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Outer Continental Shelf Environmental Assessment Program

Final Reports of Principal Investigators

Volume 30

April 1985



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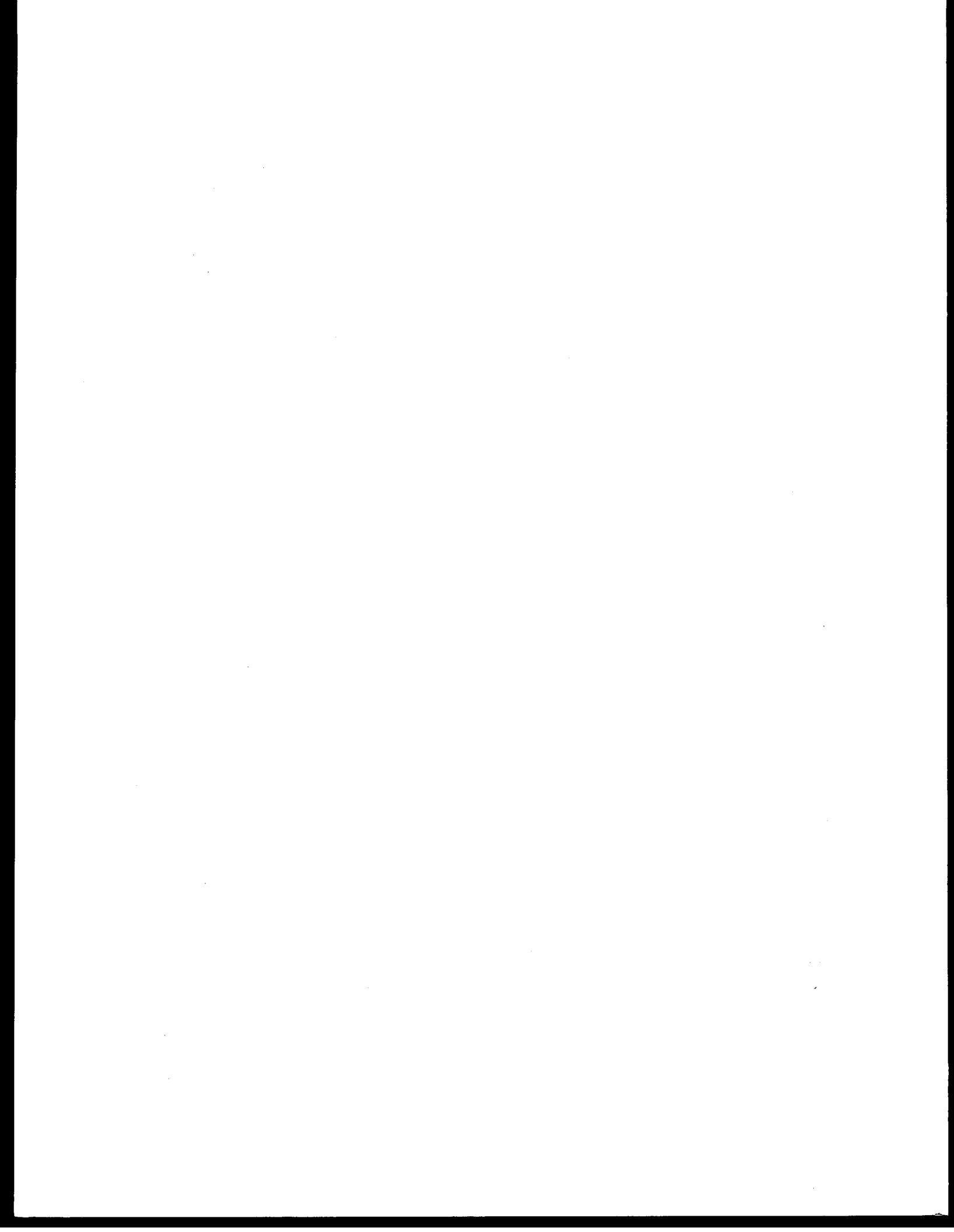
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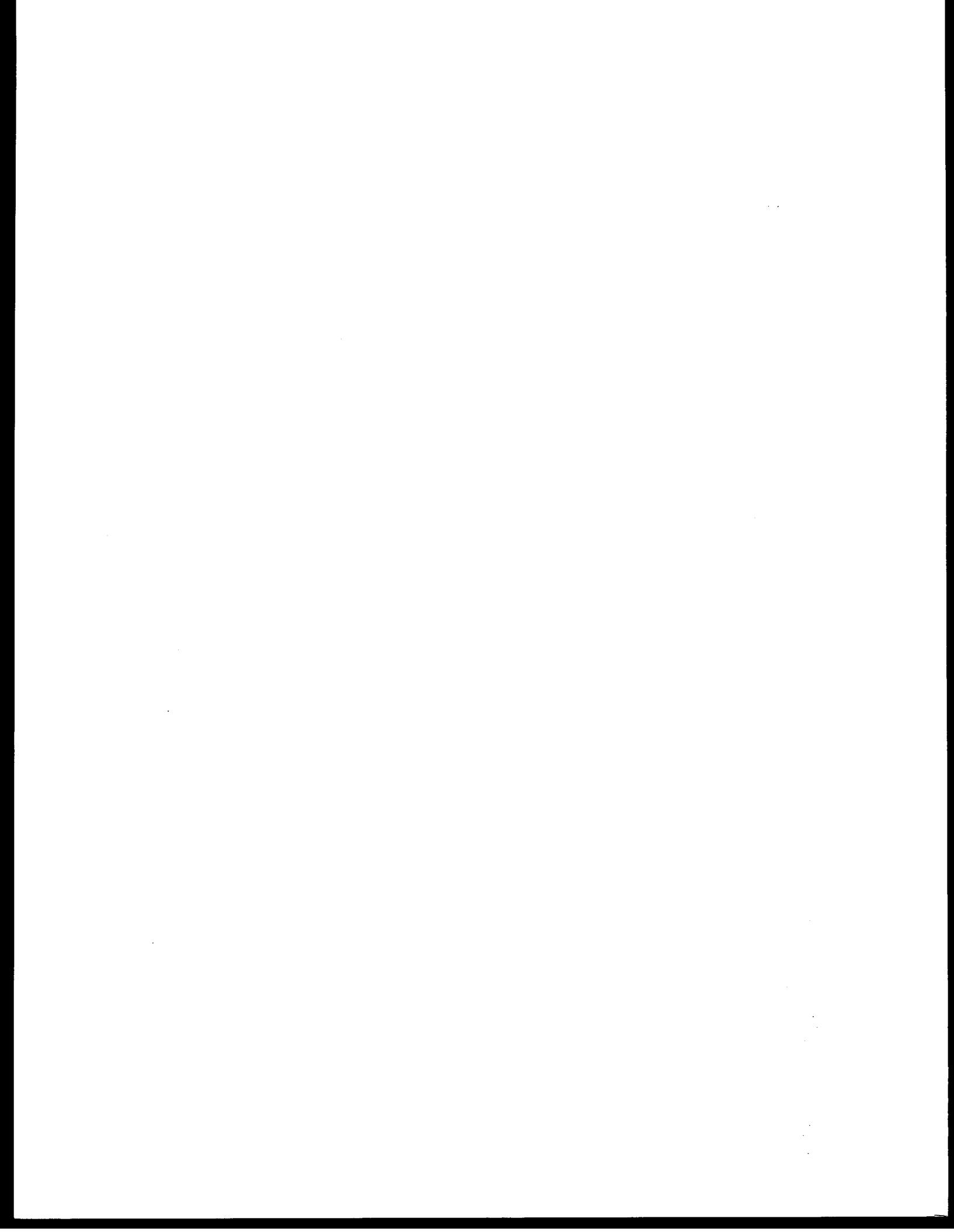
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**POPULATION AND TROPHICS STUDIES OF SEABIRDS
IN THE NORTHERN BERING AND EASTERN CHUKCHI SEAS,
1981**

by

**David G. Roseneau, Alan M. Springer,
Edward C. Murphy, and Martha I. Springer**

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**Final Report
Outer Continental Shelf Environmental Assessment Program
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April 1982

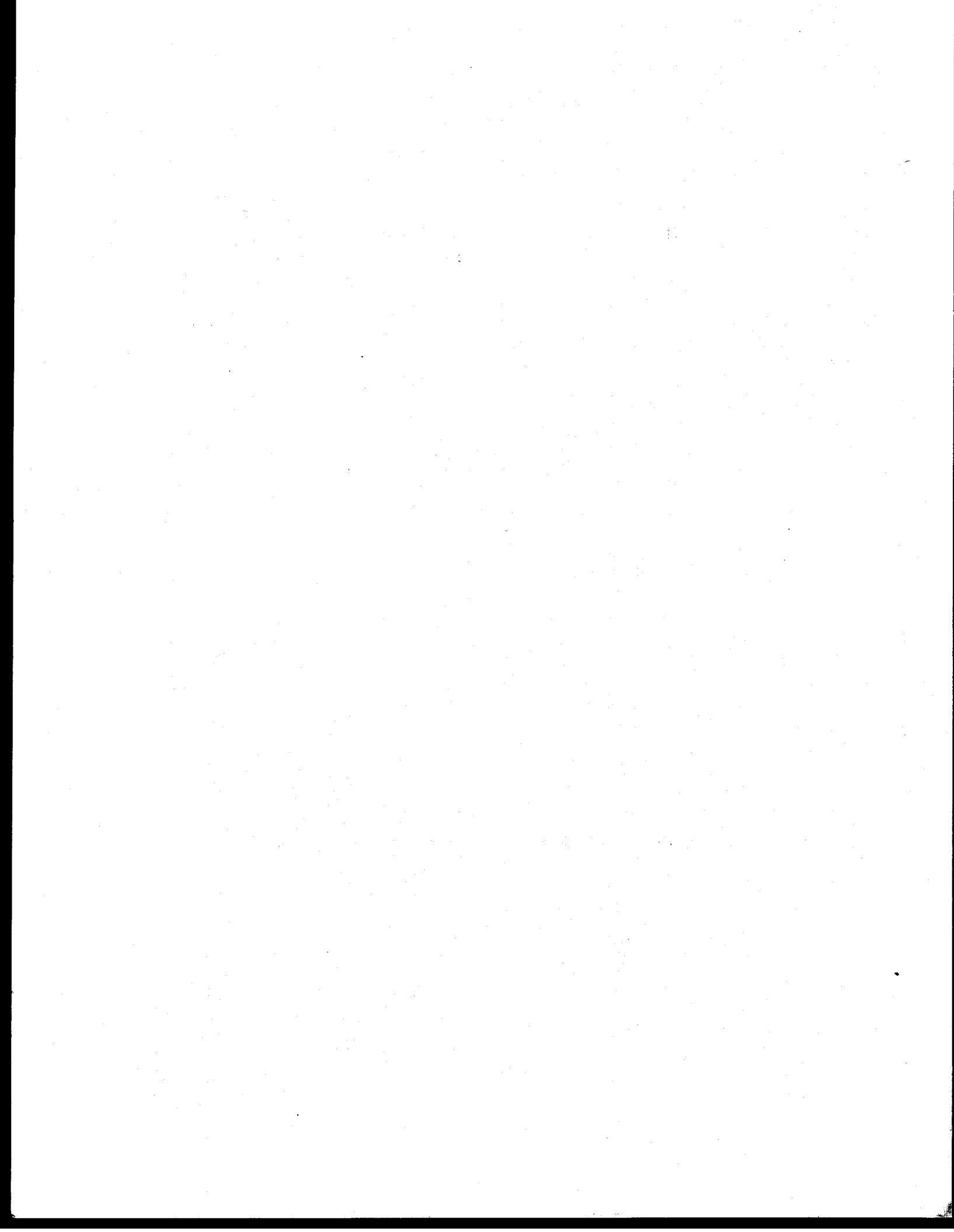


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I. SUMMARY OF OBJECTIVES, CONCLUSIONS AND IMPLICATIONS WITH RESPECT TO OCS OIL AND GAS DEVELOPMENT

A. Objectives

The general objectives of this research unit are to 1) describe relationships of seabird populations and seabird food webs to regional physical processes and environmental variation, and 2) to provide a data set which will ensure that future changes in numbers of thick-billed murres (*Uria lomvia*), common murres (*Uria aalge*) and black-legged kittiwakes (*Rissa tridactyla*) at major breeding colonies in Alaska can be detected, and that the significance of the changes can be properly interpreted.

B. Conclusions

A major decline in numbers of murres occurred at Cape Thompson between 1960 and 1976, and numbers continued to steadily decline there between 1976 and 1979. A similar downward trend in numbers of murres has occurred at Bluff in Norton Sound since 1975. That trend was still apparent in 1981. Numbers of murres at Cape Lisburne and nearby Cape Lewis have not appeared to decline during recent years. The number of murres in one colony on St. Lawrence Island, the only colony for which we have more than one year of data, was considerably lower in 1976 than in 1972; but 1972 and 1981 numbers were comparable, suggesting a short-term fluctuation in the size of the breeding population in the mid-1970's at a time when environmental conditions were unusually cold.

Environmental fluctuations during the 1970's had important repercussions on the breeding biology of murres, black-legged kittiwakes and least auklets (*Aethia pusilla*) in northern Alaska by affecting supporting food webs. Breeding phenology and reproductive success of kittiwakes in the eastern Chukchi Sea, and of kittiwakes and common murres in Norton Sound, were strongly correlated with climatic conditions. Historical data indicate that the spring and summer periods during about two decades preceding the mid-1970's were relatively cold. After 1976 the spring-summer periods became warmer. Breeding phenology was later and reproductive success was lower in colder years when conditions were less favorable for some prey populations. Breeding phenology was earlier and reproductive success was higher in warmer years when prey availability was higher. Below average natality between 1959-1976, a relatively cold period in northern Alaska, could have led to declining numbers of murres in recent years. Kittiwake and murre reproductive success has been high since 1978 when spring-summer periods have been warm. A preliminary simulation analysis has predicted that murre numbers should increase over the next several years, beginning in 1982, if differential reproductive success is responsible for the numeric changes (see Springer *et al.* 1982). Regional differences in physical processes and food web stability appear to account for changes in kittiwake productivity and could account for differences in numeric trends of local breeding populations of murres in northern Alaska.

C. Implications with Respect to OCS Oil and Gas Development

Information of the kind we are obtaining on seabird biology will help us differentiate between future changes in seabird populations that might result from OCS oil and gas development, and changes resulting from environmental fluctuations unrelated to OCS activities.

II. INTRODUCTION

A. General Nature and Scope of Study

Seabirds occupy top positions in marine food webs and thereby integrate many elements of regional ecosystems. Among the many species of seabirds, murres and kittiwakes are easily studied and are sensitive to changes in the environment. Our studies take advantage of these characteristics to examine spatial and temporal differences in several marine food webs, and the relationships between these food webs, regional physical processes and seabird biology.

Substantial declines in murre populations during recent years in northern Alaska have demonstrated the need for a system that will permit future monitoring of colonies as resource exploration and development increases on Alaska's outer continental shelf. Therefore, our studies are designed to provide methods for reliably censusing murres, thus establishing useful indices of murre numbers at major breeding colonies in Alaska.

B. Specific Objectives

Our initial plans for the FY81 field season called for colony studies at St. Lawrence Island, Little Diomede Island and Cape Thompson. The *Surveyor* would have been used to transport people and equipment to those locations. The *Surveyor* was unavailable for that purpose, and it was necessary to modify our plans concerning field sites. We elected to retain our first priority of visiting St. Lawrence Island and to continue work at two more accessible locations, Bluff and Cape Lisburne/Cape Lewis. The specific objectives of the FY81 work remained unchanged and included:

1. Censusing murres and black-legged kittiwakes at each location.
2. Establishing as many permanent murre and kittiwake census plots as possible on St. Lawrence Island for future comparison.
3. Determining breeding phenologies and levels of reproductive success of kittiwakes and other seabirds at each location.
4. Determining growth rates of kittiwake chicks at each location.
5. Collecting specimens of seabirds, primarily murres, kittiwakes, crested auklets (*Aethia cristatella*) and least auklets, for food habits data and as a means of sampling local marine organisms for distribution and relative abundance.

6. Obtaining data on other species of seabirds that would provide useful information on local marine systems.

C. Relevance to Problems of Oil Development

The success of OCSEAP will depend in part on an ability to detect changes in marine biological systems and in part on an ability to separate naturally occurring changes from changes that might result from resource development in Alaskan waters. OCSEAP sponsored studies of seabirds in the Bering and Chukchi seas have shown that population parameters such as numbers, breeding phenology and reproductive success can vary considerably between years. Such marked natural variation could make it difficult to determine if developmental activities were involved in biological changes that might be detected in future years.

Our studies have shown that annual variability is not random, but is predictable from annual changes in the physical environment and in regional food webs. Information of this kind is relevant to problems of OCS development because it provides the means to more clearly differentiate between natural phenomena and changes resulting from resource development. This aspect of our work is acquiring added importance because of the recent declines in murre numbers that we have documented at two major colonies, one in the eastern Chukchi Sea and the other in the northeastern Bering Sea.

Seabirds are appropriate species to study not only because they are sensitive indicators of changes in the environment, but also because they are relatively easy to study, especially by comparison to other high profile marine vertebrates such as seals and whales. They also offer an excellent means of sampling lower trophic levels that often defy scientific sampling methodologies. Therefore, seabird studies can provide a great amount of relatively inexpensive information on marine ecosystem dynamics. The monitoring of seabird populations at strategic locations in Alaskan waters may be one of the most effective means of detecting significant changes resulting from OCS developments and activities.

III. CURRENT STATE OF KNOWLEDGE

Prior to OCSEAP-sponsored studies, seabird colonies at Cape Lisburne and nearby Cape Lewis in the eastern Chukchi Sea, and at Bluff in Norton Sound in the northeastern Bering Sea had not been investigated.¹ Field work in 1981 at Cape Lisburne and Cape Lewis extended OCSEAP studies conducted there between 1976-1979 and previously reported by Springer and Roseneau (1977, 1978), Springer *et al.* (1979) and Murphy *et al.* (1980). Field work in 1981 extended other OCSEAP studies conducted at that site in 1975-1978 and previously reported by Drury (1976), Steele and Drury (1977), Biderman *et al.* (1978), Ramsdell and Drury (1979), Murphy *et al.* (1980) and Drury *et al.* (1981).

¹ Some general information on the relative sizes of these colonies was obtained by aerial surveys in 1970-1973 (see Bartonek and Sealy 1979).

Most previous seabird work on St. Lawrence Island has emphasized auklets (e.g., Sealy 1968, 1975, 1981; Bédard 1969a, 1969b; Sealy and Bédard 1973; Searing 1977). Reports on other species, particularly murres and kittiwakes, which are the next most abundant birds on the island, have tended to be general in nature (e.g., Murie 1936, Fay and Cade 1959, Thompson 1967, Johnson 1976, and Bartonek and Sealy 1979), although one study provides considerable information on horned puffins (*Fratercula corniculata*) (Sealy 1973).

S. R. Johnson (unpubl. data) censused murres along a portion of the west coast of St. Lawrence Island in 1972. He reported data on growth rates, heat regulation and the timing of murre chick sea-going, and on metabolism in adult murres (Johnson and West 1975). Searing (1977) visited the island in 1976 and censused murres at the same location counted by Johnson. Searing also obtained data on murre and kittiwake breeding phenology and success in 1976. Aerial surveys were made at St. Lawrence Island in 1977 and 1978, and provided some information on seabird numbers, colony locations and offshore feeding areas (Ramsdell and Drury 1979, Drury *et al.* 1981). Offshore concentrations of birds in the vicinity of the island were also reported by Gould (1977), Harrison (1977), Biderman and Drury (1978) and Hunt *et al.* (1981). Sowls *et al.* (1978) reported colony locations and numbers of seabirds on St. Lawrence Island based on the above studies. In 1979, F. Fay (pers. comm.) made a rapid boat-based estimate of seabirds along a portion of the northeastern sector of the island. Data relevant to our studies on murres, kittiwakes and auklets from these earlier investigations are included in following sections of this report.

IV. STUDY AREAS

The locations of the 1981 study areas are shown in Figure 1. Details of the Cape Lisburne, Cape Lewis and Bluff study areas were reported previously by Steele and Drury (1977), Biderman *et al.* (1978), Springer and Roseneau (1977, 1978), Ramsdell and Drury (1979), Springer *et al.* (1979), Murphy *et al.* (1980) and Drury *et al.* (1981) and we refer readers to these reports for additional information on them.

St. Lawrence Island is shown in detail in Figures 2, 3 and 4. Fay and Cade (1959), Thompson (1967), Sealy (1968, 1973, 1975), Bédard (1969a, 1969b), Sealy and Bédard (1973), Searing (1977) and Drury *et al.* (1981) have provided various descriptions of the St. Lawrence Island study area. We have drawn on these accounts and other reports relevant to the region (e.g., Hood and Kelly 1974; Coachman *et al.* 1975; Brower *et al.* 1977a, 1977b; Hood and Calder 1981) in preparing the following discussion.

St. Lawrence Island is the largest island in the Bering Sea. It is about 160 km long and varies between 18-40 km wide, with an approximate surface area of 5100² km. It lies north of the continental shelf break about 220 km south of Bering Strait, 60 km southeast of Chukotsk Peninsula (U.S.S.R.), and 200 km southwest of Seward Peninsula, Alaska (Figure 1).

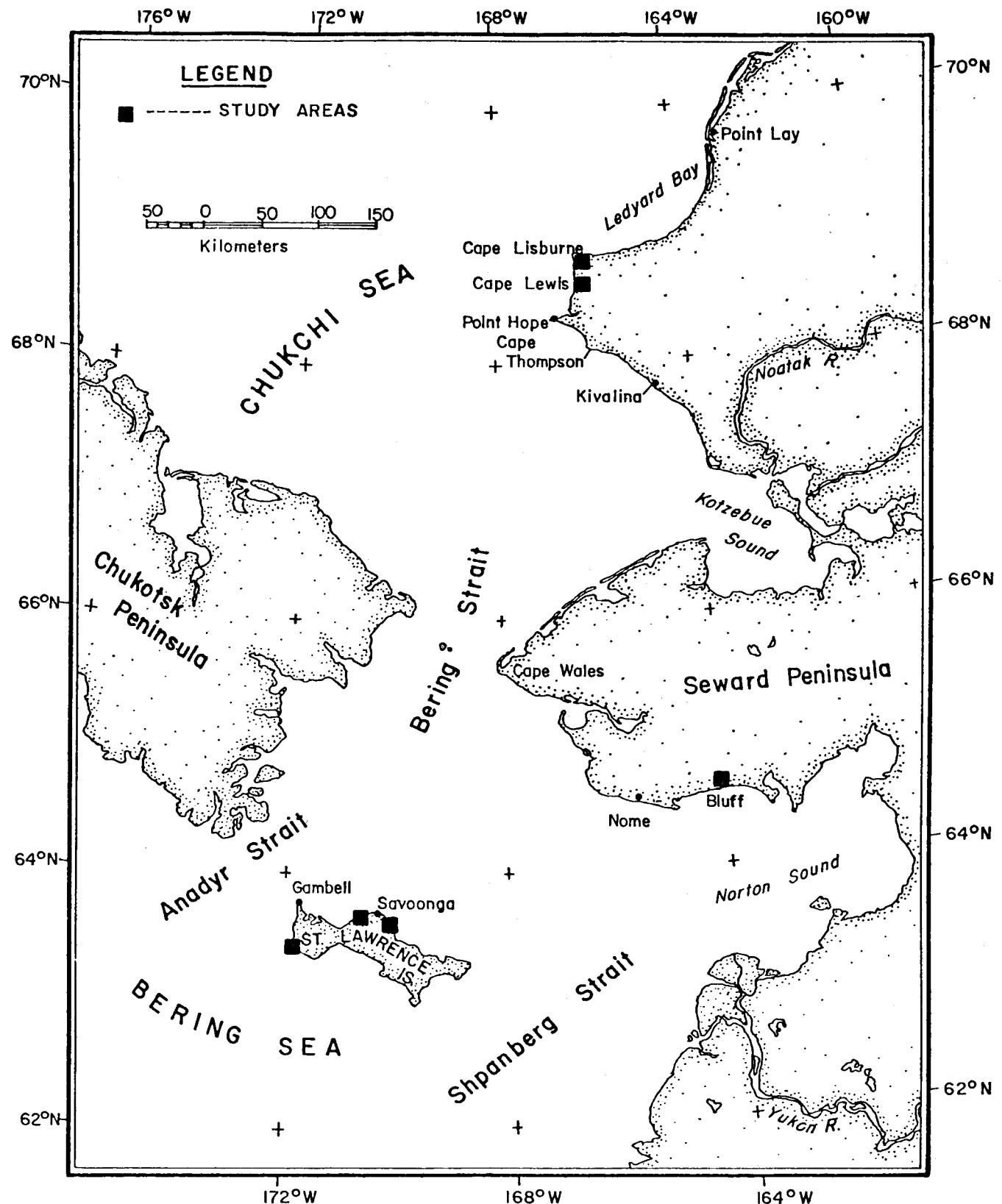


Figure 1. Study areas visited in 1981.

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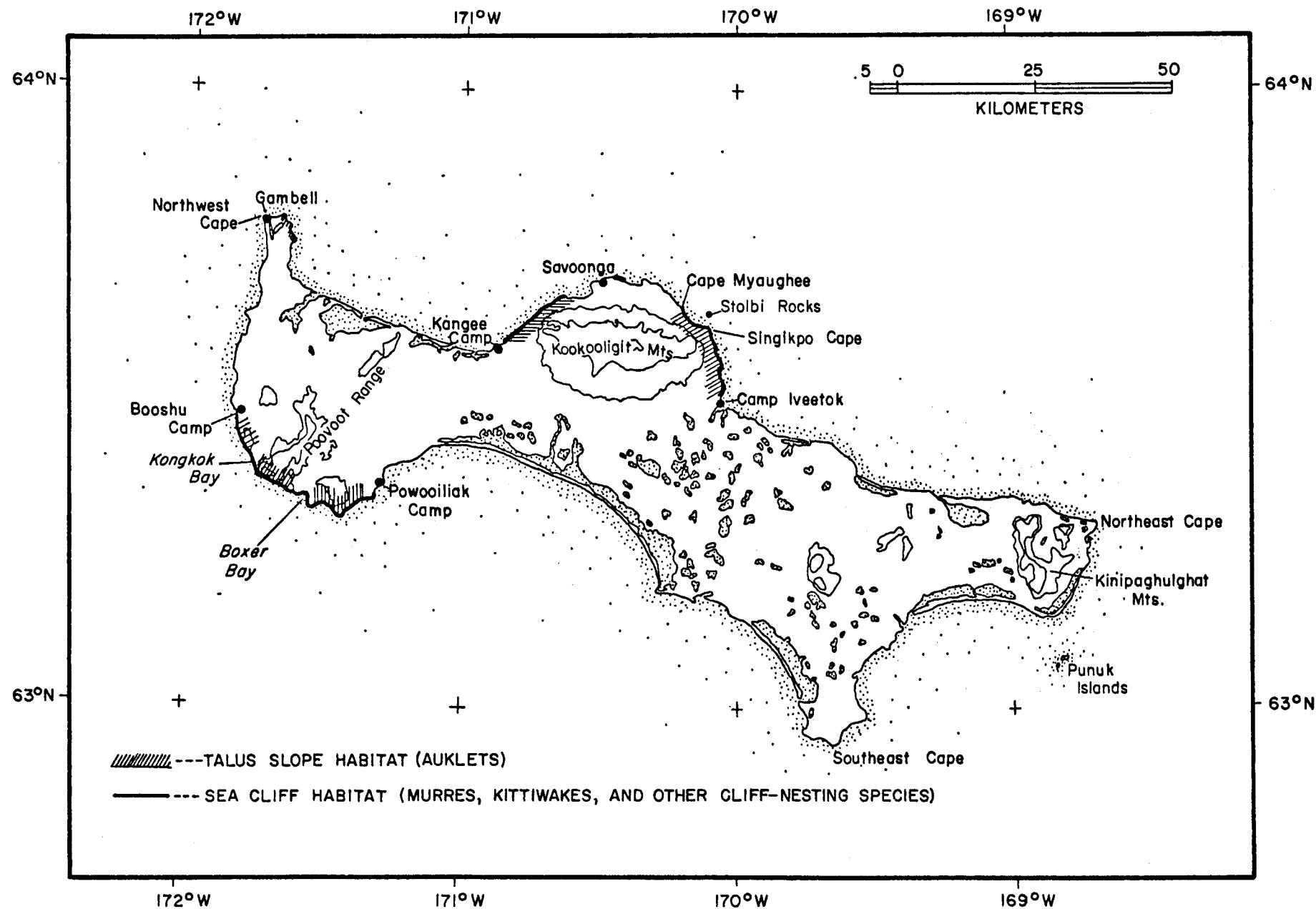


Figure 2. The St. Lawrence Island study area and locations of principal seabird nesting habitat.

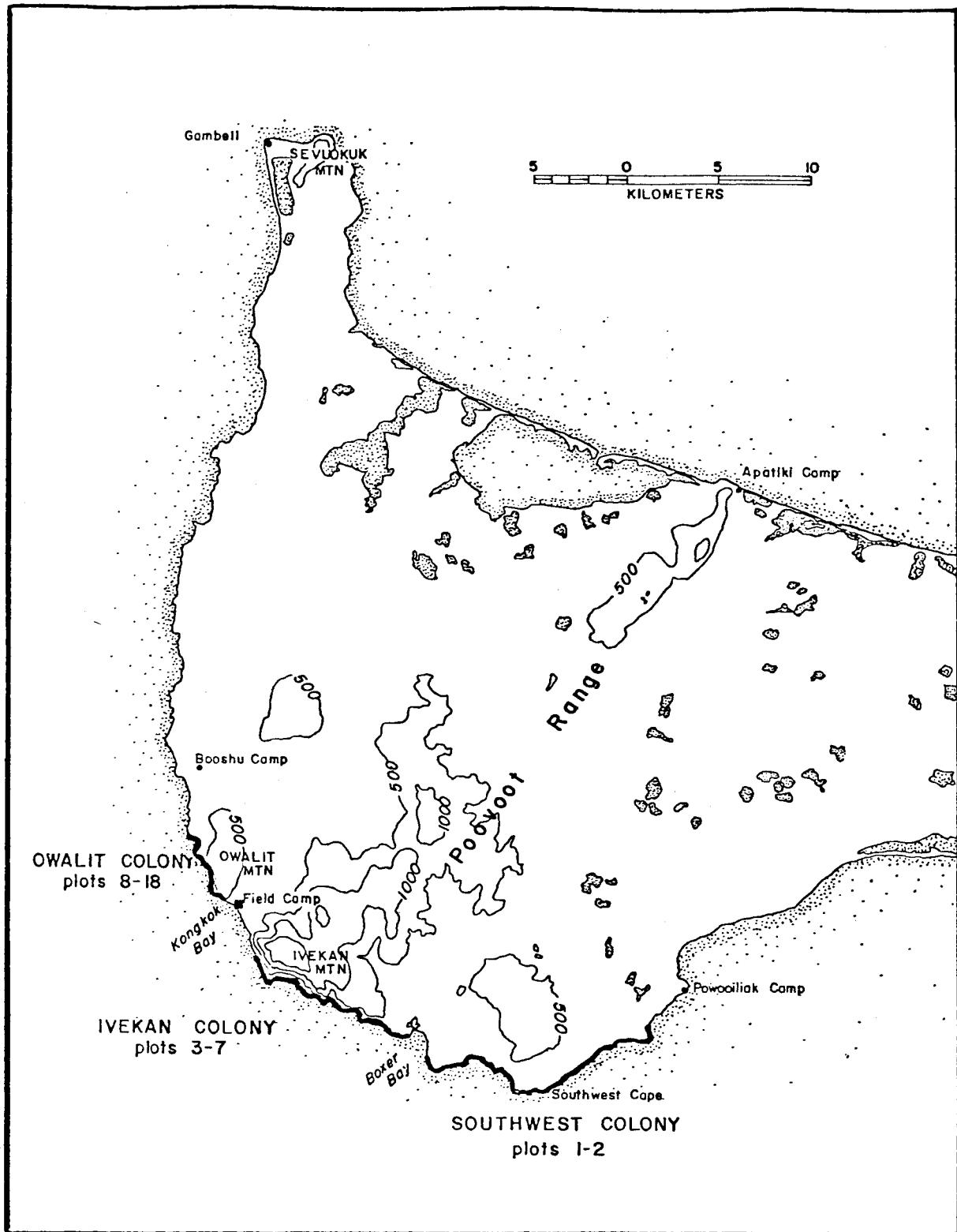


Figure 3. Murre and black-legged kittiwake colonies in the southwestern sector of St. Lawrence Island.

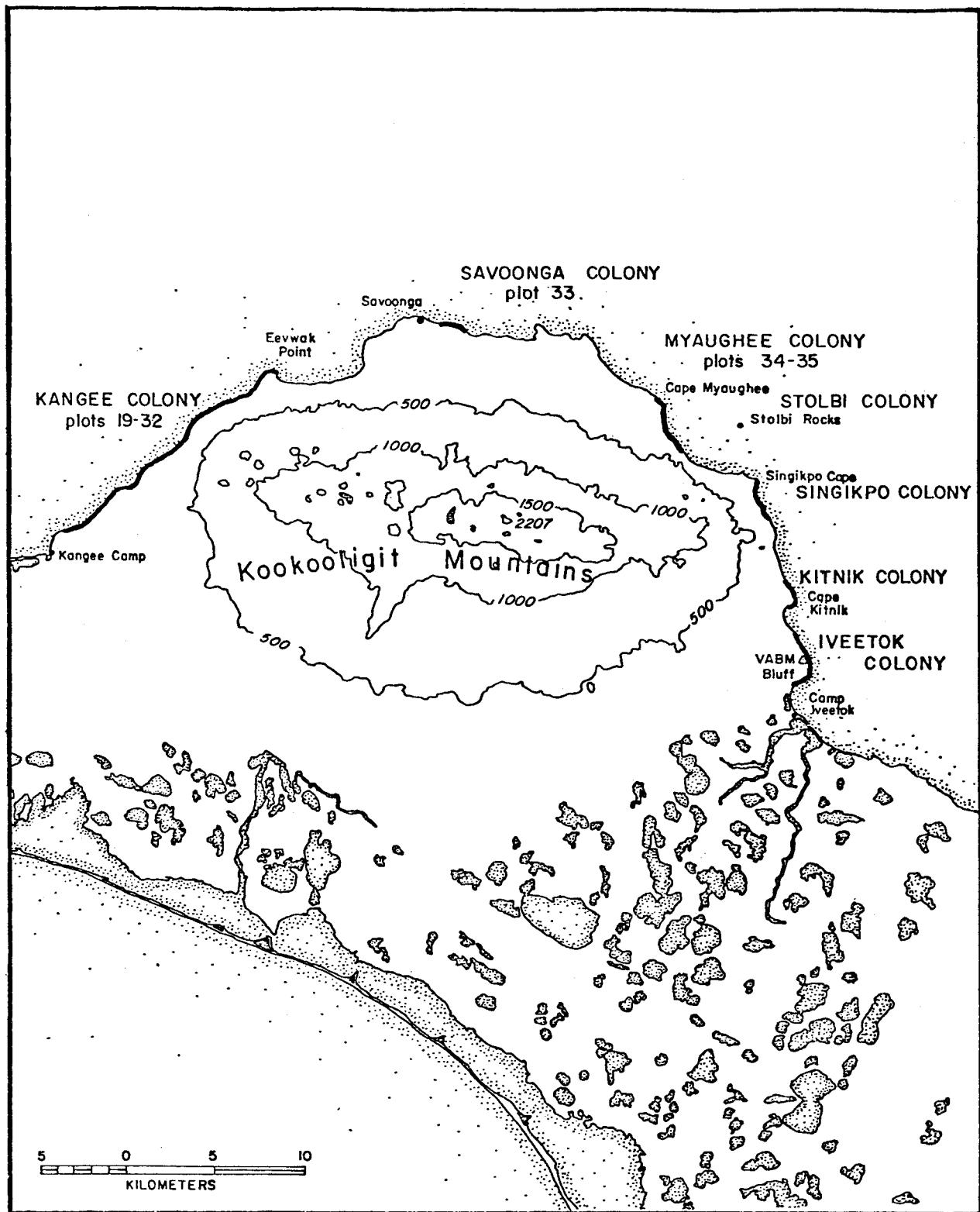


Figure 4. Murre and black-legged kittiwake colonies in the north-central sector of St. Lawrence Island.

The island has an arctic-maritime climate and seasonal weather typical of much of the northern Bering Sea region (see Brower *et al.* 1977a, 1977b). Summers are short and tend to be cooler than in nearby continental areas. Mid-summer temperatures of 10–15°C, and occasionally 20°C, are typical, and moderate to strong winds from southern quadrants are especially common during June–August. Cloudy skies, fog, drizzle and rain are also common throughout spring, summer and fall. Weather tends to be especially poor during late summer, fall and early winter when large, often violent storms track northward through the region. Winters are long, but somewhat milder than in nearby continental areas, and surrounding waters are ice-covered during much of the year. Snowfall is frequent and winds from northern quadrants are common. Blowing, drifting snow is typical of many winter days.

The highest point on St. Lawrence Island is about 670 m above mean sea level (msl); however, the majority of the island is low (60 m msl or less) and wet (Figure 2). Most of the upland areas are found in the southwestern, north-central and eastern sectors. The southwestern sector, dominated by the Poovoot Range, and the north-central sector, dominated by the Kookooligit Mountains, provide almost all of the 'rock-pile,' talus-slope and sea-cliff nesting habitat on the island (Figures 2–4; see also Fay and Cade 1959).

Sea-cliffs in the southwestern and north-central sectors of the island (Figures 3 and 4) are predominantly of volcanic origin and are relatively stable by comparison to cliffs at many of Alaska's northern mainland seabird colonies (e.g., Cape Lisburne, Cape Lewis and Cape Thompson in the eastern Chukchi Sea and Bluff in Norton Sound). They range in height from about 10 m msl to about 300 m msl and are typically highest in the southwestern sector between Booshu and Powooiliak camps where most cliffs rise about 50–200 m above the sea. In comparison, most sea-cliffs between Kangee Camp and Camp Ivetok in the north-central sector are about 10–30 m high, although some rise to heights of about 75 m msl in the central portion of Kangee Colony.

St. Lawrence Island's size, location and orientation relative to the Siberian and Alaskan landmasses and to prevailing ocean currents influence biota in the region, including seabirds. The western end of the island is separated from Chukotk Peninsula by 60 km wide Anadyr Strait (Figure 1). Shpanberg Strait, 110 km wide, separates the eastern end of the island from the mainland of Alaska. The island's long axis (160 km), equivalent to about one-third of the 430 km distance between Chukotk Peninsula and the delta of the Yukon River, is oriented perpendicularly to an ocean current flowing northward out of the Bering Sea through Bering Strait into the Chukchi Sea. Cold Bering Shelf Water and cold Anadyr Water pass through Anadyr Strait (see Coachman *et al.* 1975, Kinder and Schumacher 1981), and other elements of Bering Shelf Water, influenced by warmer, less saline Alaskan Coastal Water, pass through Shpanberg Strait (see Coachman *et al.* 1975, Ingraham 1981). The flow of water past the island affects sediment deposition, and long, linear shoals are present off its northeastern and northwestern flanks (Nelson *et al.* 1981). Currents are most pronounced through narrow Anadyr Strait, and an area of particularly intense bottom current activity is present north of the island's western end (Larsen *et al.* 1981).

The strong currents entering Anadyr Strait transport large seasonal populations of zooplankton, including a variety of endemic oceanic Bering Sea species dominated by copepods, such as *Eucalanus bungii*, *Calanus cristatus*, *C. plumchrus*, *Acartia longiremis* and *A. clausi* (see Cooney 1981), from the region of the shelf break past the western end of St. Lawrence Island during ice-free months. These currents, richly laden with zooplankton, and the turbulent mixing and upwelling northward of the island's western end create an annually important feeding area for large populations of seabirds breeding on the island and along the coast of Chukotsk Peninsula. The majority of seabirds from St. Lawrence Island, especially the alcids, forage north of Gambell (Northwest Cape) downstream in the current flow during most of the breeding season (Bédard 1969b, Searing 1977, Drury *et al.* 1981, Hunt *et al.* 1981). Many alcids favor this area well into fall, and during late summer some northern fulmars (*Fulmarus glacialis*) are also present there (Harrison 1977). Other large populations of transient seabirds, primarily shearwaters (*Puffinus spp.*), enter the northern Bering-eastern Chukchi region annually (Gould 1977). These birds may also feed heavily in the out-flow of Anadyr Strait when they are present in the area, but most of them have been observed downstream of the island's eastern end during late summer and fall (Harrison 1977, Hunt *et al.* 1981).

St. Lawrence Island is also a dominant geographic feature affecting regional patterns of winter ice cover. North winds are prevalent in winter, and as the ice front advances southward into the Bering Sea, ice converges against the island's northern shore and a large, persistent polynya forms off its southern shore (Shapiro and Burns 1975a, 1975b, McNutt 1981). Dynamic zones of fractured, divergent ice are also created on either side of the island (McNutt 1981). The polynya south of St. Lawrence Island is important to wintering oldsquaws (*Clangula hyemalis*) and eiders (*Somateria spp.*) (Fay and Cade 1959, Divoky 1981). Murres (presumably thick-billed murres), pelagic cormorants (*Phalacrocorax pelagicus*) and some large gulls (*Larus spp.*) also frequently winter there (L. Iyakitan pers. comm.). Large numbers of sea ducks (especially oldsquaws) and murres have also been observed in the zone of divergent ice south and west of the island (F. Fay pers. comm.).

V. SOURCES, METHODS AND RATIONALE OF DATA COLLECTION

Field efforts during 1981 began on 10 July and continued until 15 August. One two-man team visited Bluff from 10 July to 22 July, Cape Lisburne from 25 July to 5 August, and made a short trip to Cape Lewis (18 km south of Cape Lisburne) on 2 August. A second two-man team visited St. Lawrence Island from 14 July to 15 August. Boat trips were made along the north coast of St. Lawrence Island between Gambell and Cape Myaughee on 18-19 July, and between Gambell and Kaghkusaliq Point on 12 August. Most effort was concentrated in the southwestern sector of the island between Booshu Camp and Powooiliak Camp; a field camp at Kongkok Bay served as base of operations from 21 July to 10 August.

A total of 65 thick-billed murres, 42 common murres and 72 black-legged kittiwakes was collected at varying intervals at St. Lawrence Island, Bluff and Cape Lisburne. Ten least and 12 crested auklets were also collected at St. Lawrence Island, and the regurgitated contents from gular pouches of other least and crested auklets were obtained by flushing perching adults after they returned from foraging at sea. Data on weight, breeding condition and fat condition were taken from all birds within two hours of collection and stomach contents and gular pouch contents were preserved in 70% ethanol for future identification.

Complete censuses of murres and kittiwakes were made at Bluff and Cape Lewis using previously established plot boundaries (see Springer and Roseneau 1978, Murphy *et al.* 1980). Murres and kittiwakes were also censused on 10 of 75 plots previously established at Cape Lisburne (see Springer and Roseneau 1977). Six of the 10 plots were counted on two separate occasions. Six of 10 colonies (see Figures 2-4) of murres were completely censused at St. Lawrence Island. The six colonies were divided into 35 plots at the time of census, and include all murre breeding areas on the island except those between Ataaka's Camp and Camp Ivetok, and one offshore location on Stolbi Rocks. The boundaries of these plots were photographed for future reference.

The censuses of murres at all sites followed previously established methods, and all counts were timed to occur between mid-incubation and first sea-going of chicks, dates comparable to those of previous censuses (see Murphy *et al.* 1980). In all but one case, two observers counted murres simultaneously on each plot with the aid of binoculars from a small boat stationed offshore. The exception occurred at Bluff, where only one observer was able to count murres. Each observer estimated the number of murres by 10's at all census plots except plots 1-5 on St. Lawrence Island. These five large plots at Southwest Colony and Ivetok Colony between Powooiliak Camp and Bunnell Cape were counted by 100's. Estimation by 100's at these particularly lengthy sections of cliff allowed the observers to complete the census of murres in the southwestern sector of the island before a major storm system arrived. During each census observers intermittently counted 10 or 100 individual birds in areas of varying densities to maintain accuracy and precision. The scores of individual observers were not compared until after all counts of murres were complete at each colony.

The censuses of kittiwakes at Cape Lisburne, Cape Lewis and Bluff also followed previously established methods. These censuses were conducted in the same manner as the murre censuses; however, both individual birds and nests were counted, and all counts were by 1's.

To allow later evaluation of differences in counts of murres and kittiwakes between observers, we have adhered to and extended the notation for observers used in earlier annual reports (e.g., Murphy *et al.* 1980). As used in this report and applied to the field crews in 1981, the notations are:

<u>Code</u>	<u>Name</u>
C	A. M. Springer
E	D. G. Roseneau
F	E. C. Murphy
K	R. Mule

Four of six small study plots established by Searing (1977) were successfully located at Owalit Colony, St. Lawrence Island. Murres, kittiwakes and kittiwake nests were counted by 1's by either one or two observers from the same approximate land or sea position used by Searing. Additional kittiwake nesting areas were also photographed for future reference.

Kittiwake nests were examined at varying intervals at Cape Lisburne, Bluff and in the southwestern sector of St. Lawrence Island. On 12 August we also had an opportunity to examine a large number of kittiwake nests near Kangee Camp in the north-central sector of St. Lawrence Island. Visits to kittiwake nests at varying intervals provided data from the time of hatching through the period of maximum growth of chicks. Ratios of empty/occupied nest were obtained at each location, and clutch size, hatching success and weights of chicks were recorded at each nest. All chicks were encouraged to regurgitate food prior to weighing. In the few instances when chicks had food in their crops and did not readily regurgitate it, the weight of the retained food was estimated on the basis of known weights of similar volumes of food. Regurgitated food from chicks was collected and preserved in 70% ethanol to supplement other food habits samples.

Kittiwake chicks were weighed on Pesola spring balances. Growth rates were calculated for each chick by determining the slope of the regression equation relating all of the respective weights taken between the first weighing and the highest weight recorded that was less than or equal to 300 g. A preliminary analysis indicated that growth rates of most chicks remained linear through 300 g (also see Coulson and White 1958, Maunder and Threlfall 1972).

Because we visited nests every several days, we frequently did not know the exact hatching date of particular chicks. In such instances we estimated the hatching date if the chick was weighed two or more times before attaining 300 g. Using the regression equation for daily growth rate, we calculated the date on which the chick would have weighed 35 g and used that value as the estimated hatching date for that chick. In some instances chicks were first weighed more than ten days later than the estimated hatching date, and we eliminated such individuals from the data base on hatching phenology. This method is unbiased if the growth rate is linear, or approximately so, between hatching and 300 g. Various studies (e.g., Coulson and White 1958, Maunder and Threlfall 1972) indicate that the growth rate of kittiwakes is linear from the time of hatching until about three weeks of age.

We located several least auklet nests in Kongkok Basin at Ivezkan Mountain, St. Lawrence Island. These nests were found just prior to hatching or within a few days after hatching, and chicks were subsequently weighed and measured on several occasions for growth rate information.

Observations of flight directions of murres, kittiwakes and auklets departing and returning to their colonies were made regularly during offshore collecting trips, boat trips along the coast, and from the beaches and cliff-tops at all colonies.

VI. & VII. RESULTS AND DISCUSSION

A. Murres

Census

Results of murre censuses taken at St. Lawrence Island, Cape Lisburne, Cape Lewis and Bluff in 1981 are presented in Tables 1-4. Table 5 summarizes all censuses taken at all four locations and at Cape Thompson since 1960.

St. Lawrence Island

All previous estimates of the size of the murre population of St. Lawrence Island have been general approximations. The estimates include an average of about 200,000 individuals during the 1950's (Fay and Cade 1959); a range of about 102,000-360,000 individuals obtained during aerial surveys in 1977-1978 (Biderman and Drury 1978, Ramsdell and Drury 1979, Drury *et al.* 1981); and an estimate of about 300,000 individuals derived from the aerial estimates and from Searing's (1977) census of one colony and general observations at others in the southwestern sector of the island in 1976 (Sowls *et al.* 1978).

We conducted censuses of murres at six of the 10 breeding colonies at St. Lawrence Island¹ (Table 1). We were unable to visit the four remaining colonies at Singikpo Cape, Cape Kitnik, VABM Bluff near Ivetek Camp and Stolbi Rocks, offshore of Singikpo Cape (see Figure 4). Some recent observations at those colonies and the results of our censuses at the other six colonies suggest that the total population of murres on St. Lawrence Island is larger than was previously thought.

Aerial estimates of numbers of all species of birds at Singikpo, Kitnik and Ivetek colonies in 1977-1978 included 10,000-50,000 murres. F. Fay (unpubl. data) tried to quickly estimate numbers of all species of birds

¹Sowls *et al.* (1978) reported the presence of murres at an eleventh location, the Punuk Islands, based on Thompson's (1967) observations of a few individuals; however, even though a few murres are occasionally present, they do not breed there (B. Kelly, L. Iyakitan, V. Slwooko pers. comm.).

at these same colonies from a passing boat in early July 1979. His estimates of murres, including birds in the air, on the water and on the cliffs, totaled 76,000 ($\pm 50\%$). Stolbi Rocks also provide habitat for at least a few thousand murres (Drury *et al.* 1981).

The attempts to determine the number of murres at Singikpo, Kitnik, Ivetok and Stolbi colonies were not plot-by-plot censuses. Furthermore, the estimates were made quickly and were directed simultaneously toward all species present, including hundreds of thousands of auklets. Still, the estimates clearly suggest that a complete census of the four colonies would have increased our raw score (uncompensated for daily or diurnal differences in numbers, see Springer *et al.* 1982) of about 329,000 murres by several tens of thousands of individuals.

Owalit Colony (Figure 3) is the only location on St. Lawrence Island for which good historical data on numbers of murres are available. The colony was censused in 1972 by S.R. Johnson (unpubl. data) and in 1976 by Searing (1977). The uncompensated results of these censuses, which were conducted similarly to ours, were about 32,000 and 16,000 individuals, respectively (Table 5). Our count in 1981 totaled 34,000 murres. Searing (1977) reported the results of Johnson's census as about 60,000 individuals. That number is incorrect, and an explanation of the problem is presented in the Appendix.

We believe that the differences in numbers of murres between 1976 and the other two census years were real because the colony is not difficult to count, and because the observed changes in numbers there were large in both cases. Some of the difference between 1972 and 1976 may be explained in part by a rock-fall that occurred in a densely occupied portion of the colony after 1972, but before 1976 (Johnson per. comm.). However, our observations of the cliffs suggest that rock-falls could not account for most of the apparent change between those years. The similarity in numbers of murres present in 1972 and 1981 also suggests that other factors were responsible for the changes.

We believe that most of the differences in numbers of murres at Owalit Colony between 1972 and 1976, and between 1976 and 1981, are best explained by the unusually cold environmental conditions that prevailed in the Bering-Chukchi region in the mid-1970's (see Niebauer 1980, 1981a, 1981b). The unusually cold environment may have affected the presence of breeding murres at Owalit Colony in several ways. Local conditions may have made it physically difficult for murres to nest. Searing (1977) noted that snow cover persisted on the breeding ledges at Owalit Colony in spring 1976, and he described how the presence of snow might have affected the presence of murres on the cliffs. Also, the annually cooling climatic conditions preceding the unusually cold year of 1976 may have influenced seabird food webs. Searing (1977) noted a high usage of invertebrate prey by murres at Owalit Colony in 1976, a phenomenon that also occurred at Cape Thompson during the same year (Springer *et al.* 1982). Because murres feed predominantly on fish during the breeding season, the higher incidence of invertebrates in murre diets in 1976 indicates that fish biomass was relatively low that year. Such changes in food webs may have influenced the number of murres attempting to breed at Owalit Colony in the mid-1970's.

The effect may have been especially great on common murres, which depend even more on fish than do thick-billed murres (Swartz 1966, Springer *et al.* 1982).

Regardless of the specific reasons for the presence of fewer murres at Owalit Colony in 1976, the number of murres present on the cliffs in 1981 was about the same as a decade ago. The similarity in numbers between 1972 and 1981, both climatically mild years, and the cold environmental conditions that coincided with the 1976 breeding season suggest that the 1976 population decrease was a short-lived event rather than an actual decline in the population.

Cape Lisburne and Cape Lewis

Results of our censuses at Cape Lisburne and Cape Lewis (Tables 2 and 3) suggest that numbers of murres have remained relatively stable at these two colonies since the mid-1970's (Table 5). In contrast, murres declined at Cape Thompson between 1960 and 1976, and between 1976 and 1979 (see Murphy *et al.* 1980). The apparent stability of populations of murres at Cape Lisburne and Cape Lewis compared to decreasing numbers at Cape Thompson are discussed by Springer *et al.* 1982.

Bluff

Our earlier analysis of pre-1980 census data indicated that the number of murres declined at Bluff during 1975-1979 (see Murphy *et al.* 1980). Data we obtained in 1981 indicate that the murre population is still decreasing (Table 5).

The rate of decline of murres at Bluff was fairly steady during 1975-1981, and nearly the same as the rate of decline previously documented for murres at Cape Thompson during 1976-1979 (Murphy *et al.* 1980). We are presently examining two possible reasons for these decreases, which involve effects of a changing environment on: (1) natality of murres and (2) winter mortality of murres. A thorough discussion of these possibilities is presented in Springer *et al.* 1982.

Phenology

Dates of first hatching of murre eggs and first sea-going of murre chicks at St. Lawrence Island, Cape Lisburne, Bluff and Cape Thompson since 1959 are summarized in Table 6. Based on hatching dates, murres at St. Lawrence Island bred about one week earlier in 1981 than did murres at Cape Lisburne, but about one and a half weeks later than murres at Bluff.

Hatching of thick-billed murre eggs at Owalit Colony, St. Lawrence Island commenced about 20 July. On 23 July, a ledge used predominantly by common murres contained 21 unpipped eggs, 1 pipping egg and 2 small chicks estimated to be about two days old. Several other chicks, approximately 2-5 days old, were seen on ledges where thick-billed murres predominated. Chicks were numerous on many ledges by 30 July and hatching appeared to peak about 1-2 August, but was still occurring on 10 August. Some of the earliest chicks seen were well-developed and appeared ready to go to sea on 10 August. Sea-going may have commenced as early as the

evenings of 10-11 August, but probably did not peak until about 15-16 August.

The first common murre chick was seen at Bluff on 11 July. Most chicks hatched between 14 July and 22 July. Our early departure prevented us from determining the full extent of the hatching period at Bluff in 1981.

These data and consistent differences among the locations in previous years (Table 6) probably reflect the typically warmer, earlier spring conditions at the more southern latitudes of Bluff ($\sim 64^{\circ}30'N$) and St. Lawrence Island ($\sim 63^{\circ}30'N$) compared to the later, cooler spring conditions at the more northern latitudes of Cape Lisburne ($\sim 68^{\circ}50'N$) and Cape Thompson ($\sim 68^{\circ}10'N$) (see Brower *et al.* 1977a, 1977b).

Phenological changes among years at each location also follow a consistent trend (Table 6). Murres nested latest in the mid-1970's and earliest in the late 1970's. Changes in phenology at all murre colonies occurred concomitantly with changes in regional physical conditions (Figure 5). Relationships between phenological changes, reproductive changes and physical conditions are discussed in greater detail in Springer *et al.* (1982).

Foraging Areas

Observations of the flight directions taken by murres as they commuted between offshore foraging areas and nesting areas at St. Lawrence Island, Cape Lisburne and Bluff in 1981 are summarized below.

St. Lawrence Island

The majority of murres nesting at Owalit, Ivezkan and Southwest colonies clearly fed in Anadyr Strait and its out-flow north of Northwest Cape, where Anadyr Water mixes with Bering Shelf Water and where strong currents result in turbulence and upwelling in the vicinity of shoals (see Nelson *et al.* 1981). Throughout the day, flocks departing from colonies in the southwestern sector paralleled the coast between Boxer Bay and Booshu Camp, where they tended to disperse toward Anadyr Strait (Figure 6). Departing flocks, typically small (often only 5-30 individuals), fanned out toward the north and northwest; some flew within sight of the coast as far as Gambell, where they were lost from sight as they continued northward. Inbound flocks were typically much larger (often hundreds of individuals), and nearly unbroken strings of murres returned to the vicinity of Sevuokuk Mountain at Northwest Cape from north and northeast of the island during evening hours¹ (Figure 6). Flocks of murres flew past Northwest Cape and paralleled the island's western coast as they returned to Owalit, Ivezkan and Southwest Colonies.

¹These returning flights of murres were accompanied by large numbers of least and crested auklets and small numbers of parakeet auklets (*Cyclorrhynchus psittacula*), horned puffins, tufted puffins (*Lunda cirrhata*), some kittiwakes and occasional pelagic cormorants and pigeon guillemots (*Cephus columba*).

Table 1. Murre census results from St. Lawrence Island, 1981.^a

Colony	Plot	Date	Time ^b	Observer		\bar{x}
				C	E	
<u>South side of island</u>						
Southwest Cape	1	1 August	17:45	56,000	58,950	57,475
	2	1 August	19:25	<u>16,200</u>	<u>14,100</u>	<u>15,150</u>
Subtotals				72,200	73,050	72,625
Ivekan Mtn.	3	2 August	14:25	17,000	19,600	18,300
	4	2 August	13:40	33,800	33,200	33,500
	5	2 August	10:40	59,500	67,500	63,500
	6	24 July	17:58	11,400	11,240	11,320
	7	24 July	17:37	<u>4,520</u>	<u>4,180</u>	<u>4,350</u>
Subtotals				126,220	135,720	130,970
Owalit Mtn.	8	24 July	17:30	500	500	500
	9	24 July		372	361	367
	10	24 July		253	257	255
	11	24 July	16:00	8,280	10,050	9,165
	12	24 July	15:10	8,920	9,630	9,275
	13	24 July	14:47	6,120	7,220	6,670
	14	24 July	14:25	5,080	3,570	4,325
	15	24 July	14:04	880	870	875
	16	24 July	13:52	1,710	1,815	1,763
	17	24 July	13:42	150	175	163
	18	24 July	13:25	<u>590</u>	<u>607</u>	<u>599</u>
Subtotals				32,855	35,055	33,957
<u>North side of island</u>						
Kangee	19	19 July	14:20	5,390	5,420	5,405
	20	19 July	14:15	1,580	2,040	1,810
	21	19 July	13:45	4,030	6,860	5,445
	22	19 July	13:40	4,300	2,410	3,355
	23	19 July	13:20	3,230	2,840	3,035
	24	19 July	13:05	3,280	3,060	3,170
	25	19 July	12:46	7,080	7,170	7,125
	26	19 July	12:10	12,580	17,110	14,845
	27	19 July	11:40	6,960	10,540	8,750
	28	19 July	11:15	4,760	5,930	5,345
	29	18 July	21:25	150	130	140
	30	18 July	21:15	2,470	2,870	2,670
	31	18 July	20:30	9,080	10,910	9,995
	32	18 July	20:10	<u>1,310</u>	<u>1,220</u>	<u>1,265</u>
Subtotals				66,200	78,510	72,355
Savoonga	33	18 July	19:30	<u>4,080</u>	<u>4,310</u>	<u>4,195</u>
Subtotals				4,080	4,310	4,195
Cape Myaughee	34	18 July	18:50	5,080	6,350	5,715
	35	18 July	17:50	<u>7,170</u>	<u>10,880</u>	<u>9,025</u>
	Subtotals				12,250	17,230
TOTALS				313,805	343,875	328,840

^aEstimates are by 10's of birds except: plots 1-5 by 100's; plots 9 and 10 by 1's on several dates at varying times and numbers given here are averages of those counts.^bTimes are times at start of count, Bering Daylight Time.

Table 2. Murre census results from Cape Lisburne, 1981.^a

Plot	Time ^b	25 July			2 August			\bar{x}
		Observer F	Observer K	\bar{x}	Time ^b	Observer F	Observer K	
11	1815	950	737	844	2000	1,340	1,260	1,300
12	1840	1,550	1,624	1,587	2015	1,950	1,980	1,965
25	1910	695	624	660	2030	1,170	1,220	1,195
26	1920	1,010	769	890	2045	1,240	1,110	1,175
30	1935	3,130	2,850	2,990	2100	3,930	4,430	4,185
32	1950	1,890	1,773	1,832	2140	1,530	1,670	1,600
65	2020	2,140	2,276	2,208				
66	2045	1,450	1,450	1,450				
70	2100	1,070	1,200	1,135				
72	2110	700	583	642				
Total		14,585	13,886	14,238		11,160	11,670	11,420

^aEstimates are by 10's.

^bTimes are Bering Daylight Time.

Table 3. Murre census results from Cape Lewis, 1981.^a

Plot	Time	2 August		
		Observer F	Observer K	\bar{x}
1	1055	580	640	610
2	1115	2,050	1,610	1,830
3	1140	700	720	710
4	1150	1,030	960	995
5	1200	1,960	1,320	1,640
6	1220	1,260	1,060	1,160
7	1230	1,800	1,510	1,655
8	1255	2,480	2,890	2,685
9	1315	3,370	3,090	3,230
10	1330	200	290	245
11	1345	1,120	990	1,055
12	1355	1,070	1,200	1,135
13	1410	1,850	2,120	1,985
14	1430	1,540	1,720	1,630
Total		21,010	20,120	20,565

^aEstimates are by 10's.

^bTimes are Bering Daylight Time.

Table 4. Murre census results from Bluff, 1981.^a

Section	<u>15 July</u>	<u>19 July</u>
	Observer F	Observer F
End-C	7,410	5,080
C-D	8,485	8,415
D-E	3,900	3,820
E-F	3,750	3,990
F-G	1,520	1,280
G-H	1,230	1,430
H-I	3,400	3,630
I-J	280	200
Total	29,975	27,845
Time at end (Bering Daylight Time)	1010	1110
Time at J (Bering Daylight Time)	1935	1900

^aEstimates are by 10's.

TABLE 5 Summary of census results of murres in northern Alaska.

Year	Colony								
	Cape Lisburne		Cape Lewis		Cape Thompson ¹		Bluff	St. Lawrence Is. ²	
	Raw	Standardized ³		Raw		Raw	Standardized ³	Average ⁴	Raw
1960					251,000	357,000			
1972								32,000	
1975							70,000		
1976	130,000	184,000			157,000	199,000	50,000	16,000	
1977	131,000	184,000	19,000		143,000	171,000	38,000		
1978 ⁵	126,000	172,000					40,000		
1979 ⁵	142,000	246,000			114,000	149,000	35,000		
1980 ⁵	173,000	174,000					31,000		
1981 ⁵	149,000	153,000	21,000				29,000	34,000	

¹Data for 1960 are from L.G. Swartz (unpubl. data).

²Owallow Mtn. study area only; data for 1972 are from S.R. Johnson (unpubl. data); data for 1976 are from Searing (1977).

³Data have been standardized for differences in counting times during the day (see Springer and Roseneau 1978 and Murphy *et al.* 1980).

⁴Average of two or three complete counts (see Murphy *et al.* 1980); data for 1975-1979 are from Drury *et al.* 1981.

⁵Estimate based on partial census.

Table 6. Murre breeding phenology: dates of first hatching and first sea-going at colonies in the northern Bering Sea and eastern Chukchi Sea.

A. First Hatching

Year	Cape Lisburne ^b	Cape Thompson ^b	St. Lawrence Island ^d	Bluff ^c
1959	---	~4 Aug ^e	---	---
1960	---	30 Jul	---	---
1961	---	27 Jul	---	---
1972	---	---	30 Jul	---
1975	---	---	---	~24 Jul
1976	~6 Aug	9 Aug	31 Jul	~27 Jul
1977	1 Aug	1 Aug	---	3 Aug
1978	21 Jul	~23 Jul	---	15 Jul
1979	22 Jul	22 Jul	---	~15 Jul
1980	1 Aug	---	---	<19 Jul
1981	26 Jul	---	20 Jul	11 Jul

B. First Sea-going

Year	Cape Lisburne ^b	Cape Thompson ^b	St. Lawrence Island ^d	Bluff ^c
1959	---	25 Aug	---	---
1960	---	18 Aug	---	---
1961	---	19 Aug	---	---
1972	---	---	18 Aug	---
1975	---	---	---	~10 Aug
1976	28 Aug	~30 Aug	21 Aug	~14 Aug
1977	20 Aug	23 Aug	---	20 Aug
1978	11 Aug	13 Aug	---	31 Jul
1979	14 Aug	11 Aug	---	2 Aug
1980	~22 Aug	---	---	>24 Jul
1981	~16 Aug	---	~11 Aug	~29 Jul

^aData for 1959-1961 at Cape Thompson are from Swartz (1966 and unpubl. data); data for 1972 at St. Lawrence Island are from Johnson and West (1975) and S. R. Johnson (unpubl. data); data for 1975 at Bluff are from Drury (1976); data for 1976 at St. Lawrence Island are from Searing (1977); data for 1976 at Bluff are from Steele and Drury (1977); data for 1977 at Bluff are from Biderman *et al.* (1978); data for 1978 at Bluff are from Ramsdell and Drury (1979);

^bData for Cape Thompson and Cape Lisburne are for thick-billed murres. Approximate dates were calculated from first hatching or sea-going using an average chick age of 22 days.

^cData for Bluff are for common murres. Approximate dates were calculated from first hatching or sea-going dates using an average chick age of 19 days (see Ramsdell and Drury 1979). Wherever approximate dates are given for both hatching and sea-going in the same year, dates were estimated from whatever information the authors provided.

^dData for St. Lawrence Island in 1981 are for thick-billed murres, and data for 1972 and 1976 are assumed to be representative of this species. Johnson and West's (1975) data indicate that the phenologies of both species were similar in 1972, and Searing (1977) did not note any major differences between the two species in 1976. Since both studies reported first dates of both events, any bias would probably favor thick-billed murres as they may hatch and go to sea slightly earlier than common murres (e. g., Fay and Cade 1959, Swartz 1966).

^eSwartz (1966) reported 11 August as the date thick-billed murre chicks were first seen in 1959. We adjusted this date on the basis of a chick age of 22 days and the date of first sea-going (25 Aug) to better reflect the date of hatching that year.

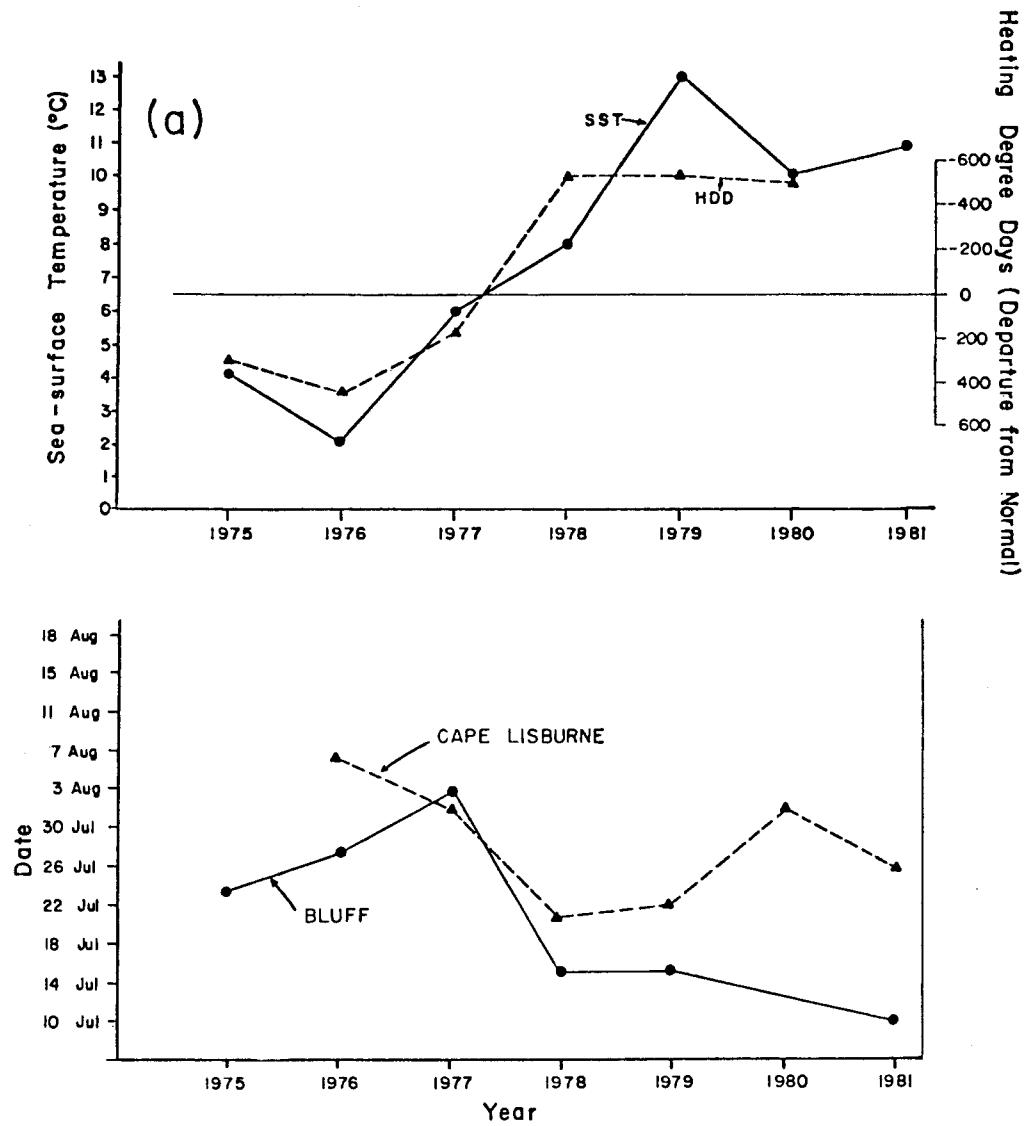


Figure 5. Relationships between environmental change and murre breeding phenology. (a) Sea-surface temperature near Cape Lisburne (mean date = 16 July, $s = 3$ days), and departure from normal heating degree days in April-July at Nome. (b) Date of first hatching of murre eggs.

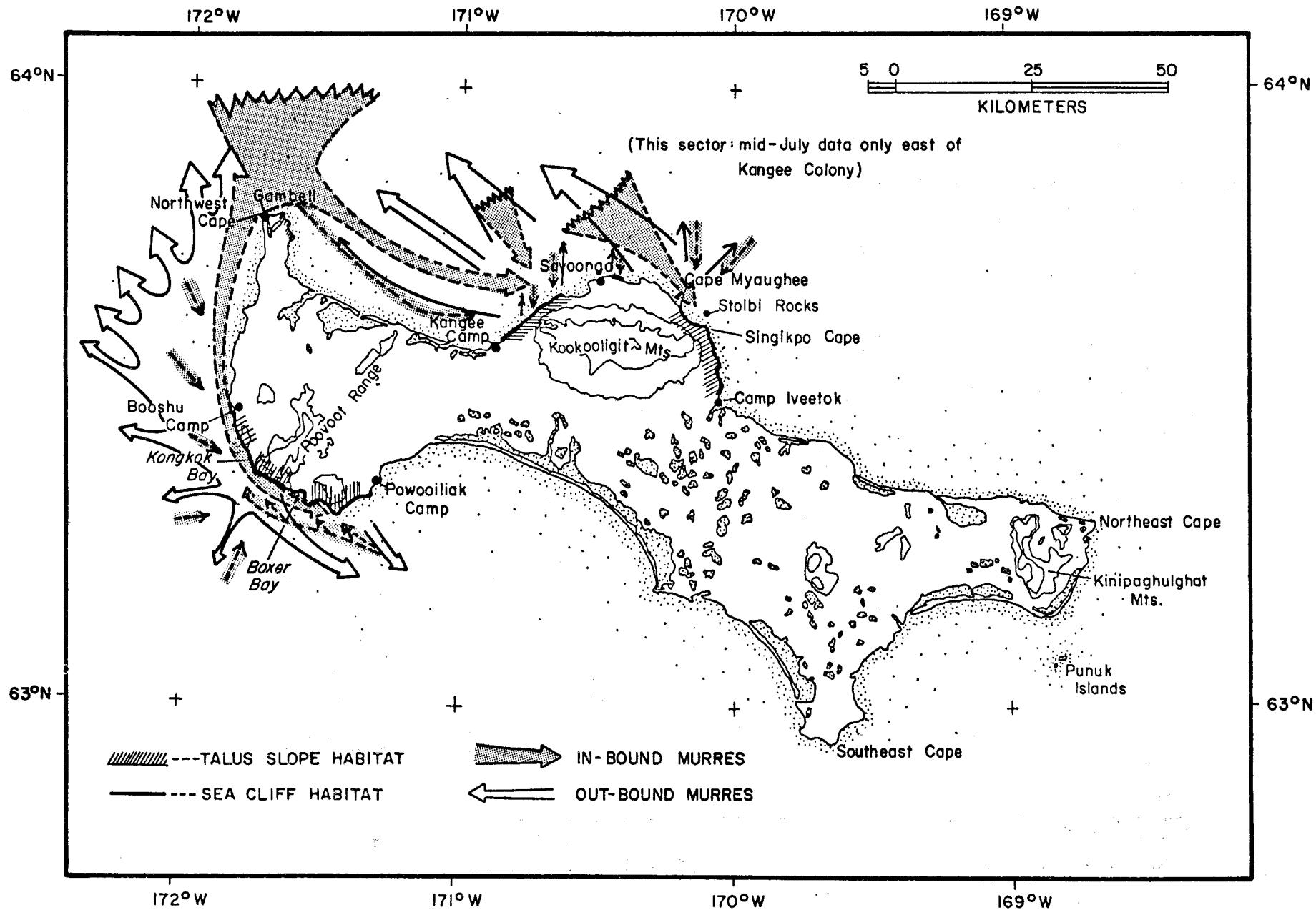


Figure 6. Flight directions followed by murres at St. Lawrence Island, mid-July through mid-August 1981.

Smaller numbers of murres nesting at Owalit, Ivezkan and Southwest colonies departed to and returned from a southeasterly direction (Figure 6). This flight pattern was most evident at Boxer Bay and Southwest Cape, where some inbound birds carrying fish turned into Southwest Colony and others continued past Boxer Bay toward Kongkok Bay. Smaller numbers of murres also occasionally fed directly offshore of all three colonies.

Flight patterns of murres nesting in the southwestern sector of the island did not change substantially during mid-July through mid-August, but murres spent more time in front of the colonies after the first week of August. Activity, including some feeding in front of the cliffs, increased as the chicks neared sea-going age. Drury *et al.* (1981) observed concentrations of murres near the southwestern sector colonies after mid-August in 1978. We believe that these concentrations were also primarily the result of sea-going activities.

We also observed the inbound and outbound flight directions taken by murres commuting between breeding colonies in the north-central sector of the island and offshore feeding areas on 18-19 July and 12 August. Most murres nesting at Kangee, Savoonga and Myaughee colonies departed to and returned from the north and northwest (Figure 6). The flight pattern indicated that these birds shared the same general foraging area used by murres nesting in the southwestern sector of the island.

Movements of murres to and from the north-central sector colonies occurred on a broad front. Many murres returned from the north and northeast to the vicinity of Sevuokuk Mountain, where they turned eastward after separating from the flocks traveling toward the southwestern sector of the island. Murres that turned eastward at Sevuokuk Mountain rarely intercepted the coast west of Kangee Colony; instead, the majority remained several kilometers or more offshore as they flew directly across the large embayment between Sevuokuk Mountain and Savoonga toward Kangee Colony. Many other flocks of murres apparently turned southeastward toward Kangee, Savoonga and Myaughee colonies at greater distances offshore. These flocks intercepted the southeasterly flow of birds at various points along the northwestern coast of the island. Some murres at Myaughee Colony also departed toward and returned from north and northeasterly directions. We have no information on flight directions taken by murres nesting southeast of Cape Myaughee at Singikpo, Kitnik or Ivetek colonies, except that some murres appeared to be flying past Myaughee Colony without stopping there.

Flight patterns of murres at St. Lawrence Island indicate that the majority travel long distances to feed during most of the breeding season. Murres from the southwestern sector colonies may regularly fly in excess of 70 km each way to forage north of Northwest Cape. Many murres from colonies in the north-central sector of the island may commute similar distances each way to feed in the same area. Flight patterns between the primary foraging area and the colonies change little from year to year. In 1981, murres from the southwestern sector of the island followed the same basic flight pattern used in 1972 (Johnson unpubl. data) and 1976 (Searing 1977), and indeed, as used in almost all years (L. Iyakitan pers. comm.). These observations demonstrate the annual importance of food-rich Anadyr Strait and its out-flow to foraging seabirds.

Cape Lisburne

The majority of murres nesting at Cape Lisburne in the eastern Chukchi Sea fed north and northeast of the colony during our late July-early August visit. Murres regularly forage northeast of the colony in Ledyard Bay during early and mid-summer, and north to northwest of the Cape after early August (see Springer and Roseneau 1977, 1978; Springer *et al.* 1979; Springer *et al.* 1982).

Bluff

The majority of murres nesting at Bluff dispersed widely to feed offshore in Norton Sound during mid-July through mid-August in 1980 and during our mid-July visit in 1981, a pattern typical of past years (see Drury *et al.* 1981).

B. Black-legged Kittiwakes

Census

Results of our 1981 censuses of black-legged kittiwakes at colonies in the northern Bering and eastern Chukchi seas are presented in Tables 7-9. All censuses of kittiwakes at these colonies, and at Cape Thompson, since 1976 are summarized in Table 10.

St. Lawrence Island

Photographs were taken of several census plots to provide a basis for comparisons of numbers in future years. Numbers of birds and nests have not yet been counted from these photographs.

Cape Lisburne

We counted kittiwakes on 10 of the 75 census plots, and recounted kittiwakes on 6 of those 10 plots at Cape Lisburne in 1981 (Table 7). These data were used to estimate the total number of birds present on the cliffs, and the resulting estimate of approximately 14,000 individuals was nearly identical to our previous estimates at this colony (Table 10). These data suggest that little change has occurred in the size of the kittiwake population during the last five years.

Cape Lewis

We first censused kittiwakes at Cape Lewis in 1977 (Springer and Roseneau 1978). Plots 1-7, half of all plots, were censused in 1978. That count indicated an increase of over 100% in the number of kittiwakes between 1977 and 1978 (Table 10). We were unable to census the colony in either 1979 or 1980; however, brief observations of it in both years also suggested that many more kittiwakes were present than in 1977. Our 1981 census of 5,228 individuals (Table 8) confirms our previous impressions - over twice as many kittiwakes were present at Cape Lewis in 1981 than in 1977.

Table 7. Black-legged kittiwake census results from Cape Lisburne, 1981.^a

Plot	time ^b	25 July						2 August						
		Observer F		Observer K		\bar{x} (birds)	\bar{x} (nests)	time	Observer F		Observer K		\bar{x} (birds)	\bar{x} (nests)
birds	nests	birds	nests	birds	nests				birds	nests	birds	nests		
11	1815	201	159	196	156	199	158	2000	193	153	216	158	205	156
12	1840	164	140	227	207	196	174	2015	161	148	161	142	161	145
25	1910	41	34	40	33	41	34	2030	42	40	54	50	48	45
26	1920	281	243	205	180	243	212	2045	258	241	238	223	248	232
30	1935	112	99	137	118	125	109	2100	142	132	161	146	152	139
32	1950	48	43	41	36	45	40	2140	37	32	43	37	40	35
SUBTOTAL		847	718	846	730	847	724		833	746	873	756	854	752
65	2020	309	281	310	262	310	272							
66	2045	45	42	41	38	43	40							
70	2100	110	109	121	117	116	113							
72	2110	129	119	127	116	128	118							
TOTAL		1,440	1,269	1,445	1,263	1,446	1,270							

^aCounts are by 1's.

^bTimes are Bering Daylight Time.

Table 8. Black-legged kittiwake census results from Cape Lewis, 2 August 1981.^a

Plot	time ^b	Observer F		Observer K		\bar{x} (birds)	\bar{x} (nests)
		birds	nests	birds	nests		
1	1055	120	90	121	81	121	86
2	1115	339	269	342	250	341	260
3	1140	80	65	75	59	78	62
4	1150	218	181	202	151	210	166
5	1200	686	592	538	454	612	523
6	1220	259	225	263	215	261	220
7	1230	513	464	584	458	549	461
8	1255	607	543	440	363	524	453
9	1315	799	729	513	473	656	601
10	1330	74	64	68	55	71	60
11	1345	493	443	406	370	450	407
12	1355	520	478	552	508	536	493
13	1410	659	575	556	497	608	536
14	1430	198	178	224	191	211	185
Total		5,565	4,896	4,884	4,125	5,228	4,513

^aCounts are by 1's.

^bTimes are Bering Daylight Time.

Table 9. Black-legged kittiwake census results from Bluff, 1981.^a

Section	15 July						19 July					
	Observer F		Observer K		\bar{x} (birds)	\bar{x} (nests)	Observer F		Observer K		\bar{x} (birds)	\bar{x} (nests)
	birds	nests	birds	nests			birds	nests	birds	nests		
End-C	2,056	1,787	2,141	1,573	2,099	1,680	2,138	1,931	2,473	2,238	2,306	2,085
C-D	2,037	1,716	2,107	1,809	2,072	1,763	2,341	1,975	2,384	2,049	2,363	2,012
D-E	963	852	1,033	893	998	873	1,502	1,260	1,419	1,243	1,461	1,252
SUBTOTAL	5,056	4,355	5,281	4,275	5,169	4,316	5,981	5,166	6,276	5,530	6,130	5,349
E-F	ND ^b	ND	1,101	996	ND	ND	1,316	1,178	1,389	1,205	1,353	1,192
F-G	ND	ND	830	705	ND	ND	923	780	1,006	847	965	814
G-H	ND	ND	381	325	ND	ND	416	332	623	450	520	391
H-I	ND	ND	1,209	971	ND	ND	1,364	1,088	1,310	1,053	1,337	1,071
I-J	353	275	394	260	374	268	352	281	460	297	406	289
TOTAL			9,196	7,532			10,352	8,825	11,064	9,382	10,711	9,106
Time at A	11:10 Bering Daylight Time						10:08 Bering Daylight Time					
Time at J	19:00		"		19:35		"					

^aCounts are by 1's.

^bND = No data (not counted or counts not completed).

TABLE 10. Black-legged kittiwake census summaries for colonies in northern Alaska, 1975-1981.

Colony	1975	1976	1977	1978	1979	1980	1981
Bluff ^a	7,250	7,000	7,400	6,600	9,000	9,900	10,700
Cape Thompson	ND ^b	10,500	10,200	15,200 ^c	16,800	ND	ND
Cape Lewis	ND	ND	2,300	5,800 ^d	ND	ND	5,200
Cape Lisburne	ND	ND	14,700	15,400 ^e	17,300 ^e	ND	16,300

^aData for 1975-1976 are from Steele and Drury (1977); data for 1977 are from Biderman *et al.* (1978); data for 1978 are from Ramsdell and Drury (1979).

^bND = no data.

^cEstimate derived from the count of Colony 4 only. The value is the mean ($S=1900$) of three estimates of the 1978 colony total. The estimates were derived by using each of the other three years as bases for extrapolating the colony total from counts at Colony 4 in 1978.

^dEstimate derived from a count of 50% of the census plots. The value is the mean ($S=380$) of two estimates of the 1978 colony total. The estimates were derived by using each of the other two years as bases for extrapolating the colony total from partial counts in 1978.

^eEstimate derived from counts of selected census plots within the colony.

Bluff

We completely censused kittiwakes at Bluff in 1981 (Table 9). The total number of individuals counted, 10,711, was nearly identical to the total number of individuals counted in 1980, but the population clearly increased after 1977-1978 (Table 10).

Phenology

Mean hatch dates of black-legged kittiwake eggs at St. Lawrence Island, Cape Lisburne, Bluff and Cape Thompson are summarized in Table 11.

Kittiwakes at St. Lawrence Island bred a few days earlier in 1981 than kittiwakes at Cape Lisburne, but about one week later than kittiwakes at Bluff. Hatching of kittiwake eggs at Owalit and Ivezkan colonies at St. Lawrence Island began about 18 July, based on weights of chicks on 21 and 23 July. The peak of hatching occurred about 22 July. Of 16 eggs checked on 21 July, 7 had hatched, 4 were pipping and 5 were unpipped. Eighteen eggs were checked on 23 July at two other plots: 11 were hatched, 3 were pipping and 4 were unpipped. Three of the 4 unpipped eggs proved to be addled and only 1 of them hatched at a later date. Hatching was essentially complete by 1 August.

Kittiwake eggs at Cape Lisburne began hatching about 21 July, based on weights of chicks on 25 July. The peak of hatching occurred about 26 July, based on chick growth rates, but actually may have occurred a few days later, based on direct observations. Sixty-seven of 237 eggs had hatched by 25 July, and by 31 July 103 of 188 eggs had hatched. Hatching was still occurring when we departed on 5 August and may not have been complete until several days later.

Weights taken of kittiwake chicks at Bluff indicated that hatching commenced about 7 July, the date of our arrival. Hatching peaked about 15 July, based on chick growth rates, but may have occurred about two days later, based on chick observations. Sixteen of 152 eggs had hatched by 10 July, and 64 of 141 eggs had hatched by 16 July. Hatching was nearly complete by 22 July.

Phenological data on kittiwakes at colonies in the northern Bering Sea and the eastern Chukchi Sea (Table 11) have followed the same pattern demonstrated for murres (Table 6). Breeding schedules at Cape Lisburne and Cape Thompson have been similar, but consistently later than breeding schedules at St. Lawrence Island and Bluff. Kittiwakes have always bred earlier at Bluff than at any of the other colonies.

Phenological changes among years at each colony have also followed a consistent trend. Kittiwakes bred latest in the mid-1970's and earliest in the late 1970's and early 1980's.

Differences between kittiwake breeding schedules at St. Lawrence Island, Bluff and Cape Thompson/Cape Lisburne are probably associated with latitudinal climatic differences, as with murres. Average spring and early summer conditions at St. Lawrence Island are somewhat warmer than at Cape Lisburne

Table 11. Black-legged kittiwake breeding phenology: dates of peak hatching at colonies¹ in the northern Bering Sea and the eastern Chukchi Sea.

Year	Cape Lisburne	Cape Thompson	St. Lawrence I	Bluff
1975	----	----	----	29 Jul ²
1976	15 Aug ³	12 Aug ⁴	27 Jul ⁵	30 Jul ²
1977	14 Aug	3 Aug	----	1 Aug ²
1978	6 Aug	----	----	22 Jul
1979	25 Jul	29 Jul	----	16 Jul
1980	26 Jul	----	----	15 Jul
1981	26 Jul	----	23 Jul	15 Jul

¹Dates are estimated from weights of chicks when first found and from subsequent growth rates, unless otherwise noted. We have standardized our method of calculating hatching dates from chick weights and growth rates, and this has resulted in some minor adjustments between dates reported here and dates reported by Murphy *et al.* (1980).

²Data are from Drury *et al.* (1981).

³Chicks were not weighed; estimate is based on sizes of chicks relative to those at Cape Thompson.

⁴Chicks were not weighed; estimate is based on direct observation.

⁵Data are from Searing (1977); estimate is based on date the first of two total eggs was found and an incubation period of 28 days (see Swartz 1966).

and Cape Thompson, but all three of these locations, aligned with Bering Strait, share typically cooler regional climates than that which occurs to the east at Bluff, in relatively well-protected Norton Sound (Brower *et al.* 1977a, 1977b).

Changes in breeding schedules of kittiwakes between the mid-1970's and the early 1980's are clearly related to regional physical conditions (Figure 7) (see Springer *et al.* 1982). Unusually cold conditions prevailed in the mid-1970's, but after 1976 conditions became warmer and kittiwakes nested progressively earlier each year during 1977-1979. Changes in breeding schedules after 1979 continued to reflect changes in environmental conditions; sea-surface temperatures were somewhat cooler in the northern Bering-eastern Chukchi region in 1980, but somewhat warmer again in 1981.

Productivity and Growth Rates

Productivity data on black-legged kittiwakes at St. Lawrence Island, Bluff and Cape Lisburne are presented in Tables 12-14 and are summarized in Figure 8. Growth rates of kittiwake chicks at these colonies and at Cape Thompson since 1977 are summarized in Table 15.

The pattern of productivity between kittiwakes nesting at colonies in the northern Bering Sea and the eastern Chukchi Sea followed the same pattern as phenology. Productivity of kittiwakes at St. Lawrence Island was perhaps slightly higher than productivity at Cape Lisburne, but apparently lower than productivity at Bluff. Productivity at St. Lawrence Island was not especially high or low in 1981, although it was considerably better than in 1976 when a reproductive failure occurred there (Searing 1977). Similar changes in productivity of kittiwakes occurred at Cape Lisburne, Cape Thompson and Bluff during the same years (Drury *et al.* 1981, Springer *et al.* 1982).

Differences in productivity of kittiwakes between the mid-1970's and the early 1980's are clearly related to regional physical conditions, just as are differences in phenology (Figure 7). Although our measurements of the physical environment are not strictly the same, they are comparable to other measurements that have been shown to be significantly correlated in the Bering Sea (Niebauer 1980, 1981a, 1981b). Air temperature affects water temperature, which is in turn related to the abundance of important prey populations for kittiwakes (Springer *et al.* 1982).

The average growth rate of kittiwake chicks at St. Lawrence Island was about 47% higher than at Cape Lisburne, and about 35% higher than at Bluff (Table 15). Also, growth rates at St. Lawrence Island were significantly higher during the second week of the weighing interval (22.5 g day^{-1} , $s=5$) than during the first week of the weighing interval (16.5 g day^{-1} , $s=3$) (Wilcoxon Rank Sum Test, $P<0.05$). These data suggest that food availability to kittiwakes during the second weighing interval was higher than during the first weighing interval, and was higher during both intervals at St. Lawrence Island than at either Bluff or Cape Lisburne.

The average growth rate of kittiwake chicks at Cape Lisburne was about

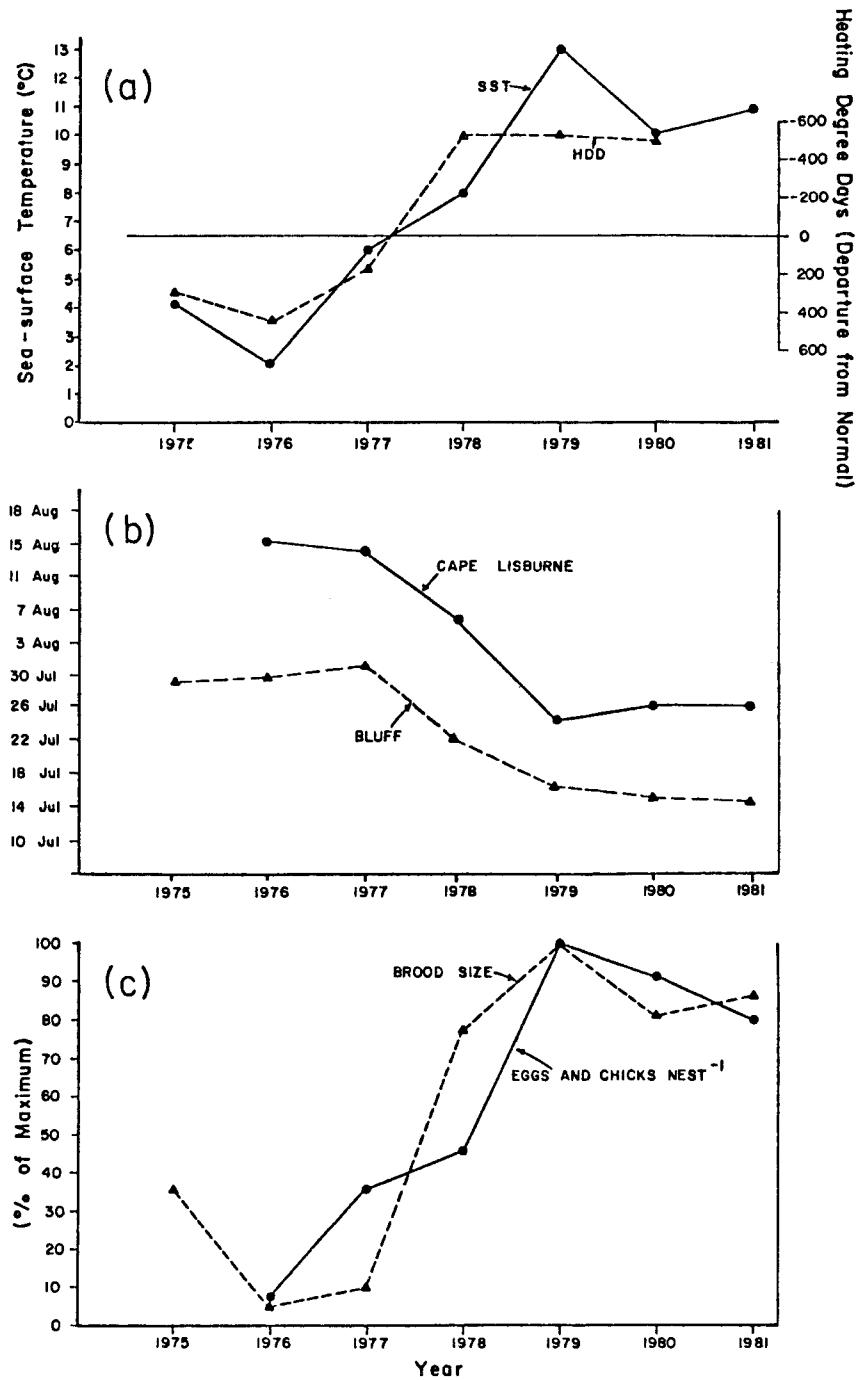


Figure 7. Relationships between environmental change, kittiwake nesting phenology and estimates of kittiwake reproductive success at Cape Lisburne and Bluff. (a) Sea-surface temperature near Cape Lisburne (mean date = 16 July, $s = 3$ days), and departure from normal heating degree days in April-July at Nome. (b) Mean date of hatch of kittiwake chicks. (c) Numbers of kittiwake eggs and chicks nest^{-1} in first week of hatch at Cape Lisburne (as a percentage of maximum = 1.7 eggs and chicks nest^{-1}), and kittiwake brood size in the late chick period at Bluff (as a percentage of maximum = 1.03 chicks nest^{-1}). Data for 1980 and 1981 at Bluff are from the early chick period; data for 1975-1978 at Bluff are from Drury *et al.* 1981.

Table 12. Black-legged kittiwake nest contents at St. Lawrence Island, 1981.

Date	Empty	1 egg	2 eggs	3 eggs	1 chick	2 chicks	1 egg & 1 chick
21-23 July	3	4	9	0	11	9	5
30 July- 1 August	4	3	2	0	28	5	1
8-9 August	9	0	0	0	31	3	0

Table 13. Black-legged kittiwake nest contents at Bluff, 1981.

Date	Empty	1 egg	2 eggs	3 eggs	1 chick	2 chicks	1 egg & 1 chick
10 July	6	18	53	2	2	4	6
16 July	8	15	23	2	16	19	10
20 July	9	11	5	0	46	14	6
22 July	11	8	0	0	53	10	9

Table 14. Black-legged kittiwake nest contents at Cape Lisburne, 1981.

Date	Empty	1 egg	2 eggs	3 eggs	1 chick	2 chicks	1 egg & 1 chick
25 July	36	39	59	1	9	24	10
31 July	51	22	24	0	42	23	15
3 August	69	13	10	0	67	15	10

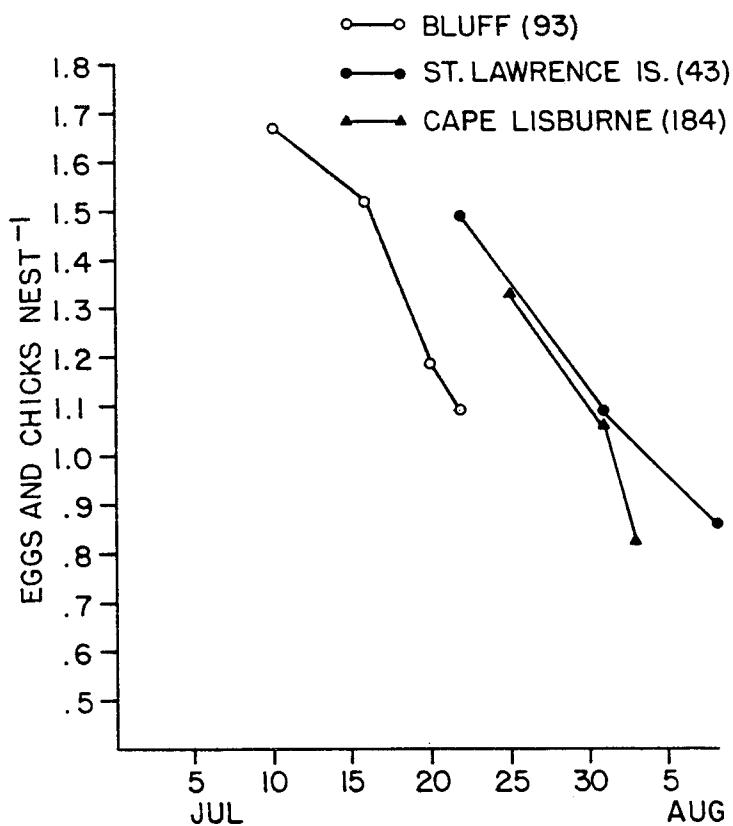


Figure 8. Contents of black-legged kittiwake nests at Bluff, St. Lawrence Island and Cape Lisburne, 1981.

20% lower in 1981 than in 1980, and about 25% lower than growth rates in 1977-1979 (Table 15).¹ A similar trend was apparent at Bluff, where the average growth rate of chicks was about 11% lower in 1981 than in 1978 and 1980, and about 24% lower in 1981 than in 1979. These data suggest that mid-season food availability declined in the eastern Chukchi Sea and Norton Sound in the cooler years following the exceptionally warm year of 1979. The differences in chick growth rates between Cape Lisburne and St. Lawrence Island, and between Bluff and St. Lawrence Island in 1981 indicate that less food was available to kittiwakes in the eastern Chukchi Sea and Norton Sound than in the waters near Anadyr Strait that year. Changes in food availability between years are related to changing environmental conditions (Springer *et al.* 1982), and differences in food availability between colonies in a single year are also probably related to annual, local differences in regional physical conditions.

C. Auklets

All data on auklets are from St. Lawrence Island, the only study area visited in 1981 where auklets breed.

¹Values reported in Table 15 differ somewhat from those reported by Springer and Roseneau (1978), Springer *et al.* (1979) and Murphy *et al.* (1980) because we have revised our method of calculation (see Methods).

TABLE 15. Growth rates of black-legged kittiwake chicks in northern Alaska.

Year	Colony			
	Bluff	Cape Thompson	Cape Lisburne	St. Lawrence I.
1977	ND ^a	12.6 ± 3.6 (16) ^b	19.3 ± 2.9 (18)	ND
1978	17.9 ± 4.1 (22)	ND	19.7 ± 6.7 (21)	ND
1979	20.4 ± 4.4 (35)	20.2 ± 4.7 (111)	18.3 ± 1.4 (24)	ND
1980	17.6 ± 7.4 (30)	ND	17.9 ± 3.7 (43)	ND
1981	15.6 ± 4.5 (31)	ND	14.3 ± 3.0 (30)	21.0 ± 7.1 (15)

^aND = no data.

^bMean growth rate (g day^{-1}) ± standard deviation (sample size).

Phenology

In 1981, hatching of least auklet eggs in Kongkok Basin on Iveykan Mountain commenced about 24-25 July. On 25 July, when 11 nests were checked, 9 contained single eggs and 2 contained tiny chicks estimated to be about one day old. Seventeen nests were checked on 28 July. Thirteen of these contained single chicks (mean weight = 17.3g ± 5.0g) and four contained single eggs. By 5 August, hatching appeared essentially complete. The only eggs found on and after that date were addled.

Searing (1977) summarized phenological data on least auklets breeding at St. Lawrence Island. Previous dates when chicks were first found include 28 July 1964, 30 July 1965, about 27 July 1966, about 15 July 1967 and 25 July 1976. These dates correspond closely with our findings, with the exception of that given for 1967, a year when warm spring air temperatures caused an early snow melt (see Sealy 1975).

Productivity

Searing (1977) reported the fate of 16 of 34 least auklet chicks which hatched successfully at Kongkok Bay in 1976. Seven (44%) died or were killed by predators and nine (56%) survived to the age of fledging (about 32 days). The fate of 11 least auklet chicks to an age of about 15-16 days is known for 1981 at Iveykan Mountain. Four (36%) died or were killed by predators and 7 (64%) were still alive and healthy on 8 August, by which time they ranged in weight from 52g to 82g ($\bar{x} = 73.3\text{g}$).

Growth Rates

Mensural data for least auklet chicks at Iveykan Mountain in 1981 are

presented in Table 16. The average rate of weight gain of seven chicks during the interval 28 July-8 August was 4.7 g day^{-1} ($s=0.82$). That rate is 27% greater than the average growth rate of 10 chicks (3.7 g day^{-1}) during the period of maximum growth in 1976 (Searing 1977), but is similar to growth rates of least auklet chicks in 1966 (Sealy 1981).

These data are the first to suggest that important oceanic food webs might have been adversely affected by the unusually cold water temperatures and late springs of 1975 and 1976, as were neritic food webs in Norton Sound and the eastern Chukchi Sea (Springer *et al.* 1982). Food brought to least auklet chicks in 1976 was predominantly *Calanus plumchrus*. A preliminary examination of food brought to chicks in 1981 indicated that *C. cristatus* was the main item in diets that year. If we assume that adult auklets feed on the species of copepod which is most abundant in terms of biomass, without being too small to be taken efficiently (see Bédard 1969b), then we would conclude that *C. cristatus* was probably in low abundance compared to *C. plumchrus* in 1976, since the former is much larger than the latter and might well be selected for if numbers of the two species were equal. Although we cannot necessarily conclude that *C. plumchrus* was uncommon in 1981, or that *C. cristatus* was uncommon in 1976, we can be reasonably certain that the overall biomass of copepods was lower in 1976 than in 1981, as indicated by differences in chick growth rates between the two years.

Growth rates of least auklet chicks during the interval 5-8 August (6.7 g day^{-1}) were significantly greater than during the interval 28 July-5 August (4.6 g day^{-1}) (Wilcoxon Rank Sum Test, $P<0.05$). During the later interval, when north winds prevailed, adult least auklets from the Owalit Mountain and Ivezkan Mountain colonies fed in large numbers along the coast near Kongkok Bay. During the earlier period they regularly traveled long distances northward to feed in Anadyr Strait north of Northwest Cape. It was not clear whether shorter commuting distances, greater copepod biomass, or both were responsible for the greater growth rates of chicks during the second interval.

Foraging Areas

We collected some information of foraging flight directions of least and crested auklets at St. Lawrence Island in 1981. These data supplement observations provided by Fay and Cade (1959), Bédard (1969b), Searing (1977) and Drury *et al.* (1981).

Owalit Colony and Ivezkan Colony

The majority of least and crested auklets and many parakeet auklets nesting at Owalit and Ivezkan colonies foraged in Anadyr Strait and its outflow between mid-July and early August. The flight pattern to and from this important feeding area is shown in Figure 9. Most flocks (typically 50 or more birds flock $^{-1}$) departed northwestward toward Cape Chukotskiy and northward toward Northwest Cape. Huge numbers of least and crested auklets and some parakeet auklets, accompanied by large numbers of murres and small numbers of horned and tufted puffins, some kittiwakes, and occasional pelagic cormorants and pigeon guillemots, returned from the north and northeast toward Sevuokuk Mountain during the evening. The inbound flights

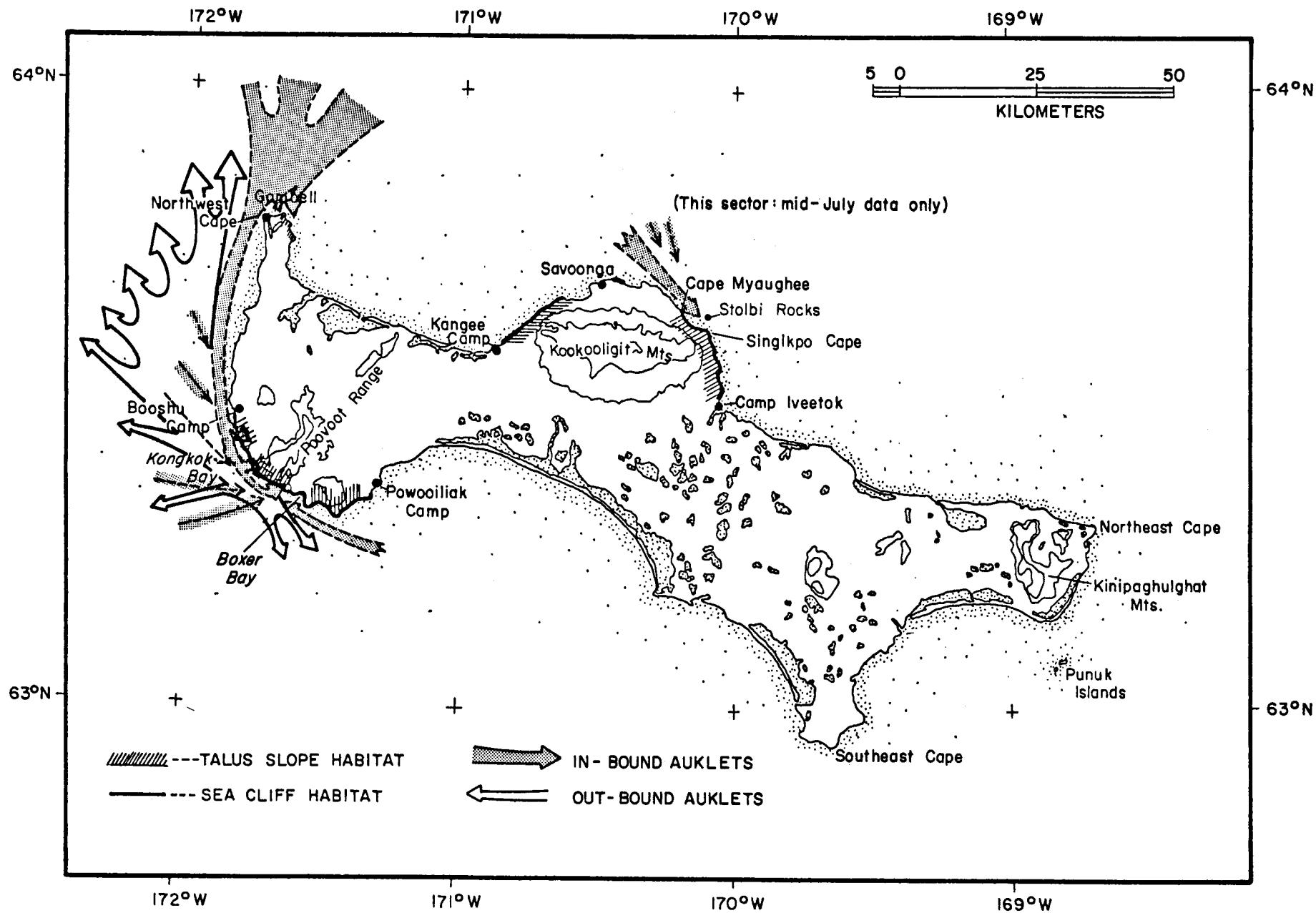


Figure 9. Flight directions followed by least and crested auklets at St. Lawrence Island, mid-July through mid-August 1981.

TABLE 16. Mensural data on least auklet chicks at St. Lawrence Island, 1981:
 T= tarsus length (mm); C= culmen length (mm); WT= weight (g).

Chick Number	28 July 1981			5 August 1981			8 August 1981		
	T	C	WT	T	C	WT	T	C	WT
1	16.0	6.0	19.5	17.5	6.5	44.0	17.8	7.0	52.0
2	16.5	6.5	22.5	17.8	8.3	60.0	18.7	8.2	79.0
3	16.0	6.5	22.5	18.3	6.8	56.0	18.7	7.5	73.0
3a				15.5	6.5	27.0	16.7	6.7	47.0
4	14.5	6.0	15.5	18.5	8.5	55.0	18.0	7.2	68.0
4a							19.0	8.4	78.0
5	17.0	6.7	26.0	18.5	7.4	60.0	19.4	7.5	80.0
6	14.3	5.5	13.0						
10	15.0	6.0	19.5	17.2	7.2	49.0	18.3	7.5	79.0
11	14.5	5.5	10.0						
12	14.5	5.5	13.5						
13	14.5	5.5	13.0	17.0	8.0	55.0			
14	16.0	6.5	22.5	19.0	8.5	54.0	18.8	7.6	82.0
14a							18.2	7.4	75.0
15	14.0	5.5	13.5						
17	14.5	5.5	14.0						

of auklets, consisting of near-constant strings of large flocks (typically hundreds of birds $flock^{-1}$), usually commenced about 1930 h, peaked between about 2030 h and 2300 h, and decreased noticeably by about 2330-2400 h. The majority of flocks in the flights approaching Sevukuk Mountain turned westward to round Northwest Cape and then streamed southward along the island's western coast.

Our best estimate of the magnitude of the southbound flights passing Gambell was obtained during a generally fog-free evening period on 17 July (Table 17). Subsequent boat trips between Gambell and Ivezan Mountain, and between Ivezan Mountain and Booshu Camp provided additional information. The returning flocks, forming a continuous stream of birds along the island's entire western coast, generally maintained a flight corridor several kilometers offshore of the island after passing Northwest Cape, and usually began to intercept and parallel the coast more closely near Booshu Camp before rounding Owalit Mountain and landing at the Owalit and Ivezan colonies.

The arrival of auklet flocks at Owalit and Ivezan colonies usually commenced about 2100 h and ended about 2400 h. On 23 July, for example, flocks began rounding Owalit Mountain and landing at the colonies at 2100 h, and by 2200 h tens of thousands of birds streamed in from the north to join those milling about in the air over the colonies. Arriving birds declined in number to about 1,000 per five-minute count by 2330 h and few birds appeared to arrive after about 0030 h. During the evening arrival period, some auklets also appeared to depart from the colonies.

A second period of intense activity occurred in the morning, usually between about 0400 h and 0800 h. Some flocks arrived at the colonies during this period, but many small flocks appeared to depart from them, dispersing northwestward, seaward of the route used by inbound flights. Many small flocks also appeared to depart throughout the remainder of the morning, and some occasionally departed or returned in the afternoon.

Although the majority of auklets nesting at Owalit and Ivezan colonies clearly fed in a major foraging area north and northwest of St. Lawrence Island's western end during mid-July through early August, small numbers also fed to the west. Several thousands of least and crested auklets, accompanied by some parakeet auklets, also fed southeast of Kongkok Bay. Flights returning from the southeast intercepted the coast near Southwest Cape, and flocks of birds with food-filled gular pouches paralleled the island's shoreline between Boxer Bay and Kongkok Bay.

Foraging flight patterns of auklets nesting at Owalit and Ivezan colonies changed in early August (Figure 10). After about 2-3 August, the majority of crested auklets ceased flying to and from the north and began departing to and returning from the west. This flight pattern was still evident at Gambell during 10-14 August; few outbound or inbound crested auklets passed Northwest Cape on those dates.

The majority of least auklets, accompanied by some parakeet auklets, continued to travel to and from the north until 6 August, by which time strong northeasterly winds had developed. The winds, varying between 30-80 $km\ h^{-1}$ and often gusting to 80-120 $km\ h^{-1}$, prevailed between the evenings

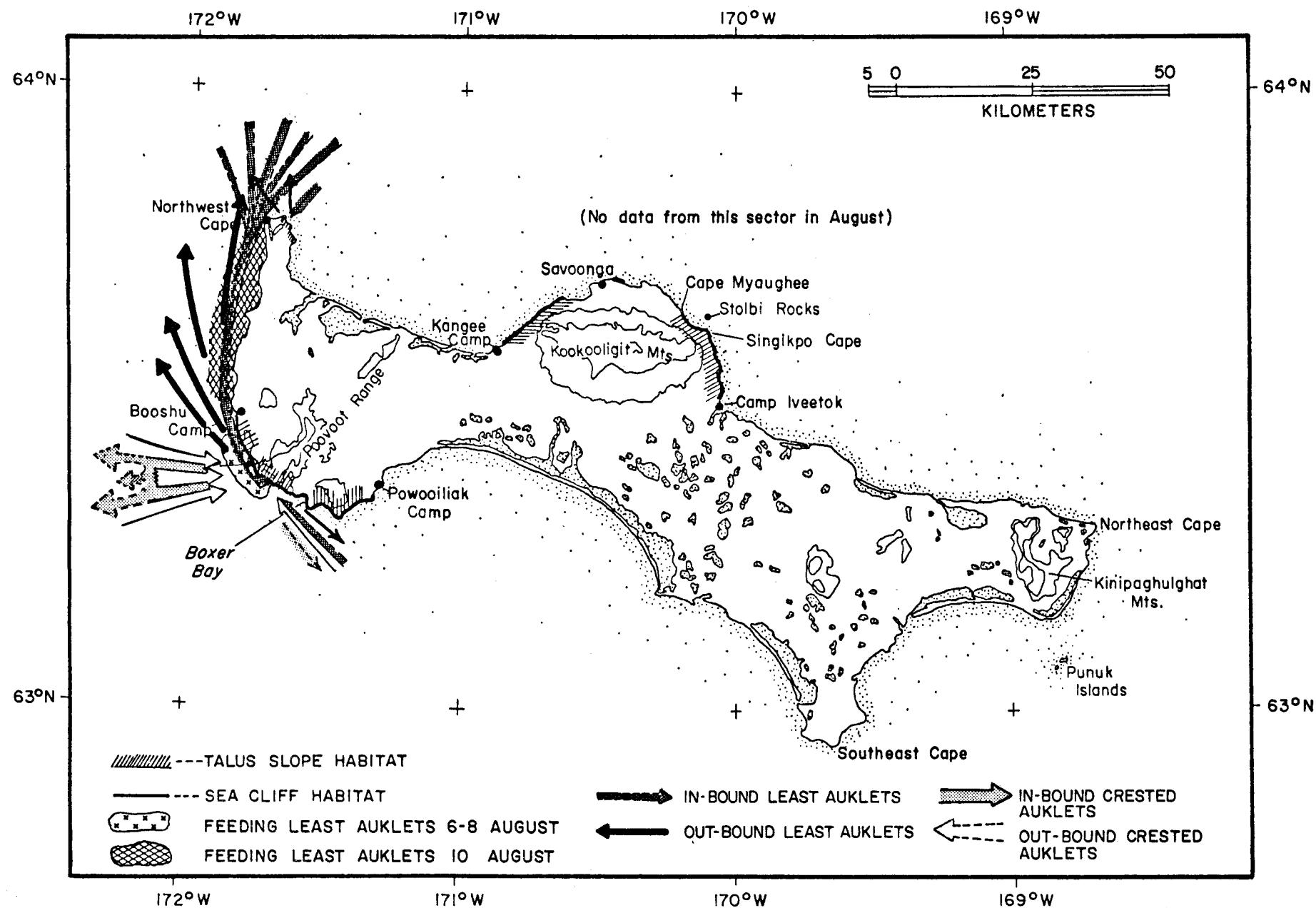


Figure 10. Flight directions followed by least and crested auklets at St. Lawrence Island, mid-August 1981.

of 5 and 8 August. During 6-8 August, large concentrations of least auklets fed in and near Kongkok Bay between the surf zone and a few kilometers offshore. Most least auklets resumed travel to and from the north with the advent of calmer conditions on 9 August, but many fed along the island's western coast in a zone of current slicks visible from the top of Ovalit Mountain. On the evening of 10 August, large numbers of feeding least auklets were dispersed over a calm sea among these north-south oriented slicks about 0.5-5.0 km offshore along the entire coast between Booshu Camp and Gambell. Surface waters in and near the slicks were richly laden with pteropods, medusae, ctenophores and other small invertebrates. Although many flocks of least auklets with distended gular pouches were flying southward past Northwest Cape, numbers were smaller than during previous weeks. Large numbers of southbound least auklets, accompanied by small numbers of parakeet auklets, passed Gambell during the evening of 11 August, but the magnitude of the evening flights appeared to decrease again during 12-14 August with the advent of increasing northerly winds.

Sevuokuk Colony

The majority of auklets nesting on Sevuokuk Mountain also foraged in Anadyr Strait and its out-flow during mid-July. Small flocks of departing least and crested auklets generally dispersed northwestward and northward from the colony, and returned from northerly and northeasterly directions. As large inbound flights approached Sevuokuk Mountain, flocks returning there separated from the streams of southbound auklets. Foraging flight patterns of Sevuokuk Mountain auklets appeared little changed in mid-August. Flocks of least and crested auklets were returning to the colony from northwesterly through northeasterly directions as we boated past Sevuokuk Mountain during the evening of 12 August.

Table 17. Five-minute counts of least and crested auklets flying south-westward past Gambell, St. Lawrence Island, ^aon 17 July 1981.

Time ^b	Observer C ^c	Observer E ^d	\bar{x}
2130-2135	20,000	18,100	19,050
2200-2205	30,000	25,000	27,500

^aThese estimates were obtained only from the eastern margin of the movement. Many other low-flying flocks were occasionally visible at much greater distances offshore.

^bBering Daylight Time.

^cObserver C estimated by 500's using 10x40 binoculars.

^dObserver E estimated by 100's using 7x50 binoculars.

Singikpo Colony

Our observations of foraging flight patterns of auklets nesting along St. Lawrence Island's northern coast, predominantly in the Singikpo Cape area, are limited to 18-19 July. On 18 July between 1600 h and 1900 h in the Cape Myaughee vicinity, we saw numerous small flocks of least and crested auklets flying southeastward. The flocks were arriving from northwesterly directions and were headed toward Singikpo Cape, the third major auklet nesting area on St. Lawrence Island. West of Kookoolik Cape, nearer Savoonga, few auklets appeared to intercept the island's coastline. Between Kookoolik Cape and Kangee Camp, small flocks of eastward traveling crested auklets were occasionally encountered between 1930 h and 2300 h. We saw only a few small flocks of crested auklets between Savoonga and Sevuokuk Mountain during the morning and afternoon of 19 July, and between Kangee Camp and Sevuokuk Mountain during the evening of 12 August. The major auklet flight corridor leading toward Singikpo Cape apparently remained well offshore.

Our observations of the foraging flight patterns of auklets nesting at St. Lawrence Island's western end corroborate other observations made there by Bédard (1969b), Searing (1977) and Drury *et al.* (1981). Observations in the north-central sector of the island provide additional evidence that auklets from all three primary nesting areas on the island feed predominantly in the same area in Anadyr Strait and its out-flow during much of the breeding season (see Bédard 1969b).

The basic flight patterns followed by auklets nesting at colonies in the western sector of the island were typical of annual patterns that have occurred regularly for many years (L. Iyakitan pers. comm.). The change in auklet foraging patterns observed after early August may also be a fairly regular event.

VIII. CONCLUSIONS

1. Numbers of murres have declined at Cape Thompson in the eastern Chukchi Sea, and a similar decline is continuing at Bluff in Norton Sound. We are currently investigating two possible reasons for these decreases, which involve effects of a changing environment on (a) natality of murres and (b) winter mortality of murres.
2. Numbers of murres have not appeared to change at Cape Lisburne or Cape Lewis as they have at Cape Thompson and Bluff. This difference could be explained by the movement of birds, particularly prospecting subadults, between colonies during a regional decline. Local differences in food availability could lead to intercolony movements by murres.
3. At Owalit Colony on St. Lawrence Island, numbers of murres were markedly lower in 1976 than in 1972 or 1981. Similarity in numbers of murres between 1972 and 1981, both climatically mild years, and the cold environmental conditions that coincided with the 1976 breeding season suggest that the 1976 decrease was a short-lived event rather than an actual decline in the population as has occurred at Cape Thompson and Bluff.
4. Environmental fluctuations during the 1970's had important repercussions on the breeding biology of murres, black-legged kittiwakes and least auklets in northern Alaska by affecting supporting food webs. Year-to-year differences in breeding phenology and reproductive success were strongly correlated with changing climatic conditions. Differences in breeding phenology and reproductive success between colonies in the same year were probably related to local differences in regional climates. Variations in food availability between locations in a given year are also probably related to local regional climatic conditions.
5. The current data base on relationships between seabird population parameters, physical conditions and food webs indicates the value of long-term, low-level monitoring efforts. The results of these integrated studies can provide the means to separate natural changes from changes that may occur as a result of resource development. The degree to which such changes can be separated will clearly measure the success of future programs that may attempt to detect and monitor effects of resource exploration and extraction.

IX. NEEDS FOR FURTHER STUDY

The data base on northern Bering-eastern Chukchi seabirds justifies the continuation of studies to monitor numbers, reproductive success and food habits of murres, black-legged kittiwakes and auklets in northern Alaska. These studies can effectively explore relationships between annual variability in population parameters of seabirds, physical environmental changes and changes in seabird food webs. Earlier OCSEAP-sponsored studies of seabirds in Alaska indicated that marked annual variability occurred in several population parameters. The current longer-term data

clearly show that annual variability in seabird populations is not random, but is related to and predictable from annual changes in the physical environment and regional food webs (see also Springer *et al.* 1982). Moderate levels of additional research in the coming years would provide a firm basis with which to more clearly differentiate between natural phenomena and changes resulting from resource development. Such an ability to separate natural phenomena from other changes is important to any monitoring effort.

Our studies have made progress toward identifying the causes of declines in murre numbers at Cape Thompson and Bluff. Additional research is necessary to refine and test our hypothesis (see Springer *et al.* 1982). We especially recommend an effort that will allow us to expand and test our population model at Bluff. Also, we have not ruled out the possibility that similar declines are occurring at other murre colonies in northern Alaska. Colonies that have been censused at least once in previous years, such as St. Matthew Island and the Pribilof Islands, should be checked again soon.

A program of studies to fulfill the above needs does not have to be especially costly; however, it needs to be well organized and designed to run for several years. Study sites would be selected on the basis of location and past history of investigation. They should range from northern latitudes (i.e., the Chukchi Sea) to southern latitudes (i.e., the southern Bering Sea and Gulf of Alaska), and should include offshore and coastal locations. Within this framework, colonies at Cape Lisburne, Cape Thompson and Bluff would serve as 'home-base' study sites because of the long histories of study at them, their northern latitudes and their location relative to regional climatic and oceanographic conditions. Bluff has a much warmer climate than Cape Lisburne and Cape Thompson, and it lies in Norton Sound well removed from the more dynamic oceanographic conditions of Bering Strait. Cooler conditions prevail in the eastern Chukchi Sea, and Cape Lisburne in particular lies on the edge of major currents flowing through that region. Colonies such as St. Lawrence Island, St. Matthew Island and the Pribilof Islands would serve as offshore study sites, and colonies in northern Bristol Bay would serve as southern coastal locations.

Within this large region it would be preferable to visit three or four study sites each year for several years; however, home-base study sites at Bluff and either Cape Thompson or Cape Lisburne would be visited every study year. Only one field team is required to accomplish the work at home-base sites because logistics are relatively simple and costs are minimal compared to many of the other colonies. One or two field teams would also work at one or two other colonies each year. These teams would alternate annually among the suite of selected study locations. Such a study design could:

1. Help clarify relationships between physical conditions, several seabird population parameters and food webs.
2. Establish a repeatable numeric monitoring system.

3. Monitor changes in seabird populations that might occur as a result of resource development.

There is a special need to resume work at St. Matthew Island as soon as possible because of strong industry interest to use part of the island as a staging area and support base for offshore exploration and development in the Navarin Basin. Development of support facilities, including a landing field for large transport aircraft, helicopter pads and fuel depots, has been proposed to begin as early as 1982. Although industry use of the island, currently designated a wilderness area, is being contested by the U.S. Fish and Wildlife Service (E. Baily pers. comm.), development may proceed in the near future. Murres have not been censused at St. Matthew Island since the first census there in 1977 (see DeGange and Sowls 1978). By the summer of FY 1982 it will have been five years since counts were made, an interval sufficiently long to allow significant changes in numbers to become apparent. A recensus of murres on St. Matthew Island would be an important precautionary measure, and would increase our understanding of declines in murres at more northern colonies. It would also increase our understanding of relationships between physical parameters, seabird food webs and seabird productivity. With little doubt, a recensus of murres would have the greatest value as an aid to understanding these changes if it were conducted before development and potential associated disturbance occurred. A recensus of murres at St. Matthew Island immediately prior to development would provide a firmer basis from which to detect effects of human actions, and to more clearly separate them from natural changes.

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APPENDIX

The estimate given by Searing (1977) of 60,000 murres at Owalit Mountain was derived from the unpublished data of S.R. Johnson, who censused this colony on 12 and 14 August 1972. Searing (1977) was not able to carefully examine Johnson's data; only raw scores for various sections of the colony were transmitted from Johnson to Searing (Johnson pers. comm.). Some details of the counting procedures were apparently omitted or unclear. Recently, we were able to examine Johnson's original field notes. Table 18 shows Johnson's 1972 censuses of Owalit Mountain. The 12 August census of the cliffs was incomplete; at least one large 'gully' and some other similar features which contained murres in plot D were not counted. A complete re-census of the cliffs was made on 14 August, when plot D was split into seven smaller areas (plots D-I, and K). Some areas counted during both censuses represented portions of adjacent air space or sea surface (area C, 12 and 14 August; areas J and L, 14 August). Searing's (1977) estimate of about 60,000 murres present in 1972 was incorrectly derived from the total of all murres counted in all habitats on both dates. The corrected estimate of approximately 32,000 murres¹ was derived from the total of all murres counted on the cliffs on 14 August 1972.

¹The 25,000 murres reported in Johnson and West (1975) refers only to the densest part of the Owalit Mountain Colony.

Table 18. Census data for Owalit Mountain, St. Lawrence Island,
12 and 14 August 1972.^a

Plot (Area)	<u>Number of Murres</u>			
	<u>12 August</u>		<u>14 August</u>	
	Flying	On Cliffs	Flying or on Water	On Cliffs
A		4,000		4,500
B		8,000		6,000
(C)	400-500 ^b		480 ^b	
D		9,500 ^c		2,500
E				6,500
F				4,500
G				6,350
H				245
I				860
(J)			1,250 ^d	
K				375
(L)			2,000 ^e	
Total	400-500	21,500	3,730	31,830

^aData are from unpublished field notes of S.R. Johnson, 1972.

^bThis number is an estimate of birds flying to and from plots A and B at the time of census.

^cThis number is an incomplete estimate of the cliff areas D-I, and K.

^dThis number is an estimate of birds on the water between areas I and K at the time of census.

^eThis number is an estimate of birds in the air offshore of plots D-I, and K at the time of census.

**POPULATION AND TROPHICS STUDIES OF SEABIRDS
IN THE NORTHERN BERING AND EASTERN CHUKCHI SEAS,
1982**

by

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**Final Report
Outer Continental Shelf Environmental Assessment Program
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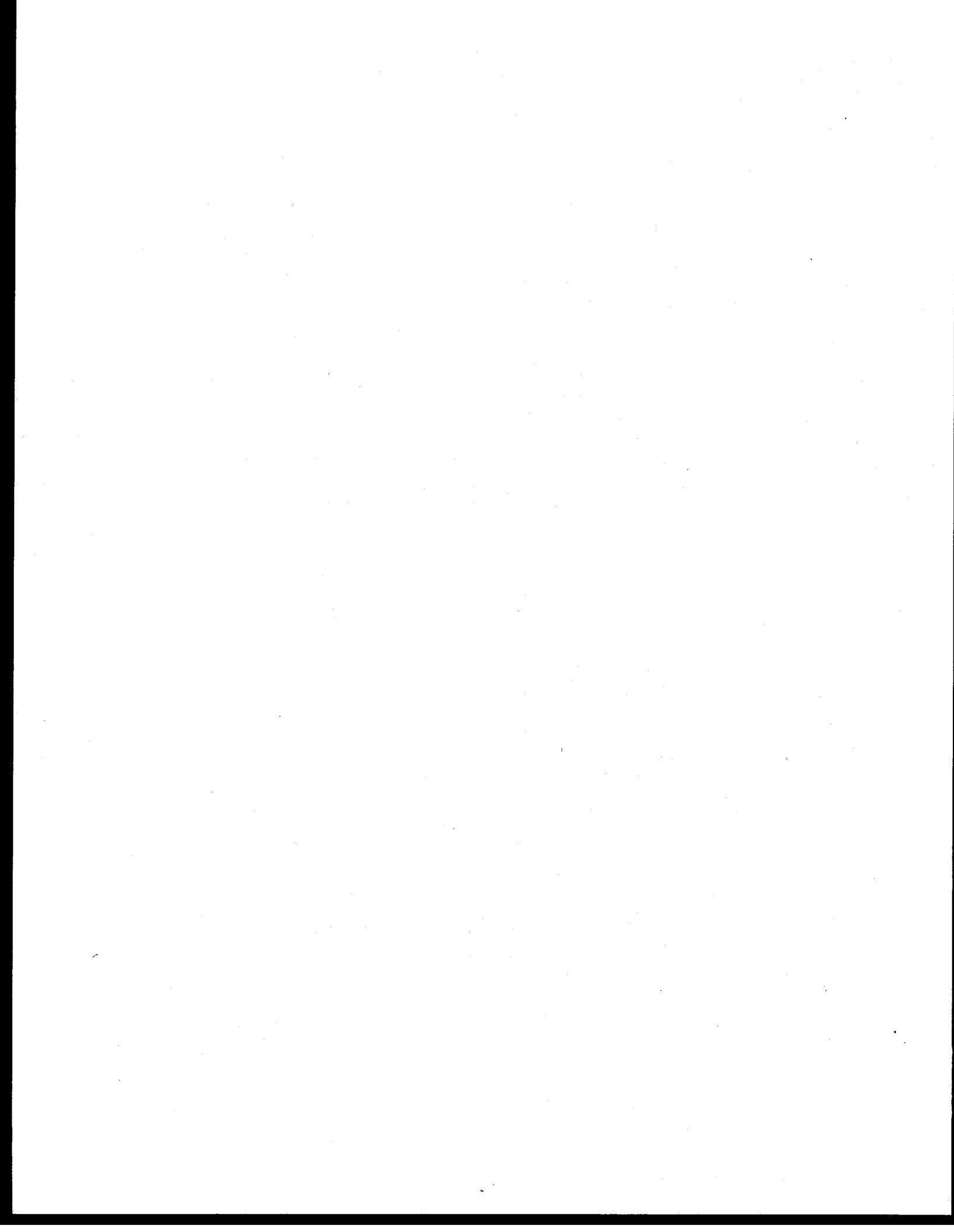


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I. SUMMARY OF OBJECTIVES, CONCLUSIONS AND IMPLICATIONS WITH RESPECT
TO OCS OIL AND GAS DEVELOPMENT

A. Objectives

The objectives of this study are to monitor numbers of seabirds at breeding colonies in the Bering and Chukchi seas, and to describe food web relationships and other ecosystem processes that determine the fate of the seabird populations.

B. Conclusions

Populations of piscivorous seabirds throughout the SE Bering Sea, particularly the murres (*Uria* sp.) and kittiwakes (*Rissa* sp.), were severely stressed in the spring and summer of 1982. As a result most pairs failed to produce young. A similar situation existed in 1981 on the Pribilof Islands and probably elsewhere that year. The numbers of murres were lower also at several colonies in 1982 than in the early-mid 1970's. We do not know if these numerical changes represent short-term decreases in response to extreme environmental conditions in the past two years, or long-term declines similar to the declines at Bluff and Cape Thompson.

The stress was apparently caused by a wide-spread food shortage, chiefly of walleye pollock (*Theragra chalcogramma*). A combination of environmental factors, such as the recent warm climatic period since 1977, and the commercial pollock fishery in the SE Bering, could have reduced pollock availability to the birds.

Limited data on the zooplanktivorous auklets in the SE Bering may indicate an opposite trend. Numbers of Least and Parakeet Auklets (*Aethia pusilla* and *Cyclorrhynchus psittacula*) were higher on the Pribilos in 1982 than in 1976, and growth rates of Least Auklet chicks were high on St. Matthew Island in 1982. Both of these observations imply that prey of the auklets was plentiful during the breeding season. If the number of juvenile pollock is depressed, it would reduce predation pressure on copepod stocks which would then become available in greater numbers to another copepod predator - auklets. Such trophic relationships have been observed elsewhere and are consistent with information on both the planktivorous and piscivorous seabird species.

Seabirds in the W Aleutian Islands and in the Gulf of Alaska reproduced normally in 1982. Reproductive success was low in Norton Sound but high at Cape Thompson. Cool spring temperatures probably account for the poor season in Norton Sound by adversely affecting fish prey populations. Fishes were abundant in the E Chukchi summer-long in 1982.

Murre numbers continued to decline at Bluff and Cape Thompson in 1982, but the decline was less than in prior years. An apparent stabilization of numbers may be a result of increasing recruitment following several years of good reproductive success, or an increasing balance between productivity and winter mortality.

C. Implications with Respect to OCS Oil and Gas Development

Information of the kind we are obtaining on seabird biology will help to differentiate between future changes in seabird populations that might

result from OCS oil and gas development, and those resulting from changes in the environment unrelated to OCS activity.

II. INTRODUCTION

A. General Nature and Scope of Study

Seabirds occupy top positions in marine food webs and thereby integrate many elements of ecosystems. Also, seabirds are easily studied and are sensitive indicators of change in the environment. Our studies take advantage of these characteristics to examine spatial and temporal differences in several marine food webs and the linkage between these food webs, regional physical processes and seabird biology.

Substantial declines in murre populations during recent years in Alaska have demonstrated the need for a system that will permit future monitoring of colonies as resource development increases on Alaska's continental shelf. Our studies are establishing present indices of seabird numbers at major breeding colonies in Alaska.

B. Specific Objectives

1. Census murres and kittiwakes on St. Matthew I., Bluff and Cape Thompson.
2. Establish permanent census plots for murres and kittiwakes on St. Matthew I.
3. Determine the breeding phenologies and levels of reproductive success of murres, kittiwakes and other seabirds at all locations.
4. Determine growth rates of murre, kittiwake and auklet chicks.
5. Collect specimens of seabirds, primarily murres, kittiwakes, Least Auklets and Crested Auklets (*Aethia cristatella*), for food habits information and as a means of sampling local marine organisms for distribution and relative abundance.

C. Relevance to Problems of Oil Development

The success of OCSEAP will depend in part on the ability to detect changes in marine biological systems and in part on the ability to distinguish naturally occurring changes from those that might result from resource development in Alaskan waters. OCSEAP sponsored studies of seabirds in the Bering and Chukchi seas have shown that many populations are very dynamic, largely the result of climatic change. Natural variability such as this could make it difficult to determine if activities or accidents were involved in species and community changes if they are detected in later years. This aspect of our work is acquiring added importance because of the recent declines in murre numbers and widespread breeding failures in the SE Bering.

III. CURRENT STATE OF KNOWLEDGE

Our 1982 field work extended long-term studies of seabirds at Bluff and Cape Thompson. Historical information on these colonies and results of past investigations of seabirds at them are summarized in Springer et al. (in press). Field work in 1982 on St. Matthew I. measurably expanded the small data base

acquired there previously. With one exception, references to seabirds on or near the island are general in nature (e.g., Townsend in Healy 1887, Hanna 1917, Bent 1919, Beals 1944, Gabrielson and Lincoln 1959, Klein 1959, Rausch and Rausch 1968, Irving et al. 1970, McRoy et al. 1971, Gould 1977, Sowls et al. 1978, Bartonek and Sealy 1979, Divoky 1981, Hunt et al. 1981). Only DeGange and Sowls (1978), as part of a faunal reconnaissance, provided detailed data on locations and numbers of birds in addition to information on species composition.

IV. STUDY AREAS

The locations of our 1982 study areas are shown in Fig. 1. Detailed information on Cape Thompson is provided in our previous annual reports (see Murphy et al. 1980) and in the Project Chariot report (see Wilimovsky and Wolfe 1966). Similar information on Bluff has been provided in the annual reports of the initial investigators (see Drury et al. 1981). We consulted DeGange and Sowls (1978) and provide the following summary information on St. Matthew I., Hall I. and Pinnacle I.

More than a million seabirds are estimated to nest on St. Matthew, Hall and Pinnacle islands (DeGange and Sowls 1978). The islands are located in the eastern Bering Sea at approximately $60^{\circ}27' N$, $172^{\circ}50' W$ which is about 350 km offshore of the Alaska mainland and 250 km northeast of the continental shelf break (Fig. 1). They are tundra-covered and are of volcanic origin (Dutro and Payne 1957). Their precipitous shorelines are composed of predominantly pillar basalt occurring in a variety of vertical, horizontal and complex configurations interspersed by large deposits of eroding breccia and tuff.

St. Matthew I., largest of the group, is 52 km long and varies between about 2-9 km wide (about 330 km^2). It supports about 44% of the islands' total seabird population. It is characterized by smoothly-worn low hills and ridges alternating with several lowlands (fault zones) that cross its width from shore to shore. The maximum elevation is 459 m above sea level. Cliffs varying from about 10-450 m high (most 60-300 m), steep escarpments and slumping rubble slopes occur intermittantly around the coast of the island wherever uplands abut the sea. The majority of the features providing suitable nesting habitat for seabirds are located in the northern and southern sectors. Extensive areas of loosely consolidated breccia, smoothly-worn tuff and unstable, actively shifting rubble slopes tend to alternate with areas of better quality and provide little usable nesting space for seabirds on the island.

Hall I. lies about 5 km northwest of St. Matthew I. across Sarichef Strait. It is less than 9 km long and 4 km wide (about 14 km^2), but provides nesting habitat for about 46% of the total seabird numbers. It rises abruptly out of the sea to a maximum elevation of 508 m asl. Vertical, continuous 300 m cliffs topped by steep escarpments dominate its northern and southern coasts and much of the coast in the southwest. Lower cliffs, eroding escarpments and a few small beaches are found on the south and southeastern coast. A large cliff surface area combined with the frequent occurrence of horizontal terraces and ledges provide much high-quality nesting habitat for cliff-nesting seabirds on the island.

Pinnacle I., smallest of the three, lies about 14 km south of St. Matthew I. It is less than 3 km long and 1 km wide (about 1.5 km^2) and it provides

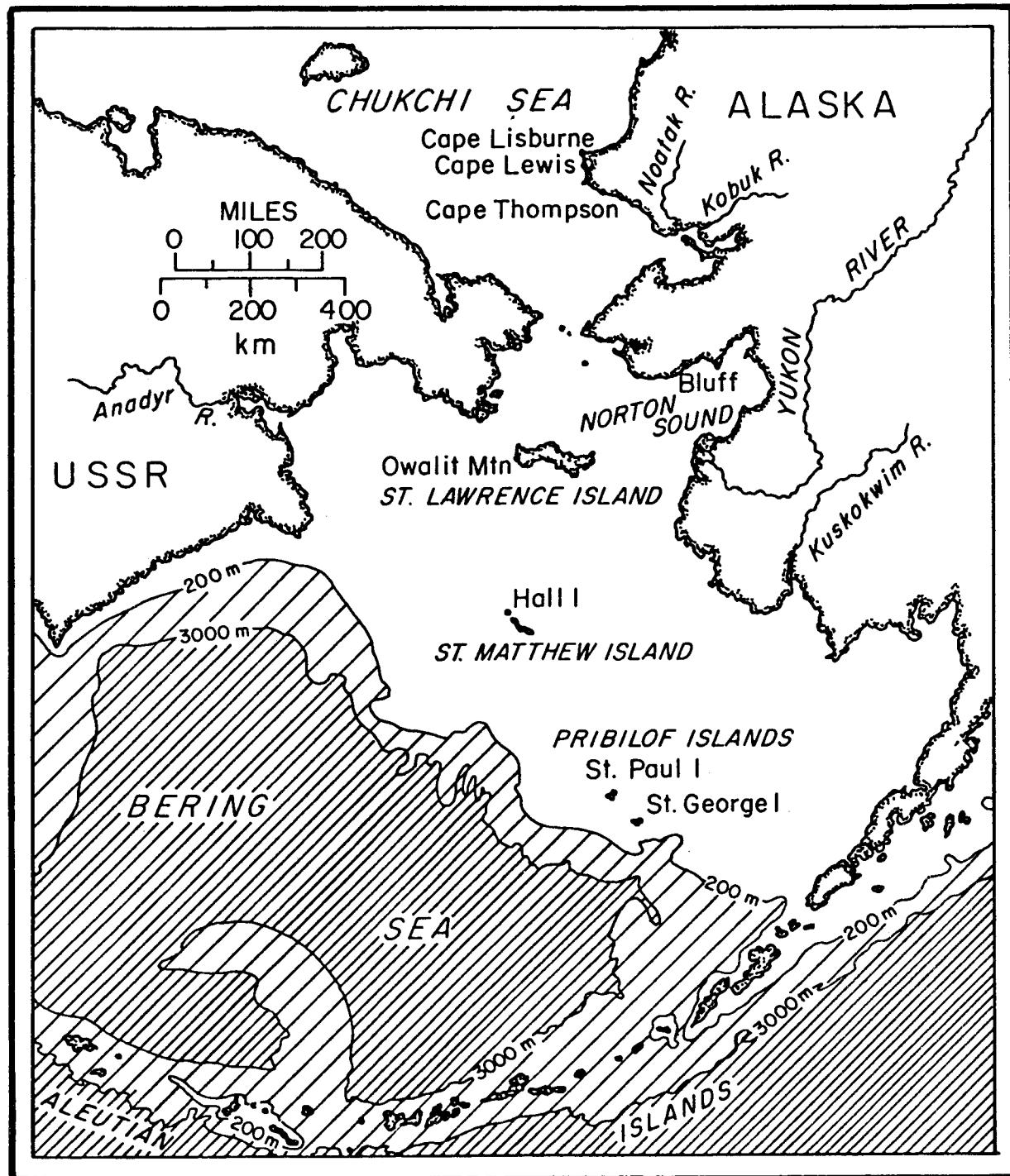


Figure 1. Locations of study sites in Alaska.

nesting habitat for about 10% of the total seabird population of the three islands. It also rises abruptly out of the sea and has a maximum elevation of 380 m asl. Sheer cliffs and rock spires over 300 m high dominate much of its coast line, especially on the southern side.

All three islands have an arctic maritime climate similar to that found on St. Lawrence Island, and seasonal weather conditions are typical of the N Bering Sea region (Brower et al. 1977). Summers are short and tend to be cool. Mid-summer air temperatures of 8-14° C are common. Mean day and night temperature were 7°C and 5°C, respectively, during the period 13 July-11 August 1982. Moderate to strong winds from the south are especially common during summer. Low pressure systems commonly track northeastward through the region after June. Cloudy skies, fog, drizzle and rain are also common throughout much of the summer and weather tends to be especially poor during late summer, fall and early winter. Winters are long and somewhat milder than in nearby continental areas, and surrounding waters are ice-covered for several months each year.

Bering Shelf Water tends to flow northwest past the islands at about 2-4 cm/sec (Kinder and Schumacher 1981). Relatively strong currents also flow northward through Sarichef Strait and past Glory of Russia Cape. Sea-surface temperature (SST) near the islands tends to be cooler than surrounding waters, a probable result of insular upwelling. During 26 July-10 August 1982, mean SST recorded at the northern end of St. Matthew I. was 4.9°C (range 3.9°-6.5°C). Mean SST recorded at the southern end of the island in July was 3.6°C (range 2.0°-6.0°C) (Sowls pers. comm.).

V. SOURCES, METHODS AND RATIONAL OF DATA COLLECTION

Four people were transported to St. Matthew I. on the *Vivienne II*, departing from Nome on 9 July and arriving at St. Matthew I. on 12 July. The field party remained on the island until 11 August when they were taken aboard the *Surveyor* and returned to Kodiak on 18 August. Two other people were flown to Bluff on 14 July and returned to Nome on 21 July. They were then flown to Cape Thompson on 22 July where they were joined by two additional people from Fairbanks. All four stayed at Cape Thompson until 10 August.

DeGange and Sowls (1978) established permanent census plots on St. Matthew I. in 1977. We used those plots in taking our census of murres and kittiwakes in 1982. We censused only the north end of the island and the locations of the plots we censused are shown in Fig. 2.

We have extended the notation for observers used in earlier reports (see Murphy et al. 1980, Roseneau et al. in press). As used in this report, the notations are: E - D.G. Roseneau, F - E.C. Murphy, K - R. Mulé, M - M. Hoberg.

Details of our methods for taking censuses, estimating breeding phenology and growth rates, and evaluating food habits can be found in Springer et al. (in press).

VI. RESULTS

A. Murres

Census

The results of the murre censuses at St. Matthew I., Bluff and Cape

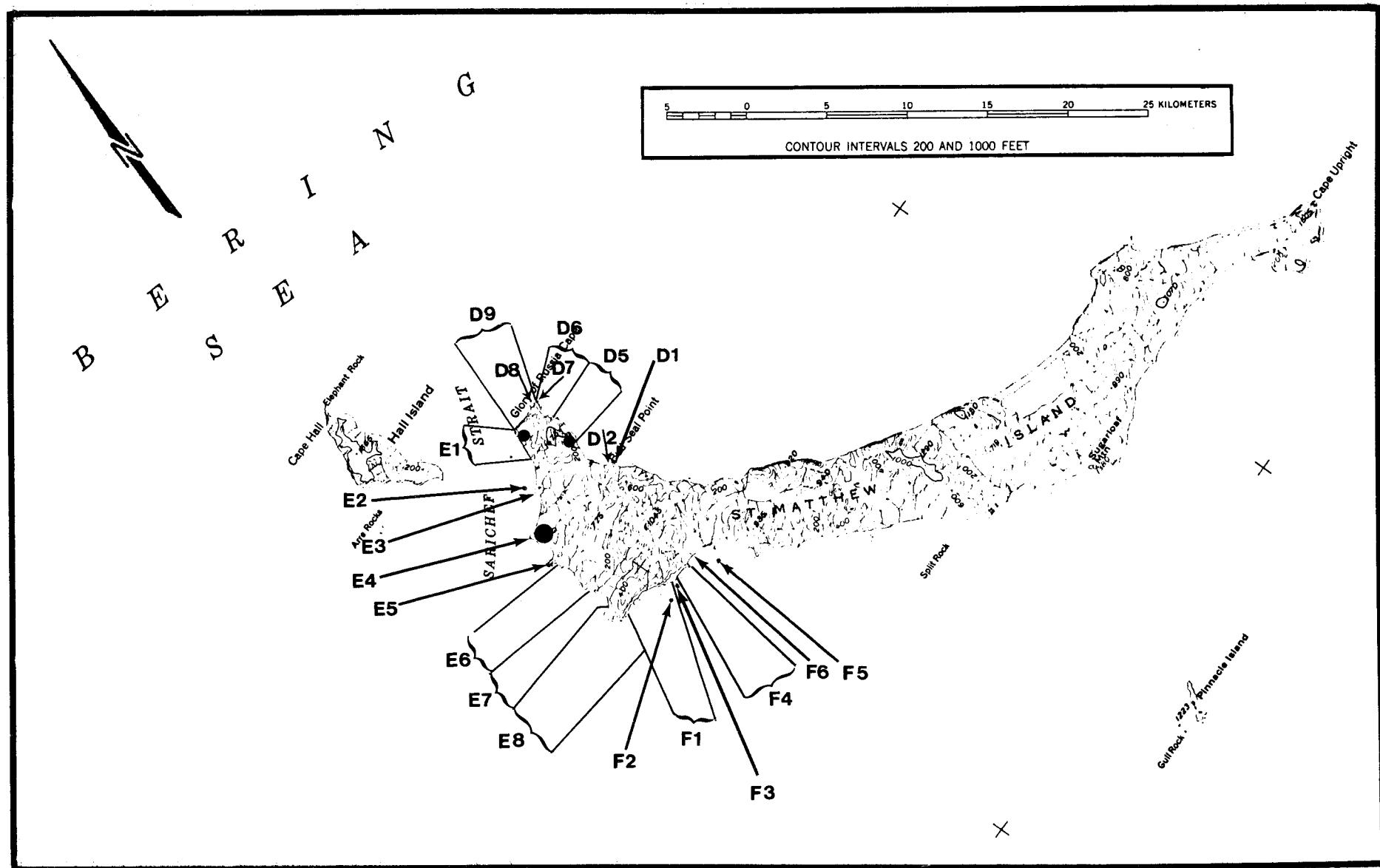


Figure 2. Locations of plots on St. Matthew I. censused in 1977 and 1982.

Thompson are detailed in Appendix Tables 1-9. Details of a portion of the census of St. Matthew I. taken by Sowls (pers. comm.) in 1977 are presented in Appendix Table 10. Diurnal compensation counts from Cape Thompson are presented in Appendix Table 11.

St. Matthew I.

Results of the 1977 and 1982 censuses of part of St. Matthew I. are summarized in Table 1. In 1977 the number of murres on this portion of the island was about a third of the island total (see Sowls et al. 1978). Both the raw and the compensated census scores indicate that the number of murres declined about 40-60% between 1977-1982. Common and Thick-billed Murres nest on the island but the two species were not differentiated in either census.

The raw census scores for both 1982 and 1977 were compensated for diurnal changes in cliff attendance using the data for Plots 9b and 9c (see Appendix Table 1). When these data are plotted against time, they closely resemble diurnal activity patterns of murres seen elsewhere (Fig. 3). This activity pattern accounts for about 30% of the variability between the values obtained for the 8 sets of replicate plot counts made in 1982 (see Appendix Table 1). The average CV of the compensated replicate counts was 0.21, $s=10$, compared to an average of 0.31, $s=19$, for the uncompensated replicate counts (Table 2).

Similar declines in murre numbers were recorded in the central Aleutians and on the Pribilofs (Table 3). The greatest percentage decline occurred in the Aleutians, where Thick-billed Murres predominate and where the combined census total of the three islands in 1982 was nearly an order of magnitude lower than in 1972 (E. Bailey pers. comm.). Craighead and Oppenheim (in press) reported that the number of Thick-billed Murres declined significantly on both St. George and St. Paul I. from 1976-1982. The number of Common Murres did not change significantly on St. Paul I. even though the total count in 1982 was only 45% of the total in 1976. Common Murre numbers increased significantly on St. George I. The percentage increase, about 27%, was similar to the decrease in numbers of Thick-billed Murres, about 24%.

Although the changes in numbers on St. George I. were small and no replicate counts were made to assess levels of daily and diurnal variability, the patterns shown in Fig. 4 support the suggestion that numbers of both species did in fact change between 1976-1982: the increase in numbers of Common Murres on different areas of the island was proportional to the decrease in numbers of Thick-billed Murres. Because the absolute change was much greater for Thick-billed Murres, the increase in numbers of Common Murres may have resulted in part from the decrease in numbers of Thick-billed Murres.

Murre numbers on Agattu I., which lies near the western end of the Aleutians, and on Middleton I. in the northern Gulf of Alaska were not apparently different in 1982 than in previous years (Table 3). Common Murres predominate on both islands (Day et al. 1979, Gould and Nysewander 1982).

Bluff

Fig. 5 shows the summarized murre census data in relationship to numbers since 1975. The data show a steady decline in numbers through 1982, although the rate of the decline appears to be slowing. Common Murres vastly out-

Table 1. Comparison of murre census results at St. Matthew Island, 1977 and 1982.

Plot	Raw		Compensated	
	1977	1982 ^a	1977	1982 ^a
D-1	696	609	nd ^b	1,740
D-2	266	27	nd	80
D-3	0	0	0	0
D-4	0	0	0	0
D-5	0	0	0	0
D-6	480	129	nd	310
D-7	1,665	1,135	nd	3,240
D-8	800	330	nd	1,100
D-9	17,440	6,323	nd	13,450
E-1	560	868	nd	1,830
E-2	0	0	0	0
E-3	170	57	710	150
E-4	290	360	1,160	490
E-5	21,900	11,203	73,000	29,670
E-6	8,775	4,670	26,590	6,910
E-7	600	774	1,670	1,200
E-8	8,800		23,160	
F-1	1,480	8,694	3,610	16,570
F-2	0	0	0	0
F-3	600	685	1,430	1,640
F-4, F-6	550	390	1,280	980
F-5	380	nd	860	nd
Total	65,452	36,254	—	79,360
Total E-3 - F-4, F-6	44,507	26,833	133,470	57,610

^aAverages of all counts if replicate counts were made.

^bnd = no data.

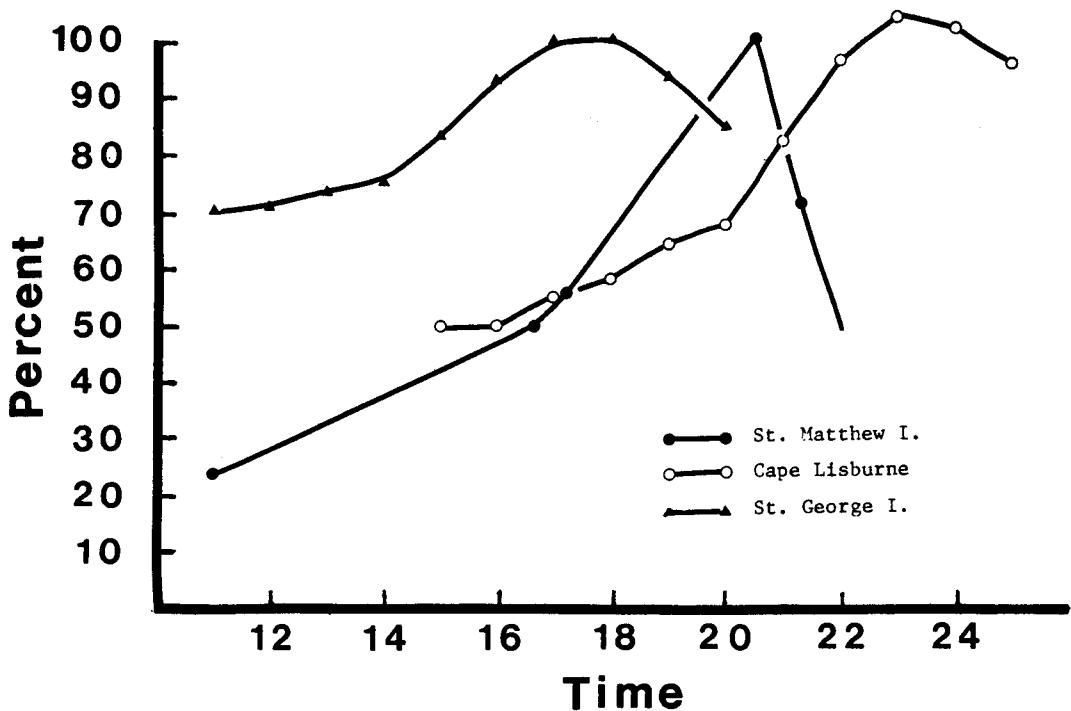


Figure 3. Diurnal activity patterns of murres. Data for St. George I. are from Hickey and Craighead (1977).

Table 2. Results of replicate counts of murres at St. Matthew Island in 1982. Arithmetic means of the time - compensated numbers.

Plot	Number of Counts	Mean Number of Murres	s	cv
D-8	2	1,100	300	.27
D-9a	2	4,360	1,010	.23
D-9d	2	4,800	230	.05
E-1	3	1,830	350	.19
E-5	2	29,670	7,380	.25
E-6	3	6,910	2,660	.38
E-7	3	1,200	175	.15
E-8,F-1	2	16,570	2,560	.15

Table 3. Numbers of murres in the S Bering Sea and the N Gulf of Alaska.

Island	1972	1973	1975	1976	1977	1978	1981	1982
Knugi ^a	5,500							0
Chagulak ^a	112,000						24,000	
Kagamil ^a	285,000						35,000	
St. George ^b				1,400,000			1,100,000	
St. Paul ^b				110,000			54,000	
St. Matthew					210,000		140,000	
Agattu ^c	21,400	12,137				18,402		19,402
Middleton ^d				5,851		6,803	5,521	6,161

^aE. Bailey pers. comm.

^bCraighead and Oppenheim 1982. Thick-billed Murres only.

^cForsell and Ambroz 1983.

^dGould and Nysewander 1982.

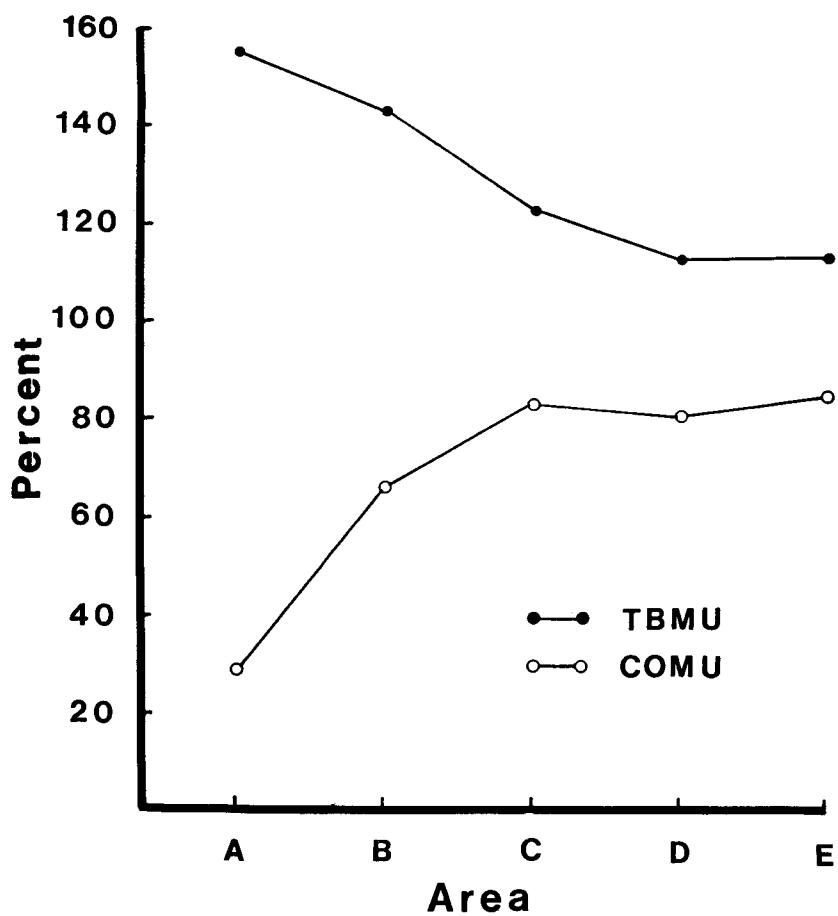
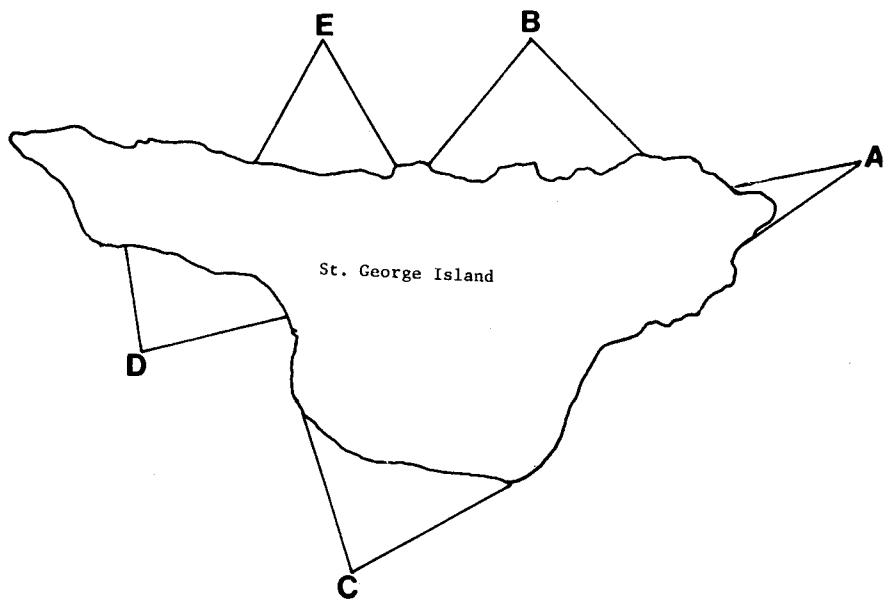


Figure 4. Changes in murre numbers in different areas on St. George I. The values are murre numbers in 1976 as percentages of numbers in 1982. Data are from Craighead and Oppenheim (in press).

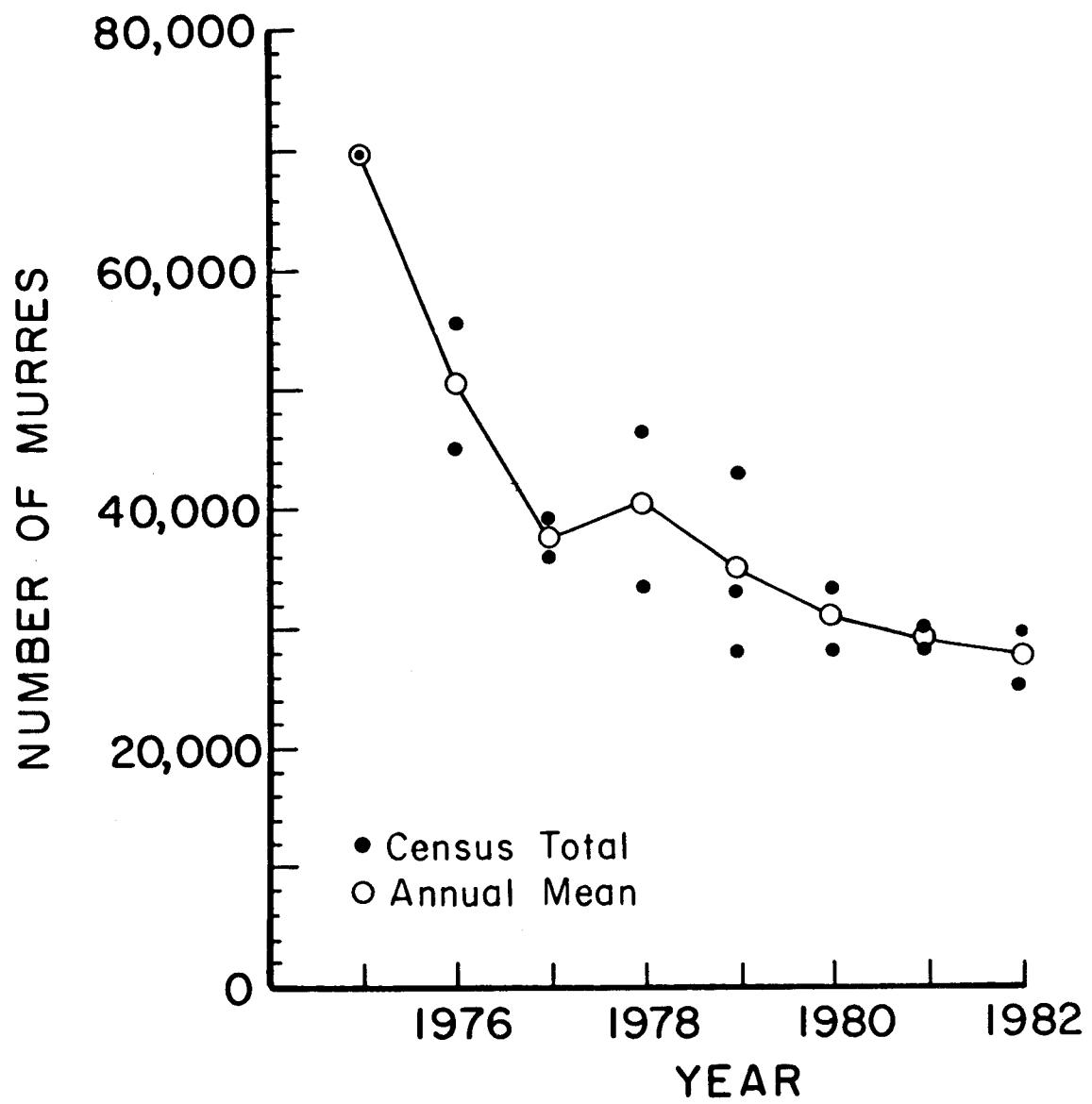


Figure 5. Numbers of murres at Bluff.

number Thick-billed Murres at Bluff so changes in numbers there can be considered as changes in numbers of Common Murres.

Cape Thompson

The murre census results from Cape Thompson are summarized and compared to results from prior years in Table 4 and Fig. 6. Both the raw census counts and the compensated counts indicate that murre numbers have declined further since 1979. However, as at Bluff, numbers appear to be stabilizing. The decline has been greatest at Colony 5, where the 1982 count was only 32% of the 1960 count and where fewer murres have been seen in each successive year since 1976.

We conducted a Chi-square test for differences in probabilities (Conover 1980) using the compensated results to examine intercolony differences in the degree of numeric change between years. Although the test statistic was highly significant ($T = 13,471$, $v = 16$, $p < 0.001$), the result is trivial since it is based on such a large sample of observations. Comparisons of observed and expected values verified that the decline has been less pronounced at Colonies 1, 2 and 4, comparable at Colony 3 and more pronounced at Colony 5 than would be expected if numbers had declined at the same rate at all five colonies.

Land-based observers distinguished between the two murre species at three census plots at Colony 5 in 1982 where comparable counts were made in 1960 (Table 5). In 1960, observers counted 2,120 Common Murres and 4,850 Thick-billed Murres on these plots, while in 1982 we counted 393 Common Murres and 1,820 Thick-billed Murres. The percentage of Common Murres thus declined from 30% in 1960 to 18% in 1982; the difference is highly significant (Chi-square test, $T = 135.384$, $v = 1$, $p < 0.001$). In conjunction with a major decline in total numbers of murres on each of these plots, the proportion of Common Murres declined as well.

Phenology and Reproductive Success

St. Matthew I.

Murres apparently laid few eggs on St. Matthew I. in 1982. We saw no eggs on two study plots which we could view well from above; the plots contained about 130 and 190 Thick-billed Murres, respectively, but no Common Murres. A. Sowls (pers. comm.) told us that he found Common Murres with several eggs on 25 June at the south end of the island, but only 2 Thick-billed eggs among many birds. Also, Sowls saw "very few" eggs and chicks on Hall I. on 4 August. Craighead and Oppenheim (in press) reported that murre reproductive success was low also on the Pribilofs in 1982, but that Common Murres might have had somewhat better success than Thick-billed Murres had.

Common Murres carrying fish to the colonies were first seen by us on 4 August, indicating that eggs at the north end of the island began hatching about that time. We did not see any Thick-billed Murres carrying fish by 11 August, the day we left the island. Sowls saw an unidentified murre carrying a fish on 24 July near Cape Upright.

Hatching dates beginning about 4 August in 1982 are much later than hatching dates reported for the Pribilofs in 1975-1978, when they averaged about 21-25 July (Hunt et al. 1981). They are also later than hatching dates

Table 4. Summary of murre census results at Cape Thompson.

Year	Census Total	
	Uncompensated	Compensated
1960	251,000	357,000
1976	157,000	199,000
1977	143,000	171,000
1979	114,000	149,000
1982	112,000	132,000

Note: Uncompensated (raw) scores are the averages of all counts made simultaneously by two or more observers on one or more days. Compensated scores are the raw scores adjusted to maximum values on the basis of diurnal patterns of activity, averaged for daily differences in numbers, and standardized for differences between land-based and boat-based counting positions (see Springer et al. in press).

Table 5. Numbers of Thick-billed Murres and Common Murres on three census plots at Colony 5, Cape Thompson.

Plot	Year	Common Murres	Thick-billed Murres
K	1960	800 (21) ^a	3,000 (79)
	1982	72 (9)	758 (91)
S	1960	1,100 (58)	800 (42)
	1982	283 (38)	461 (62)
T	1960	120 (10)	1,050 (90)
	1982	38 (6)	601 (94)

^aRow percent.

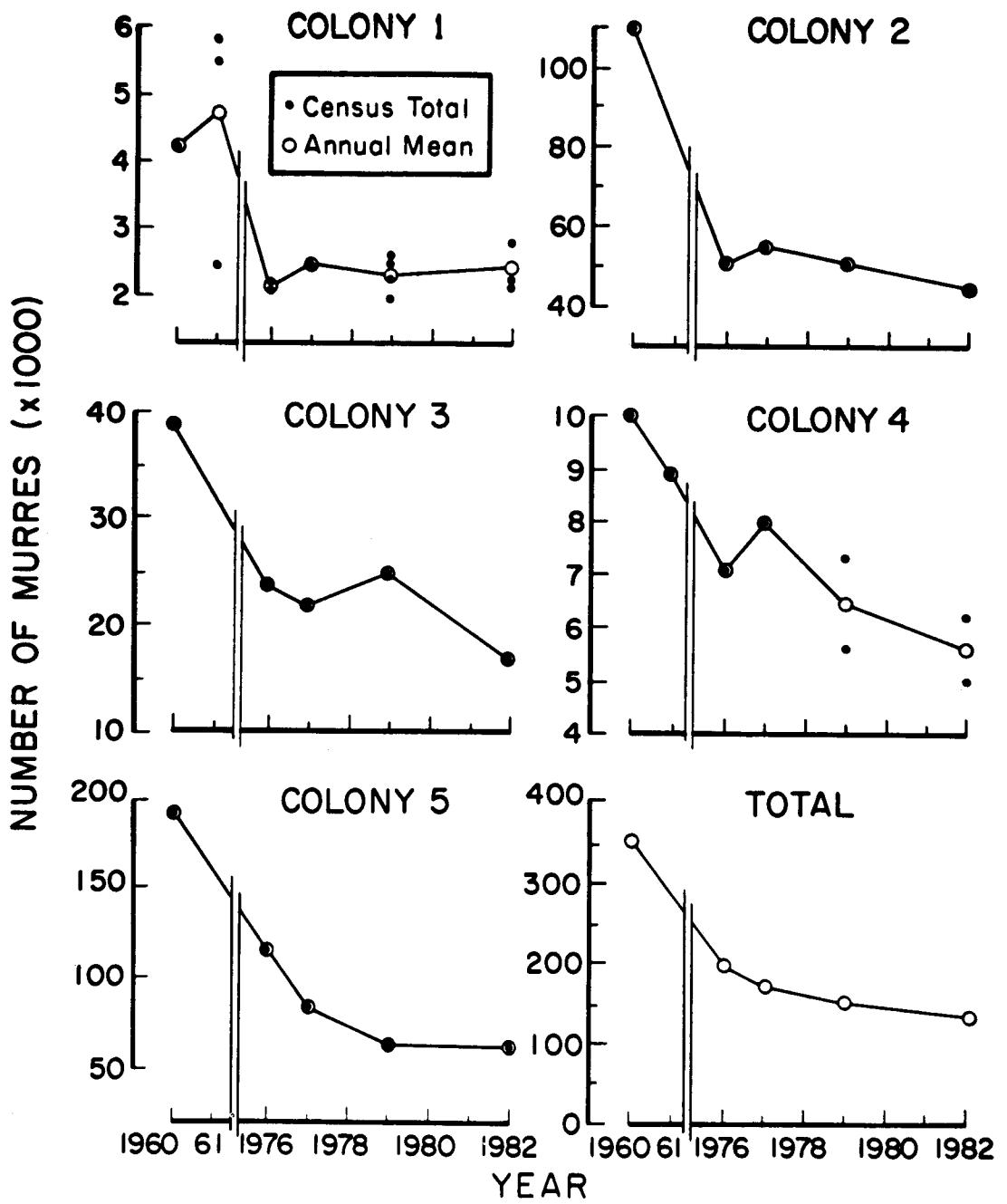


Figure 6. Numbers of murres at Cape Thompson.

reported for St. Lawrence I. where they generally range between about 20-31 July (Roseneau et al. in press).

Bluff and Cape Thompson

Phenological dates in the murre breeding season at Bluff and Cape Thompson were late compared to other years at these colonies (Table 6). Also, eggs of both species were relatively small at the two sites (Table 7). Because our departures from the colonies predated the completion of hatching and sea-going, we can only infer the levels of murre reproductive success. Birkhead and Nettleship (1981) have shown that murre reproductive success is generally lower in years when laying is later and egg sizes within populations are smaller. Although the reproductive success may have been depressed at these two sites, it was much higher than at colonies in the SE Bering.

Food Habits

St. Matthew I.

Food habits of murres collected at St. Matthew I. during the late incubation/early chick period in 1982 are summarized in Table 8. Among the fishes eaten by both species, pollock and unidentified fishes, perhaps in the family Liparidae, were the two most common taxa. Thick-billed Murres consumed typically more invertebrates than did Common Murres. Most of the invertebrates recovered from the Thick-billed Murres were shrimp, gammarid amphipods and polychaetes, while most of those found in Common Murres were the hyperiid amphipod *Parathemisto*.

Our collection of seabirds on St. Matthew I. for detailed food habits information is the first such collection from the island, so we have no basis for comparison to other years or seasons. However, on the basis of similar studies on the Pribilofs (Hunt et al. 1981) and in the N Bering and E Chukchi (Springer et al. in press), we can make the following generalizations.

Invertebrates were taken more frequently by Common Murres on St. Matthew I. than is characteristic of this species in summer elsewhere in N Alaska. Invertebrates were recovered from 45% of the Common Murres we collected on St. Matthew I. compared to about 25% on the Pribilofs (Hunt et al. 1981) and about 10% in the E Chukchi (Springer et al. in press) in the late 1970's.

Invertebrate use by both murre species is generally greater in early summer and declines as the season progresses (e.g., Fig. 7). By late July - early August, use of invertebrates is usually low. Fig. 7 also shows that annual variability in the use of invertebrates is high. In the eastern Chukchi, years when invertebrates were relatively important, such as 1976-1977, were years characterized by low levels of reproductive success among murres and Black-legged Kittiwakes (*Rissa tridactyla*) (Springer et al. in press).

Hunt et al. (1981) found pollock to be the most important prey of Common and Thick-billed Murres on the Pribilofs during the summers of 1975-1978. On St. Matthew I. in 1982, a fish taxon possibly in the family Liparidae contributed 25-30% of the total number of fishes taken by murres, and their remains were found in 29% of the Thick-billed Murres and in 65% of the Common Murres.

Murres on the northern side of St. Matthew I. and Hall I. generally flew between north and east when commuting to and from feeding areas, while murres

Table 6. Murre breeding phenology at Bluff and Cape Thompson.

Year	First Hatching		First Sea-going	
	Bluff	Cape Thompson	Bluff	Cape Thompson
1959		~4 Aug		25 Aug
1960		30 Jul		18 Aug
1961		27 Jul		19 Aug
1975	~24 Jul	---	~10 Aug	---
1976	27 Jul	9 Aug	14 Aug	~30 Aug
1977	3 Aug	1 Aug	20 Aug	23 Aug
1978	15 Jul	~23 Jul	31 Jul	13 Aug
1979	<15 Jul	22 Jul	2 Aug	11 Aug
1980	<19 Jul	---	>24 Jul	---
1981	11 Jul	---	29 Jul	---
1982	18 Jul	5 Aug	>21 Jul	>10 Aug

Table 7. Egg volumes (cc) of murres.

Year	Common Murre		Thick-billed Murre
	Bluff	Cape Thompson	Cape Thompson
1977	---	107.4 \pm 9.0 (16)	96.8 \pm 9.1 (54)
1979	---	117.3 \pm 9.9 (5)	104.5 \pm 10.0 (36)
1981	110.9 \pm 8.8 (29)	---	---
1982	106.7 \pm 8.7 (44)	111.0 \pm 10.2 (47)	91.5 \pm 10.1 (19)

ANOVA Results: 1) Common Murres (5 locality-year samples):
 $F_{L-Y(4,126)} = 2.53$, $p < 0.05$.

2) Cape Thompson, species: $F_{1,171} = 50.82$,
 $p < 0.001$; year: $F_{2,171} = 6.95$, $p < 0.005$;
 species x year: $F_{2,171} = 2.81$, $0.05 < p < 0.1$.

Table 8. Prey of Thick-billed Murres (TBMU), Common Murres (COMU) and Black-legged Kittiwakes (BLKI) at St. Matthew Island, 15 July - 8 August 1982.

	TBMU		COMU		BLKI	
	n	% ^a	n	% ^a	n	% ^a
Number examined	34	(100)	42	(100)	16	(100)
Number empty	10	(30)	9	(21)	2	(13)
Frequency of invertebrates	12	(35)	19	(45)	12	(75)
Frequency of fish	21	(62)	31	(74)	1	(6)
A. Frequency of Occurrence						
<i>Theragra chalcogramma</i>	13	54	28	85	0	0
<i>Gadus macrocephalus</i>	0	0	1	3	0	0
Cottidae	7	29	7	21	0	0
<i>Mallotus villosus</i>	0	0	2	6	0	0
Liparidae ^b	6	25	20	61	1	7
Unidentified fishes	3	13	2	6	0	0
Shrimps	6	25	0	0	1	7
Crabs	1	4	2	6	2	14
<i>Parathemisto</i> sp.	3	13	5	15	1	7
Gammaridae	5	21	1	3	1	7
<i>Thysanoessa</i> sp.	0	0	2	6	2	14
Snails	2	8	0	0	7	50
Squids	0	0	0	0	1	7
Polychaetes	8	33	4	12	8	57
Unidentified invertebrates	0	0	7	21	1	7
B. Number of individuals						
<i>Theragra chalcogramma</i>	640 ^c	54	464	38	0	0
<i>Gadus macrocephalus</i>	0	0	1	<1	0	0
Cottidae	31	3	8	<1	0	0
<i>Mallotus villosus</i>	0	0	3	<1	0	0
Liparidae ^b	266	22	169	14	1	<1
Unidentified fishes	3	<1	4	<1	0	0
Shrimps	17	1	0	0	2	<1
Crabs	1	<1	2	<1	2	<1
<i>Parathemisto</i> sp.	21	1	29	2	2	<1
Gammaridae	22	1	4	<1	2	<1
<i>Thysanoessa</i> sp.	0	0	509 ^d	42	2	<1
Snails	2	<1	0	0	320 ^e	62
Squids	0	0	0	0	2	<1
Polychaetes	193	16	6	<1	180	35
Unidentified invertebrates	0	0	7	<1	1	<1

^aValues in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency or number, respectively, among birds with identifiable prey remains.

^bTentative identification.

^cOne specimen contained 400; a second specimen contained 209.

^dOne specimen contained 500.

^eOne specimen contained 300.

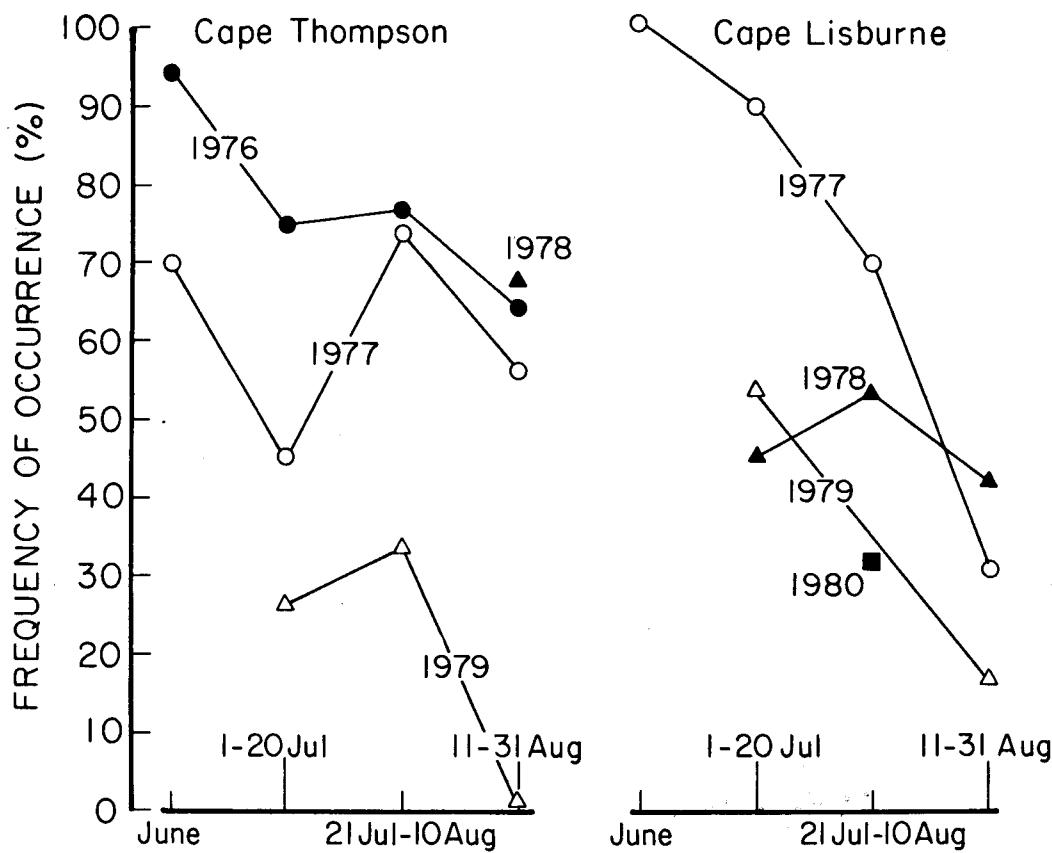


Figure 7. Frequency of occurrence of invertebrates in diets of Thick-billed Murres.

on the southern sides of the islands generally flew west and southwest (Fig. 8). Murres at Cape Upright fed southeast of that colony (Sowls pers. comm.).

Murres were seen in flocks of 10-40 flying towards St. Matthew I. when we were about 64 km northeast of it on our arrival on 12 July. Between about 64-48 km northeast of the island the frequency of observations of flying birds increased and remained relatively constant until we were nearshore and close to the colonies.

Cape Thompson

The food habits data from Cape Thompson (Table 9) indicate that fish prey were abundant in the E Chukchi Sea in 1982. Age class 0+ sculpins (Cottidae), 0+ fishes possibly in the family Liparidae or Pleuronectidae, and 1+ capelin (*Mallotus villosus*) and saffron cod (*Eleginus gracilis*) were particularly abundant. Sand lance (*Ammodytes hexapterus*) were conspicuously absent at Cape Thompson, but were apparently numerous at Cape Lisburne. Personnel at the Cape Lisburne Air Force Station told us that they found large numbers of sand lance on the beach following a storm in late July (our identification based on their description). Invertebrates were not found in any of the murres we examined, probably because of the availability of fishes.

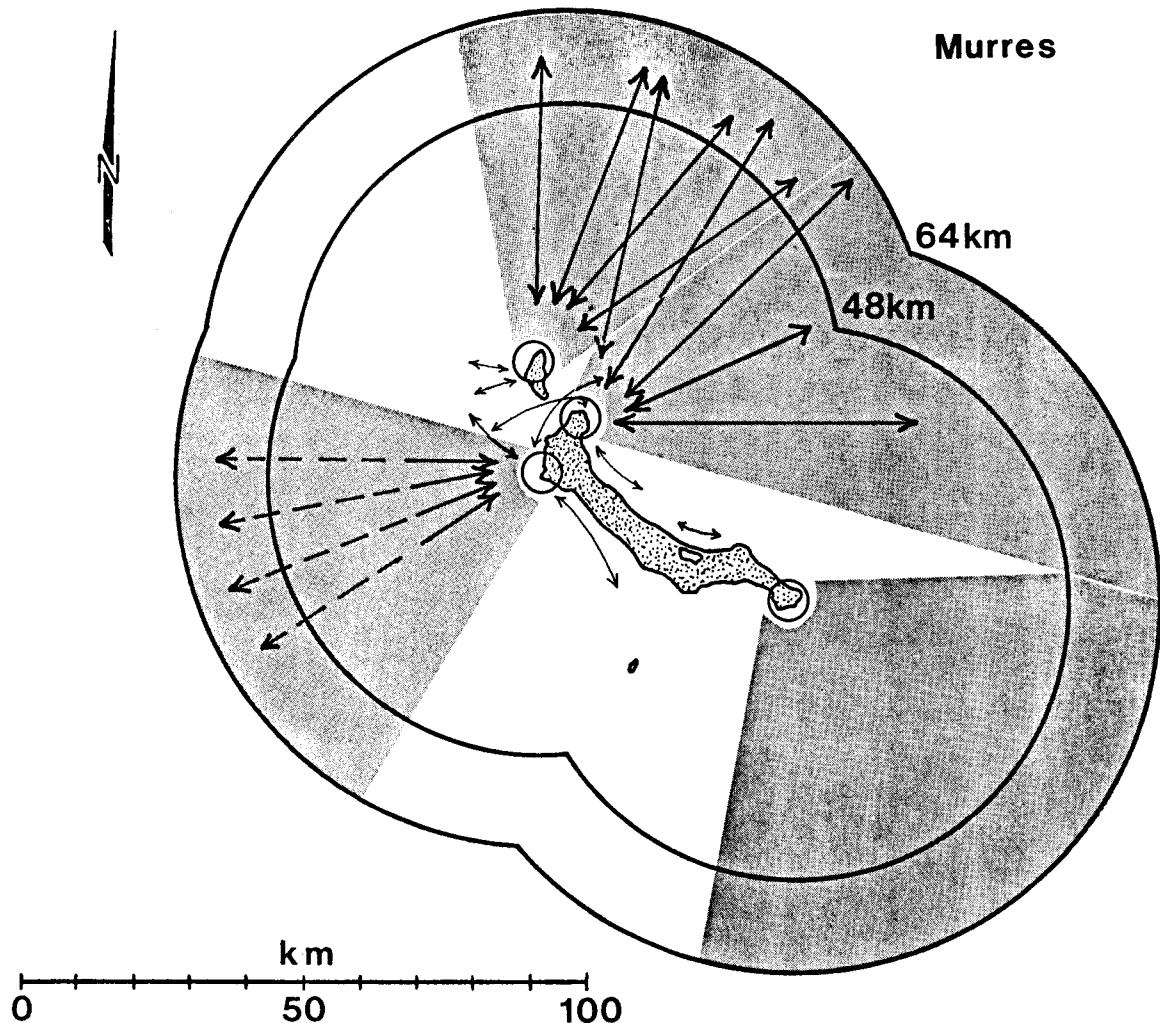


Figure 8. Feeding flight direction of murres on St. Matthew I. and Hall I. Circles on the islands indicate regions of high nesting density.

B. Black-legged Kittiwakes

Numbers, Phenology and Reproductive Success

Results of the Black-legged Kittiwake census at St. Matthew I., Bluff and Cape Thompson are detailed in Appendix Tables 12-15.

St. Matthew I.

The total number of Black-legged Kittiwake nests on 17 plots was about 25% fewer than in 1977. Seven plots showed large declines, while only two showed large increases.

A. Sowls (pers. comm.) found that laying occurred during the interval 25 June - 11 July 1982 in 60 nests he monitored at Cape Upright. Hunt et al. (1981) reported an overall mean laying date of 1 July for Black-legged Kittiwakes on the Pribilofs in the late 1970's. Thus, laying dates on St. Matthew I. in 1982 appear normal for this region of the Bering Sea.

Table 9. Prey of Thick-billed Murres (TBMU), Common Murres (COMU) and Black-legged Kittiwakes (BLKI) at Cape Thompson, 25 July - 6 August 1982.

	TBMU		COMU		BLKI	
	n	% ^a	n	% ^a	n	% ^a
Number examined	7	(100)	4	(100)	4	(100)
Number empty	0	0	0	0	0	0
Frequency of invertebrates	0	0	0	0	1	(25)
Frequency of fish	7	(100)	4	(100)	4	(100)
A. Frequency of occurrence						
Cods	7	100	4	100	0	0
Sculpins	7	100	3	75	1	25
Sand lance	0	0	0	0	1	25
Capelin	2	29	3	75	4	100
Other fishes	6	86	4	100	1	25
Euphausiids	0	0	0	0	1	25
B. Number of Individuals						
Cods	48	7	20	7	0	0
Sculpins	490	76	139	51	1	3
Sand lance	0	0	0	0	1	3
Capelin	15	2	56	20	30	83
Other fishes	91	14	60	22	2	6
Euphausiids	0	0	0	0	2	6

^aValues in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency or number, respectively, among birds with identifiable prey remains.

The reproductive success of Black-legged Kittiwakes on St. Matthew I. was very low in 1982. Only 21 eggs were laid in the 60 nests Sowls monitored and only four of them hatched before he left the island. Three of the four chicks died within a few days after hatching. We examined 132 nests at the north end of the island in early August: 101 were empty and the remainder were covered by adults in incubating/brooding posture. Sowls also examined 40 nests on Hall I. on 3 August and found 38 empty, one with one egg and one with two eggs.

The average clutch size of the 60 nests monitored at Cape Upright was 0.35 eggs/nest. The overall average on the Pribilofs during the period 1975-1978 was 0.76 eggs/nest (Hunt et al. 1981), more than twice as many as on St. Matthew I. in 1982.

Black-legged Kittiwakes on the Pribilofs and in the central Aleutians also experienced poor breeding seasons in 1982. There were 20% fewer nests on study plots on the Pribilofs in 1982 than in 1976, and only three chicks were seen on St. George I. (Craighead and Oppenheim in press). The population on Chagulak I. declined from 28,500 to 6,000 between 1972-1982 and from 10,000 to 2,850 on Knugi I. (Bailey pers. comm.).

In contrast, Black-legged Kittiwakes on Agattu I. laid an average of about 1.5 eggs/nest and produced about 0.5-0.6 chicks/nest in 1982 (Forsell and Ambroz 1983). Likewise, Black-legged Kittiwakes on Middleton I. laid about 1.6-1.7 eggs/nest and raised about 0.3-0.4 chicks/nest (Gould and Nysewander 1983). The number of nests on Middleton I. in 1982, 77,000, was similar to the number counted there in 1978 and 1981.

Bluff

The number of adult Black-legged Kittiwakes at the Bluff colony and the number of nests on five census plots were about 30% and 23% lower, respectively, in 1982 than in 1981, and were the lowest counted there since 1977 (Fig. 9). Hatching dates were later than in any other year since 1977 and they continued to be strongly correlated with regional environmental conditions (Fig. 10.). Although we departed just as the eggs began hatching, it appeared as though reproductive success was lower than average (Fig. 11).

Cape Thompson

The number of kittiwakes at Colony 4 at Cape Thompson was considerably higher in 1982 than in previous years (Table 10), although the number of nests was somewhat lower (Table 11). The number of nests and adults on 10 plots at Colony 2 in 1982, 994 and 1214, respectively, were both higher than in 1979 when the numbers of nests and adults were 848 and 928, respectively.

Approximately 25% of the kittiwake eggs had hatched at Cape Thompson when we arrived on 22 July. Based on the size of the largest chick on 26 July (124 g) and its subsequent growth rate, the first chicks began hatching about 21 July, relatively early compared to other years (Table 12). The mean hatching date of the chicks we weighed for growth rates was 26 July which was comparable to the mean hatching date in 1979 but six days earlier than in 1977.

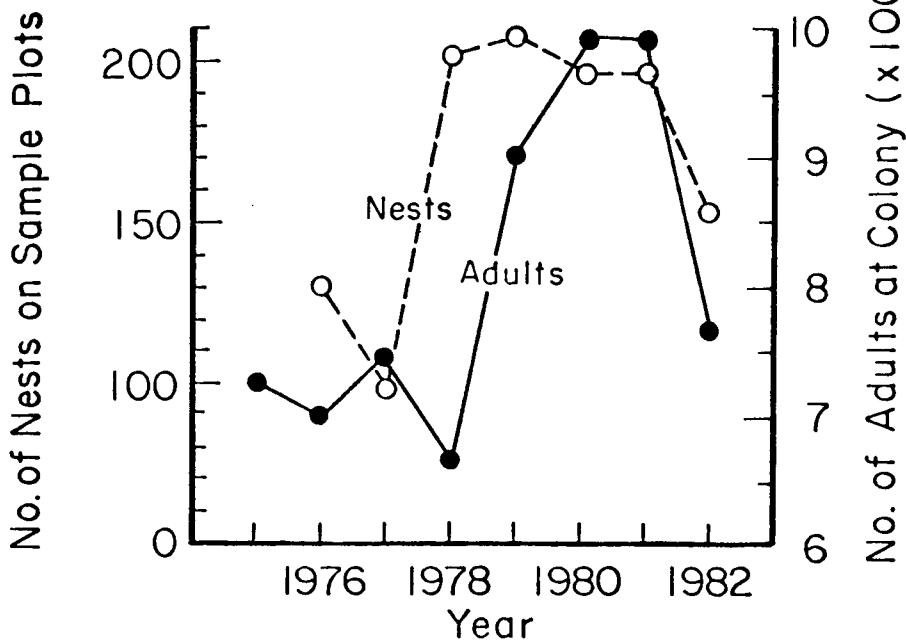


Figure 9. Numbers of adult Black-legged Kittiwakes and kittiwake nests at Bluff.

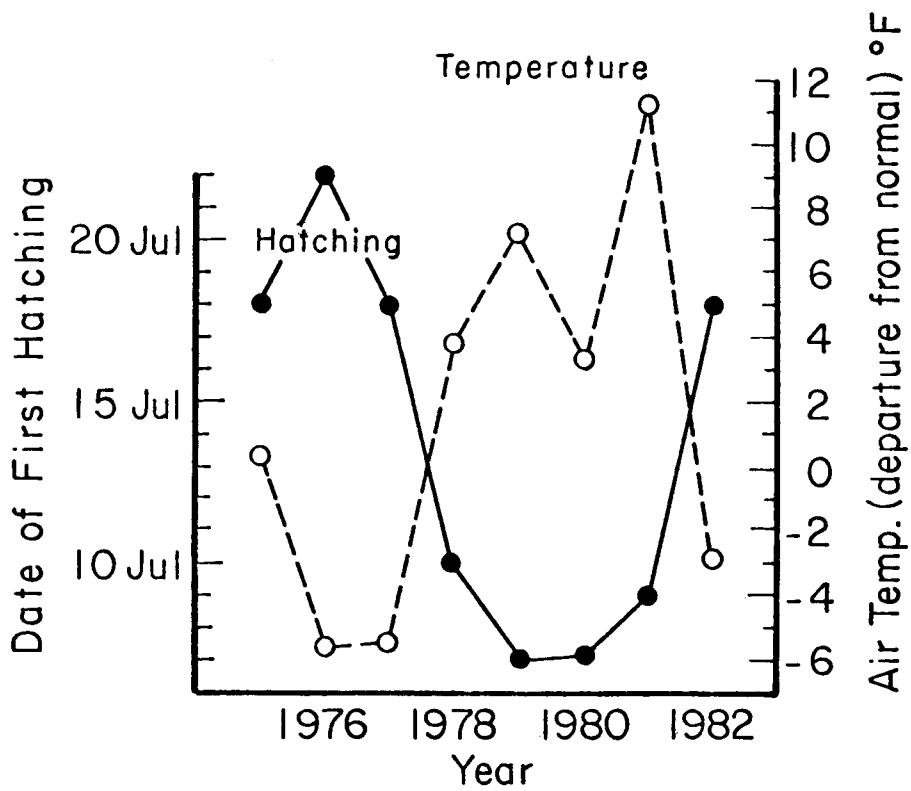


Figure 10. Black-legged Kittiwake nesting phenology and climate at Bluff, 1975-82. Air temperature at Nome, April-July.

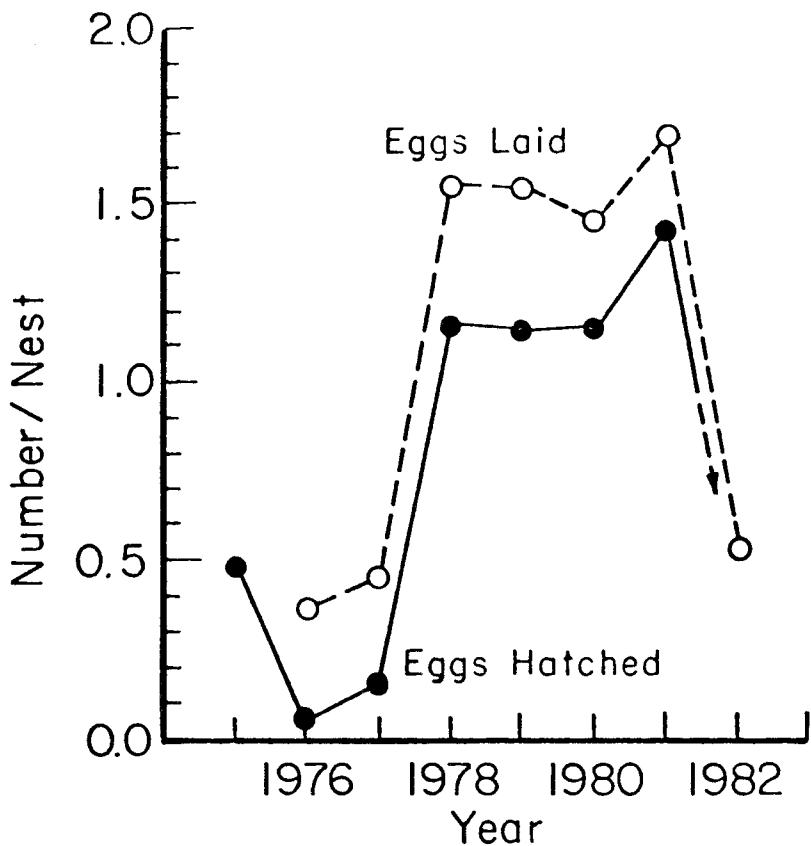


Figure 11. Productivity estimates of Black-legged Kittiwakes at Bluff.

The reproductive success of kittiwakes at Cape Thompson was good (Figs. 12 & 13). Clutch and brood sizes were large and most of the pairs that built nests successfully raised chicks. Chick growth rates were about mid-way between the highest and lowest rates measured previously at Cape Thompson and at other colonies in the N Bering and E Chukchi (Table 13).

Food Habits

St. Matthew I.

Food habits of Black-legged Kittiwakes on St. Matthew I. in 1982 are summarized in Table 8. Only one fish was found in all of the birds we examined, while invertebrates were found in 75% of them. Polychaetes and pteropods were the most important prey.

Black-legged Kittiwakes on the Pribilofs fed mainly on pollock in the breeding seasons of 1975-1978 (Hunt et al. 1981). Sand lance, capelin and myctophids (Myctophidae) were taken in smaller numbers. Invertebrates were

Table 10. Summary of the censuses of adult Black-legged Kittiwakes at Cape Thompson.

Colony	Year				
	1976	1977	1978	1979	1982
2	3,387	3,444	----	5,529	----
3	3,068	2,655	----	4,964	----
4	1,649	2,459	3,290	3,178	3,801
5	2,430	1,665	----	3,146	----
Total	10,536	10,223	----	16,817	----

Table 11. Summary of Black-legged Kittiwake nest counts at Cape Thompson.

Colony	Year				
	1960	1961	1978	1979	1982
2	5,173	----	----	4,558	----
3	2,598	----	----	3,674	----
4	3,132	2,996	1,630	2,790	2,580
5	3,191	----	----	2,489	----
Total	14,094	----	----	13,511	----

Table 12. Dates of first hatching of Black-legged Kittiwakes at Cape Thompson.

<u>Year</u>	<u>Date</u>
1959	20 July
1960	17 July
1961	22 July
1976	9 August
1977	29 July ¹
1978	25 July ¹
1979	18 July ¹
1982	21 July ¹

¹Extrapolated from weight of the heaviest nestling when first found and its subsequent growth rate.

Table 13. Growth rates of Black-legged Kittiwake chicks in northern Alaska.

Year	Colony			
	Bluff	Cape Thompson	Cape Lisburne	St. Lawrence I.
1977	nd ¹	12.6 \pm 3.6 (16) ²	19.3 \pm 2.9 (18)	nd
1978	17.9 \pm 4.1 (22)	nd	19.7 \pm 6.7 (21)	nd
1979	20.4 \pm 4.4 (35)	20.2 \pm 4.7 (111)	18.3 \pm 1.4 (24)	nd
1980	17.6 \pm 7.4 (30)	nd	17.9 \pm 3.7 (43)	nd
1981	15.6 \pm 4.5 (31)	nd	14.3 \pm 3.0 (30)	21.0 \pm 7.1 (15)
1982	nd	16.5 \pm 3.3 (48)	nd	nd

¹nd = no data.

²Arithmetic mean: g · day⁻¹ \pm standard deviation (number of chicks).

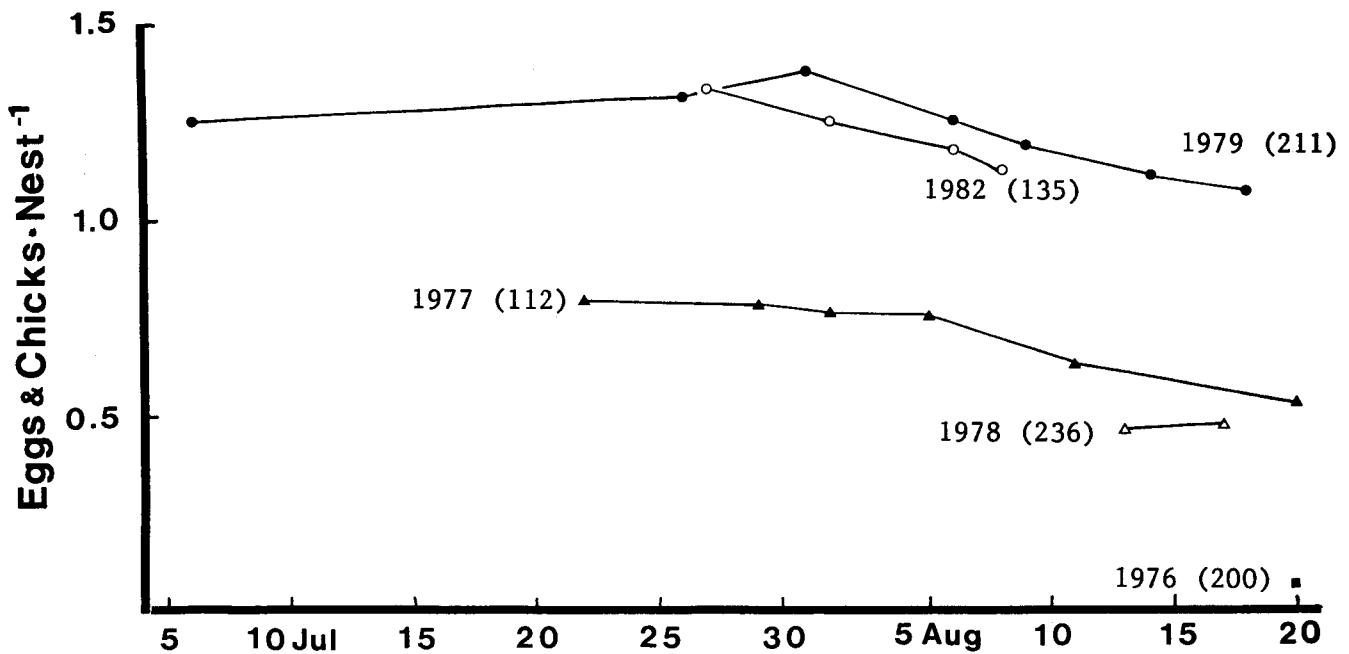


Figure 12. Mean number of Black-legged Kittiwake eggs and chicks in nests at Cape Thompson. The number of nests is in parentheses.

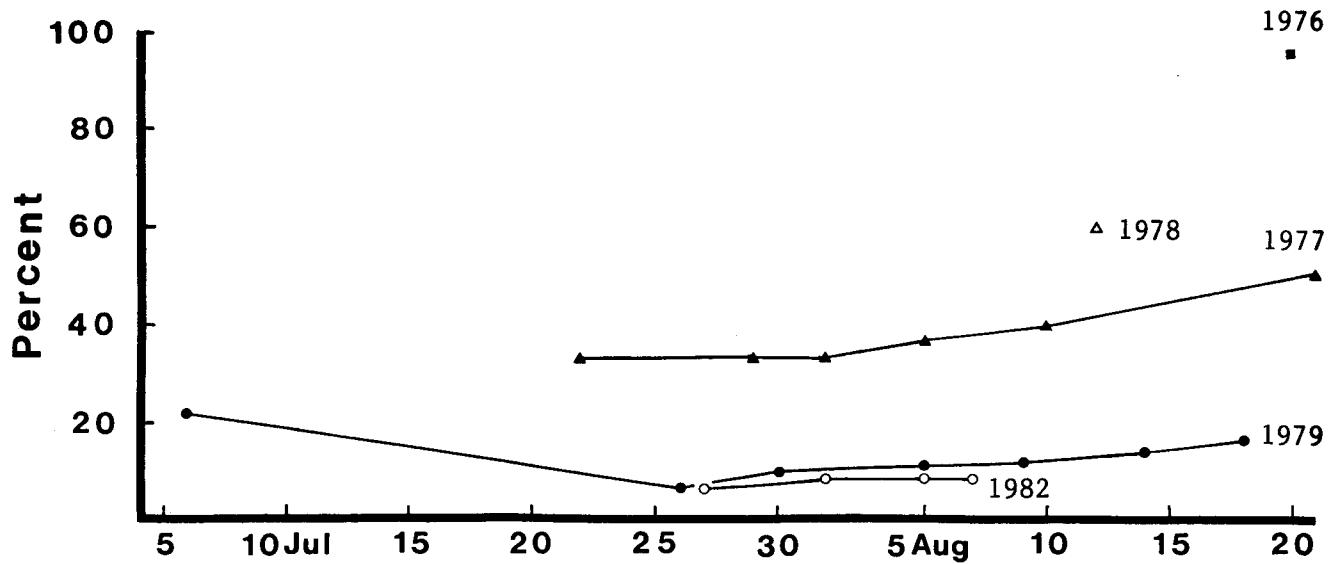


Figure 13. Percentage of empty Black-legged Kittiwake nests at Cape Thompson.

important in the diets in June, but by late July and August their importance had declined to a low level compared to that of fishes. In the E Chukchi during 1976-1980, invertebrates were generally much less important than fishes, particularly in years when kittiwake productivity was high (Springer et al. in press).

Cape Thompson

Food habits of kittiwakes at Cape Thompson in 1982 are summarized in Table 9. In contrast to St. Matthew I., fishes were recovered from all of the birds we examined, while invertebrates were recovered from only one bird. Capelin was the most important prey in the diets. In earlier years at Cape Thompson when capelin or sand lance were abundant among the prey of kittiwakes, reproductive success was high as it was in 1982.

C. Auklets

Phenology, Reproductive Success and Chick Growth Rates

St. Matthew I.

Least Auklets nest deep in the talus on St. Matthew I. and the unstable nature of most slopes makes it difficult to locate the nests without substantially disturbing them. Such disturbance might have contributed to the high failure rate, 80%, of the nests we found in 1982. Nearly 60% of the chicks we located died within 4-6 days after they were first weighed. Predation did not appear to be a factor in the deaths. On St. Lawrence I. where predation is a factor, only 36% died before the age of 15-16 days in 1981 (Roseneau et al. in press), and only 44% died before sea-going in 1976 (Searing 1977).

A 15 g Least Auklet chick was found on 19 July and most eggs had hatched by about 1 August 1982. Based on the weights of chicks when we first found them, most Least Auklet chicks began hatching about 22-23 July. This is slightly earlier than the date (24-25 July) when hatching began on St. Lawrence I. in 1981, a relatively early year (Roseneau et al. in press).

Mensural data on Least Auklet chicks from St. Matthew I. in 1982 are detailed in Appendix Table 16. The mean growth rate of five chicks over intervals of 10-15 days was 4.9 g/day ($s = 0.9$ days), a rate in the high range of values recorded on St. Lawrence I. during three years (see Roseneau et al. in press).

Food Habits

St. Matthew I.

Food habits of Least Auklets during the chick period in 1982 are detailed in Appendix Table 17 and are summarized in Table 14. *Callanus marshallae* comprised about 89% of the total volume of all prey; hyperiid and gammarid amphipods comprised about 5% and 4%, respectively. All other taxa comprised 1% or less of the total. *C. marshallae* is also important prey of Least Auklets on the Pribilofs (Hunt et al. 1981) and on St. Lawrence I. (Bedard 1969, Searing 1977, Springer and Roseneau unpubl. data).

We have examined only four of the Crested Auklet samples from St. Matthew I. *Parathemisto libellula* occurred in all four birds and totaled 250 individuals. The only other invertebrates found were six euphausiids, *Thysanoessa raschii*, in one bird. Amphipods were also important to Crested Auklets on the Pribilofs in 1975-1978, but less so than euphausiids, which constituted about 70% of the diet during the chick period (Hunt et al. 1981). Copepods were not found in the diets of Crested Auklets at either the Pribilofs or St. Matthew I., although they have been found in moderate numbers in some years in the diets of the birds on St. Lawrence I. (Bedard 1969, Searing 1977, Springer and Roseneau unpubl. data).

Auklets on the north side of St. Matthew I. tended to feed in the same direction as murres, but they appeared to stay closer to shore (Fig. 14). Auklets were often seen feeding in Sarichef Strait, an area also noted important to them by DeGange and Sowls (1978). Auklets also fed within a few kilometers of shore north of the island and within 3-4 km offshore of Glory of Russia Cape where surface slicks often occurred when waters were calm. The slicks formed under conditions of strong current flow northwest past Glory of Russia Cape and north through Sarichef Strait.

Table 14. Summary of prey taken by Least Auklets on St. Matthew Island during the chick period in 1982. Number of samples = 29.

	Number	Percent of total volume
<i>Calanus marshallae</i>	18,685	89
<i>Hyperiidae</i>	150	5.2
<i>Gammaridae</i>	216	3.9
<i>Decapod zoea</i>	187	1.1
<i>Thysanoessa</i> sp.	10	< 1
<i>Acanthomysis</i> sp.	1	< 1
<i>Diastylis bidentata</i>	1	< 1
<i>Limacina helicina</i>	73	< 1

VII. & VIII. DISCUSSION AND CONCLUSIONS

The summer of 1982 was a poor breeding season for murres and kittiwakes in the SE Bering Sea, and it was apparently the second such year in a row. D. Lloyd (pers. comm.) told us that the reproductive success of these species was also very low in 1981 on the Pribilofs. Murres and kittiwakes appeared to lay eggs in reasonable numbers in 1981, but chick mortality was very high. Red-legged Kittiwakes (*Rissa brevirostris*) were less successful than Black-legged Kittiwakes; as in 1982, few even constructed nests. R. Day (unpubl. data) saw Red-legged Kittiwakes feeding at unusually great distances from the Pribilofs in June and July of 1982. Although studies were not made on St. Matthew I. or in the central Aleutians in 1981, it is likely that birds at those colonies had breeding seasons similar to the one on the Pribilofs.

The breeding failures apparently have been caused by a wide-spread food shortage. Only one fish was recovered from all of the Black-legged Kittiwakes we examined at St. Matthew I. in 1982. Murres occasionally took very large numbers of juvenile pollock and another fish taxon, and Common Murres were seen carrying capelin and smaller numbers of larger pollock to the colonies, but on the average the consumption of fishes was low and the consumption of invertebrates was high compared to other colonies in years when reproductive success was high (Springer et al. in press). For example, reproductive success was probably above average at Cape Thompson in 1982, and the Thick-billed Murres we examined that contained fish in late July and early August had an average of 92 fish/bird ($s = 90$, $n = 7$). At the same time on St. Matthew I. the average was only 45 fish/bird ($s = 130$, $n = 21$) and the CV was very large: 15 of the birds had only 1 or 2 fish each, while one bird had 386 and another had 480. Also, at Cape Thompson in 1982, the Thick-billed Murres contained no invertebrates, while 35% of them did at St. Matthew I. and the average number was 21 ($s = 29$, $n = 12$).

We cannot be certain which prey species are most important to piscivorous seabirds on St. Matthew I. in years when reproductive success is at a higher level. It might be expected that pollock are important in most years; they were taken with greater frequency and in greater numbers by murres than any of the other fish prey at St. Matthew I. in 1982,

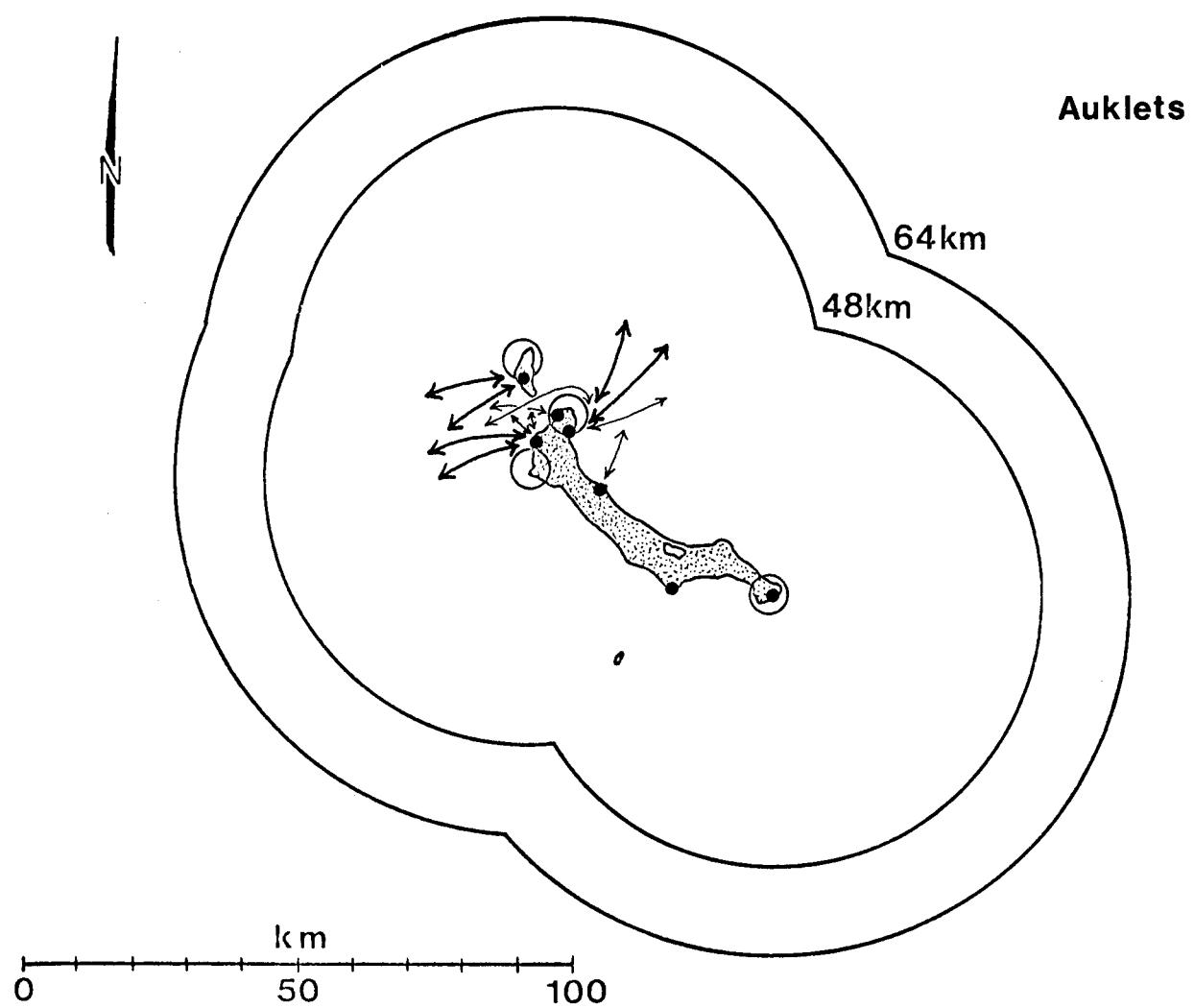


Figure 14. Feeding flight directions taken by auklets on St. Matthew I. and Hall I. Solid circles indicate largest nesting densities.

and they were the dominant prey of murres and Black-legged Kittiwakes on the Pribilofs in 1975-1978 (Hunt et al. 1981). St. Matthew I. and the Pribilofs lie in a zone of high pollock density as indicated by research vessel surveys and by catch statistics from the commercial pollock fishery (Smith 1981). If low prey availability has been responsible for the recent reproductive failure of murres and kittiwakes in the SE Bering Sea, then the implication is that the availability of pollock has been low.

During the late 1970's prey availability fluctuated considerably in the N Bering and E Chukchi, and the fluctuations led to large annual differences in reproductive success of seabirds at Bluff, Cape Thompson and Cape Lisburne. Changes in fish populations were associated with annual changes in sea-ice cover and sea-surface temperature: in colder years, like 1976 and 1977, several species of fishes in the E Chukchi tended to be smaller and less numerous than they were in warmer years such as 1979 and 1980. These temporal trends were especially pronounced in populations of sand lance and capelin, but were also apparent in populations of Arctic cod (*Boreogadus saida*) and sculpins (Springer et al. in press).

The oscillation in marine environmental conditions from unusually cold in 1975-1976 to unusually warm by 1979 (Niebauer 1979) affected regional seabird populations and their food webs to a lesser extent in the SE Bering than it did in the N Bering and E Chukchi. Average laying dates of Black-legged Kittiwakes on the Pribilofs varied by less than a week between years in the late 1970's (Hunt et al. 1981), while they varied by more than two weeks between years in the northern colonies (Springer et al. in press). The numbers of eggs laid by successful females were relatively constant at a level about mid-way between the extremes of values seen farther north (Table 15). Uniform laying dates and clutch sizes on the Pribilofs indicate that there was little variation between years in the early summer conditions that affect kittiwake breeding, in spite of the significant warming trend in the SE Bering.

Although the environmental factors and food webs affecting Black-legged Kittiwakes on the Pribilofs were stable compared to northern sites, they were not sufficiently good to allow more than a low to moderate level of reproductive success. Productivity of Black-legged Kittiwakes on the Pribilofs (Table 16) was generally in a low range of values compared to the northern colonies (e.g., see Fig. 11). This was in large part due to the high number of unsuccessful pairs, which averaged 55% ($s = 6.7$) on St. Paul I. in 1975-1979 and 52% on St. George I. in 1976-1978 (from Hunt et al. 1981). Conditions apparently remained marginal throughout several breeding seasons as Black-legged Kittiwake chicks grew rather slowly, averaging only 14.7 g/day on St. Paul I. and 12.8 g/day on St. George I. (Hunt et al. 1981).

Likewise, the phenology and reproductive success of murres on the Pribilofs were comparatively uniform during the late 1970's (Hunt et al. 1981) and the general level of reproductive success was low compared to most other colonies (Table 17), as it was for Black-legged Kittiwakes. The only value as low as those from the Pribilofs was from Cape Peirce in 1981 (D. Lloyd pers. comm.), a large coastal colony in the SE Bering.

There is some evidence that the breeding failures of Black-legged Kittiwakes in the past two years on islands in the SE Bering could represent the low points of a trend of generally declining levels of productivity since 1976 (Fig. 15). The proposed decline occurred during a period of

Table 15. Black-legged Kittiwake clutch size per completed clutch at colonies in northern Alaska.

	Year									
	1960	1961	1975	1976	1977	1978	1979	1980	1981	1982
St. Lawrence I. ^b	--	--	--	1.0	--	--	--	--	1.61	--
Bluff ^c	--	--	1.22	1.11	1.08	1.56	1.45	1.45	1.72	1.06
Cape Thompson ^d	1.92	1.88	--	1.12	1.18	--	1.58	--	--	1.48
Cape Lewis	--	--	--	--	1.17	--	1.64	--	--	--
Cape Lisburne	--	--	--	1.0	1.14	1.23	1.80	1.61	1.67	--
St. Paul I. ^e	--	--	1.42	1.49	1.52	1.33	1.47	--	--	--
St. George I. ^e	--	--	--	1.42	1.46	1.20	--	--	--	--
St. Matthew I.	--	--	--	--	--	--	--	--	--	1.04

^aValues for St. Lawrence I. in 1981, Bluff in 1979-1981, Cape Lewis in 1977 and 1979, Cape Lisburne in 1976, 1978 and 1980-1981, and Cape Thompson in 1982 are nest contents on our first visit. First visits at those colonies in those years occurred approximately when eggs were hatching so the values reported represent minimum estimates of actual clutch sizes.

^bData for 1976 are from Searing 1977.

^cData for 1975-1978 are from Drury et al. 1981.

^dData for 1960-1961 are from Swartz 1966.

^eData are from Hunt et al. 1981.

Table 16. Number of chicks fledged per nesting attempt of Red-legged Kittiwakes (RLKI) and Black-legged Kittiwakes (BLKI) on the Pribilof Islands.

Year	St. Paul Island		St. George Island	
	RLKI	BLKI	RLKI	BLKI
1975	.34	.44	---	---
1976	.63	.52	.37	.62
1977	.54	.43	.54	.45
1978	.10	.36	.13	.22
1979	.34	.54	.18	.40
1980	---	---	.27	.38
1981	---	---	.11	.07
1982	.01	.01	.01	.01

Table 17. Reproductive success of murres. Number of eggs hatching per average number of adults on plot.

Colony	\bar{x}	s	Year	Species
Prince Leopold I. ^a	.57	-	1976	TBMU
Bluff ^b	.40	.18	1975-1981	COMU
Agattu I. ^c	.57	-	1978	TBMU
Agattu I. ^c	.54	-	1978	COMU
Cape Peirce ^d	.15	-	1981	COMU
St. Paul I. ^e	.19	.03	1976, 1978	COMU
St. George I. ^e	.30	-	1978	COMU

^aGaston and Nettleship 1981.

^bSpringer et al. in press.

^cDay et al. 1979.

^dD. Lloyd pers. comm.

^eHunt et al. 1981.

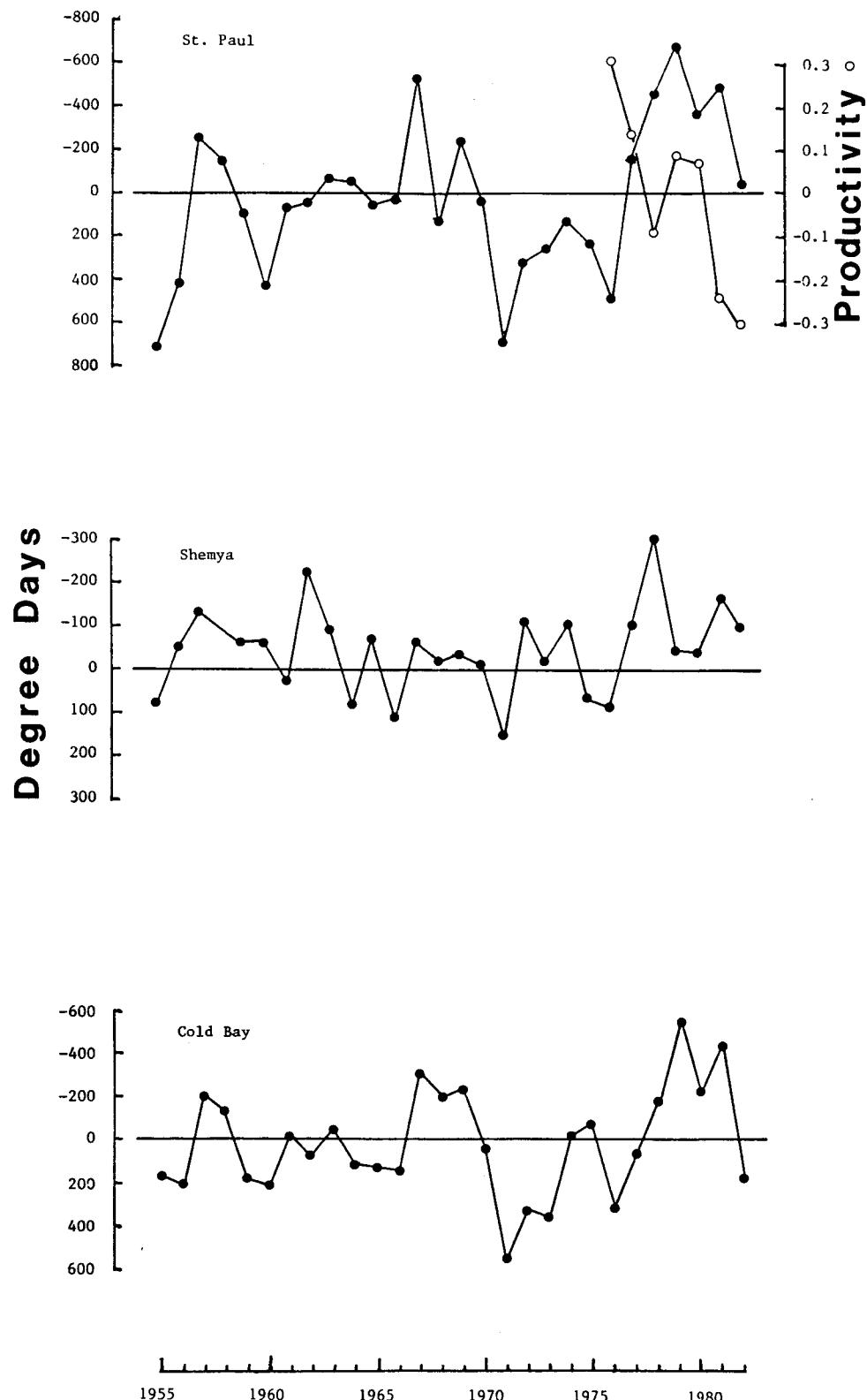


Figure 15. Black-legged Kittiwake productivity and air temperature in the S Bering Sea, April-July. Productivity measured as departure from the average number of chicks fledged/nesting attempt on St. George I. ($\bar{x} = 0.31$).

warming after 1976, although annual variability in reproductive success was not as well-correlated with climatic variability as it was in the north (e.g., see Figs. 10 & 11). A declining trend was less apparent on St. Paul I.; however, reproductive success was poor there in 1982, and probably in 1981, as it was on St. George I. Also, Hunt et al. (1981) suggested that productivity and chick growth rates were depressed on St. George I. because of competition for limited prey. Small fluctuations in prey availability in the SE Bering, therefore, would probably have a greater effect on birds at St. George I. than on birds at St. Paul I. Large fluctuations in prey availability affect the birds on the two islands similarly, as seen in 1982.

The past six years have been warmer than average during the spring and summer throughout the southern Bering Sea (Fig. 15). Niebauer (1979, unpubl. data) demonstrated a significant correlation between air and water temperatures, and showed that water temperature has been generally above average since 1977. Changes in water temperature could affect prey availability, for example, by changing the vertical and horizontal distribution of pollock. Slight changes in the vertical distribution could have major repercussions on kittiwakes, since they are restricted in their feeding to about the upper 1 meter of the water column. If such were the case, however, we might expect a closer association between Black-legged Kittiwake productivity and temperature during the breeding season.

Data from the commercial pollock fishery show that the abundance of pollock in the E Bering declined between 1969-1973 and has remained low since (Fig. 16). In spite of rapidly declining CPUE, the total tonnage taken increased, peaking in 1972. The decline of about 70% in pollock abundance from the high in 1969 could explain why even the highest estimates of reproductive success of murres and kittiwakes on the Pribilofs are lower than most estimates at other colonies. If pollock stocks are depressed, then rather small perturbations of the marine environment, for example by changes in climate, could result in disproportionately large changes in prey available to seabirds, leading to years of reproductive failure such as 1981 and 1982.

The spring and summer of 1982 were colder than the past four years in Norton Sound and the reproductive success of Black-legged Kittiwakes was correspondingly low (see Figs. 9-11). At Cape Thompson egg laying of murres was delayed, but Black-legged Kittiwake laying dates were early and reproductive success was high, indicating that conditions were much better there than at Bluff. Indeed, the farther away from the SE Bering that seabirds nested in 1982, the greater success they had in their breeding attempts (Fig. 17). It may be significant that Common Murres predominate at the colonies surrounding the SE Bering such as Agattu I., Middleton I. and Bluff, and that Common Murres apparently had somewhat better reproductive success than did Thick-billed Murres on the Pribilofs and on St. Matthew I., where Thick-billed Murres predominate.

Common Murres and Thick-billed Murres overlap geographically and trophically. Both species feed largely on various species of cods, but Common Murres take a greater number of shallow water schooling fishes, particularly sand lance and capelin, and Thick-billed Murres take a greater number of benthic invertebrates and fishes, particularly sculpins. The distribution of Common Murres generally corresponds with areas in which sand lance and capelin food webs occur, particularly shallow shelf areas such as the mainland coast and around St. Lawrence I. and the Near

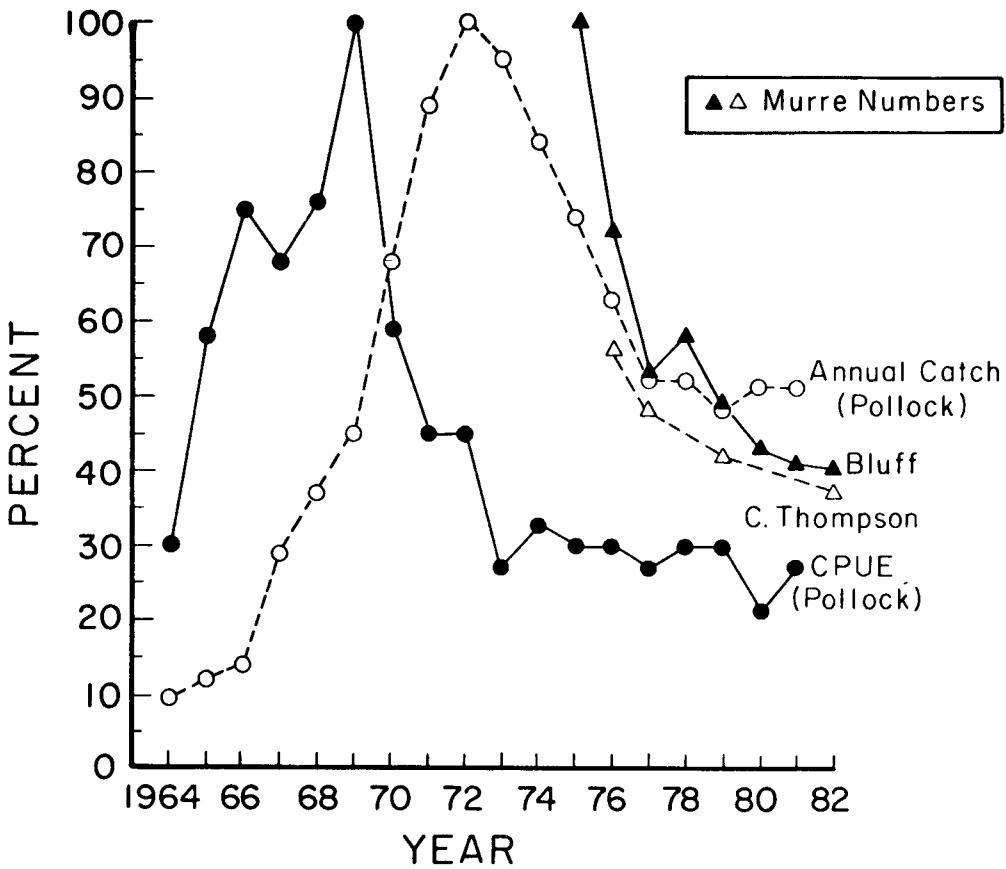


Figure 16. Annual catch and catch per unit effort (CPUE) of pollock in the eastern Bering Sea (after Bakkala and Wespestad 1982), and the changes in murre numbers at Bluff and Cape Thompson. The 100% levels of the annual catch and the CPUE were c. 1.9×10^6 tonnes and 31.5 tonnes/1000 pair trawl horsepower hour, respectively.

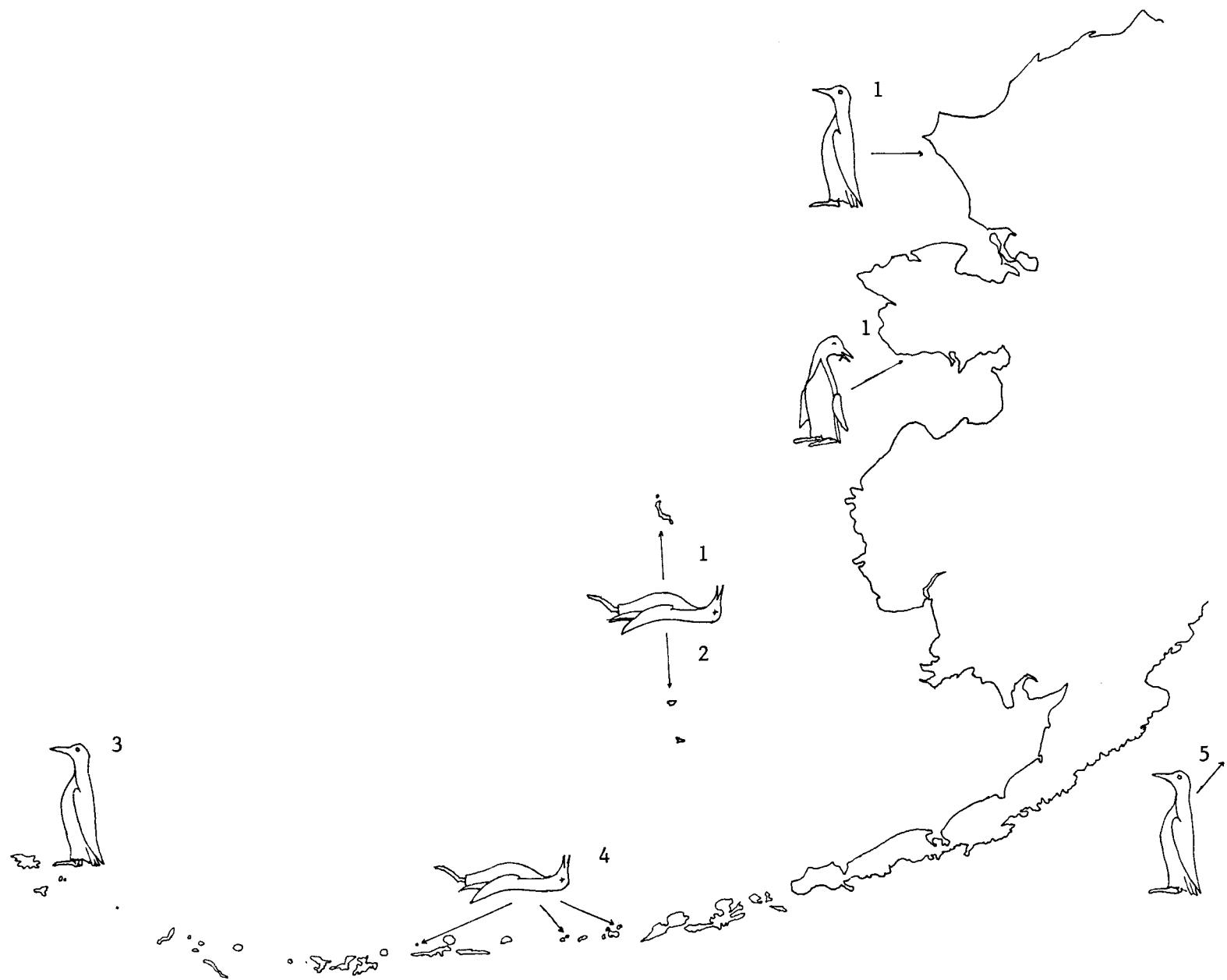


Figure 17. Locations of seabird studies in 1982, and representations of the quality of the breeding season. 1 - This study; 2 - Craighead and Oppenheim 1982; 3 - Forsell and Ambroz 1983; 4 - E. Baileypers. comm.; 5 - Gould and Nysewander 1982.

Islands, including Agattu I. Sand lance and capelin populations are enhanced in warm years and depressed in cold years (see Springer et al. in press). The breeding season in 1982 was not warm in Norton Sound and feeding conditions were presumably poor, particularly during the period preceding egg-laying. In contrast, the season was warm in the Near Islands and the murres and kittiwakes had good reproductive seasons.

Common Murres are in the minority on the Pribilofs probably because there is a limited sand lance/capelin community. Common Murres feed chiefly on pollock there since pollock is the dominant pelagic species in that area. In years when pollock abundance is low, Common Murres can probably outcompete Thick-billed Murres for the available fish since Common Murres are anatomically more streamlined and better able to capture pelagic fishes (Spring 1971); thus it is reasonable that Common Murres had better reproductive success than did Thick-billed Murres on the Pribilofs and on St. Matthew I. in 1982.

Census results showed fewer murres in 1982 at Bluff and Cape Thompson than in any earlier year, although the rate of decline appears to be slowing. We have proposed two hypotheses explaining these declines: one that involves changes in natality and one that involves changes in mortality (Springer et al. in press). In one case, generally low levels of productivity during a cool period in the mid-1970's could have caused the decline. Alternatively, poor recruitment because of high winter mortality could have been the cause. Winter mortality would have resulted from insufficient winter prey, i.e., pollock, a species thought to be important in the winter diets of murres (Divoky 1981). Because the summers of 1978-1981 were much warmer than average and reproductive success was good (Figs. 18 & 19), increasing recruitment from improved natality could be responsible for the drop in the rate of decline in murre numbers; a population model (see Springer et al. in press) indicated that murre numbers at Bluff should increase markedly between 1982-1985. On the other hand, pollock abundance has apparently stabilized at a low level, which could allow an equilibrium to develop between the numbers of summer and winter predators, including seabirds and their prey.

There are very few data concerning populations of the zooplanktivorous auklets in the SE Bering. The limited observations that have been made all suggest that 1982 was not a bad year for the auklets and, in fact, might have been a good one. For example, the numbers of Parakeet and Least Auklets were higher on the Pribilofs in 1982 than in 1976 (Craighead and Oppenheim in press). Also, the growth rates of Least Auklet chicks on St. Matthew I. in 1982 were high compared to rates measured in three years on St. Lawrence I.

Large numbers of adults and high growth rates of chicks both would require that prey be abundantly available to the birds. Least Auklets, which are an order of magnitude more numerous than either of the other two auklet species, feed mainly on copepods. Copepods are also important prey of pollock age classes 0+ and 1+ (Smith 1981), which are in turn fed on by piscivorous seabirds. Therefore, within the feeding area of the seabirds, auklets and pollock might compete for copepods. If such competition exists, large changes in numbers of one of the predators should lead to opposite changes in the other. For example, if pollock numbers are severely depressed, as commercial fisheries data and our studies indicate, much less predation pressure would be exerted on copepods, which could lead to enhanced prey availability for the auklets. May et al. (1979)

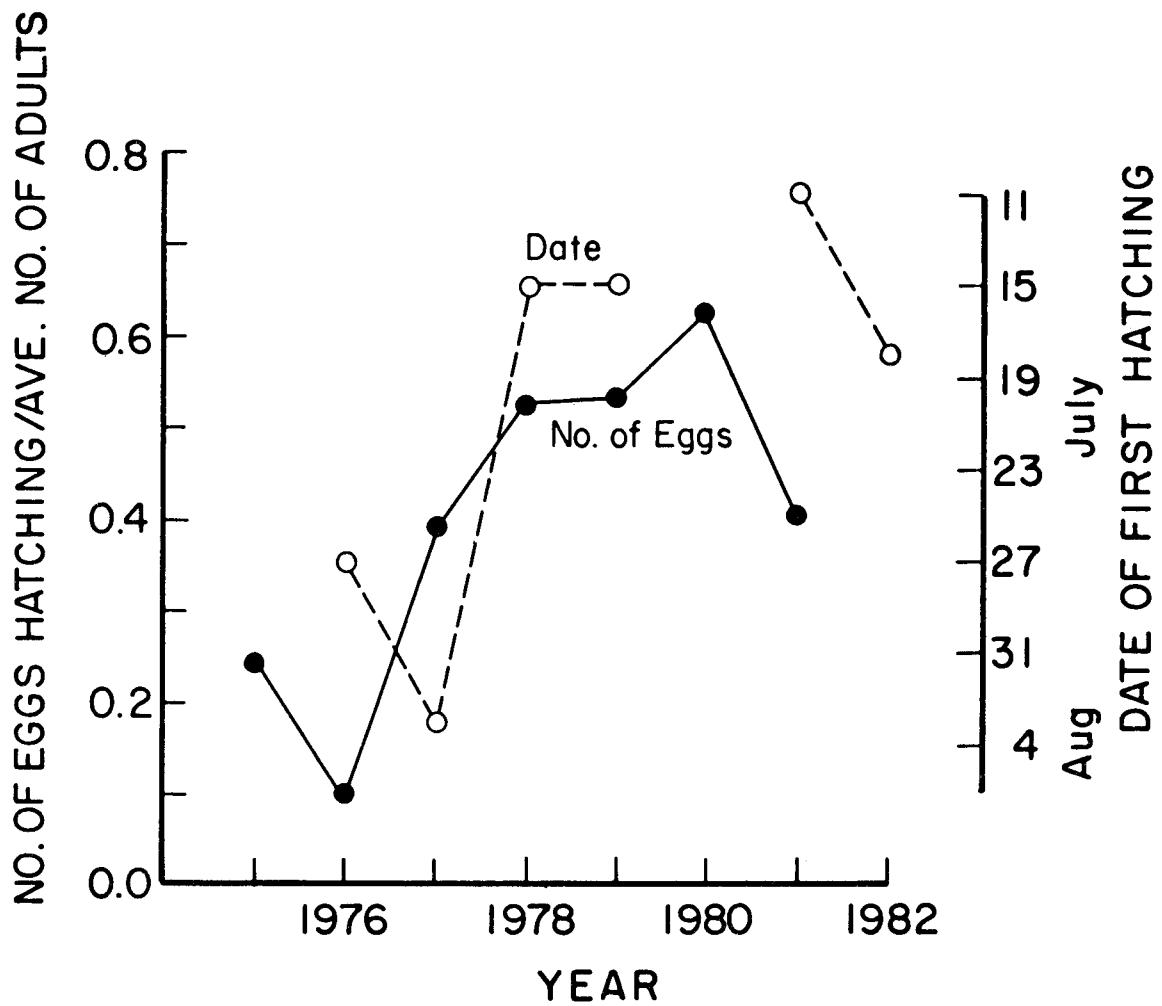


Figure 18. Murre productivity and phenology at Bluff.

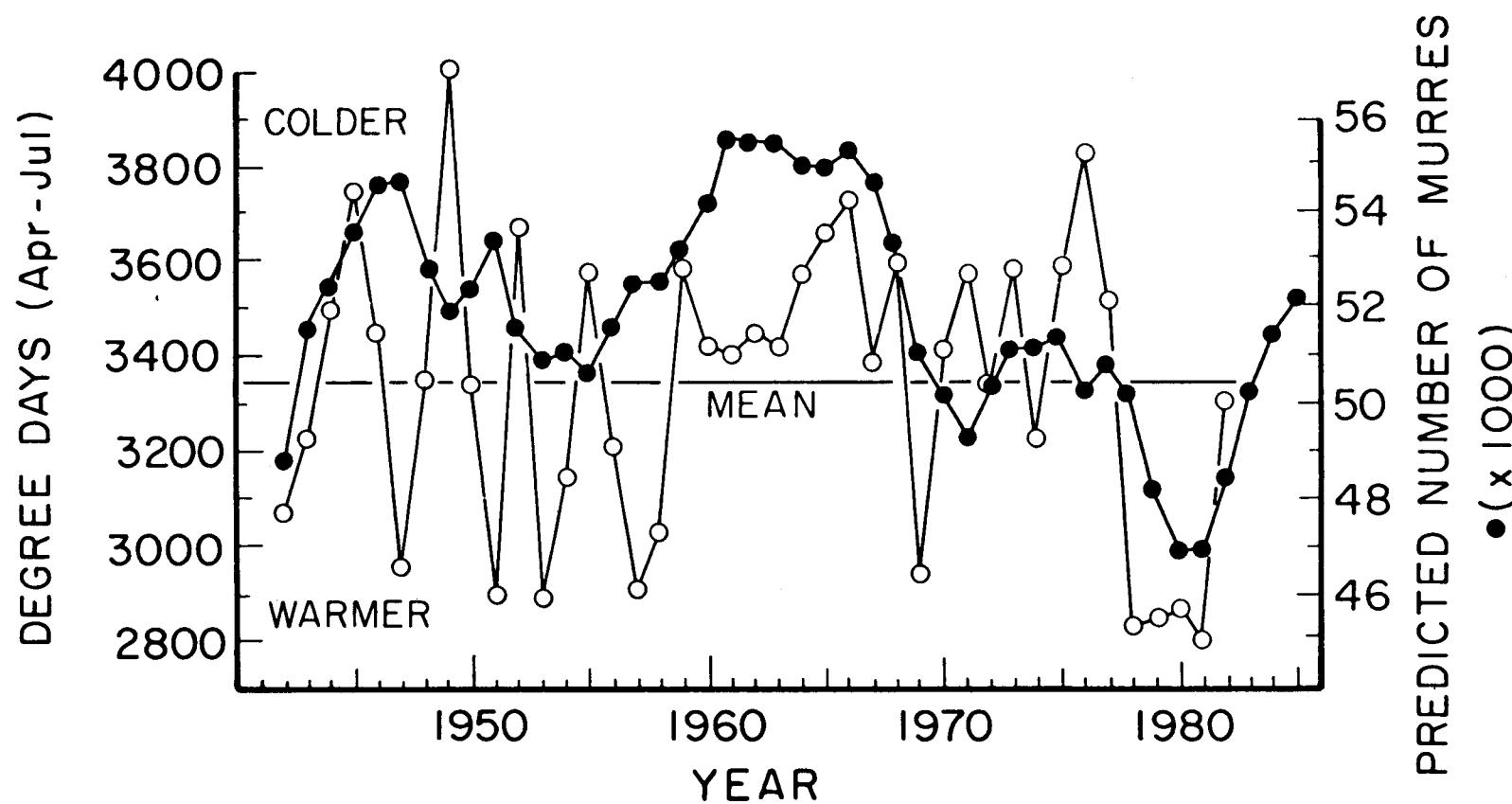


Figure 19. Air temperatures at Nome and the predicted numbers of murres at Bluff.

have discussed similar interactive systems, and Vesin et al. (1981) suggested a specific example of significant change in energy flow pathways through a copepod-mediated food web when the population of one copepod consumer declined.

IX. NEEDS FOR FUTURE STUDY

Large fluctuations in the biology of any animal or plant population are of interest since they generally signal changes of similar proportions in the environment. Such fluctuations can be disconcerting when they indicate major imbalances in ecosystems, as do the wide-spread declines in numbers of murres at several colonies in the Bering and Chukchi seas. In order to understand the causes of such changes and to provide the continuity of data necessary to address the relationship between ecosystem dynamics on Alaska's continental shelf and resource development, studies at selected seabird colonies should be continued. Field work is being conducted on St. Matthew I. in 1983 and should be continued for a third year, regardless of the outcome of the 1983 breeding season. Seabird populations in the SE Bering are not stable, as they appeared to be during the late 1970's, and it will be important to the needs of OCSEAP to understand future trends and the factors that cause those trends.

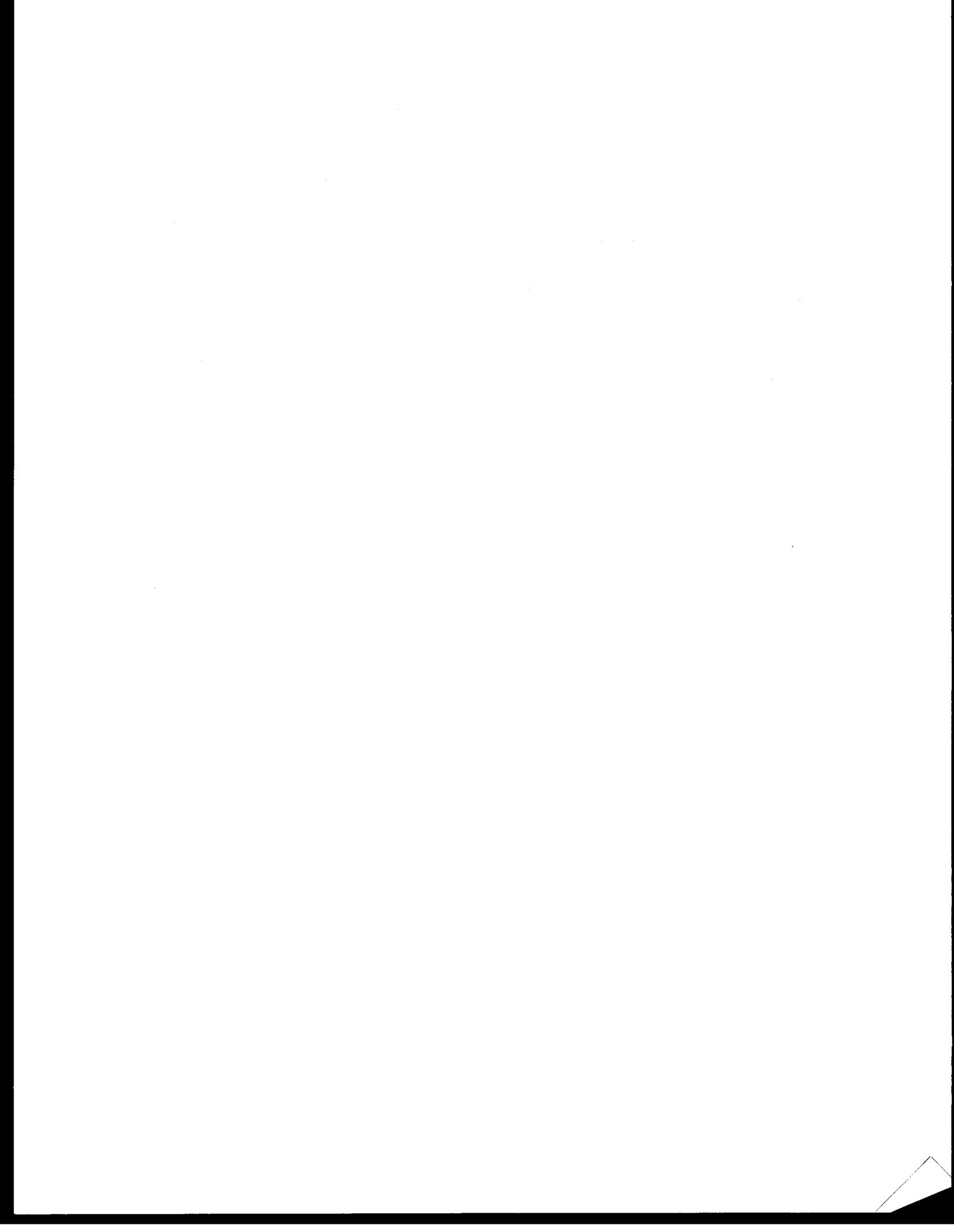
The Cape Peirce-Cape Newenham colonies, last censused in 1977, should be visited in 1984, particularly so that a census of murres can again be taken. Because large numbers of Common Murres, but few Thick-billed Murres, nest there, and because the colonies are in the SE Bering, a 1984 field season there would provide very useful comparisons with the recent information from the offshore island colonies. The value would be enhanced considerably if work took place concurrently on one of the islands, such as St. Matthew I.

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APPENDIX

Table 1. Murre census results from St. Matthew Island in 1982.

Plot	18 July		20 July			28 July		29 July		
	Time ^a	Observer E	Time	Observer E	Observer M	Time	Observer E	Time	Observer E	Observer M
D-1		1315		612	605					
D-2		1300		27	27					
D-3				0	0					
D-4				0	0					
D-5				0	0					
D-6		1500		130	127					
D-7		1515		1,250	1,020					
D-8		1600		340	300					
D-9a		1545		1,640	1,640					
D-9b		1630		1,200	990					
D-9c		1645		1,120	970					
D-9d		1745		3,570	2,390					
E-1	1400	820	1845	1,230	1,330					
E-2	1910	0								
E-3	1440	57								
E-4	1845	360								
E-5	1545	9,815								
E-6	1700	2,040				1900	6,850	1815	4,840	4,950
E-7	1730	630				1830	715	1745	820	930
E-8, F-1						1745	12,500	1615	7,710	5,870
F-2								1510	0	0
F-3								1415	740	630
F-4, F-6								1445	410	370

^aBering Daylight Time.

Table 1 (cont.).

Table 2. Murre census results from Bluff in 1982.

Section	15 July	18 July	
	Observer F	Observer F	Observer K
End-C	6,280	5,980	7,310
C-D	8,330	9,990	10,120
D-E	2,360	3,100	3,850
E-F	3,520	4,710	5,360
F-G	1,160	1,530	1,370
G-H	1,060	1,110	1,230
H-I	2,390	2,350	2,320
I-J	110	160	110
Total	25,210	28,930	31,670
Time at End ^a	0825 h	0855 h	
Time at J	1410 h	1300 h	

^aBering Daylight Time.

Table 3. Murre census results from Colony 1, Cape Thompson, in 1982.

Plot	29 July			5 August			7 August			7 August		
	Time ^a	Obser-ver F	Obser-ver K	Time	Obser-ver F	Obser-ver K	Time	Obser-ver F	Obser-ver K	Time	Obser-ver F	Obser-ver K
A	2040	0	0	2110	0	0	2230	0	0	2310	0	0
B	2035	130	130	2106	150	150	2230	140	130	2310	140	130
C	2032	220	180	2105	280	300	2225	150	190	2305	180	200
D	2028	360	370	2052	350	340	2215	280	330	2258	320	285
E	2020	1,070	940	2040	1,270	1,420	2210	1,110	880	2252	1,140	880
F	2015	0	0	2038	16	15	2102	16	15	2247	24	23
G	2010	540	560	2030	620	600	2159	500	530	2245	525	490
H	2009	13	12	2025	28	35	2155	13	16	2243	13	11
I	2005	0	0	2020	0	0	2155	0	0	2243	0	0
Total		2,333	2,192		2,714	2,860		2,209	2,091		2,342	2,029

^aBering Daylight Time.

Table 4. Murre census results from Colony 2, Cape Thompson, in 1982.

Plot	Time ^a	29 July		Time ^a	5 August	
		Observer F	Observer K		Observer F	Observer K
A1	1446	9	10	1525	20	20
A2	1448	15	10	1530	19	20
B	1453	136	110	1531	140	130
C	1458	750	770	1540	770	760
D	1506	210	240			
E	1509	1,560	1,710			
F	1516	470	540			
G	1525	1,525	1,830			
H	1533	1,870	2,000			
I	1540	1,280	1,610	1550	1,270	1,450
J	1550	1,690	1,750			
K,L	1602	2,330	2,130			
M	1610	1,430	1,970			
N	1625	1,540	1,690			
O	1634	1,610	2,250	1620	1,480	1,380
P	1641	840	900			
Q	1649	1,930	2,020			
R	1657	430	500			
S,T	1705	4,180	4,000			
U	1720	2,610	2,120	1645	1,660	1,640
V	1736	2,250	2,560			
W	1822	1,850	1,870			
X	1829	1,630	1,550			
Y	1836	2,730	2,060			
Z	1848	1,850	1,590			
AA	1853	690	760	1709	690	700
BB	1900	1,340	1,360	1717	1,010	1,090
CC	1908	1,240	1,200			
DD	1915	1,590	1,360			
EE	1922	580	500			
FF	1930	460	470			
HH	1935	700	630	1725	370	340
II	1940	190	200	1732	190	190
Total		43,780	44,370			

^aBering Daylight Time.

Table 5. Murre census results from Colony 3, Cape Thompson, in 1982.

Plot	Time ^a	3 August		Time	5 August	
		Observer F	Observer K		Observer F	Observer K
A	0852	180	200	1148	56	50
B	0905	380	340	1040	580	580
C	0908	200	190			
D	0909	570	560	1030	560	530
E	0912	510	510	1034	480	510
F	0915	310	250	1051	370	330
G-K	0930	3,720	3,430			
L	1009	180	270			
M	1011	760	750			
N	1017	1,000	1,060	1058	880	950
O	1014	250	290			
P	1021	1,150	1,250	1102	1,360	1,430
Q-O	1032	210	300			
Q-P	1035	490	530			
R-O	1040	520	680			
R-P	1043	1,130	1,070			
S-O	1050	560	700			
S-P	1054	120	110			
T	1105	1,740	1,700	1113	1,670	1,670
U	1110	1,600	1,640	1120	1,330	1,390
V	1130	1,040	800	1131	840	810
W	1135	450	500	1148	420	460
<hr/>		Total	17,070	17,130		

^aBering Daylight Time.

Table 6. Murre census results from Colony 4, Cape Thompson, in 1982.

Plot	Time ^a	28 July		Time	3 August	
		Observer F	Observer K		Observer F	Observer K
A	2030	100	120	1425	110	110
B	2028	200	290	1423	180	180
C	2025	430	320	1417	480	500
D	2007	130	70	1400	140	120
E	2014	670	660	1405	720	630
F	2013	240	300	1358	240	260
G	2010	820	1,000	1356	570	540
H	2000	410	360	1346	170	170
I	1958	90	40	1344	90	80
J	1953	460	520	1341	480	500
K	1950	90	100	1339	110	110
L	1945	360	450	1333	240	250
M	1936	370	410	1330	320	350
N	1940	370	420	1328	190	200
O	1942	90	90	1325	70	80
P	1933	610	710	1320	360	390
Q	1930	230	250	1314	260	290
R	1928	260	220	1308	240	230
Total		5,930	6,330		4,970	4,990

^aBering Daylight Time.

Table 7. Murre census results from Colony 5, Cape Thompson, in 1982.

Plot	Time ^a	28 July		Time	3 August	
		Observer F	Observer K		Observer F	Observer K
B	1402	120	90			
C	1348	110	270			
D	1355	160	200			
E	1417	40	40			
F	1418	130	110			
G	1425	450	280			
H	1424	310	580			
I	1411	270	220			
J	1456	210	240			
K,FF	1505	2,320	2,500			
L	1540	210	290			
M	1545	230	300			
N	1550	880	900			
O	1515	180	180			
P	1519	410	650			
Q	1544	230	300			
R	1630	410	530			
S	1706	420	600			
T	1704	390	520			
U,RR	1757	1,270	1,210			
V	1805	110	130			
W	1808	100	120			
X	1350	700	640			
Y	1352	1,070	1,000			
AA	1405	1,290	1,150			
BB	1434	560	240			
CC	1431	280	180			
DD	1440	1,290	1,250	1446	920	1,000
EE	1449	1,160	1,190			
GG	1552	2,290	2,810			
HH	1605	5,190	5,280	1456	4,570	4,750
II	1625	3,300	3,160			
JJ	1640	1,300	1,660			
KK	1635	1,770	2,880			
LL	1714	870	950	1515	940	980
MM	1708	2,620	2,280			
NN	1735	3,000	2,880			
OO	1729	2,620	3,160	1522	1,600	1,650
PP	1746	2,170	2,390			
QQ	1751	1,040	1,240			
Total		41,480	44,600			

^aBering Daylight Time.

Table 8. Murre census results from Colony 5, Cape Thompson, in 1982 using 1976 plots.

Plot	Observer F	Observer K
AA	810	910
BB	1,350	1,290
CC	2,320	2,230
DD	3,670	3,300
FF	4,280	4,770
HH	5,700	6,300
KK	6,930	7,720
LL	6,110	6,950
NN	5,620	6,040
QQ	3,210	3,630
RR	1,480	1,460
Total	41,480	44,600

Table 9. Land-based counts of murres at Colony 5, Cape Thompson, in 1982.

Plot	30 July		3 August		7 August	
	Time ^a	Number	Time	Number	Time	Number
B	1600	912				
E	1515	2,107	1818	2,134	1557	1,850
F	1510	455	1816	472	1615	436
G	1640	2,083	1738	1,924	1625	2,095
H	1800	1,630	1750	1,755	1640	1,804
I		2124		640		
K					1655	1,375
L					1725	823
M		2025		835		
N		2015		2,285		
O		1938		930	1732	824
P		1950		1,195	1737	1,266
Q		2005		733	1752	803
R		1932		1,858	1758	2,326
S		1937		690	1824	823
T		1910		1,245	1835	943
U		1900		440		
V		1836		515	1855	328
W		1820		760	1900	388

^aBering Daylight Time.

Table 10. Murre census results from St. Matthew Island in 1977. Data are from DeGange and Sowls (1978) and Sowls (unpubl. data). Raw scores were compensated using the diurnal activity curve derived in 1982.

Plot	Time ^a	Number	
		Raw	Compensated
D-1	nd ^b	696	--
D-2	nd	266	--
D-3	nd	0	--
D-4	nd	0	--
D-5	nd	0	--
D-6	nd	480	--
D-7	nd	1,665	--
D-8	nd	800	--
D-9	nd	17,440	--
E-1	nd	560	--
E-2	nd	0	--
E-3	1115	170	710
E-4	1130	290	1,160
E-5	1215	21,900	73,000
E-6	1300	8,775	26,590
E-7	1345	600	1,670
E-8	1415	8,800	23,160
F-1	1445	1,480	3,610
F-2	1500	0	0
F-3	1500	600	1,430
F-4, F-6	1515	550	1,280
F-5	1530	380	860

^aBering Daylight Time.

^bnd = no data.

Table 11. Numbers of murres on compensation plots at Cape Thompson in 1982.

Time ^c	Colony 2 ^a		Colony 5 ^b			
	29 Jul	5 Aug	29 Jul	30 Jul	3 Aug	7 Aug
0900					2,180	
1000					2,265	
1100					2,267	
1200					2,169	
1300			1,811		2,063	
1400			2,029		1,969	
1500	554		1,894	1,693	1,934	
1600	576	718	1,966	1,684	1,938	1,865
1700	608	731	1,922	1,727	1,883	
1800	607	813	1,918		1,943	
1900	691		2,081		1,918	
2000	661		2,139		1,965	2,020
2100	661		2,063		1,970	
2200			1,996			

^aCompensation plots A-1 and A-2.

^bCompensation plots 5-1-A, 5-1-B, 5-1-C, 5-2, 5-3.

^cBering Daylight Time.

Table 12. Black-legged Kittiwake census results from St. Matthew Island.

Plot	Nests	Time ^b	1982					
			20 July		28 July		5 August	
			Birds	Nests	Birds	Nests	Birds	Nests
D-1	411	1316	434	284				
D-2	359	1306	166	123				
D-3	0		0	0				
D-4	0		0	0				
D-5	0		0	0				
D-6	23		0	0				
D-7	50	1505	211	126				
D-8	10	1600	8	1				
D-9	857	1534	1,077	746				
E-5	1,305	1220					1,036	537
E-6	0	1800			0	0		
E-7	90	1715			79	113		
E-8	825	1630			896	nd ^c		
F-1	360	1515			810	643		
F-2	0				0	0		
F-3	0	1455			2	1		
F-4	0	1415			5	6		
Total	3,465 ^d		1982: Birds = 4,724, Nests = 2,580 ^d					

^aData from DeGange and Sowls (1978).

^bBering Daylight Time.

^cnd = no data.

^dTotals exclude plot E-8 for comparative purposes.

Table 13. Black-legged Kittiwake census results from Bluff in 1982.^a

Section	Observer F		Observer K	
	Individuals	Nests	Individuals	Nests
End-C	1,927	1,488	1,567	1,261
C-D	1,808	1,397	---	---
D-E	777	695	718	642
E-F	1,009	878	---	812
F-G	872	650	881	545
G-H	379	286	415	280
H-I	1,169	889	988	745
I-J	310	202	303	212
Total	8,251	6,485		

^aEnd-F censused on 15 July; G-J censused on 18 July.

Table 14. Black-legged Kittiwake census results from a portion of Colony 2, Cape Thompson, on 5 August 1982.

Plot	Time ^a	Observer F		Observer K	
		Individuals	Nests	Individuals	Nests
A1	1525	0	0	0	0
A2	1530	0	0	0	0
B	1535	0	0	0	0
C	1540	0	0	0	0
I	1550	222	162	211	164
O	1620	124	97	138	100
U	1645	727	633	680	---
AA	1709	83	51	92	---
HH	1725	68	42	71	44
II	1732	6	5	6	4

^aBering Daylight Time.

Table 15. Black-legged Kittiwake census results from Colony 4, Cape Thompson, on 5 August 1982.

Plot	Time	Individuals		Nests	
		Observer F	Observer K	Observer F	Observer K
A	1410	299	270	193	177
B	1405	376	274	240	192
C	1355	424	386	303	270
D	1350	42	69	23	38
E	1338	623	400	430	323
F	1332	280	210	205	169
G	1317	450	362	326	284
H	1306	143	125	98	84
I	1254	449	340	289	240
J	1246	132	136	66	87
K	1241	176	156	115	108
L	1234	266	199	156	147
M	1228	122	124	84	78
N	1223	217	221	141	156
O	1221	45	50	28	26
P	1217	108	110	62	64
Q	1214	8	11	4	4
R	1213	0	0	0	0
Total		4,160	3,443	2,723	2,437

^aBering Daylight Time.

TABLE 16. Mensural data on least auklet chicks at St. Matthew Island, 1982: T = tarsus length (mm); C = culmen lenght (mm); WT = weight (g).

Chick Number	25 July 1982			1 August 1982			5 August 1982			9 August 1982			11 August 1982		
	T	C	WT	T	C	WT	T	C	WT	T	C	WT	T	C	WT
3	17.8	5.7	16.5	21.0	7.9	45.0	22.8	8.6	65.0	23.2	8.6	90.0	22.2	8.7	83.0
4	15.8	5.9	17.0												
5				18.3	5.9	19.0									
8	17.4	6.0	17.0												
11				20.3	6.7	24.5	20.8	7.0	43.5	21.0	7.3	73.5	21.4	7.5	71.0
13				16.4	5.8	15.0	19.0	6.9	29.5	20.4	7.1	50.5	21.1	7.2	61.0
15	17.3	6.2	19.0												
16				22.6	7.0	47.0	22.8	7.4	35.0						
17				17.9	6.4	22.5									
18				16.9	5.5	14.0									
19				19.8	7.0	28.5									
21				16.3	6.4	18.5	17.0	7.0	31.5	21.5	8.0	71.5	23.6	8.5	83.0
22				15.6	5.6	11.5									
23				17.3	5.8	12.0	18.7	6.8	21.0	18.8	7.0	42.5	19.0	7.0	51.5
24				13.2	6.7	24.0									
27				14.9	5.8	14.0									
28							15.5	6.4	14.0						

Table 17. Numbers of prey taken by Least Auklets on St. Matthew Island during the chick period in 1982. Size categories are I, 0.0-7.0 mm; II, 7.1-15.0 mm; III, 15.1 mm and over (from Bedard 1969). Number of samples = 29.

	Size	Number
<i>Calanus marshallae</i>	I	18,685
<i>Parathemisto libellula</i>	I	73
	II	65
	III	4
<i>P. pacifica</i>	I	4
<i>Hyperoche medusarum</i>	I	1
	II	3
<i>Monoculodes</i> sp. zoea	II	2
<i>Pleusympetes</i> sp.	I	10
<i>Westwoodilla caecula</i>	I	1
<i>Atylus bruggeni</i>	I	104
<i>A. collingi</i>	II	1
<i>Orchomene</i> sp.	I	4
<i>Jassa</i> sp.	I	1
	II	1
<i>Iscyrocera</i> sp.	I	1
	II	11
<i>Pontogeneia makaroui</i>	I	32
<i>P. rostrata</i>	I	23
<i>Anonyx laticoxae</i>	I	4
	II	11
<i>Melita</i> sp.	II	1
<i>Anisogammarus pugettensis</i>	II	1
<i>Pleustidae</i>	II	1
<i>Stenothoidae</i>	I	1
<i>Podoceridae</i>	II	2
<i>Lysianassidae</i>	I	1
<i>Gammaridae</i>	II	4
<i>Thysanoessa</i> sp.	II	1
	III	1
<i>Euphausiid furcilia</i>	I	8
<i>Acanthomysis</i> sp.	II	1
<i>Hippolytidae</i> zoea	I	4
	II	55
<i>Crangonidae</i> zoea	I	1
	II	1
<i>Pandalidae</i> zoea	II	5
<i>Shrimp</i> zoea	II	2
<i>Paguridae</i> zoea	I	32
	II	62
<i>Lithodidae</i> zoea	I	14
	II	10
<i>Oregoninae</i> zoea	I	1
<i>Diastylis bidentata</i>	II	1
<i>Limacina helicina</i>	I	28
	II	45

**POPULATION STATUS, REPRODUCTIVE ECOLOGY,
AND TROPHIC RELATIONSHIPS OF SEABIRDS
IN NORTHWESTERN ALASKA**

by

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**Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 460**

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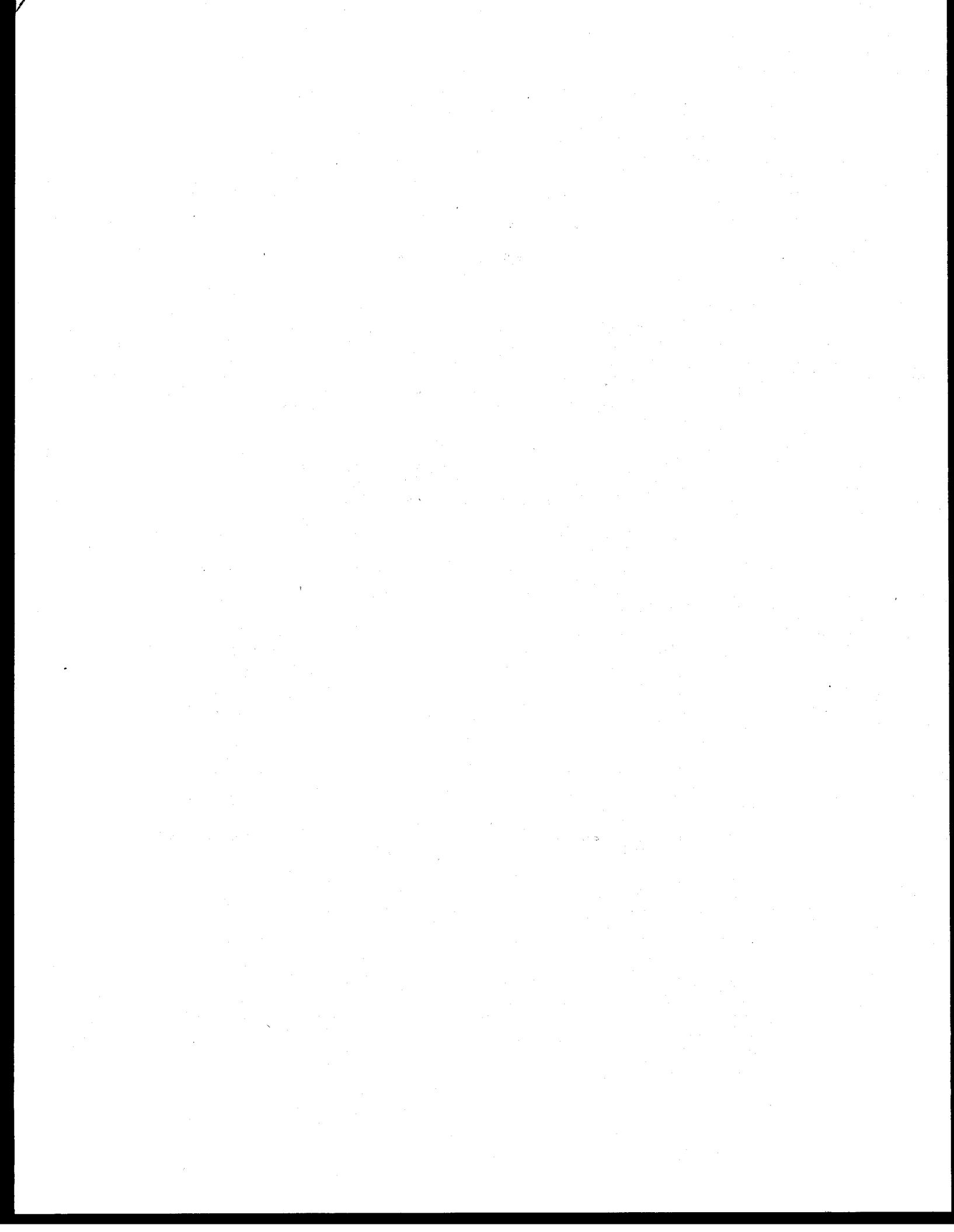
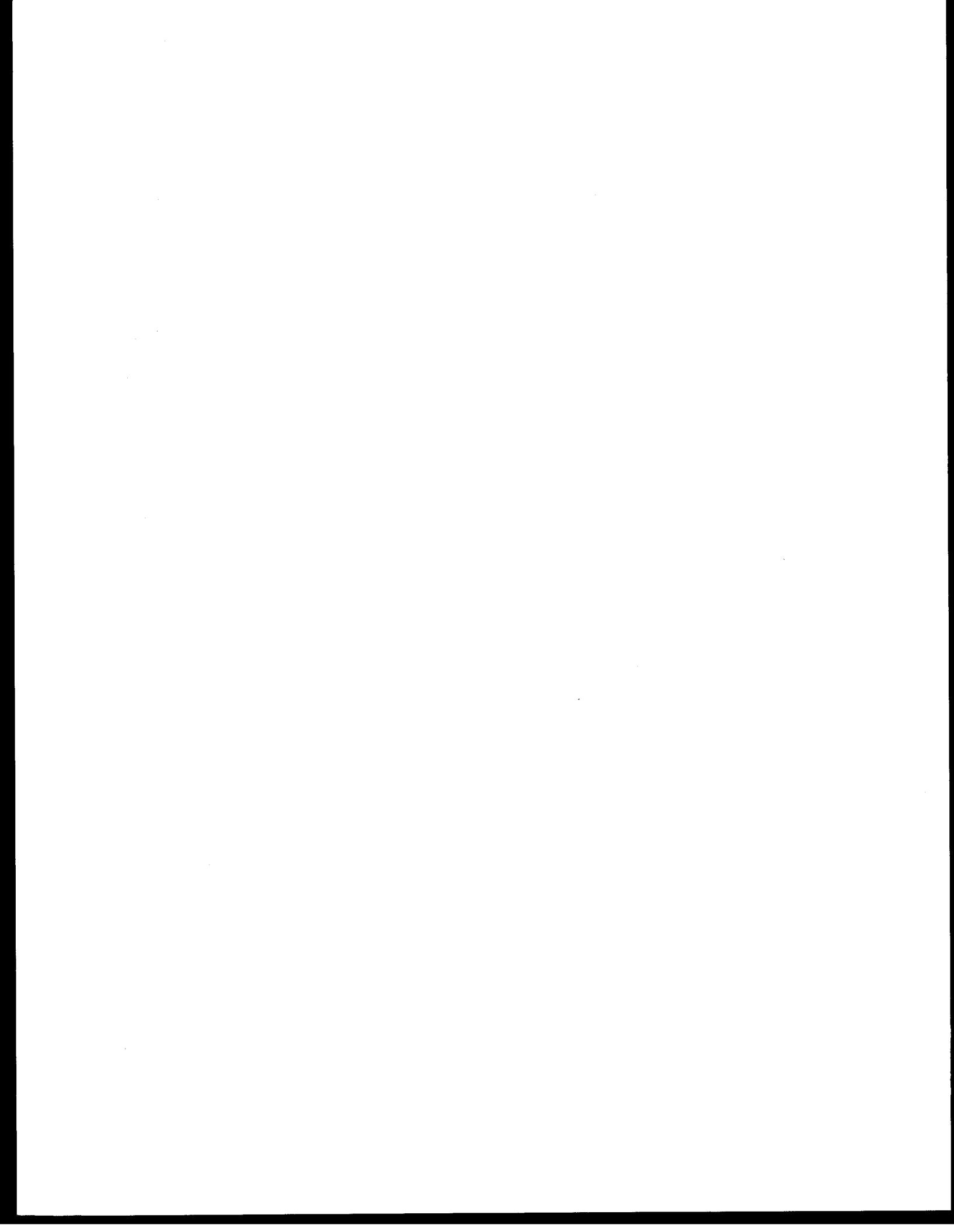


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I. SUMMARY OF OBJECTIVES, CONCLUSIONS AND IMPLICATIONS WITH REGARD TO OCS OIL AND GAS DEVELOPMENT

A. Objectives

The objective of RU 460 is to describe important components of the biology of seabirds in northern Alaska, including relationships among seabirds, their supporting food webs and the physical environment. To accomplish this objective we have concentrated on studies of thick-billed murres (*Uria lomvia*), common murres (*U. aalge*) and black-legged kittiwakes (*Rissa tridactyla*), the most wide-spread, and among the most numerous, of all seabird species in the region. Moreover, murres and kittiwakes are easily studied compared to other species, and are sensitive indicators of environmental change.

B. Conclusions

Our principal conclusions are that numbers of murres at two major breeding colonies in northern Alaska are declining and that annual variability is high in a variety of elements of murre and kittiwake breeding biology. Two possibilities that could account for declining murre numbers are decreases in natality and/or increases in winter mortality. Annual variability in murre and kittiwake breeding biology is a function of prey availability, and is predictable from conditions in the physical environment during spring and summer.

C. Implications with respect to OCS Oil and Gas Development

Seabirds are very sensitive indicators of environmental change. They are easily and economically studied by comparison to other high-profile marine vertebrates. Studies of seabirds can yield a great amount of information on changes in marine food webs important to many top-level consumers. Such information will be necessary in order to identify possible effects of oil and gas development on regional marine ecosystems.

II. INTRODUCTION

A. General Nature and Scope of Study

Seabirds occupy top positions in marine food webs and therefore integrate many elements of regional ecosystems. Among the many species of seabirds breeding in Alaska, murres and kittiwakes are easily studied and are sensitive to changes in the environment. Our studies take advantage of these characteristics to examine spatial and temporal differences in several important marine food webs, and relationships among these food webs, regional physical processes and seabird biology.

Substantial declines in murre populations that we have documented during recent years in northern Alaska have demonstrated the need for a system that will permit future monitoring of colonies as resource exploration and development increases on Alaska's outer continental shelf. Therefore, our studies are designed to provide information on the popula-

tion status of murres and on methods to reliably census them, thus establishing useful indices of numbers at major breeding colonies in Alaska.

B. Specific Objectives

The specific objectives are to:

1. Census murres and black-legged kittiwakes at major colonies in Northern Alaska.
2. Establish permanent census plots for monitoring numbers in future years.
3. Examine sources of variability in census methodologies that affect the bias and precision in estimates of numbers.
4. Determine levels of reproductive success and breeding phenologies of murres and kittiwakes.
5. Measure growth rates of kittiwake chicks.
6. Collect specimens of murres and kittiwakes for food habits information, and as a way to sample local marine fishes and invertebrates.
7. Obtain data on other species of seabirds that would provide useful information on regional marine ecosystems.

C. Relevance to Problems of Oil Development

The success of OCSEAP will depend in part on the ability to detect changes in marine biological systems and, in part, on the ability to separate naturally occurring changes from changes that might result from resource development in Alaskan waters. OCSEAP sponsored studies of seabirds in the Bering and Chukchi Seas have shown that population parameters such as numbers, breeding phenology and reproductive success can vary considerably between years. Such marked natural variation could make it difficult to determine if developmental activities were involved in biological changes that might be detected in future years.

Our studies have shown that the annual variability in seabird biology is not random, but is predictable from annual changes in the physical environment and in regional food webs. Information of this kind is relevant to problems of OCS development because it provides the means to more clearly differentiate between natural phenomena and changes resulting from resource development. This aspect of our work is acquiring added importance because of the recent declines in murre numbers that we have documented at two major colonies, one in the eastern Chukchi Sea and the other in the northeastern Bering Sea.

Seabirds are appropriate species to study not only because they are sensitive indicators of changes in the environment, but also because they are relatively easy to study, especially by comparison to other high

profile marine vertebrates such as seals and whales. They also offer an excellent means of sampling lower trophic levels that often defy scientific sampling methodologies. Therefore, seabird studies can provide a great amount of relatively inexpensive information on marine ecosystem dynamics. The monitoring of seabird populations at strategic locations in Alaska may be one of the most efficient ways of detecting significant changes resulting from OCS development.

III. CURRENT STATE OF KNOWLEDGE

The first serious attempt to study a large seabird colony in northwestern Alaska was made by L.G. Swartz at Cape Thompson in 1959-1961. We returned there in 1976, and upon completing that first field season we were faced with two interesting questions. They were 1) What happened to all the murres, and 2) What happened to all the kittiwakes? Murre numbers were about half large as in 1960, and instead of laying nearly two eggs per clutch, the majority of kittiwakes failed to lay any eggs at all.

Because other species of seabirds that nest at Cape Thompson were few in number and we saw little change in their populations compared to 1960, we devoted most of our time in the following years to studies of murres and kittiwakes. In this report, our current state of knowledge, we describe changes we saw in murre and kittiwake populations at Cape Thompson and other colonies in northwestern Alaska in the years following 1976, and discuss reasons for the changes including man-induced and natural changes in the environment.

IV. STUDY AREAS

The locations of seabird colonies visited during this study are shown in Figure 1. Also shown is the location of the Owalit Mountain study area on St. Lawrence Island which we visited in 1981.

Details concerning the colonies at Bluff, Cape Thompson and Cape Lisburne have been reviewed in our previous annual reports. Additional information on St. Lawrence Island can be found in our annual report for the FY81 field season.

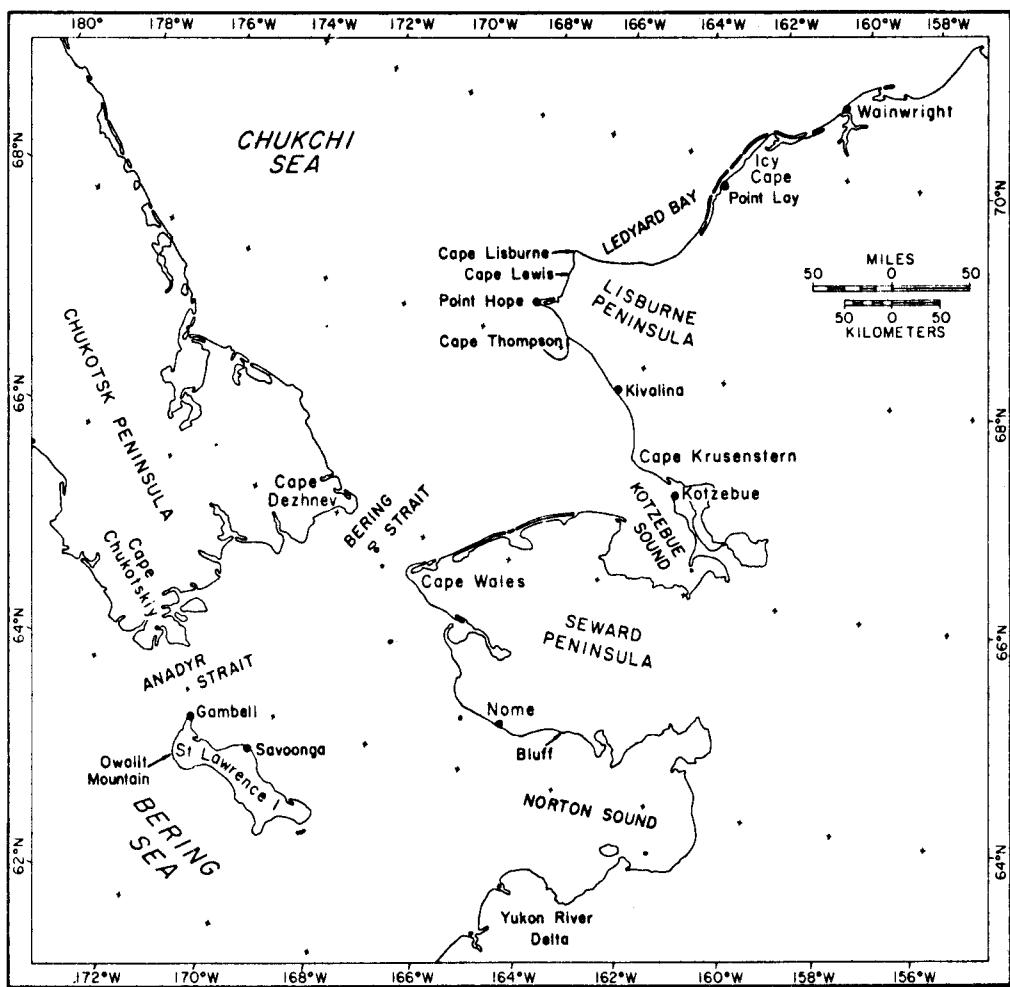


Figure 1. Study areas in northwestern Alaska.

Va. MURRE NUMBERS - SOURCES, METHODS, AND RATIONALE OF DATA COLLECTION

Cape Thompson

Swartz (1966) first censused the murres at the Cape Thompson colonies in 1960. In conducting the census, he subdivided each of the five colonies into census plots to facilitate counting and recorded the boundaries on photographs (Swartz, unpublished data). Plot boundaries were generally defined in accordance with geomorphic features such as cracks and deep ravines. In 1961, Swartz's field crews counted Colony 1 three times and Colony 4 once as well as some of the census plots at the other three colonies.

In each census of murres that we conducted at Cape Thompson we generally used the same plot boundaries as did Swartz's field crews. The principal exception was at Colony 5 in 1976 when we lacked photographs showing the original plot designations. In addition, in several instances we had difficulty discerning the boundaries in the photographs and counted adjacent plots as a single unit. In 1979 all five colonies were censused on 7 or 8 August; several additional counts of Colony 1 and randomly selected plots at the other four colonies were made during the incubation and chick periods.

All censuses at Cape Thompson have been made between the completion of egg-laying and the onset of sea-going of chicks, i.e., within the appropriate period for censusing as defined by Birkhead and Nettleship (1980). In 1979 at Cape Thompson some of the additional counts were made either shortly before the completion of egg-laying or shortly after the first sea-going of chicks. Here we include any plot counts made during the period commencing one week before the day hatching was first observed and ending one week after the first date chicks successfully left the cliffs. We define this interval as the "Census Period". Lloyd's (1975) daily counts of common murres indicate that numbers are likely highest and fluctuate least from day to day during this period.

The techniques of counting murres at Cape Thompson were similar but not identical among years. Typically two or three observers counted each plot with the aid of binoculars from a small boat anchored offshore. However, in 1960 most of the plots at higher elevations at Colony 5 were counted from vantage points along the top of the cliffs. In 1976 and 1977 these plots, like all other plots, were counted from a boat anchored offshore. In 1979, observers boat-based and land-based counted some of these plots simultaneously to compare the two methods.

Usually observers have estimated numbers by tens, intermittently counting ten individuals to maintain accuracy. However, at Colony 5 in 1960 and 1976 all boat-based estimates were in increments of 100 rather than 10.

Both thick-billed murres and common murres breed at Cape Thompson and occur in varying proportions throughout the five colonies (Swartz 1966). Although one of Swartz's field assistants differentiated between the two species in his boat-based counts, no observers in our field crews have done so successfully. All counts reported here are of the two species combined.

Cape Lisburne, Cape Lewis, St. Lawrence Island

The procedures for censusing murres at Cape Lisburne and Cape Lewis have been comparable to those at Cape Thompson. Two or three boat-based observers have conducted the counts and, except in 1976 at Cape Lisburne when observers estimated numbers by hundreds, observers have estimated numbers by tens. Complete censuses were conducted at Cape Lisburne only in 1976 and 1977. In 1978 only six of the 75 plots were counted. In 1979 and 1981, these six plots and four additional plots were counted. Cape Lewis was censused completely in 1977 and 1981. As at Cape Thompson, no differentiation between the two murre species was made in any of these censuses.

Murres on St. Lawrence Island have never been censused completely. In 1981 we counted murres at six colonies but did not count those at the remaining four colonies at the east end on the island. We counted the Owalit Mountain colony on 24 July. Previously S.R. Johnson (unpublished data) counted this colony on 14 August 1972, and two observers counted the murres there on 26 July 1976 (Searing 1977).

Bluff

Common murres so vastly outnumber thick-billed murres at Bluff (Drury *et al.* 1981) that counts there can be considered as counts of common murres only. Each census at Bluff has been conducted by one or more boat-based observers. Until 1980 observers counted from a boat moving slowly past the cliffs rather than anchoring at each plot. Beginning in 1980 field crews anchored the boat at each plot before starting the counts. Before 1980 field crews esimated the numbers of murres flushing from the cliffs in response to the approaching boat as well as counting those remaining on the cliffs. In contrast field crews at Bluff in 1980 and 1981, and in all years at the other study colonies, have simply waited several minutes to begin counting a particular plot until any murres that had flushed returned to the cliffs.

We first participated in censusing murres at Bluff in 1978 and have used the data presented by Drury *et al.* (1981) for earlier years. Several censuses at Bluff have been conducted outside of the Census Period, and we do not consider them here. Little information on phenology was available for 1975; we used only the 1 August census and excluded the 4 July and 8 September censuses which fell outside of the Census Period in all other years at Bluff. At least two censuses were conducted within the Census Period at Bluff in each year from 1976 through 1981.

At Bluff, but not at the other study localities, a variation of Birkhead and Nettleship's (1980) "full-scale method" for determining population status has been used. Numbers of common murre chicks hatching and successfully going to sea have been determined on productivity plots.

Because plot choices and boundaries were refined as the study progressed and were not finalized until 1977, we have followed the procedure of Drury *et al.* (1981) and express hatching success as a ratio between the total number of eggs hatching and the average number of individuals in adult plumage present on the plots (k') and sea-going success as a ratio between the total number of sea-going chicks and the average number of individuals present on the plots (k''). These ratios are similar to a k -value (e.g., Birkhead 1974) which is the ratio between the total number of eggs laid (number of breeding pairs) and the average number of individuals on study plots.

Compensation of Census Results

Numerous studies have documented marked diurnal variation and daily variation in numbers of murres present on the breeding cliffs (e.g., Swartz 1966, Lloyd 1975, Birkhead 1978a, Slater 1980). Consequently, Birkhead and Nettleship (1980) recommended that counts of individuals be made on selected study plots during the same time each day for five to 10 days during the Census Period. However, as Birkhead and Nettleship noted, a key assumption in the use of study plots is that numeric changes on those plots reflect changes in numbers in the whole colony. Rather than accepting this assumption we have counted the entire colony whenever possible. At Bluff a complete census requires only several hours, and two or more censuses at the same time of day have been conducted in each year since 1976, negating the effects of diurnal variation in attendance in comparisons of census results and permitting quantification of daily variation in attendance. At the larger colonies (Cape Thompson and Cape Lisburne) repeated complete censuses have not been possible and a different approach has been taken.

Swartz (1966) introduced a technique of compensating for diurnal variation in attendance and we describe our modification of the technique here. Observers stationed onshore count certain areas (compensation plots) of the colony repeatedly at regular intervals (e.g., hourly) while the census is being conducted by the boat-based observers. At Cape Thompson and our other study colonies we have noted a bimodal pattern in daily attendance of murres with peak numbers occurring in the early morning and late evening.

Continuing the counts on the compensation plots until evening peak numbers are ascertained permits adjustment of counts on census plots made earlier in the day to that peak. To calculate the number of murres that would be expected on each census plot at the time of the evening peak, we multiplied the raw count at time t , averaged between or among observers, by the maximum evening count on the compensation plots and divided by the count on the compensation plots at time t . An assumption of this procedure is that the diurnal pattern of attendance on the compensation plots accurately reflects that on the census plots.

At Cape Thompson in 1979 all census counts were coupled with 24-hour counts of compensation plots. In 1960, 1976, and 1977, however, counts of compensation plots at Cape Thompson were not always made in conjunction with the censuses. If compensation counts were not made on the day a particular census plot was counted, or if the compensation counts did not continue through the evening peak in numbers, compensation for diurnal

variation was made on the basis of all counts during the Census Period on compensation plots in that year. We first expressed each hourly count as a proportion of the evening maximum that day and then averaged values from all days counts were made for a particular hour of the day. Thus census counts made on days when no compensation plots were counted were compensated in relation to the average diurnal pattern of attendance during the Census Period in that year.

In 1979 at Cape Thompson we made several counts in addition to those during the census. We randomly chose and counted three plots at Colony 2 and one plot at Colony 3 four times during the Census Period. We counted five plots on Colony 2 on 17 August, and field crews counted four plots on each of Colonies 3, 4, and 5 on 11 August. Colony 1 was censused completely three times and Colony 4 once in addition to the censuses on 7 August. These counts provide a basis for compensation of the census results in that year for daily variation.

Once all counts of census plots were compensated for diurnal variability, we compensated results on the day of the census for daily variation within the Census Period. All plot counts for a particular colony made on a particular day were summed, and the sum was then expressed as a proportion of the census total for those plots. The results for all days that counts of census plots were made, including the day of the census, were then averaged, providing a correction factor for the departure of the census figure from the daily average in numbers during the Census Period.

At Cape Lisburne counts of compensation plots were made only in 1977. The diurnal pattern of cliff attendance in that year was therefore used as a basis of diurnal compensation in later years. Repeated counts of census plots at Cape Lisburne were made only in 1981 when six plots on the west side of the colony were counted twice. Thus compensation of the census results for daily variation at Cape Lisburne was possible only in 1981. No counts of compensation plots were made at the time of the census in any year at the Owlit Mountain colony, and we report only the raw census results for that colony.

Numerous observers have conducted the field work. We have made no estimates of personal handicaps, as we have no basis for determining which observers estimated numbers most accurately. Except on small, easily viewed plots the count obtained by each observer should be considered an estimate of the number of murres visible from that vantage point, rather than a true count. In reporting the results here we have computed the mean of simultaneous counts by different observers for each plot and have then summed the results for all plots in each colony.

Several studies have shown that weather influences the number of murres present on the cliffs (e.g., Birkhead 1978, Slater 1980). Although we have not quantified the effects of weather in the present study, by necessity all boat-based censuses have been conducted in similar weather conditions, i.e., in conditions of calm or light winds, calm seas or light swells, no precipitation, and no fog obscuring the cliffs. Tidal fluxes are slight throughout the region, precluding a relationship between tidal stage and numbers of murres present on the cliffs like that noted elsewhere by Slater (1980).

As noted earlier, 18 of the upper plots at Colony 5 at Cape Thompson were censused from the top of the colony in 1960 but from a boat at sea in later years. In 1979 we evaluated differences between these techniques by simultaneous counts by boat-based and land-based observers at eight of these plots. The ratio between the land-based and boat-based totals for the eight plots provided a correction factor for boat-based counts of those 18 plots in 1977 and of the remaining ten plots in 1979. Since plot designations at Colony 5 in 1976 differed from those in 1960, we used the ratio between the corrected 1979 total and the boat-based 1979 total as a correction factor to adjust the 1976 total. Thus our compensation for counting location adjusts boat-based counts between 1976 and 1979 so that they are comparable with any land-based counts in 1960.

Modeling of Population Fluctuations

Birkhead and Hudson's (1977) data on survivorship, age at maturity, and age-related cliff attendance, in connection with the data on numbers and reproductive success at Bluff, provide a basis for modeling changes in population numbers that would be expected to result from annual variations in reproductive success. First we determined the relationship between climatic conditions during the breeding season and reproductive success at Bluff for the years 1975-1979 using polynomial regression analysis (e.g., see Zar 1974). Secondly, we used the resultant regression equation to predict reproductive success from 1942 through 1974, years that climatic data were available but no studies of murres were conducted, and 1980, when our visit to the colony was brief and predated the period of sea-going of chicks. Thirdly, we constructed a population model based on a modified Leslie matrix, lumping all adults into a single age class (e.g., see Mertz 1971), but maintaining yearly age classes up to the age of maturity. Thus each cohort could be tracked individually until the age of maturity. Using the average predicted reproductive output for the years 1942-1980 and Birkhead and Hudson's (1977) figure of 0.915 for adult survivorhsip, we determined the value for subadult survivorship (0.339) which would result in a stationary population. Fourth, we ran the model with those particular values of survivorship inputing the predicted reproductive success in each year in succession. Due to the multi-year lag between the time chicks leave the cliffs and the time they return as subadults or adults (see Birkhead and Hudson 1977), the model can be used predictively as well as providing a simulation of observed trends. The model provides a test of the hypothesis that numeric variations are due to variability in natality, i.e., to conditions during the breeding season.

VIA. MURRE NUMBERS - RESULTS

Cape Thompson

The timing of the censuses at Cape Thompson and breeding phenology during the years complete censuses were made are shown in Table 1. Completing the census generally required several days, ranging from two days in 1979, when two crews simultaneously counted different portions of the colonies, to 14 days in 1960.

Table 2 summarizes the census results at Cape Thompson. Both the raw counts and compensated results indicate that numbers declined markedly between 1960 and 1976 and that the decline continued between 1976 and 1979. The decline occurred primarily at Colony 5, the only colony where fewer murres were counted in each successive census. Although numbers at Colonies 1-4 were also lower in recent years than in 1960, there was no clear trend in numbers at those colonies between 1976 and 1979. To evaluate the null hypothesis that there were no intercolony differences in the degree of numeric change among years, we conducted a Chi Square Test for differences in probabilities (Conover 1980:153) using the standardized results. The test statistic was highly significant ($T = 12,096$; $v = 12$, $P < 0.001$). Significantly fewer murres were present at Colony 5 in 1977 and especially in 1979 than would be expected if numbers there had changed at the same rate as at the other four colonies. Thus the murre populations have apparently consolidated at Colonies 1-4 as the decline in numbers has progressed.

Cape Lisburne, Cape Lewis, and St. Lawrence Island

Complete censuses of the Cape Lisburne colony were made in 1976 and 1977; counts of portions of the colony were made in 1978, 1979, and 1981 (Table 3). All counts were made during the Census Period. Results standardized for time of day suggest that murre numbers at Cape Lisburne were highest in 1979. In that year counts were made in the afternoon rather than in the evening as in other years. Because the 1977 counts at compensation plots showed that numbers were low in the afternoon and peaked in the evening, compensation according to those counts greatly increased only the 1979 results. Because (1) the assumption that the 1977 diurnal patterns of cliff attendance is typical of all years may not be valid and (2) no compensation for daily variation in attendance at Cape Lisburne could be made except for 1981, the apparent differences among years at Cape Lisburne may be spurious.

There have been only two censuses at Cape Lewis and the results were similar. Counts, averaged between observers, were 19,130 in 1977 and 20,564 in 1981. No compensation of these counts has been made. There is insufficient evidence to indicate that numbers have changed significantly at either Cape Lisburne or Cape Lewis, but certainly there is no evidence that numbers at these colonies have declined in synchrony with the declines at Cape Thompson.

On St. Lawrence Island in 1981 we counted approximately 329,000 murres at six of ten colonies where they are known to nest. The other four

colonies contain about 30,000 to 60,000 murres (F.H. Fay, pers. comm., Drury *et al.* 1981). At the Owalit Mountain Colony the average of the counts of two observers was 33,955 murres. S.R. Johnson (unpubl. data) counted 31,830 murres there in 1972. In 1976, the average of the counts of two observers was only 15,635 murres (Searing 1977). Searing (pers. comm.) included murres flying in front of the cliffs and those on the water as well as murres on the cliffs. Therefore, the number of murres on the cliffs was even lower than that reported for 1976. Neither diurnal nor daily variation in attendance patterns of murres were quantified in conjunction with any of the colony counts on Owalit Mountain. Although these sources of variation can be substantial, the dip in numbers in 1976 was probably the result of unusually cold weather. In 1976 snow persisted as late as 14 June on the ledges normally occupied by murres, and egg-laying did not peak until early July (Searing 1977) about two weeks later than usual (Fay and Cade 1959). The low count in 1976 could be due to the absence of many murres that would normally occupy breeding ledges or to reduced time on the ledges. No data are available to evaluate such possibilities.

The Owalit Mountain Colony constitutes less than ten percent of the murres on St. Lawrence Island. Because that colony is the only one with a history of counts, we do not know if parallel fluctuations in numbers have occurred at other colonies on the island or if they were localized to the Owalit Mountain Colony. The opinion of residents of Gambell (e.g., L. Iyakitan, pers. comm.) is that murres have been increasing in numbers. In 1981 Lane Iyakitan showed us areas in Boxer Bay, near Southwest Cape, where murres have nested only in recent years.

Bluff

At Bluff two or more censuses were made in each year from 1975 through 1981. Several censuses occurred either before eggs began to hatch or after sea-going of chicks began. Table 4 summarizes the census dates relative to breeding phenology, indicating which dates fell within the Census Period. Two or more censuses were conducted within the Census Period in all years but 1975.

Numbers of murres at Bluff declined between 1975 and 1981 (Table 5). A significant downward trend is evident (Spearman's $r = -0.96$, $n = 7$, $P < 0.005$). None of the counts in 1980 or 1981 exceeded the counts in 1975-1977.

On 11 July 1976, nine days before the start of the Census Period, only 20,779 murres were present on the cliffs. This count is substantially lower than those during the Census Period that year and perhaps indicates that the counts during the Census Period were overestimates of the average number of murres on the cliffs that year. However, even if the census on 11 July is included in the results for 1976, the average of the censuses in that year would equal 40,448, which is higher than the mean of the counts in any subsequent year. Therefore, the census results, although quite variable within years, do indicate that numbers declined at Bluff between 1975 and 1981.

In addition to the complete boat-based censuses at Bluff we conducted

counts on several days during the Census Period at two locations, Stake 10 and Stake 15, from observation sites at the top of the cliffs. Results of all counts which we started at 1700 h (Bering Daylight Time) are listed in Table 6. At Stake 10 fewer murres were present in 1980 than in either 1979 and 1981. More murres were present at Stake 15 in 1981 than in either 1979 or 1980. Thus, in contrast to the census figures, these results suggest that the decline in numbers of murres at Bluff did not continue through 1981. These counts are certainly more precise and accurate than boat-based counts but these two stakes represent only a small fraction of the cliffs which the murres use at Bluff. Changes at these two locations therefore may not be representative of numeric changes at other locations within the colony.

Table 5 shows reproductive as well as census data for Bluff. Our observations suggest that reproductive success was quite low in 1975 and 1976 and then increased at least through 1979. In 1980 and 1981 data were not obtained on "fledging" (sea-going) success. Reproductive success was also probably quite high in 1980, but in 1981 it was probably comparable to that in 1977.

Major changes between years in the past decade in the food habits of murres and black-legged kittiwakes (Sections Vb-VIIb) and reproductive success of kittiwakes (Sections Vc-VIIc) were associated with changing environmental conditions. We lacked detailed data on annual variation in water temperatures in Norton Sound. However, Niebauer (1980) showed that water temperatures and air temperatures (heating degree days) in the Southeastern Bering Sea are positively and significantly correlated. Therefore, we examined the relationship between reproductive success and air temperatures. Only limited climatic data were available for Bluff. Climatic data for Nome, 80 km west of Bluff, correspond quite closely to those at Bluff and are far more extensive. We therefore used the climatological records from Nome to examine the relationship between reproductive success and air temperature. Since the number of sea-going chicks in early August is likely related to conditions during the previous several months, we chose cumulative heating degree days during the months of April through July as our measure of air temperature during a two-month pre-breeding period and the two-month reproductive season.

We examined the relationship between reproductive success and air temperature using polynomial regression analysis. A quadratic equation provides an excellent fit, indicating that our measure of air temperature accounts for 95% of the variance in reproductive success (Figure 1). Thus air temperatures apparently are closely coupled with factors such as sea-surface temperatures and food availability, which probably more directly influence reproductive success.

Modeling the Relationship Between Reproductive Success and Population Numbers

Because reproductive success is highly correlated with temperature we examined the historical records of summer climate at Nome. During the period from 1959 to 1977 only three summers were warmer than normal; the summers of 1975 and 1976 were exceptionally cool (see Figure 2). Thus reproductive success likely was low in most years from 1959 to 1977. To

address the relevance of poor reproductive success to the decline in numbers at Bluff in recent years, we developed a model to simulate changes in population numbers of common murres at Bluff in relation to variability in reproductive success. Values for parameters in the model were either calculated from data collected there since 1975 or were obtained from studies of common murres elsewhere (see Table 7).

Data on heating degree days at Nome were available from 1942 through 1980. We used the quadratic equation (Figure 1) to predict reproductive success in each year during that period. Average predicted success in that 39-year period was 33.4 sea-going chicks/100 individuals. Assuming a stationary population between 1942 and 1980, the one remaining unknown, survival of subadults, from the time they leave the cliffs as chicks until they begin to breed, can be determined analytically from the tabulated values for adult survivorship, age at maturity, and average reproductive success. The values of age-specific subadult survivorship of second-year, third-year, and fourth-year subadults were generalized from Birkhead and Hudson's (1977) results which show that survivorship of subadults increases with age. Survivorship of first-year birds was set to 0.5545 so that the product of age-specific survivorship values of subadults would equal 0.339, the value of overall subadult survivorship (Table 7).

Our counts of murres at Bluff, as elsewhere, include not only incubating and brooding adults, but also their off-duty mates, failed breeders, non-breeding adults, and subadults (see Birkhead 1978a). The proportion of individuals present during the censuses to the total number of individuals using the cliffs was calculated using the tabulated k-value and the values of age-specific use of the ledges shown in Table 7. An assumption implicit in this calculation is that the variance in the number of individuals present among counts reflects the variable presence of adults as well as subadults. Slater (1980) demonstrated considerable diurnal variability in the presence of off-duty mates on the cliffs.

The values shown in Table 7 produce a population which is stationary in numbers. Inputting the annual values of predicted reproductive success, rather than average predicted reproductive success, during the period 1942-1980, we then simulated population changes which would be expected during that period if variability in reproductive success has been the key to changes in numbers we have observed at Bluff. In conducting this analysis we set the initial (1942) population size so that predicted and actual population size in 1976, the first year at least two censuses were conducted, would be equal.

Results of the simulation (Figure 2) suggest that numbers of murres at Bluff were high in the early 1960's, declined in the late 1960's following a series of cold summers beginning in 1959, and declined further in the late 1970's. The predicted trend between 1975 and 1981 is quite similar to that observed (Table 5). The correlation between observed and predicted numbers is positive and significant (Spearman's $p = 0.86$, $n = 7$, $P < 0.01$).

The model, like the trend at Stake 10 (Table 6), suggests that population numbers decreased through 1980 but then began to increase in 1981. As noted earlier, numbers at Stake 15 were equivalent in 1979 and 1980 but higher in 1981. Stake 15 is apparently primarily a club area;

relatively few ledges will safely accommodate an egg there and variability in numbers of murres is relatively high. In 1979 the coefficient of variation in the counts at 1700 h during the Census Period at Stake 15 (14.5%) was more than twice that at Stake 10 (6.8%) even though the counts at these two areas were conducted simultaneously (except for one additional count at Stake 10). Although Birkhead and Hudson (1977) defined clubs as aggregations of murres on tidal rocks, the slight tidal fluxes in the region of our study apparently preclude such sites for clubs. Clubs at our study colonies probably form in areas of low breeding density on the cliffs. Because clubs are comprised primarily of subadults, particularly two-year-olds (Birkhead and Hudson 1977), an increase in population numbers would occur in areas used by clubs before it would occur on the breeding ledges. Thus the trends of numeric change at Stakes 10 and 15 coincide with those expected if variability in reproductive success has been the key to changes in overall numbers at Bluff in recent years.

The magnitude of the decline in the late 1970's predicted by the model was much less than that indicated by the census results. This discrepancy may indicate that either (1) interannual variability in reproductive success was only partially responsible for observed changes in numbers from 1975 through 1981, or (2) the actual decline has been far less pronounced than is suggested by examination of the annual mean counts only. Certainly intra-annual variation in census results has been high (Table 5); consequently the sample means derived from two or three censuses have been rather imprecise estimates of mean numbers on the cliffs. However, if these estimates are accurate (unbiased), factors in addition to summer conditions probably are implicated in the declines.

VIIa. MURRE NUMBERS - DISCUSSION

In the following discussion we first address intralocality (Cape Thompson only) and then interlocality variation in changes in numbers and then factors responsible for such changes. The theoretical basis is Fretwell's (1972) theory of habitat selection; we hypothesize that a subadult will prospect at several colonies and several areas within those colonies and will subsequently establish a breeding site at the colony, and at the particular area within that colony, which will maximize its probability of reproductive success.

Although data are lacking on intercolony movements of subadult murres, detailed studies of other seabirds, e.g., fulmars (*Fulmarus glacialis*) (Coulson and Horobin 1972) and black-legged kittiwakes (Coulson and Wooler 1976), indicate that juveniles and subadults disperse widely from their breeding colonies and may visit several colonies before selecting a breeding site to which they likely will return in each subsequent breeding season. Thus intercolony transfer of individuals does occur in other species of seabirds and results from nest site selection away from the natal colony by at least some prospecting subadults.

Birkhead (1977) showed that year-to-year fidelity of adult murres to their nest sites is high; 95% of his sample of banded and returning adult common murres returned to the same portion of the breeding ledge that they occupied the previous year. However, he also hypothesized that nest site tenacity would be reduced if reproductive success is poor and cited Johnson's (1938) findings that adults abandoned nest sites on ledges that were subject to heavy predation by gulls and resettled elsewhere in the same colony in the same year. Thus, movements of adults from one area to another within a locality normally is rare but could be expected to increase during periods of population decline as sites in more suitable portions of the colony become available.

Intralocality Variation: Cape Thompson

The census results at Cape Thompson indicate a marked decline in murre numbers between 1960 and 1976 and a continuation of this decline through 1979 when censuses were last conducted there. The decline was not spread uniformly across the five colonies, suggesting either differences in natality or survivorship among the colonies or a consolidation of the population at the more suitable colonies as the overall decline progressed.

Birkhead (1974) showed that most adult mortality is restricted seasonally to the nonbreeding season. Because murres breeding at the Cape Thompson colonies likely overwinter south of the ice edge in the southeastern Bering Sea (Irving *et al.* 1970, Shuntov 1974, Divoky 1978), individuals from the five colonies certainly mingle on the wintering areas and are thus subjected to the same mortality factors.

Swartz (1967) found murres from the Cape Thompson colonies feeding up to 100 km or more away from the colonies. Because (1) the colonies span only 11 km of coastline, (2) we have observed murres from the various colonies depart in the same flocks to foraging areas and returning together from foraging areas, and (3) we have observed seasonal changes in flight

directions of murres flying to and from foraging areas, there is no evidence that murres occupying sites in the five colonies differentially exploit food resources or vary consistently in their proximity to such resources. To the extent that reproductive success is food-limited, reproductive success should not vary systematically among the five colonies.

In terms of both absolute and relative numbers the decline has been far greater at Colony 5 than at the other four colonies. As noted in the description of the Cape Thompson colonies, the rock is much softer and more extensively fragmented at Colony 5 than elsewhere. Although numerous minor rockfalls and one major rockfall occurred at the other four colonies between 1976 and 1979, such occurrences were infrequent compared to the almost incessant rock showers and occasional rock slides at Colony 5. As well as breaking eggs and killing chicks, such slides do kill adults (personal observations). Thus the major decline at Colony 5 could be due to a lack of subadult colonization of this relatively unsuitable colony and possibly to transfer by already-established adults from Colony 5 to the other four colonies as more suitable areas in the other colonies became available during the overall decline.

We were unable to distinguish the two murre species in our census counts. Swartz (1966) estimated that thick-billed murres comprise 81% of the murres using Colonies 1 and 5, 60% of those using Colony 3, and less than 50% of those using Colonies 2 and 4 (49% and 43%, respectively). Although the major decline at Colony 5 could indicate that the overall decline was due to a decline in numbers of thick-billed murres only, the compensated census results (Table 2) indicate that the decline was also both absolutely and relatively high at Colony 2, where common murres outnumbered thick-billed murres in 1960 (Swartz 1966). Thus the decline in overall murre numbers probably reflects a decline in numbers of both species.

Common murres are larger, heavier and more agile than thick-billed murres (Spring 1971) and are dominant in aggressive encounters for breeding sites at colonies where both species breed (Williams 1974). Belopolski (1961) showed that during a period when common murre numbers increased in the Murmansk region, common murres gradually displaced thick-billed murres from the broader ledges. Conversely it could be expected that thick-billed murres would again occupy broader ledges during a period of decline in the common murre population. Thus the spatial pattern of population decline among the Cape Thompson colonies is consistent with a reduction in numbers either of both species or only of common murres accompanied by a consolidation of the thick-billed murres in relatively suitable breeding areas.

Interlocality Variation in Numeric Changes

The declines at Cape Thompson have been paralleled at Bluff, where common murres predominate, but not at the other mixed species colonies at Cape Lisburne and St. Lawrence Island. The declines in recent years at Bluff can be explained, at least partially, by relatively cool summers and associated poor reproductive success in the past two decades. Compared to the climatological data base for Nome, there are few weather data available

for Cape Thompson; Allen and Weedfall (1966) showed that summer air temperatures there are well correlated with those at Kotzebue but are somewhat cooler. In turn, Kotzebue temperatures from April through July are highly correlated with those at Nome (heating degree days, $r = 0.889$, $n = 22$ (1959-1980), $P < 0.01$). Thus, interannual fluctuations in air temperatures at Cape Thompson and Bluff likely have occurred in parallel.

We lack detailed data on reproductive success at Cape Thompson and only can infer annual differences from annual variation in breeding phenology and egg sizes. In a given year common murres and thick-billed murres begin to lay eggs on virtually the same day (Swartz 1966), but the timing of breeding by both species has varied substantially among years (see Table 1). Using the Kotzebue weather data and information on hatching phenology, we found a strong correlation between date of first hatching and late-spring, early-summer temperatures (heating degree days, April-July, Spearman's $p = 0.886$, $n = 6$, $P < 0.005$). Phenology is advanced in warm years. Studies elsewhere (e.g., Birkhead and Nettleship 1981) have shown that reproductive success is higher when breeding is earlier.

Birkhead and Nettleship (1981) also documented a positive relationship between egg size and reproductive success. At Cape Thompson we obtained data on egg sizes of both murre species on several accessible ledges in 1977 and on a subset of those ledges in 1979. We grouped the egg volume ($0.50 \times \text{length} \times \text{breadth}^2$) data by species and year and then conducted a factorial ANOVA. Egg volumes of both species were greater in 1979 than in 1977 (thick-billed murres, 1977: mean = 96.4, s.d. = 9.4, $n = 55$; 1979: mean = 104.5, s.d. = 10.0, $n = 36$; common murres, 1977: mean = 107.4, s.d. = 9.0, $n = 16$; 1979: mean = 117.3, s.d. = 9.9, $n = 5$; ANOVA Year effect: $F = 4.685$, $v = 1,108$, $P < 0.033$). At Bluff reproductive success was higher in 1979 than in 1977 (Table 5). Thus both the phenology and egg volume data indicate that reproductive success of murres at Cape Thompson has likely paralleled that at Bluff. Consequently, the decline at Cape Thompson has possibly been due to relatively poor reproductive success in association with relatively cool summers in the past two decades.

Air temperatures at Cape Lisburne average several degrees cooler than those at Cape Thompson (Allen and Weedfall 1966) and are well correlated with those at Kotzebue (heating degree days, April-July, $r = 0.728$, $n = 16$, $P < 0.01$). Furthermore sea-surface temperatures measured near Cape Lisburne in July between 1974 and 1981 show a pattern of change similar in direction and magnitude to that of April-July air temperatures at Nome and Kotzebue (see Sections Vb-VIIb). On the basis of the above discussion, a decline in murre numbers would also be predicted at Cape Lisburne, but numbers appeared to remain stationary from 1976 through 1981.

Drury (1979) noted that during periods of general population increase or decline, seabird numbers at some localities may change substantially while those at others remain stationary, and he argued that proximity to food resources is probably a key factor affecting such interlocality variability.

In most years food availability near Cape Lisburne appears to be higher than that near Cape Thompson. Black-legged kittiwakes typically have higher reproductive success, and growth rates of kittiwake chicks are

faster at Cape Lisburne than at Cape Thompson (see Sections Vc-VIIc). The reasons for these differences are not well understood but are possibly related to physical oceanographic processes that make Ledyard Bay, the region northeast of Cape Lisburne, an especially favorable foraging area (see Sections Vb-VIib). Thus reproductive success of murres at Cape Lisburne is probably generally higher than at Cape Thompson.

St. Lawrence Island, like Cape Lisburne, is favorably situated with respect to foraging areas. Anadyr Strait is an extremely productive region in which enormous numbers of auklets, murres, and kittiwakes feed (Bedard 1969, personal observations). Although kittiwake reproductive success on St. Lawrence Island was similar to that at Bluff and Cape Lisburne in 1981, chicks on St. Lawrence Island grew substantially and significantly faster than did those at Bluff or Cape Lisburne (see Sections Vc-VIIc). The low count of murres at Owlait Mountain in 1976 can be related to adverse conditions early in the breeding season (Searing 1977). The influence of such conditions early in the breeding season on murre numbers during the Census Period indicates that severe conditions can affect census results. However, Birkhead (1978b) documented intense competition for breeding sites, and Williams (1974) found that prior ownership plays a key role in contests for sites. Consequently, there is likely a premium on maintaining occupancy of a site even in years when the probability of reproductive success is low, and therefore in most years numbers on the cliffs probably do provide a reasonable index of population numbers. In extremely adverse conditions numbers, as well as reproductive success, may be depressed.

The declines at Cape Thompson and Bluff are fundamentally different than the apparent short-term change at St. Lawrence Island. At Bluff numbers have declined while reproductive success has varied and generally increased (see Table 5). Although numbers of murres at Cape Thompson were substantially lower in 1979 than in 1977, the data on egg volumes and phenology suggest that reproductive success was greater in 1979. Thus the lowest census total at Cape Thompson (1979) certainly did not occur in conjunction with adverse conditions in that particular breeding season.

Differences among localities in proximity to food supplies likely results in differences in rates of numeric change during a general population increase or decrease. Such differences could result from differences in reproductive success and could be augmented by shifts to the more productive colonies. Although Drury and Nisbet (1972) showed that some adult herring gulls (*Larus argentatus*) nesting in colonies characterized by poor reproductive success move to more productive colonies, site tenacity of adult murres is extremely high (Birkhead 1977), and long-distance relocation seems unlikely. However, movement of individuals prior to age at first breeding from natal colonies characterized by relatively poor reproductive success to more productive colonies certainly is possible. However, documentation of such movements, particularly between major colonies, would be virtually impossible as it would require banding of sea-going chicks on a massive scale and detailed searching for banded birds several years later at colonies other than the natal colony.

In summary, the variable patterns in census results for the various colonies are consistent with an overall population decline, i.e., the

declines at Cape Thompson and Bluff may reflect declines in regional populations of one or both murre species rather than localized effects on breeding populations only at those colonies. Examination of factors responsible for those declines should include consideration of factors acting on regional populations as well as those acting on the murres at Cape Thompson and Bluff.

Factors Affecting Population Change

Drury (1979) reviewed several studies documenting the sensitivity of population numbers of seabirds to long-term environmental fluctuations. We have shown that in northwestern Alaska environmental conditions during the breeding season not only fluctuate widely between years but also demonstrate long-term trends. In the 39 year history of reporting of heating degree day data for Nome by the U.S. Weather Bureau and the National Weather Services, the first two decades were relatively warm and the last two decades have been relatively cool (see Figure 2). Because reproductive success at Bluff is strongly and positively correlated with late-spring, early-summer temperatures, recent population declines there are probably related, at least partially, to reduced reproductive success in the early and mid-1970's, as our simulation model shows.

At the present time agreement between observed and predicted changes in numbers at Bluff is only in terms of trends; the magnitude of the decline of one percent annually that was predicted by the simulation model (Figure 2) is considerably less than that implied by the census results (five percent annually, 1976-1981, see Table 5). We consider two explanations of this discrepancy. First, the mean of two or three counts is a very imprecise measure of numbers on the cliffs in a particular year because intra-annual variation between (among) counts is high. Thus the observed decline could be an overestimate of the true rate of decline. Alternatively, factors affecting mortality could be implicated in the decline.

As noted earlier, Birkhead (1974) showed that mortality of murres occurs primarily in the nonbreeding season. Murres breeding at all colonies in the northern Bering Sea and the Chukchi Sea, including those at Bluff, likely mingle extensively at wintering areas in the southeastern Bering Sea (see Shuntov 1974). Consequently, overwinter mortality must act on the regional population as a whole rather than differentially on individuals associated with particular colonies (Drury 1979). Factors which could reduce survivorship in wintering areas include long-term natural changes, natural catastrophes, and human influences.

Niebauer (1980) summarized the marine climate in the southeastern Bering Sea in the past decade. Beginning in 1973, a cooling trend led to a decline in sea-surface temperatures to 1.5°C below the 15-year mean by 1975; sea ice reached its maximum southern extent during the 1975-1976 winter. Between the fall of 1976 and the spring of 1979, a warming trend occurred and was characterized by annual increases of about 0.7°C in sea-surface temperatures and annual decreases in ice coverage of about ten percent. There are no data on the effect of such variation in winter climate on overwinter survival of murres. Numbers of murres at Bluff and Cape Thompson declined as the warming trend progressed while those at Cape

Lisburne and the Pribilof Islands (see Hunt *et al.* 1981) apparently remained stationary. Although winter climatic conditions could affect survival, we cannot address such a relationship with the available data.

Natural catastrophes in the region, such as the die-off of an estimated 100,000 common murres along the Alaskan Peninsula in the spring of 1970 (Bailey and Davenport 1972) would result in short-term fluctuations in numbers but not in declines persisting over several or many years.

Studies elsewhere (e.g., Cramp *et al.* 1974, Nettleship 1977) have documented the adverse consequences of oil development and particularly oil spills on murres. Oil development has not yet begun in the Bering or Chukchi Seas. McKnight and Knoder (1979:190) cited two instances of murre die-offs in Alaska which were apparently associated with oiling. Although such events will surely increase as oil development accelerates along the Alaska coast, the declines at Cape Thompson and Bluff in recent years have occurred independently of such events; i.e., oil development cannot be implicated in these declines.

Annually several hundred thousand seabirds have been caught incidentally in the salmon gill net fishery in the north Pacific Ocean (e.g., King *et al.* 1979). This fishery began in 1952 and expanded rapidly in the next several years. Estimates of seabird mortality in the early to mid 1970's ranged between about 250,000 and 750,000 birds annually (King *et al.* 1979). Agreements between Japan and the USSR resulted in a reduction in the fishery in 1977; imposition of the 200-mile territorial limit by the United States led to a further reduction in 1978. However, DeGange (1978) estimated that 290,000 seabirds were drowned in drifting salmon gill nets in 1978. Estimates of murre numbers range from 11 percent to 58 percent of all birds caught (DeGange 1978). Tull *et al.* (1972) reviewed the tremendous adverse effect of the salmon gill net fishery on murre numbers in western Greenland. However, in Alaska the fishery operates several hundred kilometers south of the colonies we have studied and principally during the summer months. Thus survivorship age classes returning to the study colonies would be unaffected by the salmon gill net fishery. Birkhead and Hudson (1977) showed that one-year-old common murres did not return and few two-year-olds returned to their study colony. The declines at Cape Thompson and Bluff could be ascribed in part to the incidental salmon catch only if such age classes remained in the wintering areas which overlap the region of the fishery.

Murres are primarily piscivorous seabirds, preying on a variety of small fishes, including young age classes of commercially important species (e.g., Strat and Haight 1979). In some regions, e.g., the North Sea, seabirds and man are competing intensely for a restricted food supply (see Furness 1978). Brown (1980) reviewed the competitive conflicts between seabirds and commercial fisheries and concluded that such conflicts will intensify particularly because fisheries pressure is shifting more and more to species which are central to the food webs of piscivorous seabirds.

Walleye pollock (*Theragra chalcogramma*) appear to be the principal winter food of both thick-billed murres and common murres in the southeastern Bering Sea (Divoky 1978). The pollock fishery in that region

started in the early 1960's as stocks of yellowfin sole (*Limanda aspera*) were depleted. Even after overexploitation in the early 1970's and continued declines in the catch per unit effort (CPUE), Bering Sea pollock still constitute the most important single species fishery in the north Pacific region (Bakkala *et al.* 1981). Thus in the past two decades commercial fisheries pressure on a principal species in the winter diet of murres has intensified greatly.

If human exploitation of pollock does constitute true competition with murres, overwinter survivorship of murres could be reduced. Population numbers of long-lived, low-fecundity taxa such as murres are extremely sensitive to slight alterations in adult survivorship (e.g., see Mertz 1971); reducing survivorship by a few percentage points would result in population declines of the magnitude we have observed at Cape Thompson and Bluff.

The CPUE of pollock is shown in Figure 3 as are the counts of murres at Bluff. The two-year lag between the decline in the pollock CPUE and the decline in murre numbers at Bluff would be expected if competition with the commerical pollock fishery has reduced primarily survivorship of the youngest age classes because there is a comparable lag between sea-going of chicks and their return to the colony (Birkhead and Hudson 1977). Young murres are inexperienced at foraging and would likely be the first individuals to suffer from a decline in food availability.

Although increased overwinter mortality would be experienced by murres from all of the study colonies, numbers at more suitable colonies could remain relatively stationary due to higher reproductive success and possibly immigration of young individuals. Numbers could decrease substantially at less productive colonies at the same time due to lower reproductive success and emigration of young individuals. Therefore, numeric declines at Bluff and Cape Thompson but stationary numbers at Cape Lisburne and short-term fluctuations on St. Lawrence Island are consistent with a regional population decline due to decreased overwinter survivorship. The discrepancy between the observed and modeled rates of decline at Bluff could be the consequence of increased overwinter mortality as well as low reproductive success in recent years.

The simulation model can be extended to provide a prediction of numbers of murres at Bluff for the next several years because there is a multi-year lag between the time chicks leave the cliffs and the time when they return as subadults (Birkhead and Hudson 1977). Because summers have been relatively warm (Figure 2) and reproductive success has been moderate or high since 1978 (Table 5), population numbers at Bluff should increase markedly over the next three years (1982-1984) if variability in reproductive success plays a key role in changes in numbers (see Figure 2). In contrast, pollock abundance and the pollock CPUE have remained low during the same period (see Figure 3; Bakkala *et al.* 1981). If competition with commerical fisheries is the key factor in the recent decline in murre numbers at Bluff, the decline should continue during the next several years.

TABLE 1. Dates of murre censuses at Cape Thompson in relation to breeding phenology.

Event	Year			
	1960	1976	1977	1979
First Hatching	30 Jul	9 Aug	1 Aug	22 Jul
First Sea-Going	18 Aug	>25 Aug ¹	23 Aug	11 Aug ²
Census Dates				
Colony 1	17 Jul	6 Aug	11 Aug	8 Aug
Colony 2	27,29,31 Jul 3 Aug	18 Aug	9 Aug	
Colony 3	21-23 Jul	23 Jul	10,12 Aug	7 Aug
Colony 4	15-17 Jul	9 Aug	12 Aug	7 Aug
Colony 5	1,2,4,12 Aug	19 Aug	13,14,17 Aug	7 Aug
Number of Census Days				
Incubation Period	8	1	0	0
Chick Period	6	4	7	2
Total	14	5	7	2

¹No murre chicks had left the cliffs when field crews left the study site on 25 August.

²One murre chick was seen on water on 7 August; none was seen again until 11 August, when many were on the water.

TABLE 2. Summary of murre census results at Cape Thompson, 1960-1979.

A. Raw results, averaged between (among) observers counting simultaneously.

Year	Colony					Total
	1	2	3	4	5 ^a	
1960	4,187(100) ^b	76,249(100)	26,814(100)	8,726(100)	134,532(100)	250,508(100)
1961	4,589(110) ^c	NC	NC	6,445(74)	NC	NC
1976	4,293(103) ^d	46,722(61)	19,098(71)	6,894(79)	79,650(59)	156,657(62)
1977	2,471(59)	52,320(69)	21,282(79)	7,621(87)	58,995(44)	142,689(57)
1979	2,302(55) ^e	50,034(66)	15,822(59)	6,157(71) ^d	39,756(30) ^f	114,071(46) ^f
					45,161(34) ^g	119,476(48) ^g

NC: No census.

^a In 1960 18 plots of Colony 5 were counted from above on land; in 1976 and 1977 those as well as all other plots were counted by observers in a boat. In 1979 nine of those 18 plots were counted from land and all others from a boat.

^b Percent of 1960 count.

^c Mean of 3 censuses.

^d Mean of 2 censuses.

^e Mean of 4 censuses.

^f Boat-based counts only.

^g Land counts at 9 plots at Colony 5.

B. Results compensated for daily (1979 only) and diurnal (all years) variation in cliff attendance of murres.

Year	Colony					Total
	1	2	3	4	5 ^a	
1960	4,200(100) ^b	110,000(100)	39,000(100)	10,000(100)	194,000(100)	357,200(100)
1961	4,500(110)	NC	NC	8,900(89)	NC	NC
1976	2,100(50)	51,000(46)	24,000(62)	7,100(71)	115,000(59)	199,200(56)
1977	2,500(59)	55,113(50)	21,951(56)	8,053(81)	83,000(43)	171,000(48)
1979	2,382(57)	51,027(46)	25,447(64)	6,621(66)	63,242(32)	148,719(42)

NC: No census.

^a Compensation was also made to correct for the discrepancy between land-based and boat-based counts (see text).

^b Percent of 1960 total.

TABLE 3. Summary of murre census results at Cape Lisburne.

Raw Census Results				
Year	Subsample A ^a	Subsample B ^b	Total	Date of First Hatching
1976	9,925	14,100	129,575	6 August
1977	10,106	15,501	131,420	1 August
1978	9,524	NA	NA	21 July
1979	10,390	16,123	NA	22 July
1981	10,108 ^c	14,236	NA	26 July

B. Results compensated for daily (1981 only) and diurnal variation in cliff attendance.

Compensated Census Results			
Year	Subsample A	Subsample B	Total
1976	NA	NA	NA
1977	14,779	22,138	184,000
1978	14,094	NA	NA
1979	17,342	26,050	NA
1981	11,968	17,735	NA

NA: Not available.

a Plots 11, 12, 25, 26, 30, 32.

b Subsample A and plots 65, 66, 70, 72.

c Average of two censuses.

TABLE 4. Dates of murre censuses in relation to breeding phenology at Bluff.

Event	Year						
	1975	1976	1977	1978	1979	1980	1981
First Hatching ^a	NA	27 Jul	3 Aug	15 Jul	< 15 Jul	< 19 Jul	11 Jul
First Sea-going ^a	NA	~ 14 Aug	20 Aug	31 Jul	2 Aug	> 24 Jul	~ 29 Jul
Census Dates	(4 Jul) ^b	(26 Jun)	(26 Jun) (11 Jul)	(26 Jun)	20 Jul	21 Jul	15 Jul
	1 Aug	26 Jul	7 Jul	18 Jul	31 Jul	23 Jul	19 Jul
	(8 Sep)	12 Aug	29 Jul	9 Aug	7 Aug		
			19 Aug	(14 Aug)			

NA: Not available.

^a If first dates of either hatching or sea-going were unknown, they were calculated assuming an interval of 18 days between hatching and sea-going (see Ramsdell and Drury 1979).

^b Dates in parentheses are out of the range of the Census Period and results of censuses on those dates have not been included in the analyses.

TABLE 5. Murre numbers and reproductive success at Bluff, 1975-1981.

Year	Census Results ^a				Reproductive Output ^b	
	Census				k^c	k^d
	1	2	3	Average		
1975	69,900	--	--	69,900(100) ^c	--	0.18
1976	45,175	55,390	--	50,283(72)	~0.10 ^f	0.04
1977	39,250	36,100	--	37,675(54)	0.39	0.34
1978	33,520	46,560	--	40,040(57)	0.52	0.44
1979	28,284	43,275	33,370	34,976(50)	0.53	0.50
1980	33,655	27,875	--	30,765(44)	0.62 ^g	ND
1981	29,975	27,845	--	28,910(41)	~0.40 ^g	ND

ND: No data, field crew left the colony before sea-going commenced.

^a Values reported here are the averages of observers' counts, if two or more observers counted murres during a particular census.

^b For values prior to 1979, see Drury et al. 1981, Ramsdell and Drury 1979 and Biderman et al. 1978.

^c Number of eggs hatching/average number of individuals on the Productivity Plots.

^d Number of sea-going chicks/average number of individuals on the Productivity Plots.

^e Percent of the 1975 count is listed in parentheses.

^f Calculated on the basis of average figures reported by Drury (1978).

^g When field crews left the colony, hatching was not yet complete. This figure represents the midpoint between the minimum number known to hatch and the maximum number that could have hatched (number of eggs plus number still being incubated).

TABLE 6. Results of counts of murres at two study plots at Bluff, 1979-1981.

Year	Location	
	Stake 10	Stake 15
1979	1,452 ± 99(15) ^a	797 ± 116(14)
1980	1,354 ± 55(5)	841 ± 39(4)
1981	1,446 ± 73(11)	991 ± 60(8)
Pairwise Comparisons ^b	1979 > 1980 < 1981	(1979 = 1980) < 1981

^a Mean ± standard deviation (sample size). All counts were started at 1700 h (Bering Daylight Time).

^b Alpha level = 0.05.

TABLE 7. Values of parameters used in the population model.

Parameter	Value	Source
A. Adult Survivorship	0.915	Birkhead & Hudson (1977)
B. Subadult Survivorship	0.339	See Text
1. First-year	0.5545	See Text
2. Second-year	0.80	See Text
3. Third-year	0.85	See Text
4. Fourth-year	0.90	See Text
C. Reproductive Success (average predicted success, 1942-1980)	0.334	See Text
D. Age at Maturity	5 years	Birkhead & Hudson (1977)
E. Ratio of Breeding Pairs/Average Number of Individuals (k)	0.61	Present Study
F. Proportion of Age Class using Breeding Ledges		Birkhead & Hudson (1977)
1. One-year olds	0	Birkhead & Hudson (1977)
2. Two-year olds	0	Birkhead & Hudson (1977)
3. Three-year olds	0.50	Birkhead & Hudson (1977)
4. Four-year olds	0.75	Birkhead & Hudson (1977)
5. Adults	1.00	Birkhead & Hudson (1977)
G. Proportion of Individuals at Ledges during Counts	0.75	See Text

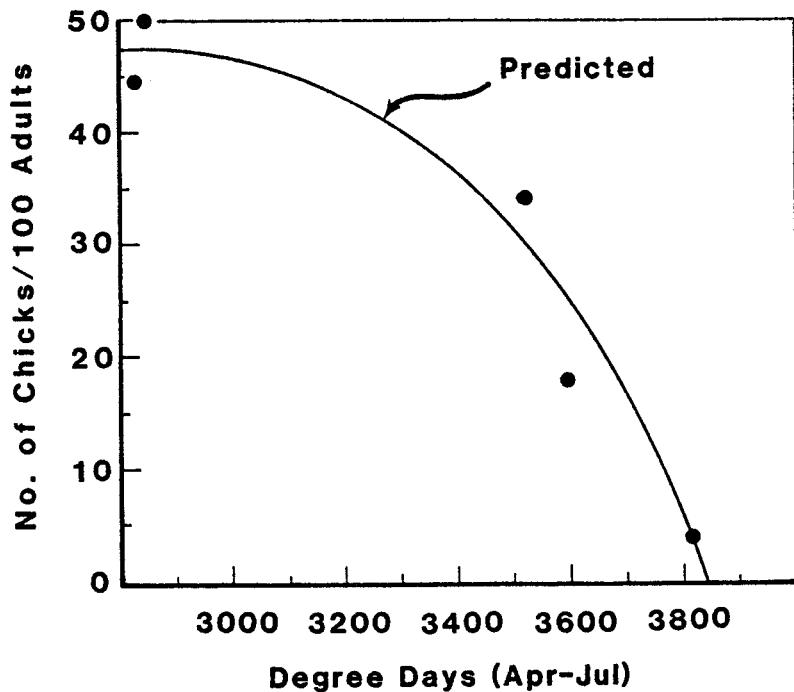


Figure 1. Relationship between reproductive success (number of sea-going chicks/100 adults) at Bluff, and cumulative heating degree days in April-July at Nome. The equation of the line is:

$$\begin{aligned} \text{Number of chicks/100 adults} = & 4.62 \times 10^1 + \\ & 2.36 \times 10^{-2} (\text{Degree days} - 2800) - \\ & 6.55 \times 10^{-5} (\text{Degree days} - 2800)^2. \end{aligned}$$

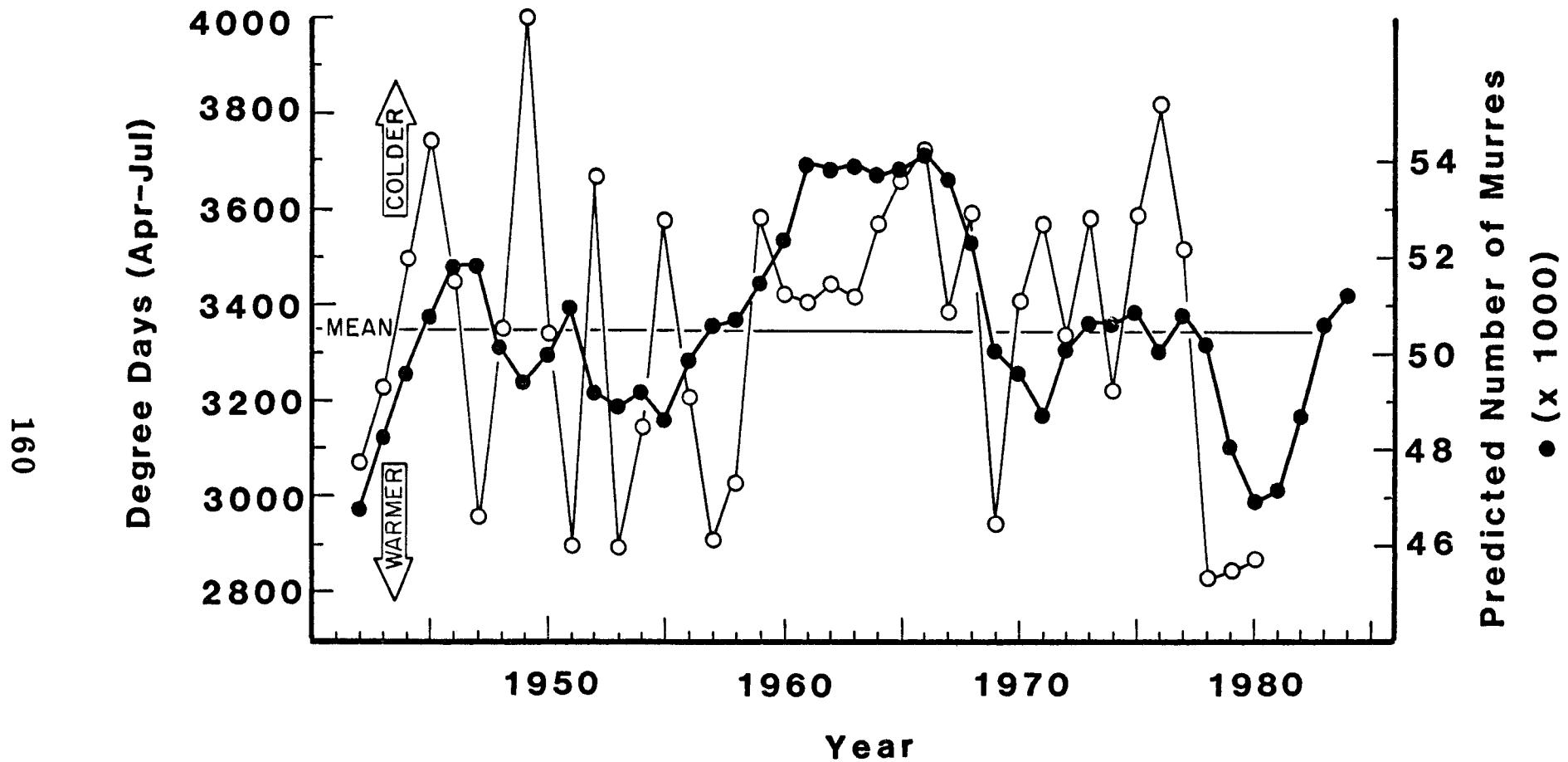


Figure 2. Cumulative heating degree days in April-July at Nome (open circles), and the predicted number of murres at Bluff (closed circles). Based on data in Figure 1.

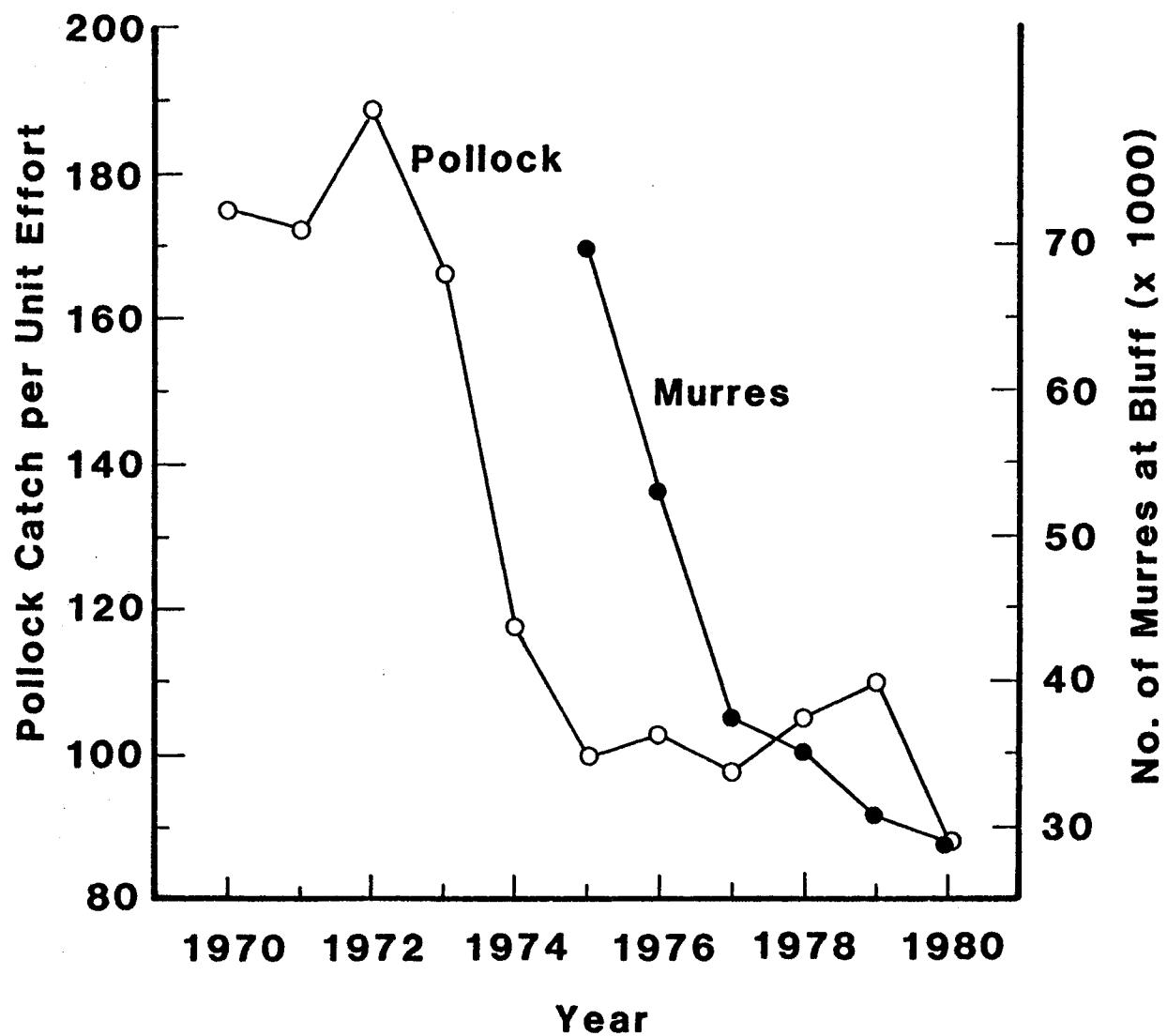


Figure 3. Catch per Unit Effort of pollock in the southeastern Bering Sea (Bakkala *et al.* 1981), and numbers of murres at Bluff.

Vb. FOOD HABITS -- METHODS

Field work was conducted during a portion of each summer of 1976-1979 at Cape Thompson and 1976-1981 at Cape Lisburne. In each year, except 1976 at Cape Lisburne, murres and kittiwakes were collected at intervals as they returned to the colonies from offshore feeding areas. Most birds fed at a considerable distance from the colonies at both sites (see Results), and it was not practical to visit these areas to collect specimens. A few birds were also collected as they fed near the colonies. Generally within two hours of collection the stomach contents and the lining of the proventriculus were removed and stored in 70% ethanol. Food items were later sorted and identified using appropriate taxonomic keys and preserved reference material.

Prey remains were usually in an advanced stage of digestion by the time the birds returned to the colonies. Invertebrate prey items were often identified by parts such as rostra, jaws, uropoda and eyes. Fishes were identified from otoliths. Sculpins (Cottidae) were also counted and identified on the basis of preopercular bones. The following data, therefore, are probably biased towards hard-bodied prey, and especially towards fishes since otoliths appear to persist in digestive tracts longer than other types of prey remains. A recent discussion of such problems associated with food habits studies of thick-billed murres has been presented by Bradstreet (1980).

The sizes of most fish prey were reconstructed from regressions of fish length on otolith length, and from fish weight on fish length. The equations used are presented in Table 1. Sculpins were often not identifiable to species or genera, and for the purposes of this analysis all were considered to be *Myoxocephalus quadricornis*. *M. quadricornis* was a common species in the region (Alverson and Wilimovsky 1966, Craig and Haldorson 1981), one that occurred regularly in prey remains, and the only species of sculpin in the eastern Chukchi for which size data were available. Two other sculpins were also frequently encountered, *Icelus* sp. and *Artedielius* sp. Righteye flounders (Pleuronectidae) were generally young-of-year fish and were assigned an average weight of 1.0 g. "Other fishes" (see Results) were a variety of taxa including snailfishes (Cyclopteridae, especially *Liparis* sp.), pricklebacks (Stichaeidae, especially *Stichaeus punctatus* and *Chirolophus* sp.), and herring (*Clupea harengus*). They occurred in several sizes but were generally small and were assigned an average weight of 2.0 g.

Intact invertebrates were measured and average weights were used to reconstruct wet weights of certain groups. Average weights of amphipods (Amphipoda) and mysids (*Neomysis* sp. and *Mysis* sp.) were about 0.2 g, euphausiids (*Thysanoessa* sp.) about 0.1 g, and shrimp (predominantly *Pandalus* sp. and *Eualus* sp.) about 0.5 g. Polychaetes (*Nereis* sp.) were assigned an average weight of 1.0 g and "Other invertebrates" (see Results), including hermit crabs (*Labidochirus splendescens*), squids (Cephalopoda) and snails (Gastropoda) were assigned an average weight of 0.5 g.

Most information on feeding areas used by murres and kittiwakes at Cape Thompson and Cape Lisburne was obtained annually by land-based observations of directions taken by birds as they flew to and from the colonies, and by similar boat-based observations along the coastline up to 60 km from the colonies. In 1978 a Cessna 336 aircraft was used to complement the land and boat-based observations during 25-29 July and 18-19 August. Transects were flown up to 130 km from the colonies at about 45 m above the water and at ground speeds of about 190 km hr.⁻¹. Observations were made from both sides of the aircraft by two or three observers. Numbers of birds on the water were summed during five minute intervals and numbers of birds in the air and their flight directions were recorded. The positions of the transects were determined from time and heading information and from radar fixes provided by U.S. Air Force stations at Cape Lisburne and Point Lay.

VIB. FOOD HABITS - RESULTS

Food Habits

Food habits of murres and kittiwakes during all years combined (Tables 2 & 3) were similar at the two colonies. A notable difference was the absence of mysids and euphausiids at Cape Thompson. Dietary differences among the three species were similar to those reported previously for Cape Thompson (Swartz 1966) and for the Pribilof Islands (Hunt *et al.* 1981). Thick-billed murres demonstrated the greatest diversity in food habits and common murres the least. Both species of murres fed on similar kinds of fishes, although common murres took many fewer sculpins and "Other fishes". Common murres also fed on very few invertebrates. Kittiwakes rarely fed on sculpins and never on flatfishes, benthic taxa that would generally not be available to kittiwakes because of the kittiwakes' restricted feeding depth. Polychaetes were taken relatively more frequently by kittiwakes than by murres at both colonies, as were euphausiids at Cape Lisburne. The apparently large contribution of amphipods to diets of kittiwakes at Cape Lisburne is misleading since all but one were recovered from a single bird.

Annual differences in the overall importance of fishes and invertebrates to thick-billed murres and kittiwakes were seen at both colonies (Table 4, Figure 1). Proportionally fewer fishes were recovered from birds in 1976, with steadily increasing relative importance in succeeding years. As suggested by data in Table 5, annual increases in fish biomass were primarily responsible for annual differences in the relative utilization of fishes and invertebrates.

Seasonal patterns were also apparent in the use of fishes and invertebrates by thick-billed murres, but the patterns were not the same at the two colonies (Table 4). The greatest proportional use of invertebrates occurred early in the summer at both colonies, with fishes assuming greater importance later in the breeding season. A regular progression of increasing dominance by fishes occurred at Cape Lisburne, while the highest proportion of fishes at Cape Thompson was taken during the interval 1-20 July in two of the three years for which the data are complete.

A seasonal pattern similar to that at Cape Thompson was reported for the Pribilof Islands by Hunt *et al.* (1981), where the importance of invertebrates in the diets of thick-billed murres was highest in June and lowest in July.

The importance of various fish taxa to murres and kittiwakes changed seasonally (Tables 6 & 7). Cods (Arctic cod, *Boreogadus saida* and saffron cod, *Eleginus gracilis*) were most common in the birds' diets early in the season and declined steadily in importance as sand lance (*Ammodytes hexapterus*) rose in importance throughout the summer. Seasonal patterns of importance of invertebrate taxa were less conspicuous and less consistent (Table 8), except that polychaetes were most common early in summer. This trend was most pronounced in kittiwakes; all of the polychaetes taken by kittiwakes at Cape Lisburne and 99% of those taken at Cape Thompson were taken during the interval 1-20 July. Polychaetes spawn in the water column in early summer (H. Feder pers. comm.), and the heteronereid worms become available to murres and kittiwakes at that time.

Seasonal and annual differences in utilization of various fish taxa by murres and kittiwakes are accentuated if the taxa are grouped as in Figure 2 and Table 9. The trend is for the combined importance of sand lance and capelin (*Mallotus villosus*) to be greater later in the season of all years, except in 1979 at Cape Thompson, and to be greater earlier in the season each year after 1976. Hunt *et al.* (1981) also reported that numbers of sand lance increased in diets of black-legged kittiwakes on the Pribilofs from early through late summer.

Characteristics of Prey Populations

Size distributions of principal taxa of prey fishes are shown in Figures 3-13. Included for comparison are data we collected in 1978 and 1980 at Bluff, a seabird colony in Norton Sound (northeastern Bering Sea), and that L. G. Swartz (unpubl. data) collected at Cape Thompson in 1960.

The average size of sand lance recovered from murres and kittiwakes was significantly larger each successive year between 1977-1980 at all three colonies (ANOVA, $P < 0.05$). Age determinations, based on opaque and hyaline zones of otoliths (see Reay 1972), indicated that the majority of the sand lance were age class 1+, with fewer age class 0+ individuals. Sand lance older than age class 1+ were infrequent, except at Cape Lisburne in 1977 when age class 2+ fish were common and accounted for the unusual bimodal size distribution that year. Andriyashev (1954) noted that sand lance in the coastal zone of Murmansk also were predominantly age class 1+, and Hatch *et al.* (1979) reported that all of the sand lance fed to tufted puffin (*Lunda cirrhata*) and rhinoceros auklet (*Cerorhinca monocerata*) chicks on Middleton Island (northern Gulf of Alaska) were age class 0 and 1.

Capelin were significantly larger in 1979 than in 1977 at Cape Thompson and were significantly larger in 1980 than in 1979 at Cape Lisburne (ANOVA, $P < 0.05$). Capelin were not aged, but they were predominantly age class 1+ according to age-length distributions of capelin from the Grand Bank reported by Pitt (1958 a).

The same trend of increasing average size in later years was also seen in Arctic cod, and differences between 1977-1978 and 1978-1979 at Cape Lisburne were significant (Kruskal-Wallis test, $P < 0.05$). The size distributions of Arctic cod tended to be bimodal; smaller fish were predominantly age class 1 and the larger fish were age class 3 (see Table 10). The annual increases in average size of Arctic cod at Cape Lisburne resulted from changes in relative numbers of the two age classes between years, as well as from apparent annual increases in average sizes of age class 1 fish. Craig and Haldorson (1981) reported that the sizes of age class as 1-5 Arctic cod in Simpson Lagoon (northeast of Cape Lisburne in the Beaufort Sea) were larger in 1978 than in 1977, and the difference was significant for age class 2 fish, which averaged 15 mm larger in 1978 ($t = 3.6$, $P < 0.001$). At Cape Thompson the average size of Arctic cod decreased between 1976 and 1977 because of a large change in proportions of age classes 1 and 3 fish. However, it appears that the average sizes of individual age classes may have increased between years, especially between 1977 and 1979, as it did at Cape Lisburne and Simpson Lagoon.

Differences between years in sizes of sculpins are even more difficult to interpret because the "population" each year consisted of various numbers of at least three species. The majority of sculpins in all years were apparently age classes 0-2 (see Table 11). Nevertheless, the average length of sculpins increased between most years at both Cape Thompson and Cape Lisburne. The increases were significant between 1976 and 1977 at Cape Thompson, and between 1978-1979 and 1979-1980 at Cape Lisburne (Kruskal-Wallis test, $P < 0.05$).

Saffron cod were considerably smaller than Arctic cod, and most were apparently age class 0 fish with perhaps a few age class 1 fish (see Table 12). Unlike Arctic cod, sand lance, capelin and sculpins, saffron cod were smaller in successive years, except between 1978-1979 at Cape Thompson, and the differences were all significant (Kruskal-Wallis test, $P < 0.05$). Conversely, saffron cod were much larger in 1980 than in 1978 in Norton Sound, although the difference in that region was apparently the result of age class changes between years rather than changes in size at age. A change in age class strength might also explain the difference in size of saffron cod between 1978 and 1979 at Cape Thompson.

Sand lance, capelin, sculpins and Arctic cod also exhibited a trend towards increasing size with decreasing latitude. Within all years that samples were collected at both Cape Thompson and Cape Lisburne, sculpins and capelin were always significantly larger at Cape Thompson. Sand lance were larger at Cape Thompson than at Cape Lisburne in 1978 and 1979 and the difference was significant in 1979. In 1977 sand lance were significantly larger at Cape Lisburne because of the unusually high occurrence of age class 2+ fish. Sand lance at Bluff were significantly larger in 1978 than at the other two colonies that year, and in 1980 they were significantly larger than any of the other samples we obtained. Arctic cod were larger at Cape Thompson than at Cape Lisburne in 1977 and 1979 and the difference was significant in 1977. Increasing fish size with decreasing latitude has also been reported by Andriyashev (1954) for sand lance in the Barents Sea, and by Lowry and Frost (1981), who showed that Arctic cod in the Bering Sea were larger than in the Chukchi and Beaufort Seas.

Size distributions of principal species of invertebrates recovered from murres and kittiwakes at Cape Thompson and Cape Lisburne are presented in Figures 14-17. *Parathemisto libellula* were significantly larger at Cape Lisburne in 1977 than in 1978, or than at Cape Thompson in 1979 (ANOVA, $P < 0.05$). Similarly, euphausiids (*Thysanoessa sp.*) were significantly larger at Cape Lisburne in 1978 and 1979 than in 1980 (ANOVA, $P < 0.05$). However, all of the individuals measured in 1978 and 65% of those measured in 1979 were taken from thick-billed murres, compared to only 2% in 1980. In 1979, thick-billed murres took significantly larger individuals than did kittiwakes (Figure 18), a fact that could account for the apparent size difference of euphausiids in 1980.

Feeding Areas

Although Cape Thompson and Cape Lisburne are separated by only about 85 km, feeding areas of seabirds from these two colonies were much farther apart during most of each summer. Generally, birds from Cape Thompson fed to the south of the colony during June and July, and shifted more to the west and north in August. Birds from Cape Lisburne fed to the northeast in Ledyard Bay during June and July, and shifted more to the north in August. Only during August of some years was there ever any overlap in foraging areas of birds from the two colonies.

Figure 19 illustrates the combined land and aerial observations we made on feeding areas of murres during this study. Most of the murres from Cape Thompson fed south of the colony in all years during June and most of July. In 1976 murres shifted more to the west in August, but few were ever seen commuting north. A clear shift to the north occurred in late July of 1977 and by early August nearly all murres from Cape Thompson fed north of the colony. Although a similar shift happened in 1978, there was less distinction between early and late season feeding areas. Many murres continued to feed south and west of the colony after many others had begun feeding to the north and northwest. In 1979 murres fed over an even broader area throughout the summer than during the previous year. Flight directions were already widely scattered between south and west in early July. About half of the murres shifted to the west and north by early August, and thereafter murres could be seen flying to and from nearly all offshore directions.

These observations of feeding areas of murres from Cape Thompson are supported by both shipboard and aerial surveys made in earlier years. Swartz (1967), reporting on shipboard transects made in the eastern Chukchi Sea during August 1960, stated that the principal feeding area of murres from Cape Thompson appeared to lie between 25-65 km south of the colony. Fewer murres were seen to the west. Harrison (1977) reported seeing concentrations of murres approximately 70 km south of Cape Thompson during aerial surveys flown in June 1975. He also reported fewer, but substantial, numbers of murres in the same region in August 1976. Concentrations of murres were also seen in the same general area by shipboard observers in early September 1976 (Gould 1977).

Very few murres were ever seen on the water between Cape Thompson and Cape Lisburne, except in the immediate vicinity of the colony at

Cape Lewis, during any of our aerial surveys or during numerous flights between the colonies at other times. When Cape Thompson murres fed north of the colony, therefore, they probably went to the same area used by birds from Cape Lisburne. In August of 1978 we intercepted several flocks of southbound murres west of Cape Lisburne and followed them to Point Hope in our survey aircraft. At Point Hope we watched other flocks arriving from the same direction and subsequently confirmed that these flocks were returning to Cape Thompson.

Other observations of murres flying south past Point Hope during the summer have been made in the past. R. M. Gilmore (unpubl. field notes) recorded watching "...endless flocks of Pallas murres fly by" as he sat at Point Hope on 4 August 1931. His conclusion was that the birds were on their southward migration because their directional orientation was from north to south. We believe that he was probably seeing flocks returning to Cape Thompson after feeding in the vicinity of Cape Lisburne. Nelson (1969) also reported that during summer murres "...constantly fly north or south over Point Hope spit...". Although he believed that the birds were flying back and forth between the colonies at Cape Thompson and Cape Lisburne, and mentioned wind as a causative factor determining northward or southward flight directions, we suggest that he too was seeing murres departing from Cape Thompson and returning there after feeding well north of Cape Lisburne.

Murres at Cape Lisburne fed to the northeast of the colony in Ledyard Bay during June and July of all years. By early August of each year they shifted their foraging effort more to the north. By late August most Cape Lisburne murres foraged to the north and northwest of the colony. The aerial transects flown in late July 1978 showed that murres were feeding in a relatively well-defined region east of a line between Cape Lisburne and Point Lay. By mid-August 1978, aerial surveys found the majority of murres concentrated north of the colony, with fewer to the west and east.

Although the pattern of seasonal feeding area use was less variable at Cape Lisburne than at Cape Thompson, some differences between years have occurred. In early September 1976 the majority of murres fed more to the northwest and west than in following years. Swartz (1967) also reported relatively large numbers of murres westward of the colony in late August 1960.

Kittiwake feeding areas tended to be closer to the colonies, but generally lay in the same direction as those of murres in June and July. Beginning in late July or early August of all years except 1976, kittiwakes concentrated along the coastline north and south of Cape Thompson and east of Cape Lisburne. The shift to coastal feeding occurred when sand lance and capelin appeared near shore east of Cape Lisburne and north of Cape Thompson. As shoals of these fishes moved west along the coast to Cape Lisburne and south to Cape Thompson, feeding intensified in front of both colonies. At Cape Thompson shoals of sand lance traveled well southeast of the colony and feeding effort shifted as far south as Kivalina in some years. When sand lance and capelin were absent in 1976, kittiwakes foraged widely offshore throughout the summer.

VIIb. FOOD HABITS - DISCUSSION

The large annual differences in abundance and size of forage fishes in the eastern Chukchi Sea indicate that there was substantial environmental variability in this region between 1976-1980. Sea ice and seawater temperature, very important elements of the highly seasonal environment of northern Alaska, fluctuated considerably during the past decade, and might have been responsible for many of the interannual and seasonal changes in seabird food webs, and hence in seabird breeding success, that occurred during that time.

The southern extent of ice in the Bering Sea has varied considerably between years, a consequence of changing weather patterns (Walsh and Johnson 1979, Johnson 1980, Niebauer 1980, 1981a, 1981b). Beginning in 1973, anomalous atmospheric circulation resulted in progressive cooling of the Bering Sea, which led to large negative deviations from normal sea-surface temperature and shelf bottom water temperature, and a large positive deviation from normal ice cover by 1976 (Dickson and Namias 1979, Niebauer 1980). Between fall 1976 and spring 1979, however, the trend reversed; sea-surface temperature, which was 1.4°C below normal in 1975, rose 0.7 - 0.8°C yr⁻¹, and sea ice, which had reached its maximum southern extent in the winter of 1975-76, decreased about 10% yr⁻¹ from 1977 through 1979 (Dickson and Namias 1979, Niebauer 1980). Annual changes in ice cover and sea-surface temperatures were not confined to the Bering Sea, but were equally pronounced in the eastern Chukchi Sea as shown in Figure 20.

Besides sea ice, the eastern Chukchi Sea is dominated by a strong barotropic current flowing north out of the Bering Sea (Coachman *et al.* 1975, Coachman and Aagaard 1981). Water velocity of 150 cm sec⁻¹ through Bering Strait is common and mean transport is in the order of 1 - 2 x 10⁶ m³ sec⁻¹. A major component of the flow is Alaska Coastal Water, a well defined warm water mass of low salinity found on the eastern side of the strait. North of Bering Strait, Alaska Coastal Water tends to follow the 40 m contour interval which takes it eastward toward the Cape Thompson-Point Hope region. North of Point Hope the current splits with part flowing northwest into the central Chukchi Sea and part flowing northeast around Cape Lisburne and into the Beaufort Sea east of Barrow (Flemming and Heggarty 1966, Hufford 1973, Coachman *et al.* 1975).

Alaska Coastal Water develops annually in the northeastern Bering Sea from cold, relatively saline water remaining from winter that is diluted by melting ice and river input, primarily from the Yukon River, and rapidly heated by insolation (Coachman *et al.* 1975). The temperature of coastal water flowing through Bering Strait may rise from near 0°C to 10°C during the first month following dissipation of sea ice (Bloom 1964, Ingraham 1981). Therefore, the seasonal development of the Alaska Coastal Water mass depends on the winter extent of ice into the Bering Sea, its rate of retreat in spring and the spring temperature of Bering Sea parent water.

The relationship of Alaska Coastal Water to the marine biology of the eastern Chukchi Sea is not well known, but it may have a major direct effect by ameliorating an otherwise colder arctic environment (Flemming and Heggarty 1966). It may have other important effects by 1) advecting into the region particulate organic matter that subsidizes local primary production and helps feed endemic zooplankton and benthic invertebrate populations, and by 2) advecting in oceanic and neritic zooplankton stocks originating in the Bering Sea, but constituting an important food source for eastern Chukchi fish populations.

The Bering Sea shelf shoreward of about 100 m has relatively high levels of primary productivity, in the order of $3 \text{ g C m}^2 \text{ day}^{-1}$ (Cooney and Coyle MS). Poor coupling to pelagic herbivores, however, results in a relatively inefficient system, with a major fraction of the annual primary production being lost to endemic pelagic food webs. The turbulent Bering Strait region also has high levels of primary productivity, comparable to upwelling areas off of the west coasts of North and South America and Africa (McRoy *et al.* 1972, McRoy and Goering 1976). Because of the volume and speed of water transported through the strait, a significant portion of the carbon fixed there during summer is probably swept downstream. Stoker (1981) suggested that such a process would explain high standing stocks of predominantly boreal Pacific benthic invertebrate macrofauna in the southern Chukchi Sea. Particulate organic matter advected off of the northern Bering Sea shelf, plus that originating in Bering Strait, could therefore be expected to contribute significantly to the annual carbon budget of the eastern Chukchi Sea.

The flow of water from the Bering Sea has also been shown to play an important role in determining the composition and abundance of zooplankton assemblages in Bering Strait and the eastern Chukchi Sea. A variety of endemic Bering Sea copepods, including *Eucalanus bungii*, *Calanus cristatus*, *C. plumchrus*, *Acartia longiremis* and *A. clausi*, are advected into the eastern Chukchi Sea during summer, and contribute significantly to diversity and standing stocks of zooplankton in the near shore waters (Johnson 1956, Redburn 1972, Cooney 1981). The intrusion of warm water also creates a temperature regime favorable for the rapid development and high production of meroplankton, particularly barnacle larvae, and as a result, zooplankton biomass in the warmer coastal zone during summer is about an order of magnitude higher than in the colder central Arctic Ocean (Redburn 1972).

Little is known about the natural histories of the various fish populations that are important to seabirds in the eastern Chukchi Sea. Information obtained elsewhere on any of the same or similar species, however, indicates that distributions and numbers of populations of prey fishes could be influenced by the effects that Alaska Coastal Water has on regional water temperatures and on zooplankton standing stocks.

Sand lance are generally considered a coastal, shallow water species except in winter when they move into relatively deeper water of 100-120 m (Macy *et al.* 1978). They spawn during a long interval between fall and spring (Andriyashev 1954, Macy *et al.* 1978, Rogers *et al.* 1981). Beginning in mid-June in the Barents Sea, shoaling sand lance composed mainly

of year class 1+ fish run towards shore where they remain until August-October (Andriyashev 1954). We observed similar behavior of sand lance at both Cape Thompson and Cape Lisburne. For example in 1977, small numbers of sand lance were available to murres and kittiwakes in early July. These were at best, however, an insignificant vanguard of shoals that were present after 25-30 July at Cape Lisburne, and after 10-12 August at Cape Thompson. Shoaling sand lance moved along the coast throughout the remainder of the summer at both colonies.

Several studies have shown that sand lance are sensitive to water temperature. Inoue *et al.* (1967) showed that sand lance eggs artificially incubated at 6°C took 33 days to hatch, whereas eggs incubated at 16°C hatched in only 13 days. Winslade (1974) reported that the emergence of sand lance (*A. marinus*) from sand where they overwintered was determined by warming water temperatures in spring. Sand lance (*A. dubious*) from the Grand Bank in the northwest Atlantic Ocean had slower first-year growth rates in colder years than in warmer years (Winters 1981).

Since sand lance spawn during winter, it might be assumed that the onshore runs in summer occur in response to seasonally abundant food. Sand lance are often found near the bottom where they apparently bury in the sand to avoid predators (Macy *et al.* 1978), but benthic organisms contribute little to their diets. Sand lance in the Barents Sea fed primarily on pelagic taxa such as *Calanus finmarchicus* and meroplanktonic forms of barnacles and larvae of euphausiids and amphipods during early summer, and shifted to small copepods, particularly *Microsetella*, *Acartia* and *Oithona*, towards late summer (Andriyashev 1954). Sand lance in the northern Gulf of Alaska fed predominantly on calanoid copepods and barnacle larvae (Blackburn *et al.* 1981, Rogers *et al.* 1979). Sand lance taken by seabirds in the eastern Chukchi Sea during this study fed on large numbers of small calanoid copepods (*cf. C. plumchrus*).

Changes in the physical environment (i.e. the extent and duration of sea ice and the development of the Alaska Coastal Water mass) of the magnitude seen in the Bering Sea and eastern Chukchi Sea during the 1970's could reasonably be expected to have led to the changes we observed in the sand lance population between 1976-1980. Smaller sizes of sand lance in colder years could have resulted from water temperature alone, by its effects on metabolism and growth for example, or could have resulted from poor coupling to seasonally abundant prey because of prolonged incubation time of eggs, delayed emergence of larvae and adults in spring, and delayed development of zooplankton populations. The annual changes in seasonal abundance of sand lance also could have been a function of differential rates of development of neritic prey populations or of delayed emergence times of overwintering fish.

Most of the capelin eaten by murres and kittiwakes were age class 1+ juveniles, although remains of a few larger adults were also recovered. The adults were spawning as evidenced by developing reproductive products in both sexes. Adult capelin do not feed while spawning, but juveniles feed intensively throughout the summer, predominantly on copepods (Vesin *et al.* 1981). The presence of juvenile capelin near Cape Thompson and

Cape Lisburne in summer could be a response to seasonally abundant food, as in the case of sand lance.

Pitt (1958b) reported that capelin on the Grand Bank will spawn in a rather broad range of water temperatures, but spawning and embryonic development is delayed in colder years. In 1950, relatively cold water temperatures resulted in spawning in mid-July, and larvae were liberated in late September. In 1951 when water temperatures were about 2°C warmer, spawning occurred in late June-early July and larvae were liberated around the first of August. Pitt (1958a) also showed that growth rates of capelin were slower in colder years than in warmer years, and suggested that the difference was a factor of water temperature and food conditions. Annual differences in seasonal warming patterns in the eastern Chukchi could easily account for the annual differences in the sizes of capelin in 1977-1980.

By far the most abundant and widespread fish fauna in the eastern Chukchi Sea are Arctic cod and sculpins (Alverson and Wilimovsky 1966, Craig and Haldorson 1981). Arctic cod feed on typically arctic copepods, amphipods and mysids (Lowry and Frost 1981, Craig and Haldorson 1981). Sculpins feed mainly on mysids, amphipods and isopods (Craig and Haldorson 1981). The degree to which these Arctic food webs might be subsidized by carbon imported from the Bering Sea is unknown. If there is a positive effect, then it should be larger in warmer years when the annual production cycle begins relatively early in summer, and it should be greatest just north of Bering Strait where the suspended particulate load would be highest. Increasing sizes of Arctic cod and sculpins between 1976-1980, and from north to south, would suggest such effects.

Cod and sculpin populations might also benefit if their prey concentrated along the front separating Alaska Coastal Water from the adjacent water mass in the eastern Chukchi Sea. A rather sharp boundary exists in summer between these two water masses (Coachman *et al.* 1975), similar to fronts separating water masses in the southeastern Bering Sea (Coachman and Charnell 1979, Shumacher *et al.* 1979). During our aerial surveys in 1978, the number of murres on the water declined sharply after we crossed a frontal line running northeast-southwest across the mouth of Ledyard Bay between Cape Lisburne and Point Lay. Kinder *et al.* (MS) have recently described a similar relationship in the southeastern Bering Sea. They found murres concentrated near a front that surrounds the Pribilof Islands in summer, and suggested that these aggregations were related to the availability of walleye pollock (*Theragra chalcogramma*) that were feeding on zooplankton concentrated along the front. Annual differences in the development of Alaska Coastal Water and the associated front separating it from the adjacent water mass in the central and northern Chukchi Sea could thereby lead to annual differences in energy flow through food webs that include Arctic cod and sculpins.

Annual and seasonal differences in murre feeding areas also indicated that arctic benthic and demersal food webs, as well as neritic food webs, might benefit from energy exported from the Bering Sea. In June and July of all years, murres at Cape Thompson fed to the south, toward the source of the flow where energy levels should be highest relatively early in the season. As summer progresses in this region, zooplankton,

for example copepods that are plentiful in the water column as eggs, nauplii and copepodids in early summer, may decline in numbers as the larval forms mature and migrate to deeper water where they overwinter. The shift in murre flight directions from south to west to north at Cape Thompson might indicate that the birds followed the movement of a passively mobile assemblage of organisms advected north before the annual production cycle began to shut down in the northern Bering-Bering Strait region. Similarly, the shift in murre flight directions from northeast to north and northwest at Cape Lisburne suggests that those birds also responded to this drifting assemblage of organisms as it passed their colony. By mid-August of several years, the center of murre prey biomass appeared to be situated north and west of Cape Lisburne, because at that time the majority of the birds from Cape Lisburne and large numbers of murres from Cape Thompson fed there. Indeed, Wing (1974) showed that copepod biomass and diversity were greatest in a region of relatively warm water northwest of Cape Lisburne in September-October 1970. The occurrence of a variety of fish species was also higher there at that time than in surrounding waters (Ingham *et al.* 1972). Annual variations in foraging patterns of murres at Cape Thompson might be explained by the way a drifting, maturing food web could be affected by differences in timing of the annual production cycle in the Bering Sea.

The changes we observed in the breeding biology of murres and kittiwakes between 1976-1979 and the corresponding changes in prey populations probably represented adjustments to the large-scale environmental fluctuation that occurred during that time. Although we lack many of the details, the effects of climatic changes during the 1970's were apparently manifested in two very different food webs, arctic benthic and demersal food webs that include cods and sculpins, and boreal neritic food webs that include sand lance. Furthermore, environmental effects on seabirds and their food webs were not restricted to Cape Thompson and Cape Lisburne. Drury *et al.* (1981) and we documented the same pattern of breeding failure followed by recovery in kittiwakes and common murres in Norton Sound between 1975-1981. Figure 21 compares the relationships between environment and productivity for kittiwakes at Bluff and Cape Lisburne. Food availability at Bluff also seemed to be the most important factor in determining annual levels of reproductive success. Apparent food shortages likewise led to a poor breeding season for murres and kittiwakes on St. Lawrence Island (northern Bering Sea) in 1976 (Searing 1977). Murres and kittiwakes in Norton Sound feed primarily on sand lance and saffron cod, and on St. Lawrence Island they feed on cods, sand lance and capelin (Springer *et al.* unpubl. data). St. Lawrence Island and Norton Sound are located in the headwaters of the marine river that flows out of the Bering Sea and into the eastern Chukchi Sea. Breeding seabirds throughout the northern Bering-eastern Chukchi region may be related by common food web dependencies that are influenced by similar physical processes.

If energy flow through food webs in northern Alaskan waters waxes and wanes in response to patterns of environmental change during intervals of a few years, as it apparently did in the 1970's, it might also adjust to longer-term fluctuations in the environment (see Cushing and Dickson 1976). For example, between the late 1940's and mid-1960's,

sea-surface temperature over the bulk of the northern Pacific Ocean (15° to 60° N and 130° E to 110° W) was generally normal or above; only about three years in the mid-1950's were slightly below normal (Namias and Cayan 1981). Since 1964, however, sea-surface temperature was above normal in only three years. Such differences may alter energy budgets in northern Alaska sufficiently to account for the declines in numbers of murres that we have documented at Bluff and at Cape Thompson (Table 13). Below average temperatures in Norton Sound for many years could have resulted in relatively less energy available to murres, relatively low levels of natality, and the recent numerical decline as recruitment fell below adult survivorship (see sections V.a - VII. a.). At Cape Thompson, murre numbers were highest in 1960, a time when water temperatures had been above normal for several preceding years. However, relatively cold temperatures prevailed from the mid-1960's until we resumed work there in 1976. A preliminary simulation analysis predicts that at Bluff, murre numbers will increase beginning in 1982 as a consequence of improved reproductive success associated with the warming trend since 1978, if the population decline resulted from climatic fluctuation and not other causes.

TABLE 1. Regression equations used to estimate lengths and weights of principal fishes identified in prey remains of murres and kittiwakes collected in the eastern Chukchi Sea.

Fish	Equation	Sample Size	Correlation Coefficient	Source
Arctic cod (<i>Boreogadus saida</i>)	fish length (cm) = 2.198 x otolith length (mm) + 1.588 log weight (g) = -5.196 + 3.031 log length (mm)	202 277	0.981 0.98	Frost and Lowry 1981 Craig and Haldorson 1981
Saffron cod (<i>Eleginops gracilis</i>)	otoliths > 8.5 mm fish length (cm) = 2.323 x otolith length (mm) - 4.839 otoliths < 8.5 mm fish length (cm) = 1.740 x otolith length (mm) log weight (g) = -5.610 + 3.233 log length (mm)	110 36 180	0.963 0.932 0.94	Frost and Lowry 1981 Frost and Lowry 1981 Craig and Haldorson 1981
Sculpins ¹ (Cottidae)	fish length (cm) = 4.009 x otolith length (mm) - 4.364 log weight (g) = -6.016 + 3.46 log length (mm)	272	0.98	Frost and Lowry unpubl. data Craig and Haldorson 1981
Sand lance ² (<i>Ammodytes hexapterus</i>)	fish length (mm) = 4.01 x otolith length (units) ³ + 19.0	31	0.91	This study
Capelin ⁴ (<i>Mallotus villosus</i>)	fish length (mm) = 3.42 x otolith length (units) ³ + 29.22	12	0.99	This study

¹Equations are derived from specimens of *Myoxocephalus quadricornis*.

²Weights are approximated as: mean weight all fish = 2.0 g, Cape Thompson 1977; = 3.0 g, Cape Thompson 1978 and Cape Lisburne 1977-78; = 4.0 g, Cape Thompson 1979 and Cape Lisburne 1980.

³12.5 units mm⁻¹

⁴Weights are approximated as: mean weight all fish = 2.0 g, Cape Thompson 1977 and Cape Lisburne 1979; = 3.0 g, Cape Thompson 1979 and Cape Lisburne 1980.

TABLE 2. Importance of major taxa in diets of thick-billed murres (TBM), common murres (CM) and black-legged kittiwakes (BLK) collected at Cape Thompson, eastern Chukchi Sea, 1976-1979.

	TBM		CM		BLK	
	n	% ¹	n	% ¹	n	% ¹
Number examined	246	(100)	62	(100)	116	(100)
Number empty	33	(13)	13	(21)	11	(9)
Frequency of invertebrates	115	54	6	12	20	19
Frequency of fish	182	85	45	92	91	87
<i>a. Frequency of Occurrence</i>						
Cods	85	40	29	59	55	52
Sculpins	87	41	14	29	0	0
Sand lance	45	21	20	41	32	30
Capelin	26	12	12	24	17	16
Righteye flounders	19	9	3	6	0	0
Other fishes	28	13	3	6	3	3
Shrimps	69	32	3	6	4	4
Amphipods	29	14	3	6	0	0
Mysids	0	0	0	0	1	1
Euphausiids	1	<1	0	0	0	0
Polychaetes	18	8	0	0	12	11
Other invertebrates	36	17	1	2	7	7
<i>b. Numbers</i>						
Cods	350	8	203	26	241	27
Sculpins	835	25	137	17	0	0
Sand lance	213	6	271	34	325	36
Capelin	199	6	138	18	146	16
Righteye flounders	180	5	4	<1	0	0
Other fishes	271	8	16	2	6	<1
Shrimps	244	7	4	<1	34	4
Amphipods	910	27	12	2	0	0
Mysids	0	0	0	0	2	<1
Euphausiids	1	<1	0	0	0	0
Polychaetes	36	1	0	0	137	15
Other invertebrates	73	2	1	<1	14	2
<i>c. Estimated Grams Wet Weight</i>						
Cods	2574	43	2210	59	2626	63
Sculpins	1555	26	414	11	0	0
Sand lance	497	8	694	19	975	23
Capelin	595	10	383	10	415	10
Righteye flounders	180	3	4	<1	0	0
Other fishes	130	2	32	<1	12	<1
Shrimps	122	2	2	<1	17	<1
Amphipods	312	5	2.4	<1	0	0
Mysids	0	0	0	0	<1	<1
Euphausiids	<1	<1	0	0	0	0
Polychaetes	36	<1	0	0	137	3
Other invertebrates	37	<1	<1	<1	7	<1

¹Numbers indicate the percentage of stomachs containing food in which the food item was represented. Values in parentheses represent frequency in the total number of stomachs examined.

TABLE 3. Importance of major taxa in diets of thick-billed murres (TBM), common murres (CM) and black-legged kittiwakes (BLK) collected at Cape Lisburne, eastern Chukchi Sea, 1977-1980.

	TBM		CM		BLK	
	n	% ¹	n	% ¹	n	% ¹
Number examined	198	(100)	48	(100)	71	(100)
Number empty	16	(8)	3	(6)	4	(6)
Frequency of invertebrates	85	47	9	20	22	33
Frequency of fish	173	95	45	100	60	90
<i>a. Frequency of Occurrence</i>						
Cods	99	54	35	78	28	42
Sculpins	89	49	10	22	4	6
Sand lance	75	41	25	56	29	43
Capelin	13	7	2	4	7	10
Righteye flounders	15	8	7	16	0	0
Other fishes	8	4	1	2	5	7
Shrimps	39	21	1	2	1	1
Amphipods	48	26	2	4	4	6
Mysids	19	10	3	7	0	0
Euphausiids	15	8	1	2	8	12
Polychaetes	12	7	0	0	13	19
Other invertebrates	11	6	1	2	2	3
<i>b. Numbers</i>						
Cods	660	13	202	31	158	5
Sculpins	529	10	17	3	5	<1
Sand lance	838	16	255	39	263	8
Capelin	55	1	60	9	29	<1
Righteye flounders	123	2	83	13	0	0
Other fishes	22	<1	6	<1	7	<1
Shrimps	165	3	5	<1	1	<1
Amphipods	985	19	4	<1	1318	42
Mysids	295	6	9	1	0	0
Euphausiids	1544	29	6	<1	1626	51
Polychaetes	8	<1	0	0	51	2
Other invertebrates	25	<1	3	<1	2	<1
<i>c. Estimated Grams Wet Weight</i>						
Cods	5028	51	1034	53	912	36
Sculpins	1135	12	18	1	30	1
Sand lance	2703	27	669	34	830	33
Capelin	132	1	122	6	87	3
Righteye flounders	123	1	83	4	0	0
Other fishes	44	<1	12	<1	14	<1
Shrimps	83	<1	2.5	<1	<1	<1
Amphipods	197	2	<1	<1	264	10
Mysids	59	<1	1.8	<1	0	0
Euphausiids	155	2	<1	<1	163	7
Polychaetes	8	<1	0	<1	52	2
Other invertebrates	13	<1	1.5	<1	1	<1

¹Numbers indicate the percentage of stomachs containing food in which the food item was represented. Values in parentheses represent frequency in the total number of stomachs examined.

TABLE 4. Fish biomass : invertebrate biomass in diets of thick-billed murres in the eastern Chukchi Sea.

Colony	June	1-20 July	21 July-10 Aug.	10-31 Aug.	Overall
Cape Thompson					
1976	2.9	15	8	11	8.4
1977	5.7	232	22	76	30
1978	---	---	---	59	---
1979	---	74	18	679	48
\bar{x}	4.3	107	16	206	29
s	2.0	112	7.2	316	20
Cape Lisburne					
1977	2.9	5.1	5.6	17	6.0
1978	---	9.0	9.3	637	11
1979	---	35	---	442	72
1980	---	---	372	---	---
\bar{x}	2.9	16	129	365	30
s	---	16	210	317	37

TABLE 5. Average weight of major taxa in diets of thick-billed murres in the eastern Chukchi Sea. Units are g bird⁻¹.

Colony	Taxon	1976	1977	1978	1979
Cape Thompson					
Cods		14	10	DI ¹	14
Scorpions		1.9	12	DI	4.4
Sand lance		0.1	4.2	DI	2.1
Capelin		0	0	DI	8.7
Righteye flounders		0	0	DI	2.4
Other fishes		1.7	0.8	DI	0.1
Total fish		17	27	DI	32
Total invertebrates		1.9	0.9	DI	0.7
Cape Lisburne					
Cods		ND ²	12	30	24
Scorpions		ND	0.9	3.6	7.5
Sand lance		ND	9.7	16	32
Capelin		ND	0	0	1.8
Righteye flounders		ND	0.02	1.5	0.6
Other fishes		ND	0.4	0	0.6
Total fishes		ND	23	51	66
Total invertebrates		ND	3.9	4.5	0.9

¹DI = data insufficient for meaningful comparison.

²ND = no data.

TABLE 6. Percentage contribution of various taxa to total weight of fish in diets of thick-billed murres in the eastern Chukchi Sea, 1976-1980.

Colony	June	1-20 July	21 July-10 Aug	11-31 Aug
Cape Thompson				
Cods	74 ± 20	69 ± 48	45 ± 45	39 ± 32
Sculpins	24 ± 21	6.7 ± 10	38 ± 47	36 ± 32
Sand lance	1 ± 1.5	2.6 ± 3.3	5 ± 5.8	10 ± 19
Capelin	0	13 ± 23	10 ± 16	3 ± 6
Righteye flounders	0	6 ± 11	1.1 ± 1.8	2 ± 3
Other fishes	1 ± 1	1.5 ± 1.4	1.4 ± 1.1	9 ± 14
Cape Lisburne				
Cods	--	88 ± 10	49 ± 4	33 ± 28
Sculpins	--	3.4 ± 2.1	9.4 ± 2.2	12 ± 10
Sand lance	--	7 ± 5.8	38 ± .08	53 ± 34
Capelin	--	.7 ± 1	0	1.5 ± 1.7
Righteye flounders	--	.3 ± .4	2.8 ± 4	.3 ± .4
Other fishes	--	.8 ± 1	.9 ± 1.3	.2 ± .4

TABLE 7. Percentage contribution of various taxa to total weight of fish in diets of black-legged kittiwakes in the eastern Chukchi Sea, 1976-1980.

Colony	1-20 July	21 July-10 Aug.	11-31 Aug.
Cape Thompson			
Cods	84 ± 25	22 ± 7	7.7 ± 6.8
Sand lance	.7 ± 1	23 ± 19	87 ± 9
Capelin	14 ± 25	55 ± 26	4.8 ± 8
Cape Lisburne			
Cods	75 ± 19	14 ± 12	--
Sand lance	25 ± 20	72 ± 28	--
Capelin	0	9.2 ± 16	--

TABLE 8. Percentage contribution of various taxa to total weight of invertebrates in diets of thick-billed murres in the eastern Chukchi Sea, 1976-1980.

Colony	June	1-20 July	21 July-10 Aug.	11-31 Aug.
Cape Thompson				
Shrimps	69 ± 17	38 ± 17	50 ± 28	54 ± 23
Amphipods	6 ± 5	25 ± 42	18 ± 27	11 ± 11
Polychaetes	18 ± 12	28 ± 26	9 ± 10	14 ± 13
Cape Lisburne				
Shrimps	27	20 ± 19	17 ± 17	8.4 ± 7.9
Amphipods	11	5.5 ± .5	42 ± 40	73 ± 16
Mysids	0	12 ± 15	6.4 ± 3.7	0
Euphausiids	22	57 ± 23	32 ± 31	0
Polychaetes	27	1.2 ± 1.3	.7 ± 1.2	0

TABLE 9. Percent weight of cod in combined weight of cods, sand lance and capelin in diets of black-legged kittiwakes in the eastern Chukchi Sea.

Colony	1-20 July	21 July-10 Aug.	11-31 Aug.
Cape Thompson			
1976	100	ND ¹	ND ²
1977	>99	26	15
1978	NF	6	ND
1979	55	17	2
Cape Lisburne			
1977	97	1	ND
1978	70	23	ND
1979	59	ND	ND
1980	ND	22	ND

¹ND = no data.

²ND = no fish recovered from birds collected during interval.

TABLE 10. Age-length relationships (derived by otoliths) and sex ratios of combined samples of Arctic cod caught in Simpson Lagoon and adjacent coastal waters, 1977-79. Data are from Craig and Haldorson (1981).

Age	Fork Length (mm)				Sex Ratio	
	n	\bar{x}	range	SD	n	% female
1	196	84	54-110	13	0	--
2	101	128	88-177	20	87	52
3	86	162	120-196	19	86	71
4	16	182	129-203	21	15	80
5	8	212	153-250	36	7	100
6	4	240	198-257	28	4	75
Total	411				199	

TABLE 11. Age-length relationships (derived from otoliths) of fourhorn sculpins (*Myoxocephalus quadricornis*) in Simpson Lagoon. Data are from Craig and Haldorson (1981).

Age	Total Length (mm)			
	n	\bar{x}	range	SD
1	55	63	46-81	8
2	46	94	74-160	15
3	34	134	102-167	17
4	31	169	133-208	17
5	31	193	168-224	14
6	24	211	176-248	18
7	5	222	197-258	25
8	3	236	220-265	25
9	1	226	--	--

TABLE 12. Age-length relationships (derived from otoliths) of saffron cod in Simpson Lagoon. Data are from Craig and Haldorson (1981).

Age	Fork Length (mm)			
	n	\bar{x}	range	SD
1	108	125	79-192	21
2	69	198	145-242	21
3	1	247	--	--
4	3	256	200-303	52

Table 13. Summary of census results of murres in northern Alaska.¹

Year	Colony						
	Cape Lisburne		Cape Lewis	Cape Thompson		Bluff	St. Lawrence Is.
	Raw	Standardized	Raw	Raw	Standardized	Average	Raw
1960				251,000	357,000		
1972							32,000
1975						70,000	
1976	130,000	184,000		157,000	199,000	50,000	16,000
1977	131,000	184,000	19,000	143,000	171,000	38,000	
1978	126,000	172,000				40,000	
1979	142,000	246,000		114,000	149,000	35,000	
1980	173,000	174,000				31,000	
1981	149,000	153,000	21,000			29,000	34,000

¹Data are from Sections Va. - VIIa.

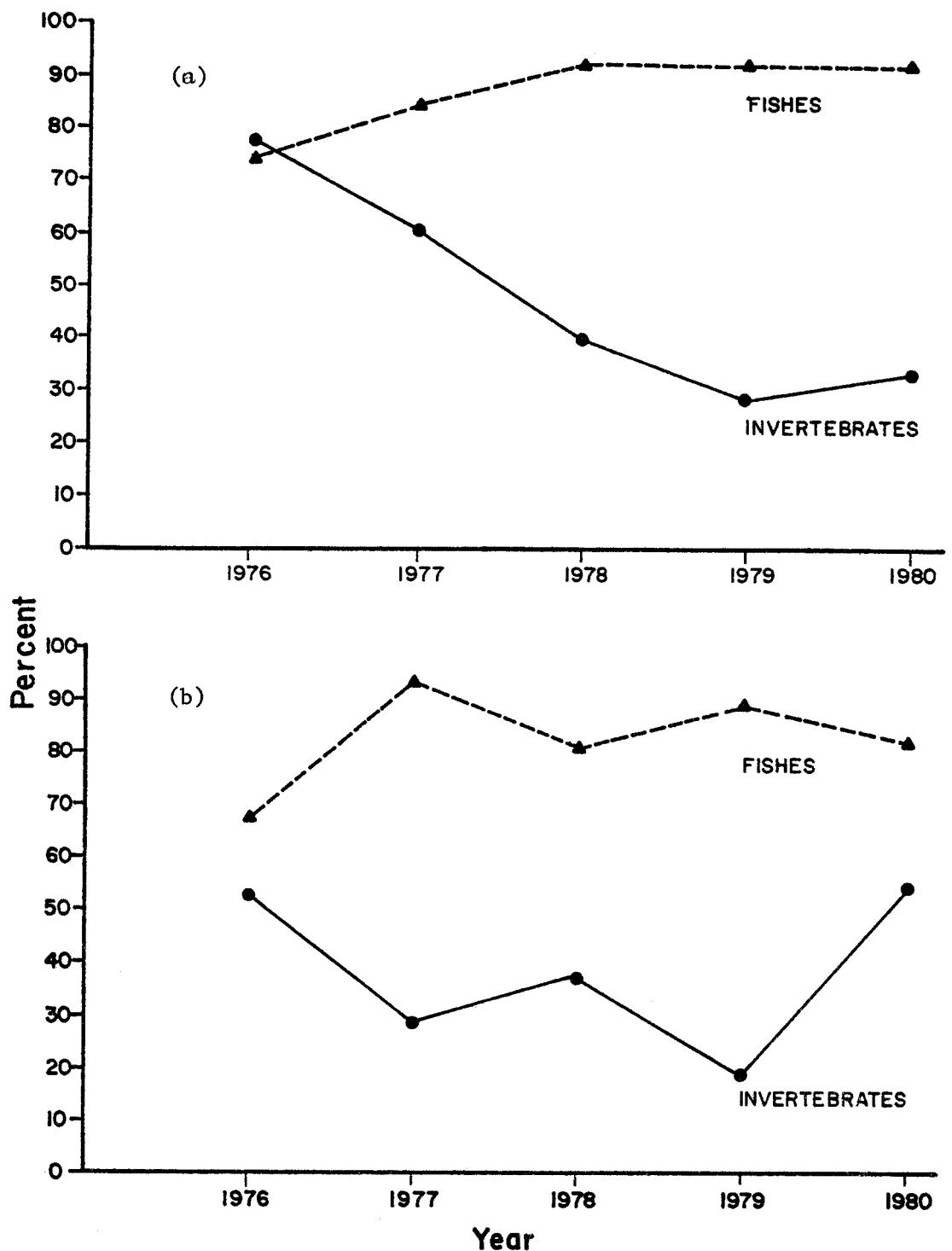


Figure 1. Frequency of occurrence of fish and invertebrates in diets of (a) thick-billed murres and (b) black-legged kittiwakes at Cape Lisburne and Cape Thompson.

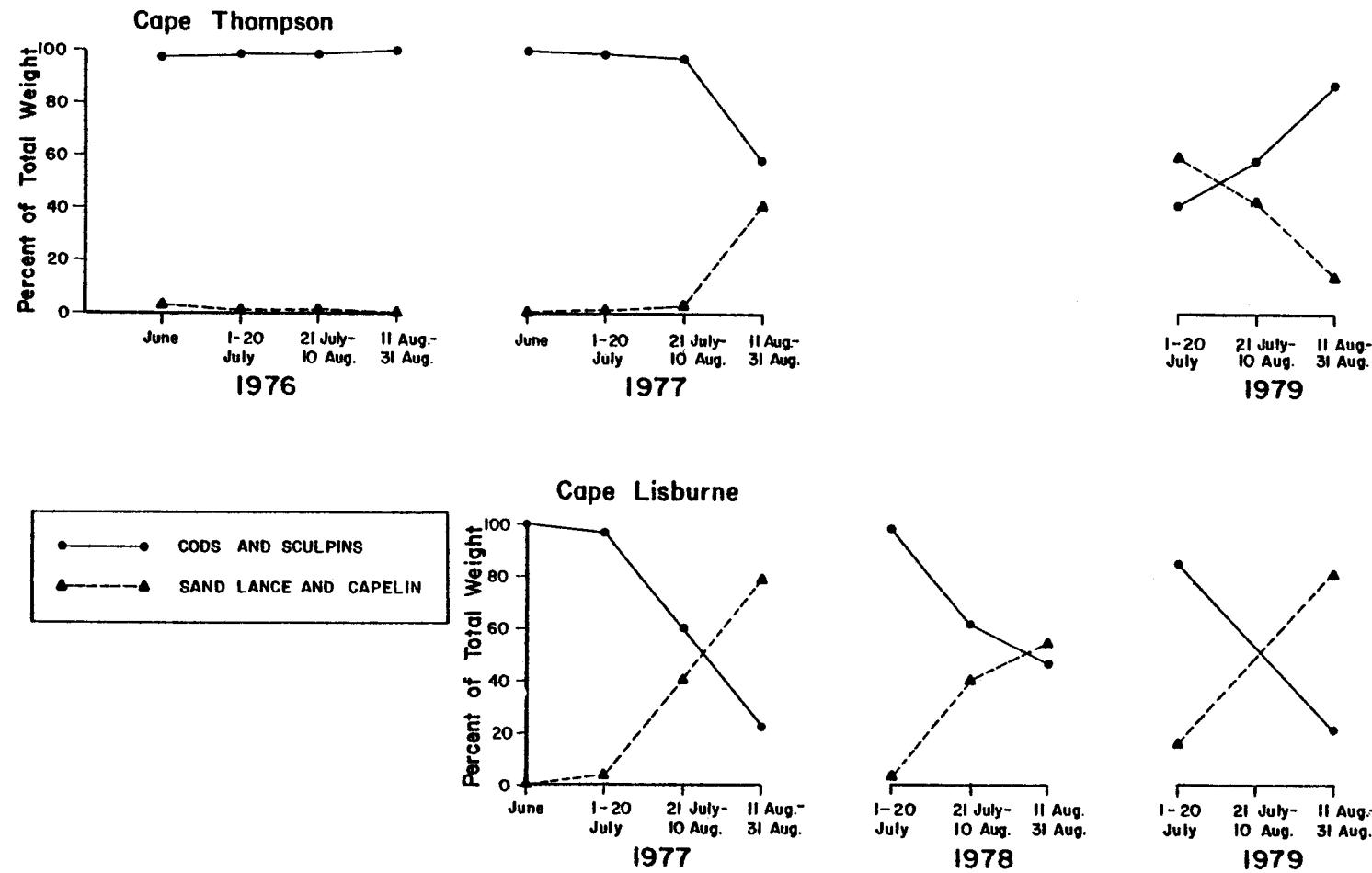


Figure 2. Combined importance of cods and sculpins compared to sand lance and capelin in diets of thick-billed murres at Cape Thompson and Cape Lisburne.

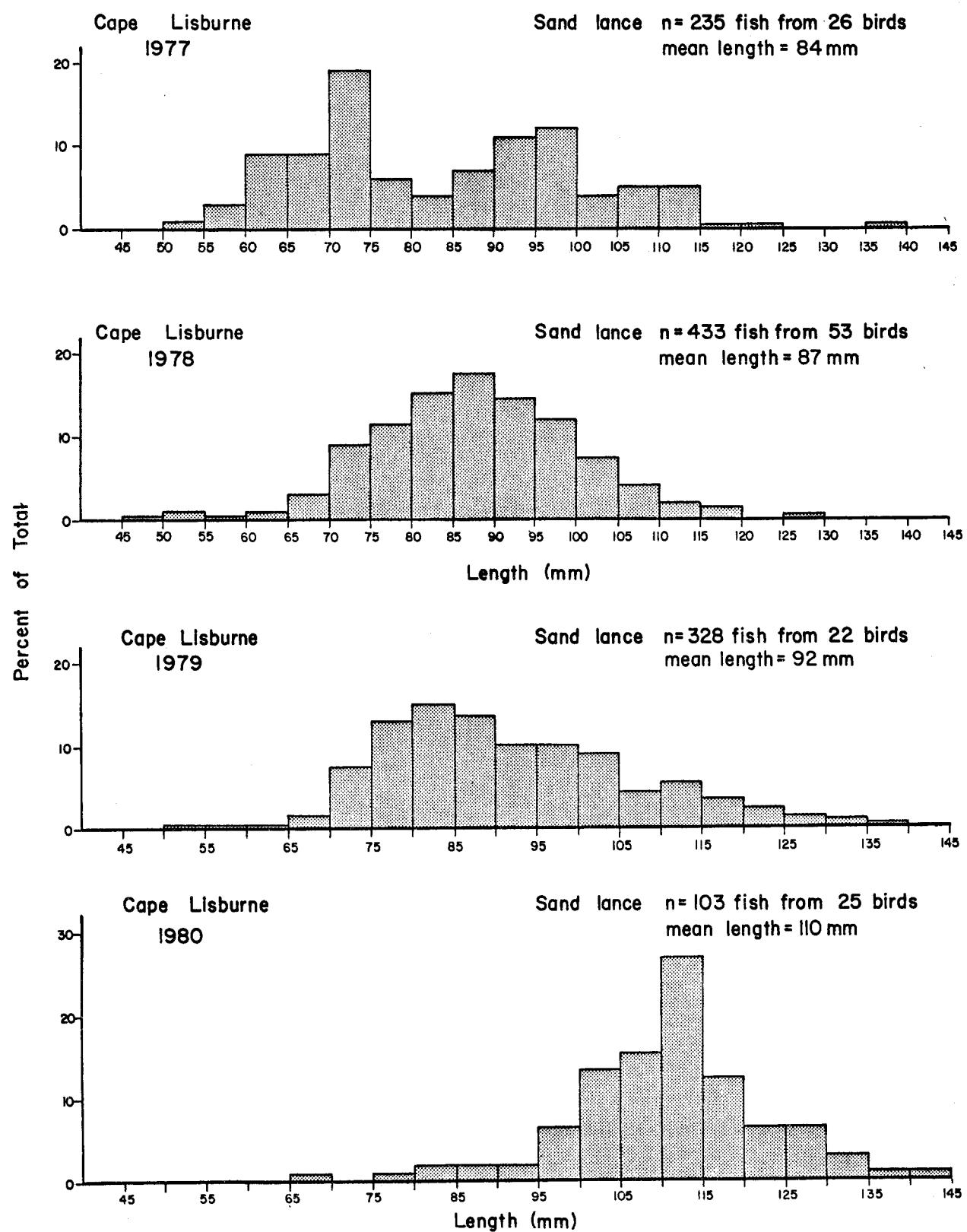


Figure 3. Sizes of sand lance in diets of murres and kittiwakes at Cape Lisburne.

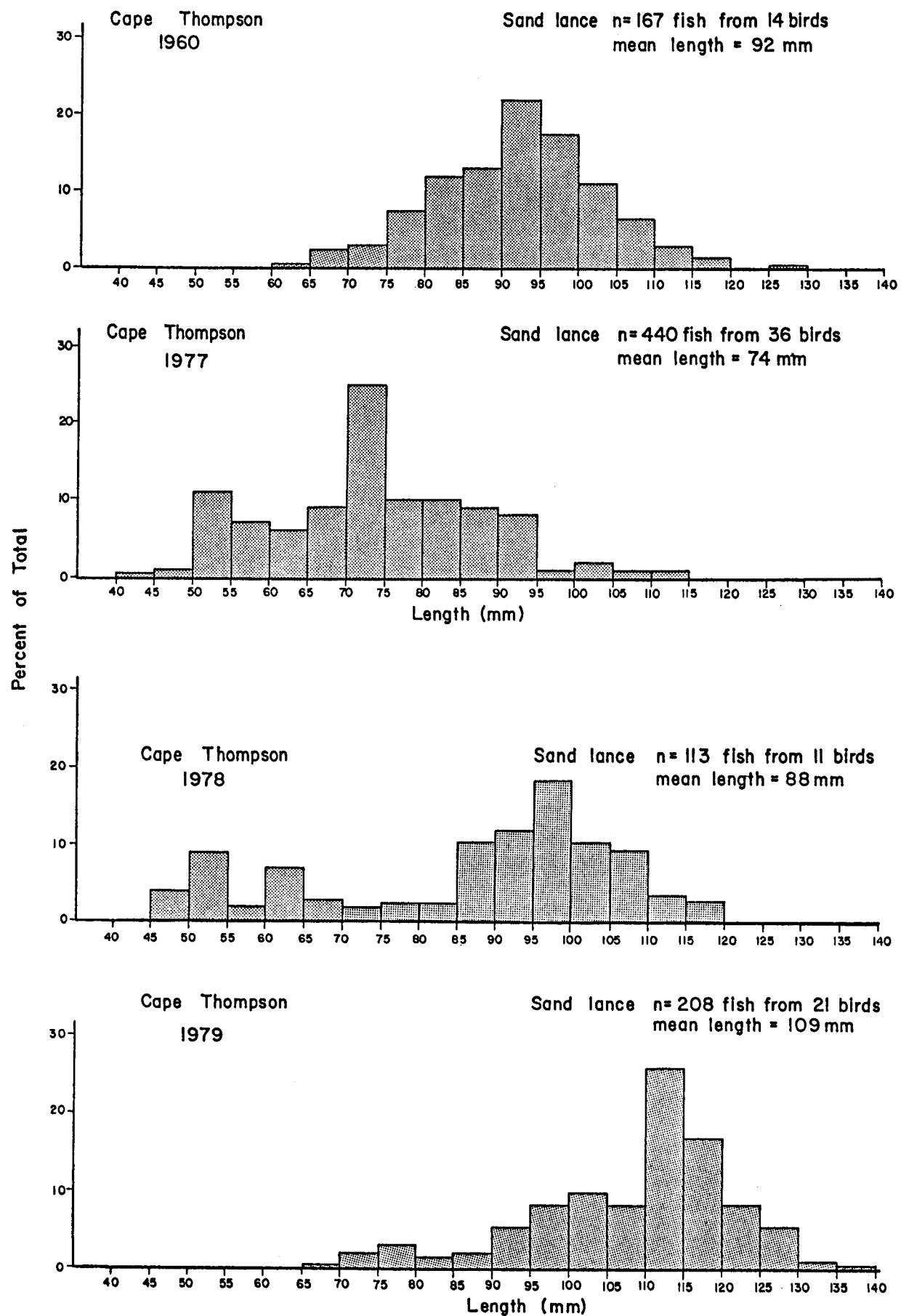


Figure 4. Sizes of sand lance in diets of murres and kittiwakes at Cape Thompson.

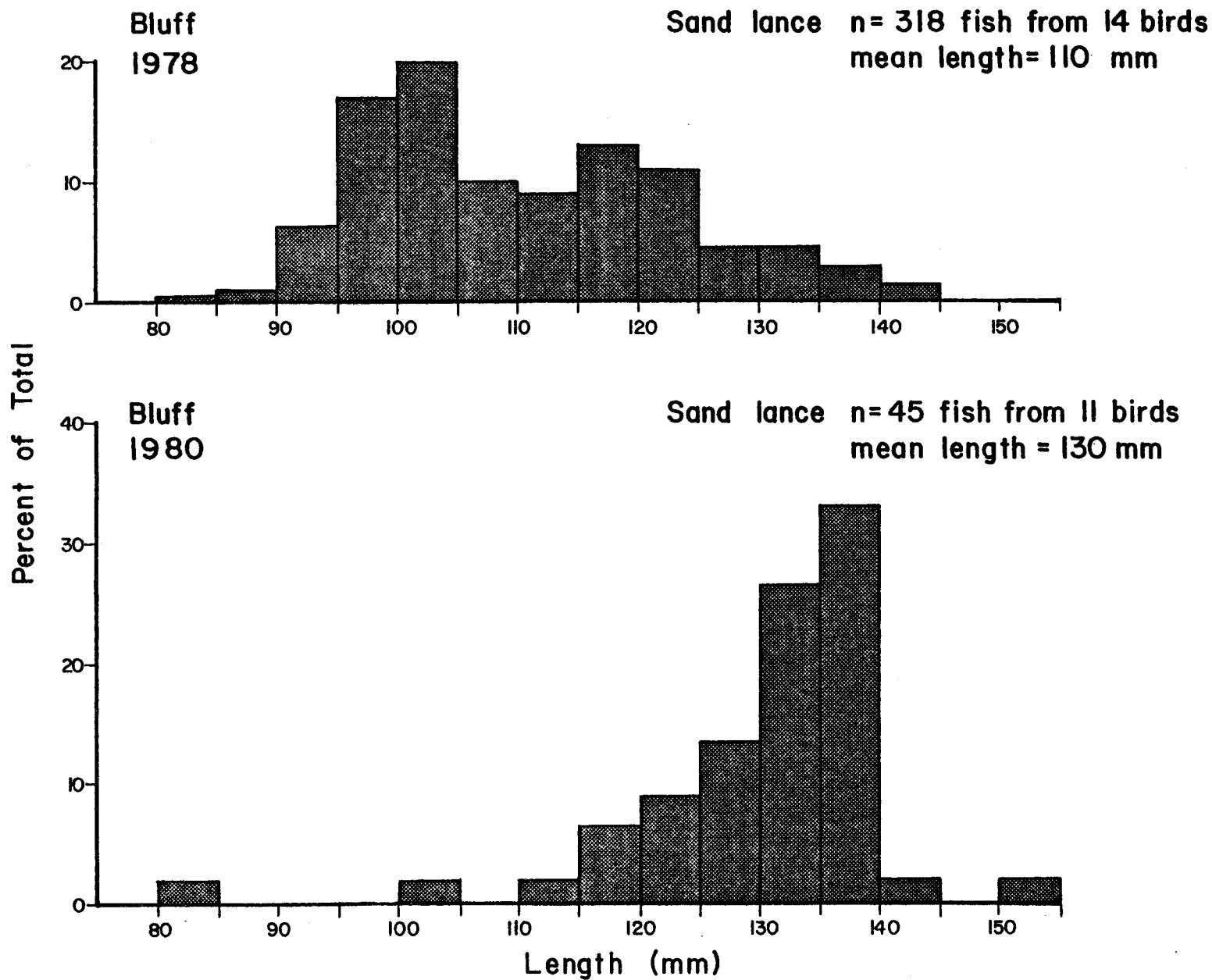


Figure 5. Sizes of sand lance in diets of murres and kittiwakes at Bluff.

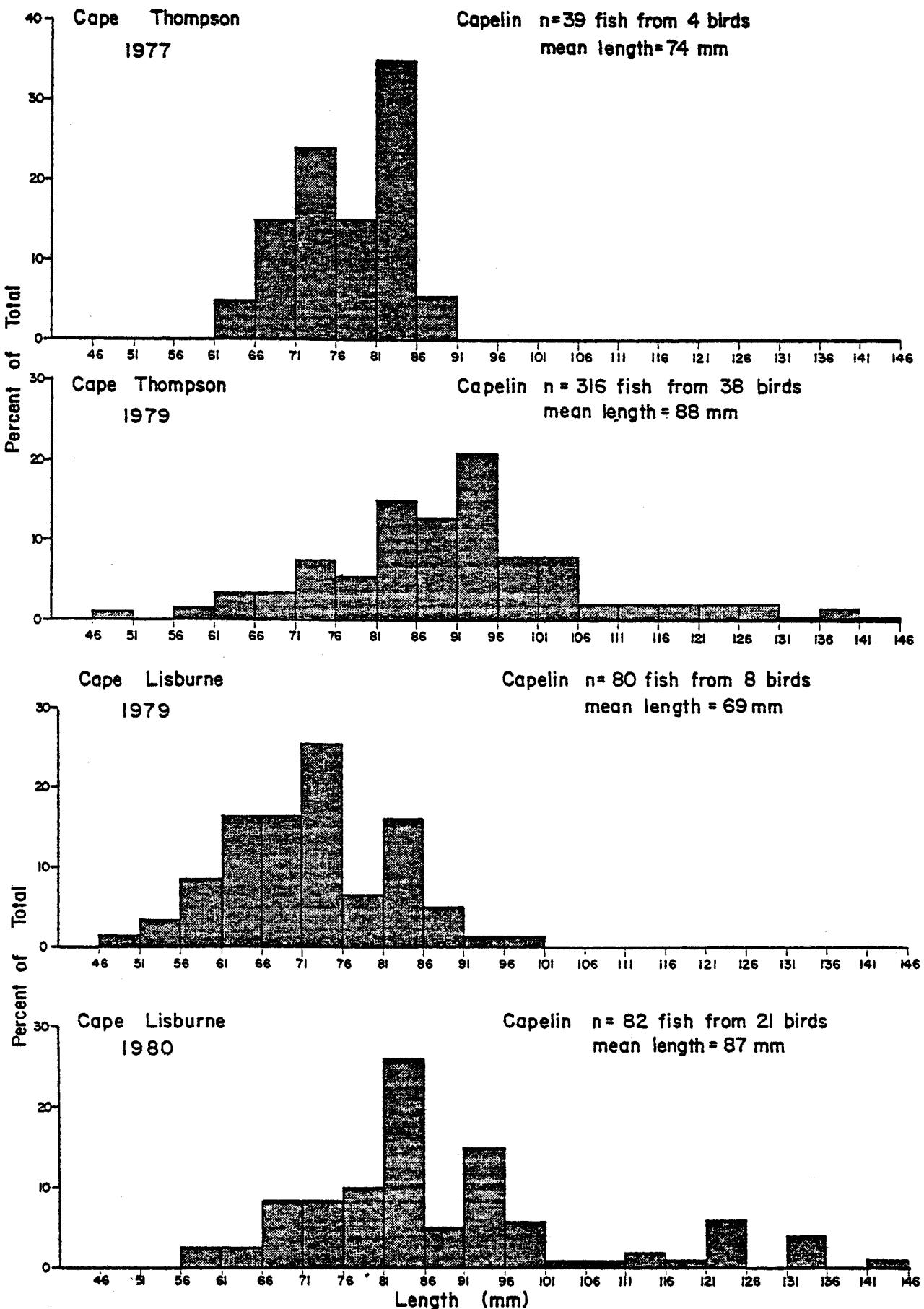


Figure 6. Sizes of capelin in diets of murres and kittiwakes at Cape Thompson and Cape Lisburne.

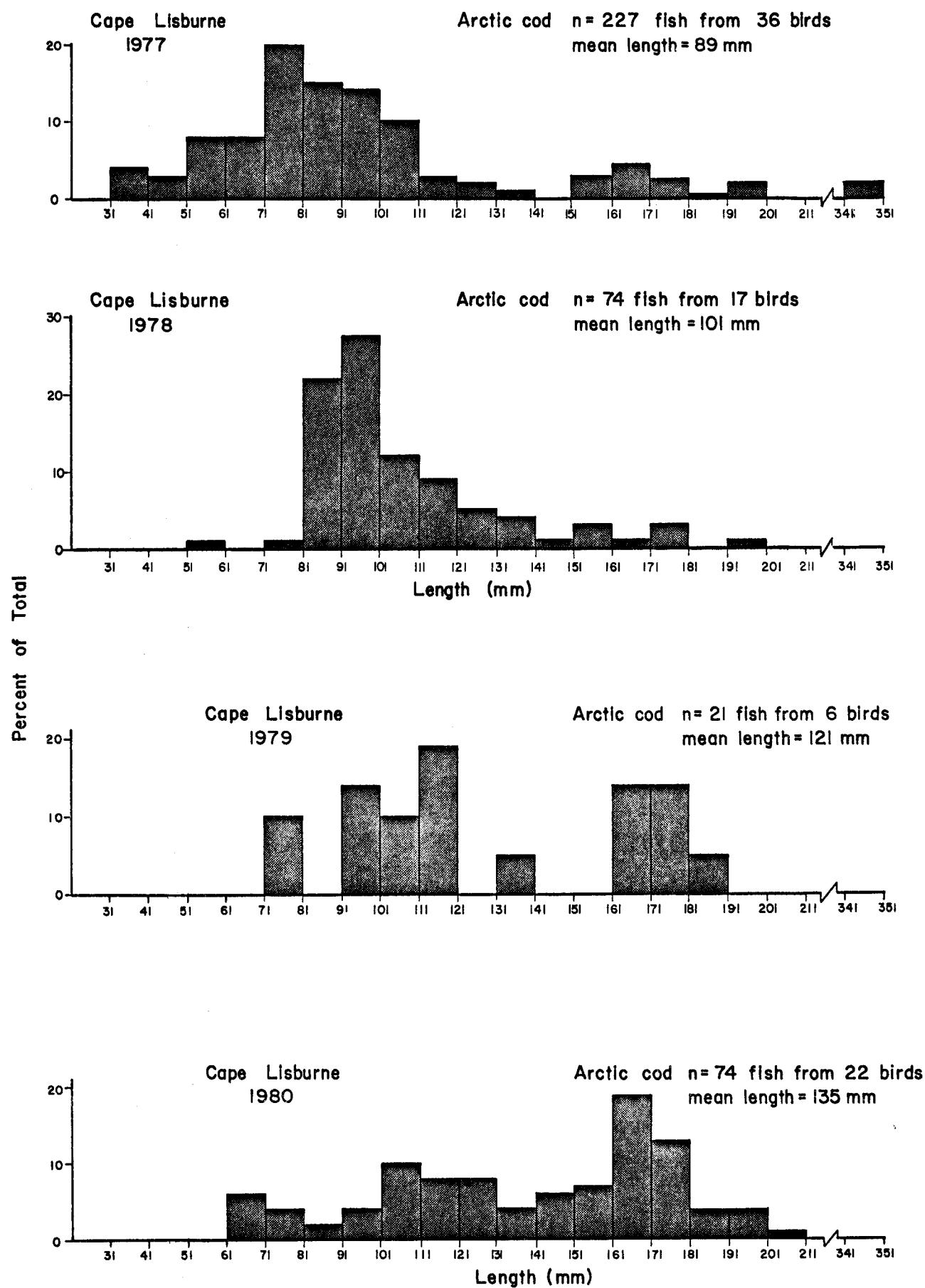


Figure 7. Sizes of Arctic cod in diets of murres and kittiwakes at Cape Lisburne.

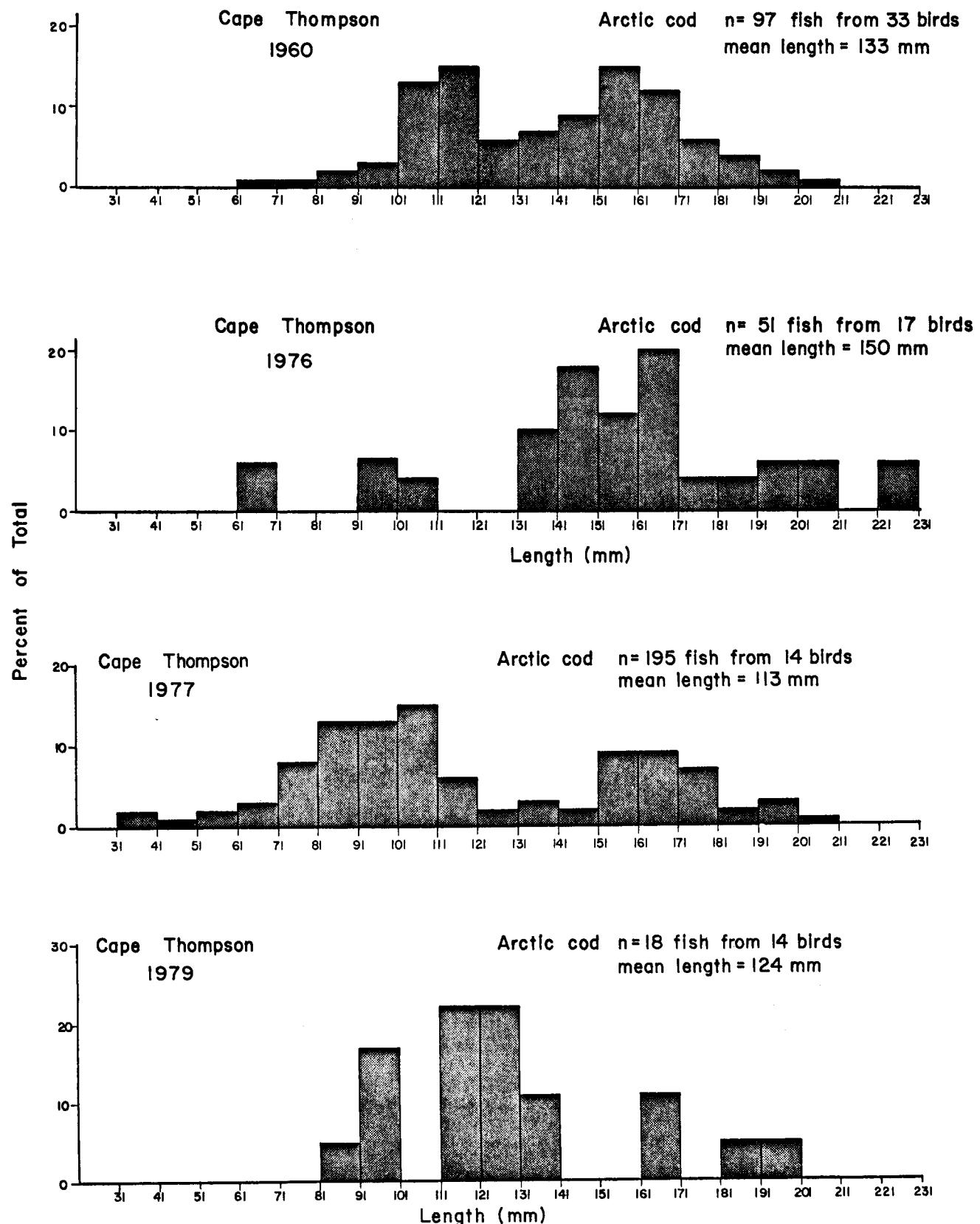


Figure 8. Sizes of Arctic cod in diets of murres and kittiwakes at Cape Thompson.

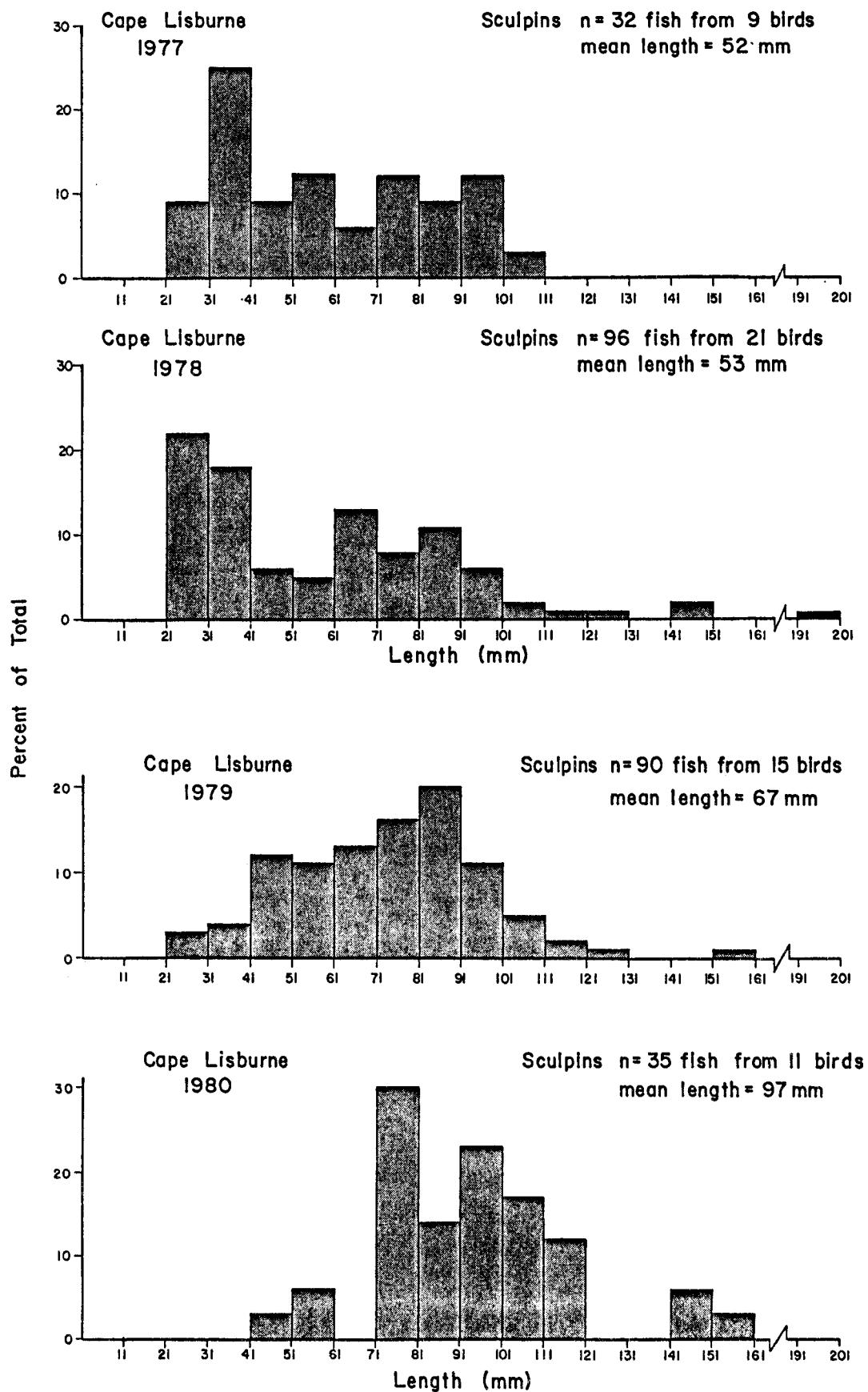


Figure 9. Sizes of sculpins in diets of murres and kittiwakes at Cape Lisburne.

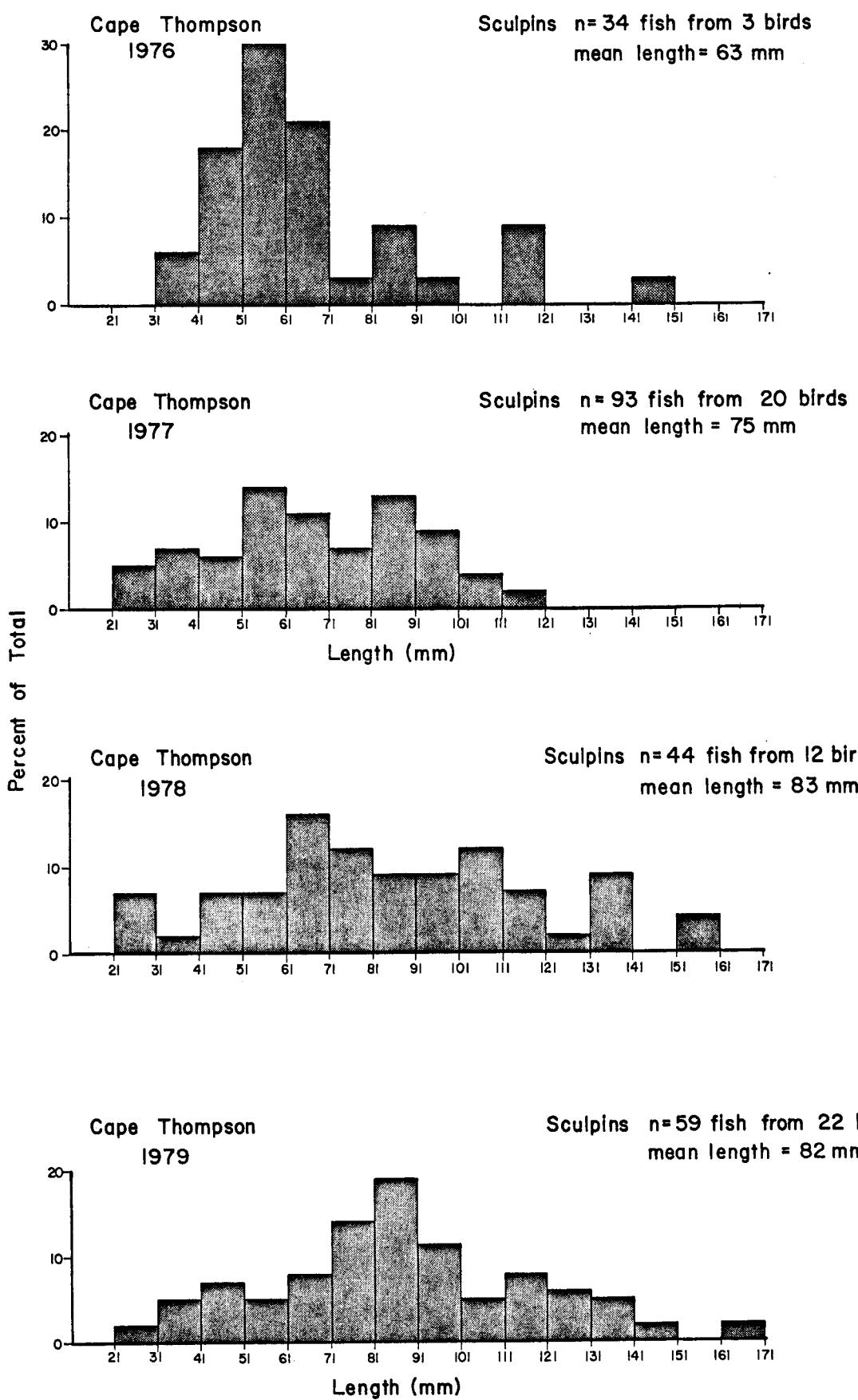


Figure 10. Sizes of sculpins in diets of murres and kittiwakes at Cape Thompson.

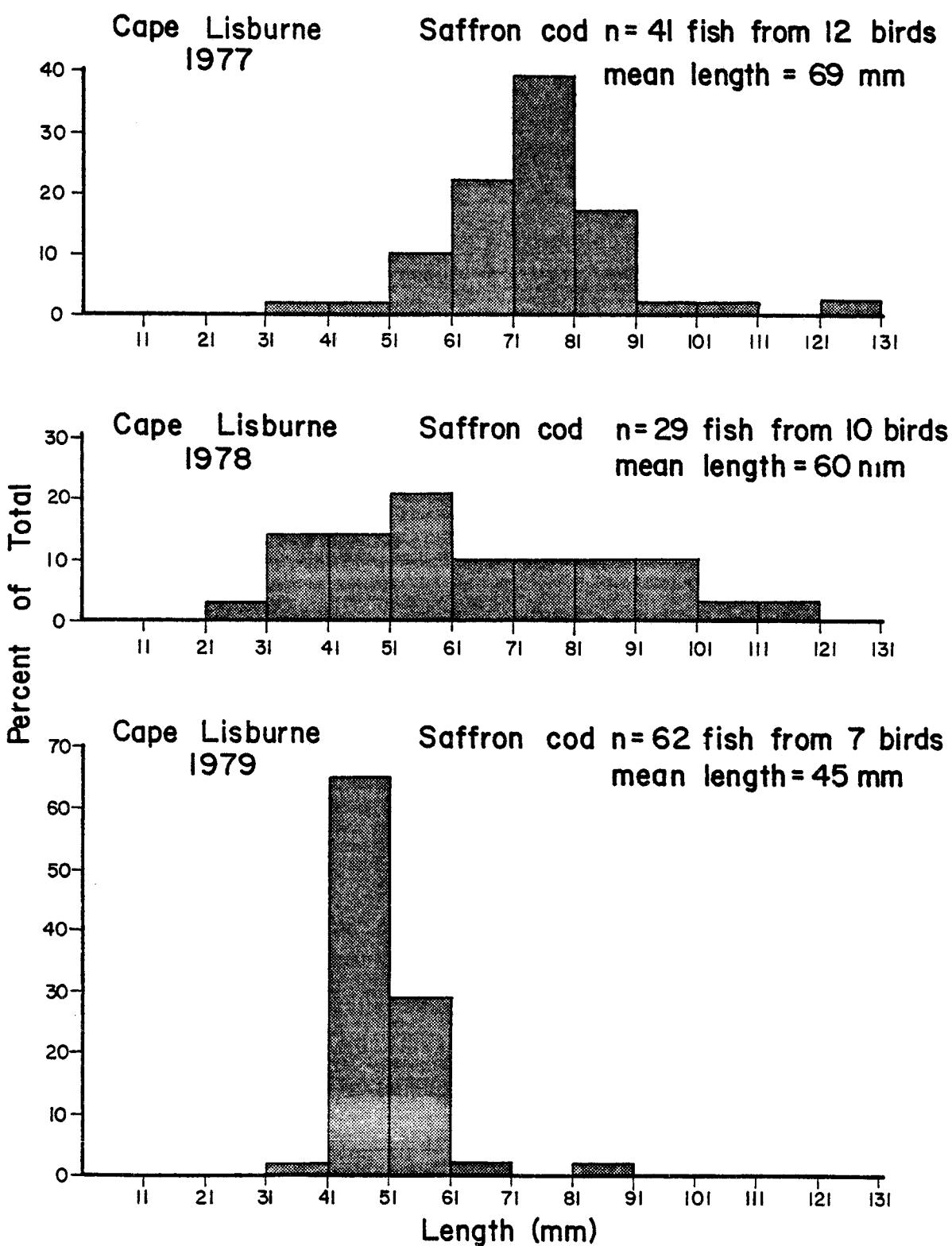


Figure 11. Sizes of saffron cod in diets of murres and kittiwakes at Cape Lisburne.

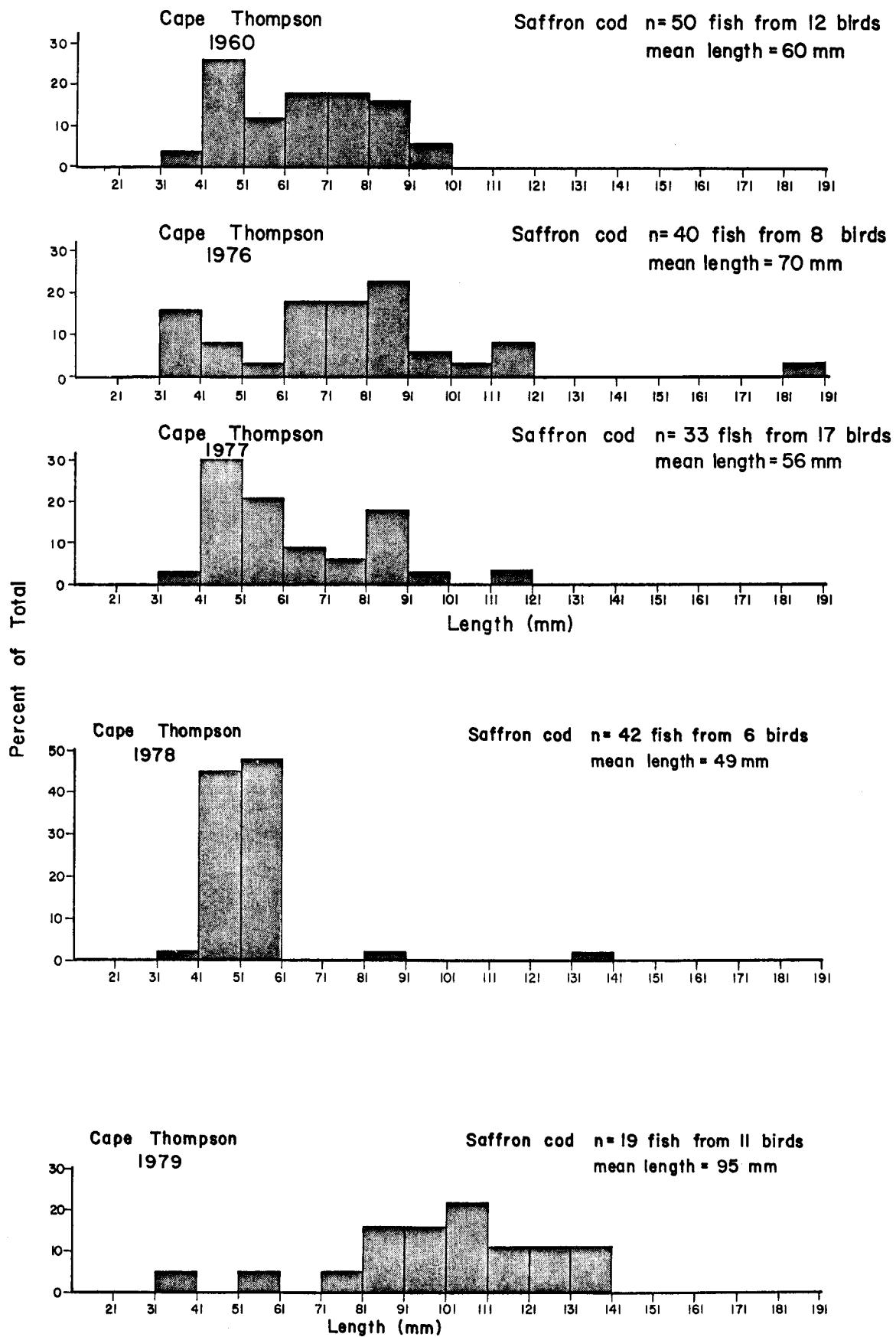


Figure 12. Sizes of saffron cod in diets of murres and kittiwakes at Cape Thompson.

761

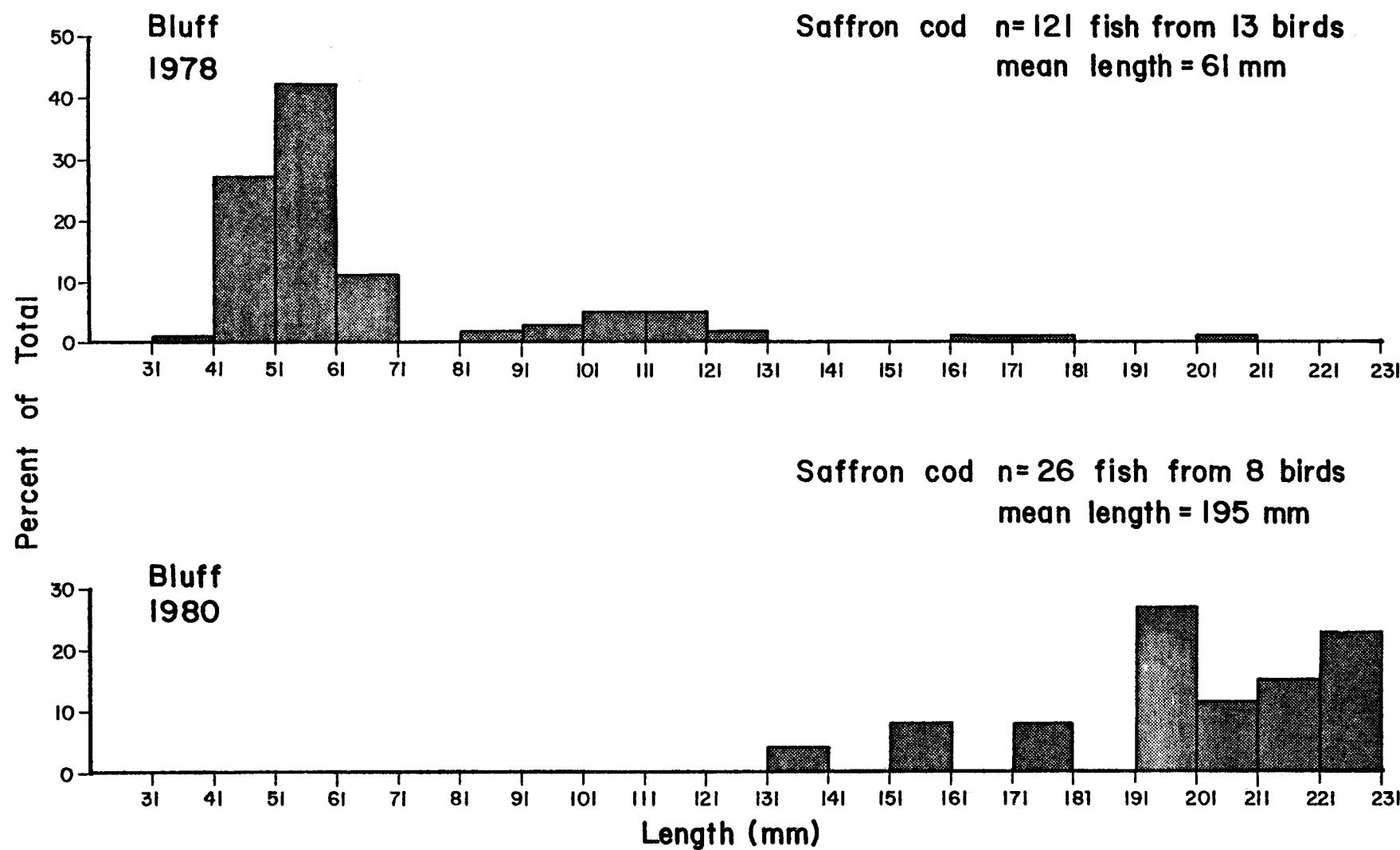


Figure 13. Sizes of saffron cod in diets of murres and kittiwakes at Bluff.

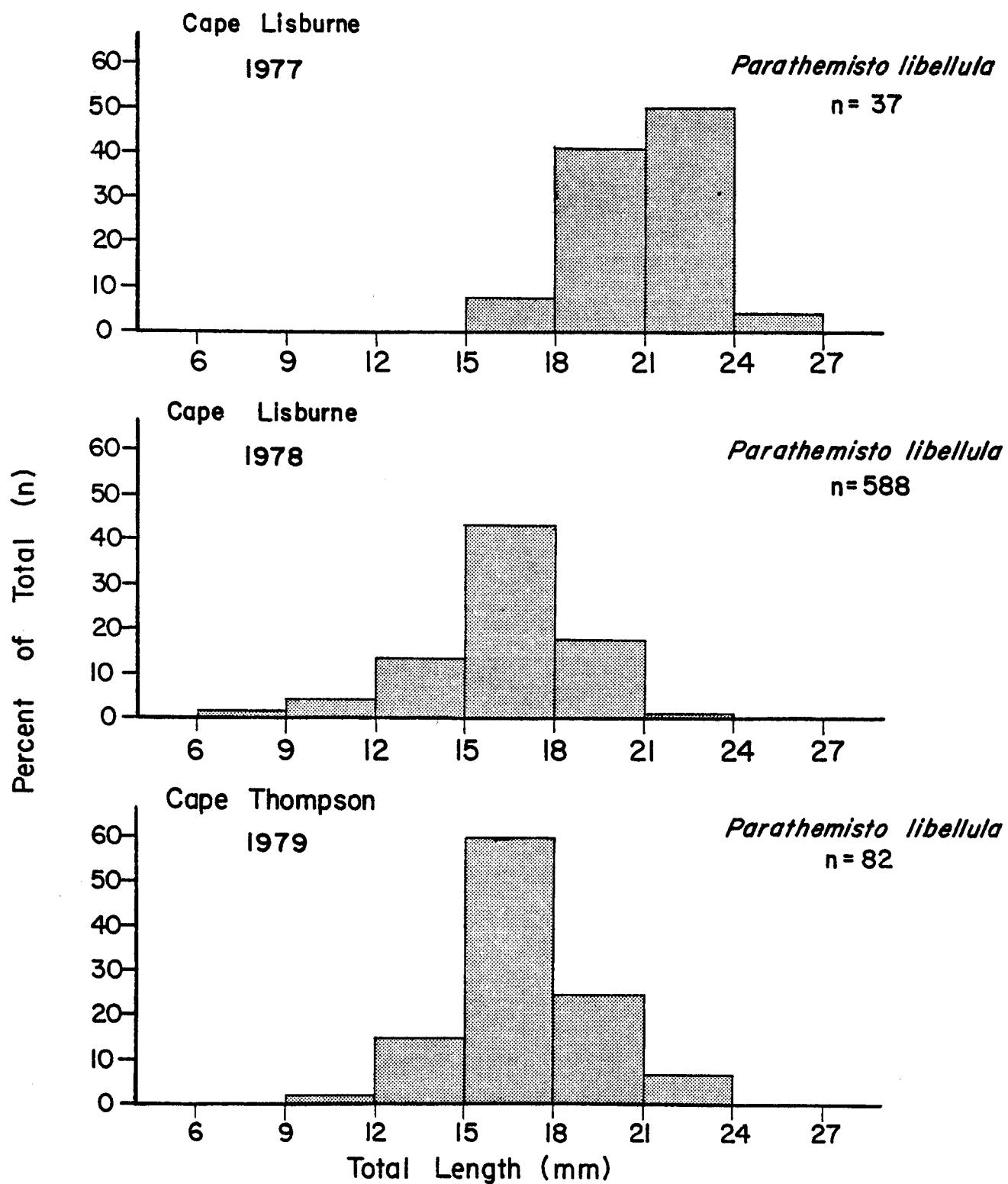


Figure 14. Sizes of *Parathemisto libellula* in diets of thick-billed murres at Cape Thompson and Cape Lisburne.

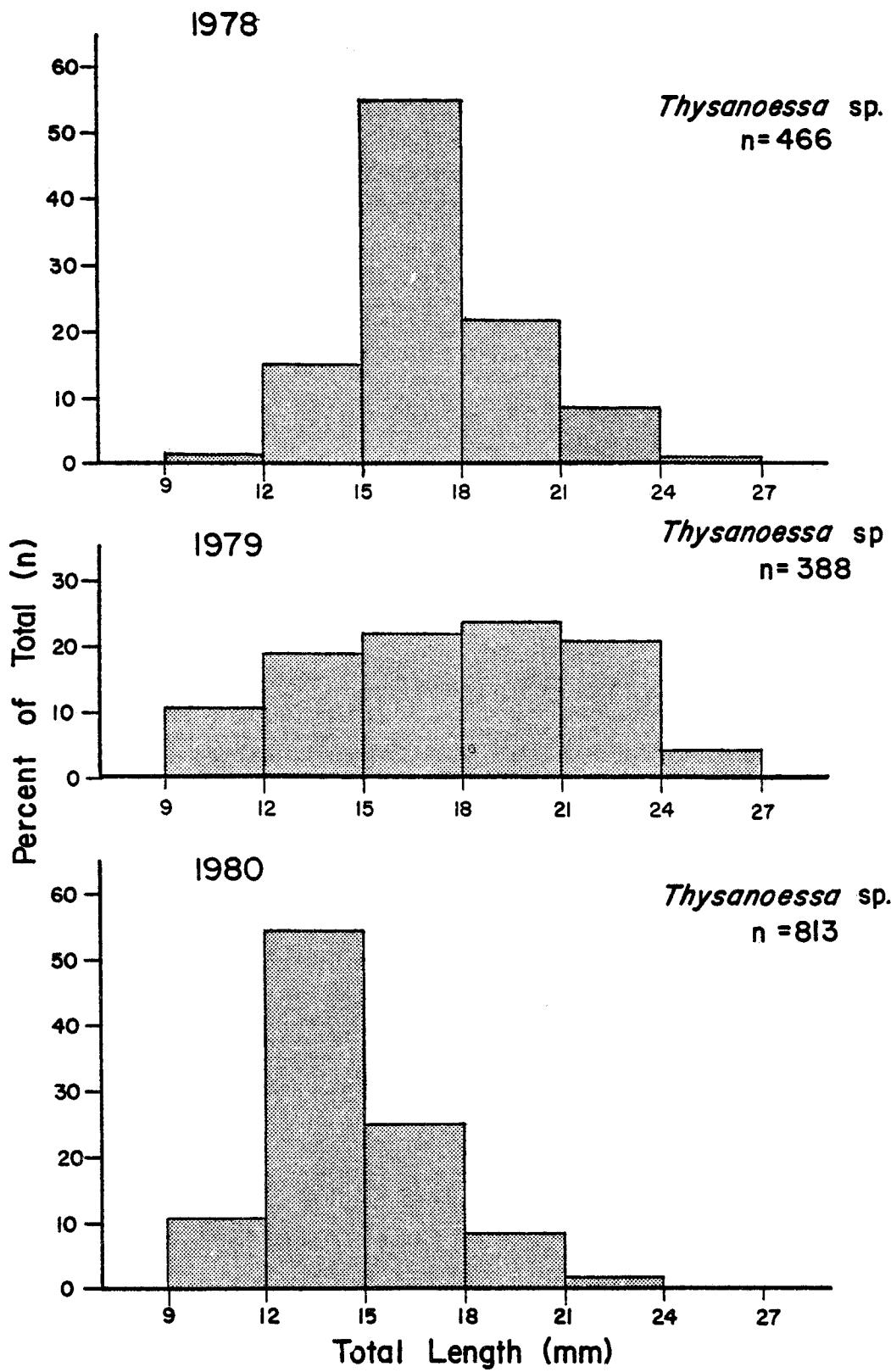


Figure 15. Sizes of *Thysanoessa* sp. in diets of murres and kittiwakes at Cape Lisburne.

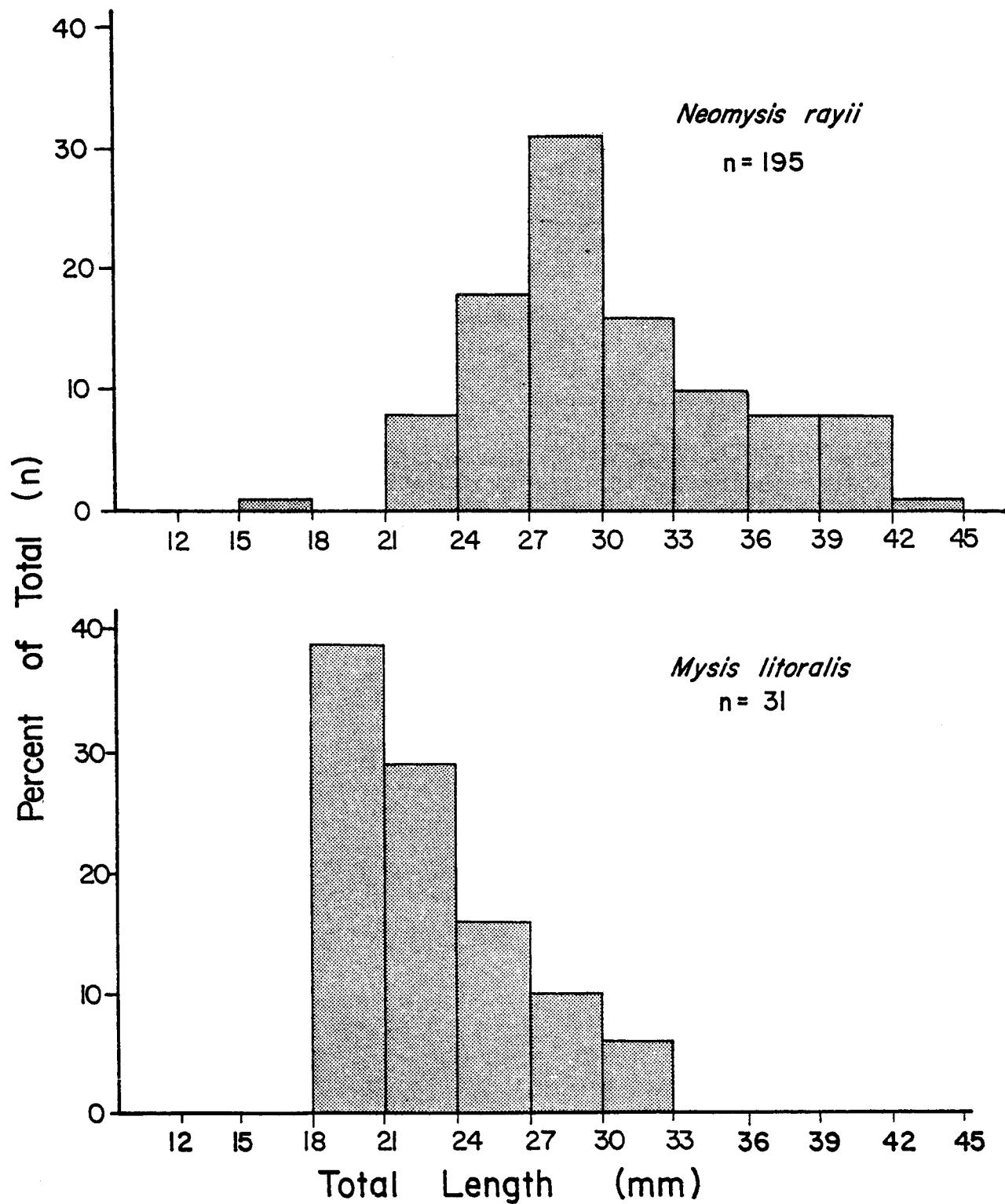


Figure 16. Sizes of mysids in diets of thick-billed murres at Cape Lisburne in 1978.

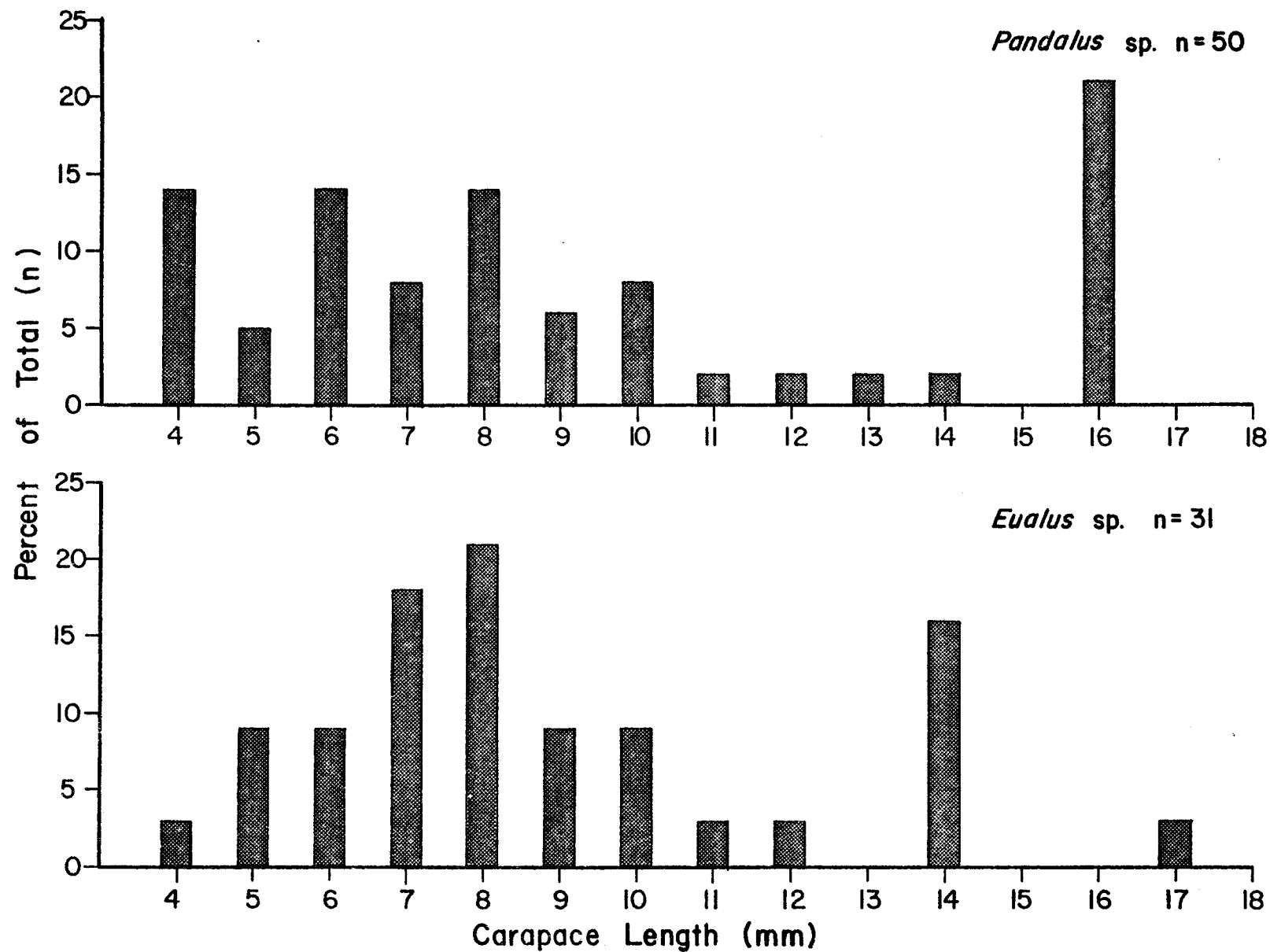


Figure 17. Sizes of shrimps in diets of murres and kittiwakes at Cape Thompson and Cape Lisburne, 1976-1978.

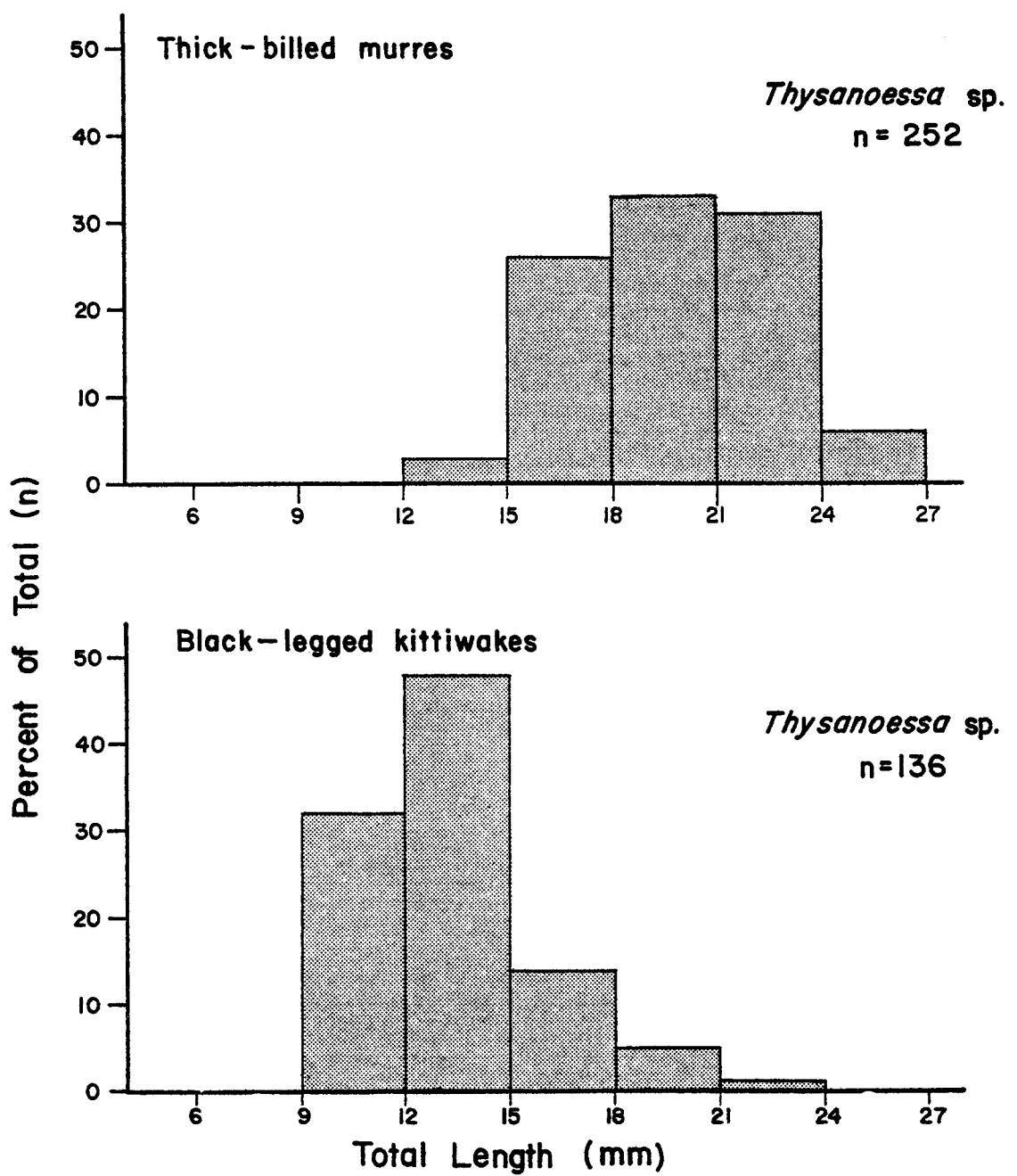


Figure 18. Sizes of *Thysanoessa* sp. in diets of murres and kittiwakes at Cape Lisburne in 1978.

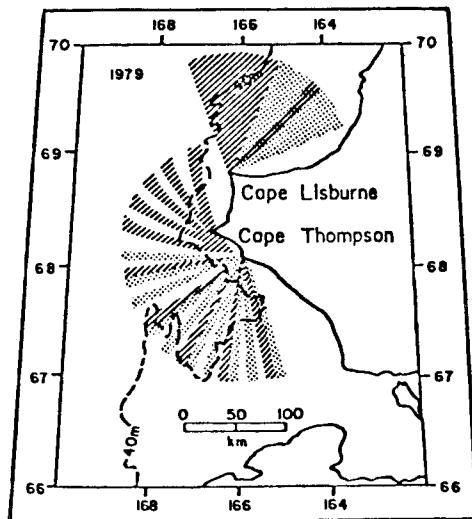
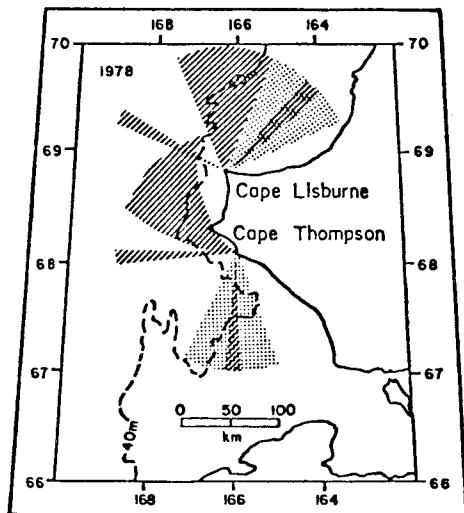
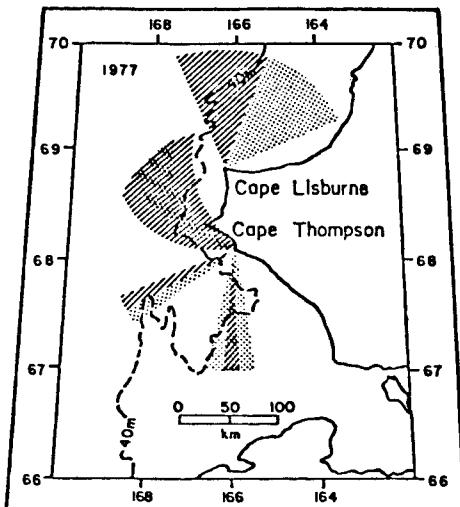
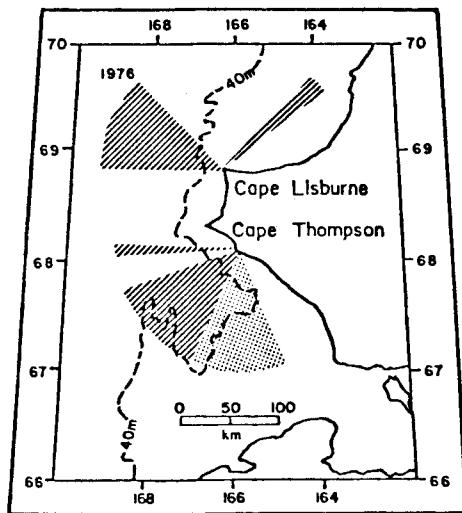


Figure 19. Directions taken by murres flying to and from foraging areas in the eastern Chukchi Sea. Stipple = July, bars = August.

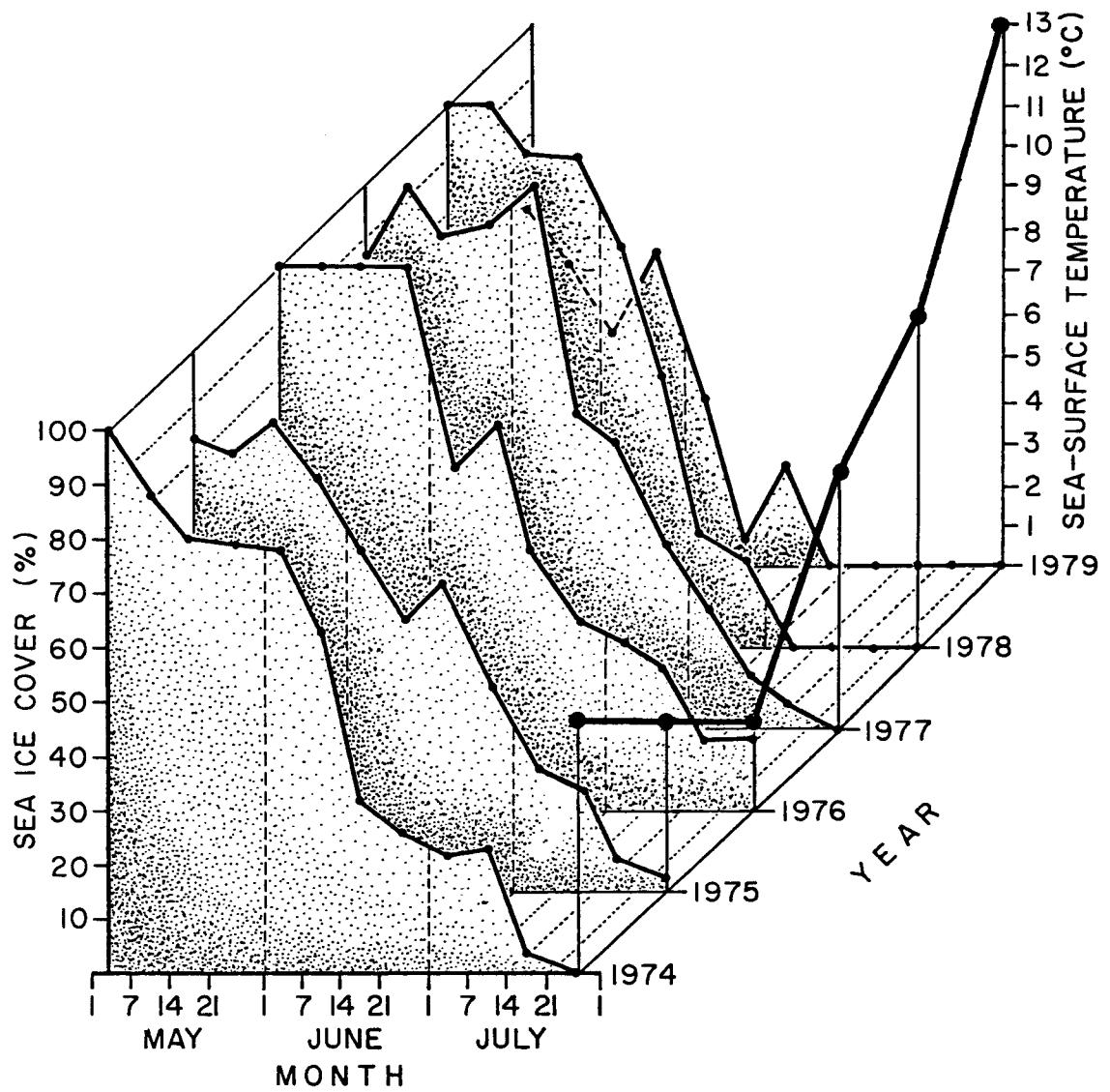


Figure 20. Sea ice cover over the northern Bering Sea and eastern Chukchi Sea, and sea-surface temperatures measured near Cape Lisburne (mean date = 16 July, $s = 3$ days).

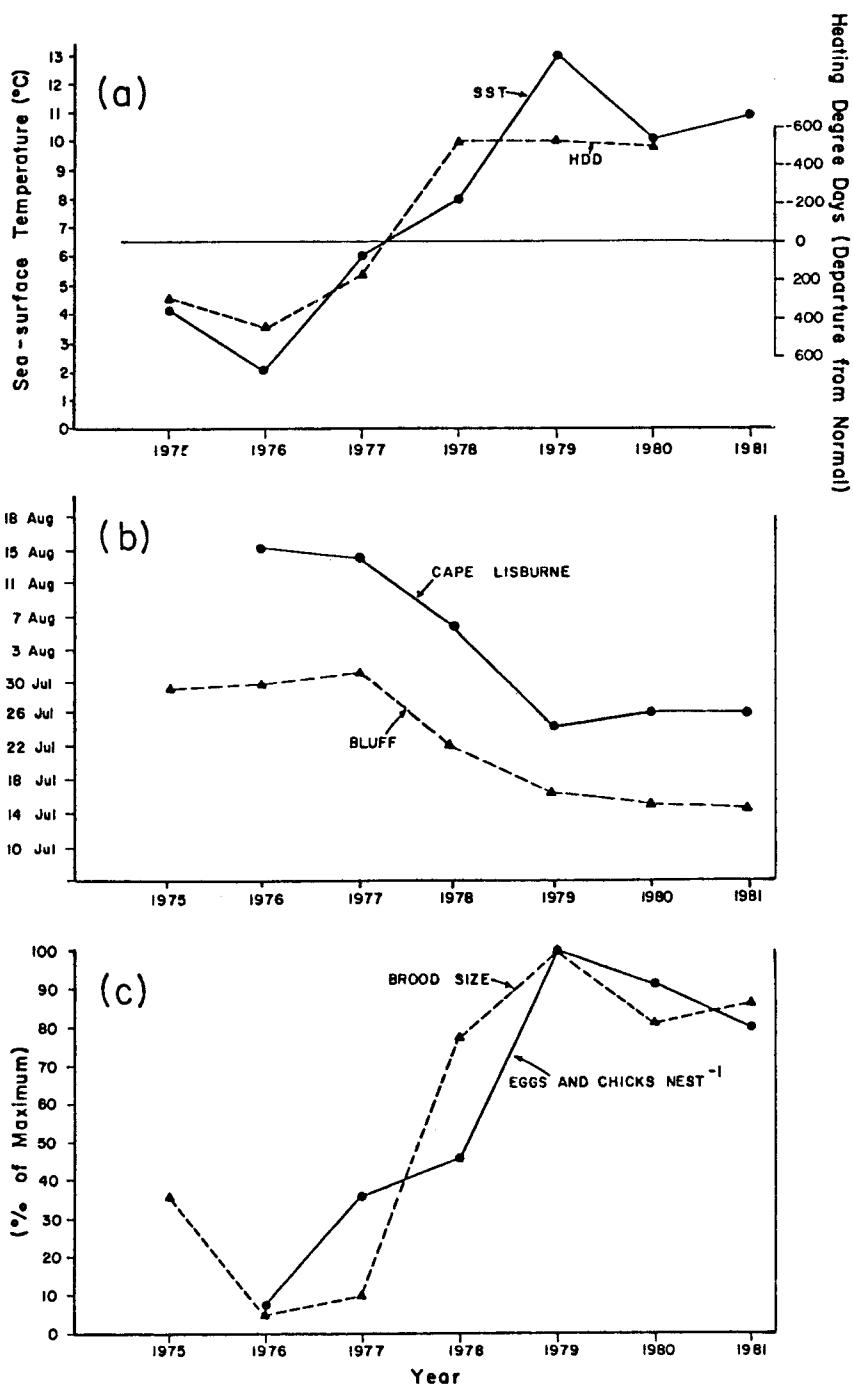


Figure 21. Relationships between environmental change, kittiwake nesting phenology and estimates of kittiwake reproductive success at Cape Lisburne and Bluff. (a) Sea-surface temperature near Cape Lisburne (mean date = 16 July, $s = 3$ days), and departure from normal heating degree days in April-July at Nome. (b) Mean date of hatch of kittiwake chicks. (c) Numbers of kittiwake eggs and chicks nest⁻¹ in first week of hatching at Cape Lisburne (as a percentage of maximum = 1.7 eggs and chicks nest⁻¹), and kittiwake brood size in the late chick period at Bluff (as a percentage of maximum = 1.03 chicks nest⁻¹). Data for 1980 and 1981 at Bluff are from the early chick period; data for 1975-1978 at Bluff are from Drury *et al.* 1981.

Vc. KITTIWAKES - METHODS

Field work was conducted at Cape Thompson in 1976-1979, at Cape Lisburne in 1976-1981, at Cape Lewis in 1977, 1979 and 1981, at Bluff in 1979-1981 and on St. Lawrence Island in 1981. The locations of these colonies are shown in Figure 1, section IV.

The length of time we spent in the field varied from year to year and from colony to colony, and was often of short duration. In most years we arrived before or during the time that kittiwake eggs were hatching and stayed until the chicks were nearly grown. Exceptions to this schedule were 1979 and 1980 at Bluff when we arrived about 5-6 days after the peak of hatching, 1981 at Bluff when we departed shortly after the completion of hatching, 1978 at Cape Thompson when we visited the colony before egg laying and again after the chicks were approximately half grown, 1976 at Cape Lisburne when we arrived mid-way through the chick period, and 1979 at Cape Lisburne when we were away from the colony for about two weeks during the chick period.

Kittiwakes were censused by counting the number of adults present on the cliffs during the late incubation or chick period. Counts were by 1's, and were made from a raft by one or two observers using binoculars. We took three complete censuses of kittiwakes at Bluff in 1979 and two each season in 1980 and 1981. At Cape Thompson we took a complete census once each season in 1976, 1977 and 1979, and a partial census in 1978. Cape Lewis was censused completely in 1977 and 1981, and half of the colony was censused in 1978. The only complete census of Cape Lisburne was taken in 1977, although partial counts of that colony were made in 1978, 1979 and 1981.

Active nests, those nests that showed evidence of attention during the current breeding season, were counted at Cape Thompson at Colony 4 in 1978, and at Colonies 2-5 in 1979. Kittiwakes do not nest on Colony 1. Nests were counted on about 80% of the plots at Cape Lisburne in 1977, on a subset of six plots in 1978 and 1979, and 10 plots in 1981. Complete counts of nests were made at Bluff in 1980 and 1981, but nests were not counted colony-wide in earlier years.

Kittiwake nests on study plots were mapped and visited at varying intervals during the summer to obtain data on clutch size, brood size and chick growth rates. Chicks were weighed on Pesola spring balances. Growth rates were calculated for each chick by determining the slope of the regression equation relating all of the respective weights taken between the first weighing and the highest weight recorded that was less than or equal to 300 g. A preliminary analysis indicated that growth rates of most chicks remained linear through 300 g (also see Coulson and White 1958, Maunder and Threlfall 1972).

A prolonged period of adverse weather and our field schedule at Cape Lisburne in 1979 precluded nest checks between the day hatching began and 22 days later when all but two chicks weighed well over 300 g. We computed daily growth rates for Cape Lisburne in 1979 by (1) assuming

that the egg hatched the day after it was found pipped (see Maunder and Threlfall 1972), (2) assigning a weight of 35 g (the average weight of newly hatched chicks) for hatching weight, and (3) computing the daily weight gain between the presumed hatching day and the day the chick was first measured about three weeks later. Our preliminary analyses and other accounts (e.g., Maunder and Threlfall 1972) suggest that daily weight gains typically decline soon after chicks reach 300-350 g; therefore the data on daily weight gains at Cape Lisburne in 1979 are minimum estimates and are not equivalent to those obtained in other locality-year samples.

Because we visited nests every several days, we frequently did not know the exact hatching date of particular chicks. In such instances we estimated the hatching date if the chick was weighed two or more times before attaining 300 g. Using the regression equation for daily growth rate, we calculated the date on which the chick would have weighed 35 g and used that value as the estimated hatching date for that chick. In some instances chicks were first weighed more than ten days later than the estimated hatching date, and we eliminated such individuals from the data base on hatching phenology. This method is unbiased if the growth rate is linear, or approximately so, between hatching and 300 g. Various studies (e.g., Coulson and White 1958, Maunder and Threlfall 1972) indicate that the growth rate of kittiwakes is linear from the time of hatching until about three weeks of age.

Before statistically analyzing the data on hatching phenology and growth rates of chicks we examined frequency distributions of each variable for each locality-year sample. In several cases, frequency distributions of hatching phenology and growth rates were skewed and/or kurtotic. Consequently we analyzed these variables nonparametrically, using the Kruskal-Wallis Test. We subsequently followed the Multiple Comparisons Procedure outlined by Conover (1980) to make pairwise comparisons among the samples.

We measured the length and maximum breadth of eggs at Cape Thompson in 1977 and 1979 and at Cape Lisburne and Bluff in 1981. We calculated egg volumes using the formula $0.4866 \times \text{length} \times \text{breadth}^2$ (see Coulson 1963). Coulson (1963) showed that the volume of eggs varies with respect to clutch size and position in the laying sequence. In Coulson's study volumes of eggs in one-egg clutches and the second egg in two-egg clutches were equivalent and about four percent smaller than the first egg in two-egg clutches. Since we typically first visited colonies after the completion of egg laying, we usually were unable to determine the laying sequence in multiple-egg clutches. Consequently we compared locality-year samples grouping the data by clutch size only and not by position in the laying sequence.

VIc. KITTIWAKES -- RESULTS

Summaries of the kittiwake censuses, including counts of kittiwakes at Bluff in 1975-1978 (see Drury *et al.* 1981), are shown in Table 1. Beginning in 1978 at Cape Lisburne and Cape Thompson, and in 1979 at Bluff, kittiwake numbers began to increase over previous years and

remained higher at least through 1979 at Cape Thompson and through 1981 at Bluff and Cape Lisburne. A similar change occurred at Cape Lewis.

The number of nests at Cape Thompson in 1979 was similar to the number reported by Swartz (1966) for 1960 and 1961, although there were large discrepancies among the four colonies where kittiwakes nest (Table 2). The number of nests at Colony 4 in 1978 was nearly 50% lower than in the other three years of study; however, this difference may not have been representative of Cape Thompson as a whole. Nests on two plots at Colony 2 were also counted in 1978 and the total, 829, was only 5% lower than the total of 870 counted on the same plots in 1979. From counts of selected census plots at Cape Lisburne, we estimated that nests numbered about 14,000 in 1977, 14,500 in 1978, 14,400 in 1979 and 13,300 in 1981. Numbers of active nests on three study plots where nest contents were monitored were 79, 76, 75 and 71 in 1978-1981, respectively. These counts and our estimates of total nests indicate little variation in the numbers of kittiwake nests among years at Cape Lisburne. At Bluff, the numbers of nests, as well as the numbers of individuals, were nearly the same in 1980 and 1981, about 8,500 and 8,300, respectively.

Replicate counts of kittiwakes on three census plots at Colony 4 at Cape Thompson in 1976 demonstrated great daily variation in attendance of adult birds. Totals of 467, 75 and 734 adults were counted at 1845 h (Bering Daylight Time) on 9 August, 1750 h on 14 August and 1835 h on 15 August, respectively. Searing (1977) reported that kittiwake numbers also varied considerably between days on St. Lawrence Island in 1976, and Drury *et al.* (1981) reported similarly erratic attendance patterns the same year at Bluff. In 1979 at Bluff, we counted kittiwakes on five areas at the same times on several days (Figure 1). Day-to-day variation in numbers was slight; overall, numbers in mid-afternoon fluctuated between 110% and 124% of the number of nests during the 17-day period.

Mean hatching dates of the chicks we weighed for growth rates are shown in Figure 2. Significance relationships among colonies and years are presented in Table 3. Three trends are apparent from these data: (1) hatching dates were progressively earlier from 1976-1977 through 1979, after which time they stabilized, (2) hatching dates within years were progressively earlier with decreasing latitude and (3) hatching synchrony among nests tended to be higher in later years than in earlier years.

As hatching dates, and thus laying dates, became earlier each year, egg production by laying females increased (Table 4). These data are not strictly comparable between years and colonies since we generally arrived relatively late in the breeding season and an unknown number of eggs probably had already been lost (see Swartz 1966). Still, they indicate the magnitude of change in clutch size that occurred between 1976 and 1979.

Table 4 also lists clutch sizes of black-legged kittiwakes on the Pribilof Islands (St. Paul Island and St. George Island) obtained by Hunt *et al.* (1981) in 1975-1979. Egg production on the Pribilof Islands was much more constant among years, never falling as low or rising as high as

production in the northern colonies. Such a pattern is consistent with the uniform laying and hatching dates on the Pribilof Islands, which varied less than a week in the years 1975-1979 (Hunt *et al.* 1981).

The number of nests that contained eggs at the northern colonies also increased after 1976 (Figure 3). That increase and larger clutch sizes led to much improved levels of productivity by 1979 (Figure 4). Many kittiwakes also laid large clutches in 1980 and 1981, but a higher incidence of chick death in those years resulted in low levels of reproductive success compared to 1979. Hunt *et al.* (1981) reported that productivity of black-legged kittiwakes (expressed as the ratio of chicks fledged to nesting attempts) fluctuated between 0.36 and 0.54 on St. Paul Island in 1975-1979 and between 0.22 and 0.62 on St. George Island in 1976-1978. Like phenological dates and clutch sizes, productivity on the Pribilof Islands was much more stable than in the northern colonies and was about midway between the lowest and highest levels we observed (see Figure 4).

Growth rates of kittiwake chicks were generally high, except in 1977 at Cape Thompson and in 1981 at Bluff and Cape Lisburne (Table 5). Growth rates at Cape Lisburne in 1980 were lower than in 1977, but higher than in 1981. Significance relationships of chick growth rates among all colonies and years are shown in Table 3.

As a group, growth rates of kittiwake chicks in northern Alaska were much higher than rates reported elsewhere. Hunt *et al.* (1981) reported growth rates ranging between 11.5 ± 2.6 g day $^{-1}$ ($n = 24$) and 16.6 ± 2.9 g day $^{-1}$ ($n = 14$) for black-legged kittiwake chicks on the Pribilof Islands in 1975-1979. Growth rates of kittiwake chicks in Newfoundland were about 13-15 g day $^{-1}$ (Maunder and Threlfall 1972). Coulson and White (1958) reported that growth rates of kittiwake chicks at a colony in England averaged 15.64 g day $^{-1}$ (range 15.07 g day $^{-1}$ - 16.21 g day $^{-1}$) in 1954-1957. Kittiwake chicks on the Farne Islands gained about 15 g day $^{-1}$ (Pearson 1968) and chicks on the east Murman coast in northern Russia gained about 12 g day $^{-1}$ (Belopolski 1957).

Table 6 lists mean volumes of kittiwake eggs measured at Bluff, Cape Thompson and Cape Lisburne. The mean value of all categories, 48.7 mm 3 , is larger than volumes of eggs laid by kittiwakes at the same latitudes in the North Atlantic Ocean (see Runde and Barrett 1981). Eggs in two-egg clutches were larger than eggs in one egg clutches in 1977 and 1981 and the difference was significant in 1977 ($t = 2.95$, $P < 0.05$). Eggs in one-egg clutches were significantly larger ($t = 2.04$, $P < 0.05$) at Cape Thompson in 1979 than in 1977.

VIIc. KITTIWAKES - DISCUSSION

The consistent pattern of change in elements of the breeding biology of black-legged kittiwakes at colonies in northern Alaska suggests that birds nesting in a large geographic area were similarly affected by a change or changes in the environment. Indeed, a close association between variation in the physical environment and estimates of kittiwake breeding phenology and productivity is apparent in Figure 5. Belopolski (1957)

described similar relationships between kittiwake reproductive success and breeding phenology and environmental change in the Barents Sea. He also said that changes in kittiwake food availability, which were associated with regional changes in water temperature, accounted for the annual differences he saw in the breeding biology of the birds.

The importance of food availability to the timing of breeding seasons and levels of reproductive success has been reviewed by Perrins (1970) for several species of terrestrial and marine birds. The pattern of change we saw in the breeding biology of kittiwakes in northern Alaska during recent years suggests that annual change in food availability was the ultimate factor affecting kittiwake breeding phenology and reproductive success.

Food habits studies of thick-billed murres, common murres and black-legged kittiwakes at Cape Thompson and Cape Lisburne revealed important annual and seasonal differences in foods used by all three species between 1976 and 1980 (see sections V. b. - VII. b.). In general, fish biomass was low in 1976 but rose steadily during later years, largely as a result of increased stocks of sand lance in particular, and capelin to a lesser extent. Changes in food availability were associated with the warming trend shown in Figure 5. Adult murres and kittiwakes ate more sand lance earlier each year between 1977 and 1979. Sand lance were apparently unavailable to kittiwakes throughout 1976. Less is known about the food habits of kittiwakes at Bluff or St. Lawrence Island, but sand lance are also important at these colonies (Drury *et al.* 1981, Springer *et al.* unpubl. data).

Early laying dates and apparently high levels of egg production by kittiwakes in 1980 and 1981, but greater chick mortality and slower growth rates than in 1979, indicate a failure of the food supply mid-way through both breeding seasons. In 1980 at Cape Lisburne, kittiwake chick diets, on a wet weight basis, consisted of about 31% sand lance, 20% capelin, 20% cod and sculpins, 28% euphausiids, and 1% other fish and invertebrates (Springer *et al.* unpubl. data). Sand lance was essentially the only food given to kittiwake chicks in all earlier years when chick mortality was relatively low and growth rates were high.

The importance of sand lance to kittiwake chick growth is also apparent from our observations in 1977. In that year chicks hatched earlier at Cape Thompson than at Cape Lisburne; however, sand lance schools arrived earlier at Cape Lisburne, at about the same time that the chicks hatched. They did not arrive in large numbers at Cape Thompson until about 10-14 days after chicks hatched there. The abnormally low rate of growth at Cape Thompson in 1977 was probably due to the lack of sand lance, or suitable alternative, until well after the chicks had hatched.

Arctic cod also contribute significantly to the diet of kittiwakes in the eastern Chukchi Sea. However, Arctic cod are demersal fish and are probably never as abundant, relative to the kittiwake's ability to catch them, as are sand lance and capelin, which form dense schools near the surface. Therefore, the contribution of sand lance and capelin to

exploitable fish biomass may be the necessary ingredient for kittiwakes to enjoy successful reproductive seasons in northern Alaska.

The differences in annual trends of breeding phenology and reproductive success between northern kittiwake populations and those that breed on the Pribilof Islands--variable versus stable--can probably be explained by the different food webs that support kittiwakes in the two regions. The Pribilof Islands lie in the open ocean in relatively deep water near the continental shelf break. Kittiwakes on the Pribilof Islands depend on walleye pollock (Hunt *et al.* 1981), the dominant fish species in the stable pelagic food web of the outer shelf zone of the southeastern Bering Sea (Iverson *et al.* 1979). Relatively stable prey populations should result in uniform dates of breeding activities, levels of reproductive success and chick growth rates. Neither growth rates nor reproductive success would be particularly high because pollock, like Arctic cod, are generally found in water deeper than kittiwakes can exploit, and occur in less consolidated schools than do sand lance and capelin. Thus, while providing a uniform level of energy, this level is probably seldom, if ever, as high as at colonies where sand lance and capelin occur in large numbers.

Although we still lack many details concerning the relationships of kittiwakes to their food webs in northern Alaska, it is clear that available fish biomass varies considerably between years, probably in response to changing climatic conditions which affect the regional marine environment. Kittiwake productivity consequently fluctuates between very low and very high levels, but over the long-term, numbers of chicks produced per breeding pair are probably similar to numbers produced at more stable colonies such as those on the Pribilof Islands. In the years 1976-1979, 100 pairs of kittiwakes on the Pribilof Islands would have produced about 185 chicks. One hundred pairs of kittiwakes would have produced about 204 chicks at Bluff, 218 chicks at Cape Thompson and 246 chicks at Cape Lisburne during the same interval. These higher overall levels of productivity would tend to offset the counter effect of fewer breeding attempts in years when reproductive success was low, and result in levels of production for the northern populations that would be about the same as for the Pribilof Islands population. Therefore northern kittiwake populations are probably maintaining themselves without relying on immigration of birds from outside of the region.

Because natural variation in reproductive success is high in kittiwake populations in northern Alaska, additional effects of resource development could be devastating. In Peru, the combination of El Nino events and commercial fishing led to a decline in the number of guano birds from 28 million to about 5 million during the 1950's and 1960's (Shaeffer 1970). The effects of commercial fishing in Alaska may already threaten certain seabird populations (see sections V. a - VII. a.). Since stocks of the more commercially valuable fishes worldwide are already heavily fished, further increases in catches will depend on the development of fisheries that target less preferred species (Gulland 1978). Capelin and sand lance are both receiving greater attention in Alaska as possibilities for expansion of the State's commercial fishing industry (Warner 1981, R. Wolotire pers. comm.). Increased interest in

these species is a cause for concern for the maintenance of trophic systems that may be critical to the success of kittiwake populations in northern Alaska.

Vd. OTHER SPECIES - METHODS

In addition to murres and black-legged kittiwakes, pelagic cormorants (*Phalacrocorax pelagicus*), glaucous gulls (*Larus hyperboreus*), black guillemots (*Cephus grylle*), pigeon guillemots (*C. columba*), horned puffins (*Fratercula corniculata*), and tufted puffins (*Lunda cirrhata*) breed at colonies in the eastern Chukchi Sea. Numbers of all of these species were small by comparison to numbers of murres and black-legged kittiwakes, and nest sites of those that bred were generally inaccessible. For these reasons, and because we saw little change in their numbers or reproductive success at Cape Thompson in 1976-1979 compared to observations made by Swartz (1966), we devoted relatively little time to them.

We censused all six breeding species in at least one year at Cape Thompson and we recorded information on reproductive success of cormorants and gulls in one or more years at Cape Thompson and Cape Lisburne. We made numerous observations-of-opportunity throughout the study. Selected data are compared to similar data reported by Swartz (1966), who made more thorough studies of most of these species at Cape Thompson in 1960. Summary information is presented in following discussions, and additional information and details are presented in previous annual reports.

Eiders (*Somateria spectabilis* and *S. mollissima*) were also common throughout the summer in Ledyard Bay, especially as they passed by Cape Lisburne during migration. We have included observations of these waterfowl because the region appears to be important to them, particularly in August as they move south out of arctic nesting areas.

VId. - VIIId. OTHER SPECIES - RESULTS AND DISCUSSION

Pelagic Cormorants

Numbers of pelagic cormorants at Cape Thompson have been variable. Numbers have fluctuated between years, especially at Colony 1 and Colony 2, but show no consistent trend (Table 1). The greatest change occurred at Colony 2. The marked difference in nesting pairs between 1959 and 1960 may have been due, in part, to less survey effort. Surveys for species other than murres and kittiwakes were less complete in 1959 than in 1960 or 1961 (Swartz, pers. comm.).

In 1960 and 1961, most of the cormorants at Colony 2 nested at one location (Swartz unpubl. data). Most of that section of cliff had sheared off since the time of Swartz's (1966) study, and the loss of that nesting area may account for much of the difference between 1959-1961 and 1976-1978.

Whereas the total number of nesting pairs of cormorants varied from 11 to 18 in 1976-1978, productivity remained relatively stable. Ten nests contained 2.2 large chicks nest⁻¹ on 16 August 1976, and 11 nests

TABLE 1. Black-legged kittiwake census summaries for colonies in northern Alaska, 1975-1981.

Colony	1975	1976	1977	1978	1979	1980	1981
Bluff ^a	7,250	7,000	7,400	6,600 ^c	9,000	9,900	10,700
Cape Thompson	ND ^b	10,500	10,200	15,200 ^d	16,800	ND	ND
Cape Lewis	ND	ND	2,300	5,800 ^d	ND	ND	5,200
Cape Lisburne	ND	ND	14,700	15,400 ^e	17,300 ^e	ND	16,300 ^e

^aData for 1975-1976 are from Steele and Drury (1977); data for 1977 are from Biderman *et al.* (1978); data for 1978 are from Ramsdell and Drury (1979).

^bND = no data.

^cEstimate derived from the count of Colony 4 only. The value is the mean ($S=1900$) of three estimates of the 1978 colony total. The estimates were derived by using each of the other three years as bases for extrapolating the colony total from counts at Colony 4 in 1978.

^dEstimate derived from a count of 50% of the census plots. The value is the mean ($S=380$) of two estimates of the 1978 colony total. The estimates were derived by using each of the other two years as bases for extrapolating the colony total from partial counts in 1978.

^eEstimate derived from counts of selected census plots within the colony.

TABLE 2. Black-legged kittiwake nest count summaries at Cape Thompson, Alaska.

Colony	1960	1961	1978	1979
1	0	0 ²	0	0
2	5,200	ND ²	ND	4,600
3	2,600	ND	ND	3,700
4	3,100	3,000	1,600	2,800
5	3,200	ND	ND	2,500
Total	14,100			13,500

¹Data from 1960 and 1961 are from Swartz (1966).

²ND = no data.

TABLE 3. Results of Multiple Comparison Procedure (Conover 1980) comparing growth rates (lower left) and hatching phenology (upper right). Significant differences between sample means ($P < 0.05$) indicated by +; no significant difference indicated by 0.

		Bluff				Cape Thompson		Cape Lisburne				St. Law. I.	
		1978	1979	1980	1981	1977	1979	1977	1978	1979	1980	1981	1981
Bluff	1978		+	+	+	+	+	+	+	0	+	+	0
	1979	0		0	0	+	+	+	+	+	+	+	+
	1980	0	+		0	+	+	+	+	+	+	+	+
	1981	+	+	0		+	+	+	+	+	+	+	+
Cape Thompson	1977	+	+	+	+		+	+	0	+	+	+	+
	1979	+	0	+	+	+		+	+	+	+	+	+
Cape Lisburne	1977	0	0	+	+	+	0		+	+	+	+	+
	1978	0	0	+	+	+	0	0		+	+	+	+
	1979	0	0	0	+	+	0	0	0		+	+	0
	1980	0	+	0	+	+	+	+	0	0		0	+
	1981	+	+	+	0	0	+	+	+	+	+		+
St. Lawrence I.	1981	0	0	0	+	+	0	0	0	0	0	+	

TABLE 4. Black-legged kittiwake clutch size per completed clutch at colonies in northern Alaska.

Colony	Year								
	1960	1961	1975	1976	1977	1978	1979	1980	1981
St. Lawrence I. ²	-	-	-	1.0	-	-	-	-	1.61
Bluff ³			1.22	1.11	1.08	1.56	1.45	1.45	1.72
Cape Thompson ⁴	1.92	1.88	-	1.12	1.18	-	1.58	-	-
Cape Lewis	-	-	-	-	1.17	-	1.64	-	-
Cape Lisburne	-	-	-	1.0	1.14	1.23	1.80	1.61	1.67
St. Paul I. ⁵	-	-	1.42	1.49	1.52	1.33	1.47	-	-
St. George I. ⁵	-	-	-	1.42	1.46	1.20	-	-	-

¹Values for St. Lawrence I. in 1981, Bluff in 1979-1981, Cape Thompson in 1976, Cape Lewis in 1977 and 1979, and Cape Lisburne in 1976-1978 and 1980-1981 are nest contents on our first visit. First visits at those colonies in those years occurred approximately when eggs were hatching so the values reported represent minimum estimates of actual clutch sizes.

²Data for 1976 are from Searing (1977).

³Data for 1975-1978 are from Drury et al. (1981).

⁴Data for 1960-1961 are from Swartz (1966).

⁵Data are from Hunt et al. (1981).

TABLE 5. Growth rates of black-legged kittiwake chicks in northern Alaska.

Year	Colony			
	Bluff	Cape Thompson	Cape Lisburne	St. Lawrence I.
1977	ND ^a	12.6 ± 3.6 (16) ^b	19.3 ± 2.9 (18)	ND
1978	17.9 ± 4.1 (22)	ND	19.7 ± 6.7 (21)	ND
1979	20.4 ± 4.4 (35)	20.2 ± 4.7 (111)	18.3 ± 1.4 (24)	ND
1980	17.6 ± 7.4 (30)	ND	17.9 ± 3.7 (43)	ND
1981	15.6 ± 4.5 (31)	ND	14.3 ± 3.0 (30)	21.0 ± 7.1 (15)

^aND = no data.

^bMean growth rate (g day^{-1}) ± standard deviation (sample size).

TABLE 6. Black-legged kittiwake egg volumes at colonies in northern Alaska.

Colony	Clutch/Size	Year		
		1977	1979	1981
Bluff	1 egg	ND ^a	ND	47.9 ± 2.0 (7) ^b
	2 eggs	ND	ND	48.9 ± 3.3 (55)
Cape Thompson	1 egg	45.1 ± 3.1 (19)	47.3 ± 4.3 (44)	ND
	2 eggs	46.9 ± 1.8 (6)	47.1 ± 3.5 (142)	ND
Cape Lisburne	1 egg	ND	ND	47.3 ± 3.0 (27)
	2 eggs	ND	ND	48.4 ± 3.5 (86)

^aND = no data.

^bMean volume (mm^3) ± standard deviation (sample size).

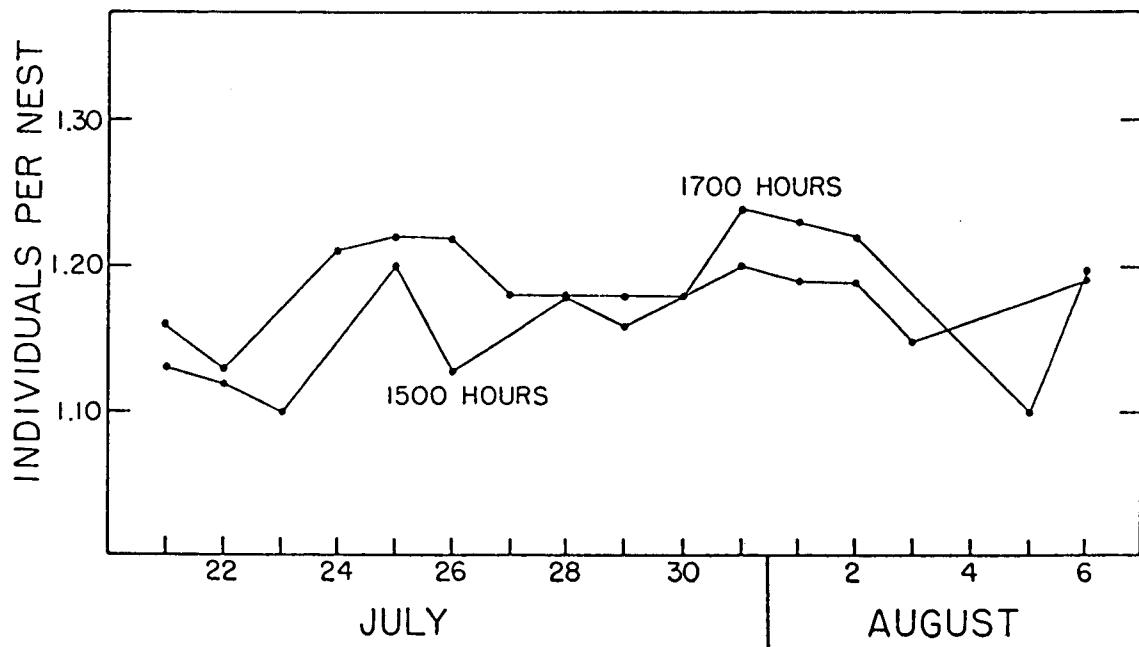


Figure 1. Daily variation in kittiwake numbers during the nestling period at Bluff in 1979.

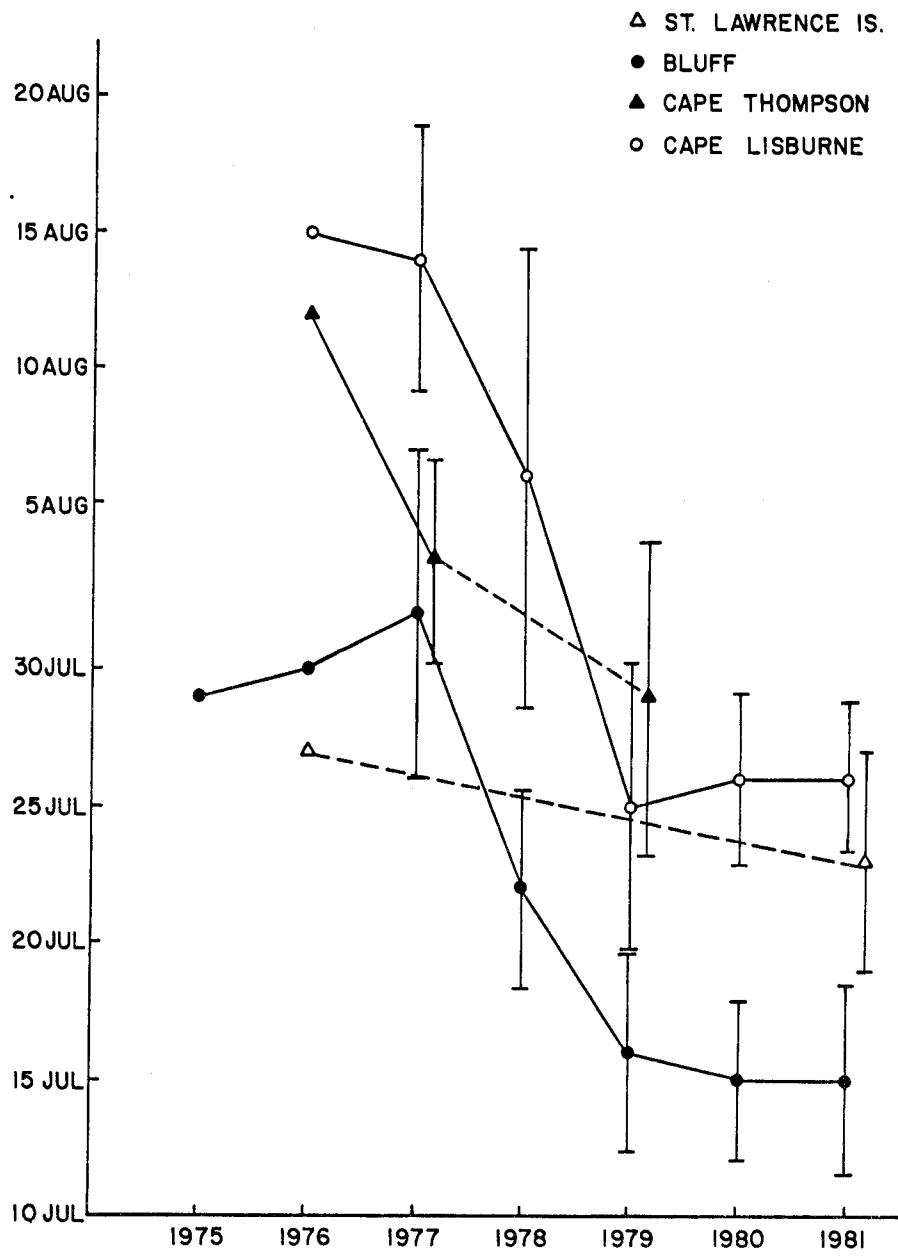


Figure 2. Mean hatching dates of kittiwake chicks. Dates for 1975-1977 are from Drury *et al.* (1981); date for 1976 at St. Lawrence Island was estimated from data reported by Searing (1977).

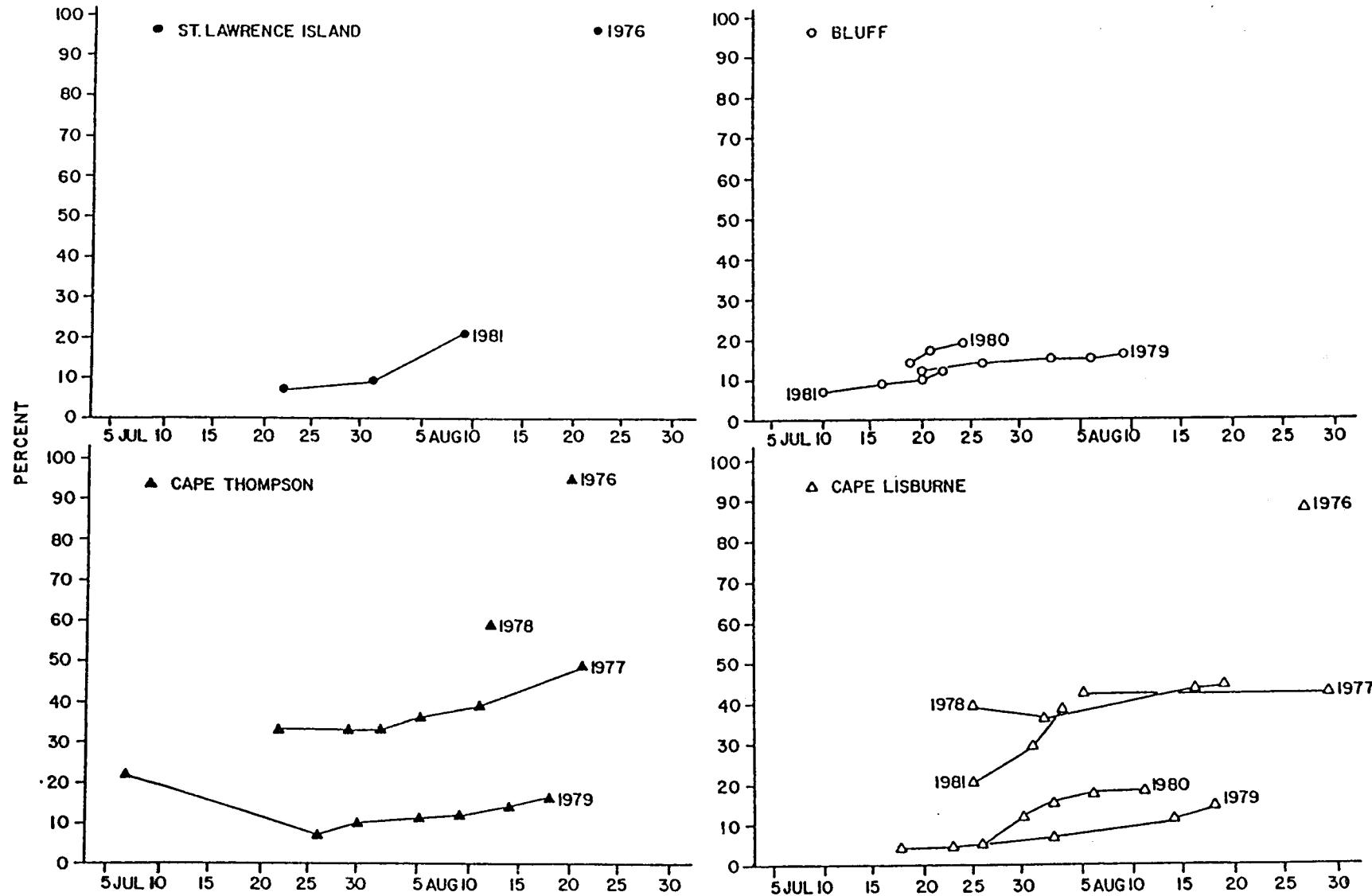


Figure 3. Percentage of empty kittiwake nests at colonies in northern Alaska.

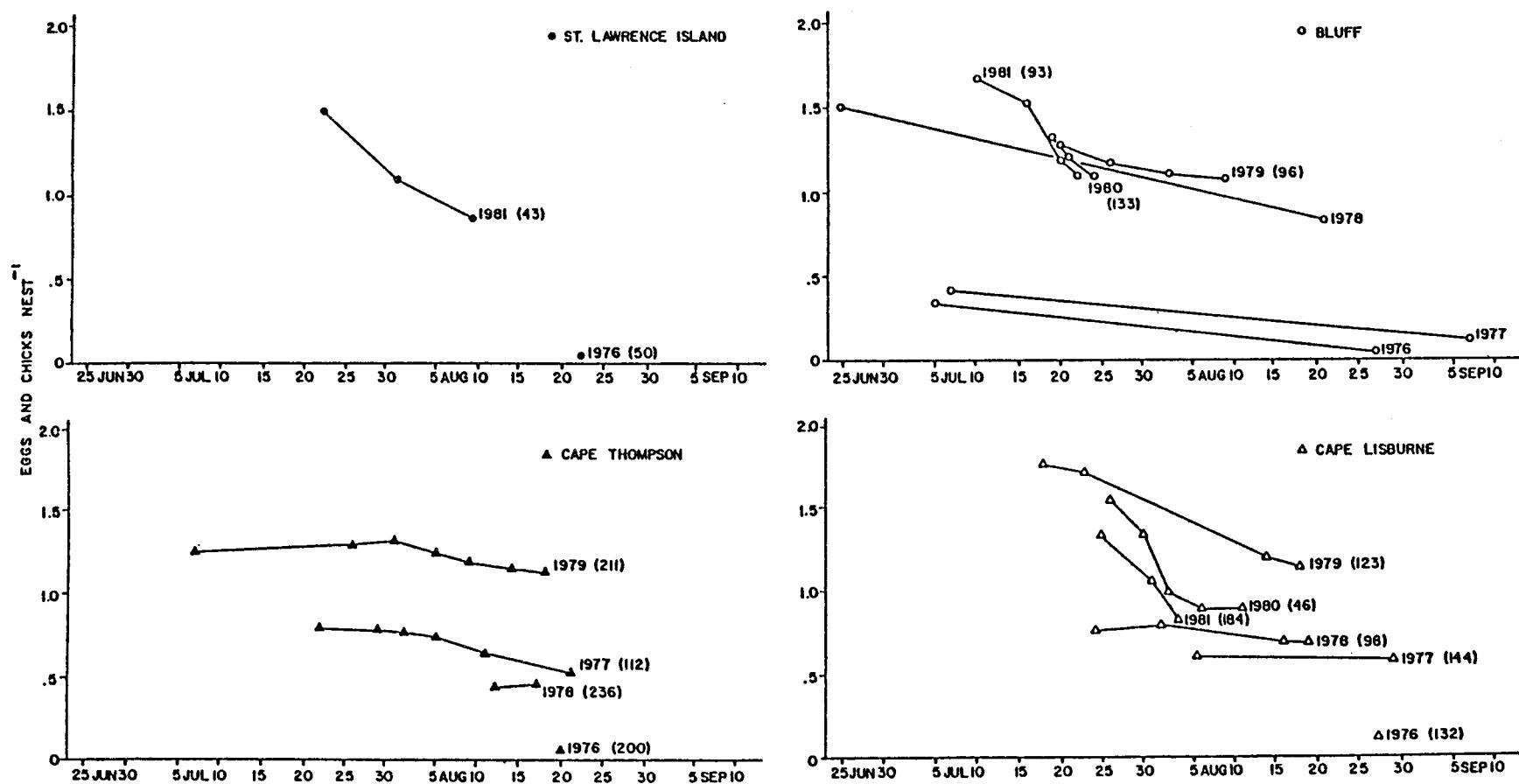


Figure 4. Mean number of kittiwake eggs and chicks per nesting attempt. Data for Bluff in 1976-1978 are from Drury *et al.* (1981); datum for St. Lawrence Island in 1976 is from Searing (1977). Sample size is in parentheses.

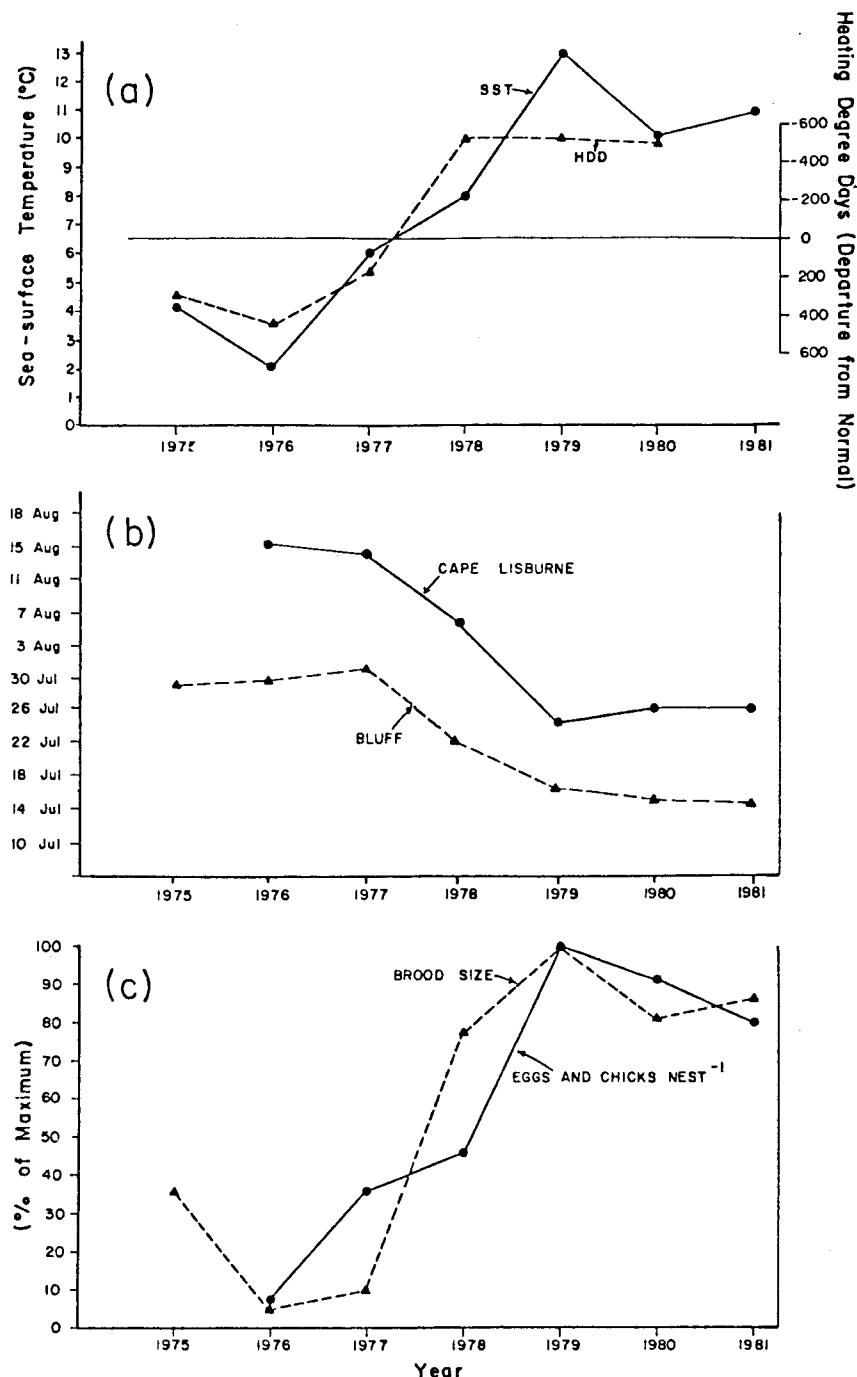


Figure 5. Relationships between environmental change, kittiwake nesting phenology and estimates of kittiwake reproductive success at Cape Lisburne and Bluff. (a), (b), and (c) as in Figure 21, page 77.

contained 2.3 large chicks nest⁻¹ on the same date in 1978. We saw the contents of only 2 nests on 23 August 1977, and although the sample size was small, the brood size of 2.5 large chicks nest⁻¹ was similar to that found in both 1976 and 1978.

Total cormorant nests declined from 39 in 1977 to 25 in 1978 at Cape Lisburne. Average brood size at the 25 nests examined on 17 August 1978, 2.6 large chicks nest⁻¹, was considerably higher than the average brood size of 2.0 large chicks nest⁻¹ at 36 of the 39 nests examined on 20 August 1977.

Numbers of cormorants at Cape Lewis increased from 28 nesting pairs in 1977 to 53 nesting pairs in 1979. Although it was difficult to determine nest contents at Cape Lewis, it appeared that the majority of the 53 nests contained three young each on 21 July 1979.

Cormorants do not nest at Corwin Bluff, about 40 km east of Cape Lisburne, but large numbers of non-breeders appear to roost there. Numbers of non-breeding birds increased steadily from 33 in 1977 to 53 in 1979 to 79 in 1980. Increases in 1979 and 1980 may have been the result of relatively good reproductive success at Cape Lisburne and Cape Lewis in 1978 and 1979. They might have also resulted from improving feeding conditions in Ledyard Bay following 1976. These increases are similar to annual increases of glaucous gulls in Ledyard Bay between 1977 and 1979.

Eiders

Large flocks of king and common eiders, generally composed of 100-500 birds, were commonly seen migrating from east to west along the northern coast of the Lisburne Peninsula each year. We first noted these migrations at Cape Lisburne in late August and early September 1976, and obtained some additional information on eiders in following years.

On 25 July 1978, while flying an aerial survey of birds in Ledyard Bay, 35 flocks of eiders were observed on the water. Flocks varied in size from about 100-400 birds. One observer estimated that these flocks totaled about 12,000 individuals, and a second observer estimated that 12,000-15,000 individuals were present. Several other flocks, varying in size from 12 to several hundred birds were also seen during the survey.

Most of the eiders were found along a 50 km section of a transect line running almost directly between Point Lay and Cape Lisburne, and the heaviest concentration occurred within a 20 km subsection near the center of the transect (see Springer *et al.* 1979). Two days later on 27 July, large numbers of eiders were seen offshore between Ayugatak Lagoon and Corwin Bluff, and by 31 July large skeins of birds were migrating westward past Cape Lisburne. Flocks of about 200 birds each passed the Cape regularly on 2 August, and on 15 August migrating flocks were seen continuously along the coast as far east as Corwin Bluff.

Eiders also migrated west along the coast of Ledyard Bay in 1979. On 17 August during a short boat trip east of Cape Lisburne, we saw four

flocks totaling about 750 common eiders about 8 km west of Ayugatak Lagoon. Three of the flocks were flying west and one was resting on the water.

Five-minute counts at Cape Lisburne in late July 1980 (Table 6) indicated the size and pattern of these annual migrations. We estimated that in the order of 50,000 individuals may have passed the Cape each day during 27-31 July that year, based on the average number of birds (464 ± 538 per 5 minute interval) observed between 1400 h and 2300 h.

We know little about the route taken by eiders after they pass Cape Lisburne, but it is clear that they remain well offshore after rounding the Cape. Southward migrations were not evident at Noyalik Peak or Cape Lewis, nor were they evident at Cape Thompson during late summer 1976-1979, a location where notable spring and early summer migrations occur (see Williamson *et al.* 1966).

The late summer molt migration of eiders is relatively well documented (e.g., Bent 1925, Thompson and Pearson 1963, Johnson *et al.* 1975), and most accounts of it are similar. From about early July to early August, flocks of male common and king eiders begin to move westward along the Beaufort Sea coast from breeding grounds in Alaska and Canada (see also Harrison 1977). Flocks of hundreds of individuals have passed given points every few minutes, especially during favorable wind conditions. Approximately 18,000 birds (mostly king eiders) passed over Point Barrow every day between 14 July and 1 September 1953 (Thompson and Pearson 1963). Until 8 August the majority of birds were males (about 22:1), but during the period 8-17 August, the sex ratio shifted to a preponderance of females. Although the largest flock contained 1,100 birds, mean flock size was 105 birds.

Major westward movements of eiders have also been recorded on radar during the last week in July and the first week in August at several locations in northern Alaska (Flock 1973). After eiders pass Point Barrow, they tend to follow the coast at distances of 1.5 km or more off shore at least as far as Point Lay.

Common and king eiders apparently molt in the vicinities of Icy Cape and Point Lay (see Thompson and Pearson 1963, Johnson *et al.* 1975). Most of the eiders seen concentrated in Ledyard Bay on 25 July 1978 were in less than full breeding plumage. Many may have been flightless since most swam from the path of the approaching aircraft.

It is also possible that eiders stage in Ledyard Bay before migrating on to their wintering grounds. Murres and kittiwakes feed extensively in the bay, and perhaps eiders, too, find the shallow waters a productive area in which to feed before resuming their southward journey.

Glaucous Gulls

Glaucous gulls were censused at Cape Thompson in 1976, 1977 and 1979. In 1976, 144 nests, the equivalent of 288 adults were counted at Colonies 1-4; neither nests nor adults were counted at Colony 5. Swartz

(1966) reported that the population at all five colonies was 304 and 300 adult gulls in 1960 and 1961, respectively. Fourteen adults were found at Colony 5 in 1960 and 28 were present in 1961. Swartz's totals for Colonies 1-4 for 1960 and 1961, 290 and 268 adults, respectively, were similar to our projected total of 288 adult glaucous gulls in 1976.

In 1977, we counted 250 adult glaucous gulls at all five colonies at Cape Thompson on 20-21 August. Most gull chicks had already fledged and some had moved a short distance from the colonies. An additional 39-50 adults with juveniles were counted along nearby upcoast and down-coast beaches, bringing the total adult population to 289-300, a figure close to the totals for all previous years.

Adult glaucous gulls were censused again at Cape Thompson on 16 August 1979. The total number, 386, was considerably greater than in any other year. The change was similar to changes we observed in numbers of breeding black-legged kittiwakes between 1976 and 1979.

The population of glaucous gulls at Cape Lisburne is smaller than the population at Cape Thompson. In 1976 we estimated that 100-200 individuals were present at or near the colony during 26-29 August; no distinction was made between adults, subadults and juveniles. In 1977 it was clear that, at most, only about 50 adults regularly occupied the Cape Lisburne colony. We only found two nests in 1977, but several other widely scattered pairs were seen along the cliff-tops at typical, grassy nesting areas where they might have been attending nests. The 1976 estimate of total numbers was probably inflated by the presence of subadults, which typically appear in greater numbers at both Cape Thompson and Cape Lisburne after late July-early August. Although counts of adult glaucous gulls were not made in 1978-1981 at Cape Lisburne, numbers did not appear to change relative to 1977.

Estimates of glaucous gull productivity were made only at Cape Thompson. We examined a total of 29 nests at colonies 1 and 4 on 28 June and 4 July, respectively. The nests contained a total of 34 eggs and 24 chicks, or 2.0 eggs and chicks nest⁻¹. Swartz (1966) reported a mean clutch size of 2.86 in 1960. If egg counts had been made earlier in the season in 1976, the difference between our data and those of Swartz would probably have been less, since some eggs were probably lost during incubation.

Nineteen nests were checked at Colony 1 on 16 July and 21 nests were checked there on 4 August 1976. Brood size fell to 1.9 chicks nest⁻¹ during the first interval and to 1.4 chicks nest⁻¹ during the second interval. No chicks had fledged by 4 August so brood size on that date does not necessarily represent fledging success.

Estimates of reproductive success were not made at Cape Thompson in 1977 or in 1979. Counts of adults and juvenile gulls in mid-late August of both years indicated that productivity was similar to productivity in 1976. We counted all gulls in the vicinity of Cape Thompson on 20 August 1977 and on 16 August in 1979. In 1977 we obtained a ratio of 0.63 juveniles per adult, or 1.26 juveniles per projected pair, and in

1979 we obtained a ratio of 0.41 juveniles per adult, or 0.82 juveniles per projected pair.

We obtained phenological information on glaucous gulls in 1976 and 1977 at Cape Thompson, and in 1977 at Cape Lisburne. Breeding schedules at Cape Thompson were similar in 1977 and 1959-1961 (see Swartz 1966), but about 10-15 days later in 1976. Only 13 of 33 eggs had hatched by 28 June 1976. In 1977 at Colony 1 adults were incubating on 8 June, and most eggs had hatched before about 1 July. Hatching was essentially complete by 6 July. Although two small downy chicks (~ 70 g each) were only about 3-5 days old on 7 July, most chicks were relatively large by early July. Seven large, well-feathered young were present at Colony 3 on 15 July, and some juveniles were capable of flight a few days later. Many juveniles were flying by the first week of August, and almost all of the chicks had fledged by 15-20 August.

In 1977, glaucous gulls may have bred about 10 days later at Cape Lisburne than at Cape Thompson, and may have followed a schedule similar to that followed at Cape Thompson in 1976; however, our data are from only two nests. The two nests contained five chicks estimated to be about 10 days old on 14 July.

The proportion of subadult to adult glaucous gulls at Cape Thompson and Cape Lisburne increased greatly between 1976 and 1979, and subadult gulls were seen earlier each summer after 1977. In 1976 subadult glaucous gulls were not observed at the Cape Thompson colonies until 1 August. Of 164 gulls in the immediate vicinity of the colonies on 20 August, only 7% were subadults.

In 1977 subadults again appeared at both Cape Thompson and Cape Lisburne during the first few days of August. By 20-21 August they accounted for about 6% of the total 440 gulls observed at Cape Thompson. Of an additional 127-152 gulls located farther away from the colonies upcoast and downcoast along the beaches, 31-33% were subadults. Area wide, subadults accounted for 17% of the 567-593 gulls counted on 20-21 August.

On 2 August 1977 at Cape Lisburne, 12 subadults (13%) were identified among 89 glaucous gulls counted between the colony and Thetis Creek. By 15 August subadults had become somewhat more numerous and were observed near the colony; however, no counts were made of the relative number of adults and subadults.

Data on subadult glaucous gulls were gathered on 29 July 1978 during a flight from Cape Thompson to Point Hope. Approximately 250 gulls were counted along the shoreline and about 25% of these birds were subadults. On a 17 September flight from Cape Thompson to Krusenstern Lagoon, 216 glaucous gulls were counted and aged and 43% were subadults. Groups totaling about 75 additional gulls were also seen during this flight and about 50-75% were estimated to be subadults.

The earliest counts of glaucous gulls in the Cape Lisburne vicinity in 1978 were made during an aerial survey flight on 25 July, but sub-

adults were already present at Cape Lisburne when we arrived on 22 July. Three flocks of about 75 gulls each were seen along the lagoons approximately 9-16 km east of Cape Lisburne; about 10% of these birds were subadults. Two days later on 27 July, 1,150 gulls were counted along the coast from a point about 35 km south of Point Lay to Wainwright. We classified 767 of these birds and 168 (22%) were subadults; however, the distribution of subadult gulls was not uniform. From the starting point south of Point Lay to Icy Cape, 9% of 487 birds were subadults, but between Icy Cape and Wainwright 44% of 280 individuals were subadults.

Glaucous gulls were also counted during several boat trips east from Cape Lisburne in 1978. On 29 July 200 gulls were seen between Cape Lisburne and Corwin Bluff, of which 10-15% were subadults, a ratio consistant with the aerial data from south of Icy Cape. Several weeks later, on 15 August, major changes had occurred in the numbers of gulls and in the proportion of adults to subadults. Within 20 km to the east of Cape Lisburne we counted six flocks of gulls and kittiwakes, each comprised of 750-1,000 birds. Each mixed flock contained between 100 and 350 glaucous gulls, or about 1,000 gulls total. Aging the birds was difficult, however, our best estimate suggested that about 90% were subadults.

We also gathered some data on gulls between Cape Lisburne and Corwin Bluff in 1979. On 20 July about 200 gulls were counted on the lagoons 9-16 km east of Cape Lisburne and about half (50-60%) were subadults. On 17 August three flocks of 25 birds each were observed near the lagoons and at least 125 additional gulls in flocks of 5-50 birds each were counted flying west between the lagoons and Corwin Bluff. On our return trip, 300-400 gulls (presumably the same birds observed in smaller flocks earlier in the day) were counted at Ayugatak Lagoon. About 80-90% of all glaucous gulls observed on 17 August were subadults.

Little information was gathered on subadult glaucous gulls at Cape Thompson in 1979. However, subadults were observed flying in the vicinity of the colonies upon our arrival on 2 July, much earlier than in previous years. We did not actively look for subadults again until 17 July when we began seeing them in larger numbers. On 21 August, 343 glaucous gulls were classified as to age between Ogotoruk Creek and Kivalina during a flight to Kotzebue, and of these, 15% were subadults.

The changes observed in total numbers of glaucous gulls at Cape Thompson and Cape Lisburne were due primarily to an increase in the subadult component of the population. Subadult gulls were observed near the colonies much earlier each year after 1978. No subadults were seen at Cape Thompson in June of 1976 or in July of 1976 and 1977, nor were subadult gulls seen at Cape Lisburne during July of 1977. In both 1976 and 1977, subadults began arriving at Cape Thompson and Cape Lisburne in August. Subadults arrived at both colonies somewhat earlier in 1978 and 1979.

After subadult gulls began arriving, they continued to increase in numbers at both colonies throughout the remainder of the season each year, and constituted progressively greater and greater proportions of the total

populations. An age structure developed solely on data obtained at Cape Lisburne in 1978 would have suggested that only 10-15% of all gulls within the region were subadults; however, by late August subadults not only accounted for about 90% of all gulls, but the total population was about an order of magnitude greater than it had been in July. Therefore, we suggest that numbers data be used cautiously in forming conclusions regarding changes in the size or age structure of glaucous gull populations in the Chukchi Sea since widely different results may be obtained, depending upon census dates.

We question whether the major changes in numbers of subadult glaucous gulls represent either recent (i.e., during the past 5 years) changes in gull productivity, or major changes in gull survivorship. A flock of subadult gulls could be composed of one, two and three year-old birds. Many of the birds in the flocks we saw at Cape Lisburne in 1978 were certainly alive in the previous 1-2 years, and may have summered offshore or in some other region. We believe subadult gulls may have occurred in the vicinity of Cape Lisburne in large numbers in 1978 as a result of early, bountiful supplies of forage fish, particularly sand lance. Except for a few breeding birds, all of the gulls were found east of the Cape Lisburne colony and were feeding, perhaps exclusively, on these fish.

The changes we have seen in the glaucous gull population at Cape Thompson and Cape Lisburne over the years are consistent with changes we have observed in other species of seabirds. We believe the causative factors underlying these changes are the same. The prey base upon which the birds depend recovered steadily between 1977 and 1979 from a low in 1976, and has remained relatively stable since then. Food subsidies for gulls, particularly at garbage dumps, may also be responsible for increases in gull populations; however, we stress that conclusions regarding the effects of these and similar sources of food on populations of northern gulls be arrived at carefully, keeping in mind parallel changes in other elements of the ecosystem.

Black Guillemots

One noteworthy event at Cape Lisburne was the discovery of a large population of black guillemots (Table 2). During a brief survey in late August 1976, fewer than ten black guillemots were found there, but in 1977 black guillemots were relatively numerous when we arrived on 6 July, and a minimum of 136-151 individuals were regularly observed at the colony from mid-July through early August. Groups of 30-40 birds commonly perched on or near the same boulder piles where most of the 1976 sightings had occurred, but after a severe storm on 8-9 August only a few pairs remained in the area. These few pairs may have been the only ones that nested successfully that year.

On 9 and 10 July 1978, 9-11 black guillemots were observed on the water in front of the cliffs on the north side of the colony. These few birds were probably not representative of the actual number present on that date because the west side of the colony was not surveyed until two weeks later. On 24 July 108 black guillemots were counted within the colony boundaries.

Conditions in 1979 did not provide an opportunity to conduct a complete census of black guillemots at Cape Lisburne. Nevertheless, approximately 50 birds were regularly observed between mid-July and mid-August on or near the beach at the east end of the colony.

Two complete counts of black guillemots at Cape Lisburne in 1980 indicated that a minimum of 126-154 birds were present at the colony that year, at least during early to mid-August. These numbers are similar to those obtained in 1977 when black guillemots were also censused more than once.

Counts of black guillemots were not as high in 1978 and 1979 as they were in 1977 and 1980; however, less effort was made to count them in 1978 and 1979. We believe that comparable census efforts would have provided comparable results among all four years.

Observations of black guillemots from the vicinity of Cape Lisburne, but outside of the colony boundaries, were also made in 1977-1980. In 1977, 14 birds were found frequenting the coast between Kay Creek, near the colony's southern boundary, and Noyalik Peak, and 24 additional birds were present at Cape Lewis. Although we did not count guillemots at Cape Lewis in 1978, some were present, and we found 46 individuals in the section of coast between Kay Creek and Noyalik Peak. Black guillemots were also regularly seen along the northern coast east to Corwin Bluff. In 1977, our highest count in that section was nine individuals, and numbers seemed comparable in 1978. A minimum of 56 individuals was present there in 1980.

Cape Thompson appears to represent the southernmost breeding location of black guillemots in Alaska. Although some individuals have been seen occasionally at colonies farther south in and near Bering Strait, nesting pairs have apparently never been documented at them.

The population of black guillemots at Cape Thompson has been consistently small and variable since 1959 (Table 3), and only one nest has been located there. Swartz (1966) found a nest containing two eggs in a crevice several feet above a talus slope in 1960. He collected one egg and found the second egg broken and deserted the next time he checked the nest.

We have found evidence of breeding by black guillemots at Cape Lisburne. A dead 14-21 day-old chick was discovered at the base of a large boulder pile on 26 August 1976. Two nests were located in 1977. One contained two eggs on 12 July, but both eggs were found broken on 5 August. One of the eggs contained the remains of a well-developed chick. A second nest only a few meters from the first was repeatedly entered by an adult carrying fish on 25 July; however, the nest contents and fate are unknown. In 1978 a nest under a split boulder had one egg in it on 11 July, and another nest containing a single egg was eventually located in a crevice on 2 August 1980.

We are uncertain as to how many black guillemots actually breed at Cape Lisburne, and we are also unsure of their breeding success. Of the

four known nests at Cape Lisburne, one failed and fates of the other three are unknown. At least two of the nests contained single eggs, whereas two-egg clutches are more typical (see Bent 1919). Divoky (1978) reported an average clutch size of between 1.75 and 1.95 in 1975-1977 at Cooper Island. However, overall breeding success of black guillemots at Cooper Island dropped dramatically in 1976 and 1977 after near perfect success in 1975. Divoky attributed the decline to increased predation by Arctic foxes and an increase in the number of inexperienced breeding pairs at new nest sites. Nests used for the first time had smaller average clutch sizes and breeding success was poorer at these nests than at nests used in previous years.

We have observed black guillemots regularly flying in and out of inaccessible cracks and crevices high on the cliffs in a variety of locations where quality of nesting habitat appears superior to the storm-lashed bases of the cliffs. At least some of the nests we found at Cape Lisburne may have been those of inexperienced pairs as indicated by their placement at the bases of the cliffs, and single-egg clutches.

East of Cape Lisburne black guillemots were often observed flying off of dirt bluffs where they may also nest (see Asbirk 1978), and some pairs probably breed along the bluffs and cliffs south of Cape Lisburne and at Cape Lewis. The full extent to which Cape Lisburne and vicinity are used for nesting is still unknown.

We have some information on prey taken by black guillemots at Cape Lisburne. Fourteen observations of birds carrying fish into boulder piles were obtained during 22-25 July 1977. In one case the fish was a sand lance, but in 12 cases the fish were clearly small cod, and in one case the fish was clearly an Arctic cod. Arctic cod were numerous under the ice floes that remained near the colony at the time these observations were made, and most, if not all, of the cod were probably of that species. Divoky *et al.* (1974) reported that Arctic cod were fed to chicks in the Beaufort Sea.

Pigeon Guillemots

A small and variable population of pigeon guillemots inhabits Cape Thompson (Table 4). Although the population is small and we have not found any nests, Swartz (1966) located four nests in boulder piles in 1960-1961. These records suggest Cape Thompson is the northernmost limit of breeding for this species in Alaska. Pigeon guillemots have been seen on only two occasions at Cape Lisburne and vicinity. Both sightings were of one bird each, and occurred on widely separated dates in 1977.

Horned Puffins

A complete census of horned puffins was taken in 1976 at Cape Thompson, and Colonies 1-4 were censused in 1977. Only Colony 1 was censused in 1978, the last year horned puffins were counted at one or more entire colonies at Cape Thompson. Results of our counts and data reported by Swartz (1966) for 1960 are shown in Table 5.

Swartz (1966) compensated his counts of horned puffins for diurnal changes in numbers like he did for murres. In 1976 we made two 24-hour counts of horned puffins and compensated counts at Colonies 2, 3 and 5 on the basis of these counts. Colonies 1 and 4 were censused several times each and we have reported only the highest of all counts. Diurnal (24-h) activity counts were not made in 1977 and the numbers in Table 5 for 1977 are uncompensated scores. Likewise, the number for 1978 at Colony 1 is the uncompensated total of one count. Although these census data are not strictly comparable among years, there is no indication of large change in the number of horned puffins at Cape Thompson since 1960.

Horned puffins were censused at Cape Lisburne only in 1977 when 55 of 75 plots were counted. The total of those plots, 1,072, indicates that the number of horned puffins at Cape Lisburne is similar to the number at Cape Thompson.

The breeding cycle of horned puffins was apparently later in 1976 and 1977 than in 1960, as it was for murres, kittiwakes and gulls. We located nine nests at Cape Thompson in 1976, each of which contained one egg. Two laying dates were obtained, one between 16-20 July and another after 20 July. None of the nine eggs had hatched by 25 August. In 1977, at least one egg was laid about 15-20 July and was hatching or had just hatched on 26 August. Swartz (1966) reported two hatch dates in 1960, one on 12 August and the other between 17-20 August.

Tufted Puffins

Several complete censuses of tufted puffins were taken at Cape Thompson in 1976 and 1977, and Colony 1 was counted once in 1978. Results of our censuses are presented in Table 6, and include only the highest scores obtained during the two census years. Numbers have been consistently small, and especially variable at Colonies 1 and 2 where the majority of pairs have nested.

We did not census tufted puffins at Cape Lisburne in 1976. The birds were generally conspicuous and there was no doubt that they were more numerous than at Cape Thompson—at least 100 individuals were apparent within the colony boundaries. In 1976 tufted puffins were also relatively numerous along the bluffs between the Cape Lisburne colony and at Noyalik Peak where we counted about 50 individuals.

The numbers of tufted puffins at Cape Lisburne and Noyalik Peak declined sharply between 1976 and 1977. A complete census of Cape Lisburne in 1977 revealed only 11 individuals within the colony boundaries, and only 12 birds were present at Noyalik Peak.

Casual observations of tufted puffins at Cape Lisburne and Noyalik Peak in 1978-1980 indicate numbers have remained low since 1977. Only about seven individuals were seen within the colony boundaries and a few other birds were seen at Noyalik Peak in each of those years.

We cannot explain the decline in numbers of tufted puffins at Cape Lisburne and Noyalik Peak after 1977; however, both Cape Lisburne and

TABLE 1. Numbers of active pelagic cormorant nests at Cape Thompson, 1959-1978.

Year	Colony					TOTAL
	1	2	3	4	5	
1959 ^a	1	1	0	4	0	6
1960 ^a	3	18	0	1	1	23
1961 ^a	4	18	0	1	0	23
1976	7	2	0	5	0	14
1977	16	0	0	2	0	18
1978	7	0	0	4	0	11

^aData are from Swartz (1966).

Cape Thompson are in the northernmost nesting range of both puffin species, and as a consequence, numbers may vary considerably from year to year. Data from Colony 1 at Cape Thompson are suggestive of this. Because of its location, Colony 1 is the most often viewed. Tufted puffins are usually conspicuous there when they are present, because of the broad, flat rock faces and small size of the cliff, and counts there are likely to be the most accurate. In five of the six census years maximum counts varied from a low of two pairs in 1959 to a high of 12 pairs in 1976.

Nesting by tufted puffins has been confirmed only once at Cape Thompson. A single egg was found in a crevice at Colony 2 on 17 August 1976. It is likely that some pairs breed at both colonies each year. Tufted puffins are regularly seen entering and leaving crevices during July and August at both locations.

TABLE 2. Populations of black guillemots in the vicinity of Cape Lisburne, 1976-1980.

Year	Cape Lisburne	Cape Lewis	Kay Creek to Noyalik Peak	Cape Lisburne to Corwin Bluff
1976	<10	NC ¹	NC	NC
1977	136-151	24	14	9
1978	108	NC	46	NC
1979	>100	NC	NC	NC
1980	154	NC	NC	56

¹NC = no count.

TABLE 3. Populations of pigeon and black guillemots at Cape Thompson.

Species	1959 ^a	1960 ^a _a	1961 ^a _a	1976	1977	1978	1979
Pigeon guillemots	< 10	4	14	4-6	2-3	--	6-8
Black guillemots	< 10	16	4	4-6	6-10	> 6	3-4

^aData are from Swartz (1966).

TABLE 4. Numbers of horned puffins at Cape Thompson.

Year	Colony					Total	
	0 ^a	1	2	3	4		
1960 ^b	86	418	470	210	178	540	1,902
1976	75	241	663	200	180	559	1,918
1977	65	265	344	256	142	NC ^c	---
1978	NC	218	NC	NC	NC	NC	---

^aColony '0' is located between colonies 1 and 2.^bData are from Swartz (1966).^cNC = no count.

TABLE 5. Numbers of tufted puffins at Cape Thompson.

Year	Colony					Total
	1	2	3	4	5	
1959 ^a	4	18	0	0	0	22
1960 ^a	20	12	0	0	4	36
1961 ^a	6	34	0	0	0	40
1976	24	13	1	0	6	44
1977	13	9	4	0	4	30
1978	10	NC ^b	NC	NC	NC	--

^aData are from Swartz (1966).^bNC = no count.

TABLE 6. Five-minute counts of eiders flying past Cape Lisburne,
1980.

Beginning Time ¹	July					August
	27	28	29	30	31	1
1045						0
1105					0	
1230						0
1400	750					
1440					500	
1450		500				
1500	750					
1545					300	
1810			750			
1820					300	
1940					750	
2005		100	500			
2045					500	
2140			500			
2310			0		300	

¹Bering Daylight Time.

VIII. CONCLUSIONS

The major population decline of murres at Cape Thompson in the past two decades and the decline at Bluff since the mid-1970's might be due, at least partially, to a long series of relatively cool summers in the region when reproductive success was reduced. Although declines have occurred at Cape Thompson and Bluff, murre numbers apparently have remained stationary at Cape Lisburne and on St. Lawrence Island. Such differences among the colonies could be related to differences in proximity to concentrations of food resources.

The observed rates of decline in numbers of murres at both Cape Thompson and Bluff are greater than would be predicted on the basis of summer conditions only. Variability among counts within years is high, and therefore a single count, or the average of a few counts, provides an imprecise estimate of numbers in any particular year. Thus, the rate implied by our results may be higher than the actual rate of decline. Alternatively, the observed and actual rates could be the same, implicating factors in the wintering areas as an additional reason for the declines. Perhaps the greatest change in winter environmental conditions in the past two decades was a reduction in the winter food supply of murres due to commercial harvest of pollock. Subsequent competition for food might have resulted in increased overwinter mortality and therefore a regional decline in murre numbers. Consolidation of murres at colonies most favorably situated with respect to prey availability could have led to the apparent differences in the status of murre populations at colonies in northern Alaska.

Like murres, kittiwake numbers also changed among years, but tended to increase rather than decrease following the particularly poor breeding season of 1976. Changes in other components of their breeding biology also occurred; for example, laying dates were earlier and reproductive success increased in years following 1976. These changes and our studies of food habits of murres and kittiwakes indicated that prey availability was low in 1976 in association with unusually cold environmental conditions. A warming trend in succeeding years led to more abundant prey and much improved breeding performance of kittiwakes.

An adequate level of fish biomass is necessary for kittiwakes to enjoy good reproductive seasons. In most years a combination of Arctic cod and sand lance probably satisfies this requirement. Arctic cod stocks appear to fluctuate little by comparison to stocks of sand lance, which were essentially unavailable to kittiwakes in 1976, but increased to very high numbers by 1979. The availability of sand lance appears to be important to kittiwake chicks which grow rapidly on diets of these fish, but more slowly when sand lance are in low numbers and their diets must be supplemented with other types of food.

Although northern kittiwake populations experience years of very poor reproductive success, they also have years of very good success. Over the long term, these extremes probably balance each other and maintain the populations at more or less uniform levels.

Two basically different food webs provide most of the energy supporting seabirds in the eastern Chukchi Sea. One includes the typically Arctic taxa of cods and sculpins and their primarily benthic prey of mysids, amphipods and isopods, as well as some arctic copepods. Arctic cod and sculpins are the most abundant and widely distributed fish fauna in northern regions. The other principal food web includes sand lance and their primarily neritic, seasonal prey of boreal copepods and meroplankton. Because sand lance form dense schools near the surface, they provide a concentrated source of energy to kittiwakes and other seabirds.

The factors responsible for maintaining these food webs are imperfectly understood. Particulate organic matter and zooplankton are advected into the Chukchi Sea by the northward flow of water from the Bering Sea. This imported energy may subsidize annual primary and secondary production north of Bering Strait and be important to food web organisms. The warming effect of Alaska Coastal Water appears to be especially important to seasonally abundant sand lance and their supporting neritic food web.

We have identified one area in the eastern Chukchi Sea that is consistently used by large numbers of a variety of seabirds and marine mammals throughout the summer. Ledyard Bay, on the north shore of the Lisburne Peninsula, provides critical feeding habitat for the majority of the birds nesting at the Cape Lisburne colonies. Moreover, large numbers of migrating eiders, non-breeding cormorants and gulls, walrus, phocid seals and gray whales are found there during much of each season. We do not fully understand the physical processes responsible for the biological richness of Ledyard Bay. The year-to-year consistency of use underscores the importance of the bay, and demonstrates a clear need to preserve the integrity of biological systems found there.

IX. NEEDS FOR FUTURE STUDY

Murre numbers should be monitored at colonies where counts have been made in the past. We recommend that the Pribilof Islands should receive high priority because a very good census was taken there in 1975 and 1976, but not since then. The Pribilof Islands lie near the heart of the region of the pollock fishery, and murre numbers on the islands also might have declined if competition for pollock has become a significant source of winter mortality. Also, competition for pollock could lead to lowered natality of murres on the Pribilof Islands, since pollock is the main food of breeding murres there. Knowledge of the current status of murres on the Pribilof Islands would contribute greatly to our understanding of factors affecting murre numbers in northern colonies.

Studies should be resumed at the Cape Pearce-Cape Newenham colonies. Common murres attain their greatest density in this region and knowledge of their status would provide valuable counterpoint to information from the Pribilof Islands where thick-billed murres are in the vast majority.

To aid in the assessment of fisheries-seabird interactions, a colony located away from the area of possible conflict should also be investigated. Middleton Island would be a suitable site. Because it lies in the Gulf of Alaska, neither breeding nor wintering murres should be affected by activities in the Bering Sea. Moreover, the murre population on Middleton Island has increased dramatically since the mid-1950's, indicating very favorable regional environmental conditions compared to those farther north.

Low-level effort should continue at Cape Lisburne and Bluff where we now have information for six and seven consecutive years, respectively. Both sites are logistically simple and inexpensive, and the return on the investment is high. These long-term studies have been invaluable to our understanding of marine ecology in northern Alaska.

Studies of kittiwakes should be made at all sites where murres are censused. Kittiwakes are easy to work with and are very sensitive indicators of local environmental conditions.

Murres and kittiwakes should be collected at all study sites for food habits information and as a way of sampling marine organisms. An understanding of trophic relationships among seabirds and of seabird food webs is critical to any study of seabird ecology.

A program of studies that alternates among several colonies should be planned for a period of at least ten years. During that interval, each colony would be visited two or three times, and one or two colonies would be visited each year. A program of this kind would be the most efficient, accurate and precise method to monitor changes in regional ecosystems that occur naturally or in response to resource development.

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**POPULATION AND TROPHICS STUDIES OF SEABIRDS
IN THE NORTHERN BERING AND EASTERN CHUKCHI SEAS,
1983**

by

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I. SUMMARY OF OBJECTIVES, CONCLUSIONS, AND IMPLICATIONS WITH RESPECT TO
OCS OIL AND GAS DEVELOPMENT

A. Objectives

The objectives of this study were to monitor population numbers, reproductive success and food habits of key seabird species in the Bering and Chukchi seas. The work was undertaken in order to understand the relationships of seabird populations to the physical and biological processes controlling regional marine communities.

B. Conclusions

Black-legged Kittiwakes (Rissa tridactyla) suffered a third consecutive year of reproductive failure in the SE Bering. Few, if any, chicks were produced on the Pribilof Is. or on St. Matthew I. The starvation of young shortly after hatching indicated that food availability was low, as it apparently has been in recent years. Common murres (Uria aalge) and thick-billed murres (U. lomvia) on St. Matthew I. had better success than Kittiwakes and apparently had a better reproductive season in 1983 than in 1982. Although the census results are somewhat equivocal, murre numbers on St. Matthew I. apparently were higher in 1983 than in 1982 and similar to numbers in 1977.

Invertebrates were important to murres and Kittiwakes on St. Matthew I, particularly during June, while walleye pollock (Theragra chalcogramma) was the dominant prey during July and August. The biomass of pollock in diets of both Kittiwakes and murres was higher in 1983 than in 1982, suggesting that food availability improved between the two years.

Least auklets (Aethia pusilla) on St. Matthew I. during the breeding season depend on Calanus marshallae, the dominant large copepod in the middle shelf domain. Feeding occurs near the island where local oceanographic features may concentrate prey. Declines in the number of copepods fed to auklet chicks and declines in chick growth rates between 1982-83 contrast with the general improvement in availability of pollock and in the apparent effect of the improvement on the biology of piscivorous murres and Kittiwakes, suggesting multispecies interactions among members of copepod-based food webs in the SE Bering Sea.

Murre and Kittiwake numbers at Cape Lisburne showed no change from previous years and reproductive success was good. Arctic cod (Boreogadus saida) were extremely abundant in Ledyard Bay in 1983, accounting for the majority of the carbon flux between lower trophic levels and the seabirds throughout the summer. In spite of the super-abundance of cod, however, the growth rates and survival of Kittiwake chicks were lower than in years when sand lance (Ammodytes hexapterus) were available, indicating the pivotal role of sand lance in the economy of Kittiwakes in the E Chukchi Sea.

Measurements of water temperature, phytoplankton abundance and zooplankton abundance in Ledyard Bay throughout the summer revealed a close correspondence between changes in all three in late summer and the appearance of sand lance in seabird diets. The results indicate an association between sand lance and numbers of their principal prey and support the hypothesis that hydrographic conditions in spring and early summer on the Bering-Chukchi shelf determine the availability of sand lance to seabirds by affecting the development of prey populations.

C. Implications with Respect to OCS Oil and Gas Development

Information of the kind we have gathered on the biology of seabirds, particularly on the magnitude of fluctuations in population, food web and environmental parameters, will help us to detect future changes in seabird populations and to distinguish between those that are natural and those that result from human activity in the marine environment.

II. INTRODUCTION

A. General Nature and Scope of Study

This study has attempted to monitor seabird populations, including their numbers, reproductive success and food habits. Also, we have attempted to elucidate the relationship of seabirds to marine food webs and oceanography. We have focused our attention on murres, kittiwakes and auklets, "key" species in the sense that they are among the most easily studied, the most numerous, and the most sensitive indicators of environmental change.

B. Specific Objectives

1. Census murres, kittiwakes and auklets at breeding colonies on St. Matthew I. and at Cape Lisburne.
2. Establish permanent census plots for auklets on St. Matthew I.
3. Determine the breeding phenologies and reproductive success of murres, kittiwakes and auklets.
4. Determine growth rates of kittiwake and auklet chicks.
5. Determine the food habits of murres, kittiwakes and auklets.
6. Determine seasonal changes in water temperature and phytoplankton and zooplankton stocks in Ledyard Bay.

C. Relevance to Problems of Oil Development

Accidental oil discharges in the vicinity of seabird congregations elsewhere in the world have caused the deaths of large numbers of birds. Uncertainties associated with oil development in Alaskan waters and the possibility of spills near colonies of important biological significance are causes for concern. In the event of an accident or other negative impact of development, it will be necessary to document the extent of the effect on seabirds and other marine organisms. Our studies are designed to provide baseline information on seabird populations in the Bering and Chukchi seas with which the possible effects of oil development can be assessed.

III. CURRENT STATE OF KNOWLEDGE

Field work on St. Matthew I. in 1983 enlarged upon our studies there in 1982 and those of DeGange and Sowls (1978) in 1977. Results of previous work on the island are presented in Springer et al. (in press a). Our work at Cape Lisburne extended the long-term studies conducted there and at Cape Thompson each year since 1976. A summary account of the work between 1976 and 1981 is

presented in Springer et al. (in press b). Additional information on seabird trophic relationships and regional physical processes in the Bering and Chukchi seas is presented in Springer et al. (1984) and in Springer and Roseneau (in press).

IV. STUDY AREAS

The locations of Cape Lisburne and St. Matthew I. are shown in Fig. 1. Detailed information on these sites is presented in our previous annual reports.

We conducted the auklet studies in two of the major auklet colonies on St. Matthew I. (Fig. 2.). "Pterodactyl Colony" is located on north and west facing talus slopes between about 15-150 m above sea level and has large areas of slumpblock and boulder rubble at the bottom leading into the sea. These lower areas were covered with lichens and generally contained lower auklet densities than higher in the talus. The second colony, "Arch Colony", is located on northwest-facing talus slopes about 30-200 m above sea level. Large areas of this colony also were covered with lichens as well as a thin layer of soil supporting sphagnum mosses and mat-cushion tundra.

V. SOURCES, METHODS AND RATIONALE OF DATA COLLECTION

Transportation to and from St. Matthew I. was provided by ARCO Alaska in cooperation with the Alaska Office of NOAA/OMPA. Transportation from the island was provided also by the U.S. Fish and Wildlife Service.

Two people arrived on the island on 8 June after sailing on the work-vessel Bhiel Trader, chartered by ARCO, from Dutch Harbor to an exploration support barge anchored near the island. They were lightered ashore from the tug Marine Constructor, also chartered by ARCO. Two additional people arrived on 13 July after a similar trip aboard the Bhiel Traveler. Departing the island, two people were lightered to the barge on the tug on 4 August and were then flown to Nome aboard an ARCO-chartered twin engine helicopter on 7 August. The other two people left the island on 11 August, sailing to Homer on the Western Pacific, chartered by the USFWS.

Field work at Cape Lisburne was carried out by two or three people between 16 June - 28 August. Transportation to Cape Lisburne is via commercial air carrier.

Murres and Kittiwakes at both sites were censused on plots established during earlier work. Additional monitoring plots were established at St. Matthew I. The methods for taking the censuses, as well as for determining breeding phenology, chick growth rates and food habits were the same as those used in all other years (see Springer et al. 1984, in press b) with the following additions. The equations used for estimating the sizes of pollock were:

$$\begin{aligned} \text{Otoliths } > 10.0 \text{ mm} \quad Y &= (3.175 X) - 9.770 \\ \text{Otoliths } < 10.0 \text{ mm} \quad Y &= (2.246 X) - 0.510 \end{aligned}$$

where Y = fish length in cm

X = otolith length in mm; from Frost and Lowry (1981),

and, $W = 0.0075 L^{2.977}$

where W = fish weight in g

L = fish length in cm; from Pereyra et al. (1976) in Smith (1979).

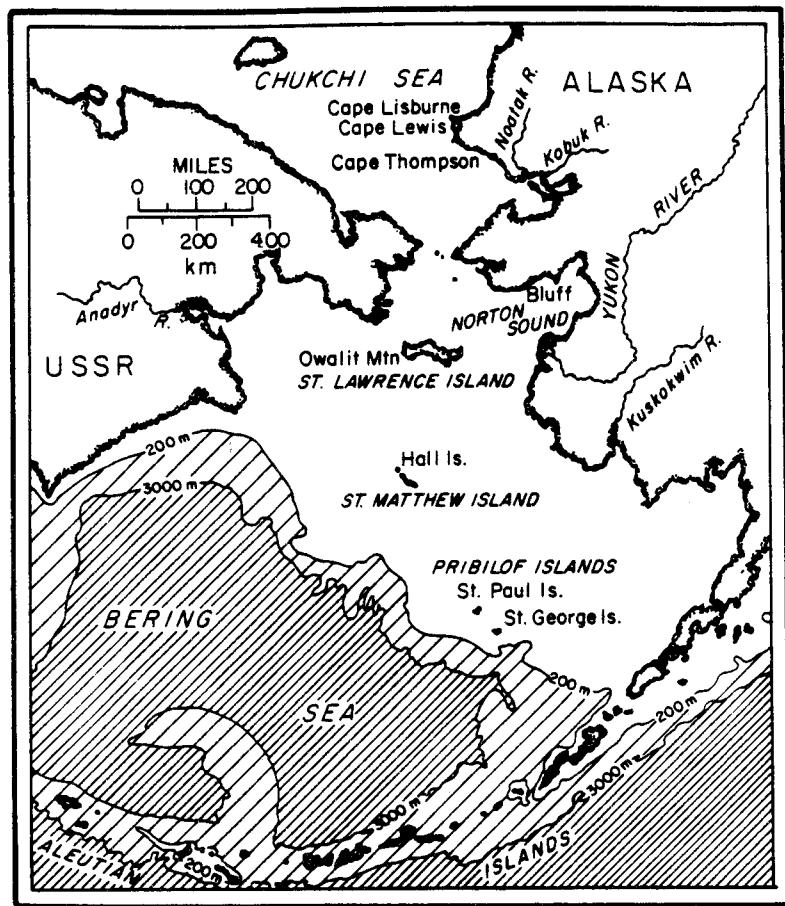


Fig. 1. Map of the study area in the Bering and Chukchi seas.

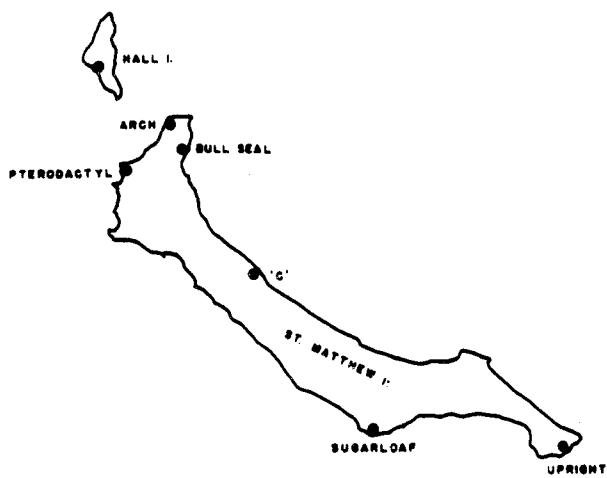


Fig. 2. Approximate location of the largest auklet breeding colonies on St. Matthew I. and Hall I.

Young-of-year pollock were all assigned a weight of 0.5 g, the approximate midpoint of weights of young-of-year pollock determined by T. Nishyama (unpubl. data). The length-weight estimates for capelin were taken from K. Pahlke (unpubl. data) and are as follows:

fish length < 80 mm, weight estimate = 5 g
80 mm < fish length < 115 mm, weight estimate = 10 g
fish length > 115 mm, weight estimate = 20 g.

The auklet census plots were chosen on the basis of visibility and representativeness with regard to auklet density. The plots were placed variously in areas of high, medium and low density and in transition zones between areas of different density. Counting positions were located in most cases such that more than one plot could be censused from each position. All positions were at least 40 m away from the plots to minimize disturbance of birds during the counts. Photographs were taken to document the locations of all plots.

Two methods were employed to establish indices of auklet numbers on the census plots, the "net movement" method described by Byrd et al. (1983) and a modification of the "surface average" method described by Bedard (1969a).

Bedard (1969a) counted the number of birds in 14.2 x 14.2 m plots every half hour between 0500 and 0800 hours during the last few days preceding egg-laying. The censuses were taken on three successive days and the second, third and fourth-highest counts were averaged. For our surface average counts we established 11 census plots in Pterodactyl Colony and 6 plots in Arch colony. The plots were 10x10 m in surface area. We counted the number of each species of auklet on each plot once every 15 minutes during the entire morning and early-afternoon activity period, generally between the hours of 0500-1500 in early June. Hours of peak activity became later as the season progressed, so we adjusted our census period to correspond to that change. Counts were made during three phenological periods: pre-laying (arrival of birds on the plots until 17 June), incubation (18 June - 16 July), and chick feeding (17 July - sea-going). We averaged the five highest counts from each day counts were made. Additional counts were made of the proportions of immature auklets and of adults carrying food.

Two water sampling stations at Cape Lisburne were occupied at intervals of about three days or less except when ice or weather conditions prevented boat travel. The stations were approximately 2 km offshore; one station was directly north of the Cape Lisburne Air Force Station and the other was directly west of Kay Creek on the west side of the cape. The bottom depth of each was approximately 16 m. One liter water samples for the determination of chlorophyll-a were taken in replicate from the depths of 1, 5 and 15 m. The samples were filtered through glass fiber filters within 30 minutes of collection, buffered with magnesium carbonate and frozen in air-tight, dark containers over calcium carbonate within 20 minutes of filtration according to the method of Strickland and Parsons (1972). The samples remained frozen until they were extracted in 90% acetone and read with a Turner Designs fluorimeter in the laboratory (Strickland and Parsons 1972).

Zooplankton were collected in a 0.5 m, 0.250 mm mesh net towed vertically from the bottom to the surface. The samples were preserved in 5% formalin and

identified by K. Coyle at the Institute of Marine Science, University of Alaska. Fresh sand lance regurgitated by Kittiwake chicks were preserved in 5% formalin and the contents of their stomachs also were analysed by K. Coyle.

We have extended the notation for observers used in our earlier reports. As used in this report, the notations are: C - A. Springer, E - D. Roseneau, N - D. McGuire, O - G. van Vliet, P - P. Martin, Q - B. Cooper, R - S. Cooper.

VI. RESULTS

A. Murres

1. Census

The results of the murre censuses on St. Matthew I. and Cape Lisburne are detailed in Appendix Tables 1 and 2, respectively. Included in Appendix Table 1 are the diurnal compensation counts of murres from St. Matthew I.

St. Matthew I.

Results of the murre census on 15 plots on St. Matthew I. that contained murres and that were censused in all three years of study [1977 - DeGange and Sowls (1978), 1982 - Springer et al. (in press a)] are summarized in Table 1. Friedman's and Multiple Comparisons tests of significance indicated that the uncompensated scores in 1982 were significantly lower than those in 1977 and 1983, which were equivalent (.01< P<.025).

Interpretation of the scores compensated for diurnal activity patterns are less straight-forward. DeGange and Sowls (1978) noted the counting times for only 8 of the plots and did not make any diurnal activity counts in 1977. We counted a particular plot at several different times of the day in 1982, but all counts were not on the same day. Therefore, daily (day-to-day), as well as diurnal, changes in attendance were incorporated into the activity pattern we used to compensate the 1982 scores. In 1983 we made repeated counts of a plot at different times of the day on the same day. A strong correlation over the daily cycle existed between the 1982 and 1983 curves (Fig. 3), however, the magnitude of the hourly changes differed considerably; in 1982 there was a larger proportional change between the morning low and the evening peak numbers, perhaps reflecting the overall effect of daily changes in attendance.

The 1982 census scores for all 15 plots compensated by using both the 1982 and 1983 diurnal activity curves, and the 1983 scores compensated by using the 1983 curve are summarized in Table 1. Table 2 summarizes the uncompensated and compensated scores for 8 plots where the counting times were recorded in 1977; the 1977 and 1982 scores have been compensated using both the 1982 and 1983 diurnal curves. When the scores from all three years are compensated using the 1983 curve, the same pattern as in the uncompensated scores is obtained, i.e., numbers in 1977 and 1983 are equivalent, while the number in 1982 is about 40% lower. However, when the 1982 curve is used to compensate the 1977 and 1982 scores, as done in our previous report, the numbers in 1982 and 1983 are equivalent and are about 45% lower than the number in 1977.

Table 3 summarizes the results of repeated counts of 3 subplots at St. Matthew I. in 1982 and 1983. The sum of the 1983 counts averaged 84% higher than the sum of the 1982 counts. Table 4 lists the results of repeated counts in 1982 and 1983 of a subplot containing only thick-billed murres. The mean of the

Table 1. Numbers of murres on Plots D-1, 2 and 6-9; E-1, 3, and 6-8; and F-1, 3, 4 and 6 at St. Matthew Island. Data for 1977 are from DeGange and Sowls (1978).

Year	Uncompensated Scores	Compensated Scores
1977	42,882	--
1982 ^A	24,634	49,120
1982 ^B	--	30,782
1983	37,094	50,436

^A Scores compensated using 1982 diurnal counts.

^B Scores compensated using 1983 diurnal counts.

Table 2. Numbers of murres on Plots E-3 and 6-8; and F-1, 3, 4 and 6 at St. Matthew Island. Data for 1977 are from DeGange and Sowls (1978).

Year	Uncompensated Scores	Compensated Scores
1977 ^A	20,975	54,450
1977 ^B	--	29,559
1982 ^A	15,270	27,450
1982 ^B	--	18,858
1983	22,562	30,444

^A Scores compensated using 1982 diurnal counts.

^B Scores compensated using 1983 diurnal counts.

Table 3. Uncompensated numbers of murres on three subplots at St. Matthew Island where replicate counts were made in 1982 and 1983.

Subplot	1982			1983		
	n	x	s	n	x	s
9a	2	1,502	194	2	4,157	730
9b	5	1,621	833	6	1,985	690
9d	2	2,232	1,057	3	3,086	333
Total:		5,355			9,842	

Table 4. Counts of common murres (COMU) and thick-billed murres (TBMU) on two subplots in plot E-1 on St. Matthew Island, 1982 - 1983^a.

Year	Date	Subplot	Time ^b	COMU	TBMU
1982	25 Jul	1	1521	0	124
		2	1732	0	187
	1 Aug	1	1530	0	139
			1930	0	133
	9 Aug	1	1520	0	83
1983	16 Jul	1	1905	0	154
	20 Jul	1	1241	0	163
	28 Jul	1	1611	0	161
	5 Aug	2	1630	13	134

^a All counts were made by Observer E.

^b Bering Daylight Time.

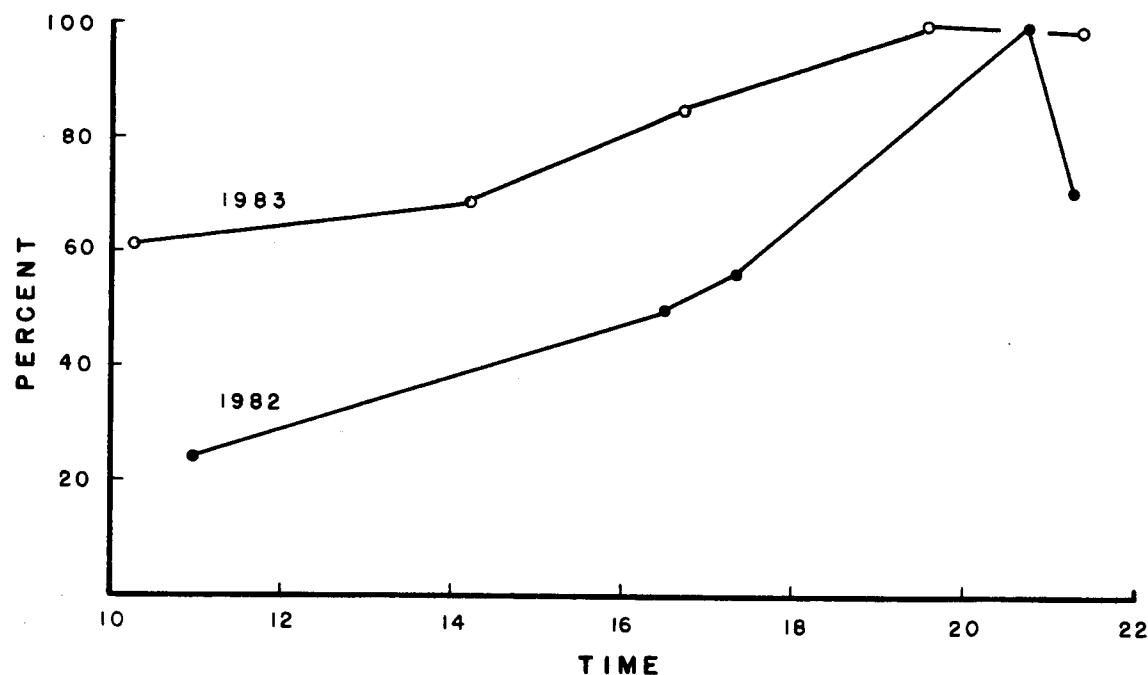


Fig. 3. Diurnal activity patterns of murres on St. Matthew I. in 1982 and 1983.

counts in 1983, 159, is 33% higher than the mean of the counts in 1982, 120.

Common and thick-billed murres were differentiated during single counts of 7 subplots on St. Matthew I. (Table 5) and of 13 subplots on Hall I. (Appendix Table 3). Six of the subplots on St. Matthew I. were counted similarly by DeGange and Sowls in 1977. A comparison of the proportions of the two species in 1977 and 1983 shows no consistent difference in relative numbers of the two species between years. Three additional areas were established in 1983 where repeated counts of all species were made (Appendix Tables 4-6).

Cape Lisburne

A summary of the murre censuses at Cape Lisburne is presented in Table 6, including the results from 1984 (Springer and Byrd, unpubl. data). Compensation in all years was done using the diurnal curve obtained in 1977. The results are remarkably consistent with other years, suggesting that there has been no long-term change in numbers since 1976.

2. Phenology and Reproductive Success

St. Matthew I.

Two plots were located where nesting thick-billed murres could be easily viewed. Our counts of the numbers of eggs, chicks and adults on those plots are listed in Tables 7 and 8. We were unable to find similar plots where sufficient numbers of common murres were visible for meaningful information. The counts of the thick-billed murre egg plots will provide a basis for comparing productivity in future years.

Table 5. Ratios of common murres (COMU) and thick-billed murres (TBMU) at St. Matthew Island, 1977 and 1983. Data for 1977 data are from DeGange and Sowls 1978; A. Sowls, unpubl. data.

Location	Time ¹	Date	COMU	TBMU	COMU/TBMU
Glory of Russia Cape					
(1st Cove - left)	ND ² 1303	12 Jul 1977 21 Jul 1983	59 44	203 339	0.3 0.1
(1st Cove - right)	ND 1415	12 Jul 1977 21 Jul 1983	19 300	95 466	0.2 0.6
(2nd Cove - left) ³	1700 1440	19 Jul 1977 21 Jul 1983	0 22	276 137	0 0.2
(2nd Cove - right)	ND 1440	19 Jul 1977 21 Jul 1983	ND 49	ND 236	ND 0.2
(Shore-side of D-8)	1730 1338	19 Jul 1977 21 Jul 1983	194 235	0 0	0 0
(Sea-side of D-8)	ND 1338	19 Jul 1977 21 Jul 1983	ND 270	ND 52	ND 5.2
Bull Seal Point					
(Northwest side)	1130 1040	9 Jul 1977 1 Aug 1983	125 197	57 47	2.2 4.2
(Southeast side)	1100 ND	8 Jul 1977 1983	26 ND	39 ND	0.7 ND
Cape Upright					
(Plot No. 1)	ND ND	15 Jul 1977 1983	6 ND	274 ND	<0.1 ND
(Plot No. 2)	ND ND	15 Jul 1977 1983	13 ND	37 ND	0.4 ND
<hr/>					
Totals (1977 plots recounted in 1983):		1977 1983	272 798	631 989	0.4 0.8
Totals (all plots counted each year):		1977 1983	442 1,117	981 1,277	0.5 0.9

¹ Bering Daylight Time.

² ND = no data.

³ The "2nd Cove" total reported by DeGange and Sowls (1978) is a count of the cove's north side (see DeGange and Sowls 1978, Figure 6).

Table 6. Summary of murre census results at Cape Lisburne.

Year	Uncompensated Scores		Compensated Scores	
	Sample A ¹	Sample B ²	Sample A	Sample B
1976	9,925	14,100	NA	NA
1977	10,106	15,501	14,779	22,138
1978	9,524	NA	14,094	NA
1979	10,390	16,123	17,342	26,050
1981	10,108	14,236	11,968	17,735
1983	9,401	16,395	15,110	25,151
1984	11,228	16,283	22,148	30,622

¹ Plots 11, 12, 25, 26, 30, and 32.² Plots 11, 12, 25, 26, 30, 32, 65, 66, 70 and 72.

Common murres laid earlier than thick-billed murres as they did in 1982. Common murres began carrying fish, particularly capelin, to the colonies about 15 July and many were carrying fish by 26 July. The first common murre chick was seen on 19 July and the smallest chicks seen on 9 August were about 8-10 days old. These hatching dates are about 2-3 weeks earlier than in 1982 (see Springer et al. in press a) and are comparable to hatching dates on the Pribilof Is. during 1975-79 (Hunt et al. 1981a). Sea-going of common murres was first seen on 1 August, but few chicks left the cliffs before about 10-14 August. Thick-billed murres were first seen carrying fish on 27 July and many were carrying fish by 9 August. The first thick-billed murre chicks were seen on 7 August and were less than about five days old. On 9 August the estimated ages of 18 thick-billed murre chicks were: 1-2 days old, 6; 2-4 days old, 4; 4-6 days old, 8; > 6 days old, 0.

Cape Lisburne

The first murre chick was seen on 2 August, a date somewhat later than average (Table 9). Murre eggs and chicks were abundant on the ledges indicating that reproductive success was good.

3. Food Habits

St. Matthew I.

Food habits of murres at St. Matthew I. in 1982 and 1983 are summarized in Tables 10 and 11, respectively. Pollock and a taxon we have tentatively identified as belonging to the family Pleuronectidae were both important contributors

Table 7. Counts of adult thick-billed murres, eggs and chicks on eggplot 1 at Arch Colony, St. Matthew Island, 1983.

	27 Jun	4 Jul	13 Jul	22 Jul	1 Aug
Number of adults (time ¹)	72 (1500) 31 (1500)	37 (0600) 28 (1135)	24 (0845) 47 (1335)	66 (0900) 49 (1530)	ND ²
Number of eggs	12	3	ND	ND	2
Number of chicks	0	0	ND	ND	3
Number of adults sitting on eggs or chicks	0	6	ND	ND	0
Number of eggs laid since last visit	12	0	ND	ND	0
Number of eggs or chicks lost since last visit	0	3	ND	ND	7

¹ Bering Daylight Time.

² ND = no data.

Table 8. Counts of adult thick-billed murres, eggs and chicks on eggplots 1-3 at North Camp Colony, St. Matthew Island, 1983.

	27 Jun	3 Jul	22 Jul	1 Aug
Number of adults (time ¹)	116 (1615)	98 (1750)	116 (0900) 89 (1530)	63 (ND ²)
Number of eggs	21	24	ND	10
Number of chicks	0	0	ND	10
Number of adults sitting on eggs or chicks	0	0	ND	2
Number of eggs laid since last visit	21	5	ND	6
Number of eggs or chicks lost since last visit	0	2	ND	7

¹ Bering Daylight Time.

² ND = no data.

Table 9. Approximate date of first hatching of murre chicks at Cape Lisburne.

Year	First Hatching
1976	6 Aug
1977	1 Aug
1978	21 Jul
1979	22 Jul
1980	1 Aug
1981	26 Jul
1983	2 Aug

Table 10. Occurrence of major taxa in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) on St. Matthew Island, 15 July - 8 August 1982.

	TBMU		COMU		BLKI	
	n	% ^a	n	% ^a	n	% ^a
Number examined	34	(100)	42	(100)	16	(100)
Number empty	10	(30)	9	(21)	2	(13)
Frequency of invertebrates	12	35	19	45	12	75
Frequency of fishes	21	62	31	74	1	6
A. Frequency of Occurrence						
<i>Theragra chalcoptera</i>	13	54	28	85	0	0
<i>Gadus macrocephalus</i>	0	0	1	3	0	0
Cottidae	7	29	7	21	0	0
<i>Mallotus villosus</i>	0	0	2	6	0	0
Pleuronectidae ^b	6	25	20	61	1	7
Unidentified fishes	3	13	2	6	0	0
Shrimps	6	25	0	0	1	7
Crabs	1	4	2	6	2	14
Parathemisto spp.	3	13	5	15	1	7
Grammatidae	5	21	1	3	1	7
<i>Thysanoessa</i> spp.	0	0	2	6	2	14
Mysidae	1	2	1	1	0	0
Snails	2	8	0	0	7	50
Squids	0	0	0	0	1	7
Polychaetes	8	33	4	12	8	57
Unidentified invertebrates	0	0	7	21	1	7
B. Numbers of Individuals						
<i>Theragra chalcoptera</i>	640 ^c	68	464	71	0	0
<i>Gadus macrocephalus</i>	0	0	1	<1	0	0
Cottidae	31	3	8	1	0	0
<i>Mallotus villosus</i>	0	0	3	<1	0	0
Pleuronectidae ^b	266	28	169	26	1	100
Unidentified fishes	3	<1	4	<1	0	0
C. Estimated Wet Weight (g)						
<i>Theragra chalcoptera</i>	536	63	1,247	90	0	0
<i>Gadus macrocephalus</i>	0	0	5	<1	0	0
Cottidae	170	20	0	0	0	0
<i>Mallotus villosus</i>	0	0	35	3	0	0
Pleuronectidae ^b	133	16	85	6	0.5	100
Unidentified fishes	6	<1	8	<1	0	0

^a Values in parentheses are the frequency among the total number of birds examined. Values not in parentheses are the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains.

^b Tentative identification.

^c One specimen contained 400 individuals, and a second specimen contained 209 individuals.

Table 11. Occurrence of major taxa in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) on St. Matthew Island, 7 June - 9 August 1983.

	TBMU		COMU		BLKI	
	n	% ^a	n	% ^a	n	% ^a
Number examined	57	(100)	79	(100)	53	(100)
Number empty	5	(9)	4	(5)	3	(6)
Frequency of invertebrates	39	75	18	24	35	70
Frequency of fishes	37	71	71	95	21	42
A. Frequency of Occurrence						
<i>Theragra chalcoptera</i>	34	65	63	84	17	36
Cottidae	2	4	2	3	0	0
<i>Mallotus villosus</i>	1	2	20	27	3	6
<i>Culpea harengus</i>	1	2	1	1	0	0
Pleuronectidae ^b	15	29	24	32	0	0
Shrimps	1	2	2	3	1	2
Crabs	1	2	0	0	0	0
<i>Parathemisto</i> spp.	6	12	2	3	3	6
Gammaridae	10	19	0	0	4	9
<i>Thysanoessa</i> spp.	2	4	7	9	1	2
Mysidae	1	2	1	1	0	0
Isopoda	3	6	0	0	2	4
Squids	0	0	0	0	3	6
Polychaetes	8	15	1	1	12	26
Pteropoda	0	0	0	0	8	17
Unidentified crustaceans	15	29	9	12	5	11
Mollusca	0	0	0	0	3	6
B. Numbers of Individuals						
<i>Theragra chalcoptera</i>	317	84	786	64	41	91
Cottidae	15	4	4	<1	0	0
<i>Mallotus villosus</i>	2	<1	52	4	4	9
<i>Culpea harengus</i>	1	<1	2	<1	0	0
Pleuronectidae ^b	43	11	378 ^c	31	0	0
C. Estimated Wet Weight (g)						
<i>Theragra chalcoptera</i>	1,533	90	5,773	83	388	80
Cottidae	75	4	7	<1	0	0
<i>Mallotus villosus</i>	40	2	955	14	100	20
<i>Culpea harengus</i>	30	2	60	<1	0	0
Pleuronectidae ^b	22	1	189 ^d	3	0	0

^a Values in parentheses are the frequency among the total number of birds examined. Values not in parentheses are the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains.

^b Tentative identification.

^c One specimen contained 310 individuals.

^d One specimen contained 155 individuals.

of biomass to murre diets in 1982. The importance of the flatfish in 1983, however, was much less than pollock, which dominated murre diets that year. Capelin (Mallotus villosus) were of moderate importance to common murres in 1983.

Invertebrates were taken frequently by thick-billed murres in both years (Table 12) and probably contributed significantly to their diets, particularly during early summer. Common murres characteristically took fewer invertebrates, except in the June sample period. It was not possible to estimate the numbers or biomass of the invertebrate fraction of the stomach contents in most cases because the prey organisms were highly fragmented.

The numbers and estimated biomass of total fishes in murre diets are summarized in Tables 13 - 16. A greater number of fishes with a greater estimated biomass was recovered from common murres than from thick-billed murres. For both species, the biomass of fishes was lowest in June and increased steadily throughout the summer in both years. The numbers of fishes and their estimated biomass were much higher in 1983 than in 1982.

The importance of young-of-year pollock declined dramatically between 1982-1983 (Table 17).

Cape Lisburne

Food habits of murres at Cape Lisburne in 1983 are summarized in Table 18. Cods, primarily Arctic cod with smaller numbers of saffron cod (Eleginus gracilis), dominated the diets of both species throughout the summer. The availability of cods in 1983 was unprecedented in the many prior years of study at Cape Lisburne. Other prey taxa were of little importance.

A sense of the magnitude of the contribution of cods can be seen in Table 19, which compares the numbers and estimated biomass of fishes in thick-billed murre diets between years. The average numbers of fishes/bird were not very different than in other years, although the average biomass/bird was generally much higher. This is because in other years taxa such as sculpins, sand lance and capelin contributed substantially to total numbers; however, because these taxa were generally smaller than cods, particularly Arctic cod, their contribution in terms of biomass was relatively small.

B. Black-legged Kittiwakes

1. Census

St. Matthew I.

Results of the census of black-legged kittiwakes on St. Matthew I. are detailed in Appendix Table 7. The results of the censuses of 12 plots counted in three years of study are summarized in Table 20. The total number of birds and nests on the 12 plots increased from 1982 to 1983, but the increase in the number of nests was small. Little difference in the number of nests on those plots has been recorded in the three years that censuses have been taken.

2. Phenology, Reproductive Success and Chick Growth Rates

St. Matthew I.

On 19 July we saw one nest with two small chicks and on 24 July we found

Table 12. Frequency of occurrence (%) of invertebrates in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged Kittiwakes (BLKI) at St. Matthew Island. Values in A include all specimens; values in B exclude empty specimens.

Year		Jun			1-20 Jul			21 Jul-10 Aug		
		TBMU	COMU	BLKI	TBMU	COMU	BLKI	TBMU	COMU	BLKI
1982	A	ND ¹	ND	ND	33	11	100	40	54	71
	B				100	17	100	50	67	100
1983	A	71	50	63	47	0	86	85	9	38
	B	89	52	68	47	0	86	85	9	43

¹ ND = no data.

Table 13. Numbers and estimated biomass of fishes in diets of common murres at St. Matthew Island. Arithmetic mean number and weight (g)/bird.

Year		Jun			1-20 Jul			21 Jul-10 Aug		
		n	\bar{x}	s	n	\bar{x}	s	n	\bar{x}	s
<u>Numbers</u>										
1982			ND ^a		9	2	3	33	20	43
1983		30	7	10	13	14	14	34	24	56
<u>Biomass</u>										
1982			ND		9	10	17	33	46	62
1983		30	54	80	13	115	73	34	130	127

^a ND = no data.

Table 14. Numbers and estimated biomass of fishes in diets of thick-billed murres at St. Matthew Island. Arithmetic mean number and weight (g)/bird.

Year	Jun			1-20 Jul			21 Jul-10 Aug		
	n	\bar{x}	s	n	\bar{x}	s	n	\bar{x}	s
Numbers									
1982		ND ^a		9	<1	1	25	37 ^b	119
1983	24	2	4	14	10	19	19	10	16
Biomass									
1982		ND		9	3	6	25	48 ^c	118
1983	24	9	21	14	39	43	19	52	59

^a ND = no data.

^b One specimen contained 480 individuals and a second specimen contained 386 individuals.

^c One specimen contained 359 g and a second specimen contained 459 g.

Table 15. Numbers and estimated biomass of fishes in diets of common murres at St. Matthew Island. Geometric mean number and weight (g)/bird.

Year	Jun			1-20 Jul			21 Jul-10 Aug		
	n	\bar{x}	$\pm 1s$	n	\bar{x}	$\pm 1s$	n	\bar{x}	$\pm 1s$
Numbers									
1982		ND		9	2	.8-4	33	6	1-25
1983	30	3	.9-10	13	10	3-28	34	12	4-36
Biomass									
1982		ND		9	3	.4-17	33	11	1-99
1983	30	16	2-110	13	63	11-365	34	73	16-327

ND = no data.

Table 16. Numbers and estimated biomass of fishes in diets of thick-billed murres at St. Matthew Island. Geometric mean number and weight (g)/bird.

Year	Jun			1-20 Jul			21 Jul-10 Aug		
	n	\bar{x}	$\pm 1s$	n	\bar{x}	$\pm 1s$	n	\bar{x}	$\pm 1s$
Numbers									
1982		ND		9	1	.9-1	25	3	.5-16
1983	24	2	.7-4	14	4	.5-16	19	6	2-17
Biomass									
1982		ND		9	1	.3-4	25	3	.3-31
1983	24	1	.2-79	14	14	2-101	19	22	4-125

ND = no data.

Table 17. Relative importance (%) of young-of-year pollock among all pollock in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) at St. Matthew Island, 15 July - 8 August 1982 and 7 July - 9 August 1983.

	TBMU		COMU		BLKI	
	1982	1983	1982	1983	1982	1983
Frequency of occurrence	69	37	82	45	0	0
Number	99	68	88	21	0	0
Biomass	59	8	16	1	0	0

Table 18. Occurrence of major taxa in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) at Cape Lisburne, 16 June - 28 August 1983.

	TBMU		COMU		BLKI	
	n	% ^a	n	% ^a	n	% ^a
Number examined	104	(100)	25	(100)	61	(100)
Number empty	2	(2)	0	(0)	1	(2)
Frequency of invertebrates	46	45	7	28	7	12
Frequency of fishes	101	99	25	100	60	100
A. Frequency of Occurrence						
Cods	89	87	25	100	60	100
Scorpions	44	43	7	28	3	5
Sand lance	11	11	5	20	2	3
Capelin	2	2	1	4	3	5
Other	28	27	7	28	9	15
Shrimps	11	11	0	0	0	0
Amphipods	8	8	5	20	0	0
Mysids	4	4	1	4	0	0
Euphausiids	0	0	0	0	0	0
Polychaetes	18	18	1	4	5	8
Other	29	28	1	4	3	5
B. Numbers of Individuals						
Cods	1,005	73	513	73	617	92
Scorpions	216	16	32	5	2	<1
Sand lance	53	4	135	19	29	4
Capelin	7	<1	1	<1	6	<1
Other	91	7	17	2	19	3
C. Estimated Wet Weight (g)						
Cods	11,531	94	5,324	94	8,688	99
Scorpions	535	4	40	<1	2	<1
Sand lance	100	<1	270	5	58	<1
Capelin	14	<1	2	<1	11	<1
Other	120	<1	34	<1	24	<1

^a Values in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains.

Table 19. Number and estimated biomass of fishes in diets of thick-billed murres at Cape Lisburne. Arithmetic mean number and weight (g)/bird; data for 1977-80 are from Springer et al. (1984).

	Jun			1-20 Jul			21 Jul - 10 Aug			11-31 Aug		
	n	\bar{x}	s	n	\bar{x}	s	n	\bar{x}	s	n	\bar{x}	s
Numbers												
1977	6	5	7	22	6	8	15	7	9	9	9	12
1978		ND		17	8	14	29	20	20	10	15	13
1979		ND		17	12	14		ND		19	23	25
1980		ND			ND		32	6	8		ND	
1983	37	10	15	21	13	14	20	21	20	24	18	17
Biomass												
1977	6	10	13	22	19	29	15	14	18	9	23	36
1978		ND		17	23	44	29	43	70	10	53	55
1979		ND		17	64	81		ND		19	57	67
1980		ND			ND		32	54	84		ND	
1983	37	100	102	20	187	144	20	151	124	24	72	79

ND = no data.

Table 20. Black-legged Kittiwake census summary for 12 plots on St. Matthew Island that were counted in each of three years.

Year	Birds	Nests
1977	---	2,160
1982	2,785	2,036
1983	3,629	2,283

5 small chicks among 34 successful nests. Using the average incubation period of 28 days (Swartz 1966), the eggs from which the 5 chicks hatched were laid before 26 June. Laying dates in late June through early July are the same as in 1982 (Springer et al. in press a).

The reproductive success of kittiwakes in 1983 was the same as in 1982 - few, if any, chicks were raised. The average clutch size was small, but was comparable to that reported for the Pribilof Is. during the late-1970's (see Hunt et al. 1981a); chick survival was very poor (Table 21). We examined an additional 28 nests on St. Matthew I. on 7 August, one of which had one egg and another of which had one chick, and 51 nests on Hall I. on 9 August, two of which had one chick each. All failures during incubation appeared to be caused by adults deserting the nests. Chicks generally died within a few days after hatching, apparently from starvation and exposure.

Cape Lisburne

The mean hatching date of kittiwake chicks at Cape Lisburne was about 30 July, a date midway between the earliest and latest dates in past years (see Springer et al. in press b).

The clutch size of kittiwakes (Table 22) was large compared to other years at Cape Lisburne (see Springer et al. in press b). However, most of the second chicks hatched in two-chick broods died within a few days of hatching. Starvation appeared to be the cause of death. Growth rates of the surviving chicks were relatively slow (Table 23).

3. Food Habits

St. Matthew I.

Kittiwakes at St. Matthew I. fed on pollock, capelin and a variety of invertebrates in 1983 (Table 11). They were frequently seen carrying fish, especially capelin, to the colonies during mid-July, but not after that time when the birds foraged more widely offshore. The shift coincided with the period when large schools of 'bait' fish were detected at depths of 6-24 m in nearshore waters instead of at the surface (J. Anderson, pers. obs. from July-August bathymetry surveys from the Marine Constructor). Considerably more fishes were taken in 1983 than in 1982, when only one fish was recovered from 16 kittiwakes collected in July and August. Invertebrates were taken frequently in both years, but perhaps somewhat less so in 1983 (Table 12). Young-of-year pollock were not taken in either year.

Cape Lisburne

Cods, over 99% Arctic cod, were the principal food of kittiwakes in 1983, as they were for the murres (Table 18). Other species of fishes and invertebrates were not important, except during August when the adults were able to obtain limited numbers of sand lance.

C. Auklets

1. Census

Least auklets, crested auklets (Aethia cristatella) and parakeet auklets (Cyclorrhynchus psittacula) nest on St. Matthew I. Results of the

Table 21. Reproductive success of black-legged kittiwakes at Tusk Colony on St. Matthew Island, 1983.

	Plot 2A	Plot 2B
No. nests	58	172
No. empty nests	29	94
No. 1-egg clutches	22	75
No. 2-egg clutches	7	3
Clutch size / nest	0.6	0.5
No. chicks fledged	0	<3

Table 22. Reproductive success of black-legged kittiwakes at Cape Lisburne, 1983.

No. nests	103
No. empty nests	8
Clutch size / nest	1.6
No. chicks fledged	<3

Table 23. Growth rates of black-legged kittiwake chicks at Cape Lisburne.

Year	Grams/day \pm s (n)
1977	19 \pm 3 (18)
1978	20 \pm 7 (21)
1979	18 \pm 1 (24)
1980	18 \pm 4 (43)
1981	14 \pm 3 (30)
1983	16 \pm 3 (45)

surface average counts of auklets are detailed in Appendix Tables 8 and 9. The census was not designed to estimate the total numbers of auklets on St. Matthew I. or in the two study colonies, but was designed to provide indices of population numbers for future comparisons.

The surface average numbers of auklets on the plots in the two colonies during the three phases of the breeding cycle are summarized in Table 24. Least auklets were generally in the lowest abundance during the prelaying period. Crested auklets were most numerous during incubation. The small numbers of parakeet auklets on the plots preclude similar generalizations for this species. The presence of immature birds, plus the fact that many courtship activities take place underground (Bedard 1969a) may explain our higher numbers during the incubation and chick periods.

Comparisons of net movement and surface average counts of auklets are presented in Table 25. While some variation in the surface average counts occurred, the net movement counts were extremely variable. Thus, the surface average technique appears to be better suited for establishing an index of numbers in the St. Matthew I. colonies than does the net movement technique.

Bedard (1969a) found that immature auklets arrived on St. Lawrence I. in early June and comprised 30-35% of the total number present by 20 June. Immature least auklets were not present in the colonies on St. Matthew I. until nearly the end of June and they comprised about 20% of the total number by mid-July (Fig. 4). Immature crested auklets were not seen until 20 July and also comprised about 20% of the total number (Fig. 4).

2. Phenology and Chick Growth Rates

Upon our arrival on 8 June, auklets had formed pairs and several copulations were seen. Three female least auklets collected on 15 June each had fully developed follicles within one day of laying. The first egg was found on 21 June. On 17 July, chicks from 1-5 days old were found in 8 of 14 nests. The number of adults carrying food also began to increase about that time (Fig. 5). The first sea-going chick was seen on 7 August.

Growth rates of 22 least auklet chicks weighed during intervals of 5-18 days averaged 3.9 g/day ($s = 0.96$ g/day); growth rates of 12 chicks weighed during intervals of at least 10 days averaged 3.6 g/day ($s = 0.78$ g/day). The growth rate of 3.6 g/day was significantly lower than the average growth rate of five chicks in 1982 (4.9 g/day, $s = 0.9$ g/day) weighed during intervals of at least 10 days (Mann-Whitney $P < 0.025$).

3. Food Habits

Food habits of least auklets during the chick period in 1983 are detailed in Appendix Table 10. They are summarized and compared to food habits in 1982 in Table 26. No important differences in the composition of the prey were apparent between years; least auklets on St. Matthew I. depend on one species of copepod, Calanus marshallae, for the majority of their food during the chick period. Comparative data on auklet food habits from the Pribilofs and St. Lawrence I. are presented in Tables 27 and 28. Calanus marshallae, the species characteristic of the middle shelf domain of the SE Bering Sea (Cooney 1981; Smith and Vidal 1984), was replaced in importance on both the Pribilofs and St. Lawrence I. by C. plumchrus and C. cristatus, species characteristic of the outer shelf domain. The location of the Pribilofs relative to the outer shelf domain and of

Table 24. Surface average counts of crested auklets (CRAU), least auklets (LEAU), and parakeet auklets (PAAU) during the pre-laying (PL), incubation (IN), and chick-feeding (CF) periods on study plots at Pterodactyl and Arch colonies on St. Matthew Island, 1983.

Colony	Plot	CRAU			LEAU			PAAU		
		PL	IN	CF	PL	IN	CF	PL	IN	CF
Pterodactyl										
	1	3	2	2	57	62	102	0	<1	0
	2	2	4	2	83	141	131	<1	0	0
	3	<1	1	<1	40	51	49	<1	0	0
	4	<1	2	2	32	46	35	2	<1	<1
	5	3	4	3	59	73	62	0	<1	0
	6	8	12	9	114	126	182	0	0	0
	7	11	18	11	55	51	59	0	0	0
	8	11	25	21	42	52	58	0	0	0
	9	ND	0	0	ND	29	23	ND	0	0
	10	ND	0	0	ND	12	13	ND	0	0
	11	ND	6	6	ND	85	106	ND	0	0
Arch										
	1	0	<1	0	31	69	68	0	0	0
	2	4	7	6	70	96	95	2	<1	0
	3	<1	<1	0	42	44	47	0	0	0
	4	0	<1	0	52	47	51	0	<1	0
	5	ND	8	12	ND	80	80	ND	0	0
	6	ND	<1	0	ND	36	31	ND	0	0

Pre-laying period = arrival to ~17 June, incubation period = ~18 June to ~16 July, and chick-feeding period = ~17 July to fledging.
 ND = no data (plot added after the pre-laying period).

Table 25. Comparisons of surface average and net movement estimates of crested auklet (CRAU), least auklet (LEAU), and parakeet auklet (PAAU) numbers on study plots at Pterodactyl and Arch colonies on St. Matthew Island, 1983.

Colony	Plot	Date	CRAU	LEAU	PAAU	Method of Estimation
Pterodactyl						
	1	11 Jun	3 14	57 400	0 0	Surface average Net movement
		24 Jun	3 0	63 12	<1 0	Surface average Net movement
	2	11 Jun	2 0	129 -554	<1 0	Surface average Net movement
		24 Jun	2 -2	83 -4	0 0	Surface average Net movement
	6	13 Jun	8 4	114 226	0 0	Surface average Net movement
		24 Jun	11 -22	131 -1,252	0 0	Surface average Net movement
	8	13 Jun	11 6	42 -396	0 0	Surface average Net movement
		24 Jun	14 -34	50 -272	0 0	Surface average Net movement
Arch						
	2	16 Jun	4 0	70 16	2 0	Surface average Net movement
	3	16 Jun	<1 2	42 6	0 0	Surface average Net movement

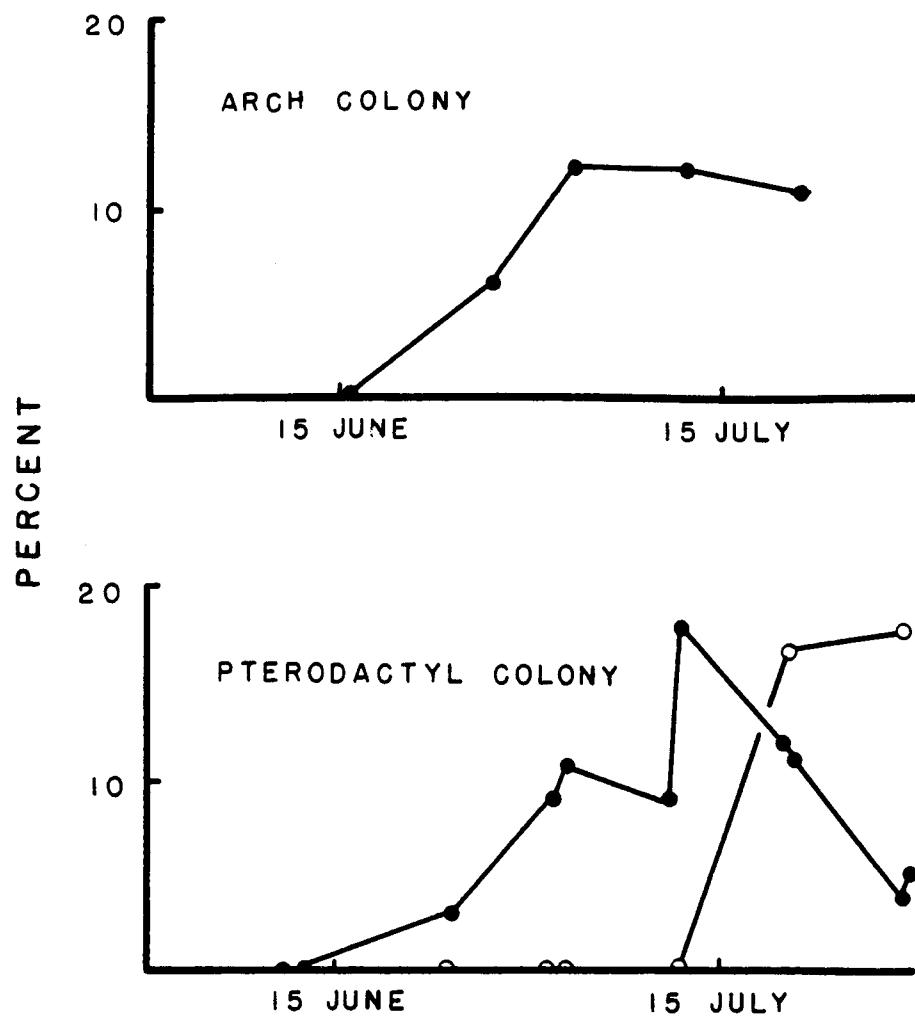


Fig. 4. Proportion of immature auklets in breeding colonies on St. Matthew I. in 1983. Solid circles are least auklets, open circles are crested auklets.

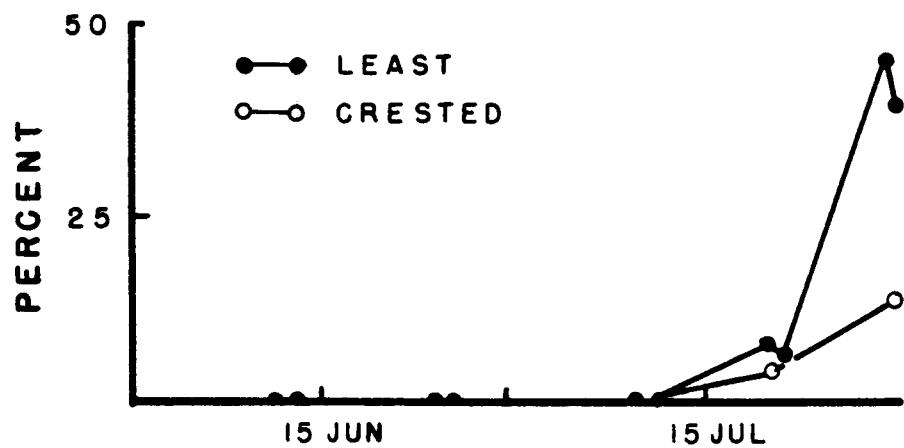


Fig. 5. Proportion of adult auklets carrying food to breeding colonies on St. Matthew I. in 1983.

Table 26. Prey of least auklets on St. Matthew I.

Taxon	1982 (n=29)		1983 (n=40)	
	Number	Volume (%)	Number	Volume (%)
<u>Calanus marshallae</u>	18,658	89	17,668	84
<u>C. plumchrus</u>	0	0	1	<0.1
Hyperiidae	150	5	59	3
Gammaridae	216	4	209	9
Decapod zoea	187	1	460	3
<u>Thysanoessa</u> spp.	10	<0.1	80	1
<u>Limacina helicina</u>	73	<0.1	8	<0.1
Other	1	<0.1	1	<0.1

Table 27. Prey of least auklets on the Pribilof Is., 1975-78. Numbers (%) are from Hunt et al. (1981a); volume (%) is according to text. N=258.

Taxon	Number (%)	Volume (%)
<u>Calanus marshallae</u>	65	30
<u>C. plumchrus</u>	11	5
<u>C. cristatus</u>	24	48
Hyperiidae	2	9
Gammaridae	2	5
Decapod zoea	0	0
<u>Thysanoessa</u> spp.	<1	2
<u>Limacina helicina</u>	0	0
Other	0	0

Table 28. Prey of least auklets on St. Lawrence I. Data for 1964-66 are from Bedard (1969); data for 1976 are from Searing (1977).

Taxon	1964-66 (n=124)		1976 (n=12)		1981 (n=24)	
	Number	Volume (%)	Number	Volume (%)	Number	Volume (%)
<u>Calanus marshallae</u>	77,908	65	344	3	3,132	26
<u>C. plumchrus</u>	0	0	9,047	90	6,205	50
<u>C. cristatus</u>	1,444	8	32	2	197	11
<u>Eucalanus bungii</u>	169	<1	9	<1	0	0
Hyperiidae	2,102	9	57	1	32	<1
Gammaridae	533	3	9	<1	21	<1
Decapod zoea	2,808	3	47	<1	643	7
<u>Thysanoessa</u> spp.	2,325	7	2	<1	1	<1
<u>Limacina helicina</u>	6	<1	34	<1	3	<1
Other	311	1	31	<1	0	0

St. Lawrence I. relative to the Bering Slope current probably accounts for the differences between the composition of the prey of auklets on these islands and that on St. Matthew I. (Springer and Roseneau in press).

Although there were no important differences in the composition of auklet prey on St. Matthew I. between 1982 and 1983, quantitative differences in prey between years may exist. Comparisons of this kind can be misleading, however, it is interesting that the difference between the average number of copepods recovered from sublingual pouches of adult least auklets in 1982 and 1983, 640 \pm 460, respectively, or a decline (Mann-Whitney $P<0.001$) of about 30%, is nearly the same as the percentage decline in the growth rates of chicks between the two years. The prey in sublingual pouches is that which is fed to chicks.

Least auklets on St. Matthew I. apparently fed close to the island at most times. Hunt et al. (1981a) suggested that auklets feed generally within 30 km of shore in the Pribilof Is. Auklets nesting in the northwestern part of the island flew westward to feed during July, while those nesting in the northeastern part of the island flew northeast to feed. After 30 July, auklets in the northeast fed in large concentrations within a zone from about 5 m - 1 km of shore. We have seen similar episodes of auklets feeding nearshore on St. Lawrence I. during periods of strong upwelling (Springer and Roseneau in press).

D. Food Web Dynamics

Cape Lisburne

Primary production, as measured by the integrated chlorophyll-a concentration, underwent a typical bloom in early summer as the sea ice broke up (Fig. 6). Following the bloom, phytoplankton populations remained low throughout the summer. However, beginning in early August, the chlorophyll concentration began to rise, increasing about 3-fold over the lowest levels by the end of the month. We do not know if the increase resulted from in situ production or from advection into the region from the south.

From the examination of stomach contents of sand lance, we found that the fish were feeding on a meroplanktonic stage of a bivalve, the cladocerans Podon spp. and Evdne spp. and the copepods Pseudocalanus spp. and Acartia clausi. The ambient concentrations of all five taxa were generally low until early August, when they increased dramatically in abundance (Fig. 7). The increases occurred at the same time as that of chlorophyll-a, postdating the seasonal rise in water temperature by about 2 weeks (Fig. 7).

A concurrent increase in the importance of sand lance in murre and kittiwake diets occurred in early August (Fig. 8). Sand lance were not an abundant item in the birds' diets in 1983, a characteristic typical of cold years. Water temperature in mid-July was only 3°C which is in the low range of temperatures for that time of year (Table 29).

E. Characteristics of Prey Populations

The majority of pollock eaten by murres and kittiwakes at St. Matthew I. were age class 1 according to the length of the fishes, as determined from their otoliths, and data on pollock size-at-age reported by Smith (1979). The distribution of the lengths of intact otoliths recovered from murres and kittiwakes in 1983 (Fig. 9) indicates the sizes of length cohorts of pollock. For reference, fish lengths can be calculated by using the regression equations

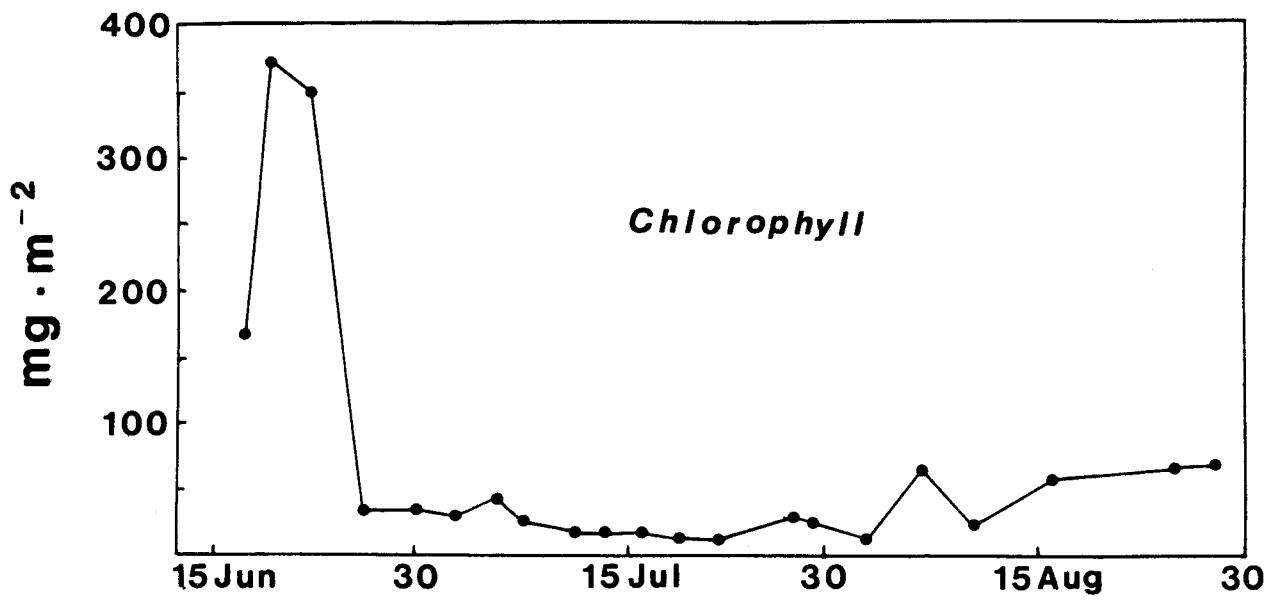


Fig. 6. Integrated chlorophyll-a at Station A, Cape Lisburne, 1983. Surface to bottom, mean depth about 15 m.

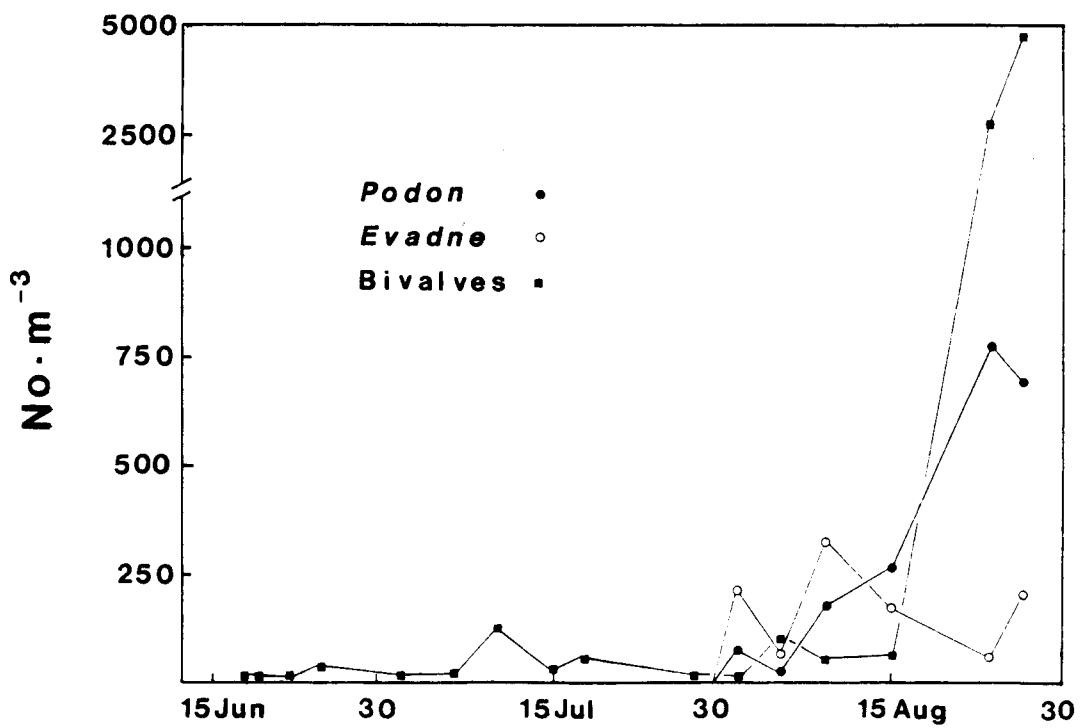
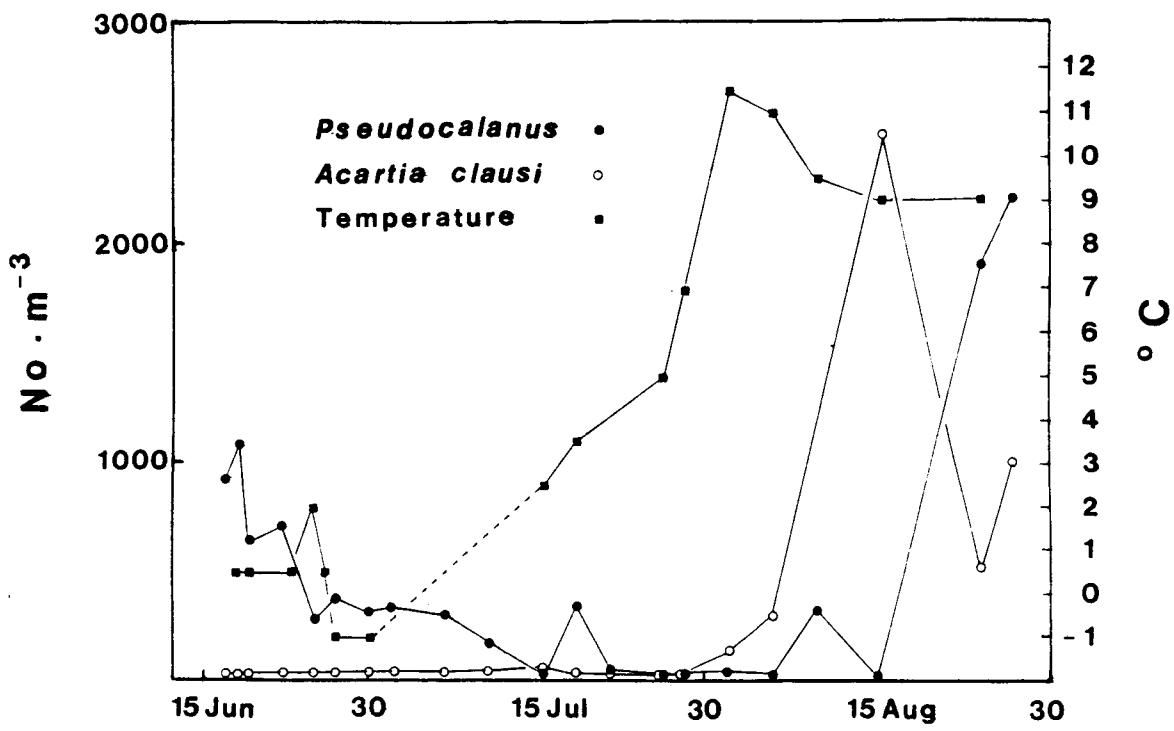


Fig. 7. Water temperature and the ambient concentrations of the five most abundant taxa in diets of sand lance near Cape Lisburne, 1983.

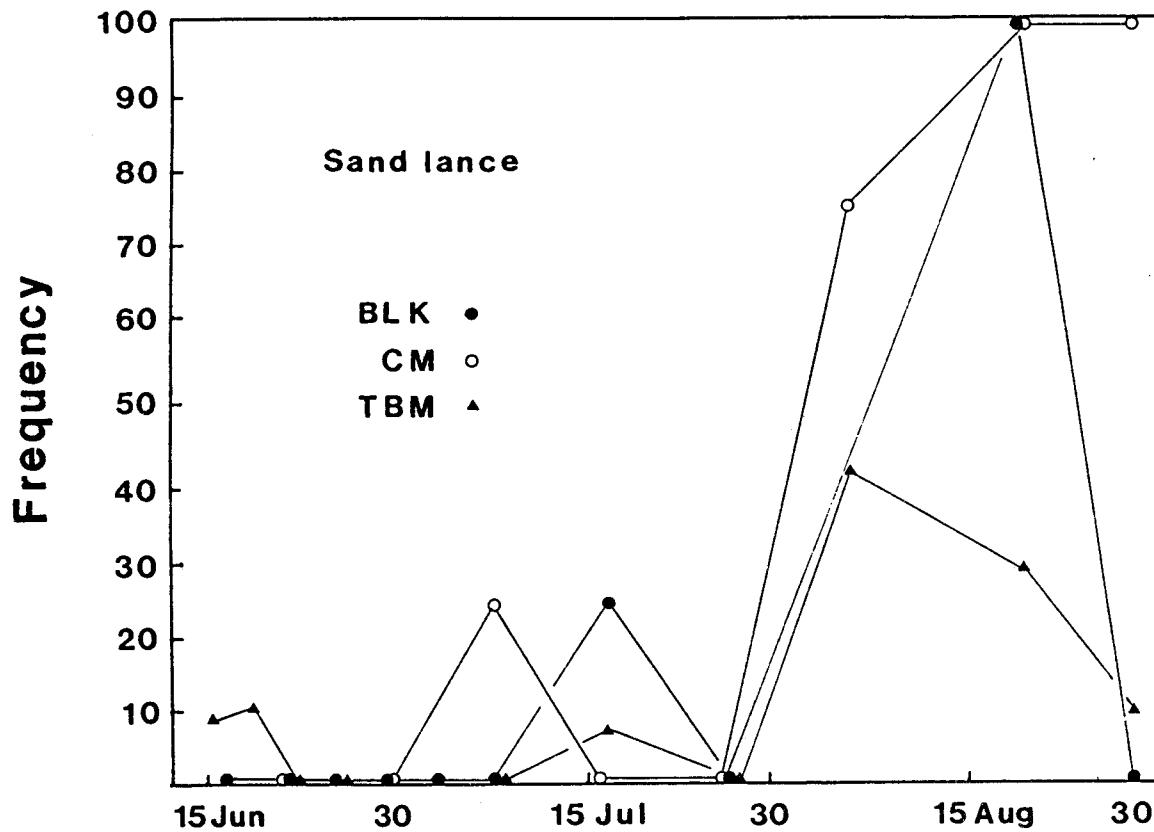


Fig. 8. Frequency of occurrence of sand lance in the diets of murres and kittiwakes at Cape Lisburne, 1983.

Table 29. Water temperature during mid-July at Cape Lisburne.

Year	Degrees C
1974	7
1975	4
1976	2
1977	6
1978	8
1979	13
1980	10
1981	11
1982	10
1983	3

reported above. There was apparently no difference between the distributions in 1982 and 1983, although the 1982 sample size was too small ($n = 32$) for meaningful comparison. The 1983 distribution does not necessarily reflect the absolute contribution of each cohort to the total numbers of pollock taken, since many of the otoliths were broken and could not be included in the above distribution. Also, the young-of-year cohort referred to in Table 17 is not shown in Fig. 9. Otoliths of that cohort were less than 14 otolith units.

The three principal size cohorts of sand lance in the 1983 sample (Fig. 10) ranged in age from 0+ - 1+. The two smallest cohorts were somewhat larger than those in 1977, but considerably smaller than those in 1980. This pattern is similar to that previously observed, when fishes tended to be larger in warmer years (Springer et al. 1984). In 1983, the size distributions of each of the three cohorts were bimodal, and the differences in size between modes of the smaller size range were proportional to those of the larger size range. This pattern suggests that individuals from two populations are represented among the otoliths, perhaps a local population and one that was advected into the region from the south. We have shown previously that sand lance taken by seabirds at Cape Thompson were larger than at Cape Lisburne, and that sand lance taken at Bluff were largest (Springer et al. 1984; in press b)

Two distinct size-age cohorts of saffron cod were taken by murres and Kittiwakes at Cape Lisburne in 1983 (Fig. 11). During the first half of the summer, larger fishes were taken, while later in the summer smaller fishes were taken. The lengths apparently represent fishes that differ in age by one year (0+ and 1+ age classes) according to Craig et al. (1981), who report length-at-age data for saffron cod in the Beaufort Sea. Advection possibly played a role also in the change in size of saffron cod during the summer. The average length of the smaller fishes was larger in 1983 than the average length of the same age class collected during the same interval in 1979 (Fig. 11). This pattern is consistent with the trend recorded in 1976-79, when saffron cod were smaller in warmer years than in colder years (Springer et al. 1984).

VII. & VIII. DISCUSSION AND CONCLUSIONS

SE Bering Sea

The breeding season of 1983 was the third consecutive year of failure for black-legged Kittiwakes on islands in the SE Bering Sea. Kittiwakes failed on the Pribilof Is. in 1981 (D. Lloyd pers. comm.), 1982 (Craighead and Oppenheim 1982) and 1983 (A. Merculieff pers. comm.) and on St. Matthew I. and Hall I. in 1982 and 1983. Our impression is that low prey availability during those years was responsible for the failures. Because pollock are the most important prey of Kittiwakes on the Pribilof Is. (Hunt et al. 1981a) and on St. Matthew I., an absence of pollock in surface waters apparently has been the direct cause.

Murres had a better season than they had in 1982, and they had a better season than Kittiwakes had in 1983. The uncompensated numbers of birds on the census plots on St. Matthew I. in 1983 were similar to numbers in 1977 and higher than 1982. There is little evidence of a long-term decline in the murre population on St. Matthew I. as has occurred at Cape Thompson and Bluff (see Springer et al. in press b). Similarly, murre numbers on St. Lawrence I. were lower in the particularly severe year 1976 than in 1971 and 1981 (Roseneau et al. in press). Murre numbers on the cliffs at Bluff in mid-July 1984 were only about a third as large as numbers in recent years, but are not expected to remain that low since the summer of 1984 was extremely severe oceanographically in Norton

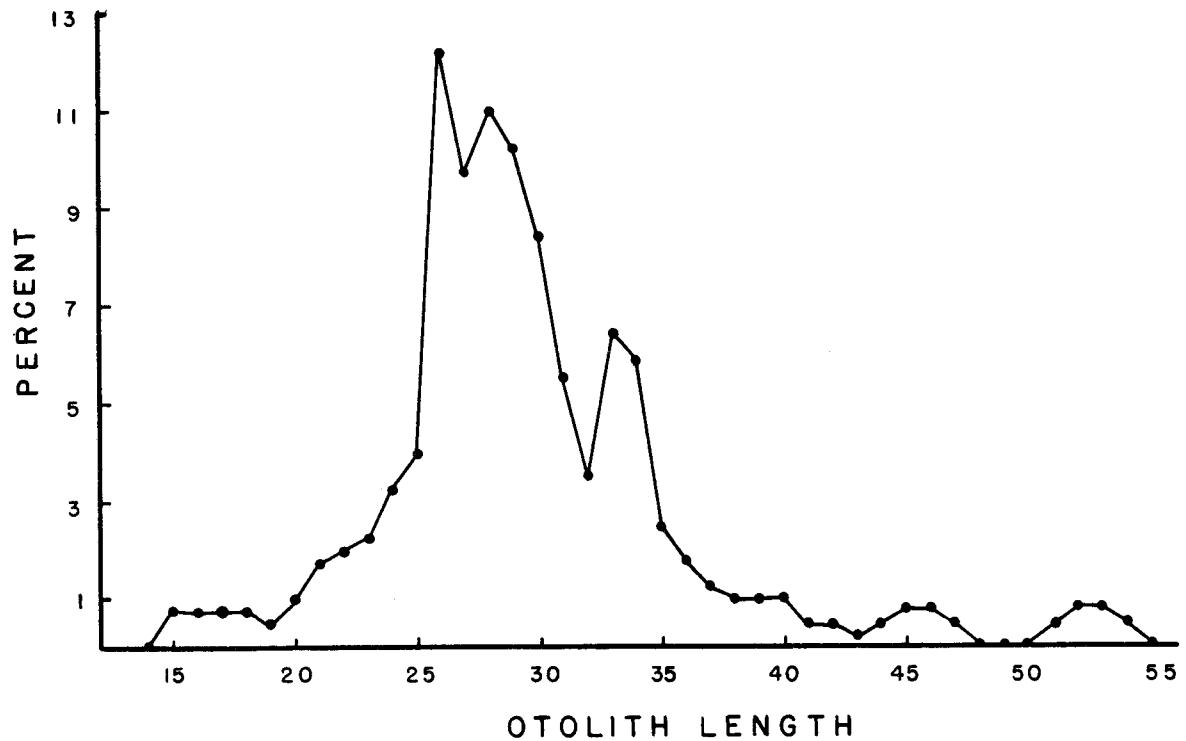


Fig. 9. Size frequency distribution of otoliths of pollock eaten by murres and kittiwakes on St. Matthew I., 1983. Otolith length in units, 6.25 units/mm.

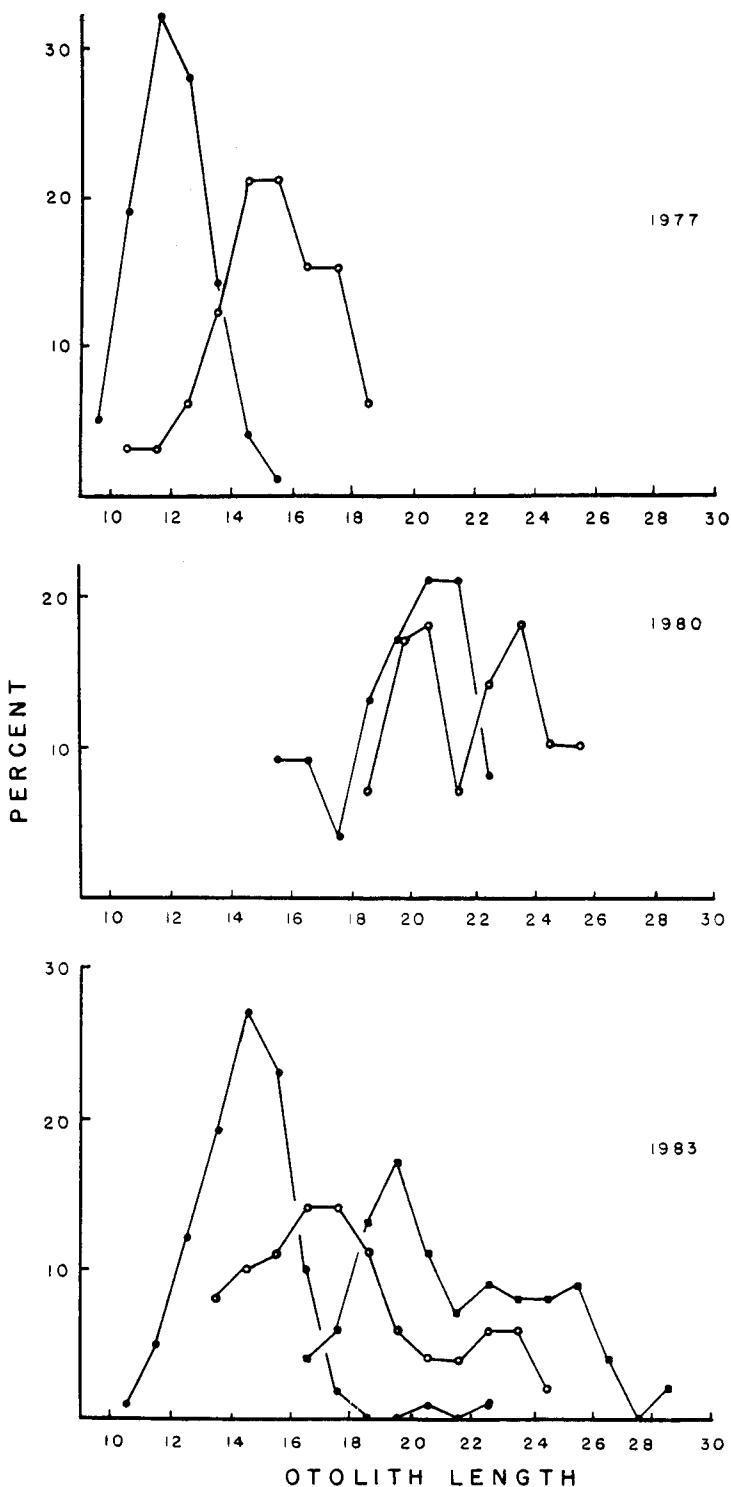


Fig. 10. Size frequency distribution of otoliths of sand lance eaten by murres and kittiwakes at Cape Lisburne, 1983. Solid circles are youngest age, open circles are older age, solid squares are oldest age. Otolith lengths are in units, 12.5 units/mm.

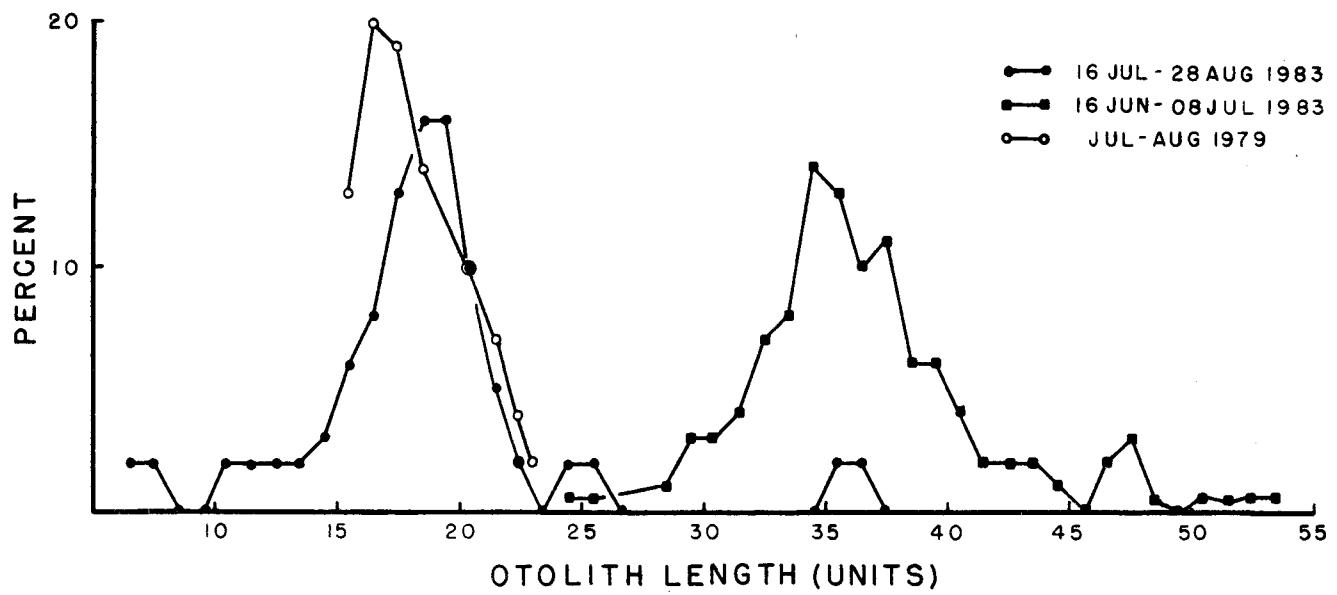


Fig. 11. Size frequency distribution of otoliths of saffron cod eaten by murres and kittiwakes at Cape Lisburne, 1983. Otolith length in units, 6.25 units/mm.

Sound (Springer et al. unpubl. data). Because pollock are the most important prey of murres in the SE Bering Sea, particularly low availability of pollock in 1982 might account for the low murre numbers that year.

The majority of pollock biomass in murre and kittiwake diets is contributed by year class 1 fish. Fishery survey data obtained by the Northwest and Alaska Fisheries Center (NAFC) indicate that the abundance of age 1 pollock in the SE Bering Sea in 1983 was about three times greater than in 1981 or 1982 (Bakkala and Traynor 1984). Our food habits data, which show a marked increase in consumption of pollock between 1982-83, are consistent with these survey data.

The NAFC data also show that the recruitment of the 1979-1981 year classes was low compared to that of the 1974 and 1978 year classes, i.e., the abundance of age 1 pollock in 1980-1982 was low compared to 1975 and 1979. Unfortunately, comparable data are not available for the year-class years 1975-1977. Still, the information generally fits well with the pattern of reproductive success of black-legged kittiwakes on St. George I. since 1976 (Table 30). It is not inconsistent that reproductive success in 1983 remained low, since the estimated abundance of age 1 pollock in 1983, while about three times greater than the previous two years, was still only 40% of the 1979 estimate (Bakkala and Traynor 1984).

Another interesting relationship involves the auklets and the connection between the abundance of their main prey, copepods, and the abundance of pollock. We have discussed the possibility elsewhere that tight coupling in the pelagic copepod-based food web of the SE Bering Sea might lead to multispecies interactions when stocks of pollock wax and wane (Springer and Roseneau in press). Age class 1 pollock feed on large calanoid copepods (Clarke 1978; Smith 1981; T. Nishyama unpubl. data) that are also the major prey of least auklets. Smith and Vidal (1984) have suggested that declines in the numbers of calanoids from the outer shelf domain during spring represent losses to vertebrate consumers, including whales, birds and fishes. Thus, years in which recruitment of age 1 pollock is low, as in 1982, would be favorable for auklets, since the auklets would face less competition from the fish for prey biomass. The observations from St. Matthew I. during the past two years support such an hypothesis. In 1982, a poor pollock year, auklets apparently were able to feed their chicks more, resulting in faster chick growth, than in 1983, a much improved pollock year. In contrast, murres and kittiwakes, which depend on pollock, had better seasons in 1983 than in 1982.

On a larger scale, the distribution in the Bering Sea of pollock and copepod biomass may contribute to the geographical differences in the numbers of murres and auklets at insular breeding colonies. Copepods are apparently supplied to the northern shelf by the Bering Shelf current, which advects zooplankton from the outer shelf domain onto the northern shelf (Springer and Roseneau in press). However, pollock are rarely found on the northern shelf, where they are replaced by Arctic and saffron cod (Frost and Lowry 1981a; Wolotira et al. 1979). Probably because of harsher environmental conditions, populations of these cods, as well as of other fishes, are small compared to the pollock population as indicated by test fishery data (Wolotira et al. 1979) and by the absence of a commercial fishery on the northern shelf. In summer, the baleen whales are represented only by the gray whale (Eschrichtius robustus), which feeds primarily on benthic amphipods (see Frost and Lowry 1981b). Thus, competitors of auklets for copepod biomass are probably few compared to those in the outer shelf domain, while at the same time copepod biomass is apparently large.

Table 30. Black-legged Kittiwake reproductive success on the Pribilof Is. and St. Matthew I. (number of chicks fledged/total nests), and recruitment of age class 1 pollock in the eastern Bering Sea (billions of fish). ND = no data. Pollock data are from Bakkala and Traynor (1983).

Year	Pollock recruitment	Kittiwake reproductive success		
		St. George I.	St. Paul I.	St. Matthew I.
1975	ND	ND	0.44	ND
1976	ND	0.62	0.52	ND
1977	ND	0.45	0.43	ND
1978	ND	0.22	0.36	ND
1979	8.7	0.40	0.54	ND
1980	1.0	0.38	ND	ND
1981	1.0	0.07	ND	ND
1982	0.9	0.01	ND	0.01
1983	3.5	0.01	ND	0.01

Pollock is the largest contributor of biomass to diets of piscivorous seabirds in the SE Bering Sea. On St. Lawrence I. piscivorous seabirds feed on a variety of fishes including Arctic cod, sand lance and capelin (Springer and Roseneau unpubl. data). The ratio of the numbers of murres, the numerically dominant avian piscivores at Bering Sea breeding colonies, to the number of least auklets (Fig. 12) indicates a shift in the proportions of available fish and copepod biomass from predominantly fish in the south to copepods in the north. This trend is consistent with the reported distribution of pollock and with the inferred competition for copepods in the SE Bering Sea.

The persistent failures of black-legged Kittiwakes in the SE Bering Sea contrast with the pattern of average to good success punctuated by occasional failures lasting only one year at colonies in the N Bering and E Chukchi seas. The long-term nature of the kittiwake failures at southern colonies indicates a prolonged inadequacy of pollock, and is now a cause for concern for Kittiwakes breeding at those colonies.

Unfortunately there are no systematic data on seabirds from the Pribilofs or St. Matthew I. collected before the inception of the commercial pollock fishery in the late 1960's. Preble and McAtee (1923) quoted from Palmer (1899), "... St. Paul Island, August 2, 1890, most nests with young, but a few had a young and an egg, or sometimes two or three eggs." Thus, we do not know if the levels of reproductive success reported for the Pribilofs during the period 1975-79 (Hunt et al. 1981a) are typical of levels in such a pelagic system. During the late 1970's, the average clutch sizes of laying pairs were about in the middle of the range of clutch sizes at northern colonies (see Springer et al. in press b). Chick growth rates were slow-moderate and mortality was relatively high.

The availability of pollock to surface-feeding seabirds, such as kittiwakes, on islands in the SE Bering Sea may never be as high as is the availability of sand lance and capelin to coastal populations. Sand lance and capelin form dense shoals in shallow water and are easily captured by kittiwakes. The availability of these fishes accounts for generally high chick growth rates and survival. Pollock do not form such near-surface shoals and therefore they are less available to kittiwakes, even though the total biomass of pollock may greatly exceed that of the other forage species. Major changes in the abundance of pollock, such as in the recent years of poor recruitment of age 1 fish, are likely to have major effects on kittiwake reproductive success. Generally lowered recruitment, which might have resulted from the reduction of adult pollock by the commercial fishery (Fig. 13), might have contributed to the low-moderate levels of kittiwake reproductive success during the late 1970's.

E Chukchi Sea

Murre numbers at Cape Lisburne apparently have varied little between years since censuses were first taken there in 1976. This trend contrasts with those at all other colonies in the Bering and Chukchi seas where we and others have made systematic counts in two or more years during the same interval. Such numerical constancy suggests that murre food webs in Ledyard Bay are also stable compared to those elsewhere, and may be more effectively buffered in some way against disruption by seasonal and annual variations in the physical environment.

The great abundance of Arctic cod at Cape Lisburne in 1983 allowed kittiwakes to lay large clutches of eggs, but was not sufficient to maintain all

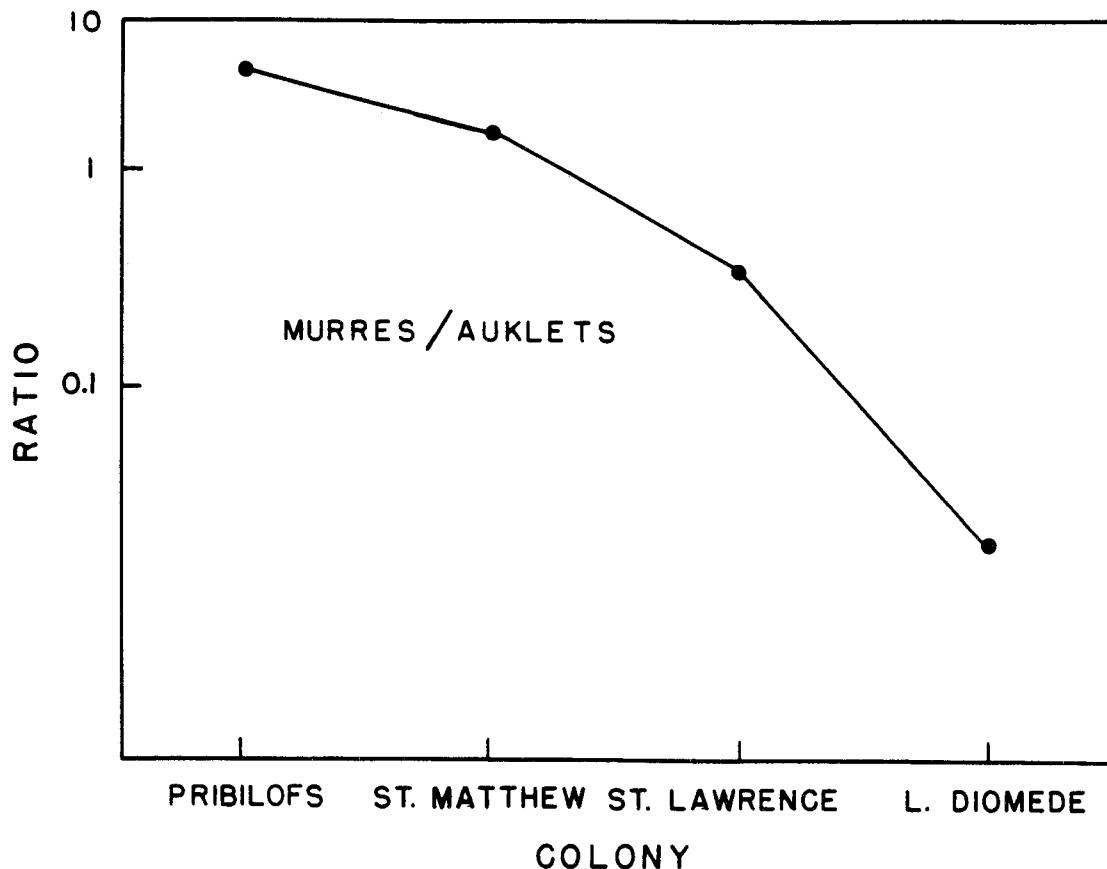


Fig. 12. Relative numbers of murres and least auklets at colonies in the eastern Bering Sea. From Sowls et al. (1978) and Roseneau et al. (in press).

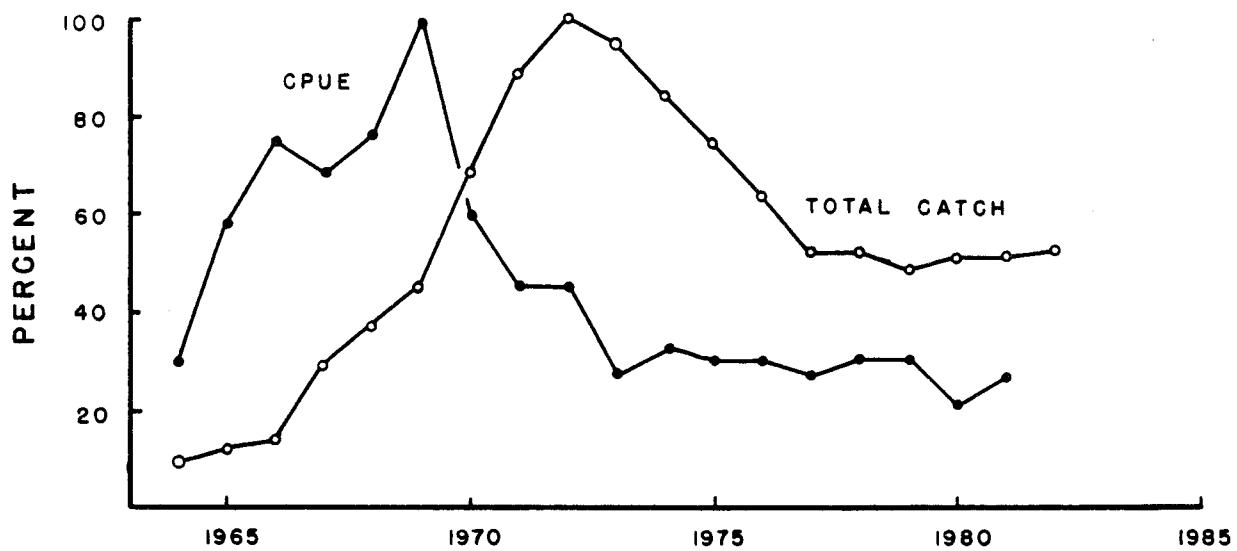


Fig. 13. Total catch and catch per unit effort (CPUE) of pollock in the eastern Bering Sea. The 100% levels of the annual catch and the CPUE were about 1.9 million tonnes and 31.5 tonnes/1000pair horsepower hour, respectively. From Bakkala and Traynor (1984).

of the chicks at the colony. Chick mortality was high - most of the second chicks to hatch in two chick broods died - and growth rates of the surviving chicks were slow compared to other years at Cape Lisburne when sand lance have been available during the chick period. Thus, sand lance appear to be a key species to Kittiwakes in terms of the overall production of young. While Arctic cod is probably always important to Kittiwakes during the egg-laying period, sand lance seem to be necessary for the birds to enjoy a highly successful breeding season.

The close correspondence between the increases in chlorophyll-a, zooplankton populations and the availability of sand lance to seabirds in Ledyard Bay suggests interactions between three trophic levels of the neritic community. We do not know if warming conditions beginning about mid-July promoted the increases in zooplankton, or if they all resulted from the advective import of associated food web organisms from the south. Neimark (1976) found a significant positive correlation between numbers of Acartia clausi and warming water temperatures in Norton Sound; in 1976, an environmentally cold year, the number of Acartia clausi began to increase rapidly beginning in the interval 16-31 July and peaked during the interval 1-15 August. The increase followed the rise in water temperature in Norton Sound by about two weeks, as it did in Ledyard Bay in 1983. However, the period of maximum abundance of the cladocerans was two weeks earlier than that of Acartia, while the period of maximum abundance of bivalve veligers was two weeks later. At Barrow, Redburn (1974) suggested that the abundance of Acartia and the cladocerans was a function of advection from the south, since the peak in numbers coincided with the intrusion of warmer water and the presence of other neritic copepod taxa.

Although many details remain undescribed, it seems that oceanographic conditions on the Bering-Chukchi shelf play a major role in determining annual levels of seabird reproductive success at colonies in Norton Sound, on St. Lawrence I., in the E Chukchi Sea, and probably on the Diomede Is. Two marine "rivers" having sharply contrasting physical and chemical properties flow northward through Bering Strait during summer. In the east, Alaskan Coastal Water, a warm, low-salinity water mass normally develops in early summer following the dissipation of sea ice in Norton Sound, breakup of the Yukon River and increased insolation (Coachman et al. 1975). Annual variability in the development of this seasonal water mass is thought to have significant effects on the coastal zone food webs supporting coastal seabird populations (Springer et al. 1984). Contrasting in the west, Bering Shelf-Anadyr water consists of Bering Shelf Water and Anadyr Water, both of which originate at depth in the Bering Sea and are cold, high salinity water masses (Coachman et al. 1975). The flow of this water across the northern shelf promotes exceptionally high levels of primary production during summer (Sambrotto et al. 1984) and advects sufficient copepod biomass from the south to apparently influence the breeding distribution of least auklets in the Bering Sea (Springer and Roseneau in press).

Ordinarily, the presence of the two flow regimes, Alaskan Coastal Water and Bering Shelf-Anadyr water, maintains two very different marine environments on the Bering-Chukchi shelf, in which characteristic food webs have adapted to the prevailing physical conditions. However, in some years the juxtaposition of these water masses breaks down leading to major disruptions of regional food webs. For example in 1984, anomalous circulation in the N Bering Sea carried Bering Shelf-Anadyr water deep into Norton Sound, a situation that persisted from early summer through about mid-August (Springer et al. unpubl. data). Consequently, the normally very warm environment of the NE Bering and E Chukchi seas was unusually cold throughout the summer. In Norton Sound where the anomaly

was greatest, murres and kittiwakes experienced the worst breeding season ever recorded (Murphy and Springer unpubl. data). The normal kittiwake breeding population of about 10 thousand pairs at Bluff was reduced to 500-750 birds total. Adult kittiwakes were found dead and dying along the Unalakleet River. Five emaciated specimens we examined had eaten berries and apparently had starved to death. Murres were less severely affected, but only about a third of the normal number was at the colony during mid-July. The reproductive success of murres and kittiwakes was nil. It seems certain that the availability of fishes normally taken by murres and kittiwakes in Norton Sound, particularly sand lance and saffron cod (Springer et al. unpubl. data), was very low. The analysis of zooplankon samples collected at Bluff (Springer and Murphy in progress) may indicate whether the prey of the fishes was reduced as well.

IX. NEEDS FOR FUTURE STUDY

The persistent reproductive failures of black-legged kittiwakes on the Pribilofs and St. Matthew I. pose an important question about the stability of the pollock population in the SE Bering Sea. They also emphasize the need for the monitoring of selected seabird colonies each year, especially during periods of anomalous breeding performance such as that during the 1980's. The insight provided by long-term data is that which will be needed to adequately assess the affect of OCS oil and gas development on regional seabird populations. Thus, certain colonies should be designated for low-level surveys each year, such as those we have done in the E Chukchi and at Bluff. Colonies that would be appropriate are those on the Pribilofs, at Bluff and at Cape Lisburne, since they are in distinct environmental regimes and have long histories of nearly uninterrupted study. A schedule for visiting other colonies at regular, but less frequent intervals, should be considered for a period of 10 years.

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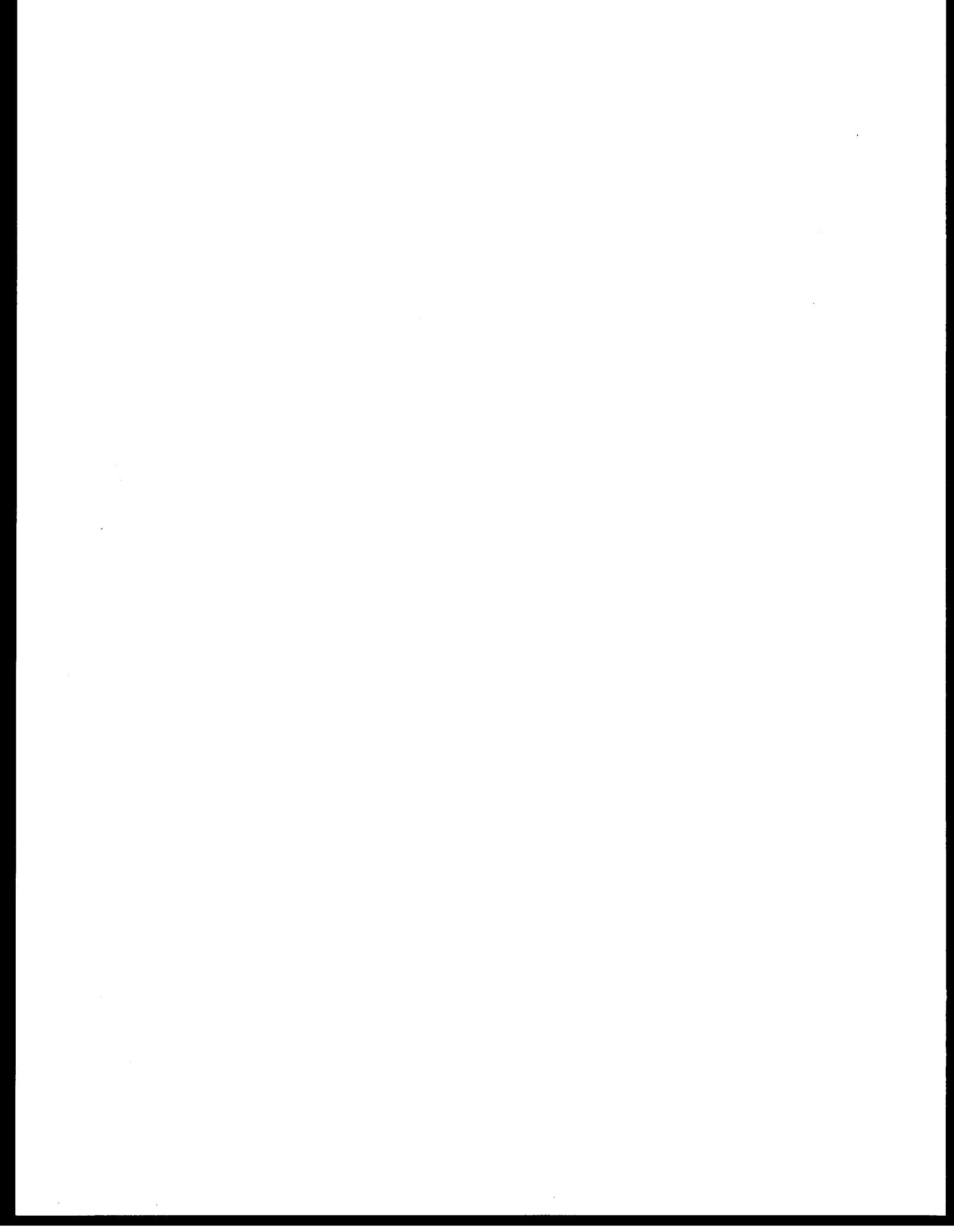
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APPENDIX

Table 1. Murre census results from St. Matthew Island, 1983.

Plot	21 Jul				26 Jul				27 Jul			
	Time ^A	Obs. E	Obs. P	\bar{x}	Time	Obs. E	Obs. P	\bar{x}	Time	Obs. E	Obs. P	\bar{x}
C-1												
C-2,3												
C-4,6												
C-8					1525			28	28			
C-9					1530			81	81			
D-1,2	1145	1,209		1,209								
D-6	1230	390		390								
D-7	1245	2,930		2,930								
D-8	1340	557		557								
D-9a	1315	3,225		3,225				1345	2,740	2,430	2,585	
D-9b	1425	2,245		2,245				1315	1,570	1,820	1,695	
D-9c	1455	1,100		1,100								
D-9d	1520	2,440		2,440				1200	2,320	2,130	2,225	
E-1	1600	1,190		1,190								
E-3												
E-4												
E-5												
E-6												
E-7												
E-8,F-1												
F-2												
F-3												
F-4,6												

^A Bering Daylight Time.

(Table 1, cont.)

(Plot)	29 Jul				30 Jul				1 Aug					
	Time ^A	Obs. E	Obs. P	Obs. Q	\bar{x}	Time	Obs. E	Obs. P	\bar{x}	Time	Obs. E	Obs. P	\bar{x}	(%)
(C-1)						1710	2,600		2,600					
(C-2,3)						1555	410	410	410					
(C-4,6)						1340	1,640		1,640					
(C-8)														
(C-9)														
(D-1,2)										1015	735	595	665	(61)
										1410	723	783	753	(69)
										1645	887	854	871	(80)
										1935	1,151	1,022	1,087	(100)
										2120	1,114	1,034	1,074	(99)
(D-6)														
(D-7)														
(D-8)														
(D-9a)														
(D-9b)	1815	2,430	2,700		2,565					0930	1,570	1,410	1,490	
										1115	1,090	1,010	1,050	
(D-9c)														
(D-9d)														
(E-1)														
(E-3)	1215	90			90									
(E-4)														
(E-5)														
(E-6)	1340	8,260	8,980		8,620									
(E-7)	1355	340			375	357								
(E-8,F-1)	1515	12,080	12,580		12,330									
(F-2)														
(F-3)	1655	740			740									
(F-4,6)	1705	440	410		425									

^A Bering Daylight Time.

(Table 1, cont.)

(Plot)	Time ^A	9 Aug			Raw \bar{x}	Compensated \bar{x}^B
		Obs. E	Obs. P	\bar{x}		
(C-1)				2,600	2,600	3,132
(C-2,3)				410	410	518
(C-4,6)				1,640	1,640	2,309
(C-8)				28	28	36
(C-9)				81	81	105
(D-1,2)				943	943	1,474
(D-6)					390	582
(D-7)					2,930	4,309
(D-8)					557	785
(D-9a)					2,798	4,158
(D-9b)	1900	3,120	2,610	2,865	1,961	2,606
(D-9c)					1,100	1,467
(D-9d)	1945	2,730	2,710	2,720	2,466	3,086
(E-1)					1,190	1,526
(E-3)					90	136
(E-4)						
(E-5)						
(E-6)					8,620	12,140
(E-7)					357	502
(E-8,F- 1)					12,330	16,223
(F-2)						
(F-3)					740	925
(F-4,6)					425	518
Total:					41,631	56,537

^A Bering Daylight Time.^B Raw x compensated using diurnal counts at Plots D-1,2 on 1 Aug (see above).

Table 2. Murre census results from Cape Lisburne, 1983.

Plot	21 Jul				6 Aug				11 Aug			
	Time ^A	Obs. N	Obs. O	\bar{x}	Time	Obs. N	Obs. C	\bar{x}	Time	Obs. N	Obs. O	\bar{x}
11	2000	1,230	1,110	1,170								
12	2045	1,260	1,740	1,500								
25	2115	820	690	755								
26	2130	1,040	810	925								
30	2220	3,140		3,140								
32	2245	1,860	1,960	1,910								
65			1430		2,470 ^B	2,740		1500	2,220 ^B		2,220	
66			1630		2,140	1,870	2,005	1330	1,635		1,635	
70			1500		2,130 ^B	2,130		1430	2,100 ^B	2,340 ^B	2,220	
72			1640		1,010	1,190	1,100	1415	870		870	
73			1650		590	630	610	1410	410		410	

^A Bering Daylight Time.^B Counts made from shore; all other counts made from raft.

(Table 2, cont.)

(Plot)	19 Aug				27 Aug ^C		28 Aug ^C		Raw \bar{x}	Compensated \bar{x}
	Time ^A	Obs. N	Obs. O	\bar{x}	Time	Obs. N	Time	Obs. N		
(11)									1,170	1,746
(12)									1,500	1,923
(25)									755	888
(26)									925	1,051
(30)									3,140	3,237
(32)									1,910	1,949
(65)	1850	2,000 ^B	2,612 ^B	2,306	1700	1,156	1100	2,426	2,236	4,366
(66)									1,820	3,526
(70)	1930	1,490 ^B	1,530 ^B	1,510	1715	1,000	1120	1,520	1,953	3,662
(72)									985	1,888
(73)									510	965
								Total:	16,904	25,201

^A Bering Daylight Time.^B Counts made from shore; all other counts made from raft.^C These counts were made outside of the census period and are not included in the raw and compensated means.

Table 3. Ratios of common murres (COMU) and thick-billed murres (TBMU) at Hall Island, 1983.

Location ¹	Time ²	Date	COMU	TBMU	COMU/TBMU
Subplot No. 3	1321	18 Jul	398	51	7.8
Subplot No. 4	1321	18 Jul	26	325	0.1
Subplot No. 5	1350	18 Jul	205	46	4.5
			-----	-----	-----
		(Subtotal)	(629)	(422)	(1.5)
Subplot No. 6	1350	18 Jul	467	266	1.8
			-----	-----	-----
		Total (18 Jul)	1,096	688	1.6
Subplot No. 3	1240	9 Aug	442	44	10.1
Subplot No. 4	1220	9 Aug	52	224	0.2
Subplot No. 5	1257	9 Aug	213	40	5.3
		-----	-----	-----	-----
		(Subtotal)	(707)	(308)	(2.3)
Eggplot No. 1	1315	9 Aug	9	102	0.1
Eggplot No. 2	1330	9 Aug	0	51	0
Eggplot No. 3	1345	9 Aug	3	23	0.1
Eggplot No. 4	1400	9 Aug	26	50	0.5
Eggplot No. 5	1430	9 Aug	11	17	0.6
Eggplot No. 6	1415	9 Aug	18	12	1.5
		-----	-----	-----	-----
		(Subtotal)	(67)	(255)	(0.3)
		-----	-----	-----	-----
		Total (9 Aug)	774	563	1.4

¹ All subplots and eggplots are located near the boundary separating Plots H-1 and H-2 (see DeGange and Sowls 1978).

² Bering Daylight Time.

Table 4. Counts of seabirds on subplots 1-4 at Tusk Colony, St. Matthew Island, 1983.

Date	Subplot	Time ¹	TBMU ²	COMU ³	BLKI ⁴
17 Jun	1	1217	0	0	77
		1758	0	0	60
	2	1240	32	125	224
		1747	33	115	212
	3	1245	32	6	92
		1734	38	7	93
	4	1255	22	12	109
		1713	38	11	100
29 Jun	1	1430	0	0	70
	2	1435	17	111	331
	3	1445	17	10	105
	4	1500	13	14	117
9 Jul	1	1400	0	0	53
	2	1400	28	102	238
	3	1415	24	12	57
	4	1430	21	7	88
15 Jul	1	1700	0	0	56
	2	ND ⁵	ND	ND	ND
	3	1700	27	10	87
	4	1715	35	12	99
19 Jul	1	1625	0	0	49
	2	1640	25	163	257
	3	1655	48	13	76
	4	1715	34	13	90
28 Jul	1	1420	0	0	66
	2	1430	19	167	303
	3	1445	28	9	81
	4	1455	18	13	95
1 Aug	1	1020	0	0	53
	2	1030	18	95	154
	3	1040	19	9	28
	4	1055	0	11	54

¹ Bering Daylight Time.

² TBMU = thick-billed murre.

³ COMU = common murre.

⁴ BLKI = black-legged Kittiwake.

⁵ ND = no data.

Table 5. Counts of seabirds on subplot 1 at Arch Colony, St. Matthew Island, 1983.

Date	Time ¹	TBMU ²	COMU ³	NOFU ⁴
15 Jun	1400	136	8	10
	1700	142	4	8
	2000	142	5	12
	2200	110	5	12
16 Jun	1400	305	17	7
26 Jun	1830	120	13	8
	2030	143	13	8
27 Jun	0400	202	10	8
	1445	307	14	9
4 Jul	0600	141	12	7
	1500	142	15	12
13 Jul	0845	74	2	9
	1135	150	20	8
	1335	163	19	7
22 Jul	0900	262	18	6
	1230	169	10	6
	1530	219	15	6

¹ Bering Daylight Time.

² TBMU = thick-billed murre.

³ COMU = common murre.

⁴ NOFU = northern fulmar.

Table 6. Counts of thick-billed murres (TBMU) on subplots 1-4 at North Camp Colony, St. Matthew Island, 1983.

Date	Subplot	Time ¹	TBMU
18 Jun	1	1127	36
		1240	38
	2	1127	6
		1240	11
27 Jun	1	1615	48
		1630	17
	3	1645	51
		1700	21
3 Jul	1	1750	37
		1800	20
	3	1815	41
		1825	28
22 Jul	1	0900	44
		1530	32
	2	0915	19
		1545	15
	3	0930	53
		1600	42
	4	0945	20
		1615	17
1 Aug	1	ND ²	20
			12
	3		31
			14

¹ Bering Daylight Time.

² ND = no data.

Table 7. Black-legged kittiwake census results from St. Matthew Island, 1983.

Plot	20-21 Jul			29-30 Jul		
	Time ¹	Birds	Nests	Time	Birds	Nests
C-1				1700	215	150
C-2				1600	0	0
C-3				1600	0	0
C-4,6				1330	379	324
D-0 ²	1330	545	335			
D-1a	1110	158	95			
D-1b	1130	521	281			
D-2	1200	0	0			
D-3	1200	0	0			
D-4	1200	0	0			
D-5	1200	0	0			
D-6	1230	43	26			
D-7	1245	248	115			
D-8	1345	0	0			
D-9a	1315	717	344			
D-9b	1420	337	178			
D-9c	1450	403	161			
D-9d	1520	2	0			
E-1	1600	0	0			
E-6				1300	10	4
E-7				1350	86	59
E-8				1515	977	740
F-1				1615	1,104	1,020

¹ Bering Daylight Time.² Plot D-0 = Tusk Colony, a concentration of murres and kittiwakes not reported by DeGange and Sowls (1978).

Table 8. Numbers of crested auklets (CRAU), least auklets (LEAU), and parakeet auklets (PAAU) on Plots 1-6 at Pterodactyl Colony on St. Matthew Island, 1983.

Plot	Date	Observer	Surface Average			Net Movement		
			CRAU	LEAU	PAAU	CRAU	LEAU	PAAU
1	11 Jun	Q/R	3	57	0	+14	+400	0
	24 Jun	R	3	63	<1	0	+12	0
	3 Jul	Q	2	56	0			
	11 Jul	R	1	66	0			
	20 Jul	R	3	100	0			
	30 Jul	R	1	104	0			
2	11 Jun	Q/R	2	129	<1	0	-554	0
	24 Jun	R	2	83	0	-2	-4	0
	2 Jul	Q	5	175	0			
	11 Jul	Q	5	164	0			
	21 Jul	R	4	167	0			
	31 Jul	R	<1	96	0			
3	11 Jun	Q/R	<1	40	<1			
	24 Jun	R	0	15	0			
	2 Jul	Q	1	65	0			
	3 Jul	Q	2	67	0			
	11 Jul	Q	<1	56	0			
	21 Jul	R	2	61	0			
	31 Jul	R	0	37	0			
4	11 Jun	Q/R	1	32	2			
	24 Jun	R	2	36	1			
	2 Jul	Q	4	64	2			
	11 Jul	R	2	37	0			
	21 Jul	R	4	43	1			
	31 Jul	R	<1	27	0			
5	13 Jun	R	3	59	0			
	24 Jun	Q	5	86	<1			
	2 Jul	R	6	70	<1			
	12 Jul	R	2	64	0			
	21 Jul	Q	4	68	0			
	31 Jul	Q	2	55	0			
6	13 Jun	R	8	114	0	+4	+226	0
	24 Jun	Q	11	131	0	-22	-1,252	0
	2 Jul	R	17	136	0			
	12 Jul	R	8	111	0			
	21 Jul	Q	12	195	0			
	31 Jul	Q	5	169	0			

Table 8, cont. Numbers of crested auklets (CRAU), least auklets (LEAU), and parakeet auklets (PAAU) on Plots 7-11 at Pterodactyl Colony on St. Matthew Island, 1983.

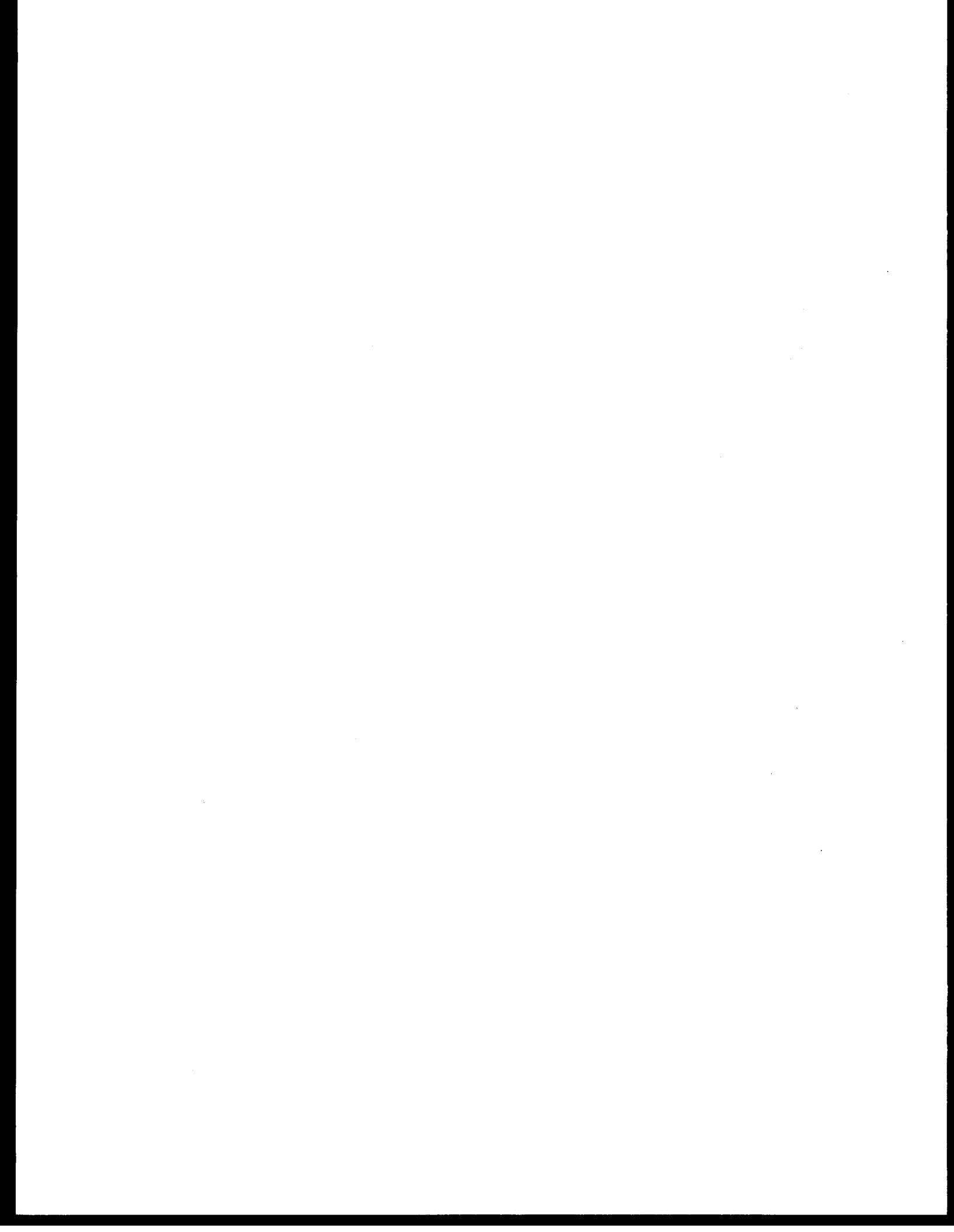
Plot	Date	Observer	Surface Average			Net Movement		
			CRAU	LEAU	PAAU	CRAU	LEAU	PAAU
7	13 Jun	Q	11	55	0			
	25 Jun	Q	16	45	0			
	3 Jul	R	18	62	0			
	12 Jul	Q	19	48	0			
	20 Jul	Q	18	71	0			
	30 Jul	Q	4	48	0			
8	13 Jun	Q	11	42	0	+6	-396	0
	25 Jun	Q	14	50	0	-34	-272	0
	3 Jul	R	34	49	0			
	12 Jul	Q	27	58	0			
	20 Jul	Q	31	64	0			
	30 Jul	Q	10	51	0			
9	3 Jul	R	0	25	0			
	12 Jul	Q	0	33	0			
	20 Jul	Q	0	28	0			
	30 Jul	Q	0	19	0			
10	2 Jul	R	0	10	0			
	12 Jul	R	0	14	0			
	21 Jul	Q	0	19	0			
	31 Jul	Q	0	7	0			
11	3 Jul	Q	9	95	0			
	11 Jul	R	3	76	0			
	20 Jul	R	7	98	0			
	30 Jul	R	4	115	0			

Table 9. Numbers of crested auklets (CRAU), least auklets (LEAU), and parakeet auklets (PAAU) on Plots 1-6 at Arch Colony on St. Matthew Island, 1983.

Plot	Date	Observer	Surface Average			Net Movement		
			CRAU	LEAU	PAAU	CRAU	LEAU	PAAU
1	16 Jun	R	0	31	0	0	+16	0
	27 Jun	R	2	92	0			
	4 Jul	R	0	69	0			
	14 Jul	R	0	45	0			
	22 Jul	R	0	68	0			
2	16 Jun	R	4	70	2	0	+6	0
	27 Jun	R	8	117	1			
	4 Jul	R	9	95	0			
	14 Jul	R	5	75	<1			
	22 Jul	R	6	95	0			
3	16 Jun	Q	<1	42	0	0	+6	0
	27 Jun	Q	1	52	0			
	4 Jul	Q	<1	49	0			
	14 Jul	Q	0	30	0			
	22 Jul	Q	0	47	0			
4	16 Jun	Q	0	52	0	0	+6	0
	27 Jun	Q	<1	56	1			
	4 Jul	Q	0	44	1			
	14 Jul	Q	<1	41	0			
	22 Jul	Q	0	51	0			
5	4 Jul	R	13	87	0	0	+6	0
	14 Jul	R	3	73	0			
	22 Jul	R	12	80	0			
6	4 Jul	Q	<1	42	0	0	+6	0
	14 Jul	Q	0	29	0			
	22 Jul	Q	0	31	0			

Table 10. Numbers of prey taken by least auklets on St. Matthew Island during the chick period in 1983. Size categories are I, 0.0-7.0 mm; II, 7.1-15.0 mm; III, 15.1 mm and larger (from Bedard 1969). Number of samples = 40.

Taxon	Size	Number
<u>Calanus marshallae</u>	I	17,668
<u>C. plumchrus</u>	I	1
<u>Parathemisto libellula</u>	I	11
	II	43
<u>Parathemisto</u> spp.	I	4
<u>Hyperoche medusarum</u>	II	1
<u>Monoculodes</u> spp.	I	2
<u>Westwoodilla caecula</u>	I	2
<u>Atylus bruggeni</u>	I	1
	II	146
<u>Orchomene</u> spp.	I	4
<u>Jassa</u> spp.	I	1
	II	3
<u>Iscyroceras</u> spp.	?	1
<u>Pontogeneia</u> spp.	I	6
	II	20
<u>Anonyx</u> spp.	I	2
<u>Lepidepecreum</u> spp.	I	1
<u>Pontoporeia affinis</u>	I	1
<u>Stenothoidae</u>	I	4
	II	9
<u>Melphidipidae</u>	?	1
<u>Oedicerotid</u>	II	5
<u>Thysanoessa raschii</u>	II	1
	III	2
<u>Thysanoessa</u> spp.	II	45
	III	1
<u>Euphausiid</u> furculia	I	30
	II	1
<u>Hippolytidae</u> zoea	II	147
<u>Crangonidae</u> zoea	II	2
<u>Pandalidae</u> zoea	II	7
<u>Shrimp</u> zoea	II	12
<u>Paguridae</u> zoea	I	53
<u>Lithodidae</u> zoea	I	130
	II	15
<u>Paralithoides</u> zoea	I	3
<u>Anomuran</u> zoea	I	12
<u>Argis</u> spp.	II	79
<u>Limacina helicina</u>	I	8
<u>Cumacean</u>	II	1



**POPULATION ESTIMATES AND TEMPORAL TRENDS
OF PRIBILOF ISLAND SEABIRDS**

by

F. Lance Craighead and Jill Oppenheim

**Alaska Biological Research
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**Final Report
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Research Unit 628**

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EXECUTIVE SUMMARY

Replicate counts were made in 1982 of study areas established on St. Paul and St. George islands in 1976. Eleven species of seabirds were represented. Study area populations totaled 16,700 on St. Paul in 1976 and 8,862 in 1982. On St. George the totals were 35,739 in 1976 and 32,394 in 1982. In 1982, thick-billed murre and red-faced cormorant numbers had decreased significantly over 1976 on both islands, common murre, parakeet auklet, and horned puffin numbers had increased significantly on St. George, least auklet numbers had increased significantly on both St. George and St. Paul islands. A significant increase of tufted puffins on St. George should be viewed in light of a small sample size.

Red-legged and black-legged kittiwake numbers had not changed significantly in 1982, but the number of active nests had decreased for both species. No significant change was detected in crested auklet or northern fulmar numbers on either island. Fulmar estimates, however, are probably low, especially on St. George, due to the inaccessibility of their nesting habitat.

Population estimates were made using the 1976 estimates as a baseline and assuming the study population comprises the same proportion of the total population in both years. Estimates for 1976 and 1982 are listed below.

	<u>St. Paul</u>		<u>St. George</u>	
	<u>1976</u>	<u>1982</u>	<u>1976</u>	<u>1982</u>
Thick-billed murres	110,000	54,000	1,400,000	1,100,000
Common murres	39,000	39,000	220,000	280,000
Black-legged kittiwakes	42,000	42,000	94,000	94,000
Red-legged kittiwakes	3,600	3,600	220,000	220,000
Parakeet auklets	34,000	34,000	158,000	290,000
Least auklets	24,000	44,000	220,000	310,000
Crested auklets	6,000	6,000	28,000	28,000
Horned puffins	4,400	4,400	30,000	36,000
Tufted puffins	1,000	1,000	5,200	9,100
Red-faced cormorants	2,500	700	6,300	4,500
Northern fulmars	700	700	79,000	79,000

These estimates are considered accurate to order-of-magnitude with one significant digit. Confidence limits vary with species, but approximate a 95 percent confidence interval of ± 36 percent.

Comparisons between years suggest that 1976 was a year of high productivity for the fish-eating seabirds while 1982 was a year of reproductive failure. Burrow and crevice nesters, and/or inshore feeders, in general increased in numbers. These changes in seabird numbers are most likely due to changes in food supply but may be due partly to weather effects, habitat modification, and possibly, on St. Paul, human disturbance.

INTRODUCTION

The Pribilof Islands contain the largest nesting colonies of seabirds along the Alaskan Continental Shelf. Eleven species of seabirds totaling over two million birds breed there¹. Much of the baseline data on the ecology, population numbers, species composition, distribution, and foraging of seabirds has been acquired through NOAA/OCSEAP supported projects (Hickey 1976, 1977; Hunt 1976, 1977, 1978). Population estimates in 1975 and 1976 were made on the basis of a stratified random sampling technique using photos of birds on the nesting ledges. Reference areas were established on both St. Paul and St. George islands during 1976. Our visit was made to attempt to resurvey these discrete segments of cliff.

Specific objectives of this study were:

1. To re-census representative study areas of seabird nesting habitat, examining as many species as possible;
2. To develop population estimates for nesting seabird species, including in the estimates measures of confidence in the data;
3. To compare seabird populations estimates made during this study with previous investigations on the Pribilof Islands, especially 1976;

4. To test a time and cost-efficient methodology for indexing these seabird populations and their species composition; and
5. To acquire additional baseline data in preparation for proposed oil development activities in the St. George Basin.

¹Scientific names for these species are listed in Appendix 7.

STUDY AREA

The study areas are located on St. George and St. Paul islands, in the Pribilof Islands. These study areas are well-defined sections of cliff-nesting habitat that can be approached and censused on foot. Study area locations are detailed in Figures 1 and 2.

FIGURE I. ST. PAUL ISLAND STUDY AREAS

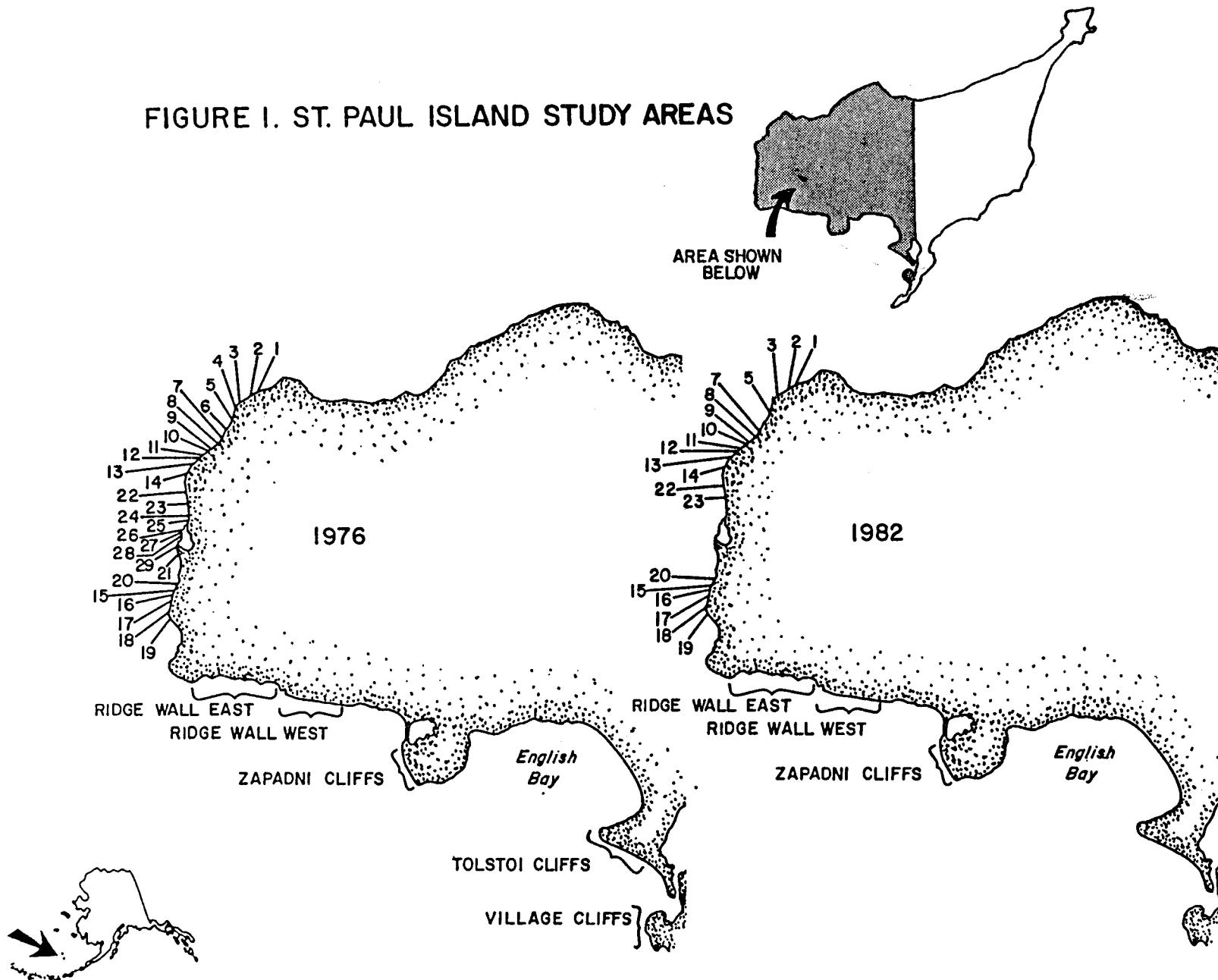
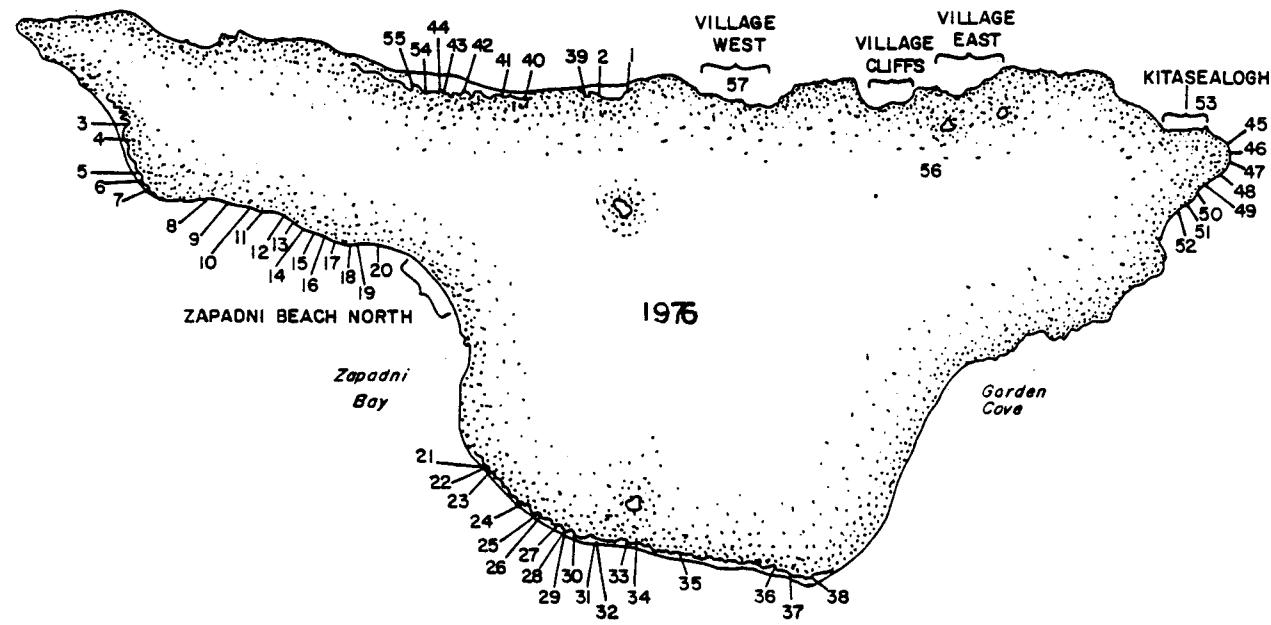
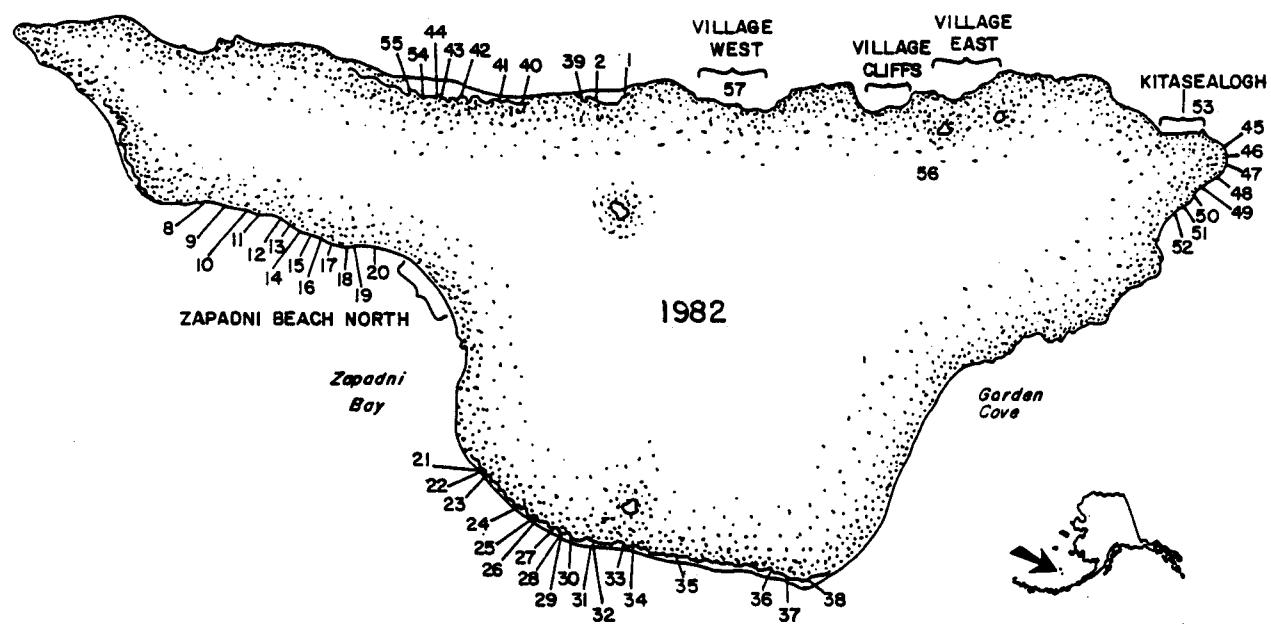


FIGURE 2 . ST. GEORGE ISLAND STUDY AREAS



METHODS

Census Procedures

Four days were spent on St. Paul and two weeks on St. George in late July 1982. Counts of all birds present on study areas and all active kittiwake nests were recorded. Active was defined as containing an incubating adult, an egg, or a chick. All red-faced cormorant nests were also recorded, and all successful nests were noted. Observers used photos taken in 1976, with the study area outlined to locate the identical area, and made counts from the 1976 observation points. The resultant count was then a re-census of the area delineated in 1976 and a replicate count of that area's bird numbers.

In order to make comparisons between years as close as possible, efforts were made to re-census each ledge at the same phase of the breeding cycle and at the same part of the diurnal cycle as in the previous census. Most censuses of study areas in 1976 were timed to coincide with an afternoon peak in ledge attendance of the smaller alcids that occurred between 1200 and 1500 hours, during the late incubation period of thick-billed murres. This peak was established by a series of counts made at 30-minute intervals throughout the day at various ledges.

In 1982, a similar series of counts was made at 30-minute intervals at ledge 29 on St. George to determine the afternoon peak of alcid numbers on the cliffs. Censuses of study areas in 1982 were timed to coincide with this afternoon peak which occurred between 1300 and 1700 hours.

Nine study areas censused in 1976 on St. Paul were not censused in 1982 due to poor weather, time constraints, or gross physical changes in the study area. Similarly, five areas on St. George were not re-censused due to weather and time constraints.

Data Analysis

Counts made in 1982 are replicate counts of the numbers of birds present on clearly defined study areas, previously counted in 1976. The study areas were chosen on a basis of accessibility and location, and vary greatly in area. Therefore, the sampled populations cannot be assumed to be normal and have equal variances. Nonparametric statistics were used to determine levels of confidence; in particular, Wilcoxon's paired-sample test was applied:

$$T' = m(n+1) - T$$

where m = the number of the ranks with the less frequent sign,
 n = the number of samples,
 T = the sum of the ranks with the less frequent sign
for ranked differences in sample populations between 1976 and 1982 data.

This test was the basis for determining whether or not observed differences in bird populations on study areas were significant between years. Differences were considered significant when $p < 0.05$ and highly significant when $p < 0.01$.

Secondly, overall estimates of the population of each bird species were derived. This estimate was derived in 1976 using stratified random samples from photos of the entire cliff area of St. George. Parametric statistical methods used with these data gave an accuracy of order-of-magnitude with one significant digit. Confidence limits varied among species estimated, but approximated a 95 percent confidence interval of ± 36 percent.

Following the final report of NOAA/OCSEAP in 1976 (Hickey 1977), some further refinements were made in overall species estimates (Craighead, Hickey, and Squibb 1977; Craighead, Hickey, and Cary 1977). These refined 1976 estimates are presented in Tables 1 and 2.

Using this overall population estimate as a basis, we have used the significant changes in 1982 in the sub-population on study areas to extrapolate 1982 overall population estimates for each species on each island (Tables 1 and 2). This overall estimate has the same accuracy as the 1976 estimate: order-of-magnitude with one significant digit. Corrected proportions are presented for various species as follows. On St. Paul, the census of Ridge Wall was taken earlier in the day than the expected afternoon peak in alcid attendance in 1982, and the Zapadni census was taken before the afternoon peak in 1976. Since the correspondence in times for these counts was not close, these data were ignored in the case of parakeet, least, and crested auklets, and horned puffins. This edited data set results in the corrected 1982/1976 proportions for St. Paul (Table 1). The closest correspondence

in time and date of replicate counts on St. George occurred on the lowest and highest cliff strata, although all occurred within the incubation phase of thick-billed murres. Using data from only these strata for parakeet and least auklets and horned and tufted puffins results in the corrected 1982/1976 proportions for St. George (Table 2).

In most cases, the corrected proportion also reflected significant population changes. In these, the more conservative 1982/1976 proportion was used to derive the 1982 estimate, since this figure represented a larger sample size. In only one case, tufted puffins on St. George, was a corrected proportion found to be significant where the overall proportion was not. Since the data for the other auklet species indicate that overall counts are reliable, this edited count (tufted puffins) must be viewed with skepticism, particularly as it is based upon a very small sample size.

RESULTS AND DISCUSSION

Our observations in 1982 suggest a number of changes in seabird numbers in the Pribilof Islands since 1976. Population estimates for each seabird species and differences between 1976 and 1982 are presented for St. Paul (Table 1) and St. George (Table 2) islands. Population changes summarized in these tables can be described in relation to changes in years for each seabird species and comparisons between islands.

The results of counts at individual study areas are presented in Appendices 1 through 5B. Appendix 1 contains daily ledge attendance counts made at 30-minute intervals on ledge 29, St. George, to determine peak attendance times for census purposes. Appendices 2A through 5B present census counts at study ledges.

Species Accounts

Thick-billed murre

Thick-billed murres were censused during both 1976 and 1982 just prior to hatching. The mean hatching date in 1976 was 3 August. There was little change in numbers of murres on ledges between 1300 and 1700 hours when censuses were made. Attendance of ledge 29, St. George Island, 25 July, is summarized in Figure 3.

On both St. Paul and St. George and in all vertical strata, numbers of thick-billed murres were significantly ($p<0.05$) lower than in 1976 (Tables 1 and 2). On St. Paul, the greatest decrease, 49 percent of the

1976 total, was recorded. Thick-billed murres constituted 53 percent of the total birds on study areas on St. Paul in 1976 and 49 percent in 1982. A total of 54,000 thick-billed murres was estimated on St. Paul in 1982.

Thick-billed murres declined in numbers to 81 percent of the 1976 total on St. George. Their numbers represented 64 percent of the total birds estimated in 1976 and 57 percent in 1982. A total of 1,100,000 thick-billed murres was estimated on St. George in 1982.

1982 was almost certainly a year of nesting failure for thick-billed murres. A single chick was observed on 25 July. Additionally, very few eggs were observed on St. George study areas as compared to 1976. This failure may have attributed to the decline in numbers of birds observed on the cliffs.

Common murre

On St. Paul in 1982, there was no significant change in numbers over 1976 (Table 1), although there was an apparent decline in numbers. Apparently common murres decreased in some study areas but increased in others, perhaps shifting to new sites. Several of the St. Paul ledges that previously had common murres were covered with debris, while others were bare, but unused. Common murres were estimated at 39,000 on St. Paul in 1982.

Common murres on St. George, however, showed a 27 percent increase in population (Table 2) which was highly significant ($p<0.01$). Overall,

KEY TO ABBREVIATIONS IN TABLES 1 AND 2.

TM	Thick-billed murre	HP	Horned puffin
CM	Common murre	TP	Tufted puffin
RK	Red-legged kittiwake	RC	Red-faced cormorant
PA	Parakeet auklet	LF	Northern fulmar (light phase)
LA	Least auklet	DF	Northern fulmar (dark phase)
CA	Crested auklet	BK	Black-legged kittiwake

Table 1. Estimated total population of cliff-nesting seabirds, St. Paul Island, 1976 and 1982.

	TM	CM	BK	RK	PA	LA	CA	HP	TP	RC	LF
1976 Total Estimate	110,000	39,000	42,000	3,600	34,000	24,000	6,000	4,400	1,000	2,500	700
1982 Total Estimate ¹	54,000 ²	39,000	42,000	3,600	34,000	44,000 ³ (52,000) ³	6,000	4,400	1,000	700 ²	700

¹Numbers in parentheses refer to estimates made which ignored counts made when auklets were not at peak attendance.

²Represents a highly significant change ($p<0.01$).

³Represents a significant change ($p<0.05$).

8
21

Table 2. Estimated total population of cliff-nesting seabirds, St. George Island, 1976 and 1982.

	TM	CM	BK	RK	PA	LA	CA	HP	TP	RC	LF
1976 Total Estimate	1,400,000	220,000	94,000	220,000	158,000	220,000	28,000	30,000	5,200	6,300	79,000
1982 Total Estimate ¹	1,100,000 ²	280,000 ³	94,000	220,000	290,000 ² (290,000) ²	310,000 ² (630,000) ²	28,000	36,000 ² (77,000) ²	5,200 (9,100) ³	4,500 ³	79,000

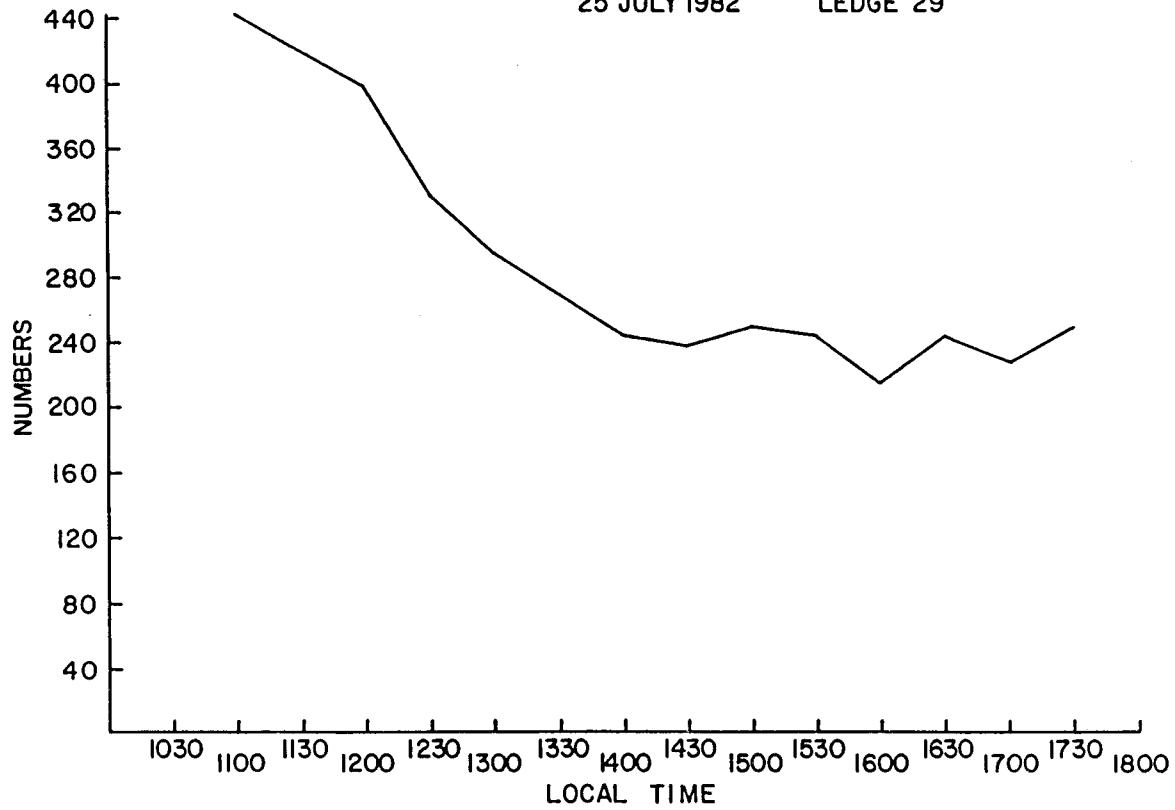
¹Numbers in parentheses refer to estimates made that ignored counts made when auklets were not at peak attendance.

²Represents a highly significant change ($P<0.01$).

³Represents a significant change ($P<0.05$).

FIGURE 3. LEDGE ATTENDANCE OF THICK-BILLED MURRES, ST. GEORGE ISLAND

25 JULY 1982 LEDGE 29



there was an increase in the lower cliffs and in the higher cliffs with little change in the cliffs of medium height. Some of the ledges that previously had common murres were empty in 1982. Common murres were estimated at 280,000 on St. George in 1982.

Although few eggs and no chicks were observed in the study areas, common murres may have fared better than thick-billed murres. A common murre ledge at Egg Rock on St. George, for instance, was cleared of eggs for subsistence; a second laying of about 160 eggs (from roughly 200 birds) was then collected on 25 July (D. Roby, pers. comm.).

Common murre phenology and daily ledge attendance is similar to that of thick-billed murres (Hickey 1977). Although common and thick-billed murres eat similar food items, they exhibit differences in relative proportions of various prey species and foraging zones [common murres generally forage closer to shore than thick-billed murres (Hunt 1977)].

Black-legged kittiwake

Although black-legged kittiwake numbers did not change significantly ($p<0.05$) on either island (Tables 1 and 2), they experienced a severe reproductive failure. Only three black-legged kittiwake chicks were observed on St. George: one was almost fully feathered while the other two were small and downy. In 1976 most young were well feathered at this date in late July. These significant declines in success occurred at all elevations and appeared to occur early in the nesting season since few birds completed nests and many birds did not even attempt to build nests. On St. Paul in 1982 there were only 17 percent (highly significant, $p<0.01$) as many active nests as in 1976. Similarly, the number of active nests on St. George in 1982 was only 19 percent (highly significant, $p<0.01$) of the 1976 total. In 1976, however, estimates were derived only from the low and high cliffs. Furthermore, many nests described as active may have been inactive (see Results and Discussion: Census Problems).

Black-legged kittiwake populations were estimated at 42,000 and 94,000 for St. Paul and St. George, respectively. Numbers of both black- and red-legged kittiwakes on cliffs showed little variation throughout the day according to 1976 data. Our 1982 sample size at

ledge 29, St. George was too small to use for a daily ledge attendance curve.

Red-legged kittiwake

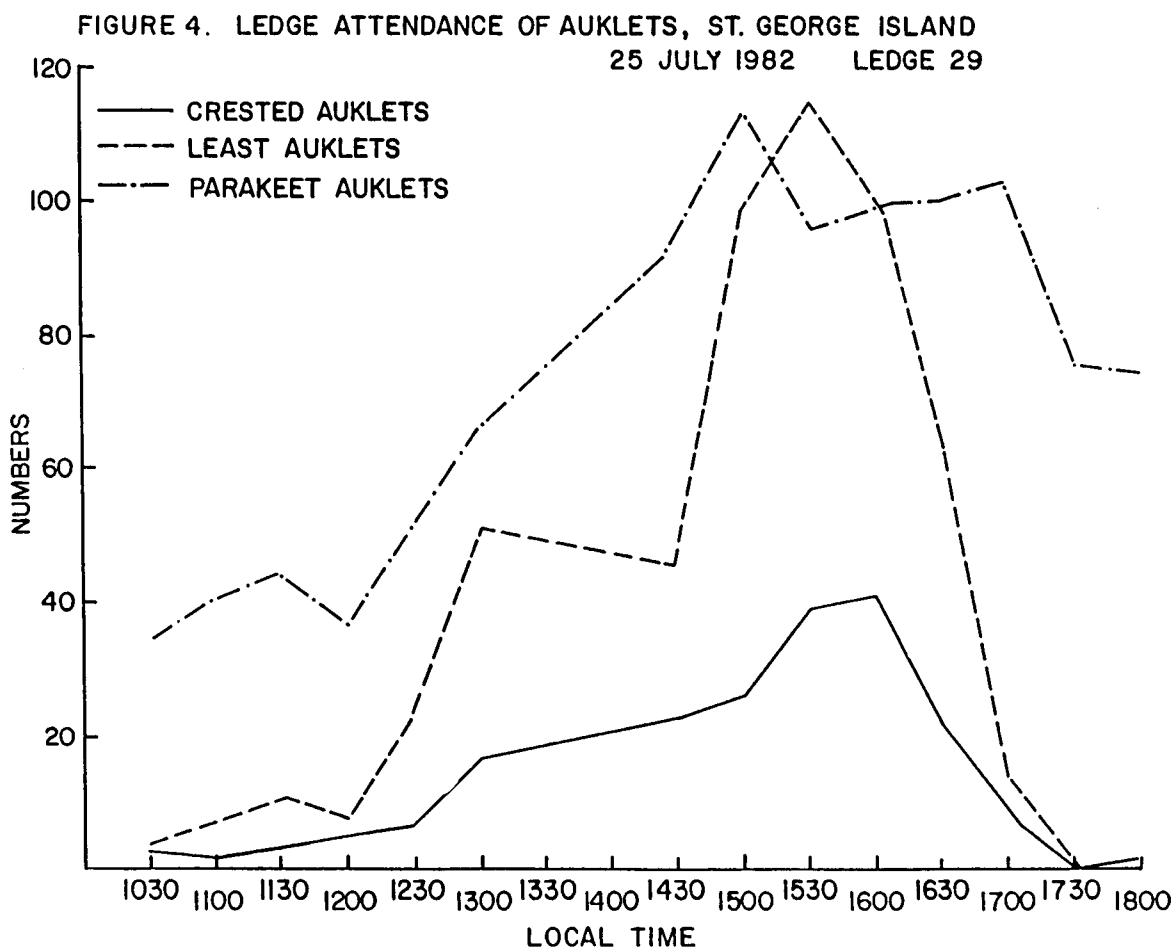
Red-legged kittiwakes also experienced a severe breeding failure (only three chicks and one addled egg were noted), although numbers of birds present on cliffs were not significantly ($p<0.05$) reduced on either island (Tables 1 and 2). The difference in number of active nests between 1976 and 1982 was highly significant ($p<0.01$) for both islands, however.

No active red-legged kittiwake nests were seen on St. Paul's lower cliffs. The higher (400 ft) cliffs could not be surveyed because of fog. Three thousand six hundred red-legged kittiwakes were estimated on the cliffs of St. Paul in 1982.

On St. George the number of active nests on high and low cliffs in 1982 was only eight percent (highly significant, $p<0.01$) of the 1976 total. There is a marked zonation in kittiwake habitat with elevation on St. George: as elevation increases there is a relative increase of red-legged kittiwake nests and a decrease in black-legged kittiwakes. In 1982 there appeared to be a slight increase in nesting of red-legged kittiwakes with elevation: on the low cliffs, active nests were five percent of the 1976 total, while on the high cliffs active nests were nine percent of the 1976 total. An estimate of 220,000 red-legged kittiwakes, the majority of the world population, was made for St. George.

Parakeet auklet

Parakeet auklet numbers were unchanged on St. Paul (Table 1), but increased on St. George (Table 2). As mentioned before, auklet numbers fluctuate greatly during the day (Figure 4). Some counts were made at times when low numbers would be expected, and some were made at a different point in the diurnal cycle than the previous count in 1976. Accordingly, these counts were left out of the analysis for corrected proportions.



On St. Paul there was no significant difference between the 1976 and the 1982 counts. Thirty-four thousand birds were estimated.

The closest correspondence in timing of replicate counts on St. George occurred on the lowest and highest cliff strata. Using data from only these strata shows a highly significant ($p<0.01$) increase of 82 percent between study years. A similar estimate was derived from counts at all study areas (Table 3). The result, which is probably conservative, is an estimate of 290,000 parakeet auklets on St. George in 1982.

Parakeet auklets also nest on several large talus piles at the bases of cliffs. We were unable to census these in 1982, and they represent a small fraction of the total population.

Least auklet

There are three types of nesting habitat for least auklets on the Pribilof Islands: beach boulder piles and talus, crevices on cliffs, and an inland colony in a boulder slope of Ulukaia Hill on St. George. No attempt was made to census the beach boulder and talus habitat in 1976 or 1982. The number of least auklets censused on cliffs increased significantly ($p<0.05$) in 1982 on both islands (highly significant on St. George, $p<0.01$) (Tables 1 and 2). Daily ledge attendance on cliffs is summarized in Figure 4.

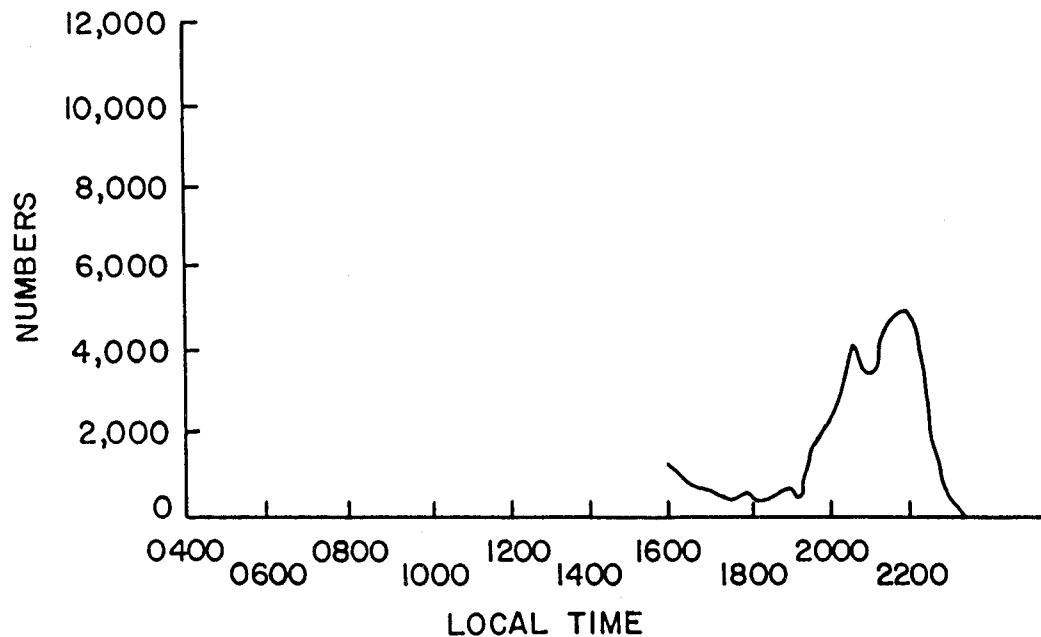
On St. Paul, the study population was at least 82 percent greater than that recorded in 1976, if all study areas are included in the estimate. This is a conservative estimate.

On St. George the 1982 estimate is at least 43 percent greater than the 1976 estimate if all cliff counts are included in the estimate.

Although the numbers of cliff-nesting least auklets has increased greatly, there has been a decrease in the number of birds nesting in the Ulukaia Hill colony. Flight counts of least auklets flying into the Ulukaia Hill colony on 31 July 1982 from the afternoon low, until darkness prevented counting, revealed a total of 72,760 parakeet auklets (Appendix 6 and Figure 5). This flight count can be compared to two similar counts made in 1976: 26 July and 10 August (Figure 6). Our closest actual count was 26 July 1976, which totaled 96,700. Phenologically, the count made in 1982 should be similar to counts made in 1976 (mean date of hatching was 13 July in 1982 [Dan Roby, pers. comm.] and 17 July in 1976). Counts in both years were made before fledging at a time when adults were making repeated trips to the colony to feed young.

It appears that the colony size in 1982 has been reduced to roughly 75 percent of its size in 1976. This decrease may be due to loss of habitat. In 1976 it was estimated that the colony covered an area of 126,500 square meters mapped on 17 June. The east end of the colony, which was used intensely for nesting in 1976 was heavily overgrown with moss and rye grass, Elymus spp., in 1982. Soil and debris has apparently filled in the boulder interstices where auklets nest. No least auklets were found to nest in this area in 1982 (Dan Roby, pers. comm.). This area appears to be slightly less than 25 percent of the former colony area. The 1976 estimate of population size for this colony was 106,700 breeding birds.

FIGURE 5. 1982 LEAST AUKLET FLIGHT COUNTS FROM SEA TO COLONY



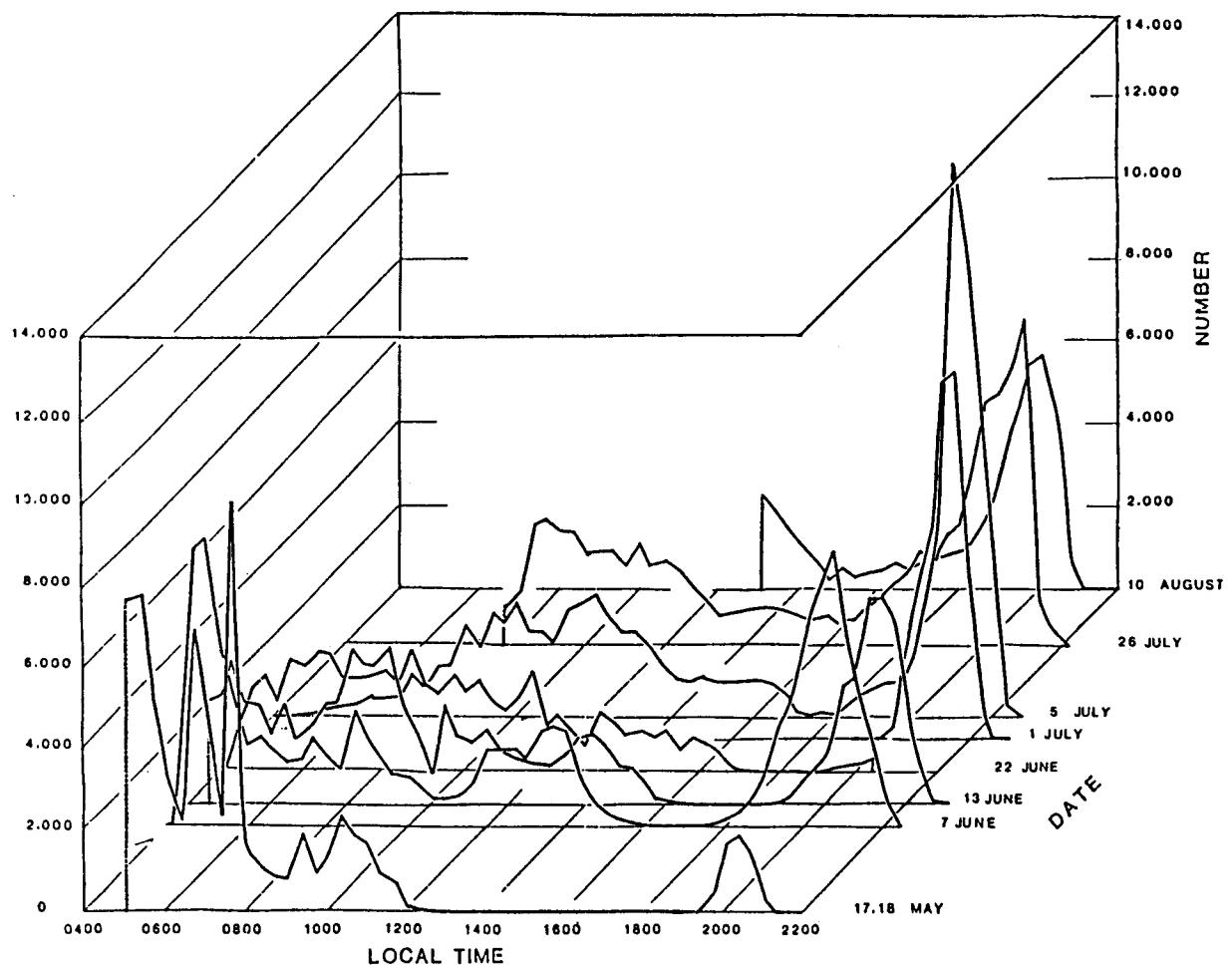
A 25 percent reduction in 1982 would result in approximately 80,000 birds remaining. This figure closely resembles our 1982 estimate.

The number of least auklets breeding on St. George in 1982, exclusive of beach nesters but including Ulukaia colony, was approximately 390,000. It is likely that beach-nesting birds may number on the order of 100,000 more. The numbers of birds on both islands, therefore, increased greatly over the 1976 population, perhaps even doubling in size.

Crested auklet

Crested auklet numbers did not change significantly on the cliffs of either island (Tables 1 and 2). Small sample sizes and the secretive habits of this species preclude a lengthy discussion. Crested auklets nest in crevices on cliffs and in three or more large boulder slopes

FIGURE 6. 1976 LEAST AUKLET FLIGHT COUNTS FROM SEA TO COLONY



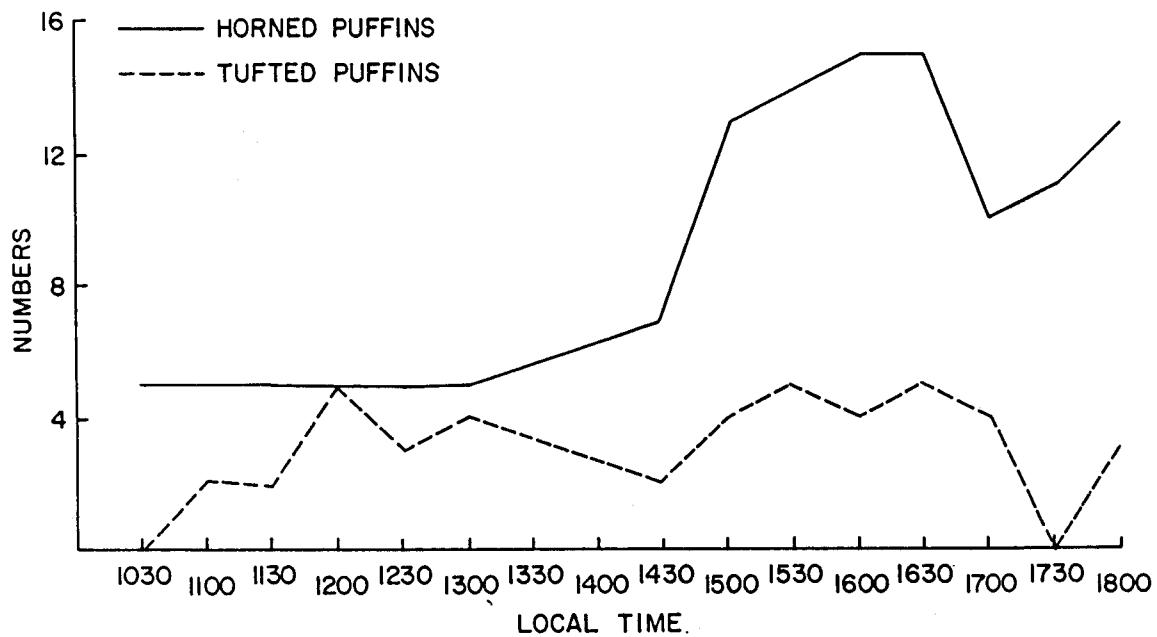
below the cliffs of St. George. Their daily ledge attendance patterns are summarized in Figure 4.

Horned puffin

Both horned and tufted puffins are found in relatively small numbers on both islands. Consequently, sample sizes for daily ledge attendance figures are small. The data for 1982 indicate that there was a slight afternoon peak in ledge attendance for horned puffins (Figure 7).

FIGURE 7. LEDGE ATTENDANCE OF HORNED AND TUFTED PUFFINS, ST. GEORGE ISLAND

25 JULY 1982 LEDGE 29



The St. Paul data for horned puffins include counts at Ridge Wall and Zapadni that probably missed an afternoon peak (Table 1). Neither these sets of data, nor a corrected form ignoring these counts reveal any significant change in population, however.

On St. George the data show a highly significant increase ($p < 0.01$) in numbers when all study ledges are considered, and also when a corrected estimate is made using only data from the high and the low cliffs (Table 2). Selecting the larger sample size, we estimated 36,000 horned puffins on St. George.

Tufted puffin

The daily ledge attendance counts do not show an afternoon peak for tufted puffins, but the sample size is very small (Figure 7).

There is no indication that the tufted puffin population has changed significantly on St. Paul (Table 1). Approximately 1,000 tufted puffins occupy St. Paul. On St. George, though, if only the high and the low cliffs are used to obtain a corrected estimate, a significant increase ($p<0.05$) can be described (Table 2). If an increase of 75 percent over the 1976 population is accepted, 9,100 tufted puffins were estimated for St. George in 1982.

Red-faced cormorant

On St. Paul there was a highly significant decrease ($p<0.01$) in numbers of red-faced cormorants. There was no significant difference in numbers of completed nests, but only one nest was successful. Three nests contained dead, downy chicks.

On St. George there was a significant decrease ($p<0.05$) in adults present, but no decrease in number of completed nests compared with 1976. Eleven of 38 nests were successful. No dead chicks were observed on St. George.

Although there was no decrease in nesting attempts, there was probably a decrease in successful nests on both islands in 1982. It appears that this was a year of reproductive failure for cormorants and it is likely that nest failure was the reason that fewer adults were found on study cliffs during surveys.

Northern Fulmar

Nesting, light-phase fulmars predominate on the Pribilofs. Ship-board transects of foraging fulmars reveal that birds at sea near the Pribilofs are primarily dark-phase fulmars presumed to be nesting in the Aleutians (Hunt 1978). No change in the ratio of light-phase to dark-phase fulmars was noted in 1982 and there was no significant change in numbers present on cliffs.

St. Paul has a relatively small population of fulmars, with only 700 estimated for both 1976 and 1982.

St. George had an estimated population of 79,000 fulmars in 1976 and 1982. There are large areas of cliffs that appear to be prime fulmar habitat. Because these ledges are inaccessible, population estimates are probably low for both islands.

Fulmars are the one species breeding on the Pribilofs that would be expected to be the least susceptible to the vagaries of environmental change: they nest early, selecting the most sheltered nesting cavities; they can select from a wide variety of prey items; and they can forage far afield when necessary without reducing the amount of food used for feeding chicks.

Comparisons Between Islands

St. Paul and St. George are about 100 km apart. For all practical purposes they share the same weather. Foraging areas for the larger, offshore feeding seabirds are essentially the same. Any significant relative changes in seabird numbers between islands should therefore reflect differences in nesting habitat or differences in disturbance.

Exceptions to this generalization might be the plankton-feeding alcids and perhaps the common murres, which appear to forage inshore.

There are differences in nesting habitat, due to the differing geologic histories of the two islands: St. George is older and is composed of high basaltic cliffs reaching 305 m (1,000 ft) in elevation, while St. Paul is largely composed of cinder cones and scoria with small cliffs along the southwestern end of the island. Consequently, there are differences in the numbers and proportions of seabirds nesting on each island.

The St. George cliffs are relatively undisturbed. Subsistence activity (egg collecting and shooting of adults) occurs, but is probably negligible considering the size of the colony. St. Paul, on the other hand, has a much smaller seabird population and a greater degree of disturbance. During the breeding season, tourists visit the cliffs near Southwest Point several times per week. It is possible that the greater magnitude of the decrease of thick-billed murres is due in part to this disturbance. The feature of disturbance may explain why there was no change in numbers of common murres on St. Paul while they increased on St. George.

Census Problems

Using established study areas located throughout the cliff-nesting habitat for replicate counts of nesting seabirds appears to be a feasible method for assessing population trends on the Pribilof Islands. There are, however, some difficulties with this method.

First, gross physical changes of cliffs reduce opportunities to standardize counts. The basaltic rock composing nesting ledges is subject to collapse, accumulation of debris, and a resultant growth of vegetation. These types of changes were noticeable, particularly on St. Paul. Four study areas on St. Paul had some accumulation of debris and one contained a small area of recent rock fall (occurring since the previous census in 1976). Similarly, even though no study areas were noticeably altered, a quick survey around the island of St. George by boat in 1982 revealed three large rockfalls and 20 small ones since 1976.

Second, nesting success for many species is difficult to determine and there is little information available to correlate adult numbers on cliffs with breeding pairs and reproductive performance. At this stage of the reproductive cycle one might assume that increased numbers on cliffs represent an increase of breeding pairs. Numbers of murres, however, increase in the late breeding season as non-breeding birds "prospect" for nest sites (Tuck 1969). Similar behavior may apply to other species as well. Similarly, failed pairs of some species may spend more time loitering on the cliffs rather than foraging and returning with food.

Kittiwakes also exemplify problems with determining breeding success from these censuses. One problem encountered is determining whether a nest is 'active' or 'inactive', due to the fact that some adults that appear to be incubating are actually sitting on empty nests. It is likely that in a bad year, such as 1982, a greater number of nests would be identified as active due to this behavior.

SUMMARY AND CONCLUSIONS

Several species of seabirds nesting on study areas on St. George and St. Paul islands experienced significant population changes between 1976 and 1982. Although 1976 was a year in which the onset of breeding began relatively late, due in part to delayed snow melt, it was a good year, reproductively, for kittiwakes, murres, and cormorants. In contrast, 1982 was a poor reproductive year for these species.

Thick-billed murres present on study areas decreased significantly. Common murres increased on St. George. Although no quantitative measure of reproductive success was obtained for either species of murre, it appeared to be much lower than in 1976.

There was no significant change in kittiwake numbers on either island, but both red-legged and black-legged kittiwakes experienced a significant breeding failure. Red-faced cormorants decreased in numbers on both islands.

Although there was no significant decrease in nesting attempts by red-faced cormorants in 1982, it appeared that most nests were unsuccessful.

In general, the plankton-feeding alcids appeared to have increased in numbers. Parakeet auklet numbers increased on St. George. Least auklet numbers increased on both islands although the least auklet colony on Ulukaia Hill, St. George, decreased in numbers. No significant change in crested auklet numbers could be detected on either island.

Horned puffin numbers increased on St. George, and tufted puffin numbers probably increased, although our sample size was small. Puffin numbers on St. Paul did not change significantly. Increases in numbers present on cliffs represent either an actual increase in breeding birds or an apparent increase due to the behavior of unsuccessful nesters. We are assuming an actual increase.

No change in numbers of northern fulmars could be detected. It appears that estimates of the fulmar populations on both islands may be low.

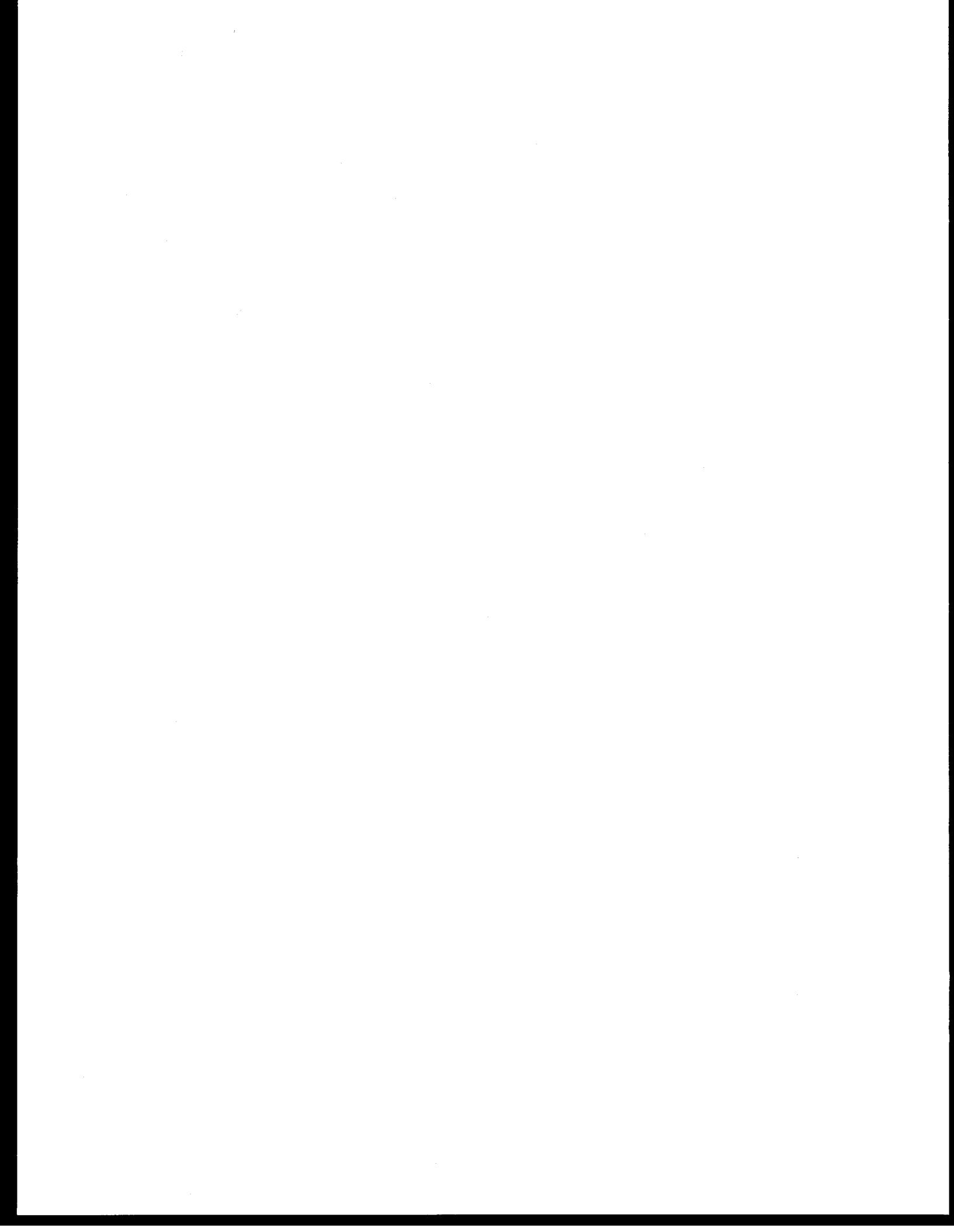
Several avenues of speculation are possible to explain these changes. A decrease in fish food items could explain the reproductive failure of murres, kittiwakes, and cormorants; the plankton feeding alcids may have been relatively successful. If this were the case, the puffins may have suffered a reproductive failure also, since they feed on many of the same prey items (Hunt 1977).

Severe weather effects could also have inhibited the reproduction of the cliff-nesting murres, kittiwakes, and cormorants. Presumably, the burrow- and crevice-nesters with their more sheltered nesting habitats would be less adversely affected. In this case, the puffins and auklets would have probably been reproductively successful in 1982. Weather effects, however, seem unlikely because of the nature of the kittiwake failure. If nests had been destroyed by weather, many birds would have still been building nests at the time of the census.

Finally, especially on St. Paul, human disturbances may have influenced seabird attendance and reproductive success.

Some problems are involved with using established ledges to monitor population trends. Physical changes in the cliffs can be accommodated by careful observation and appear to be less critical to survey procedures on St. George with its much larger area of cliffs than on St. Paul.

A conceptual model of ecosystem stability for the Southeast Bering Sea has been proposed (McRoy and Walsh 1980) which predicts that successful reproduction in species nesting on the Pribilof Islands is coupled to primary production with less influence by the variegation of seasonal events (i.e., storm frequency) than coastal populations. Coastal populations are expected to have frequent reproductive failures, while the more stable Pribilof populations should not. In light of the breeding failures on the Pribilofs in 1981 (Robert Day, pers. comm.) and in 1982, some modifications of this model may be necessary.



APPENDICES

KEY TO ABBREVIATIONS

TM	Thick-billed murre
CM	Common murre
RK	Red-legged kittiwake
PA	Parakeet auklet
LA	Least auklet
CA	Crested auklet
HP	Horned puffin
TP	Tufted puffin
RC	Red-faced cormorant
LF	Northern fulmar (light phase)
DF	Northern fulmar (dark phase)
BK	Black-legged kittiwake

APPENDIX 1. Ledge attendance of nesting seabirds of St. George Island, 25 July 1982 [Ledge 29].

Time	TM	CM	BK	RK	PA	LA	CA	HP	TP	LF
1030	--	--	--	--	35	4	2	5	0	--
1100	443	2	12	8	41	7	1	5	2	14
1130	420	1	12	5	44	11	3	5	2	16
1200	399	0	13	7	37	7	5	5	5	14
1230	330	2	12	4	51	24	6	5	3	15
1300*	294	0	12	5	66	51	16	5	4	16
1330*	221	--	--	--	43	28	5	--	5	3
1400*	244	0	13	5	72	42	10	7	2	16
1430	238	0	10	4	93	44	22	7	2	17
1500	249	0	10	9	114	99	26	13	4	20
1530	241	0	14	8	95	115	39	14	5	20
1600	214	0	7	7	99	101	41	15	4	24
1630	243	1	9	7	100	63	22	15	5	25
1700	226	1	8	6	103	13	8	10	4	25
1730	249	1	9	6	75	0	0	11	0	23
1800	234	0	12	5	74	0	2	22	13	3

* fog at time of count.

APPENDIX 2A. Reference ledge counts, St. Paul Island, 17-21 July 1976.

Location	Time	TM	CM	BK	BK		RK		PA	LA	CA	HP	TP	RC		
					Active Nests	RK	Active Nests	RK						Nests	LF	
1	1225	72	15	35	28	9	5		1	0	0	0	0	14	12	0
2SW	1255	26	2	26	10	0	0		16	11	0	1	0	4	0	0
3	1310	79	3	47	24	2	0		14	19	0	2	0	10	7	0
5SW	1430	266	0	93	51	0	0		28	10	0	2	0	15	5	0
5NE	1405	120	1	14	8	0	0		5	1	0	0	0	3	2	0
7	1515	142	256	47	30	0	0		7	0	0	0	0	2	1	0
8	1525	253	20	20	9	0	0		20	3	0	0	0	4	3	0
9	1545	133	104	94	50	5	2		16	0	0	5	1	1	1	2
10	1600	284	648	44	24	0	0		8	0	0	0	0	4	2	3
11	1625	40	0	21	13	0	0		5	0	0	1	0	0	0	0
12	1345	193	0	78	37	0	0		3	0	0	1	0	23	10	0
13	1355	110	0	40	23	1	0		13	0	0	0	0	2	2	0
14	1415	369	184	20	8	6	2		15	0	0	3	1	3	1	2
15	1200	206	11	50	31	2	0		2	0	0	5	0	7	2	4
16	1145	187	106	60	28	1	1		17	7	0	4	0	0	0	1
17	1130	88	21	24	14	1	0		5	0	0	5	0	1	0	0
18	1115	254	192	40	17	3	1		3	0	0	0	0	8	5	0
19	1100	179	133	43	27	0	0		8	7	0	2	0	1	0	2
20	1220	37	0	15	13	0	0		0	0	0	1	0	0	0	1
22	1430	563	6	66	47	2	0		44	3	0	8	0	1	1	3
23	1510	1,073	25	80	56	11	5		42	0	0	11	0	2	2	17
Ridge Wall	1000-1700	2,179	752	914	492	61	26		696	246	14	113	13	64	43	3
Zapadni	1030-1230	1,952	558	720	462	15	8		322	135	12	29	5	48	19	2
TOTAL		8,805	3,037	2,591	1,502	119	50		1,290	442	26	193	20	217	118	40

APPENDIX 2B. Reference ledge counts, St. Paul Island, 18-20 July 1982.

Location	Time	TM	CM	BK	BK		RK		PA	LA	CA	HP	TP	RC		
					Active	Nests	RK	Active						Nests	LF	
1	1237	9	0	30	4	3	0	0	0	0	0	0	0	3	3	0
2SW	1247	26	0	24	3	0	0	0	0	0	0	0	0	17	0	0
3	1259	57	15	46	5	3	0	3	0	0	0	0	0	1	0	0
5SW	1400	179	81	79	15	1	0	10	18	0	3	0	0	13	1	0
5NE	1408	27	0	18	4	0	0	5	1	0	0	0	0	0	0	0
7	1426	117	2	20	3	0	0	0	0	0	0	0	0	4	2	0
8	1434	122	109	4	0	1	0	0	0	0	0	0	0	0	0	0
9	1455	191	75	56	6	2	0	6	5	0	6	0	0	1	1	2
10	1520	157	0	60	6	0	0	6	7	0	1	0	0	1	0	3
11	1511	38	0	10	2	0	0	6	5	0	0	0	0	0	0	0
12	1538	49	0	68	8	10	0	3	0	0	0	0	0	8	3*	0
13	1550	186	11	34	6	13	0	0	14	5	0	0	0	0	0	0
14	1611	244	6	23	4	2	0	19	0	0	0	0	0	0	0	6
15	1605	107	113	62	7	0	0	2	28	0	12	0	0	0	0	4
16	1550	26	0	24	2	0	0	23	17	0	9	0	0	0	0	1
17	1545	59	0	4	1	0	0	3	0	0	3	0	0	0	0	1
18	1535	72	0	23	6	4	0	20	14	0	4	1	0	0	0	0
19	1524	48	118	26	10	0	0	4	11	0	2	0	0	0	0	1
20	1620	82	0	11	0	0	0	9	0	0	1	0	0	0	0	0
22	1621	308	11	81	16	9	0	27	9	0	15	0	6	4	26	
23	1640	259	0	56	6	7	0	38	11	0	5	4	0	0	20	
Ridge Wall	1130-1330	1,383	417	390	86	35	0	71	255	11	71	26	7	0	7	
Zapadni	1445-1622	598	407	207	63	0	0	188	418	122	10	7	0	0	1	
TOTAL		4,344	1,365	1,356	263	90	0	457	804	133	142	38	61	14	72	

*One nest with chicks.

APPENDIX 3A. Reference ledge counts (low cliffs), St. George Island, 24-29 July, 2-3 August 1976.

Location	Time	TM	CM	BK	BK		RK		PA	LA	CA	HP	TP	RC	RC	
					Active Nests	RK	Active Nests	Nests							LF	DF
Zapadni Beach	1230-1300	675	23	46	13	45	5	115	8	0	15	2	18	0	4	0
Village W	1230-1415	986	141	368	144	210	55	197	205	14	1	0	21	8	42	0
Village E	1500-1630	1,836	254	172	95	55	20	183	44	49	6	3	15	2	66	2
8	1525	307	2	6	2	0	0	60	23	1	9	0	2	0	22	0
9	1445	295	0	38	23	7	2	23	2	0	3	0	1	0	24	0
10	1420	348	15	2	1	7	3	22	9	0	4	0	0	0	36	0
11	1400	115	52	8	6	0	0	1	1	0	1	0	0	0	0	0
12	1345	180	22	4	0	1	0	11	0	0	0	0	0	0	5	0
13	1330	105	0	0	0	0	0	9	5	0	0	0	0	0	15	0
14	1250	177	28	34	14	17	4	15	13	2	3	0	0	0	12	0
15	1210	193	0	6	4	0	0	14	10	0	2	0	0	0	27	0
16	1150	169	0	5	3	0	0	7	12	0	2	0	0	0	0	0
17	1130	148	6	8	3	0	0	12	13	0	2	0	0	0	11	0
18	1105	70	0	0	0	0	0	6	8	0	3	0	1	0	2	0
19	1050	91	16	26	22	0	0	6	0	0	0	0	2	0	10	0
20	1035	58	0	0	0	0	0	4	1	0	0	0	0	0	0	0
45	1110	202	8	5	4	1	1	18	1	0	8	0	2	3	16	1
46	1140	184	0	31	19	7	1	11	0	0	0	0	3	3	0	0
47	1215	156	3	20	7	1	0	14	3	0	2	0	0	0	28	0
48	1255	237	2	17	8	6	1	11	2	0	0	0	13	0	10	0
49	1345	31	0	21	5	59	26	0	0	0	0	0	0	0	0	0
50	1400	119	3	5	4	4	3	4	0	0	0	0	0	0	0	0
51	1510	96	0	50	16	18	5	19	0	4	4	2	0	0	10	0
52	1540	52	0	103	52	15	5	0	0	0	0	0	4	5	4	0
53	1030	188	3	49	25	94	44	2	0	0	0	0	9	7	0	0
38 lower	1925	181	0	1	0	1	0	0	0	0	2	0	0	0	1	0
26	1200	155	574	3	0	1	0	4	7	0	2	0	12	0	2	0
Village	1630-1730	730	41	358	165	293	41	103	3	0	23	4	10	3	0	0
TOTAL		8,084	1,193	1,386	635	842	216	871	370	70	92	11	113	31	347	3

APPENDIX 3B. Reference ledge counts (low cliffs), St. George Island, 23-28 July, 1-3 August 1982.

Location	Time	TM	CM	BK	BK		RK		PA	LA	CA	HP	TP	RC	RC Nests	LF	DF
					Active Nests	RK Nests	Active Nests	RK Nests									
Zapadni Beach	1145-1235	563	50	36	4	23	0	71	102	0	19	2	5	0	2	0	
Village W	1300-1530	805	164	321	36	220	1	329	308	9	36	3	34	16	48	0	
Village E	1425-1625	1,124	455	195	21	97	3	401	290	65	26	5	8	2	51	1	
8	1715	258	7	5	0	2	0	65	47	1	15	0	0	0	30	0	
9	1645	273	8	24	1	7	0	51	20	0	10	0	0	0	21	1	
10	1616	354	21	2	0	9	0	56	40	5	6	0	0	0	34	0	
11	1600	109	59	1	0	0	0	8	0	0	1	0	0	0	0	0	
12	1540	198	29	5	0	0	0	26	23	0	4	0	0	0	11	0	
13	1525	96	0	1	0	0	0	11	0	4	3	0	0	0	7	0	
14	1505	82	0	5	0	0	0	28	16	2	4	4	0	0	8	0	
15	1438	160	0	9	2	5	0	34	39	0	3	2	8	1	16	0	
16	1430	161	12	4	2	1	0	20	33	0	3	0	2	0	0	0	
17	1415	120	10	5	2	1	0	28	50	0	4	1	3	0	8	0	
18	1350	90	4	6	0	1	0	41	25	0	10	0	0	0	2	0	
19	1333	94	2	15	3	0	0	15	7	0	8	0	0	0	6	0	
20	1325	33	0	1	0	0	0	5	4	0	0	0	0	0	0	0	
45	1715	61	0	12	2	2	0	39	0	0	22	0	0	0	3	0	
46	1348	196	61	44	2	1	0	13	0	0	1	0	0	0	2	0	
47	1407	161	2	16	3	48	1	32	26	0	14	0	0	0	20	0	
48	1455	141	0	13	3	4	0	24	5	0	18	3	1	0	4	0	
49	1630	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
50	1515	50	2	5	0	9	0	3	0	0	0	0	0	0	0	0	
51	1530	65	0	45	2	14	0	22	10	5	5	2	0	0	4	0	
52	1550	34	0	82	16	14	0	0	0	0	2	0	2	1	4	0	
53*	1216, 1750	92	0	37	3	59	0	4	3	0	0	0	3	0	1	0	
38 lower	1840	610	13	0	0	1	0	22	0	0	4	0	0	0	8	0	
26	1610	67	822	0	0	0	0	3	0	0	0	0	1	0	0	0	
Village	1520-1650	494	44	414	26	199	5	249	9	5	27	6	18	5	0	0	
TOTAL		6,523	1,765	1,304	128	719	10	1,597	1,057	96	245	28	85	25	306	0	

*Average

APPENDIX 4A. Reference ledge counts (medium cliffs), St. George Island, 9-13 July 1976.

Location	Time	TM	CM	BK	BK	RK	RK						RC Nests	LF	DF	
					Active Nests ¹	Active Nests ¹	PA	LA	CA	HP	TP	RC				
21	1400	104	0	0	0	6	3	0	0	0	0	0	0	0	0	
22	1400	174	0	0	0	6	3	1	0	0	0	0	0	0	0	
23	1400	268	0	1	0	14	4	3	0	0	0	0	0	0	0	
24 middle	1625	779	54	0	0	0	0	11	0	0	3	0	0	0	126	
24 upper	1617	825	123	9	--	16	--	12	1	2	4	0	0	0	59	
25	1215	857	83	25	(19)	3	0	60	122	16	9	1	0	0	51	
27	1225	979	10	41	(24)	60	(31)	26	57	0	6	7	7	5	99	
28	1300	704	93	21	(19)	50	(31)	77	126	12	11	2	0	0	85	
29	1320	592	21	12	(9)	18	(9)	61	76	26	14	3	0	0	40	
30	1345	640	137	20	(14)	16	(11)	56	57	38	19	4	0	0	45	
31	1514	210	38	0	0	0	0	11	2	15	6	3	0	0	3	
32	1520	371	55	3	(3)	0	0	16	0	24	2	1	0	0	44	
33	1600	1,202	2	18	(13)	475	(285)	16	0	0	2	0	0	0	47	
34	1730	116	0	1	0	46	(27)	8	0	0	4	0	0	0	0	
35	1730	682	0	27	(21)	3	(2)	3	0	1	9	9	2	0	108	
36	1820	760	2	14	(10)	8	(5)	0	0	0	26	1	2	2	72	
37	1900	669	15	22	(17)	42	(18)	1	0	0	2	0	0	0	17	
38 upper	1925	459	0	5	(4)	67	(53)	1	0	0	6	0	1	0	15	
39	1350	530	89	57	20	67	23	43	0	0	54	2	0	0	80	
TOTAL		10,921	722	276	(173)	897	(505)	406	441	134	177	33	12	7	896	2

¹Numbers in parentheses include nests of undetermined status.

APPENDIX 4B. Reference ledge counts (medium cliffs), St. George Island, 29 July-1 August 1982.

Location	Time	TM	CM	BK	BK		RK		RC							
					Active Nests	RK	Active Nests	PA	LA	CA	HP	TP	RC	Nests	LF	DF
21	1300	49	0	2	0	8	0	0	0	0	0	0	0	0	0	0
22	1300	51	0	0	0	3	0	0	1	0	0	0	0	0	0	0
23	1315	200	0	1	0	14	0	14	10	0	3	0	0	0	79	0
24 middle	1430	476	12	0	0	0	0	44	11	0	2	0	0	0	17	0
24 upper	1400	486	80	29	2	5	0	75	35	16	6	2	0	0	23	0
25	1600	335	92	15	0	1	0	83	8	20	4	2	0	0	35	0
27	1640	1,227	11	33	3	97	4	55	2	0	10	1	0	0	100	0
28	1717	561	90	29	1	58	0	109	1	20	4	0	0	0	57	0
29	1740	338	4	10	2	5	0	119	1	6	4	0	0	0	13	0
30	1315	480	67	6	0	6	0	72	6	1	5	4	0	0	27	0
31	1350	138	40	1	0	1	0	6	1	2	0	0	0	0	1	0
32	1415	299	100	10	0	20	0	13	2	10	2	0	0	0	24	0
33	1510	1,745	36	19	1	433	14	19	0	0	5	0	0	0	29	0
34	1545	98	0	0	0	0	0	9	1	0	2	0	0	0	0	0
35	1630	420	13	16	2	14	0	25	2	2	3	5	0	0	75	0
36	1730	262	18	3	0	3	0	17	0	0	4	0	4	1	27	0
37	1755	680	55	20	0	54	1	39	0	2	3	0	0	0	17	0
38 upper	1840	182	0	4	0	18	0	15	0	0	3	0	0	0	10	0
39	1220	547	100	51	2	45	0	70	21	3	18	0	0	0	71	0
TOTAL		8,574	718	249	13	785	19	784	102	82	78	14	4	1	605	0

APPENDIX 5A. Reference ledge counts (high cliffs), St. George Island, 29 July-5 August 1976.

Location	Time	TM	CM	BK	BK		RK		PA	LA	CA	HP	TP	RC	RC Nests	LF	DF
					Active Nests ¹	RK	Active Nests ¹	RK									
1	1300	116	0	1	0	46	(27)	8	0	0	4	0	0	0	0	0	0
2	1445	466	100	3	0	22	12	6	0	0	2	0	0	0	0	4	0
40	1645	113	0	17	9	169	77	0	0	0	0	0	0	0	0	0	0
41	1830	1,760	362	38	27	334	170	0	0	0	0	0	0	0	0	0	0
42	1450	185	1	4	0	362	141	0	0	0	0	0	0	0	0	0	0
43	1435	196	0	21	14	580	260	3	0	0	0	0	0	0	0	0	0
44	1950	473	0	12	6	521	277	0	0	0	0	0	0	0	0	1	0
54	1600	222	0	0	0	299	98	3	0	0	0	0	0	0	0	0	0
55	1650	425	181	19	12	326	135	4	0	0	0	0	5	0	0	26	0
TOTAL		3,956	644	115	68	2,659	1,197	24	0	0	6	5	0	0	31	0	
GRAND TOTAL (all cliffs)		22,961	2,559	1,777	(876)	4,398	1,918	1,301	811	204	275	49	125	38	1,274	5	

¹Numbers in parentheses include nests of undetermined status.

APPENDIX 5B. Reference ledge counts (high cliffs), St. George Island, 30 July-2 August 1982.

Location	Time	TM	CM	BK	BK		RK		PA	LA	CA	HP	TP	RC	RC Nests	LF	DF
					Active Nests	RK	Active Nests	RK									
1	1130	298	0	14	0	77	1	1	1	0	4	0	0	0	0	2	0
2	1205	33	15	0	0	16	0	0	0	0	0	0	0	0	0	8	0
40	1310	75	0	9	0	153	1	0	0	0	0	0	0	0	0	0	0
41	1835	1,715	496	40	6	410	15	3	0	0	0	0	0	0	0	1	0
42	1430	178	7	3	0	255	6	0	0	0	0	0	0	0	0	0	0
43	1500	156	0	3	0	491	25	9	0	0	0	0	0	0	0	0	0
44	1545	311	0	5	2	462	38	3	0	0	0	0	0	0	0	0	0
54	1630	261	0	0	0	277	18	6	0	0	0	0	0	0	0	0	0
55	1700	381	238	10	0	220	3	13	0	0	2	0	0	0	0	12	0
TOTAL		3,408	756	84	8	2,361	107	35	1	0	6	0	0	0	23	0	
GRAND TOTAL (all cliffs)		18,505	3,239	1,637	149	3,865	136	2,416	1,160	178	329	42	89	26	934	2	

APPENDIX 6. Least auklet flight count from sea to Ulukaia Hill colony,
St. George, 30-31 July 1982.

Time	Least Auklets	Time	Least Auklets
1550	1,470	1930	1,460
1600	1,400	1940	1,640
1610	1,290	1950	2,220
1620	890	2000	2,040
1630	630	2010	2,610
1640	900	2020	3,800
1650	690	2030	4,860
1700	650	2040	4,260
1710	630	2050	3,290
1720	620	2100	2,970
1730	380	2110	4,480
1740	490	2120	3,440 ²
1750	620	2130	5,040
1800	400	2140	5,500
1810	450	2150	4,360
1820	330 ¹	2200	5,100
1830	540	2210	5,510
1840	550	2220	2,310
1850	460	2230	2,300
1900	730	2240	1,150
1910	730	2250	540
1920	870	2300	0

TOTAL OF EVENING PEAK 72,760

¹Evening low.

²Average of 2 counts.

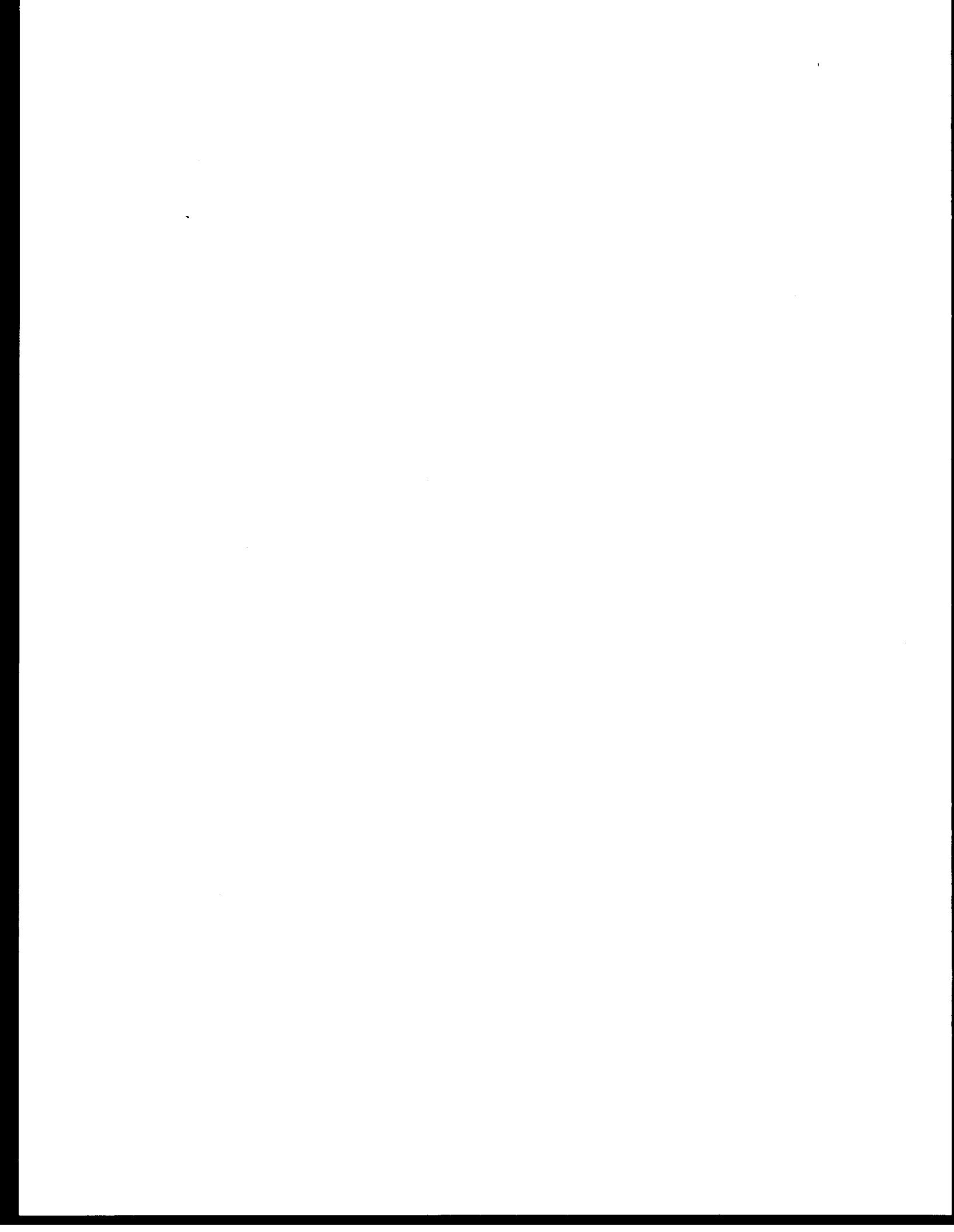
Appendix 7. Scientific names of seabird species discussed in this report¹.

Species	Abbreviation	
Northern fulmar (light phase)	<i>Fulmarus glacialis</i>	LF
Northern fulmar (dark phase)	<i>Fulmarus glacialis</i>	DF
Red-faced cormorant	<i>Phalacrocorax urile</i>	RC
Black-legged kittiwake	<i>Rissa tridactyla</i>	BK
Red-legged kittiwake	<i>Rissa brevirostris</i>	RK
Common murre	<i>Uria aalge</i>	CM
Thick-billed murre	<i>Uria lomvia</i>	TM
Parakeet auklet	<i>Cyclorrhynchus psittacula</i>	PA
Least auklet	<i>Aethia pusilla</i>	LA
Crested auklet	<i>Aethia cristatella</i>	CA
Tufted puffin	<i>Fratercula cirrhata</i>	TP
Horned puffin	<i>Fratercula corniculata</i>	HP

¹Phylogenetic sequence, scientific nomenclature, and English names of species all follow the American Ornithologists' Union (34th Supplement to the AOU Check-List of North American Birds [Auk 99(3):1CC-16CC, 1982]).

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**PELAGIC DISTRIBUTION OF MARINE BIRDS
ON THE CENTRAL BERING SEA SHELF
AND ANALYSIS OF RISK FOR THE NAVARIN BASIN**

by

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**Final Report
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SUMMARY OF OBJECTIVES, CONCLUSIONS AND IMPLICATIONS WITH RESPECT TO OCS OIL AND GAS DEVELOPMENT

The purpose of this study was to obtain information on avian use of the Navarin Basin, and to evaluate the potential risk to birds of offshore oil development in this region. We used data from our five OMPA sponsored cruises which covered the central shelf area of the Bering Sea ($59^{\circ}30'N$ to $63^{\circ}N$). We also used data from other OSCEAP surveys of the area, and our data from PROBES sponsored cruises.

Despite the number of cruises surveying the Navarin Basin, only about half of the area has been covered in any season and there is no coverage for the winter. Sample sizes are generally low in the Navarin Basin (a maximum of 40 transects per 30' latitude by 60' longitude block). Hence, we pooled observations by location into larger geographic areas on the basis of oceanographic and biological features: coastal water, middle shelf water, outer shelf water, deep water and areas within 60 km of the major breeding colonies at St. Lawrence and St. Matthew Islands (Figure 1). While the use of zones is useful for providing patterns of bird distribution and abundance within habitats, it does not reveal specific sites of high density.

Average Densities

The analysis of bird distribution by zone (Table 1) showed birds concentrated in the middle shelf and outer shelf regions of the Navarin Basin in the spring, with average densities of about 40 birds/km². Least Auklets (Aethia pusilla) were the most abundant species in both the outer shelf and middle shelf waters surveyed, although Thick-billed Murres (Uria lomvia) were also abundant on the middle shelf.

In summer, birds were concentrated around the colonies at St. Lawrence Island (average density 343 birds/km², mostly auklets) and St. Matthew Island (average density 193 birds/km², mostly murres). Bird densities in outer shelf waters were also high (97 birds/km²) and represented storm-petrels (Oceanodroma

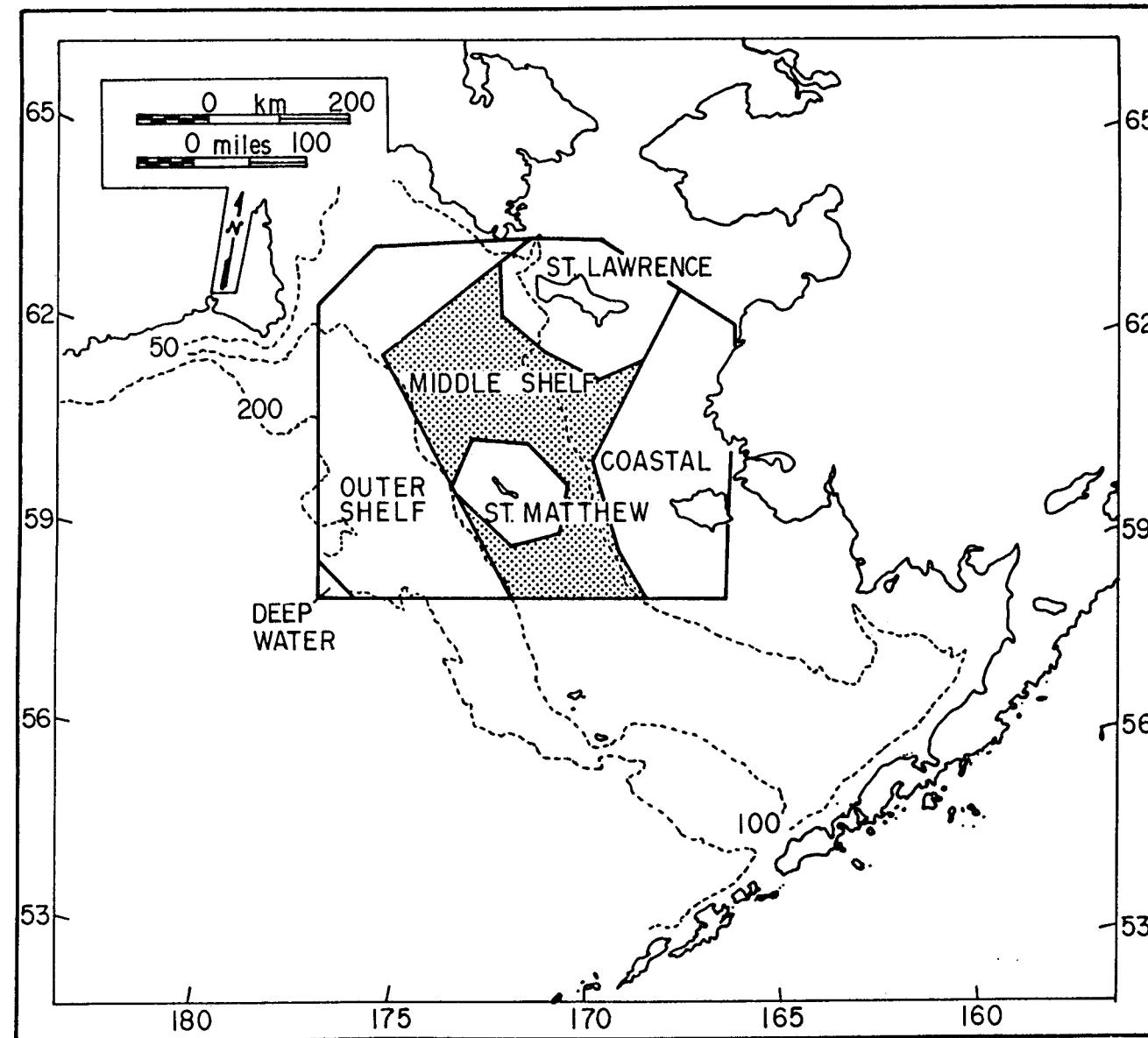


Figure 1. Zones for the central Bering Sea shelf.

Table 1. Mean densities (birds/km²) of birds on the central Bering Sea shelf by zone and season. The abbreviations¹ in parentheses stand for the most abundant species. See tables 3-5 for sample sizes.

ZONE	SPRING	SUMMER	AUTUMN
Coastal	*	75 (MURR)	3
Middle Shelf	44 (LEAU)	19 (MURR)	12 (SMAL)
Outer Shelf	38 (LEAU)	97 (STPE)	21 (SMAL)
Deep	6 (NOFU)	24 (STPE)	22 (SHER)
St. Matthew	16 (MURR)	193 (MURR)	7 (BLKI)
St. Lawrence	*	343 (SMAL)	*
Total	28	98	13
All seasons	56		

* no data

¹ BLKI= Black-legged Kittiwake, LEAU = Least Auklet, MURR = murres, NOFU = Northern Fulmar, SHER = shearwaters, SMAL = small auklets, STPE = storm-petrels.

sp.) and phalaropes (Phalaropus sp.). Coastal waters showed moderate use in the summer (average density 75 birds/km²) by murres, Black-legged Kittiwakes (Rissa tridactyla) and Crested Auklets (Aethia cristatella).

In the fall, the Navarin Basin supported low densities of birds. The highest densities were found in outer shelf waters and in the deep waters beyond the shelf (average density 20 birds/km²). Auklets were the predominant birds in outer shelf waters while shearwaters were the most abundant species beyond the shelf.

Figures 2-4 show average bird density on a finer scale (30' latitude by 60' longitude blocks) and show high average densities (≥ 75 birds/km²) within the Navarin Basin during all seasons we sampled. In general, average densities were lower and areas of high density were not as widespread in portions of the southeastern Bering Sea (e.g. the inshore waters of Bristol Bay and portions of the outer and middle shelf domains). In the spring, high bird densities were found west of St. Matthew Island, near the 100 and 200 m isobaths. Large numbers of birds were also seen in the polynyas around St. Matthew Island (N. Harrison, B. Braun, pers. obs.), but, no formal censuses were made. In summer, average densities were highest around St. Matthew Island, the site of a breeding colony of 1.4 million seabirds (Sowls et al. 1978), St. Lawrence Island, with 1.8 million breeding seabirds, and at the shelf edge in the northwest corner of the Navarin lease sale area. In the fall, bird densities were moderate or low (≤ 30 birds/km²) except at the shelf edge in the southwest corner of the lease sale area where the average densities of Northern Fulmars (Fulmarus glacialis) and shearwaters (Puffinus sp.) reached 75 birds/km².

Encounter rate for high bird densities

Figures 5-8 show the encounter rate for four levels of bird density (50, 100, 500 and 1000 birds/km²) averaged throughout the year. Since oil spills may occur in any season, these figures give a rough estimate of the number of birds that might be affected in any region. Large numbers of birds are likely to be affected near St. Matthew and St. Lawrence Islands and at the shelf break in

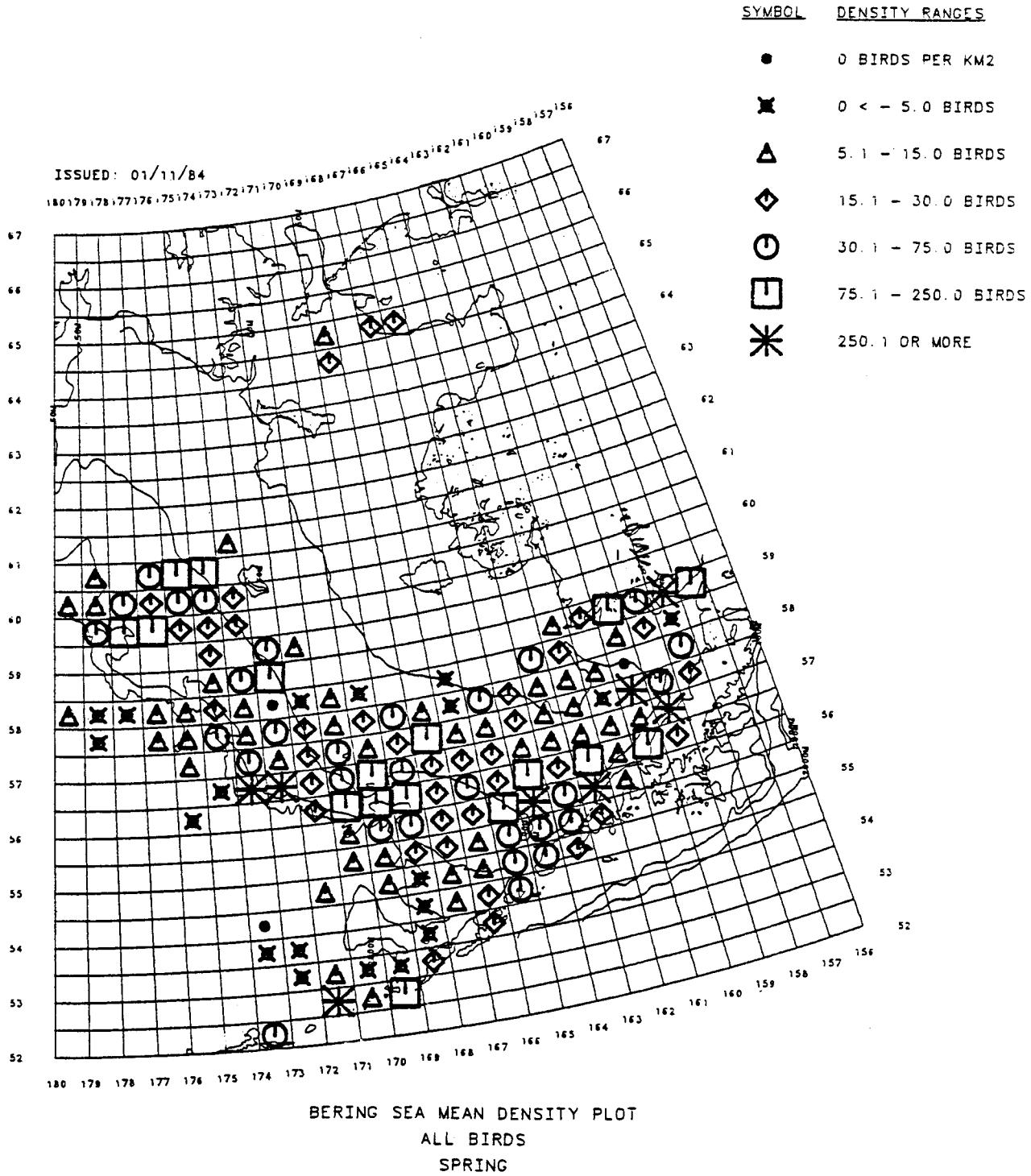


Figure 2. Mean densities, all birds: Spring.

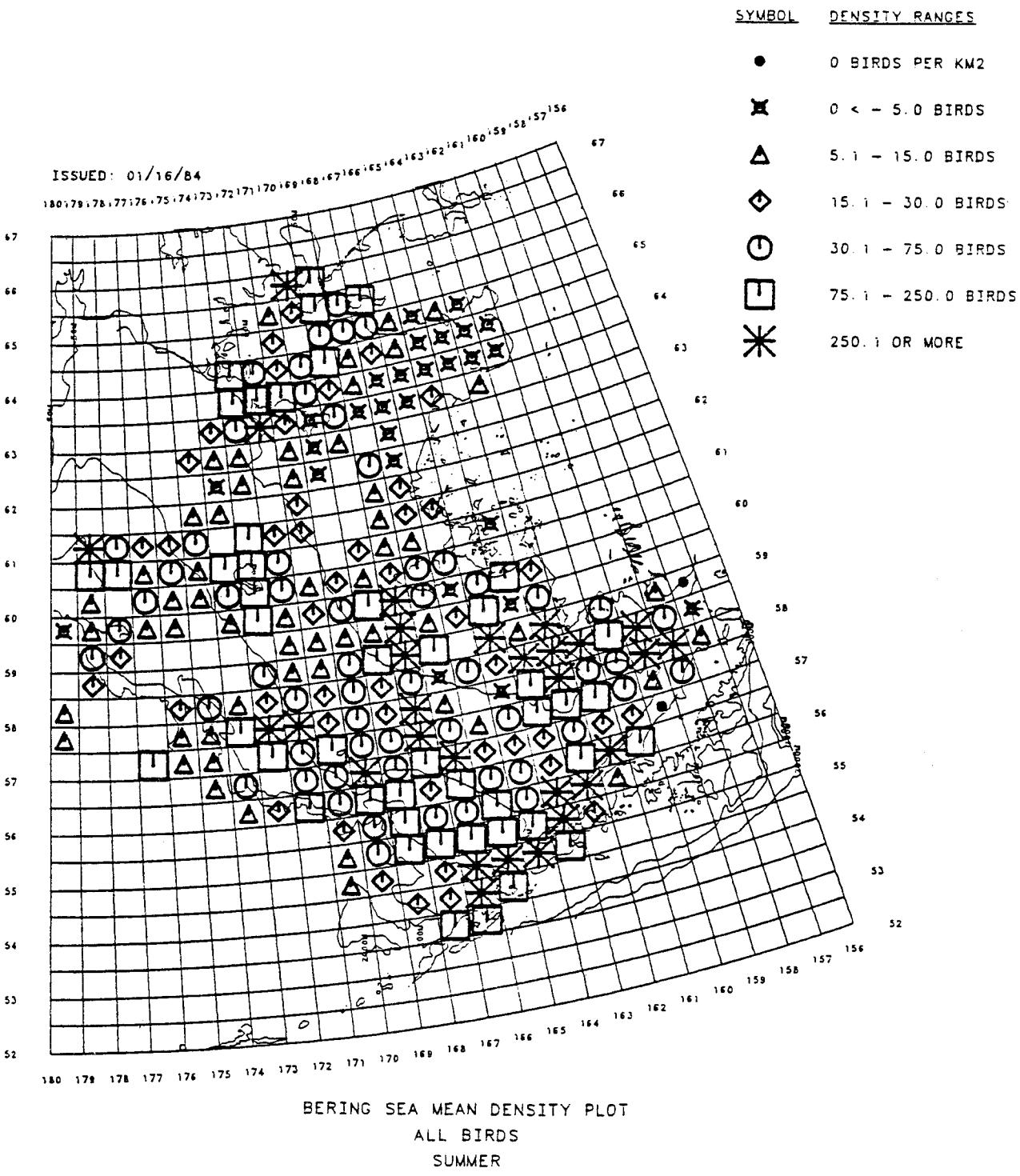


Figure 3. Mean densities, all birds: Summer.

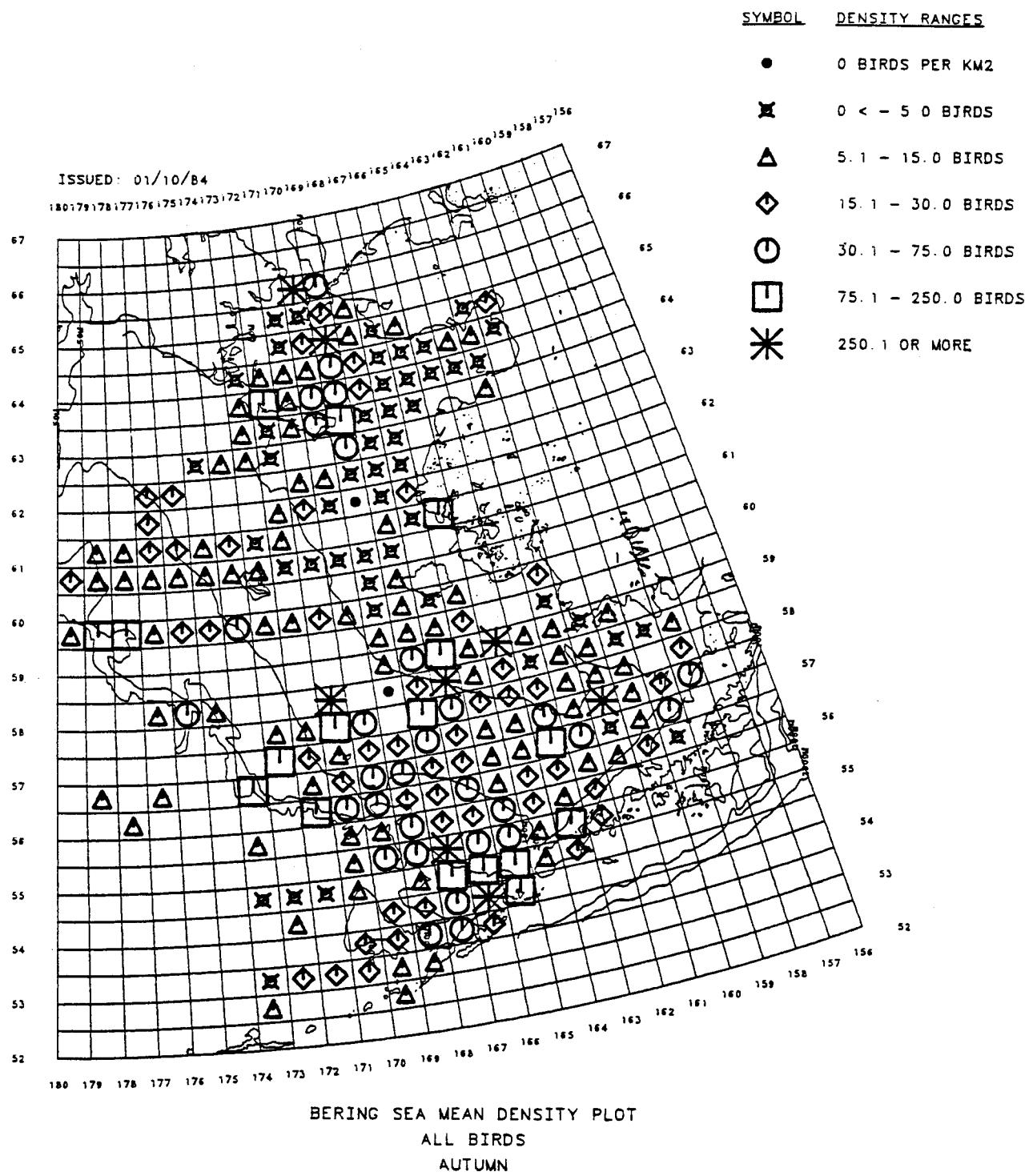


Figure 4. Mean densities, all birds: Autumn.

the northwest corner of the lease-sale area (Figure 7). High bird densities in these areas were largely confined to the summer (Table 6, p. 33), when they occurred more frequently than figures 5-8 suggest. In the summer, bird densities \geq 250 birds/km² were encountered in 10% of the transects in outer shelf waters (mostly storm-petrels and phalaropes), in 22% of the transects around St. Matthew Island (mostly murres and auklets), and in 27% of the transects around St. Lawrence Island (mostly auklets).

Summary and recommendations for future work

Most of the avian biomass of the Navarin Basin was composed of resident, breeding birds, with Thick-billed Murres and Least Auklets being the most abundant species. The only migrants which occurred in large numbers were phalaropes (mostly Red Phalaropes Phalaropus fulicaria) which occurred in high densities at the shelf break during summer. Migrant shearwaters, which dominated the avifauna of the southeastern Bering Sea, were a minor constituent of the Navarin Basin avifauna, and were only found in high densities at the shelf break in the fall. Additional survey work around St. Lawrence and St. Matthew Islands in the spring could be useful given our observations of large numbers of birds and Divoky's (1980) suggestion that most bird biomass in the ice-influenced portion of the Bering Sea in spring is associated with polynyas around colonies. Although almost half of the Navarin Basin hasn't received sampling, all marine habitats have been censused and consistently low counts were found in most censused areas (Figures 14-16, pp. 30-32). Further survey efforts are unlikely to provide new insights into the locations of seabird concentrations in the Navarin. Emphasis should now focus on protecting critical habitat, particularly the areas around colonies. The development of a staging area on St. Matthew Island is of particular concern as increased ship traffic in the area may result in chronic oil pollution of the foraging areas of breeding birds. Hunt (MS) has suggested that chronic pollution may have more serious consequences for population stability than occasional spills.

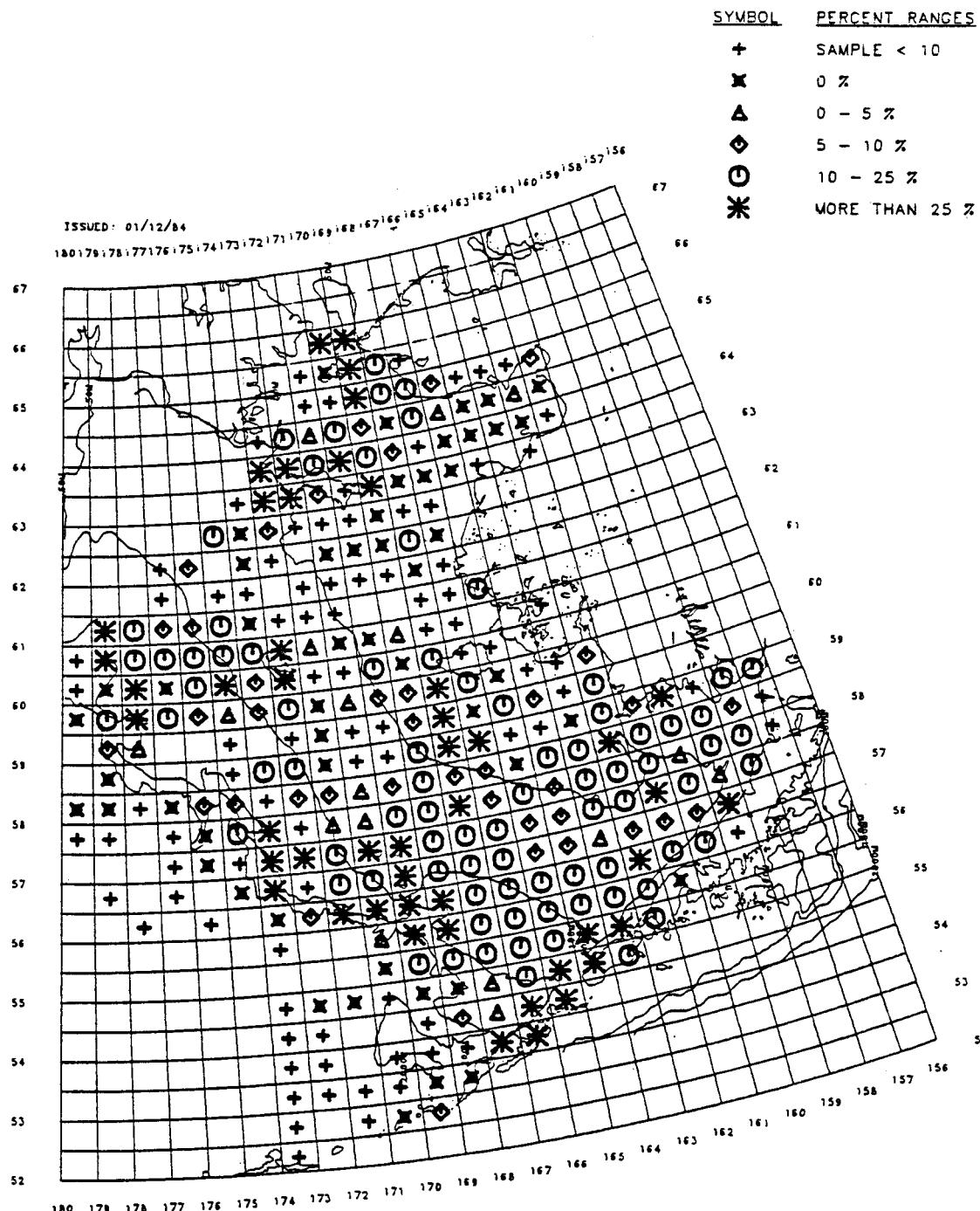


Figure 5. Frequency distribution of transects with densities ≥ 50 birds/km 2 .

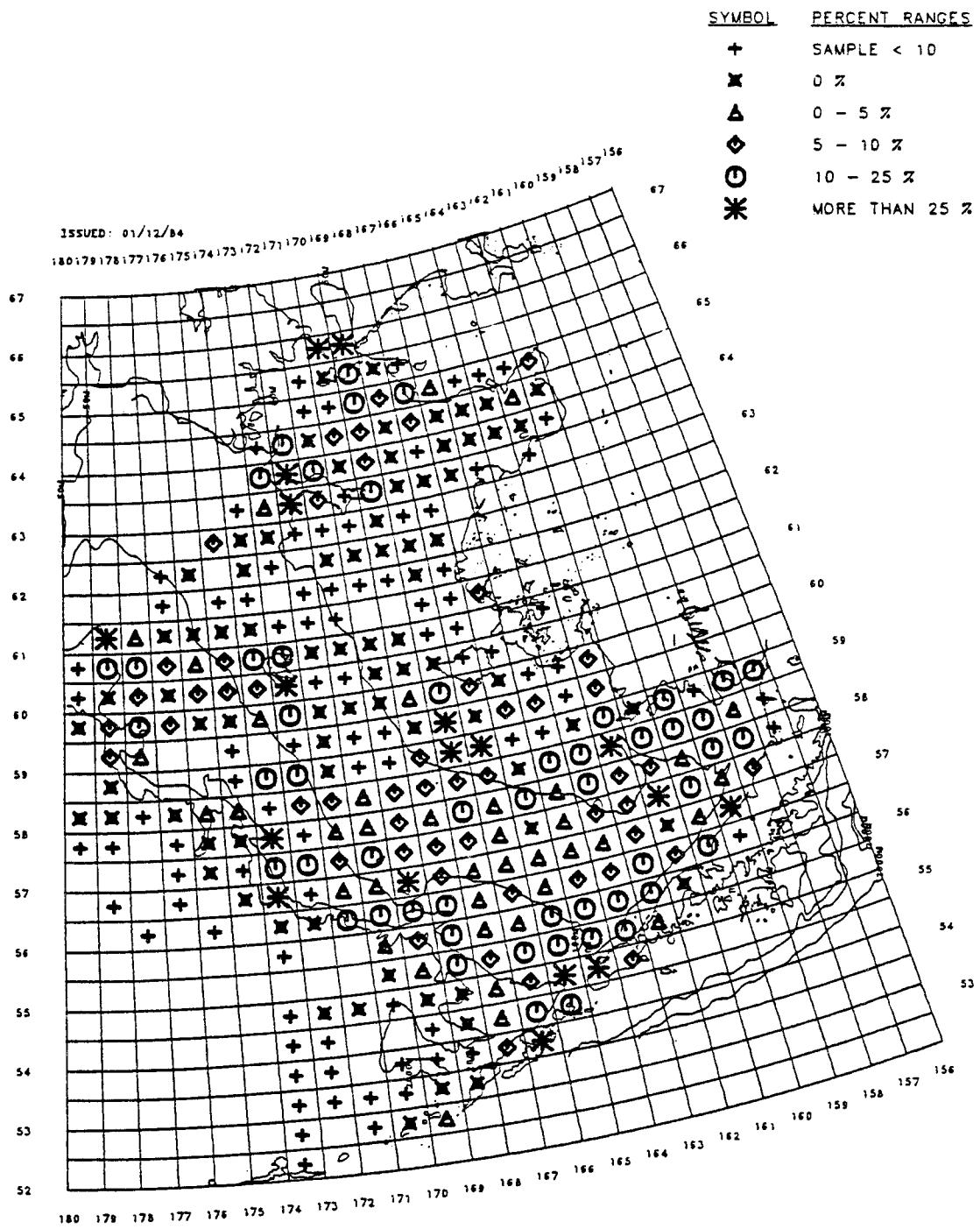


Figure 6. Frequency distribution of transects with densities ≥ 100 birds/km 2 .

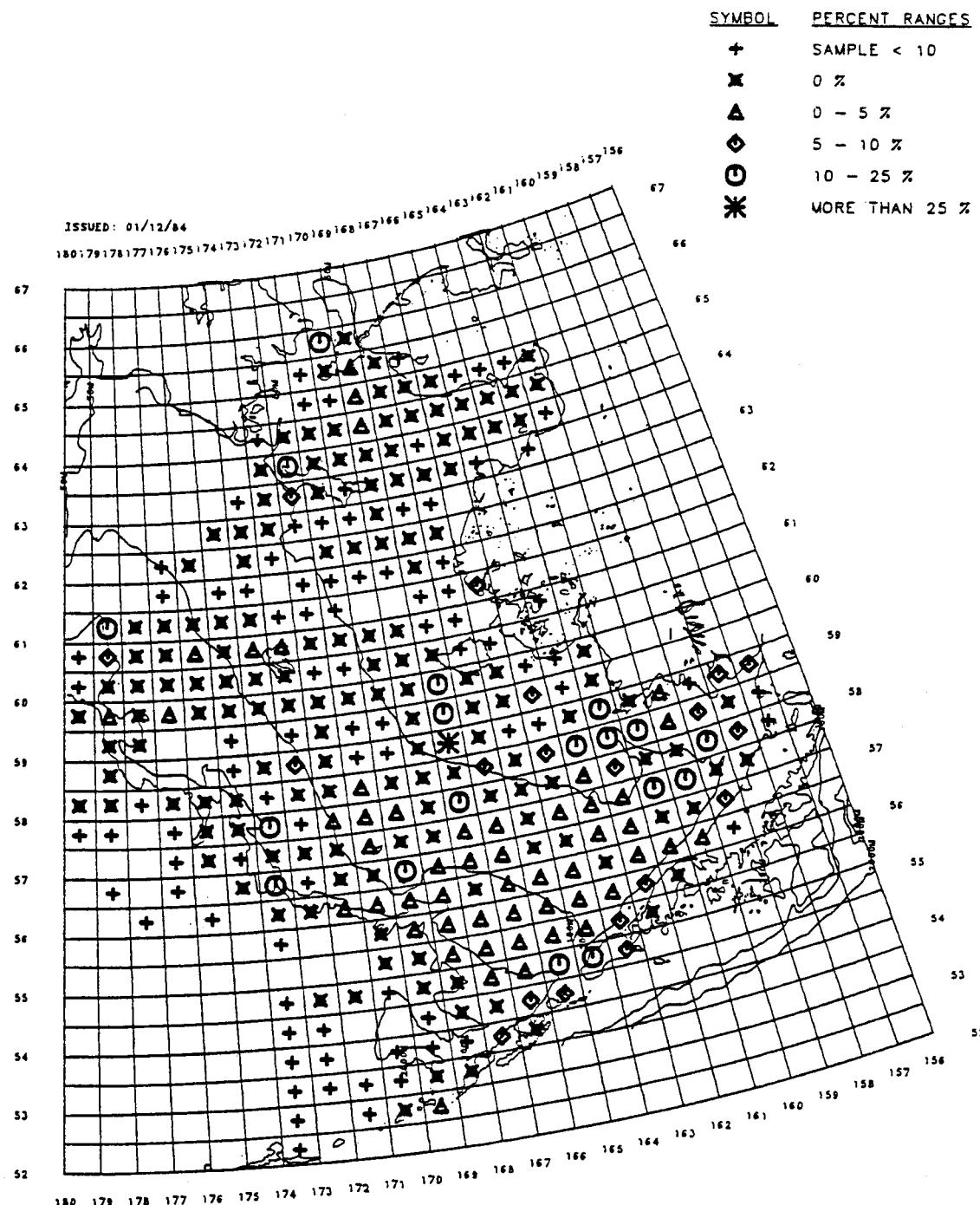


Figure 7. Frequency distribution of transects with densities ≥ 500 birds/km².

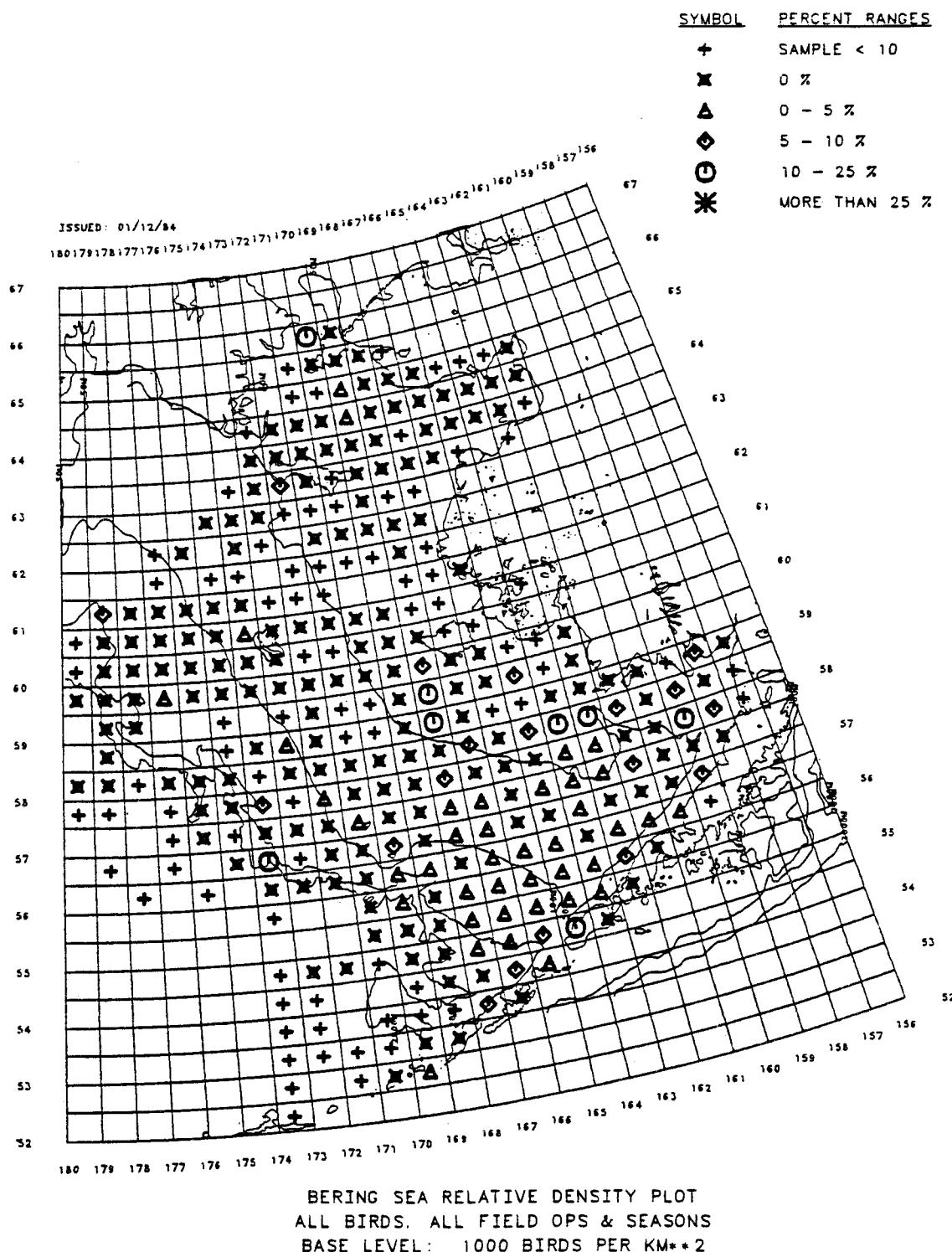


Figure 8. Frequency distribution of transects with densities $\geq 1,000$ birds/km 2 .

INTRODUCTION

This study examines seabird use of the Navarin Basin and central shelf region of the Bering Sea. We discuss the seasonal patterns of bird use of the Navarin Basin and compare average densities and dominant species with other regions of the Bering Sea. We discuss the importance of the region for species sensitive to oil spills and point out important habitats where high bird densities may be expected. We identify areas within the Navarin Basin which lack adequate censusing and make recommendations for future study. Here, we also present the latest compilation of bird distribution data for the eastern Bering Sea, including new data from five 1982 cruises. These cruises largely covered previously uncensused areas on the central shelf of the Bering Sea ($59^{\circ}30'N - 63^{\circ}N$). Two cruises we made in 1983 in the Navarin Basin and adjacent deep waters are not included in this presentation, but are being entered into the seabird data base available from NODC and the Data Projects Group at the University of Rhode Island.

We have previously reported on the patterns of seabird distribution relative to the risk of encountering oil for the southeastern Bering Sea (Hunt et al. 1982) and for the North Aleutian Shelf (Eppley et al. 1982). Our knowledge of bird densities in the Navarin Basin is based on a relatively small data base compared to that available for the St. George Basin or the PROBES area in central Bristol Bay. For these regions which have received extensive sampling, we previously found significant differences between water masses in the abundance of birds and species present which accounted for up to 30% of the variation in bird numbers. In the Navarin Basin, for which we have a relatively small data set and where there are several water masses, it was necessary to focus on avifaunal differences among water masses in generating our estimates of bird numbers.

CURRENT STATE OF KNOWLEDGE

Oceanographic setting

The Navarin Basin contains several different hydrographic domains: deep waters beyond the shelf, outer shelf waters, middle shelf waters, and shallow water habitat around St. Matthew Island and nearby St. Lawrence Island (Figure 9). Much of the eastern Navarin Basin consists of middle shelf waters, 50 to 100 m deep. A strong thermocline develops in these waters, limiting nutrient input to the euphotic zone. The central and western part of the Navarin Basin contains outer shelf waters, which are complexly stratified. Upwelling is expected at the shelf break front, which crosses the western corner of the lease sale area. East of the Navarin Basin, there is extensive middle shelf and coastal water habitat. St. Matthew Island, which rests in middle shelf water, presents a topographic discontinuity in this two-layer system, and its coastal waters may support different prey populations.

The water masses of the Navarin Basin are similar in their vertical structure to the domains of the southeastern Bering Sea studied by the PROBES program. In the southeastern Bering Sea, these water masses have little net horizontal advection (Coachman and Charnell 1979) and are associated with distinct faunal assemblages and food webs (Iverson et al. 1979); in the northern Bering Sea, analogous water masses form currents. While there are similarities between the faunas of the analogous northern and southern water masses, there are important differences in biomass and species composition of the faunas. Presumably the central shelf of the Bering Sea is a transitional area for these water masses and it is difficult to apply directly the results of studies done on the northern or southern water masses to this central region. The physical oceanography of the Navarin Basin is not well studied and little information is available on the fauna and food webs of this region.

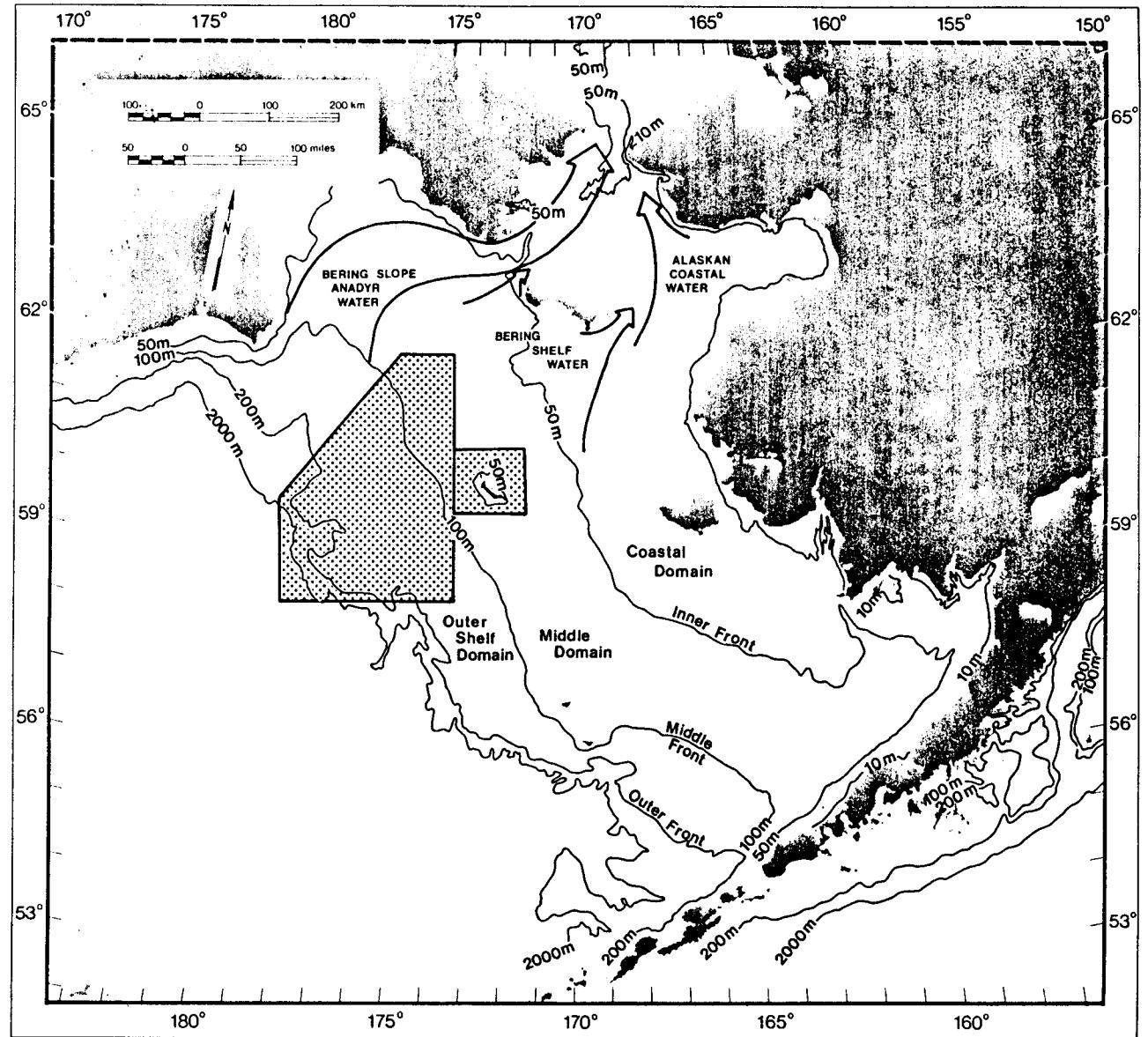


Figure 9. Navarin Basin relative to the hydrographic domains of the Bering Sea.

Ornithological background

As part of their efforts to census pelagic bird abundance in the Bering Sea, the U. S. Fish and Wildlife Service has conducted bird censuses in the Navarin Basin. These data have not been presented for the Navarin Basin per se, but have been included in the general ornithological data base and are included in the present analysis. Other ornithological work on the Bering Sea shelf has not been localized in the Navarin Basin, but the results may be applicable. Previously, Shuntov (1972), Wahl (1978) and Hunt et al. (1981b) have reported summer densities of birds on the Bering Sea shelf to be between 15 and 32 birds/km². Surface-feeding seabirds such as kittiwakes, fulmars and storm-petrels, have been found to be associated with outer shelf waters, while sub-surface foragers have been found to be associated with middle shelf waters (Schneider and Hunt 1982). Thick-billed Murres and Sooty Shearwaters (*Puffinus griseus*) have also been associated with outer shelf waters (Schneider and Hunt 1982).

The number of different water masses in the Navarin Basin probably increases the local heterogeneity of the avifauna. Fronts and eddies formed at the boundaries of water masses, the upwelling region along the continental slope, and outer shelf areas may possibly support larger standing stocks of prey than surrounding waters and may therefore be areas where high bird densities are likely to be encountered.

There are two large bird colonies fairly near the Navarin Basin which serve to increase bird densities in the region, St. Matthew Island with 1.4 million birds and St. Lawrence Island with 1.8 million birds (Sowls et al. 1978). Only St. Matthew Island is close enough to the Navarin lease-sale area so that breeding birds might forage there. However, the Navarin Basin is likely to be important to birds associated with other northern colonies as a staging or recovery area before or after breeding.

The Navarin Basin has not been censused for birds during the winter, largely due to the logistical problems caused by ice cover between January and June (Brower et al. 1977). McRoy et al. (1971) visited St. Matthew Island in February and found concentrations of murres, Harlequin Ducks (Histrionicus histrionicus), Oldsquaw (Clangula hyemalis) and eiders in the leads around the island. In March, Divoky (1981) found that the ice front is an important habitat for birds where high densities were common (up to 10,000 birds/km² with 1000 birds/km² occurring commonly). Murres were the most numerous species he found associated with ice. Later in the spring, high bird densities (\geq 100 birds/km²) were limited to polynyas near breeding colonies, and bird densities elsewhere were lower (30-50 birds/km²) (Divoky 1981). The impact of oil spilled during winter on Navarin Basin avifauna may be very different than oil spilled in other seasons due to the concentrating effect of polynyas on birds and oil, the transport of oil in ice and the release of unweathered oil from the melting ice edge in the spring (Vermeer and Anweiler 1975, Gaston and Nettleship 1981, Brown 1982).

In the past few years, methods have been presented to evaluate the risk of oil to bird populations (King and Sanger 1979) and to compare the risk to birds among regions (Kaiwi and Hunt 1983). King and Sanger's oil vulnerability index for North Pacific bird species indicates the likelihood that an individual of a species will become oiled and the sensitivity of the species given its population size, breeding range and productivity. Kaiwi and Hunt (1983) developed a method to assess the relative risk to birds within segments of a lease-sale area and to compare these assessments. They polled ornithologists, conservationists and ecologists and found that respondents preferentially voted to protect areas where birds breed and those containing bird populations with low reproductive rates.

We are still a long way from being able to predict the consequences of oil spills on Alaskan seabird populations. Hunt (MS) has summarized recent literature on birds and oil pollution, emphasizing the applicability and limitations of simulation models of seabird population response. He points out that oil-related mortality in some cases is only a small fraction of natural mortality. If oil-related mortality is additional to natural mortality, then oil spills could have major effects on seabird populations, especially if spills occurred close to large colonies. However, if most natural mortality is density-dependent, then oil-related losses could be largely compensatory. In Alaska, losses due to oil pollution might be recovered through increased production via a reduction of density-dependent depression of reproduction found at the large colonies (Hunt et al. MS). Alternatively, the concentration of birds in a few large colonies makes these populations extremely vulnerable to a single spill. Most of the information we have on the effects of oil pollution on marine bird populations comes from the North Sea where bird colonies are relatively small (<100,000 birds) and dispersed. In Alaska, marine birds are concentrated in a few very large colonies (>1,000,000 birds). The models of bird population recovery rely on age-specific survivorship curves derived from European seabird populations; these may be different from values for Alaskan seabird populations which live in a different environment.

Clark (1984) and Hunt (MS) suggest that chronic, low-level pollution may be more damaging to population stability than occasional spills. The plan to use St. Matthew Island as a staging area raises concern about increased ship traffic resulting in chronic pollution of the foraging areas of breeding birds. Preliminary results from our NSF-sponsored study of seabird foraging suggests that tidal fronts and eddies may be important foraging sites for St. Matthew birds. These features may tend to concentrate and confine oil in what may be preferred foraging areas of breeding birds.

METHODS

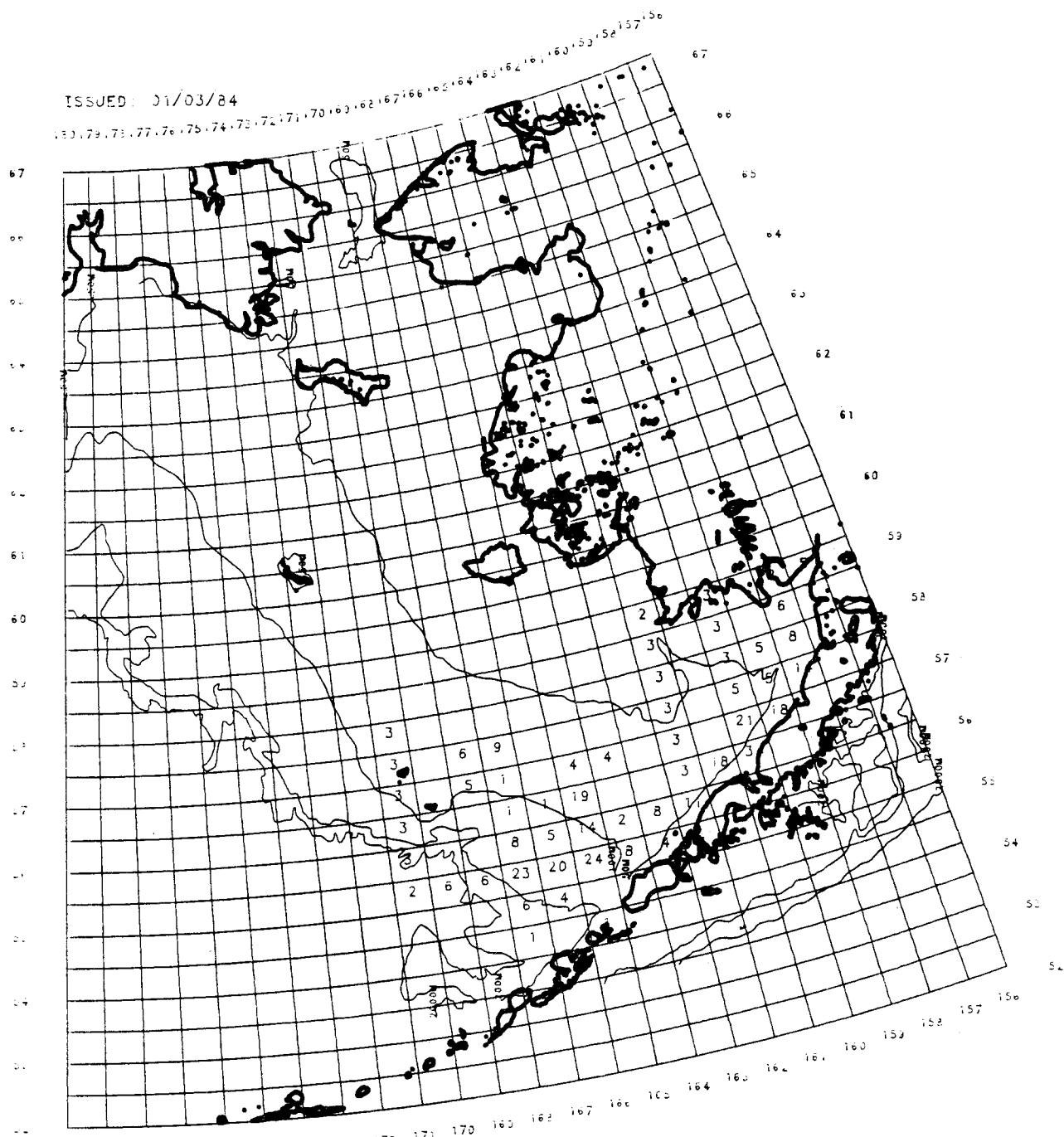
Data collection

The data presented in this report were obtained on five OMPA sponsored cruises made in 1982, and on other cruises made by ourselves (including PROBES cruises) and other OCSEAP investigators (see Appendix 4). Bird densities were estimated using a line transect method modified for use at sea (Hunt et al. 1982). Counts were made from ships, using a 90° sector extending 300 m abeam and forward. Counts were made while the ship was underway at speeds ranging from 10 to 20 km/hr (5-11 knots). Ship following birds were counted and thereafter excluded from counts. The ship's position, to the nearest tenth of a minute of latitude and longitude, was recorded at the start and end of each 10 minute count. Bird identifications were made to the lowest possible taxonomic level. Bird densities were computed for each 10 minute count based on the area scanned (distance traveled x transect width). Data from aircraft surveys (using either fixed-wing craft or helicopters) were treated in a similar fashion, and both ship and air transects were included in the data base. The sampling effort by season is given in Figures 10-13.

Analysis

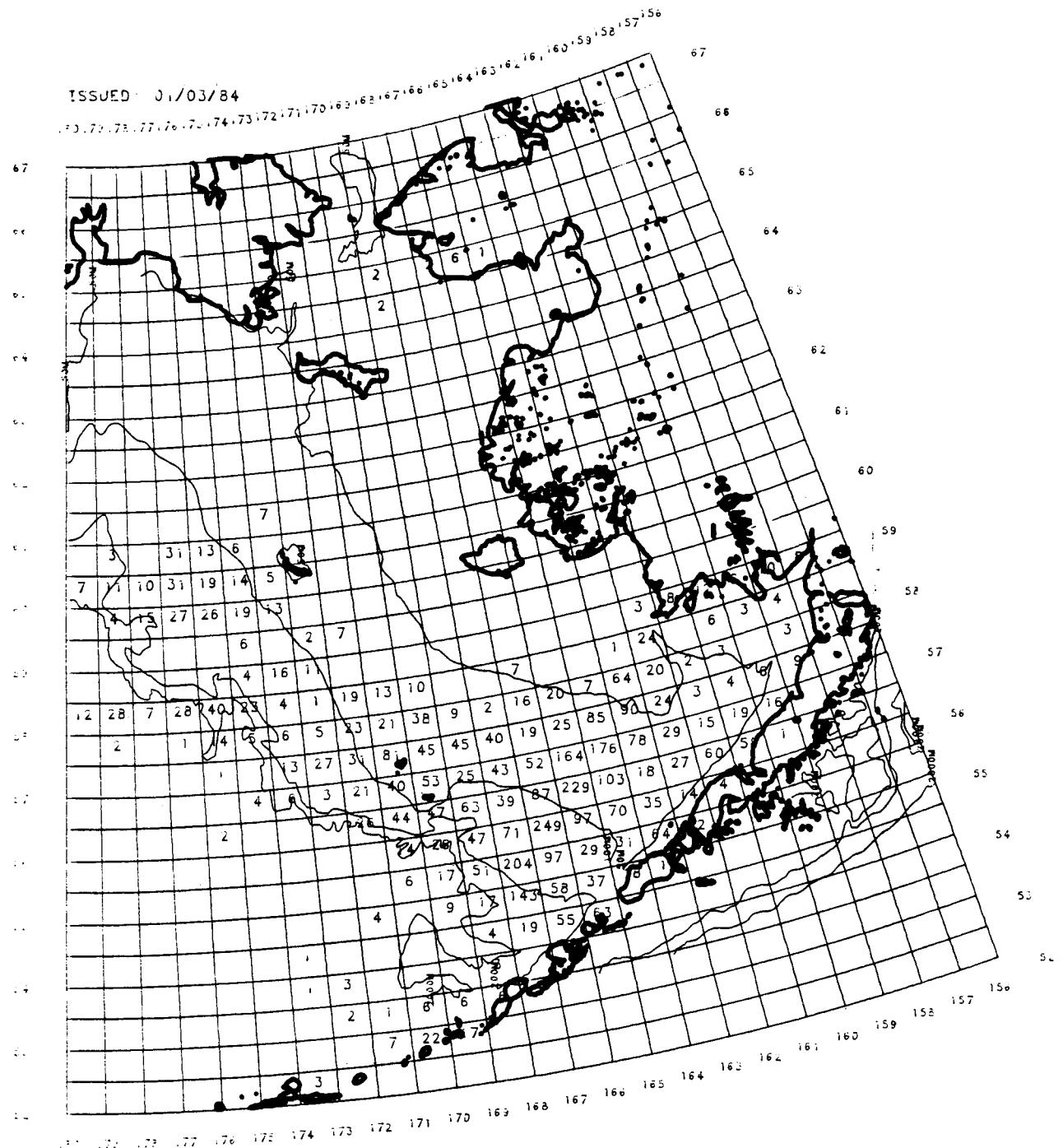
Average bird densities within 30' latitude by 60' longitude blocks for the eastern Bering Sea were calculated by season for individual species, all birds, and all birds on the water (see Appendix 4 for species groups). These figures show the seasonal pattern of species distribution and abundance, but do not reflect the great variability in bird densities. The frequency distribution of bird densities within each 30' latitude by 60' longitude block was calculated, for all seasons combined. These plots indicate how often bird densities of ≥ 50 , 100, 500 and 1000 birds/km² were encountered.

To incorporate variability, a coefficient of variation (standard deviation/mean) was also calculated for each block. Blocks having a high mean (high rate of



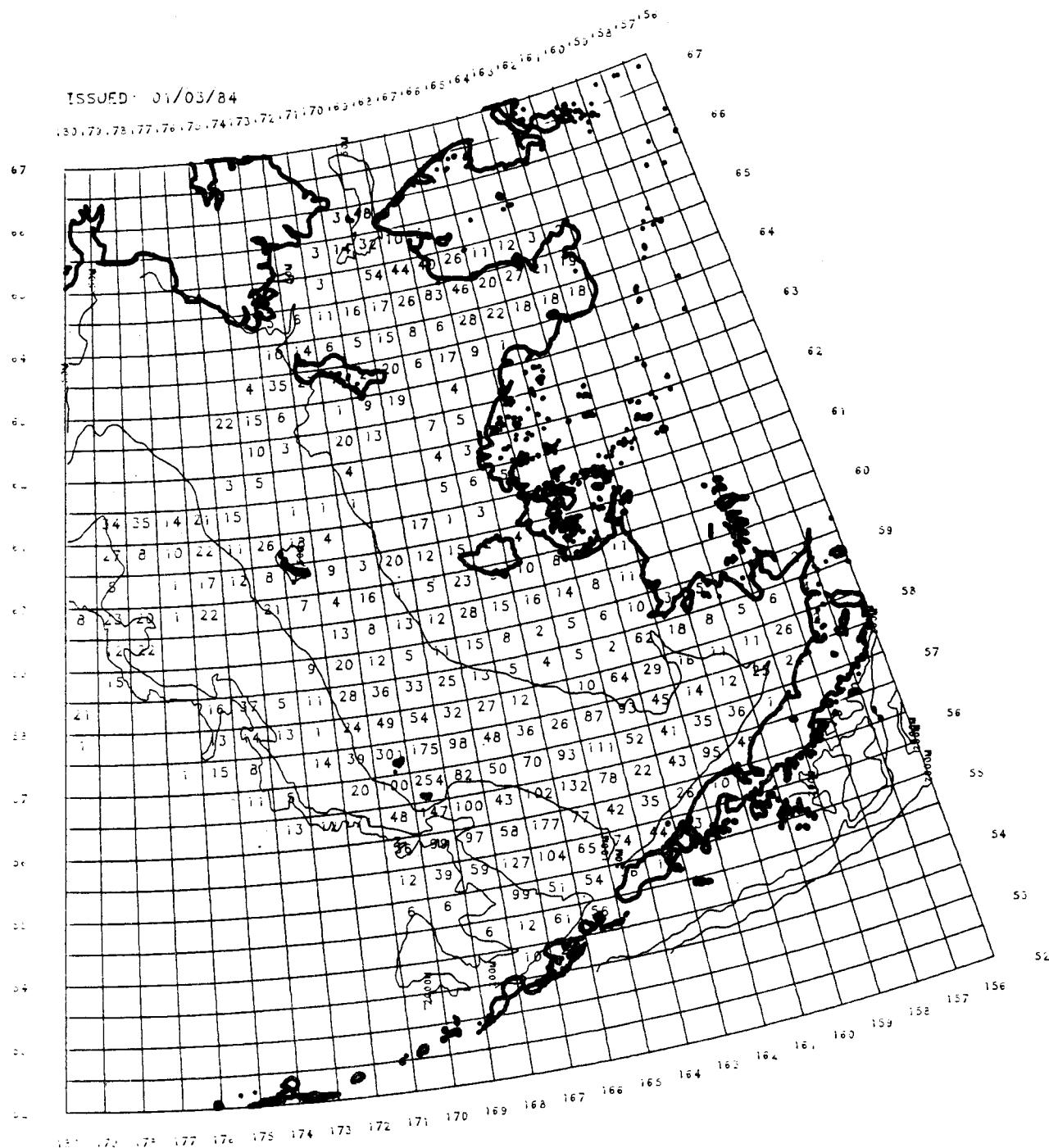
BERING SEA EFFORT PLOT
 FILE TYPE 033 BIRD DATA
 WINTER

Figure 10. Effort plot, all field observations, 1975-1982: Winter.



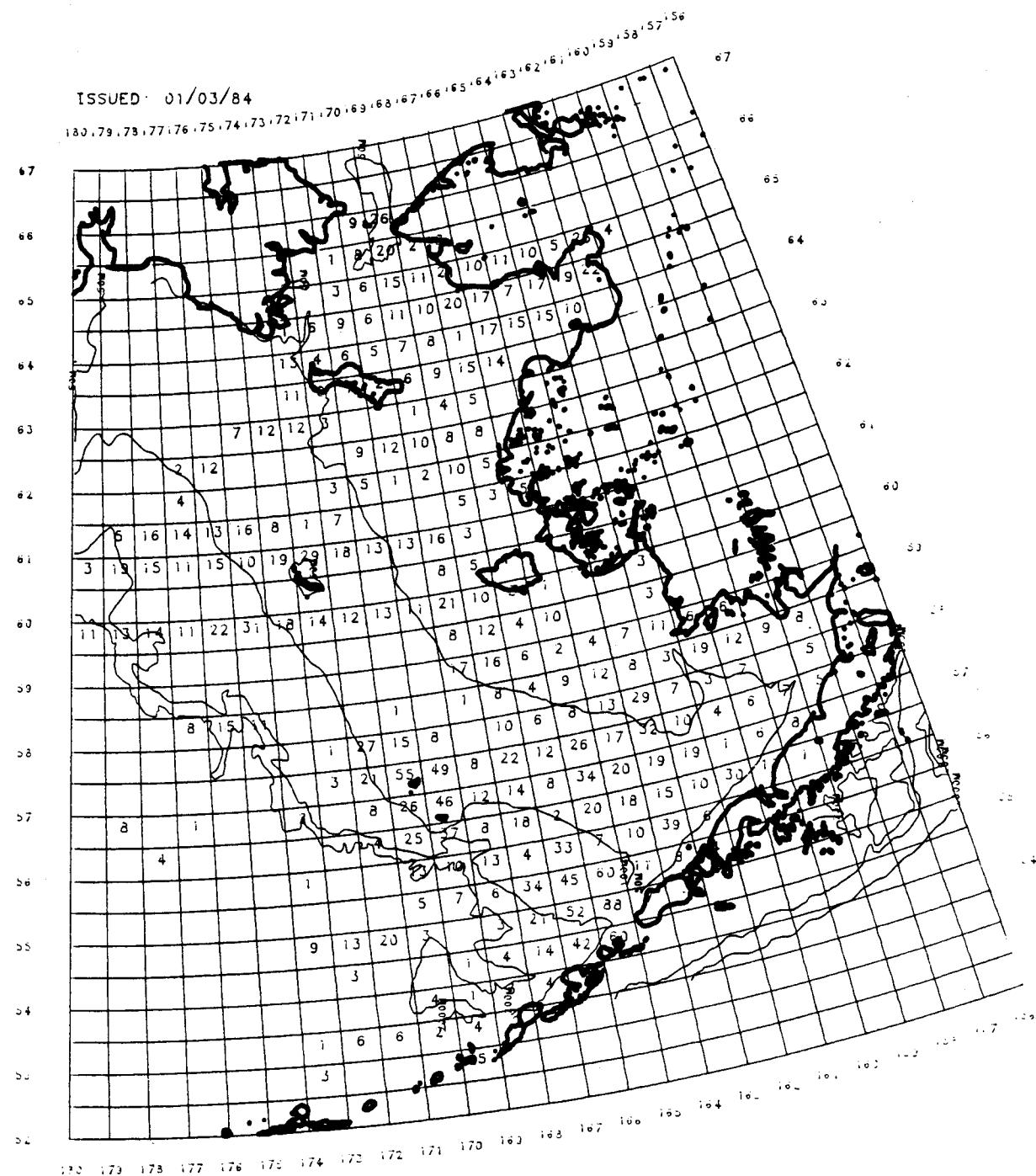
BERING SEA EFFORT PLOT
 FILE TYPE 033 BIRD DATA
 SPRING

Figure 11. Effort plot, all field observations, 1975-1982: Spring.



BERING SEA EFFORT PLOT
 FILE TYPE 033 BIRD DATA
 SUMMER

Figure 12. Effort plot, all field observations, 1975-1982: Summer.



BERING SEA EFFORT PLOT
 FILE TYPE 033 BIRD DATA
 AUTUMN

Figure 13. Effort plot, all field observations, 1975-1982: Autumn.

encounter) and a low coefficient of variation (a reliably high rate of encounter) were identified as high risk areas (see Hunt et al. 1982 for a more complete discussion of the use of coefficients of variation). This method uses subjective cut-off values to separate high and low means and high and low coefficients of variation. These cut-off values were selected on the basis of arbitrary considerations and must be evaluated on those terms. Also, at this time we have no reliable method to mathematically describe the true overall distribution of the bird population; only modest confidence can be placed on the stability of means for small areas and thus, also on the coefficients of variation.

To reduce the statistical problems caused by local patchiness of seabird distributions, we categorized the data into mutually exclusive density categories and looked at the frequencies of transects in the different categories. This method greatly minimizes the number and strength of the assumptions required for analysis and allows the application of relatively simple discrete probability models to the problem of estimating the likelihood of encountering large numbers of birds (see Appendix 1). Confidence limits for the proportions observed in each category were computed for the both the case where no assumptions were made about the distribution of birds (nonparametric) and for the normal approximation. The confidence interval is the observed encounter rate \pm the error rate (d), where

$\alpha = 0.95$ and

$$d = \frac{1}{2[N(1-\alpha)]^{.5}} \quad \text{or} \quad \sqrt{\frac{1.96^2}{4N}} \quad \text{for the normal approximation}$$

These are the same formulas used in Hunt et al. 1982 and in Eppley et al. 1982 to calculate error rates. However, a typographical error occurred in both these works for the nonparametric formula, giving it as:

$$\frac{1}{2} \frac{1}{[N(1-\alpha)]^{.5}} \quad \text{instead of} \quad \frac{1}{2[N(1-\alpha)]^{.5}}$$

In order to provide areas within which sampling effort was sufficient to provide meaningful frequency distributions and for which there would be a biological rationale for the boundaries, we divided the Navarin Basin and adjacent waters into zones (Figure 1, p. 2). The zones are drawn to represent different water masses: coastal, middle shelf, outer shelf and the deep waters off the shelf. Two other zones were constructed around St. Lawrence and St. Matthew Islands, extending 60 km around each island. We used 60 km as an approximation of the foraging range of most breeding birds, as we had previously found to be the case at for a similar suite of species at the Pribilof Islands (Hunt et al. 1981a). Only RU83 cruises were included in this analysis. Ship-following birds were excluded from this analysis, as were transects shorter than 10 minutes or with visibility less than 300 m.

The analysis of bird distribution by zone provided information on the average densities of species using each habitat by season as well as information on the frequency distribution of bird densities. We used density categories of: 0-5, 5.1-15, 15.1-30, 30.1-75, 75.1-250 and >250 birds/km².

RESULTS

Patterns of bird use of the Navarin Basin

The Navarin Basin is one of several areas of moderately high bird density within the eastern Bering Sea (Figures 2-4, pp. 5-7). In the spring, the middle and outer shelf regions of the Navarin Basin supported bird densities of about 40 birds/km² (Table 1, p. 3). The most abundant birds were auklets and murres. In the summer, birds were concentrated near breeding colonies resulting in high average densities: 193 birds/km² around St. Matthew Island and 343 birds/km² around St. Lawrence Island. Murres were the most numerous birds around St. Matthew

Island, while auklets were the predominant species at St. Lawrence Island. In the fall, the highest bird densities (about 20 birds/km²) were found in outer shelf waters (mostly auklets) and in deep waters off the shelf (mostly shearwaters).

Surface foraging seabirds were more abundant in outer shelf waters, while there was little difference in the abundance of diving seabirds among water masses (Table 2). Particular species were more abundant in outer shelf waters: Northern Fulmar, storm-petrels, shearwaters and phalaropes (spring and summer only); while others were associated with middle shelf waters: Crested Auklet, Common Murre (Uria aalge), Black-legged Kittiwake, Thick-billed Murre (spring only).

Several species were found in the Navarin Basin in densities as high or higher than in other censused regions of the Bering Sea. These species were: storm-petrels (Figure 30, p. 64), phalaropes (Figure 42, p. 75), Black-legged Kittiwakes (Figure 50, p. 84), Thick-billed Murres (Figure 66, p. 100), small alcids (Figure 70, p. 104) and Least Auklets (Figure 78, p. 112) during the spring; phalaropes (Figure 43, p. 77) during the summer; and murres (Figure 60, p. 94) during the fall. In addition, murres in the spring (Figure 58, p. 92), storm-petrels in the summer (Figure 31, p. 65), and shearwaters (Figure 28, p. 62) and Least Auklets (Figure 80, p. 114) in the fall occurred in high densities in the Navarin Basin, although these densities were not the highest for these species in the Bering Sea.

Risk assessment

In previous reports (Hunt et al. 1982, Eppley et al. 1982) we have used a base level of 30 birds/km² encountered in $\geq 50\%$ of the transects to identify important areas for birds. The frequency distribution of densities for each zone in the central Bering shelf region are given for spring, summer and fall in Tables 3-5. High frequencies of counts with densities ≥ 30 birds/km² were relatively scarce in spring and especially fall. More than half of the transects

Table 2. Mean densities (birds/km²) of surface and sub-surface foraging seabirds in outer shelf and middle shelf waters of the central Bering Sea shelf.

		SPRING	SUMMER	AUTUMN
SUB-SURFACE FORAGERS: alcids, shearwaters	Outer shelf	25.28	16.54	15.29
	Middle shelf	36.16	15.11	8.08
SURFACE FORAGERS: kittiwakes, fulmars, phalaropes, storm- petrels	Outer shelf	12.07	79.06	1.52
	Middle shelf	5.78	3.08	2.38

Table 3. Spring frequency distribution of bird densities (birds/km²) by zone (percent of transects) for the central Bering Sea shelf.

ZONE	N	DENSITY CATEGORY						
		0	0.1- 5.0	5.1- 15.0	15.1- 30.0	30.1- 75.0	75.1- 250.0	>250
Coastal	0							
Middle Shelf	113	0	5.3	28.3	21.2	31.9	12.4	0.9
Outer Shelf	168	0.6	11.9	36.3	28.6	15.5	5.4	1.8
Deep	146	6.8	47.3	39.0	6.8	0	0	0
St. Matthew	10	0	10.0	40.0	40.0	10.0	0	0
St. Lawrence	0							

Table 4. Summer frequency distribution of bird densities (birds/km²) by zone (percent of transects) for the central Bering Sea shelf.

ZONE	N	DENSITY CATEGORY						
		0	0.1- 5.0	5.1- 15.0	15.1- 30.0	30.1- 75.0	75.1- 250.0	>250
Coastal	36	2.8	0	8.3	16.7	41.7	27.8	2.8
Middle Shelf	291	2.4	25.4	34.7	22.0	12.4	2.7	0.3
Outer Shelf	223	2.7	13.9	24.7	18.4	18.8	11.2	10.3
Deep	140	15.7	41.4	14.3	6.4	15.0	5.7	1.4
St. Matthew	67	0	0	3.0	14.9	26.9	32.8	22.4
St. Lawrence	113	3.5	10.6	8.0	8.0	15.9	27.4	26.5

Table 5. Autumn frequency distribution of bird densities (birds/km²) by zone (percent of transects) for the central Bering Sea shelf.

ZONE	N	DENSITY CATEGORY						
		0	0.1- 5.0	5.1- 15.0	15.1- 30.0	30.1- 75.0	75.1- 250.0	>250
Coastal	76	22.4	63.2	11.8	1.3	1.3	0	0
Middle Shelf	223	1.3	31.4	43.0	17.5	5.8	0.9	0
Outer Shelf	137	2.2	23.4	46.7	18.2	5.1	2.9	1.5
Deep	57	3.5	28.1	49.1	8.8	7.0	0	3.5
St. Matthew	74	10.8	45.9	33.8	6.8	2.7	0	0
St. Lawrence	0							

in the coastal zone (72%) and the areas around St. Matthew (82%) and St. Lawrence (70%) Islands had bird densities > 30 birds/km² during the summer. For comparison, in the southeastern Bering Sea, bird densities ≥ 30 birds/km² were encountered in the summer in more than half of the transects around the Pribilof Islands and Cape Newenham, both sites of large bird colonies, and in Unimak Pass. As in the southeastern Bering Sea, important areas for birds in the central Bering Sea are the areas around colonies and the coastal zone.

To refine this classification of areas in which spilled oil would pose a high risk for birds, we analyzed the Navarin lease-sale area in 30' latitude by 60' longitude blocks in terms of mean densities and variability using coefficients of variation. Figures 14-16 classify blocks as having high (> 75 birds/km²) or low densities, and whether these densities were consistent ($CV \leq 2.0$) or were highly variable. Consistently high densities were found associated with the shelf break front during spring, summer and fall; the 100 m front in the spring; and with St. Matthew Island in the summer. The high densities associated with the fronts were localized along portions of the fronts and were spatially variable. Other areas of the Navarin Basin which received sampling generally showed consistently low densities, although much of the Basin has yet to be adequately sampled.

Averaging over all seasons, bird densities ≥ 500 birds/km² were rarely encountered in the central Bering Sea shelf (Figures 7 and 8, pp. 11-12). The encounter rates were highest near St. Matthew and St. Lawrence Islands and at the shelf break in the northwest corner of the Navarin lease sale area (Figures 7 and 8). At St. Matthew Island, 5% of the transects contained bird densities ≥ 500 birds/km², while at St. Lawrence Island and at the shelf break 10-25% of the transects contained high bird densities (Figure 8).

The likelihood of encountering high densities during a particular season may be much greater than figures 5-8, averaged over a year, indicate. We therefore

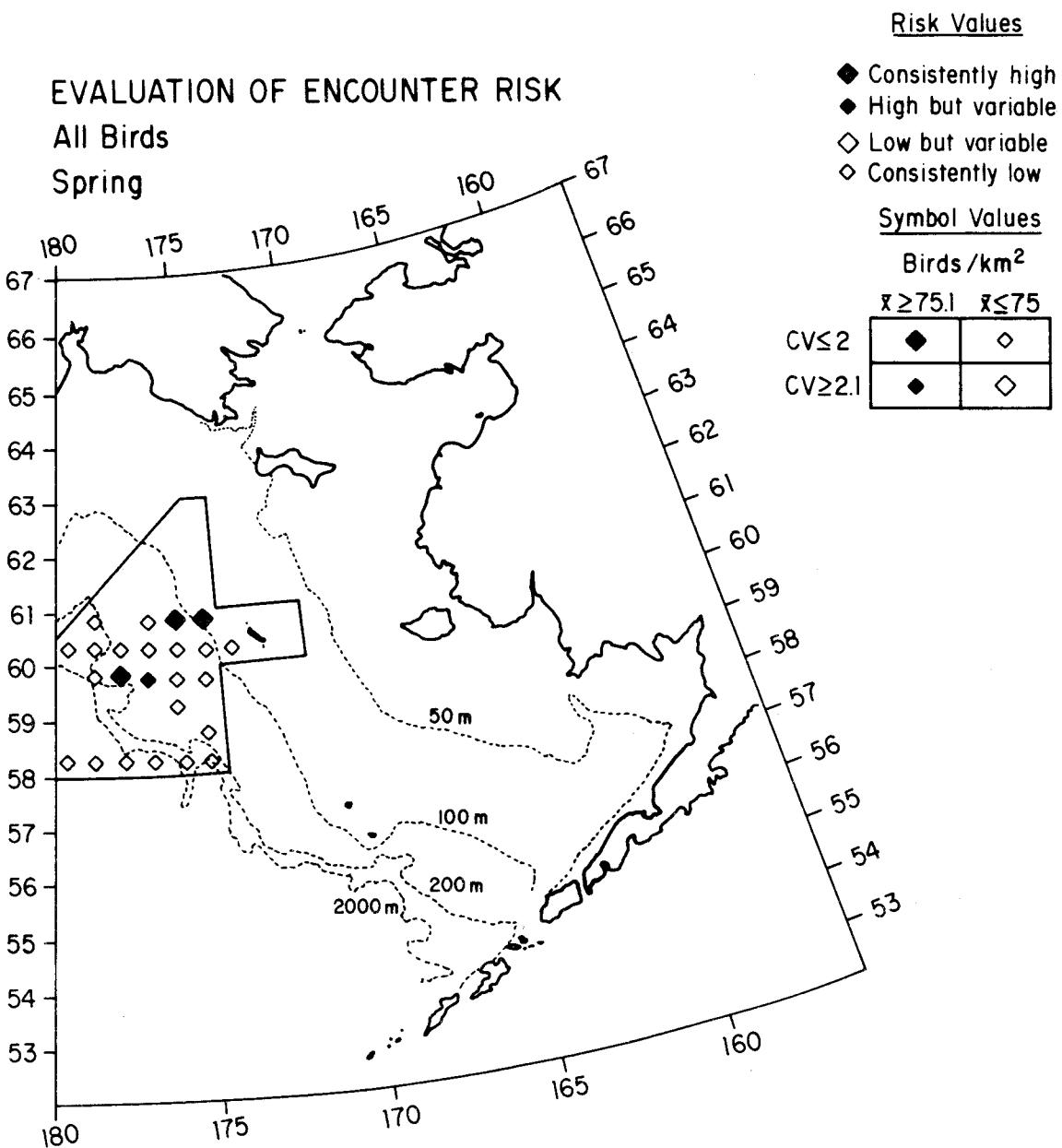


Figure 14. Evaluation of encounter risk for birds in the Navarin Basin:
Spring.

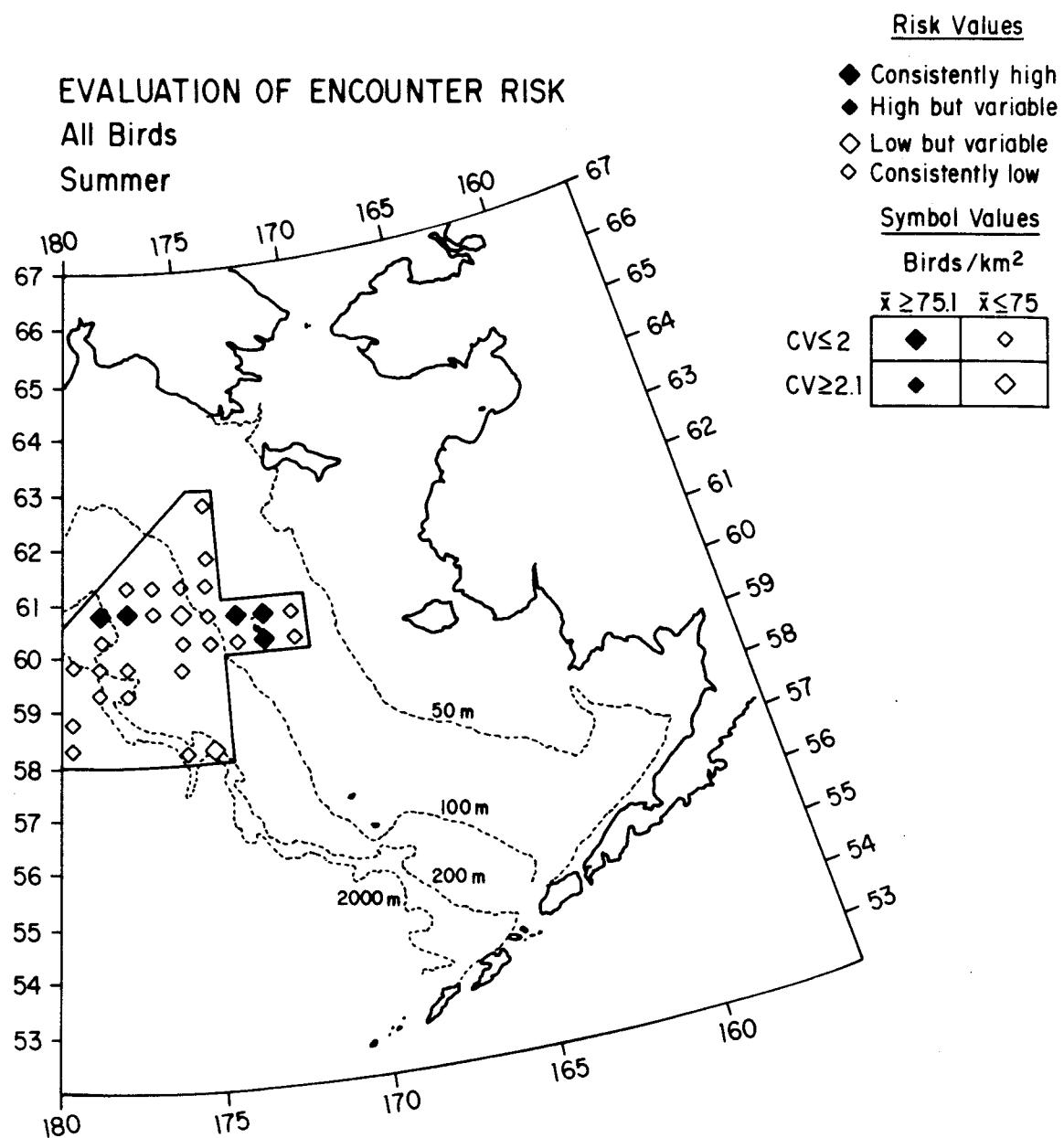


Figure 15. Evaluation of encounter risk for birds in the Navarin Basin:
Summer.

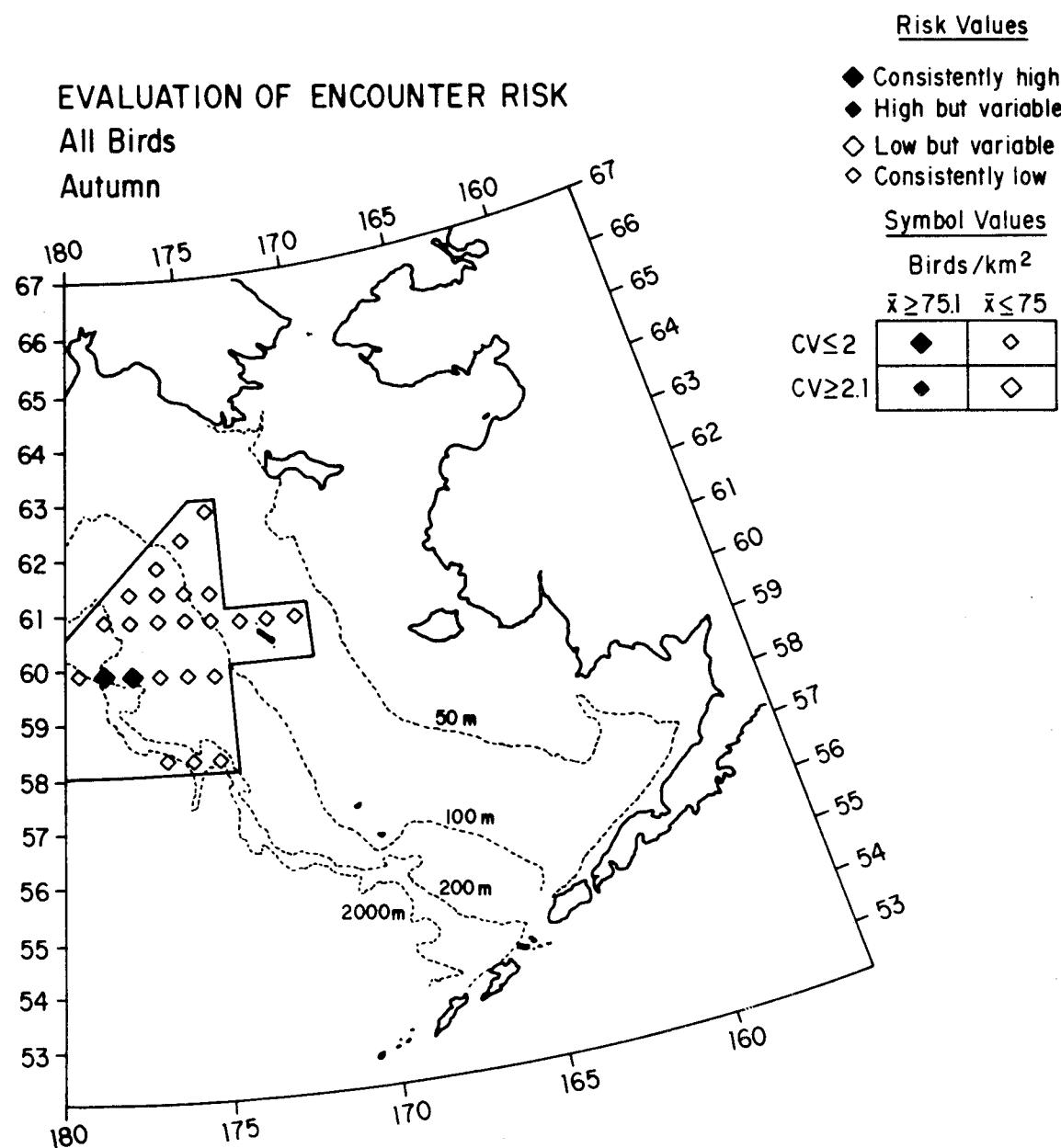


Figure 16. Evaluation of encounter risk for birds in the Navarin Basin:
Autumn.

Table 6. The occurrence of bird densities greater than 250 birds/km² on the central Bering Sea shelf by season, zone and species, based on RU83 data only. Confidence intervals (95%) are given.

SPRING:	<u>middle shelf</u>	<u>outer shelf</u>		
	all 0.9%	all 1.8%		
	small alcids 0.9% (Least Auklets 0.9%)	small alcids 1.2% (Least Auklets 1.2%)		
	<u>± 9%</u>	storm-petrels 0.5%		
		<u>± 8%</u>		
SUMMER:	<u>middle shelf</u>	<u>outer shelf</u>	<u>St. Matthew</u>	<u>St. Lawrence</u>
	all 0.3%	all 10.3%	all 22.4%	all 26.5%
	murrels 0.3%	storm-petrels 5.4%	murrels 16.4%	small alcids 17.7%
	<u>± 6%</u>	phalaropes 3.1%	small alcids 4.5%	(Least Auklets 12.4%)
		shearwaters 1.3%	(Least Auklets 3.0%)	murrels 6.2%
		Northern Fulmars 0.4%	Northern Fulmars 1.5%	(Crested Auklets 3.5%)
	<u>± 7%</u>		<u>± 12%</u>	Black-legged Kittiwakes 1.8%
				<u>± 9%</u>
AUTUMN:	<u>deep</u>	<u>outer shelf</u>		
	all 3.5%	all 1.5%		
	shearwaters 3.5%	<u>± 8%</u>		
	<u>± 13%</u>			

used a subset of the data used in figures 5-8 (RU83 data) to examine the occurrence of transects with high bird densities within the central Bering Sea shelf (Figure 1, p. 2) for each zone and season (Table 6). In spring and fall the scarcity of counts with high densities remained as before. In summer, at St. Matthew and St. Lawrence Islands, bird densities >250 birds/km 2 occurred commonly; over 26% of the transects near St. Lawrence Island and 22% of the transects near St. Matthew Island had bird densities >250 birds/km 2 . These data emphasize our finding that summer is the period when high concentrations of birds are most likely to be found, and that the waters near the two large colonies on St. Lawrence and St. Matthew Islands are particularly important. The shelf edge region (outer shelf and deep water zones) was also important in summer when concentrations of birds were frequently encountered there. Large numbers of phalaropes migrate through this region on their return to breeding areas and it is heavily used by storm-petrels that may either be from Aleutian Islands colonies, or be non-breeding birds.

DISCUSSION

Estimates of the accuracy of encounter rates

We have used a confidence level of 95% throughout this report. These data could be described using different confidence levels. For comparison, we provide tables giving the required sample size associated with four different confidence levels and two different error rates for both the nonparametric calculation (Table 7) and the normal approximation (Table 8). These tables also appeared in Hunt et al. 1982 with a typographical error, which is corrected here.

Our estimates of the encounter rates for specific bird densities are within about 10% of the true encounter rates (95% confidence) for most zones and seasons (Tables 9-11). Unfortunately, our error rates are much higher for the zones around St. Matthew and St. Lawrence Islands in spring, when Divoky's (1981) findings suggest that areas near colonies may harbor large bird concentrations.

Table 7. Sample size (N) required for a given confidence level (α) and error rate (d).

$$N = .25 d^2 (1 - \alpha)$$

d	.1	.25
α		
.99	2500	400
.95	500	80
.90	250	40
.75	100	16

Table 8. Sample size (N) required for a given confidence level (α) and error rate (d), with the normal approximation (k is the z score associated with a given α level).

$$N = .25 (k/d)^2$$

α	d	.05	.10	.25	k
.99	665	166	27	2.58	
.95	384	96	15	1.96	
.90	272	68	11	1.65	
.75	135	34	5	1.16	

Table 9. Spring error rates (d) for zones in the central Bering Sea shelf, $\alpha = 0.95$.

$$d = \frac{1}{2[N(1-\alpha)]^{.5}}, \text{ nonparametric calculation; } d^* = \sqrt{\frac{1.96^2}{4N}}, \text{ normal approximation}$$

	COASTAL	MIDDLE SHELF	OUTER SHELF	DEEP	ST. MATTHEW	ST. LAWRENCE
Sample size (N)	0	113	168	146	10	0
Error rate (d)	-	21.0%	17.3%	18.5%	70.7%	-
(d*)	-	9.2%	7.6%	8.1%	31.0%	-

Table 10. Summer error rates (d) for zones in the central Bering Sea shelf, $\alpha = 0.95$.

$$d = \frac{1}{2[N(1-\alpha)]^{.5}}, \text{ nonparametric calculation; } d^* = \sqrt{\frac{1.96^2}{4N}}, \text{ normal approximation}$$

	COASTAL	MIDDLE SHELF	OUTER SHELF	DEEP	ST. MATTHEW	ST. LAWRENCE
Sample size (N)	36	291	223	140	67	113
Error rate (d)	37.3%	13.1%	15.0%	18.9%	27.3%	21.0%
(d*)	16.3%	5.7%	6.6%	8.3%	12.0%	9.2%

Table 11. Autumn error rates (d) for zones in the central Bering Sea shelf, $\alpha = 0.95$.

$$d = \frac{1}{2[N(1-\alpha)]^{.5}}, \text{ nonparametric calculation; } d^* = \sqrt{\frac{1.96^2}{4N}}, \text{ normal approximation}$$

	COASTAL	MIDDLE SHELF	OUTER SHELF	DEEP	ST. MATTHEW	ST. LAWRENCE
Sample size (N)	76	223	137	57	74	0
Error rate (d)	25.6%	15.0%	19.1%	29.6%	26.0%	-
(d*)	11.2%	6.6%	8.4%	13.0%	11.4%	-

Further sampling around these islands in winter and spring could be useful but would require an icebreaker. We already know that high bird densities may be expected around the colonies, at the shelf break and at the 100 m front and that encounter rates for high densities are greatest in spring and summer. Further sampling is unlikely to provide major new insights about the locations of bird concentrations in the Navarin Basin for spring, summer and fall. While much of the Navarin Basin has not received sampling (Figures 10-13, pp. 20-23), consistently low counts were found in most censused areas (Figures 14-16, pp. 30-32). Although surveys are still needed for winter and spring, effort should now be focused on protecting the critical areas around the colonies and perhaps also the shelf break region. The areas around the colonies are particularly important because they harbor large concentrations of breeding birds of species which are susceptible to oiling. The development of a staging area on St. Matthew Island is of great concern, not only because of the direct disturbance of the colony, but also because of the likelihood that the foraging areas around the colony used by breeding birds will be affected by chronic, low-level pollution due to increased ship traffic.

In contrast to the southeastern Bering Sea, where almost all high density counts of birds away from the Pribilof Islands were due to non-breeding, migrant shearwaters (Table 12), many species of locally breeding birds were found in high densities on the central Bering Sea shelf (Table 6). In both the central and southeastern Bering Sea shelf, we found large concentrations of vulnerable species close to colonies (Table 6 and 12). These were diving species which are likely to become oiled (King and Sanger 1979). In pelagic waters, high bird densities in the southeastern Bering Sea involved less vulnerable populations, either non-breeding birds (shearwaters) or species whose foraging method reduces their probability of becoming oiled (aerial foragers: storm-petrels, fulmars) (King and Sanger 1979). On the central Bering Sea shelf, high pelagic bird densities involve species which are vulnerable because 1) they are breeding (small auklets,

Table 12. The occurrence of bird densities greater than 250 birds/km²* in the southeastern Bering Sea by season, zone and species. Confidence intervals (95%) are given.

SPRING:	<u>Alaska Peninsula</u> all 5% shearwaters 4.2% <u>+ 9%</u>	<u>Unimak</u> all 2.3% shearwaters 2.3% <u>+ 34%</u>	<u>outer shelf</u> all 0.9% shearwaters 0.9% <u>+ 4%</u>	<u>Pribilof Islands*</u> all 10.3% murres 7.5% Black-legged Kittiwakes 1.8% small alcids 0.9% <u>+ 7%</u>
SUMMER:	<u>coastal</u> all 16.1% shearwaters 15.2% <u>+ 9%</u>	<u>Alaska Peninsula</u> <u>coastal</u> all 6.3% shearwaters 6.3% <u>+ 9%</u>	<u>Alaska Peninsula</u> <u>offshore</u> all 5.8% shearwaters 5.8% <u>+ 8%</u>	<u>Pribilof Islands*</u> all 28.1% murres 12.3% small alcids 1.8% storm-petrels 0.7% shearwaters 0.6% Black-legged Kittiwakes 0.4% Red-legged Kittiwakes 0.4% <u>+ 3%</u>
	<u>Cape Newenham</u> all 30.4% shearwaters 30.4% <u>+ 47%</u>	<u>middle shelf</u> all 2.5% shearwaters 2.5% <u>+ 4%</u> <u>middle shelf</u> all 2.5% shearwaters 2.5% <u>+ 4%</u>	<u>outer shelf</u> all 3.1% Northern Fulmar 1.6% shearwaters 0.9% storm-petrels 0.1% <u>+ 4%</u>	<u>Unimak</u> all 7.4% shearwaters 6.2% <u>+ 11%</u>
AUTUMN:	<u>Unimak</u> all 30% <u>+ 71%</u>	<u>middle shelf</u> all 2.4% <u>+ 9%</u>	<u>outer shelf</u> all 2.7% <u>+ 11%</u>	<u>Pribilof Islands*</u> all 3.3% <u>+ 7%</u>

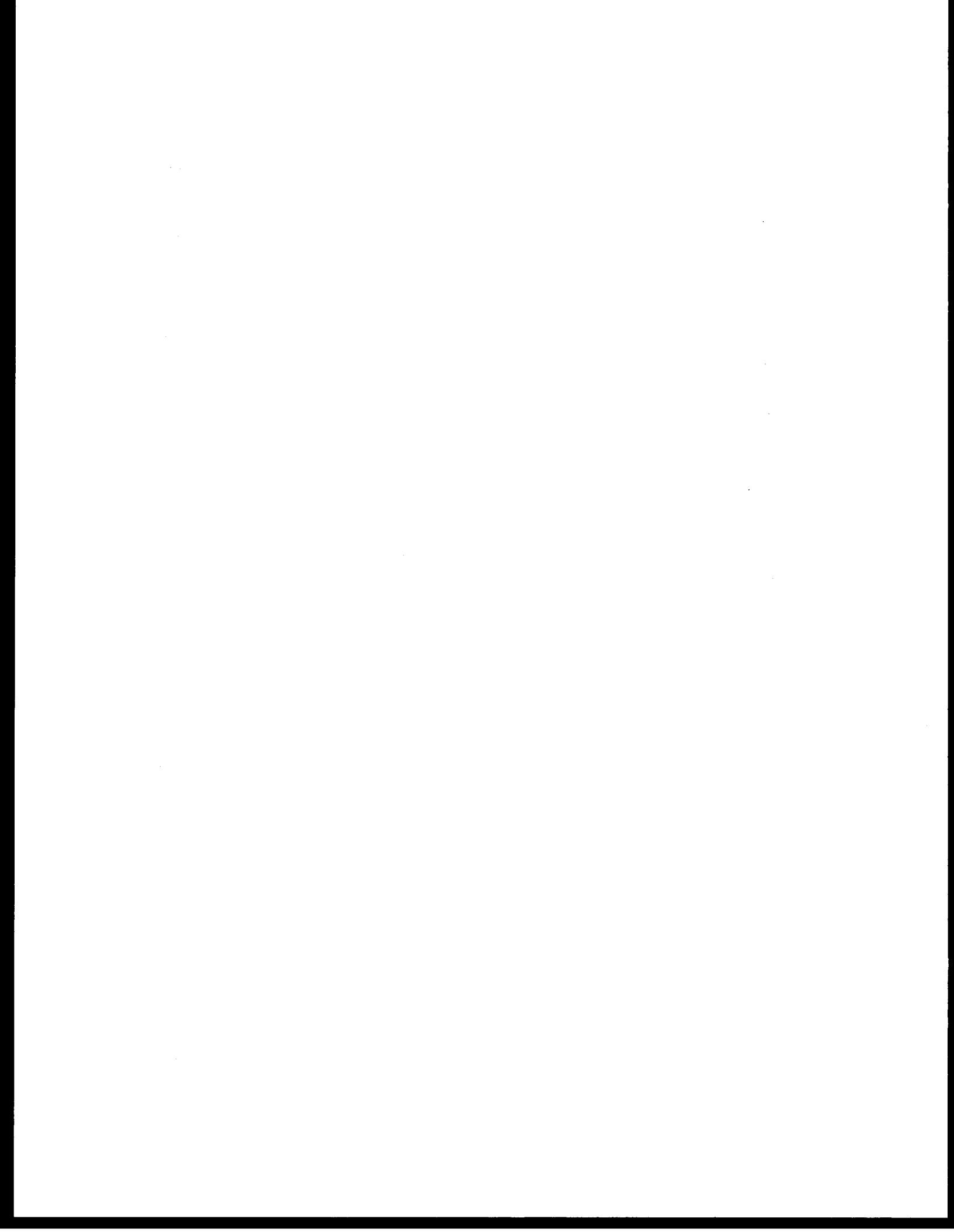
* Pribilof Islands, densities > 100 birds/km²

kittiwakes, murres, fulmars), or 2) their foraging method makes them likely to become oiled (small auklets, phalaropes), or 3) because a large proportion of the world's population of the species is concentrated in the region, as may be the case with the Aethia auklets and the Red Phalarope during their spring migration.

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APPENDIX 1

Derivation of statistical analysis of density categories

J. Kaiwi

APPENDIX 1

Density estimates derived from transect samples can be categorized into c disjoint intervals with the following assumptions:

- (1) Each sample is considered to be an independent Bernoulli trial.
- (2) For each i , $i = 1, \dots, c$, π_i is the probability that the sample statistic (in this case the mean) will fall within interval i and therefore belong to category i . For categories $1, \dots, c$;

$$\pi_1 + \pi_2 + \dots + \pi_c = 1 .$$

- (3) The number of transects (samples) belonging to category i is the number of successes S associated with the category;

$$N = S_1 + S_2 + \dots + S_c .$$

- (4) The probability of obtaining a particular set of successes is given by the multinomial model as follows:

$$m(S_1, S_2, \dots, S_c; \pi_1, \pi_2, \dots, \pi_c) = \binom{N}{S_1, S_2, \dots, S_c} \pi_1^{S_1} \pi_2^{S_2} \dots \pi_c^{S_c}$$

where

$$\binom{N}{S_1, S_2, \dots, S_c} = \frac{N!}{S_1! S_2! \dots S_c!} .$$

- (5) If the number of categories is reduced by combining two or more of the original set then, for example,

$$m(S_1, S_2, S'_3; \pi_1, \pi_2, \pi'_3) = \binom{N}{S_1, S_2, S'_3} \pi_1^{S_1} \pi_2^{S_2} \pi'_3^{S'_3}$$

where $S'_3 = N - (S_1 + S_2)$

and $\pi'_3 = \pi_3 + \pi_4 + \dots + \pi_c$.

- (6) If only one category is of interest then the multinomial model given in (4) reduces to the Binomial model so that:

$$b(S_i; N, \pi_i) = \binom{N}{S_i} \pi_i^{S_i} (1 - \pi_i)^{N - S_i}.$$

The practical application of statements (1) through (6) requires estimations of the probabilities π_1, \dots, π_c . This entails the derivation of a formula which provides, for any given confidence level and interval, a lower bound on the required sample size. This formula, for any given sample size and confidence level, also yields an upper bound on the associated confidence interval. The derivation is straight-forward and requires only Chebyshev's Inequality and the weak law of large numbers. The version of the former used here can be stated as follows: at least $1 - 1/h^2$ of the probability associated with any random variable will lie within h standard deviations of the mean. In particular,

(A) $\Pr(|x - \mu| < h\sigma) \geq 1 - \frac{1}{h^2}$

which is read as: the probability that the absolute value of the difference between a random variable and its mean is less than $h\sigma$ is equal to or greater than $1 - 1/h^2$. The Chebyshev Inequality holds for any distribution so long as it has a mean and variance and therefore can be used to validate Khintchine's Theorem for the weak law of large numbers, described next.

Given a random sample of n observations taken from a population with mean μ and variance σ^2 , the expectation of the sample mean \bar{x} is σ^2/N . This last statement implies that as n gets large the variance of the sample mean approaches zero which is the significant implication of the law of large numbers. That is, for any $d > 0$,

$$(B) \quad \Pr(|\bar{x} - \mu| < d) \rightarrow 1 \text{ as } n \rightarrow \infty .$$

To show this analytically, Chebyshev's Inequality can be written as

$$(C) \quad \Pr(|x - \mu| < d) \geq 1 - \frac{1}{h^2}$$

where $d = h\sigma$ and $h = \frac{d}{\sigma}$.

Consequently, if we substitute \bar{x} for x and σ^2/N for σ^2 , the result is Khintchine's theorem:

$$\Pr(|\bar{x} - \mu| < d) \geq 1 - \frac{1}{\left(\frac{d}{\sqrt{\sigma^2/N}}\right)^2} = 1 - \frac{\sigma^2}{Nd^2}$$

Since σ^2 and d^2 are fixed, as $N \rightarrow \infty$, $\sigma^2/Nd^2 \rightarrow 0$ giving (B).

The equation relating sample size to confidence level and confidence interval can now be derived using the Bernoulli model and statements (A) through (C). In this model, each transect is considered to be one of N independent Bernoulli trials with population probability π_i associated with category i . If S is the number of transects in category i (i.e., the number of successes) then the sample mean is S/N and

$$\Pr\left(\left|\frac{S}{N} - \pi_i\right| < d\right) \rightarrow 1 \text{ as } N \rightarrow \infty .$$

This is the Bernoulli law of large numbers, first published in 1713. In words, as N gets large the proportion of successes in the sample will get arbitrarily close to the population proportion π_i . The question is, how large must N be for S/N to be a "good" estimate of π_i ? To answer this we wish to estimate the size of N such that the observed frequency of success in the sample will be within a specific distance d of π_i at a given high level of probability α . Formally, we wish to find an integer N such that

$$\Pr\left(\left|\frac{S}{N} - \pi_i\right| \leq d\right) \geq \alpha \text{ for all } \pi_i \text{ in } 0 \leq \pi_i \leq 1 .$$

To find a lower bound on N , note that from (C)

$$\alpha = 1 - \frac{\sigma^2}{Nd^2} ,$$

and from the Bernoulli model the variance of S/N is $\pi_i(1 - \pi_i) / N$.

Furthermore,

$$\begin{aligned}\pi_i(1 - \pi_i) &= \pi_i - \pi_i^2 \\ &= \frac{1}{4} - \left(\frac{1}{4} - \pi_i + \pi_i^2\right) \\ &= \frac{1}{4} - \left(\frac{1}{2} - \pi_i\right)^2\end{aligned}$$

so $\pi_i(1 - \pi_i)$ is maximum at $\pi_i = 1/2$. Therefore,

$$(D) \quad \Pr\left(|\frac{S}{N} - \pi_i| \leq d\right) \geq 1 - \frac{1}{4Nd^2}$$

since $\frac{\sigma^2}{N} = \pi_i(1 - \pi_i)/N \leq \frac{1}{4N}$.

The relation in (D) is satisfied if

$$N \geq \frac{1}{4d^2(1 - \alpha)}$$

The estimates given above for sample sizes required for particular values of α and d can be improved if S is the sum of a large number of independent trials (usually greater than 30). If this is true then the Central Limit Theorem holds approximately and S/N can be assumed to be nearly normal. In this case, the error

$$d = k\sigma_{S/N}$$

$$= k\sqrt{\frac{\pi_i(1 - \pi_i)}{N}}$$

and

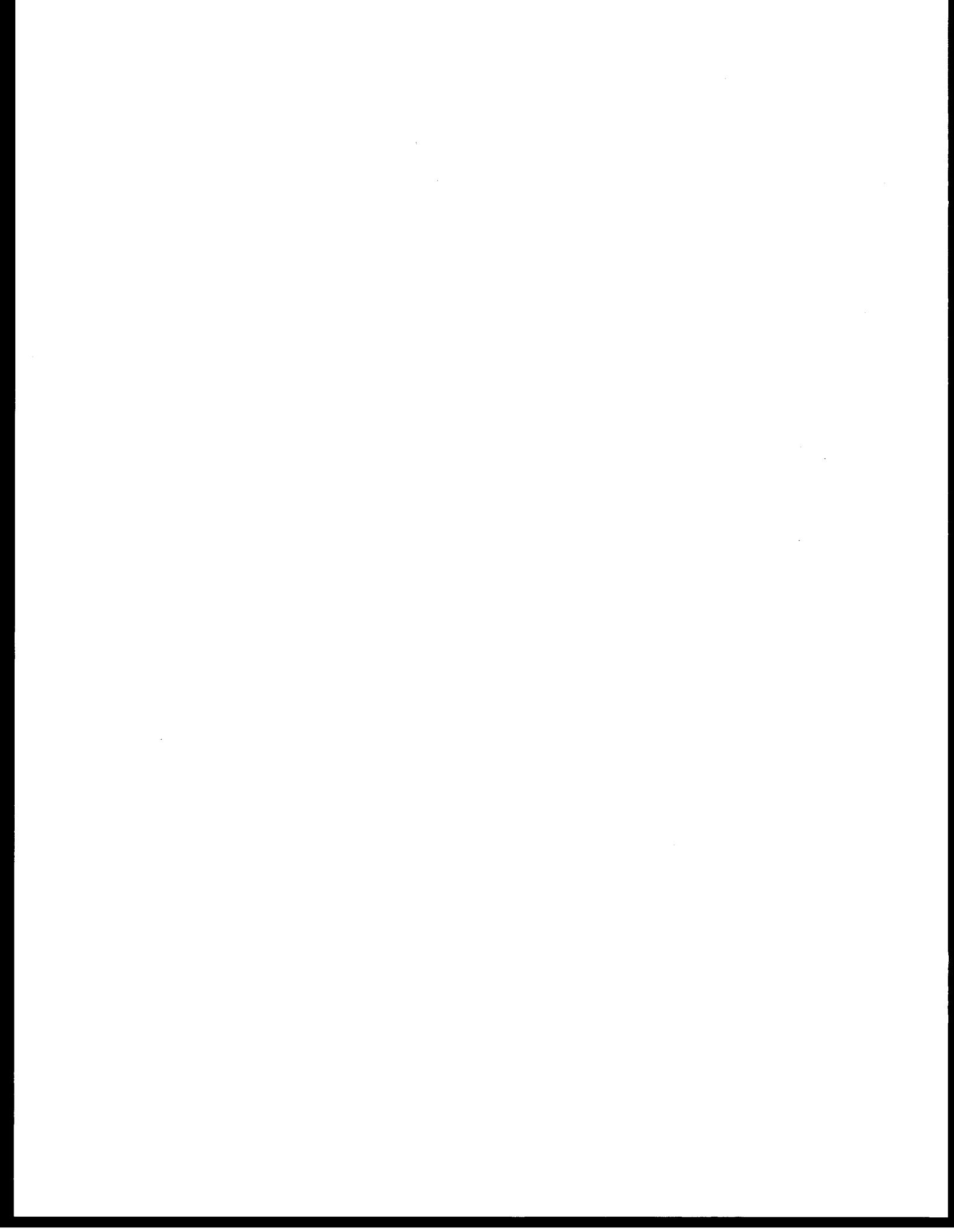
$$N \geq \pi(1 - \pi) \left(\frac{k}{d}\right)^2 .$$

Once again $\pi(1 - \pi)$ is a maximum at $\pi = 1/2$. Therefore

$$N \geq \frac{1}{4} \left(\frac{k}{d}\right)^2$$

and also,

$$d = \sqrt{\frac{k^2}{4N}} .$$



APPENDIX 2

Distribution maps for individual species in the Bering Sea

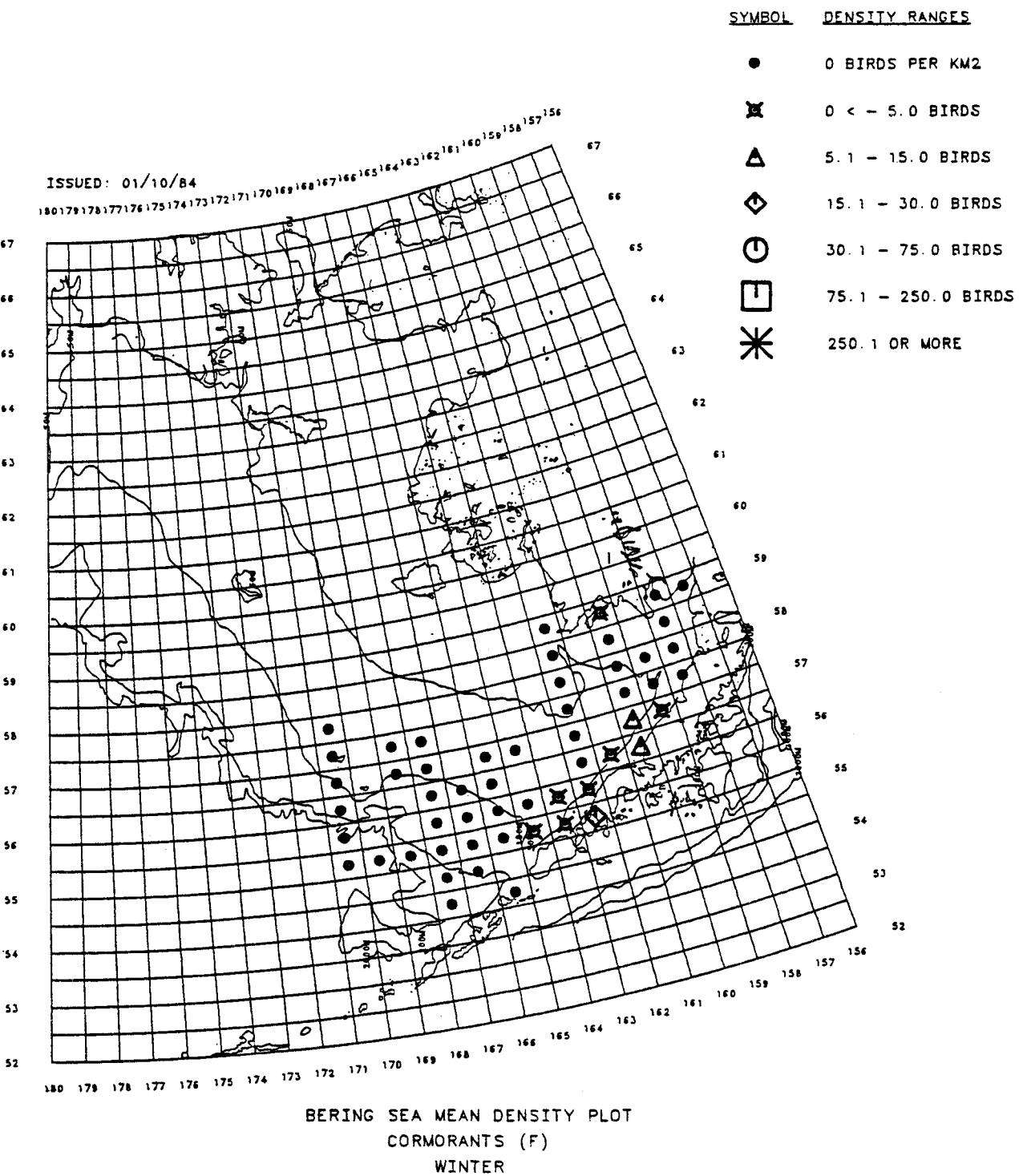


Figure 17. Mean densities, cormorants: Winter.

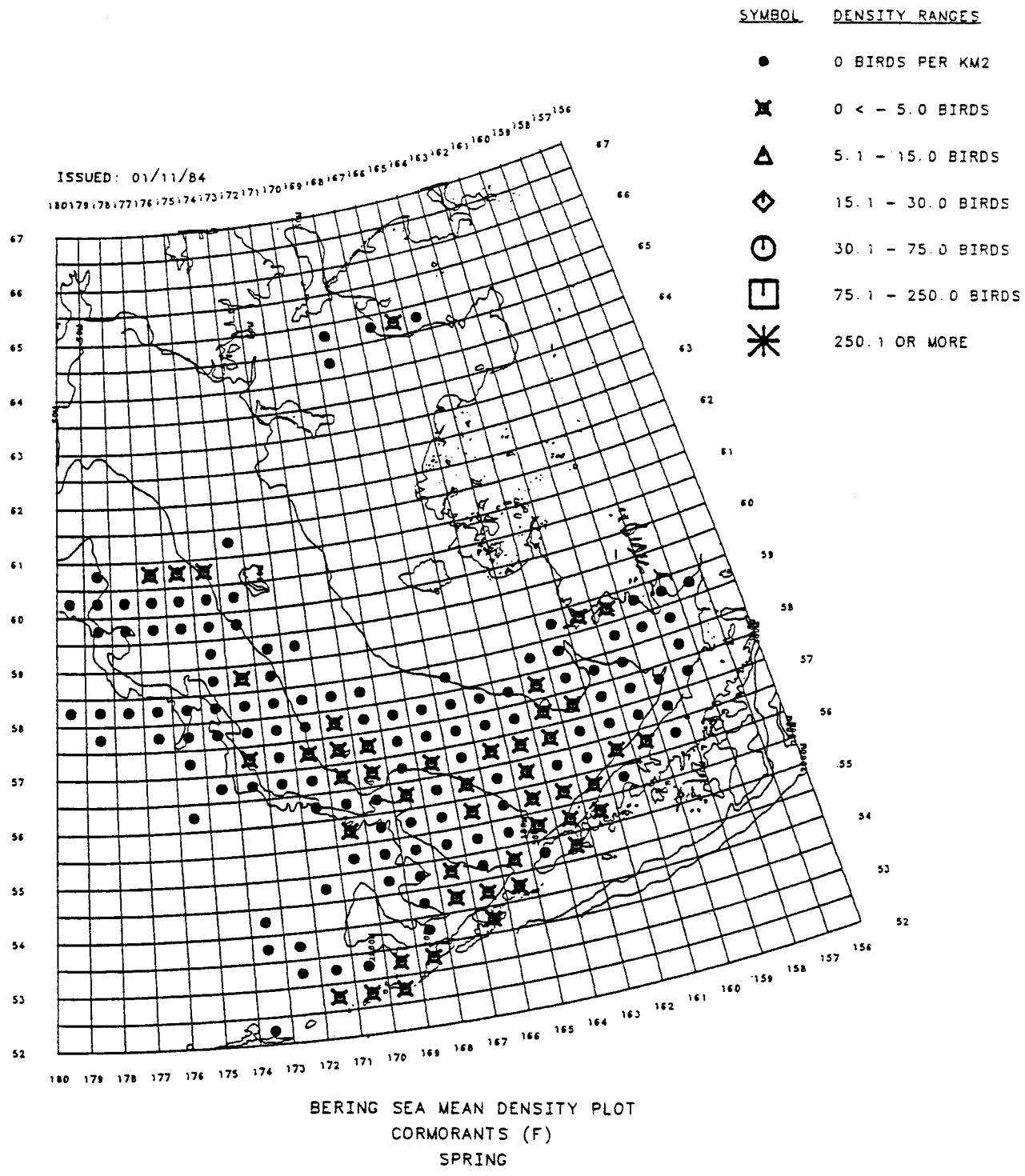


Figure 18. Mean densities, cormorants: Spring.

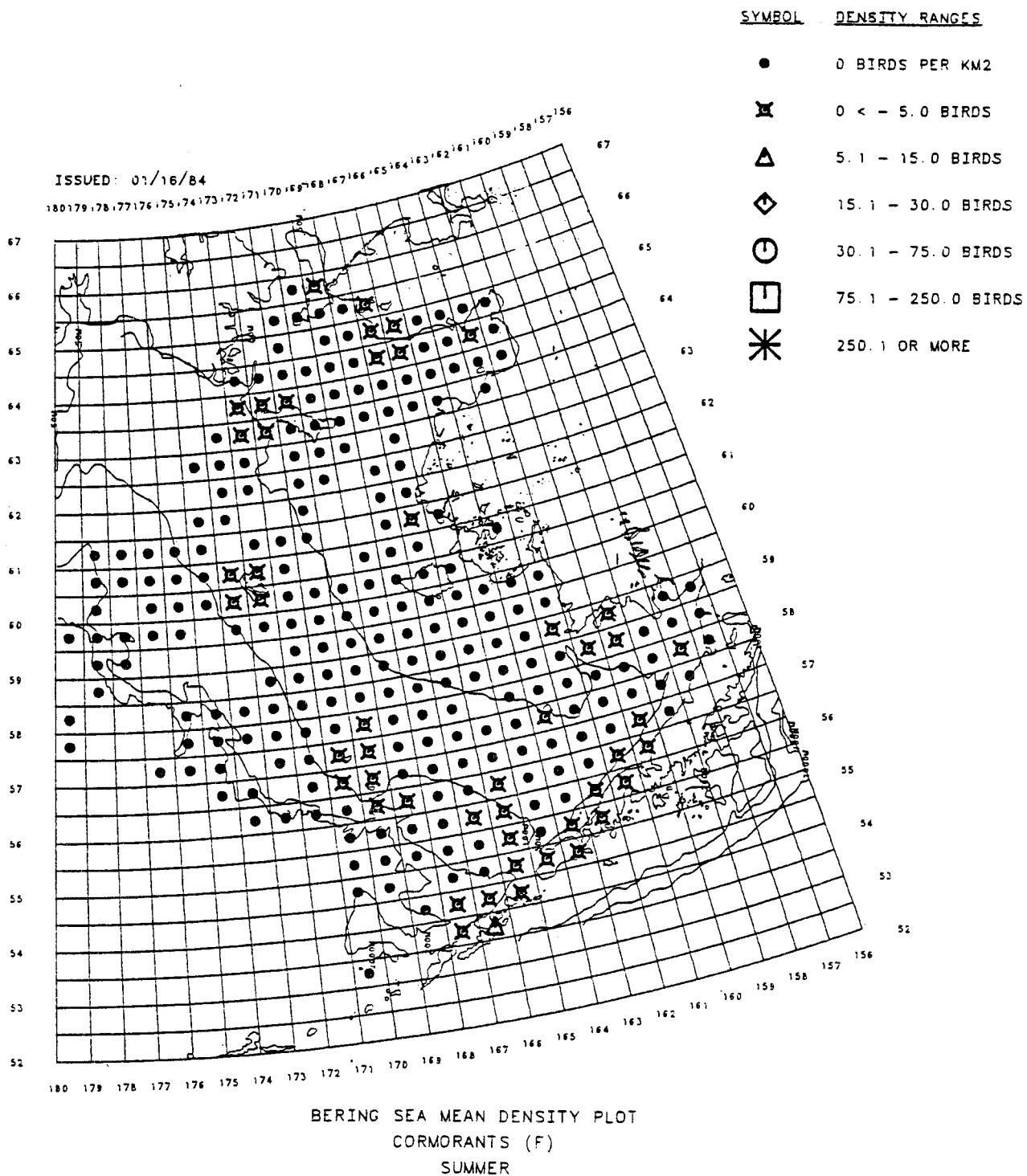


Figure 19. Mean densities, cormorants: Summer.

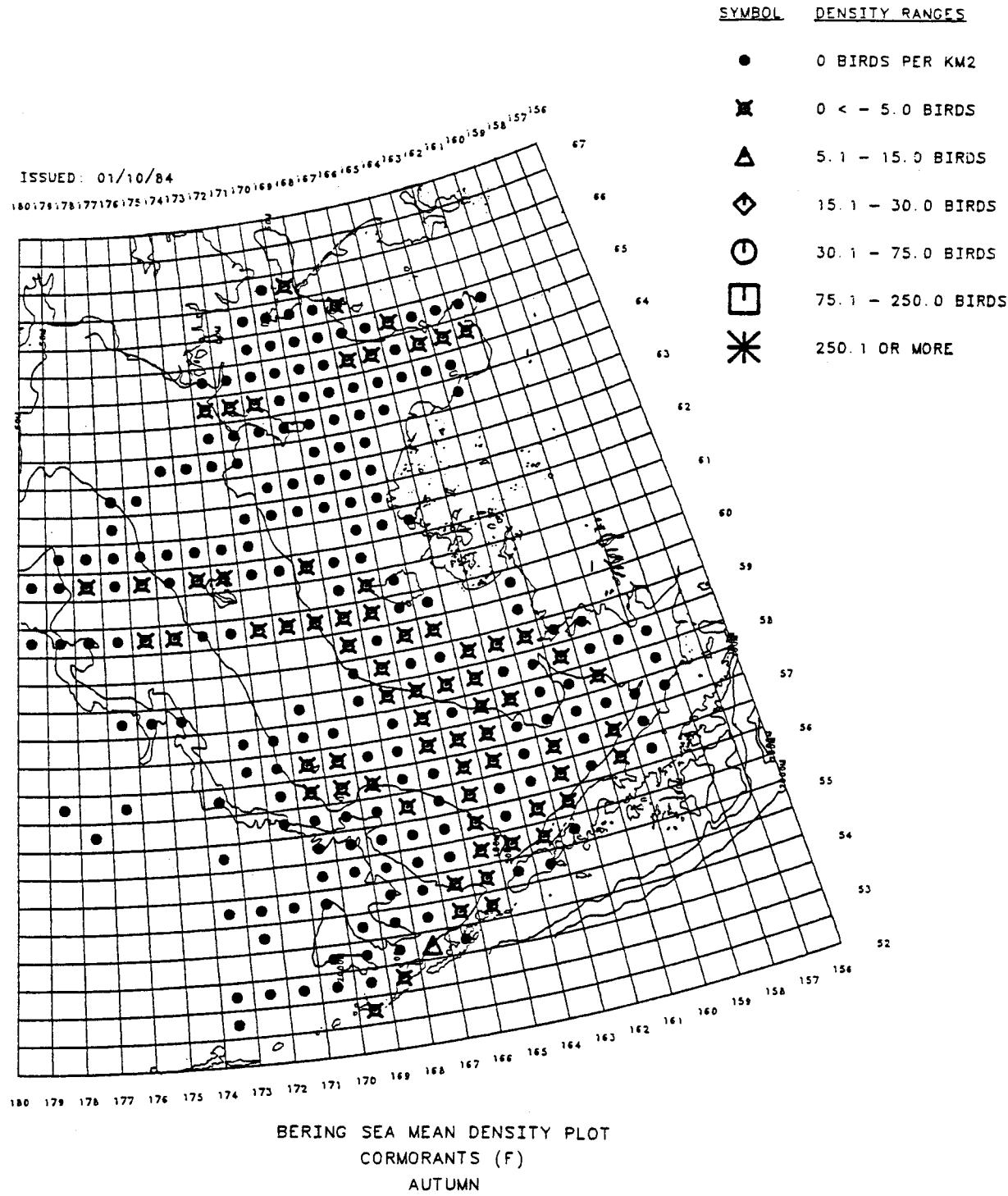


Figure 20. Mean densities, cormorants: Autumn.

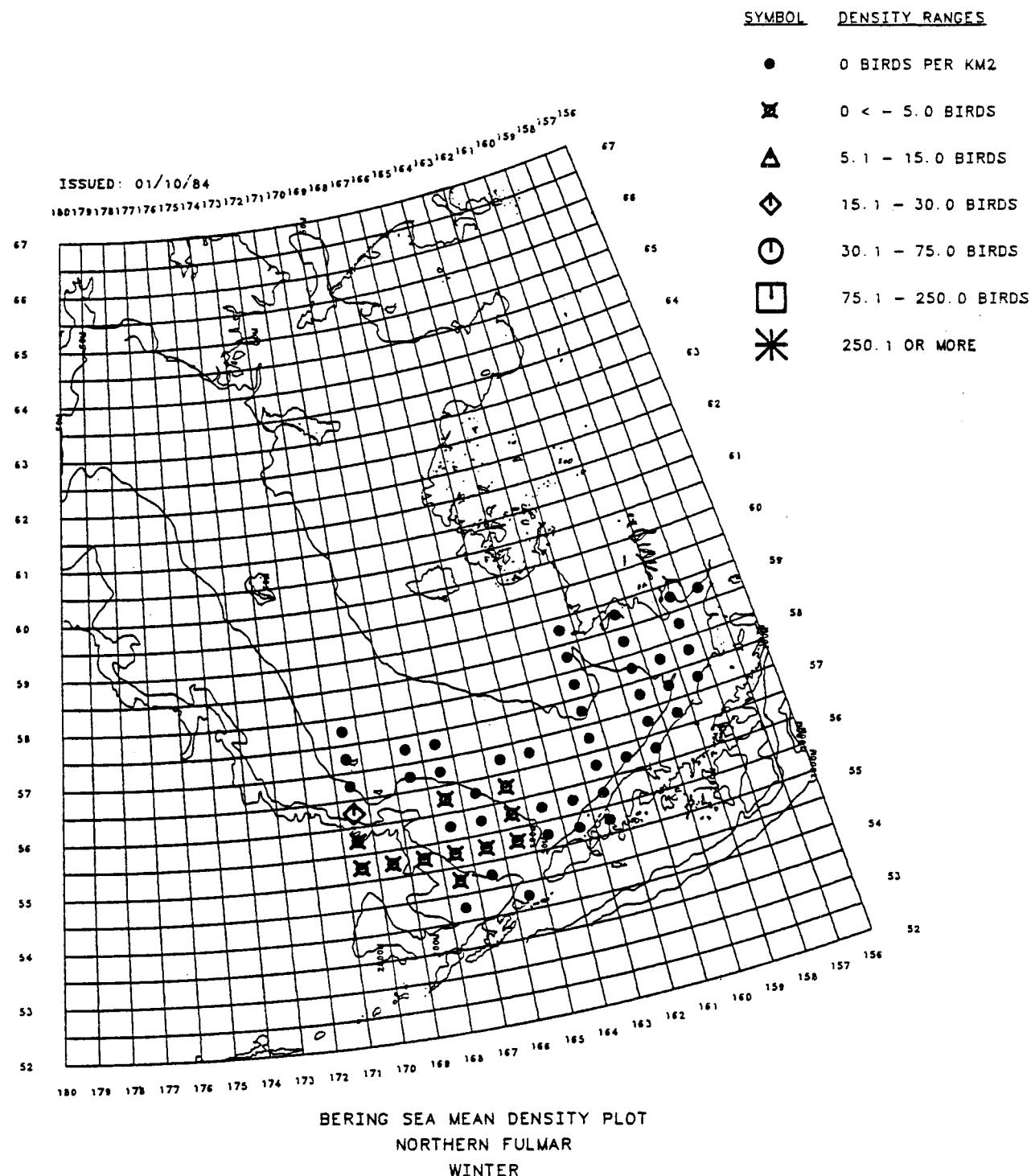


Figure 21. Mean densities, Northern Fulmars: Winter.

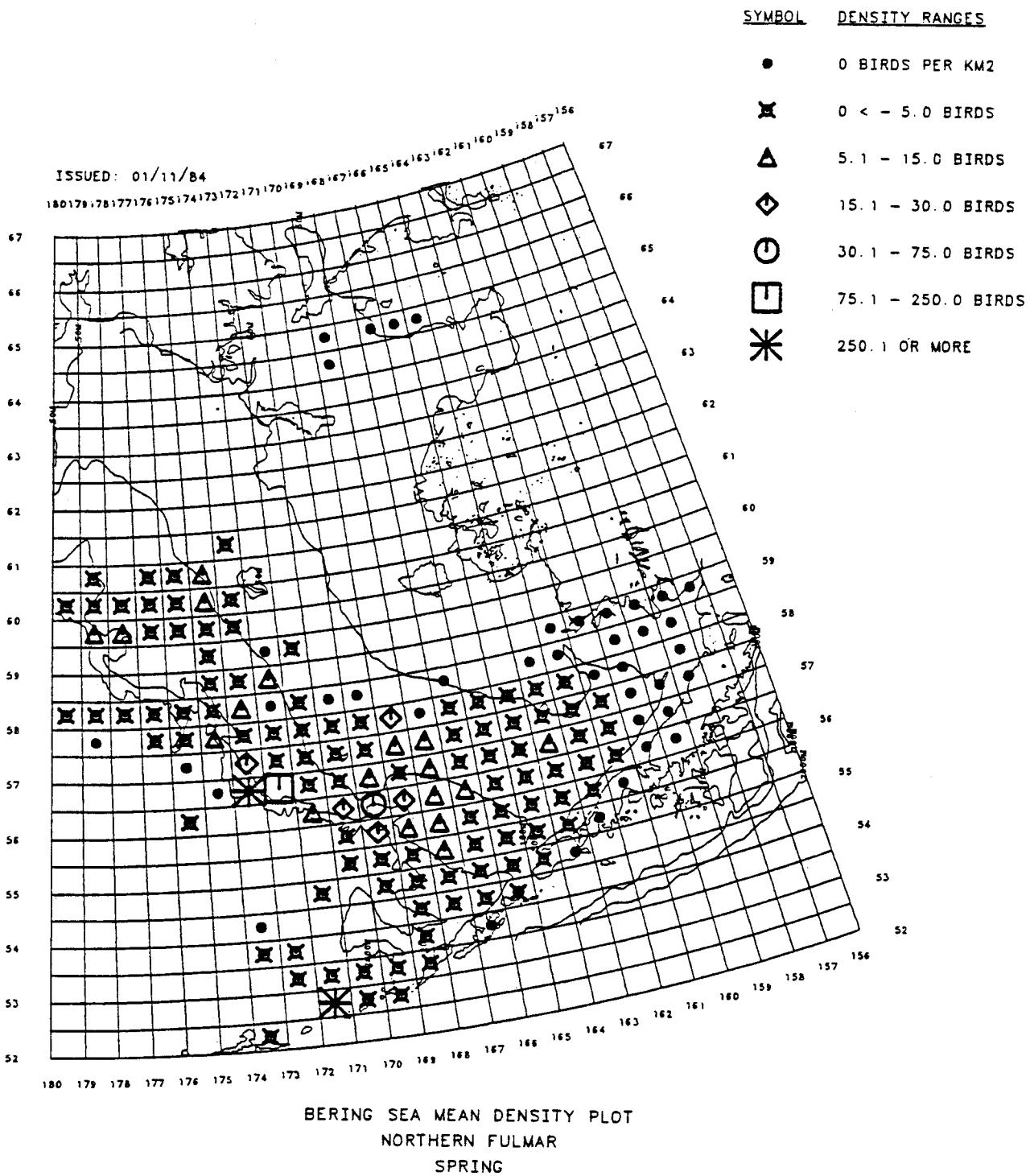


Figure 22. Mean densities, Northern Fulmars: Spring.

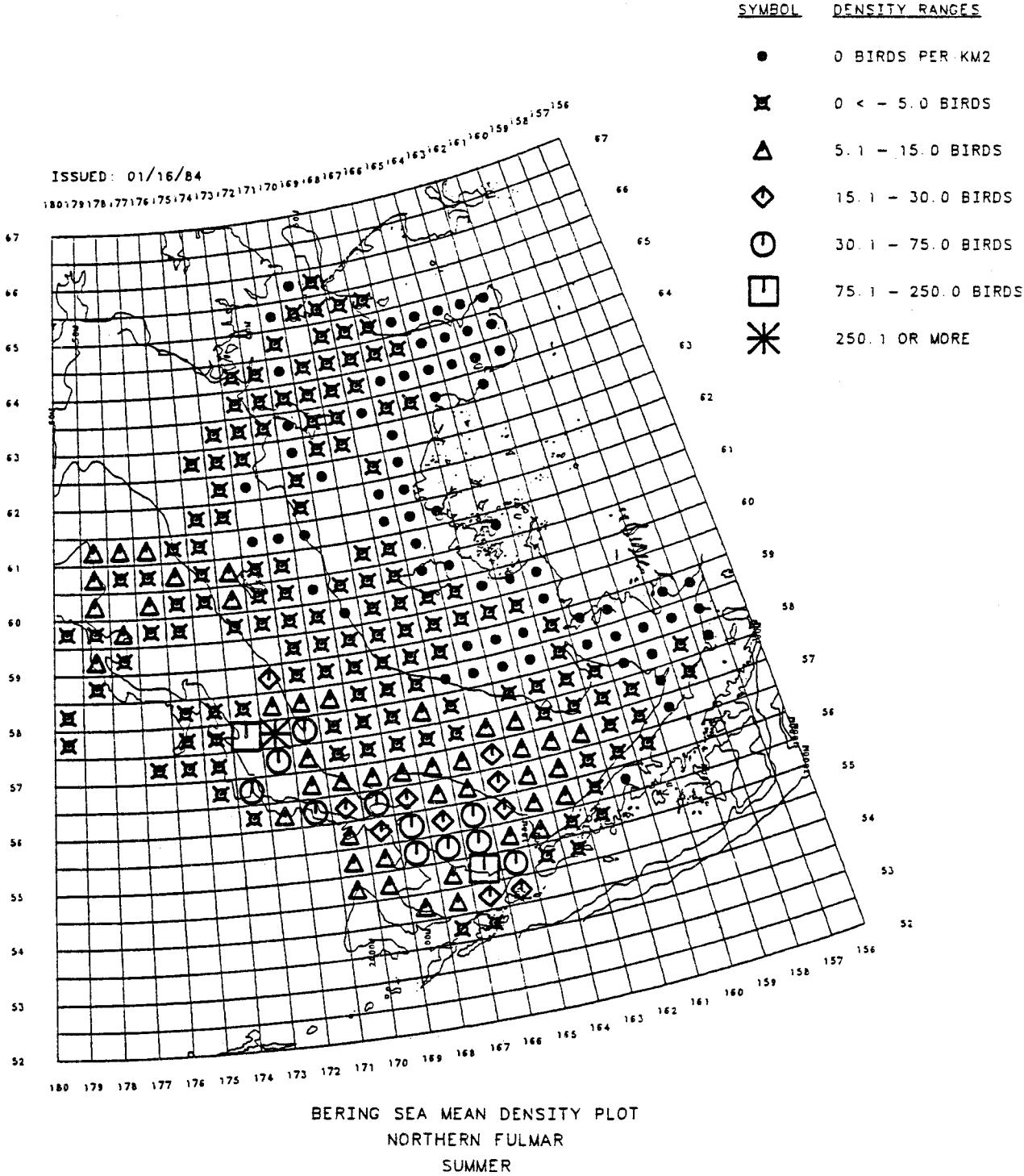


Figure 23. Mean densities, Northern Fulmars: Summer.

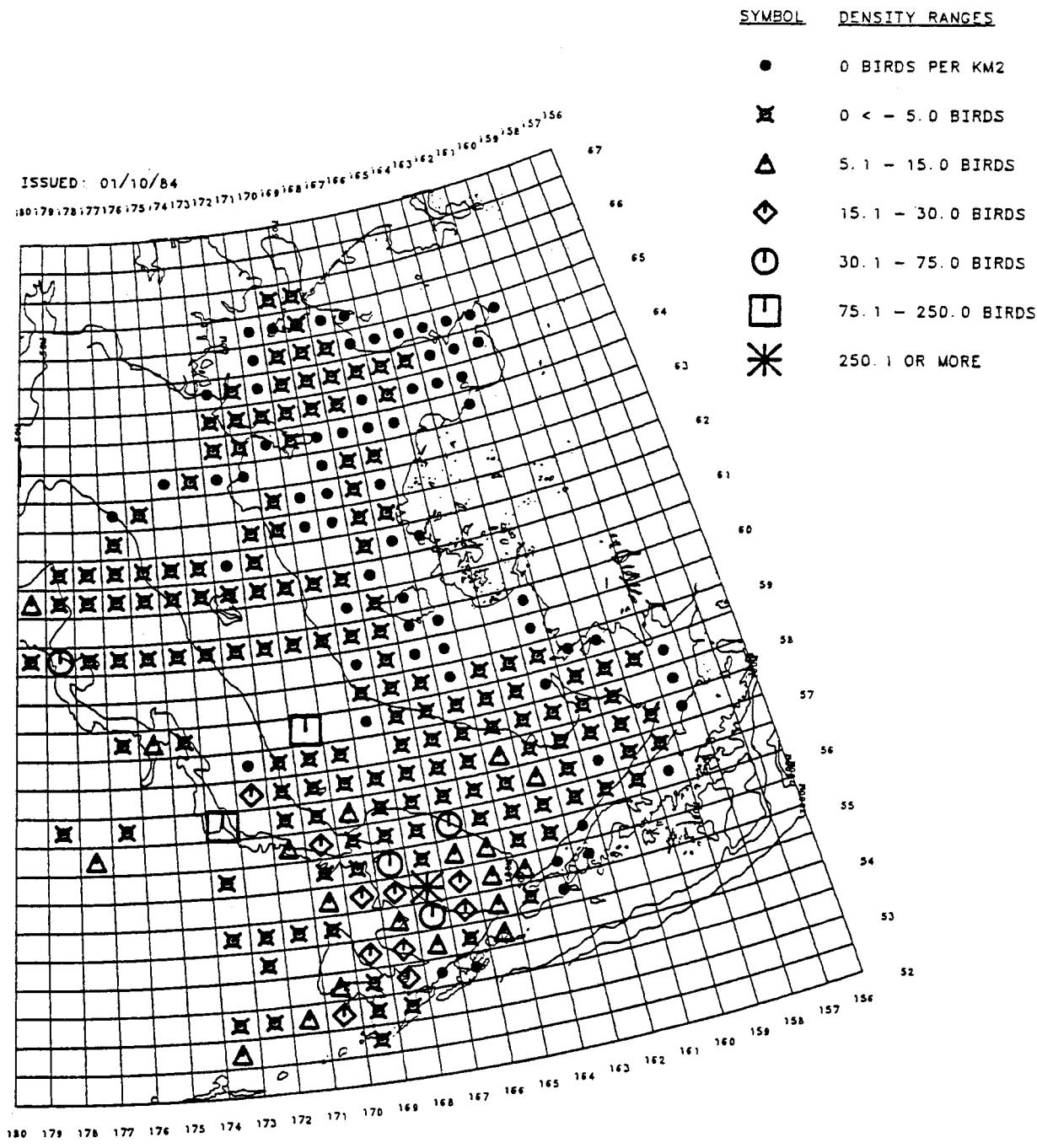


Figure 24. Mean densities, Northern Fulmars: Autumn.

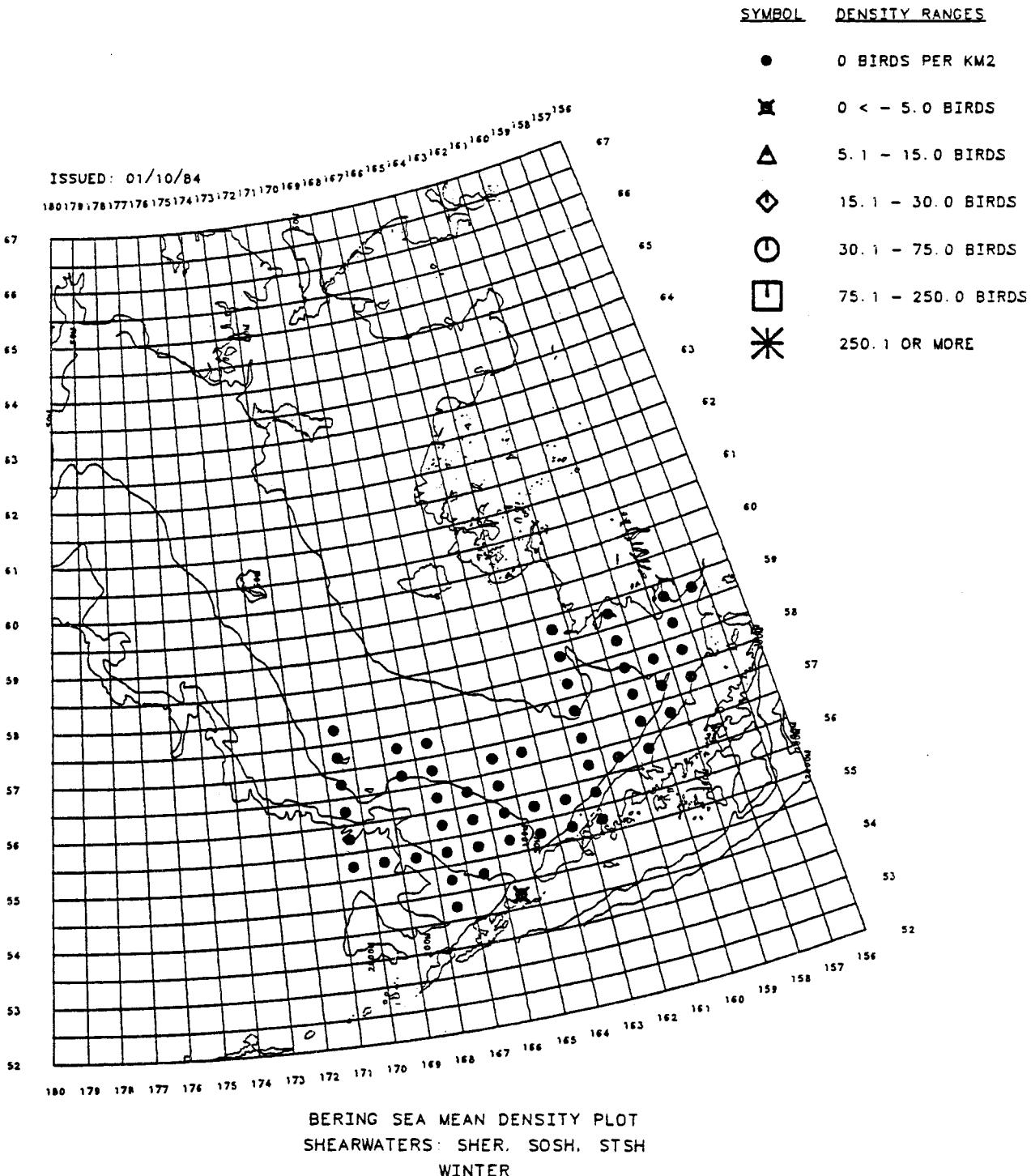


Figure 25. Mean densities, shearwaters: Winter.

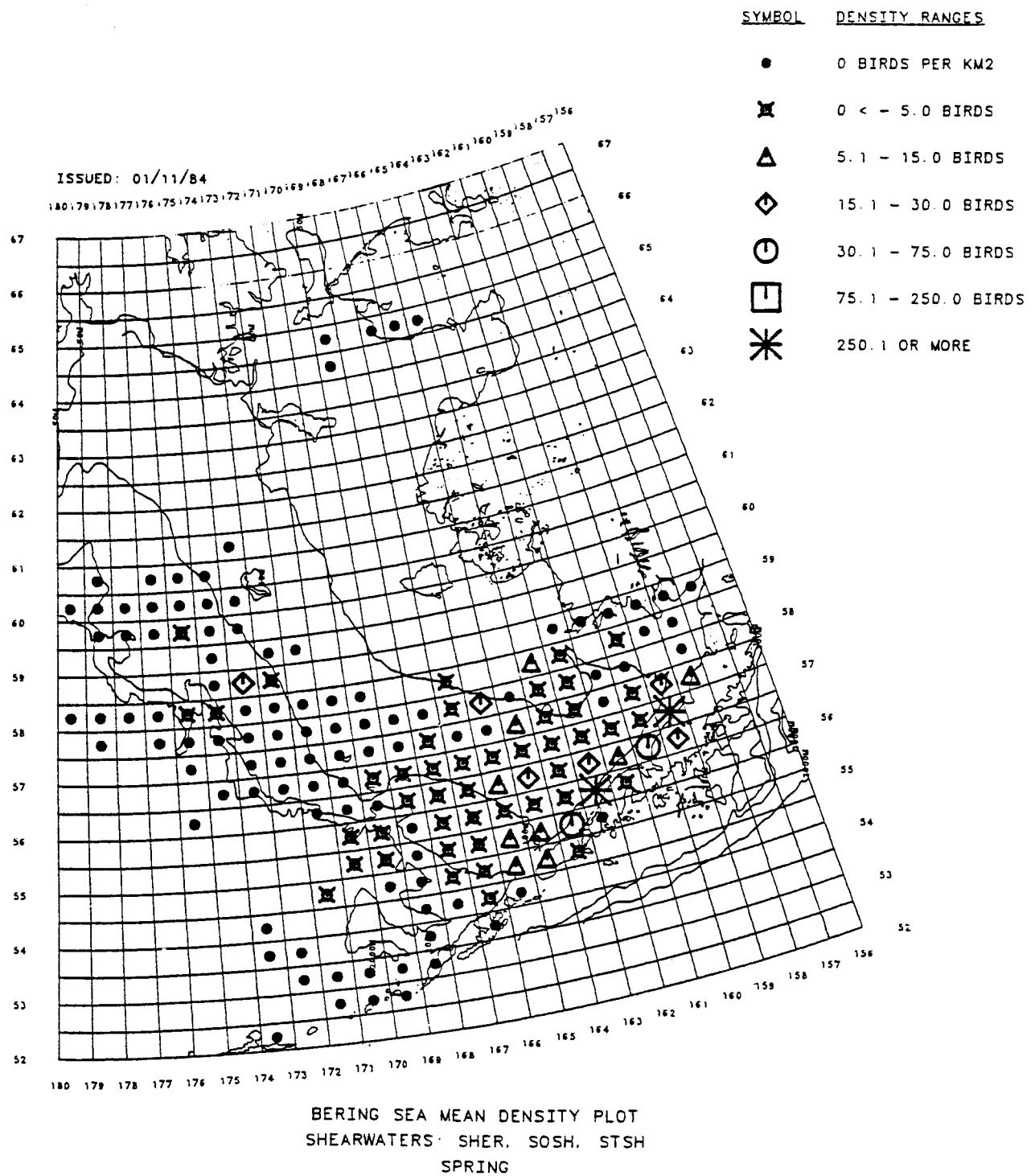


Figure 26. Mean densities, shearwaters: Spring.

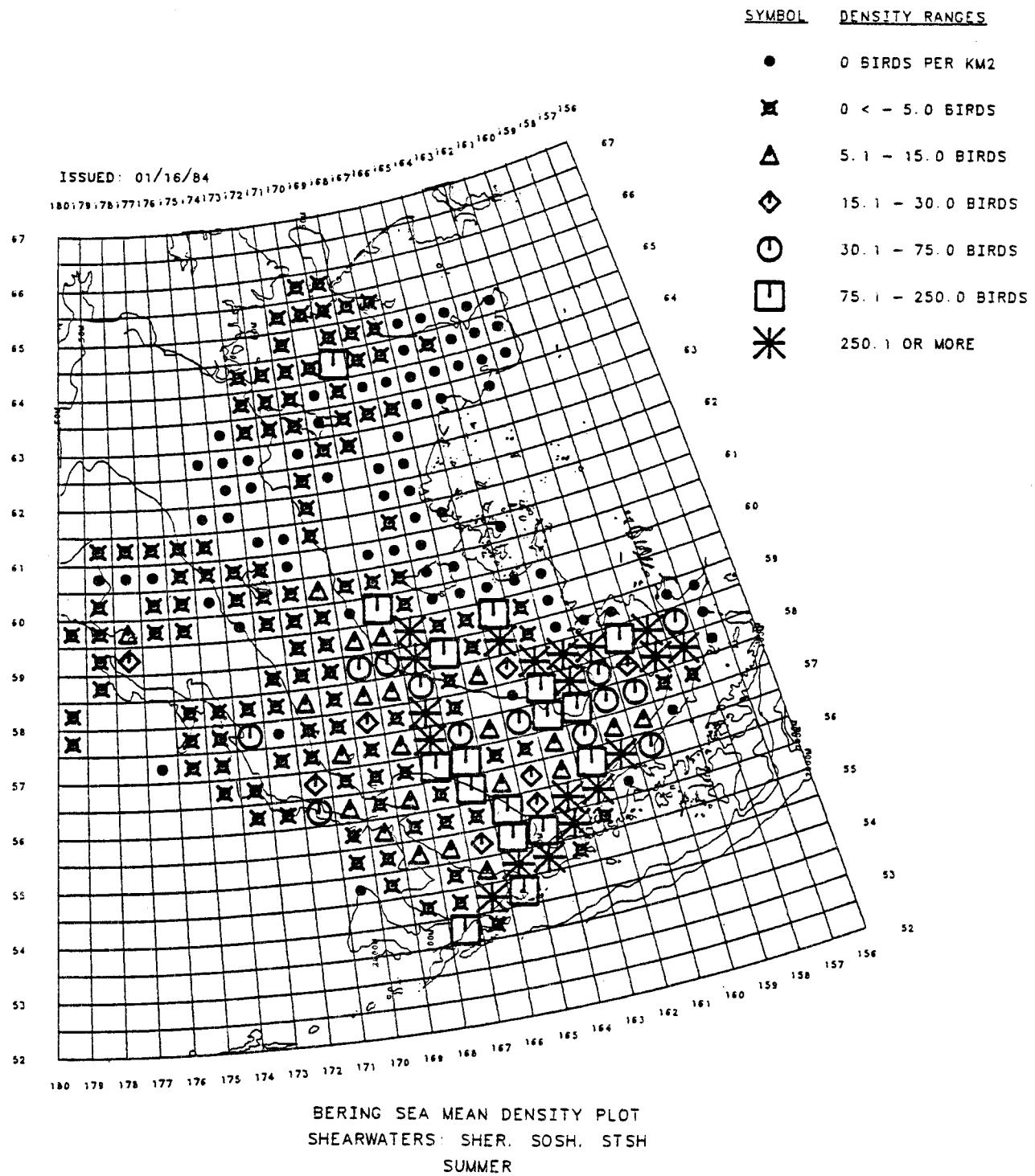


Figure 27. Mean densities, shearwaters: Summer.

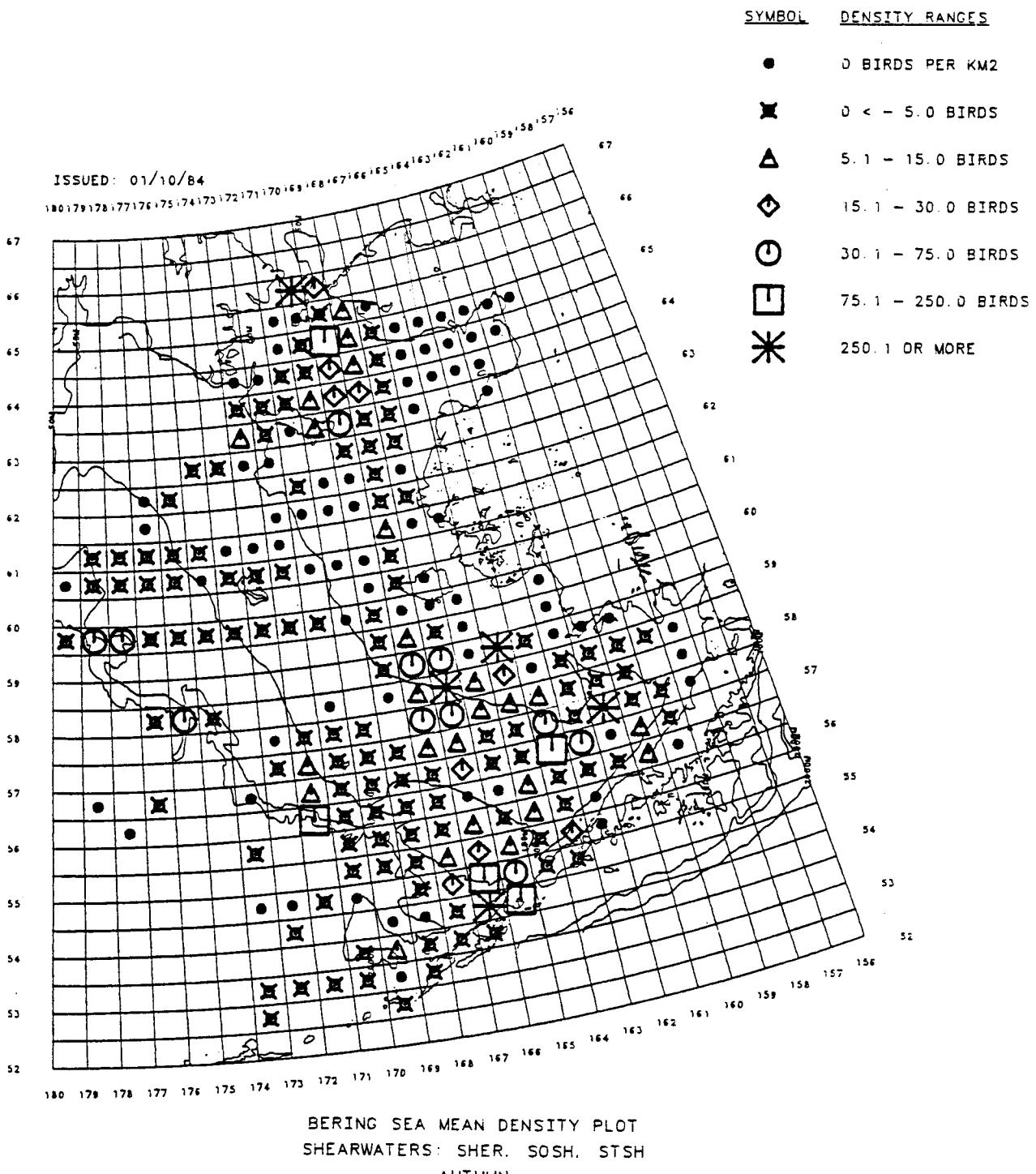


Figure 28. Mean densities, shearwaters: Autumn.

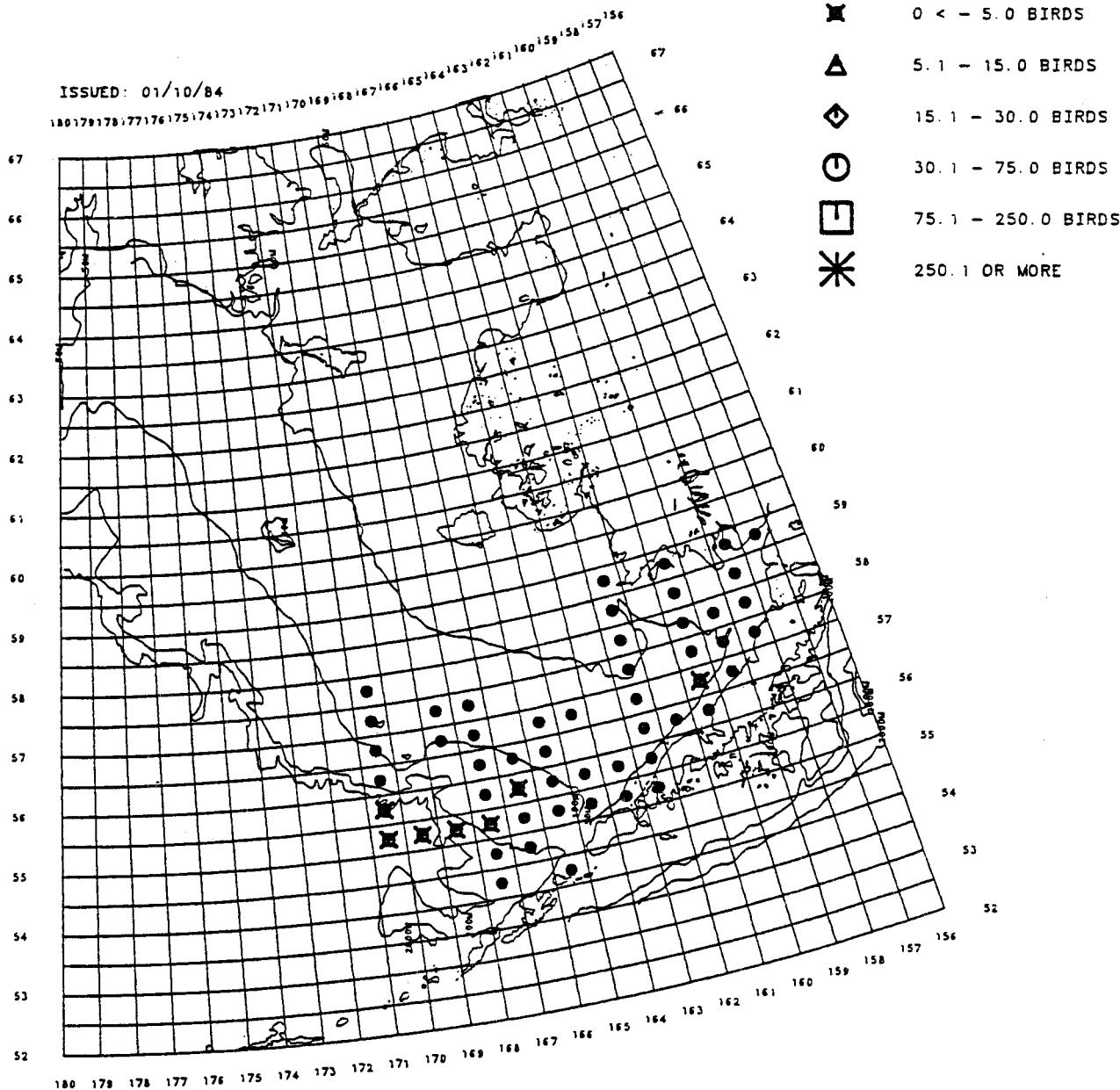


Figure 29. Mean densities, storm-petrels: Winter.

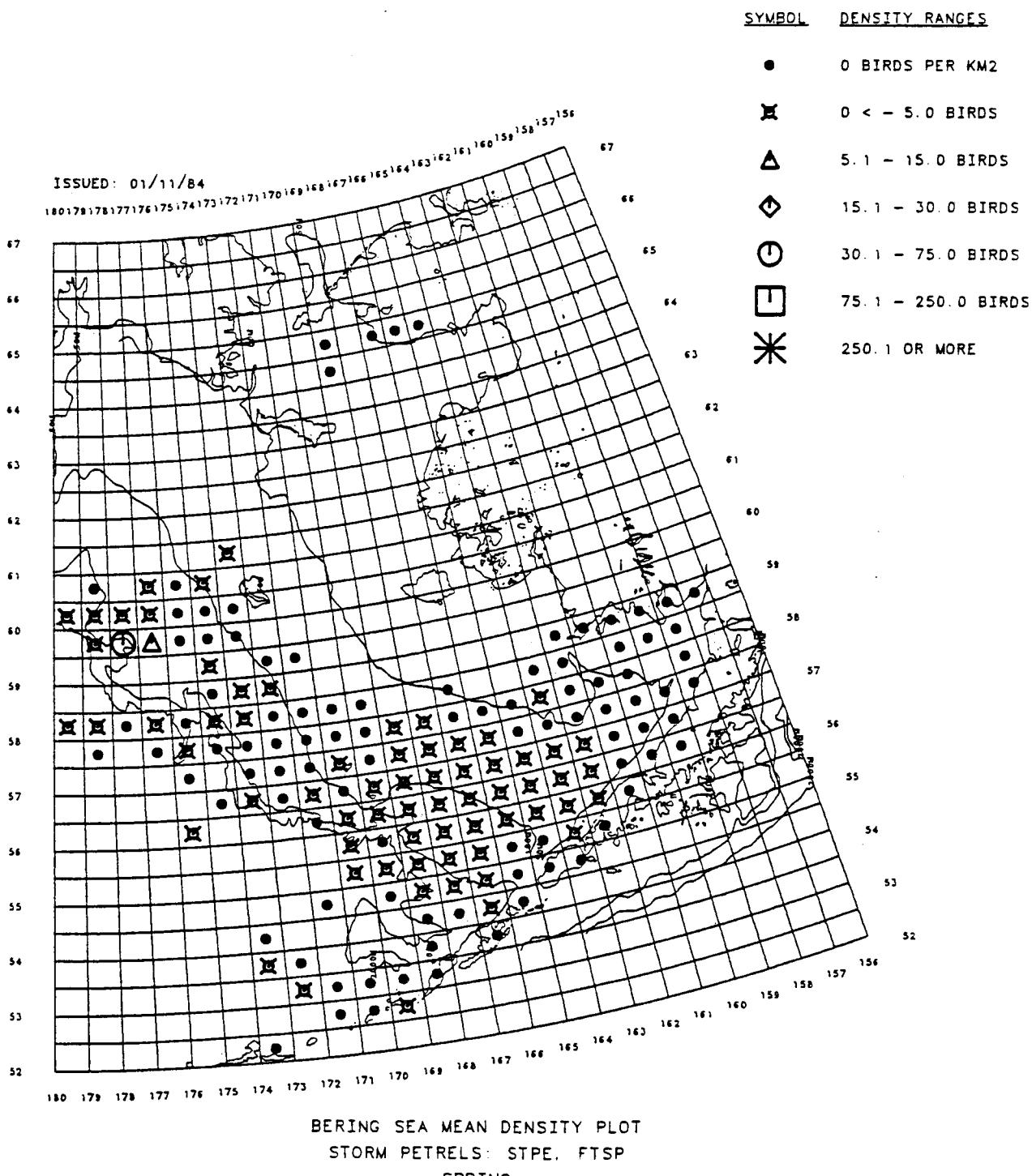


Figure 30. Mean densities, storm-petrels: Spring.

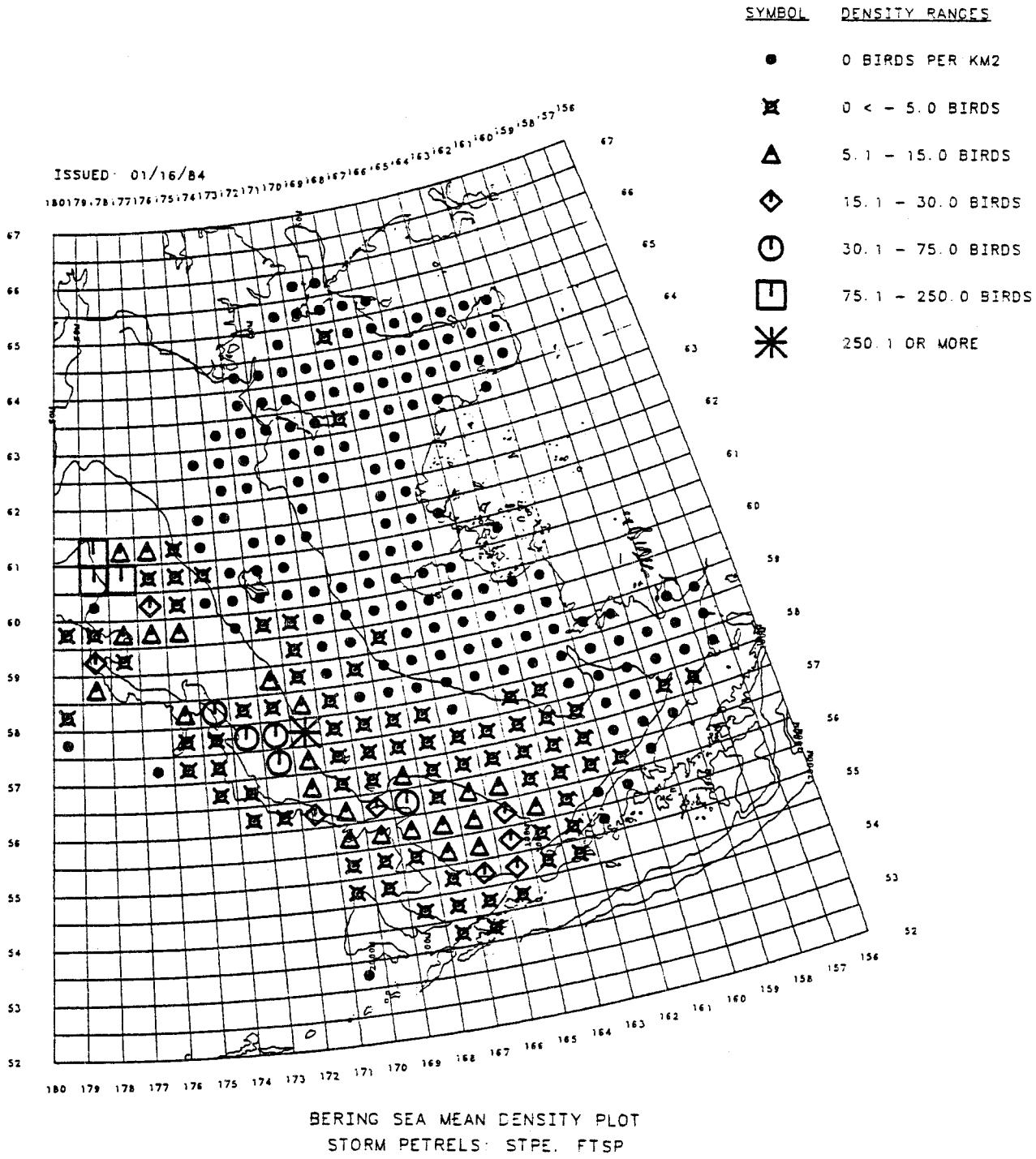


Figure 31. Mean densities, storm-petrels: Summer.

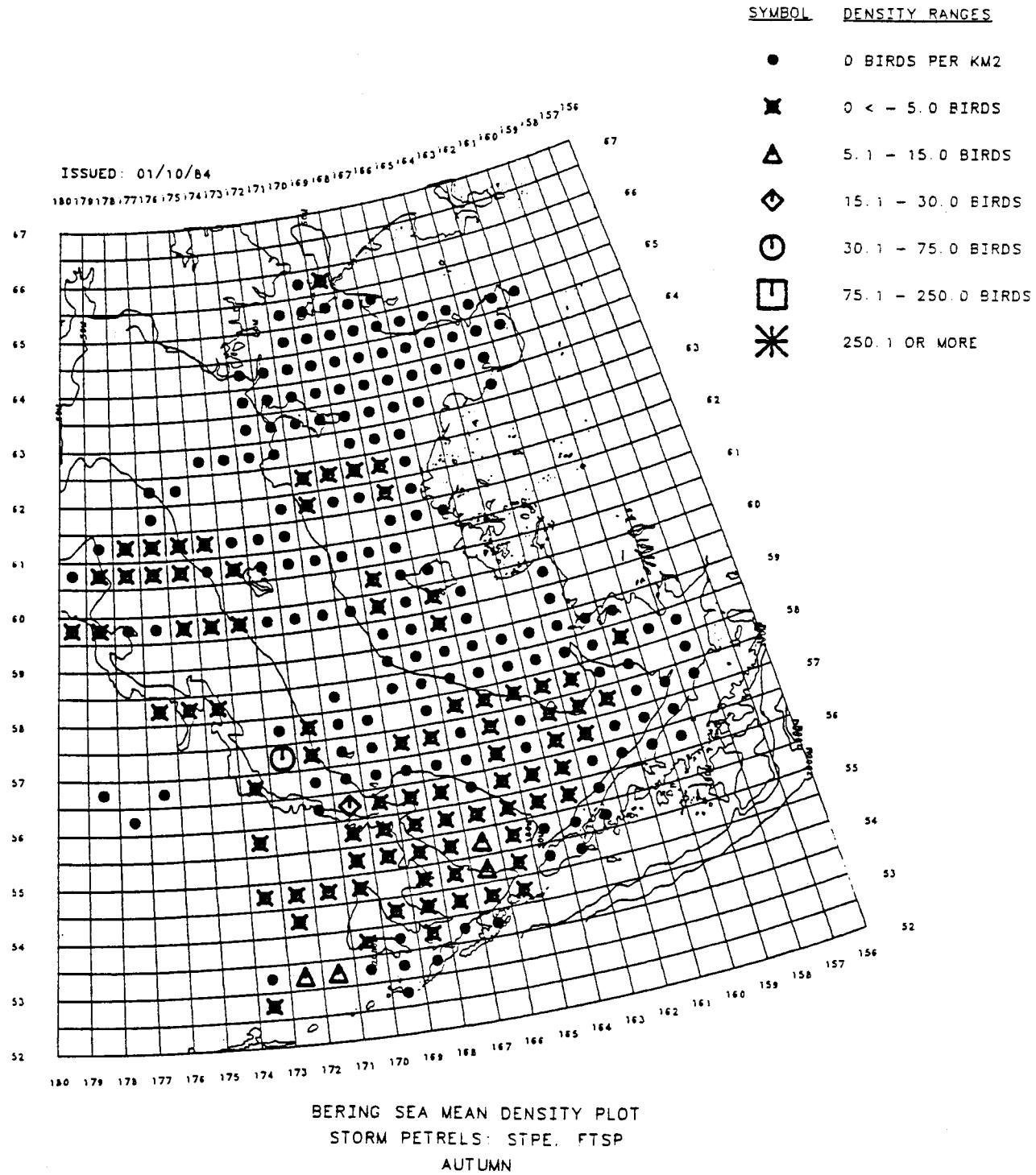


Figure 32. Mean densities, storm-petrels: Autumn.

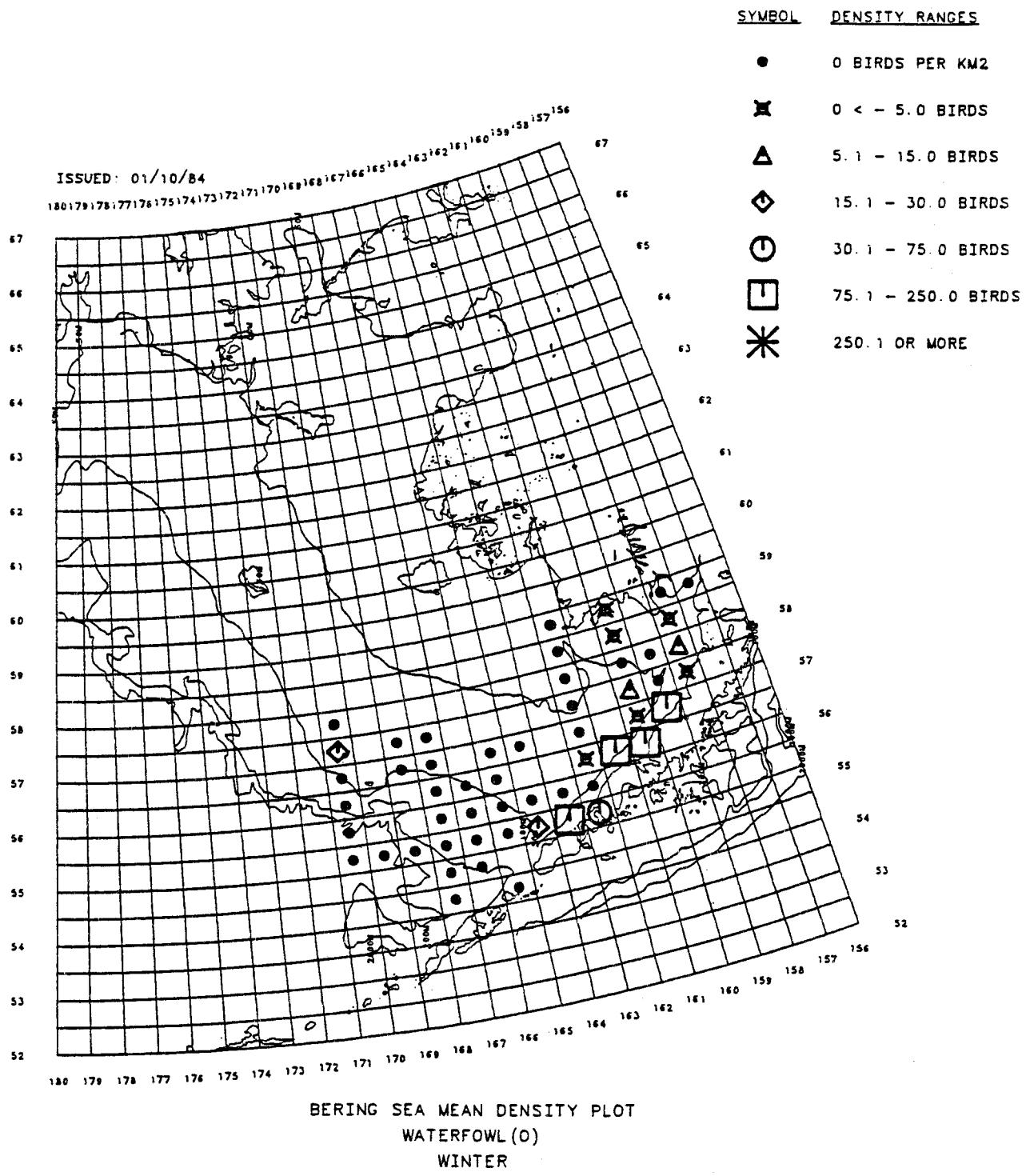


Figure 33. Mean densities, waterfowl: Winter.

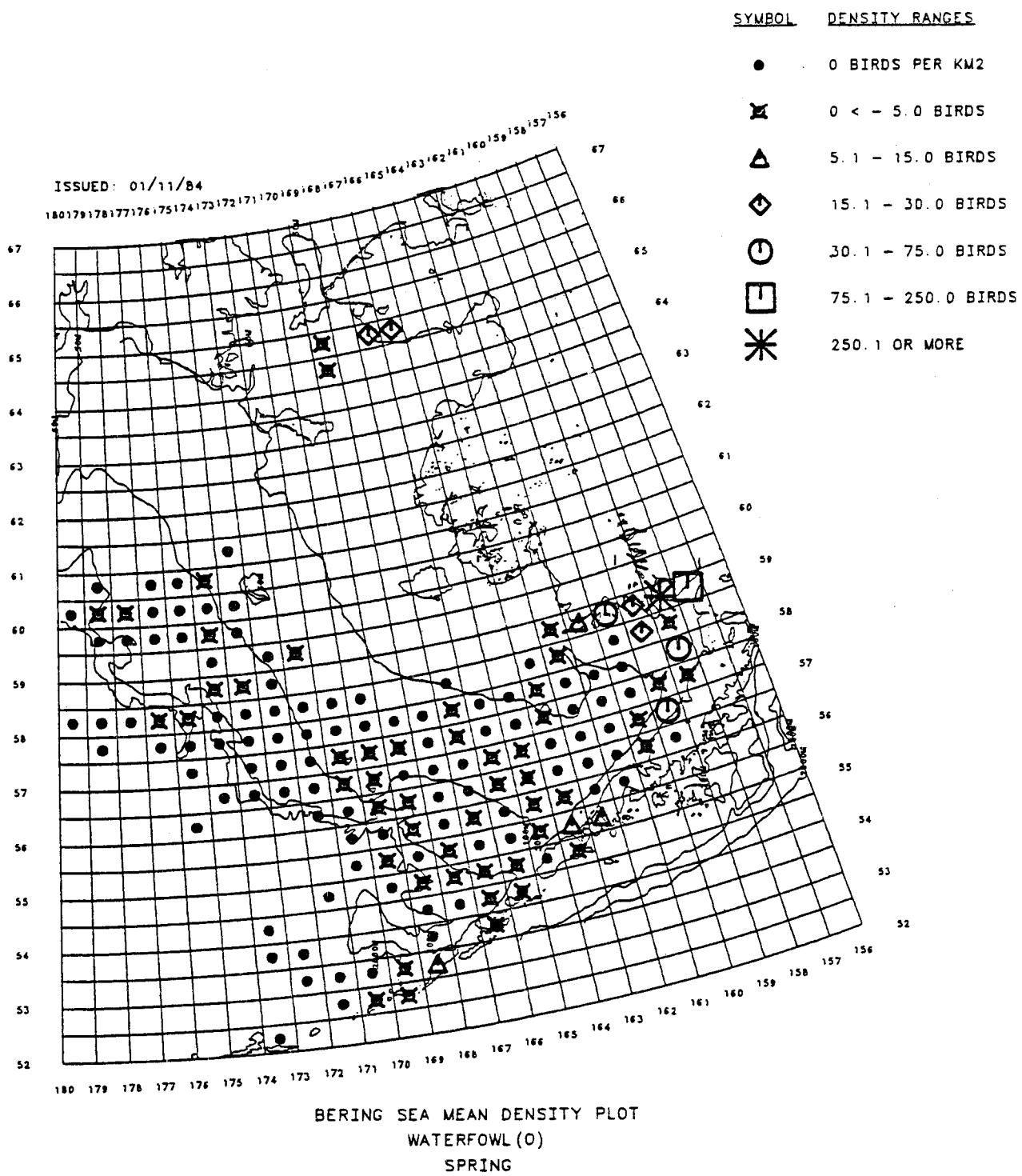


Figure 34. Mean densities, waterfowl: Spring.

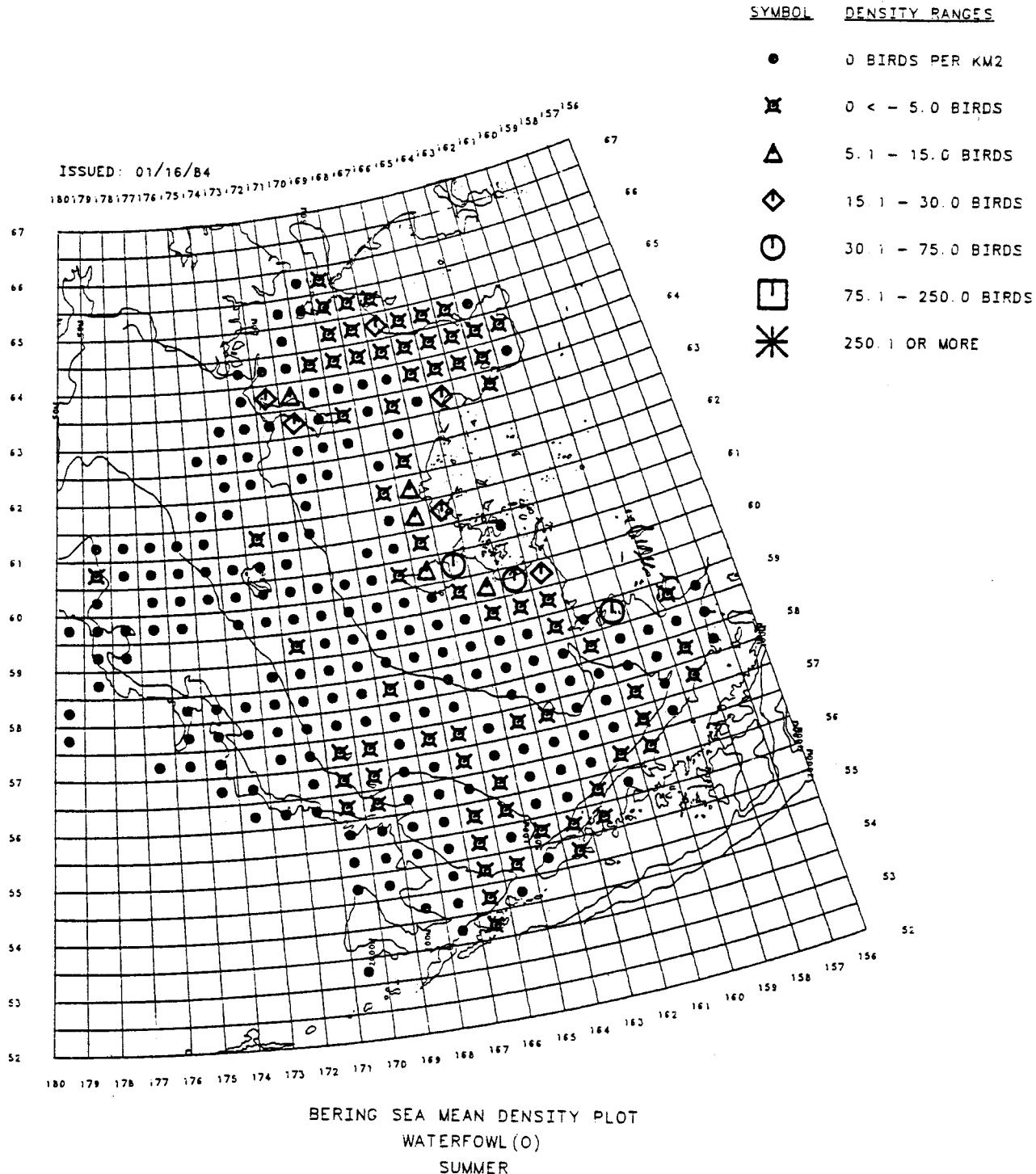


Figure 35. Mean densities, waterfowl: Summer.

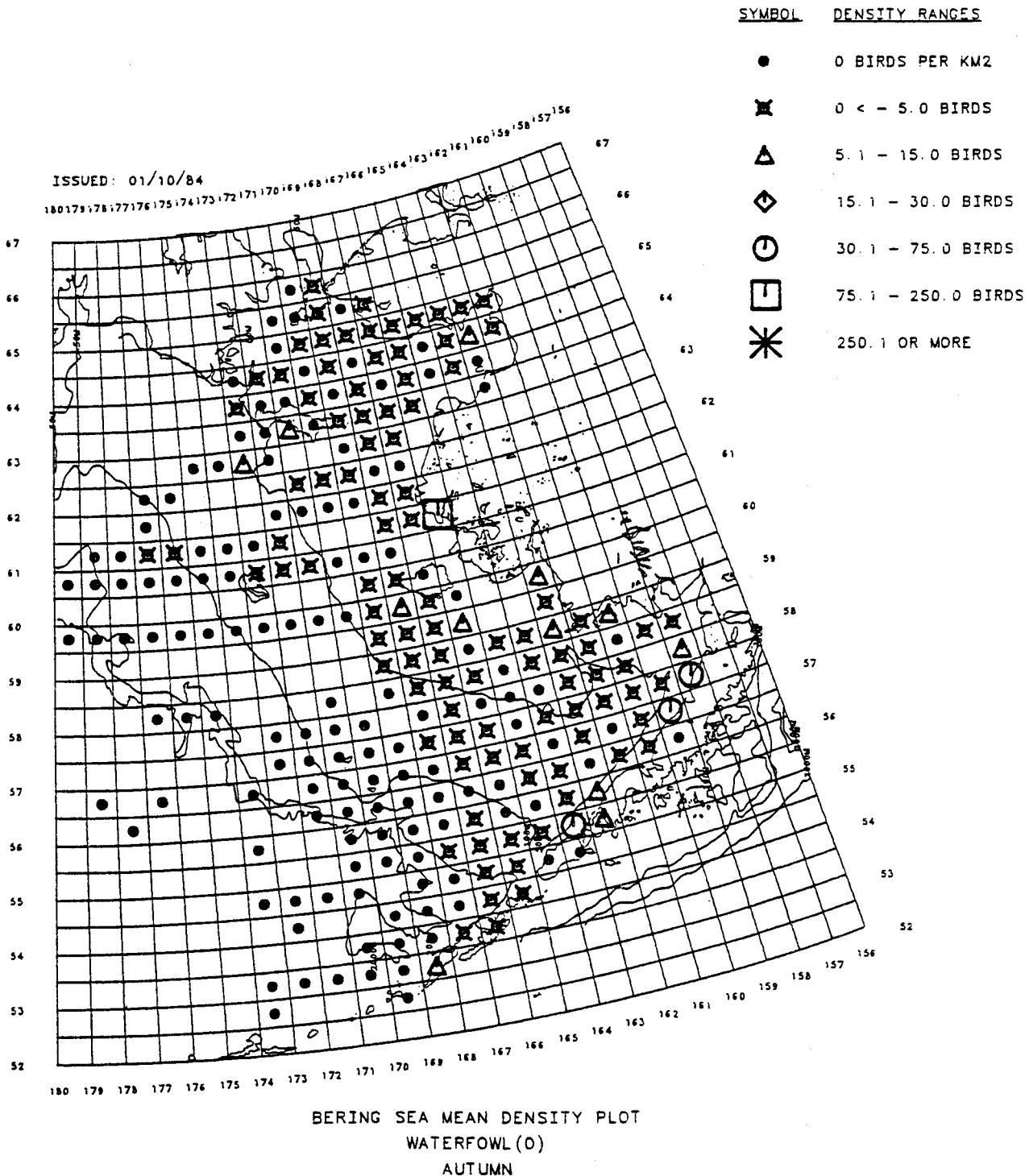


Figure 36. Mean densities, waterfowl: Autumn.

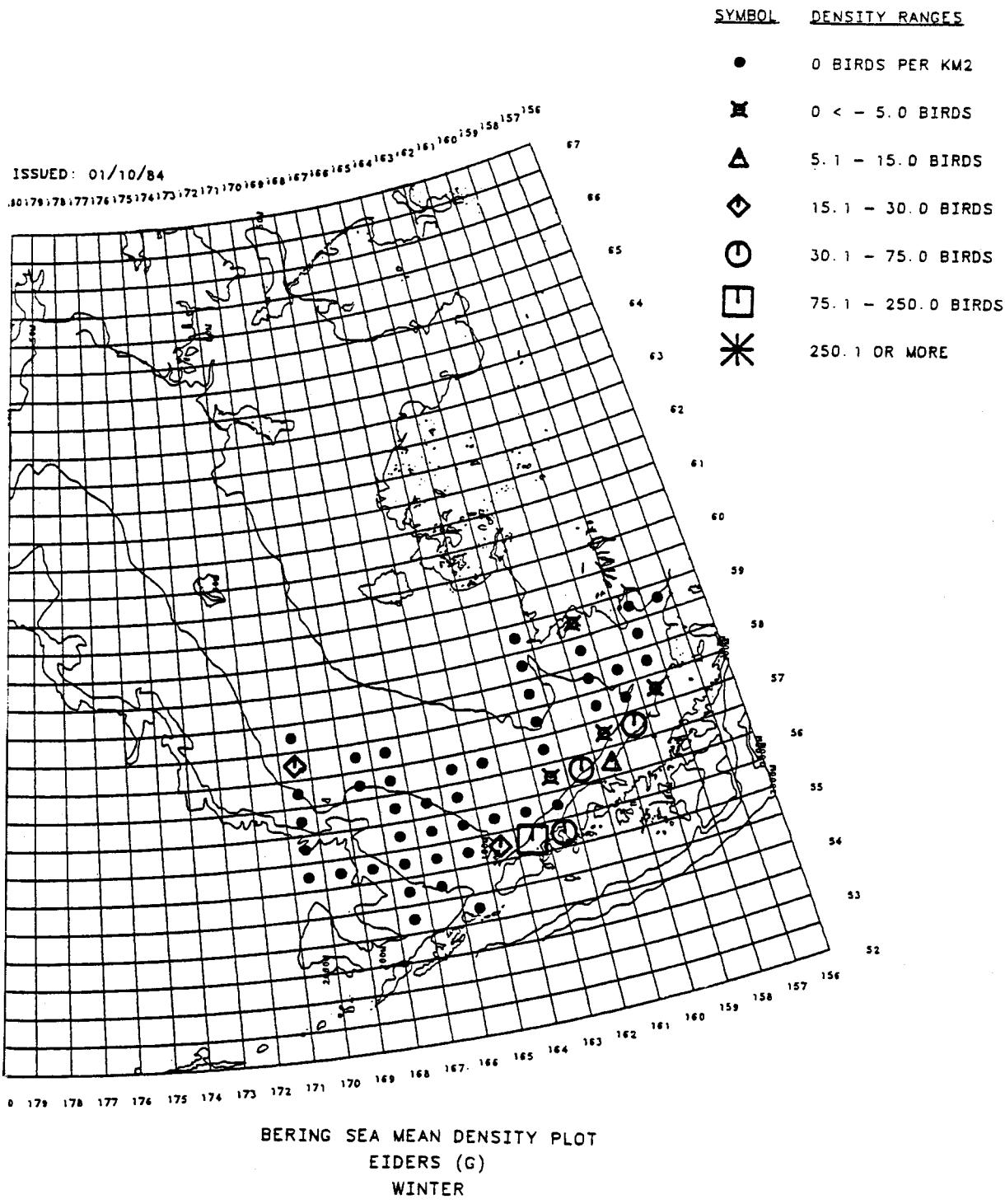


Figure 37. Mean densities, eiders: Winter.

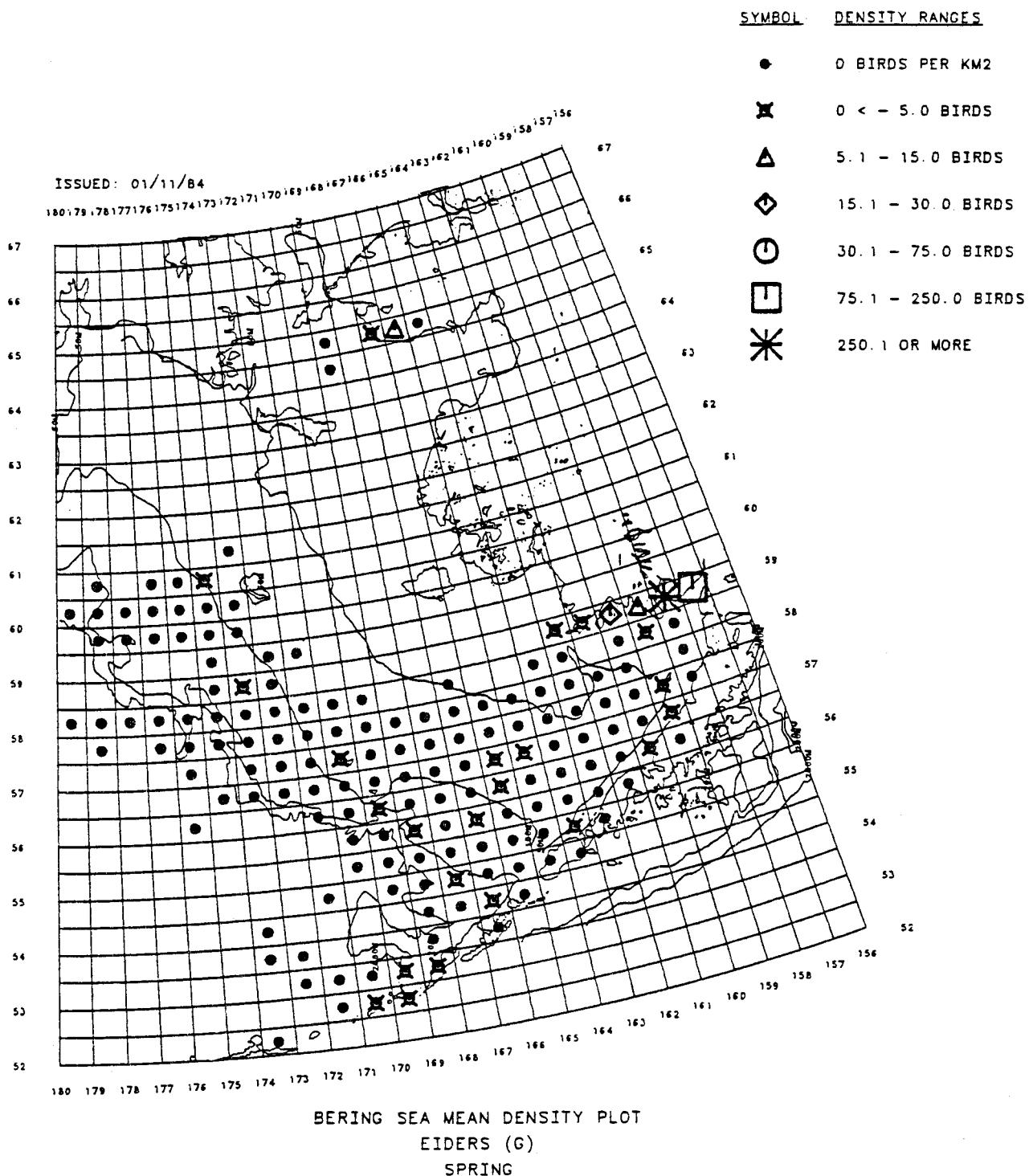
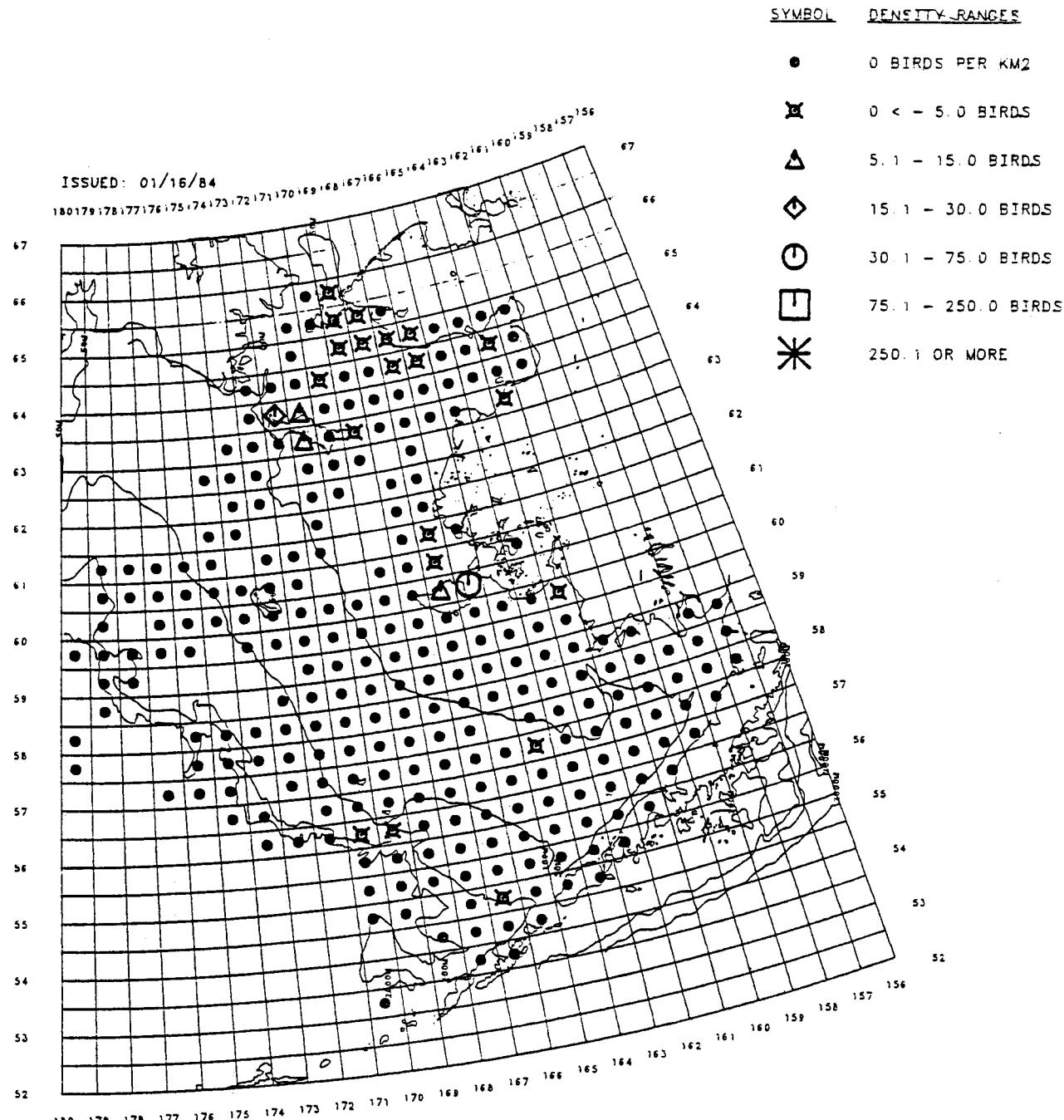


Figure 38. Mean densities, eiders: Spring.



BERING SEA MEAN DENSITY PLOT
EIDERS (G)
SUMMER

Figure 39. Mean densities, eiders: Summer.

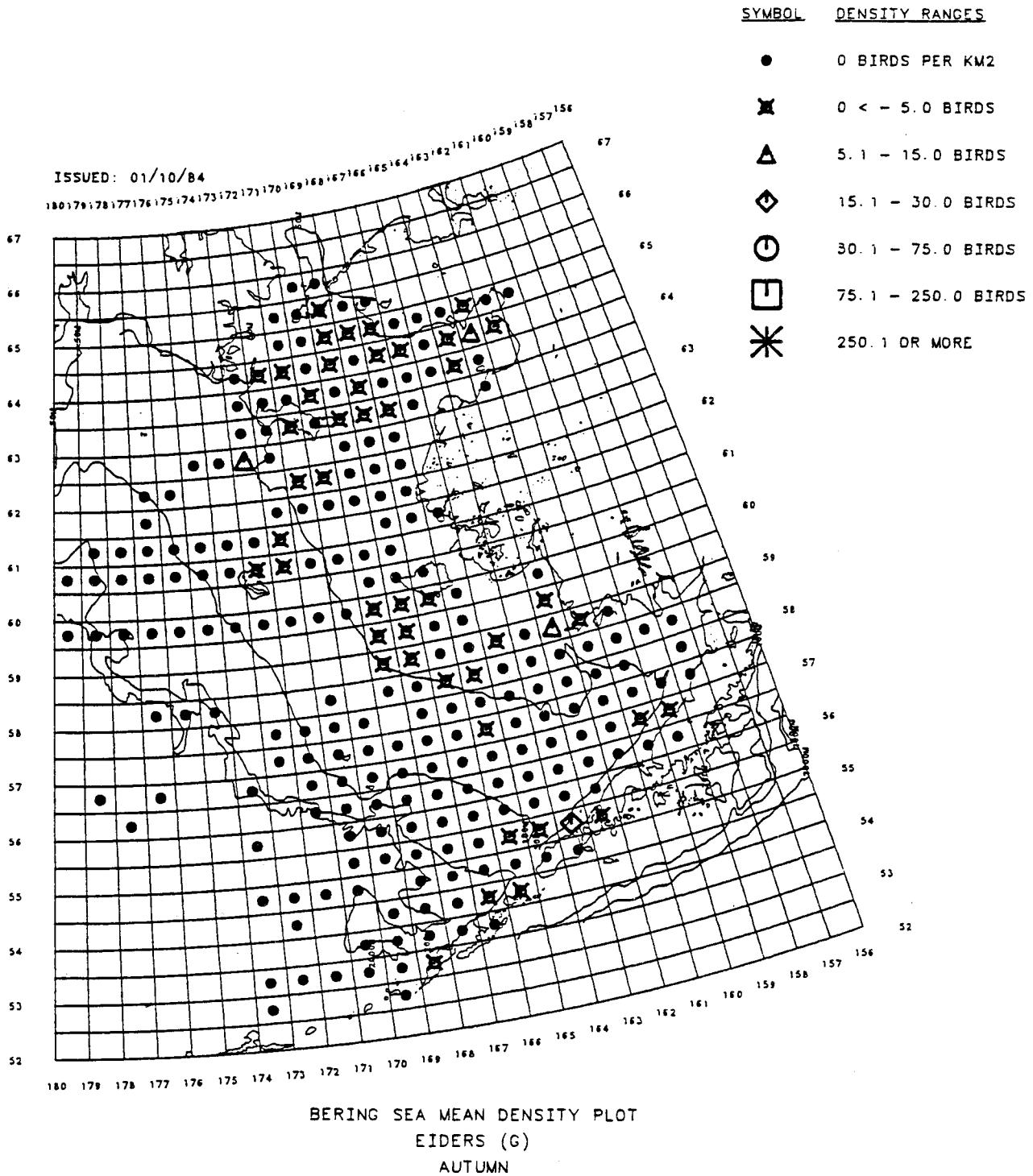


Figure 40. Mean densities, eiders: Autumn.

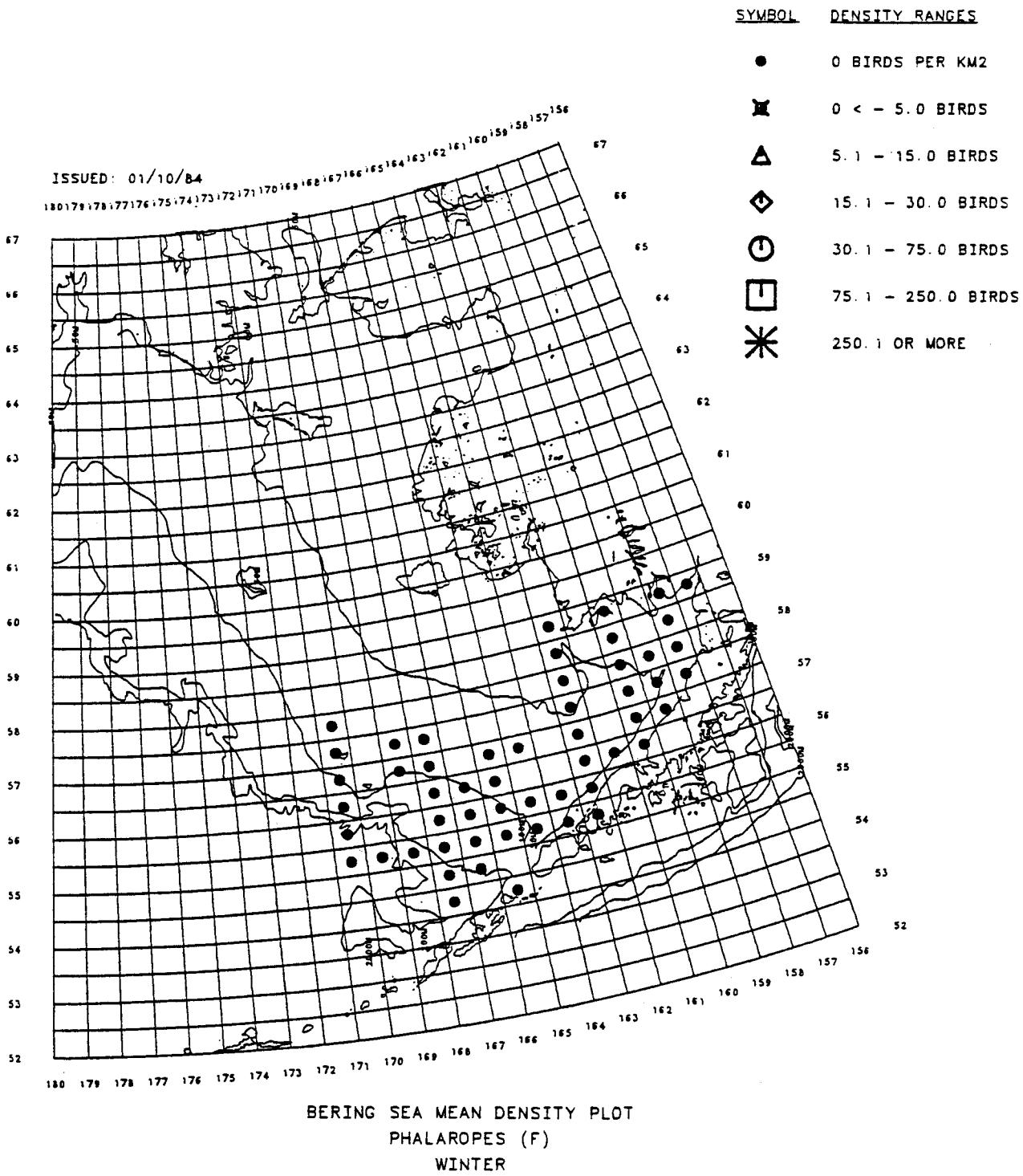


Figure 41. Mean densities, phalaropes: Winter.

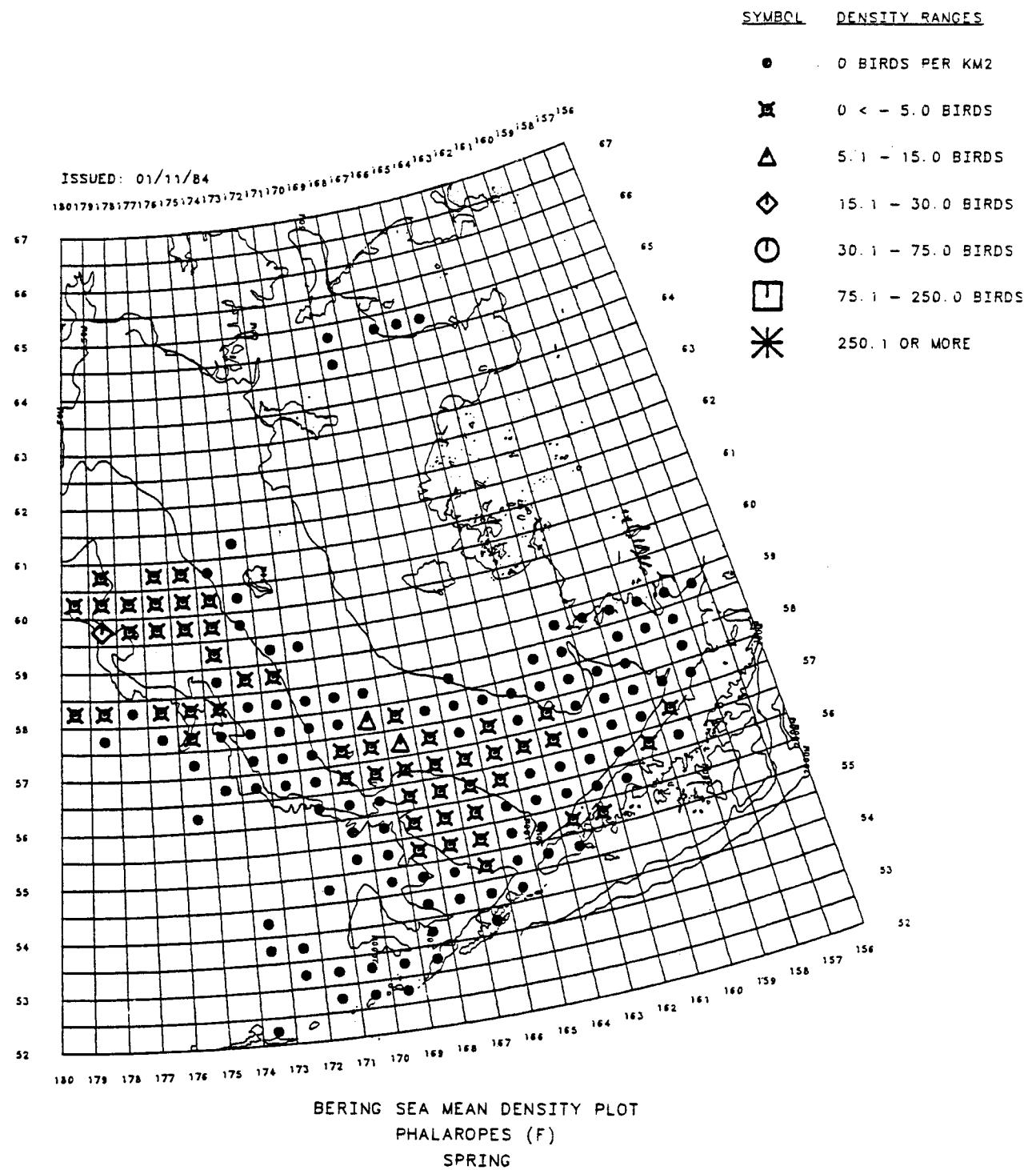


Figure 42. Mean densities, phalaropes: Spring.

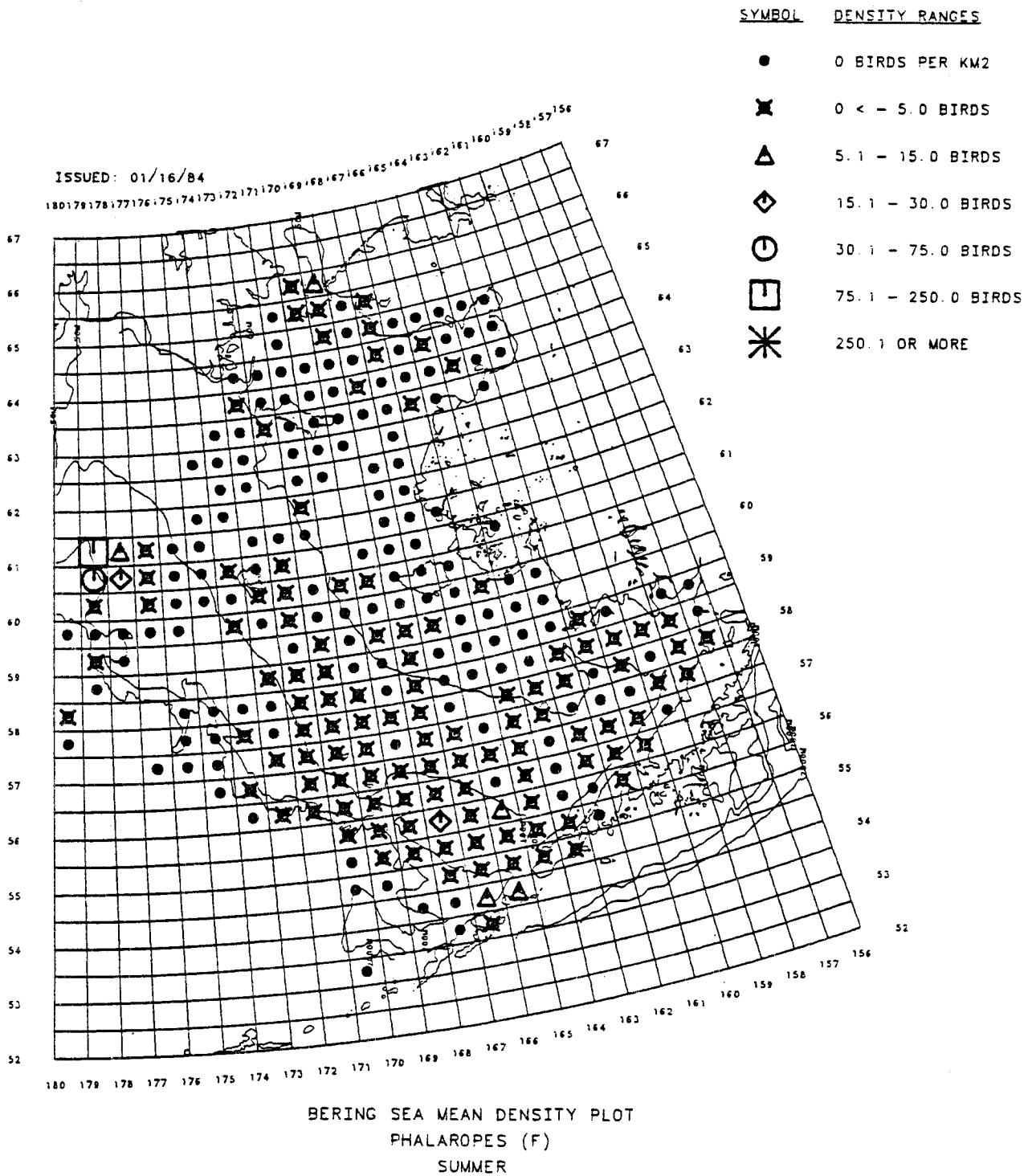


Figure 43. Mean densities, phalaropes: Summer.

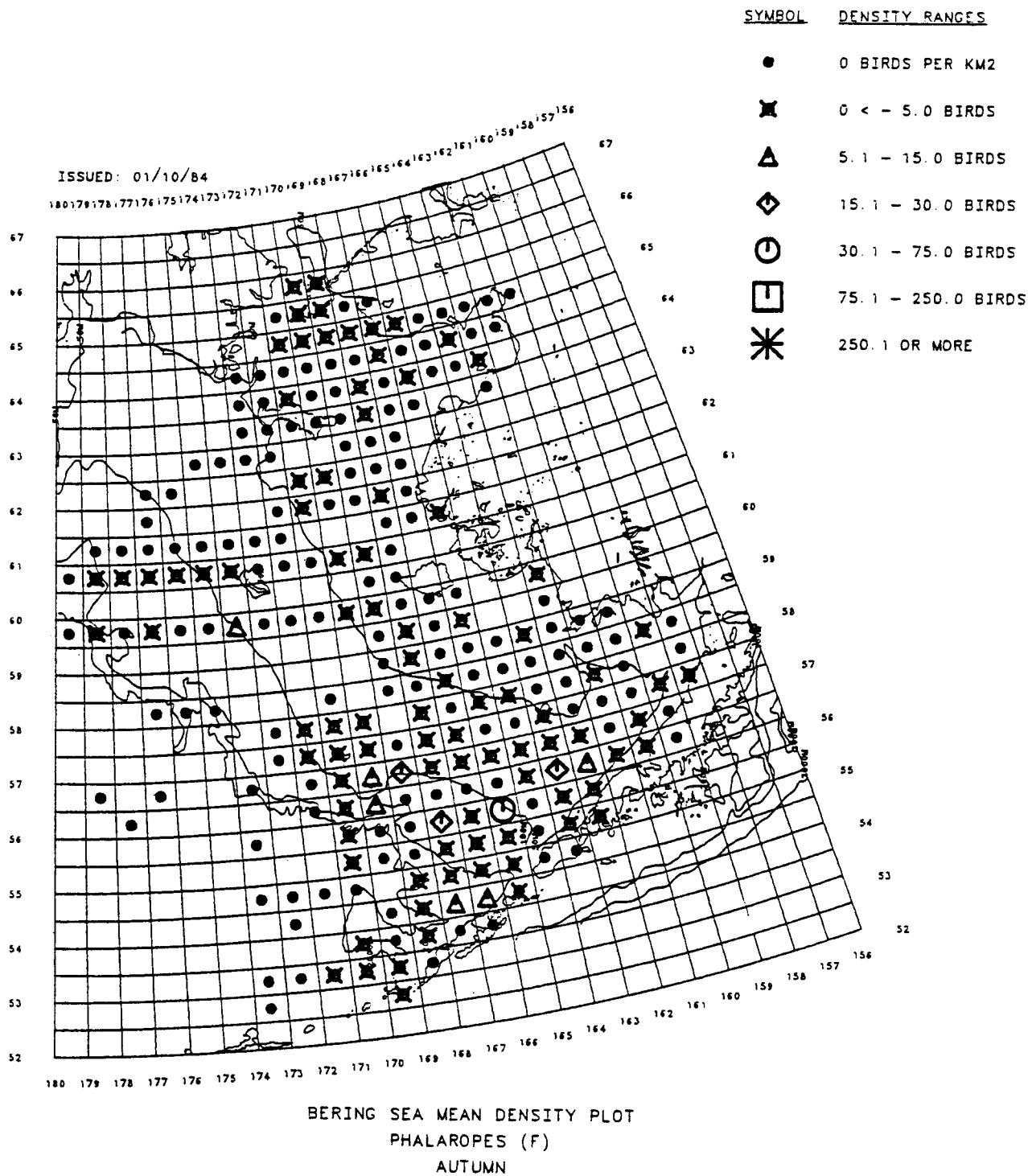


Figure 44. Mean densities, phalaropes: Autumn.

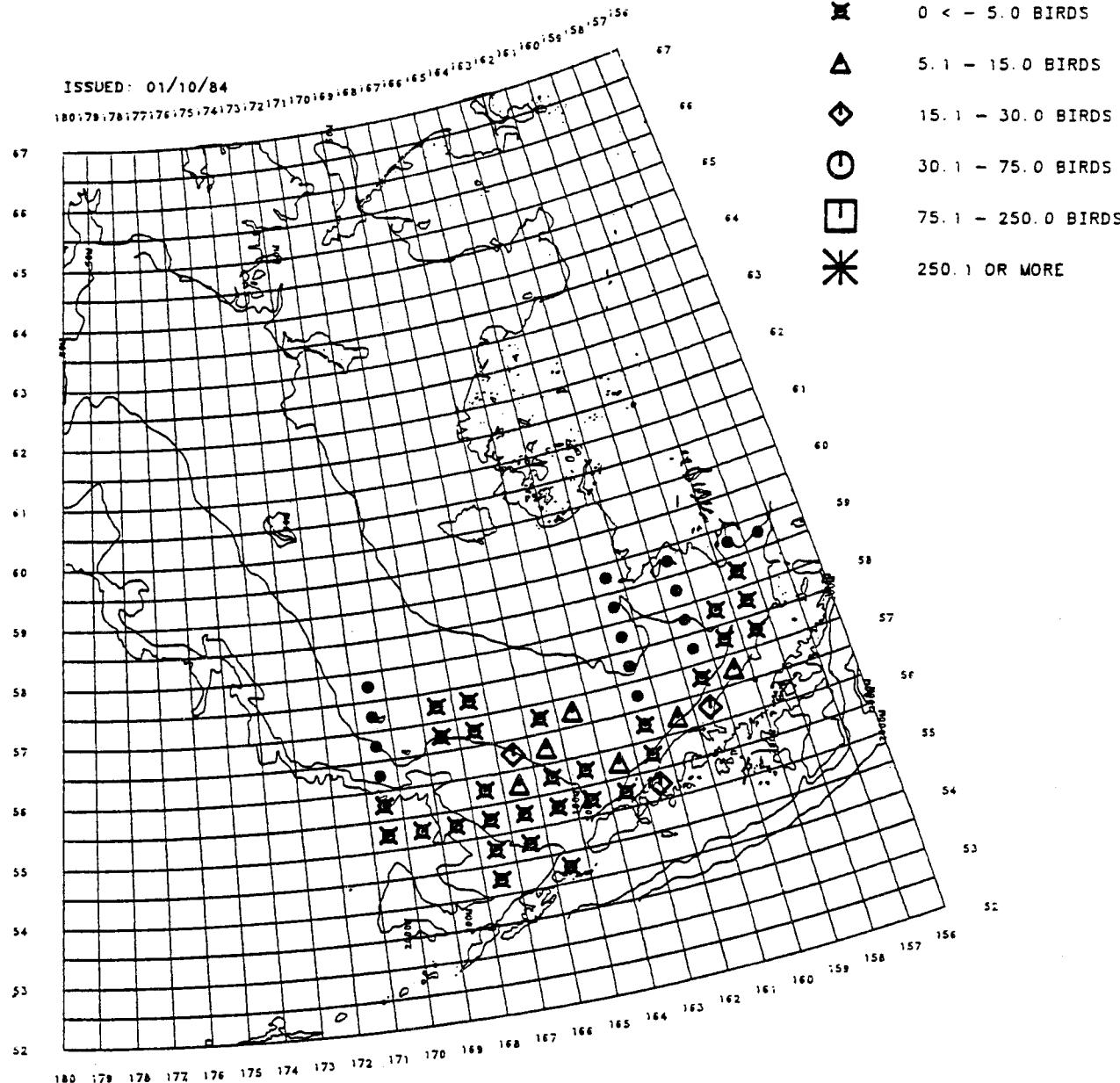


Figure 45. Mean densities, Larus gulls: Winter.

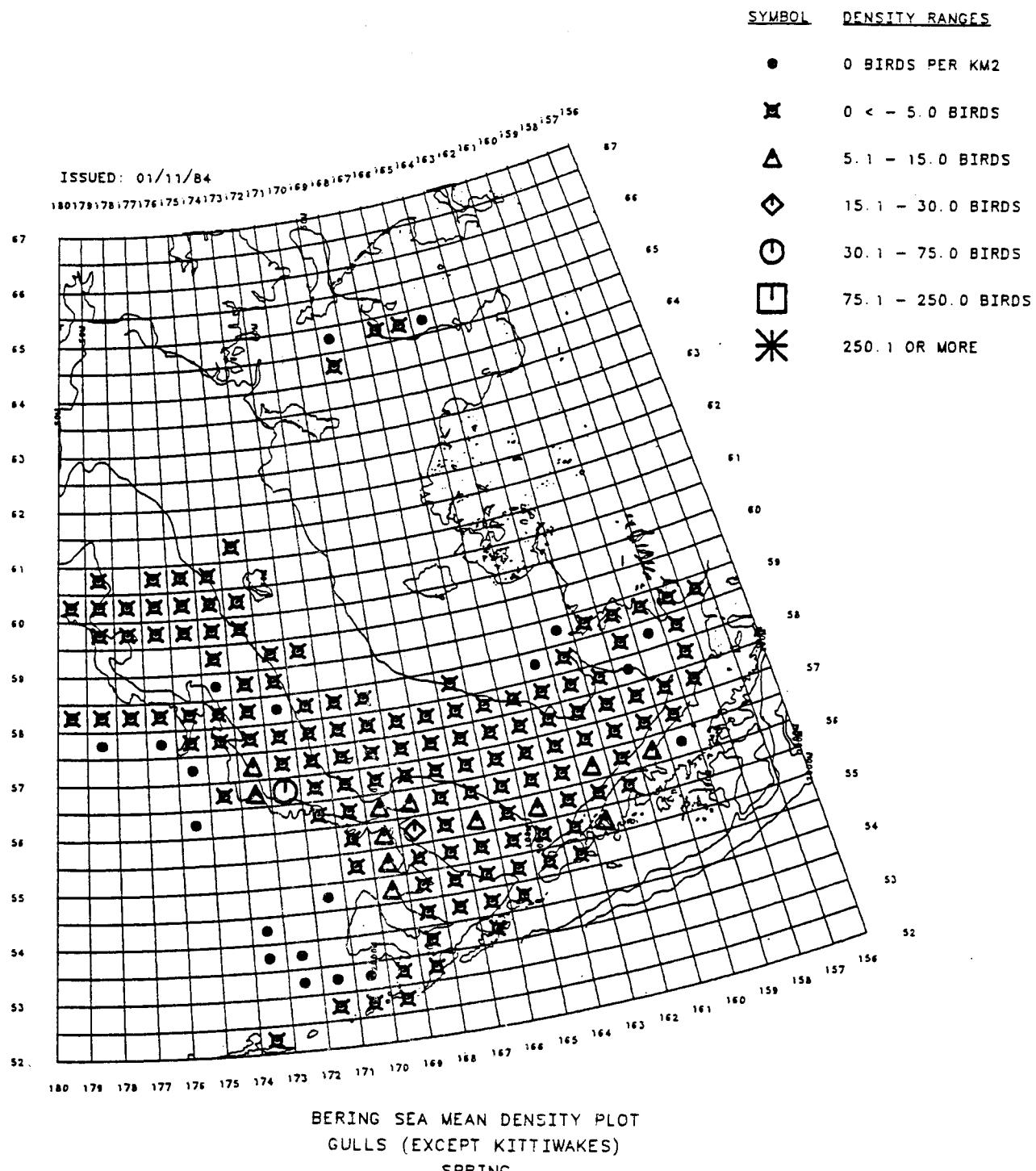


Figure 46. Mean densities, Larus gulls: Spring.

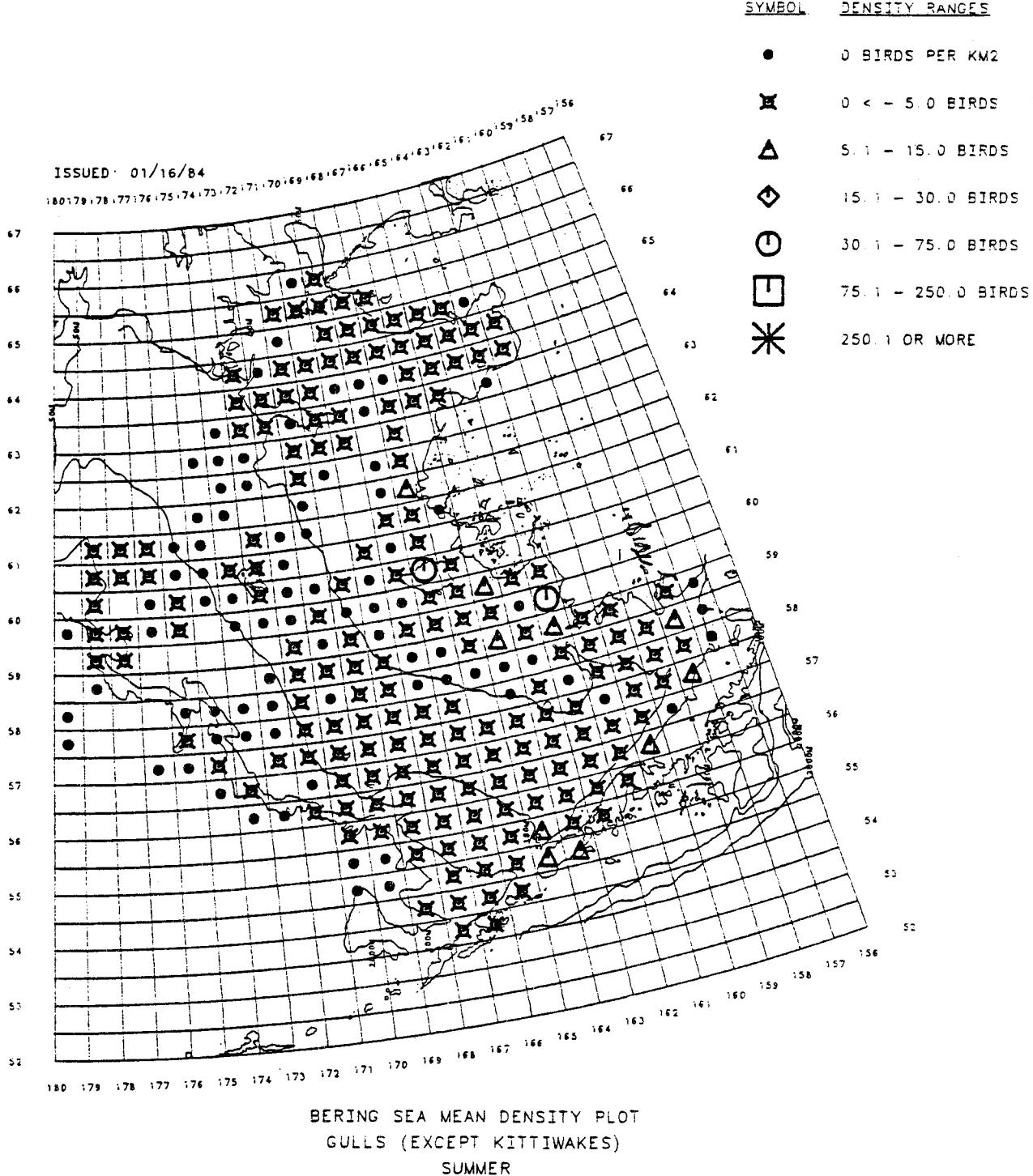


Figure 47. Mean densities, Larus gulls: Summer.

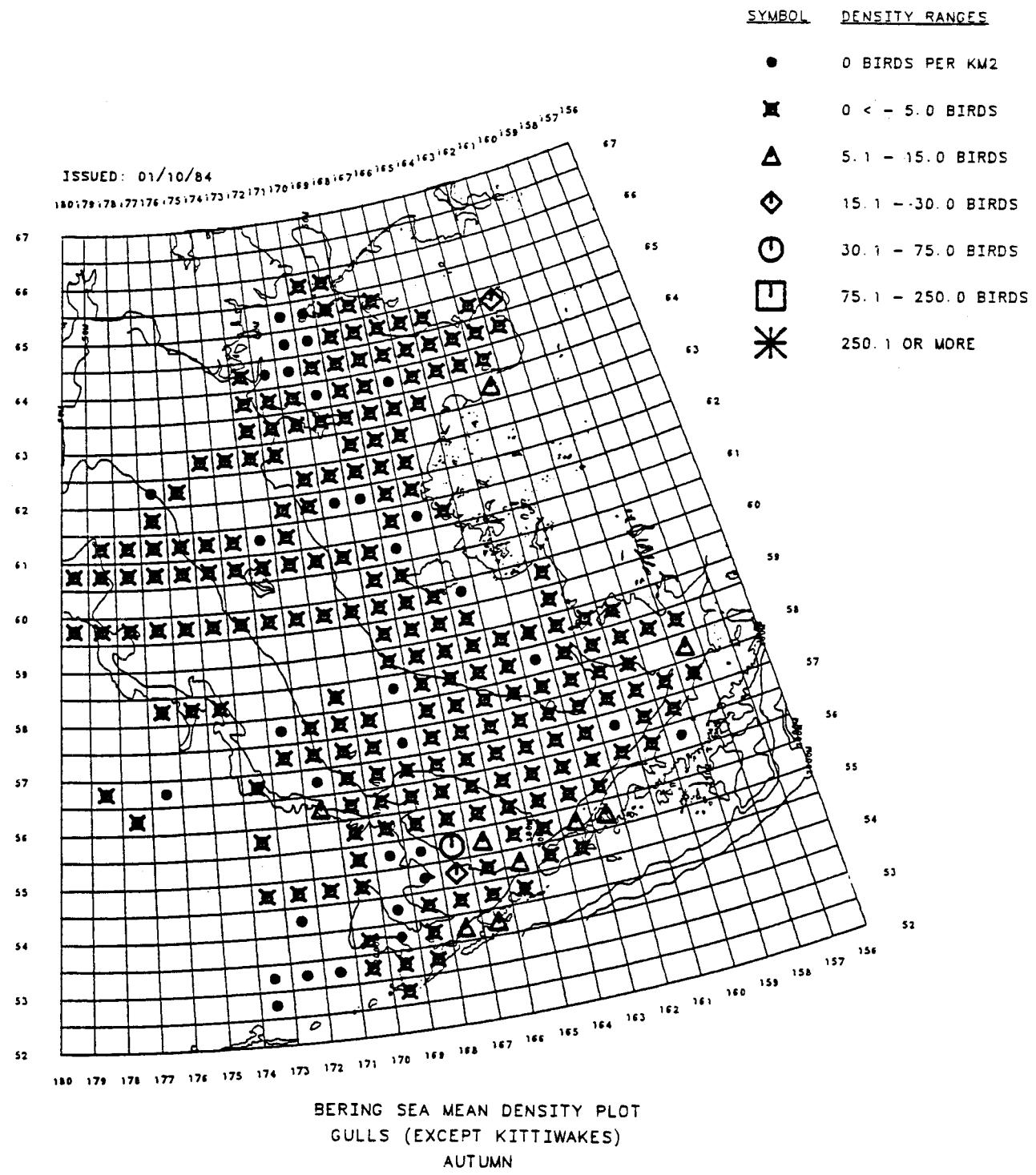


Figure 48. Mean densities, Larus gulls: Autumn.

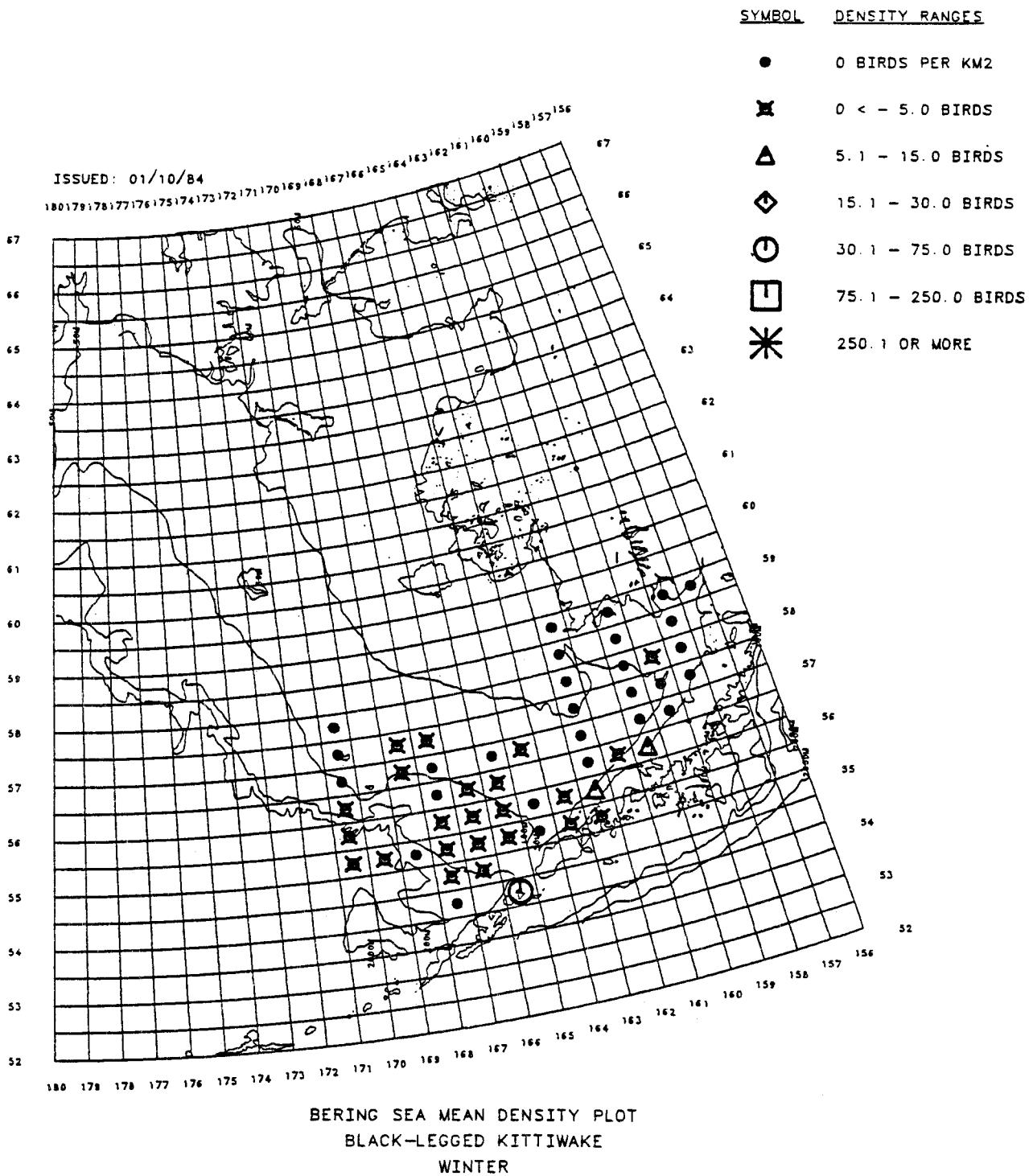


Figure 49. Mean densities, Black-legged Kittiwakes: Winter.

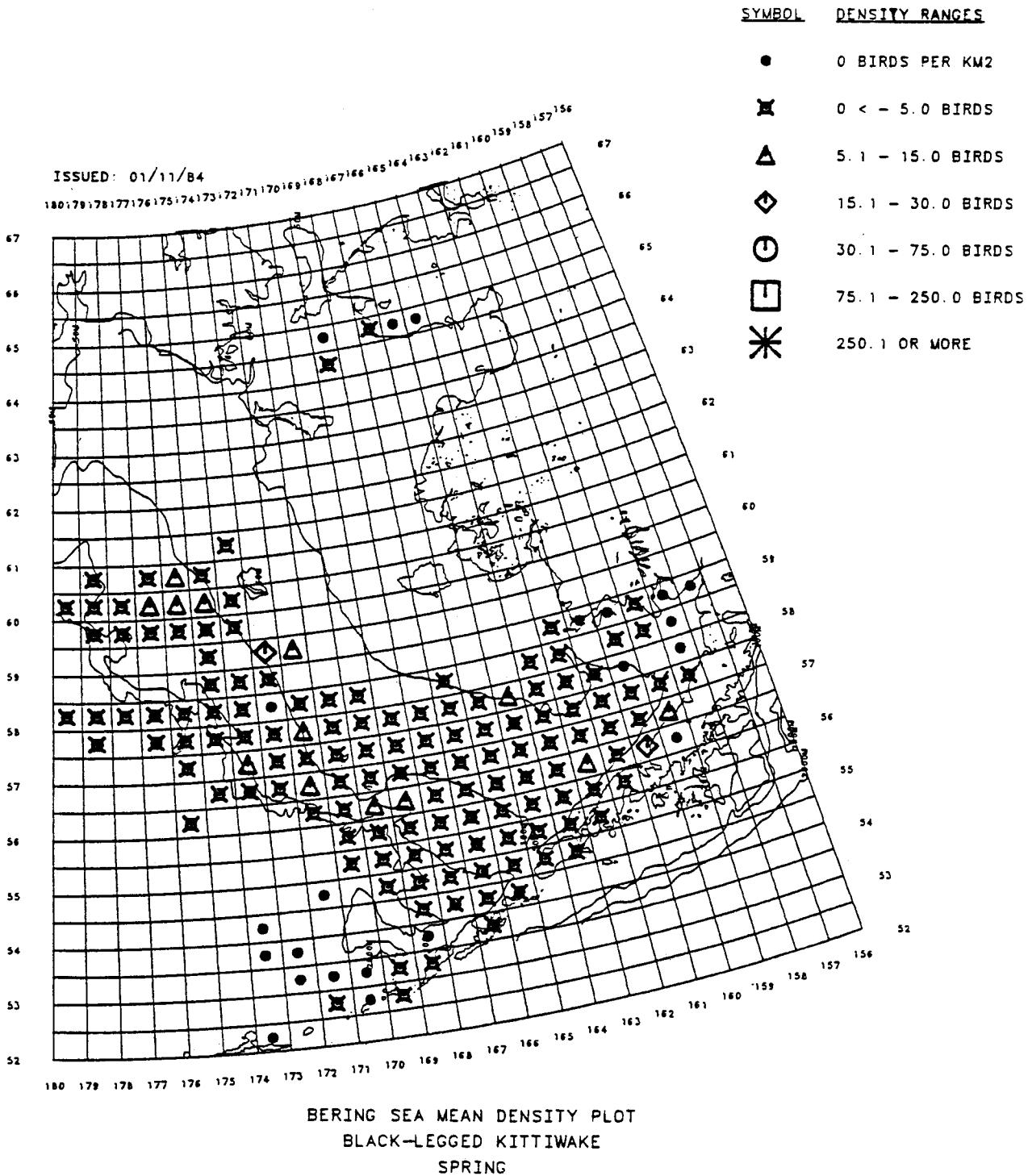


Figure 50. Mean densities, Black-legged Kittiwakes: Spring.

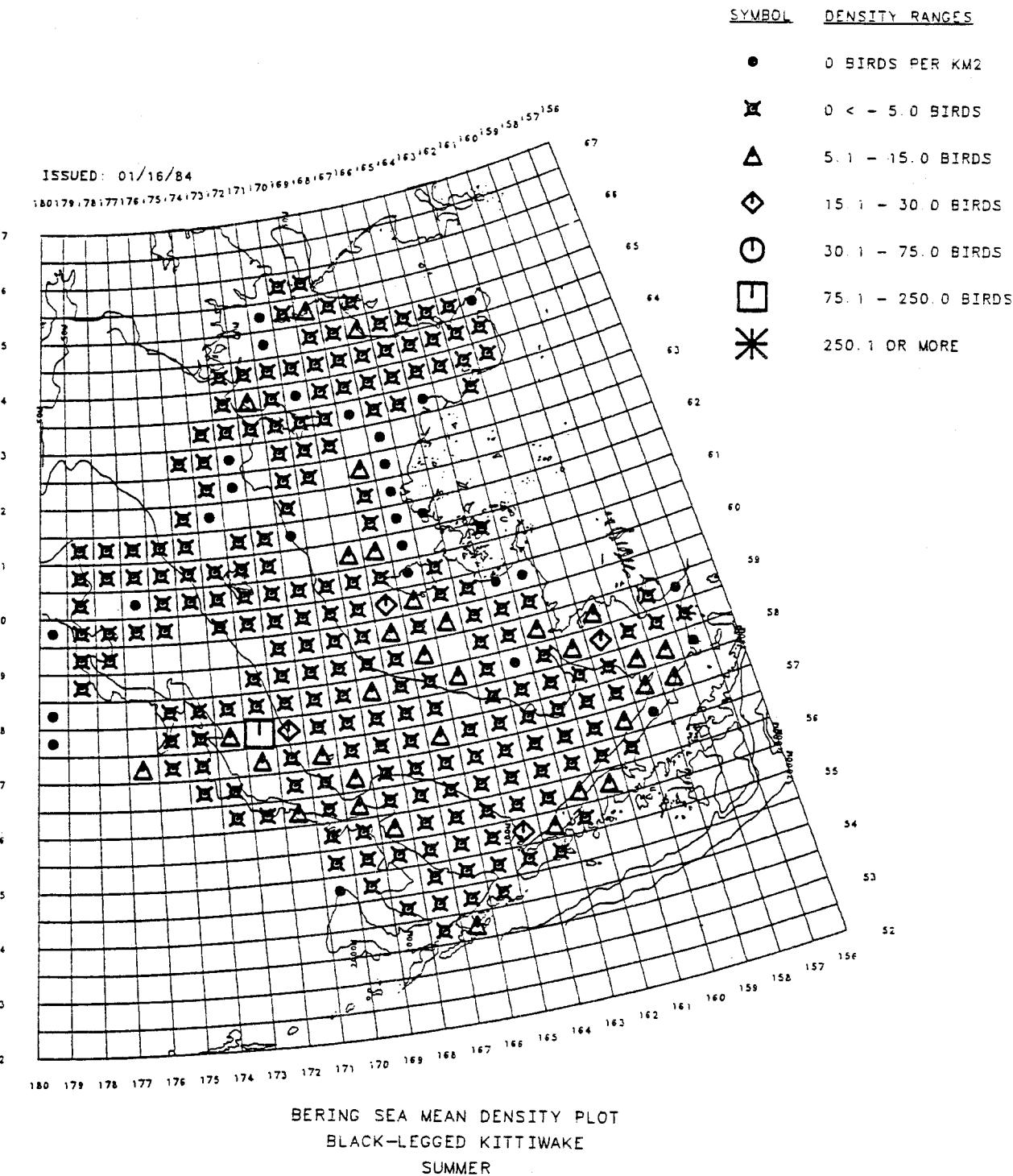


Figure 51. Mean densities, Black-legged Kittiwakes: Summer.

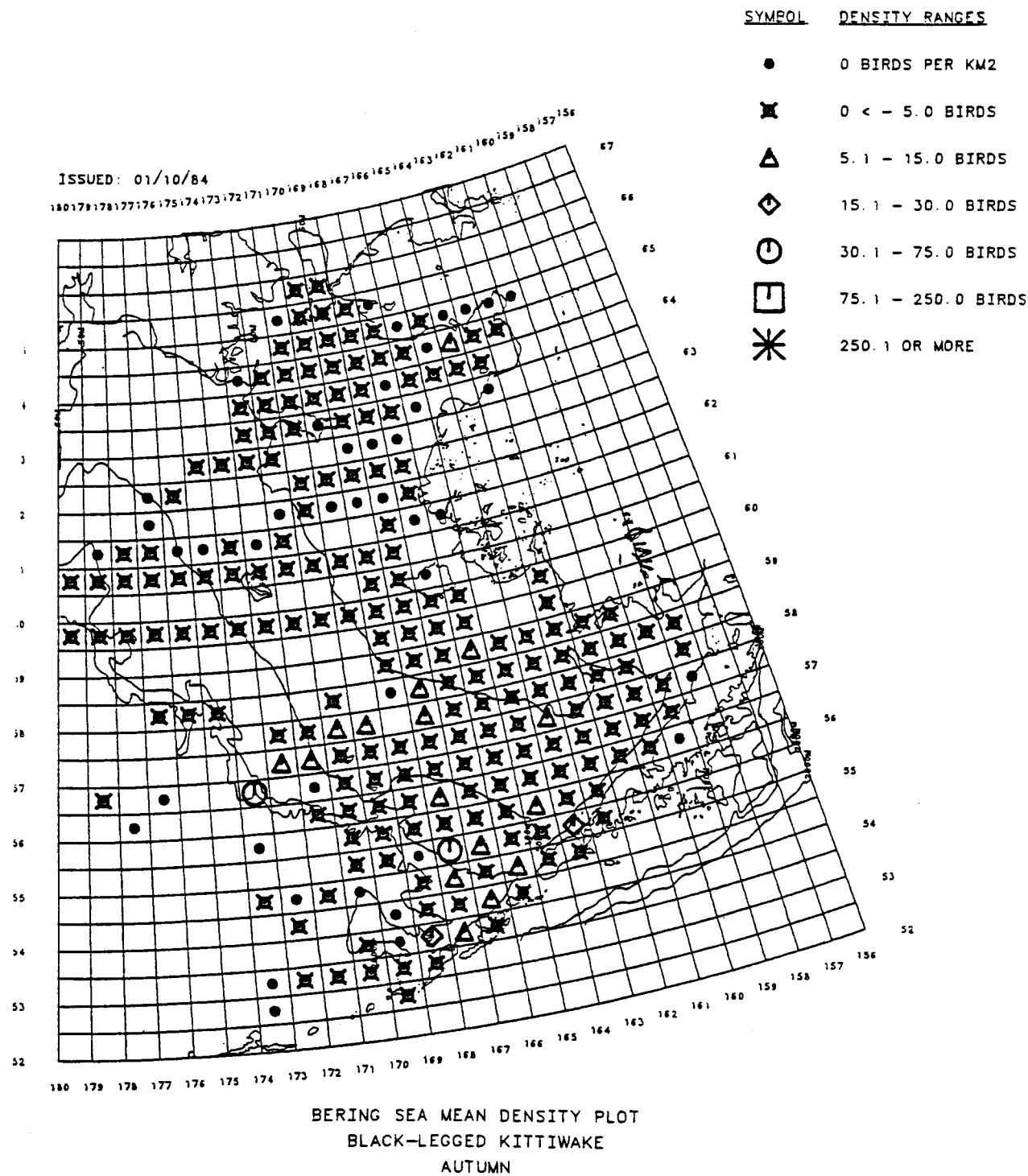


Figure 52. Mean densities, Black-legged Kittiwakes: Autumn.

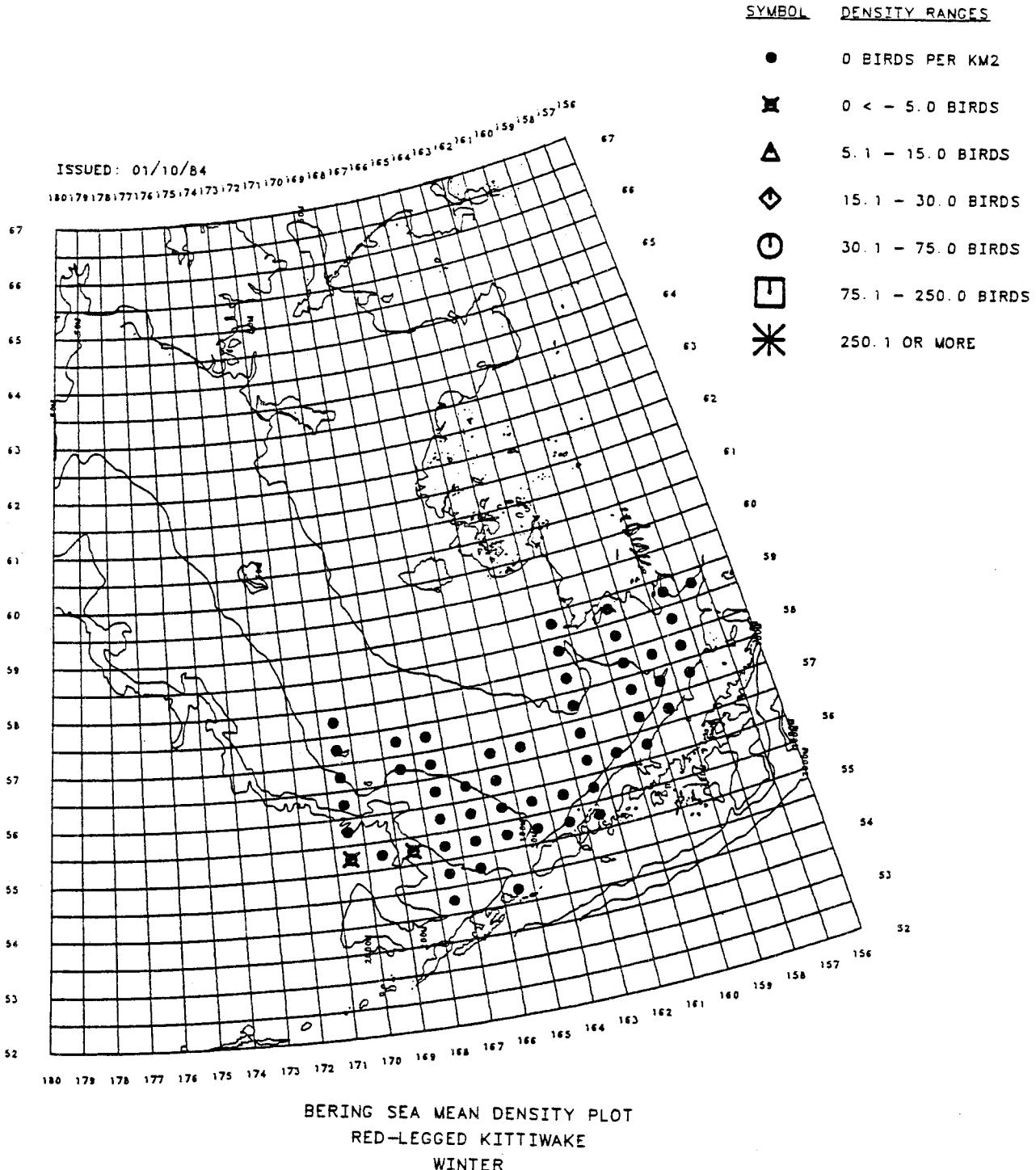


Figure 53. Mean densities, Red-legged Kittiwakes: Winter.

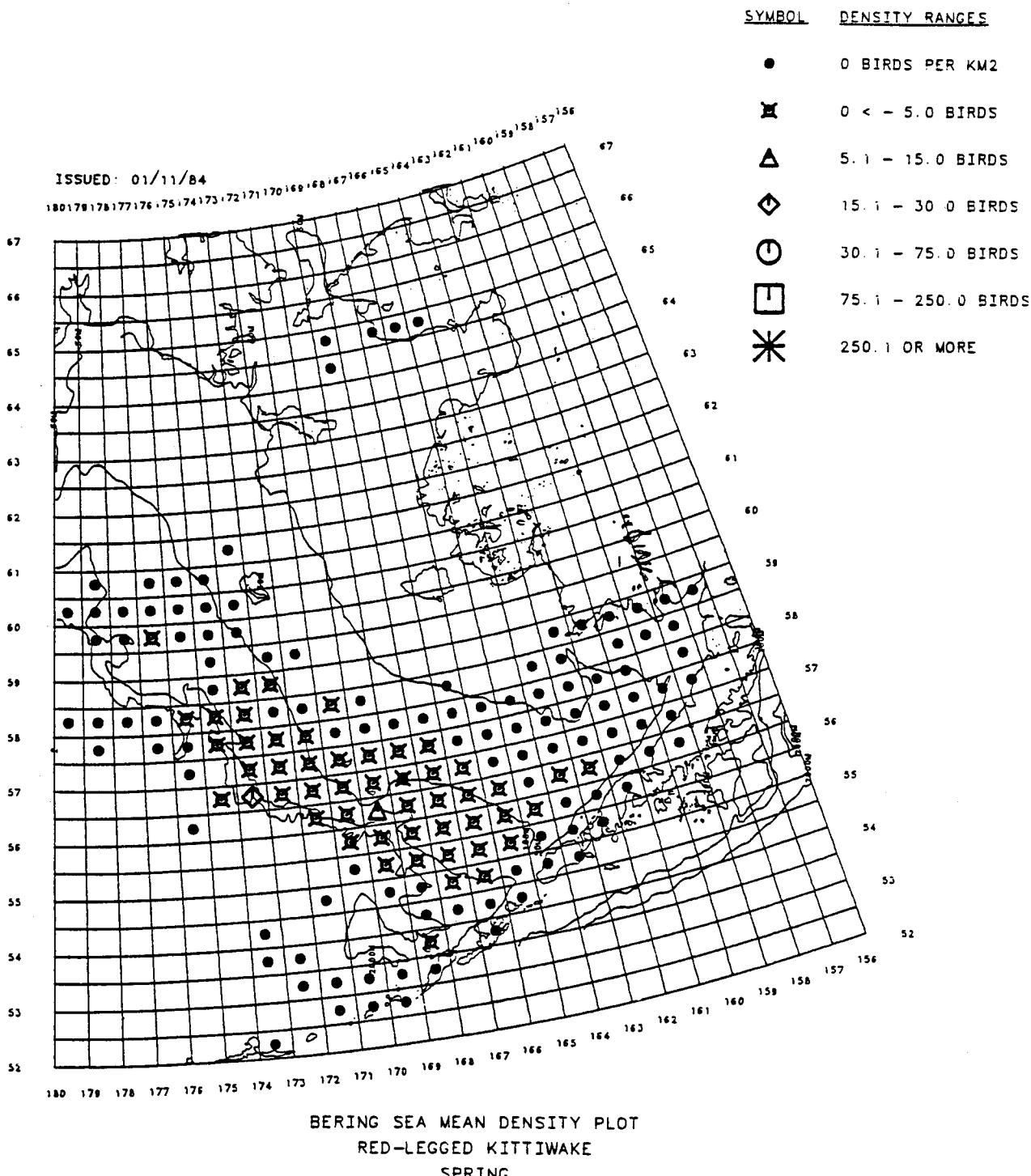


Figure 54. Mean densities, Red-legged Kittiwakes: Spring.

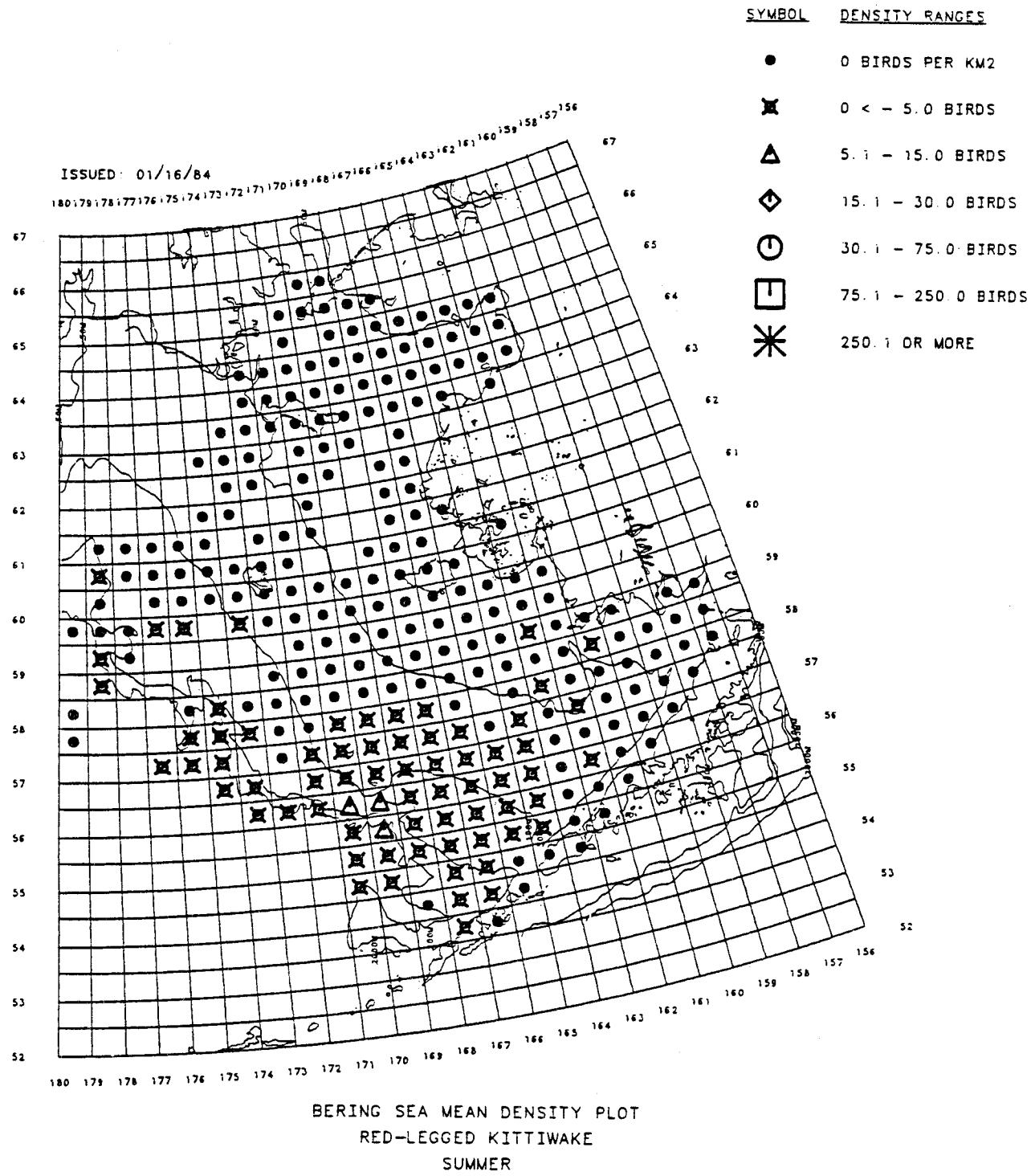


Figure 55. Mean densities, Red-legged Kittiwakes: Summer.

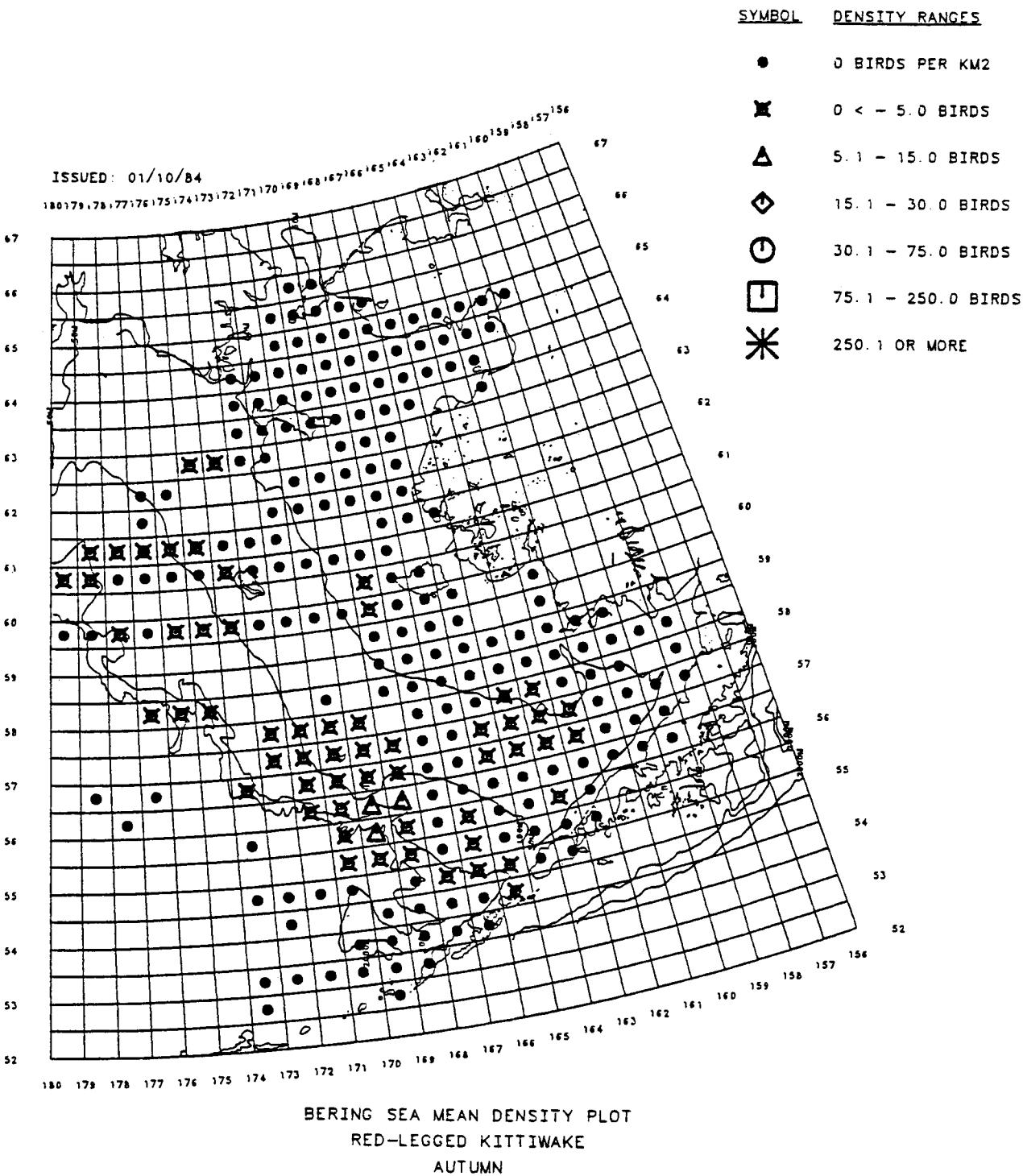


Figure 56. Mean densities, Red-legged Kittiwakes: Autumn.

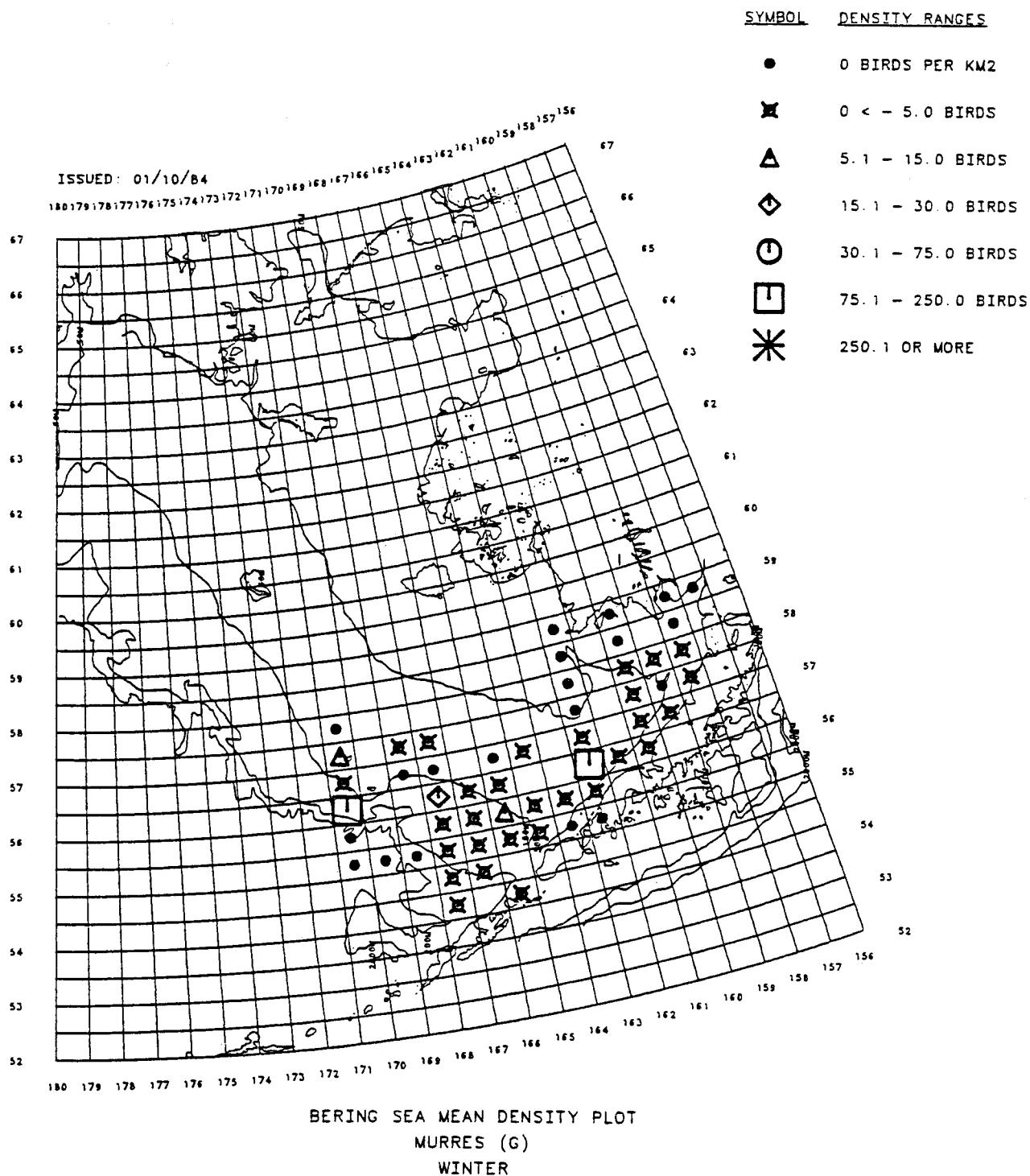


Figure 57. Mean densities, murres: Winter.

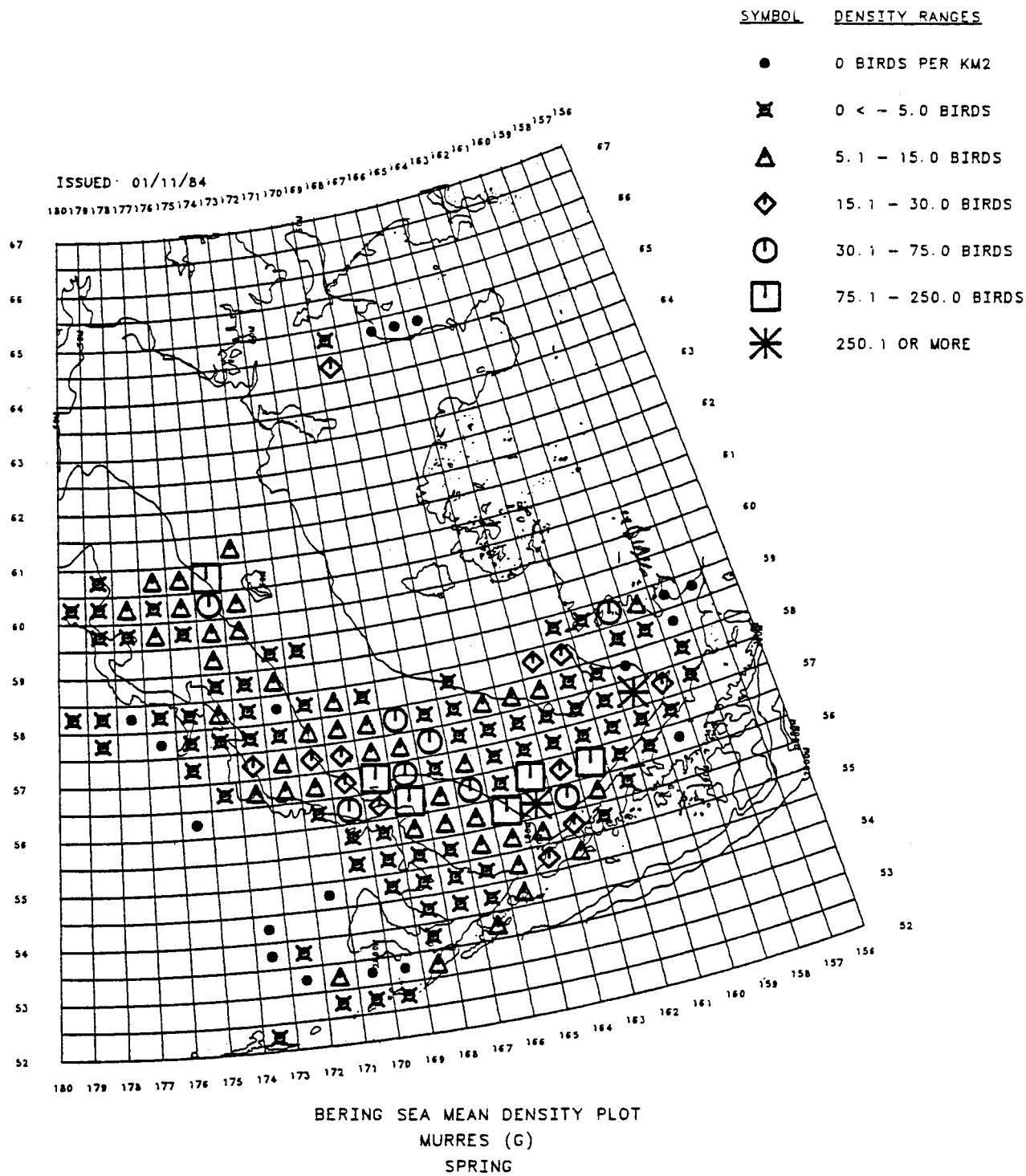


Figure 58. Mean densities, murres: Spring.

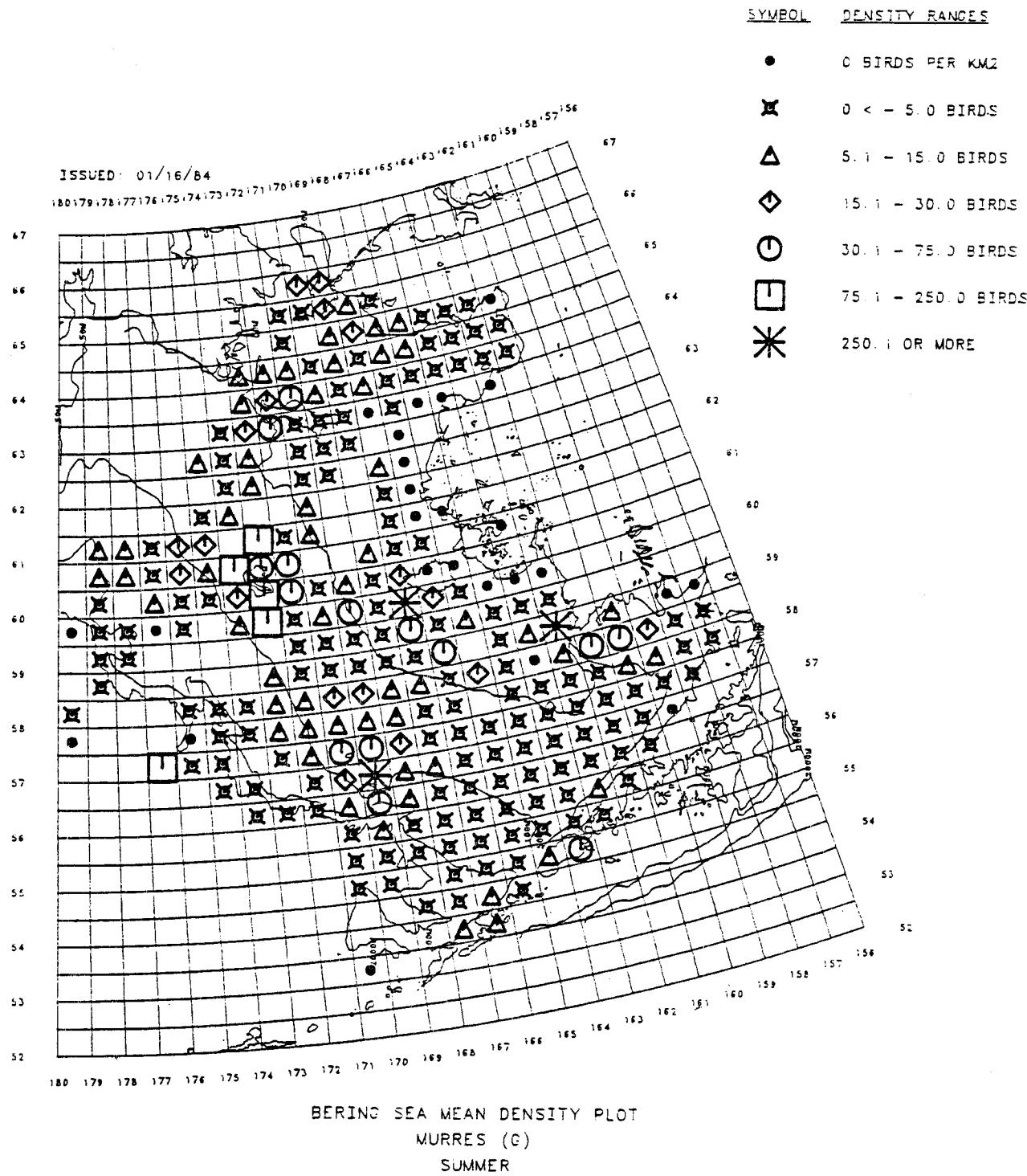


Figure 59. Mean densities, murres: Summer.

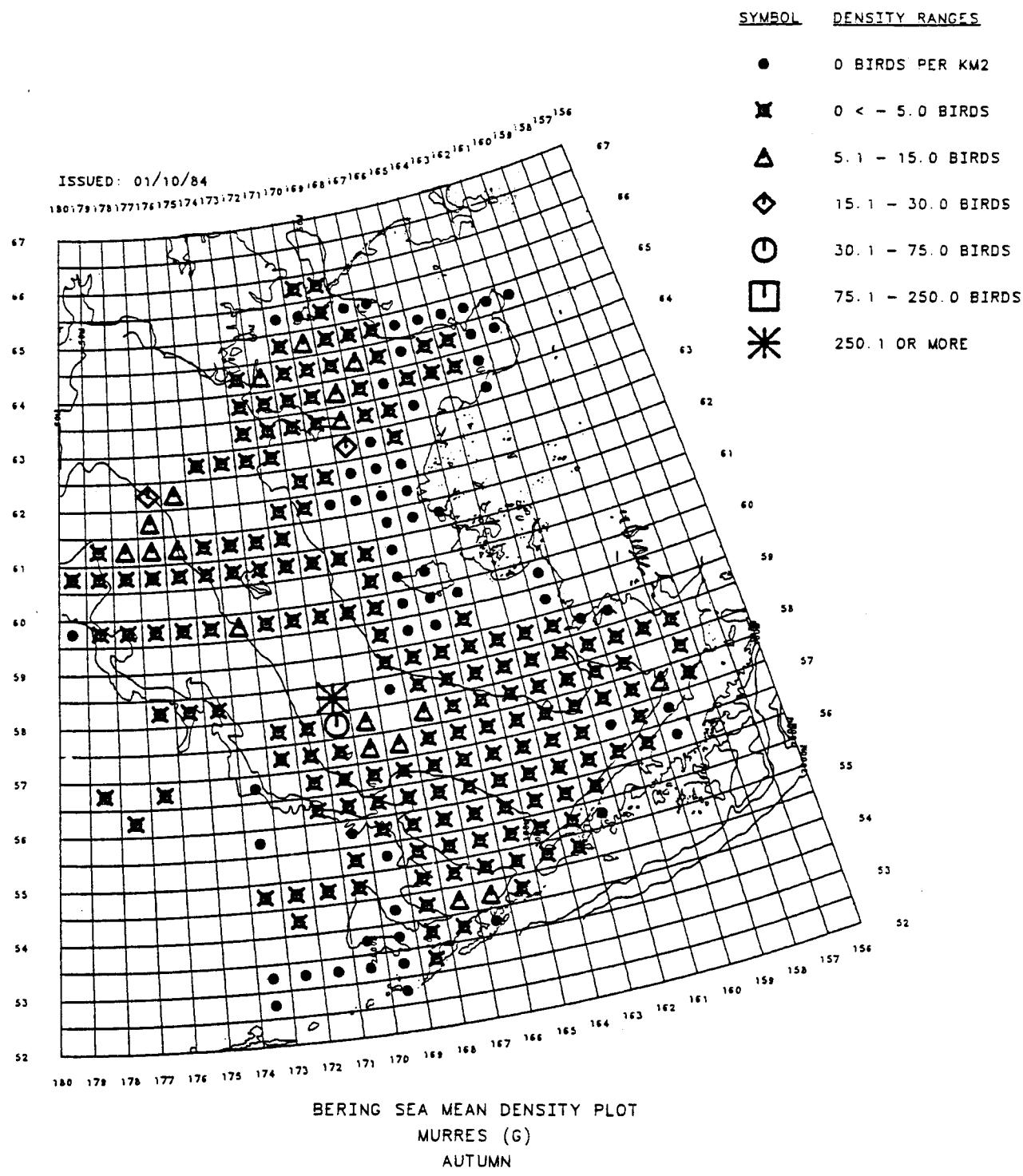


Figure 60. Mean densities, murres: Autumn.

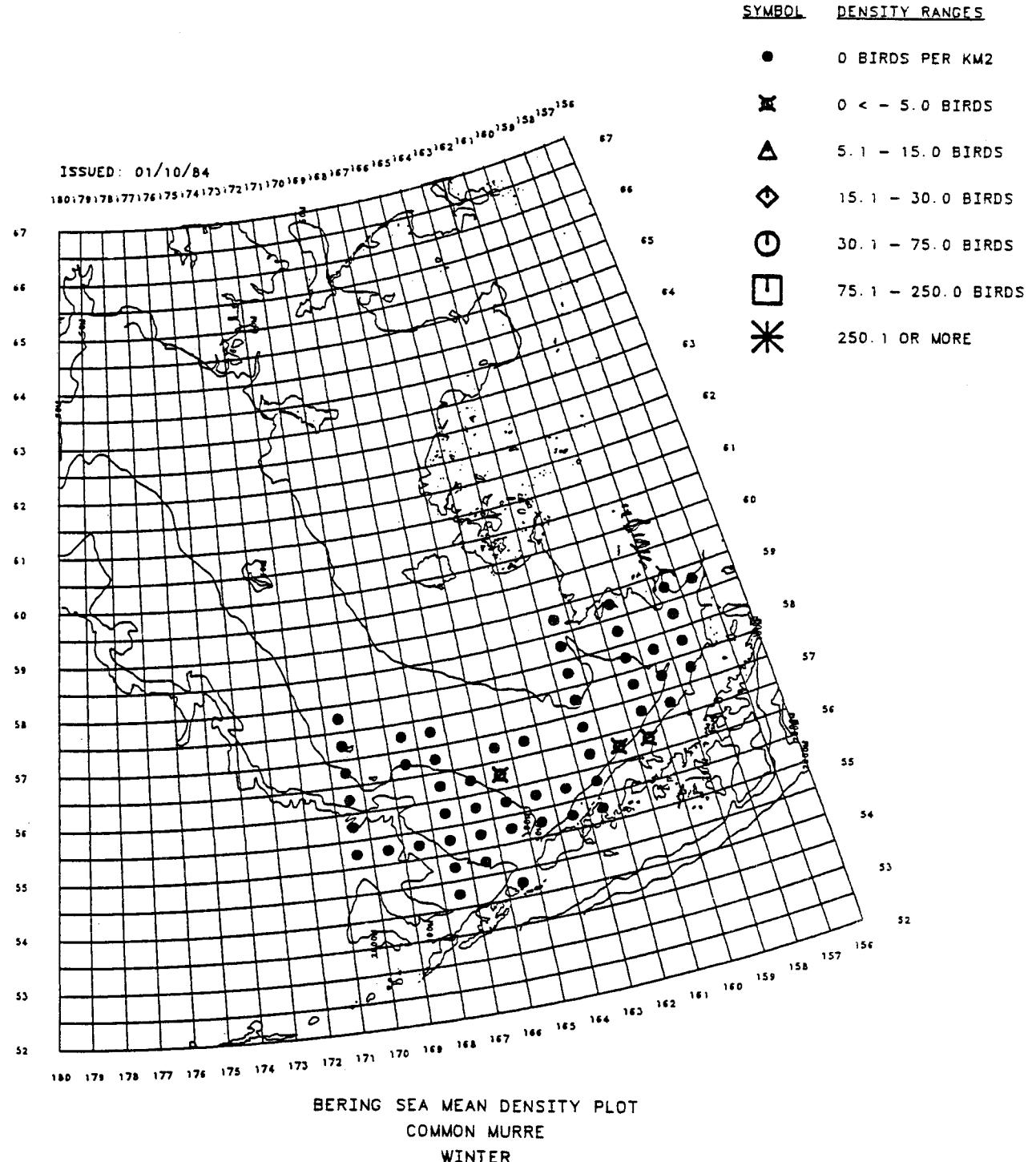


Figure 61. Mean densities, Common Murres: Winter.

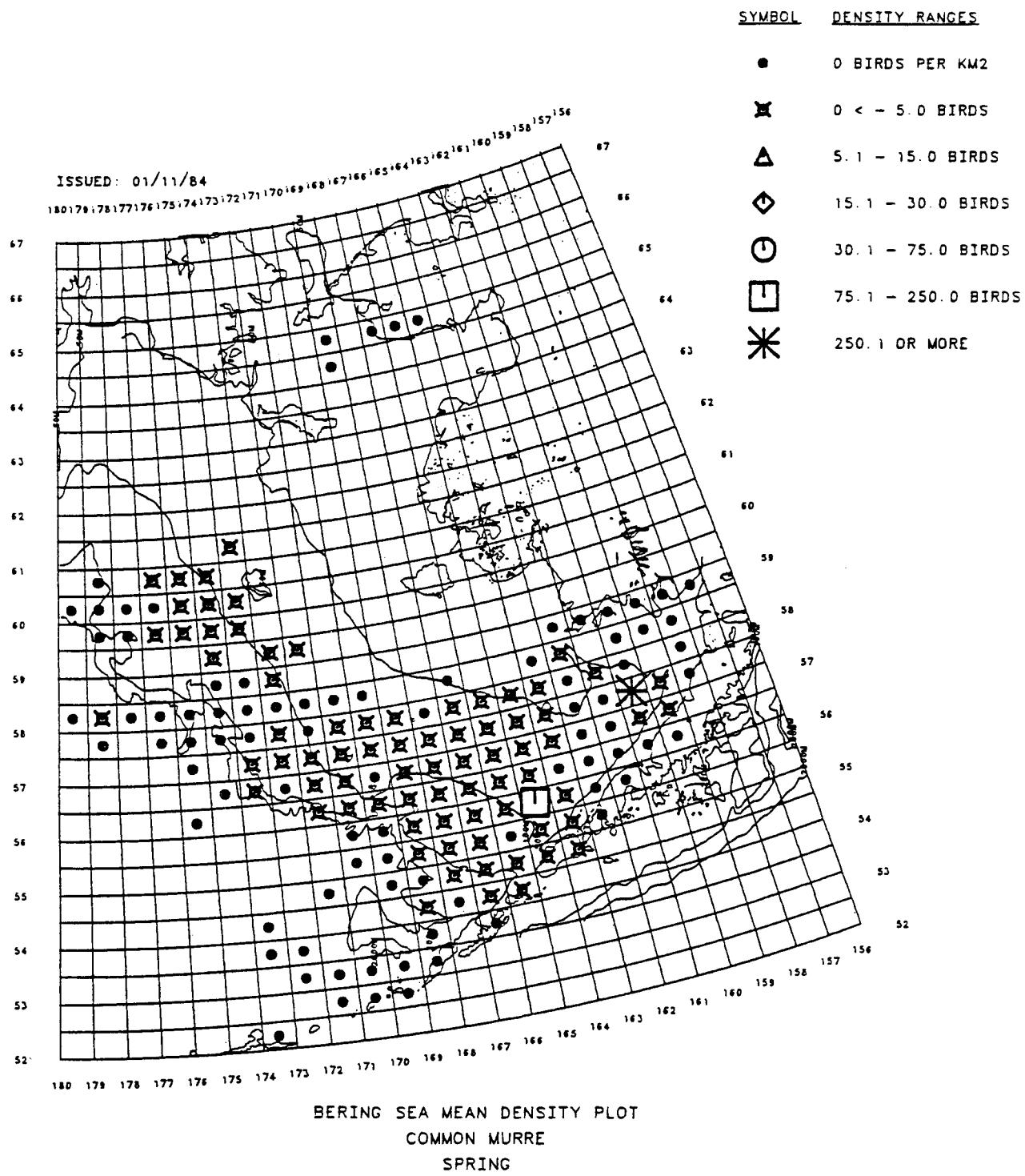


Figure 62. Mean densities, Common Murres: Spring.

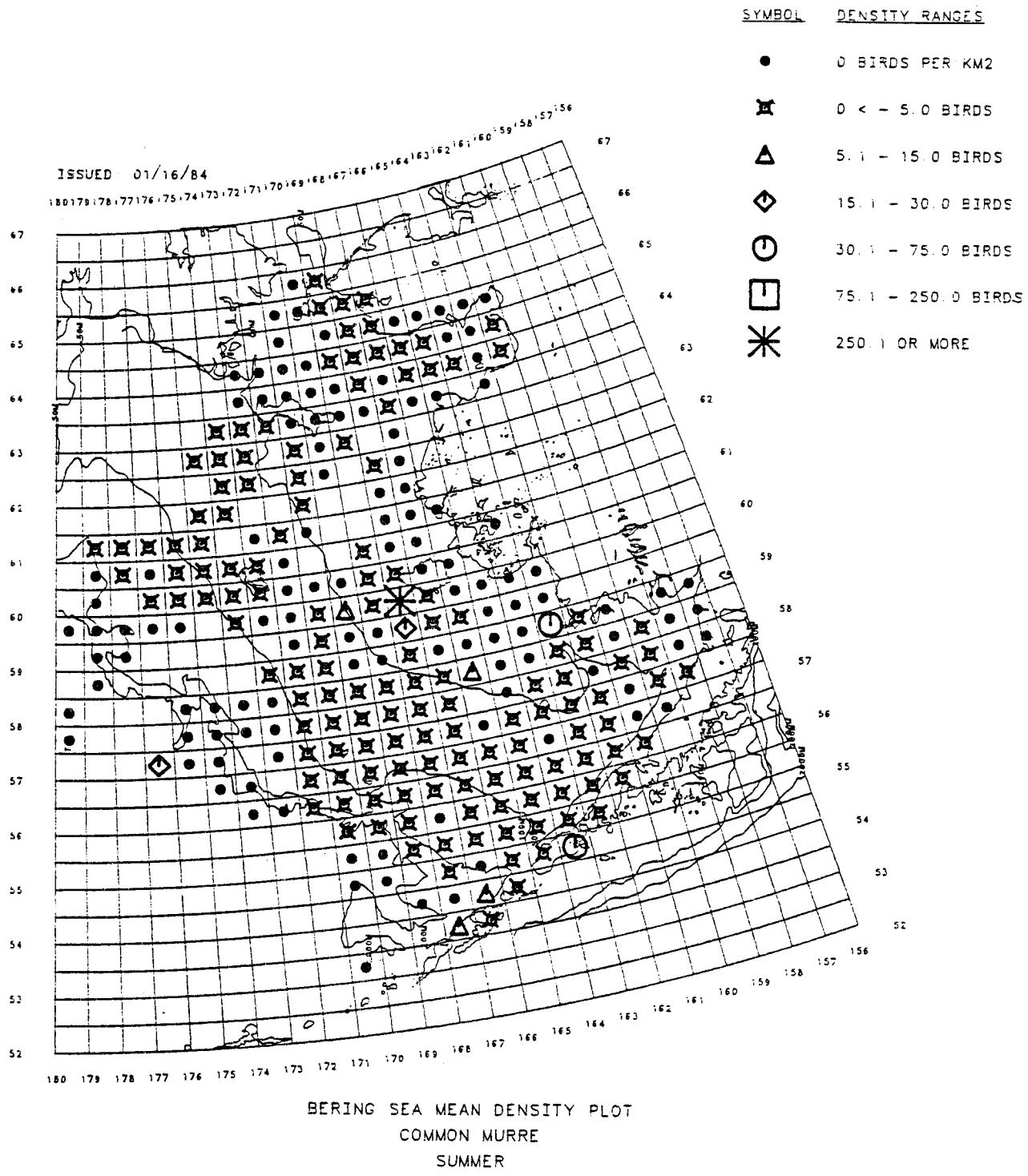


Figure 63. Mean densities, Common Murres: Summer.

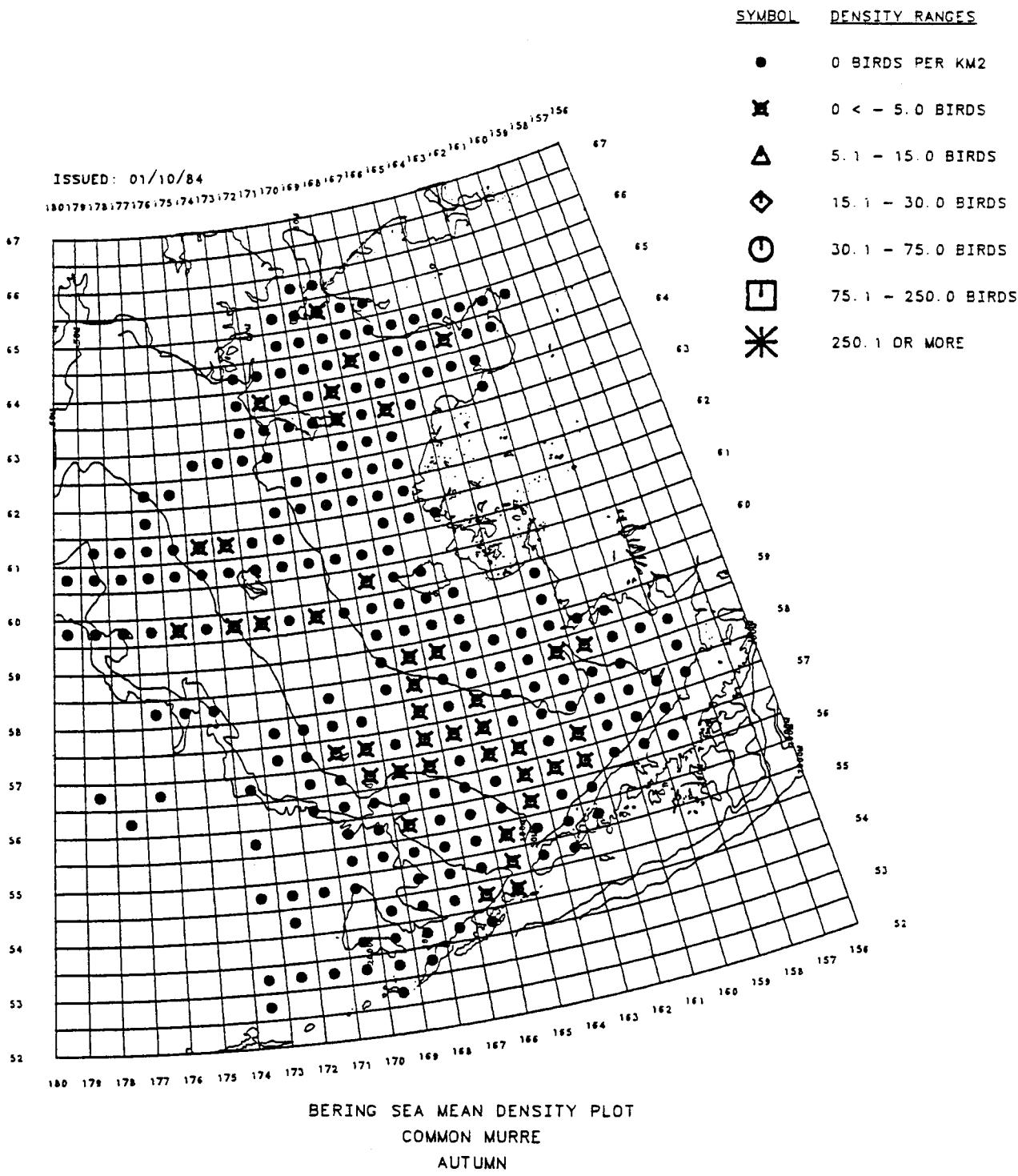


Figure 64. Mean densities, Common Murres: Autumn.

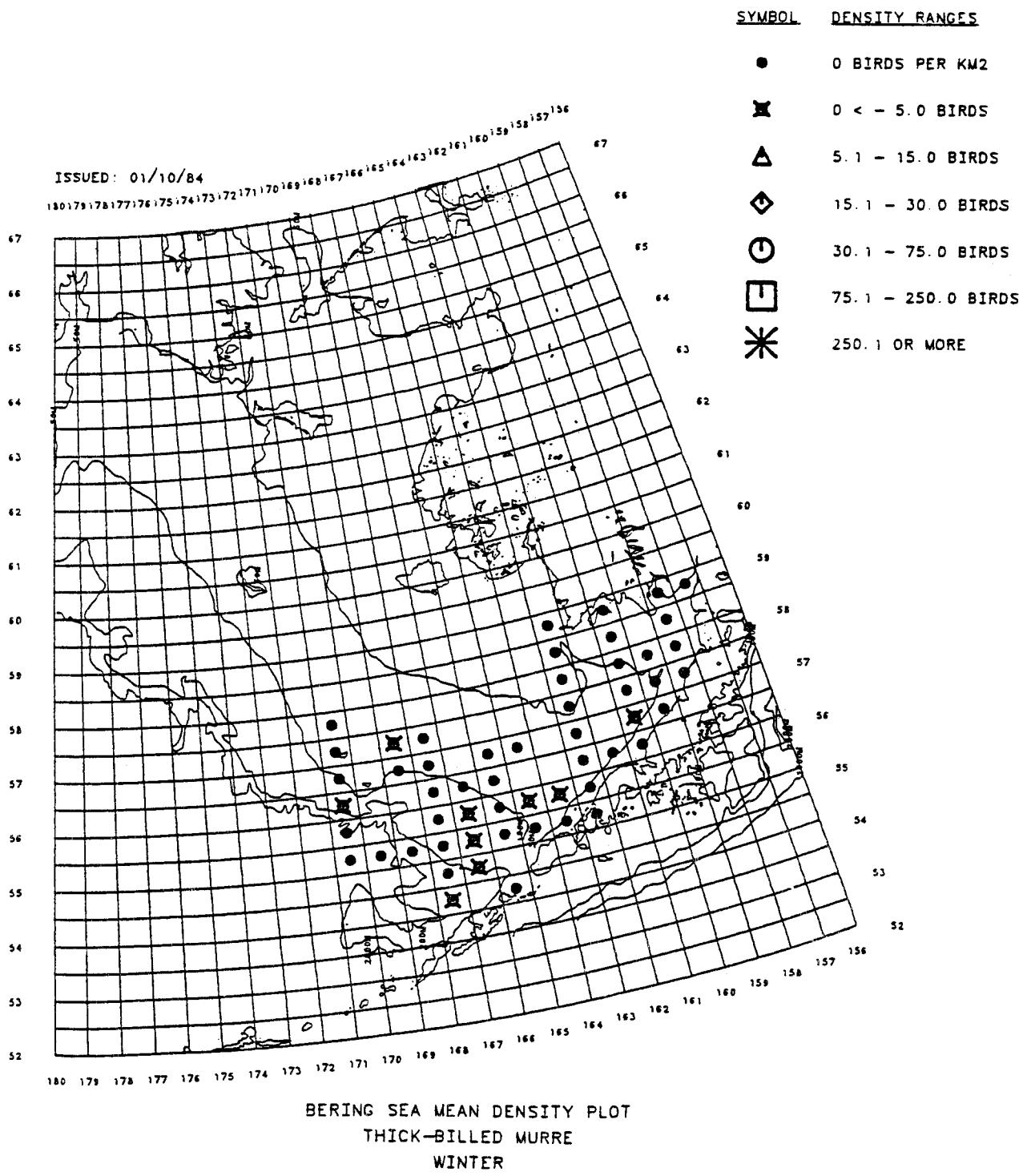


Figure 65. Mean densities, Thick-billed Murres: Winter.

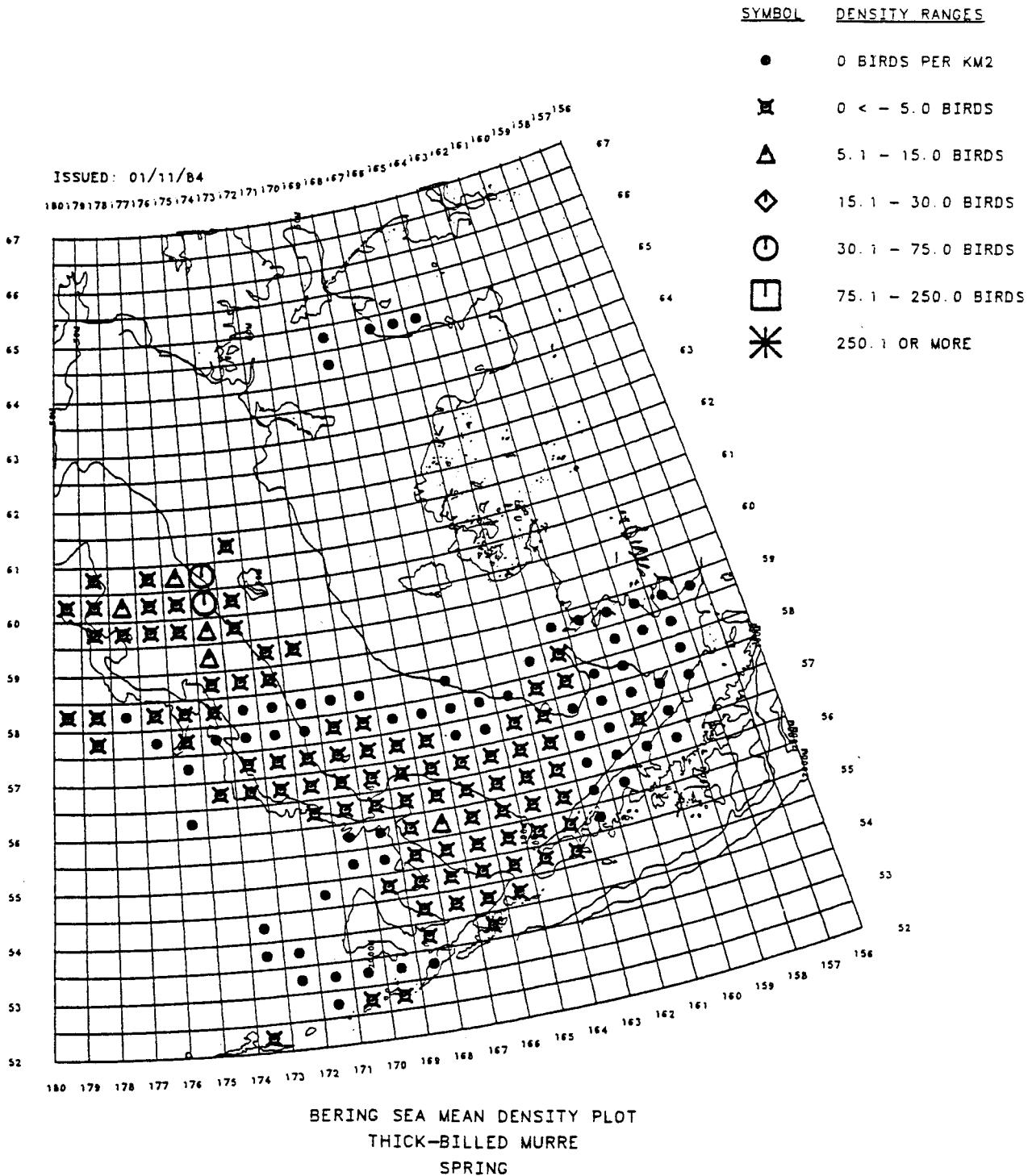


Figure 66. Mean densities, Thick-billed Murres: Spring.

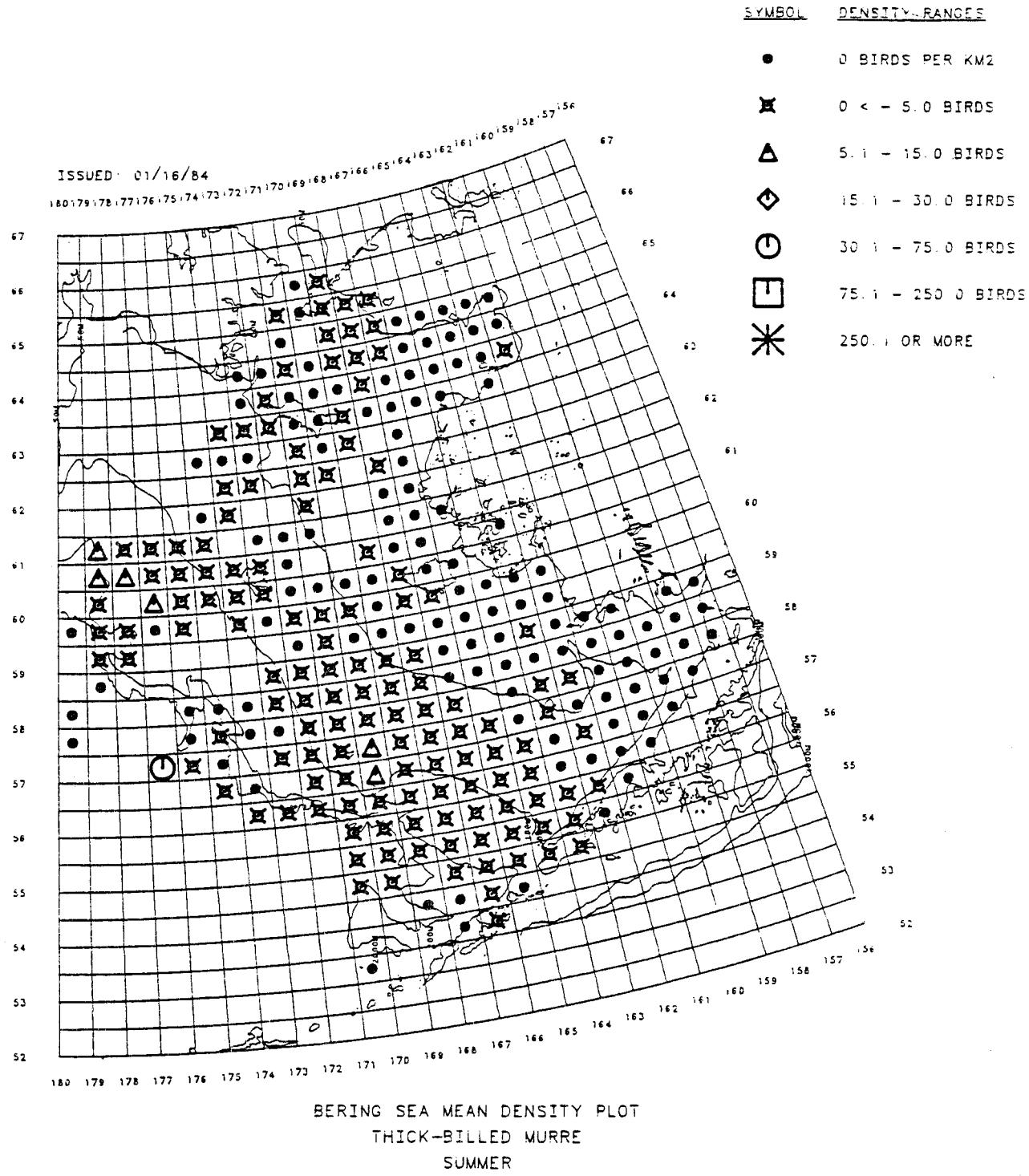


Figure 67. Mean densities, Thick-billed Murres: Summer.

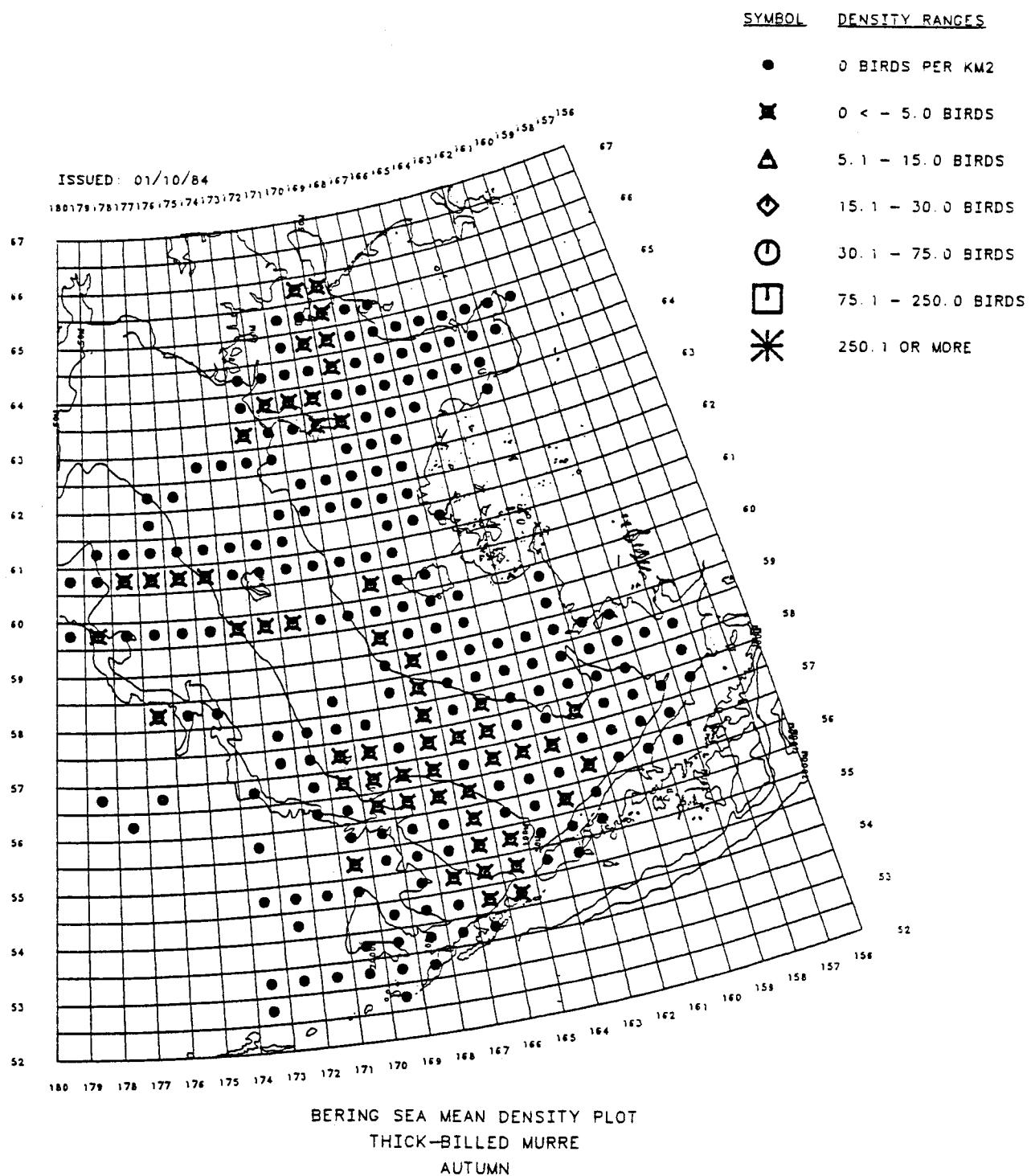


Figure 68. Mean densities, Thick-billed Murres: Autumn.

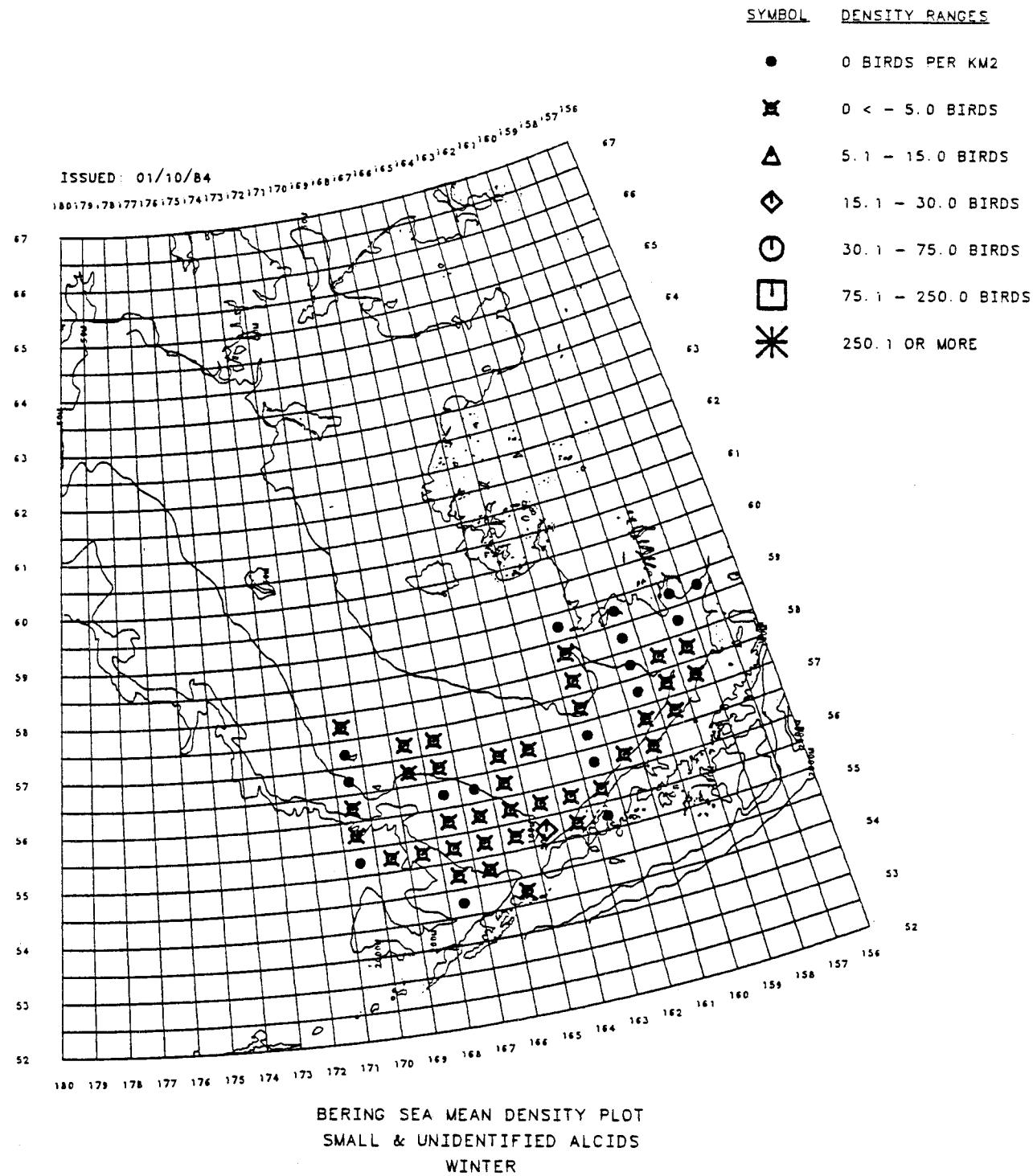
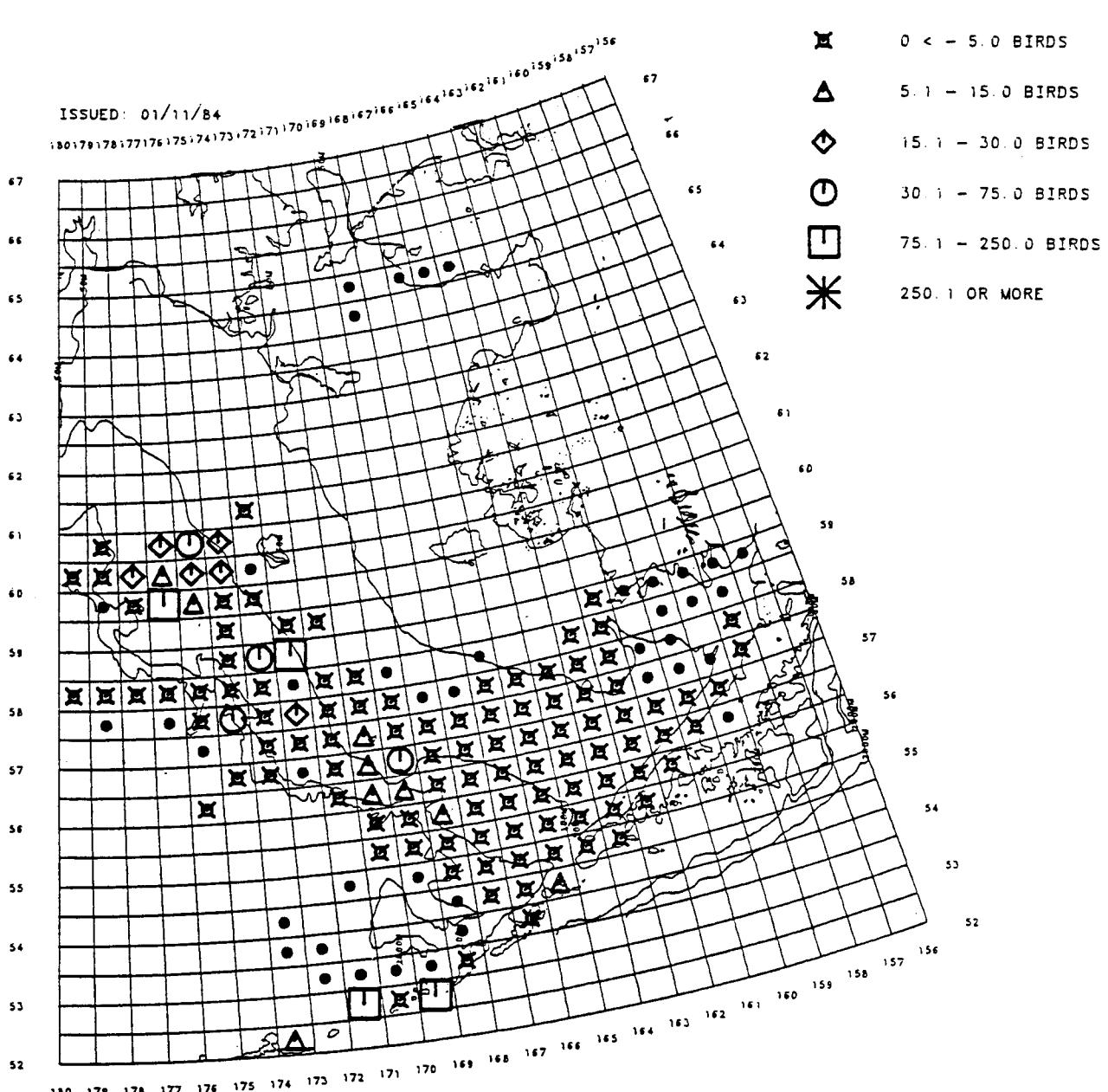


Figure 69. Mean densities, small alcids: Winter.



BERING SEA MEAN DENSITY PLOT
 SMALL & UNIDENTIFIED ALCIDS
 SPRING

Figure 70. Mean densities, small alcids: Spring.

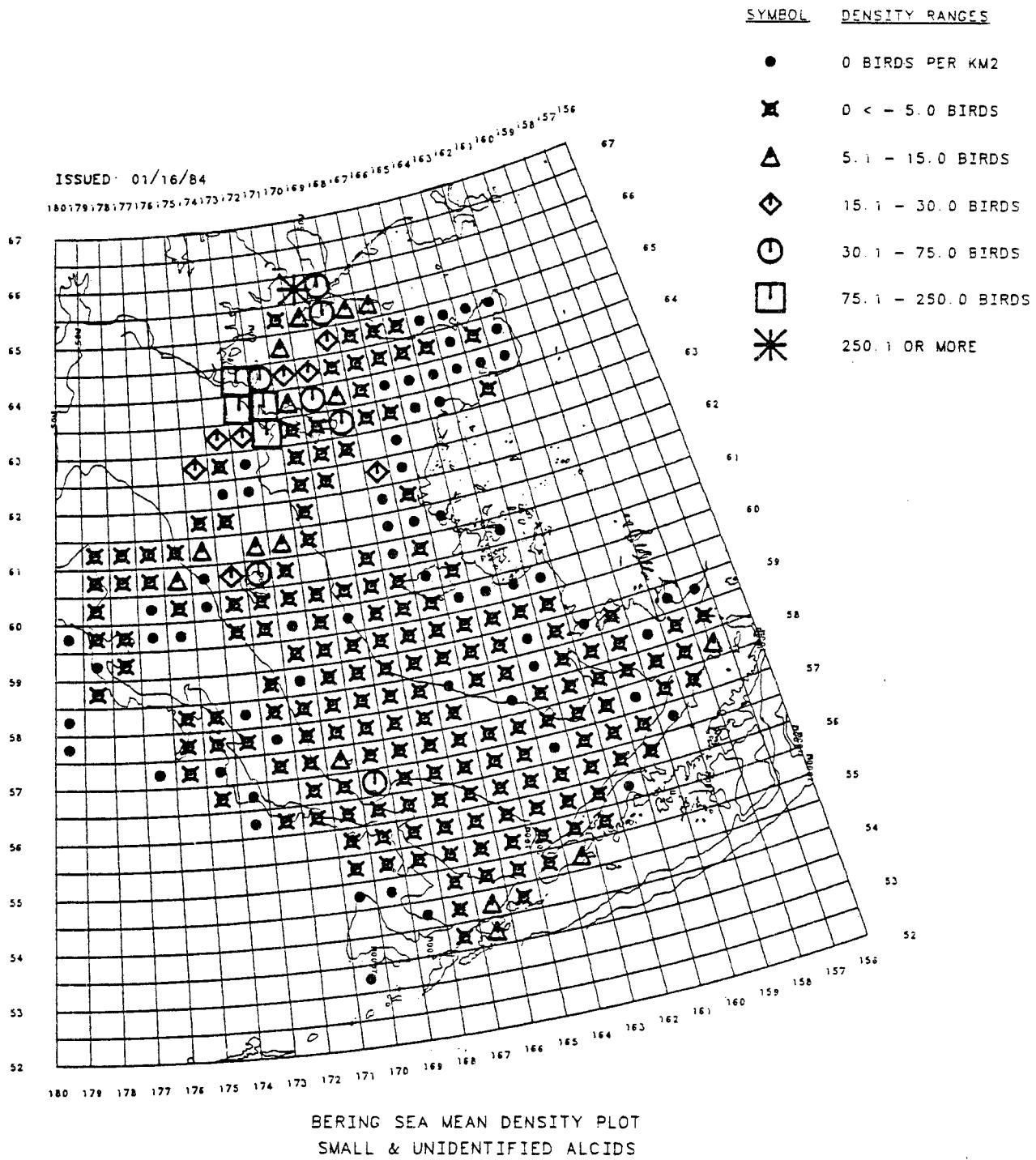


Figure 71. Mean densities, small alcids: Summer.

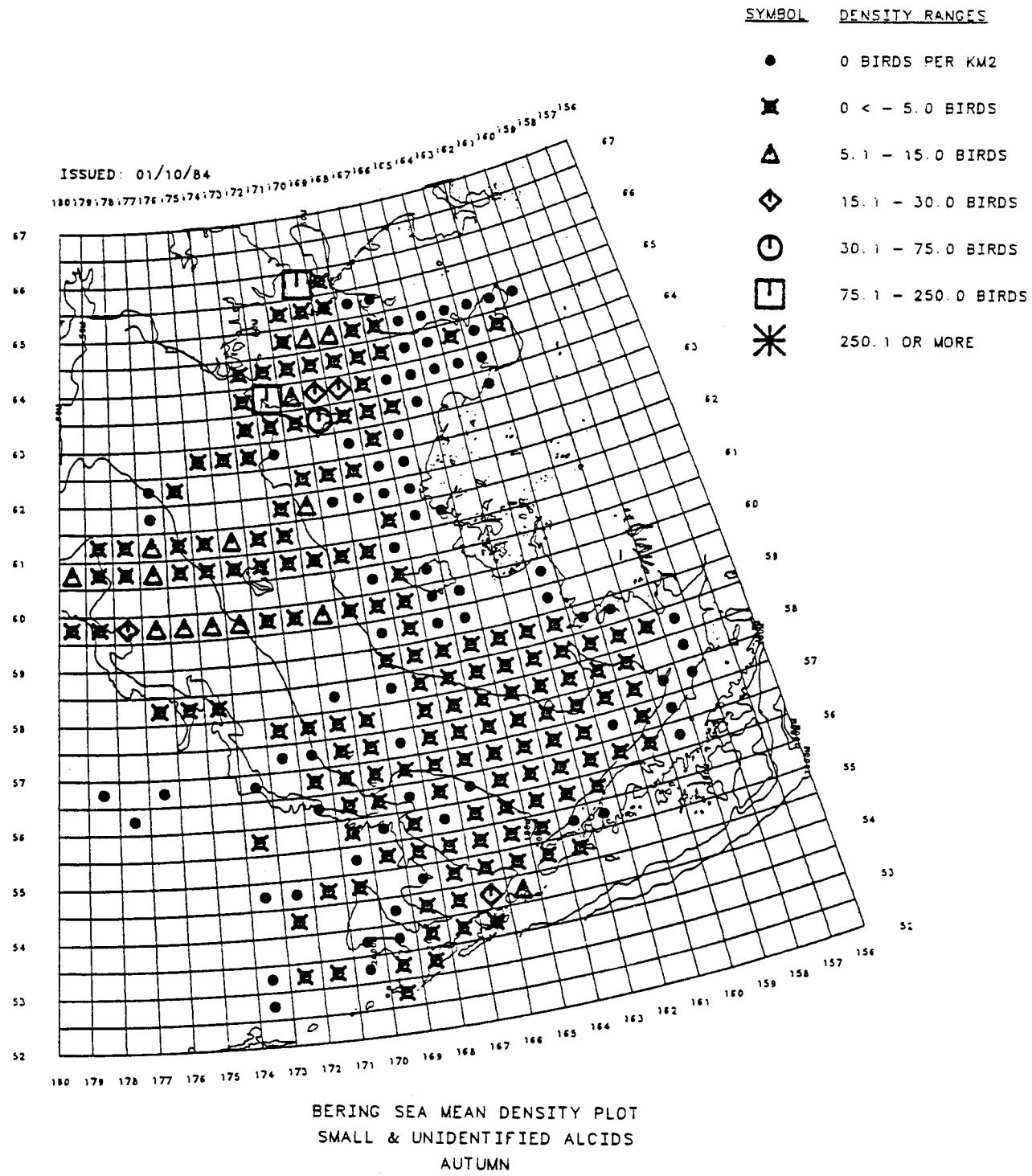


Figure 72. Mean densities, small alcids: Autumn.

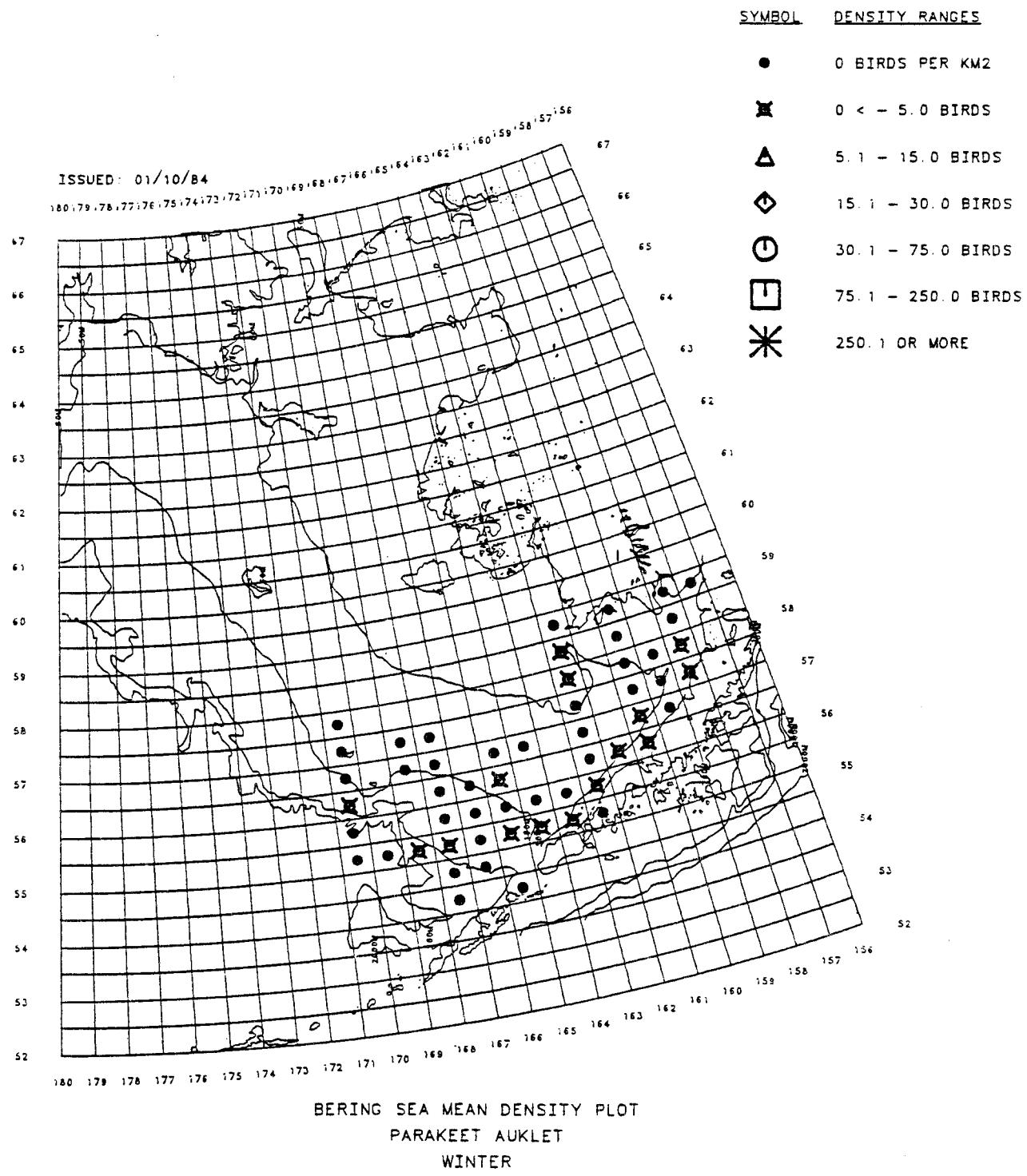


Figure 73. Mean densities, Parakeet Auklets: Winter.

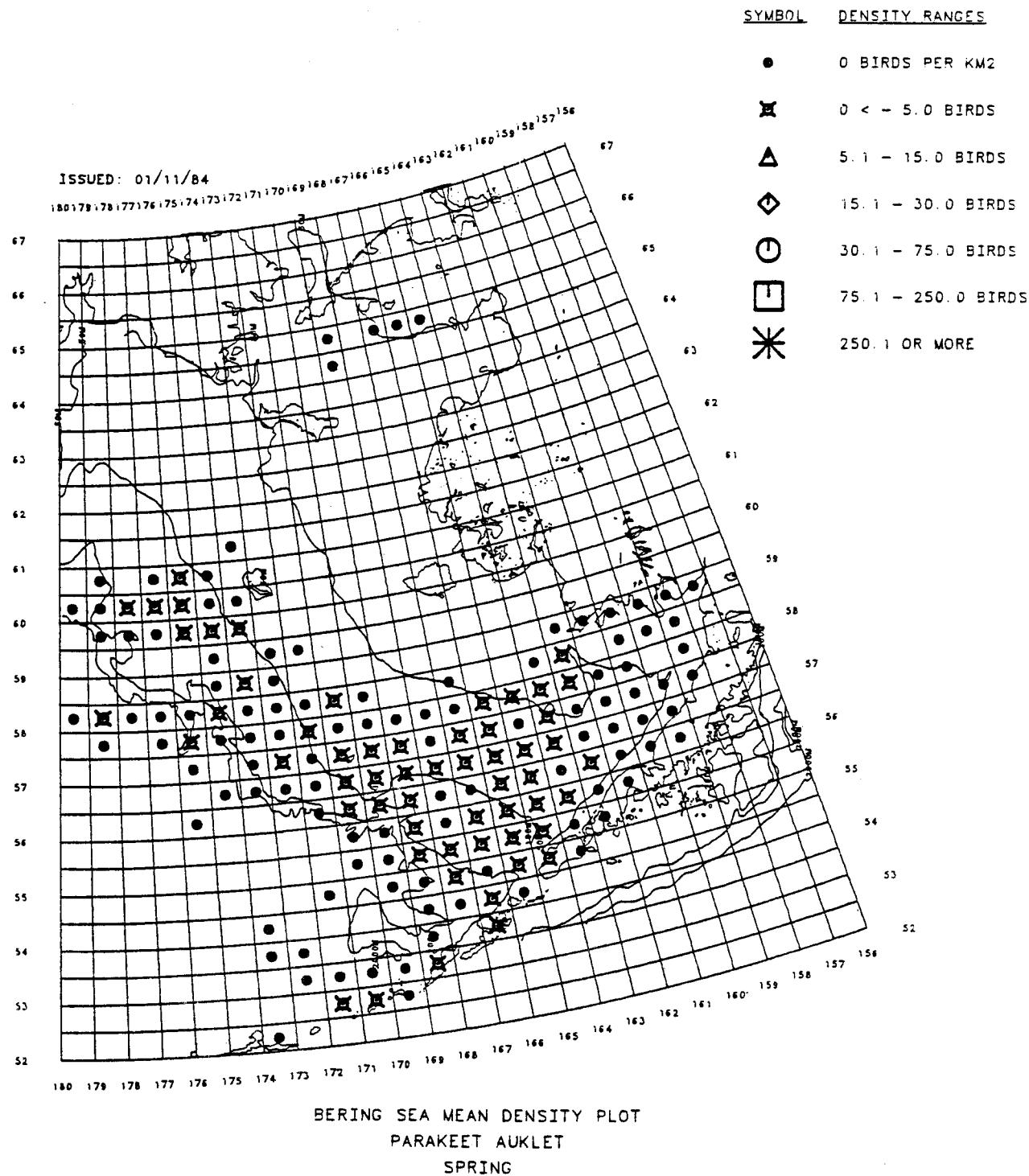


Figure 74. Mean densities, Parakeet Auklets: Spring.

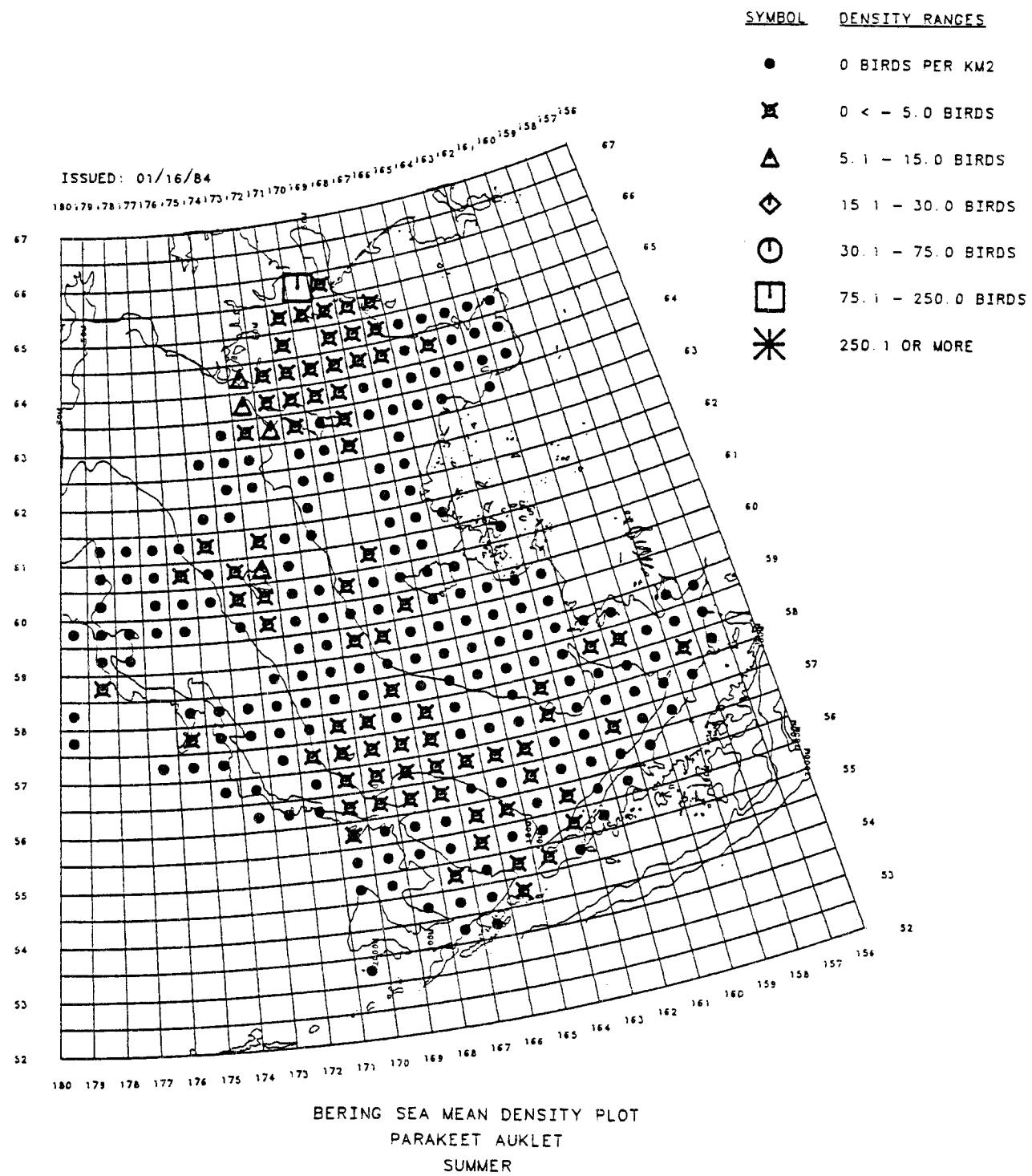


Figure 75. Mean densities, Parakeet Auklets: Summer.

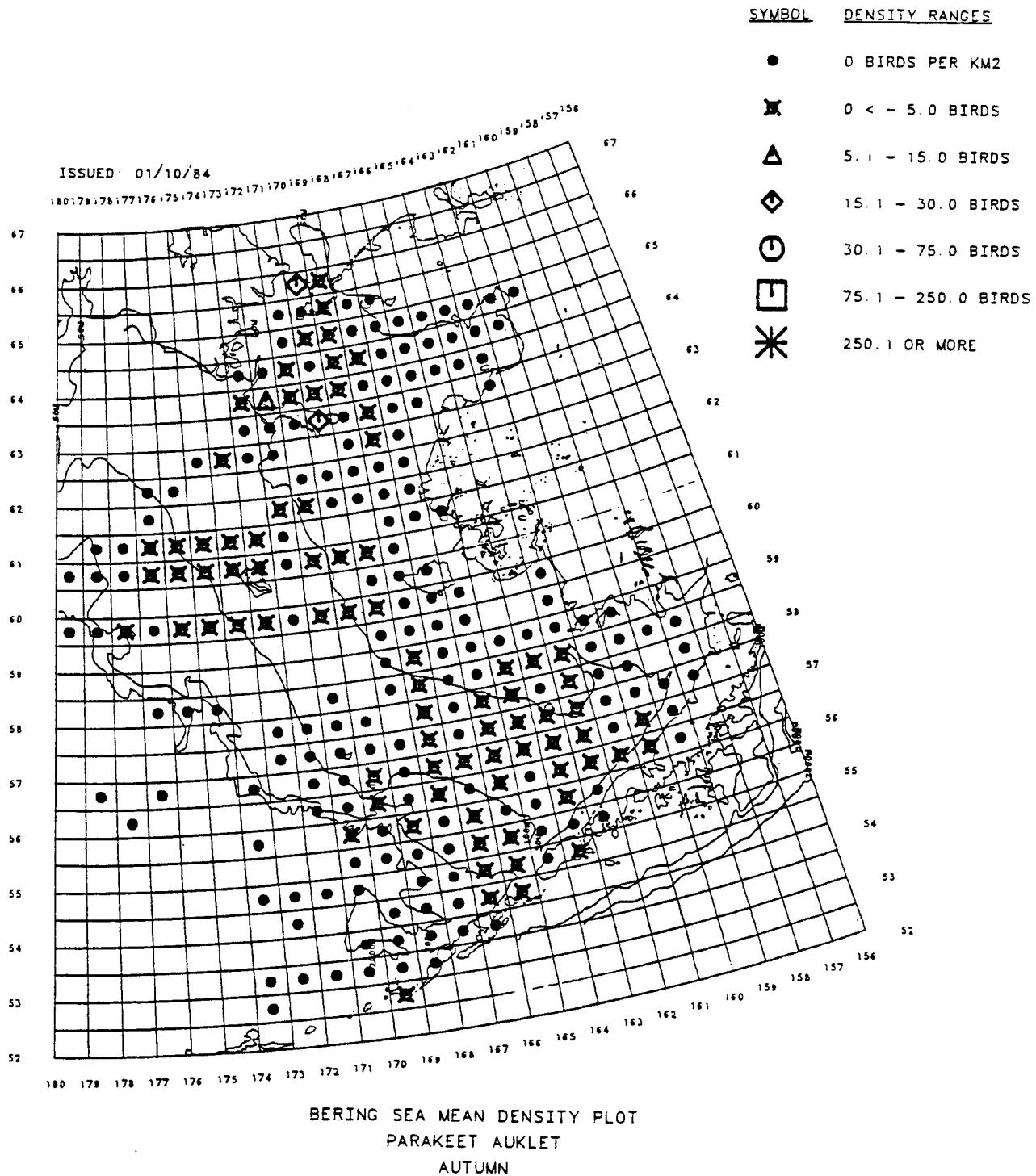
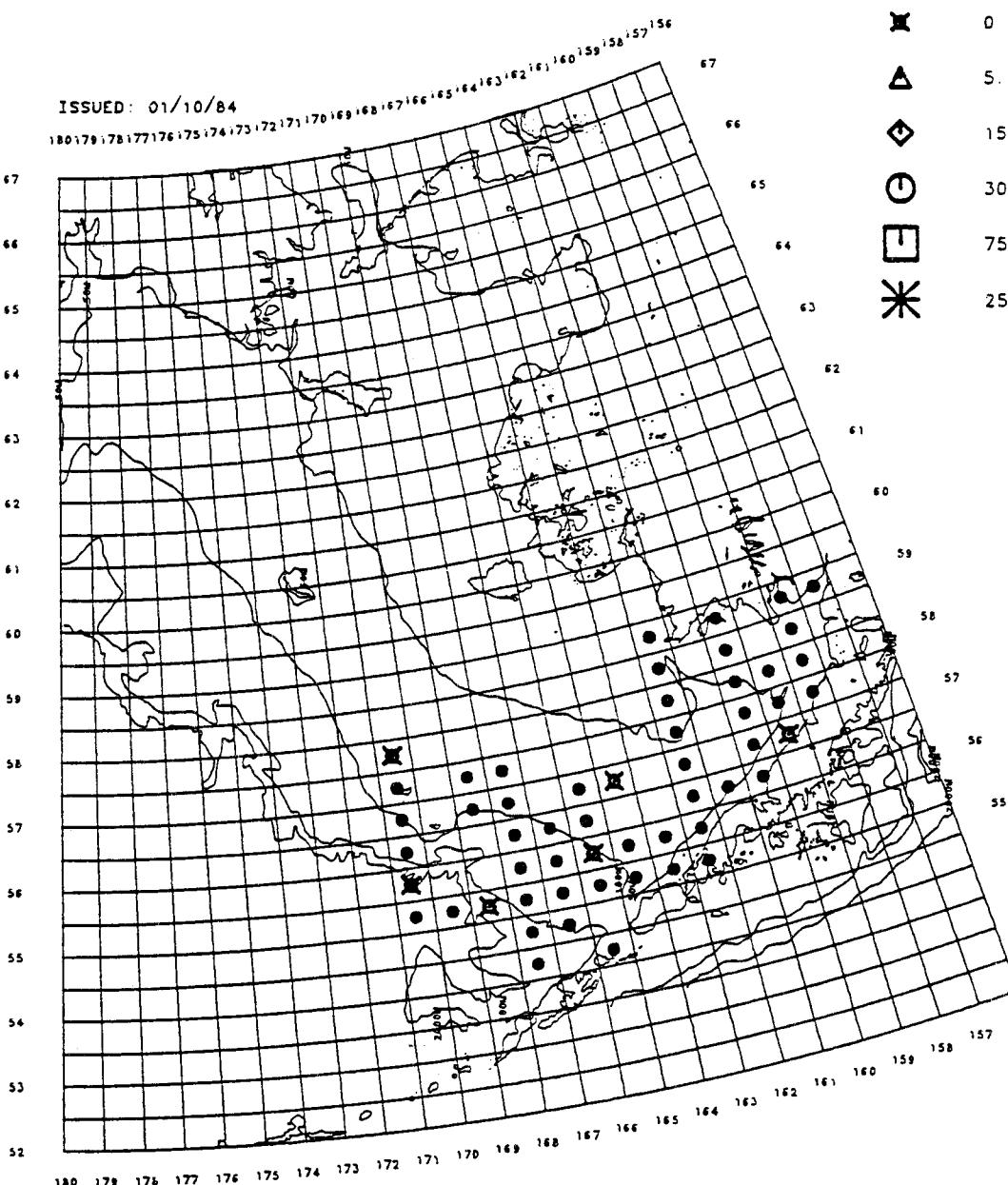


Figure 76. Mean densities, Parakeet Auklets: Autumn.



<u>SYMBOL</u>	<u>DENSITY RANGES</u>
●	0 BIRDS PER KM ²
✖	0 < - 5.0 BIRDS
△	5.1 - 15.0 BIRDS
◊	15.1 - 30.0 BIRDS
○	30.1 - 75.0 BIRDS
■	75.1 - 250.0 BIRDS
*	250.1 OR MORE

BERING SEA MEAN DENSITY PLOT
 LEAST AUKLET
 WINTER

Figure 77. Mean densities, Least Auklets: Winter.

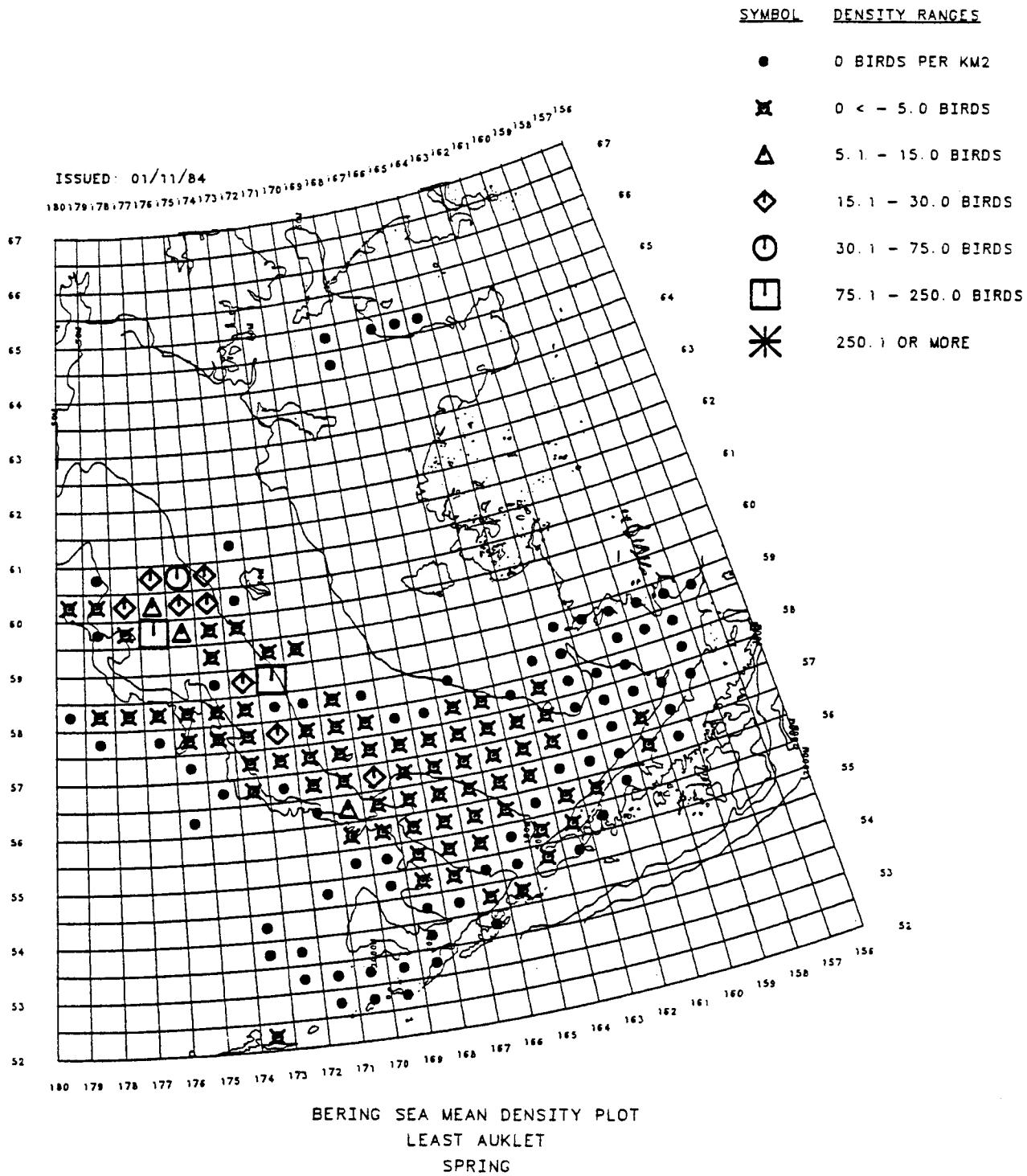


Figure 78. Mean densities, Least Auklets: Spring.

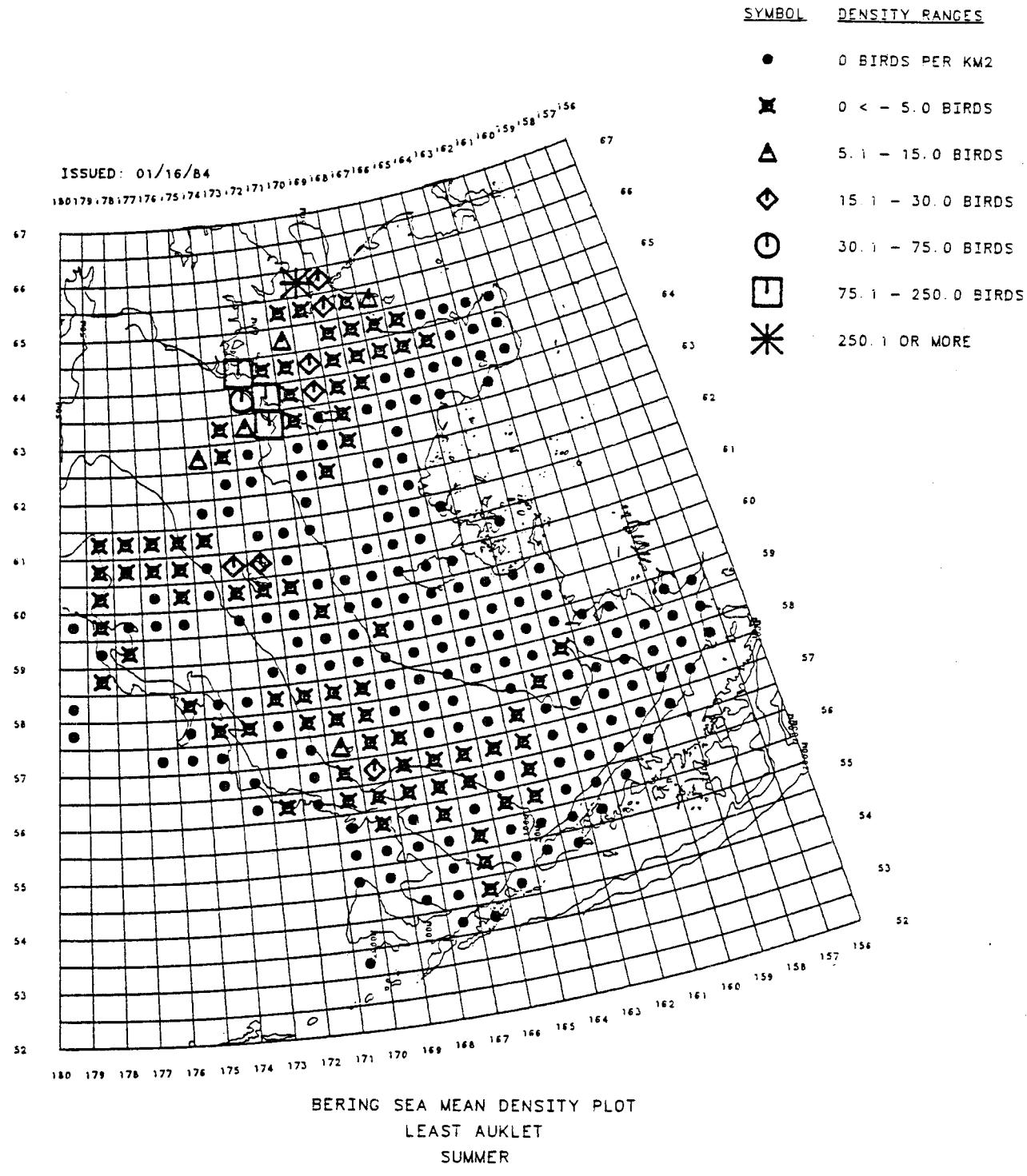


Figure 79. Mean densities, Least Auklets: Summer.

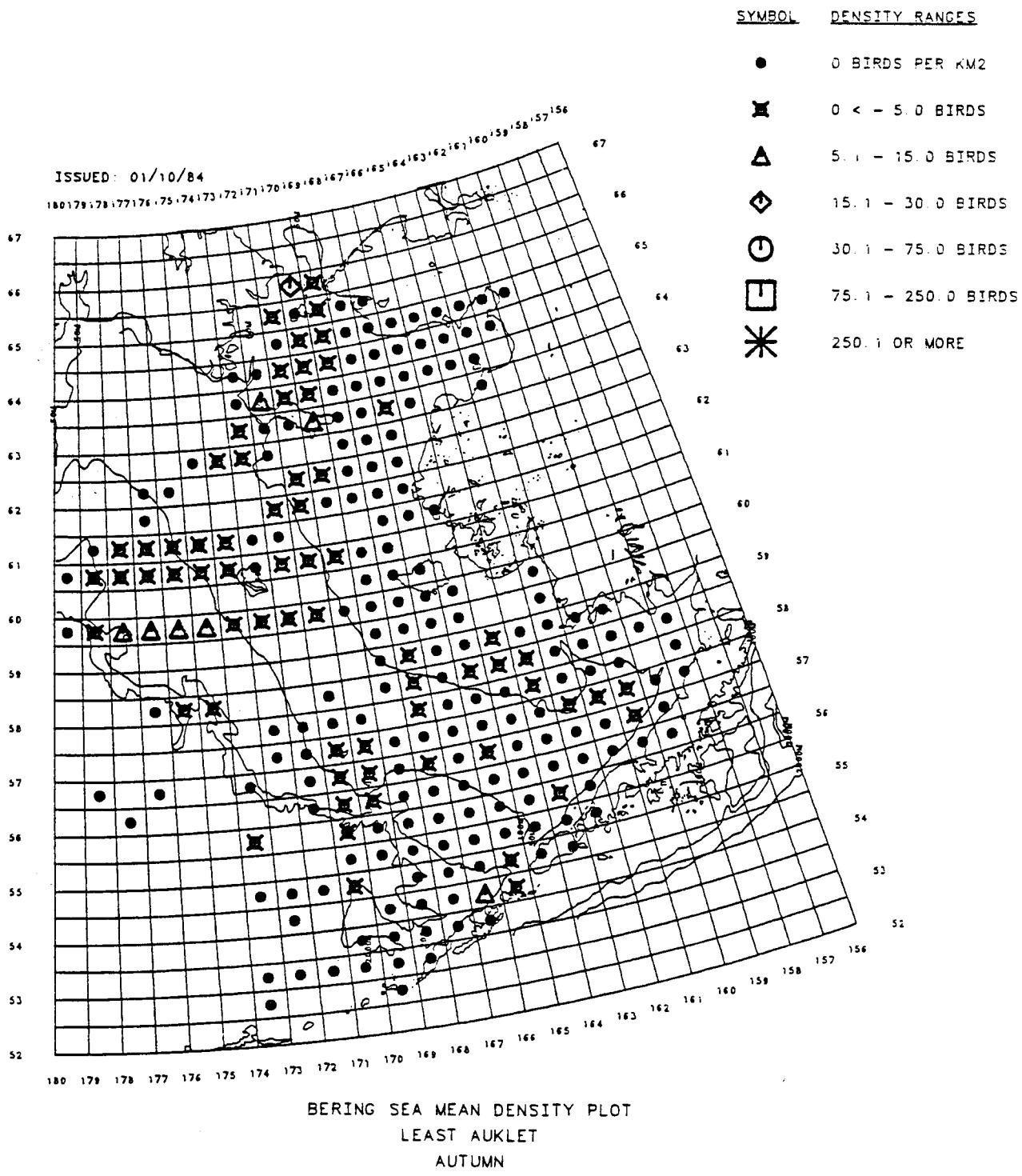


Figure 80. Mean densities, Least Auklets: Autumn.

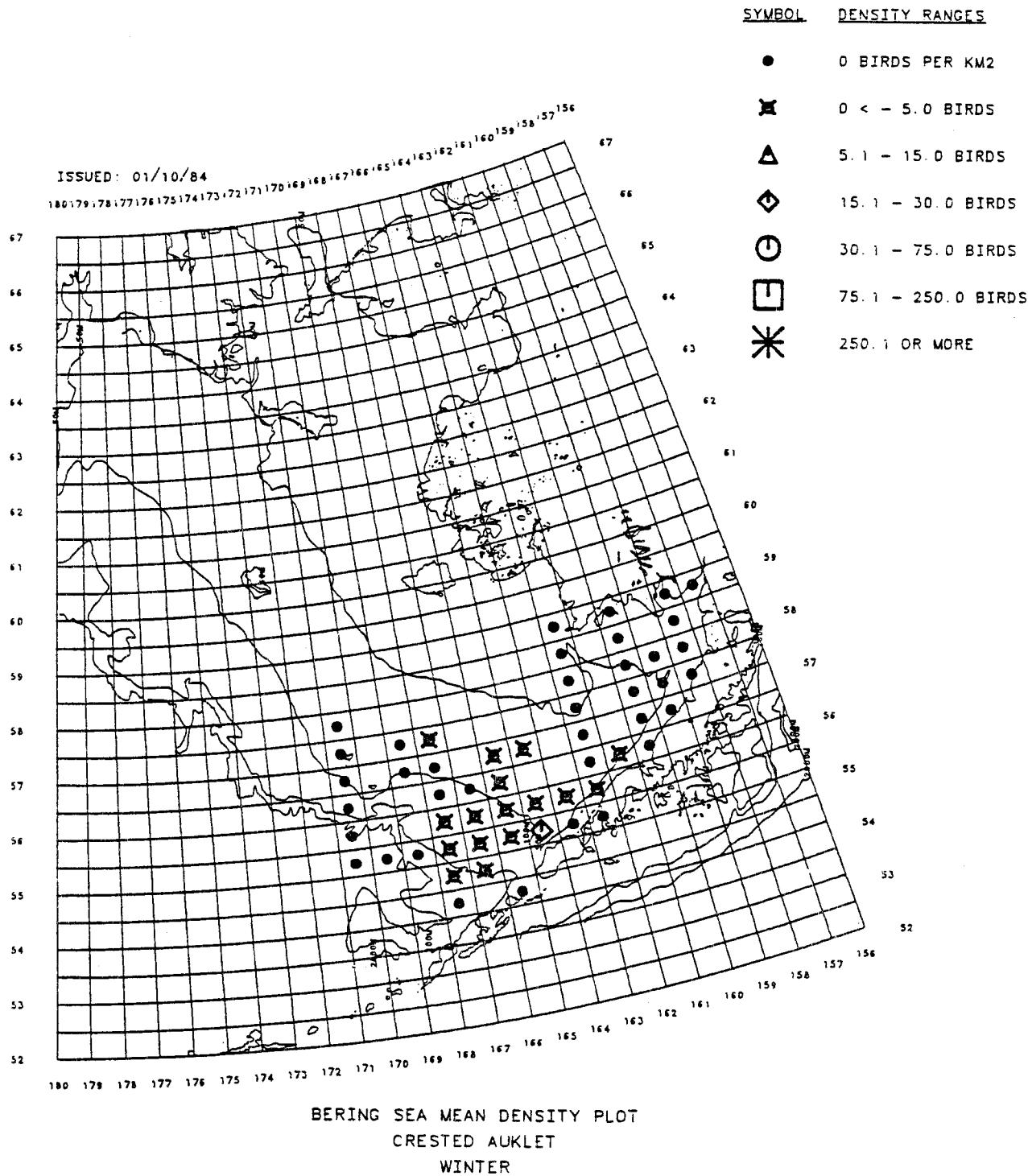


Figure 81. Mean densities, Crested Auklets: Winter.

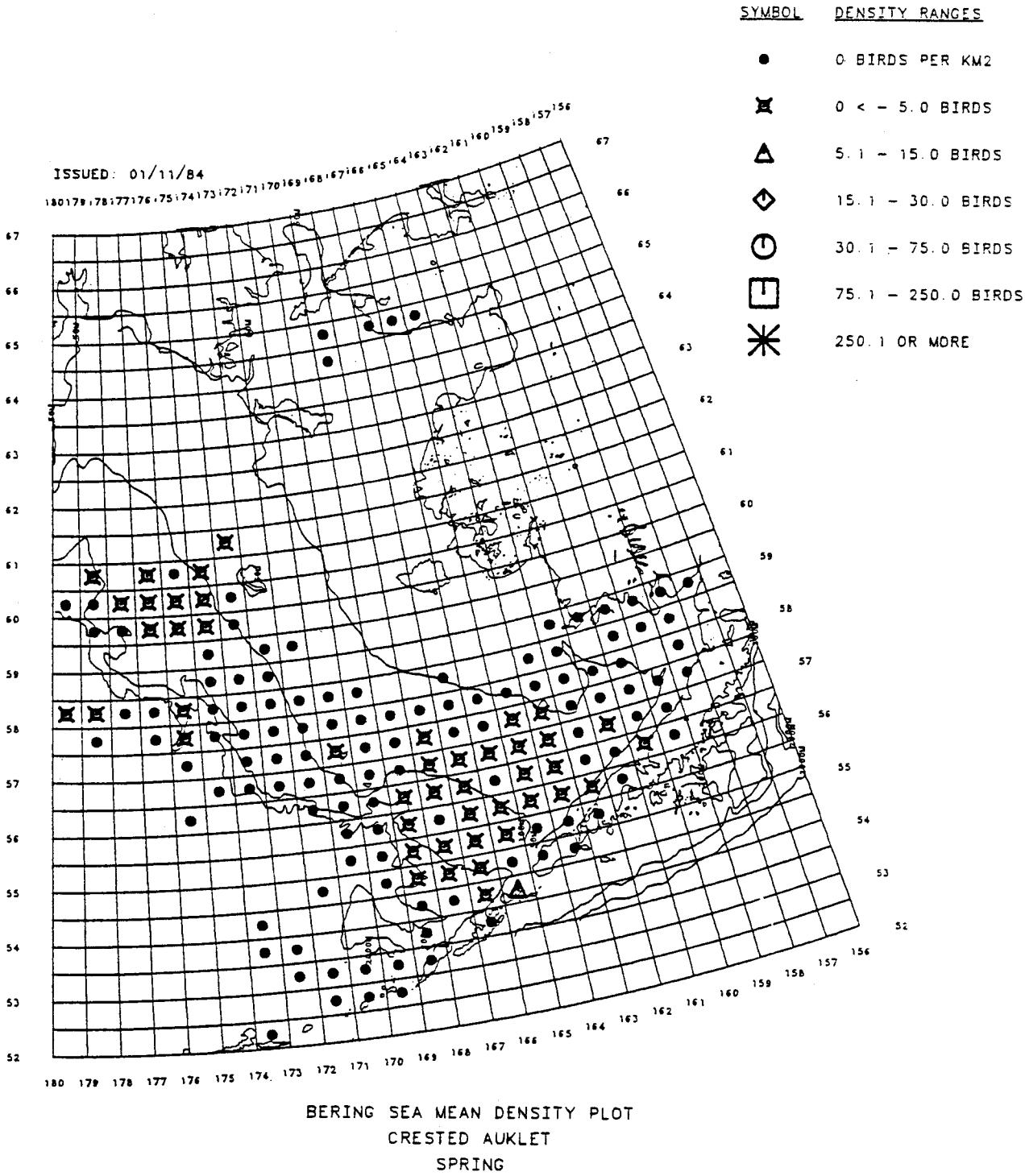


Figure 82. Mean densities, Crested Auklets: Spring.

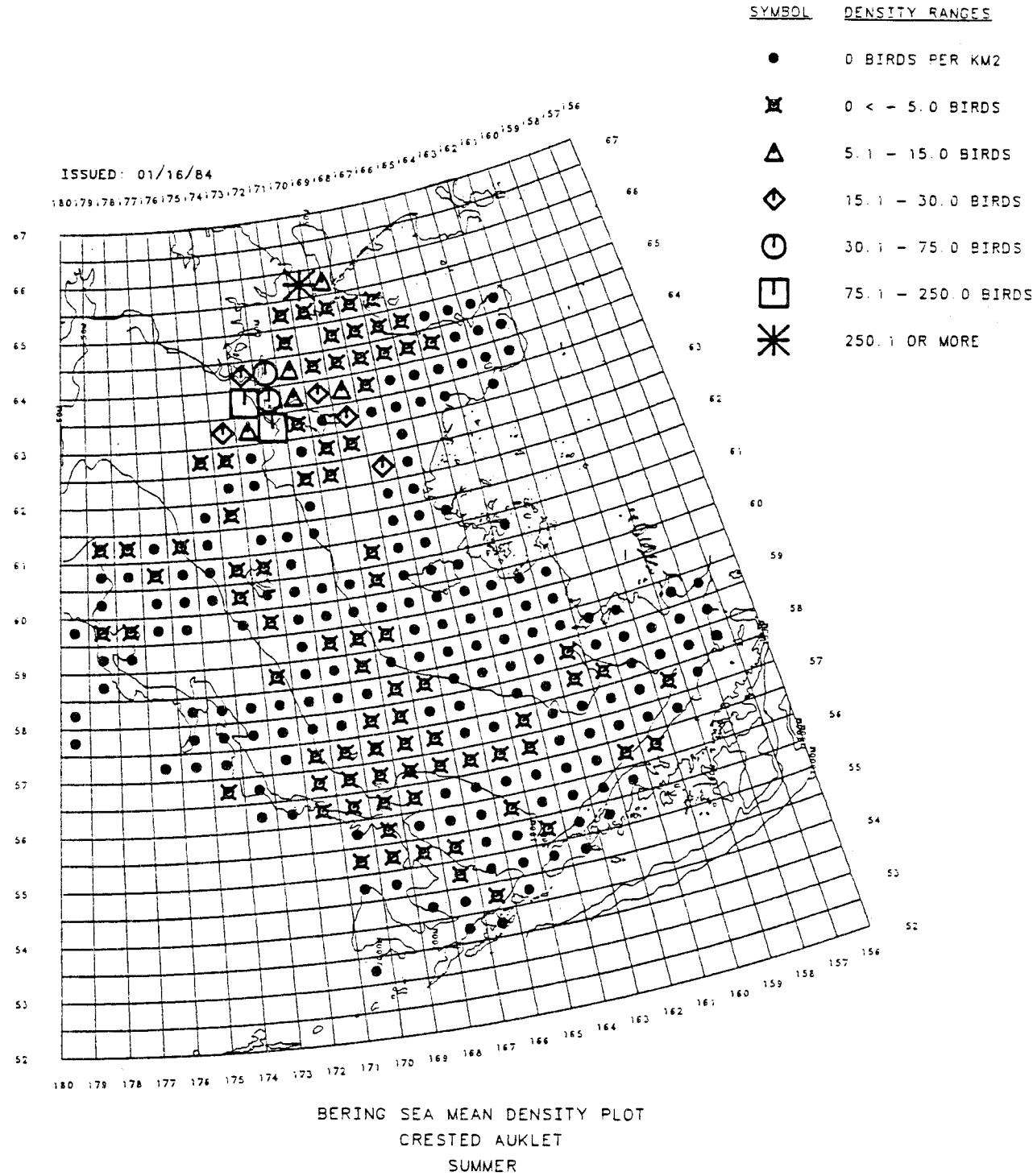


Figure 83. Mean densities, Crested Auks: Summer.

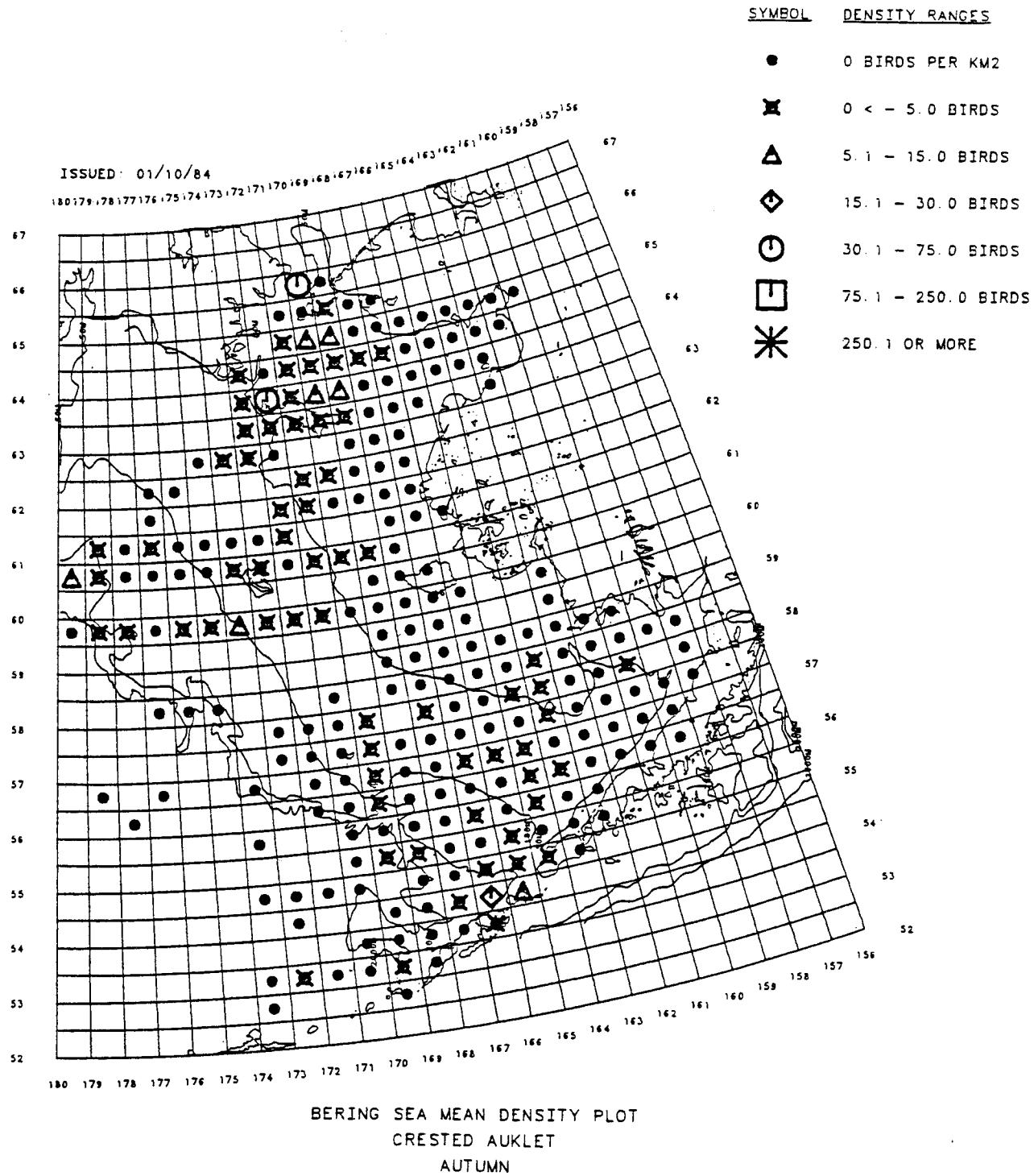


Figure 84. Mean densities, Crested Auklets: Autumn.

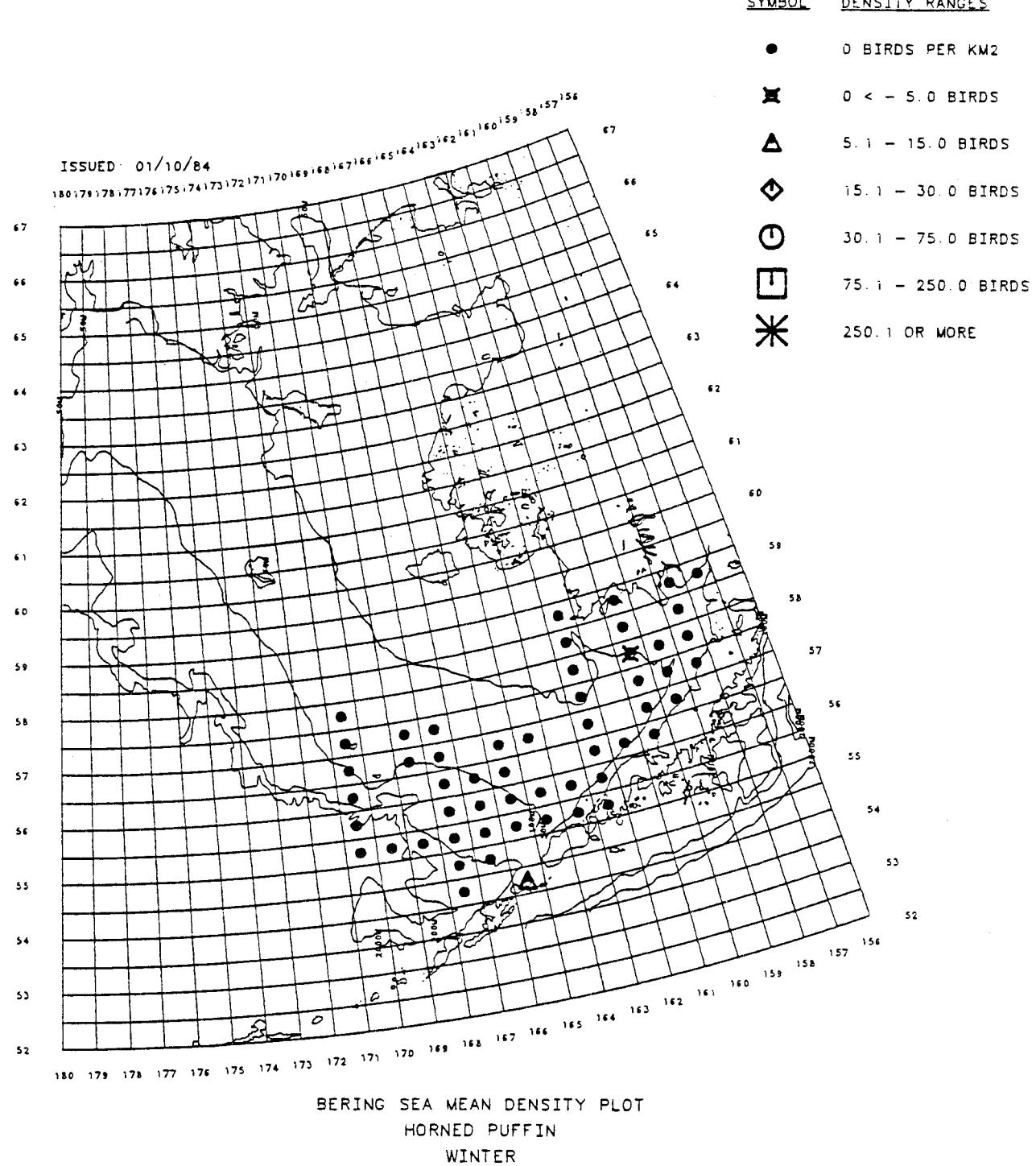


Figure 85. Mean densities, Horned Puffins: Winter.

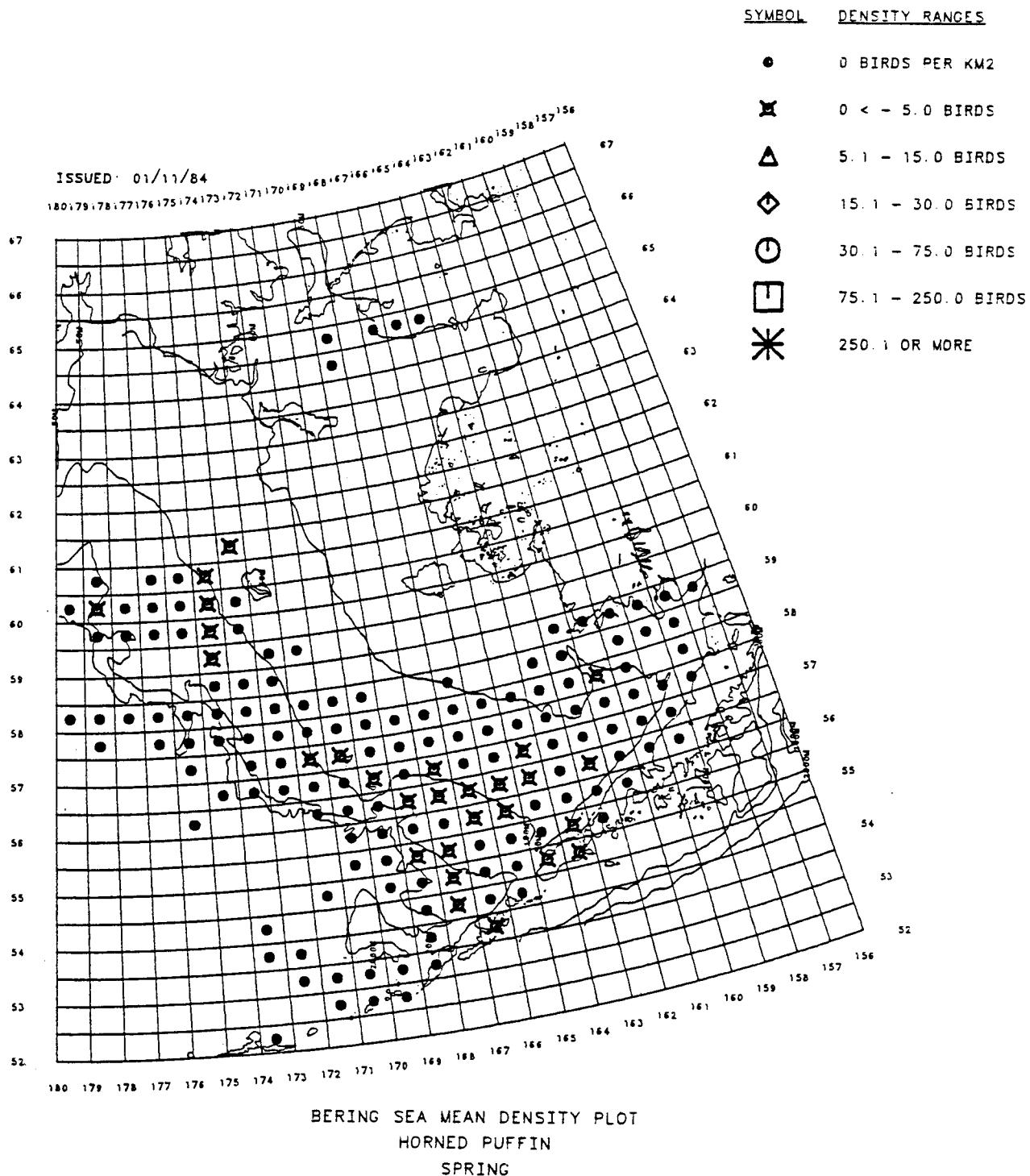


Figure 86. Mean densities, Horned Puffins: Spring.

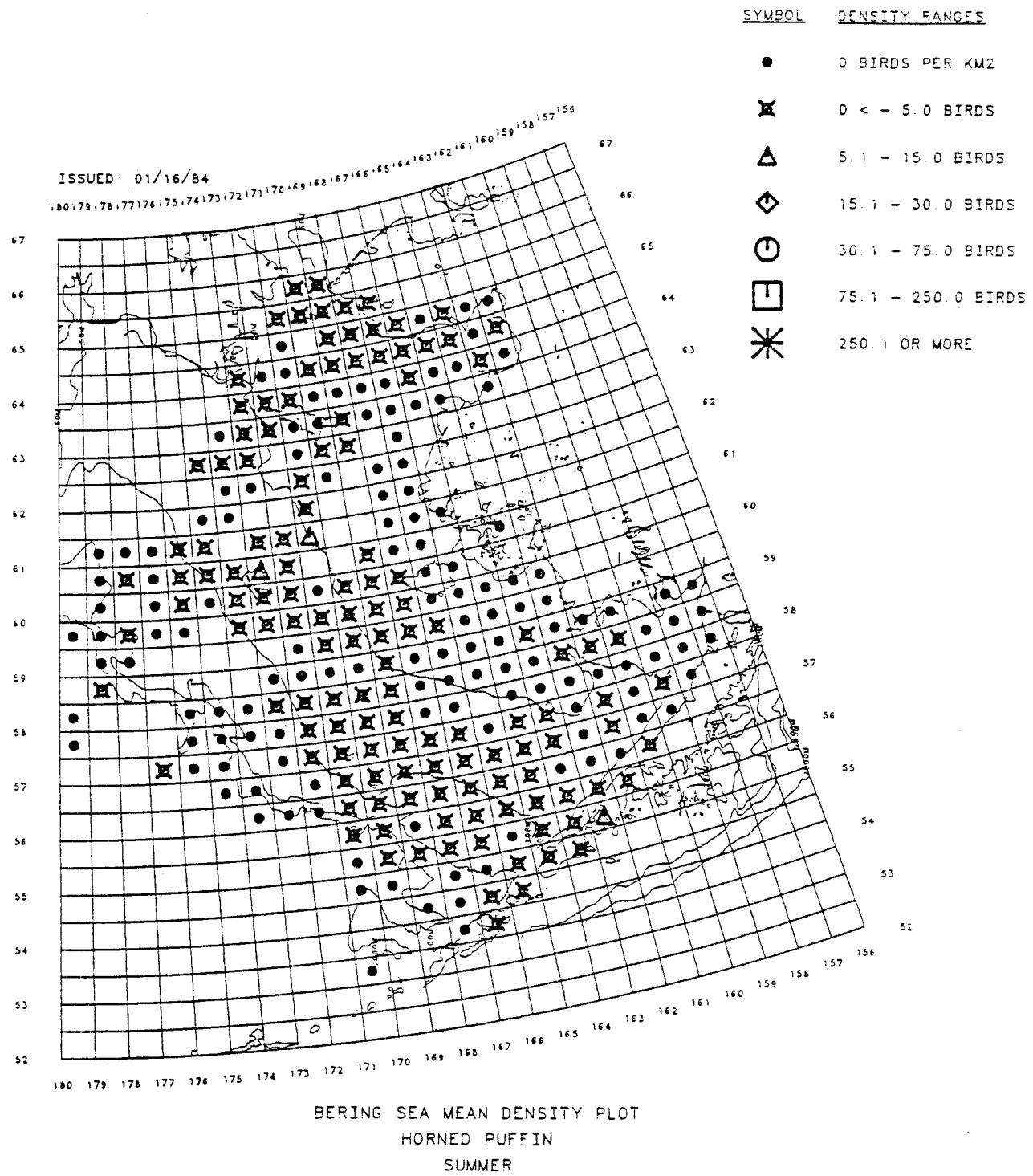


Figure 87. Mean densities, Horned Puffins: Summer.

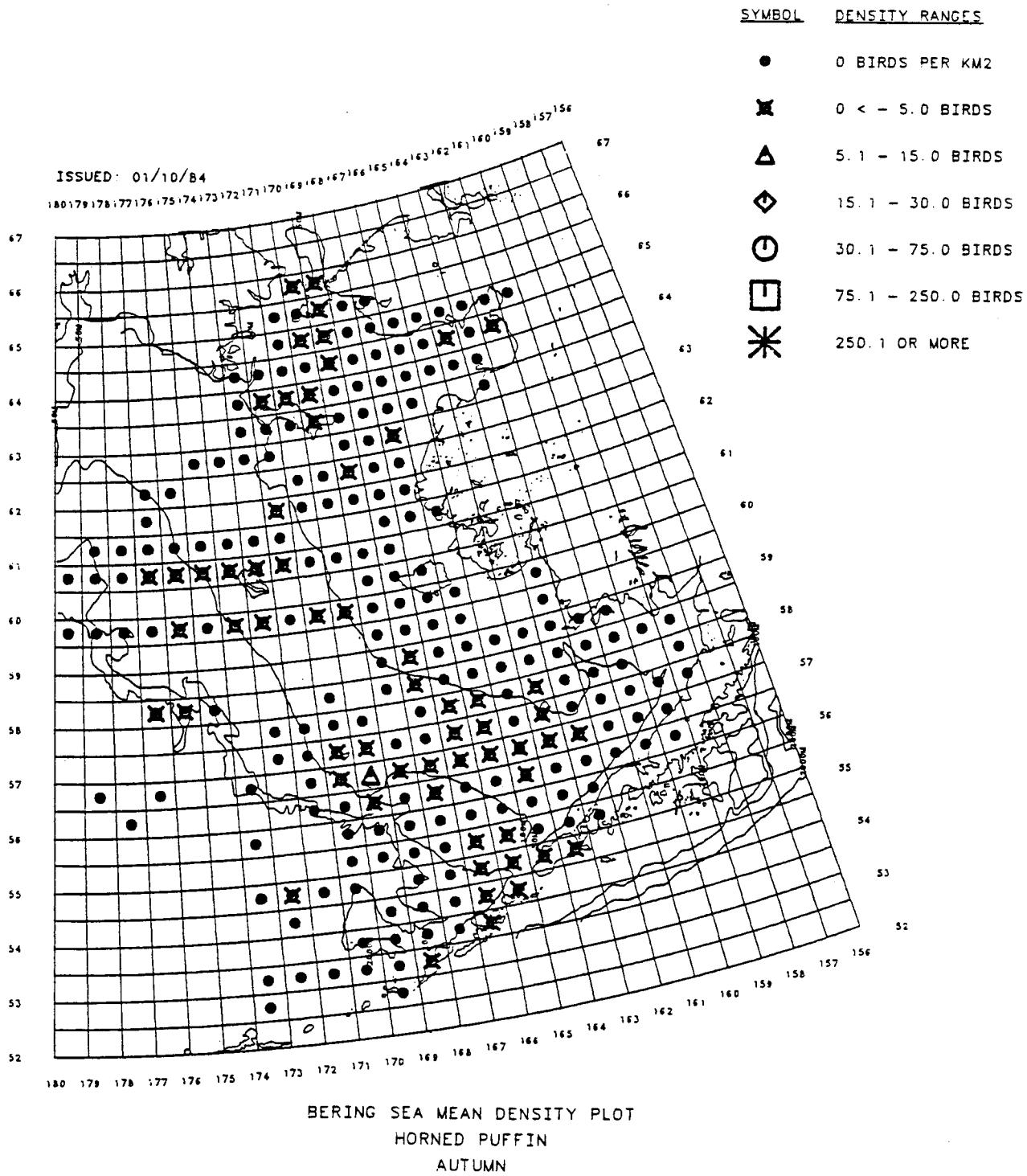


Figure 88. Mean densities, Horned Puffins: Autumn.

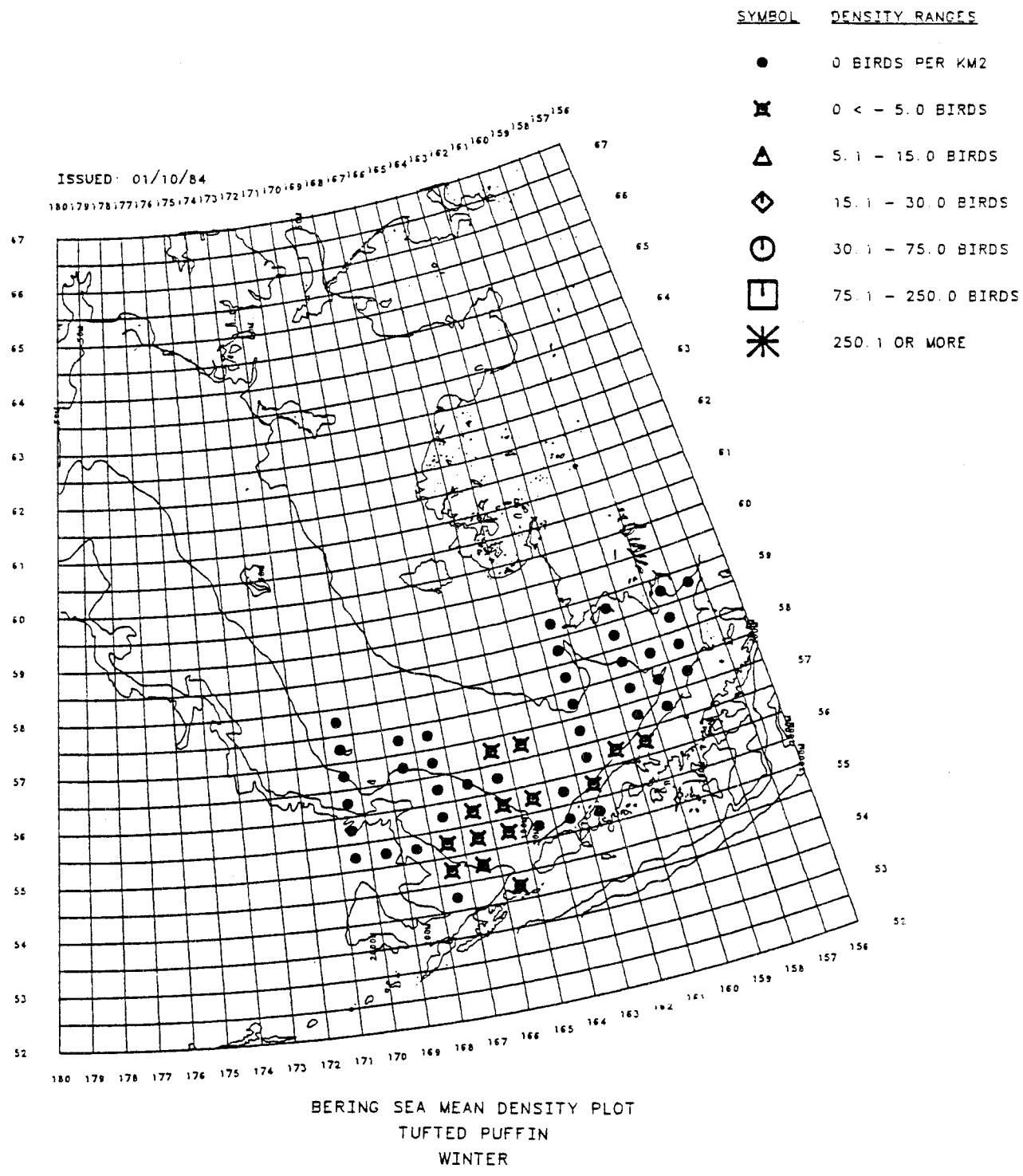


Figure 89. Mean densities, Tufted Puffins: Winter.

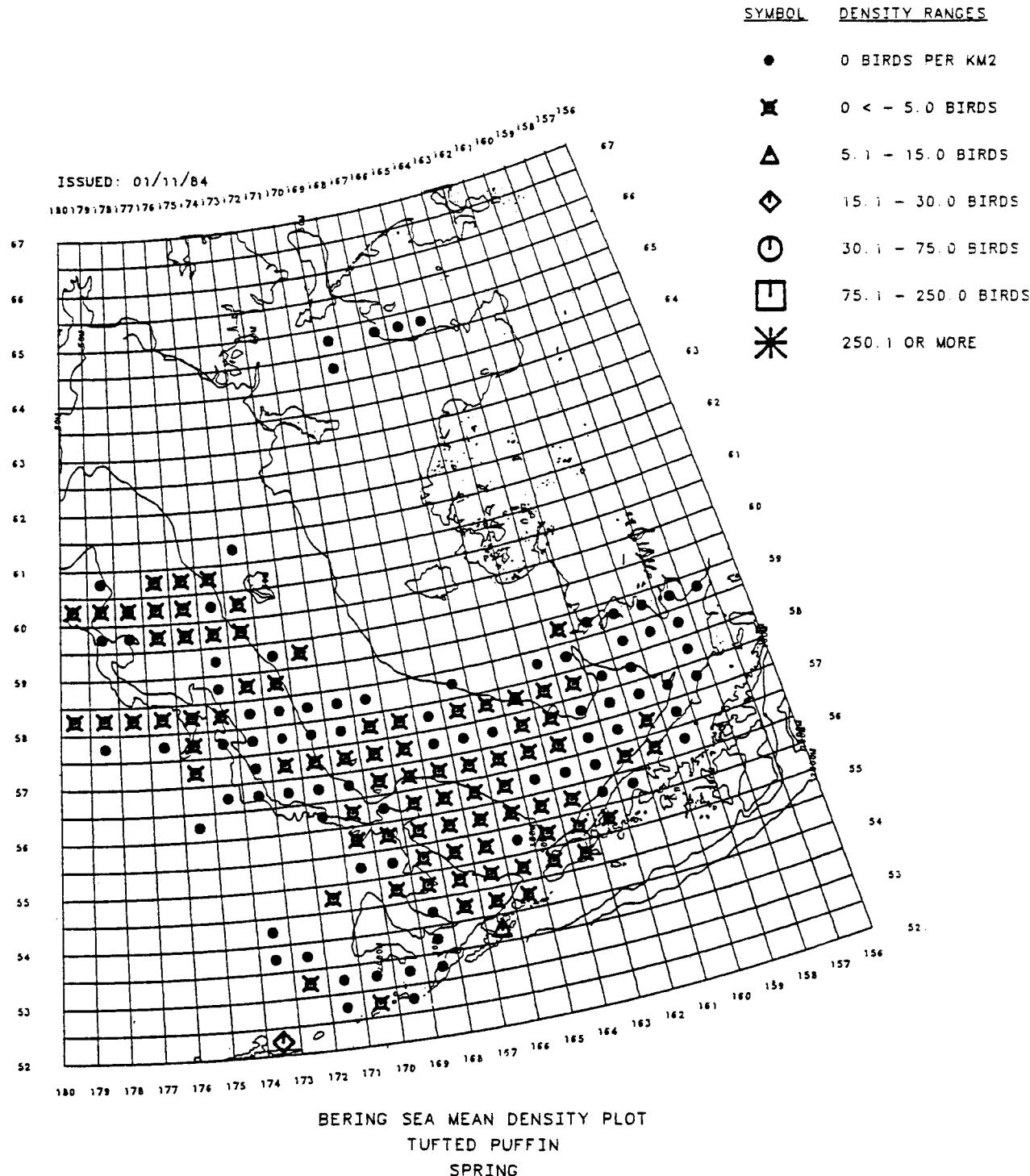


Figure 90. Mean densities, Tufted Puffins: Spring.

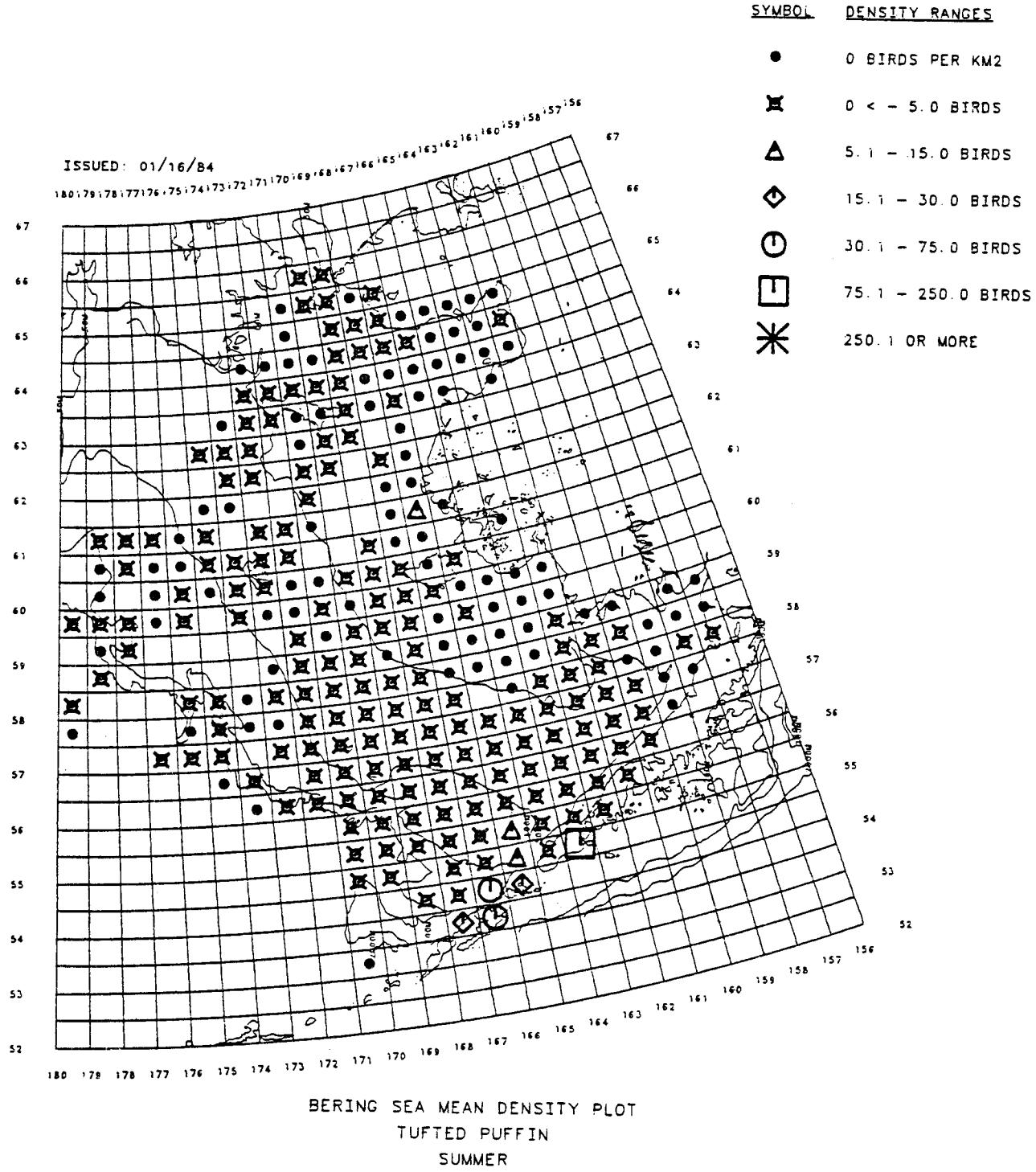


Figure 91. Mean densities, Tufted Puffins: Summer.

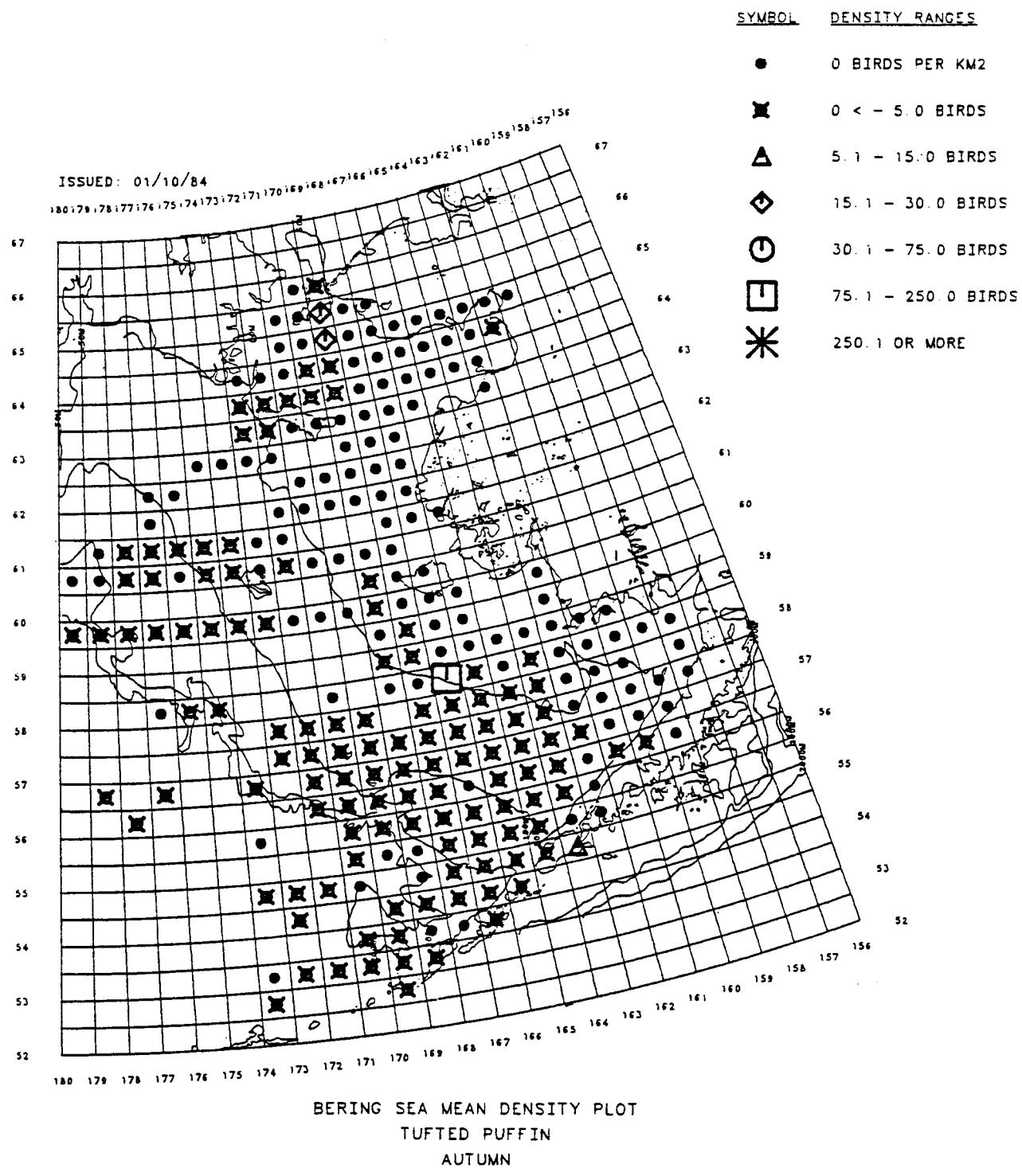
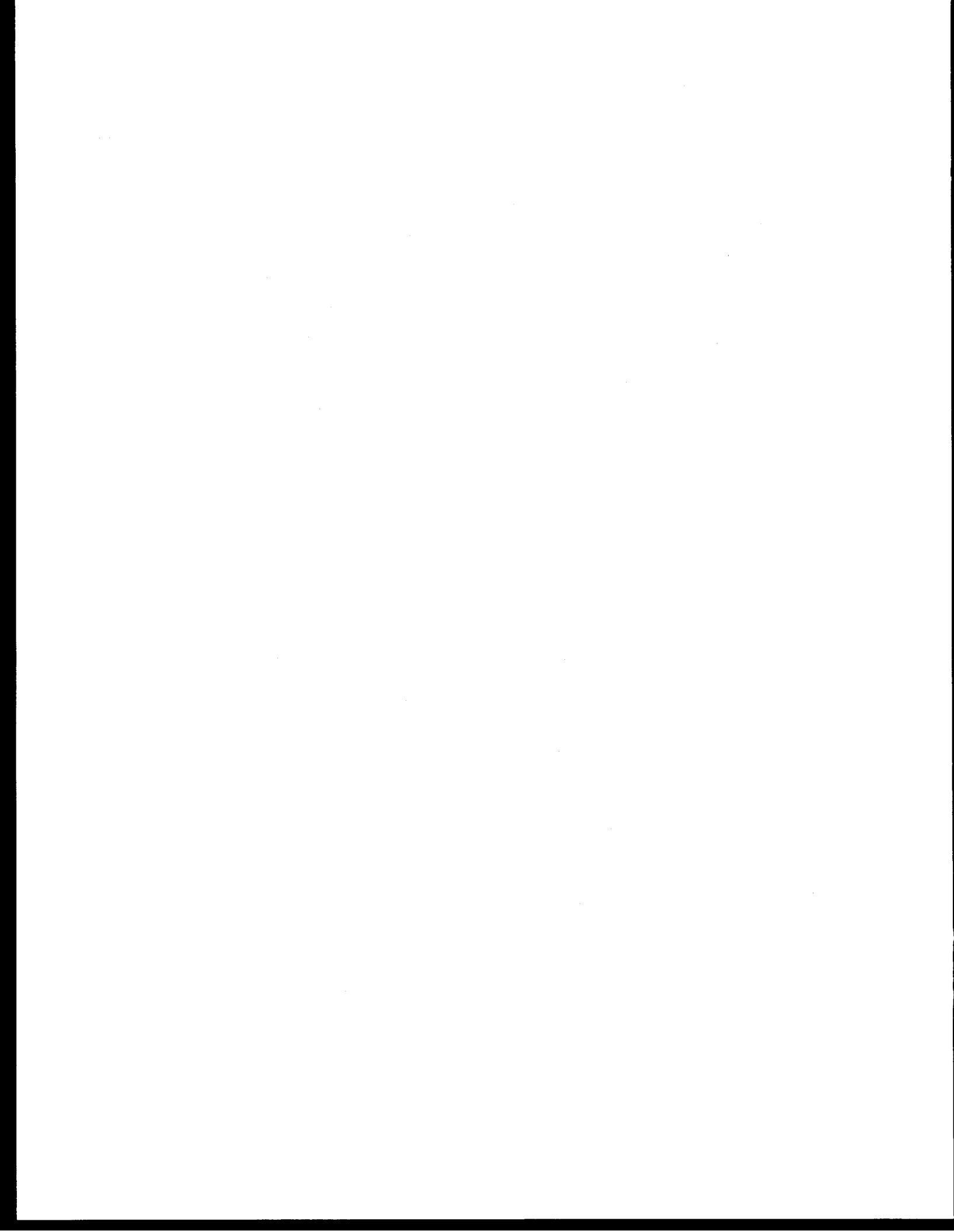


Figure 92. Mean densities, Tufted Puffins: Autumn.



APPENDIX 3

Summary plots for bird distribution in the Bering Sea

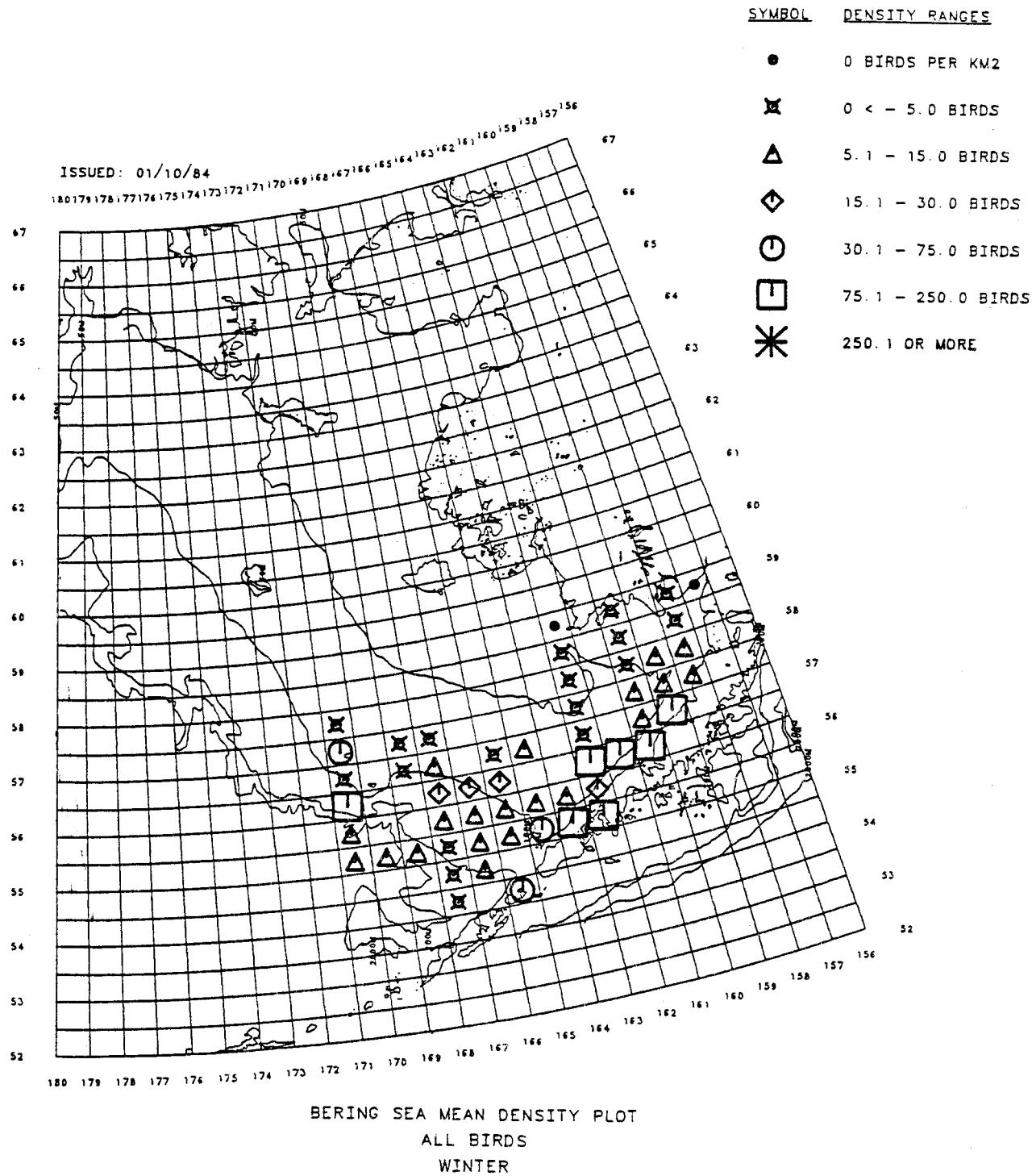


Figure 93. Mean densities, all birds: Winter.

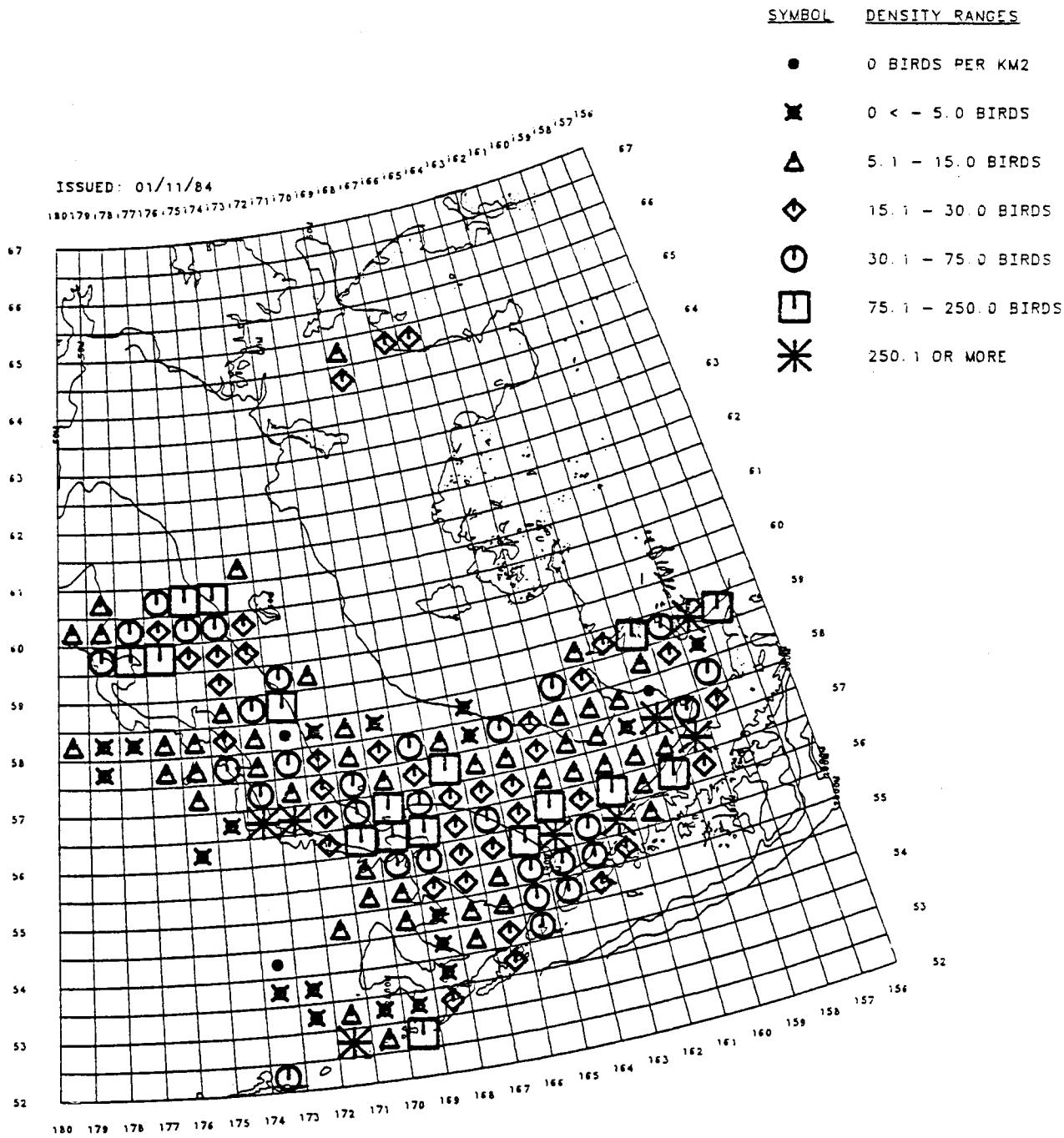


Figure 94. Mean densities, all birds: Spring.

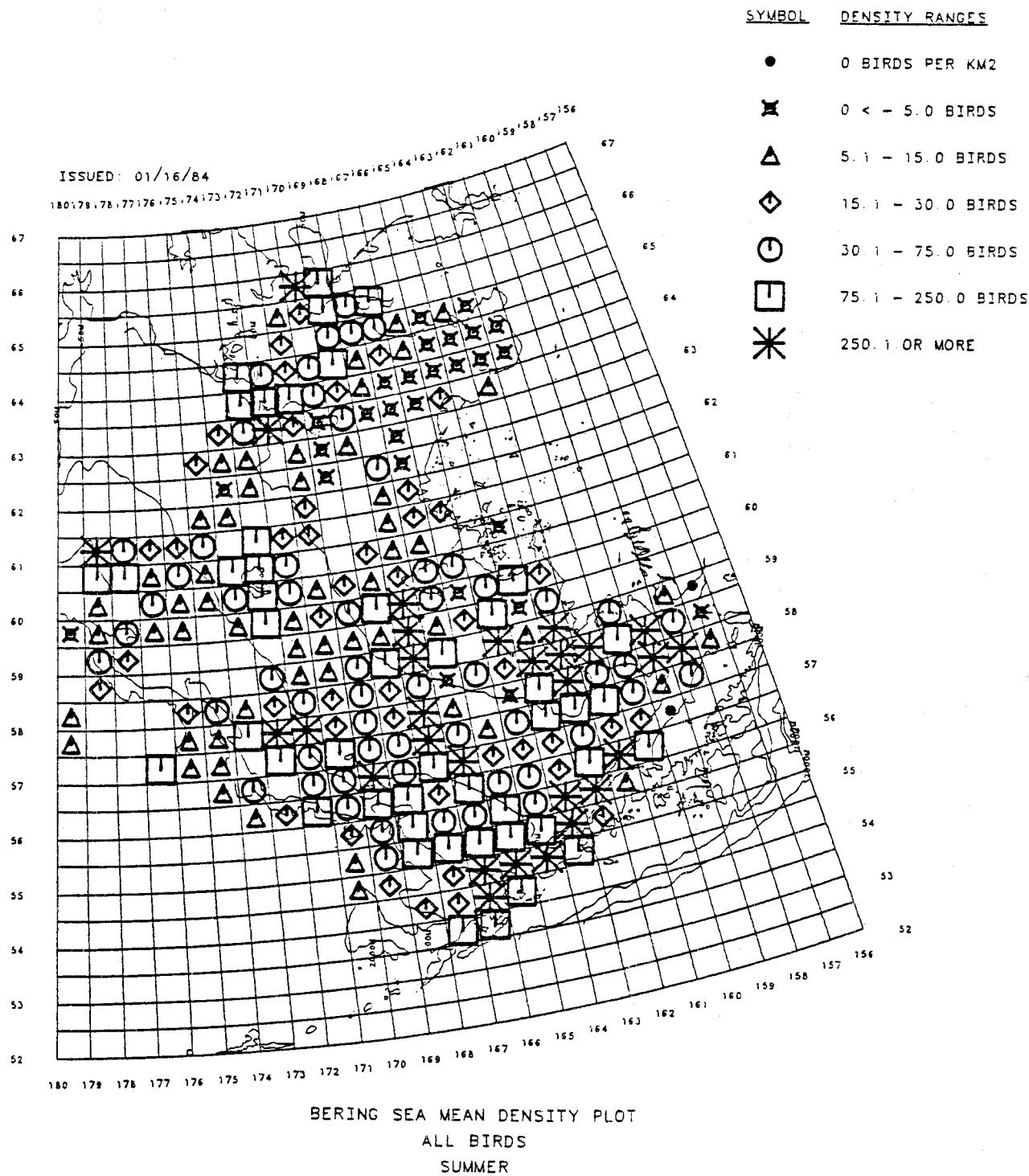


Figure 95. Mean densities, all birds: Summer.

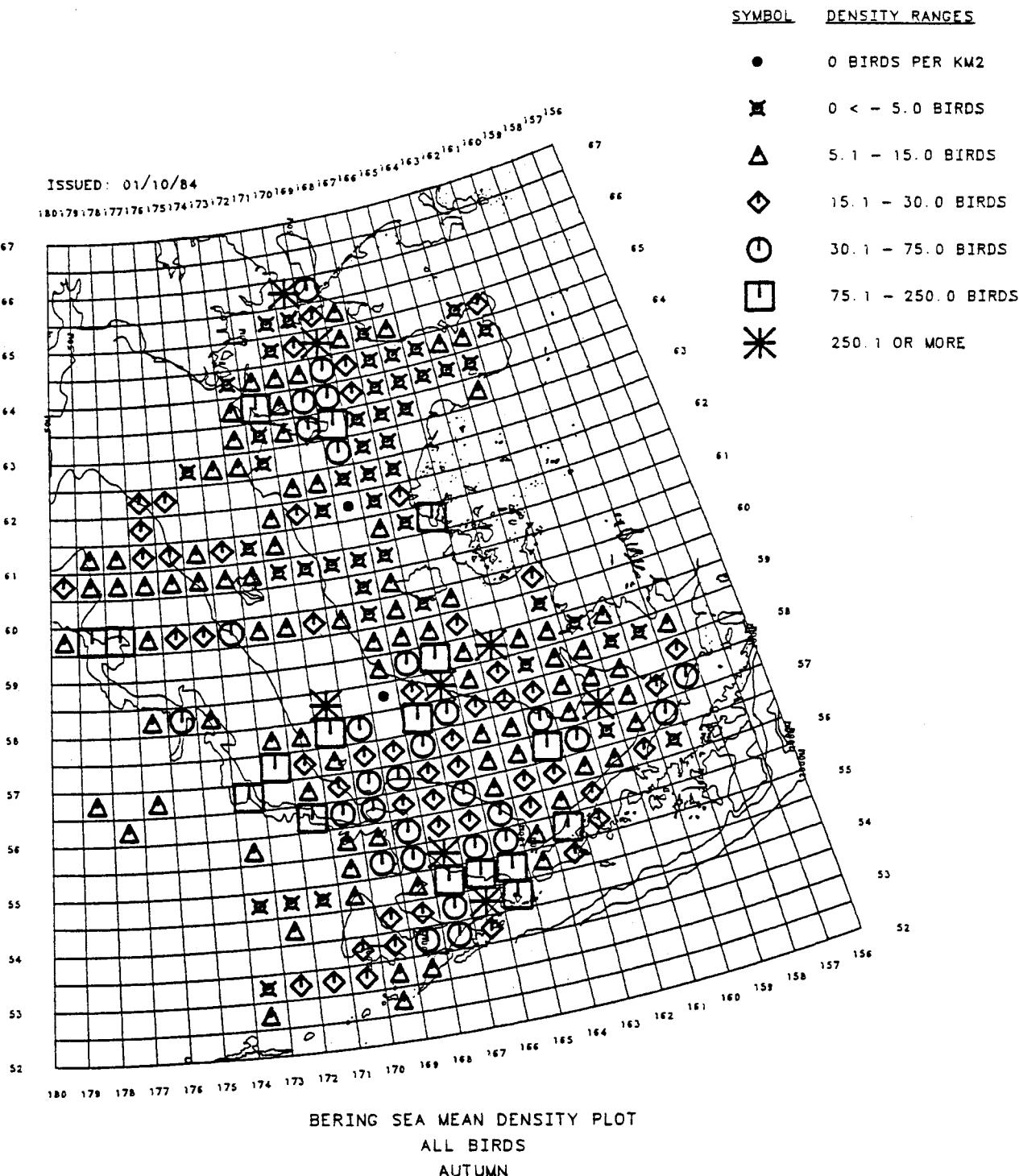


Figure 96. Mean densities, all birds: Autumn.

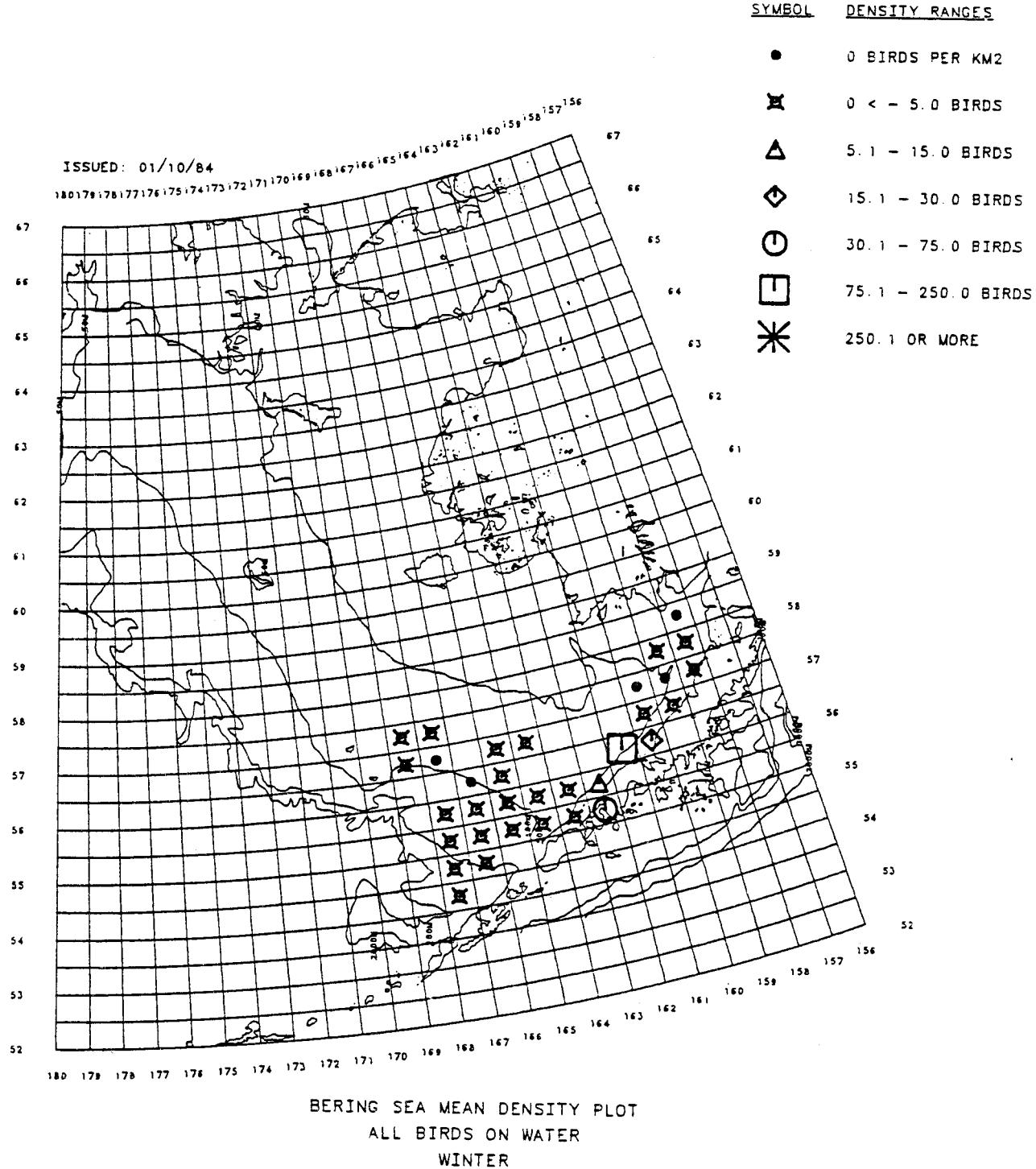


Figure 97. Mean densities, birds on the water: Winter.

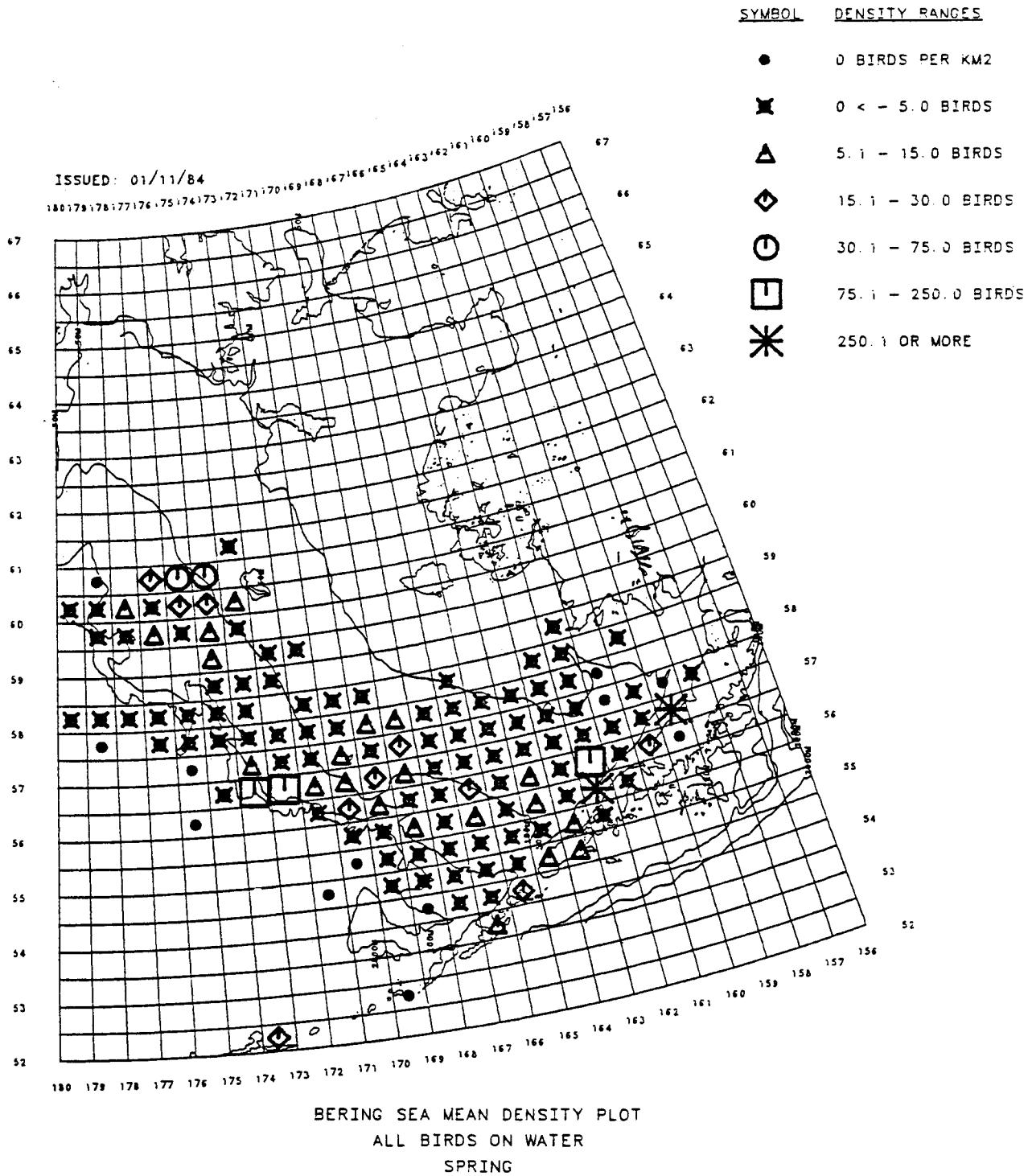


Figure 98. Mean densities, birds on the water: Spring.

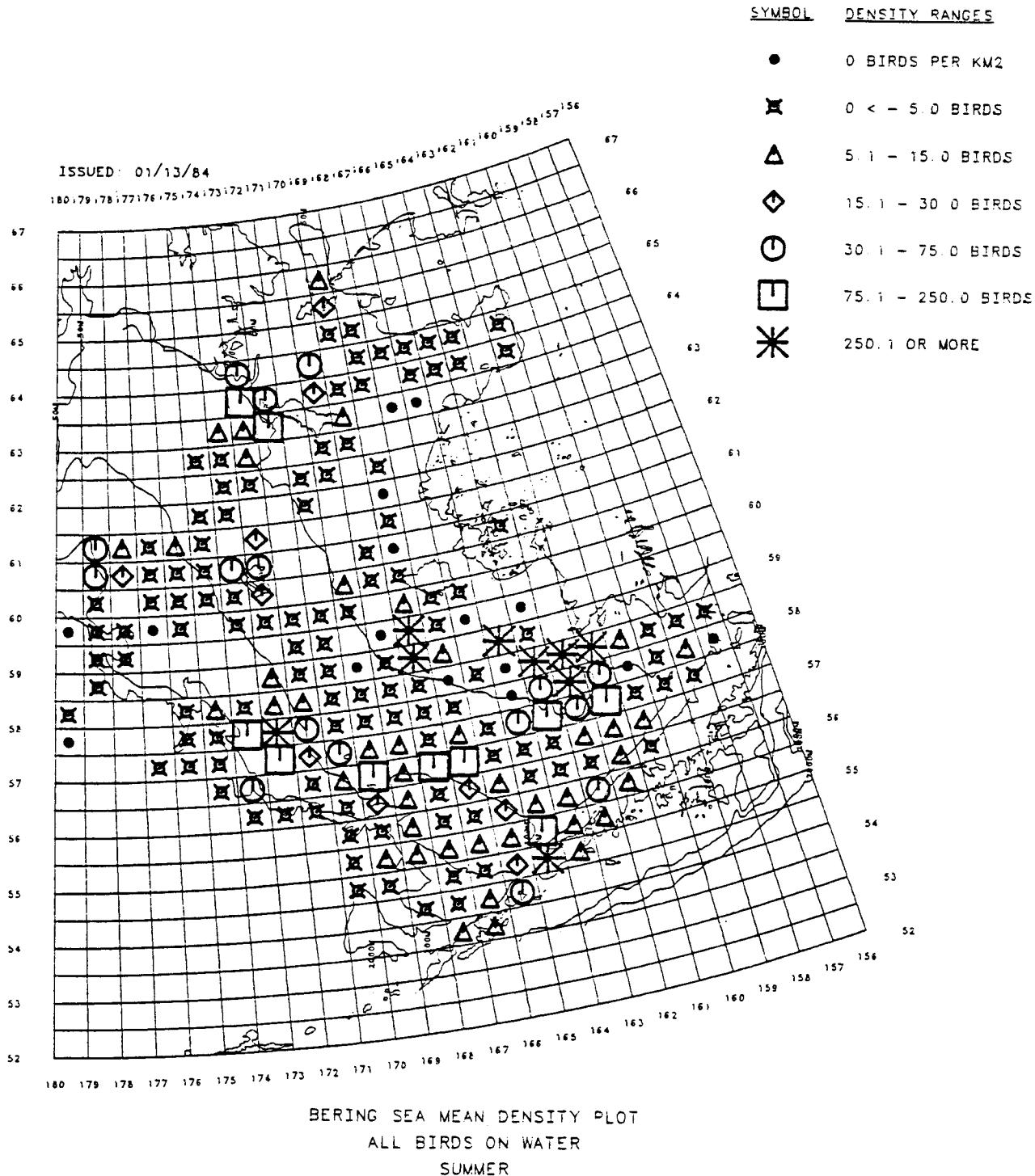


Figure 99. Mean densities, birds on the water: Summer.

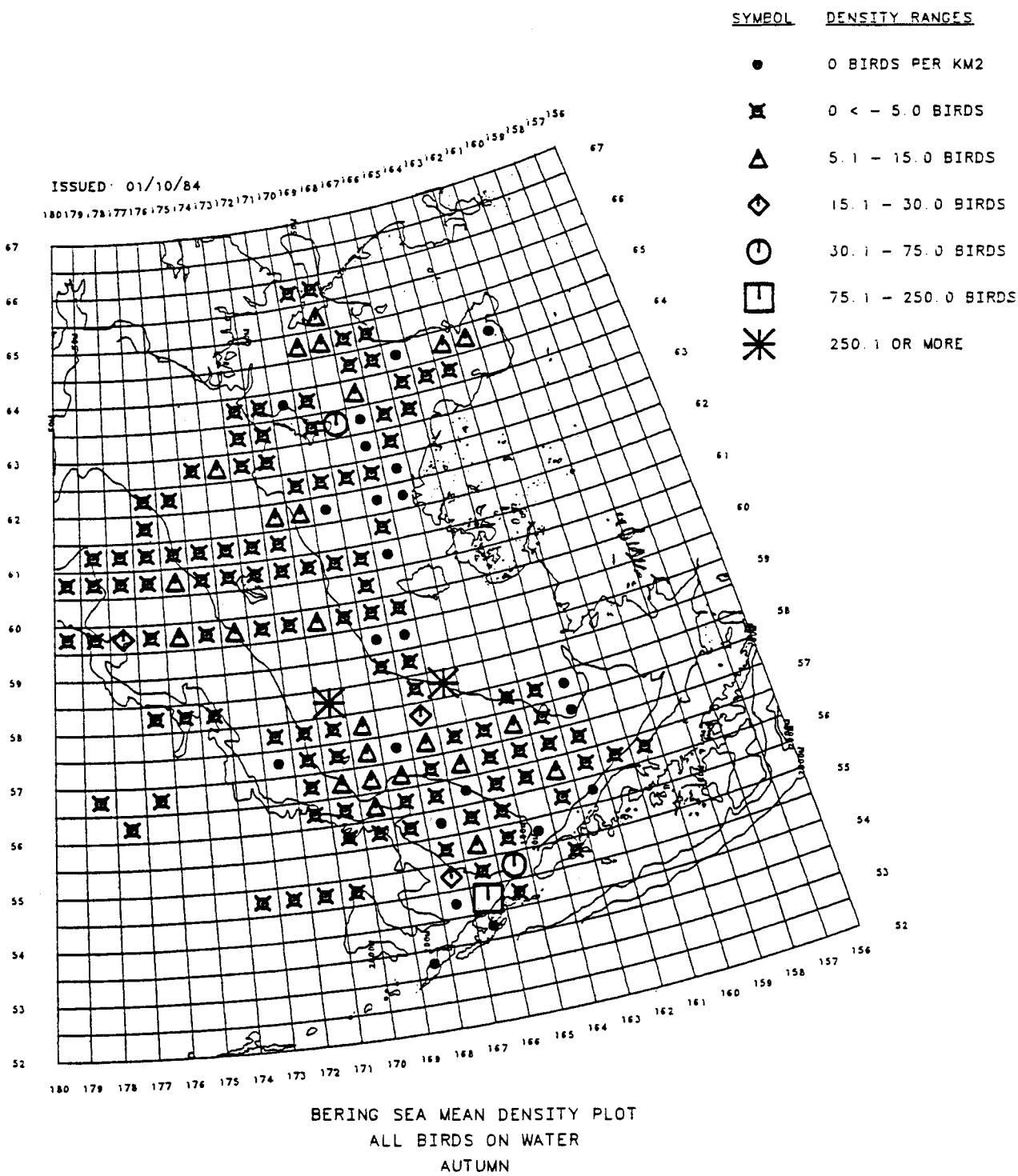
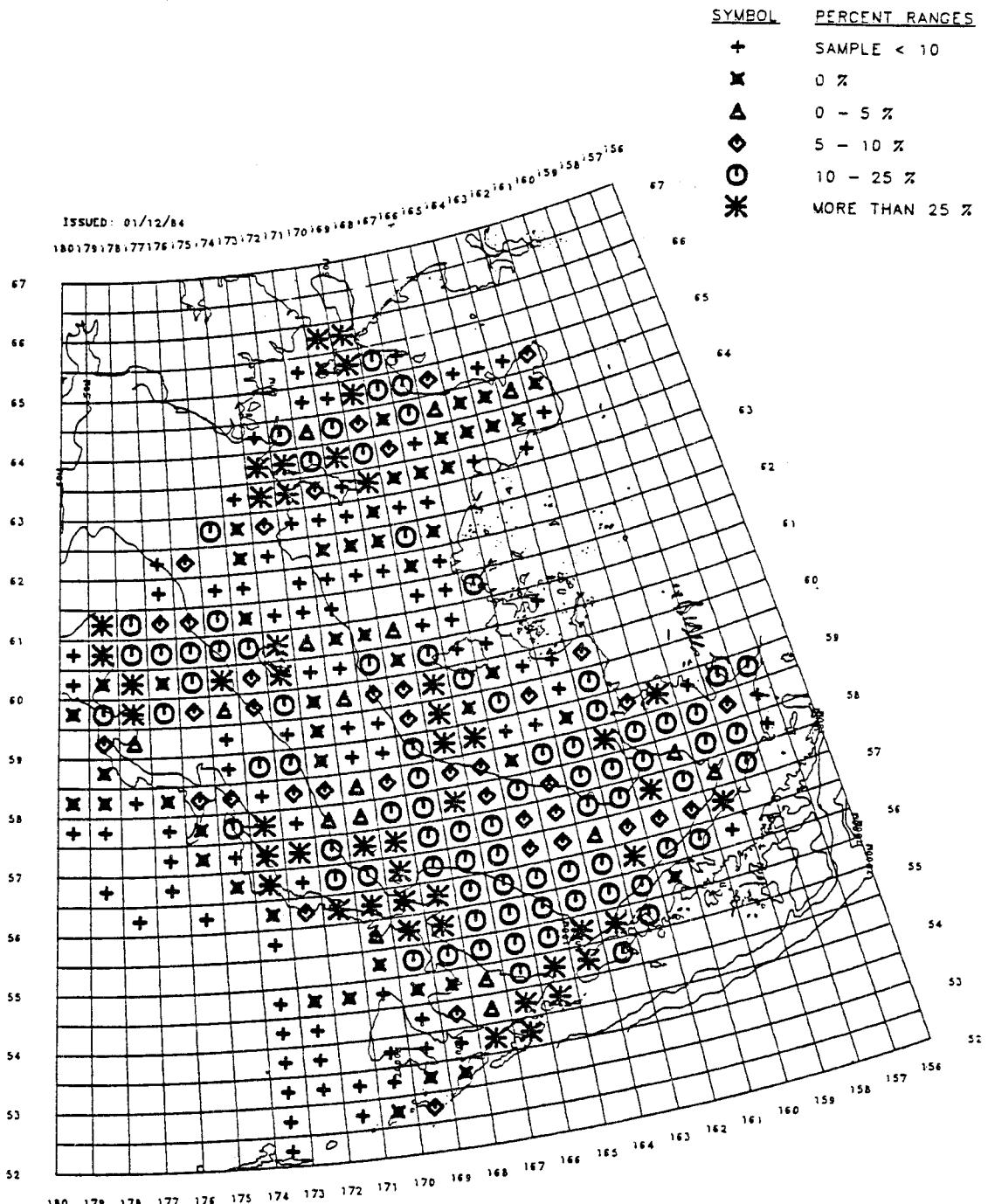


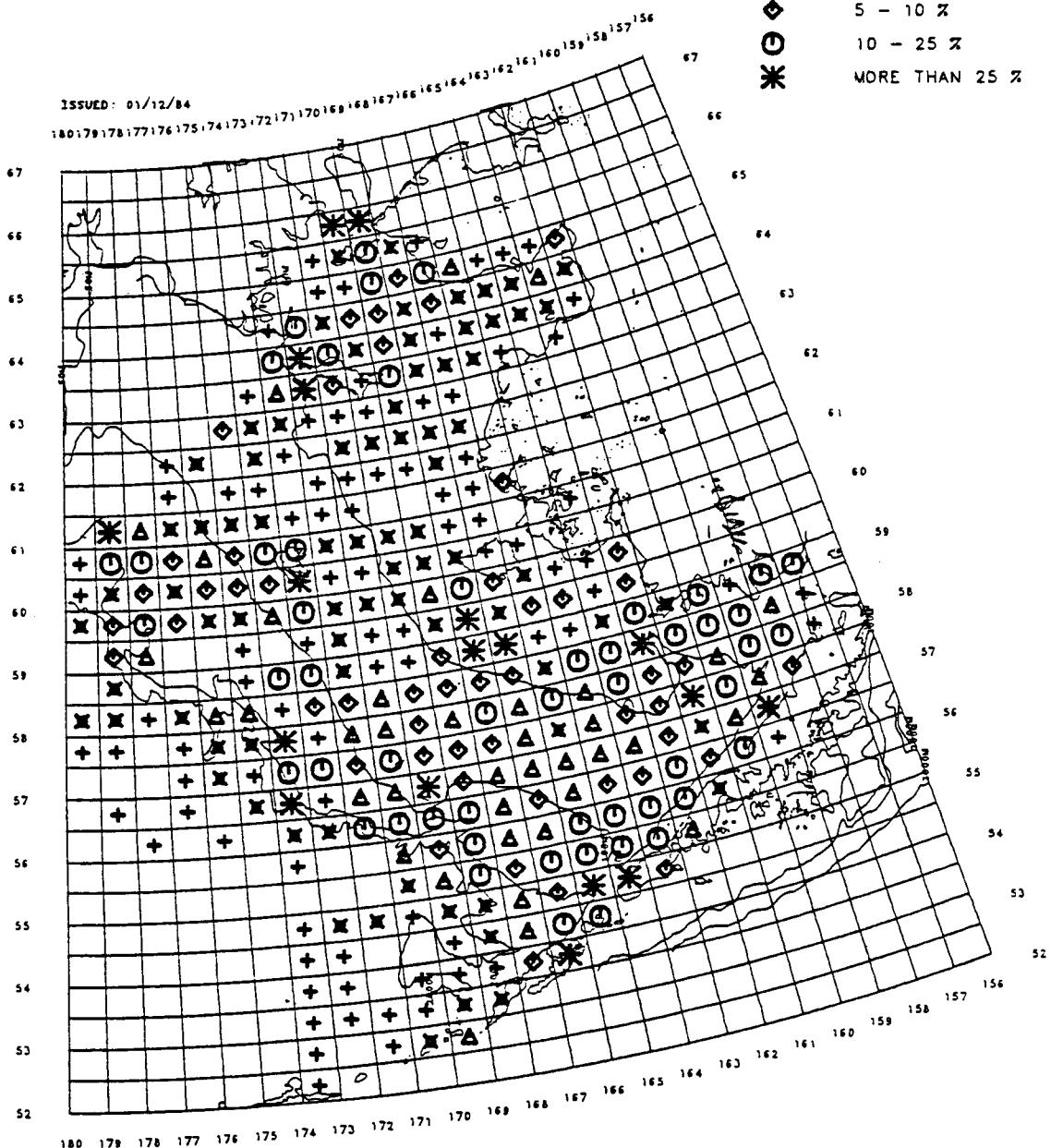
Figure 100. Mean densities, birds on the water: Autumn.



BERING SEA RELATIVE DENSITY PLOT
ALL BIRDS, ALL FIELD OPS & SEASONS
BASE LEVEL: 50 BIRDS PER KM²

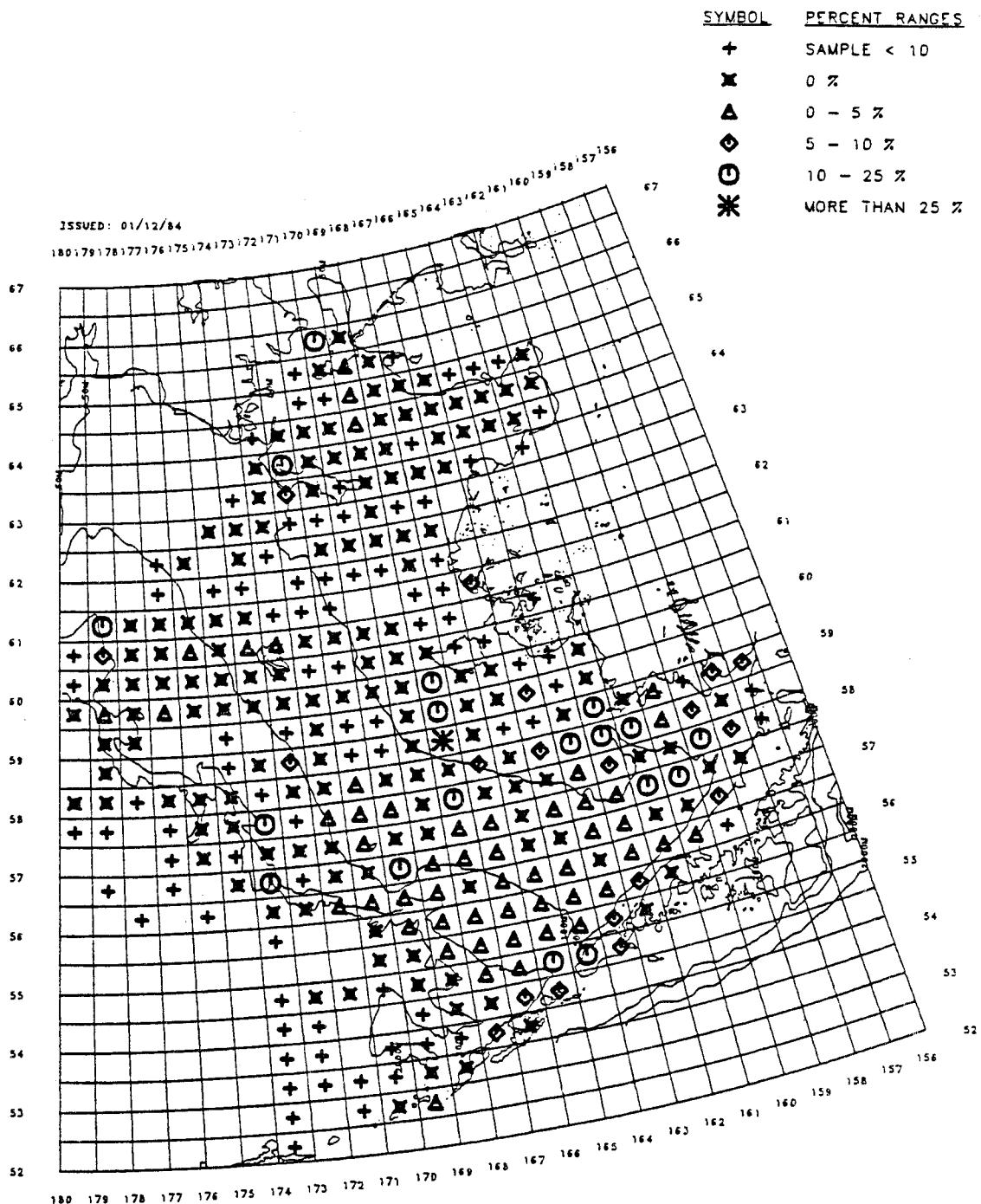
Figure 101. Frequency distribution of transects with densities ≥ 50 birds/km².

<u>SYMBOL</u>	<u>PERCENT RANGES</u>
+	SAMPLE < 10
×	0 %
△	0 - 5 %
◊	5 - 10 %
○	10 - 25 %
*■	MORE THAN 25 %



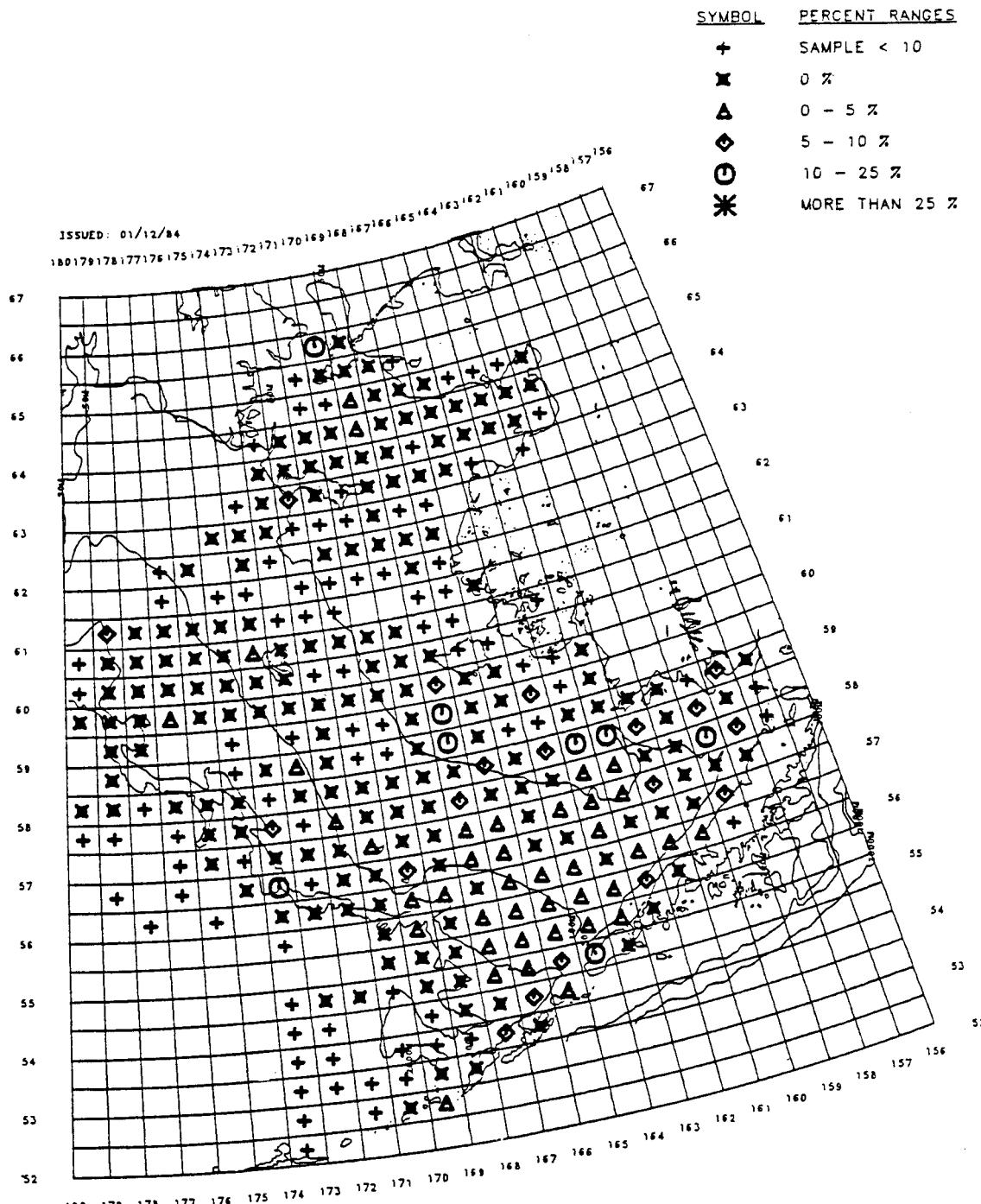
BERING SEA RELATIVE DENSITY PLOT
 ALL BIRDS, ALL FIELD OPS & SEASONS
 BASE LEVEL = 100 BIRDS PER KM² * 2

Figure 102. Frequency distribution of transects with densities ≥ 100 birds/km².



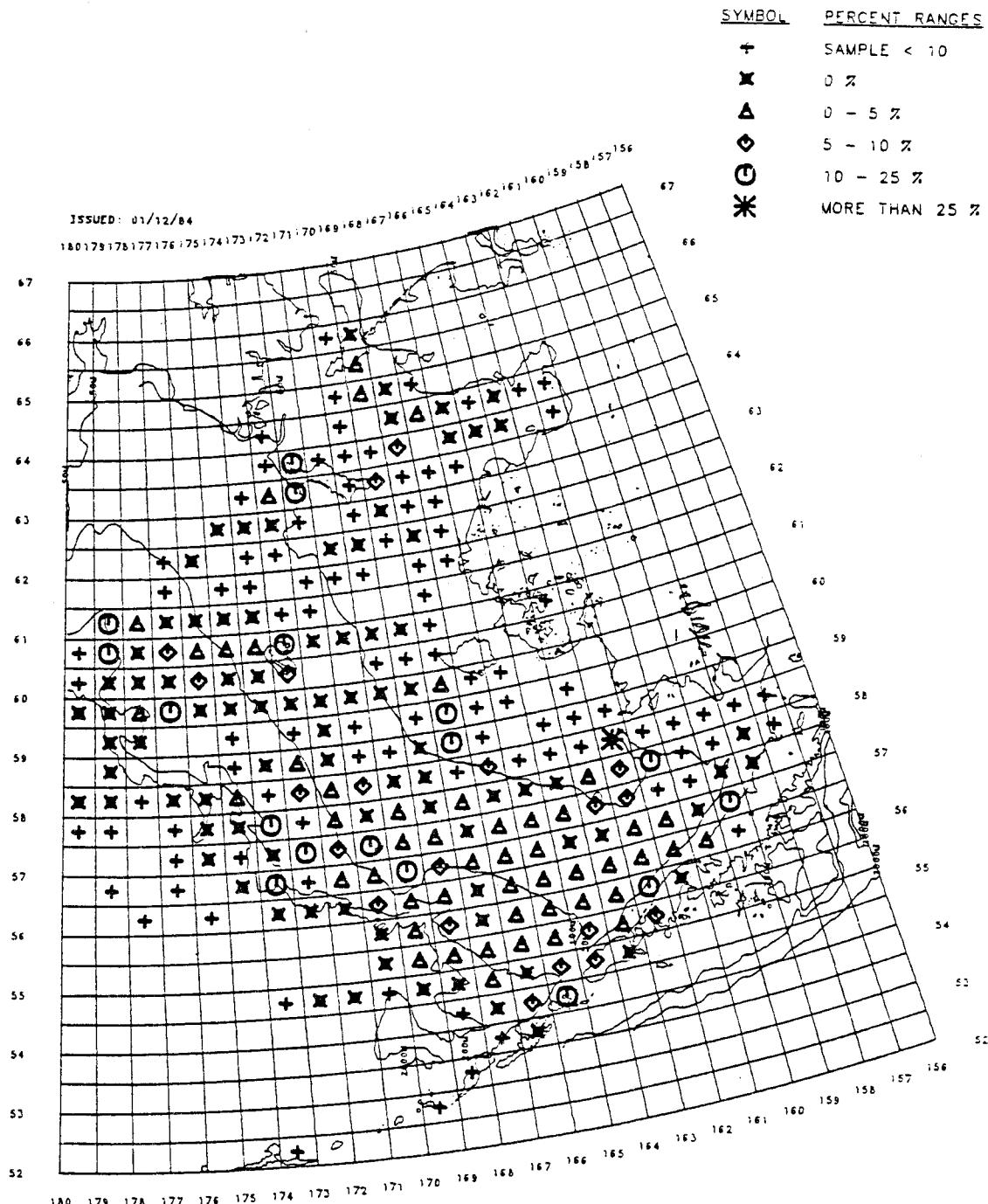
BERING SEA RELATIVE DENSITY PLOT
ALL BIRDS, ALL FIELD OPS & SEASONS
BASE LEVEL: 500 BIRDS PER KM²

Figure 103. Frequency distribution of transects with densities ≥ 500 birds/km².



BERING SEA RELATIVE DENSITY PLOT
ALL BIRDS. ALL FIELD OPS & SEASONS
BASE LEVEL: 1000 BIRDS PER KM**2

Figure 104. Frequency distribution of transects with densities $\geq 1,000$ birds/km 2 .



BERING SEA RELATIVE DENSITY PLOT
 BIRDS ON WATER ALL FIELD OPS & SEASONS
 BASE LEVEL 50 BIRDS PER KM²

Figure 105. Frequency distribution of transects with densities ≥ 50 birds/km 2 : Birds on the water.

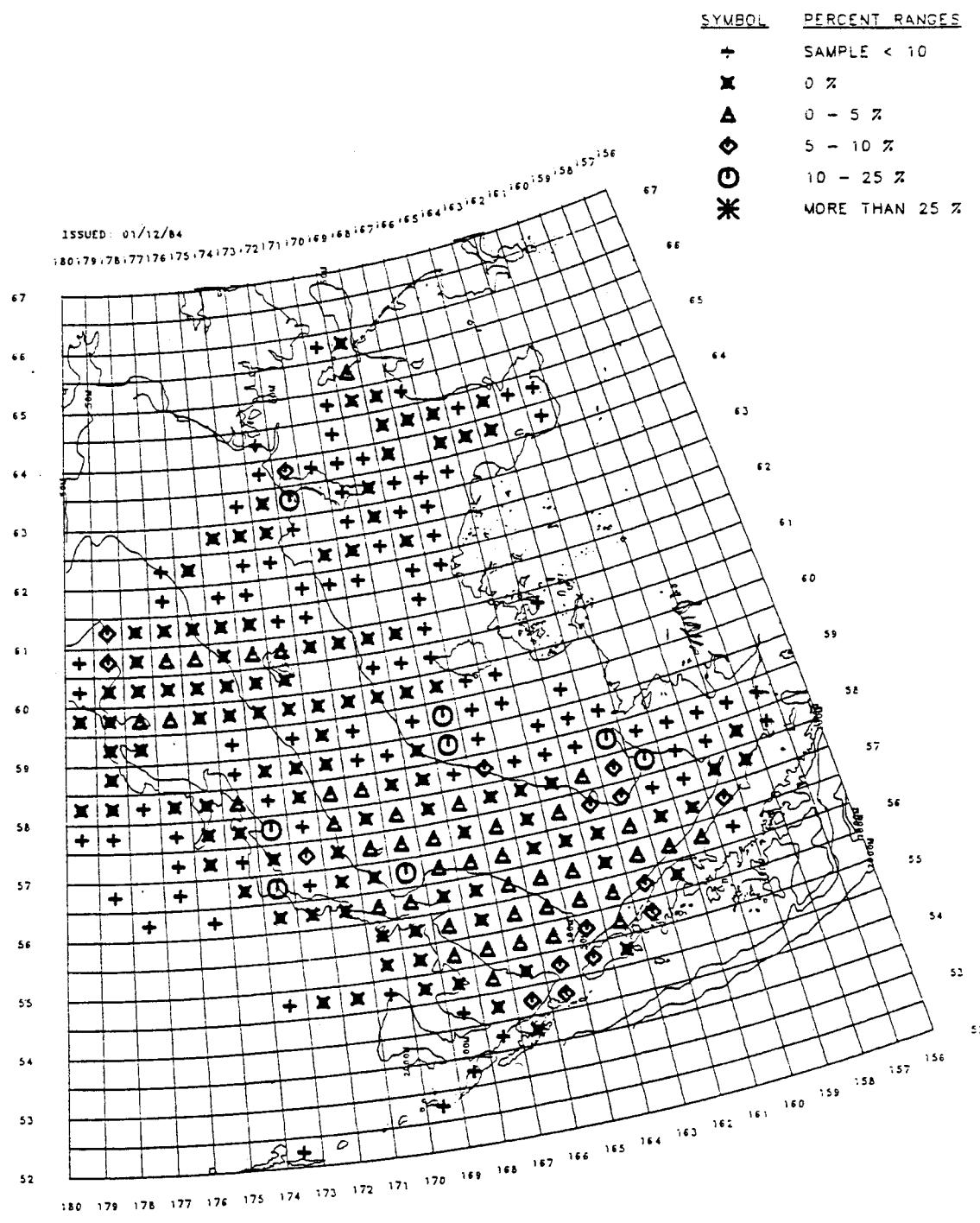
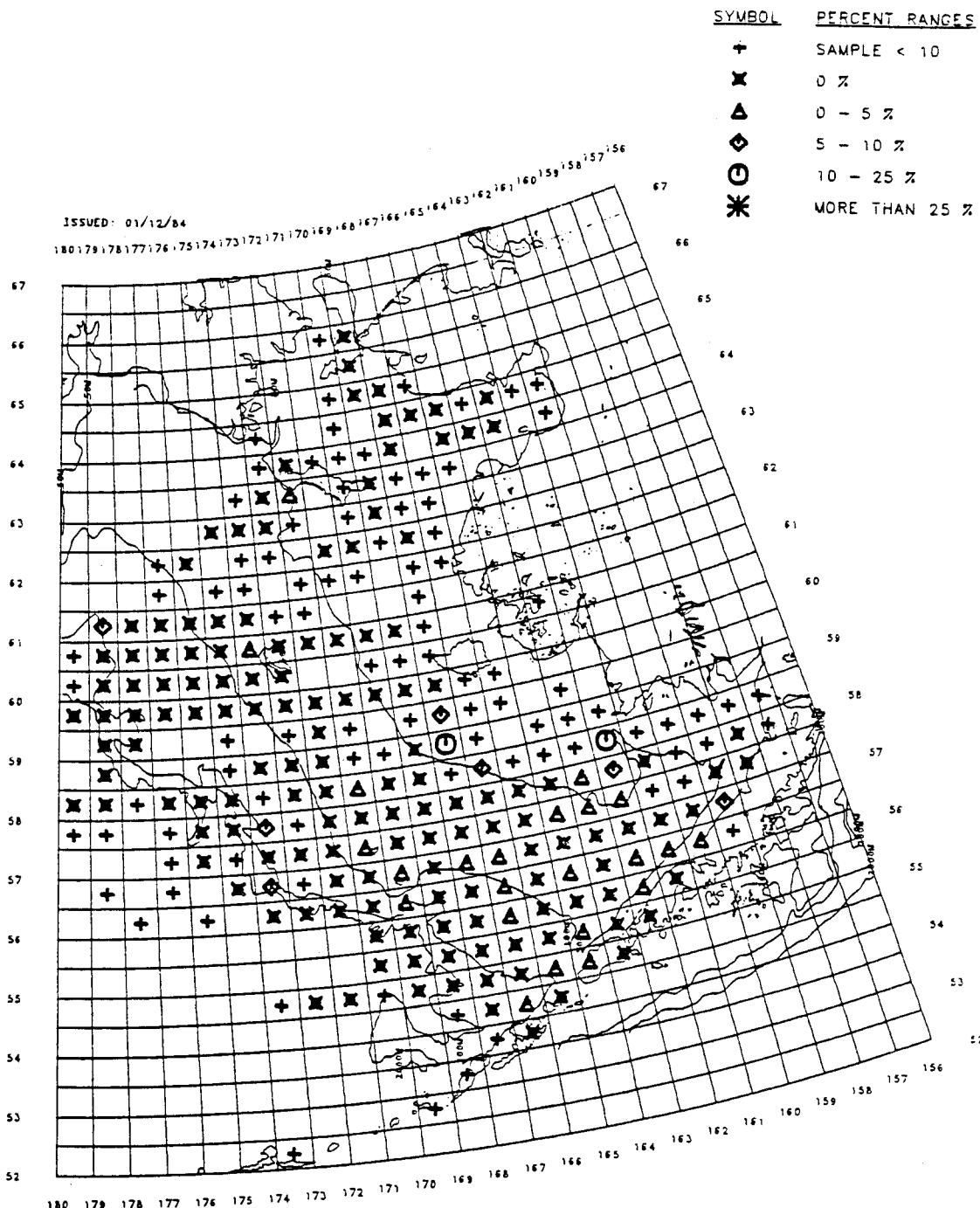
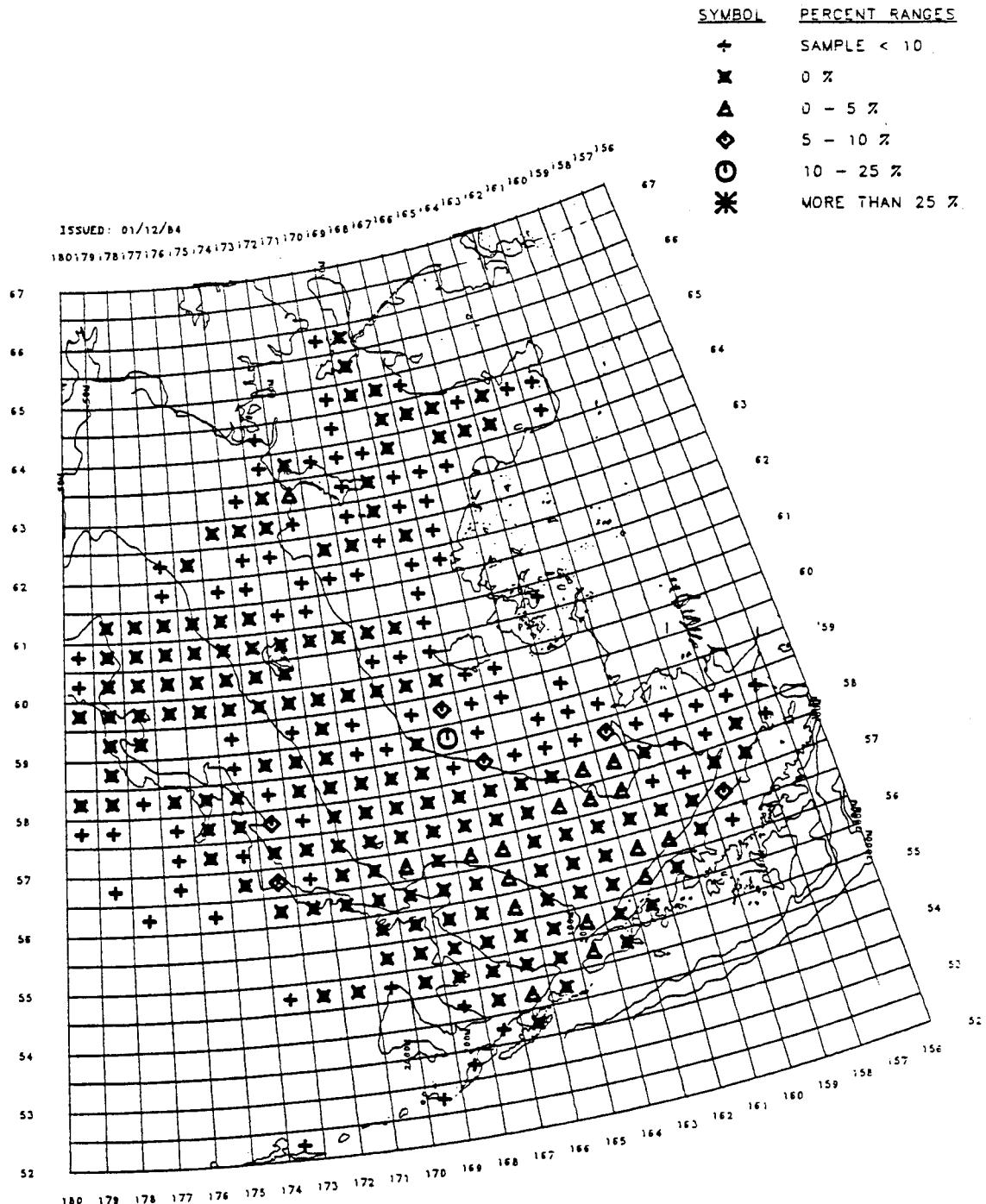


Figure 106. Frequency distribution of transects with densities ≥ 100 birds/km 2 : Birds on the water.



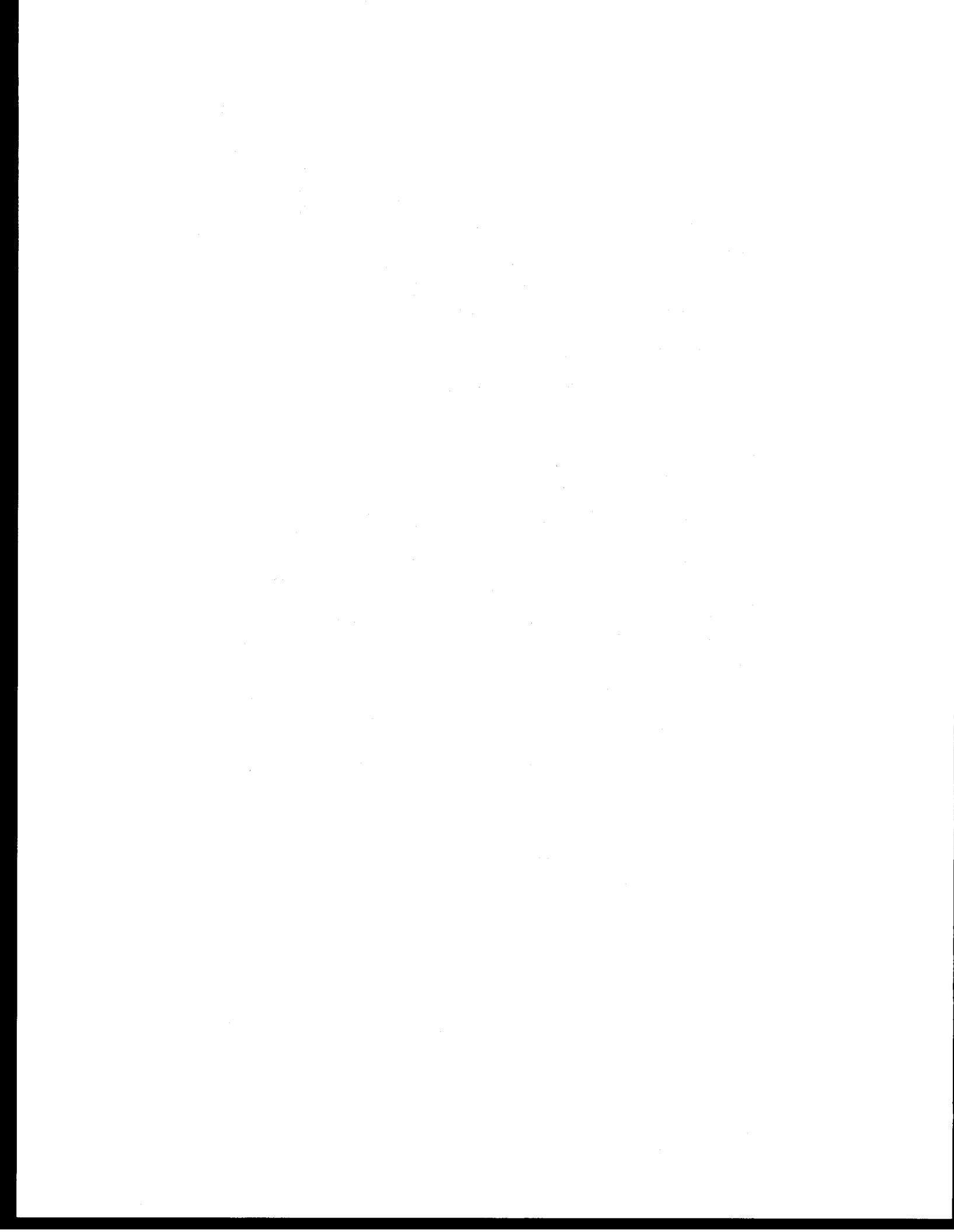
BERING SEA RELATIVE DENSITY PLOT
 BIRDS ON WATER. ALL FIELD OPS & SEASONS
 BASE LEVEL 500 BIRDS PER KM²

Figure 107. Frequency distribution of transects with densities ≥ 500 birds/km 2 : Birds on the water.



BERING SEA RELATIVE DENSITY PLOT
BIRDS ON WATER. ALL FIELD OPS & SEASONS
BASE LEVEL: 1000 BIRDS PER KM²

Figure 108. Frequency distribution of transects with densities $\geq 1,000 \text{ birds/km}^2$: Birds on the water.



APPENDIX 4

**Cruises and species groups used in generating distribution maps
and other URI products**

DATA SETS FOR HUNT PRODUCTS
29 DEC 1983

DATA SETS FOR HUNT PRODUCTS
29 DEC 1983

FILE TYPE	RU	FILE ID	TRACK NUMBER	PROBES	REQUESTED AREA	FILE TYPE	RU	FILE ID	TRACK NUMBER	PROBES	REQUESTED AREA
---	---	-----	-----	-----	-----	---	---	-----	-----	-----	-----
033	083	UCI501	TR3957		*	033	108	0622 1	TR0566		
	083	UCI601	TR3958		*		108	1614 0	TR0580		
	083	UCI602	TR3959		*		108	0621 1	TR0581		*
	083	UCI703	TR3960		*		108	2614 0	TR0609		*
	083	UCI704	TR3961		*		108	0531 1	TR0610		*
	083	UCI801	TR4179		*		108	0522 1	TR0611		*
	083	UCI802	TR4180		*		108	0522 0	TR3251		*
	083	UCI803	TR4181		*		108	0531 0	TR3252		
	083	UCI804	TR4182		*		108	0532 0	TR3253		
	083	UCI805	TR4183		*		108	0532 5	TR3254		
	083	UCI806	TR4184		*		108	1615 0	TR3255		
	083	UCI808	TR4185		*		108	3607 0	TR3256		
	083	UCI580	TR6852		*		108	3607 4	TR3257		
	083	UCI480	TR6946	P	*		108	3607 6	TR3258		
	083	UCI680	TR6947	P	*		108	0622 3	TR3479		
	083	UCI280	TR6948	P	*		196	1DI577			
	083	UCI380	TR6949	P	*		196	1SR377			
	083	UCI180	TR6950	P	*		196	1SR477			
	083	UCI901	TR7487	P	*		196	1SR578			
	083	UCI902	TR7488	P	*		196	1SR678			
	083	UCI903	TR7489	P	*		196	3A1A76	TR2339		
	083	UCI281	TR7601	P	*		196	3A2A76	TR2340		
	083	UCI381	TR7602	P	*		196	2A2776	TR2341		
	083	UCI781	TR7603	P	*		196	3A1676	TR2342		
	083	UCI181	TR7654		*		196	3A2676	TR2343		
	083	UCI481	TR7655		*		196	3A3676	TR2344		
	083	UCI701	TR7656		*		196	3A2776	TR2345		
	083	UCI702	TR7657		*		196	3A3776	TR2346		
	083	UCI581	TR7897	P	*		196	3A4776	TR2347		
	083	UCI681	TR7898	P	*		196	3A5776	TR2348		
	083	UCI881	TR7899	P	*		196	3A6776	TR2349		
	083	UCI182	TT0479		*		196	3A1876	TR2350		
	083	UCI282	TT0480		*		196	3A2876	TR2351		
	083	UCI382		P	*		196	3A1976	TR2352		
	083	UCI482	TT0501	P	*		196	3A2976	TR2353		
	083	UCI582	TT0481		*		196	3A3976	TR2354		
	096	290676	TR1299				196	2A1576	TR2355		
	108	1616 1	TR0565				196	2A2576	TR2356		

DATA SETS FOR HUNT PRODUCTS
29 DEC 1983

DATA SETS FOR HUNT PRODUCTS
29 DEC 1983

FILE TYPE	RU	FILE ID	TRACK NUMBER	PROBES	REQUESTED AREA	FILE TYPE	RU	FILE ID	TRACK NUMBER	PROBES	REQUESTED AREA
-----	---	-----	-----	-----	-----	-----	---	-----	-----	-----	-----
033	196	2A1676	TR2357			033	196	2IC976	TR2761		
	196	2A2676	TR2358				196	2BW576	TR2762		
	196	2A1776	TR2359				196	2KL676	TR2763		
	196	2A3676	TR2360				196	3BL676	TR2764		
	196	2A5676	TR2361				196	2KL776	TR2765		
	196	2A6676	TR2362				196	3P1776	TR2766		
	196	2A7676	TR2363				196	3PB876	TR2767		
	196	2A3776	TR2364				196	2BW076	TR2769		
	196	2A4776	TR2365				196	2CL976	TR2789		
	196	2A1876	TR2366				196	1SR376	TR2838	*	
	196	2A2876	TR2367				196	1SR476	TR2839	*	
	196	2A1976	TR2368				196	2GLA76	TR2840	*	
	196	2A2976	TR2369				196	2GL976	TR2841		
	196	2A3976	TR2370				196	2DI976	TR2842	*	
	196	2A4976	TR2371				196	2GL876	TR2843		
	196	2A1A76	TR2372				196	2BI776	TR2844		
	196	2A1B76	TR2373				196	2GL875	TR2845	*	
	196	2PD976	TR2738				196	3AL876	TR2846		
	196	2WR976	TR2739				196	3C0776	TR2916		
	196	3OK676	TR2740				196	3C0676	TR2917		
	196	2PD676	TR2741				196	3C0876	TR2918		
	196	2IC676	TR2742				196	UCI478	TR4796	P	*
	196	2CL676	TR2744				196	3AL878	TR6114		
	196	2WR676	TR2745				196	3AL877	TR7395		
	196	3PP776	TR2746				196	3GL877	TR7396		
	196	2CB776	TR2747				196	GL3976	TR7434		
	196	3CR776	TR2748				196	C03976	TR7436		
	196	3BR776	TR2749				196	NW3878	TR7437		
	196	3OK776	TR2750				237	WD5WFS	TR1689	*	
	196	2BW776	TR2751				237	WD6OSI	TR1690	*	
	196	3BB776	TR2752				237	WD6SUI	TR1691	*	
	196	2UP776	TR2753				237	WD6WFS	TR1692	*	
	196	2WR776	TR2754				237	WD77BS	TR5392	*	
	196	2PD776	TR2755				237	A6D8BS	TR5393	*	
	196	2IC876	TR2756				237	WD78BS	TR5393	*	
	196	2CL876	TR2757				237	WD78CS	TR5394	*	
	196	3PP876	TR2758				239	01UC75	TR3106	*	
	196	3OK976	TR2760				239	02UC75	TR3107	*	

608

DATA SETS FOR HUNT PRODUCTS
29 DEC 1983

DATA SETS FOR HUNT PRODUCTS
29 DEC 1983

FILE TYPE	RU	FILE ID	TRACK NUMBER	PROBES	REQUESTED AREA	FILE TYPE	RU	FILE ID	TRACK NUMBER	PROBES	REQUESTED AREA
033	239	03UC75	TR3108		*	033	337	FW7035	TR2850		
	239	01UC76	TR3109				337	FW7036	TR2851		*
	239	02UC76	TR3110				337	FW7042	TR2852		
	239	03UC76	TR3111		*		337	FW7045	TR2853		
	239	04UC76	TR3112				337	FW7046	TR2854		
	239	05UC76	TR3113		*		337	FW5008	TR3481		*
	337	FW5007					337	FW5009	TR3482		
	337	FW5028					337	FW5014	TR3483		*
	337	FW6069					337	FW5027	TR3484		
	337	FW6096					337	FW5030	TR3485		
	337	FW6100					337	FW5032	TR3486		*
	337	FW6200					337	FW6001	TR3487		
	337	FW6300					337	FW6015	TR3488		
	337	FW7047					337	FW5004	TR3571		
	337	FW7050					337	FW5018	TR3572		*
	337	FW7051					337	FW5034	TR3573		
	337	FW7052					337	FW6025	TR3574		
	337	FW7053					337	FW6026	TR3575		
	337	FW7054					337	FW6028	TR3576		
	337	FW8006					337	FW6029	TR3577		
	337	FW8007					337	FW6093	TR3578		*
	337	FW8008					337	FW7026	TR3579		
	337	FW8012					337	FW7027	TR3580		
	337	FW8014					337	FW7029	TR3581		*
	337	FW8015					337	FW5010	TR3584		
	337	FW8016					337	FW5021	TR3585		*
	337	FW8017					337	FW6085	TR3586		*
	337	FW8018					337	FW6086	TR3587		*
	337	FW8025					337	FW6186	TR3588		*
	337	FW8027					337	FW6088	TR3589		*
	337	FW8028					337	FW5013	TR3590		*
	337	FW8100					337	FW5023	TR3591		*
	337	FW9001					337	FW5024	TR3592		
	337	FW7032	TR2377				337	FW6066	TR3593		*
	337	FW7033	TR2378				337	FW5011	TR3634		*
	337	FW7028	TR2847				337	FW5012	TR3635		*
	337	FW7031	TR2848				337	FW5015	TR3636		*
	337	FW7034	TR2849				337	FW5016	TR3637		*

DATA SETS FOR HUNT PRODUCTS
29 DEC 1983

DATA SETS FOR HUNT PRODUCTS
29 DEC 1983

FILE TYPE	RU	FILE ID	TRACK NUMBER	PROBES	REQUESTED AREA	FILE TYPE	RU	FILE ID	TRACK NUMBER	PROBES	REQUESTED AREA
---	---	---	---	---	---	---	---	---	---	---	---
033	337	FW5020	TR3638	*		033	337	FW6027	TR3859	*	
	337	FW5022	TR3639	*			337	FW6050	TR3860		
	337	FW5026	TR3640	*			337	FW6051	TR3861		
	337	FW5033	TR3641	*			337	FW6052	TR3862		
	337	FW5035	TR3642	*			337	FW6064	TR3863		
	337	FW5036	TR3643	*			337	FW6077	TR3864		
	337	FW5037	TR3644	*			337	FW6078	TR3865		
	337	FW5038	TR3645	*			337	FW6083	TR3866		
	337	FW6006	TR3804	*			337	FW6092	TR3867		
	337	FW6009	TR3805	*			337	FW6094	TR3868		
	337	FW6012	TR3806	*			337	FW6095	TR3869		
	337	FW6021	TR3807	*			337	FW4001	TR6497		
	337	FW6057	TR3808	*			337	FW9002	TR6498		
	337	FW6067	TR3809	*			337	FW6400	TR7397		
	337	FW6068	TR3810	*			337	FW8019	TR7398		
	337	FW6070	TR3811	*			337	FW8023	TR7399		
	337	FW6074	TR3812	*			337	FW8024	TR7400		
	337	FW6082	TR3813	*			337	FW8026	TR7401		
	337	FW6084	TR3814	*			337	FW8029	TR7402		
	337	FW6087	TR3815				337	FW8032	TR7403		
	337	FW6089	TR3816	*			460	EC1978	TR7914		
	337	FW5003	TR3842				467	AERSR1	TR4318		
	337	FW5006	TR3843	*			467	AERSR2	TR4319		
	337	FW5025	TR3844				467	AERSR3	TR4320		
	337	FW5029	TR3845				467	AERSR4	TR4321		
	337	FW5031	TR3846				467	AERSR5	TR4322		
	337	FW6002	TR3847				467	AERSR6	TR4323		
	337	FW6004	TR3848				467	AERSR7	TR4324		
	337	FW6005	TR3849				467	AER801	TR5395		
	337	FW6010	TR3850				467	AER802	TR5396		
	337	FW6007	TR3851				467	AER803	TR5397		
	337	FW6008	TR3852				467	AER804	TR5398		
	337	FW6011	TR3853				467	AER805	TR5399		
	337	FW6013	TR3854				467	AER806	TR5400		
	337	FW6014	TR3855				467	AER807	TR5401		
	337	FW6016	TR3856				467	AER808	TR5402		
	337	FW6018	TR3857				467	AER809	TR5403		
	337	FW6019	TR3858				467	AER810	TR5404		

SPECIES LIST FOR HUNT PRODUCTS

Bering Sea

FT033, Marine Bird Sightings, Ship/Aircraft

Small and Unidentified Alcids

881010000000
881010060000-881010119999
912901000000
912901060000-912901119999

Crested Auklets

881010110100-881010110199
912901110100-912901110199

Least Auklets

881010110200-881010110299
912901110200-912901110299

Parakeet Auklets

881010100100-881010100199
912901100100-912901100199

Cormorants

880404000000-880404999999
911004000000-911004999999

Eiders

880601170000-880601179999
911201170000-911201179999

Northern Fulmars

880302020100-880302020199
910902020100-910902020199

Gulls except Kittiwakes

881008000000-881008029999
881008040000-881008059999
912802000000-912802029999
912802040000-912802059999

Black-legged Kittiwakes

881008030000-881008030199
912802030000-912802030199

Red-legged Kittiwakes

881008030200-881008030299
912802030200-912802030299

Common Murres

881010030100-881010030199
912901030100-912901030199

Murres

881010030000-881010039999
912901030000-912901039999

Thick-billed Murres

881010030200-881010030299
912901030200-912901030299

Storm Petrels:

Unidentified Storm Petrels and Fork-tailed Storm Petrels

880303000000-880303020199
910903000000-910903020199

Phalaropes

881006000000-881006999999
912707000000-912707999999

Horned Puffins

881010130200-881010130299
912901130200-912901130299

Tufted Puffins

881010140100-881010140199
912901140100-912901140199

Shearwaters:

Unidentified Shearwaters, Sooty Shearwaters,
and Short-tailed Shearwaters

880302040000
880302040700-880302040899
910902040000

910902040700-910902040899

Waterfowl

880600000000-880699999999
911200000000-911299999999

APPENDIX 5

Mean, standard deviation and frequency of densities for selected species
in the central Bering Sea shelf by zone

Platform type code: 1

Number of tapes: 1

Tape number 1 assigned to unit: 16 Files skipped before reading: 0 Number of files searched: 6

Number of cruises accepted: 6

Cruises accepted: UCI182 UCI282 UCI382 UCI482 UCI582 UCI999

Number of tax code sets: 12

Number of tax codes for each set: 1 1 1 1 2 1 1 1 1 1 1 4

Species mnemonics and codes:

ALL	All birds	9100000000	8		
NOFU	Northern Fulmar	9109020201	0		
SHER	shearwaters	9109020400	2		
STPE	stormpetrels	9109030000	4		
BLKI	Black-legged Kittiwake	9128020300	9128020301		
PHAL	phalaropes	9127070000	4		
LEAU	Lauant Aukslet	9129011102	0		
MURR	Murres	9129010300	2		
CRAU	Crested Aukslet	9129011101	0		
COMU	Common Murk	9129010301	0		
TBMU	Thick-billed Murk	9129010302	0		
SMAL	small alcid	9129010000	9129011001	9129011101	9129011102
		0	0	0	0

Number of seasons: 3

Season mnemonics and months:

SPRING	3	4	5
SUMMER	6	7	8
AUTUMN	9	10	11

Zone files accepted:

NBSCO.ZON	63.	63.	58.	58.	59.	60.	62.
Cooler	32.	0.	0.	0.	27.	57.	22.
	167.	165.	165.	167.	169.	170.	168.
	38.	0.	0.	20.	53.	27.	10.
NBSMI.ZON	60.	59.	58.	58.	59.	60.	61.
Middle Shelf	57.	27.	0.	0.	42.	18.	22.
	170.	169.	167.	171.	173.	176.	173.
	27.	53.	20.	30.	43.	45.	2.
NBSSL.ZON	58.	58.	59.	59.	60.	60.	62.
Outer Shelf	0.	0.	0.	39.	10.	47.	10.
	171.	174.	177.	178.	177.	180.	180.
	30.	0.	43.	25.	57.	0.	0.
STM60K.ZON	61.	61.	60.	60.	59.	59.	60.
St. Matthew	12.	2.	52.	25.	59.	46.	16.
	173.	172.	171.	171.	171.	172.	174.
	5.	12.	44.	9.	48.	45.	6.
STL60K.ZON	63.	62.	62.	62.	62.	63.	64.
St. Lawrence	32.	22.	23.	40.	46.	6.	32.
	167.	168.	169.	170.	171.	172.	173.
	38.	10.	28.	48.	47.	49.	4.
NBSDP.ZON	60.	60.	59.	59.	58.	58.	56.
Deep Water	47.	10.	39.	0.	0.	0.	0.
	180.	177.	178.	177.	174.	180.	0.
	0.	57.	25.	43.	0.	0.	0.

Zone map
(180.00, 64.23)

(165.00, 64.23)



(165.00, 58.00)

Cruise UCI182 reading

Rejection list Width: 0 Platform: 0 Length: 10 Latitude: 0 Longitude: 0 Zone: 82 Month: 0

Records written on file : 0

Cruise UCI282 reading

Rejection list Width: 0 Platform: 0 Length: 21 Latitude: 0 Longitude: 0 Zone: 30 Month: 0

Records written on file : 0

Cruise UCI382 reading

Rejection list Width: 0 Platform: 0 Length: 4 Latitude: 0 Longitude: 0 Zone: 171 Month: 0

Records written on file : 0

Cruise UCI482 reading

Rejection list Width: 0 Platform: 0 Length: 21 Latitude: 0 Longitude: 0 Zone: 1 Month: 0

Records written on file : 0

Cruise UCI582 reading

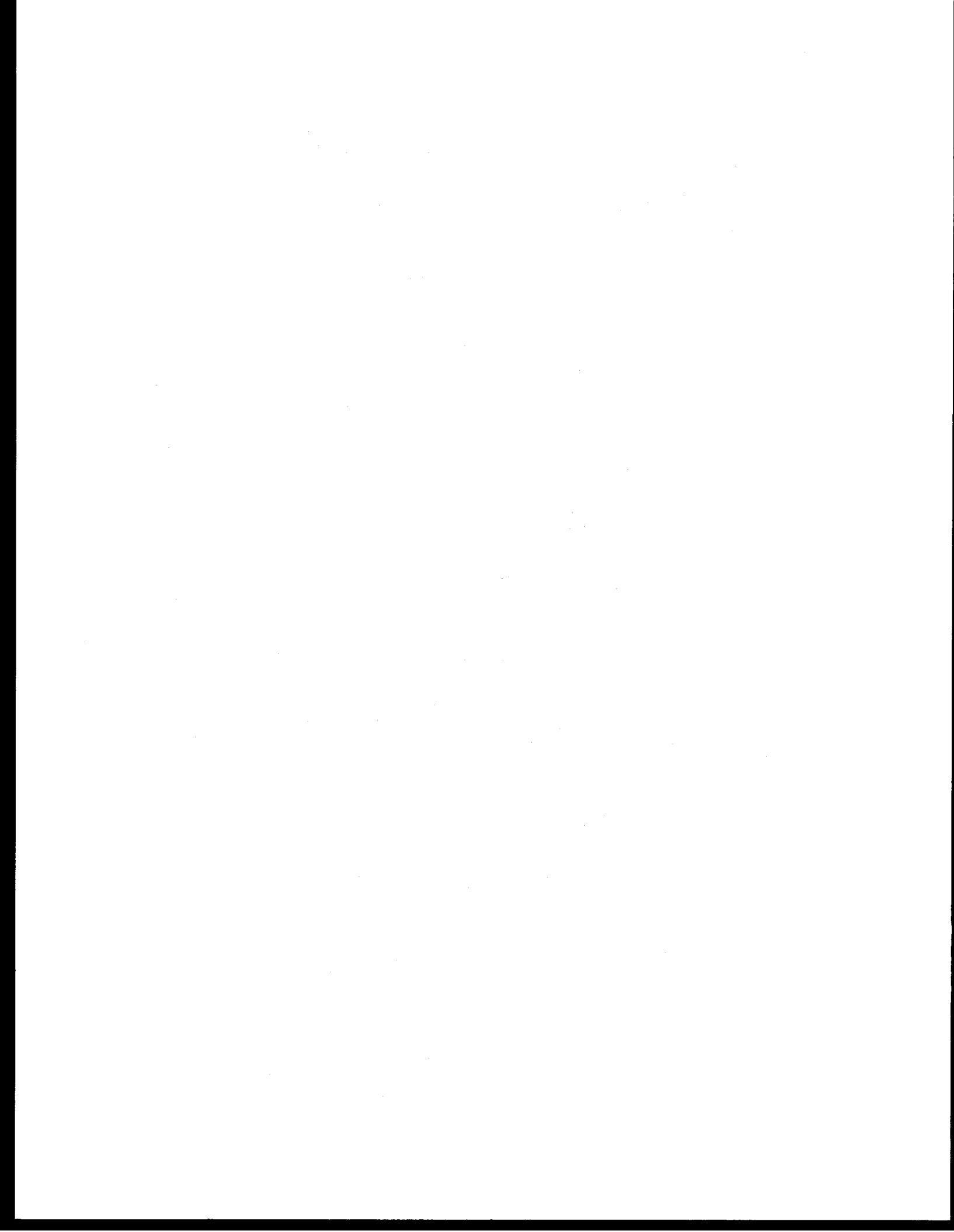
Rejection list Width: 0 Platform: 0 Length: 10 Latitude: 0 Longitude: 0 Zone: 275 Month: 0

Records written on file : 0

Cruise UCI999 reading

Rejection list Width: 0 Platform: 0 Length: 13 Latitude: 0 Longitude: 0 Zone: 108 Month: 0

Records written on file : 0



APPENDIX 6

Prey taken by birds at St. Matthew Island

We made two collections of birds at St. Matthew Island to compare diets of species between the colonies at St. Matthew Island and the Pribilof Islands. We collected 25 birds in October 1982 and another 41 birds in July 1983 (Table 15). We are only able to compare the July collection with the Pribilof data because of seasonal shifts in diet and because our Pribilof collections were limited to the summer. This comparison must be considered preliminary due to the small sample size for St. Matthew Island.

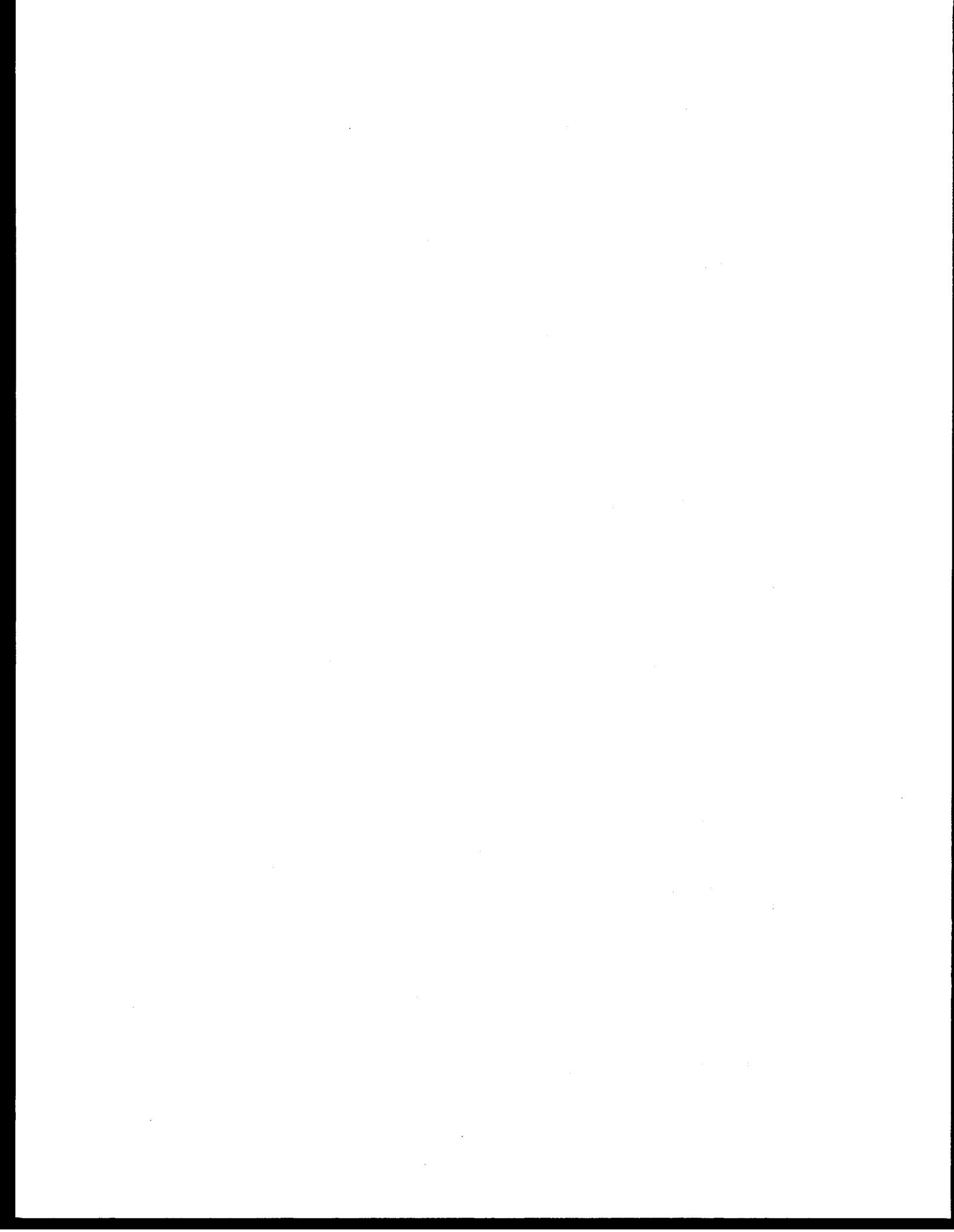
Food samples were treated as given in Hunt et al. (1981a), with the exception that we are now able to detect jellyfish both through microscopic detection of nematocysts and by visual identification of the dehydrated gelatinous tissue (Harrison, in press).

During the summer, dietary diversity for birds at St. Matthew Island was either equal (COMU, TBMU, LEAU) to that shown by the same species at the Pribilof Islands, or was greater (NOFU, BLKI, PAAU). While Common Murres and Least Auklets used the same major prey (gadids and Calanus, respectively) at both St. Matthew and the Pribilof Islands, the other species we collected used different prey at the two locations. At the Pribilof Islands, fish (primarily gadids) were the major prey for Northern Fulmars, Black-legged Kittiwakes, Thick-billed Murres and Parakeet Auklets. At St. Matthew Island the major prey found in Northern Fulmars was squid, in Black-legged Kittiwakes and Parakeet Auklets the major prey was jellyfish and hyperiid amphipods (mostly Hyperia), and in Thick-billed Murres the major prey was the amphipod Parathemisto pacifica. Although gadids do not appear to be the major prey for many species at St. Matthew Island, when fish appeared in our collections they were mostly gadids. In the summer, the prey which appeared most frequently in our collection from St. Matthew Island were jellyfish and hyperiids (occurring together) and gadids. In the fall collection, squid, gadids and crustaceans appeared most frequently. In the fall, dietary diversity of birds at St. Matthew appeared to be less than during the summer.

Table 13. Prey (% occurrence) taken by seabirds at St. Matthew Island, based on collections in October 1982 (25 birds) and July 1983 (41 birds). NOFU=Northern Fulmar, BLKI=Black-legged Kittiwake, TBMU=Thick-billed Murre, LEAU=Least Auklet, CRAU=Crested Auklet, PIGU=Pigeon Guillemot, HOPU=Horned Puffin, GLGU=Glaucous Gull, COMU=Common Murre, PAAU=Parakeet Auklet

	NOFU	BLKI	TBMU	LEAU	CRAU	PIGU	HOPU
N (OCTOBER)	11	4	1	3	2	1	3
Jellyfish	9%				50%		
Nereid	9%						
Squid	82%						
Unid. Copepod		25%		66%			
<u>Parathemisto pacifica</u>	9%			33%			
Unid. Hyperiid				33%			
Unid. Amphipod							33%
<u>Thysanoessa raschii</u>				33%			
<u>Spirontocaris tridens</u>					50%	100%	
Unid. Crustacean	27%						33%
<u>Theragra</u>	9%	25%			100%		
Unid. Gadid			100%				33%
Osmeridae		50%					33%
Unid. Fish	27%	25%				100%	33%

	NOFU	BLKI	TBMU	LEAU	GLGU	COMU	PAAU
N (JULY)	8	8	5	3	1	8	8
Jellyfish	37%	75%	20%		100%	25%	50%
Nereid	12%	25%					25%
Pteropod		12%					25%
Squid	87%						
Unid. Copepod	12%			66%			12%
<u>Parathemisto pacifica</u>		25%	60%	33%			25%
Unid. Hyperiid	50%	87%	20%		100%	12%	50%
Unid. Gammarid	37%	37%					
Unid. Amphipod	12%						
Unid. Euphausiid	12%		20%				
Unid. Decapod		12%					
Unid. Crustacean	25%	12%	20%		100%		12%
Unid. Gadid		37%	40%	33%		87%	
Unid. Myctophid		12%				12%	12%
Unid. Fish	12%	12%	40%			12%	12%
Fork-tailed Storm-petrel		12%					



ASSESSMENT OF OIL SPILL RISK TO BIRDS

by

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**Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 83**

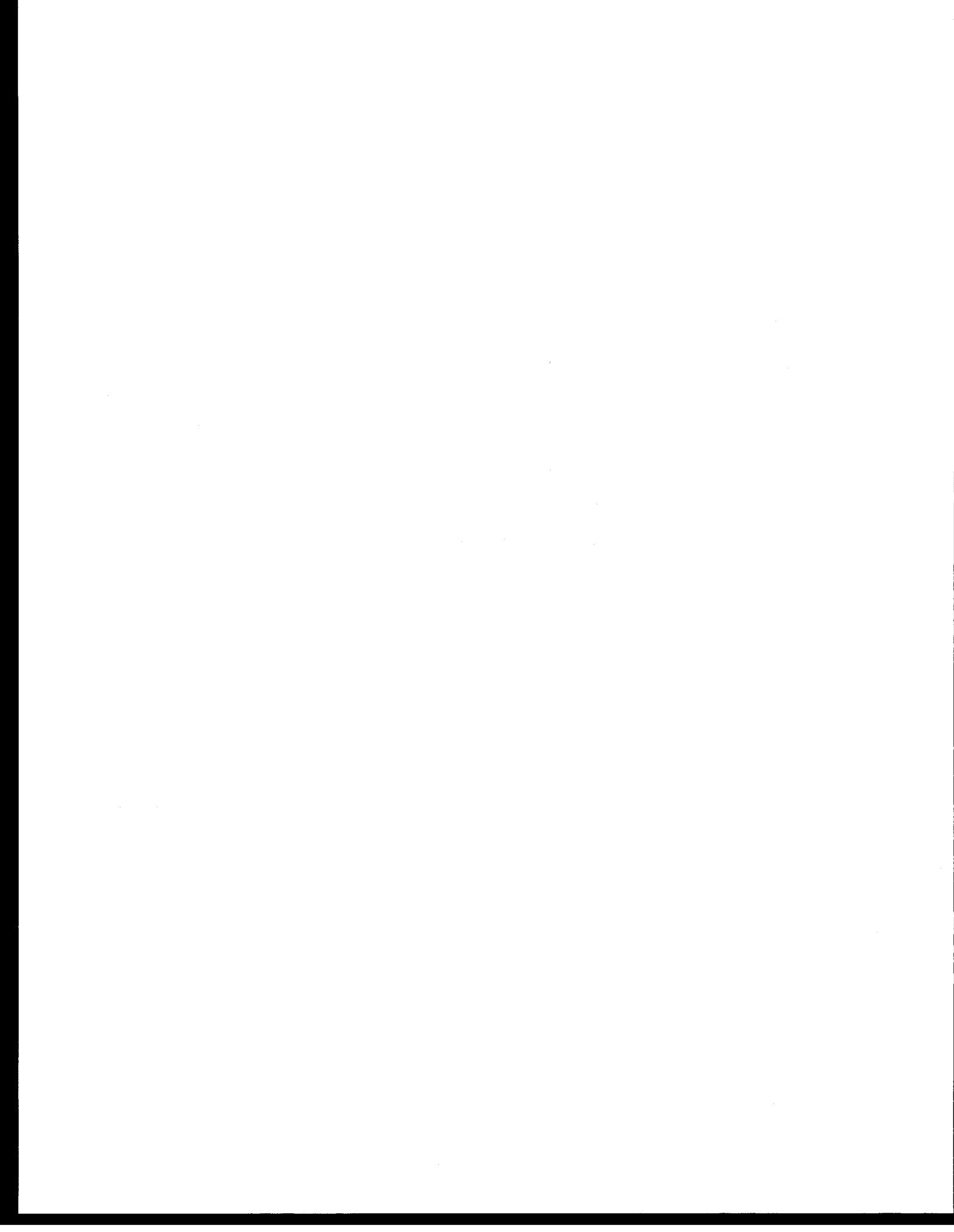
October 1983

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SUMMARY OF OBJECTIVES, CONCLUSIONS, AND IMPLICATIONS
WITH RESPECT TO OCS OIL AND GAS DEVELOPMENT

The objective of this project was to develop a procedure for ranking areas with respect to the relative risk of oil spills to resident and visiting bird populations. Our methods were based on the assumption that the prospect theory of Daniel Kahneman and Amos Tversky (1979) is the most appropriate descriptive model of the way individuals respond to questions concerning decisions about environmental risk.

We found that breeding bird populations were singled out as the most important group to protect, and that respondents showed little inclination to rank moulting, migratory or wintering populations separately from one another. Birds that are about to commence or that have begun breeding have a higher reproductive value than birds that will not breed again for several months or more. Thus this result focuses on the importance of expected reproductive value.

We also compared preferences for avoiding putting various species groups at risk of losing some fraction of their population. We found, not surprisingly, that respondents were least willing to risk populations of species defined as having low reproductive rates, and conversely, species with high reproductive rates were seen as of lesser concern. Alcids were accorded high levels of concern, as were swans. While the alcids fit the category of species with low reproductive rates, swans may not. Possibly small population size, true especially of Trumpeter Swans (Olor buccinator), was a factor, or possibly more emotional/aesthetic considerations influenced the high degree of protection sought for them.

We found that respondents tended not to differentiate between our bird-groups when the local population put at risk was equal to or less than 10% of the world population, or when the local population was equal to or greater than 50% of the world population of the bird-groups in question. The biological interpretation of this result is that below 10% of the world population, the risk to each species as a whole is small enough that no one species category was singled out as of greater concern. On the other hand, when there is a potential loss of 50% or more of the world population, all species again tend to be of equal concern. A loss of that magnitude would apparently makes any species immediately equivalent to a threatened, if not an endangered, species. These results can be summarized as saying that our respondents would vote to protect preferentially areas where birds breed and areas with bird populations having low reproductive rates.

Our results complement the King and Sanger (1979) Oil Vulnerability Index (OVI) in several ways. First, the high level of agreement between the rankings obtained by our method and one based on the OVI is evidence that biologists do compare birds in a measureable and consistent way. Second, the relatively small number of categories used with success in our study suggests that when risk is being evaluated, differentiation of birds into species is redundant because reproductive potential is the factor attended to most. Third, our data demonstrate the feasibility of obtaining an interval scale of risk, a level of measurement necessary if comparisons between combinations of species or groups of species are to be made. The OVI, being a ordinal scale, cannot be used in this way.

Our findings that respondents' behavior was consistent with prospect theory (Kahneman and Tversky 1979) means that evaluations of risk to birds may be dependent on the manner in which questions concerning that risk are posed.

For example, options described in terms of saving birds may receive different responses than options described in terms of bird losses - as in our questionnaire - even if the expected risks are exactly the same in both cases (Thaler 1980, Tversky and Kahneman 1981). Even if the rank orderings were to remain constant, changes in the relative value of species might result, affecting the overall evaluation of several species taken together. If synthesis meetings for lease areas, or questionnaires are expected to provide consistent information, the possible effects of different ways of presenting the available options should be taken into account.

INTRODUCTION

The prospect of oil exploration, extraction and associated hazards over much of the outer continental shelf of the United States has prompted a program of baseline studies of this region. Included in this program have been a variety of studies of the distribution, abundance, reproductive biology and food habits of marine birds. These studies have successfully identified the places where high concentrations of birds are found, and when they are likely to be there. While there remains much to be learned about these avian populations, we now have for several regions sufficient data to allow preliminary predictions about where and when birds might encounter oil.

We have also made a start on addressing the question of which species are most likely to become oiled if an oil spill should occur in a specific area. The Oil Vulnerability Index (OVI) of King and Sanger (1979) includes 6 factors (Marine Orientation, Roosting, Foraging, Escape, Flocking on Water, History of Oiling) out of 20 that specifically relate to the likelihood that a member of a given species will become oiled. Additional field work addressing the behavior of marine birds when they encounter floating oil is in progress in

southern California (Varoujean, pers. comm.).

A second question that needs to be addressed is the relative value of the individual birds that might become oiled. The loss of an individual from the population of an endangered species is clearly of greater significance to its population than is the loss of an individual of a species that has a large, widely dispersed population. The OVI of King and Sanger (1979) addresses this second question by including a number of factors related to species range, population size, productivity, mortality unrelated to oil, and seasonal changes in distributions. Their index is designed for the northeast Pacific region as a whole, and it is useful for assessing the relative impact of a spill on two or more different species. It is more difficult to apply their index when comparing the risk of an oil spill in two or more small adjacent areas. If each area contains several species, how should the index scores for the different species be combined into a measure which allows inter-area comparison?

A third question is therefore, how should the relevant evidence be evaluated when choosing between alternative oil lease-sale plans. This question includes not only the likelihood of birds present in the area being oiled, but also an assessment of the seriousness of the loss and possibly other factors, not directly linked to biology, that may influence a decision. The decisions as to how to weight the available data clearly go beyond a strictly biological context.

Ideally, one would like to have a scale, derived from biological considerations, that would allow an assessment of the overall risk to birds within a segment of a lease-sale and the ability to compare this assessment to that of any other area. If such a scaling method were at hand, and if all the required data were available, then a panel of experts would have an objective basis for decision making. Additionally, if the decision

procedure itself were also known, managers and others would have much greater success at using the expert's choices in their own decisions.

The need for information about how to rank various options became painfully obvious to us during the St. George Synthesis meeting (BLM 1981) held in Anchorage in April 1981. After careful review of the available data on distribution, abundance and status of birds throughout the area of the lease-sale, we were faced with making recommendations on a variety of lease-sale options. These included the extremes of no sale, selling all nominated tracts or recommending deletions of tracts that would either protect the colonies on the Pribilofs or protect the lagoons of the north side of the Alaska Peninsula, important migratory rest stops and foraging areas for waterfowl. We knew what species were present, how long they were present and what they were doing. We did not have an objective guideline for ranking the two intermediate options and we had to rely on intuition and experience.

These perceived needs led to the project summarized here. When we set out, we had as our main objective the development of a method whereby the choices of experts evaluating risky alternatives for avifauna could be simulated for the purposes of ranking oil lease-areas. In this we have been partially successful. We have obtained by means of a questionnaire rankings for several groups of bird species that agree substantially with the ranks predicted by the OVI. However, unlike the OVI, the scale which ranks our groups of species also provides information about the distance between groups so that the relative value of combinations of groups or species can be compared. We have been only partially successful because, within the scope of this study, relative values for groups of species at all levels of risk could not be obtained. Our evaluation of the risk levels for which we have data suggests our procedures can be used in a way beneficial to both biologists and managers.

METHODS

In order to obtain data about individual choices among risky alternatives, we designed a questionnaire patterned after past research in decision theory (Allais 1953, Kahneman and Tversky 1979, Thaler 1980, Tversky and Kahneman 1981). These other efforts were concerned mostly with fairly simple situations, so our first task was to construct similar questions in terms of birds and their environments.

Questions used in this study were of two types:

1) "Within a specified area, assume endangered species will suffer 0% losses with probability .50 and 100% losses with probability .50. What certain % loss for a species of large birds would you accept as an equivalent substitute?"*

2) "Within a specified area, assume a species with a high reproductive rate will suffer 0% losses with probability .50 and 100% losses with probability .50. What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% of the world population? _____
- c. 10% of the world population? _____
- d. 25% of the world population? _____
- e. over 50% of the world population? _____".

Thirteen bird groups (Table 1) were compared using 3 levels of risk (.25, .50, .75) and 5 levels of local population (1%, 5%, 10%, over 50% of the world population). In addition, 4 types of habitat (migratory, wintering, breeding, moulting) were considered. Included in each questionnaire was a glossary

*The complete questionnaire can be found in Appendix A

defining the bird group labels and habitat names used, along with a lengthy introduction explaining gambles and their expected value. Approximately 35 individuals and organizations were asked to fill out a questionnaire (Table 2); of about 15 replies, 7 were judged suitably complete to be included in our analysis.

Ranking of Bird Groups

Rankings for the thirteen bird groups were obtained from each individual's responses as follows. Consider first type (1) questions. According to prospect theory (see references cited above) many people will over-weight a sure loss relative to gambles having the same expected value. For example, given a choice between a gamble with an expected value of 50% losses for an endangered species and a sure loss of 50% for the same species, most people prefer the gamble, implying the certain loss has the greater negative value. This in turn implies the gamble would be judged equivalent to a certain loss smaller than 50%, say 45%. It follows that if the same gamble is judged equivalent to a certain loss for another species of only 40%, then the latter species must be more valuable than the species involved in the gamble. Similiarly, if the same gamble is judged equivalent to a certain loss for another species that is greater than 45% then the second species must be less valuable than the endangered species. In this manner, using the same gamble, equivalent sure losses for all groups of species can be obtained and transformed into ranks. Gambles involving three levels of risk - .25, .50, .75 probability of 100% losses - to an endangered species were compared to equivalent sure losses for the other twelve groups of birds.

Type (2) questions were used to derive rankings when world populations were taken into account. If the procedures described above were repeated

Table 1
Bird Group Codes *

- 0 Endangered Species
- 1 Large Birds
- 2 Small Birds
- 3 Game Birds
- 4 Subsistence Birds
- 5 Alcids
- 6 Shore Birds
- 7 Gulls
- 8 Swans
- 9 Ducks
- 10 Tubenoses
- 11 Birds with high reproduction rates
- 12 Birds with low reproduction rates

* Brief explanations of these categories are in the glossary of Appendix A

Table 2
Individuals and organizations contacted

Dr. Kees Vermeer, President Pacific Seabird Group Point Reyes Bird Observatory 4990 Shoreline Highway Stinson Beach, CA 94970	Dr. R. A. Paynter, Jr., Editor Nuttall Ornithological Club c/o Museum of Comparative Zoology Harvard University Cambridge, MA 02138
Dr. James A. Tucker, Exec. Direc. American Birding Association P.O. Box 4335 Austin, TX 78765	Dr. Abbot S. Gaunt, President Wilson Ornithological Society Museum of Zoology University of Michigan Ann Arbor, MI 48109
Dr. Ned K. Johnson, President Cooper Ornithological Society Department of Biology University of California Los Angeles, CA 90024	Dr. Paul G. Risser, Secretary Ecological Society of America Office of the Chief, Ill. Nat. His. Sur. 607 E. Peabody Champaign, IL 61820
Dr. Charles Walcott, Exec. Direc. Cornell University Lab. of Ornithology 159 Sapsucker Woods Road Ithaca, NY 14850	Dr. Robert Cahn, Acting Chair The Institute of Ecology Holcomb Research Bldg. Butler University Indianapolis, IN 46208
Mr. Steve Wilson, Chair National Waterfowl Council Arkansas Game and Fish Commission Game and Fish Building Little Rock, AR 72201	Dr. Russell W. Peterson, Pres. National Audubon Society 950 Third Ave. New York, NY 10022
Mr. William D. Blair, President The Nature Conservancy 1800 N. Kent St., Suite 800 Arlington, VA 22209	Dr. Jeffry B. Mitton, Secretary Society for the Study of Evol. 110 Ramalex, Campus Box B-334 University of Colorado Boulder, CO 80309
Mr. Michael McCloskey, Exec. Direc. Sierra Club 530 Bush St. San Francisco, CA 94108	Ms. Karla Slap, Executive Director American Cetacean Society P.O. Box 4416 San Pedro, CA 90731
Ms. Margaret T. Donnald, Sec. Eastern Bird Banding Association 11501 S. Glen Road Potomac, MD 20854	Mr. David Brower, Founder & Board Chair Friends of the Earth 1045 Sansome St. San Francisco, CA 94111
Mrs. John Lueshen, Exec. Officer Inland Bird Banding Association R.F.D. 2, Box 26 Wisner, NE 68791	Chris Cook, Administrative Director Greenpeace U.S.A. 2007 R St., N.W. Washington, D.C. 20009
Ms. Sarah B. Laughlin, Secretary Northeastern Bird-banding Association c/o Vermont Inst. of Natural Science Woodstock, VT 05091	Dr. Russell E. Train, President World Wildlife Fund-U.S. 1601 Connecticut Ave., N.W. Washington, D.C. 20009

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Dr. Dennis M. Power, Secretary
American Ornithologists' Union
National Museum of Natural History
Smithsonian Institution
Washington, D.C. 20560

Ms. Beverly A. Bevan, Secretary
North American Habitat Preservation Society
P.O. Box 869
Adelphi, MD 20783

for all five local population levels our questionnaire would have been prohibitively long, so we ranked each bird group by the magnitude of its equivalent loss. We assumed that for any particular gamble, the more valuable a species, the smaller the corresponding equivalent loss. When bird groups or habitats were judged to have the same rank, each was assigned the average of the ranks they would have been assigned had no ties occurred (Siegal 1956).

The question of how well people agree on their bird group preferences is important for managers because strong agreement suggests a strong concensus of opinion is possible, and it is important for biologists because strong agreement suggests the concept of value may have a substantive basis. To test the level of agreement, individual rank-orderings of the bird groups were compared across risk levels and different population proportions using the Kendall coefficient of concordance. If this statistic was significantly large, we could assume each individual had an underlying rank ordering of the bird groups which we could estimate as suggested by Kendall (1948). Using the same statistic, these individual rankings were compared and tested for a single ranking aggregated across subjects. Rankings based on the Oil Vulnerability Index and our methods were compared using the Kendall rank correlation coefficient τ .

Habitats were compared at each level of risk by counting the number of subjects that ranked birds in one kind of habitat as more or less valuable than birds in another. For example, if a subject indicated a 30% sure loss for birds in a breeding area was equivalent to a .25 chance at 100% losses in a breeding area, but the same gamble was equivalent to a 40% sure loss in a migratory route, then we assumed that subject valued birds in a breeding area more than birds in a migratory route.

Table 3

Equivalent sure losses for endangered species within a breeding area.

Gambles*			
Subj.	(-100%, .25)	(-100%, .50)	(-100%, .75)
A	-.85	-.95	-.98
B**	-.10	-.05	-.05
C	-.75	-.85	-.90
D	-.125	-.25	-.50
E	-.60	-.70	-.80
F	-.30	-.80	-.90
G	-.10	-.10	-.10
Expected Value	-.25	-.50	-.75

$$\chi^2 = 8.33, p < 0.016 \text{ (N = 6)}$$

*(-100%,x) represents the gamble; an x chance of 100% losses and an 1-x chance at 0% losses.

**not included in the chi-square test, see text page 13.

RESULTS

Table 3 gives our respondents' sure losses for gambles involving endangered species in a breeding area; subject A indicated a sure loss of 85% was equivalent to a .25 chance at 100% losses. This table was derived from the first set of questions asked. These questions were the least complex of all the questions and were designed to both familiarize the subject with the form of the questionnaire and to test our assumption that risk was evaluated in a manner consistent with prospect theory. If, contrary to prospect theory, subjects compute the expected value of risky choices, in the present context they should tend to evaluate a .25 chance of 100% losses of an endangered species as close to a certain loss of 25%. The data in Table 3 and throughout our study do not support this assumption. Table 3 does offer evidence that our subjects understand the questions to the extent that larger equivalent losses are associated with greater risk ($\chi^2 = 8.33$); as the size of the expected loss (risk level) increases, more birds would be given up to avoid the gamble. (An exception is subject B, but this individual does not repeat the pattern seen in Table 3 in the rest of the questionnaire.)

Table 4(A) shows that 6 of the 7 respondents valued birds in a breeding area over each of the other three habitats when comparisons were made based on a .25 chance at 100% losses. At the same level of risk, 3 subjects valued birds in a migratory route over birds in a moulting area, 3 subjects valued moulting over migratory and 1 subject was indifferent between these two habitats, and so on. The exhibited preference of breeding to other habitats has a multinomial probability of less than 0.01 of being due to chance. For the .5 gamble, the only significant preference was breeding over moulting, and at the .75 level of risk, no significant preferences are evident.

Table 4(B) further illustrated the homogenizing effect of increasing risk. At each level of risk, three comparisons were made, breeding against migratory,

breeding against moulting, and breeding against wintering. Each habitat could receive a maximum score of 7 (i.e. 7 subjects showed a preference for one over the other) in each comparison for a total of 21. The preference exhibited by our subjects for birds in a breeding ground clearly is reduced as risk increases.

Rank Ordering of Bird Groups

Table 5 summarizes the ranks assigned to the thirteen bird groups based on the equivalent losses indicated by respondent A for three different gambles, as in the type (1) question described earlier. The first row corresponds to the gamble where an endangered species has a .25 probability of suffering 100% losses, the second row to a .50 probability of 100% losses, and the third row to a .75 probability of 100% losses. For example, at the .25 level of risk, Subject A indicated bird groups coded 8 and 10 were more valued than any other bird group but equal to each other, thus each received a rank of 1.5. The Kendall coefficient of concordance for this table is sufficiently large ($W=.874$) to justify the assumption that this subject's ranking of the bird groups is independent of the risk level, and to accept as the best estimate of the underlying ranking the column sums given in row 4 (Kendall 1948).

Two rankings of the bird groups were obtained from type (1) questions (i.e., those questions not mentioning world populations). First, a ranking across gambles was obtained for each subject as in Table 5. Table 6 gives these rankings with the derived overall ranking in the last row. The second ranking was obtained by deriving a ranking for each gamble across subjects and then summarizing across gambles. Table 7 gives the derivation for the .25 gamble and Table 8 the summary rank order.

Type (2) questions were used to construct a third ranking of the bird

Table 4(A)

Habitat Preference by Subject
 The number of respondents ranking the row category over the column category

		Br	Mi	Mo	Wn
	Br/	-	6*	6*	6*
.25	Mi/	1	-	3.5	4.5
	Mo/	1	3.5	-	4
	Wn/	1	2.5	3	-
		Br	Mi	Mo	Wn
	Br/	-	4	5*	4
.50	Mi/	3	-	4	4
	Mo/	2	3	-	3.5
	Nr/	3	3	3.5	-
Risk Level (gamble)		Br	Mi	Mo	Wn
	Br/	-	3.5	3.5	3.5
.75	Mi/	3.5	-	4	3
	Mo/	3.5	3	-	2.5
	Wn/	3.5	4	4.5	-

Key Br = Breeding
 Mi = Migratory
 Mo = Moultling
 Wn = Wintering

*p < .01

**p < .05

Table 4(B)

Habitat Preference by Subject
Breeding Area Against All Others

		Breeding Area	Other Areas
Risk Level (gamble)	.25	18	10.5
	.50	13	10.5
	.75	10.5	10.5

$p < .05$, $df = 2$ ($\chi^2 = 5.952$)

Table 5

Subject A Rankings

Bird Group Code*

	0	1	2	3	4	5	6	7	8	9	10	11	12	
.25	3	7.5	12.5	7.5	7.5	7.5	7.5	7.5	1.5	7.5	1.5	12.5	7.5	
.50	1	8	12.5	8	8	8	8	8	3	8	3	12.5	3	
Risk	.75	2.5	9.5	12.5	9.5	9.5	6	6	2.5	2.5	6	2.5	12.5	9.5
Col Sum	6.5	25	37.5	25	25	21.5	21.5	18	7	21.5	7	37.5	20	
Rank	1	10	12.5	10	10	7	7	4	2.5	7	2.5	12.5	5	

$W = .874^{**}$, $\chi^2 = 31.45$, $df = 12$, $p < .01$

*See Table 1 for explanations of bird-group codes

**Kendall coefficient of concordance

groups. Only when the local population at risk totaled 25% of the world population did subjects exhibit consistent rankings for each type of gamble. At the 25% population level all subjects except F (this person inverted ranks unintentionally) gave consistent rankings so we removed F from this particular analysis and proceeded as in Tables 7 and 8. Table 9 gives the rankings obtained.

Comparison to the Oil Vulnerability Index

Table 10 compares the rankings we obtained in Tables 6, 8 and 9 to one based on the King and Sanger OVI (1979). This OVI based ranking was constructed by categorizing all the species considered by King and Sanger into our species groups, calculating the average OVI score for each species group, and ranking the averages. The overall agreement between the four rankings is very high ($W=.748$), so an aggregate ranking was estimated as before and placed in the last column. Table 11 gives the same four rankings rearranged into order of vulnerability. Notice that the two rankings having the greatest degree of association (Kendall's τ) are W_1 and W_2 ($\tau=.929$) while the smallest τ is between the OVI ranking and W_3 ($\tau=.258$).

DISCUSSION

The relatively small proportion of responses obtained in this study can be attributed not only to an inclination on the part of many biologists to avoid value judgements, but also to difficulties inherent in the nature of the study.* The amount of information necessary for this kind of analysis is best obtained by repeated interviews, but unfortunately this was not possible. Our only alternative was to make use of a questionnaire which

*See Appendix B for some comments by respondents.

Table 6
Bird Group Ranks Across Subjects*

Bird Group Code**

SUBJECT	0	1	2	3	4	5	6	7	8	9	10	11	12
A	1	10	12.5	10	10	7	7	4	2.5	7	2.5	12.5	5
B	13	5	5	11	9.5	5	5	5	1.5	9.5	8	12	1.5
C	13	6	6	6	6	3	10	12	1.5	6	10	10	1.5
D	13	7	7	7	7	7	7	7	7	7	7	7	1
E	1	8.5	12	6.5	4	2.5	11	5	2.5	2.5	6.5	13	10
F	1	7.5	7.5	7.5	7.5	7.5	7.5	7.5	7.5	12	2.5	13	2.5
G	6	4	9.5	9.5	5	1	11.5	13	7	8	3	11.5	2
Sum	48	48	59.5	57.5	49	33	59	53.5	29.5	58	39.5	79	23.5
Rank	5.5	5.5	12	8	7	3	10	11	2	9	4	13	1

$W = .349^{***}$, $\chi^2 = 29.30$, df = 12, p < .01

*derived from type (1) questions

**See Table 1

***Kendall coefficient of concordance

Table 7
Bird Group Ranks across Subjects at .25 Risk Level

Bird Group Codes*

SUBJECT	0	1	2	3	4	5	6	7	8	9	10	11	12
A	3	7.5	12.5	7.5	7.5	7.5	7.5	7.5	1.5	7.5	1.5	12.5	7.5
B	12	5.5	5.5	12	9.5	5.5	5.5	5.5	1.5	9.5	5.5	12	1.5
C	10.5	6	6	6	6	7	10.5	13	2	6	10.5	10.5	2
D	13	7	7	7	7	7	7	7	7	7	7	7	1
E	1	8	11.5	8	3.5	3.5	11.5	3.5	3.5	8	8	13	8
F	1	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	12.5	6.5	12.5	6.5
G	3	3	8.5	8.5	6	3	12.8	13	8.5	8.5	3	12.5	3
Sum	43.5	43.5	57.7	55.5	46	35	61	56	30.5	59	42	80	29.5
Rank	5.5	5.5	12	8	7	3	10	11	2	9	4	13	1

$W = .354^{**}$, $\chi^2 = 29.77$, df = 12, p < .01

*See Table 7

**Kendall coefficient of concordance

Table 8

Bird Group Ranks across Subjects and Risk Levels

Bird Group Code*

RISK	0	1	2	3	4	5	6	7	8	9	10	11	12	W	p(χ^2)
.25	5.5	5.5	10	8	7	3	12	9	2	11	4	13	1	.354	<.01
.50	7	6	11	8	4	3	9	11	1	11	5	13	2	.283	<.05
.75	7	5	12	9.5	8	4	11	9.5	2	6	3	13	1	.309	<.02
Sum	19.5	16.5	33	25.5	19	10	32	29.5	5	28	12	39	4		
Rank	7	5	12	8	6	3	11	10	2	9	4	13	1		

W = .923**, χ^2 = 33.23, df = 12, p < .001

*See Table 1

**Kendall coefficient of concordance

Table 9
Bird Group Ranks at the .25 population level*

RISK	Bird Group Code*												
	0	1	2	3	4	5	6	7	8	9	10	11	12
.25	9	6.5	6.5	11	11	2	6.5	3	4	11	6.5	13	1
.50	10	5	3	11.5	9	2	7	5	5	11.5	8	13	1
.75	9	6	6	11	11	2	6	6	3	11	6	13	1
Sum	28	17.5	15.5	33.5	31	6	19.5	14	12	33.5	20.5	39	3
Rank	9	6	5	11.5	10	2	7	4	3	11.5	8	13	1

w = .959, $\chi^2 = 34.54$, df = 12, p < .001

*See Table 1

**N = 6

Table 10

Comparison of Derived Ranks to Oil Vulnerability Index

Ranking by different criteria

Species Group	OVI*	W_1^{**}	W_2^{***}	W_3^{****}	Aggregate Rank
Endangered Species	1	5.5	7	9	5.5
Large Birds	6	5.5	5	6	5.5
Small Birds	9	12	12	5	10
Game Birds	12	8	8	11.5	11
Subsistence Birds	8	7	6	10	7
Alcids	2	3	3	2	2
Shore Birds	3	10	11	7	12
Gulls	11	11	10	4	8
Swans	5	2	2	3	3
Ducks	7	9	9	11.5	9
Tubenoses	4	4	4	8	4
Birds with high reproduction rates	10	13	13	13	13
Birds with low reproduction rates	3	1	1	1	1

OVI*: Ranks based on Oil Vulnerability Index;

W_1^{**} : Ranks based on table 6;

W_2^{***} : Ranks based on table 8;

W_3^{****} : Ranks based on table 9.

Table 11

Bird Groups In Order of Vulnerability*

		OVI	W_1	W_2	W_2	Aggregate Rank
High	1	Endangered Birds	Birds with low reproduction rates			
	2	Alcids	Swans	Swans	Alcids	Alcids
	3	Birds with low reproduction rates	Alcids	Alcids	Swans	Swans
	4	Tubenoses	Tubenoses	Tubenoses	Gulls	Tubenoses
	5	Swans	Endangered Species	Large Birds	Small Birds	Endangered Species
	6	Large Birds	Large Birds	Subsistence Birds	Large Birds	Large Birds
	7	Ducks	Subsistence Birds	Endangered Species	Shore Birds	Subsistence Birds
	8	Subsistence Birds	Game Birds	Game Birds	Tubenoses	Gulls
	9	Small Birds	Ducks	Ducks	Endangered Species	Ducks
	10	Birds with high reproduction rates	Shore Birds	Gulls	Subsistence Birds	Small Birds
	11	Gulls	Gulls	Shore Birds	Ducks	Game Birds
	12	Game Birds	Small Birds	Small Birds	Game Birds	Shore Birds
Low	13	Shore Birds	Birds with high reproduction rates			

$$\begin{aligned}\tau(W_1, W_2) &= .929, P(z=4.42) < .001 \\ \tau(OVI, W_1) &= .568, P(z=2.70) < .003 \\ \tau(OVI, W_2) &= .538, P(z=2.56) < .006 \\ \tau(W_2, W_3) &= .452, P(z=2.15) < .015 \\ \tau(W_1, W_3) &= .429, P(z=2.04) < .02 \\ \tau(OVI, W_3) &= .258, P(z=1.22) > .10\end{aligned}$$

*Rankings defined in Table 10

was necessarily very long and complex, and to limit our formal analysis to order statistics. Nevertheless, we have some substantive results to report.

Comparing Rankings. First of all, the rankings of our bird groups were obtained in a way very different from that used by King and Sanger to construct their OVI, and yet the results of both methods are similar (Tables 10 and 11). This is reassuring because it is evidence that biologists evaluate risk to birds in a reliable manner. It also suggests both ways of measuring vulnerability are sensitive to the same factors. Our results have shed some light on the nature of these factors.

The data in Tables 10 and 11 support our contention that risk is evaluated primarily on the basis of features closely related to reproduction rates. Species having high reproductive rates tend to be ranked as least vulnerable while species with low reproductive rates tend to be ranked as most vulnerable. The large concordance statistic associated with the four rankings ($W=.748$) suggests all four have the same underlying rank order with the observed differences accounted for mostly by a confounding of the notions of risk and the meaning of a species being "endangered".

If vulnerability is mostly a function of reproductive ability, then as more birds are put at risk the class of endangered species will tend to contain additional species so that the property of being endangered can no longer be used to discriminate between species. The rank of an endangered species is therefore likely to drop as risk increases, and this is what we see in Tables 10 and 11.

The strongest pair-wise relationship in Table 11 is between rankings W_1 and W_2 which were constructed from answers to questions that did not draw attention to the size of the local bird population put at risk, relative to the world population of the same species. The weakest association is

that between the OVI derived ranking and W_3 . The W_3 ranking is based on answers to questions that drew the respondents attention to the size of the local population at risk relative to the world population, increasing the absolute level of risk. What is most obvious about these different rankings is the movement of the rank assigned to endangered species. The OVI automatically forces any endangered species - a category defined almost exclusively in terms of numbers of birds - to be ranked as most vulnerable. Our method on the other hand, did not prejudge the relative importance of any particular species, whether or not it was endangered, and we have found a decreasing relative preference for endangered species as perceived risk increases.

Utilizing Ranks. The ordered rankings we have constructed and the OVI of King and Sanger can be used for management decisions when the distance between ranks is not important. This would be the case, for instance, if all the species in one lease-area were ranked lower than all the species in another area, and the higher ranked species were in numbers at least as great as the lower ranked species. It is true that population size is one of the factors in the King and Sanger index but this does not allow one to claim that an OVI score of 80 is twice as large as an OVI score of 40, and this is what is essential if combinations of species with different size local populations are to be compared.

If a selected group of individuals were made available for repeated testing, the methods used in this study would provide an interval scale of vulnerability. Several estimates of the equivalent losses used in our analysis could be used to calculate the distance between ranks so that any combination of ranks and populations could be compared to any other combination. To illustrate, if for a given gamble the sample estimate of the equivalent loss for species with a high reproduction rate was .6 and

the sample estimate of the equivalent loss for species with a low reproduction rate was .2 then we could say the latter was rated as three times as vulnerable as the former, i.e. one individual was equivalent to three individuals of the other type.

Several levels of complexity are available with this procedure. We have so far discussed rank order aggregated across subjects and the corresponding interval scales. Management decisions could be made at a lower level of aggregation by using the individual interval scales of each subject to "vote" on alternatives. Each individual, as represented by his or her scale, would indicate yes or no and management could then use the total vote count as an indication of general preference.

A still lower level of aggregation is also available. Our work so far indicates that the way individuals rank order species is fairly constant - except for endangered species - over different gambles, but between rank distances may change and this would affect the evaluation of combinations of species. This problem would be reduced if several scales were constructed for each individual, each scale corresponding to a particular level of risk. If the format of our study were used, every respondent would have three scales of vulnerability, one for each gamble (.25, .50, .75 probability of total loss). Management could then take a vote on alternatives as described in the previous paragraph, using the appropriate scale for individual voters.

Prospect Theory. If management chooses to solicit opinions with questionnaires or especially in an open forum such as a synthesis meeting, they should be aware that "Individuals who face a decisive problem and have a definite preference (i) might have a different preference in a different framing of the same problem (ii) are normally unaware of alternate frames and their potential effects on the relative attractiveness of options, (iii) would wish their preferences to

be independent of frame, but (iv) are often uncertain how to resolve detected inconsistencies" (Slovic and Tversky 1974).

The following generic problems (Tversky and Kahneman 1981) illustrate the inconsistencies which may arise when framing effects are not paid attention to (the proportion of respondents preferring each alternative is given in brackets).

Problem 1. [N=152]

Imagine that the U.S. is preparing for the outbreak of a rare Asian disease, which is expected to kill 600 people. Two alternative programs to combat the disease have been proposed. Assume that the exact scientific estimates of the consequences of the program are as follows:

If program A is adopted, 200 people will be saved [72%].

If program B is adopted, there is a 1/3 probability that 600 people will be saved and a 2/3 probability that no people will be saved [28%].

Which of the two programs would you favor?

Problem 2. Same cover story [N=155].

If program C is adopted, 400 people will die [22%].

If program D is adopted there is a 1/3 probability that nobody will die and a 2/3 probability that 600 people will die [78%].

Notice that programs A and C have identical outcomes (400 dead) and programs B and D have identical expected values (400 dead). The only difference in the two problems is the wording of the options and yet the majority of people in the study reversed preference. People tend to value the "sure thing" over a gamble having an expected value equal to the "sure thing".

Program A is seen as a gain of 200 lives and is therefore preferred to program B. Program C is seen as a loss of 400 lives and this has a more negative value than the preferred option program D. Frames of reference that interpret

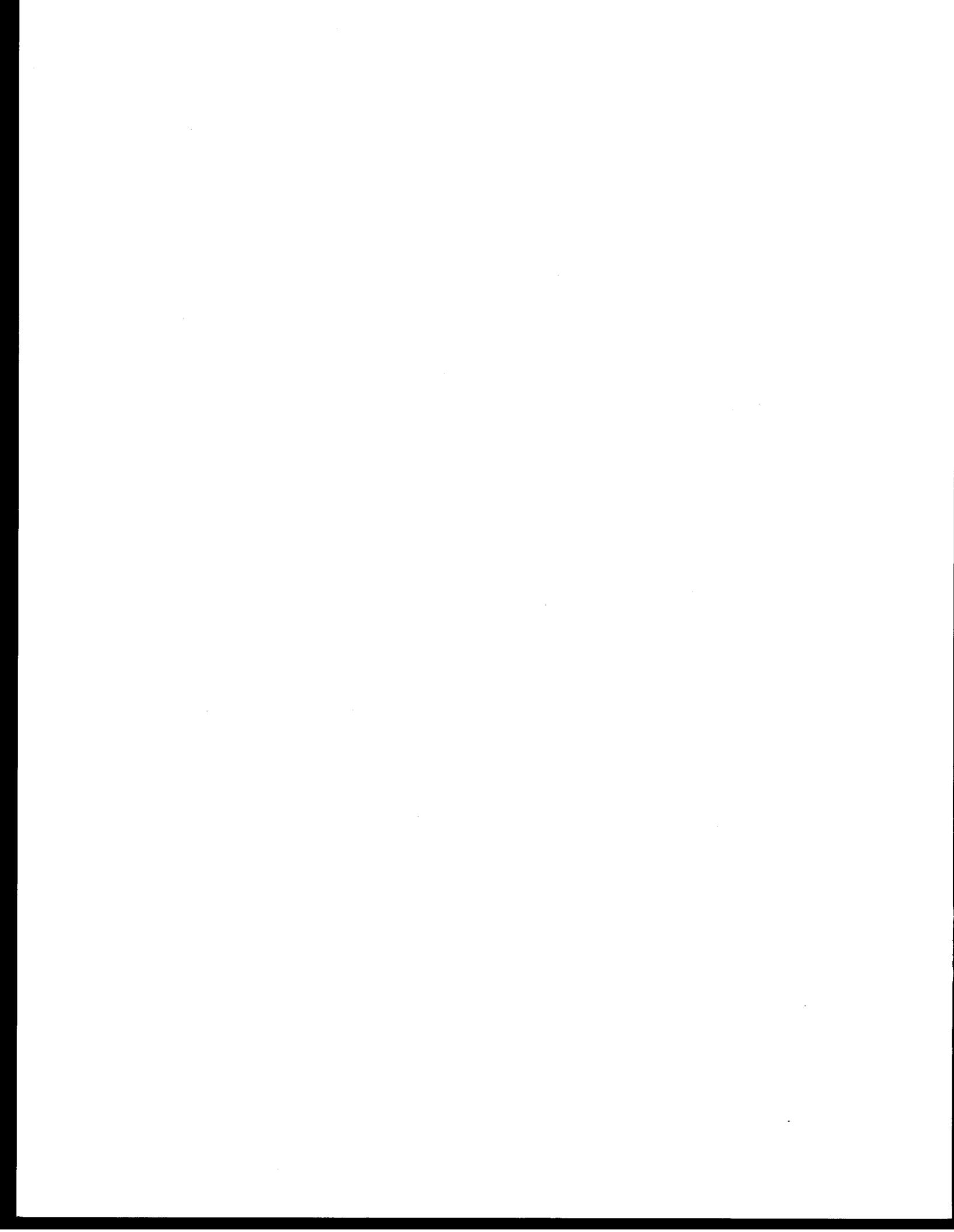
as gains or losses can affect preferences.

Another source of difficulty is the tendency to group the costs and benefits associated with an object. "Imagine you are about to buy a jacket for \$125 and a calculator for \$15. The calculator salesman tells you that the calculator you want to buy is on sale for \$10 at the other branch of the store, a 20-minute drive away. Would you make the drive? (Kahneman and Tversky 1982)" The majority of people who answered this question said they would make the trip. However, when another group of respondents were given a similar problem with the cost of the jacket changed to \$15 and the cost of the calculator changed to \$125 and \$120 in the other store, most people said they would not make the trip. In both cases the costs and benefits were the same but a reduction from \$15 to \$10 was seen as more valuable than a reduction from \$125 to \$120.

The point we are making with these examples is that carefully worded questions are mandatory if reliably consistent preferences are to be obtained. The questionnaire used in this study was constructed with these considerations in mind and a number of individuals were able to understand the questions and give sensible answers without prompting from us other than the written introduction and directions. We would expect open discussions such as those conducted at synthesis meetings to have little chance at producing a reliable concensus of opinion if a comparable level of attention is not paid to the structure of options.

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Appendix A. Questionnaire

PREFACE

George Hunt and I are working on an application of decision theory to the problem of rank-ordering different geographical regions in terms of their environmental sensitivity. We intend to develop a decision rule that incorporates both the best available quantitative field work and the subjective expertise of knowledgeable persons. The enclosed questionnaire is our first attempt at designing a quantitative measure of ecological risk. The answers supplied by yourself and others will provide data necessary for the derivation of a preference structure in the context of bird ecology. This project, funded by the Bureau of Land Management through the National Oceanic and Atmospheric Administration, is primarily concerned with analyzing the risk to Alaska seabirds associated with oil spills, but we believe our methodology can be adapted for applications in other natural situations.

The mathematical details of our methodology will be made available to respondents or other interested parties as requested. In brief, we propose to derive a set of mathematical functions which approximate individual preferences for risky situations. These functions will be combined into a single decision rule and this, in turn, used to rank-order potentially hazardous situations for seabirds. We acknowledge the fact that preferences implied by a group decision are not necessarily identical to those based on any particular individual's preferences, and consequently the particular method used to obtain group choices is likely to be somewhat controversial. We would be most happy to reply to any

comments or suggestions you might have concerning this matter. We, of course, are solely responsible for any short-comings of our methodology and do not presume to speak for any person generous enough to contribute to our effort.

INTRODUCTION

As we mentioned previously, our goal is to devise a rule whereby any number of geographical regions can be compared and ranked in terms of their ecological value. To do this we have selected a particular method of quantifying your judgments of relative value that requires a series of choices between hypothetical future events, which can occur for certain, and alternative gambles--or lotteries as they are sometimes called--in which the ultimate outcomes are generally uncertain. This method, as we have interpreted it in the context of bird ecology, is based on research done by Howard Raiffa, Duncan Luce, Amos Tversky, Daniel Kahneman, and others, in the fields of decision theory and the psychology of choice.

To illustrate the ideas underlying our approach, consider first the situation where each possible consequence of an oil spill within a specified region is assigned a cost in dollars and a probability of occurrence so that the sum of all the probabilities equals 1.0. Under these circumstances, one way to rank-order regions is to simply compute the expected dollar cost associated with each region (the cost of each consequence multiplied by its probability, summed over each region) and assign preferences based on the assumption that smaller expected costs are more valued than larger expected costs.

One immediate objection to this scheme is the observation that expected costs do not reflect the full range of consequences of a choice. For example, a region with a 75% chance of a moderate oil spill (estimated cost = \$50,000.00) and a 25% chance of a small spill

(estimated cost = \$30,000.00) would have the same value as a region with a 50% chance of little oil damage (\$10,000.00) and a 50% chance of considerable damage (\$80,000.00); the expected cost in each region is \$45,000.00. It is not unreasonable to suggest some people might consider the latter region to be more risky, especially if \$80,000.00 were an intolerable, or unrecoverable loss. Expected value schemes do not take into account factors such as threshold conditions. In fact, when individuals are asked to make real choices with risk involved, they typically do not make their choice based on expected values. This result cannot be interpreted merely as irrational or inconsistent behavior. It is evidence that external factors are commonly taken into account when a choice must be made between risky alternatives. This point of view has led researchers such as those mentioned above to expend considerable effort in perfecting methods for determining mathematical descriptions of the choices people actually make when ranking hypothetical risky outcomes. Their findings (e.g., Schlaifer¹⁹⁶⁹) form the basis upon which our questionnaire is structured.

Since we are dealing in a context where money is not a direct consideration, we have selected as the unit of analysis individual birds rather than dollars. In an effort to capture some of the complexity of an ecological system, we have included questions which are intended to reveal relationships between different categories of birds and different types of bird habitats. The particular hazardous event we had in mind when constructing the questions is an oil spill which impacts a finite region for a finite amount of time. The consequences of this event are

always given as potential levels of bird mortality, in terms of either classifications of birds or classifications of habitat. What we ask is that you place a value on each of the risky sets of consequences we describe.

The complication is that the values you indicate must be in terms of proportions of birds lost, either when the birds are those typically found in the region being considered or when the birds are all members of a particular category. All the questions you will see are composed of two parts, a description of a gamble having two possible consequences and a request for the "sure thing" alternative consequence you judge to be an equivalent substitute for the gamble. With consequences in terms of proportion of birds lost, the gamble in a typical question is phrased thusly: "Suppose within a region x there is a .25 probability of 0% mortality for birds of Type Y and a .75 probability of 100% mortality for birds of Type Y." The value you place on this gamble is the "certain" loss--i.e., a proportional loss with probability 1.0--that you would be willing to substitute for the gamble.

- Given a colony/breeding ground, assume birds of an endangered species will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this endangered species would you accept as an equivalent substitute for the above gamble?

answer _____

- Given a colony/breeding ground, assume an endangered species will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this endangered species would you accept as an equivalent substitute for the above gamble?

answer _____

- Given a colony/breeding ground assume an endangered species will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this endangered species would you accept as an equivalent substitute for the above gamble?

answer _____

- Assume 0% bird losses will occur in a colony/breeding ground with probability 1.0.

Given the same size population in a moultling area, what certain % loss for birds typical of this area would you accept as a substitute?

answer _____

5. Assume 0% bird losses will occur in a colony/breeding ground with probability 1.0.

Given the same size population in a migratory route, what certain % loss for birds typical of this region would you accept as a substitute?

answer _____

6. Assume 0% bird losses will occur in a colony/breeding ground with probability 1.0.

Given the same size population in a wintering ground, what certain % loss for birds typical of this area would you accept as a substitute?

answer _____

7. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .75 and 100% bird losses will occur with probability .25.

Given the same size population in a moultling area, what certain % bird loss would you accept as equivalent to the above gamble?

answer _____

8. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .75 and 100% bird losses will occur with probability .25.

Given the same size population in a migratory route, what certain % bird loss would you accept as equivalent to the above gamble?

answer _____

9. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .75 and 100% bird losses will occur with probability .25.

Given the same size population in a wintering ground, what certain % bird loss would you accept as equivalent to the above gamble?

answer _____

10. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .50 and 100% bird losses will occur with probability .50.

Given the same size bird population in a moultling ground, what certain % loss would you accept as equivalent to the gamble?

answer _____

11. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .50 and 100% bird losses will occur with probability .50.

Given the same size bird population in a migratory route, what certain % loss would you accept as equivalent to the gamble?

answer _____

12. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .50 and 100% bird losses will occur with probability .50.

Given the same size bird population in a wintering ground, what certain % loss would you accept as equivalent to the gamble?

answer _____

13. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .25 and 100% bird losses will occur with probability .75.

Given the same size bird population in a moultling ground, what certain % loss would you accept as equivalent to the gamble?

answer _____

14. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .25 and 100% bird losses will occur with probability .75.

Given the same size bird population in a migratory route, what certain % loss would you accept as equivalent to the gamble?

answer _____

15. Assume, at a colony/breeding ground, 0% bird losses will occur with probability .25 and 100% bird losses will occur with probability .75.

Given the same size bird population in a wintering ground, what certain % loss would you accept as equivalent to the gamble?

answer _____

16. Within a specified area, assume 0% losses for an endangered species has probability 1.0.

a. What certain % loss for a species of large birds would you accept as an equivalent substitute?

answer _____

b. What certain % loss for a species of small birds would you accept as an equivalent substitute?

answer _____

c. What certain % loss for a species of game birds would you accept as an equivalent substitute?

answer _____

d. What certain % loss for a species of subsistence birds would you accept as an equivalent substitute?

answer _____

e. What certain % loss for a species of Alcids would you accept as an equivalent substitute?

answer _____

f. What certain % loss for a species of shore birds would you accept as an equivalent substitute?

answer _____

g. What certain % loss for a species of gulls would you accept as an equivalent substitute?

answer _____

h. What certain % loss for a species of swans would you accept as an equivalent substitute?

answer _____

i. What certain % loss for a species of ducks would you accept as an equivalent substitute?

answer _____

j. What certain % loss for a species of tubenoses would you accept as an equivalent substitute?

answer _____

k. What certain % loss for a species with a high reproductive rate would you accept as an equivalent substitute?

answer _____

l. What certain % loss for a species with a low reproductive rate would you accept as an equivalent substitute?

answer _____

17. Within a specified area, assume endangered species will suffer 0% losses with probability .75 and 100% losses with probability .25.
- a. What certain % loss for a species of large birds would you accept as an equivalent substitute?
answer _____
- b. What certain % loss for a species of small birds would you accept as an equivalent substitute?
answer _____
- c. What certain % loss for a species of game birds would you accept as an equivalent substitute?
answer _____
- d. What certain % loss for a species of subsistence birds would you accept as an equivalent substitute?
answer _____
- e. What certain % loss for a species of Alcids would you accept as an equivalent substitute?
answer _____
- f. What certain % loss for a species of shore birds would you accept as an equivalent substitute?
answer _____

g. What certain % loss for a species of gulls would you accept as an equivalent substitute?

answer _____

h. What certain % loss for a species of swans would you accept as an equivalent substitute?

answer _____

i. What certain % loss for a species of ducks would you accept as an equivalent substitute?

answer _____

j. What certain % loss for a species of tubenoses would you accept as an equivalent substitute?

answer _____

k. What certain % loss for a species with a high reproductive rate would you accept as an equivalent substitute?

answer _____

l. What certain % loss for a species with a low reproductive rate would you accept as an equivalent substitute?

answer _____

18. Within a specified area, assume an endangered species will suffer 0% losses with probability .50 and 100% losses with probability .50.

a. What certain % loss for a species of large birds would you accept as an equivalent substitute?

answer _____

b. What certain % loss for a species of small birds would you accept as an equivalent substitute?

answer _____

c. What certain % loss for a species of game birds would you accept as an equivalent substitute?

answer _____

d. What certain % loss for a species of subsistence birds would you accept as an equivalent substitute?

answer _____

e. What certain % loss for a species of Alcids would you accept as an equivalent substitute?

answer _____

f. What certain % loss for a species of shore birds would you accept as an equivalent substitute?

answer _____

g. What certain % loss for a species of gulls would you accept as an equivalent substitute?

answer _____

h. What certain % loss for a species of swans would you accept as an equivalent substitute?

answer _____

i. What certain % loss for a species of ducks would you accept as an equivalent substitute?

answer _____

j. What certain % loss for a species of tubenoses would you accept as an equivalent substitute?

answer _____

k. What certain % loss for a species with a high reproductive rate would you accept as an equivalent substitute?

answer _____

l. What certain % loss for a species with a low reproductive rate would you accept as an equivalent substitute?

answer _____

19. Within a specified area, assume an endangered species will suffer 0% losses with probability .25 and 100% losses with probability .75.
- a. What certain % loss for a species of large birds would you accept as an equivalent substitute?
answer _____
- b. What certain % loss for a species of small birds would you accept as an equivalent substitute?
answer _____
- c. What certain % loss for a species of game birds would you accept as an equivalent substitute?
answer _____
- d. What certain % loss for a species of subsistence birds would you accept as an equivalent substitute?
answer _____
- e. What certain % loss for a species of Alcids would you accept as an equivalent substitute?
answer _____
- f. What certain % loss for a species of shore birds would you accept as an equivalent substitute?
answer _____

g. What certain % loss for a species of gulls would you accept as an equivalent substitute?

answer _____

h. What certain % loss for a species of swans would you accept as an equivalent substitute?

answer _____

i. What certain % loss for a species of ducks would you accept as an equivalent substitute?

answer _____

j. What certain % loss for a species of tubenoses would you accept as an equivalent substitute?

answer _____

k. What certain % loss for a species with a high reproductive rate would you accept as an equivalent substitute?

answer _____

l. What certain % loss for a species with a low reproductive rate would you accept as an equivalent substitute?

answer _____

20. Within a specified area, assume large birds will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

21. Within a specified area, assume large birds will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

22. Within a specified area, assume large birds will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

23. Within a specified area, assume small birds will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

24. Within a specified area, assume small birds will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

25. Within a specified area, assume small birds will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

26. Within a specified area, assume game birds will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

27. Within a specified area, assume game birds will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

28. Within a specified area, assume game birds will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

29. Within a specified area, assume subsistence birds will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

30. Within a specified area, assume subsistence birds will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

31. Within a specified area, assume subsistence birds will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

32. Within a specified area, assume Alcids will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

33. Within a specified area, assume Alcids will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

34. Within a specified area, assume Alcids will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

35. Within a specified area, assume shore birds will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

36. Within a specified area, assume shore birds will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

37. Within a specified area, assume shore birds will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

38. Within a specified area, assume gulls will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

39. Within a specified area, assume gulls will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

40. Within a specified area, assume gulls will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

41. Within a specified area, assume swans will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

42. Within a specified area, assume swans will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

43. Within a specified area, assume swans will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

44. Within a specified area, assume ducks will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

45. Within a specified area, assume ducks will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

46. Within a specified area, assume ducks will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

47. Within a specified area, assume tubenoses will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

48. Within a specified area, assume tubenoses will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

49. Within a specified area, assume tubenoses will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

50. Within a specified area, assume a species with a high reproductive rate will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

51. Within a specified area, assume a species with a high reproductive rate will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

52. Within a specified area, assume a species with a high reproductive rate will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

53. Within a specified area, assume a species with a low reproductive rate will suffer 0% losses with probability .75 and 100% losses with probability .25.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

54. Within a specified area, assume a species with a low reproductive rate will suffer 0% losses with probability .50 and 100% losses with probability .50.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

55. Within a specified area, assume a species with a low reproductive rate will suffer 0% losses with probability .25 and 100% losses with probability .75.

What certain % loss for this species would you accept as an equivalent substitute, if the local population totaled:

- a. 1% of the world population? _____
- b. 5% _____
- c. 10% _____
- d. 25% _____
- e. over 50% _____

Appendix B

Selected comments of respondents

"Although I hate to make value judgements in these hypothetical situations, I agree with you that it is better to make the value judgements on biological bases rather than let developers and oil companies make them on other bases."

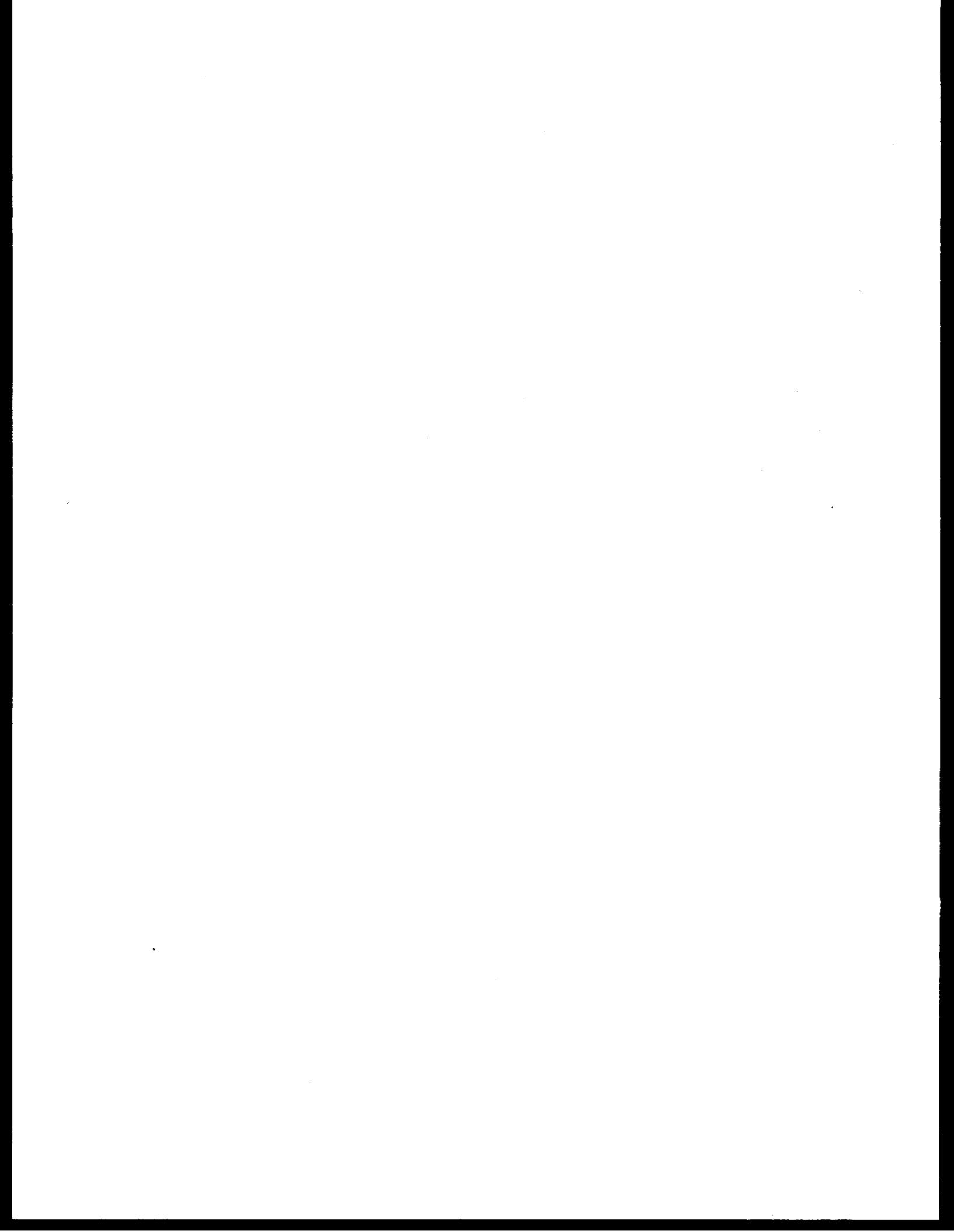
"Sorry - I just don't have time to do this justice - if that is, indeed, possible. I'd be happy to comment on specific cases but I can't deal with these questions biologically - there are too many uncertainties. I would suggest, however, that our concern, as a nation, with 'endangered species' hasn't done us or wildlife much good."

"I feel very uneasy about my responses.... Are you asking which species are more highly valued - large, small, alcids, swans, etc.? If one believes in equality of species, no such judgements are appropriate."

"...Also, transfixation of attention on large oil spills is a totally unrealistic view of reality, when the chronic, low level pollution is far more important. The questionnaire cannot be generalized; it would be easier if the real situation was presented and more valid, too."

"My experience in real life has been that survival of any individual bird is secondary to the protection of habitat and salmonid habitat in particular... I accepted a much more dangerous gamble for expanding species (Trumpeter Swans, Brandts, Cormorants, Glaucous-winged Gulls) and for boom-bust reproductive strategists such as game birds and shore birds...theoretical species identity changed as I progressed through the lists of increasing percent of the world's population."

"I accept that these are the questions you have to ask yourself when the crunch comes, but I don't see much point in asking them in the abstract, in advance. They have to be asked about an actual situation, even if they have to be asked in a hurry. I'm always saying this to people who draw up elaborate contingency plans for emergency oil spill operations - they're of very little use in practice because no oil spill yet, to my knowledge, has ever been quite like any preceding one."



**SIMULATION MODELING OF MARINE BIRD POPULATION ENERGETICS,
FOOD CONSUMPTION, AND SENSITIVITY TO PERTURBATION**

by

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**Final Report
Outer Continental Shelf Environmental Assessment Program
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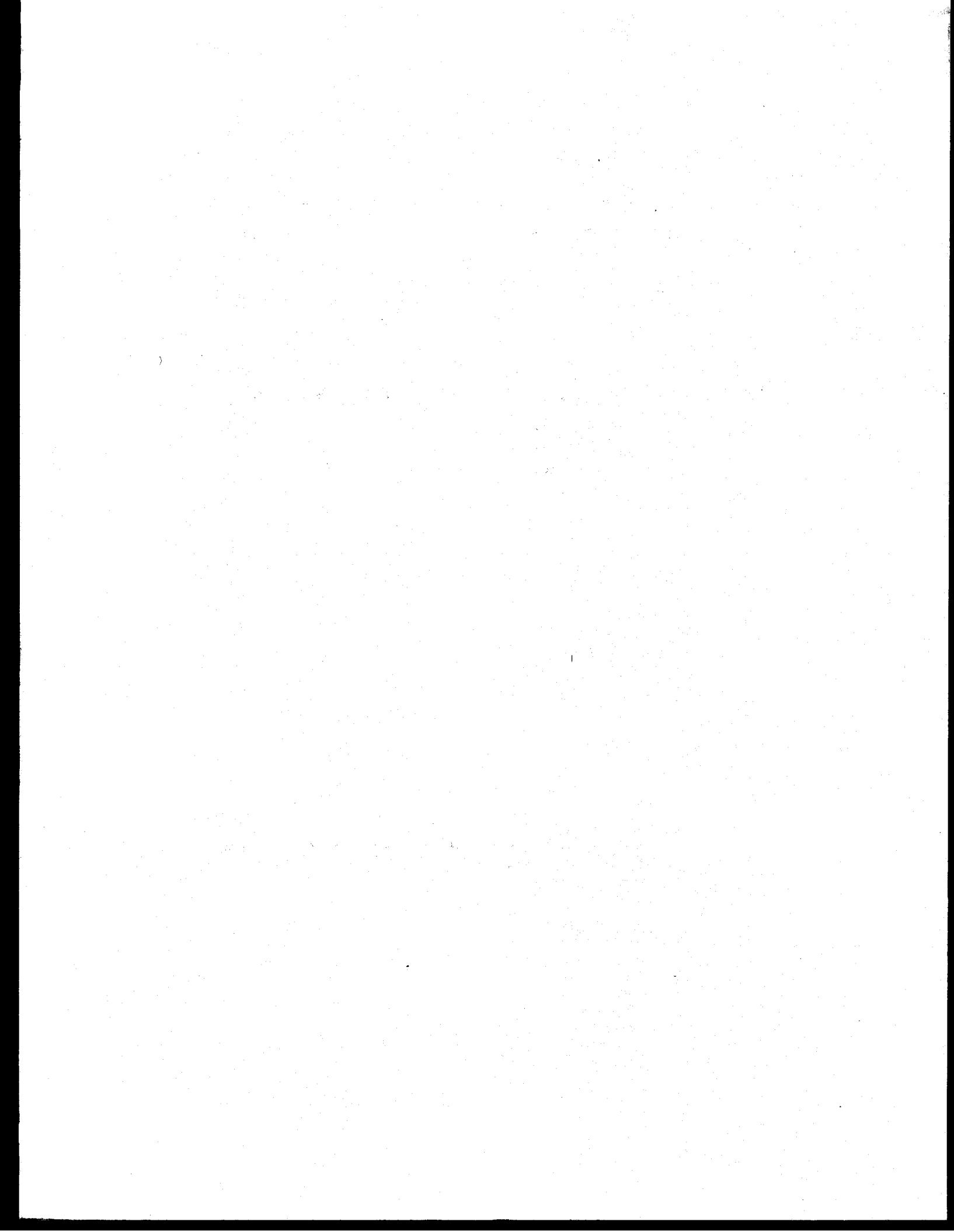
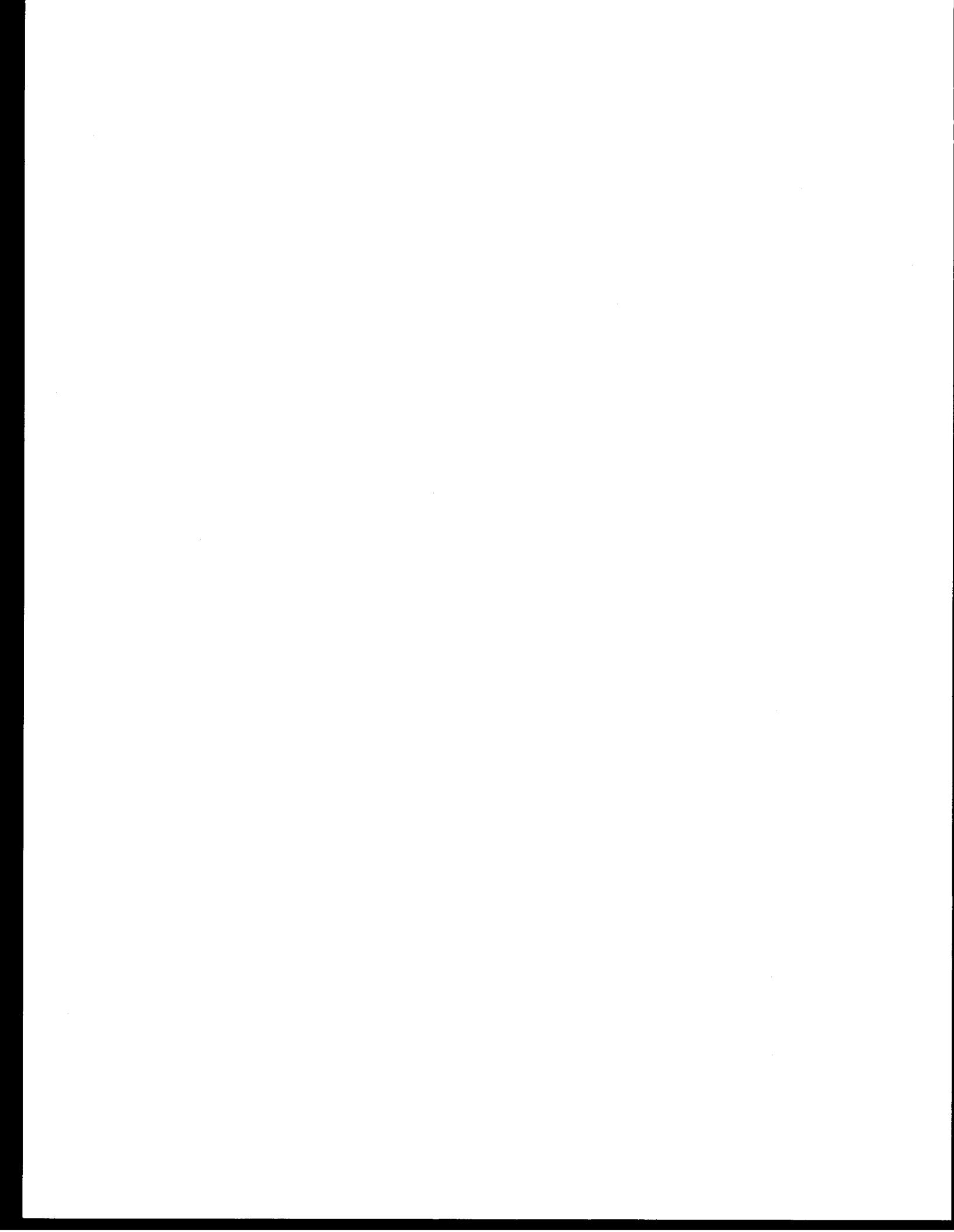


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SUMMARY

The objective of our research has been to develop methods of assessing the sensitivity of marine birds in Alaskan waters to petroleum-related environmental perturbations. Our approach has combined field observations and information with various analytic and computer simulation models. This report completes our documentation of the population energy flow patterns, at-sea distributions, and sensitivity to oil spills of the dominant marine bird species breeding at major colonies on Kodiak Island and using the surrounding oceanic areas for foraging. We employed data from 8 major colony locations of breeding Tufted Puffins and Black-legged Kittiwakes, in combination with other information obtained from the seabird literature, to conduct model analyses of the level of mortality of these species that might accompany selected oil-spill scenarios. The model that we used was a simplification of one developed earlier in this research and previously applied to the Pribilof Islands system. In the Kodiak model, we excluded consideration of chick mortality due to death of parents or to diminished growth rate accompanying a shift in parental foraging distributions caused by a spill, and we modeled the spatial distribution of the birds about Kodiak using a system of rectangular coordinates rather than the polar coordinate system employed in the Pribilof analysis. The Kodiak model required 12 parameters, which considered features of population size and distribution, flight speed and trip time, time spent foraging in specific areas and the sizes and locations of those areas, daylength, the probability that adults encountering a spill will suffer mortality, the mortality suffered by birds from a given colony foraging in a given area, and the extent of a simulated oil spill and time required for the affected area to return to an equilibrium following the spill. Spill trajectories were simulated from four launch points at two times of the breeding season, using 50 simulation runs to establish the frequency distributions for each site-season scenario. The results of our modeling indicated that for most scenarios, adult mortality of puffins and kittiwakes was quite low, usually less than 1% of the breeding populations at a given colony. Puffins were somewhat more susceptible than kittiwakes, and spills originating close to a colony generally effected greater mortality than those launched at greater distances, although this was influenced in important ways by the foraging distribution characterizing the birds inhabiting a given colony. For each spill scenario, however, there was a frequency distribution of estimated mortalities that resulted from the influences of the various factors affecting spill trajectory and duration. As a result, some spill scenarios did cause substantial mortality among the breeding birds, although these generally were not likely to occur very often. Monte Carlo analyses indicated that a considerable amount of the variation in the estimates of spill-related mortality of adult puffins and kittiwakes was due to uncertainty in the estimation of various model parameters. This emphasizes the need for good information on those population or colony attributes.

The second part of this report reviews the general status of the information or data base on marine birds and their environments in Alaskan waters that we have found to be necessary to our modeling efforts. From a consideration of a large number of parameters on populations, foraging, energetics, and characteristics of the perturbations themselves, we identify the following as having a high priority for obtaining accurate, colony- or area-specific field data: (1) The size of the colony. (2) The patterns of at-sea distributions of the birds. (3) The trip times of foraging adults. (4) The pattern of age-specific survivorship of the population. (5) The probability that an adult bird encountering an oil spill will suffer mortality. (6) The frequency with which adults shift their foraging distri-

distribution to other areas upon encountering an oil spill. (7) The ways in which a spill may influence resource availability to foraging birds in the affected area. In addition, the following parameters are assigned an intermediate priority: (1) The breeding structure of the population. (2) The foraging pathways of individuals. (3) The metabolic costs of foraging activity. (4) The spatial and temporal patterns of food availability about the Colony. (5) The ways in which changes in food delivery rate to chicks affects their growth rate and survivorship. (6) The distributional dynamics of oil spills.

PART I. AN ANALYSIS OF KODIAK ISLAND COLONIES

A. Introduction

Colonially breeding seabirds are a conspicuous and important element of most marine ecosystems. They often occur in vast concentrations, especially in areas of high productivity. They may have major effects on energy flow in these systems, consuming perhaps 22-27% of the annual production of small pelagic fishes (Wiens and Scott 1975, Furness 1978), and their concentration of nutrients about breeding colonies may have major influences on local patterns of marine nutrient cycling (Tuck 1960, Zelickman and Golovkin 1972) or on the contributions of nutrients to adjacent terrestrial systems (Burger et al. 1978, Smith 1979). As marine ecosystems become subject to increasing demands for human development, especially through activities related to petroleum resources, the probability that the seabirds and their positions in marine trophic dynamics will be disturbed increases (Nettleship 1977, Nisbet 1979, Birkhead and Nettleship 1980). Intelligent management or conservation of marine birds requires some means of anticipating the effects of various perturbations, rather than continued reliance on post facto assessments of development-related mortality.

The objective of our research over the past several years has been to develop methods of assessing the sensitivity of marine birds in Alaskan waters to environmental perturbations such as might accompany petroleum development. The approach has combined the analysis of field observations on the distributions of the birds at sea and on their life history, reproductive, and demographic attributes with simulation modelling of population foraging distributions and demography. This approach was initially developed and applied to colonially breeding seabirds on the Pribilof Islands, Bering Sea (Wiens et al. 1979a, Ford et al. 1981). More recently, we have extended the analysis to the marine birds associated with Kodiak Island and the surrounding waters of the northeast Gulf of Alaska. This report completes the presentation of the results of our investigation of that system.

This research has involved three distinct phases. In the first (Wiens et al. 1979b), we used simulation models to estimate population energy flow patterns for the dominant breeding species in the Kodiak region. We found that Tufted Puffins¹ were the most important consumer species, in terms of their energy demands upon the system. We estimated that the puffin population consumed 5.90×10^9 kcal during the course of the breeding season, compared with 2.12×10^9 kcal consumed by the Black-legged Kittiwake population and 1.73×10^9 kcal consumed by Glaucous-winged Gulls. Total energy demand by these three dominant species was thus estimated to be 9.75×10^9 kcal during the breeding season, which converts (following the procedures of Wiens and Scott 1975) to 8,100 metric tons of prey. These values are nearly an order of magnitude less than those we calculated for the Pribilof

¹Scientific names of bird species are given in Appendix I.

system (Wiens et al. 1978a). The Kodiak values, however, do not include several major species, such as shearwaters and murres, that do not breed (at least at high densities) on Kodiak but that exploit the nearby waters, so the comparison is of doubtful value.

The second phase of the research involved an analysis of the distributional patterns of the dominant breeding species about Kodiak Island, and a statistical evaluation of the results of seabird sensuses in the region (Wiens et al. 1980). Because of the heterogeneity in censusing circumstances and conditions, it was necessary to adjust the raw census values in various ways in order to synthesize the distributional patterns of the birds in the Kodiak area. Our analyses of the distributions of Black-legged Kittiwakes, Glaucous-winged Gulls, murres, Sooty Shearwaters, and Tufted Puffins indicated distinct regions of high and low densities. Some of the high-density areas were probably the result of chance encounters of large aggregations of individuals during censusing, but others were clearly associated with bathymetric features or nearby breeding colonies. In general, the areas around the Semidi and Barren islands, over Portlock North (the eastern end), and South Albatross banks, and the area between the Trinity Islands and Cape Ikolik appeared to be important foraging areas for these species, while Shelikof Strait and the eastern end of North Albatross Bank had consistently low densities, as did the off-shelf areas.

Our statistical analyses of the results of pelagic bird censusing in the Kodiak region was not encouraging. When densities were calculated from censuses in 20 x 20-km blocks of the region around Kodiak, our analyses indicated that only 6% of the area had been surveyed with sufficient intensity to permit the derivation of statistical confidence intervals about the mean density estimates. Of that proportion of blocks, only 3% had been sampled sufficiently enough that the upper confidence limits were within an order of magnitude of the calculated mean, even though the data were pooled over seasons to enhance sample sizes. Thus, while the at-sea censuses available to us at that time were sufficient to permit estimations of densities for the various blocks of ocean about Kodiak, we were generally unable to attach meaningful statistical significance levels to the spatial variations in the densities. Obviously, this lack of statistical validation of the distributional patterns that we (and others) have derived poses a serious constraint on any subsequent efforts to define areas of greater or lesser sensitivity to perturbations.

This report contains the results of the third phase of our research, which has concentrated on employing models to estimate the effects of various petroleum-related perturbation scenarios on mortality of birds associated with breeding colonies on Kodiak Island.

B. The Data Base

Any modeling analysis is constrained by the nature of the data available as it related to the objectives of the analysis (see Section II of this report). Our analysis of the dynamics of the Kodiak seabird systems was constrained by the availability of detailed information on the demography of well-studied colonies and by the quality of the information regarding the distribution of the birds at sea. Partly for this reason, and partly on the basis of the results of our earlier analysis of the Pribilof Islands marine bird system (Ford et al. 1981), we adopted a simplified approach to modeling the Kodiak system. As a result, we required information on basic features of breeding colonies, such as size and location, and on the at-sea

distributions of birds. Colony data were provided for colonies in Sitkalidik Strait and the Chiniak Bight by U.S. Fish and Wildlife Service personnel (Pat Baird, Gerry Sanger, and Pat Gould), and were supplemented with information from the Catalog of Alaskan Seabird Colonies (Sowls et al. 1978). Because little information was available on many of the colonies listed in the catalog, we restricted our consideration to those colonies or colony-groups indicated in Fig. 1 (See also Table 1).

Table 1. Seabird colonies in the Kodiak area used in our modeling analyses (See Fig. 1). Colony names and locations (in parentheses) follow the notation of the Catalog of Alaskan Seabird Colonies (Sowles et al. 1978).

Colony (location)	Numbers of Individuals (x 10 ³)	
	Colonies	Total
TUFTED PUFFIN		
1. Flat Is. (033 002)	30	30
2. Cathedral Is. (034 005)	12	12
3. Ladder Is. (034 007), Ermine Pt. Is. (034 060), Dusk Is. (034 061)	6, 1, 1.5	8.5
4. Gull Pt. (034 010), Long Is. (034 067)	5, 2.2	7.2
5. Chiniak Is & Rks (034 014)	7	7
6. Kekur & Middle Is. (034 015), Svitlak & Utessitoi Is. (034 016), Queer Is. (034 017), Viesoki Is. (034 018), Puffin Is. [1] (034 022), Jug & Kalsin Is. (034 047), Zaimka Is. (034 087), Cliff Is. (034 088), Bird, Kulichkof, Holiday & Popof Is. (034 089), Long Is. & Islets (034 090)	.6, .9, 1.3, 1.8, 1.3, .7, 2.1, .8, .2, 1.7	11.4
7. The Triplets (034 046)	60	60
BLACK-LEGGED KITTIWAKE		
1. Flat Is. (033 002), Jap Bay (033 003)	1, 3	4
2. John Is. (034 003), Middle Triangle (034 050)	3, .4	3.4
3. Cathedral Is. (034 005)	4.1	4.1
4. Inner Right Cape (034 059), Ermine Point Is. (034 060), Dusk Island (034 061)	1.4, 5.5, 1.7	8.6
5. W. Boulder Bay (034 008)	40	40
6. Chiniak Is. & Rks (034 014)	9.8	9.8
7. Kekur & Middle Is. (034 015), Svitlak & Utessitoi Is. (034 016), Viesoki Is. (034 018), Bird, Kulichkof, Holiday & Popof Is. (034 089), Gibson Cove (034 099)	1.2, 2.5, 2.6, .4, .4	7.1
8. Anton Larsen Bay (034 097), N. Barbara Cove Point (034 028), Whale Is. (034 044)	1.5, 2, 4	7.5

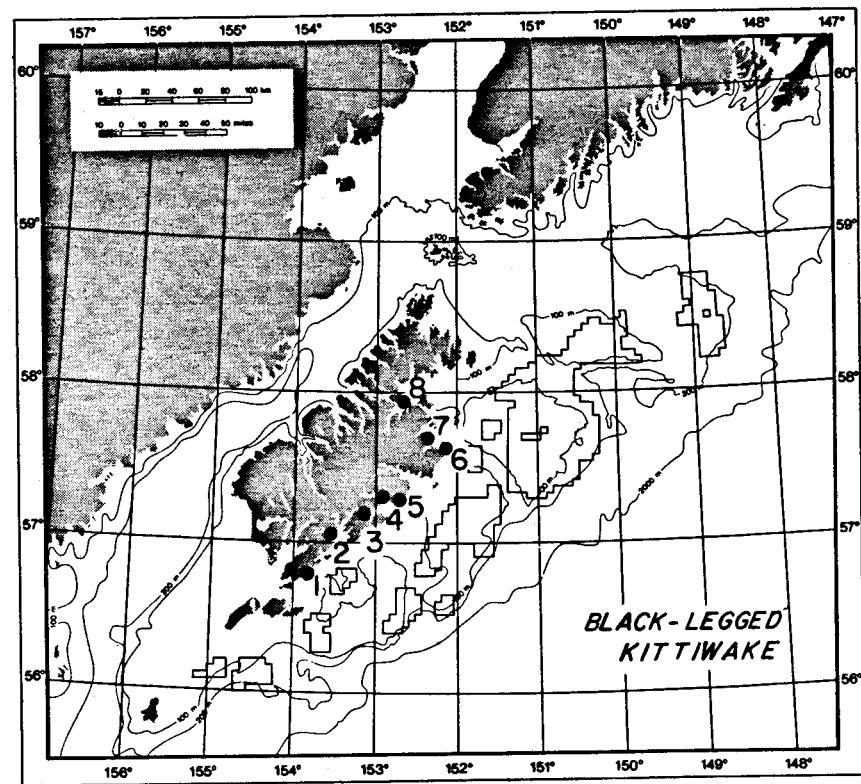
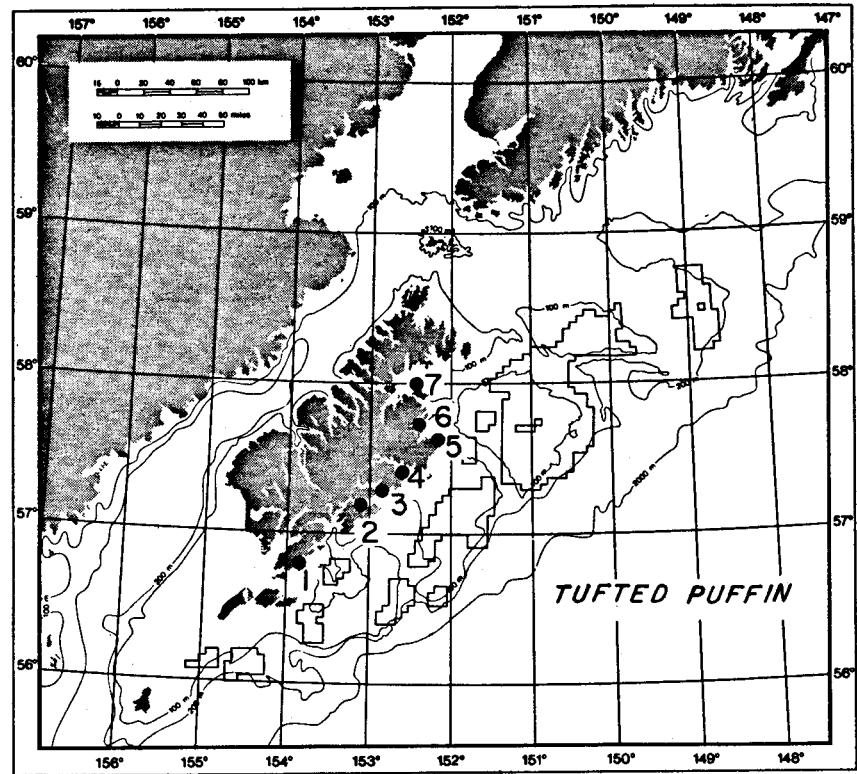


Fig. 1. Locations of colonies of Tufted Puffins (above) and Black-legged Kittiwakes (below) considered in our analysis of oil-spill impacts upon seabird populations. The parameters for these colonies are given in Table 1.

A large array of marine birds species occurs at these colonies and in the waters adjacent to Kodiak Island. Many of these, however, occur at low densities (e.g. Arctic Terns, Pelagic Cormorant), are primarily associated with island groups other than Kodiak itself (e.g. Common and Thick-billed murres), or are not directly associated with the breeding colonies on Kodiak (e.g. Sooty Shearwaters). Accordingly, we restricted our attention to the two major breeding seabirds on Kodiak, Tufted Puffins and Black-legged Kittiwakes. Collectively, these two species contribute roughly 94% of the birds breeding in the Kodiak colonies that we considered.

Information on the distribution of the birds at sea in the areas adjacent to Kodiak was obtained from shipboard and aerial transects conducted by U.S. Fish and Wildlife Service personnel during 1975-1977. These data were included in our earlier analysis of distributional patterns (Wiens et al. 1980). That analysis evaluated distributional patterns by estimating the densities of species in 10 km x 10 km blocks of ocean area. We used the same information to conduct the model analyses reported here, except that distributions were combined into 20 km x 20 km blocks. This change was necessitated by computer limitations: the run time and size of the model increase exponentially with the number of spatial blocks that must be considered. We believe that this slightly coarser spatial scale is appropriate for the sort of spill scenarios we consider.

C. Model Structure

In the present analyses we have used a modified version of the modeling approach that was employed for the Pribilof Islands (Ford et al. 1982). The Pribilof analysis indicated that the effects of oil spills on mortality of nestling birds had a relatively minor long-term effect on population sizes and recovery rates as compared with adult mortality. We therefore simplified the model approach to consider only adult mortality. While sacrificing some elegance and fine-scale resolution, this approach is more appropriate for systems in which relatively few data on reproductive and demographic parameters of species in specific colonies are available. In addition, we use a rectangular coordinate system to model the spatial distributions of the birds rather than the polar coordinate system employed in the Pribilof model. This change was required by the greater complexity of the Kodiak and mainland coastlines and the larger number of spatially separated colonies that we considered.

The Kodiak model is based upon 12 parameters, which represent three categories: (1) input parameters for which we have a reasonable empirical basis for their values, (2) input values for which we have little or no empirical basis for their estimation and that are part of the Monte Carlo analysis, and (3) values based upon intermediate calculations within the model itself. These parameters may be defined as follows:

Category 1.--Empirical Input Values

- C_j The population size of a species in colony j .
- S Flight speed (km min^{-1}).
- A_i The area of sector i (km^2).
- A'_i The area of sector i covered by an oil spill (km^2).
- L Daylength (min).
- N_{ij} The mean number of birds from colony j in sector i , where i is a 20 km x 20 km block defined in rectangular coordinates.

Category 2.--Monte Carlo Input Values

- T Mean trip time (min).
ρ The probability per minute that foraging in a spill region will lead to fatal spill contact (min^{-1}).
τ The time required for an area depleted of birds by spill mortality to return to an equilibrium density of birds.

Category 3.--Internally Calculated Parameters

- D_{ij} The distance from colony j to the midpoint on sector i (km).
F_{ij} The time spent by birds from colony j foraging in sector i (min).
M_{ij} The mortality suffered by colony j in sector i (birds day $^{-1}$).

Our modeling approach is based on the following major assumptions:

Assumption 1.--There exists a foraging distribution of birds at any time that is in a state of "equilibrium." This means that although individuals may shift the focus of the activities from day to day, the density of birds remains constant within a given area. The Pribilof model makes a similar assumption, except that the equilibrium level is determined by the relation between the "food supply" and the absolute number of birds, and when perturbations occur that balance is used to readjust the foraging distribution. In the Kodiak model, equilibrium is determined only by the proportion of a given colony that forages in a given sector (see Figs. 2 and 3). Thus, if the population of a colony were to be halved, the equilibrium number foraging in all sectors would similarly be halved. This means that we do not take into account density-dependent depletion of food supply, as was done in the Pribilof model. The problems with the complexity of the Kodiak area and the data base, however, preclude that sort of analysis in the Kodiak system.

Assumption 2.--The equilibrium proportions of birds in the sectors are constant in time. This, of course, is patently absurd, but it should not affect estimates of mean mortality rates. It does, however, significantly lower estimates of the variability in kill rates, which are of considerable importance. The available data base would need to include far more replication of transects within blocks than it does, or alternatively some sort of a priori stratification (zonation) scheme would be necessary in order to relieve us of this assumption.

Assumption 3.--Birds forage throughout the daytime period.

Assumption 4.--Birds fly in straight-line flight between the colony and their foraging areas. This is a conservative assumption, as it implies that the birds spend the maximum proportion of their time in areas in which they are vulnerable to oil spills.

Assumption 5.--The probability of fatal oil contact is constant per unit time while foraging in the area of the spill.

Additional assumptions will be discussed where appropriate in the following narrative.

Assuming linear flight to and from colony j to the foraging area i, the mean time spent per day foraging in i by birds from j is:

$$F_{ij} = (T - 2D_{ij}/S)(L/T)$$

where the first term, $T - 2D_{ij}/S$, is the time spent foraging per trip, and L/T is the number of trips per day. The expected time spent in a spill is the product of F_{ij} and the proportion of i that is covered by the spill, A'_i/A_i . The probability of death per day for birds from j utilizing i is:

$$(1 - \rho) \exp(F_{ij} A'_i / A_i)$$

The total number of birds from j dying in i per day is the product of the probability of death per day and the number of birds utilizing i . The number of individual birds utilizing i will be greater than N_{ij} because each individual spends only part of its time in i , and the remainder in transit between j and i . The number of individuals is estimated as $N_{ij}T/(T - 2D_{ij}/S)$. Thus, if the observed density was 300 birds, trip time was 200 min, and $(T - 2D_{ij}/S)$ was 10, the number of individuals utilizing i would be 600 birds.

Total expected mortality is then the product of the daily probability of death and the number of birds at risk:

$$M_{ij} = (1 - \rho)[\exp(F_{ij} A'_i / A_i)] N_{ij} T / (T - 2D_{ij}/S).$$

The new density in i is thus $N_{ij} - M_{ij}$, and the new colony size is $C_j - \sum_i M_{ij}$. The following day M_{ij} is reset, assuming that at equilibrium the proportion of j that is utilizing i is the same as that prior to the perturbation. Equilibrium is not achieved in only 1 day, however, but rather moves a fraction $(1/\tau)$ of the distance from the perturbed value to the equilibrium value. Each day, the total mortality is assessed as $\sum_i M_{ij}$.

In order to use this model to estimate the mortality of breeding birds that might be expected from a given oil spill scenario, initial estimates of parameter values must be obtained. In our application of this model to the Kodiak kittiwake and puffin populations, this was accomplished as follows.

C_j - Colony size estimates were based on the values reported in the Alaskan Seabird Colony Catalog (Sowles et al. 1978). These were combined to give a total "colony" value when several nearby colonies were grouped together in our analysis (see Fig. 1 and Table 1).

S - Flight speeds were based upon estimates made by Ford and Heinemann on St. Paul Island in the Pribilof Islands in 1978 (Wiens et al. 1979a, Ford et al. 1982).

A_i - Sector areas were based upon the gridding scheme that we adopted for this analysis. As each sector was 20 km x 20 km, its area equaled 400 km².

L - Average daylength was assumed to be 900 min; this value was also used in our earlier analyses (Wiens et al. 1979a, Ford et al. 1982).

N_{ij} - The procedures used to calculate the densities of birds at sea from transect survey results were described in detail previously (Wiens et al. 1980). The values obtained in the earlier analysis, which was based upon 10 km x 10 km sectors, were converted to the appropriate values for the 20 km x 20 km sectors used in the present analyses. It was also necessary, however, to estimate the proportion of the birds in each sector that originated from each colony. The estimation of colony-specific foraging distributions was based on the assumption that a given area of water will be dominated by the nearest colony, and that individuals will move the

shortest possible distance to their foraging site. As noted above, minimization of flight time is a conservative assumption. We begin with the estimated values of N_i and C_j . An incremental group of birds (i.e. 100) is "released" from each colony. Each group moves to the nearest unoccupied sector relative to its colony. This process is iterated until a given sector is filled (that is, when the sum of the increments is equal to N_i , the estimated density of birds in the sector). At the next step, the incremental flight of birds is directed to the next nearest sector; this procedure is repeated until all the sectors are filled to their observed densities. The colony-specific foraging distributions generated for each species in this manner are depicted in Figs. 2 and 3).

This approach thus assigns proportions of birds from a colony to sectors in such a way that individual transit time is minimized. This procedure tends to bias the results in the direction of higher mortalities, as birds will spend more of their time foraging (and thus potentially vulnerable to spill contact) than in transit.

A'_j - The area of a sector covered by a spill in a given scenario was derived from the results of the spill trajectory analysis, which is described below.

T - Although some data on trip times of individuals from nest sites to foraging areas and back were available for both Tufted Puffins and Black-legged Kittiwakes from the Sitkalidik Strait colony, we were unable to use them. Our estimates of time spent moving between colonies and foraging areas based upon the distributional data indicated minimal transit times that were 2-3 times greater than the total trip times observed for both species. We therefore concluded that these data were not representative, and based our estimates of trip times on our experience on the Pribilof Islands. Using estimates of mean minimal transit times, we assumed that birds spent 30-70% of their foraging trips in transit; we used 50% as our best approximation.

For this input parameter (and for ρ and τ), however, we do not have a firm empirical base from which to estimate values. This does not mean that we know nothing about them, but it does imply that what we do know is perhaps best described as an "educated guess." There are several alternative approaches to dealing with this uncertainty. First, we could simply make our "best guess" for a parameter value, and use that. This has the disadvantage that we lose sight of the potential variability in the outcome due to our uncertainty, and it thus ignores the problem of sensitivity. Another approach would be to estimate the upper and lower limits of possible values for the parameter. The model could then be run repeatedly (Monte Carloed) using different parameter values selected from a uniform distribution of possible values, where the endpoints of the uniform distribution are defined by the upper and lower limits of our guesses. This technique is an improvement in that it does not mask the variability in the outcome due to uncertainty, but it perhaps has the disadvantage of overemphasizing the extreme possible values. Our approach is to use a triangular ("house top") probability density function in which the peak is the "best guess" and the endpoints are the estimated maximum and minimum parameter values (Fig. 4). This approach preserves the potential variability in the estimated parameter values without loosing sight of the fact that, by definition, the "best guess" is the most likely value. Thus, in determining values for trip time, we conducted Monte Carlo runs using a house-top distribution in which the range of reasonable values (30-70% of the mean transit time) defined the endpoints of the distribution and 50% of the mean transit time was the mode.

ρ - The probability of fatal spill contact per minute was varied in the same manner as T , using 0.0 and 0.00264 as the range and 0.002 as the "best guess." These values were based upon the analyses of Wiens et al. (1979a).

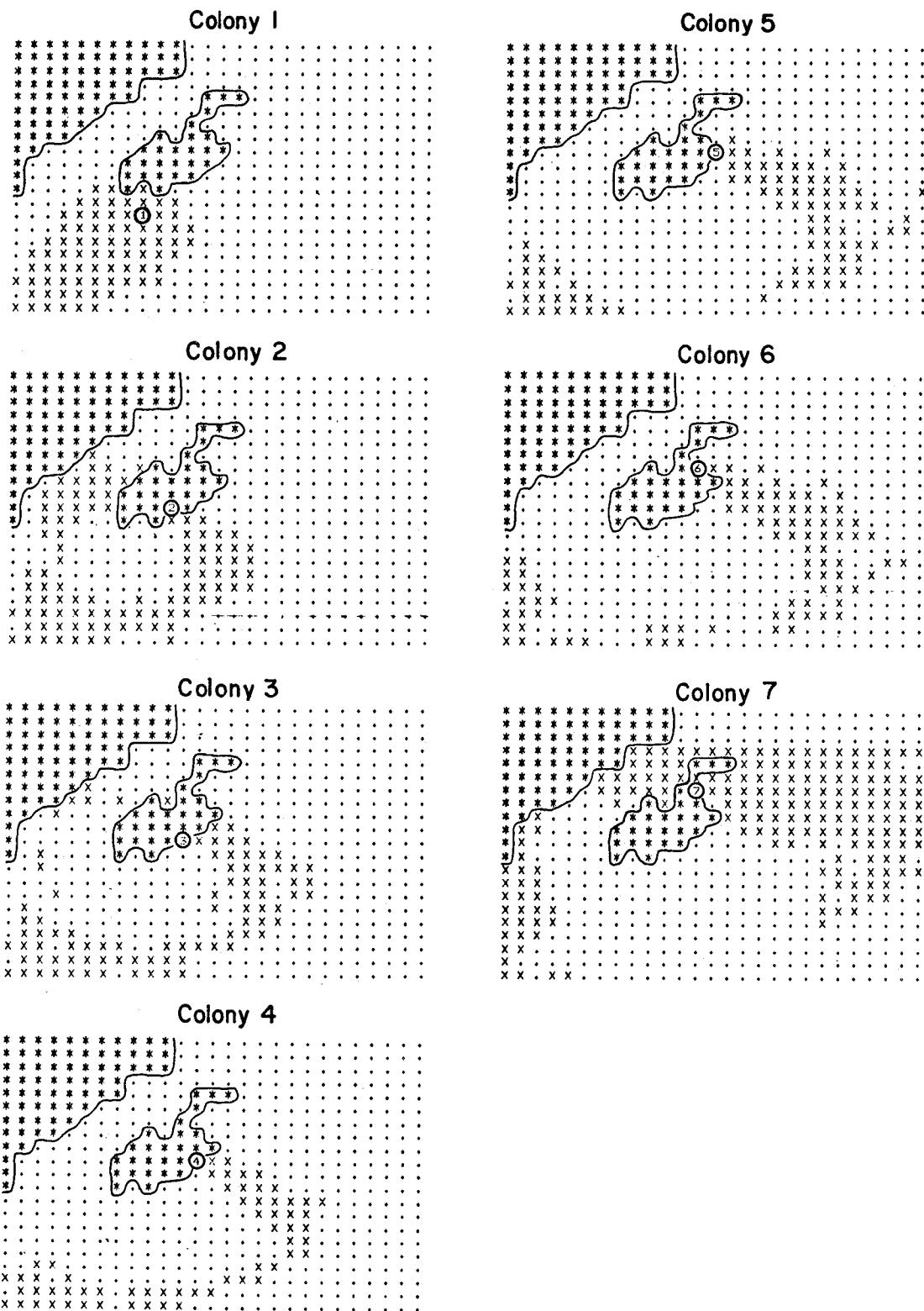


Fig. 2. Projected foraging distributions for individuals breeding in each of the Tufted Puffin colony locations shown in Fig. 1. In these computer-generated plottings, the stars represent grid blocks located on the mainland (upper left corner) or Kodiak Island (center); Xs represent grid blocks in which foraging occurred, and dots represent grid blocks in which little or no foraging by birds from a specified colony occurred. See text for derivation of these maps.

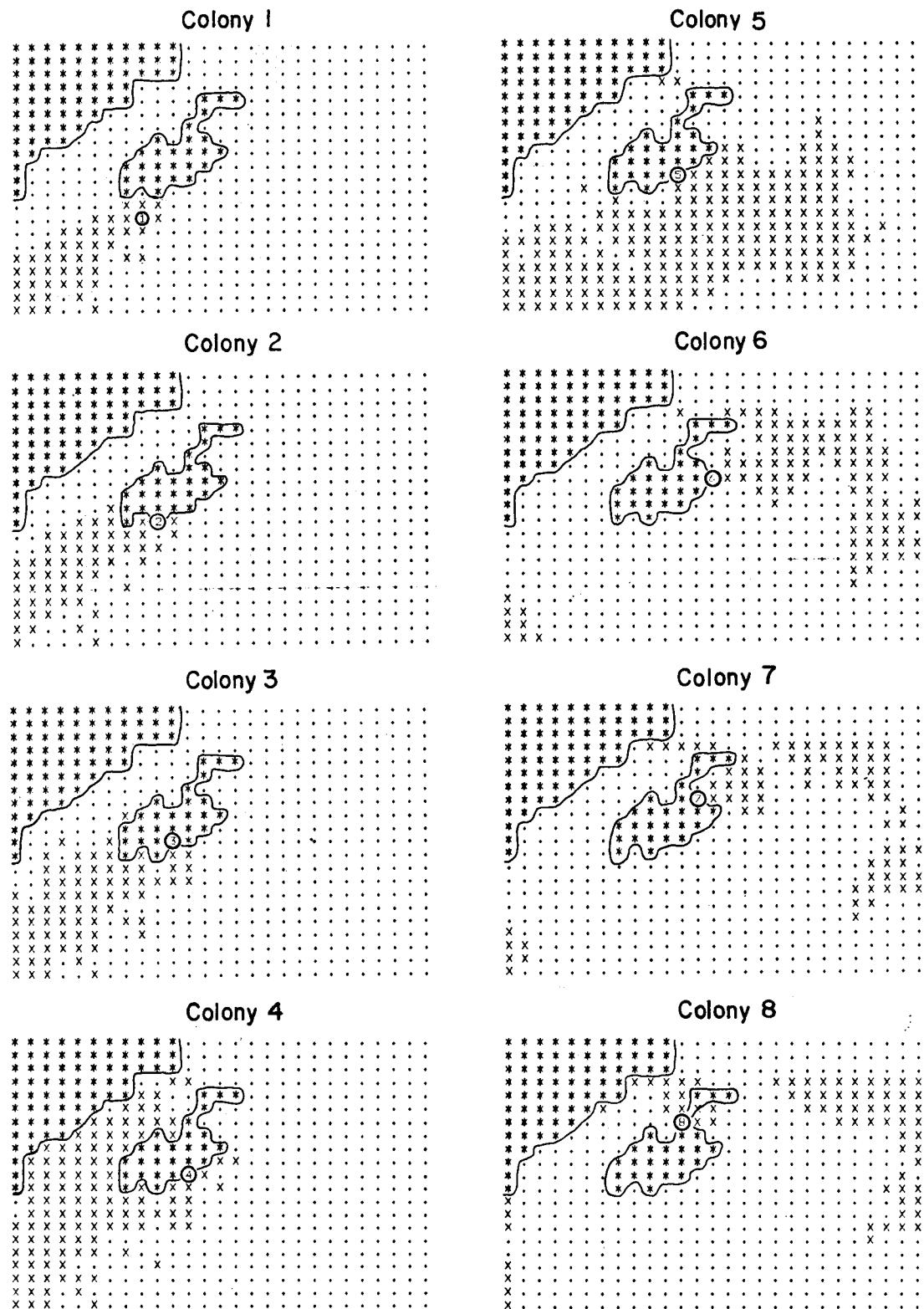


Fig. 3. Projected foraging distributions for individuals breeding in each of the Black-legged Kittiwake colony locations shown in Fig. 1. See Fig. 2 for explanation.

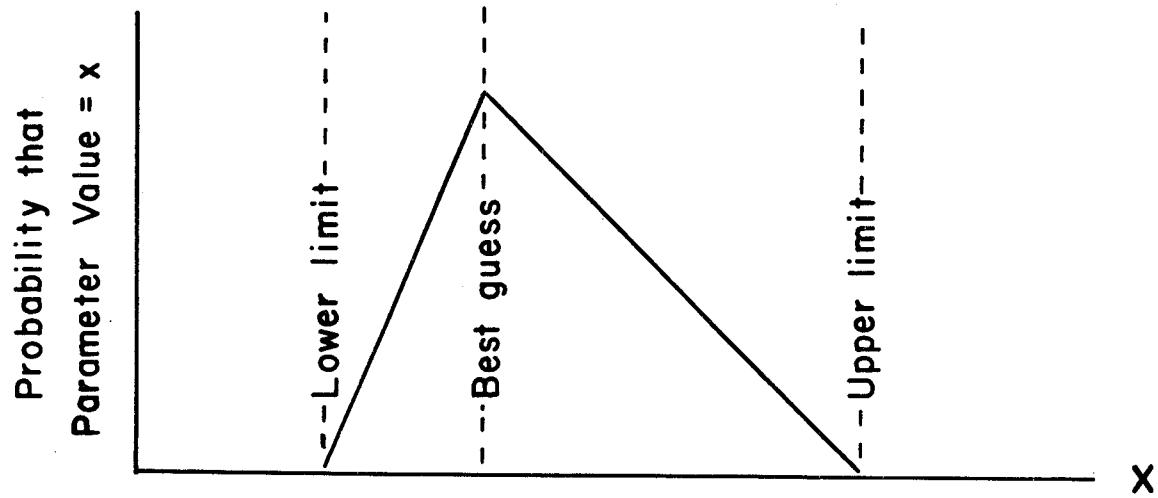


Fig. 4. The "housetop" distribution of parameter values employed in sensitivity tests. "X" represents a range in parameter values, with lower and upper limits, and a "best guess" value determined from field data, literature reports, or intuition. The curve gives the probability distribution of values from which individual parameter values were randomly drawn in Monte Carlo simulations, as described in the text.

τ - Values for this parameter were also estimated using Monte Carlo procedures. Time to equilibrium was estimated to range between 1 and 10 days, with 5 days being the "best guess" (Wiens et al. 1979a).

Spill trajectories.--Model runs were made using output from the USGS spill trajectory model (W. Samuels, pers. comm.). Spill trajectories were provided in the form of point locations at 3-h time steps, starting from four different spill launch points distributed evenly through the lease tract on a north-south gradient (Fig. 5). The trajectory model is stochastic, so we used 10 sample trajectories per launch point. Because wind and current vectors vary on a seasonal basis, we used two sets of trajectories, one for spring and another for summer. Thus, there were 4 (launch points) x 2 (seasons) = 8 scenarios. For each launch point-season scenario, there were 10 trajectories simulated.

We assumed that each spill was a circular area of 50 km²; this defined the parameter value for A_i , the area of sector i covered by a spill. Spills were assumed to persist without change until they hit land, moved beyond the geographic limits of the model, or had been in existence for 30 days.

To evaluate the sensitivity of the model to our estimates of the values of the parameters T , ρ , and τ , we also varied these in a Monte Carlo fashion. For each of the 80 (4 x 2 x 10) trajectories, we made five model runs using different values of T , ρ , and τ that were selected at random from the previously described distributions of parameter values. Thus, each launch point-season scenario entailed a total of 10 x 5 = 50 simulation runs. Each of the frequency distributions that we present below (Figs. 6 and 7) is thus based upon five versions of 10 possible trajectories.

D. Results

The estimated mortality of adults accompanying each of the spill scenarios depicted in Fig. 5 is given in Tables 2 and 3. Several features are apparent. First, the mortality rates are generally quite low, usually less than 1% of the birds estimated to be present at a colony. Second, mortality of Tufted Puffins is generally greater than that of Black-legged Kittiwakes for a given spill scenario. This is a consequence of the differences in the foraging distributions of the species, as kittiwakes forage over a border area about a colony (Figs. 2 and 3), and the probability of individual encounter with oil in a restricted spill is thus less for kittiwakes than for puffins. Third, the proportion of a colony suffering mortality is generally a function of the distance from the colony to the spill launch point, but this is influenced in important ways by the pattern of foraging distribution of the birds associated with a colony. Thus, for Tufted Puffins, birds from colony 1 suffer little mortality in any of the spill scenarios, even though two launch points (A10 and A11) are not far from the colony. Colony 2 is most strongly affected by spill A11 in spring, while colony 3, located not far away, is most sensitive to spills originating from point A7, especially during summer. A glance at Fig. 2 indicates that these differences are associated with the foraging distribution patterns assigned to birds from these two colonies. Colony 4, with a foraging distribution similar to that of colony 3, is likewise most sensitive to spills from point A7. Colonies 5 and 6 are most strongly affected by summer spills from A3, but are influenced only slightly less by spring spills from A7. Colony 7 is by far the most sensitive of the puffin colonies, suffering in excess of 10% mortality for spring and summer spills originating at point A3, and mortality greater than that of any other colony with spring and summer spills from A7 and spring A10 spills. The wide foraging distribution of birds assigned to this colony (Fig. 2) is at least

Table 2. Mean mortality (numbers of adults killed) of Tufted Puffins by colony and oil-spill scenario. Percentages of total colony population are given in parentheses.

Spill Scenario	Colony (size)						
	1 (30,000)	2 (12,000)	3 (8,500)	4 (7,000)	5 (7,000)	6 (11,500)	7 (6,000)
A3 Spring	12 (0.04)	6 (0.05)	9 (0.11)	7 (0.10)	16 (0.23)	26 (0.23)	650 (10.83)
A3 Summer	0 (0.00)	21 (0.18)	54 (0.64)	55 (0.79)	132 (1.89)	218 (1.90)	762 (12.70)
A7 Spring	41 (0.14)	130 (1.08)	149 (1.75)	90 (1.29)	88 (1.26)	142 (1.23)	279 (4.65)
A7 Summer	24 (0.08)	88 (0.73)	176 (2.07)	140 (2.00)	40 (0.57)	71 (0.62)	179 (2.98)
A10 Spring	229 (0.76)	140 (1.17)	46 (0.54)	27 (0.39)	15 (0.21)	19 (0.17)	130 (2.17)
A10 Summer	120 (0.40)	15 (0.13)	40 (0.47)	39 (0.56)	23 (0.33)	33 (0.29)	76 (1.27)
A11 Spring	150 (0.50)	171 (1.43)	42 (0.49)	17 (0.24)	0 (0.00)	10 (0.09)	0 (0.00)
A11 Summer	348 (1.16)	127 (1.06)	33 (0.39)	3 (0.04)	0 (0.00)	2 (0.02)	0 (0.00)

Table 3. Mean mortality (numbers of adults killed) of Black-legged Kittiwakes by colony and oil-spill scenario. Percentages of total colony population are given in parentheses.

Spill Scenario	Colony (size)							
	1 (4,000)	2 (3,500)	3 (4,000)	4 (8,500)	5 (40,000)	6 (10,000)	7 (7,000)	8 (7,500)
A3 Spring	0 (0.00)	0 (0.00)	1 (0.03)	0 (0.00)	57 (0.14)	138 (1.38)	58 (0.83)	42 (0.56)
A3 Summer	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	144 (0.36)	10 (1.00)	20 (0.29)	20 (0.27)
A7 Spring	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	194 (0.48)	3 (0.03)	0 (0.00)	0 (0.00)
A7 Summer	2 (0.05)	0 (0.00)	2 (0.05)	5 (0.06)	202 (0.51)	27 (0.27)	8 (0.11)	0 (0.00)
A10 Spring	0 (0.00)	0 (0.00)	4 (0.10)	22 (0.26)	340 (0.85)	18 (0.18)	0 (0.00)	0 (0.00)
A10 Summer	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.02)	101 (0.25)	8 (0.08)	7 (0.10)	0 (0.00)
A11 Spring	1 (0.03)	0 (0.00)	6 (0.15)	3 (0.04)	134 (0.09)	0 (0.00)	0 (0.00)	0 (0.00)
A11 Summer	7 (0.18)	1 (0.03)	14 (0.35)	8 (0.09)	196 (0.49)	0 (0.00)	0 (0.00)	0 (0.00)

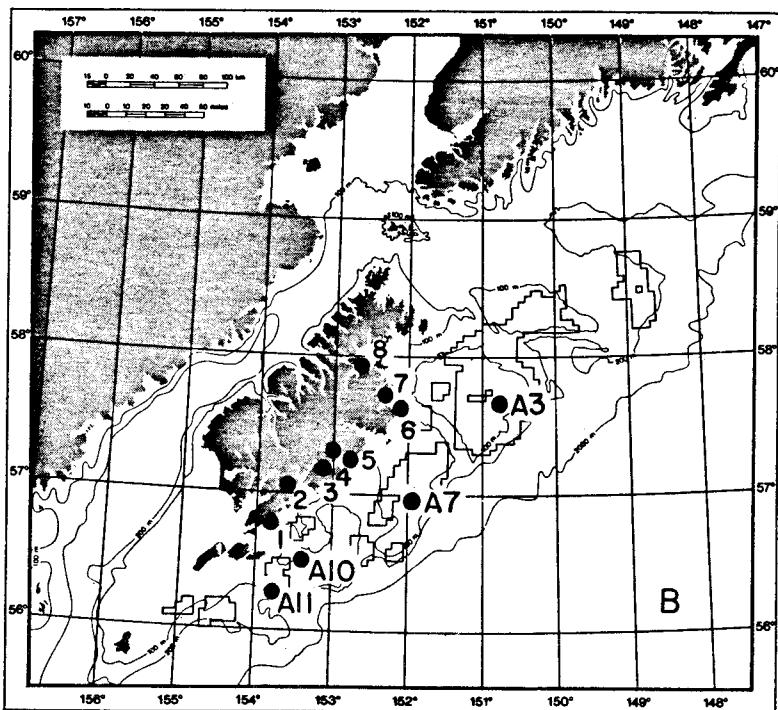
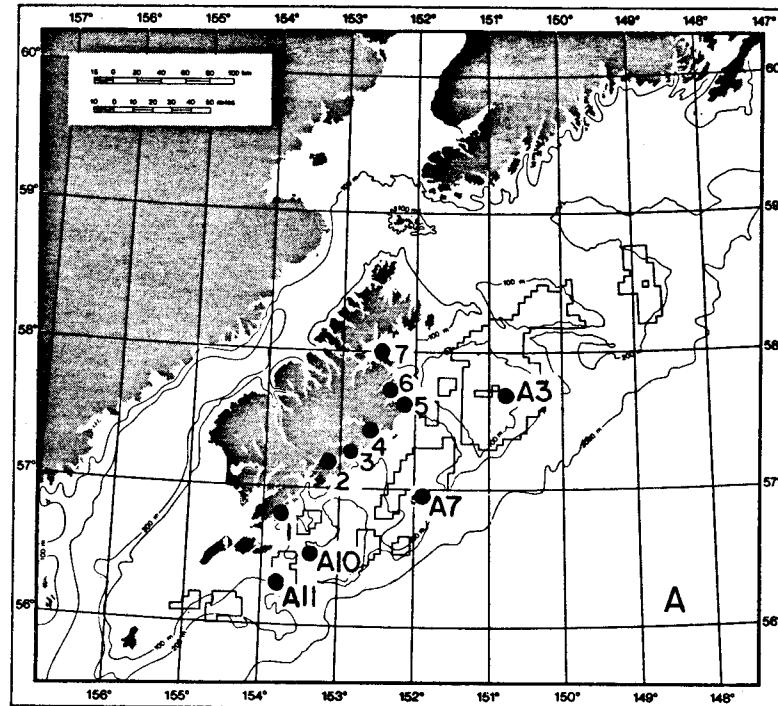


Fig. 5. Launch points for oil spills (A3-A11) in relation to the locations of Tufted Puffin (A) and Black-legged Kittiwake (B) colonies considered in our analyses.

partly responsible for these mortality patterns. For Black-legged Kittiwakes, the only spill scenarios that effected in excess of 1% mortality were spring and summer spills from A3 for colony 6.

These figures relate to the effects of the different spill scenarios on specific breeding colonies. If we instead ask what degree of mortality of puffins and kittiwakes from all of these colonies is associated with each of the spill scenarios, we find that in only one situation (spring runs of spills from launch point A7 on puffins) is the overall mortality in excess of 1% of the breeding population (Table 4). In general, then, none of these spill scenarios seems to exert a powerful direct effect on survivorship of breeding birds in these colonies, given the constraints and assumptions of our modeling approach. One must remember, however, that even small alterations in annual survivorship of adults can affect the age-structure of a population, and increase its susceptibility to devastating long-term effects of one-time perturbations of greater magnitude (Wiens et al. 1979a, Ford et al. 1982).

The values presented in Tables 2-4 all represent average mortalities associated with the 50 runs of each spill scenario. Although these are instructive in a general sense, they may be somewhat misleading, in that they do not consider the fact that the mortality accompanying some runs may be substantially greater than that associated with others. In Figs. 6 and 7 we present the frequency distributions of total mortalities of the two species (summed over all colonies) for the 50 runs of each spill scenario. For some (e.g. A3 spring and A7 summer for puffins), the mortality estimates are more or less normally distributed about the mean. For others, however, the distributions are distinctly skewed. Scenarios A10 and (especially) A11 exhibit frequency distributions with a preponderance of low or zero-mortality values. Others, such as A3 summer and A7 spring, contain a substantial number of individual runs predicting rather high mortalities for each species, even though the overall average mortalities accompanying these scenarios are not especially great (Table 4). Thus, on this basis, we attribute somewhat greater potential impact to spills originating from the areas of points A3 and A7, at least some of the time.

One important source of variation in our estimates of spill-associated mortality is that associated with our uncertainty in the values of the parameters T , ρ , and τ , which were Monte Carloed in our simulation runs. In an attempt to assess the proportion of the variance in our estimates of mortality that is associated with this parameter uncertainty, we conducted an ANOVA of the 50 simulated runs for each scenario, for each of the two species. Table 5 presents the proportion of the variance in estimated mortalities attributed to parameter uncertainty in the model. The apparent importance of this variation (and thus in the precision with which we estimate the values of T , ρ , and τ) varies considerably, but is seemingly substantial for spring spills at launch point A3 and summer spills from points A7 and A11 for puffins, and for spring and summer spills from A7 and spring spills from A3 and A10 for kittiwakes. These are not generally those spill scenarios that accounted for the greatest proportionate mortality of the species (Table 4), perhaps alleviating somewhat our concern about the need for accuracy in the estimation of these parameters. Nonetheless, they may contribute substantially to the variation in our estimates of the mortality potentially associated with given spill events.

E. Discussion

As the modeling approach we have followed in treating spill-related mortality of seabirds in the Kodiak system is a simplification and extension of that employed in

Table 4. Mean mortality (number of adults killed) of Tufted Puffins and Black-legged Kittiwakes for all colonies combined, by spill launch point.

Spill Origin	Tufted Puffin		Black-legged Kittiwake	
	Spring	Summer	Spring	Summer
A3	725 (0.88)	347 (0.42)	296 (0.35)	284 (0.45)
A7	991 (1.21)	718 (0.88)	430 (0.51)	245 (0.29)
A10	599 (0.73)	345 (0.42)	386 (0.46)	118 (0.14)
A11	288 (0.35)	512 (0.62)	145 (0.17)	228 (0.27)

Table 5. Proportion of the variance in number of individuals killed that is attributable to uncertainty in the model parameters. See text for explanation.

Spill Scenario	Tufted Puffin	Black-legged Kittiwake
A3 Spring	0.46	0.23
A3 Summer	0.15	0.11
A7 Spring	0.11	0.35
A7 Summer	0.24	0.39
A10 Spring	0.13	0.33
A10 Summer	0.04	0.05
A11 Spring	0.17	0.07
A11 Summer	0.29	0.12

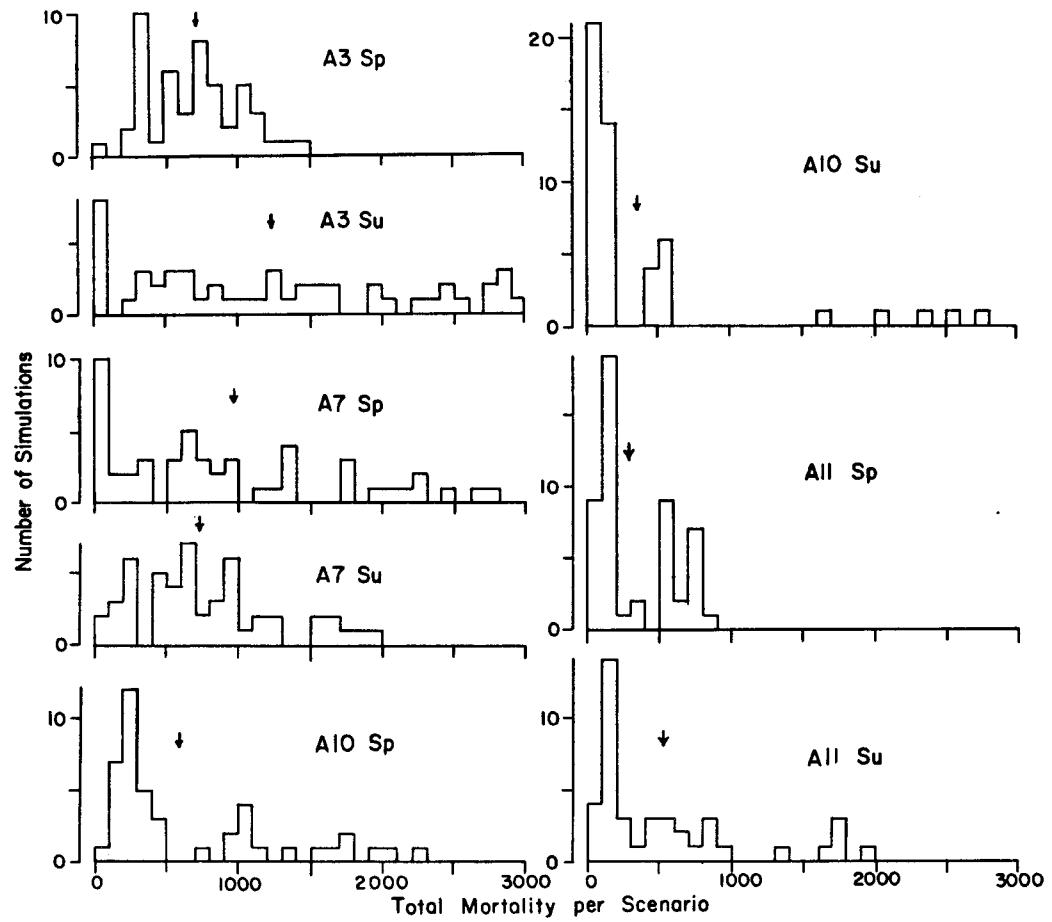


Fig. 6. Frequency distributions of Tufted Puffin adult mortality (number of individuals killed) associated with 50 simulations of each of 8 oil-spill scenarios. The arrow indicates the average mortality. See text for description of the procedures.

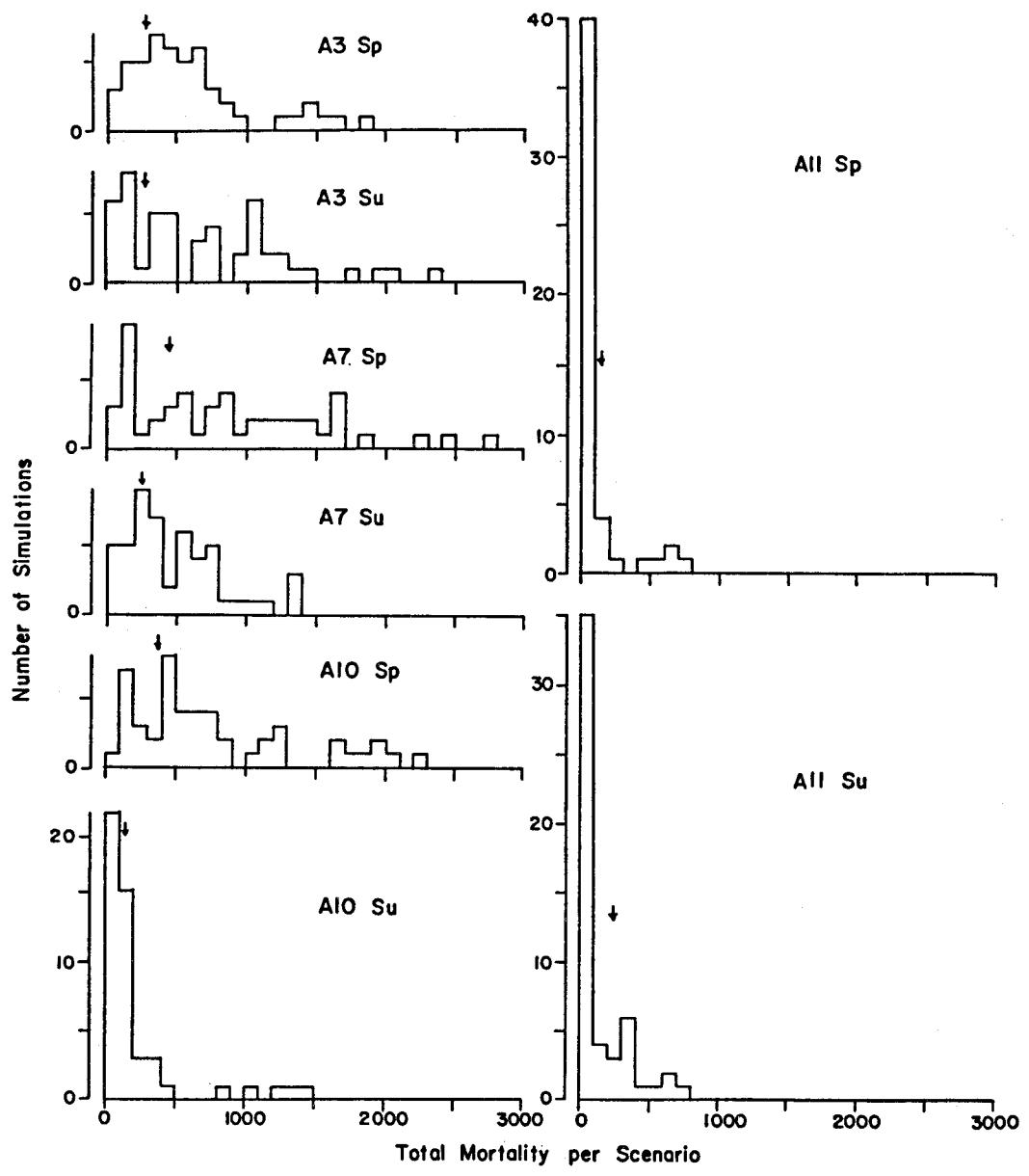


Fig. 7. Frequency distributions of Black-legged Kittiwake adult mortality (number of individuals killed) associated with 50 simulations of each of 8 oil-spill scenarios. The arrow indicates the average mortality. See text for description of the procedures.

our earlier analysis of the Pribilof Islands system, it seems appropriate to compare the models and their results. The model we developed for the Pribilofs could almost be considered an art form, in that it represented an attempt to portray the actual form of biological patterns, and incorporated a good deal of elegance. The slimness of the data base from Kodiak for many of the parameters of that model precluded its direct application to the Kodiak system, and therefore a simplified modeling approach was necessary. In a sense, however, the Pribilof model represented a necessary ontogenetic stage in our modeling development, as we were able to employ the results of analyses using that model to determine which functions could be dispensed with or modified considerably with minimal effects on the overall model predictions. It was on the basis of the Pribilof results, for example, that we felt justified in omitting the chick growth/survivorship features of the Pribilof model in developing the Kodiak model. We thus assumed that chick mortality results from adult mortality, not from food deficiency of the young. Given these and other simplifying assumptions that we have made in its development (see above), the Kodiak model seems to provide a reasonable approach to producing general projections of the mortality that might accompany specific spill scenarios, although it lacks some of the biological richness of the Pribilof model. Both approaches, of course, are constrained by our inability to verify the model estimations directly, by comparing model projections against the mortality patterns accompanying actual spills. Until controlled spill experiments and attendant monitorings of the accompanying mortality of marine birds are undertaken, our projections must remain in the realm of educated (albeit sophisticated) guesses.

PART II. ASSESSING THE SENSITIVITY OF MARINE BIRDS TO OIL SPILLS: INFORMATION GAPS AND PRIORITIES

A. Introduction

Industrialized societies are demonstrating an increasing dependence on and demand for petroleum. As these demands grow, it is inevitable that perturbations of the marine systems that are used for producing or transporting petroleum will increase in frequency and magnitude. As such seepages, spills, blowouts, wrecks, and the like are likely to have major repercussions on the biota of marine systems, it is imperative that we be able to predict their consequences and plan petroleum-related activities and development accordingly. Unfortunately, at present we seem largely restricted to after-the-fact assessments of damage once the perturbations have occurred, and while these may lead to some understanding of the dynamics and consequences of oil pollution in oceanic systems, they do not provide much guidance in developing means to minimize such effects.

We have recently attempted to approach the problem of predicting the effects of petroleum-related perturbations on colonially breeding marine birds through the development of mathematical models (Ford et al. 1982). This exercise led us to consider the existing information on marine birds, their activities, and their resources from a perspective that is not commonplace. In the process, we became aware of gaps in the available information, sampling problems, and inefficiencies in the approach of most studies of marine birds that severely constrained our attempts to structure realistic and intelligent models. Because we believe that these problems are likely to thwart any attempts to develop *a priori* means of assessing petroleum-related perturbation effects, and because some of the problems and deficiencies might be reduced if field investigations were more cognizant of them, we believe that a discussion of the difficulties that we have encountered is warranted. In this paper we will briefly describe our modeling approach, indicate the sorts of

data that are required in the model structure and the problems associated with obtaining reliable information on each, and assign provisional priorities to our information needs.

B. Model Structure

The models we have developed (Ford et al. 1982, Part I of this report) predict the mortality that might be expected in colonially breeding seabirds (murres, puffins, and kittiwakes) if a portion of the ocean area about the breeding colony were to experience a pollution event (a spill, in the examples we have considered). Such mortality may be of two kinds: direct mortality of adults caused by their encounter with the spill, and indirect mortality of offspring caused by the death of their parent(s) or by diminished growth, a consequence of the redistribution of foraging birds away from the spill area and the accompanying decrease in their rate of food delivery to the young. These mortality effects are expressed through the operation of a demographic submodel, which projects the number of individuals present in each of several age classes of a population at any point in time as a consequence of immigration, reproduction, emigration, growth, and mortality. Survivorship of the young is modeled as a function of the food (energy) delivery rate of the adults in relation to the energy demands of the chicks at given phases of their growth.

Food delivery rates and direct mortality via spill encounter by adults are projected through a foraging submodel. This submodel derives a distribution of birds from the population in the ocean area about the colony by considering daily movement patterns of foraging birds in relation to projected resource levels in various areas. Using optimality assumptions, we presume that birds will forage so as to minimize the length of time spent in foraging trips (trip time). Trip time may then be considered as a function of the distance from the colony to the foraging area, flight speed, the rate of food capture while foraging, and the overall energy demands (adult + young) that must be satisfied on a daily basis. Breeding individuals thus must obtain more food while foraging than adults without young, as they must balance both their own and their chicks' energy demands. Food capture rate is assumed to decline with increasing density of birds present in an area, as greater densities should lead to either localized depletion of food resources or interference, increasing the birds' search time. The spatial distribution of individuals at sea under conditions of optimal foraging (minimal trip time) should thus reflect a compromise between seeking out areas of high resource abundance and avoiding areas of high densities of foraging birds.

The effects of oil spill perturbations are then modeled by effecting a reduction in food supply and a proportionate direct mortality of adults in areas affected by the spill. Birds that do not suffer direct mortality must shift their foraging to other areas, and because the previous distribution was defined as optimal, this shift will lead to a reduction in foraging efficiency (greater costs of foraging associated with reduced prey capture rates in the new area) and an increase in trip time. This, in turn, will reduce the rate of food delivery to the young, affecting their growth rate and leading to mortality of the young if the growth rate falls below survival levels.

These submodels predict the short-term consequences of a specified perturbation for populations of breeding seabirds. Because the perturbation effects mortality of individuals, however, there will in addition be long-term results, as the mortality will reduce population density and alter the age structure of the population. In

another model, we evaluate these long-term effects by using the mortality rates projected from the short-term model as inputs to a simple set of population dynamics algorithms. Given information on the age-dependence and density-dependence of fecundity, mortality, and emigration and immigration rates in an unperturbed population, we can project the length of time required for a population to return to an equilibrium age structure and size following a spill event, or the magnitude of perturbation beyond which the population is unlikely to be able to recover and will suffer local extinction.

C. Information Needs

This modeling approach provides general predictions of the likely response of marine bird colonies to perturbations in the oceanic areas about the colony. The models are built upon details of the biology of the species, and as such, they are realistic and potentially quite useful. The predictions that emerge however, are limited in their accuracy by the levels of precision and accuracy of our knowledge of the basic biological parameters on which the models are founded. Unfortunately, there are some dismaying gaps in our knowledge of these systems, and some problems in the use of the information that does exist. These indicate that conventional field studies of marine birds have not addressed some important aspects of seabird biology and have perhaps addressed others incorrectly. We therefore discuss the information requirements of our modeling approach and the status of the information that is available to fill our needs. In Table 6 we summarize the status of available information for the critical model parameters for two Alaskan situations that we have modeled, and for the seabird literature in general.

Table 6. Estimations of the quality and availability of data for various parameters of seabird biology required to model the sensitivity of populations to oil spills, and an importance rank (research priority) for each.

Parameter	Quality of Data ^a			Importance rank ^b
	Pribilof Islands	Kodiak Island	In literature	
Population (colony) size	3	2	1-3	3
Time of occupancy	3	2	1-4	1
Population age structure and % breeding	1	0	0-2	2
At-sea densities	2	1	1	3
Food availability in foraging areas	1	0	0-1	2
Reproductive phenology	4	3	2-4	1

Table 6 continued

Parameter	Quality of Data ^a			Importance rank ^b
	Pribilof Islands	Kodiak Island	In literature	
Reproductive success	4	3	1-4	1
Chick growth rate	4	3	0-4	1
Body weight	4	4	2-3	1
Probability of death on spill encounter	0	0	1	3
Age-specific fecundity and survivorship	0	0	1-2	3
Foraging trip time	2	1	0-2	3
Foraging activity budget and flight path	0	0	0	2
Perturbation tracking	0	0	0	3
Metabolic rate	0	0	2	1
Thermoneutral zone	0	0	1	1
Digestive efficiency	0	0	1	1
Chick growth efficiency	0	0	1	1
Foraging (flight) cost	0	0	1	2
Flight speed	2	0	2	1
Food load size	2	0	0-2	1
Chick response to food deprivation	1	0	0	2
Foraging rate as a function of resource density	0	0	0	3
Oil spill dynamics	0	1	1	2
Changes in food availability due to perturbation	0	0	0	3

^a 0 = absent, 1 = poor, 2 = marginal, 3 = good, 4 = excellent^b 1 = low, 2 = intermediate, 3 = high

1. Population Parameters

Population size and density.--In order to initiate any consideration of the possible impacts of oil development on colonially breeding seabirds, it is necessary to know the size of the colony, when it is occupied, the age structure of the population (especially the proportion of the population that is actually involved in breeding activities), the density of birds at sea in defined areas, and the temporal variations in this at-sea distribution. General approximations of the sizes of breeding colonies have been developed for some areas (e.g. Sowles et al. 1978, U.S. Fish and Wildlife Service 1980), and these often provide a workable estimate of colony size. For many of the species, these estimates are derived from "cliff counts," in which the number of individuals of a species occupying breeding sites on a designated area of cliff-face is counted directly or from photographs, and that count extrapolated to the total area of cliff-face available in an area. Such sampling is rarely done in a systematic fashion, however, and there may be substantial errors involved in extrapolating from a few counts to a total colony estimate, because of the difficulty of assessing the total area of suitable cliff habitat that is available to the birds or that is actually occupied by the colony (see Lloyd 1975). Further, such cliff counts cannot be used to obtain accurate estimates of the densities of burrow- or crevice-nesting species (e.g. storm-petrels, auklets, puffins, guillemots).

If cliff counts are taken frequently, they may provide information on the seasonal flux of colony size, but generally this is not done. Thus, the initial arrivals and departures of birds at the colony at the onset and termination of the breeding season are often missed because observers are present only during the peak of breeding activities. In our modeling exercises, we have been forced to assume that no birds are present in the area prior to the onset of immigration to the colony in the spring or following the completion of emigration in late summer, an assumption we know to be false for some species. We have also assumed that the immigration and emigration rates are constant between initiation and completion of these phases, and that the population size remains unchanged during the period between the completion of immigration and the initiation of emigration. Cliff counts conducted on the Pribilof Islands by S.D.L. Causey-Siegel and R. Squibb (pers. comm.) suggest that the rate of arrival of birds during immigration may indeed be relatively constant, but otherwise we have no data available to test these assumptions for the seabird systems we have studied.

In order to estimate the potential reproductive output of a colony and the way in which it may be affected by perturbations, information on the proportion of the population that is actually breeding is required. In most seabird species maturation is delayed, and a proportion of the birds using the waters adjacent to colonies may not be reproductively active. In some species, age-dependent plumage changes provide a way to index population age structure and at least separate subadult individuals from adults. In other species, however, plumage does not differentiate age classes; moreover, a significant portion of adult birds may not participate in breeding in a given year, for various reasons. Age-structure data were not available for any of the Alaskan populations that we studied (Table 1). Such data are available, however, for Atlantic populations of murres and Black-legged Kittiwakes (Tuck 1961, Coulson and Woller 1976, Birkhead 1977, Woller and Coulson 1977). These can be used as estimates of the values for the Alaskan populations, although the only justification for doing this is that the data relate to the same species that we studied. Interpopulational differences in other parameters, however, cast doubt on the precision of this procedure (see below). Unfortunately,

information on the age structure or breeding status of individuals in populations is difficult to obtain, usually requiring marking studies. Resightings of marked individuals at sea are not likely to be obtained in sufficient quantity to permit anything beyond a coarse estimate of the proportion of the at-sea population that is affiliated with a breeding colony.

At the foundation of any attempt to predict perturbation impacts on marine birds is an accurate knowledge of the distributions of the populations at sea, as this will influence the likelihood that birds will encounter a spill in a given area.

Considerable effort has been devoted to determining the distributional patterns of marine birds at sea (e.g. Summerhayes et al. 1974, Brown et al. 1975, Lensink and Bartonek 1976, Lensink et al. 1976, Gould 1977, Harrison 1977, Lensink et al. 1978, Nettleship and Gaston 1978, Pocklington 1979, Brown 1980, Hunt et al. in press). Generally, these estimates are derived from shipboard or aerial transects that are run through specified areas. As such, the procedures suffer from all of the problems that are inherent in line transect population census methods (Wiens et al. 1978b, Burnham et al. 1980), which are aggravated by the fact that movements of the ship or aircraft are not generally linear and thus determination of the area actually sampled by a transect is subject to error. Our analysis of transect densities derived from aerial and ship transects in the Kodiak region of the Gulf of Alaska (Wiens et al. 1980) indicate that the probability of detecting no birds is always greater for aerial transects than for ship transects, and that for most species the mean/variance ratio is consistently higher for the aerial transects. These discrepancies hinder attempts to combine aerial and ship transects in any straightforward manner, although if both types of transects are available for some areas one may be standardized against the other to obtain at least relative consistency.

Observation conditions (e.g. visibility, attentiveness of observers) also may vary substantially among transects. If one adds to this the between-observer variation that is inevitable when many different individuals record observations on different transects, the variability attributable to sampling error of the transect counts becomes substantial. Further variation is introduced because the area of concern about breeding colonies is usually far too large to permit adequate sampling of the entire region in a short period of time. Surveys are often taken on an opportunistic basis as ship-time becomes available, and some areas may be surveyed frequently while others receive little or no attention. In particular, close inshore areas may be neglected because ships generally avoid them; such areas, however, may be important foraging zones for many of the less pelagic colonial seabirds (e.g. guillemots, glaucous-winged gulls, terns, cormorants). Thus, even in intensive studies such as those that are part of the OCSEAP, censusing is unevenly distributed over areas of ocean and through time.

The censuses that are available for estimation of at-sea densities thus exhibit substantial heterogeneity in time, area, and method of sampling. As a consequence, some degree of pooling of transect samples over space and time is necessary, and this inevitably is accompanied by a loss of resolution in the at-sea density distribution patterns that emerge. In our analysis of the perturbation sensitivity of populations breeding at several colonies on Kodiak Island, we were compelled to combine survey data collected at different times of year to produce overall annual density distribution patterns in spite of our knowledge that the pattern varied considerably during the year. Spatially, the frequency of surveys taken in the major ocean areas about the island was sufficient to permit us to consider distributions in 10 km x 10 km blocks, although we found it necessary to develop means of weighting the density estimates in relation to the number and location of transects

run through a given area (Wiens et al. 1980). Even with such broad lumping of transect data, however, some critical portions of time and space were still not represented, necessitating extrapolations to derive density/distribution estimates.

Information on the at-sea distributional patterns of marine birds is thus confounded by variability. Some of this is a consequence of the methods and observers, some a result of the patchy distribution of sampling effort in different areas at different times. Most of the variation, however, is due to the birds themselves. Many species are distributed in a distinctly aggregated fashion, presumably in response to oceanographic and/or resource conditions. Densities of a given species may vary over 3-4 orders of magnitude during time intervals of hours or days and distances of only 5-10 km. As a consequence, the frequency distributions of transect densities are extraordinarily skewed--very low densities per transect are most common, but densities orders of magnitude higher occur with regularity. This means that standard statistical approaches to establishing confidence limits to the density estimates for given blocks of ocean or for testing for differences in densities between areas are invalid unless sample sizes are extremely large (which, as noted above, they generally are not). In our work with seabird distributions in Alaskan waters, we were compelled to develop new statistical procedures for estimating confidence limits, based upon the gamma distribution (Wiens et al. 1980, Ford and Qualls ms). Our applications of this procedure to the transect density estimates for the areas adjacent to Kodiak Island (employing coarser 20 km x 20 km blocks of area and combining surveys over the year) indicated that our confidence in any estimates of Kodiak area seabird densities is quite low. There are two basic problems. First, within the area we considered (approximately 90,000 km²), only 3-6% of the area was sampled with sufficient intensity to provide any estimate of density confidence limits, despite our generous lumping procedures. Second, if a block was sampled sufficiently to provide confidence intervals, only 30-80% of these blocks (depending on species) yielded confidence limits such that the observed mean density and the upper confidence limits were within an order of magnitude of each other. The problem was most severe with shearwaters because of their highly skewed abundance distributions in the transects, but the more important foraging areas appeared to show more severely skewed distributions for all species, so that our confidence in the density estimates was often lowest where it was most important. These conclusions are quite discouraging, especially when one considers the fact that we were employing data sets generated in a rather massive transect sampling program (OCSEAP).

Reproduction and survivorship.--Operation of models to assess the proximate effects of perturbations on populations and the long-term effects on the recovery or persistence of the population requires a variety of demographic data. Fortunately, some aspects of the reproductive biology of populations are easily studied and are often included in conventional breeding biology investigations. Other parameters, however, are difficult to measure or are generally ignored in seabird studies. Our modeling exercises suggest that some of these may be critical to predicting the population consequences of perturbations.

Perhaps the most readily available data concern the timing of reproduction in the populations occupying a given colony. If a colony has received any on-site study at all, it is likely that information on the onset of incubation, the distribution of breeding attempts among individuals in the population, the mean and variance of hatching dates, and the timing of fledging of young will be available, at least in the form of coarse phenological measures. When colonies do receive close study, aspects of reproductive success are often a primary focus, and thus

data on the average hatching success of eggs laid and the average fledging success of young hatched are frequently available, perhaps accompanied by variance measures for these parameters. These data are most easily obtained for open-nesting species, can be gathered with considerable effort for cavity or burrow nesters (e.g. Hunt et al. in press), and are extremely difficult to obtain for species that nest in deep crevices. Information on the breeding success of populations is thus likely to vary substantially among species. Obviously, accurate information on both the timing and success of reproductive efforts in local populations under "normal" conditions is essential if we are to predict the effects of perturbations occurring at various times through the breeding season with any degree of accuracy.

In one of the models we developed (Ford et al. 1982), indirect mortality of young in response to an oil spill is effected by a reduction in the rate at which adults deliver food to them, and thence in the rate at which the young grow. In order to assess such effects, we must know how young grow under normal circumstances. Growth studies have been especially fashionable in seabirds because their patterns and rates of growth and maturation differ so markedly from the typical passerine patterns (e.g. Ricklefs 1973, 1979), and there is thus a moderate amount of information available in the literature. Growth rates may therefore be available for most of the species at a given colony, although colony- or area-specific growth rates for the populations are likely to be available only if populations in the area have been subjected to intensive breeding-biology studies. Between-colony or between-year differences in growth rates of chicks of a given species may sometimes be substantial (e.g. Mahoney and Threlfall 1981, Hunt et al. in press). In addition, the disparity among species of different nesting habits noted above is likely to be even more extreme for growth data than for success measures.

Unfortunately, obtaining accurate measures of the reproductive success or chick growth rates for populations requires fairly intensive field study, especially for those species nesting in burrows or crevices. The activities of investigators about the colonies or the nest sites disturbs the breeding birds, and the more intensive the studies, the greater this disturbance effect may be. Several studies have documented the degree to which even moderate levels of investigator activity about breeding colonies may depress reproductive success (e.g. Ellison and Cleary 1978, Tremblay and Ellison 1979, Lenington 1979, Duffy 1979, Ellison 1979). We are thus confronted with the paradox that the more effort we put into obtaining really precise measures of reproductive success or chick growth rates, the less natural and accurate those values are likely to be.

Information on normal body weights of adults is usually (but, regrettably, not always) gathered when collections are made for dietary studies or other purposes. Such information is required in any model that attempts to evaluate perturbation effects through estimation of individual or population energy demands (see below). If energetic analyses are to be employed to gauge the effects of varying food delivery rates on chicks, then additional weight data must be available for eggs, chicks at hatching, and fledglings. Such data are usually not obtained unless growth studies are conducted, and even then egg weights are often not recorded.

In our models, the sole source of adult mortality accompanying oil spills is the direct death of birds that encounter a spill while at sea. We can model the probability of a bird encountering a spill by relating the at-sea distribution patterns and the foraging dynamics of the birds to the specific area occupied by a spill. We do not know the details of individual behavioral responses to spills or oil slicks (e.g. attraction vs. repulsion), however, and such behaviors would influence the

probabilities of spill encounter calculated solely from distributional information. In addition, however, we must know the probability that a bird encountering a spill will actually suffer mortality. No direct measures of this parameter are available, and in our modelling exercises to date we have been forced to estimate values from descriptions of oiled birds available in the literature (e.g. Bourne et al. 1967, Bourne 1968, Holmes and Cornshaw 1974, Vermeer and Vermeer 1975, King and Sanger 1979).

The remaining features of reproduction and survivorship that are required relate to attempts to translate the proximate, short-term effects of perturbations into predictions of the long-term population consequences of those effects. To do this, any realistically structured model requires information on the patterns of age-specific fecundity and survivorship in the population, as these are the basic features of demography upon which life-table analyses are built. Moreover, if one has reason to believe that any degree of density-dependence influences these population processes, the magnitude of these density-dependent effects must be determined. Such information is difficult to obtain, as it generally requires long-term investigations. A few such studies have been conducted on seabirds in the North Atlantic (murres, Tuck 1960; Black-legged Kittiwakes, Coulson and White 1959, Coulson and Wooler 1976, Wooler and Coulson 1977; Gannets, Nelson 1978; Fulmars, Dunnet et al. 1979; Shags, Potts et al. 1980), but no information of this sort exists for any of the North Pacific breeding species. In the absence of other data, one is tempted to apply the information from Atlantic populations to Pacific populations of the same species. For kittiwakes, this is obviously inappropriate, as the fecundity reported for the two populations differs considerably (Coulson and White 1959, Coulson and Woller 1976, Wooler and Coulson 1977, Wiens et al. 1979a), and incorporation of the Atlantic values into a life-table model for the Pacific populations yields rates of change in population size from current levels that are unrealistic (Wiens et al. 1979a). Given the magnitudes of inter- and even intracolony variations in reproductive parameters that may occur for many seabirds (e.g. Harris 1980, Mahoney and Threlfall 1981, Birkhead and Nettleship 1981, Hunt et al., in press), such extrapolations may be generally suspect.

2. Foraging Parameters

The modeling approach that we have followed places heavy emphasis upon features of the foraging behavior of the birds. This is because birds generally use the oceanic areas where pollution is most likely to occur primarily for feeding, and as breeding birds are restricted to using areas within range of the breeding colony, their options for responding to a perturbation will be rather limited. The key variable that we have employed in structuring our models is trip time, which includes the time taken by a foraging adult to travel from the colony to a foraging location, the time spent in searching for and capturing prey sufficient to make a load for the return trip, and the time taken to return to the colony. Information on trip times is rarely gathered in seabird studies (but see Pearson 1968), even in those that devote considerable effort to documenting the various reproductive parameters (e.g. Birkhead 1977). When trip time has been determined, it has usually been obtained from only a few individual birds at one colony (or one location within a colony), on just a few days. The slimness of this data base makes it impossible to model the temporal dynamics of foraging patterns without making some assumptions (e.g. the optimality of foraging; see Norberg 1981), which are largely untested. It seems surprising that trip time information is often not gathered in association with continuous observations of colony sections (as in some cliff counts) or nest

sites. Possibly this is because the importance of information on trip times has not generally been realized.

Our use of trip time in the models is based upon two important assumptions. One is that the allocation of time to activities during a trip is optimal, that is, once the birds arrive in the foraging area they spend their time foraging at the maximum efficiency in relation to resource availability. This assumption requires testing, and the information that would provide the test is basic activity-budget data taken from birds at sea. How much of the time spent in a foraging area is actually spent in foraging? How much is spent "resting" or "loafing"? How does foraging success rate (and thus the time spent in foraging activities) relate to resource density? No information on any of these aspects of foraging behavior is available for any of the Alaskan populations, and data on dive times and success rates obtained in studies elsewhere (e.g. Stonehouse 1967, Scott 1973) provide only part of the requisite information.

The second assumption of our trip time calculations is that birds use the shortest, most direct flight path between the colony and the foraging area at sea. This, of course, presumes that a foraging individual knows precisely the location of its destination when it leaves the colony, and that decisions to change foraging locations are made with little time expenditure in searching for new areas. We know very little of the actual flight paths of foraging birds, although radio-tracking of tagged individuals could supply this information rather easily, at least for those species that forage relatively close to the colony.

When an area used for foraging by birds from a colony suffers an oil spill, we expect that the individuals that do not suffer direct mortality from the spill will adjust their foraging distribution to avoid the polluted area. It is unlikely that this response will be instantaneous, however, as birds that have been foraging in a traditional feeding area may exhibit some reluctance to leave it and forage elsewhere, especially if the spill is not massive. There will thus be a lag time in the response to a spill, and it may require several days for a population to adjust its at-sea foraging distribution to a new optimum dictated by the perturbation event. Because no studies of the proximate response of seabird populations to oil spills have been conducted, information on this "tracking" parameter is completely lacking, and intuition provides relatively little guidance. This is the sort of parameter that is generally not even defined unless one undertakes a modeling exercise, such as ours.

3. Energetic Parameters

Our modeling approach relies upon estimates of the balance between the energy demands of adults and chicks and the availability of energy (food) in various foraging areas to project perturbation-related alterations in the foraging patterns of adults and the growth rates and survival of young. Previous attempts to model the energetic patterns of seabird populations (e.g. Wiens and Scott 1975, Furness 1978) have followed the basic procedure of determining individual metabolic energy demands as they are modified by various environmental or behavioral factors, converting these to population-wide estimates, and then converting the energy demand values into estimates of food consumption rates. The derivation of such estimates is dependent upon knowledge of the values of several basic energetic parameters, and these also figure in the energetic calculations we have employed in assessing spill impacts.

The foundation of the energetic estimations is some procedure for deriving the metabolic rate of individuals on a daily basis, unadjusted for activities such as foraging. In our earlier modeling of seabird energetics (Wiens and Scott 1975, Wiens et al. 1978a), we used the equations presented by Kendeigh et al. (1977), which project daily existence energy requirements for nonpasserines as functions of body weight, ambient temperature, and photoperiod. Because it provides estimates of similar accuracy but requires less input information, we used the equation of Aschoff and Pohl (1970) for the daily energy requirement of a nonactive bird at thermoneutrality in our more recent models. Such general equations must be used to estimate metabolic rates because so few seabirds have been studied directly (but see Johnson and West 1975). Use of the Aschoff-Pohl equation required that we establish that the birds we studied were normally at thermoneutrality. This assumption seems justified for seabirds; Johnson and West (1975) reported a lower critical temperature for murres of 4.5°C, and the sea-surface temperatures recorded in the Bering Sea during the May-August breeding period rarely fall below that level (Wiens et al. 1978c). Use of this equation instead of the Kendeigh et al. equations also assumes that the effects of photoperiod are unimportant. The influences of photoperiods at high latitudes on metabolic rates are generally unstudied, although a series of sensitivity tests we performed on the estimates of seabird energy demands derived using the Kendeigh et al. equations indicated that small variations in photoperiod had relatively little effect on the overall energy requirements (Wiens et al. 1978c). In the absence of species-specific metabolic studies of seabirds, use of the Aschoff-Pohl equation thus seems justified, although the energy requirement estimates derived may not be very precise. As they are used in the models primarily to predict the magnitude of change accompanying a perturbation, however, their primary value is as a relative rather than an absolute measure, and for this they are probably quite suitable.

The estimates of daily individual energy requirements derived from this (or some other) equation must be adjusted for several costs in order to determine the actual energy demands that are placed upon the environment (and that thus will be affected by alterations in resource availability or energy capture rate associated with perturbations). One such cost is that associated with the inefficiency of the digestive process; an individual must consume somewhat more food than that dictated by its metabolic energy demands alone, as not all of it will be digested and made available for metabolic action. For a wide variety of avian species and food types, digestive efficiency is close to 70% (Ricklefs 1974). Little direct information is available on the efficiency with which various seabirds process food, although data from Sooty Shearwaters (L. Krasnow, pers. comm.) suggest that birds feeding on fish and squid may have a digestive efficiency as high as 80%. Beyond this cost, chicks have the additional cost of converting food input into new tissue during growth. Again, no information on the value of growth efficiency is available for seabird species, and we must resort to using the general value of 75% provided by Ricklefs (1974).

A basic premise of the approach that we have taken to predicting responses to perturbations is that a disruption of foraging areas will force feeding birds to fly farther from the colony to obtain food, and that the indirect consequences of the perturbation will thus be mediated through the increased costs in time and energy spent in foraging. In terms of energetics, this means that we must have some means of adjusting the nonactive metabolic energy requirements for the additional costs of activities such as foraging. Unfortunately, little is known of the degree to which activity elevates energy demands in any birds (King 1973, 1974; Tucker 1974; Pennycuick 1975, Rayner 1979, Walsberg 1980, Norberg 1981), much less seabirds. In

previous work with passerines, we have used a value of 0.25 times existence energy demands to adjust for the additional costs of free-living activity (Wiens and Innis 1974, Wiens and Scott 1975). In the absence of additional data, a similar value would seem appropriate for seabirds, although this is really little more than an educated guess. This is unfortunate, as foraging costs are distance-dependent, and thus would seem to be important to predicting space-dependent perturbation impacts.

Other parameters, while not specifically energetic, relate to these energy-based calculations. Thus, in order to evaluate the additional time costs associated with a shift in foraging area accompanying an oil spill, we must know the average straight-line flight speed of each species. Such information is not generally gathered in colony studies, although it is not especially difficult to obtain. Some estimates for seabirds have been published (e.g. Meinertzhagen 1955); in our modeling we used these values, as modified by our own observations of murres and kittiwakes on the Pribilof Islands. Another important parameter is load size, the quantity of food (or energy) that an adult carries back to the colony on a foraging trip to feed the young. This value, combined with the frequency of feeding trips per day and the energetic features of the young, will determine the growth patterns of the young and their survivorship probability. For species such as murres that carry a single prey item on each trip, load size may be estimated by recording the type and size of prey when it is brought to the young, and then converting to biomass or energy by comparison with voucher specimens of the prey types. For species that bring multiple items per trip, or that carry back partially digested food in the crop or stomach (e.g. auklets, gulls, fulmar), estimation of load size is much more difficult.

In our model (as in nature), a reduction in food delivery rate to the young is reflected by a reduction of their growth rate. At some point this growth reduction becomes debilitating, and the probability of mortality of the chicks increases dramatically. A few studies (e.g. Birkhead 1977, 1978; Harris 1978, Braun and Hunt ms) have investigated the degree to which growth is reduced under conditions of reduced food delivery. The effects of such reduced growth rate on survivorship may be cumulative: a chick may be able to tolerate a day or two of reduced growth and still fledge on schedule (albeit at a below-average weight), but several successive days of depressed growth may affect the chick so that fledging weight is abnormally low or fledging is delayed, decreasing survivorship (but see Hedgren 1981). Information on the growth dynamics of seabirds under different food-delivery regimes could be obtained from carefully controlled feeding trials or deprivation experiments, but few such studies have been conducted.

Finally, in order to assess the foraging dynamics of birds during the time that they are present in a foraging area, we should know the food capture rate as a function of the density or availability of the resource. While some information on the dive success rates of foraging seabirds is available (e.g. Scott 1973), this does not serve to relate the success rates to resource availability (which was not measured in these studies). Indeed, no information of this sort exists for foraging seabirds. Not only would we require data on prey capture success rates, but on the resource densities in various areas of the ocean about the colony, the rates of depletion of these resources as a function of prey uptake by the birds, and the temporal dynamics of these parameters.

4. Perturbation Parameters

When the effects of an oil-related perturbation of a marine system are considered after the fact, determining the physical features of the event (e.g. its composition, size, distribution, duration) is generally rather straightforward and of high priority. If one instead wishes to predict these effects *a priori*, determination of spill parameters and dynamics are much more difficult (see Audunson 1980). In our initial modeling efforts we developed several spill scenarios arbitrarily, using information regarding oil spills available in the literature to make these fairly realistic. A much more accurate and powerful approach involves using data on ocean current patterns, surface conditions, and wind flows to predict the trajectories likely to be followed by surface oil launched (i.e. spilled) from a specified point at sea. Such a model has been developed by W. Samuels and his colleagues (pers. comm.). Because the trajectories for any given spill event are probabilistic, varying with the patterns of currents, wind conditions, and so on, we have used the spill trajectory model to generate spill scenarios for our impact analyses by conducting multiple spill model runs for each launch point at a given time. This yields estimates of the probability of spill encounter for various areas located about the spill source. When combined with the estimations of spill effects on the birds that are generated from our models, this enables us to predict the possible effects of a given spill scenario in a probabilistic fashion. Unfortunately, such spill trajectory models are available for relatively few ocean areas, although the Samuels et al. model is equipped to analyze spill characteristics for any area for which the requisite measures of physical features of the ocean area are available. These are much more likely to be available than are the many biological parameters that we have discussed above.

D. DISCUSSION: PARAMETER PRIORITIES

The approach that we have advocated to generating predictions of the possible impacts of oil developments and perturbations upon colonially breeding marine birds requires information on a substantial number of parameters of seabird biology. The data base available for some of these parameters is reasonably good (Table 6). This is especially true of those measures that pertain directly to the reproductive biology of individuals, such as clutch sizes, reproductive success, or breeding phenology. For many of the parameters, however, little or no information is available, and the preceding text reads like an inventory of what we do not know about seabird biology.

Does this mean that our approach, or any attempt to predict seabird responses to perturbations based on knowledge of their biology, is doomed to failure, and that we must continue to be content with post facto assessments? Perhaps not. Perhaps intelligent and reasonably accurate predictions can be generated without precise knowledge of the values of all of the parameters for a given colony. In our modelling we have often been forced to use general species-specific values of parameters rather than population-specific values, and in some instances we have resorted to approximating values for a species from literature values from other species in other areas in the absence of any more specific data. For those parameters lacking any sort of quantitative data base, we have derived educated guesses of "reasonable" values from our own intuition or that of other seabird workers.

In an attempt to justify the use of all these approximations, and to evaluate the possible effects of errors in their estimation on the output or predictions of

our models, we have conducted several sensitivity tests of the parameters and the models (Wiens et al. 1978c, 1980; Ford et al. 1982). In one exercise, we systematically varied the estimated values of parameters relating to the breeding structure of the population, photoperiod length (as it might influence daily energy demands), and the degree to which metabolism is elevated by activity (i.e. foraging). These sensitivity tests indicated that variations in the first two parameters had relatively minor consequences on the values of model output, but the variations in the costs of foraging activity over a reasonable range of values produced variations in model output on the order of $\pm 10\%$ (Wiens et al. 1978c).

A more robust and thorough approach to sensitivity analysis involves the use of Monte Carlo simulations, in which each of the input variables to the model is simultaneously drawn at random from a specified probability distribution of values of the variable. We conducted such sensitivity tests on multiple runs of our model of seabird dynamics in the Pribilof Islands system (Ford et al. 1982), using most of the variables that we have described above. We used variations in the model output values of adult survivorship and number of chicks fledged as an index of the sensitivity of model predictions to variations in parameter values. Standard errors of the model predictions ranged from 0.03 to 0.21 for most oil-spill scenarios, suggesting that our ability to generate predictions of perturbation consequences using this approach was relatively insensitive to reasonable variations in the values of most input parameters. This implies that general, qualitatively reasonable estimates of values for many of the parameters we have discussed may be quite satisfactory for generating reasonable predictions of perturbation effects.

Three model parameters were not included in these sensitivity tests: the probability of adult death associated with spill encounter (ρ), the rate of population response ("tracking") to the occurrence of a spill (τ), and the amount of change in food availability in a foraging area due to a perturbation (Δ). A separate set of sensitivity tests in which these parameters were varied over the range of reasonable values indicated that variations in ρ produced variations in model output on the order of $\pm 25\%$, while similar variations in the values of τ altered model predictions by as much as $\pm 50\%$; large variations in Δ produced substantial changes in model output. These parameters (especially τ and Δ), then, seem to require some accuracy in their estimation.

Other indications of the relative importance of various sets of parameters can be gained directly from the model output, especially when considered in the context of the long-term population consequences of perturbation events. Thus, the likelihood that a perturbation will seriously impair the capacity of a population to return to equilibrium is greater if the adult age class rather than the chick age class suffers the greatest mortality. If chronic, low-level pollution reduces average fecundity and/or survivorship of adults by only a few percent, the ability of the population to then recover from a one-time, large-scale oil spill may be drastically affected; effects on survivorship are more important than those on fecundity (Ford et al. 1982). Collectively, these results point to the relatively greater importance of factors influencing survivorship than reproduction or fecundity, and to the relative unimportance of the chicks in comparison to adults.

Overall, then, our experiences in developing these models, in assembling parameter values, and in conducting sensitivity tests lead us to define several variables as critical to attempts to generate predictions of oil-spill impacts on marine birds (Table 6). We may consider these in two priority categories.

I. Intermediate priority

A. The breeding structure of the population, in particular the proportion of the at-sea "pool" of birds that is not breeding and not associated with a given colony.

B. The foraging pathways of individuals. We have assumed straight-line flight in our models, but if individuals move about in the foraging areas or take a wandering course to or from the colony, the proportion of the foraging trip during which a bird will be vulnerable to spill contact will be diminished.

C. The metabolic costs associated with foraging activity, especially flight.

D. The spatial and temporal patterns of food availability in the areas about a colony (as these play a major role in setting the distributional patterns of the birds).

E. The manners in which changes in food delivery rates to chicks affect the growth rates and survival probabilities of the chicks.

F. The distributional dynamics of oil spills in specific areas.

II. High priority

A. The size of a breeding colony.

B. The patterns of at-sea distributions of birds associated with a given colony under normal conditions, including estimates of their spatial and temporal variability.

C. The distribution of trip times of adults foraging under normal conditions.

D. The normal pattern of age-specific survivorship characteristic of a population.

E. The probability that an adult encountering an oil spill will suffer mortality.

F. The frequency with which individual members of the population shift their foraging region, which determines the rate at which "naive" birds encounter the spill area.

G. The manner in which a spill influences resource availability and thus the potential rate of prey capture by birds that forage in the spill area.

Gathering information on these parameters will not be easy, and it is discouraging (although not entirely unexpected) that those parameters that seem most critical to producing accurate predictions are generally the most difficult to measure or estimate. Conversely, if we continue to measure with considerable precision the various parameters of reproductive biology that are readily obtained in typical colony studies, this may contribute rather little in our ability to form predictive models of the dynamics of seabirds and oil spills. It is our hope that, by drawing attention to the relative importance of these parameters, and by specifying those that seem most important, individuals or groups involved in seabird research may redirect some of their efforts to exploring some of these difficult, but essential, parameters.

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APPENDIX A. Scientific Names of Bird Species

Fulmar	<u>Fulmaris glacialis</u>
Sooty Shearwater	<u>Puffinus griseus</u>
Gannet	<u>Morus bassanus</u>
Shag	<u>Phalacrocorax aristotelis</u>
Pelagic Cormorant	<u>Phalacrocorax pelagicus</u>
Glaucous-winged Gull	<u>Larus glaucescens</u>
Black-legged Kittiwake	<u>Rissa tridactyla</u>
Arctic Tern	<u>Sterna paradisaea</u>
Common Murre	<u>Uria aalge</u>
Thick-billed Murre	<u>Uria lomvia</u>
Tufted Puffin	<u>Lunda cirrhata</u>

APPENDIX B. Publications

- Wiens, J.A. 1979. Summarizing remarks, Part II. Pp. 259-261 in Shorebirds in marine environments (F.A. Pitelka, Ed.). Studies Avian Biol. No. 2.
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- Wiens, J.A., R.G. Ford, and D. Heinemann. (in preparation). Assessing the sensitivity of marine birds to oil spills: information gaps and priorities.
- Heinemann, D., R.G. Ford, and J.A. Wiens. (in preparation). Confidence and the estimation of numbers of pelagic marine birds.
- Ford, R.G., and C. Qualls. (in preparation). Estimation of confidence limits by the gamma distribution.

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