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Relationships among Beringian marine mammals and sea ice

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The distributions of the nine dominant marine mammal species of the Bering, Chukchi, and Beaufort Seas have been subjected to principal components analysis. The six species assemblages that result imply some degree of habitat partitioning. The distribution patterns of these assemblages appear to correlate with sea-ice conditions. For example, a "northern Bering Sea assemblage" is strongly associated with "broken pack". Also, some areas lack strong association with any assemblage, notably Shpanberg Strait, east of St. Lawrence Island. However, these associations are hypothetical and in need of further testing.

It is obvious that other factors than sea ice must be taken into account to clarify these relationships and that remote-sensing techniques that can record marine mammals and their habitats must play a major role in future research. Both marine mammals and environmental attributes will need to be examined quantitatively, together and at a range of time and space scales, in order that a predictive capability be attained for improved environmental and natural-resource management.

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Introduction

A major problem for ecologists and managers lies in understanding the associations among biota and environmental attributes. This is especially challenging when attempting to predict the outcome of human perturbation or environmental variation. For polar regions, this problem is most obvious because of the relative paucity of data and for logistic and other reasons.

The Beringian region has been defined as including the coastal plains and continental shelves of the Bering and Chukchi Seas that have been influenced by large sea-level excursions (Hopkins, 1967). Oceanographically and biogeographically, it is a transition area between the North Pacific and Arctic Oceans (Dunbar, 1985). For our purposes, we also include the Beaufort Sea, although it is oceanographically more closely related to the Arctic Ocean than to Beringia. The marine mammals of Beringia and adjacent waters represent both the Pinnipedia and the Cetacea. The nine species included here constitute only about a third of the species that occur in the region, but the vast majority of marine mammal biomass over the shelf. All nine are adapted to fluctuating sea-ice conditions.

We hypothesize that species assemblages are more useful than single species for understanding the relationships among biota and their environments. Assemblages may be derived by means of multivariate methods, and we believe that the data now available for marine mammals are sufficient for this purpose. Each assemblage may be considered as a single variable, although each represents more than one species. We believe that synthesis of species into assemblages has the potential to simplify the daunting task of environmental analysis.

Marine mammal distributions

The data presented here derive from NOAA (1988). Preparation of this *Atlas* consumed seven years. Its marine mammal maps and descriptions were drawn from more than 400 references and more than two dozen personal communications. Obviously, we cannot cite all these references here; therefore, the reader should consult the *Atlas* for this material.

The purpose of the *Atlas* was to synthesize the best available information and to present average, long-term conditions. For each species, a fairly complete natural history was attempted, including adult range, areas of major density and/or numbers, temporal factors, and such life history functions as reproduction and feeding. The areas shown in Figure 1 are taken directly from the *Atlas* and are current to about 1986. Each area depicts only where adults are thought to occur in greatest density. A consensus for each species was often difficult to

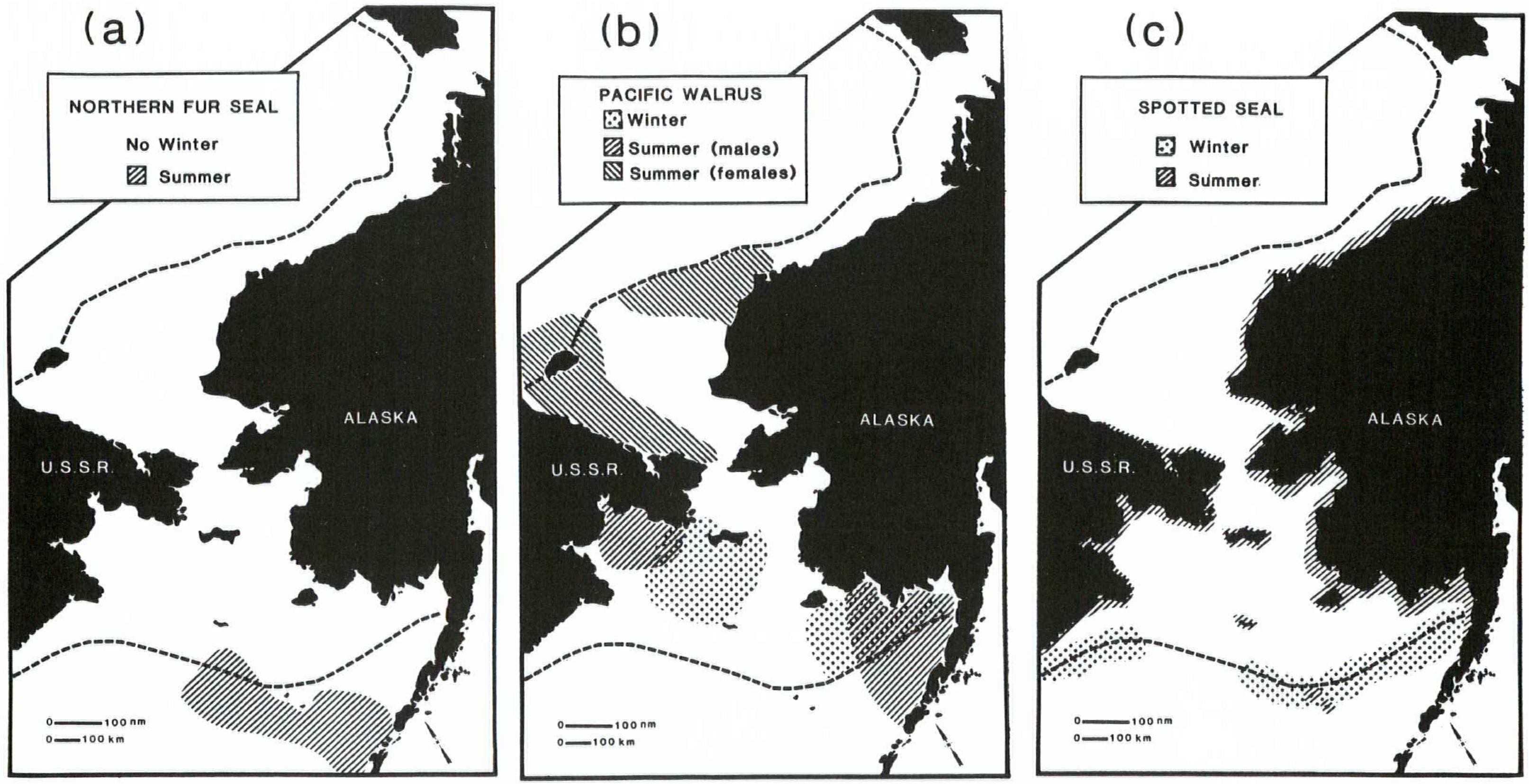


Figure 1 (a–c). Major adult areas for three of nine species of Beringian marine mammals. Areas shown are derived from NOAA (1988) and indicate where the greatest densities of each species are thought to occur. Winter (stippled) and summer (hatched) are shown separately. For walrus (b), summer females and summer males are shown separately; for no other species are the sexes so markedly segregated.

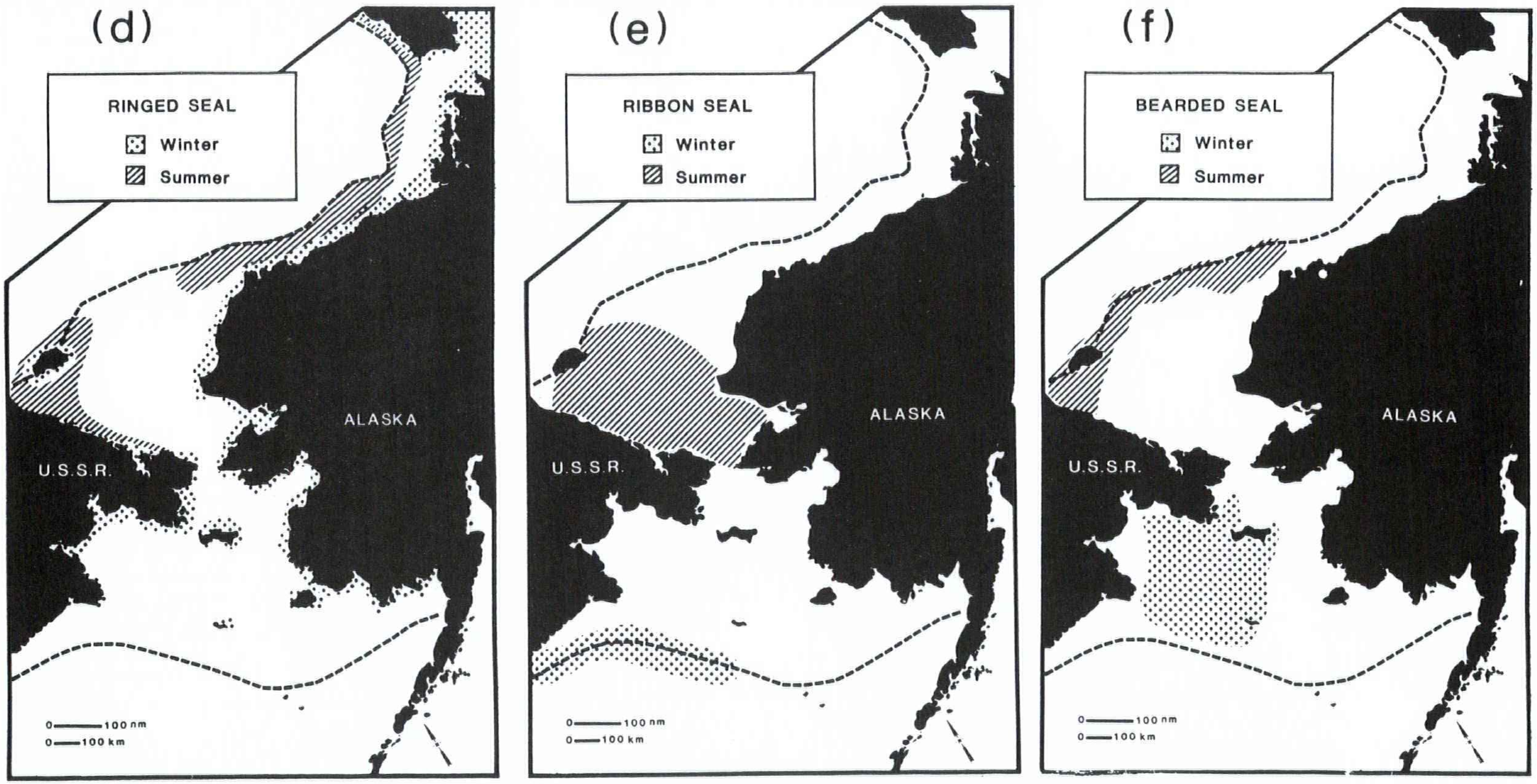


Figure 1 (d–f). See Figure 1 (a–c).

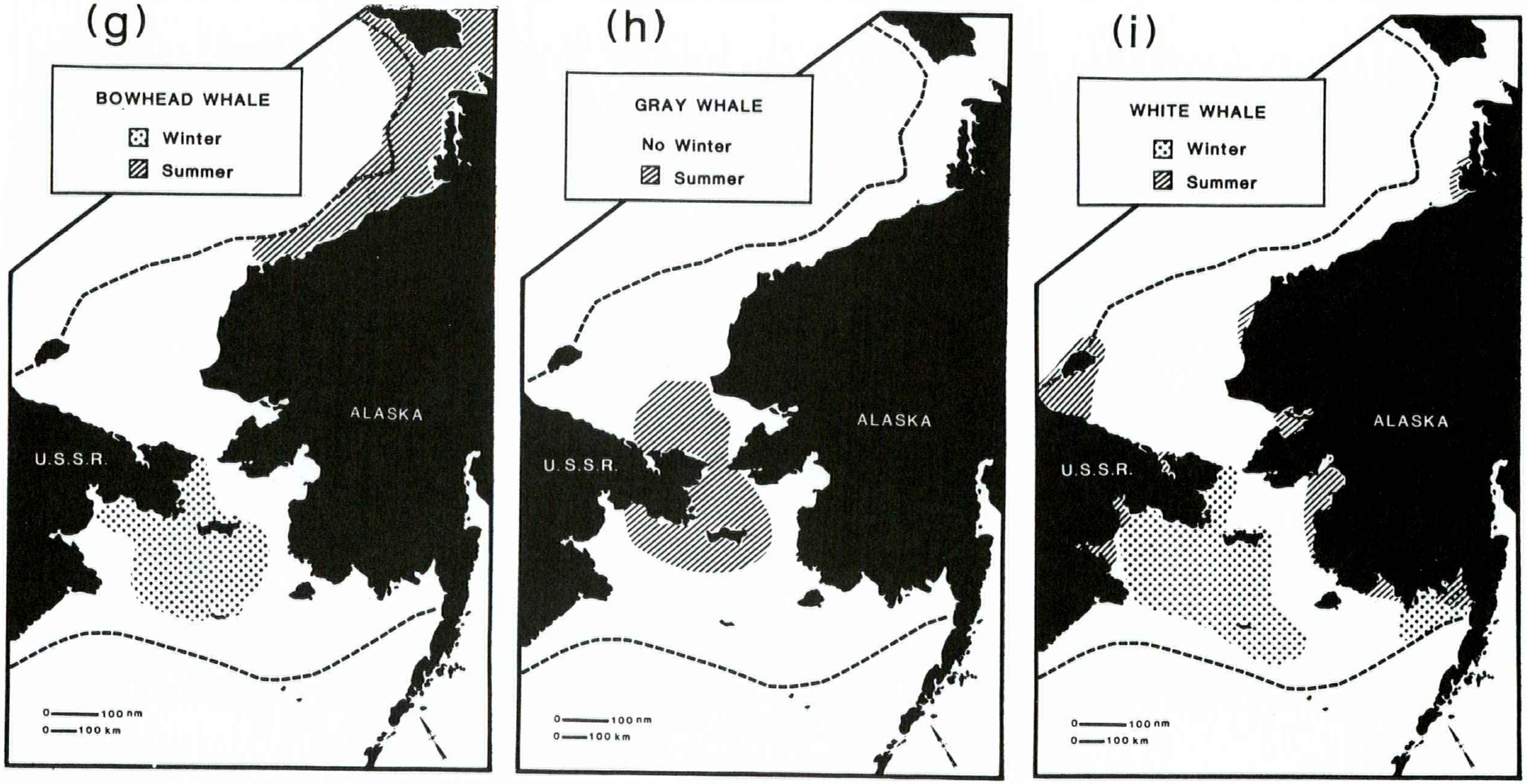


Figure 1 (g–i). See Figure 1 (a–c).

achieve, and opinions varied on the adequacy of the data. Not all species are equally well known, nor have variances in distributions been calculated. However, variances and/or more recent information would not affect the general results of our analysis.

The species are as follows:

1. Northern fur seal (*Callorhinus ursinus*), Figure 1a. The current population is about one million animals for the entire Bering Sea, of which eight-tenths is of the Pribilof Islands subpopulation. The fur seal is pelagic, except when breeding, when it hauls out on insular rocky shores. High densities of feeding animals occur during summer on the outer continental shelf and over the slope and adjacent waters of the Bering Sea.

2. Pacific walrus (*Odobenus rosmarus*), Figure 1b. The population was perhaps at its maximum of 200 000–300 000 animals in 1980 and may have been declining slowly since then. The walrus is closely associated with broken, angular ice floes. Only during summer do mature males haul out on rocky, gravelly, or sandy shores. Breeding concentrations occur in winter in the north-central and southeastern Bering Sea. Concentrations of males in summer occur around terrestrial haul-out areas in Bristol Bay, the Bering Strait region, and the Gulf of Anadyr; females and most juveniles move into the Chukchi Sea at that time.

3. Spotted seal (*Phoca largha*), Figure 1c. This species consists of about 200 000–250 000 individuals. In March–April, most of the population occurs within marginal ice where reproduction takes place. During May–June, adults and pups occur in remnant ice in the northern Bering Sea. The animals then disperse to coastal, near-shore areas during summer.

4. Ringed seal (*Phoca hispida*), Figure 1d. This species concentrates, sometimes densely, in shorefast ice. The regional population is perhaps 1–1.5 million individuals, which constitutes about a quarter of the world population. Greatest densities occur in winter throughout shorefast ice of the region where reproduction takes place. In the Bering Sea during spring, adults and pups concentrate on northern portions of remnant ice. During summer, seals are most dense in the marginal ice of the Chukchi and Beaufort Seas.

5. Ribbon seal (*Phoca fasciata*), Figure 1e. This may be the least abundant pinniped of the region. The population is estimated to be only 90 000–100 000. In March–April, the bulk of the population appears to occur in Bering Sea marginal ice where reproduction takes place. During May–June, adults and pups occur in the remnant ice of the northern Bering Sea. The animals then move north into the western and south-central Chukchi Sea where they spend the summer.

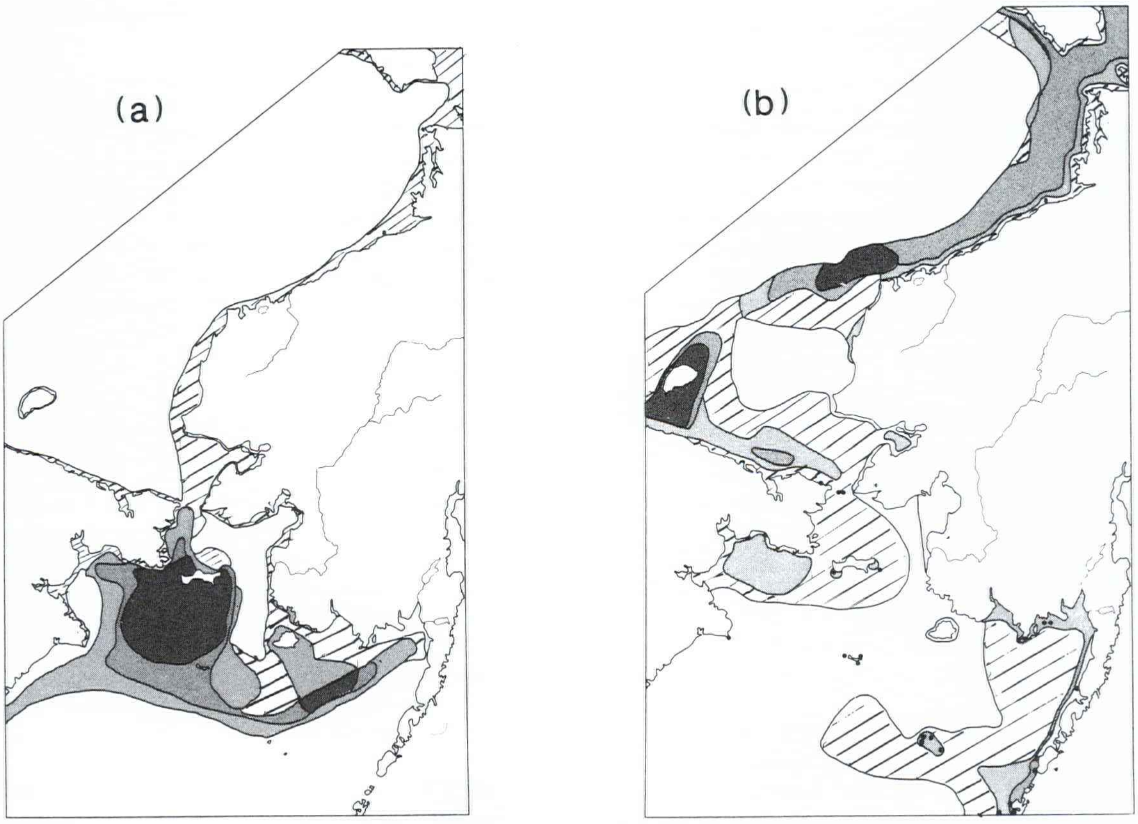


Figure 2. Simple overlay of the winter (a) and summer (b) areas of Figure 1. The darkest shading indicates where four species are present, the hatching where only one occurs. Neither abundance of individuals nor biomass is implied.

Table 1.

	I	II	III	IV	V	VI
Winter						
V1 Walrus	−0.798[a]	0.057	0.022	−0.005	0.029	−0.088
V2 Spotted seal	0.001	0.018	0.018	0.852[a]	0.062	−0.075
V3 Ringed seal	−0.078	0.856[a]	−0.028	−0.193	−0.062	0.190
V4 Ribbon seal	0.000	−0.068	−0.076	0.774[a]	−0.026	0.089
V5 Bearded seal	−0.872[a]	−0.025	−0.033	0.028	−0.047	0.007
V6 Bowhead whale	−0.868[a]	0.060	−0.079	−0.108	−0.121	−0.017
V7 White whale	−0.878[a]	0.070	0.033	−0.004	0.026	−0.093
Summer						
V8 No. fur seal	0.069	−0.141	−0.073	0.501[a]	0.111	−0.185
V9 Walrus	−0.125	0.153	0.756[a]	0.016	−0.235	0.136
V10 Spotted seal	−0.130	0.871[a]	−0.088	0.013	−0.136	−0.039
V11 Ringed seal	0.137	−0.008	0.632[a]	−0.079	−0.115	0.627[a]
V12 Ribbon seal	0.220	0.037	0.278	−0.100	−0.803[a]	−0.085
V13 Bearded seal	0.096	−0.137	0.834[a]	−0.111	0.053	0.024
V14 Bowhead whale	0.120	0.050	−0.151	−0.114	0.152	0.889[a]
V15 Gray whale	−0.408	0.113	−0.105	−0.080	−0.765[a]	−0.030
V16 White whale	0.116	0.599[a]	0.460	−0.084	0.126	−0.157

Assemblages	*Per cent of variance explained*
Northern Bering Sea	20.2
Inner Shelf	12.2
Northern Chukchi Sea	12.6
Bering Sea Outer Shelf	10.5
Bering Strait	8.7
Southwestern Beaufort Sea	8.4
Total	72.6 %

[a]Strongest species associations within the assemblage.

6. Bearded seal (*Erignathus barbatus*), Figure 1f. The population is estimated at 300 000 individuals. In March–April, this species occurs principally within the pack ice of the Bering Sea; lesser densities of animals occur in the southeastern Bering Sea and in the flaw zone of the Chukchi Sea. The greatest density of animals in summer occurs within the marginal ice of the Chukchi Sea.

7. Bowhead whale (*Balaena mysticetus*), Figure 1g. This is the only baleen whale that lives its entire life in a polar and subpolar environment. It is highly adapted to sea ice, which, owing to this whale's large size, offers little impediment. The number of animals in the population is believed to be growing and is estimated to be more than 5000 at present.

Concentrations occur in winter within the pack ice of the north-central to northwest Bering Sea. During May, migratory concentrations occur in the eastern Chukchi flaw zone. In summer and early fall, the bulk of the population occurs in the eastern to southern Beaufort Sea.

8. Gray whale (*Eschrichtius robustus*), Figure 1h. The population is estimated to be about 15 000–18 000 animals. Gray whales migrate from lagoons in Mexico, where they bear young, to spend their summers in the Bering and Chukchi Seas, where they concentrate in the Bering Strait region.

9. White whale (*Delphinapterus leucas*), Figure 1i. This small whale (also referred to as the belukha or beluga) is widely distributed in summer in small, coastal sub-populations throughout the region. The total regional population may be about 10 000–15 000 animals. The winter concentrations appear to be in the north-central Bering Sea pack ice and in the southeastern Bering Sea.

Synthesis of marine mammal concentrations

The marine mammal distributions shown in Figure 1 have been analysed to reveal assemblages of species by principal components analysis (PCA). This method results in an expression of data that could not arise through visual inspection alone. For example, Figure 2 illustrates the result obtained by overlay of these same distributions. The complex pattern resembles the mental image that emerges through visual inspection. This image illustrates spatial variability in species richness, but habitat associations are difficult to interpret.

For our PCA, we constructed a grid of 341 one-half-degree latitude by one-degree longitude cells. The cells are "cases" for which we scored the 16 species distributions shown in Figure 1 as variables. Table 1 lists these

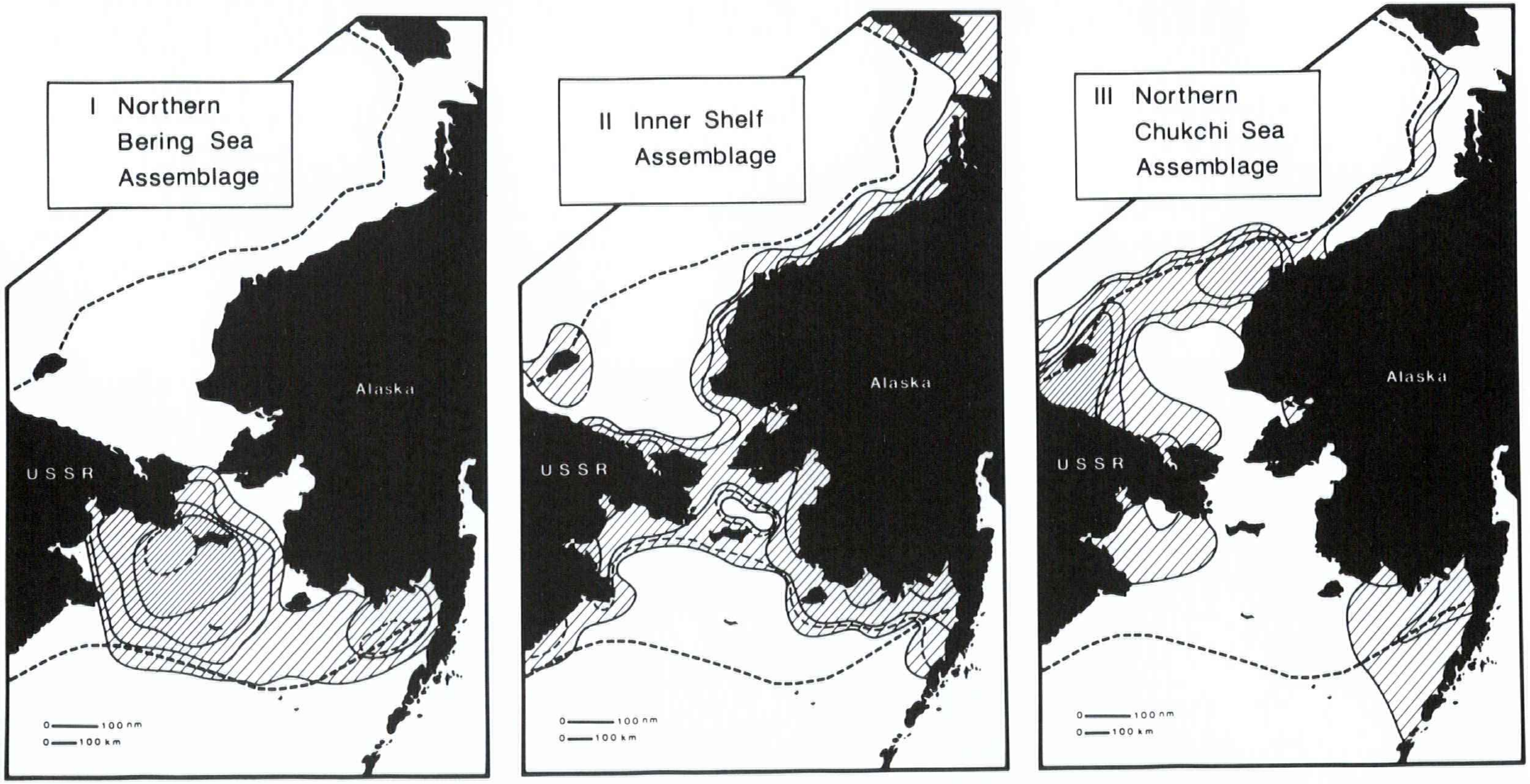


Figure 3 (I–III). Spatial characteristics for three (of six) assemblages, resulting from principal components analysis of the areas shown in Figure 1. The legend (Figure 3 (IV–VI)) indicates factor score intervals. The highest factor score interval includes the area where the assemblage is most likely to occur. A dashed contour indicates an intermediate value: for example, in assemblage I the dashed contour west of St. Lawrence Island indicates a value of 3.5 and the dashed contour in Bristol Bay indicates 1.5. The dashed lines near the northern and southern boundaries represent the summer (northern) and winter (southern) average minimum and maximum sea-ice extents.

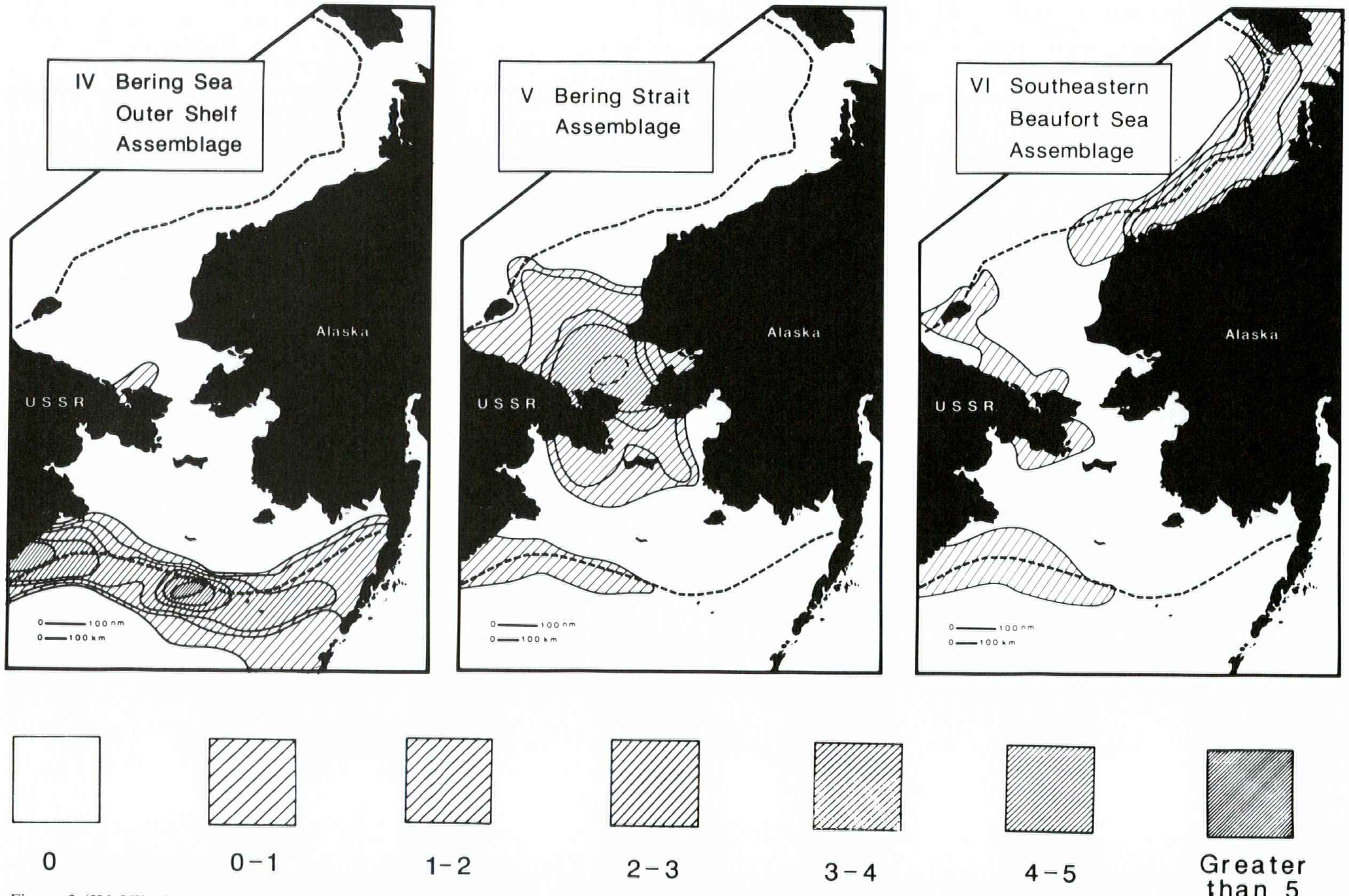


Figure 3 (IV–VI). See Figure 3 (I–III).

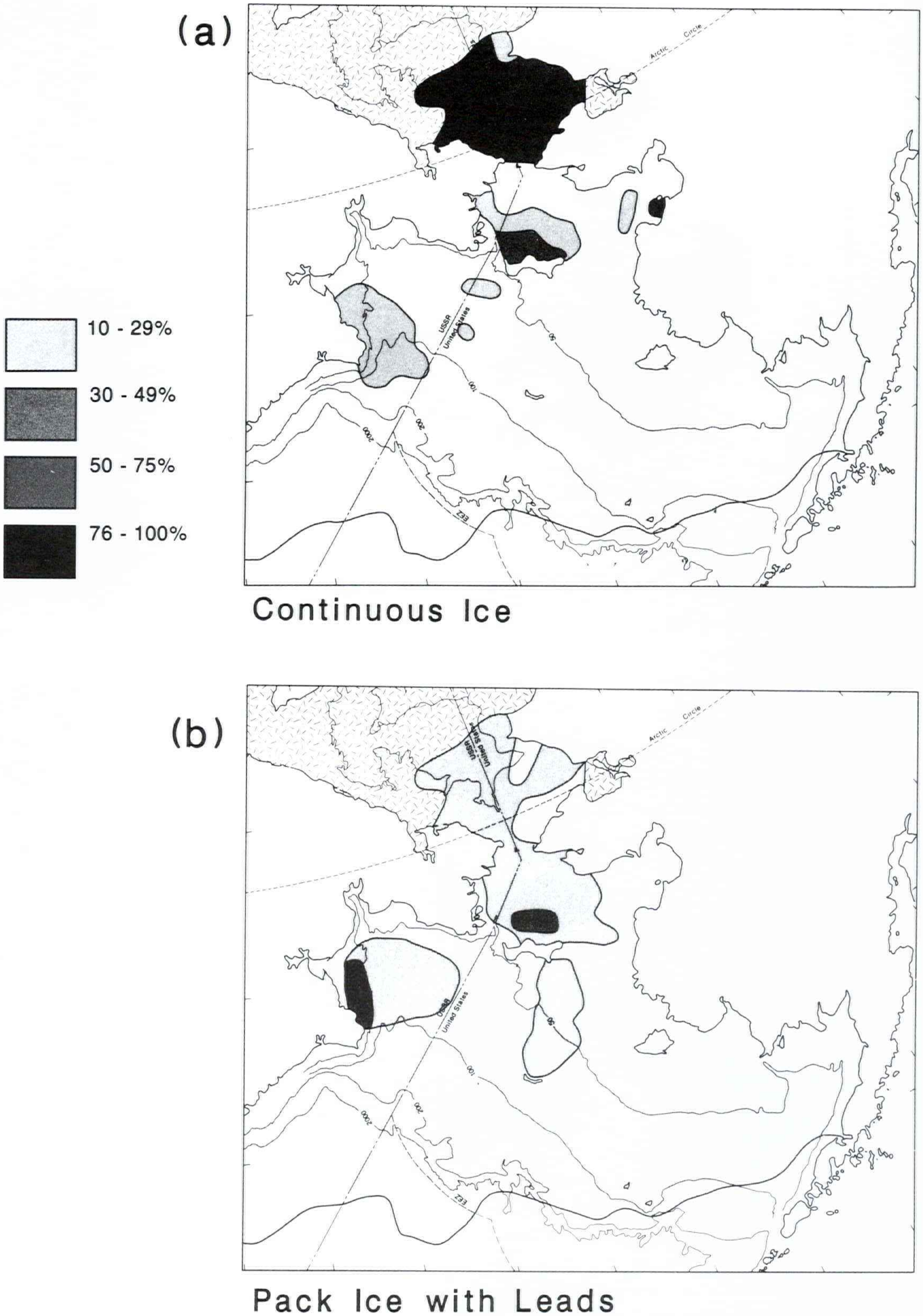
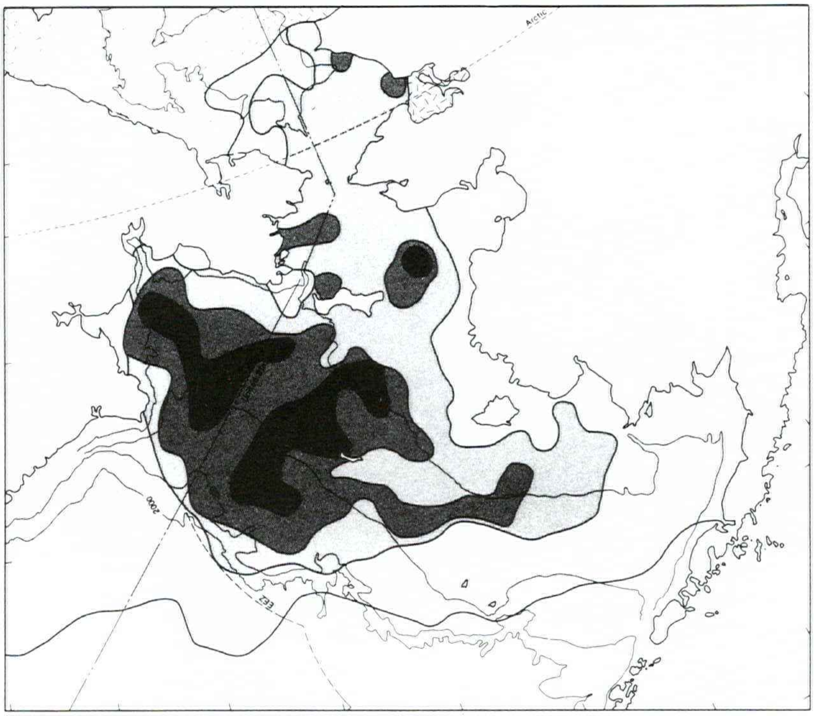


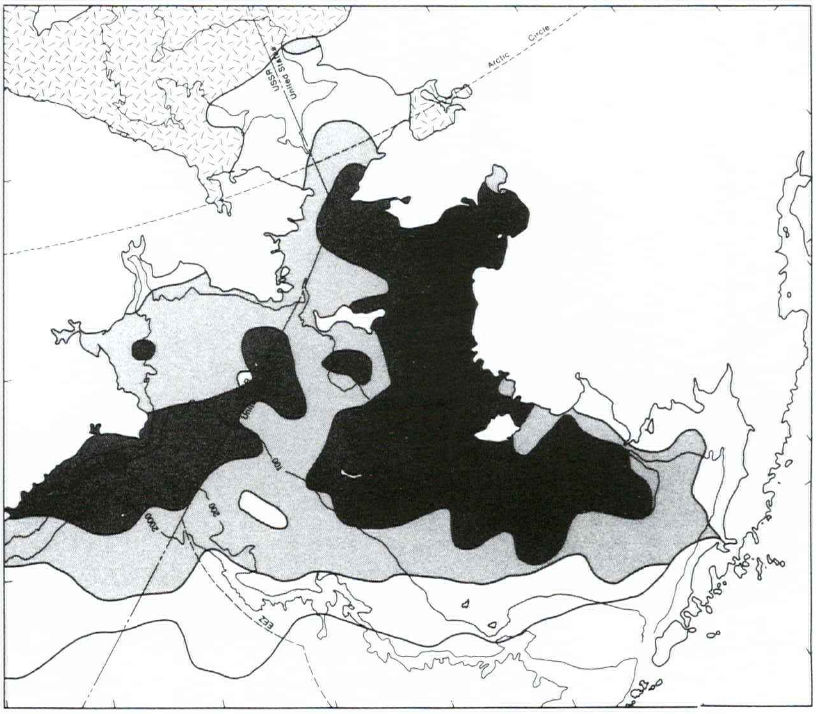
Figure 4 (a–b). Probabilities of occurrence for two (of six) sea-ice or sea-ice-related conditions from Ray *et al.* (1988). The legend gives probabilities as percentages. For example, (c) shows a 50–75 % probability of broken pack ice for a very large area over the Bering Sea shelf south and west of St. Lawrence Island; included are two areas where the probability rises to 76–100 %. Conversely, (d) shows a mirror image of this pattern for rounded pack ice (see reference to "jumbled pack" in text) wherein probabilities are highest in the northeastern to southeastern Bering Sea. These two sea-ice conditions appear to exert strong influences on marine mammal distributions.

(c)



Broken Pack Ice

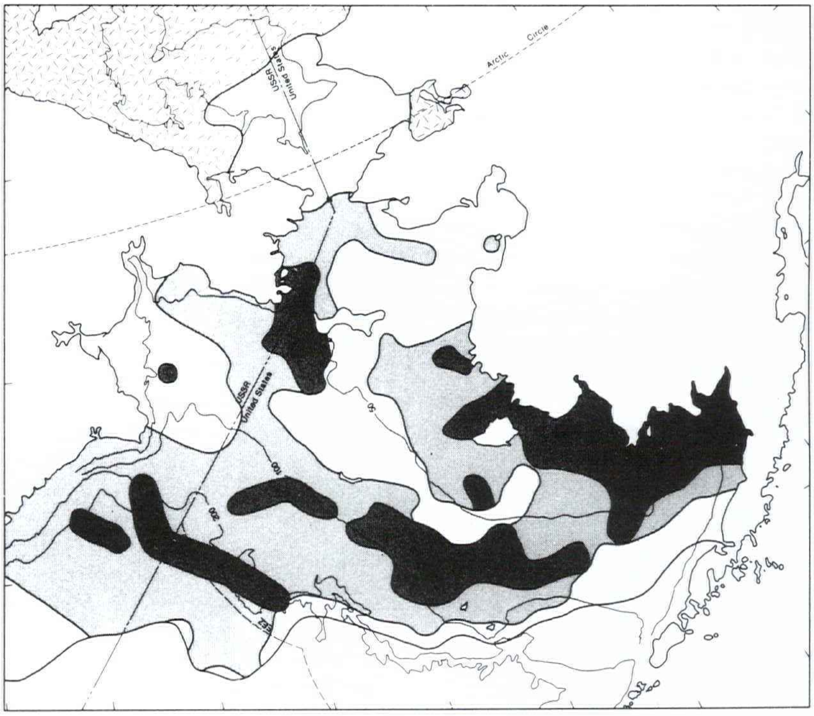
(d)



Rounded Pack Ice

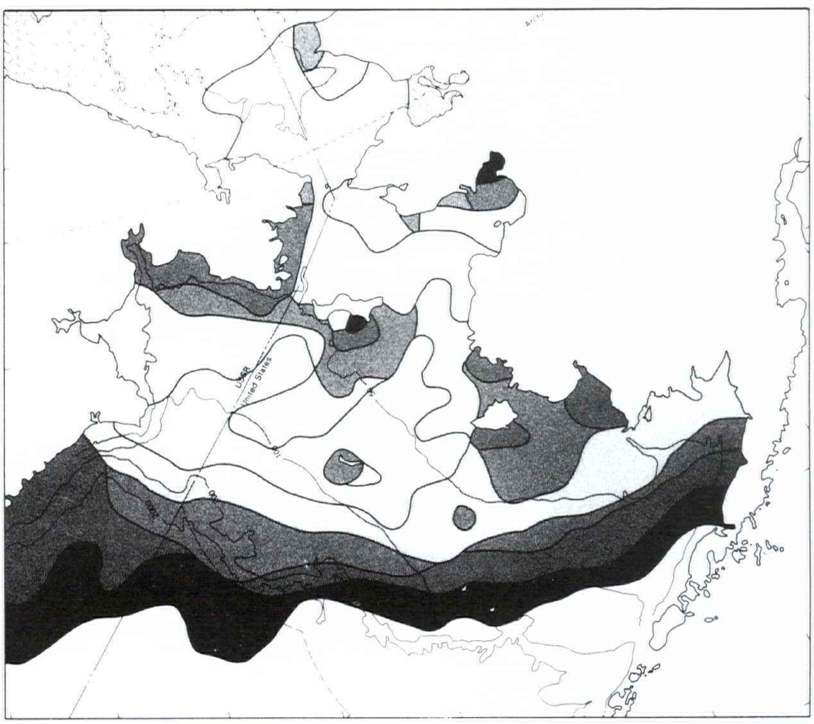
Figure 4 (c–d). See Figure 4 (a–b).

(e)



Loose Pack Ice

(f)



Open Water

Figure 4 (e–f). See Figure 4 (a–b).

variables and gives the results of our PCA. We refer the reader to statistical texts for an explanation of PCA, but wish to note that rotated loadings gave the best result, as is often the case with data sets of this sort. The first six eigenvectors explain more of the total variance than could be explained by any single variable alone, or than could be accounted for by chance. These vectors, taken together, explain about 73 % of the total variance of the sample. Each may be considered as a single variable, and it is important to note that the original 16 variables have now been reduced to six. Table 1 lists values that express strengths of associations among species for each eigenvector. If several variables have high values, whether positive or negative, the association among them is strong. The strongest species associations within each assemblage are noted in the table. The assemblages are spatial and do not necessarily express behavioral or ecological associations among species. Thus, names for the assemblages given in the table represent geographic space within Beringia.

Figure 3 gives the spatial characteristics for each of the six eigenvectors. PCA yields values for each assemblage within each grid cell. The higher the value, the stronger the association between the assemblage and the individual cell. In Figure 3, contours have been drawn around these values. Where the contours are close together, a strong environmental gradient is inferred. For example, eigenvector 1 indicates strong associations in winter (Table 1) for walrus, bearded seal, bowhead whale, and white whale. These species are associated in space most strongly just west of St. Lawrence Island (Fig. 3I), reasonably strongly in the northwestern Bering Sea, and weakly in the southeastern Bering Sea.

It is instructive to note from Table 1 that only a few species have high values in more than one assemblage. One exception is the white whale in summer, which has fairly high values in both vectors II and III. The fact that six eigenvectors are necessary to explain three-fourths of the total variance argues strongly for the occurrence of several distinctive species assemblages for which there is strong likelihood of habitat partitioning.

Sea ice

There are still many gaps in our knowledge of physical processes in the Beringian region. Recent studies have increased our understanding enough so that we can define many distinctive physical characteristics that have marked effects on biota. This is especially true of sea ice, which is a dominant physical attribute of Beringia and the physical attribute most easily measured quantitatively, as well as also being dominant in the lives of Beringian marine mammals. The Beringian shelf has a recurring annual ice cover that in cold years may reach southwards over the deep Bering Sea basin. The advance and retreat of sea ice in this region occur over 1000 km, south to north from winter to summer. Bering Sea ice is formed 97 % *in situ*, with the remainder being carried south from the Chukchi Sea. Ninety per cent of Chukchi Sea ice is formed there, with the remainder coming from the Arctic Ocean. The maximum extent of sea ice occurs during March–April; the Bering Sea is generally free of ice by the end of June. The minimum ice extent occurs in the Chukchi and Beaufort Seas in September. The extent of sea ice can vary considerably from year to year. For example, in 1975 the ice remained along the Beaufort Sea coast throughout summer; in April 1979, the Bering Sea ice cover was 35 % below normal.

Sea ice in the Beringian region has long been recognized as producing predictable zones such as shorefast ice, marginal ice, polynyas, and flaw zones. This is especially the case for the Bering Sea. Burns *et al.* (1980) proposed 11 categories of ice or ice-related conditions, six of which have been analysed by Ray *et al.* (1988) using satellite imagery. These conditions are: continuous ice, pack ice with leads, broken pack, rounded pack, loose pack, and open water. Figure 4 shows the spatial probabilities of occurrence of these conditions for the decade of 1973–1982. These conditions may be interpreted as major habitat components.

These sea-ice conditions, although persistent, do show considerable spatial and temporal variability. Figure 5 is an infrared NOAA AVHRR image obtained on 30 March 1988 that shows the six pack-ice conditions. It also illustrates the northerly wind that is the primary driving force largely responsible for winter ice characteristics. The long streaks of "rope clouds" at the bottom of the image are indicative of the wind and its direction. Several studies have shown that winter ice can be described by a "conveyor belt" concept; ice is formed along south-facing northern coasts, is pushed southwards by persistent northerly winds, then drifts southwards until it reaches its thermodynamic limit and melts (Overland and Pease, 1982).

Temporal variability is illustrated by Figure 6. This is a visible NOAA AVHRR image obtained on 22 March 1981. The dark areas adjacent to the west coast of Alaska and the north shore of the Gulf of Anadyr are mostly open water. Normally, these areas would be ice covered at this time of year. An example of spatial variability is seen in Figure 7, taken on 3 April 1988. It shows a zone of "jumbled pack" from Bering Strait through Shpanberg Strait. Southward "outbreaks" of sea ice from the Chukchi Sea into the Bering Sea occur a number of times during the winter. This zone forms where there is a large tidal component (T. L. Mofjeld, pers. comm.) that, with initial deformation of ice as it moves southwards past St. Lawrence Island, helps maintain the broken, jumbled pack.

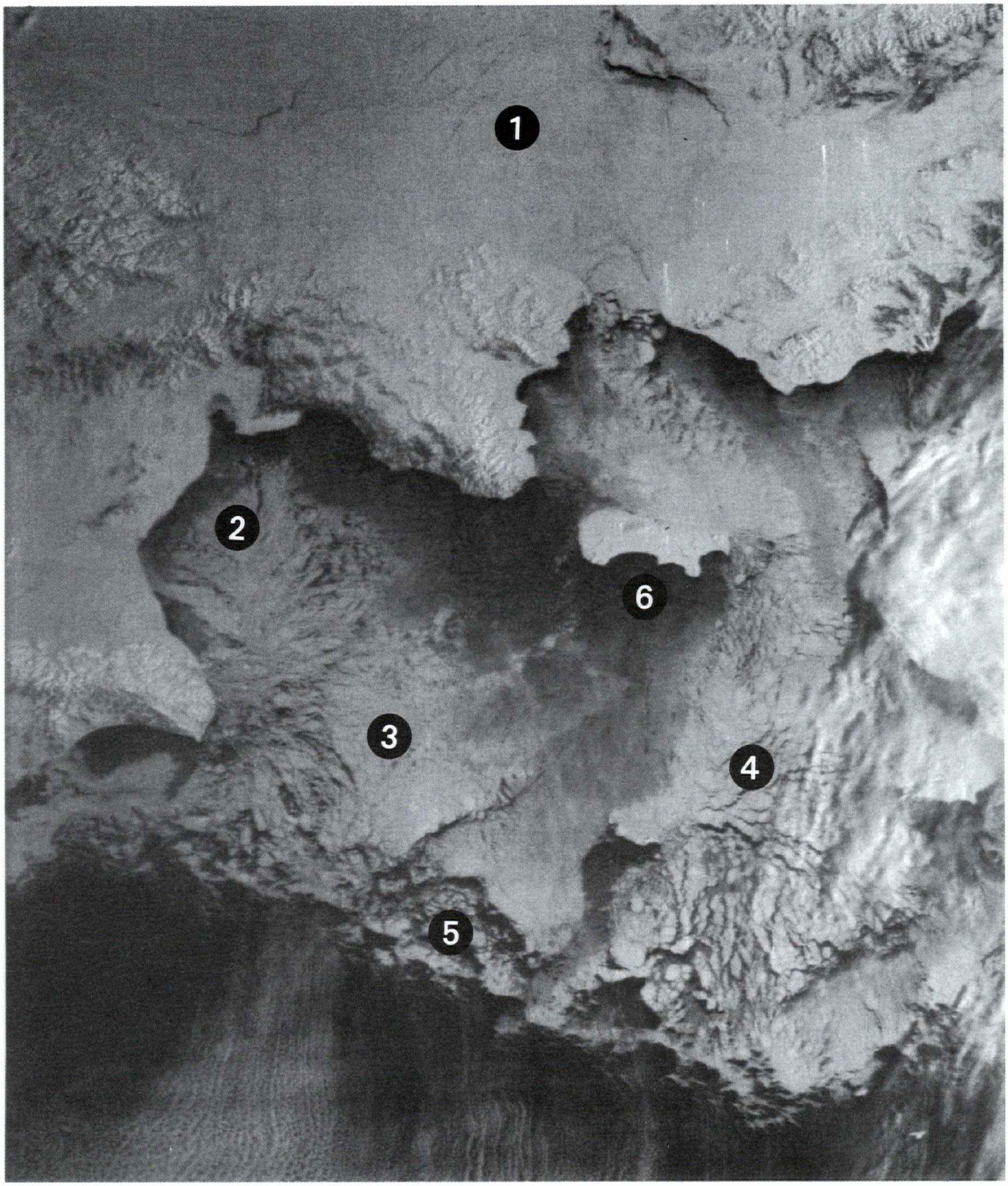


Figure 5. Infrared NOAA AVHRR (National Oceanic and Atmospheric Administration, Advanced Very High Resolution Radiometer) image of 30 March 1988 showing six sea-ice conditions: (1) continuous ice, (2) pack ice with leads, (3) broken pack ice, (4) rounded pack ice, (5) loose pack ice, and (6) open water.

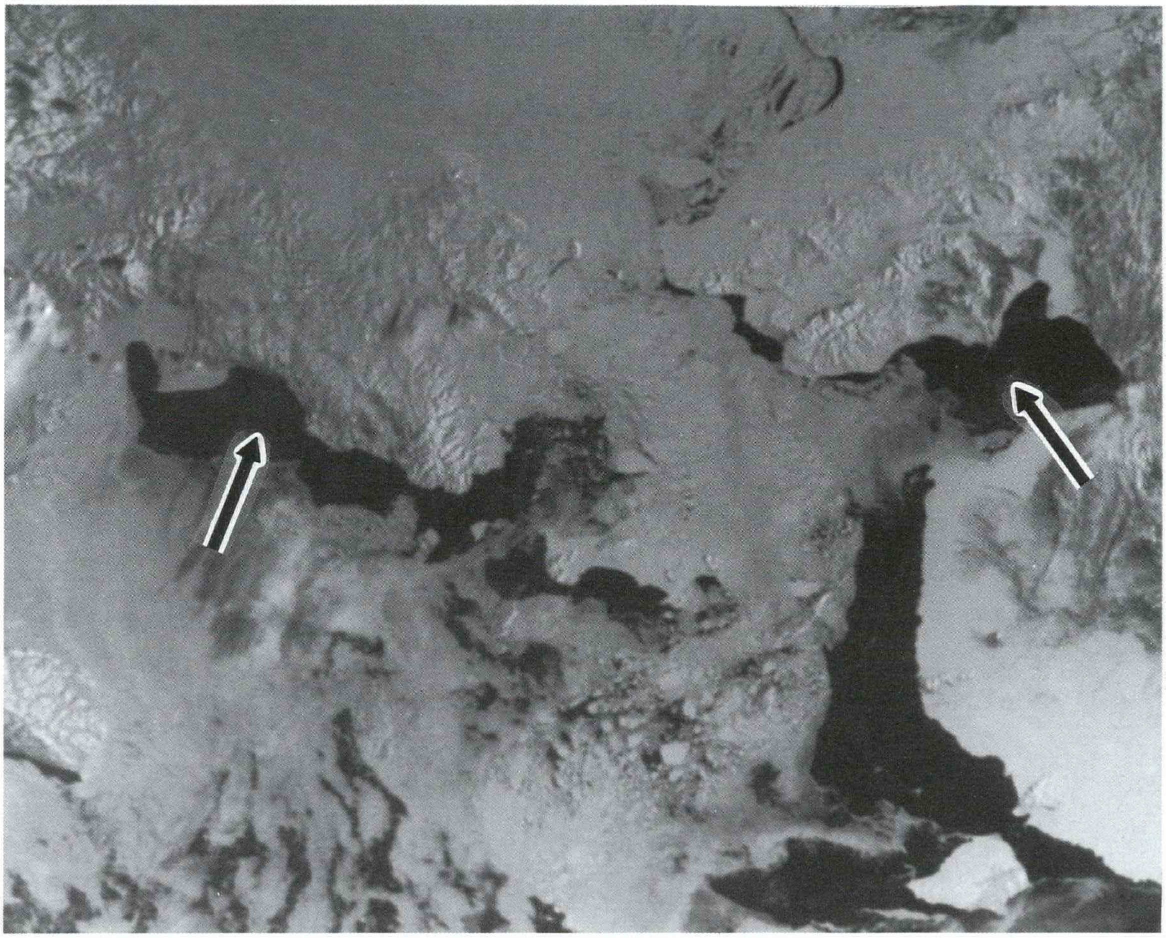


Figure 6. Example of temporal variability of pack ice: visible NOAA AVHRR image of 22 March 1981. Arrows indicate open water that would normally be ice covered at that time of year.

Species assemblages and pack ice

As stated above, habitat partitioning is indicated by the existence of well-defined species assemblages. The association among assemblages and environmental attributes can only be revealed through species and habitat analysis, undertaken jointly. Braham *et al.* (1984) illustrate possible habitat partitioning for Beringian marine mammals by virtue of the spatial separation of species observed during a variety of surveys for one year. However, surveys must take into account the fluctuations in hydrographic regimes that take place among years (Aagaard *et al.*, 1985) and to be most instructive, should also include quantitative habitat analysis.

A prerequisite for deriving species-environmental associations is prior knowledge of habitat requirements, as well as the examination of species and habitats together and at appropriate and comparable time and space scales, preferably quantitatively. Unfortunately, very few data of this sort exist for Beringian marine mammals. An exception is the remote-sensing analysis performed by Ray and Wartzok (1980) for walrus in which aerial photography that included both sea ice and walrus groups was analysed to show a statistically significant relationship between broken pack (Fig. 4c) and walrus winter concentrations (Fig. 1b) in the north-central Bering Sea. A similar analysis for bowheads and white whales was carried out by Ray *et al.* (1984).

We shall now give some examples of how the assemblages of Figure 2 relate to the sea-ice analysis of Figure 4. First, the fit between eigenvector I (Fig. 3I) and broken pack (Fig. 4c) is apparent. Second, no assemblage occurs strongly in the Shpanberg Strait region. The probability of occurrence of rounded pack, i.e., the "jumbled pack" mentioned above (Fig. 4d), is high in this area. The combination of wind and tidal forcing is responsible for highly uncertain lead structure, making this ice type not conducive to the occurrence of marine mammals. We conclude that these two ice types, the more westerly broken pack and the more easterly rounded pack, are major determinants of marine mammal distributions in the northern to southeast-

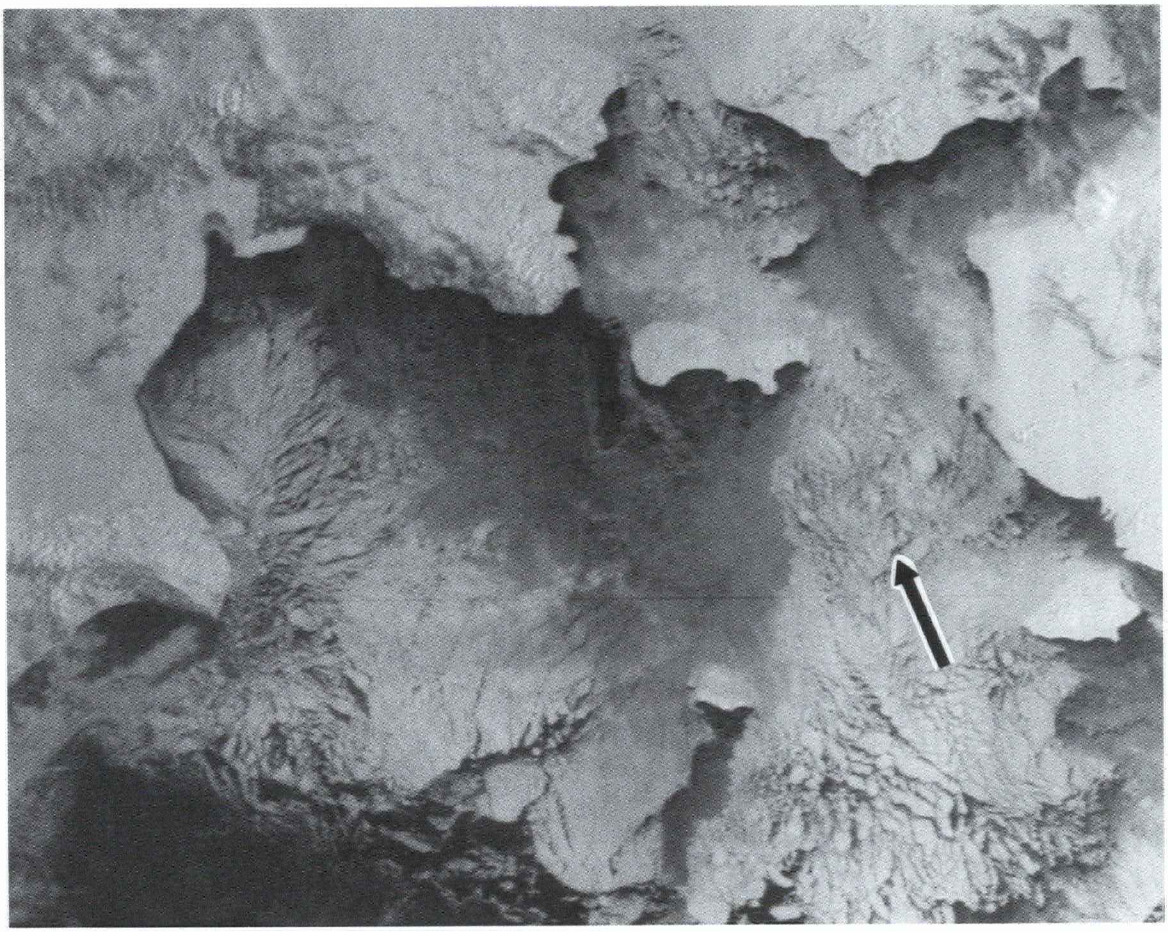


Figure 7. Example of spatial variability of pack ice: visible NOAA AVHRR image of 3 April 1988. The arrow indicates a zone of "jumbled pack" that resulted from an "outbreak" of sea ice through Shpanberg Strait.

ern Bering Sea shelf region. Third, PCA resulted in high values for ribbon and spotted seals in eigenvector IV (Fig. 3IV), an area that contains the marginal ice zone. This is entirely to be expected from the distributions of Figures 1c and e. Figure 8 is a satellite image taken on 25 March 1982 that shows quite clearly where the marginal ice forms in bands somewhat normal to the wind. There is a disjunct concentration of marginal ice in which the western and eastern portions have smaller sea-ice concentrations (50–80 %) than the middle portion (80–100 %). It is interesting that these seals have similar disjunct distributions. Finally, Figure 9 is an image taken in August 1981 and is typical of ice conditions in the Beaufort Sea along Alaska's north coast. The association of eigenvector VI (Fig. 3VI) with numerous ice eddies (indicative of gyres and also possibly of upwellings in surface waters) may be significant. Bowhead whales are heavy consumers of zooplankton in this area. Further, white whales were first observed in the marginal ice of the Beaufort Sea in September 1974 by Ray *et al.* (1984), and this may be a regular occurrence (Burns and Seaman, 1988).

Conclusion

Sea ice has long been known to be a major determinant of marine mammal distributions in Beringia. However, means for quantifying this relationship must be found. Principal components analysis (PCA) offers one such method. PCA has the advantage of quantifying boundary conditions, reducing the number of variables to be considered, estimating the strengths of species associations, and ranking various assemblages in terms of their statistical variances. However, we emphasize that the results that we have given here remain hypothetical. Questions about marine mammal/sea-ice associations and habitat requirements are obviously in need of further quantitative investigation. This will only be possible with the aid of remote-sensing techniques whereby the animals and their environments are examined together at several space scales and over daily to decadal time spans. Should the concurrence of species assemblages and sea-ice conditions prove statistically significant, as has been indicated by Ray and Wartzok (1980)

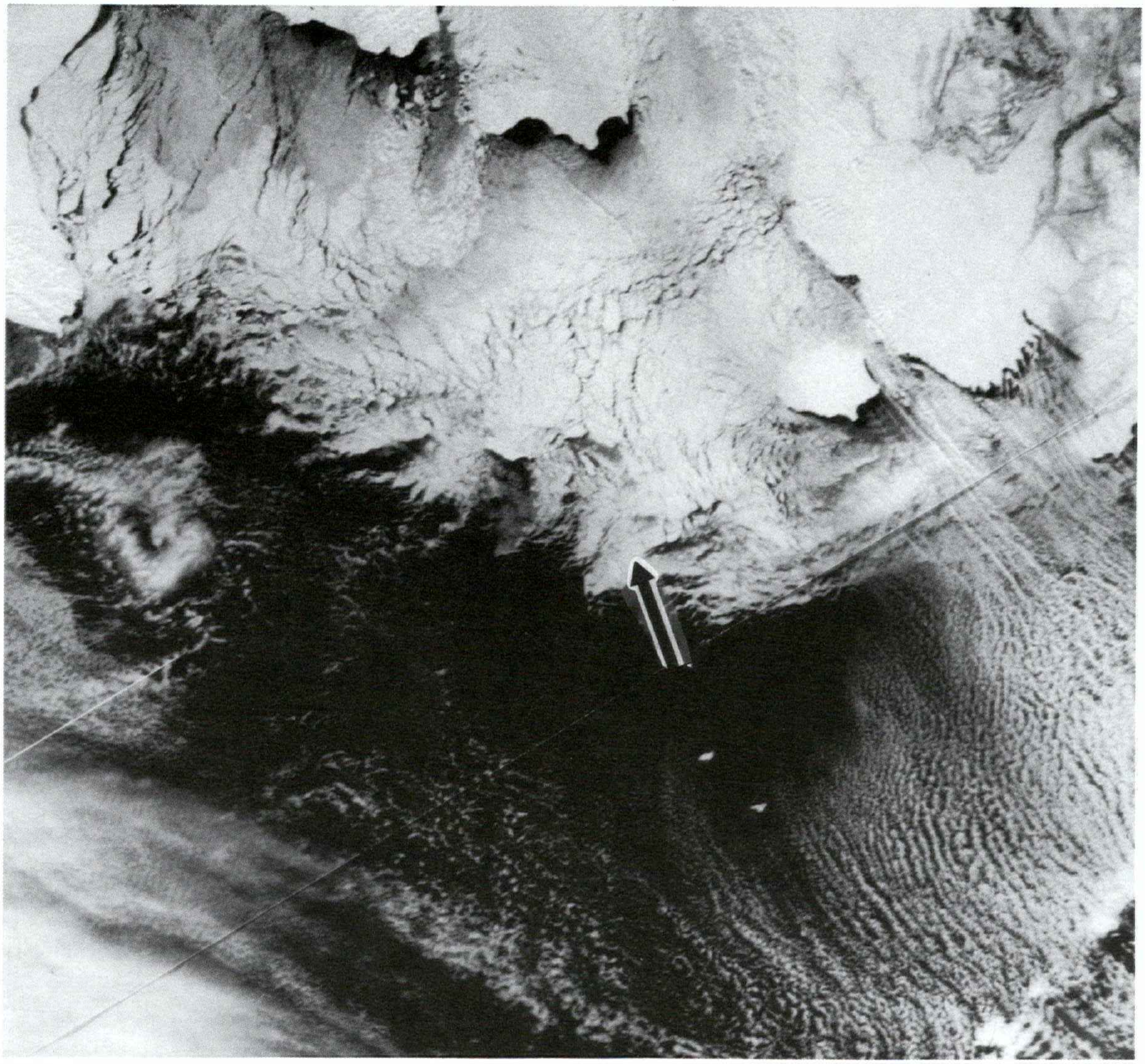


Figure 8. Visible NOAA AVHRR image of 25 March 1982 showing where marginal ice forms in bands somewhat normal to the wind. The arrow points to a zone of 80–100 % ice cover between east and west zones of 50–80 % cover.

for the walrus, a valuable predictor for marine mammal distributions will have been achieved.

Environmental factors are often used to predict the occurrence of biota. This would be particularly useful for marine mammals in such difficult-to-study areas as ice-dominated seas. However, other important attributes deserve attention. For example, circulation patterns are complex and highly variable. Even given this variability, mean flow patterns can be discerned. Over the Bering Sea shelf, three flow regimes can be recognized that are nearly coincident geographically with three distinct hydrographic domains. These domains are separated by persistent fronts that lie roughly over the 50-m, 100-m, and 150-m shelf contours (Coachman, 1986). In the Chukchi Sea, Anadyr and Bering shelf waters mix and flow northwestwards to Herald Canyon, then into the Beaufort Sea basin as a mid-layer (75-m depth) temperature maximum. The relatively warm Alaska coastal water, reinforced by river discharge, follows the Alaska coast as a coastal jet to Barrow canyon, then along the Beaufort Sea shelf break (Hufford, 1974). This flow can continue eastwards as far as Amundsen Gulf (Mountain, 1974). Because of the split flow in the Chukchi Sea, a "null zone" exists over the central shelf. This zone is easily identifiable in early summer from polar-orbiting satellite imagery that shows two embayments of water in the ice pack separated by a south-extending tongue of ice (Fig. 10).

These circulation patterns and water-mass characteristics influence the distribution and structure of sea ice,

Figure 9. Infrared NOAA AVHRR image of August 1981 of marginal ice off the north coast of Alaska in the Beaufort Sea. The arrow points to a gyre that may indicate upwelling.

and also productivity and biotic distributions at several levels. Marine mammals are not merely reflective of sea ice, but of whole ecosystems. Especially from this perspective, it will be more instructive to examine marine mammal assemblages than single species one at a time, in order to determine, for example, the degree to which these spatial assemblages function as guilds or communities. The data required for this task will be complex, requiring integrative, up-to-date data-gathering and analytic techniques. Nevertheless, if predictive capability is the objective, there appears to be no alternative to such an approach. This is to say that surveys of marine mammals without equal emphasis on environmental variables, or oceanographic investigations undertaken without equal reference to major components of the biota, will not result in either predictive capability or improved management of important living resources.

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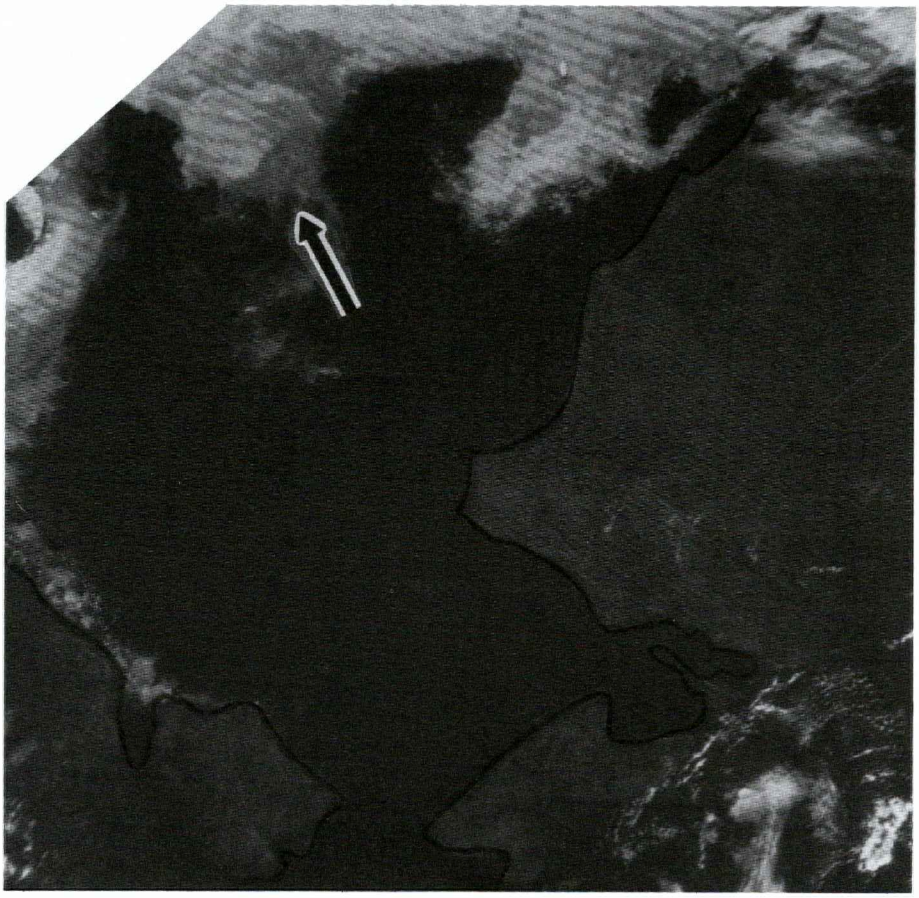

Figure 10. Visible NOAA AVHRR image of 19 July 1982 of sea ice of the northern Chukchi Sea. The arrow points to a tongue of ice that separates two embayments of open water.

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