2	4.9	1.5	11.5	8.6	69.0	23.2
	sd	-	-	-	-	-	-	0.2	1.0	0.5	1.0	12.8	10.1	38.2	5.5
Pontoporeia affinis	$\bar{x}$	9.3	4.5	6.0	2.9	0.5	0.2	-	-	0.6	0.5	-	-	-	-
	sd	4.9	2.2	2.0	0.7	0.8	0.4	-	-	1.0	0.9	-	-	-	-
Parathemisto spp.	$\bar{x}$	-	-	-	-	-	-	0.6	0.3	6.1	13.3	1.0	0.1	4.6	40.3
	sd	-	-	-	-	-	-	1.1	0.5	4.9	9.1	1.7	0.2	5.5	40.8
Amphipod spp.	$\bar{x}$	3.7	1.1	-	-	0.5	0.1	2.5	0.6	25.5	5.8	3.5	0.5	64.2	11.1
	sd	2.1	0.4	-	-	0.8	0.2	2.2	0.5	12.7	4.3	6.1	0.9	15.7	7.8

Appendix 9 (continued).

		10 July		22 July		4 August		17 August		30 August		14 September		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 3 Water Column															
Mysis litoralis	$\overline{x}$	339.8	184.6	20.9	10.4	-	-	9.6	7.2	17.1	20.4	3.3	4.1	41.1	53.3
	sd	224.9	13.9	23.3	12.2	-	-	9.1	7.9	18.2	19.8	5.8	7.1	17.0	27.8
Mysis relicta	$\overline{x}$	212.5	46.7	8.2	2.3	-	-	5.4	3.7	1.1	0.4	3.0	3.1	398.3	539.2
	sd	52.7	11.2	5.3	0.9	-	-	4.8	2.8	1.1	0.5	4.0	4.2	19.8	31.1
Mysid spp.	$\overline{x}$	20.5	1.9	16.5	2.5	-	-	0.6	0.2	-	-	1.3	0.8	13.4	4.4
	sd	18.4	2.6	12.5	2.4	-	-	1.0	0.4	-	-	3.1	1.4	18.6	7.4
Onisimus glacialis	$\overline{x}$	27.5	1.7	4.0	0.9	8.0	2.9	13.2	9.6	6.8	3.4	54.8	19.8	25.7	6.2
	sd	1.3	0.9	2.9	0.6	3.4	0.1	7.5	4.3	3.2	2.2	33.9	12.5	29.4	7.6
Gammarus setosus	$\overline{x}$	-	-	-	-	-	-	-	-	1.8	0.6	0.4	0.03	-	-
	sd	-	-	-	-	-	-	-	-	1.7	0.9	0.8	0.06	-	-
Apherusa glacialis	$\overline{x}$	-	-	0.3	0.1	-	-	24.2	13.9	22.6	9.9	159.8	110.4	73.9	73.1
	sd	-	-	0.5	0.2	-	-	13.2	10.0	5.9	6.7	67.8	69.9	6.2	8.0
Halirages mixtus	$\overline{x}$	-	-	-	-	-	-	4.2	1.7	1.6	0.9	3.4	2.4	7.5	6.8
	sd	-	-	-	-	-	-	2.1	1.0	2.8	1.6	3.3	2.5	1.0	2.1
Pontoporeia affinis	$\overline{x}$	1.4	0.8	1.7	0.8	-	-	-	-	-	-	-	-	-	-
	sd	0.6	0.5	2.2	1.0	-	-	-	-	-	-	-	-	-	-
Parathemisto spp.	$\overline{x}$	-	-	-	-	-	-	0.6	0.6	1.1	1.4	3.1	2.6	3.9	15.9
	sd	-	-	-	-	-	-	1.0	1.0	1.1	1.3	2.8	2.7	3.3	14.2
Amphipod spp.	$\overline{x}$	14.7	2.9	0.3	0.04	-	-	9.6	7.1	7.2	7.6	1.3	0.2	-	-
	sd	5.0	2.4	0.5	0.07	-	-	4.5	5.8	5.1	5.6	2.2	0.3	-	-

Appendix 9 (continued)

		10 July		22 July		4 August		17 August		30 August		14 September		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 4 Water Column															
Mysis litoralis	$\bar{x}$	367.9	117.5	15.2	7.0	2.2	2.6	103.9	92.3	18.8	22.3	5.8	7.6	157.2	222.4
	sd	304.8	87.5	15.1	7.7	0.8	2.4	150.5	135.6	11.9	9.7	7.5	10.0	73.4	116.6
Mysis relicta	$\bar{x}$	183.7	50.4	2.0	0.8	-	-	3.3	3.0	20.5	19.4	0.8	0.9	92.3	134.7
	sd	158.4	35.7	1.8	0.7	-	-	2.9	4.2	34.2	32.4	1.4	1.5	65.1	93.3
Mysid spp.	$\bar{x}$	80.2	5.6	4.9	1.5	-	-	1.6	0.5	0.5	0.3	-	-	3.5	1.4
	sd	37.3	0.5	2.5	1.9	-	-	2.7	0.9	2.0	0.5	-	-	3.1	2.2
Onisimus glacialis	$\bar{x}$	293.5	36.2	10.8	2.1	4.9	1.8	22.9	11.1	31.5	14.9	51.6	15.7	26.6	7.3
	sd	70.1	26.1	8.0	1.7	4.3	2.3	15.1	8.7	8.5	1.3	12.2	3.9	3.3	1.8
Gammarus setosus	$\bar{x}$	1.6	11.0	-	-	-	-	1.8	1.3	-	-	2.2	1.2	1.0	0.1
	sd	2.8	19.0	-	-	-	-	3.1	2.3	-	-	0.4	0.7	1.7	0.1
Apherusa glacialis	$\bar{x}$	-	-	-	-	-	-	20.9	19.0	218.3	173.1	43.9	36.2	86.2	78.0
	sd	-	-	-	-	-	-	14.7	13.7	124.0	62.5	28.3	6.2	20.1	15.6
Halirages mixtus	$\bar{x}$	-	-	-	-	-	-	8.8	3.0	2.8	1.6	13.8	7.7	11.1	8.1
	sd	-	-	-	-	-	-	7.0	2.4	2.6	1.9	10.1	6.7	1.1	0.4
Pontoporeia affinis	$\bar{x}$	-	-	0.6	0.3	-	-	-	-	-	-	-	-	-	-
	sd	-	-	1.1	0.5	-	-	-	-	-	-	-	-	-	-
Parathemisto spp.	$\bar{x}$	-	-	-	-	-	-	0.9	1.6	4.8	9.1	22.7	58.4	6.3	52.9
	sd	-	-	-	-	-	-	1.6	2.8	3.0	8.0	5.3	34.9	5.2	43.1
Amphipod spp.	$\bar{x}$	9.1	1.6	0.3	0.05	0.5	0.6	31.6	10.4	15.5	8.6	28.2	17.9	33.3	11.7
	sd	4.8	1.1	0.5	0.08	0.8	1.1	43.3	10.7	4.9	3.3	29.7	9.9	17.3	2.4

Appendix 9 (continued)

		10 July		22 July		4 August		17 August		30 August		14 September		23 September*	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 7 Water Column															
Mysis litoralis	$\bar{x}$	16.0	13.6	136.7	94.6	12.3	5.2	2.7	4.1	0.4	0.2	-	-	No Samples	
	sd	11.3	18.7	103.2	42.7	3.9	3.5	4.7	7.2	0.7	0.3	-	-	Collected	
Mysis relicta	$\bar{x}$	19.6	18.2	57.1	29.3	0.6	2.3	-	-	-	-	-	-	"	
	sd	19.0	27.7	60.8	37.2	1.1	4.0	-	-	-	-	-	-	"	
Mysid spp.	$\bar{x}$	1.3	0.1	34.7	4.8	1.8	0.6	-	-	-	-	-	-	"	
	sd	2.3	0.1	57.3	5.3	2.0	0.9	-	-	-	-	-	-	"	
Onisimus glacialis	$\bar{x}$	46.3	4.5	23.7	4.6	1.5	0.9	0.7	0.1	0.8	0.7	1.6	0.7	"	
	sd	36.2	3.6	21.4	3.5	1.7	1.4	1.2	0.2	1.4	1.3	2.5	1.0	"	
Gammarus setosus	$\bar{x}$	0.3	0.03	0.3	0.02	0.5	1.9	-	-	-	-	-	-	"	
	sd	0.6	0.05	0.5	0.04	0.9	3.2	-	-	-	-	-	-	"	
Apherusa glacialis	$\bar{x}$	-	-	2.6	0.4	1.4	0.3	93.6	89.1	89.9	127.6	59.6	49.1	"	
	sd	-	-	2.6	0.5	1.3	0.3	21.2	22.5	81.1	117.8	63.5	34.3	"	
Halirages mixtus	$\bar{x}$	1.7	2.0	0.5	0.2	6.8	2.1	6.0	2.3	3.6	1.7	-	-	"	
	sd	1.3	3.1	0.5	0.2	9.1	3.2	9.0	2.9	3.2	1.5	-	-	"	
Pontoporeia affinis	$\bar{x}$	0.4	0.3	-	-	-	-	-	-	-	-	-	-	"	
	sd	0.6	0.6	-	-	-	-	-	-	-	-	-	-	"	
Parathemisto spp.	$\bar{x}$	-	-	-	-	2.2	1.9	1.2	0.5	24.5	26.9	3.6	2.9	"	
	sd	-	-	-	-	1.0	1.3	2.1	0.9	32.8	26.4	3.6	2.8	"	
Amphipod spp.	$\bar{x}$	3.8	2.4	1.7	0.8	1.4	1.4	3.1	4.9	0.5	0.6	-	-	"	
	sd	3.1	1.5	3.0	1.4	1.3	1.2	2.6	4.5	0.9	1.0	-	-	"	

*No sample was taken on 23 September 1978 at Station 7 due to ice conditions.

Appendix 10. Abundance (No./m^2) and biomass (mg ash-free dry weight/m^2) of important species of epibenthic invertebrates collected near the bottom in drop net samples in Simpson Lagoon and nearshore areas, 8 July-23 September 1978. (N=5 for each station-day.)

		8 July		19 July		3 August		18 August		30 August		14 September		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 1 Bottom															
Mysis litoralis	$\bar{x}$	193.3	38.2	38.0	16.1	148.0	88.7	18.0	28.4	4.0	4.0	3.0	3.6	-	-
	sd	126.6	23.1	34.7	10.0	87.6	53.5	19.6	36.0	4.2	3.7	4.5	5.4	-	-
Mysis relicta	$\bar{x}$	101.7	38.8	5.0	1.3	143.0	87.6	21.0	21.1	10.0	12.6	166.0	244.7	102.0	145.9
	sd	93.0	30.6	8.7	2.3	49.6	32.6	24.8	25.2	6.1	10.7	98.1	136.1	68.3	82.4
Mysid spp.	$\bar{x}$	38.3	5.9	4.0	1.2	9.0	1.5	9.0	4.7	3.0	2.0	2.0	11.4	-	-
	sd	27.5	7.4	6.5	2.3	4.2	0.8	4.2	2.3	4.5	3.0	2.7	15.7	-	-
Onisimus glacialis	$\bar{x}$	28.3	25.4	72.0	122.8	44.0	36.2	4.0	2.2	27.0	32.9	7.0	12.1	70.0	98.0
	sd	22.5	20.5	48.2	80.2	34.2	24.9	6.5	4.3	23.6	33.2	5.7	17.7	43.0	49.3
Pontoporeia affinis	$\bar{x}$	1.7	4.3	3.0	5.0	2.0	2.2	3.0	4.1	1.0	3.4	-	-	-	-
	sd	2.9	7.4	6.7	11.3	2.7	3.1	2.7	4.1	2.2	5.3	-	-	-	-
Halirages mixtus	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	1.0	0.3	2.0	0.2
	sd	-	-	-	-	-	-	-	-	-	-	2.2	0.8	2.8	0.3
Apherusa glacialis	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	sd	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gammarus setosus	$\bar{x}$	-	-	4.0	18.1	-	-	-	-	-	-	-	-	-	-
	sd	-	-	8.9	40.6	-	-	-	-	-	-	-	-	-	-
Parathemisto spp.	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	sd	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphipod spp.	$\bar{x}$	3.3	0.5	6.0	7.0	5.0	3.6	6.0	7.7	5.0	4.2	53.0	27.2	28.0	8.0
	sd	5.7	0.9	6.5	10.5	6.1	5.8	5.5	9.7	3.5	4.2	26.6	29.5	20.8	6.6

Appendix 10 (continued).

		8 July		19 July		3 August		18 August		30 August		14 September		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 2 Bottom															
Mysis litoralis	$\bar{x}$	18.3	5.1	572.0	196.6	353.0	229.2	175.0	153.7	49.0	66.2	34.0	41.2	2.0	2.4
	sd	7.6	0.9	390.2	116.6	87.9	51.9	60.9	49.5	15.6	30.9	7.4	8.7	2.7	3.3
Mysis relicta	$\bar{x}$	40.0	29.6	75.0	62.0	13.0	16.3	4.0	11.5	13.0	24.4	123.0	164.3	92.0	117.7
	sd	32.8	36.4	35.7	41.0	9.1	12.3	4.2	11.6	9.1	12.9	66.6	76.1	19.2	23.1
Mysid spp.	$\bar{x}$	10.0	1.1	25.0	6.1	29.0	12.8	7.0	3.6	-	-	2.0	11.3	1.0	1.7
	sd	10.0	1.2	31.0	5.0	17.8	9.6	5.7	3.0	-	-	2.7	19.9	2.2	3.8
Onisimus glacialis	$\bar{x}$	45.0	65.5	14.0	16.5	79.0	81.9	81.0	87.6	45.0	96.9	59.0	80.2	37.0	43.0
	sd	34.6	58.2	6.5	10.6	23.8	22.2	29.0	34.0	7.9	44.7	37.3	56.3	18.6	29.9
Pontoporeia affinis	$\bar{x}$	3.3	2.2	1.0	1.8	2.0	2.2	17.0	18.7	-	-	1.0	0.8	-	-
	sd	5.8	3.9	2.2	4.1	2.7	3.1	15.7	18.5	-	-	2.2	1.9	-	-
Halirages mixtus	$\bar{x}$	-	-	-	-	-	-	4.0	1.3	-	-	8.0	7.7	-	-
	sd	-	-	-	-	-	-	8.9	2.8	-	-	7.6	1.1	-	-
Apherusa glacialis	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	sd	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gammarus setosus	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	2.0	1.7	1.0	1.4
	sd	-	-	-	-	-	-	-	-	-	-	2.7	2.9	2.2	3.0
Parathemisto spp.	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	sd	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphipod spp.	$\bar{x}$	13.3	14.9	1.0	0.9	23.0	26.7	37.0	24.5	22.0	8.9	33.0	21.7	51.0	16.3
	sd	14.4	23.7	2.2	2.0	9.7	24.4	22.2	24.7	14.4	9.9	25.6	30.3	48.3	18.4

Appendix 10 (continued).

		8 July		19 July		3 August		18 August		30 August		14 September		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 3 Bottom															
Mysis litoralis	$\bar{x}$	12.0	13.3	98.7	181.3	121.0	89.1	471.0	426.1	38.0	34.5	17.0	20.9	23.0	29.1
	sd	7.6	15.3	54.5	102.3	66.4	47.7	217.8	184.9	7.6	14.6	13.0	15.8	13.5	13.8
Mysis relicta	$\bar{x}$	10.0	15.6	25.0	30.4	8.0	12.2	26.0	32.0	22.0	42.0	46.0	72.9	90.0	116.2
	sd	10.0	12.3	17.3	29.0	7.6	14.2	27.7	49.6	9.1	21.2	37.3	65.7	24.2	22.7
Mysid spp.	$\bar{x}$	-	-	10.0	7.5	-	-	21.0	9.9	-	-	-	-	3.0	3.6
	sd	-	-	7.1	12.7	-	-	24.6	11.8	-	-	-	-	2.7	3.5
Onisimus glacialis	$\bar{x}$	8.0	7.0	98.8	106.0	102.0	50.8	159.0	161.2	115.0	93.3	77.0	100.5	48.0	57.0
	sd	11.5	15.5	53.0	75.0	17.2	17.7	28.2	76.9	76.4	66.9	102.7	197.1	37.8	24.6
Pontoporeia affinis	$\bar{x}$	3.0	2.3	8.8	18.3	10.0	10.7	12.0	16.2	1.0	1.3	-	-	-	-
	sd	2.7	2.7	7.5	11.3	9.4	10.2	5.7	7.3	2.2	3.0	-	-	-	-
Halirages mixtus	$\bar{x}$	-	-	-	-	-	-	4.0	9.0	-	-	8.0	1.6	3.0	1.4
	sd	-	-	-	-	-	-	5.5	1.5	-	-	9.7	1.0	4.5	2.2
Apherusa glacialis	$\bar{x}$	-	-	-	-	2.0	0.7	-	-	-	-	5.0	2.0	-	-
	sd	-	-	-	-	4.5	1.5	-	-	-	-	5.0	1.9	-	-
Gammarus setosus	$\bar{x}$	-	-	-	-	1.0	4.9	-	-	-	-	-	-	-	-
	sd	-	-	-	-	2.2	10.9	-	-	-	-	-	-	-	-
Parathemisto spp.	$\bar{x}$	-	-	-	-	-	-	-	-	1.0	1.0	-	-	1.0	14.3
	sd	-	-	-	-	-	-	-	-	2.2	2.2	-	-	2.2	32.0
Amphipod spp.	$\bar{x}$	4.0	1.4	10.0	5.9	23.0	17.1	19.0	13.9	13.0	8.9	9.0	5.0	29.0	12.1
	sd	8.9	3.0	7.1	1.7	20.8	10.3	4.2	12.1	9.7	9.9	9.6	6.4	10.2	7.3

Appendix 10 (continued).

		8 July		19 July		3 August		18 August		30 August		14 September		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 4 Bottom															
Mysis litoralis	$\bar{x}$	No Samples		398.0	587.3	65.0	51.2	47.0	49.0	19.0	19.1	3.0	4.2	22.6	36.5
	sd	Collected		264.9	950.9	47.2	35.1	11.5	21.3	5.5	6.8	2.7	4.0	18.9	34.1
Mysis relicta	$\bar{x}$	"		68.0	78.9	3.0	3.2	24.0	35.2	22.0	26.3	-	-	16.0	30.9
	sd	"		36.2	90.8	4.5	4.5	17.8	27.8	9.7	19.6	-	-	15.6	33.6
Mysid spp.	$\bar{x}$	"		11.0	2.5	2.0	1.0	6.0	2.9	1.0	0.3	2.0	1.9	1.0	0.8
	sd	"		6.5	2.5	2.7	1.4	8.9	4.7	2.2	0.8	2.7	2.8	2.2	1.8
Onisimus glacialis	$\bar{x}$	"		523.0	555.3	112.0	76.3	271.0	195.9	35.0	68.5	88.0	86.2	12.0	25.2
	sd	"		348.0	602.1	66.7	51.7	173.4	94.7	29.4	24.8	136.3	114.0	9.1	18.0
Pontoporeia affinis	$\bar{x}$	"		1.0	1.3	-	-	8.0	3.4	-	-	-	-	-	-
	sd	"		2.2	3.0	-	-	9.1	4.4	-	-	-	-	-	-
Halirages mixtus	$\bar{x}$	"		-	-	-	-	-	-	10.0	3.3	-	-	-	-
	sd	"		-	-	-	-	-	-	11.2	2.7	-	-	-	-
Apherusa glacialis	$\bar{x}$	"		4.0	2.2	-	-	-	-	-	-	-	-	-	-
	sd	"		4.2	2.5	-	-	-	-	-	-	-	-	-	-
Gammarus setosus	$\bar{x}$	"		4.0	1.3	-	-	6.0	2.7	15.0	16.7	-	-	1.0	0.1
	sd	"		4.2	1.3	-	-	8.2	4.0	20.0	20.4	-	-	2.2	0.2
Parathemisto spp.	$\bar{x}$	"		-	-	-	-	-	-	-	-	-	-	-	-
	sd	"		-	-	-	-	-	-	-	-	-	-	-	-
Amphipod spp.	$\bar{x}$	"		28.0	20.2	20.0	7.6	42.0	6.5	42.0	9.8	64.0	30.6	26.0	15.7
	sd	"		17.5	10.9	12.2	7.8	23.6	2.4	27.9	7.1	69.0	27.7	13.9	10.7

Appendix 10 (continued).

		8 July		19 July		3 August		18 August		30 August		14 September		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 5 Bottom															
Mysis litoralis	$\bar{x}$	5.0	2.0	18.0	10.8	76.0	50.5	39.0	33.9	7.0	6.1	-	-	1.0	1.2
	sd	8.7	3.4	17.2	11.7	62.4	39.5	29.0	27.4	9.7	8.8	-	-	2.2	2.7
Mysis relicta	$\bar{x}$	16.6	5.9	4.0	1.6	5.0	3.0	22.0	17.4	2.0	1.6	1.0	0.8	-	-
	sd	11.5	6.6	4.2	1.9	3.5	3.0	8.4	6.9	2.7	2.2	2.2	1.8	-	-
Mysid spp.	$\bar{x}$	-	-	5.0	0.3	9.0	2.3	2.0	0.8	-	-	1.0	1.4	-	-
	sd	-	-	4.5	0.8	7.4	2.3	2.7	1.5	-	-	2.2	3.1	-	-
Onisimus glacialis	$\bar{x}$	8.3	15.4	167.0	106.0	69.0	25.7	47.0	195.9	11.0	22.9	25.0	36.8	7.0	7.3
	sd	14.4	26.7	137.6	75.0	22.5	7.2	25.4	94.7	11.4	23.2	16.6	33.3	8.4	9.1
Pontoporeia affinis	$\bar{x}$	-	-	1.0	2.9	-	-	-	-	-	-	-	-	-	-
	sd	-	-	2.2	6.6	-	-	-	-	-	-	-	-	-	-
Halirages mixtus	$\bar{x}$	-	-	-	-	-	-	2.0	0.7	-	-	-	-	-	-
	sd	-	-	-	-	-	-	4.5	1.5	-	-	-	-	-	-
Apherusa glacialis	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	sd	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gammarus setosus	$\bar{x}$	-	-	-	-	1.0	1.4	-	-	-	-	-	-	1.0	0.1
	sd	-	-	-	-	2.2	3.0	-	-	-	-	-	-	2.2	0.2
Parathemisto spp.	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	1.0	11.2	-	-
	sd	-	-	-	-	-	-	-	-	-	-	2.2	25.0	-	-
Amphipod spp.	$\bar{x}$	1.7	0.3	1.0	0.5	51.0	16.5	89.0	13.9	20.0	10.3	15.0	8.6	6.0	1.7
	sd	2.9	0.5	2.2	1.0	32.1	22.0	57.5	8.3	7.9	7.2	11.2	9.8	5.5	1.7

Appendix 10 (continued).

		8 July		19 July		3 August		18 August		30 August		14		23 September	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 6 Bottom															
Mysis litoralis	$\bar{x}$	497.0	395.2	1.0	0.4	379.0	267.4	6.4	58.7	4.0	3.5	-	-	1.0	1.2
	sd	487.0	563.1	2.2	0.8	287.0	215.0	9.6	7.3	4.2	5.0	-	-	2.2	2.7
Mysis relicta	$\bar{x}$	420.0	193.4	2.0	0.5	5.0	10.8	-	-	-	-	14.0	3.3	22.0	31.3
	sd	393.8	196.0	2.2	1.0	7.1	20.0	-	-	-	-	28.6	26.2	16.8	29.0
Mysid spp.	$\bar{x}$	-	-	-	-	44.0	13.1	8.0	5.6	-	-	4.0	3.0	-	-
	sd	-	-	-	-	51.9	16.6	4.5	7.6	-	-	8.9	6.7	-	-
Onisimus glacialis	$\bar{x}$	74.0	56.4	75.0	37.5	27.0	31.0	6.0	8.9	4.0	9.2	10.0	77.3	15.0	33.0
	sd	45.6	56.2	42.9	45.1	20.8	31.9	5.5	9.4	4.2	17.1	6.1	102.5	7.1	29.6
Pontoporeia affinis	$\bar{x}$	1.0	4.9	-	-	1.0	0.9	-	-	-	-	-	-	-	-
	sd	2.2	11.0	-	-	2.2	2.0	-	-	-	-	-	-	-	-
Halirages mixtus	$\bar{x}$	-	-	-	-	-	-	1.0	0.3	-	-	1.0	0.3	-	-
	sd	-	-	-	-	-	-	2.2	0.3	-	-	2.2	0.8	-	-
Apherusa glacialis	$\bar{x}$	-	-	4.0	2.2	-	-	-	-	-	-	-	-	-	-
	sd	-	-	4.2	2.5	-	-	-	-	-	-	-	-	-	-
Gammarus setosus	$\bar{x}$	4.0	18.1	-	-	-	-	1.0	0.01	-	-	-	-	-	-
	sd	8.9	40.6	-	-	-	-	2.2	0.01	-	-	-	-	-	-
Parathemisto spp.	$\bar{x}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	sd	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphipod spp.	$\bar{x}$	2.0	0.6	6.0	2.7	24.0	1.5	16.0	2.3	15.0	3.9	12.0	8.0	8.0	3.8
	sd	2.7	0.8	4.2	2.2	42.6	1.7	9.6	1.7	9.4	1.9	7.6	9.4	7.6	4.2

Appendix 10 (continued).

		8 July*		19 July*		3 August		18 August		30 August		14 September		23 September*	
		Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass	Abun.	Biomass
Station 7 Bottom															
Mysis litoralis	$\bar{x}$					57.0	46.5	430.0	683.4	147.0	204.5	66.0	72.0		
	sd					27.1	22.8	237.8	335.5	30.5	158.6	19.8	23.3		
Mysis relicta	$\bar{x}$					1.0	0.8	6.0	23.8	4.0	13.4	4.0	9.2		
	sd					2.2	1.8	6.5	34.8	4.2	12.6	4.2	11.1		
Mysid spp.	$\bar{x}$					1.0	0.1	62.0	29.4	2.2	19.2	7.0	15.9		
	sd					2.2	0.3	66.0	22.6	10.2	12.4	5.7	17.7		
Onisimus glacialis	$\bar{x}$					-	-	-	-	1.6	0.2	-	-		
	sd					-	-	-	-	2.2	0.4	-	-		
Pontoporeia affinis	$\bar{x}$					-	-	-	-	-	-	-	-		
	sd					-	-	-	-	-	-	-	-		
Halirages mixtus	$\bar{x}$					-	-	1.0	0.3	-	-	-	-		
	sd					-	-	2.2	0.8	-	-	-	-		
Apherusa glacialis	$\bar{x}$					-	-	2.0	1.4	-	-	-	-		
	sd					-	-	4.5	3.0	-	-	-	-		
Gammarus setosus	$\bar{x}$					-	-	-	-	-	-	-	-		
	sd					-	-	-	-	-	-	-	-		
Parathemisto spp.	$\bar{x}$					-	-	-	-	25.0	62.8	2.0	22.4		
	sd					-	-	-	-	25.7	36.3	4.5	50.1		
Amphipod spp.	$\bar{x}$					76.0	9.8	7.0	3.0	5.0	2.7	37.0	24.8		
	sd					37.8	8.4	5.7	5.1	8.7	4.0	21.7	13.5		

*No sample was taken at station 7 due to ice conditions on 8 and 19 July and 23 September.

PART 6. PRIMARY PRODUCTION AND NUTRIENTS

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SUMMARY

The algae are the suppliers of new fixed energy and carbon to the marine ecosystem and thus, all other life forms using the marine environment depend upon them directly or indirectly. In the arctic, planktonic primary production is low by comparison to that in other oceans because nutrients are optimally available only during periods of little or no light. Light is available only during the season of maximum water stratification, which impairs nutrient circulation and replenishment in the photic zone. Diatoms are generally the more common plankton types near the shore and in river plumes; flagellates become more prevalent further offshore where the water is colder, clearer and lower in nutrient concentrations. Rapid successional changes, very common among arctic phytoplankton communities, lead to considerable variability in species dominance over space and time.

The epontic (ice) algae are patchy in distribution but they provide an early season production upon which invertebrates may graze and begin their reproductive season earlier than can planktonic or benthic animals. Thus, the total contribution of epontic productivity is more important because of its timing than because of its magnitude. And, although benthic micro- and macroalgae are probably less productive per area per season than are planktonic algae, they are located strategically on a two-dimensional surface which raises their probability of encounter by a potential grazer.

Production in nearshore arctic waters is usually nitrogen-limited during the peak light season. Usable nitrogen is scarce because of stratification of the water-column, low activity or absence of nitrogen fixers, low rates of ammonification, and undependable resupply from upwelling of deeper waters. Although phosphorus and silicon supplies are generally low in arctic coastal waters, nitrogen limitation normally takes effect before these elements can become limiting to phytoplankton growth. Oxygen supplies under-ice can become low due to biological consumption but are usually present in excess of the needs of the heterotrophic community during most of the year. Nutrient supply mechanisms include coastal upwelling of deeper water, horizontal circulation and *in situ* nutrient regeneration.

Connections between trophic levels may be hypothesized by following the proportions of carbon isotopes in primary producers and the successive consumers up through the food web. Current estimates are that 50% of nearshore (within 10 km of shore) arctic carbon that ends up in coastal areas comes from terrestrial sources (via fluvial transport and tundra erosion) and the balance comes from marine productivity (epontic, benthic and planktonic). Of the samples analyzed thus far, carbon from peat appears most concentrated in benthic-dwelling isopods and amphipods and in their benthic predator, the four-horned sculpin. Apparently the trophic link between peat and invertebrates is the bacteria and their consumers (probably protozoans).

The primary producers depend directly upon timely regeneration of nutrients for their productivity. The only significant link between leaked photosynthetic production of recalcitrant organic compounds such as peat is by passage through bacteria into protozoan grazers and up through the food web. Very little is known about the distribution, activities, or sensitivities of the bacteria which function in ecosystems as nutrient regenerators, primary production scavengers, and directly as prey organisms for higher trophic level consumers. None of these trophic roles are trivial to the net productivity of the lagoon ecosystem.

ACKNOWLEDGEMENTS

Since no research was conducted by LGL Ecological Research Associates, Inc. (LGL) pursuant to this section of the report, this is only a review of the work performed by others. I am therefore totally indebted to those who obtained funding to go into the field, conduct experiments and gather the data described herein. I am particularly grateful to Dr. D.M. Schell both for conducting critical experiments and for many informative discussions. I also wish to thank Mr. D. Thomson and W. Cross of LGL Limited, Toronto, for sharing their compilations of productivity data from unpublished reports.

INTRODUCTION

In arctic coastal waters, as elsewhere, primary production assembles inorganic materials to produce organic materials that fuel the food web. Primary production is regulated (when there is adequate light) largely by the availability of nutrients; the two which are normally in shortest supply in marine systems are nitrogen and phosphorus. The purpose of this section of the Beaufort Sea Barrier Island-Lagoon Ecological Studies report is to evaluate the available data in an attempt to determine which aspects of primary production and their nutrient sources are important to the food webs that support the more conspicuous fish and birds in the nearshore environment. The processes and components involved in primary production and nutrient supply and regeneration are discussed as background from which to analyze the possible consequences to the food web of petroleum exploration and development. This report is based on a review of published and unpublished literature. No field research concerning primary production or nutrients was conducted as part of RU467, although Schell's (1979) recent studies on these topics were done in coordination with RU467.

PRIMARY PRODUCTION

Primary production is the term used to designate fixation of inorganic compounds into biological material using either light or oxidation of inorganic compounds as the energy source. This is the only means by which new organic material is produced ('fixed') in the biosphere. In the ocean, algae and some bacteria are capable of primary production and are known as autotrophs. All other life forms that utilize food resources of the oceans are ultimately dependent upon these fixers of new material. Although less conspicuous than the kelps and seaweeds, the unicellular algae and photosynthetic bacteria are quantitatively more productive and are ubiquitous throughout the oceans. The algae are the preeminent primary producers in oceanic waters and, with only a few exceptions, also dominate the production of neritic (nearshore shallow) waters. Autotrophic primary production depends upon solar radiation and inorganic nutrients occurring simultaneously and for a sufficiently long time to develop a population that can avail itself of these potentially productive circumstances.

The chemistry and biology of primary producing- and nutrient-regenerating microbes found in the coastal and oceanic waters of the arctic are not well documented. This is due primarily to a paucity of detailed process-oriented spatial and temporal sampling. The extremely severe climate has precluded systematic investigation of both the quantitative and rate aspects of the biota and inorganic constituents of this environment except in brief, intense spot sampling. Data that have been collected are from such a variety of locations and seasons that general trends can be surmised only by analysis of pooled sampling results.

Light and temperature regimes are seasonally extreme in the arctic, and dictate the scope and sequence of possible biological activities. The orderly progression from the total darkness and extreme cold of winter to the 24-h daylight and moderate temperatures of summer forces life processes into annual cycles. Light-mediated synthetic processes must await the reappearance of the sun. Upon its return in early spring, the heavy snow cover reflects most of the incoming sunlight. Eventually the sun does warm the air and ice surface enough to melt some of the upper surfaces of the snow and ice. This, along with stresses induced by winds and currents, permits cracks to form and widen into open water leads. Winds induced by movement of heated air cause widening of the leads, which allows the ocean surface more access to sun and air.

In terms of environmental factors that regulate the growth of arctic marine plants and the availability of their nutrient supply, there are about five physically distinguishable seasons (at least in the Beaufort Sea).

1. The period from October through April is characterized by increasing sea ice thicknesses. Salinity increases in the surface waters during this period, and there is limited vertical circulation of water under the ice in shallow areas. There is little or no solar radiation between November and February.
2. The period from April to June is characterized by a slowing in the thickening rate of the still-present sea ice. During this period there is increasing solar radiation, increased sublimation of snow, high salt and nutrient concentrations in surface waters, and weak under-ice currents.

3. In June and July the snow cover disappears, the sea ice melts, and a large pulse of river water is discharged into the nearshore ocean from mountain snow melt. During this time, periods of intense solar radiation are often interrupted by ground fog and highly stratified areas of open water (cold, high-salinity coastal water overlain by fresh water) runoff.
4. From July to September the ice breaks up and (in some areas) eventually disappears. There is a diminishing of solar radiation, and periodic wind-driven mixing of the water-column produces coastal salinities similar to those found in the ocean.
5. In September and October slush ice slowly forms along the shore, concomitant with the rapidly decreasing quality and quantity of solar radiation. The salinity of coastal waters increases as ice forms, and sporadic wind-driven water circulation becomes less common as the sea ice coalesces into larger floes.

Photosynthetic determinations of epontic, planktonic, and attached algal populations by use of ^{14}C uptake rates are providing the beginnings of an understanding of primary production processes in arctic marine systems (Clasby et al. 1973; Matheke and Horner 1974; Hsiao et al. 1977). More information is needed about the leakage of photosynthate directly into bacteria under arctic conditions. Failure to account for this energy flow may be introducing significant underestimates of autotrophic fixation of carbon.

Planktonic Primary Productivity

Dunbar (1970) and Platt and Subba-Rao (1975) note that the Arctic Ocean is the least productive of the world's oceans. This low productivity is caused by a short period of available light and during the period when there is a light, very stable vertical stratification of the water-column that limits nutrient circulation and nutrient replenishment during the time it is most critically needed. Arctic Ocean productivity is estimated to be less than 10 g C/m^2/yr (English 1961) and the nearshore Beaufort Sea is estimated to be less than 20 g C/m^2/yr (Alexander et al. 1974). By comparison, primary productivity in the Bering Sea is estimated at 121 g C/m^2/yr (McRoy and Goering 1976), and productivity of Atlantic shelf waters is estimated at 150 g C/m^2/yr (Platt and Subba-Rao 1975).

By comparison, productivity estimates for the shelf waters of the Indian and Pacific Oceans are even higher, and the highest overall productivity estimates are from the Antarctic Ocean, 325 g C/m^2/yr (Platt and Subba-Rao 1975).

Productivity values for various arctic areas are tabulated in Table 1. Moreover, data are insufficient to characterize specific areas of the arctic as being more or less productive than others because of the spotty data base. Values from Frobisher Bay in the eastern Canadian subarctic are intermediate between those from the High Arctic and those from the Atlantic, and are roughly equivalent to those from West Greenland (Petersen 1964). The southeastern Beaufort Sea was found to have an hourly fixation rate of 14.8 to 22.7 mg C/m^2/h (Hsiao et al. 1977) as compared to 17.6 to 23.8 mg C/m^2/h in the Chukchi Sea (Matheke and Horner 1974) and 6.9 mg C/m^2/h in the western Beaufort Sea (Alexander 1974). There appears to be a general trend toward decreasing primary productivity as well as decreasing standing stock with increasing distance from shore. Alexander et al. (1975) noted a general increase in phytoplanktonic biomass with increasing depth in nearshore Beaufort Sea waters within 10 km of shore.

Phytoplankton Standing Stock and Succession

Phytoplankton standing stock is usually estimated by measuring the concentration of the photopigment chlorophyll α or by directly counting cells under a microscope. Cell counting is a labor-intensive exercise that gives little information on population health, viability, or activity. Measurement of chlorophylls by fluorometric or spectrophotometric methods provides indices only of present and/or recent past organismal presence, and cannot give information on the size, activity or origin of the population responsible for the pigments measured (Patterson and Parsons 1963; Jacobsen 1978). Extrapolation of data from either of these methods into an inference about productivity (Jassby and Platt 1976) or process dynamics cannot be performed reliably (Jacobsen 1978). An extensive compilation or review of all arctic "chlorophyll α" data is beyond the scope of this work.

Table 1. Annual primary productivity estimates from locations in the arctic.

Location	Primary Productivity (g C/m^2/yr)	Reference
Arctic Ocean	0.6	Apollonio (1959)
Dumbell Bay, Ellesmere Island, Canada	9-12	Apollonio (1976a)
Western Beaufort Sea	9-18	Carey (1978)
Cornwallis Island, Canada	14	Apollonio (1956)
NE Chukchi Sea	18-28	Carey (1978)
Jones Sound, N.W.T., Canada	20-35	Apollonio (1976b)
West Greenland	29-98	Steeman Nielsen (1958)
Gulf of Finland	30-40	Bagge and Niemi (1971)
Resolute Bay, Cornwallis Island, Canada	32	Welch and Kalff (1975)
West Greenland	36	Petersen (1964)
Frobisher Bay, N.W.T., Canada	50-99	Grainger (1975)

Expanded from information in unpublished table prepared by D. Thomson, LGL Ltd.

The first report of primary producers from western hemisphere arctic regions concerned diatoms collected during the Canadian Arctic Expedition of 1913-1918 as described by Mann (1925). Usachev (1947) (English review in Zenkevitch 1963) has reviewed phytoplankton sampling from European and Russian arctic expeditions of the early twentieth century. A brief discussion of relative phytoplankton abundance near Point Barrow, Alaska, is given in MacGinitie (1955), and Bursa (1963a) examined the quantitative dynamics of some taxonomic groups of marine flagellates from nearshore waters at Barrow. Horner (1969, 1972) observed a bimodal phytoplankton cycle in the Barrow nearshore area (the peaks were in spring before ice break-up and again in fall). Hsiao et al. (1977) reported that in the southeastern Beaufort Sea, cell densities ranged from 2 to 4800 x 10^3 cells/L at depths to 10 m, and Alexander et al. (1975) reported that total cell numbers in the nearshore Alaskan Beaufort Sea ranged up to 10^7 cells/L.

Phytoplankton depends upon hydrographic and meteorological forces to move it vertically (into or away from light) and horizontally. These movements can transfer phytoplankton into or away from zones of usable nutrients. Because each planktonic diatom species has requirements and tolerances different from those of every other species, dynamic seasonal patterns of succession occur as environmental conditions change. Succession is effected as the phytoplankton communities modify their surrounding waters, as they are passively moved into other waters, and as they are grazed upon by marine fauna (Braarud 1962; Guillard and Kilham 1977). In response to these and other changing environmental conditions, phytoplankton community succession is both common and rapid (Lillick 1940; Lund 1966).

High concentrations of suspended sediment sometimes occur where rivers discharge into the nearshore arctic waters; this is likely to cause light limitations for phytoplankton near river deltas (Grainger 1975). Farther away from rivers, turbidity is less, but farther offshore, ice cover can produce severe light attenuation and stratified waters can produce severe limitation of available nutrients. The temperature and salinity stratifications created by ice melt add another dimension of complexity to the factors affecting phytoplankton distribution and productivity.

There are a few relationships between environmental factors and phytoplankton type that have been observed in other systems. Diatoms generally tend to occur in highest densities with high nutrient levels, low illumination levels, and warm temperatures (Sverdrup et al. 1942; Ryther 1956; Raymont 1963; Hulburt 1970); flagellates are most prevalent under conditions of higher illumination intensity and lower nutrient concentrations (Raymont 1963; Fogg 1965).

Some data about responses of plankton communities to environment in the arctic are available. Bursa (1963a) found that phytoplankton succession at Point Barrow paralleled changes in temperature and salinity. Horner et al. (1974) reported that the communities in nearshore waters and river plumes near Prudhoe Bay were totally dominated by diatoms as did Hsiao et al. (1977) for the southeastern Beaufort Sea, and Bursa (1961a, 1963a,b) in Foxe Basin. Flagellates comprised a larger proportion of total numbers farther offshore but were usually not dominant. At specific locations and times in the arctic, localized patches of other phytoplankton species frequently were found dominant over the seemingly ubiquitous diatoms (Seidenfaden 1947; Bursa 1961a,b; Raymont 1963; Alexander et al. 1974; Hsiao et al. 1977).

Presented in Fig. 1 is a diagram compiled by M.G. Foy of LGL Ltd. from reports at a variety of sites in the Alaskan and Canadian arctic taken from Bain et al. (1977). A more detailed tabulation appears in Table 2. In general it appears that phytoplanktonic communities are dominated by diatoms, with occasional patches of flagellates. Pennate diatoms predominate early in the summer, and centric diatoms become more important later in the summer.

Phytoplankton production is supplemented in polar regions by epontic production (see below) and forms the basis of the marine food web that helps support fish, birds, marine mammals, and man. The effect of any natural or man-made phenomenon or mechanism that serves to increase or decrease primary productivity over a long period of time will be felt throughout the extent of the food web. Both the quantity and quality of light received by the phytoplankton community affect the amount of primary

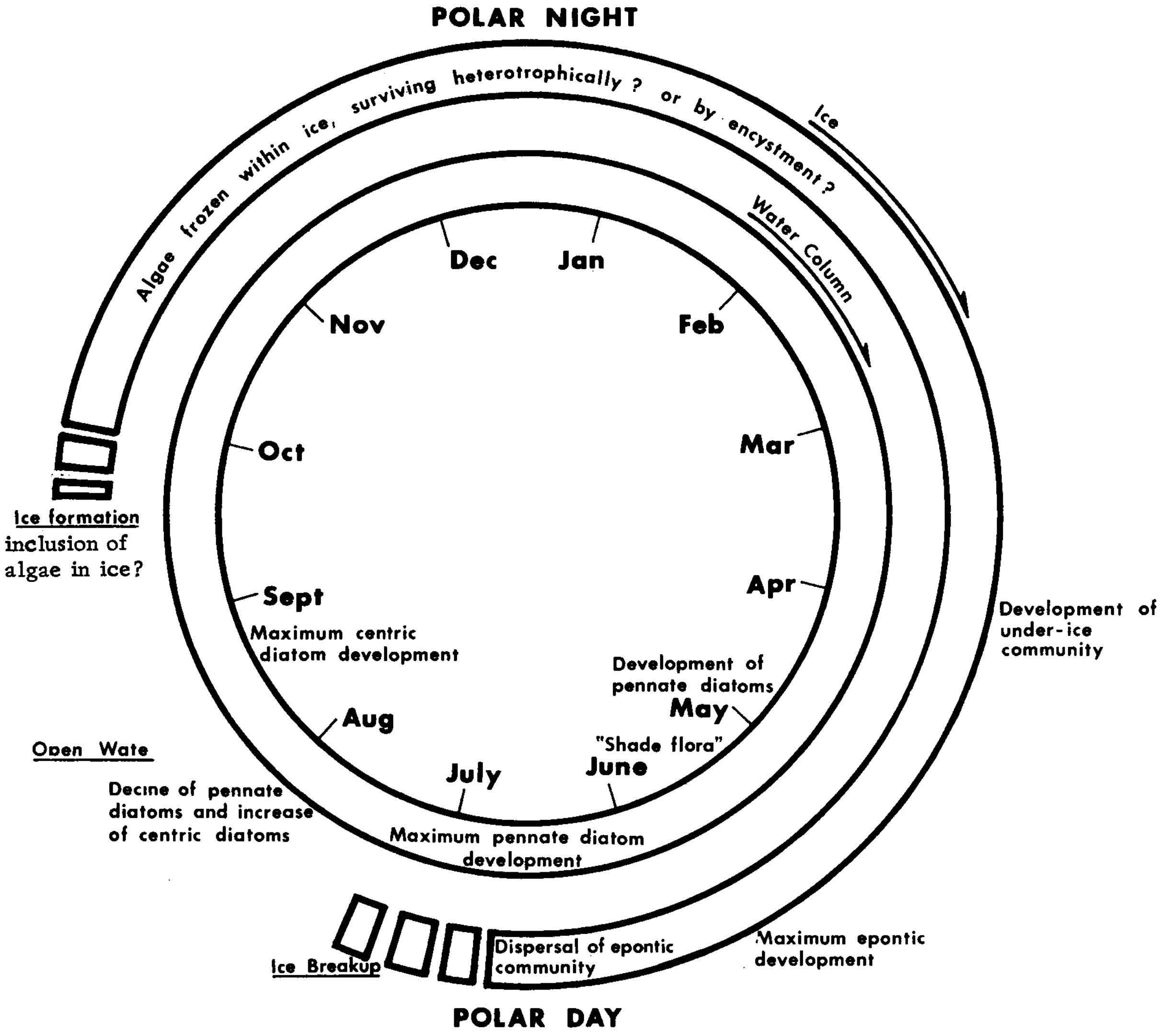

Figure 1. Seasonal sequence of algal succession in the arctic. (Redrawn from figure prepared by M.G. Foy, LGL Ltd., from data compiled by Bain et al. 1977.)

Table 2. Chronological listing of phytoplankton abundance and dominant species.

Location	Date	Depth (m)	Mean Depth-Weighted Cell No./ℓ x 10^4	Dominant Organism	References
High Arctic					
Barrow Strait	8 May	0-30	6.2*	*Nitzschia delicatissima*	Thomson et al. (1975)
Brentford Bay	2-3 May	0-25	0.1*	Microflagellates	Thomson et al. (1978)
Bridport Inlet	9-14 Jun	0-25	2.0*	*Nitzschia* spp., *Navicula* spp.	Buchanan et al. (1977)
Wellington Channel	2-29 Jun	0-25	161.0**	*Nitzschia grunowi*	Bain et al. (1977)
Resolute Passage	5 Jul	0-25	7.7	Microflagellates	Bain et al. (1977)
Creswell Bay	2 Aug	0-50	53.1	*Nitzschia seriata*	Sekerak et al. (1976b)
Bridport Inlet	5-28 Aug	0-25	42.7	*Chaetoceros socialis*	Buchanan et al. (1977)
Assistance Bay	25 Aug	0-40	83.2	*Chaetoceros socialis*	Sekerak et al. (1976b)
Peel Sound	30 Aug	0-50	1.23	Microflagellates	Thomson et al. (1975)
Brentford Bay	2 Sep	0-40	1.8	*Chaetoceros* sp.	Thomson et al. (1978)
Lancaster Sound	22-25 Jul	0-50	306.0	*Chaetoceros socialis*	Sekerak et al. (1976a)
	3 Aug-1 Sep	0-50	294-164	*Chaetoceros socialis*	Sekerak et al. (1976a)
	7-13 Sep	0-50	107.0	*Chaetoceros socialis*	Sekerak et al. (1976a)
Davis Strait	Feb	0-50	0.1†	Dinoflagellates	(Imperial Oil Limited, Aquitaine Co. Can. Ltd., Canada-Cities Service Ltd., 1978; Esso Resources Canada Ltd., Aquitaine Co. Can. Ltd., and Canada-Cities Serv. Ltd. (1979).
	Apr-May	0-50	100†	*Chaetoceros* spp.	
	Jul	0-50	14†	*Chaetoceros* spp.	
	Oct-Nov	0-50	5†	Diatoms	

*Under-ice **Ice-edge †Approximate values
Reproduced from unpublished table compiled by D. Thomson, LGL Ltd.

production (carbon fixation per unit time and volume) that can occur, and also affect the species composition of the community that is responsible for this production (successional events) (Schindler et al. 1974; Kalff and Welch 1974; Welch and Kalff 1974).

The process of photosynthesis requires light as the driving energy for fixation of carbon. Radiant energy is transformed into usable chemical energy within the chloroplasts and chromatophores by means of the photon absorbing characteristics of the chlorophylls and accessory pigments. For plant photopigments, the most commonly absorbed wavelengths of light lie in the visible spectrum at wavelengths from 400 to 700 nm. However, each algal group contains a different assemblage of accessory pigments and thus possesses different optimal lighting spectra. Wavelengths shorter than 600 mm are absorbed by accessory pigments and the energy subsequently is transferred to chlorophyll *a*; wavelengths longer than 600 nm are absorbed and used directly by chlorophyll *a*.

Temporal and spatial changes in photosynthetically usable solar radiation within the ocean have been reviewed by Strickland (1958) and Jerlov (1968). Local sky conditions such as cloud cover, fog, dust, and smoke can alter both the intensity and spectral distribution of light reaching the ocean or ice surface. When covered by ice and snow, especially when the snow cover is greater than 20 cm thick, the underlying water is shaded extremely effectively by the high surface albedo (Maguire 1975). Surface reflectivity of snow-free ice is considerably less but still quantitatively important (Langleben 1971; Campbell and Martin 1974; Kukla and Kukla 1974). The presence of a dense community of ice algae at the bottom of the ice can also reduce the transmission of light to phytoplankton in the water below. The angle of solar incidence and the sea surface state (which are functions of solar season and local winds) can also substantially affect illumination below the surface of open water. Surface reflectivity can range from only a few percent on a calm day to over 30% for conditions of moderate to strong winds (solar angle 30°). As the solar angle decreases from 30° to 10°, the surface reflection increases rapidly to over 30% in calm weather (von Arx 1962). Water transparency also affects the quantity and quality of photosynthetically available light that reaches to a given depth in the water-column.

Suspended particulates and dissolved organic and inorganic ions contribute to localized alteration and spectral shifting of solar radiation throughout the photic zone. Particulates selectively scatter blue light, which leaves only that remaining small fraction of red light that was not absorbed previously in the surface waters.

Diminution of light intensity can have either a positive or negative effect on local primary productivity rates, depending upon several other variables. For a phytoplankton population that is in high light intensity (0.2 ly/min) and that has become adapted to this light intensity, a rapid decrease in intensity would cause an immediate (scale of 10 min) decrease in productivity rates. Over the short term the organisms could respond by the physiological mechanism of light-adaptation (Brown and Richardson 1968). However, different species are adapted to use different light intensities with different nutrient concentrations for optimal growth (Dugdale 1967). If the diminution of light intensity were severe enough and persisted sufficiently long (or were coupled with a nutrient shortage), a successional event could occur in favor of a different species that was more efficient in the new illumination or nutrient circumstances. For example, Wright (1964) described an under-ice phytoplankton species adapted for growth at 0.00014 ly/min. If, after some stage of succession were attained, the effective solar intensity were again increased (e.g., by shifting ice floes, passage of a storm front, or dissipation of oil spill), the shade-adapted organisms would likely experience photo-inhibition and depressed productivity (Takahashi et al. 1971). They would probably begin to leak photosynthetically produced glycolic acids, carbohydrates and polysaccharides (Fogg 1966; Watt 1966; Anderson and Zeutschel 1970). Depending upon the subsequent conditions of illumination, successional events toward a more light tolerant or less light tolerant population could then proceed (Bursa 1961a; see also Fig. 1).

The release of short-chain fatty acids and sugars is not restricted to light stressed phytoplankton but rather it becomes more extreme when they are subjected to light stress. Release or "exudation" (Sieburth 1969) of primary photosynthetic fixation products (photosynthate) has been reported to be as high as 50% of daily productivity (Fogg 1952;

Allen 1956). Under normal conditions, healthy phytoplankton release from 15% (Eppley and Sloan 1965; Hellebust 1965) to 30% (Watt 1966) of daily carbon fixation as extracellular photosynthate. These soluble organics, along with the cellular debris from previously unsuccessful stages of successional events, provide a pool of readily assimilatable sugars, amino acids, and carbohydrates with which both phytoplankton (Lewin and Lewin 1960; Kuenzler 1965) and bacterioplankton (Wright and Hobbie 1965; Hobbie and Crawford 1969) can grow heterotrophically (photoautotrophs may function heterotrophically in the dark).

Marine bacteria have been shown to have an average assimilation efficiency of 45% for algal debris (Sorokin 1970), 67% for glucose, and 78% for amino acids (Williams 1970). The bacterioplankton are primarily responsible for remineralization of essential nutrients. Thus leakage of photosynthate by phytoplankton and its subsequent uptake and use by bacterioplankton may be one mechanism by which fixed carbon compounds are "traded" for production of biousable forms of inorganic ions and in some cases production of essential compounds (vitamins) by bacteria (Burkholder and Burkholder 1956; Starr 1956). Under most circumstances a growing bacterioplankton population could effectively out-compete a phytoplankton community for essential nutrients in a potentially limiting environment. Bacteria have much higher affinities for nutrients than do algae. Thus bacteria are capable of stripping nitrate and ammonia (Wright and Hobbie 1965) and phosphate (Rigler 1956; Rhee 1972) out of the water to well below the minimum levels necessary for algal growth (Wright and Hobbie 1966). Some phytoplankton have been reported to produce antibacterial substances (Sieburth 1964; Duff et al. 1966), possibly as a defensive mechanism.

The principal reason arctic waters are the least productive of ocean waters is that plant productivity, which is the foundation of all animal productivity, is very low. This stems from the fact that in winter little or no light is available for photosynthesis, although nutrients are plentiful, whereas in summer there is 24-h of sunlight. But there is also extremely severe nutrient limitation brought on by strong stratification of the water-column. Of the production that does occur, production by flagellates is most important in offshore waters where nutrients are generally in low concentrations but light penetration of the clear water is high. Diatoms tend to be more abundant in nearshore waters and around river plumes where the water is warmer, turbid and richer in nutrients. Complex interactions between bacterioplankton and phytoplankton provide both nutrient supplements to the algae and effective scavenging mechanisms between fixed carbon compounds and small animals. Successional events among algae, bacteria, protozoans, and copepods are common as local environmental conditions, such as sky, water, wind, stream and ice conditions, change.

Epontic Primary Productivity

During the first submarine voyage under the north polar ice cap, the commander of the USS *Nautilus* observed, "The ice looks like the inside of a fish bowl that hasn't been cleaned in years" (Anderson 1959). Responsible for this appearance were the epontic biota--the organisms associated with the underside of sea ice. The epontic biota includes both plants (algae) and animals. The unique habitat and concentrated algal production provided by the under-ice epontic community during the spring season is utilized by a diverse assemblage of animals. The reported microscopic fauna includes heliozoans, hypotrichous cilates, and nematodes; turbellarians, polychaete larvae, harpacticoid copepods, cyclopoid copepods, and copepod larvae have also been found in great abundance in the epontic zone (Horner and Alexander 1972a, b; Horner et al. 1974; Thomson et al. 1975; Buchanan et al. 1977; Thomson et al. 1978; MacLaren Marex Inc. 1979a). Macro-invertebrates often closely associated with the above potential food resources include several species of amphipods (MacGinitie 1955; Barnard 1959; English 1961; Apollonio 1961, 1965; Emery 1973; Alexander et al. 1974; Green and Steele 1975; Welch and Kalff 1975; Divoky 1978) and mysids (Thomson et al. 1978). Amphipods and mysids are less densely distributed in the epontic zone than in benthic zones (Buchanan et al. 1977; Thomson et al. 1978). However, the epontic animals are significant because of the large areal extent of under-ice habitat during the period of peak epontic algal production, and because these animals are accessible, wherever there is some open water, to diving birds. This early season production provides a significant supply of food to those animals exploiting epontic primary productivity.

The probable contribution of this community to the total productivity of polar marine ecosystems lies more in the timing of its appearance than in its net productivity per unit area of ocean. The epontic algal community appears during the latter part of winter (as the sun returns to the sky but when air temperatures are still low enough for the thickness of the sea ice to be increasing). This algal growth is absolutely dependent upon growing or stable (not melting) ice for physical support. The early appearance of primary production effectively lengthens the growing season for algae and algal grazers (Usachev 1949; Meguro et al. 1966; Dunbar 1968; Alexander 1974; McRoy and Goering 1974, 1976; Horner 1976, 1977).

Microalgae occur in low concentrations throughout sea ice, from the time it first forms (Horner 1977) through the period of thickening, between layers of fragile clear ice (Usachev 1949; Bursa 1961a,b; MacLaren Marex Inc. 1979a). Their concentration reaches a peak during late winter and early spring in the delicate, three dimensional crystalline areas in the lower few centimeters of the underside of sea ice (Meguro et al. 1967; Horner and Alexander 1972b; Thomson et al. 1975, 1978). Although very patchy in appearance, intense local blooms of epontic algae occur long before planktonic algae are abundant or productive in the water-column (Apollonio 1961; Alexander 1974; Matheke and Horner 1974). The attached under-ice phytoplankton populations near Devon Island have been estimated to include 3.0 to 23.0 mg chlorophyll/m^2, based on colorometer measurements of chlorophyll (Apollonio 1961, 1965). These values are one order of magnitude higher than reported coastal diatom blooms and two orders of magnitude higher than those from open ocean samples (Parsons 1963).

Horner (1976, 1977) has reviewed published research on epontic communities in the arctic and antarctic as well as unpublished data from workers at the University of Alaska. A restatement of her reviews is beyond the scope of this work. We will instead present information from arctic research reports that review and discuss the ecological implications of the autotrophic members of the epontic community. Many of the following data have been extracted from appendices and in some cases recalculated to correct errors by the original authors. Additional data in unreduced form are found in the original reports and publications.

Early reports of arctic ice-associated algae were species lists reported by Cleve 1896 (in Gran 1904) from coastal Baffin Bay, Canada, and those reported by Vanhoffen 1897 (in Gran 1904) from Karajak Fiord, Greenland. Observations of algae living in sea ice have been known since 1841 (Ehrenberg 1841). Nansen (1906) first reported ciliate protozoans in the under-ice community. Studies of ice organisms in the central arctic include chlorophyll measurements from coastal Devon Island from two summers (Apollonio 1961, 1965), measurements of epontic algal biomass (15 samples) and productivity offshore from Resolute Bay (Welch and Kalff 1975), measurements of chlorophyll in Barrow Strait and Austin Channel (Thomson et al. 1975), and measurements of cell abundance in several bays (Buchanan et al. 1977; Thomson et al. 1978). The most detailed data concerning arctic epontic productivity have been obtained at Barrow and several nearshore sites in northern Alaska (Horner 1972, 1976, 1977; Horner and Alexander 1972a,b; Clasby et al. 1973; Alexander 1974; Alexander et al. 1974; Matheke and Horner 1974). The only offshore studies in Alaskan waters were those by Meguro et al. (1966, 1967) from 8 to 16 km off Point Barrow. To our knowledge the only quantitative winter sampling by divers was conducted at Prudhoe Bay in February 1979 (LGL Ltd. in prep.).

Epontic Standing Stock and Productivity

The under-ice epontic community is usually dominated by pennate diatoms (both motile and sessile), which reside as colonies within brine cells in the interstices of the matrix of vertically oriented ice crystals (Meguro et al. 1967; Horner and Alexander 1972b). The particular species composition in one patch can be very different from that in a nearby patch (Alexander et al. 1974; Buchanan et al. 1977). Thus the observed shifts in dominant species at one sample site from year to year (Alexander et al. 1974) and from week to week (Hsiao 1979) should not be surprising. The most commonly dominant pennate diatoms described so far have been *Nitzschia frigida*, *N. cylindrus*, *Navicula pelagica*, *N. marina*, *N. quadripedis* and *Achnanthes taeniata*.

Centric diatoms are generally a small proportion of the epontic diatom community, but some genera occur regularly in low concentrations (*Chaetoceros* and *Thalassiosira* --Buchanan et al. 1977; Horner 1977; Thomson et al. 1978; MacLaren Marex Inc. 1979a). Some species occur occasionally in relatively high numbers (*Melosira* spp.--Hsiao 1979; and *Chaetoceros atlanticus* and *Detonula crystifera*--MacLaren Marex Inc. 1979a). The remainder of the epontic algal community is composed of lesser but varying numbers of flagellates, dinoflagellates, and cryptomonads.

Cell counts of plankton in ice have been made at several locations. Total cell numbers (standing stock) in the bottom ice layer at Barrow were as low as 41 x 10^3 cells/L in January (Alexander et al. 1974), averaged 1 x 10^6 cells/L in February-March and 3 to 4 x 10^6 cells/L in April, and reached a maximum in May when they averaged 14 to 18 x 10^6 cells/L (Table 3). Monthly averages for standing stock at Barrow were very similar in 1972 and 1973. Somewhat lower values (5 to 6 x 10^6 cells/L) have been reported for the Canadian high arctic during late May and early June by Buchanan et al. (1977) and Thomson et al. (1978), and for the Davis Strait ice pack in early May by MacLaren Marex Inc. (1979a). These data are so few as to be attributable to regional difference, or lower productivity, higher grazing pressure, successional phenomena or other factors. The unusually high counts reported by Hsiao (1979)--average of 73 x 10^6 cells/L for May--are not comparable as he used the bottom 1 cm of a core section, whereas previous results were based on bottom sections 10 to 20 cm in length.

Biomass estimates of epontic microalgae in fast ice (as measured by chlorophyll *a* content) have been made at several locations in the Arctic (Table 3). When those arctic and subarctic areas of fast ice for which there are considerable data are compared, there is close agreement in biomass per unit area averaged over the bloom period (May-June); viz. from 7.7 to 16.2 mg chlorophyll *a*/m^2 in Jones Sound (1961, 1963), in Barrow Strait (1973-1974), at Barrow, Alaska (1971-1973), and in Frobisher

Table 3. Biomass (mg chlorophyll *a*/m^3 and /m^2) and standing stock (cells/L) of epontic algae, from studies in the Beaufort Sea and Northwest Passage.

Location	Dates	Biomass (mg chl *a*/m^3) Mean	Biomass (mg chl *a*/m^3) Max.	n	Biomass (mg chl *a*/m^2) Mean	Biomass (mg chl *a*/m^2) Max.	n	Standing Stock (cells/L x 10^6) Mean	Standing Stock (cells/L x 10^6) Max.	n	Method	Authority
Barrow (offshore)	27-29 July 1964	120.3	427.0	14	24	-	14	-	-	-	1	Meguro et al. (1966,1977)
Barrow (inshore)	13-31 May 1971	65.5	119.9	13	(11.5)	(21.0)	13	-	-	-	1	Horner (1972)
	2 June-3 July 1971	15.8	52.0	26	(2.8)	(9.1)	26	-	-	-	1	Horner (1972)
	28 Jan-27 Mar 1972	7.1	12.4	11	0.8*	2.3*	11	1.01	3.26	11	1	Horner (1972),Alexander et al. (1974)
	3 Apr-1 May 1972	33.0	103.4	5	2.3*	5.2*	5	3.25	11.89	5	1	Horner (1972),Alexander et al. (1974)
	7 May-8 June 1972	170.4	707.2	8	7.7*	30.5*	9	14.14	28.84	9	2	Alexander et al. (1974)
	5-19 Jan 1973	-	-	-	0.2	0.2	3	0.15	0.26	2	1	Alexander et al. (1974)
	5-30 April 1973	-	-	-	3.6	8.3	8	3.64	5.78	5	2	Alexander et al. (1974)
	7 May-8 June 1973	-	-	-	15.8	23.0	10	18.43	42.73	9	2	Alexander et al. (1974)
N. coast Alaska++	2-3 June 1971	67.8	213.2	5	(11.9)	(37.3)	5	-	-	-	1	Horner (1972)
Prudhoe Bay**	2 Feb 72,27 Mar 71	3.7	5.7	4	(0.6)	(1.0)	4	-	-	-	1	Horner et al. (1974)
	10 May 71, 4 Jun 71, 18-25 May 1972	25.8	97.9	7	(4.5)	(17.1)	7	-	-	-	1	Horner et al. (1974)
S. Melville Island	7-13 June 1977	-	-	-	-	-	-	4.95	12.19	13	2	Buchanan et al. (1977)
Barrow Strait	8, 13 May 1973	-	-	-	15.2	22.0	15	-	-	-	?	Welch and Kalff (1975)
Austin Channel/Barrow St.	1-14 May 1974	-	-	-	10.9	12.4	3	-	-	-	1	Thomson et al. (1975)
N.E. Boothia Peninsula	22-27 May 1977	-	-	-	-	-	-	5.10	7.13	6	2	Thomson et al. (1978)
Jones Sound	4-13 June 1961	409.6	645.0	9	15.5*	23.0*	7	-	-	-	1	Apollonio (1965)
	16-27 June 1961	82.3	196.0	6	-	-	-	-	-	-	1	Apollonio (1965)
	11 May-12 June 1963	646.4	1460.0	18	10.7*	23.0*	17	-	-	-	1	Apollonio (1965)
Eclipse Sound	15-27 May 1976	-	-	-	-	-	-	72.77	160.23	9	1	Hsiao (1979)
	21 March 1977	-	-	-	-	-	-	0.03	0.04	3	1	Hsiao (1979)
Frobisher Bay	9 Jan-23 Apr 1970	16.0	44.1	3	-	-	-	-	-	-	1	Grainger (1971)
	27 May, 13 June 69	37.4	66.9	2	-	-	-	-	-	-	1	Grainger (1971)
	21 May-13 June 1970	39.7	141.5	4	(4.0)	4.6*	4	-	-	-	1	Grainger (1971)
	27 Apr-16 June 1971	162.0	300.6	7	(16.2)	9.1*	7	-	-	-	1	Grainger (1971)
Davis Strait	20-28 April 1978	4.9	40.9	58	(0.3)	(2.5)	58	-	-	-	1	MacLaren Marex Inc. (1979a)
	4-17 May 1978	11.3	160.4	152	(0.7)	(9.5)	152	5.91	30.37	25	1	MacLaren Marex Inc. (1979a)

*data given as mg/m^3 and mg/m^2-method of conversion not stated () indicate conversion of mg/m^3 (first column) to mg/m^2 by multiplying by core length (m).

++includes Waiwright, Peard Bay, Harrison Bay and Dease Inlet.

**includes inner and outer (Reinder Island) Prudhoe Bay Stations.

Method: 1: SIPRE corer; 2: Diver-operated corer.

Adapted from information in unpublished table prepared by W. Cross, LGL Ltd.

Bay (1971). In brief surveys, high spatial variability in biomass at the same time has been found both over large distances (e.g., from 0.4 to 37.3 mg chlorophyll a/m^2 at 6 sites from Wainwright to Prudhoe Bay during 2-4 June 1971--Horner 1972) and over short distances (0.3 and 17.1 mg chlorophyll a/m^2 at inner and outer Prudhoe Bay stations, respectively, on 10 May 1971--Horner et al. 1974; 0.03 and 14.2 mg chlorophyll a/m^2 at outer and inner Frobisher Bay stations during 21-23 May 1970--Grainger 1971). This variability may result from differences in snow cover (Grainger 1977; Horner et al. 1974) or differences between sites in the timing of the bloom (Horner et al. 1974).

A few biomass estimates of microalgae in pack ice have been made. Off Barrow, Alaska, during late July 1964 an average biomass of 24 mg chlorophyll a/m^2 was reported by Meguro et al. (1966, 1967). Considerably lower average biomass (0.3 to 0.7 mg chlorophyll a/m^2 for April and May, respectively) can be calculated from the data of MacLaren Marex Inc. (1979a) for the outer edge of the ice pack in Davis Strait between 60 and 64°N. The latter data are much more extensive and include many floes with a considerable biomass of epontic algae (maximum value 9.6 mg chlorophyll a/m^2--Table 3; maximum floe average 3.1 mg chlorophyll a/m^2--MacLaren Marex Inc. 1979a.) The difference in the timing of the pack ice bloom between Barrow (late July) and Davis Strait (April-May) is considerable, and apparently real, as both Meguro et al. (1967) and MacLaren Marex Inc. (1979a) reported observations indicating that the epontic community was in conditions typical of blooms under fast ice reported elsewhere.

Experimental data supporting estimates of annual primary productivity of the epontic community are few. To our knowledge, all are from ^{14}C studies in northern Alaska (Horner 1972; Clasby et al. 1973; Alexander et al. 1974; Horner et al. 1974), and in Davis Strait (MacLaren Marex Inc. 1979b), and are based on laboratory or *in situ* incubation of samples collected with a SIPRE corer (expressed as mg $C/m^3/h$) (Table 4).

Alexander (1974) calculated an annual productivity of 5 g C/m^2 (25 to 30% of total annual primary production) for coastal regions near Barrow, Alaska, based on data from 1973 (Alexander et al. 1974) and non-specified assumptions on the diel regimes and seasonal productivity

Table 4. Epontic productivity of arctic sea ice.

Diver-operated *in situ* studies (mg C/m^2/h)

Location	Dates	Primary Productivity Mean	Min.	Max.	n	Source
Barrow	7 May- 8 Jun 1972	2.0	0.3	4.6	6	3
	6-30 Apr 1973	1.2	0.3	1.9	7	3
	7 May- 8 Jun 1973	5.5	0.4	14.9	8	3

Other Studies (mg C/m^3/h)

Location	Dates	Primary Productivity Mean	Min.	Max.	n	Source[5]
Barrow	13-31 May 1971	11.3	1.6	32.4	13	1
	2 Jun-3 Jul 1971	3.9	0.1	28.2	18	1
	28 Jan-27 Mar 1972	0.1	0.0	0.2	12	1
	3 Apr-1 May 1972	0.6	0.0	2.2	5	1
N. Alaska*	2-3 Jun 1972	42.2	0.1	133.0	4	1
Prudhoe Bay	10 May, 4 Jun 1971	11.9	0.1	23.6	2	2
Davis Strait	21-25 Apr 1978	0.03	0.01	0.08	6	4
	9-15 May 1978	1.3	0.1	3.9	5	4

[5] Sources are: 1 = Horner (1972); 2 = Horner et al. (1974); 3 - Alexander et al. (1974); 4 = MacLaren Marex Inc. (1979b).

*Wainwright, Harrison Bay, Smith Bay, Dease Inlet.

Adapted from information in unpublished table compiled by W. Cross, LGL Ltd.

curve. This estimate was further cited by Horner (1976--incorrectly, as 5 mg C/m^2/yr; 1977) and applied to offshore lagoons near Prudhoe Bay where it comprised 6% of the total annual productivity (Horner et al. 1974:61).

Annual epontic productivity in Frobisher Bay was estimated to be 1-10 g C/m^2, based on an observed maximum biomass (in 1970) of 5 mg chlorophyll *a*/m^2, 'a carbon-to-chlorophyll *a* ratio of between 50 to 100, and a factor of between 3 and 10 for the ratio of maximum bloom value to the year's total...' (Grainger 1975:265). In comparison, phytoplankton production (based on ^{14}C studies) in Frobisher Bay was about 40 to 70 g C/m^2 in 1968 and 1969, respectively.

In the high arctic near Resolute, Cornwallis Island, epontic algae was estimated to contribute 33% of total annual productivity (i.e., about 15 g C/m^2/yr) (Welch and Kalff 1975). This estimate is based on the statement, "This epontic community seems to be producing about the equivalent of the shallow water benthos" (Welch and Kalff 1975:72), which in turn is based on few data (i.e., two "not--very reliable data" points, p. 71).

MacLaren Marex Inc. have estimated standing stock (1979a) and ^{14}C primary productivity (1979b) of the epontic and phytoplanktonic communities over deep water near the outer edge of the Davis Strait ice pack. They interpreted their standing stock data to mean that 10-15% of total annual primary productivity came from epontic algae (MacLaren Marex Inc. 1979a, Table 18 and p. 4-75), and their ^{14}C data to mean that less than 1% was attributable to epontic algae. Both estimates are based on questionable assumptions and faulty calculations (e.g., in converting mg chlorophyll *a*/m^3 to mg chlorophyll *a*/m^2), and both are apparently too high. Based on their data, we estimate that the ice algae contributed only about 0.01% towards total daily production in April and 0.07% in May. For these calculations we used average primary production per unit chlorophyll *a*, not the maximum figure used by MacLaren Marex Inc. (1979b, p. 4-12).

As reviewed above, a number of estimates of annual productivity by epontic algae and of their contribution to total productivity have been made. However, many such estimates are extrapolated from few data and are based on assumptions that need to be tested by further experimental research.

Benthic Primary Productivity

Algal forms growing attached to the bottom or to rocky substrates are patchy in distribution but generally decrease in density from east to west in the North American arctic (Mohr et al. 1957; Lee 1973). Whenever light and substrate are available, attached algae will grow. However, the larger macrophytic algae require firm substrates for hold fast attachment in order to remain stationery if buffeted by waves and currents. The paucity of large stands of kelp in the Alaskan arctic is due directly to the dearth of rocky zones for attachment (MacGinitie 1955; Mohr et al. 1957; Buchanan et al. 1977; Dunton and Schonberg 1979).

The few collections of rocks and cobbles in the Beaufort Sea afford the only attachment sites for kelps. Patches of cobbles are dominated by *Laminaria solidungla* with smaller accumulations of *Alaria esculenta* and *L. sacharina*. The dominant macroalgae in the understory and in places where large kelps were absent were *Phycodrys rubens*, *Neodilsea integra*, *Phyllophora truncata* and *Lethothamnion* (Dunton and Schonberg 1979). Regions with many rocks and dense stands of kelps support very diverse patches of associated marine animals. The large plant biomass (average 3.3 kg/m^2) in these kelp beds associated with coble patches has been hypothesized to be a source for net export of fixed carbon, since macrophytic algae are usually not consumed directly (Dunton and Schonberg 1979). The principal contributions of these localized zones of intense benthic production are probably as (1) attachment sites for nutrient trapping epiphytic algae and bacteria, and (2) habitat for the invertebrates and fish that graze upon the algae and one another in an area of otherwise featureless soft sediment bottom.

Work on the productivity of arctic marine benthic kelp is presently being conducted by Dunton and Broad of Western Washington State College. They are performing productivity and areal measurements but do not project completion of this ongoing research until perhaps summer 1980. Any comment on this research project would be premature except to note that such work is essential to understanding productivity of this region.

To our knowledge, only one study of the productivity of arctic benthic microalgae along the coasts of the Beaufort and Chukchi seas has been reported (Matheke and Horner 1974). Productivity ranged from less than 0.5 mg $C/mg^2/h$ in winter to almost 57.0 mg $C/m^2/h$ in August. Although this latter value, if extrapolated to the entire bottom for the entire summer season, would give a total annual production twice that reported for planktonic algae and eight-fold higher than that reported for epontic algae, these measurements of benthic productivity were made on visually selected (certainly not ubiquitously distributed) small patches of benthic algae. The extrapolation of these results to productivity on a square meter basis could be very misleading until the areal distribution of such small patches is determined and until results for an "average" square meter of benthos are obtained. Whatever their areal extent though, they provide benthic grazers with occasional oases of edible plant material on an otherwise depauperate benthos.

NUTRIENTS AND NUTRIENT SUPPLY

Plant growth is possible only when there is an adequate supply of inorganic nutrients. Nutrient concentrations in the water-column are a complex function of consumption, *in situ* nutrient regeneration rates, upwelling of deeper waters, sediment resuspension, and input from terrestrial sources. The nutrient supply for algae must be drawn from their immediate surroundings since their powers of locomotion are rather limited and they must absorb nutrients directly from the water. Once the supply of available nutrients surrounding an individual phytoplankter has become depleted below a minimal concentration, growth must cease even though light and carbon dioxide may still be available. If many phytoplankters are present in the same area (usually the case since most reproduce by binary fission), diffusion processes are insufficient to resupply the growing cells because all of the neighboring bloom organisms have been taking up the same nutrients from nearby waters.

Water Stratification

During late spring and summer, when waters of the arctic may be ice-free, these waters usually become stratified. Ice melt water (which is essentially fresh water) and river drainage water are less dense than the oceanic water, and this relatively fresh water forms a surface layer. This surface layer tends to warm fastest because it is closest to the sun and warming air. This makes the surface layer even less dense, which further stabilizes the vertical stratification. The nutrient supply near the surface is rapidly exhausted by phytoplankton growing in the intense light, and by the previous pre-breakup growth of epontic algae. The near-surface nutrient supply is replenished from deeper waters only when localized wind-generated currents break the stratification and cause vertical exchange with deeper waters below the photic zone or with the sediments below shallower waters. Only when the nutrient supply of the surface waters is replenished by vertical circulation or *in situ* regeneration does the planktonic algal community obtain enough inorganic nutrients to sustain even a brief bloom. A representative example of near-surface nutrient depletion by a phytoplankton community in Brentford

Bay, N.W.T., is shown in Table 5 from Thomson et al. (1978). The combination of a short season of intense light and stable stratification during the period of sunlight makes the Arctic the least productive of the world's oceans (Dunbar 1970; Platt and Subba-Rao 1975).

Upwelling of Nutrients

Several mechanisms of upwelling have been shown to operate in various circumstances. Wind-induced coastal upwelling results in the transport of nutrient-rich deep water to the surface and permits an increase in production at the primary and subsequent trophic levels. The worldwide distribution of large-scale areas of upwelling, and the biological effects of these upwellings, are reviewed in Dragesund (1971). The physical mechanisms responsible for these large upwellings are reviewed by Smith (1968). Wind-induced upwelling may occur on a seasonal or shorter time scale, especially at higher latitudes (Dragesund 1971). Greisman and Ingram (1977) have demonstrated that internal waves can cause local periodic upwelling in the Gulf of St. Lawrence. Wind-induced divergence of the surface layer may cause open-ocean upwelling (Smith 1968). In estuaries, outflowing fresh water entrains nutrient-rich deep water, which causes mixing and an increased nutrient supply at the surface. Thomson et al. (1975) have shown that even small arctic rivers may entrain deeper water. Some or all of these upwelling phenomena may occur in the arctic but remain to be documented.

Ice edges are often areas of intense biological activity, and the factors responsible for the seemingly high productivity in such areas have been of considerable interest (McRoy and Goering 1974; Bain et al. 1977; Sekerak and Richardson 1978; Bradstreet 1979, in prep). Along the Bering Sea shelf, 65% of the annual primary productivity occurs in spring, and most of this production is the result of action at the edge of the pack ice in May (Alexander and Cooney 1979). The bloom may extend 50 km from this ice edge, and the greatest intensity of production is under the pack ice. When the ice edge is over the continental shelf, most of the production from the ice edge bloom goes into benthic food chains. When the ice edge is over deeper water, most of the production

Table 5. Nutrient concentrations in Brentford Bay, Boothia Peninsula, N.W.T., in May and September 1977 (from Thomson et al. 1978).

Date	Depth (m)	Nitrate + Nitrite (mg-at N/m^3)	Phosphate (mg-at P/m^3)	Silicate (mg-at Si/m^3)
23 May	0	7.9	1.40	19.0
	7.5	8.3	1.32	20.1
	15	8.3	1.36	19.4
	25	8.9	1.44	22.7
	40	8.4	1.35	20.1
2 Sept	0	<0.1	0.40	<0.1
	7.5	1.1	0.70	3.3
	15	0.2	0.80	1.1
	25	2.4	0.96	7.6
	40	2.0	0.96	5.7

Adapted from information in unpublished table prepared by D. Thomson, LGL Ltd.

goes to the pelagic food web (Alexander and Cooney 1979). They hypothesize that high production at the edge of large areas of pack ice occurs because the ice at the edge is broken into small floes by the wind; this allows high light penetration but at the same time a restricted fetch inhibits mixing and thus minimizes dispersal of local bloom populations. This bloom condition could persist only until the nutrient supply became depleted or until new areas of previously ice-covered water opened up to permit lateral extension of the bloom. Upwelling may be another factor responsible for high productivity at ice edges. Clarke (1978) has shown that wind-driven upwelling at an ice edge is possible, and Buckley et al. (1979) have demonstrated its existence near Spitzbergen.

Under-Ice Movement of Nutrients

At the end of winter, as the sunlight returns to the arctic, the ice-covered oceanic and nearshore waters are rich in inorganic nutrients as a result of winter-long heterotrophic remineralization in the absence of planktonic uptake. Growth of the algae attached under the ice (epontic algae) commences, and this immediately begins to decrease nutrient concentrations in the surface waters. The ice is still increasing in thickness at this time, and this may provide the power for a hypothesized nutrient pump (Schell 1975, 1979). As the ice freezes, a zone of a very cold, dense water is formed around each growing crystal. These cold, saline waters are denser than the surrounding waters, so they sink and displace an equal volume of water upward toward the under-ice algal community. Thus a thermohaline convective pump is generated.

More nutrients may be available to epontic algae over shallow nearshore waters than to epontic algae over deep water. The 'nutrient pump' is probably of more importance in nearshore shallow areas than in areas of deep water where turbulent mixing may limit the effective vertical range of the pump. In shallow regions the bottom of the ice is close to the benthos, and the thickening of the ice moves the epontic algal community closer to the bottom. The benthos is an important source of nutrients since it receives the bulk of sinking particulate material and because it is the site of the largest concentrations of heterotrophic bacteria (Sverdrup et al. 1942); thus the benthos is the most likely site for rapid remineralization processes in the ocean. In this shallow nearshore environment, a short-range nutrient pump could be very effective in enhancing nutrient availability to epontic algae. Another advantage that a nearshore epontic community would have is that water exchange would be more limited in shallow than in deep waters. As ice formation proceeds, inorganic ions (such as nitrate, phosphate, and silicate) are excluded and thus concentrated between the ice and the sediment. In shallow waters these nutrients are more likely to remain available in concentrated form to epontic algae.

Nutrient Regeneration

Very few experimental or synoptic studies have been performed on nutrient regeneration processes of the arctic coastal waters. Kinney et al. (1970) reported chemical data from the water-column of the Beaufort Sea, and occasional observations have been reported by Gudkovich (1955), English (1961) and Kusunok et al. (1962). The effects of river input (Lena River) into coastal arctic seas (East Siberian and Laptev seas) were noted by Codispoti and Richards (1963), and Arnborg et al. (1966, 1967) examined the major ionic elements delivered to Harrison Bay (Alaskan Beaufort Sea) by the Colville River.

Nitrogen

Nitrogen is one of the most biogeochemically active elements and often is the most limiting nutrient to marine phytoplankton communities (Ryther and Dunstan 1971). Coastal arctic waters are usually nitrogen-limited (Schell 1975). Only two ionic forms of nitrogen are commonly utilized by marine microflora--nitrate and ammonia. Although ammonia is usually the preferred form (Eppley et al. 1969), it is also volatile and hence is seldom found in high concentrations (1.7 μg atoms/L in coastal Beaufort Sea; Schell 1975). The principal sources of ammonia are excretion from zooplankton and fish or ammonification of detrital organic nitrogen by bacteria.

Nitrate is not volatile and thus is the more common inorganic form of nitrogen found in marine systems. The primary sources of nitrate within the photic zone are the physical upwelling of nitrate-enriched deep water, release from detritus by bacteria, and nitrification of ammonia by bacteria.

Nitrogen fixation, another source of usable inorganic nitrogen, is known to occur in tundra ponds (Alexander and Schell 1973) and marine sediments (Bavendamm 1932; Waksman et al. 1933; Barker 1940; Pshenin 1963; Truper et al. 1969; Patriquin and Knowles 1974; Buchanan and Gibbons 1974). Most of the heterotrophic organisms known to fix nitrogen are anaerobic and thus are usually found in sediments rather than in the water-column. Measurements of nitrogen fixation in sediments from the eastern Beaufort Sea provide an estimate of only 25 mg nitrogen fixed/m^2/day, which is a very low rate (Knowles 1975). The highly active autotrophic nitrogen-fixing cyanobacteria (blue-green algae) have been sought but not found in oceanic and neritic sediments of the western Beaufort Sea (Alexander and Schell 1973; Schell and Alexander 1973). These cyanobacteria are known to be present and very active in coastal arctic tundra ponds (Alexander and Schell 1973). Thus the marine nitrogen supply receives only minor contributions from fixation within the sediments and from leakage of primary-fixed atmospheric dinitrogen from tundra ponds.

Ammonification, the process by which heterotrophic bacteria release ammonia from organic nitrogen compounds such as amino acids, urea and complex organic detritus, is one of the pathways used for *in situ* regeneration of nitrogen. Ammonification rates of 0.04 to 0.49 μg atoms NH_3/ℓ/day have been measured for amino acids in the Beaufort Sea, but organic nitrogen contained in peat was found to be somewhat resistant to ammonification (Schell 1975).

Nitrification, the energy-yielding bacterial oxidations of ammonia to nitrite and then nitrite to nitrate, has been measured in coastal and marine waters of the Beaufort Sea (0.068 to 0.15 μg atoms NO_3/ℓ/day) but remains undetected in the Colville River channel (Schell 1975). Nitrification takes place year-round in oceanic waters, and below the photic zone a lack of active planktonic uptake leads to accumulations of nitrate-rich waters which, when upwelled, are available to the phytoplankton community. Nitrification is usually an oxygen requiring reaction and would be sensitive to oxygen depletion of the water.

Ammonification and nitrification processes both proceed during the winter months in the hypersaline nearshore waters and in the rivers at temperatures at or below 0°C (Schell 1975). The absence of light during the winter leads to cessation of plant growth in river waters. These waters are extremely deficient in phosphate, which leads to accumulations of 3.6 to 6.9 μg atoms of inorganic nitrogen/ℓ in Colville River waters (Alexander et al. 1975). The nitrogen in the Colville River waters is in the form of nitrate, nitrite, and ammonia. In addition, storm-driven erosion of the tundra vegetation from shorelines transports organic nitrogen into nearshore waters. The inorganic forms of nitrogen are consumed almost immediately upon reaching the sunlit nitrate-depleted coastal waters, whereas nitrogen bound to the more refractory peat compounds forms the basis of the detrital nitrogen supply which awaits heterotrophic remineralization during the following winter (Alexander et al. 1975).

Phosphorus

Phosphorus is the second most commonly limiting nutrient for marine phytoplankton communities. The biologically useful ion of phosphorus is phosphate, which is non-volatile but does undergo abiological transformations in and near anoxic zones (the top 5 cm of marine sediment is generally anaerobic, but when stressed with sufficient biochemical oxygen demand and poor circulation, large portions of the water-column can become anoxic also). Arctic fresh waters are generally poor in phosphate (Schindler et al. 1974; Sekerak and Graves 1975). The phosphate content of the Colville River has been measured at 0.02 to 0.18 μg atoms phosphate/ℓ (average = 0.08); offshore marine waters contained 0.2 to 0.8 μg atoms phosphate/ℓ (average = 0.3). The levels in the Colville River are below the minimum requirement for growth of freshwater phytoplankton, and this probably accounts for the appreciable accumulation of inorganic nitrogen in fresh waters. Although near-limiting levels of phosphate also are present in the marine system, it is hypothesized that in arctic marine waters nitrogen becomes limiting before phosphorus (Alexander et al. 1975; Schell 1975).

Silicon

Silicon is another non-volatile and potentially growth-limiting nutrient. It is utilized biologically in its ionic form (silicate) and also undergoes abiological transformation. Although not used as a direct metabolite in cellular protoplasms, silicon is essential for the siliceous tests constructed as the outer shell of diatoms, some of the most prolific and conspicuous members of the phytoplankton and epontic communities. Colville River waters had the highest silicate concentrations measured (21.0 to 57.6 μg atoms silicate/ℓ) along the Alaskan Beaufort coast (Schell 1975). Silicate concentrations in offshore waters were depleted as low as 3.0 μg atoms silicate/ℓ. This latter value is approaching the concentrations limiting to diatom growth, but the extreme nitrogen depletion of these offshore waters precludes silicate being a likely limiting nutrient (Alexander et al. 1975; Schell 1975).

Oxygen

Oxygen, although not required for primary production, is essential to animal life and to many other processes in the marine environment. The principal sources of oxygen input to the arctic marine system are from wind-generated aeration, oxygenic photosynthetic release, and 'freeze exclusion concentration'. Wind-generated aeration, coupled with typically low temperatures, can easily lead to oxygen supersaturations such as the 125% value reported by Hufford (1974). Supersaturation can occur when open water is subjected to wind stirring. Photosynthetic oxygen release from free and attached algae can occur only during concurrent periods of nutrient availability and illumination in excess of compensation levels. Freeze exclusion concentration occurs because, when water freezes, it excludes not only ions but also oxygen. The solubility of oxygen in water increases with decreasing temperature up to the freezing point. During the summer, oxygen levels in nearshore arctic waters remain high (10.5 to 12.5 ppm), probably due to a combination of wind action and high solubility in cold water (Hufford 1974; Alexander et al. 1975; Sekerak et al. 1976a). During the winter, offshore under-ice oxygen concentrations are generally low (0.28 to 7.11 ppm) (Alexander et al. 1975), presumably due to biological consumption and lack of photosynthetic or wind-driven replenishment. Values at the lower end of this range could be of some concern as they are below or close to the lower limits of tolerance for animals and bacterial mineralizers.

Measurements of potential heterotrophic metabolic activity of microbial populations provide a means of determining types of activities and relative rates found in natural microbial populations (Griffiths et al. 1978) with respect to nutrient regeneration. Measurement of radioactive phosphorus (^{32}P) uptake rates (Schell 1979) will provide much more information on phosphorus dynamics within coastal waters than will any quantity of static phosphate concentration determinations. Ammonification rates measured under *in situ* conditions will demonstrate likely rates of nitrogen resupply from amino acid release (Schell 1975).

Carbon Supply

Carbon is an active part of the carbonate-bicarbonate buffering system of all oceans. Its concentration is seldom, if ever, limiting to plant growth within the photic zone.

Photosynthetic and chemosynthetic autotrophic organisms utilize photon energy and oxidation of inorganic compounds, respectively, to supply their energy requirements. Both autotrophs and heterotrophs require carbon compounds as cellular building materials and for growth. Autotrophic organisms such as algae and some bacteria fix carbon dioxide from the atmosphere as their carbon source and once this carbon is fixed, its ratio of isotopes no longer changes. The animals which graze on these organisms and those which consume the grazers derive carbon for incorporation into their cellular material from the carbon of their prey. This flow of carbon compounds through trophic interactions has led to the theory that analysis of the isotopic types of carbon in a consumer (e.g., heterotrophic) animal should give an indication of the principal sources of food consumed by that animal. This assumes that potential food resources have distinguishable carbon isotopic proportions and that carbon present in the animal is a direct consequence of what it consumes for incorporation into body material.

Three common, stable and distinguishable forms of carbon are found in the biosphere--^{12}C, ^{13}C, and ^{14}C. The first two are non-radioactive isotopes which can be distinguished from one another by mass spectrum analysis. Marine primary producers have a less negative (-16 to -27%) ratio of del $^{13}C/^{12}C$ (due to 'Hatch-Slack' or C_4 metabolism) than do terrestrial primary producers (-28 to -30 %) (which tend to have Calvin or C_3 carbon metabolism). The unit of del ^{13}C has been developed as a means of discriminating a very small difference between two large numbers. It is defined as

$$\text{del } ^{13}C = \frac{^{13}C/^{12}C \text{ sample}}{^{13}C/C^{12} \text{ standard}} - 1 \quad \times 1000$$

Thus, the tissues of the animals which prey on marine primary producers should also have a less negative ratio (Hatch and Slack 1970; Haines 1976; McConnaughey 1978). The common radioactive isotope ^{14}C has a half-life of 5800 years and decays in specific activity at a known rate. This allows an age determination of tissue samples. Since the mean age of terrestrial arctic peat is approximately 4000 to 5000 years (Lewellen 1973), organisms using this "fossil" terrestrial detrital carbon source, and the animals that consume these organisms, would be expected to have effectively "older" tissues than organisms using recent primary production as food.

The above concepts should allow discrimination among marine modern carbon (young ^{14}C and less negative $^{13}C/^{12}C$), terrestrial modern carbon (young ^{14}C and more negative $^{13}C/^{12}C$) and terrestrial old carbon (old ^{14}C and more negative $^{13}C/^{12}C$). However, there are several potential difficulties with these methods. The ^{14}C analysis is expensive and requires large quantities of cellular material. The $^{13}C/^{12}C$ method is relatively insensitive but less costly than ^{14}C analysis. Both analytical techniques depend upon the procedures of sample collection and preparation of their absolute accuracy. If stomach or gut contents are included in the samples, material ingested but not necessarily digested (e.g., eaten but not normally usable to the animal) will be part of the material analyzed even though it was not and would not become part of the animal tissues. Different animal tissues have different turnover times for carbon compounds and thus selecting or not selecting certain organ tissues may induce an error in estimation of carbon contents. If animals feed on different materials at different seasons, the recent feeding history of the animal may strongly influence the measured carbon composition. Similarly, different growth stages of the animals can include periods of intensive incorporation of carbon into new cellular material followed by periods of relatively little growth. This variability could potentially bias carbon apportionment away from an "average" animal composition.

Preliminary analyses of some of the radioactive and stable carbon contents of potential food resources and the organisms which could be involved in consumption of them have been performed and allow for tentative inferences. Schell (1979) estimated that >50% of carbon resources in the nearshore (10 km) were derived from terrestrial carbon sources (fluvial transport and tundra erosion) and the remainder from marine sources (benthic, epontic and planktonic production). The amphipods and isopods and the sculpin which eat them all dwell in benthic zones where old peat carbon is present and they have up to 13% old carbon in their body tissues, whereas the arctic cisco and humpback whitefish were found to have very little, if any, old peat carbon. Since the amphipods and isopods were not able to digest a cellulose substitute peat it was hypothesized that bacteria (which do digest peat) are the intermediates in this link of the food web (Schell 1979). The remaining samples are being analyzed at the time of this writing and these results may modify the following conclusions. Based upon ^{14}C analysis it appears that carbon derived from terrestrial peat (old carbon) does occur in significant quantities in bottom dwelling marine fish and invertebrates and to a lesser extent in anadromous and marine fish. Analysis of ^{14}C does not provide a distinction between river-input new carbon and marine-origin new carbon production. The food resource utilization implications to higher trophic levels are discussed in the sections dealing with the respective consuming populations.

If dietetic estimates as to the proportions of "fossil" carbon as opposed to new marine carbon as opposed to terrestrial and freshwater new carbon are to be made, more accurate information on the ages, erosional rates and areal extents of peat along the Alaskan Beaufort Sea coastline will have to be performed. River inputs of both terrestrial erosion and freshwater algal production will also be necessary.

BACTERIAL ACTIVITIES

The capacity for marine bacteria to decompose a wide spectrum of naturally occurring materials is well documented. They are known to metabolize chitin (Hock 1940; Seki 1965a,b), cellulose (Waksman et al. 1933), protein (Wood 1953) and carbohydrates (Meland 1962) in addition to their role in transforming essential inorganic nutrients. The role of bacteria in nutrient regeneration is discussed above with respect to the specific nutrients. They also have known roles as detoxifiers of natural and synthetic inhibitors. Furthermore, bacteria are a significant food source (Pavlova and Sorokin 1970; Pavlova et al. 1971; Peterson et al. 1978; Hollibaugh et al. 1980) for many deposit-feeding benthic animals (Mann 1973) and for ciliate protozoans in the water-column (Porter et al. 1979). Thus they are not merely "mineralizing service" organisms or dead end sinks for energy and nutrients (Pomeroy 1979). Bacterial uptake of photosynthetic production released into the water can occur within four hours (Paerl 1974, 1978). With generation times as short as three hours in some marine environments (Sheldon and Sutcliffe 1978) and the ability to survive freezing in sea ice for many months (Kaneko et al. 1977), these versatile micro-producers interact in the total food web of the ocean at several different trophic levels and on different time scales.

Bacteria are difficult to count due to their small size, wide range of physical characteristics, and extreme versatility in metabolic activities. The most actively growing marine bacterial forms are from 0.2 to 0.6 μm in diameter (Hoppe 1976). They are adapted to grow in extremely dilute media. Bacteria adapted to grow in rich media such as laboratory cultures are generally from 0.8 to 1.0 μm in diameter and are, metabolically, considerably less active in natural environments than are the smaller forms (Ferguson and Rublee 1976). Optical microscopy has a lower limit of resolution of 0.2 μm under ideal conditions and thus direct counting is tedious and often inaccurate. Even cells stained with fluorescent dye are difficult to discern, much less categorize as being alive, dead or cell-sized debris (Zimmerman and Meyer-Reil 1974; Daley and Hobbie 1975). Electron microscopy has much better resolution than light microscopy but all samples are fixed and dried before observation and this precludes any distinction between living cells, non-living cells, and cell-sized debris. Cultivation/plate counting techniques for estimating densities of natural microbial populations select against the small active bacteria and are known to underestimate actual population densities by one to three orders of magnitude (Zobel 1946; Skinner et al. 1952; Jannasch and Jones 1959; Casida 1968; Francisco 1970). Autoradiography has been advocated as a means to distinguish active cells from debris (Peroni and Laverello 1975; Hoppe 1976) but has yet to be applied to arctic waters. The more facile technique of adenylate pool measurement as an indication of living microbial biomass (Hamilton and Holm-Hansen 1967) also has apparently not yet been utilized in arctic marine environments.

Kriss (1963) reported that surface waters of the central Arctic Ocean contained less than one viable (plate culturable) bacterial cell per ml of water. Boyd and Boyd (1963) found 6-2000 viable (plate culturable) bacteria per ml of surface waters in the coastal Beaufort-Chukchi Sea and indicated that most were of terrestrial origin. Cultivation methods have yielded 10^3 to 10^4 viable bacteria per ml of Mackenzie Delta surface waters (Bunch and Harland 1976), and Kaneko et al. (1978) reported 10^2 to 10^5 viable (cultured) bacteria/ml and up to 10^5 microorganisms/ml by direct microscopic observations of surface waters from the western Beaufort Sea. The latter authors found up to 10^8 bacteria/ml in the sediments between Point Barrow and Oliktok Point.

Kaneko et al. (1977) analyzed the species diversity of bacteria collected from the Beaufort Sea during two seasons; they used an agar plate cultivation method. They concluded that below population densities of 10^4 viable cells per ml, species diversity was inversely correlated with population size (this situation occurred during winter). They found that culturable bacterial populations had extensive requirements for growth factors, which were hypothesized to be supplied by the algal community. Sediment samples were found to have high densities (greater than 10^4/ml) and high species diversity of bacteria regardless of season; there was no significant correlation between population size in the sediments and diversity.

Griffiths et al. (1978) measured heterotrophic potential, direct microscopic counts, and salinity tolerance of the bacterial populations of water, ice and benthic sediments in the Beaufort Sea; this was done over two summers and one winter. They found generally lower direct counts of bacteria in the water-column in winter (average 1.5 x 10^5 cells/ml) than summer (3.7 to 4.5 x 10^5 cells/ml). This agrees in trend to similar counts for the Beaufort Sea reported by Kaneko et al. (1978) (1.8 x 10^5/ml winter; 5.2 to 8.2 x 10^5/ml summer). Griffiths et al. (1978) also found lower potential activity of planktonic heterotrophs in winter (0.2 to 12 μg glutamate/h/g) than in summer (3 to 113 μg glutamate/h/g). They also found, at all seasons, generally higher respiration rates of labeled substrates in water samples (average 46-85%) than in sediment samples (average 23-39%). Viable cultivatable bacteria found frozen in the sea ice included a lower proportion (29%) of psychrophiles (i.e., cells that will grow at 4°C but not at 20°C) than occurred in the water-column (56%) at the same time (Kaneko et al. 1978). The complete tolerance of arctic marine bacteria to changes of up to 50% (26% to 17%) in the salinity of their surroundings was noted by Griffiths et al. (1978).

Standing stock estimates give no information about processes or rates. Large populations of microorganisms simply indicate presence. How they came to be there and what they are now, or were recently doing, is not knowable from measurements of numbers and densities. Langmuir-type circulations can concentrate small planktonic organisms from distant locations. Unlike birds and fish, microorganisms lack stomachs by which one could discern their gustatorial habits. In addition, it is virtually impossible to distinguish the difference between live, healthy microorganisms and those that have been moribund for many days. Thus the roles and importance of microorganisms in the functioning of nearshore arctic ecosystems are poorly known.

IMPACT ANALYSIS

From the standpoint of primary productivity and its associated nutrient recycling, the consequences of most anthropogenic disturbances in natural arctic marine environments would be impossible to project beyond the most rudimentary and intuitively obvious. This circumstance is not due so much to a lack of information on individual components of the system but is instead related to the extreme variability in the timing of weather and ice events, and the dependence of autotrophic producers on those events. The magnitude of an impact would depend upon the timing of the disturbance event with respect to not only the local season but also the successional stages achieved by the local populations of algae, bacteria and consumers. As an example of factors to be considered, one of the most commonly discussed potential hazards from petroleum development in the barrier island-lagoon system is discussed very briefly below.

An oil spill on top of the barrier island-lagoon system could have a range of consequences from almost unnoticeable to disastrous for an entire season over large expanses of the lagoon system depending upon the size of the spill and the timing of its occurrence. During the winter, when the lagoon is covered with a solid layer of ice, a surface release of crude petroleum could probably be substantially removed manually. The remainder would likely be weathered so as to cause only small and localized blockages in illumination during the epontic algal bloom and negligible introduction of toxic light petroleum fractions (Baker 1971; Snow and Scott 1975) into the water upon ice breakup. If breakup had already begun and toxic fractions were allowed to enter the water-column before good circulation and exchange began, the likely outcome would be localized killing of most elements of the late-spring epontic community and most of the planktonic and benthic nutrient-regenerating bacteria. This could delay the beginning of the planktonic algal bloom. The extent of these effects would depend not only on the size and nature of the spill, but also on currents and many other factors. If this were followed by particularly overcast, cold, short summers with little wind, the net productivity for the entire lagoon could be considerably below that necessary to sustain the invertebrates and other animals dependent upon this food web. In other words, a marginal season could, by unfortunate timing of a man-made perturbation, be turned into a disastrous season for some or all of the Simpson Lagoon inhabitants.

One of the few realistic experimental attempts to evaluate oil effects on primary productivity in the arctic is described in detail in Adams (1975). He found an increase in ^{14}C uptake rates of 15% (4 h incubation) to 55% (24 h incubation) in oiled as opposed to control under-ice sites. His results also gave indications of a slight enhancement in phytoplankton abundance and a greater diversity index for oil contaminated sites. The above results were interpreted by Adams to be due to the greater toxicity of oil to grazers than to producers. This depressed the consumption of primary producers but did not cause a real increase in system productivity. This illustrates a common problem of measurements on complex ecosystems. The leakage of photosynthate from algae discussed under "Phytoplankton Standing Stock and Succession" is also not correctly assessed by ^{14}C methodologies and thus the entire bacteria-as-prey portion of the trophic interactions may not have been represented in the experiments. The absence of animals grazing on algae and bacteria would terminate the food web at the first steps in production and provide little or no real production for higher trophic levels.

The crux of the above hypothetical construction is that we cannot know the exact date of any particular seasonal event and we cannot know the nature of weather which will follow any particular event. All primary productivity is dependent upon the seasons and weather. As long as the lagoon systems are allowed sufficient access to oceanic and river runoff waters, and not made eutrophic, we may be relatively confident that the microbial (autotrophic and heterotrophic) population will restore itself by innoculation from surrounding waters and sediments. The major question to be answered is not will the microbes survive over the long term but rather how many seasons or critical portions of seasons of curtailed production can the higher trophic levels (birds and fish) tolerate before they lose reproductive potential and become regionally extinct and how much of this is acceptable.

Data Gaps

Primary production, nutrient regeneration and microbial activities have been considered together in this report because they are all interwoven in a very complex and poorly understood milieu. The enumeration of autotrophic and heterotrophic organisms from arctic marine systems by classical methods has provided many volumes of data which substantiate the conclusion that changes in the densities and types of biota reflect variations in the physical environment of the arctic. A good example is demonstrated in a recent investigation (Griffiths et al. 1978) of heterotrophic uptake potential of coastal Beaufort Sea microbes; variations of entire orders of magnitude occurred from one week to another at one sample site.

The gaps in information about this subject are many, but the gaps which are both knowable over the forseeable future and relevant to immediate planning needs are considerably less numerous. To define the areas in which new research should be done, we must define what are the likely development activities, and what are the most sensitive sections of the ecosystem. At present the four principal areas of concern with respect to development of oil resources on the arctic continental shelf and within barrier island-lagoon systems appear to be effects of petroleum leakages, increased siltation, domestic waste disposal, and drilling mud and tailings disposal.

The main questions relating to sensitive aspects of ecosystems concern impacts on the biota and the time scales over which deleterious effects, if any, may persist. Implicit within this question is the debate over whether some particular region constitutes a unique and/or irreplacable habitat which, if damaged beyond some threshold, would functionally terminate some aspect of productivity normally used by man (e.g., avifauna and ichthyofauna). From the standpoint of primary productivity and nutrient regeneration, the shallow nearshore zones would be expected to be more productive and potentially sensitive than deeper waters on an area or volume basis because the water-column is more compressed. Benthic concentrations of nutrients and mineralizing microorganisms are physically closer to the surface (light and phototrophs) and closer to sources of terrestrial nutrient supplements (e.g., river runoff and tundra erosion).

Neither the potential impacts to microbial populations nor the linkage between these trophic levels and steps further up the food web have thus far been adequately addressed although some studies directed toward answering portions of this problem have begun (Schell 1979).

To summarize the substantial, but attainable, tasks yet to be accomplished toward the end of comprehending the role and potentially sensitive aspects of primary production and nutrient regeneration in the arctic marine ecosystem, specific processes need to be quantified over much more expansive areas and with greater resolution and replication. Dynamics (not just concentrations) of nitrogen, phosphorus and silicate in rivers, from the shore, across the lagoons, and into the ocean need seasonal definition. The areal extent and large scale contribution to total primary productivity rates from epontic, attached and planktonic algae need seasonal definition. Direct photosynthate leakage to and consumption of bacterioplankton as a food resource need to be addressed.

RECOMMENDED FURTHER RESEARCH

As has been summarized in detail above, the majority of the extant data base is comprised of sporadic samplings over the entire northern coast of North America spread over decades of taxonomic collections with little attention to process rates. Some refining of data from preliminary studies would be helpful but will not likely cause extreme revision of the poor understanding we now possess of the microbes (e.g., further analysis of samples already collected for carbon resource partitioning and field surveys of the areal extent of epontic and benthic macro- and microalgae). Simultaneous and systematic intensive investigation of rate processes of productivity, nutrients and microbiology will be the only realistic approach to learning what are the significant and sensitive aspects of the trophic levels responsible for maintenance of the more conspicuous residents of the Beaufort Barrier Island-Lagoon system.

Now that the methodologies have been devised and most of them tested under arctic conditions, critically important rate and process studies could provide answers to the questions of how much and how long can this system sustain a particular type of injury and still function.

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PART 7. SYNTHESIS, IMPACT ANALYSIS, AND A MONITORING STRATEGY

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SUMMARY

The results of the Beaufort Sea Barrier Island-Lagoon Studies are discussed in this report within the context of relevant information from various other places. Important components and processes are described, an analysis of probable impacts of development is presented, and an environmental monitoring strategy is proposed.

Ecosystem Components and Processes

Prevailing wind regimes in the nearshore region in summer cause rapid water exchange between coastal water bodies, but there are more restricted rates of exchange between the shallow nearshore and the deeper marine environments. Both phenomena of exchange are important. The longshore exchange promotes rapid mixing and great mobility of coastal waters and entrained materials. The nearshore/marine exchanges are probably characterized by a net landward component in the near-bottom currents that promotes landward delivery (and subsequent nearshore retention) of materials entrained in the lower part of the water-column. Consequently, the nearshore shallow waters appear to function as a sink for an assortment of entrained materials and organisms transported from the land and from the sea as well as for those arising *in situ* (e.g., primary production).

Estuaries and other shallow coastal waters of the world are typically highly productive in comparison to the open ocean because they (1) accumulate and rapidly recycle nutrients and organic materials, (2) have short and efficient food webs, and (3) support rapid growth stages of migrant populations of organisms. Likewise many arctic ecosystems have simple food webs and support migrant animals during periods of rapid growth; this enhances their secondary production despite the constraints of seasonal cold and darkness. The coastal ecosystem of the Alaskan Beaufort Sea has qualities typical of both coastal and arctic systems that signal its importance to the important vertebrates--oldsquaw, phalaropes, arctic and least ciscoes, arctic char, fourhorn sculpin, and arctic cod--that assemble there in summer. It provides an abundant and constantly replenished (through growth and immigration) source of prey, the mysids and amphipods. The mysids and amphipods are abundant because they are among the few species that have become adapted to the extremes of arctic estuarine environments--they find little competition for the abundant (largely marine-produced) food supply delivered to the nearshore environment. They are so abundant relative to the needs of their vertebrate consumers that there is very little of the kind of partitioning of prey types among the predators that exists in areas where competition for food is significant.

It appears that the nearshore (<~ 20 m deep) Beaufort Sea has relatively high primary and secondary production in comparison to deeper areas of the continental shelf, and as well, accumulates materials produced outside the nearshore zone. It is in that sense an important fish and bird habitat that is not found elsewhere. The fish and birds that consume the secondary production in summer further confine most of their utilization of the nearshore zone to the shallower (<~ 5 m) areas, especially the lagoons and bays, despite the apparent abundance of their favored foods in the other parts of the nearshore waters. Presumably this selective utilization of very shallow nearshore waters is related to the fact that the habitat features there (shallow depths, presence of emergent land forms, warm waters, etc.) are optimum and that food abundance is such that nearshore areas without these features need not be utilized. It appears reasonable that fish and birds could opt for other feeding sites within this relatively productive nearshore region should the sites they favor become uninhabitable because of development activities.

The habitat qualities and the biological and physical processes found to be important to fish and birds in the Simpson Lagoon area appear to be shared by other regions along the Alaskan Beaufort Sea coast. Lines of evidence supporting this view include (1) the general documented and theoretical similarities among coastal sites of physical processes (e.g., wind and current regimes, etc.) that control the general biological production, and (2) the similarities in biological processes and structural characteristics among coastal sites. Ecosystems similar within themselves but different from adjacent systems exist within long, narrow bands that follow depth contours along the coast. There is great mobility of the key species and probably also of their principal prey within these linear systems. These similarities among coastal sites suggest that extrapolation of data among coastal areas is reasonable and the mobilities of components within the coastal ecosystems probably increase the resilience of the system to effects of localized development.

Impact Analysis

Because of the structural and functional attributes it possesses, the Beaufort Sea coastal ecosystem is probably highly resilient to disturbance in general. The expected levels and kinds of responses of fish, birds and their major food chain constituents to the probable kinds of development are as follows:

1. The types of man-made structures most likely to cause adverse ecological effects are solid-fill causeways that are perpendicular to shore, or that block critical passageways of exchange (e.g., inlet channels, bays off river mouths, etc.) between the shallow nearshore waters and the ocean. The critical food web and habitat changes likely to be effected by such development actions are (a) changes in the rate of nutrient and detritus supply to, and entrapment in, the nearshore environment, (b) alterations in the normal migration patterns of epibenthic invertebrates and fish, and (c) alterations in temperature and salinity regimes in the nearshore area.

   Effects of development on food supply and habitat availability would need to be fairly extensive before the effects on fish and birds could be detected, because fish and bird numbers appear to be considerably lower than could be supported by the existing food and habitat resources. This suggests that they probably could tolerate significant decreases in the general quality or quantity of food and habitats. Likewise, locally extreme alterations in food and habitat quality would probably have little general effect, because most species of fish and birds appear to be highly mobile and are probably capable of opting for undisturbed sites.

2. Development-caused increases in water turbidity (promoted by drilling operations, island and causeway construction, boat traffic, etc.) and alterations in inputs of terrigenous detritus and nutrients (caused by shoreline stabilization and/or damming of streams) will likely be insignificant in comparison with normal annual and seasonal

variations in the same factors. The measurable consequences of these changes to fish and bird populations are therefore expected to be nil.

3. Direct disturbances to birds caused by visually detectable and audible activities of men and machines are expected to be inconsequential except where common eiders, snow geese and brant nest on islands. Along the Alaskan Beaufort coast, nest sites of these species are restricted to islands, and they (particularly the common eider) are easily disturbed when they are nesting. Other species are not very site-specific in their need for nearshore habitats; neither are they very sensitive to the expected kinds of activities.

4. Significant direct mortality and/or morbidity of birds and fish may stem from oil spills or from increased harvests by humans. Should massive oil spills reach coastal bays and lagoons during the times when oldsquaws and other seabirds are abundant there (mid-summer to early fall), very large numbers of birds would probably be killed. Fish, by contrast, may be able to avoid oil in the water and are probably relatively immune to the direct effects of oil spills. Conversely, increased access by human hunters and fishermen may affect populations of anadromous fish adversely, but would probably not have serious effects on birds.

   Food chains subjected to contaminants are not likely to be depleted such that fish and birds would be greatly affected, because of the extreme mobility of the fish and birds and the probability that any contaminated areas would be quickly replenished by food chain materials from adjacent areas. However, lack of information about medium and long-term effects of oil on arctic epibenthic invertebrates (especially mysids) makes this conclusion speculative to some extent.

5. It is our general view that the effects of development (as it is currently conceived) are more likely to be felt directly by fish (via excessive harvests) and birds (via oil spills or disturbance at nesting sites) than to manifest themselves measurably through changes in food chains and habitats, except that certain island-nesting birds may be sensitive to changes in island habitats. Both food web materials and habitats appear to be superabundant relative to the needs of fish and birds, and large changes in them might be sustained without consequence. Furthermore, the food webs themselves are likely to be resilient to adverse alteration by development.

Monitoring Strategy

We believe that a monitoring program to assess the ecological impacts of petroleum development should focus on selected important species and their food webs and habitats. The monitoring program would ideally be conducted in two phases, a planning phase and a research phase.

During the planning phase the animal species of primary concern would be identified, methods of measuring supportive functions critical to the well-being of these species would be planned in detail, and field trials of previously untried procedures would be performed. The final product of the planning phase would be a detailed work plan for field measurements and observations that would distinguish development caused changes from normal changes in (1) the general health of the important species and (2) critical processes (interactions) between these species and the environment.

The research phase of the monitoring program would include field sampling and periodic review workshops. The field data to be collected should include (1) selected measurements that reflect the "health" of the organisms (e.g., stomach fullness and content, fatness, growth rates, etc.), and (2) measurements of critical organism/environment interactions that are deemed susceptible to change by development (e.g., mysid movement vs. currents, predator-prey interactions, etc.). These data should be collected in both test (developed) and control (undeveloped) areas so that development-caused change can be effectively discriminated from natural fluctuation. Periodic workshop sessions that evaluate findings and maintain an appropriate research direction should be an integral part of the research phase of the program.

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INTRODUCTION

This report summarizes and interprets information about coastal ecosystems that appears particularly relevant to assessing the impacts of petroleum development activities in the Alaskan Arctic coastal zone. It also provides an impact analysis and a monitoring strategy based on these data. The primary sources of data are the reports of the disciplinary research units of the Barrier Island-Lagoon Studies Program (see earlier parts of this volume), supplemented by outside literature. The material presented responds generally to the three original objectives of the Barrier Island-Lagoon Studies Program, and more specifically, to tasks that evolved from these objectives. These general objectives and the original scope of each are as follows:

1. To identify and analyze those components and processes that contribute significantly to the structure and productivity of the nearshore ecosystem.

   Since it was obviously impossible to address all of the components and processes that contributed to the structure and general productivity of a barrier island-lagoon ecosystem, this objective was accordingly narrowed so that research focused on the processes and components essential to the well-being of species identified to be "key" to the interests of data users. These "key species" were defined to be those birds, fish, and mammals common in the nearshore environment that (1) had significant commercial or recreational value, (2) were important to the subsistence of local residents, (3) were considered otherwise "important" and/or (4) were considered to perhaps influence the well-being of any of the above species by competition, predation, etc. Certain additional species, most notably several invertebrates that proved to be the main trophic links between lower trophic levels and the key species of birds and fish, were not considered to be key species by the above definitions, but were studied intensively because of their critical roles in the support of the key vertebrate species.

2. To evolve mechanisms whereby the important components and processes can be evaluated for their reaction to man's activities.

   In addition to learning what processes and components in the environment were critical to the maintenance of biota, there was a need to evaluate how man's activities would affect the processes and components. The purpose of this objective became, therefore, to identify research strategies to meet this end.

3. To determine the feasibility of detecting and quantifying the temporal changes in important ecosystem components and processes.

   Research strategies to evaluate how man's activities would affect the components and processes would be valid only if they provided feasible methods for measuring changes in ecosystem components and processes, and for segregating "man-caused" from normally expected changes. The purpose of this objective was to determine whether man-caused changes in components and processes were, practically speaking, detectable.

During the course of the program, an additional need arose--to determine to what extent the information collected in the Simpson Lagoon-Jones Islands area could be validly extrapolated to other sites along the south coast of the Beaufort Sea.

Given the realities of the program in terms of the ecosystem that was studied, the expected development activities, and the new issues that arose after the program's inception, the program's objectives may now be more usefully and concretely rephrased as four questions:

1. Is the Simpson Lagoon-Jones Islands system essential to the well-being of the key species that use it, and, if so, what are the characteristics of its components and processes that make it so?
2. Do the components and processes that regulate populations of these key species in Simpson Lagoon also regulate similar populations in similar ways in other Beaufort Sea coastal systems? That is, can the results acquired in this study be broadly applied to other parts of this coast?
3. How are proposed development activities likely to alter important processes and components, and how will populations of key species be affected?
4. What does this study tell us about how future ecological studies and monitoring programs should be structured to best test for the predicted ecological impacts as petroleum development proceeds in north coastal Alaska?

The first of these questions corresponds to the first of the original program objectives. The fourth question corresponds to the second and third of the original objectives. The second question, concerning extrapolation, and the third question, concerning impact predictions, were not among the specific objectives at the start of the program, but it soon became apparent that they were important issues that should and could be addressed.

The following sections of this synthesis are organized to respond to the above questions as follows:

Section 1.	The Coastal Ecosystem: An Interdisciplinary Synthesis (Questions 1 and 2)
Section 2.	An Environmental Impact Analysis (Question 3)
Section 3.	An Environmental Monitoring Strategy (Question 4)

SECTION 1. THE COASTAL ECOSYSTEM: AN INTERDISCIPLINARY SYNTHESIS

The first part of this section will review and interpret available information that helps answer the following question:

> Is the Simpson Lagoon-Jones Islands system essential to the well-being of the key species that use it, and, if so, what are the characteristics of its components and processes that make it so?

(Later parts of this Section [the 'Discussion'] will address also the issue of extrapolating information to other areas.)

The strategy for examining this question is to proceed from general knowledge about barrier island-lagoon systems and estuaries (which are similar in many respects [Carriker 1967]) to a specific treatment of the Simpson Lagoon-Jones Islands area. Note that the term 'nearshore' as used herein refers to shallow coastal waters inside and outside of bays and lagoons to a depth of approximately 15-20 m. This zone is highly disturbed throughout by the action of ice and waves, and tends to be generally warmer and less saline in summer than do the deeper shelf areas.

Ecological Perspectives

A general knowledge of physical and biological characteristics of estuaries, of other coastal systems and of arctic ecosystems can promote improved interpretation of research findings of any study of Arctic sea coasts. Some important general considerations about coastal and Arctic systems are discussed below, as background from which to evaluate current knowledge about coastal ecosystems of the Alaskan Beaufort Sea.

Estuaries, Lagoons, and Barrier Islands

Estuaries are "semi-enclosed coastal bodies of water which have few connections with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage" (Cameron and Pritchard 1963). Some kinds of estuaries have been called lagoons (e.g., some on the Alaskan Beaufort Sea coast) because they are long and narrow, parallel to the coast, and skirted by barrier islands also parallel to the coast. The terms 'estuary and lagoon' are therefore sometimes used synonymously in this report.

Formative Mechanisms, Geomorphology and Sedimentology. Truett (1980) discusses the formative mechanisms and geology of coastal systems. The net worldwide rise in sea level since the last glaciation (15,000-20,000 years ago) has been important to the formation of most barrier islands, their associated lagoons and estuarine basins. Shallow coastal areas have given rise to barrier islands (and therefore to lagoons and estuaries) by one or more of the following three independently-operating mechanisms (all of which have been influenced to some extent by the rising of the sea):

1. Accretion of sand thrown up by wave action from the continental shelf.
2. Elongation, and eventual breaching, of sand spits that have been built from headlands by longshore drift.
3. Gradual submergence of low-lying areas behind coastal topographic highs.

There is some doubt that the first mechanism commonly operates to create emergent features under the regime of a rising sea. It appears, therefore, that most present-day barriers were probably created by sand spit elongation, by submergence of adjacent coastal features, or both. The islands created by submergence may or may not (depending on the nature of coastal and continental shelf substrates and the nearshore hydrographic regime) be nourished significantly by delivery of sediments from elsewhere.

Estuaries located where the continental shelf is extensive are usually shallow (several meters or less in depth). They tend to accumulate sediments from streams and also from the ocean because characteristic circulation patterns near estuaries (described below) normally cause a net landward transport of sediments from marine environments. Inlets, sometimes relatively deep and narrow, connect estuaries with the sea and accommodate the exchange of water and its entrained materials.

Hydrographic Processes. General hydrographic processes in coastal waters are reviewed by Truett (1980). Several aspects of water circulation in estuaries are biologically significant--freshwater inputs from the land, water exchange between the estuary and the adjacent ocean, and the associated sediment and detritus transport patterns.

Estuaries receive fresh water from the land; the mixing processes that occur when the fresh waters of streams meet the estuarine waters are similar among estuaries. As the less dense fresh water is discharged, it advances as a floating wedge at the surface of the brackish estuarine water; simultaneously, the heavier estuarine or marine water flows landward at the bottom. Mixing of the two water masses is slow except where wind stress on the water's surface creates strong oscillatory motion in the water-column. Thus, in ice-free estuaries where there is little wind, or in estuaries where water depths are sufficient that wind-induced wave motion does not stir the entire water column, a distinct salinity stratification persists. But, in shallow estuaries subject to strong and constant winds, the water may be well-mixed except near the mouth of the stream. Typically, shallow estuaries are fairly well-mixed and organisms at all points in the water-column are subjected to brackish water conditions. However, because of the seasonal and areal variation in amounts of fresh water reaching points within estuaries, salinities fluctuate greatly in time and space.

Water exchange patterns between estuaries and the sea are very important ecologically. In a simple estuarine situation where the main exchanges occur perpendicular to the coastline and where there are no major connections between the estuary and adjacent estuaries, there is net seaward movement of brackish water at the surface and landward movement of the more saline sea water at the bottom. If there are lateral entrances to the estuary, currents moving parallel to the coast may superimpose themselves on this exchange pattern, obscuring it to some extent. Frequently augmenting this pattern of exchange is the phenomenon of upwelling, whereby winds cause coastal waters to move seaward at the surface and shelf waters to move landward at the bottom and then upward to emerge at or near the land's margin. In the northern hemisphere upwelling occurs when winds blow parallel to the coast with the coast on the left as one looks downwind. As discussed below, this vertically-stratified exchange pattern has important influences on the transport and deposition of organic and inorganic materials in coastal regions.

As noted above, estuaries characteristically accumulate sediments and detritus from both the land and the sea. From the land, suspended loads introduced by streams are carried seaward in the surface layers. This particulate load gradually settles because the water slows and becomes less turbulent as it enters the estuarine basin, and because chemical aggregation of fine particles into larger, heavier particles occurs rapidly as fresh water meets saline water. This settling or "rain" of particles is typically returned landward by the bottom currents and deposited in the shallow reaches of estuaries. From the sea, dead plankton, fecal material and other waste products produced by animals in the water-column sink; many of these become entrained by the landward flowing currents at the bottom and eventually are deposited in the coastal shallows. In coastal areas subject to storms that stir the ocean bottom at considerable depths, detritus and inorganic sediments initially deposited on the continental shelf may be resuspended and moved landward.

Estuarine Biology

The physical properties and processes characteristic of estuaries sustain biological systems that are markedly different from those of the adjacent land and sea. However, important similarities exist among estuaries. A consideration of what these similarities are is important so that we may more fully interpret the information provided about North Alaskan estuaries by the Barrier Island-Lagoon Program. Described below are some of the significant ecological attributes of those systems where land meets sea.

Estuaries and other coastal waters are among the naturally richest waters on earth in terms of the availability of those essential nutrients that determine levels of biological productivity (normally nitrogen and/or phosphorus) (Darnell and Wissing 1965; Odum 1968; Clark 1977:40; and others). Two phenomena cause nitrogen and phosphorus to be more available in the estuaries than elsewhere--the net accumulation of the nutrients in the estuaries, and the high rate of nutrient turnover, or recycling. Nutrients, like sediments, are concentrated in the estuaries and other coastal waters by the combined processes of stream and/or marsh discharge of nutrients from the land and landward transport of nutrients from the sea (Ketchum 1967; Odum 1968; USDI Fish and Wildlife Service 1970:21; Clark 1977:43, 695; and others). The open ocean has relatively low nutrient levels and is, in comparison, a virtual biological desert (Johnson 1957; Tabb 1965; Clark 1977:43). Additionally, the cycling of nutrients is rapid in shallow coastal waters. In contrast, in the deep parts of the continental shelf, nutrients released on the bottom must be brought to the photic zone before they can be reinjected into the food web (Warme 1969). Indeed, it is thought that the turnover rate of nutrients may be more important than is nutrient concentration in maintaining highly productive systems (Pomeroy 1960).

As a consequence of this high nutrient availability at the edge of the sea, assimilation of these nutrients by plants and the associated rates of primary production are relatively high despite the fact that coastal waters are usually more turbid and admit less light than waters of the open sea (Johnson 1967; Segerstråle 1957, and others). And in addition to the *in situ* primary production that occurs in estuaries, the benefits of much of the phytoplanktonic growth that occurs in the adjacent sea frequently accrue to the estuarine system because of landward transport of planktonic production.

Because of the limited penetration of light into the sea, photosynthesis is impossible at the bottom of deep water. Along coasts and in estuaries, plants attached to the bottom often receive sufficient light for photosynthesis and growth, despite the high turbidity and reduced penetration of light that commonly occur near shorelines. Thus, in shallow waters photosynthesis can occur in a habitat--the bottom--where photosynthesis is reduced or absent in deeper water.

Secondary productivity in the estuary (the net increase in biomass of the animals, i.e., consumers) is fueled by primary producers (plants) (Schell 1980), and is typically high for several reasons:

1. The estuary is a zone of abundant production, accumulation, and availability of phytoplankton that is produced in the estuary and the nearby ocean.
2. The estuary may act as a sink for terrigenous sources of organic detritus carried in by fresh water inflow (Gabur 1977). This detritus, originally produced by green plants on land or in nearby marshes, may also be a major source of food to consumers (Odum et al. 1973), particularly after it has been assimilated by microbial action.
3. Estuaries are "disturbed" environments and undergo periodic and relatively drastic changes in those chemical and physical properties (water temperature and salinity, substrate quality, etc.) that strongly influence biota (Tabb 1966; Copeland et al. 1974; Hatcher and Segar 1976; and others). Biological communities that occupy recently disturbed habitats have relatively low diversities of species in comparison to similar communities at a later successional stage (Odum 1969; Nicholson and Monk 1974; and others). For example, estuaries exhibit a paucity of species in comparison to the adjacent sea (Hedgepeth 1957; Copeland et al. 1974; Copeland and Nixon 1974; Glooschenko and Harriss 1974; Steele 1974:29), presumably because the recurring stresses of physical and chemical changes maintain the estuaries in a "disturbed" state (Teal 1962; Tabb 1966). Because estuaries have relatively few biotic constituents, they have relatively short and simple food chains; this results in a high efficiency in energy transfer through the food web to the highest-level consumers (Steele 1974:7-9), and correspondingly high production by these top consumers.
4. Another reason for the high rates of secondary production in estuaries is that most estuarine-dependent species are migrants, and their migrations into the estuaries occur at times when they have demands for rapid growth, and when environmental conditions (especially temperature) in the estuaries are better than they are elsewhere for their growth (Day 1973; Gonor 1979). Likewise their emigrations from the estuaries coincide with sharp decreases in growth rates (and, in many, entry into maturity). Since ecological efficiencies of organisms are greatest during periods of rapid growth (Steele 1974:12), the simple fact that estuaries are "nursery areas" provides them with a relatively high secondary production potential in comparison with nearby oceans where more energy is funneled into maintenance and reproduction of organisms.

In summary, estuaries (and to some extent other shallow coastal water bodies) are highly productive in comparison to adjacent land or ocean (Fig. 1). They are sites where the availability of nutrients essential for primary production is relatively great in comparison with nutrient availability in fresh water or oceanic systems. Secondary production in estuaries likewise is great; it is enhanced by abundant *in situ* primary production, by accumulation of plant-derived detritus from adjacent terrigenous and oceanic systems, by the existence of high ecological efficiencies resulting from the relatively simple food webs, and by the tendency of organisms to use estuaries for growth instead of for maintenance and reproduction. These high primary and secondary productivities of estuarine ecosystems are a consequence of the estuaries' geographic location at the edge of the sea, their geomorphic configuration as shallow coastal basins, and the characteristic coastal regimes of water circulation and exchange.

Arctic Ecosystems

Arctic environments are thought to be stressful to life because they represent extremes in temperature and light regimes. Consequently, few species have evolved mechanisms to cope with arctic conditions compared with the numbers of species that have adapted to regions having more "average" conditions. However, Arctic organisms are well-adapted to these extremes and may function with no more "stress" than is experienced by organisms living in and adapted to temperate zones (Dunbar 1976).

Since arctic ecosystems function in basically the same ways as temperate ecosystems, the dominant functional attributes of the two can be compared. One way of productively comparing these attributes is to look at the ways arctic ecosystems have adjusted functionally to the controlling environmental constraints, and to find analogous types of adjustments in non-polar ecosystems. In this way, existing knowledge about all ecosystems can be pooled to promote extended interpretations of the functions of polar systems.

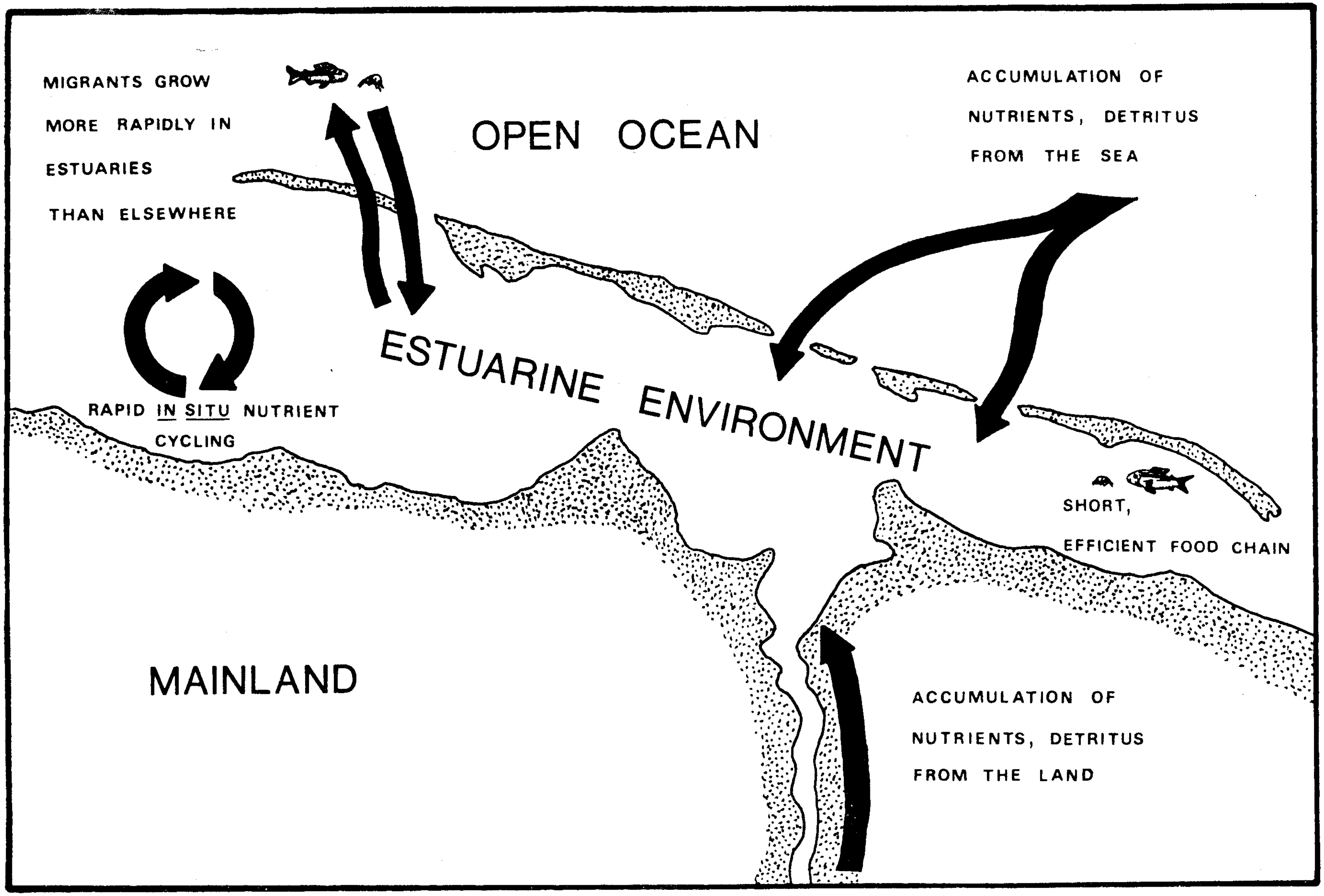

Figure 1. Several factors contribute to the high productivity of waters at the sea's margin.

Physical Constraints. Three attributes of polar regions that have important influences on ecosystem structure and function are the regimes of temperature, light and ice (Thorson 1957:462; Dunbar 1968:9, 68). For much of the year, temperatures in the arctic do not rise appreciably above 0°C (and in terrestrial environments thay may drop far below freezing). Even in the unfrozen marine waters of the arctic, the temperature is often slightly below 0°C. Temperatures below zero are critical because at these temperatures poikilothermic (cold-blooded) organisms must possess special mechanisms to avoid freezing and to continue functioning. Similarly, because of extensive periods of darkness at polar latitudes, special adjustments are required to enable biological systems to function.

Ice has profound influences on the functioning of arctic systems. It physically reduces or blocks the transfer of light, wind energy, and animals. The isolation of underlying waters from the wind reduces vertical mixing and horizontal circulation of the water, but on the other hand mixing can be promoted by the sinking of heavy brine produced during ice formation. In shallow areas, ice can completely replace water during the winter, and thereby exclude mobile marine organisms during winter and non-mobile forms year-round. Even where free water persists beneath the ice in shallow regions, the brine produced during freeze-up can make the water uninhabitable by salinity-sensitive forms. Ice motion can cause disruption of the bottom to considerable depths through rafting, formation of pressure ridges, and drifting of ice islands into shallow areas. This action disrupts one substrate, but the presence of the ice creates another substrate--the ice undersurface--where biological processes can occur.

Biological Adaptations. Three important general mechanisms of adaptation to arctic extremes of cold and dark by biological systems are adaptations in ecosystem structure, physiological adaptations of species, and behavioral adaptations of populations. Related strategies of adjustment to extremes are observable in non-polar systems.

Some of the structural attributes of arctic ecosystems are common to ecosystems in other extreme types of environments--the number of species is low (Teal 1962; Steele 1974:29; Gunter 1975), most species are adapted to utilize periodic spurts of resource availability (Dunbar 1968:68), and competition among individuals for space and nourishment is commonly reduced to a low level (Dunbar 1968:59).

The functional temperature-dependent responses of arctic organisms are similar to those of temperate-zone organisms. Birds and mammals in arctic environments maintain their normal body temperatures and are in this sense relatively independent of environmental temperatures, whereas poikilotherms in the arctic and elsewhere have temperature tolerance ranges within which their rates of activity (metabolism, growth, locomotion, etc.) increase with temperature. Arctic species have simply adjusted biochemically to cold climates and have lower ecological temperature ranges (Dunbar 1968:9, Gunter 1975). (Note, however, that even for arctic poikilotherms, the lowest temperatures at which they remain active are normally only a few degrees below 0°C.)

Arctic primary producers must have light to fix the energy on which the consumers depend. Although some of the plants have evolved mechanisms whereby production can be extended into the periods of very low light incidence, the major bursts of production occur during periods when light availability is greatest (e.g., spring and summer). Most arctic animals have life cycles timed such that periods when they need to grow coincide with times when plant production is greatest (Dunbar 1968:66-68). At other times the animals' growth, and perhaps other metabolic processes as well, slow to accommodate the scarcity of food. Likewise, migrations and other movements of arctic animals are timed and routed to promote cropping of the seasonally abundant food supply (Johnson et al. 1975; Bellrose 1976; Craig and Haldorson 1980; Davis et al. 1980; Griffiths and Dillinger 1980; Johnson and Richardson 1980). Such synchronization of growth and movement patterns with periodic bursts of food is characteristic of animal species in other extreme environments as well, and has important implications to understanding the functionings of those systems.

An Arctic Barrier Island-Lagoon System

The Setting

The field research for the Barrier Island-Lagoon Program focused on Simpson Lagoon and vicinity, a relatively short section of the Beaufort Sea coast (Fig. 2). The nearshore waters along the Alaskan shore of the Beaufort Sea are shallow, and discontinuous chains of barrier islands skirt about 50% of the coastline. The islands occur primarily in chains that are generally parallel to the mainland. The islands are characteristically low (1-1.5 m above sea level) and narrow (0.1-2.0 km wide), and range in length from a few hundred meters to 15 km. Offshore bars, also aligned parallel to the shore, exist on the seaward sides of the barrier islands and along some stretches of exposed mainland coast. The bottoms of unprotected nearshore areas are roughened by the gouging action of ice floes and icebergs.

It is generally accepted that those Beaufort Sea coastal islands capped with tundra vegetation and peat are remnant mainland features (Cannon and Rawlinson 1978; Weller et al. 1978:127) that were isolated from the mainland by a rising sea. A phenomenon that has promoted the formation of islands is the coalescing of lakes behind coastal highs, and the breaching of land separating these lakes from the sea.

Barrier islands not capped with tundra are probably also relict features; they have been eroded and extensively reshaped by wave action and ice. Their large-grained materials (mostly gravel) are probably deposits dropped in place as the islands eroded; gravel is not currently being transported to these islands from elsewhere. Whether sand from the deeper marine areas of the continental shelf is transported and added to the barrier islands is not known, but such accretion has not been postulated to be significant.

Coastal waters begin to freeze in late September or October. Ice forms first on lagoons because they are more sheltered, shallower, and less saline than the nearby ocean, and therefore cool faster. During late fall and early winter, surface ice throughout the nearshore environment is still relatively thin and may be moved about considerably by

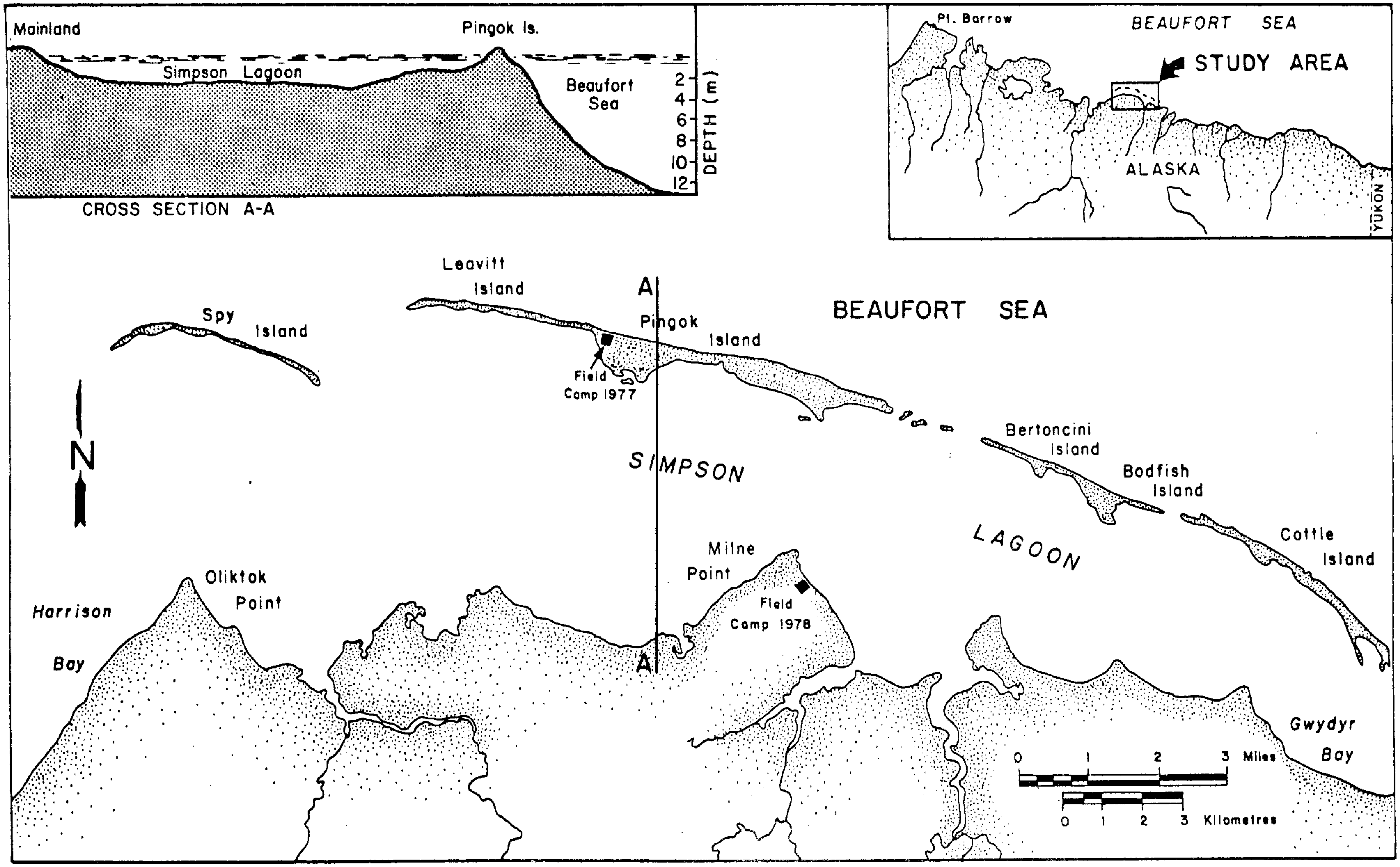

Figure 2. The Simpson Lagoon area, site where most of the research of the Barrier Island-Lagoon Ecological Process studies occurred.

wind. Consequently, large areas of open water periodically appear during this time. Thereafter, a continuous sheet of landfast ice covers the lagoons and other shallow waters of the nearshore Beaufort Sea. Ice thickens by about 1 cm per day throughout winter so that by April it is about 2 m thick. The ice begins to melt in May, and its rate of melt is soon accelerated near river deltas by river discharge.

Waters from melting streams reach the coast in late May or early June; these streams carry large amounts of silt and detritus which they discharge into the nearshore environment. Sixty to 80 percent of the annual discharge of most streams occurs within several weeks after flooding begins, during which time nearshore waters are still mostly ice-covered. The water that reaches the coast first is discharged over the sea ice; most of this fresh water eventually drains through cracks and holes and into the marine water beneath. Within a few days, however, much of the ice adjacent to stream mouths has melted, allowing the river water to flow directly into coastal waters and under the ice. Discharges rapidly decrease during the course of the summer and are minimal by freeze-up.

During the open-water period the nearshore currents of the region are extremely variable and wind-dependent; they are modified by bottom topography, coastal configuration and presence of islands. Solar/lunar tides are of low amplitude and are of secondary importance in affecting currents. Current velocities decrease greatly as the winter ice cover forms and thickens.

The mainland coastline retreats an average of 1-2 m annually, and the island margins are also eroded away and reworked. This erosion is episodic in nature; most occurs during intense summer and fall storms. During severe storms, high waters (storm surges) can inundate considerable portions of both the barrier islands and the coastal mainland. At such times large amounts of organic material (tundra mat and underlying peat) and inorganic sediments are transported from mainland and island shores to lagoon and marine environments.

Sediments are continually introduced to nearshore areas via river floodwaters and coastal erosion, and perhaps also from deeper continental shelf areas by landward transport. Most inorganic sediment particles in the lagoons and other nearshore basins are the size of sand or silt; gravels occur sparingly. Sediments are poorly sorted because sediment resuspension and transport patterns are extremely variable. Wind-generated waves and currents produce a net westerly longshore sediment drift.

The Biotic Components

The biological components of primary interest in the barrier island-lagoon study are the key species and their major food chain components. These food chain components include the prey items of key species, sources of nourishment for the prey, and the nutrients that are vital to the production of the sources of nourishment. The key species are birds (oldsquaw ducks and red and northern phalaropes) and fish (arctic and least cisco, arctic char, fourhorn sculpin and arctic cod). Their principal foods are mysids and amphipods (and also copepods in the case of the phalaropes and arctic cod). Recent (probably pelagic) primary production is the main fuel of the prey base, and the essential nutrients nitrogen and phosphorus limit primary production. Marine mammals occur in and near the lagoon only irregularly and in small numbers, and are not considered here.

Oldsquaw. The oldsquaw breeds throughout the arctic regions of the old and new worlds, and is probably the most common species of nesting waterfowl in the Beaufort Sea area (Johnson et al. 1975). Oldsquaws are present along the Beaufort Sea coast only between May and October; in fall they migrate south to winter in coastal waters of the Bering Sea and the Pacific Ocean.

Oldsquaws nest on tundra ponds, and their use of coastal waters is restricted largely to the period of their molt (early July-late August), when males and non-breeding females congregate in bays and lagoons, and to the staging period (late August-early October), when they gather prior to southward migration (Johnson and Richardson 1980).

During their residence in lagoons, oldsquaws feed mainly on mysids and amphipods and secondarily on molluscs. Feeding at this time is important because the birds are either experiencing the stress of molt or are accumulating fat for migration southward.

Phalaropes. Both northern and red phalaropes are circumpolar breeders. These birds are highly migratory; they nest on the arctic tundra in summer and the Beaufort Sea populations spend the winter at sea in the Pacific Ocean (Johnson et al. 1975). Only juveniles make extensive use of the coastal areas; they are there for a short period in late summer.

Juvenile northern and red phalaropes arrive to feed along the shorelines of the barrier islands and mainland during August; thousands of individuals concentrate along the beaches of the barrier islands during the middle and late parts of August (Connors et al. 1979; Johnson and Richardson 1980); they have left by early September.

Both northern and red phalaropes are specialized shoreline feeders that pick their food from the beach or from the water's surface near the beach. Phalaropes concentrating on coastal shorelines in August eat primarily copepods, small amphipods and small mysids. The diets of red and northern phalaropes are very similar to each other.

Arctic Cisco. The arctic cisco is circumpolar in distribution except for Greenland and Scandinavia, and is adaptable to either anadromous or freshwater life styles. It is an important species in Alaskan Arctic waters. Available information on the biology of arctic cisco in Alaska and Canada has been obtained largely as a result of coastal studies of the anadromous segment of the population (summarized in Craig and Haldorson 1980). Few data exist for the freshwater segments of these populations. It is thought that coastal populations of arctic cisco overwinter in fresh or brackish water, move to the coast in early summer, migrate along the coast for sometimes considerable distances, and return to their river of origin in the fall. Spawning individuals may move into freshwater earlier in the summer than non-spawners. Spawning locations of arctic cisco occurring along the Alaskan arctic coast in summer are unknown but believed to be in the Colville River system. Arctic cisco inhabit only the lower reaches of the Colville with none recorded as far upstream as Umiat (summarized in McElderry and Craig 1980). The lack of information regarding spawning times and areas and overwintering areas represents a major data gap.

In north Alaska coastal waters, arctic cisco feed primarily on mysids and secondarily on amphipods throughout the open-water season (Craig and Haldorson 1980).

Least Cisco. The least cisco, like the arctic cisco, is nearly circumpolar in distribution and can have either an anadromous or fresh water mode of life. It is common along the entire Beaufort Sea coastline, and several Beaufort Sea drainages in Alaska (east to the Colville River) are known to be sources of large populations of least cisco (summarized in Craig and Haldorson 1980). Some data indicate that females have a greater tendency than males to become anadromous. Similarly to arctic cisco, least cisco spawn and overwinter in fresh or brackish water, and utilize coastal areas primarily during the open-water season. The Colville River is thought to be a major source of least cisco that summer along the Alaskan coast (Craig and Haldorson 1980).

The diet of least cisco in North Alaska coastal waters is, like that of arctic cisco, primarily mysids and secondarily amphipods (Craig and Haldorson 1980).

Arctic Char. The arctic char is also essentially circumpolar in distribution and has both anadromous and freshwater life modes. Like the ciscoes, its anadromous populations overwinter in freshwater streams and spend the summer in shallow coastal waters (Craig and McCart 1976; Craig 1977). The Sagavanirktok River supports one of the largest char populations on the Alaskan North Slope, whereas the Colville River, the largest river on the Alaskan North Slope, supports a small char population. Beaufort Sea drainages west of the Colville do not appear to support char populations (Hablett 1980).

Char foods in the nearshore Beaufort Sea are, like those of the ciscoes, primarily mysids and amphipods.

Fourhorn Sculpin. The fourhorn sculpin is a circumpolar marine species that seldom invades fresh water, although it is very abundant in estuaries and lagoons. It is typically the most common marine fish found along the Beaufort Sea coastline. It is present in virtually all nearshore habitats, including the deeper waters not frequented by anadromous species (Craig and Haldorson 1980).

Fourhorn sculpins are relatively sedentary. Numbers of this species increase in lagoons (presumably having moved in from the ocean) as the open-water season progresses; most of them apparently leave the lagoons again in winter. It appears that they then move to deeper nearshore waters, where they probably spawn (Craig and Haldorson 1980).

Fourhorn sculpins consume approximately equal amounts of mysids, amphipods and bottom-crawling isopods (Craig and Haldorson 1980).

Arctic Cod. The arctic cod is a circumpolar marine species, more commonly encountered in oceanic environments than in shallow nearshore areas. It is an important food item for many species of arctic waterbirds and marine mammals. Arctic cod tend to travel in large schools and are highly mobile (Bain and Sekerak 1978; Craig and Haldorson 1980); thus, their abundance and occurrence are extremely variable. Furthermore, little is known about their spawning activities and seasonal movements. They occasionally appear in nearshore areas in extremely large numbers.

This species provided the most dramatic example of annual variability recorded during this study. Only a modest increase in cod numbers was encountered as freeze-up approached in 1977, but an estimated several million cod swept through the lagoon in mid-August of 1978. During a nine-day period in 1978 (14-22 August), 124,200 arctic cod were caught. This cod run was not restricted to Simpson Lagoon, but was also observed elsewhere along the Beaufort Sea coastline. No cod were found in the lagoon after November.

Arctic cod in the lagoon fed mainly on mysids, copepods and amphipods.

Mysids. *Mysis litoralis* and *M. relicta* comprised the overwhelming portion (and perhaps all) of the mysids collected in the lagoon and eaten by fish and birds. *M. litoralis* was normally the most common in both the lagoon and in bird and fish stomachs.

The general distribution and life-history patterns of both these species are similar in many ways. Both are circumpolar in distribution, and both are coastal species adapted to conditions of varying salinity. Of the two, *M. litoralis* appears less tolerant of fresh water (Holmquist 1963). Along the Alaskan arctic coast both species apparently recolonize the shallow lagoon and estuarine environments each spring and retreat again to the adjacent ocean in winter as the ice thickens on lagoon surfaces (Griffiths and Dillinger 1980).

In both species, breeding apparently occurs in early winter (October-November). The young develop in the brood pouches of the adult females during winter. This occurs in the marine waters adjacent to the shallow nearshore lagoons and estuaries. In spring the young are released from the brood pouches (in the ocean and/or the lagoons), rapidly recolonize the shallow lagoons and estuaries, and grow rapidly throughout the summer.

Data from Schell (1979 and pers. comm.) indicate that mysids probably depend for almost all their nourishment on recent primary production rather than peat detritus. Whether they consume phytoplankton and other plants directly is not known; nothing is known about differences in feeding dependencies of the two species.

Amphipods. Several species of amphipods were common in the lagoon, but by far the most common in terms of biomass was *Onisimus glacialis*. It was also an important prey item for birds and fish (Craig and Haldorson 1980; Johnson and Richardson 1980).

Onisimus glacialis is circumpolar in distribution and is a characteristic species of shallow, brackish waters. At least during the open-water season it is epibenthic in habit, living near, on, or sometimes burrowing into the substrate. In the winter, it is sometimes abundant on the ice undersurface (Thomson et al. 1978), although it also occurs on the bottom. In the nearshore Alaskan Beaufort Sea, it exists in lagoons and estuaries throughout the year, and as well may be found in the nearshore marine environment. Its growth rate is much slower than that of mysids, and like that of mysids, appears to slow but not stop during winter. Most individuals of *O. glacialis* appear to breed in the fall; females brood the developing young during the winter and release them sometime in late winter (February-March) (Griffiths and Dillinger 1980). The great majority of individuals found in the lagoon in summer are juveniles. The principal foods of this species appear to be other crustaceans and diatoms.

Marine Primary Producers. Most of the non-terrestrial primary production made available to the consumers in the lagoon system is presumed to be production by phytoplankton (mostly diatoms) in the lagoon and nearby ocean. Recent speculation holds that production by kelp in the large boulder patch in nearby Stefansson Sound may also be significant (Schell, pers. comm.). The primary production supporting the pelagic community in the Beaufort Sea (and other polar waters) occurs in two distinct phases. The initial algal bloom occurs in the spring well before the 2 m thick ice cover has begun to melt, but after the returning daylight reaches intensities sufficient to supply the necessary energy beneath the ice (Bunt 1963; Apollonio 1965; Horner 1977). At this time attached (epontic) algal populations grow within the bottom few centimeters of ice and at the ice-water interface, and thrive until the ice begins to melt near the beginning of June. As the ice cover melts, phytoplankton production in the water-column begins to become the major type of photosynthetic activity. In deeper waters (below 50 m) there is little primary production because of the dim light at such depths. Even in shallower waters, production soon wanes because of nutrient depletion. Melting of the ice and freshwater runoff from land strengthen the stratification of the water-column, which prevents the advection of deep-water nutrients to the photic zone (Schell 1979).

Terrestrial Primary Producers. The arctic coastal plain adjacent to the Beaufort Sea sustains an annual production by terrestrial plants, and as well is a depot for plant materials that have accumulated for thousands of years as peat. Both the plants of recent origin and the peat are dumped annually (via river input and coastal erosion) into the coastal waters, collectively in amounts that are comparable to the annual production by phytoplankton in the coastal waters (Cannon and Rawlinson 1978; Schell 1978). The great preponderance of this terrigenous material is peat, which accumulates along with other detrital materials in the lagoons and estuaries.

Although this peat is apparently decomposed biologically at a fairly rapid rate, neither it nor recent terrestrial primary production appear to enter the mysid-amphipod-fish-bird food web in large quantities (Schell 1979). However, data suggest that recent terrestrial primary production may significantly contribute to food webs in and near major river deltas (Schell, pers. comm.). All sources of terrestrial production appear to be very important contributors of nitrogen (Schell, pers. comm.).

Limiting Nutrients. As in most coastal aquatic systems, the essential nutrients that appear to control productivity in the nearshore Beaufort Sea are nitrogen and phosphorus. The land appears to contribute the major supply of nitrogen and the sea contributes most of the phosphorus. Consequently, the water-column has a low nitrogen:phosphorus ratio in offshore waters but in areas impacted by freshwater runoff, the reverse is true. For example, the waters near the mouth of the Colville River have high nitrogen and low phosphorus concentrations because of the terrestrial runoff (Schell 1979).

The overall nutrient concentrations increase in the nearshore waters over the winter months in response to:

1. *in situ* regeneration processes mediated by heterotrophic bacteria,
2. nitrogen exclusion from the ice as waters freeze, thereby increasing nitrogen concentrations in pockets of water beneath the ice, and
3. resupply from deeper and offshore waters as a result of thermohaline convection.

Late winter concentrations of nitrate, ammonium, and phosphate ions in nearshore waters (within 10 km of shore) are much higher than at the same locations in June and July. The sharp decrease in summer concentrations reflects nutrient uptake by populations of ice algae and phytoplankton, and the dilution of the coastal waters by melt of nutrient-poor ice (Schell 1979).

The Important Processes

Biological and physical processes support the birds and fish and their food webs. The biological processes function within and among the components of the food web (e.g., the nutrients phosphorus and nitrogen, the primary producers, the invertebrate consumers, and the consumers that are the key species). The important physical processes are the geologic forces reponsible for the origin of the nearshore environment and the hydrologic transport mechanisms that deliver nutrients and important components of the food web to critical sites and control the important water qualities (temperature, salinity, etc.).

Crustacean Eaters. A highly significant characteristic of the barrier island-lagoon ecosystem is that all the key species are supported largely by a few species of epibenthic crustaceans despite the presence of abundant alternate food sources (Griffiths and Dillinger 1980; Craig and Haldorson 1980) (Fig. 3). The key species are oldsquaw, red and northern phalaropes, arctic cisco, least cisco, arctic char, arctic cod, and fourhorn sculpin. Some significant characteristics of these predators in the nearshore ecosystem are as follows:

1. They are all seasonal (usually summer) visitors to the shallow lagoon. They all spend large portions of the year in other places, where they are subject to the population regulating factors of those environments. Time spent in the lagoon system ranges from less than a month for the phalaropes to 5-6 months for some of the fish.
2. The major life function for which the key species use the lagoon appears to be feeding for fattening, growth, or both. There is little reproduction of the key species in the lagoon. Oldsquaws obtain the energy necessary for their molt and growth of new feathers, and both oldsquaws and phalaropes accumulate or maintain the reserves needed for their southward migration. Fish grow and fatten in readiness for spawning and/or to carry them through the winter.
3. The key species partition the available feeding habitats and food resources in the lagoon to only a limited extent (Craig and Haldorson 1980). The partitioning that does occur appears to be largely unrelated to competition for food resources, because the species that feed in the same habitats often eat the same foods.

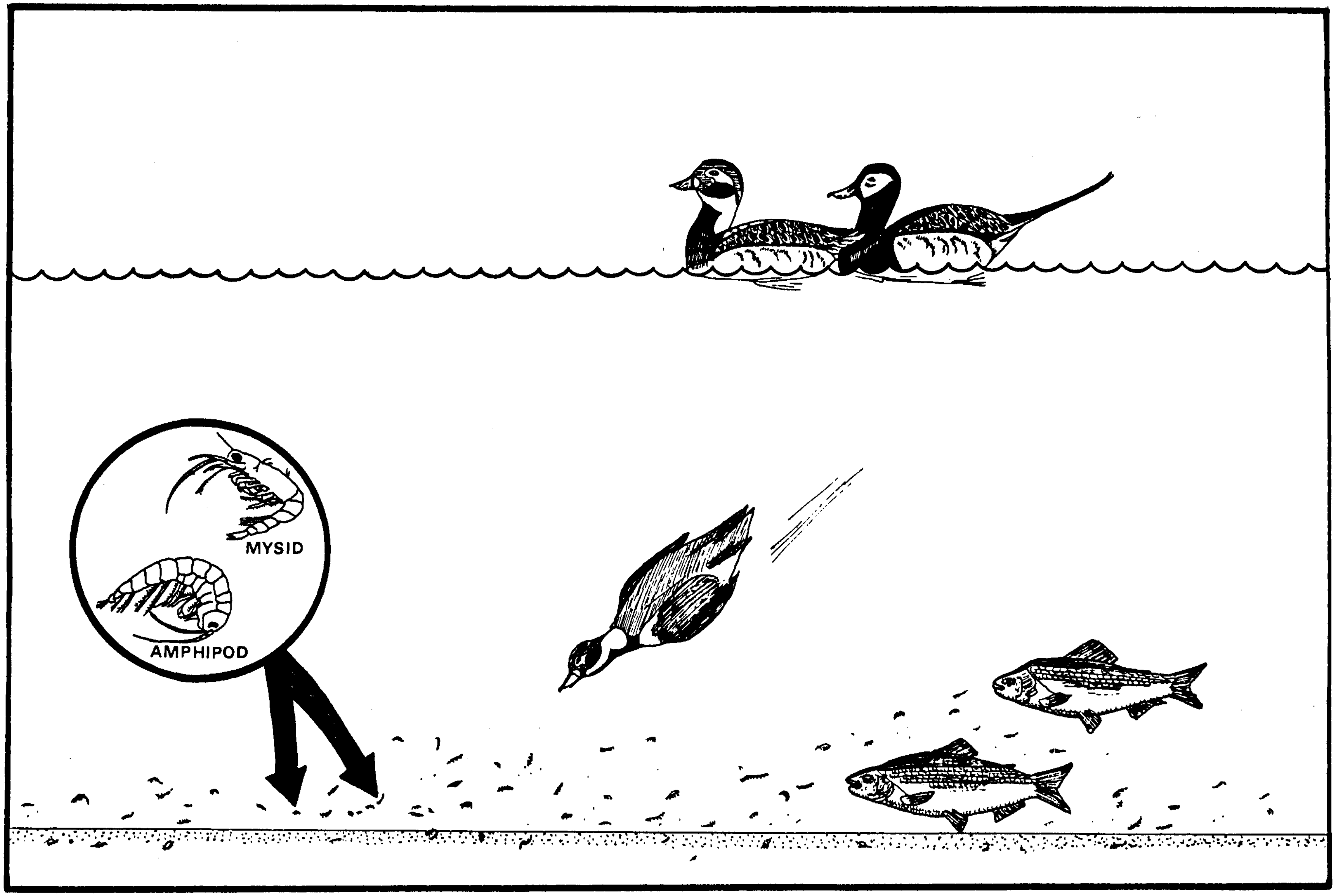

Figure 3. Epibenthic crustaceans (mainly mysids and amphipods) form the great preponderance of foods of vertebrates in the nearshore Beaufort Sea.

4. None of the key species (except arctic cod) habitually ventures far seaward beyond the lagoon environment; however, all (except the fourhorn sculpin) are highly mobile and may use several lagoon systems during the course of a summer.

To summarize, all of these major predators eat primarily crustaceans (despite the availability of other foods), most are summer visitors only, most use the lagoon only for feeding, the various species do not appear to compete for food amongst themselves, and most are largely restricted in distribution to nearshore habitats (as opposed to inhabiting the open ocean beyond).

The epibenthic crustaceans that support the vertebrate populations are mysids and amphipods. The two species of mysids (*Mysis litoralis*, *M. relicta*) comprise the majority of food biomass consumed by the key species. The most rapid growth of mysids (especially young) occurs during the open-water season; in winter their growth rates decrease but growth does not cease (Griffiths and Dillinger 1980). These mysids are highly mobile, apparently using water currents to augment their mobility. They rapidly repopulate the lagoons from the nearby ocean as the ice thaws in early summer, and it is suspected that they may also move rapidly along the coast. Thus, mysids, which comprise the major foods of the predators, are also seasonal residents in the lagoon; their season of greatest secondary productivity (summer) coincides in time with the period of greatest cropping by predators.

The amphipod of primary importance is *Onisimus glacialis*. In contrast to the mysids, it overwinters in the lagoon. It has a slower growth rate than mysids; its growth rate, like that of mysids, decreases to a low but non-zero value in the winter. Little is known about the movements of individuals or about what portion of the summer population overwinters in the lagoon.

The quantitative relationships between the key species and their prey in the lagoon have been discussed in detail by Griffiths and Dillinger (1980) and Craig and Haldorson (1980). Several points bear scrutiny:

1. Alternate sources of food are present but are not utilized significantly by the key predators. These alternate foods include infaunal organisms (molluscs), sedentary epibenthos (other crustaceans, molluscs, tunicates), other mobile epibenthos (polychaetes), and water-column organisms (small fish, zooplankton). The key species of fish are probably not adapted to feed on these alternate foods, since they do not utilize them significantly in other areas, but oldsquaws do feed on some of the alternate food types in other areas.
2. The mysid biomass available in the lagoon greatly exceeds the estimated daily energy requirements of the predators in the lagoon at all times during the open-water period.
3. Partitioning of available food resources among the key species, the normal pattern in environments where competition exists, is not apparent in the lagoon.

The implication of these points is that the lagoon is a system where there is an overabundant food supply for the key species (and other predators). The relevance of this surfeit of food to the assessment of impacts will be discussed later.

Carbon Sources. Some lines of evidence from studies in coastal environments indicate that detrital carbon from peat may be less important to estuarine food chains than the more rapidly cycled carbon from recent production. Hughes (1979) noted that most debris particles from St. Margaret's Bay in Nova Scotia appeared rather refractory (presumably because peat was a major part of this detritus) and not readily assimilated into food chains. Although it is recognized that most of the detritus from more recent terrestrial production is fairly rapidly broken down and incorporated into estuarine food chains (Odum et al. 1973; De la Cruz 1975; and others), Haines (1976, 1977) found evidence that marine phytoplankton production provided the great majority of carbon even in an estuary where input of recent terrestrial production was considerable.

There are two obvious general sources of carbon that could potentially fuel the food webs of lagoons along the Alaskan arctic coast--terrestrial carbon from river discharge and coastal erosion, and carbon fixed by aquatic primary production within the lagoon and adjacent ocean.

The majority of carbon delivered to the lagoon from terrestrial sources is in the form of peat with an average age of several thousand years. The two sources of "recent" production are plants on land and plants (mostly plankton) in the lagoon and ocean. Carbon isotope studies by Schell (1979) indicated that peat carbon formed a relatively small percentage (∿10%) of the food base of key species and their prey in the nearshore Beaufort Sea. Schell found further, by analyzing C^{12}/C^{13} ratios of food web components that most (> 80%) of the "recent" carbon that fuels the critical food chains was marine (phytoplankton) in origin.

If, as the evidence indicates, the critical carbon supply to the lagoon system is marine in origin, there are two major implications:

1. The times of greatest carbon fixing activity of consequence to key species and their prey are April-May (by ice algae) and July-August (by water-column phytoplankton) (Schell 1979). These times are immediately preceding and during the time (summer) of maximum growth of the consumers (mysids, amphipods, and their predators) that benefit directly or indirectly from the increased carbon availability.
2. Since the majority of the carbon appears to be fixed in the water-column, or released directly into the water-column when the ice melts, it is highly mobile and its depositional fate is closely tied to the hydrographic regime.

<u>Nutrient Sources</u>. As we have seen (see 'Limiting Nutrients', above), the primary source of nitrogen is from the land, and that of phosphorus is from the sea (Schell 1979). The coastal waters, including the lagoons and bays as well as the shallow shelf waters for some distance beyond, are the zone of maximum availability of nitrogen and phosphorus in ratios optimum for primary production (Hamilton et al. 1974; Schell 1979). Because the nearshore waters are shallow, nutrients are retained in the photic zone and the biological systems thus can make relatively efficient use of the nutrients present. Nutrients assimilated where the water is deeper tend to become entrapped in bottom waters after they settle, and become unavailable to food chains of vertebrate consumers. However, as we shall see below, these deep waters may be a

secondary source of both nitrogen and phosphorus. Theoretical evidence and some field observations support the idea that net landward movement of bottom waters and entrained materials and nutrients occurs, and that the repository for much of the transported materials is the coastal shallows.

Delivery Mechanisms. The Simpson Lagoon system is an open system; exchanges of organisms, nutrients, energy in various forms, and water masses occur continually between the lagoon and outside areas. Birds and fish can move to and from the lagoon through their own actions, and light, heat and wind energy can enter the lagoon from above. However, the delivery of carbon and nutrients to their sites of utilization, as well as the movements of some of the epibenthic invertebrates, are controlled by water circulation and exchange patterns. Water movement patterns contribute in a major way to making the shallow estuaries and lagoons valuable habitats for fish and birds.

In summer along the Beaufort Sea coast, prevailing wind regimes cause water to exchange rapidly between adjacent coastal water bodies (Callaway and Koblinsky 1976; Mungall 1978). Exchange between coastal and offshore waters is, on the other hand, sufficiently restricted so that the two systems remain measurably different in their temperatures and salinities, and presumably in other attributes as well. Temporal fluctuations in the rate of transport of mysids between the lagoon and offshore waters are correlated with fluctuations in currents. In winter, coastal circulation and exchange rates are much reduced from those of summer (Barnes and Reimnitz 1977).

The water exchange that occurs between the relatively warm and brackish nearshore waters and the colder, more saline ocean waters is probably affected during periods of significant stream discharge by an exchange pattern characteristic of many estuaries--a landward intrusion of saline ocean water near the bottom as brackish estuarine water moves seaward at the surface (Truett 1980). It appears that this process along the Beaufort coast may commonly be augmented by coastal upwelling (Barnes et al. 1977), whereby prevailing easterly winds cause surface water to move seaward and bottom water to move landward.

Currents near the bottom are more important in transporting ecologically significant materials than are currents higher in the water-column, because nutrients and organic suspensoids tend to settle and because the important invertebrates (mysids, amphipods) are epibenthic in habit. Existing data strongly suggest that the landward component that exists in the bottom currents in summer may promote net landward delivery of nutrients, materials and organisms in the lower part of the water-column (Truett 1980). And, characteristically, these materials are not returned seaward in the surface waters but remain near the land. The coastal lagoons and estuaries thus act as sinks for these materials and accumulate them to the benefit of the biological community there.

Temperature and Salinity Regimes. Closely tied to the water circulation patterns are temperature and salinity patterns in the coastal waters. Although birds and mammals are relatively insensitive to normal fluctuations in water temperature and salinity, fish and invertebrates are, in contrast, very sensitive. In fact it is generally conceded that temperature and salinity are probably the two water properties that are most important in regulating the distribution and functioning of cold-blooded (poikilothermic) estuarine organisms (Kinne 1963; Clark 1977:19). An important difference between the effects of salinity and temperature should be noted. Salinity tends to control the distributions of species in nature (Gunter 1956, 1961; Barrett and Gillespie 1973), but does not appreciably affect rates of metabolism or growth (Kinne 1960; Wood 1967) if it is well within the tolerance range of the species. And, since most estuarine organisms have broad salinity tolerances, stress caused by salinity is not often a problem. On the other hand, temperature has a major controlling effect on metabolism and growth of organisms, and therefore on energy turnover rates and primary and secondary productivity in ecosystems (Carriker 1967; Kinne 1963; Mihursky 1967; Dunbar 1968:9; Clark 1977:19; and others).

It appears that all of the species of fish and invertebrates of major concern in the Beaufort Sea barrier island-lagoon study are able to tolerate, at least temporarily, the considerable ranges of salinities (0-35 ppt) to be encountered in the lagoon in the open-water season.

Some (amphipods, mysids, fourhorn sculpins) have been shown by data collected in the field (Craig and Haldorson 1980; Griffiths and Dillinger 1980) to be able to withstand even higher salinities such as those encountered under the lagoon ice in winter (> 60 ppt). Correlated seasonal changes in invertebrate distributions and salinities in the nearshore area do occur (Griffiths and Dillinger 1980), but a causal relationship has not been proven to exist.

Whether the increased summer temperatures of lagoon waters along the Beaufort Sea coast cause increased metabolic and/or growth rates in fishes and invertebrates has not been documented. However, the fact that the major mysid and amphipod species grow faster in summer when water temperatures were higher, suggests that there might be a correlation between temperature and growth. Likewise, the evidence from other studies of the effects of temperature on fish and invertebrates is overwhelmingly in support of the hypothesis that temperature increases should accelerate metabolic and growth rates of poikilothermic animals in Beaufort coastal waters. This issue will be explored further in the 'Discussion' section that follows.

Discussion

This discussion presents and interprets evidence from the research of this program and from other sources that provides the best answers to the questions:

1. Is the Simpson Lagoon-Jones Islands system essential to the well-being of the key species that use it, and, if so, what are the characteristics of its components and processes that make it so?
2. Do the components and processes that regulate populations of these key species in Simpson Lagoon also regulate similar populations in similar ways in other Beaufort Sea coastal systems? That is, can the results acquired in this study be broadly applied to other parts of this coast?

The Nearshore Environment--A Critical Habitat?

The object of this portion of the discussion will be to compare the lagoon to the adjacent marine and terrestrial environments in terms of its life-support qualities. Comparisons among lagoons and between lagoons and other coastal habitats will follow in the next part of the discussion.

Available information documents that, during the periods of the open-water season when the key vertebrate species congregate in the nearshore waters, they are absent from or rare in ocean and terrestrial habitats, i.e., they apparently prefer the lagoon habitats. We cannot conclusively demonstrate, however, that this preference is equivalent to a need. What we can do is discuss the relative utilities of each of these habitats (particularly lagoon vs. ocean) in terms of their apparent provision of nutritional and habitat needs of key species. Then, depending on whether and how the lagoon area appears to exceed the ocean and/or terrestrial environments in its ability to fulfill these needs, we may postulate whether and why lagoon habitats are critical and necessary.

The following sections entitled, 'Food Resources' and 'Habitat Quality', compare the shallow lagoons with oceanic habitats in terms of needs of key species. Note that the terms estuary and lagoon will be used interchangeably, because by definition and function, all lagoons along the Beaufort Sea coast are estuaries.

Food Resources. Availability of resources at all levels in the food chains of key species are influenced by two processes--(1) transport and delivery patterns, and (2) *in situ* turnover or productivity (both primary and secondary). These processes regulate food availability in the ocean, the estuaries, and in fresh water.

As we have seen, net delivery of vital links in the food chain should accrue to the shallow coastal waters from the fresh waters on land and the deep waters of the ocean. The vital nutrients P and N are delivered to the shallow coastal waters in abundance and in the more or less balanced proportions that are most suitable for their assimilation by phytoplankton. In comparison, the fresh waters tend to be low in phosphorus while neritic (continental shelf) waters are low in available nitrogen (Campbell 1980). Likewise, particulates (plankton, feces and other zooplankton by-products, and other detrital material) that serve as food for the important mysids and amphipods should also accumulate in the shallow coastal zone (Truett 1980). On an average basis, both the fresh water systems and the deep ocean probably contain lower densities of these food materials. Some of the important invertebrates themselves (e.g., mysids) appear to show a net circulation-assisted immigration to the shallow lagoon waters during the summer, the time when the lagoon is accessible to and utilized by the key species, and the time when those species feed on these mysids.

In terms of *in situ* production, primary production rates are considerably higher (per unit volume of water) in shallow nearshore waters than they are in fresh water streams or in deeper continental shelf waters (Campbell 1980). Primary production is normally low in arctic fresh water streams because it is severely phosphorus-limited. Over the deeper parts of the shelf it is also relatively low (on a per-unit-volume basis but not necessarily on a surface-area basis) because it is nitrogen-limited. In the shallow coastal waters, nitrogen and phosphorus from the land and sea, respectively, mix and are available in near optimal concentrations for primary production. In addition, the nutrients that are released in shallow waters where light is abundant, in contrast to those in the deeper shelf waters that have settled to the bottom and become trapped below the photic zone, are rapidly reused by primary producers.

Several lines of evidence (mostly from other systems) suggest that net secondary production (growth) of the prey of fish and birds should be greater in the nearshore zone than net production rates of similar organisms in adjacent oceanic habitats. First, summer temperatures of lagoons and other Beaufort Sea coastal waters average several degrees C higher than those of the adjacent deeper ocean. As discussed earlier, this presumably should augment the growth rates of poikilotherms living in the shallows. Second, the shallow nearshore environment is a highly disturbed one (by ice and wave action) and very unstable in the qualities that regulate aquatic life (substrate integrity, temperature, salinity, turbidity, nutrient levels, etc.). As such, it would be expected to support pioneering (early successional) species (Krebs et al. 1973) that characteristically have high reproductive and population growth potentials compared to species that live in more stable environments, such as the adjacent ocean. Third, most shallow nearshore zones, in contrast to oceans, support relatively simple biological communities with correspondingly short food chains, because the communities are, in fact, "pioneering" types. Such communities have relatively high ecological efficiencies and, consequently, higher net secondary productivities. Although it is not known whether the Beaufort Sea food chains in the deeper shelf waters are less efficient, the biological communities are reportedly more complex (see Carey et al. 1974; Feder and Schamel 1976), which normally correlates with decreased efficiency. Fourth, the nearshore shallows function primarily as a "growing place" for some of the major food organisms (mysids, etc.) that overwinter at slower rates of growth in the ocean. Assuming that the system functions in a way similar to some analogous temperate systems, the net secondary production is thereby augmented, because ecological conversion efficiencies are greatest during growth stages of organisms.

In summary, two types of evidence suggest that the nearshore shallows of the Beaufort Sea (in comparison to adjacent terrestrial or oceanic environments) provide relatively great quantities of food resources. First, the nearshore environment probably acts as a sink for nutrients and food that come from the land and from the sea. Second, the *in situ* production of food resources is probably greater in the nearshore than in adjacent environments. It should be noted that there are no data about secondary production in deep continental shelf waters of the Beaufort Sea to confirm this last speculation; the evidence is circumstantial.

Habitat Quality. General principles suggest that those habitats for which animals show a preference provide the animals with the best chances for survival, and vice versa. However, existing data cannot prove this assumption. If we are to assess the probable consequences of development-caused changes in the preferred habitats, we must attempt to define not only what the preferences of the key species are, but also why these species demonstrate such preferences.

The preceding section clearly indicates that the shallow coastal region is relatively rich in food. However, the characteristic distributions of key species within this region are not clearly correlated with their food organisms, suggesting that physical or chemical constraints further affect their distribution. This study and others have established correlations between some of the species' distributional patterns and some of the measurable habitat features. Further speculation is supported by available knowledge about the species' preferences elsewhere. The apparent importance of some habitat features to the key species follow.

1. Oldsquaw - Oldsquaw distribution is more restricted than the distribution of their prey. They tend to congregate in lagoons, small bays, and other protected sites, and tend to avoid sites more exposed to wind and wave action (e.g., seaward of the barrier islands; in large, open bays) (Johnson and Richardson 1980). During molt they also congregate on leeward beaches. Oldsquaws can dive to great depths when necessary (50 m), but the energetic cost of doing so probably is a further reason for their concentration in shallow lagoons, where epibenthic prey are available nearer the surface. There is some indication that, within lagoons, they preferentially assemble in the deeper (2-3 m) waters to feed.
2. Phalaropes - Phalaropes (juveniles) feed at the water's edge, and sometimes at the water's surface near the edge, appearing to prefer barrier island beaches to mainland beaches. They too tend to seek shelter in the lee of islands.
3. Other Birds - Two species of birds not considered key species, but that nest almost exclusively on barrier islands, are the common eider and brant. In these cases preference for islands as nesting sites is essentially obligate. Isolation from arctic foxes is apparently important to the nesting success of such species. Islands sometimes provide such isolation.
4. Anadromous Fishes (arctic and least cisco, arctic char) - Our data (Craig and Haldorson 1980) show that in summer these fish collectively show a marked preference for lagoon waters that are very near the shores of the mainland or barrier islands. These species occur at much lower densities nearer the lagoon center and are almost absent from waters seaward of barrier islands. Moreover

the fish are much more numerous near mainland shores than near islands. Postulated reasons for this preference are that fish might use shorelines as navigation aids and/or that they might prefer the warmer and/or less saline water normally found near mainland shores. It is possible that some anadromous species cannot accumulate sufficient energy reserves to survive the winter or reproduce if they spend the entire summer in the colder mid-lagoon waters. However, the data are insufficient to establish causal relationships. In winter virtually all anadromous species appear to vacate shallow nearshore habitats and return to rivers to overwinter.

5. Marine Fishes (fourhorn sculpin, arctic cod) - Habitat preferences of these species in the nearshore area are less apparent than for anadromous species. These species are common in summer in deeper marine environments as well as in coastal waters. Available data (Craig and Haldorson 1980) indicate that sculpins may be more abundant near the mainland in summer, but the differences in density are not large. Arctic cod appear in nearshore areas in sudden large 'runs' in late summer, but their abundance has not been proven to be associated with any particular feature of the habitat. Both sculpins and cod were, in contrast to the anadromous species, found in bays and lagoons in winter, but appeared to exhibit a general distributional shift seaward as winter progressed.

Excepting marine fishes, all key species of birds and fish show marked associations with shallow nearshore habitats (mostly in lagoons and other estuaries) in summer. They each show preferences for specific habitats within the nearshore area, although reasons for these preferences have not been confirmed for all species.

Extrapolations--Are they Warranted?

A very important question bearing on the issue of impact assessment in the Beaufort Sea coastal zone is whether research information collected at one site can be extrapolated to answer questions about impacts in other sites. If such extrapolations are warranted, data collected in local areas such as Simpson Lagoon would be useful in developing environmental regulations to be applied on a coastwide basis. This would greatly increase the cost-effectiveness and relevance of each assessment study. It would also mean that the design of new studies could be improved by taking into account the results of studies done elsewhere along the coast.

First, it should be noted that the important functional properties (and, to a lesser extent, structural properties) of the coastal ecosystems are conservative as one moves parallel to the coast, and change rapidly as one moves perpendicular to the coast. Biological communities with similar functions and structures within themselves exist as narrow bands that follow water depth contours (Fig. 4) in the nearshore environment. This characteristic of coastal environments is widely recognized in the arctic (Carey 1978) and elsewhere (Smith 1966:221-242).

Coincidentally, because of differences in construction methods and environmental hazards associated with different water depths, petroleum resource development will proceed in the same fashion, i.e., specific technologies will be applied in particular "bands" defined largely on the basis of water depth. This phenomenon is already evident in offshore development activities and plans in the Canadian portion of the Beaufort Sea. Since the very shallow waters are likely the first to be developed, it is important that the relevance of the Simpson Lagoon studies to other shallow coastal areas be examined so that the impact studies and statements that will soon be needed may benefit.

Intra-Coastal Similarities. To investigate whether other Alaskan Beaufort Sea coastal sites are ecologically similar to the Simpson Lagoon area in important functions, we should first evaluate (on a coastwide basis) existing data about critical processes and ecosystem components. Only some kinds of data are available; fortunately the most comprehensive data from other areas are about some of the controlling variables that "drive" the ecological system (e.g., winds that drive circulation, water exchange characteristics, etc.).

Wind stress is the dominant force controlling water circulation and exchange during the open-water season (Mungall 1978). Dominant wind direction and average monthly speed are remarkably predictable along the coast, and are very consistent within the area that extends from immediately east of Barrow to the Alaskan-Canada border (Kozo 1979a,b). (The immediate Barrow area is different because it is

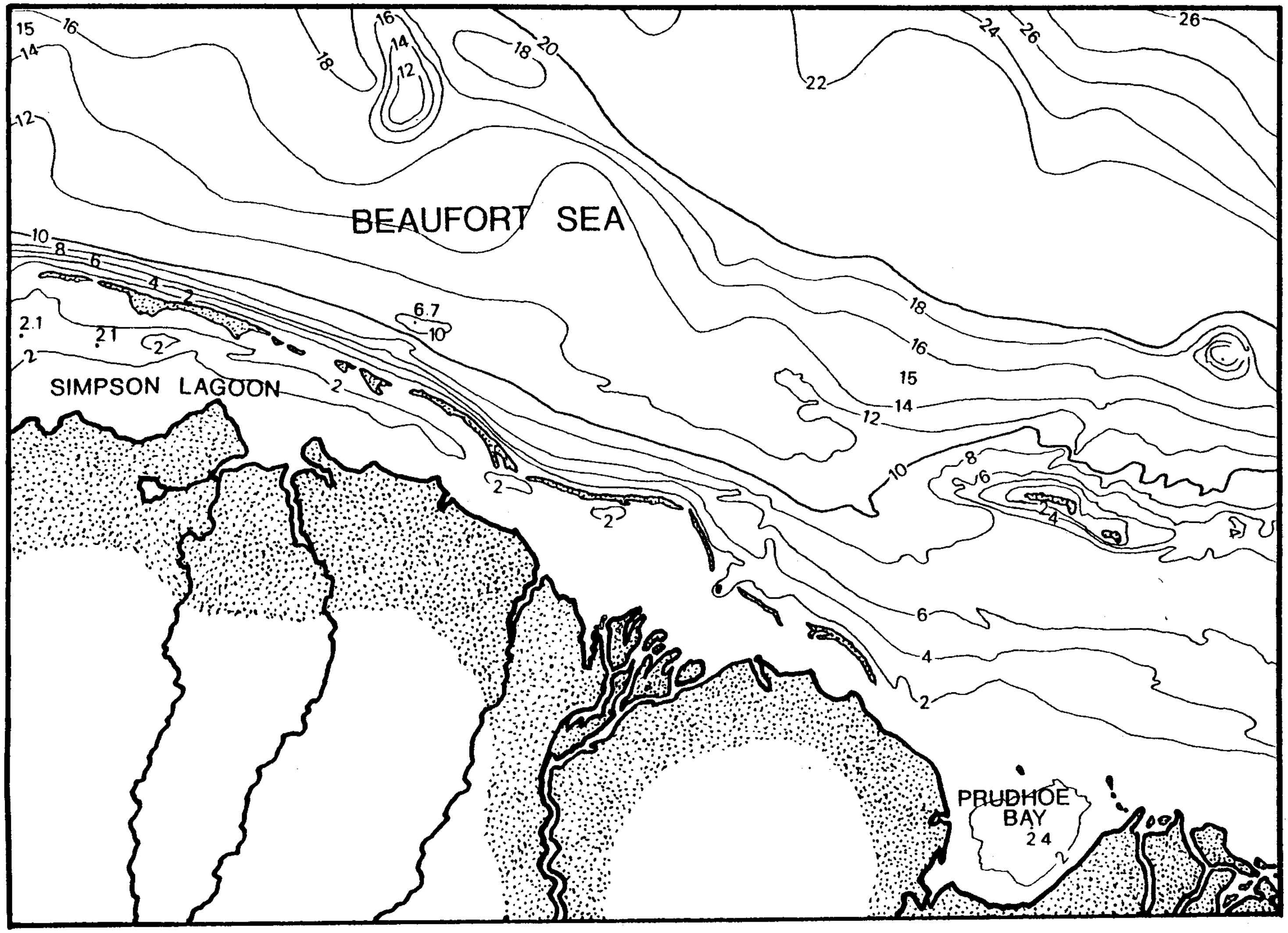

Figure 4. Depth contours (2-m isobaths) in the nearshore Beaufort Sea. Biological communities are delineated by depth contours such that nearshore ecosystems are long, narrow, and roughly parallel to the coast.

influenced by weather from the Chukchi Sea.) Likewise, the general orientation of the coastline and the gross topographic configurations (e.g., barrier island chains, shallow lagoons, and a gently sloping continental shelf) are generally similar all along the coast. Winds, coastline orientation, and topography are important in that they affect such important water exchange phenomena as upwelling and the tendency of the nearshore shallows to function as a sink for water-transported materials.

Sites of discharge of large rivers, important because of the characteristic water exchange processes that occur there, are all in shallow bays or lagoons. They also all have very similar annual discharge regimes (e.g., peak discharges over and under the ice in early summer, little or no flow in winter, etc.). Therefore, the important aspects of their discharge (e.g., dilution and heating of the saline and cold nearshore waters, layered exchange that causes the transport of materials in bottom waters to the nearshore shallows, etc.) should be very similar in quality.

Other critical processes about which data from several coastal localities are available are general feeding and habitat preferences of fishes. These data (Craig and Haldorson 1980) show that the dominant anadromous fishes eat primarily epibenthic crustaceans (largely amphipods and mysids) everywhere along the coast, despite the presence of other invertebrates, some of which are presumably alternative sources of food. Likewise these fishes generally appear to prefer the very shallow waters near the shores at all points where relevant observations have been made.

Oldsquaws and phalaropes use the same types of coastal habitats at all places along the Alaskan coast of the Beaufort Sea (Johnson and Richardson 1980). Oldsquaws feed in sheltered lagoons and bays, and rest in the lee of islands; phalaropes feed at and near the water's margin. Too few data about feeding preferences of these species at other coastal sites are available to allow reliable conclusions about longitudinal similarities. However, Johnson and Richardson (1980) note that phalaropes may tend to consume whatever organisms have been deposited at the water's edge; this may change considerably in time, and presumably in space as well.

Ecosystem Boundaries. When the functioning of a biological system is to be studied, and when development-caused changes in functioning are to be assessed, spatial units within which major biological processes are judged to be similar are normally defined. Within each unit, samples are taken, and the characteristics of those samples are ascribed to the unit as a whole, or to definable strata within the unit. Various criteria are applied to define the boundaries of discrete units; the boundaries are normally assumed to represent places where rates of exchanges of biological materials and organisms are relatively low compared to exchange rates that occur within the unit. These units so bounded have been called ecosystems.

A striking quality of the shallow, nearshore environment of the Alaskan Beaufort Sea is the longshore mobility of its organisms and materials. During the time they are resident along the coast, most of the fish and birds can and do move rapidly within a narrow band that extends seaward from the coast only a few kilometers, but that follows the coast for hundreds of kilometers. Likewise the important nutrients, detrital materials, and other entities entrained in the water column are extremely mobile coastwise, but not perpendicularly to the coast. This coastwise mobility of entrained materials occurs because the dominant component of water motion is parallel to the coast (Callaway and Koblinsky 1976; Mungall 1978). In short, this longshore mobility of components describes an ecosystem that, by conventional criteria, extends along the coast for hundreds of kilometers, but that extends seaward from the coast only a few kilometers. Given the normal assumption about the within-system similarities of major functions, processes that support the key species should be similar all along the Beaufort Sea coast. The obvious correlary is that broad extrapolations about the findings of this study (and presumably of other studies as well) may be warranted if they relate to ecosystem function and to sites within the shallow, nearshore region.

Conclusions

We have discussed the results of the Beaufort Sea Barrier Island-Lagoon Studies within the context of relevant ecological information from various other sources. A number of conclusions bearing on the issues of ecosystem function and impact assessment appear warranted. These follow, with appropriate qualifying remarks.

Prevailing wind regimes in summer cause rapid water exchange between coastal water bodies but more restricted rates of exchange between the shallow nearshore and the deeper marine environments. The nearshore/marine exchanges are probably characterized by a net landward component in the near-bottom currents that promotes landward delivery (and subsequent nearshore retention) of materials entrained in the lower part of the water-column. Consequently, the nearshore shallow waters function as a sink for materials transported from the land and from the sea as well as for those arising *in situ* (e.g., primary production) in the nearshore environment.

Estuaries and other shallow coastal waters in general are typically highly productive in comparison to the open ocean because they accumulate and rapidly recycle nutrients and organic materials, have short and efficient food webs, and support growth stages of migrant populations of organisms. Many arctic ecosystems likewise have simple food webs and support migrant animal populations that live in the arctic only during growth stages of their lives. The coastal ecosystem of the Alaskan Beaufort Sea has qualities typical of both coastal and arctic systems that enhance its quality to the important vertebrates--oldsquaw, phalaropes, arctic and least ciscoes, arctic char, fourhorn sculpin, and arctic cod--that assemble there in summer. It provides an abundant and constantly replenished source of prey, the mysids and amphipods. These prey species are so abundant relative to the needs of their vertebrate consumers that there is very little of the kind of partitioning of prey types among the predators that exists in areas where competition for food is significant. The mysids and amphipods are abundant because they are among the few species that have become adapted to the extremes of arctic estuarine environments--they find little competition for the abundant (largely marine-produced) food supply delivered to the nearshore environment.

Based on evidence from this study and from studies of other coastal systems, it appears that the nearshore (<~ 20 m deep) Beaufort Sea has and/or accumulates relatively high primary and secondary production in comparison to deeper areas of the continental shelf and is in that sense an important fish and bird habitat that is not found elsewhere. However, the fish and birds that consume the secondary production in summer further confine most of their utilization of the nearshore zone to the shallower (<~ 5 m) areas, especially the lagoons and bays, despite the apparent abundance of their favored foods in the deeper parts of the nearshore waters. Presumably this selective utilization of very shallow nearshore waters is related to the fact that the habitat features there (shallow depths, presence of emergent land forms, warm waters, etc.) are optimum and that food abundance is such that other habitats need not be utilized. The question that remains is whether fish and birds can opt for other feeding sites within this relatively productive nearshore region should the sites they favor become uninhabitable because of development activities.

The habitat qualities and the biological and physical processes found to be important to fish and birds in the Simpson Lagoon area appear to be shared by other regions along the Alaskan Beaufort Sea coast. Lines of evidence supporting this view include the general documented and theoretical similarities among coastal sites of physical processes (e.g., wind and current regimes, etc.) that control the general biological production of the nearshore region, and (2) the similarities in biological processes and structural characteristics among coastal sites. Ecosystems similar within themselves but different from adjacent systems exist as long, narrow bands that parallel the coast and have boundaries that follow depth contours. There is great mobility of the key species and probably also of their principal prey within these linear systems. The implications to impact assessment of these similarities among sites and mobilities of components will be discussed in the following section.

SECTION 2. AN ENVIRONMENTAL IMPACT ANALYSIS

An assessment of probable ecological impacts of petroleum exploration and development activities in the nearshore zone has become a natural and expected product of the Barrier Island-Lagoon Studies. The assessment provided herein is couched in general and broadly applicable terms and is based on findings of research conducted in the Beaufort Sea (Alaskan and Canadian) and in other coastal areas of the world. It provides information that helps answer the question:

> How are proposed development activities likely to alter important processes and components such that populations of key species will be affected?

The purpose of this assessment is to evaluate the general vulnerability of the coastal ecosystem to the expected kinds of activity, and to identify the critical points of interaction between significant ecosystem components and the activities. In keeping with the scope and objectives of the Barrier Island-Lagoon Program, focus will be on the ecosystem attributes (species) of major concern to humans. These include abundant species of birds (oldsquaw ducks, phalaropes), fish (arctic and least cisco, arctic char, arctic cod, fourhorn sculpin) and their food web constituents. Although the focus is on these species, it will become apparent that the data can be applied to other system components as well.

The previous synthesis has examined the major structural and functional attributes of the Simpson Lagoon-Jones Islands ecosystem, and generally of other Arctic Alaska coastal waters as well. As we saw, the species of direct concern to people are all top-level consumers (predators) that use the nearshore environment primarily in summer (May-October). They feed primarily on epibenthic crustaceans (mysids and amphipods) despite the presence of other invertebrates. With some exceptions, the key species occur at much higher densities in the shallow, brackish lagoons, bays and estuaries than in the deeper marine waters. Their foods, the mysids and amphipods, depend largely on phytoplankton production in, and delivery to, the coastal waters; this production is probably relatively high in the nearshore zone largely because nutrients are optimally available there. The key species (with the probable exception of fourhorn sculpins) and all levels of their food web are highly mobile, and collectively exhibit characteristics of pioneering-type communities that are adapted to naturally-stressed environments.

To evaluate the probable responses of these biological assemblages to OCS activities, we will begin by discussing what their expected levels of resilience are.

Resilience to Disturbance--An Ecological View

For the purposes of impact assessment, "disturbances" may be defined as relatively drastic changes in the levels of environmental factors and processes that regulate ecosystems and their constituents. A most important connection to make at the outset is that the kinds of disturbance introduced by the activities of man do not necessarily affect ecosystems differently than do natural disturbances. All ecosystems and their constituents are adapted to (tolerant of) natural disturbances to which they have been exposed during the course of their development. Coastal ecosystems, for example, naturally experience and are adapted to wide ranges of temperature, salinity, turbidity, oxygen content, current regime and even in some cases petroleum content, all of which affect populations of organisms that inhabit these systems. One object of an impact assessment, therefore, is to evaluate whether and how man's activities are likely to cause abnormal changes to which ecosystems have not previously been exposed and therefore to which they may not be tolerant. Such abnormalities could include not only perturbations of types or magnitudes not naturally experienced, but also perturbations at times of year when such perturbations do not naturally occur, or perturbations in combinations that do not naturally occur.

The likelihood that an ecosystem will be significantly changed by man's activities depends partly on the natural resilience of the system. Although different ecosystems obviously are resilient to different kinds of disturbance (depending on the evolutionary history of each ecosystem and its component species), certain kinds of ecosystems and species can be expected to be generally resilient, and others to be relatively sensitive. A discussion of some of the qualities that make ecosystems and species resilient follows.

Resilient ecosystems are normally found in environments that are subject to extreme climatic conditions (Holling 1973; Frost 1978), or that normally are subject to extreme fluctuations in environmental condition (Holling 1978:34). Conversely, systems sensitive to disturbance are typically those that are not accustomed to environmental extremes or to drastic fluctuations in environmental factors.

Similarly, species in naturally disturbed or rigorous environments have intrinsic qualities that may improve their ability to accommodate disturbance. In comparison with similar species in more benign environments, these species tend to have large maximum population sizes, high reproductive and mortality rates, short generation times, and the ability to disperse rapidly (Grassle and Sanders 1973). These qualities promote high genetic variability, which insures that the populations can survive unpredictable events. (These kinds of species are also the most likely to be preyed upon, and the least likely to have ways of avoiding predation; consequently, systems that support them are likely to be rich feeding grounds for predators.)

Another indicator of the resilience of ecosystems is the array of available options that the constituent species have for meeting their life requirements. That is, if populations are utilizing most or all of the food and/or habitat available (i.e., have no unused options), they tend to be sensitive to disturbances that reduce these resources. But if species normally utilize only a small portion of the foods and habitats available to them (i.e., have options in terms of space and food), considerable reductions in such availability may pass unnoticed. It is noteworthy that ecosystems that have periodic spurts of productivity (such as the Alaskan Arctic coast) tend to be populated during these times of high productivity by immigrants whose population levels are limited elsewhere. Consequently, food (and frequently habitat as well) is available in superabundance relative to the immigrants' needs. Such superabundances of food resources in seasonal feeding areas of migrants have been noted in anadromous fishes in estuaries (Connors 1978; Craig and Haldorson 1980), estuarine-feeding diving ducks (Nilsson

1969; Johnson and Richardson 1980), and migrating shorebirds in littoral habitats (Recher 1966). Other examples of migrant fishes and birds that feed in estuaries and are limited in number elsewhere (and thereby presumably have overabundant resources in estuaries) are provided by Talbot (1966), Bellrose (1976:391), and others.

As described in this synthesis, the estuarine systems and associated species that are found on the North Alaska coast possess general qualities that should lend them extreme resilience. That is, the systems are subject to climatic extremes and great fluctuations in environmental factors, most of the species in the systems are early successional types specifically adapted for mobility and exploitation of highly disturbed environments, and food (and perhaps habitat) resources of the key fish and birds are superabundant.

To try to determine more specifically whether these arctic estuarine systems will be relatively immune to man's activities, we will examine in the sections that follow whether the probable stresses to be imposed by man will be of the types and within the ranges of naturally-imposed stresses. Furthermore, we will attempt to identify the kinds of man-caused disturbances to which the key species of birds and fish, and their food webs and habitats, will be most vulnerable.

Consequences of Development--An Evaluation

In order to address efficiently the effects of man's activities on the key species and their life-support needs, those activities must be categorized by type according to how we suspect the ecosystem will respond. A set of activity categories expected to accompany development in the Beaufort Sea was constructed using information from Milne and Smiley (1976), Walker et al. (1977), Hopkins and Broad (1978), Hudson (1978), and Weller et al. (1978) (Table 1). The important interactions between the activities and the key species and support processes are noted. The discussions that follow evaluate the relative importance of each suspected interaction. The interactions are discussed according to the kinds of environmental alterations expected to result.

Table 1. **Development-related activities and the ecologically significant alterations they may cause in the nearshore Beaufort Sea.**

Alterations in Processes/Components

Activity	Alter longshore transport and water exchange	Alter transport and water exchange between nearshore and ocean	Modify water turbidities	Alter input of detritus/ nutrients from land	Alter temperature/salinity regimes	Block fish, invertebrate migration routes	Directly disturb birds	Kill or weaken fish, birds, invertebrates
Removing existing islands (part or all)		X	X		X		X	
Drilling, staging from existing islands							X	
Constructing and using causeways parallel to shore		X	X	X	X	X	X	
Constructing and using causeways perpendicular to shore	X		X		X	X	X	
Constructing and using artificial (gravel or ice) islands			X				X	
Subsea dredging to acquire fill, to bury pipes, and to create shipping lanes		X	X		X			
Intercepting terrigenous inputs to coastal waters		S	X	X	X	X		
Increasing air and boat traffic							X	
Releasing toxic materials								X
Increasing fish and bird harvests							X	X

The predictions below concern only the shallow nearshore waters along the coast of the Alaskan Beaufort Sea. Additional activities are likely to accompany development farther offshore, and additional activities such as icebreaking may occur in deeper waters in support of development in shallow waters. Additional species (e.g., various marine mammals) and processes are likely to be affected by development activities in offshore waters. These additional topics are not addressed here.

The assessments that follow are qualitative rather than quantitative. The intentions are to identify the types of species and processes that are likely to be most severely affected by various development activities, and to identify species and processes that probably are less susceptible than might, on first consideration, be suspected.

Alterations in Longshore Water Movement and Transport

As we have seen, the characteristically rapid longshore movement of coastal waters and the associated transport of entrained materials in the nearshore Beaufort Sea promotes (1) the rapid replenishment of zones naturally or otherwise depleted of food web materials (nutrients, detritus, epibenthos, ect.) and (2) rapid dispersal and mixing of waters and associated materials. The coastwise water exchange that occurs during the open-water season tends to obliterate local anomalies in physical conditions and primary and secondary production (including those caused by man's activities) and to provide somewhat similar food supplies and water quality at all points along the coast.

Only one facet of development is thought likely to cause potentially significant interruptions to longshore water exchange--construction of solid-fill causeways from the coastline seaward. Indeed, measurements at the one existing causeway (the ARCO causeway near Prudhoe Bay) show that it is a major interruption to the normal longshore flow of water (Mungall 1978). No adverse consequences of this causeway to fish and birds have been documented; however, this is not unexpected considering the natural resilience of the coastal ecosystem and the difficulty in validating impacts because of the inherent spatial and temporal variability in the factors that have been measured. The consequences of a number of such causeways might be more evident, and causeways extending seaward to barrier islands would have major effects on transport processes within lagoons.

Emergent features projecting long distances seaward do not exist in nature on the Beaufort Sea coast, presumably because the existing hydraulic pressures would tend to breach and realign features that oppose the normal longshore movement of water (Riggs 1976). Consequently there is reason to suspect that a series of such causeways that would greatly alter longshore water movements and transport, plus obstruct migration of fish, might adversely affect fish and birds, probably via alterations in the accessibility, productivity, and/or distribution of food web constituents. Transport of waterborne materials and invertebrates is, according to our results, essential to the maintenance of an adequate food supply in Simpson Lagoon. If a lagoon were partially or totally impounded by causeways, important effects on food availability are anticipated.

Causeways in some coastal areas have been found to adversely affect biota by altering circulation and/or by blocking migration routes. In Aransas Bay on the Texas coast, access causeways to oil well pads have apparently restricted water circulation to the detriment of fish and/or shellfish (USDI Fish and Wildlife Service 1970a). Diener (1979) states that estuarine production is generally lowered wherever dikes and levees cause diminished access by migrants to broad estuarine areas. Some scientists feel that causeways, levees, and jetties can be constructed to avoid damaging effects on estuarine circulation and longshore currents (USDI Fish and Wildlife Service 1970b). For example, solid-fill hurricane barriers constructed in Narragansett Bay, Rhode Island, had small openings (sills) that allowed for normal fish migrations that would otherwise have been disrupted (Saila 1965).

Alterations in Water Exchange between Nearshore and Ocean

Exchange of water between the ocean and the bays and estuaries is much slower than that between adjacent nearshore areas, but its characteristics are vitally important for several reasons.

1. The ocean is a reservoir from which the important nutrient phosphorus, as well as ocean-produced detritus, are supplied to the nearshore environment.
2. Current-assisted migrations of mysids between winter refugia in the ocean and estuarine areas, where these food organisms grow in summer, are vital. The key vertebrates concentrate in the coastal zone in summer and feed largely on these mysids. These vertebrates do not now concentrate outside the shallow and often protected nearshore waters, even though mysids are not restricted to these areas. Thus, it is doubtful that alternate habitats would be as suitable to the vertebrates if their food organisms were prevented from reaching the presently used habitat.
3. The nearshore environment apparently acts as a general sink for food web materials from both land and sea; the topographic structure and consequent estuarine-ocean water exchange patterns promote this tendency. Specifically, the exchange is dominated by net seaward flow in surface waters and net landward flow at the bottom. The latter is probably critical in delivering food web materials and organisms to the nearshore zone in summer; there is evidence that this process can operate at the mouths of even rather small rivers in the arctic (Thomson et al. 1975).

The barrier island chains and submerged bars parallel to shore probably enhance the effectiveness of the nearshore zone as a sink. The inlets or passes between islands and at the mouths of bays and estuaries help regulate the estuary/ocean water exchange and may accommodate the seasonal migrations of mysids. Development that would remove chains of barrier islands or submerged bars, or alternatively extend island chains by means of causeways across inlets, might adversely affect the rates of the exchanges. Likewise, alterations of the characteristics of the inlets (particularly those off river mouths where typical estuarine/ocean exchanges may promote the enrichment of nearshore areas) might decrease the potential productivity of the nearshore zone.

The wide range of configurations that exist naturally in the island chains that skirt the Beaufort Sea coast, and the rapid changes that occur naturally in inlet position and configuration, suggest that the coastal ecosystem should be able to withstand considerable topographic changes in features parallel to the coast with little noticeable effect on birds and fish. Certain general topographic features, however, remain fairly consistent in space and time and appear important to maintaining the productivity of the nearshore zone. Changes in these may have adverse consequences. As one example, most of the large rivers maintain ready access to the sea either via large, open bays (e.g., Colville River-Harrison Bay, Sagavanirktok River-Stefansson Sound) or via deep inlets between barrier islands (e.g., Kuparuk River-Egg Island Channel). Such an arrangement should enhance characteristic estuarine-marine water exchange that replenishes (via landward currents at the bottom) the nearshore zone with nutrients, detritus, and epibenthic invertebrates from the ocean. An example of potentially important consistency in topography is the relatively uniform flatness and shallowness of the bottoms of all nearshore waters (except at narrow inlets). This arrangement enhances the warming of these waters in summer and resists mixing between nearshore and ocean waters. Mixing may be enhanced where deep channels lead from the ocean into the shallows (Clark 1977: 40), or where causeways perpendicular to shore cause landward intrusions of oceanic water on the lee side of the causeway. Mungall (1978) provides evidence of the latter phenomenon.

Important changes have been caused in some coastal ecosystems because conservative topographic features were changed, with consequent changes in nearshore-offshore water exchange. Reid (1957) found that densities of estuarine populations of the dominant shrimp and fish species changed when a barrier skirting an estuary in the Gulf of Mexico was breached by man; the populations then reverted to near original conditions as the inlet was partially blocked. Drastic alterations in the surface:volume ratios of estuaries as a consequence of dredging and filling also alter exchange rates, with potentially adverse consequences to biota (see LaRoe 1979; Gonor 1979; Diener 1979).

Alterations in Water Turbidity

Turbidity levels are important in aquatic ecosystems for several reasons. Turbidity regulates light penetration, which controls photosynthetic activity and primary production rates (Grainger 1975; LaRoe 1977). High turbidities may also be associated with increased oxygen demands (see Gordon 1974) which may be critical in poorly aerated waters. Exceptionally high turbidities might clog the gills of aquatic organisms (Hopkins and Broad 1978), reduce their feeding efficiency (Sherk et al. 1974), or otherwise impair their health. It has even been postulated (Clark 1977:428) that localized turbidities might act as barriers to migrating fish.

Turbidities would be locally increased in the nearshore Beaufort Sea by any actions that remove or deposit substrate material (silt, sand, etc.). Included would be dredging operations in coastal waters, building of earth-fill causeways and artificial islands, burying of structures to provide ice-scour protection, and propellor wash in shallow waters (Gordon 1974; Hopkins and Broad 1978). Decreased turbidities might be induced by any significant interception of stream flow during the early summer flood period. (Although damming of major streams has not been proposed to accompany development, such may be advocated if water needs [Jahns 1978] continue to be critical.)

Extremely variable and periodically high turbidities are a natural phenomenon in the shallow waters along the Beaufort Sea coast (Gordon 1974; Craig and Haldorson 1980), sometimes even under the ice in winter (Schell 1979). It is generally felt that turbidities caused by man's activities in the nearshore zone would not exceed those that normally occur because of storm waves, ice gouging, bottom scour by focused currents, and the direct influx of muddy stream water (Hopkins and Broad 1978). Implications are that the increased turbidities that almost certainly will accompany development are not likely to adversely affect fish and birds or their food webs.

The effects on biota of turbidity caused by dredging/filling in other coastal areas have been addressed sparingly. In coastal Louisiana the normal seasonal variations in turbidity, controlled largely by the Mississippi River discharge, were much greater than those caused by extensive petroleum development operations (Beckman 1976:114). Construction of sand and gravel artificial islands in the shallows of the Canadian Beaufort Sea caused turbidity levels less than those normally expected as a consequence of storms (Gordon 1974). Dredging in the Mackenzie estuary apparently produced only short-term (and not always negative) effects on plankton (Duval 1977). Some localized smothering of inbenthic animals occurred in the sediment plume, and there were additional sublethal effects (Olmstead 1977), but even in this arctic area infaunal recolonization may commence within one year (Bengeyfield 1976).

In spite of the paucity of extensive experimental data, it is our view that increased water turbidities caused by oil and gas development in the nearshore Beaufort Sea will be insignificant compared to those periodically caused by storms and other natural phenomena. Consequently, any measurable adverse effects on biota will probably be extremely local, and consequences to fish and birds will likely be nil.

Alterations in Inputs of Terrigenous Detritus and Nutrients

Large amounts of organic and inorganic materials from land are delivered to nearshore waters via shoreline erosion and stream discharge. As discussed earlier, the ecological importance of these inputs appears to be that they are the major source of nitrogen to the system and secondarily that they provide a small but perhaps significant source of energy to the food webs with which we are concerned (Schell 1978, 1979).

Development activities that might significantly reduce the average annual inputs of these terrigenous materials include (1) interception of stream discharges (which would be especially critical during early summer when streams carry most of their annual detrital loads), (2) stabilization of large portions of mainland shorelines or shorelines of tundra-covered islands so as to block the input of detritus, and (3) construction of causeways such that storm waves are prevented from exerting a normal erosional force against the islands or mainland. Whether either of the first two activities is likely to occur at significant levels is uncertain; indications from industry are that they are not (see Hudson 1978). Likewise the effects of causeways (which probably will be constructed) in reducing coastal erosion are largely speculative.

Terrigenous inputs to the nearshore environment vary considerably from year to year, primarily because extensive shoreline erosion, which contributes a large proportion of these inputs, is associated with irregularly-occurring storm events. Major storms that cause most of the coastal erosion may occur as much as several years apart. The decomposition of the terrigenous organic detritus is gradual, and the expected peaks and lows in available nitrogen are smoothed correspondingly. However, it is likely that most of the usable nitrogen received from land at any one time is made available within a year (Campbell 1980). It is probable, therefore, that nearshore ecosystems naturally tolerate considerable annual variability in nitrogen supply from the land, even though they may be dependent on the long-term regularity of this supply.

Notable also is the fact that the quantity of terrigenous materials delivered to the nearshore environment varies spatially. Large quantities are delivered to river delta areas and at rapidly-eroding headlands, whereas relatively small amounts reach the nearshore area from the margins of quiet bays and lagoons. However, because of the rapid longshore transport and intra-coastal water exchange rates, these local differences in supply may be largely obscured before they reach the invertebrate and vertebrate levels in the food web.

In most coastal systems, the bulk of land-derived nutrients and organic materials are discharged by large streams and not by coastal erosion. Some researchers (Riley 1937-38; Anderson 1974; Ho and Barrett 1975; Bagur 1977; Clark 1977:695) have found that the nutrients annually supplied by stream discharge are very important in maintaining estuarine productivity. However, Odum (1968) found that nutrients from other sources (e.g., marshes and the open ocean) may sometimes predominate in estuarine production, although the ultimate nutrient source might still have been streams. However, documentation that man-caused interceptions of these terrigenous nutrient inputs caused decreased production in coastal systems are almost non-existent, although such may be sometimes inferred.

As implied above, short-term and localized disruptions to terrigenous inputs of nitrogen and organic materials to the nearshore environment would probably be inconsequential to birds and fish and their food webs. Evidence supporting this is largely circumstantial, and based on the fact that the coastal ecosystem is already adapted to high variability in the spatial and temporal distribution of terrigenous inputs of these materials. In addition, terrigenous organic materials do not seem to be the main source of energy for the lagoon invertebrates that comprise the main foods of key vertebrates. Long-term or spatially extensive blockage of such inputs might, however, cause gradual decreases in the primary productivity in the nearshore zone, and therefore in the capacity of the nearshore waters to support birds and fish.

Alterations in Temperature-Salinity Regimes

Temperature and salinity strongly affect the functioning and distributions of poikilothermic organisms inhabiting coastal ecosystems, despite the fact that many of these organisms can tolerate wide ranges in these water quality parameters. Salinity appears to regulate the general distribution of organisms, but within normal ranges it appears to have little effect on their metabolic and life-history functions (Kinne 1960; Wood 1967). Temperature, on the other hand, appears to control such critical life functions as migration, breeding, and growth (Carriker 1967; Kinne 1963; Dunbar 1968:9). Increased temperatures are known to stimulate important shoreward migrations of coastal invertebrates in early summer (see Clark 1977:19), cause increases in growth rates of coastal invertebrates, and trigger other critical life-history functions (breeding, etc.). Moreover, the high summer temperatures of shallow estuaries appear to enhance the overall productivity of coastal ecosystems.

It is during the open-water season when temperatures and salinities in the Beaufort Sea appear to be most vulnerable to ecologically important changes. Since temperature and salinity regimes depend mainly on water circulation and exchange patterns, development-caused changes in circulation may result in general temperature and/or salinity changes in the nearshore environment. The potential effects of development on circulation and exchange have already been discussed (e.g., construction of causeways, dredging, etc.). However, quantitative relationships between changes in circulation and exchange on the one hand, and changes in temperatures and salinities in the nearshore Beaufort Sea on the other, are difficult to develop because of the many unquantified variables. There are some qualitative relationships, however, that should be noted:

1. In summer the waters flowing from the land are fresh and relatively warm, and the waters from the ocean are cold and saline. Changes in the amounts of water coming from either of these sources would presumably cause changes in the normal temperature and salinity regimes of coastal waters.
2. Because the shallow nearshore waters are usually well-mixed in summer, the waters at the bottom (where most of the important secondary production takes place) are not as cold and saline as they might be should the water be deepened significantly by development.

As we have noted several times, there naturally exists considerable spatial and temporal variability in temperature and salinity in the nearshore environment in summer. In fact, it is not conceivable that development would cause the ranges of temperatures or salinities normally encountered to increase appreciably over a significant area. It is more likely that development might affect the average temperature-salinity regimes and thereby affect the biota. One way to evaluate whether the biological systems would be able to accommodate to the changes in average conditions would be to determine whether there naturally exists such variability among years. Too few data are available to determine this; however, indirect evidence (e.g., annual variation in the extent of ice cover, etc.) indicates that there may be considerable annual variability in at least the temperature of the water. And, as we have noted, small-scale variations in salinity regimes would probably not significantly affect critical life functions of the organisms that live in the nearshore environment. However, responses to temperature and salinity may interact (Busdosh and Atlas 1975; Percy 1975), so development activities that would affect both parameters warrant special attention.

Few data are available from other studies describing the responses of estuarine biota to changes in salinity or to general decreases in temperatures, but much has been done on the effects of temperature increases. In high latitudes many species live at temperatures far below their upper limits of tolerance and readily survive, indeed frequently do better at, unnaturally high temperatures (Gray 1974). Thermal increases are frequently "beneficial" in the sense that they raise the productivity of a system by increasing biochemical reaction rates and metabolic rates (Mihursky 1967). Conversely it would be expected that significant temperature decreases might reduce the general productivity of a system. No specific data are available, but widespread decreases in temperatures in the shallow water along the mainland shore might significantly reduce the ability of anadromous fish to accumulate energy reserves. Accumulation of these reserves appears to be the main reason for anadromy.

In summary, because of the existing wide variability in normal temperatures and salinities to be encountered in the nearshore Beaufort Sea, the estuarine biota should probably be able to accommodate to considerable levels of man-induced changes in temperature and salinity. The only kinds of changes likely to significantly alter productivity or ecosystem structure would be those that exceed the normally expected levels through extended periods of time and over broad areas during the open-water season.

Blockage of Fish and Invertebrate Migration Routes

Craig and Haldorson (1980) and Griffiths and Dillinger (1980) note that seasonal migrations of anadromous fishes and of epibenthic invertebrates (mysids), respectively, in the coastal waters of the Beaufort Sea are presumably important to the well-being of these animals. The fish move along the coast in summer to feed, and return to freshwater streams in winter; mysids move into coastal shallows from the ocean in early summer, feed and grow throughout the summer, and move to deeper ocean water in the fall.

Solid-fill structures that would significantly block the longshore or up- and downstream movements of fish, or the sea-lagoon-sea movements of mysids, are likely to be harmful. These structures might include dams on streams, causeways extending perpendicular to shores, or causeways blocking major lagoon-sea passageways. However, both fish and mysids may have options to blocked routes of movement, so it is difficult to evaluate the consequences of 'incomplete' barriers. Fish swim around the end of the existing ARCO causeway (Doxey 1977), and there are many potential access routes between ocean and nearshore that mysids might utilize should some routes be blocked.

It is instructive to examine whether natural barriers exist that resemble those that man might construct, and, if they do, to evaluate how fish and invertebrates accommodate to them. Natural barriers to fish movements do not appear to be common. The prevailing circulation patterns maintain open routes parallel to the coast, and in fresh water streams, there appear to be no important barriers to normal fish movements. It is likewise probable that few barriers to important movements of the mysid populations exist. Mysid migrations (both coastwise and between lagoon and sea) probably depend greatly on currents (Griffiths and Dillinger 1980), and natural barriers are breached by hydraulic pressures to accommodate the prevailing water exchange patterns (Emery and Stevenson 1957). However, some of the apparent consequences to fish and invertebrates of natural barriers in "unexpected" locations are interesting. Nunaluk Lagoon, an estuary on the Canadian Beaufort Sea coast, is closed off, except at the east end, by a continuous sand/gravel spit several kilometers long. This spit prevents coastwise passage of water between the spit and the mainland and prevents ready exchange of water between the ocean and the lagoon. Anadromous fish appear to enter and utilize the lagoon readily, but there are some indications that they consume little food therein; the invertebrate fauna is depauperate and very different from that in lagoons that are more open to the ocean (P. Craig and W. Griffiths, pers. comm.). This lends support to the view that blocking of migration routes might have adverse effects, either directly or through alteration of water mass characteristics. However, the necessity and extent of migrations are not clear enough to permit a quantitative estimate of the consequences of such blockage.

Adverse effects of partially blocking routes of movements of both fish and invertebrates have been noted to occur in other coastal areas (Diener 1979), and are thought to be a frequent consequence of constructing levees and causeways in the estuarine environment. Breaching of barriers to allow flounders access to coastal areas was a successful mitigative measure to barrier construction in Narragansett Bay, Rhode

Island (Saila 1965). Likewise we believe that in the Beaufort Sea it may be possible to construct solid-fill causeways that fulfill the needs of industry and that also allow for passage of migrating fish and invertebrates. Suggested methods are to create gaps in causeways at the critical points where passage would allow the animals to most nearly retain their normal migration patterns. For example, gaps located near the shoreline might be most beneficial for passage of fish (see Craig and Haldorson 1980). Locations of the critical migration pathways of mysids (and therefore of the places that should be left open) are not known with certainty, but are probably the passages through which the largest volumes of water move.

Direct Disturbance to Birds

Disturbance to birds in areas where they nest or feed could result in nest failure, failure to acquire sufficient food, or depletion of energy reserves. Primary interest in this respect on the Alaskan Arctic coast are large populations of birds that feed in the nearshore zone (e.g., oldsquaw ducks, red and northern phalaropes, and a few other species) and birds that nest primarily or exclusively on islands (e.g., brant, common eider).

The primary predicted forms of direct disturbance on both feeding and nesting birds are noises and movements of men and machines. These kinds of activities will accompany construction of service facilities, seismic activities, drilling and operation of wells, and the movements of air, ground and water traffic. Although man has been a part of the Beaufort coastal environment for centuries, the activities projected to accompany future petroleum development have only very recently been approached in kind and magnitude. The implications are that the coastal environments in which the birds evolved probably did little to prepare them to accommodate to the forthcoming man-related activities.

The behavioral responses of birds to man's activities can differ among species, among populations of the same species that have had different histories of exposure to man, and among seasons or circumstances. For example, common eiders did not flush from their nests when overflown at altitudes as low as 40 m (Gollop et al. 1974), but most migrating common and king eiders flush far ahead of survey aircraft (Alliston et al. 1976). Consequently, data from other times and places must be applied with caution. Fortunately, there are existing data from the Beaufort coastal area to assist in the interpretation of data from elsewhere; a few points should be mentioned:

1. Several studies have found human disturbance to reduce nesting success or chick survival of birds: e.g., Canada geese, MacInnes and Misra (1972); loons, Davis (1972) and Booth (1978); common eider, Cooch (1965); various gulls, Hunt (1972), Gillett et al. (1975), Robert and Ralph (1975). Of the two principal island nesters in the Beaufort coastal area--the common eider and brant--the common eider is by far the most sensitive to man-caused disturbance. The brant is more bold and aggressive in the presence of man and less prone to abandon its nest (S.R. Johnson, pers. comm). Both of these species are more likely to abandon their nests during the early parts of the nesting period than they are later, although development activities near their nests may potentially have adverse effects any time the birds are nesting.

2. The only known colony of snow geese on the Alaskan north coast is a small colony at Howe Island in the Prudhoe Bay area. Pre-nesting and nesting snow geese in the Canadian Beaufort Sea area sometimes leave their nest sites temporarily when overflown at low or moderate altitudes (up to 300 m AFL) (Bany and Spencer 1971; Gollop et al. 1974). Brood-rearing, fall staging and migrating snow geese often react to aircraft as much as several kilometers away (e.g., Davis and Wiseley 1974; Alliston et al. 1976). Consequences of these types of disturbance are uncertain, but disturbance of the nesting colony could be minimized by restrictions on aircraft routes and altitudes.

3. All birds that commonly feed and/or molt in the nearshore zone in large numbers (oldsquaw, phalaropes, glaucous gulls, etc.) are relatively insensitive to most kinds of predicted activities of men and machines. Frequent aircraft overflights may have the most potential for disturbing these birds, and oldsquaws are the most sensitive. However, even the oldsquaws exhibit no noticable response unless aircraft passes are very low and frequent (S.R. Johnson, pers. comm.; Ward and Sharp 1974). Smaller birds (phalaropes, other shore birds, longspurs, etc.) are normally insensitive to activities that occur more than several meters distant.

In terms of potential adverse impacts caused by disturbance, then, common eiders (and secondarily brant) nesting on islands are the most vulnerable of the species common in the Simpson Lagoon area. (Snow geese on Howe Island would also be relatively sensitive.) Oldsquaws are the next most vulnerable but are relatively resistant to all disturbance except close and frequent airplane overflights. It would be very difficult to cause significant levels of disturbance in populations of smaller birds, although individuals could be affected in local areas.

Mortality and Morbidity of Birds, Fish, and Food Chain Constituents

Birds, fish, and organisms in their food chains that become debilitated or die directly or indirectly because of disturbances associated with development will be the most dramatic examples of OCS-related impact. Two major potential causes of morbidity or death are related to development. These are exposure to contaminants released accidentally (oil) or chronically (drilling mud, oil, etc.), and increased harvests of birds and fish by humans.

Exposure to Contaminants. Two classes of contaminants normally associated with petroleum development in continental shelf waters have been of most concern in the Beaufort Sea. These are drilling muds and oil.

The toxic and smothering effects of drilling muds and formation cuttings and their constituents have been studied and reviewed extensively. General reviews include Falk and Lawrence (1973), Ray and Shinn (1975), Beckman (1976) and Monaghan et al. (1976). Studies and reviews dealing specifically with arctic organisms and/or drilling operations include Bryant and Hrudey (1976), B.C. Research (1976), Hrudey and McMullen (1976), Moore et al. (1976), Hrudey (1979) and Newbury (1979). Our interpretation of these and other studies is that the effects of drilling muds and cuttings are mostly localized and insignificant in most areas, as noted by Beckman (1976:12). In our judgement this would also be true in the Beaufort Sea, although it would be prudent not to discharge these materials into shallow nearshore areas, such as lagoons, where water volume and (in winter) circulation are limited.

There is a wide array of potential scenarios of oil introductions into the coastal environment. Potential levels of release range from low-volume chronic releases of crude or refined oil, to sudden and massive spills such as might be associated with a well blowout or the rupture of a subsea pipeline. Also, each kind of crude oil is different in the makeup of its toxic or otherwise harmful constituents. Since it is not possible to predict the times of occurrence or the magnitudes of spills, or the toxic nature of the oils that might be spilled, we will deal with the issue of oil contamination in a broad and general sense. And, as we will point out, there are physical and biological qualities of the nearshore ecosystem that may suggest, even more than will attempts to predict the nature of oil spills, how the ecosystem will respond.

The first thing to note is that the Beaufort Sea nearshore environment has several qualities that should make the food chains that are important to birds and fish resilient to oil-induced perturbations. Here, as in most coastal waters, there are oil-degrading bacteria (Bunch and Harland 1976; Atlas 1977; Atlas et al. 1978) that are normally the major agents for removal of oil from environments (McAuliffe 1977a). And despite the fact that oil dispersal and degradation in cold environments is normally slower than in more temperate areas (Beckman 1976:119; McAuliffe 1977b; Michael 1977), it is felt that general recovery of the ecosystems affected would probably require less than a decade at the maximum (Milne and Smiley 1976:43). The food chain components of major concern (i.e., those supporting birds and fish) in the Beaufort nearshore environment are water-column or epibenthic rather than inbenthic. Hence the toxic effects of oil spills to them would tend to be short-lived, because the long-lasting fractions usually persist only in sediments (Cox 1977:1; Ray 1978). Nonetheless, low-level effects are expected to persist, at least intermittently, for long periods after a major spill. Storms and ice action rework the sediments in shallow near shore waters, and thereby would occasionally release oil trapped in the sediments (Sanders 1977). Both the fish and birds and their food chain components are highly mobile, implying that oiled areas could be rapidly repopulated to speed recovery. Furthermore, fish and birds not directly contaminated by oil might be able to avoid depleted food supplies by moving into uncontaminated areas.

A detailed review of effects of oil on arctic food chains is beyond the scope of this report; the following is a summary of our understanding of the relative effects on various food-chain constituents:

1. Phytoplankton shows various short-term changes in the presence of oil, but the medium and long-term effects seem negligible (Adams 1975; Prouse et al. 1976; Hsiao et al. 1978).
2. Beds of marine macrophytes, which are an uncommon feature of nearshore waters in the Beaufort, might be severely affected by a major oil spill (North et al. 1965; Hsiao et al. 1978).
3. Epontic communities in the immediate vicinity of a major oil spill will be smothered or otherwise affected by oil accumulating under the ice.
4. Zooplankton can be killed by oil in the water column, but the concentrations necessary to cause lethal effects, at least in the short-term, are high (Percy and Mullin 1975; Foy 1979).
5. The larvae of fish and invertebrates are often more sensitive to oil than is zooplankton, and might be severely affected by the concentrations of oil that can occur in the water-column beneath an oil slick. However, nearshore areas of the Alaskan Beaufort Sea are not major rearing areas for fish larvae.
6. Short and medium term effects of a major oil spill on benthic invertebrates in nearshore areas can be severe, especially in areas with soft substrates in which the oil can become incorporated (e.g., Boesch et al. 1974; Hyland and Schneider 1976; Sanders 1977). Recolonization may sometimes be rapid even in the arctic, but the species composition after recolonization may differ from that before contamination (Atlas et al. 1978). Isopods and polychaetes would likely become more prevalent, and amphipods and bivalves would become less prevalent. Effects of oil on arctic mysids are unknown, but Anderson et al. (1974) found temperate mysids to be the most susceptible of the crustaceans tested.

The ecosystem-level effects of the above types of perturbations are uncertain. It appears doubtful that planktonic production would be severely affected by even a major oil spill. An under-ice spill would locally eliminate or (over a larger area) reduce epontic production for a one-season period. Benthic communities in nearshore areas would probably be the most severely affected, but the effects on mobile epibenthic animals (the most important to vertebrates) are poorly known.

Other than potentially depleting food-chain materials, oil might directly kill or debilitate fish or birds. Behavioral and physiological responses of fish to petroleum are poorly understood, because of variability in response within and among fish species and variability in toxicity among oils (Patten 1977). Available evidence from oil-contaminated continental shelf areas in various parts of the world strongly indicates that oil pollution has not significantly affected fish populations directly (Beckman 1976:1; Sanborn 1977), although such evidence remains somewhat speculative because of inherent difficulties in quantitative evaluations of impacts (Hay 1977). Although fish populations may not be significantly affected by oil contamination, individual fish can be killed or affected deleteriously (Patten 1977). Salmonids are apparently especially sensitive on arrival in the ocean from fresh water, possibly because of the additional stress of adapting to higher salinity (Rice et al. 1978). Furthermore, the flesh of fish can become tainted by oil, and this can render it unpalatable (Mackie et al. 1972; Connel 1974) and of no commercial value.

In contrast to fish, seabirds have been found to be very susceptible to oil spills (Beckman 1976:114; Bourne 1976; Milne and Smiley 1976:43; Hay 1977; Clark 1978; and others) in that they frequently do not avoid oil on the water's surface (e.g., Bourne 1968). Their feathers become coated with oil and as a consequence many perish as a result of physical and thermal effects (Clark 1978). In recent years there have been many studies of systemic and pathological effects of ingestion of oil, and of its effects on reproduction. While such effects do occur, it can be argued that direct mortality after external coating by oil is by far the most important effect (Bourne 1979). External oiling impairs insulation and feeding capability. Thus, the lethal effects of external coating are likely to be especially rapid in the arctic, where the insulating effect of plumage and the ability to feed and replenish energy reserves are especially important.

All birds that habitually use the nearshore waters would be vulnerable to oil spills that contaminate those areas. Particularly susceptible would be oldsquaws in the summer molt period, during which time they are flightless and abundant in lagoon waters. Oil in open leads in sea ice or along shores in early spring would also pose extreme hazards to early-arriving migrants of several kinds (Barry 1970; Milne and Smiley 1976:42-43), as would oil on coastal waters or wetlands in fall (mid-August to October), when many migrants land in nearshore areas on their way to wintering areas.

In summary, the most serious contamination threat posed by development would be the direct effects of large oil spills on seabirds such as oldsquaws. The direct effects of oil on fish and on food chains of fish and birds are expected to be less consequential to fish and birds.

Increased Bird and Fish Harvests. An inevitable consequence of any kind of resource development that promotes increased access to remote areas is the associated opportunities presented to man (both native and immigrant) to harvest fish and wildlife. These increased opportunities almost certainly result in increased harvests, sometimes despite legal constraints. We will discuss the issue of increased fish and wildlife harvests in very general terms, since levels of impact will depend very specifically on the extent and effectiveness of harvest and travel regulations, which are not precisely predictable. Moreover, these kinds of impacts cannot always be controlled by industry or regulatory authority.

Birds and fish in the nearshore zone of the Beaufort Sea are particularly susceptible to harvest by man because they concentrate predictably in time and space. Furthermore, modern harvest methods present a hazard to which fish and birds are not "pre-adapted" and therefore to which they may not have innate resistance. Although localized harvests, especially of fish, have occurred for years, the observed impacts have been low.

For several reasons, we do not think that overharvest of key bird species in the nearshore system will pose a problem. First, only one species (oldsquaw) is potentially attractive as a game species, and even the oldsquaw is not a preferred species by native hunters (who prefer king and common eiders) (Bailey 1948:171-173; Johnson et al. 1975:64). Second, it should be relatively easy to monitor both the population levels and the non-native harvests of oldsquaws so that, were hunting of oldsquaws to become an adverse impact, steps could be taken to control it.

Overharvest of fish is likely to be a more severe problem, however. First, evidence from elsewhere suggests that commercial fishing has the potential to adversely affect anadromous and estuarine fish populations. In temperate zone estuaries, overfishing has had more adverse impacts on finfishes than has any other of man's activities (Beckman 1976:154; McHugh 1976). Moreover, arctic fishes are more susceptible to fishing pressures than are fishes in temperate zones, because their population recruitment rates are relatively low. Second, because fishing for anadromous fish with commercial gear is part of the traditional life style of people who live along the coast, increased access to fishing sites such as might be promoted directly or indirectly by petroleum development is likely to be accompanied by increased "commercial-type" fishing pressures. Moreover, regulation may not be able to constrain these harvest efforts.

Conclusions

Given the probable resilience of the Beaufort Sea coastal ecosystem to disturbance in general, and the expected responses of fish, birds and their major food chain constituents to the probable kinds of development, we predict that:

1. The types of man-made structures most likely to cause adverse ecological effects are solid-fill causeways that are perpendicular to shore, or that block critical passageways of exchange (e.g., inlet channels, bays off river mouths, etc.) between the shallow nearshore waters and the ocean. The critical food web and habitat factors likely to be affected by such development actions are changes in the rate of nutrient and detritus supply to and entrapment in the nearshore environment, alterations in the normal migration patterns of epibenthic invertebrates and fish, and alterations in temperature and salinity regimes in the nearshore area.

Effects of development on food supply and habitat availability would probably have to be fairly extensive before the effects on fish and birds could be detected. Fish and bird numbers appear naturally to be considerably lower than could be supported by the existing food and habitat resources available. Although proof is lacking, this suggests that they probably could tolerate significant decreases in the general quality or quantity of food and habitats. Likewise, locally extreme alterations in food and habitat quality in the nearshore zone would probably have little effect on fish and bird populations, because most species of fish and birds appear to be highly mobile and capable of exerting options in choices of habitats.

2. Development-caused increases in water turbidity (promoted by drilling operations, island and causeway construction, boat traffic, etc.) and alterations in inputs of terrigenous detritus and nutrients (caused by shoreline stabilization and/or damming of streams) will likely be insignificant in comparison with normal annual and seasonal variations in the same factors. The measurable consequences of the changes to fish and birds are therefore expected to be nil.

3. Direct disturbances to birds caused by activities and noises of men and machines are expected to be inconsequential except where common eiders, snow geese and brant nest on islands. Along the Alaskan Beaufort coast, nest sites of these species are restricted to islands, and they (particularly the common eider) are easily disturbed when they are nesting. Other species are not very site-specific in their need for nearshore habitats; neither are they very sensitive to the expected kinds of activities.

4. Significant direct mortality and/or morbidity of birds and fish may stem from oil spills or from increased harvests by humans. Should massive oil spills reach coastal bays and lagoons during the times when oldsquaws and other seabirds are abundant there (mid-summer to early fall), very large numbers of birds would probably be killed. Fish, by contrast, may be able to avoid oil in the water and are probably relatively immune to the direct effects of oil spills. Conversely increased access by human hunters and fishermen would be likely to affect populations of anadromous fish adversely, but not to have serious effects on birds.

   Food chains subjected to contaminants are not likely to suffer direct mortality in such a manner that fish and birds would be greatly affected, because of the extreme mobility of the fish and birds and the probability that any contaminated areas would be quickly replenished by food chain materials. However, lack of information about medium and long-term effects of oil on arctic epibenthic invertebrates (especially mysids) makes this conclusion speculative.

5. It is our general view that the effects of development (as it is currently conceived) are more likely to be felt directly by fish and birds (via excessive harvests or via oil spills and disturbance at nesting sites, respectively) than to manifest themselves through changes in food chains and habitats. Except for the case of certain island-nesting birds, both food web materials and habitats appear to be superabundant relative to the needs of fish and birds, and large changes in food webs might be sustained without consequence. Furthermore, the food webs themselves are likely to be resilient to adverse alteration by development.

SECTION 3. AN IMPACT MONITORING STRATEGY

Society at large and a number of environmental groups and native corporations are concerned about the potential environmental consequences of petroleum development activities in the Alaskan Beaufort Sea. These concerns generally relate to birds, fish, and mammals that live for part or all of the year in the Beaufort Sea coastal waters. The research findings of the Beaufort Sea Barrier Island-Lagoon Studies imply how investigations might be designed to study how these animals respond to petroleum development. In this section we will propose and discuss a strategy for monitoring that is based on the concepts and findings of these studies, to help answer the question:

> What does this study tell us about how future ecological studies and monitoring programs should be structured to best test for the predicted ecological impacts as petroleum development proceeds in north coastal Alaska?

The Important Issues

Because environmental monitoring studies are expensive and time-consuming, they should be focused on the most important issues. Historically, monitoring studies have attempted to address a broad range of changes thought likely to occur because of development. This approach is impractical because of the large array of ecosystem attributes potentially altered: the issues are too many to address given normal time and money constraints. The need exists, therefore, to focus environmental assessment and monitoring studies on selected priority topics. In our view, such studies should address ecosystem attributes that are (1) of direct or indirect concern to society, (2) deemed likely to be affected by development, and (3) deemed measurable with the precision necessary to validly assess change.

Objectives

We propose that a program to monitor the ecological consequences of development in the Alaskan Beaufort Sea have five major objectives.

These are as follows. (Note that major portions of Objectives 1-3 already have been accomplished by the Barrier Island-Lagoon Studies.):

1. Identify the socially and politically important biological attributes of the nearshore ecosystem. (For purposes of this monitoring proposal, and similarly to what was done in the Barrier Island-Lagoon Studies, we will assume that selected species populations are the important attributes. However, the monitoring approach to be discussed can readily accommodate other kinds of attributes.)
2. Identify measurable indicators of the immediate health or well-being of these attributes (species populations).
3. Identify measurable indicators of the quality of the food webs and habitats of these populations.
4. Develop a strategy for, and conduct, repeated measurements of selected indicators of the health of the key species populations and the quality of their food webs and habitats, such that development-caused changes in these indicators can be detected and discriminated from changes caused by naturally-occurring phenomena.
5. In cases where development-caused changes in structural attributes would be difficult to detect and/or discriminate from normal change, investigate interactions between organisms and their environment such that man's impacts on organisms via the altering of these interactions can be predicted or documented.

Strategy

We think that a monitoring program should have two phases. Phase I would be a planning session to define, and to some extent test, a practical program of annually repeatable measurements and research concerning specified functional relationships. Phase II would be the actual field measurements and their analysis.

Phase I

Phase I would commence with a workshop conducted similarly to those of the Barrier Island-Lagoon Studies (see Truett et al. 1980). The purposes of the workshop are to (1) identify species considered to be important for monitoring purposes, (2) construct a conceptual model of factors (food webs, habitats, and physical processes) supporting these selected species, (3) determine how these species or support factors are likely to be affected by development, and (4) determine how the responses to development of the selected species and their support factors can be measured. Workshop participants would include representatives from industry and various resource user groups (e.g., native groups, regulatory agencies and conservation organizations) as well as appropriately qualified biologists, physical process scientists (oceanographers, etc.), and systems modelers. The product of the workshop would be a detailed research plan for testing the responses of the important species and their support mechanisms to development activities. Following the workshop, a work schedule and budget would be drafted based on decisions made during the course of the workshop.

Some of the system attributes likely to be appropriate for monitoring have not previously been measured in the ways or with the precision that would be necessary. Field trials of proposed measurement procedures would be needed to confirm their effectiveness, or perhaps to refine the procedures. It is important that this be done before the operational monitoring program (Phase II) begins, since data must be collected in a standardized way from the outset of Phase II. In cases where it is obvious that trials to develop or verify measurement procedures are needed, the trials might be done before the workshop proposed above. The need for trials of other measurement procedures may not become apparent until the workshop. Thus, the workshop should be held well in advance of the time when operational monitoring must begin.

Phase II

Phase II would be the performance of the monitoring plan that is developed in Phase I. Annual workshop sessions should be held to reevaluate the success and continued relevance of the monitoring efforts.

A Monitoring Plan

We have shown how environmental monitoring should be focused on the basis of society's interests and how it should be designed to measure factors supporting the attributes (species) of such interest. These factors must be susceptible to impact and capable of being measured if they are to be useful in a monitoring program. Furthermore, unless normally expected changes in these factors can be segregated from development-caused changes, the monitoring program cannot succeed. Following is a discussion of the important concepts and the design of a monitoring plan.

Test and Control Sites

Regardless of which ecosystem attributes are to be measured, simultaneous measurements at test (developed) and control (undeveloped) sites are imperative. Only by using data from test and control situations can development-caused change be readily separated from normal seasonal or annual fluctuation. Test site(s) should be established in nearshore area(s) that is (are) to be subject to exploration and/or development activity. Control site(s) should be established in a similar coastal area that is upstream (east) of and similar in geomorphic and oceanographic characteristics to the selected test site(s). Different pairs of test and control sites are likely to be necessary in order to monitor different ecosystem attributes, although at some pairs of sites it is likely to be feasible to monitor more than one attribute.

Measurement Types and Constraints

Monitoring programs normally entail periodically repeated measures of ecosystem structure. However, findings of this program and concensus among some ecologists (Reichle 1975; Kerr and Neal 1976) indicate that functional (process-type, or interactive) rather than structural attributes in ecosystems are the most logical factors to monitor. Important system functions control populations and are normally more uniform in space and time than are structural properties. Additionally, predictable types of interactions may occur between particular kinds of ecosystems and particular kinds of perturbations (Odum and Cooley 1976), so that monitoring of important functions (interactions) may provide information that is easier to interpret on the basis of "impact" information from elsewhere.

Several difficulties with establishing an effective program of biological measurements that is valid for quantifying the nature and rates of these processes in the nearshore Beaufort Sea should be noted.

1. There exists great seasonal, annual, and spatial variation in animal densities and movements, and perhaps to a lesser degree in animal growth, diet and habitat utilization. It is, therefore, extremely difficult to identify the causes of observed differences in these attributes between test and control areas.
2. Most of the important organisms and their food-chain components are highly mobile; they can and do move long distances relative to the sizes of discrete development areas. Effects of development would tend to be masked by immigration and emigration.

Pre-Development Control Data

Pre-development control data should be obtained from each of the future test and control sites. These data would help to determine whether there are any fundamental between-site differences in system attributes or processes independent of the development activity. Because of the great natural spatial and temporal variations in many structural attributes (e.g., densities of animals) of arctic systems, process attributes are the best candidates for this type of analysis. It is likely to be impractical to obtain more than 1 or 2 years of predisturbance control data. Spatial and temporal variability are likely to make it impossible to define adequately the relationships of structural attributes in the future test and control areas within a 1 or 2 year pre-development period. It is more likely that any differences in process attributes that exist between these areas can be documented in such a period.

Sampling Design

This section describes a monitoring program sampling design in terms of test area location, control area location, and examples of the types of measurements that should be made in each location.

Test Area(s). Test areas should be located where intensive exploration and development are deemed most likely to occur. The areas that have been leased to date are in very shallow waters, similar in many respects to areas studied in the Barrier Island-Lagoon Studies. As discussed in the preceding "Synthesis", we assume that coastal sites of similar depth and topography are ecologically similar among themselves in many important respects. (This is important in that the control area(s) to be selected should initially [prior to development] resemble the test area(s) in attributes that are to be measured.)

Control Area(s). The control area(s) for an attribute should, ideally, be located in a shallow nearshore area similar in water depth and geomorphology to the test area. It should be located upstream (east) of the test area at a distance sufficient to ensure effective isolation from the development activities anticipated to be responsible for anticipated impacts. Also it should be located as far as possible from any other ongoing development activities that resemble those associated with petroleum development. Of the prospective control areas that would satisfy these requirements, the one closest to the development area should be chosen. The most appropriate distance between test and control areas might vary widely among the attributes to be measured. It might be possible to measure several attributes in one test area, but a variety of different control areas at different distances might be necessary.

Measurements of Ecosystem Structure. Note that the measurements described herein must be replicated within both test and control areas to establish a basis for comparison. Note also that the measurements proposed will, with some exceptions, be measures of structure from which processes or function (e.g., process rates, relationships between physical processes and biota, etc.) may be inferred.

Several system processes are thought to be critical to the well-being of important fish and bird species in the nearshore waters of the Beaufort Sea (this report). Some of the processes that are thought to be important, how they are important, and recommended ways of making measurements to quantify each are discussed below.

Birds - Key bird species (e.g., oldsquaw, phalaropes) are highly mobile; therefore, populations of birds found at test and control sites at any one time may not necessarily have been there long, and as transients may not reflect the stresses imposed by their immediate surroundings. The only portions of populations of these key species that are sedentary in nearshore areas for any length of time are oldsquaws in molt during summer. Molting individuals remain localized for several weeks. We suggest that this segment of the bird populations would be the most likely candidate for meaningful monitoring.

A tentative scheme of data collection that would reflect the well-being of these molting oldsquaw is to measure:

1. their fatness (to indicate the state of health),
2. stage of molt (as an indication of how long they have been there),
3. stomach fullness (to indicate to what extent they have been able to acquire food), and
4. stomach content (to indicate whether their diet is significantly different between test and control areas).

Oldsquaws would have to be captured to measure (1) and (2), and sacrificed to measure (3) and (4). (Attribute (1) could be measured more precisely if the birds were sacrificed.) Differences found between test and control areas in these characteristics of oldsquaw populations should be viewed in light of information collected about their food base at the same test and control sites (see 'Invertebrates' below) to see whether the differences might be caused by differences in food availability.

Fish - Fish, like birds, are highly mobile. Individuals might move quickly into and out of test and control sites, thereby obscuring any measurable responses to localized environmental changes. For example, it is known that most of the anadromous species may travel up to 150 km or more along the coast during the course of a month or two (Craig and Haldorson 1980).

A few species, however, are relatively sedentary (e.g., fourhorn sculpin, and, to some extent, least cisco). We suggest establishing length/weight regressions (fitness indices) for populations of highly sedentary species in test and control areas. The fish would need to be captured near the end of their seasonal period of residence in the respective study areas, assuming that they do not remain there year-round. Preliminary analyses of covariance on length-weight regressions at different seasons suggest that, at least in some species, the relationship does change during the period of residence in the nearshore area (P. Craig, pers. comm.).

For mobile fish species, as with birds, we suggest that a measure of stomach fullness of individuals captured in test and control areas might indicate foraging success, which presumably can be used as an index of the species' well-being. The assumption here is that the items contained in the fish stomachs were obtained by the fish near where the fish were captured.

<u>Invertebrates</u> - As we have seen, the major foods of important fish and birds are epibenthic invertebrates (mysids and amphipods). There are two reasons for measuring populations of these. First, because we are proposing to use stomach contents of fish and birds, and perhaps observations of bird feeding behavior, as tests of their well-being in test vs. control areas, data about the availability of foods (invertebrates) are useful for interpretation of these data. Second, we propose to try to evaluate the intrinsic health of the invertebrates as a food base, without necessarily trying to establish a correlation between them and what their predators (fish, birds) are eating at the time.

A problem with this latter objective is that, although we know mysids and amphipods are mobile, we do not know <u>how</u> mobile. It is unknown whether they would commonly move, within a short period of time, into and out of a test or control area. If we assume that their movements are relatively slow, and that many would reside for much or all of an open-water season in an area that is being developed, then measurements of their growth rates and fecundities, for example, would be useful for assessing the effects of development. On the other hand, if they are as mobile as fish and birds, then such measurements might have little utility. In fact, if mysids and amphipods are highly mobile, it may be very difficult to directly acquire a measure of the well-being of populations of these invertebrates that would be useful for assessing the effects of development.

Despite these uncertainties that might make data interpretation difficult, we propose a sampling scheme that will enable investigators to estimate densities, age structure, and growth rates of mysids and amphipods in test and control areas. The sampling methods would resemble those used in this study (Griffiths and Dillinger 1980); the analytical methods would be geared to process many samples in a relatively short period, because the expected great variability among samples would require many replications for a reasonable level of precision. Although less common than mysids in fish and bird diets, amphipods may be more useful as monitors of local environmental change because they are believed to be more sedentary than mysids.

Measurements of Ecosystem Interactions. The above methods of attempting to assess impacts depend on measuring qualities of the animals or their populations that presumably reflect their health.

This section proposes a way of avoiding some of the uncertainties inherent in that approach. The strategy is to focus measurements where critical ecosystem interactions occur. It appears that many of the important interactions are between oceanographic processes (e.g., water movement) and organisms, and between predators and their prey. Examples are as follows:

1. Epibenthic invertebrates appear to respond to currents such that they are transported through inlets and passes to habitats that we presume are optimum for their growth and survival. For example, in early summer mysids move into shallow waters where they grow rapidly. Circumstantial evidence indicates that these shallow areas may be better habitats for mysid growth than are the adjacent deeper continental shelf waters. If we could make measurements at inlets or other locations to quantify the way in which mysids and currents interact to accomplish these critical migrations, we

would be in a better position to predict or assess the consequences of altering these currents (e.g., by inlet filling or bridging). The drift net technique (Griffiths and Dillinger 1980), with refinements and complementary physical measurements, would appear to be a useful approach.

2. Oldsquaw ducks dive for their food, and the required frequency and duration of diving efforts are presumably inversely correlated with the availability of food. Observations made during the course of this study indicate that oldsquaw diving activity can be quantified. We propose to monitor by observation the diving behavior (frequency, duration, etc.) of individual oldsquaws, and the lengths of feeding periods of flocks, as a reflection of how much effort is needed for oldsquaws to acquire food in test and control areas. Observations on marked birds would be preferable, but incidental observations suggest that useful data could also be derived from unmarked birds. Since the feeding observations mentioned above have not been attempted previously, the approach needs to be tested before being used in an operational monitoring system.
3. Solid seaward-extending causeways may be a significant barrier to migrating fish. It has been postulated that gaps (bridges) in these causeways would allow fish to pass directly through the causeway. In fact, it has been proposed that such a gap be opened in the existing ARCO causeway near Prudhoe Bay. We propose that a research effort to monitor fish passage through such a gap would provide useful information about the interactions of migrating fish and narrow passageways. The results would be especially useful if, for experimental purposes, the gap could be closed partly or completely by a gate arrangement.

Detailed research plans for measuring selected interactions--those mentioned above or others--would be developed during Phase I of the proposed two-phase monitoring project.

Summary

We believe that a monitoring program to assess the impacts of petroleum development should focus on selected important species and their food webs and habitats. The monitoring program would ideally be conducted in two phases, a planning phase and a research phase.

During the planning phase the animal species of primary concern would be identified, methods of measuring supportive functions critical to the well-being of these species would be planned in detail, and field trials of previously untried procedures would be performed. The final product of the planning phase would be a detailed work plan for field measurements and observations that would distinguish development-caused changes from normal changes in (1) the general health of the important species and (2) critical processes (interactions) between these species and the environment.

The research phase of the monitoring program would include field sampling and periodic review workshops. The field data to be collected should include (1) selected measurements that reflect the "health" of the organisms, and (2) measurements of critical organism/environment interactions that are deemed susceptible to change by development. The former type of measurement would include such things as stomach fullness and content, fatness, and growth rates; the latter would include mysid movement vs. currents, predator-prey interactions, etc. Periodic workshop sessions that evaluate findings and maintain an appropriate research direction should be an integral part of the research phase of the program.

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