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REVIEW OF MARINE MAMMAL POPULATION AND PREY INFORMATION FOR BERING SEA ECOSYSTEM STUDIES

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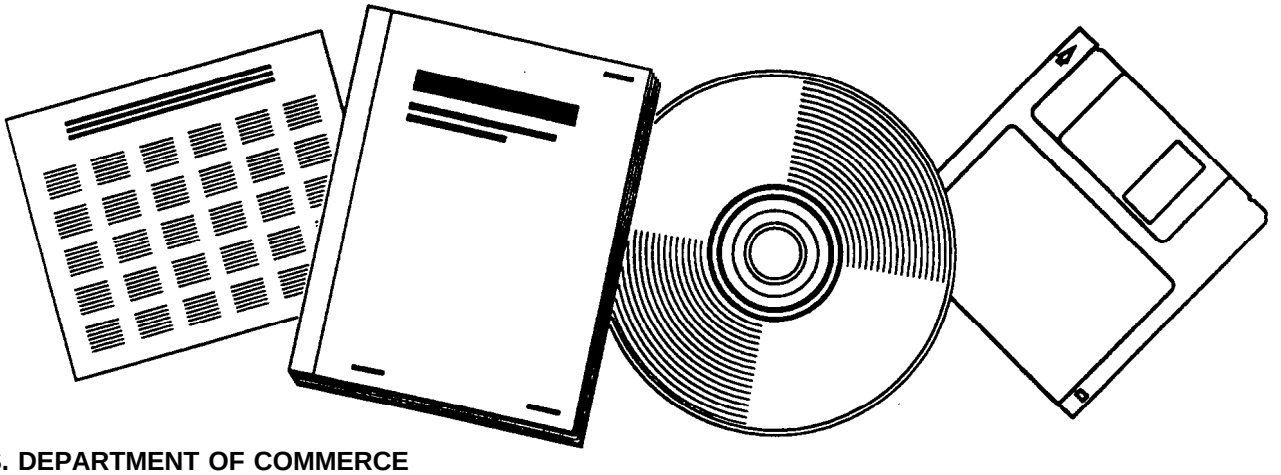
AUG 90



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Abstract: Twenty-eight marine mammal species are found in the Bering Sea and Aleutian Islands area, although only 21 species (8 pinnipeds, 12 cetaceans, and 1 mustelid) are present often enough and in adequate numbers to contribute significantly to the Bering Sea ecosystem. The quantity and quality of data available on distribution, abundance, and biomass vary widely among the species in the Bering Sea. In order to estimate the biomass of total food consumption by marine mammals of the eastern Bering Sea, it is necessary to estimate total abundance, average body mass, diet composition, and energy value of the diet of each resident marine mammal species. The paper summarizes the data in the literature through 1987 to obtain average annual values of these estimates for each marine mammal species for use in ecosystem studies assessing marine mammal impacts on their prey resources in the Bering Sea.

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National Oceanic and Atmospheric Administration
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REVIEW OF MARINE MAMMAL POPULATION AND PREY INFORMATION FOR BERING SEA ECOSYSTEM STUDIES

by

Michael A. Perez

National Marine Mammal Laboratory
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way N.E.
Seattle, WA 98115

August 1990

ABSTRACT

Data in the literature through 1987 were summarized to obtain estimated average annual values of total abundance, body mass, diet composition, and energy value of the diet of each of 21 resident marine mammal species in the eastern Bering Sea and Aleutian Islands region. For some species it was necessary to estimate the Bering Sea population using information on seasonal distribution and relative abundance of these species in the North Pacific, or diet composition of populations in other parts of the world. The average annual energy value of the diet of each marine mammal species was based on estimated annual diet composition and the energy equivalent of each prey species in the diet.

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INTRODUCTION

Twenty-eight marine mammal species are found in the Bering Sea and Aleutian Islands area, although only 21 species (8 pinnipeds, 12 cetaceans, and 1 mustelid) are present often enough and in adequate numbers to contribute significantly to the Bering Sea ecosystem (Lowry et al. 1982; Lowry and Frost 1985; Perez and Loughlin 1986). The quantity and quality of data available on distribution, abundance, and biomass vary widely among the species in the Bering Sea (Loughlin and Jones 1984; Lowry 1984).

Reliable population values are available for most of the pinniped species (Lowry et al. 1982), but, apart from data on the northern fur ***seal (Callorhinus ursinus),*** information on diet composition and prey availability is incomplete, especially by season. Only limited population and diet composition data exist for most cetaceans. Empirical data on the feeding habits of free-ranging marine mammals are variable and less certain for most species than population dynamics data.

The Bering Sea (Fig. 1) has an approximate total surface area of 2.3×10^6 km^2, of which 44% is continental shelf (depth <200 m), 13% is continental slope, and 43% is abyssal (Hood and Kelley 1974). This large continental shelf is one of the most biologically productive areas in the world's oceans (Hood and Kelley 1974; Sambrotto and Goering 1984). In summer the Bering Sea is free of ice. During the winter, part of the shelf is covered with ice that may reach as far as the continental slope in the southeastern Bering Sea. The seasonal movement of sea ice significantly affects the distribution and abundance of marine mammals in the Bering Sea during the year (Tikhomirov 1964; Burns 1970; Fay 1974).

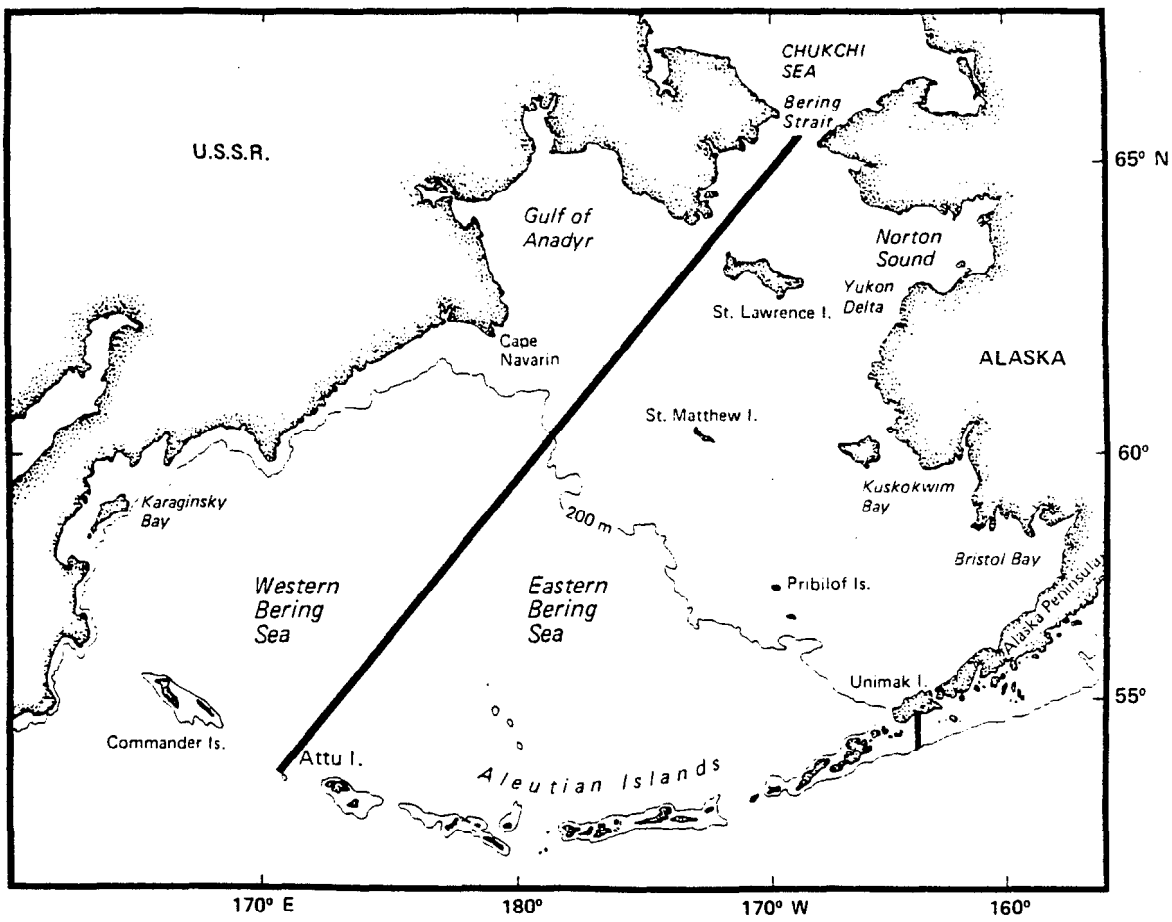

Figure 1.--The Bering Sea region. A line separates the western and eastern Bering Sea from the Bering Strait to the North Pacific Ocean and a shorter line denotes the eastern boundary of the Aleutian Islands area in the Gulf of Alaska at Unimak Pass (164° W). The Aleutian Islands shelf area (depth <200 m) is the southernmost boundary of the region. The 200 m depth contour is also indicated.

In order to estimate the biomass of total food consumption by marine mammals of the eastern Bering Sea, it is necessary to estimate total abundance, average body mass, diet composition, and energy value of the diet of each resident marine mammal species. This paper summarizes the data in the literature through 1987 to obtain average annual values of these estimates for each marine mammal species for use in ecosystem studies assessing marine mammal impacts on their prey resources in the Bering Sea.

METHODS

Biomass and Diet

Individual species abundances were calculated from population data available in the literature. For some species, it was necessary to estimate the eastern Bering Sea population size using published data of seasonal distribution and relative abundance of these species in the North Pacific. Average body mass has been taken from life tables for pinnipeds and from estimates of body size for cetaceans. The data used to estimate average body mass of pinniped species (except the: Pacific walrus, ***Odobenus rosmarus divergens)*** in this report are discussed by McAlister (1987).

Information on prey species and their relative contributions to the diets of marine mammals is incomplete for all marine mammal species except the northern fur seal. Prey species were assumed to be eaten by marine mammals throughout the year at the same average level of diet importance unless there was sufficient information to indicate a difference between summer and winter diets. In the latter case, seasonal data on diet were averaged to account for seasonal changes in the abundance of the marine mammal

predator. Migration patterns or seasonal changes in abundance of prey species were not incorporated as part of the estimates of diet composition. Except where noted in the species accounts below, the percentage of total fish in the diet of each cetacean species and the sea otter ***(Enhydra*** lutris) was divided equally among fish species reported to have been eaten by the respective predator; otherwise, the relative importance of each fish species to the diet (as cited in the literature) was used, as in the case of all pinnipeds.

In the case of some species, such as the northern sea lion, ***Eumetopias jubatus,*** data on diet are limited for the Bering Sea region, and data from nearby regions, such as the Gulf of Alaska or the Okhotsk Sea, were used as an approximate estimate of diet composition. For some cetacean species, such as the Bering Sea beaked whale, ***Mesoplodon stejnegeri,*** there are no published data on diet composition. For such species, it was necessary to approximate diet based on other taxonomically similar species.

Energy Value Estimates

The energy value of the diet of Bering Sea marine mammals was estimated using caloric values (kcal/g) of the edible portion of whole specimens (raw, wet mass) for their prey given in the literature (e.g., Watt and Merrill 1963; Kizevetter 1971; Stansby 1976; Sidwell 1981). These energy values (Appendix Table 1) were either estimated from proximate composition data on the percentages of fat, protein and carbohydrate in the prey species samples using the energy factors for these components cited by Watt and Merrill (1963), or based on published data from heats of combustion of whole specimens.

For many prey species, data on the energy value of whole, raw specimens were unavailable. For some fish species it was possible to estimate comparative energy values based on the summation of the estimated energy values (wet mass) from the percentage composition of the component body parts (Kizevetter et al. 1965; Kizevetter 1971). However, for many other fish species, caloric data were available only for muscle tissue. In this case, energy values were scaled to the estimated value for whole specimens by multiplying the estimated muscle tissue value by a factor of 1.1. This factor was based on the average ratio of caloric data (Sidwell 1981) for whole fish (capelin, ***Mallotus villosus;*** herring, ***Clupea harengus;*** walleye pollock, ***Theragra chalcogramma;*** and rainbow smelt, ***Osmerus mordax)*** to that of only muscle tissue of the same fish species. Data for octopus and crab were based only on muscle tissue values, and no correction factor was used to estimate energy values for whole specimens. The comparative energy value of mammals (as prey of other mammals) was based either on values from data for whole animals or muscle tissue values scaled to whole animal values using a factor of 1.5 for pinnipeds and 2.5 for cetaceans (these factors were derived using data in Tomilin (1957) and Stansby (1976)).

Caloric values from taxonomically related species (genus or family) were used as an approximation for prey species for which energy data were unavailable. For other fish and invertebrate prey species (not listed in Appendix Table 1) which are discussed in the marine mammal diet information later in this paper, there were no available data on their caloric content; 1.0 kcal/g was assumed for these species. Data were unavailable to

estimate energy values of prey species on a seasonal basis, except for capelin ***(Mallotus villosus)*** and Pacific herring ***(Clupea harengus pallasi).***

MARINE MAMMAL POPULATION AND DIET ESTIMATES

Lowry et al. (1982) estimate the total number of marine mammals using the Bering Sea and Aleutian Islands region at between 2 and 3 million. However, the numbers and species composition of marine mammals varies seasonally. The quality of the population data upon which these estimates are based is good for some pinniped species (such as the northern fur seal, which may be effectively counted at rookeries and haul-out sites) but poor for pagophilic pinnipeds and most cetacean species. Likewise, data on average body mass and diet composition for species by age, sex, and seasonal variability range from good to poor (Lowry et al. 1982; Loughlin and Jones 1984; Lowry 1984).

Pinnipeds

Two species of the family Otariidae, the northern fur seal and northern sea lion; five species of the family Phocidae, the Pacific harbor seal ***(Phoca vitulina richardii),*** the spotted seal ***(Phoca largha),*** the ringed seal ***(Phoca hispida),*** the ribbon seal ***(Phoca fasciata),*** and the bearded seal ***(Erignathus barbatus);*** and one species of the family Odobenidae, the Pacific walrus, occur regularly in the Bering Sea where they congregate annually to reproduce.

Northern Fur Seal

The northern fur seal migrates and feeds in water off western North America (Kajimura et al. 1980a; Gentry 1981; Bigg 1982). The total population of northern fur seals was estimated at 1,190,000 to 1,225,000 in 1983 (North Pacific Fur Seal Commission 1984). This estimate included 871,000 animals from the Pribilof Islands, Alaska; 4,000 from San Miguel Island, California; 200,000 to 220,000 from the Commander Islands; 70,000 to 80,000 from Robben Island, Okhotsk Sea; and 45,000 to 50,000 from the Kuril Islands (North Pacific Fur Seal Commission 1984). The population on the Pribilof Islands declined at a rate of 5-8% from 1976 to 1980 and 0-4% from 1980 to the present (North Pacific Fur Seal Commission 1985). York and Kozloff (1987) suggest that this decline in the birth rate of the Pribilof Islands population may have ended.

The estimated abundance of northern fur seals in the eastern Bering Sea and Aleutian Islands area was based on life table data in Lander (1981), pelagic sampling data (Kajimura et al. 1979, 1980a; Lander 1980a), land sampling data (Johnson 1968; Lander 1980b), data from the annual male harvest during 1973-84 (Kozloff 1986), and the calculated average birth rate during 1981-86 (Kozloff 1985; York and Kozloff 1987). The summer (May-October) population, excluding pups, was estimated at 399,500 (McAlister 1987), and the winter (November-April) population was estimated at 40,000 (Table 1). Based on pelagic distribution data for the North Pacific, these estimates assume that 10% of the population, primarily adult males and some immature animals, remain in the southern portion of the region during winter, and that most immature animals of ages 1 and 2 years remain outside the Bering Sea during summer.

Table 1.--Estimated total pinniped abundance in the Bering Sea, average feeding abundance in the eastern Bering Sea and Aleutian Islands region by season, and average body mass.

Species	Abundance: Bering Sea	Abundance: Eastern Bering Sea and Aleutian Islands: May-Oct.	Abundance: Eastern Bering Sea and Aleutian Islands: Nov.-April	Body mass (kg)	Data sources[a]
Northern fur seal	871,000	399,500	40,000	30 S 70 W	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13
Northern sea lion	30,000-35,000	32,000	32,000	212	13, 14, 15, 16, 17, 18
Pacific harbor seal	110,000[b]	45,000	45,000	49	13, 19, 20, 21, 22, 23, 24, 25
Spotted seal	280,000-330,000	14,000	140,000	72	13, 23, 26, 27, 28, 29
Ringed seal	1-1.5 million	1,000	600,000	34	13, 23, 26, 22, 29, 30, 31, 32, 33
Ribbon seal	100,000-110,000	66,000	66,000	46	13, 23, 26, 27, 34, 35, 36
Bearded seal	300,000	5,000	150,000	172 S 243 W	13, 23, 27, 37, 38, 39
Pacific walrus	270,000-290,000	10,000	200,000	900	26, 27, 32, 40, 41

[a] Data sources: (1) Scheffer and Wilke 1953; (2) Johnson 1968; (3) Kajimura et al. 1979; (4) Kajimura et al. 1980a; (5) Lander 1980a; (6) Lander 1980b; (7) Lander 1981; (8) North Pacific Fur Seal Commission 1984; (9) North Pacific Fur Seal Commission 1985; (10) Kozloff 1985; (11) Kozloff 1986; (12) York and Kozloff 1987; (13) McAlister 1987; (14) Fiscus 1961; (15) Calkins and Pitcher 1982; (16) Merrick et al. 1987;

Table 1.--Continued.

(17) Loughlin et al. 1990; (18) unpublished data, National Marine Mammal Laboratory, Alaska Fisheries Science Center, NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115; (19) Bigg 1969; (20) Pitcher 1977; (21) Everitt and Braham 1980; (22) Fiscus et al. 1981; (23) Lowry and Frost 1981; (24) Burns and Gol'tsev 1984; (25) Pitcher 1985; (26) Popov 1982; (27) Braham et al. 1984; (28) Lowry 1985a; (29) Burns 1986; (30) Fedoseev 1965; (31) Frost and Lowry 1981a; (32) Lowry et al. 1982; (33) Frost 1985; (34) Shustov 1969; (35) Burns 1981a; (36) Lowry 1985b; (37) Burns and Frost 1979; (38) Burns 1981b; (39) Nelson et al. 1985; (40) Fay et al. 1977; (41) Lowry 1985c.

[b] Total abundance does not include harbor seals on the Commander Islands.

S = Summer
W = Winter

The average body mass of northern fur seals was estimated at 30 kg (Table l), or 40 kg if pups are excluded from calculation of average body mass, based on data in Scheffer and Wilke (1953), Johnson (1968), Kajimura et al. (1979), Lander (1980a, 1980b, 1981), and McAlister (1987). Because adult males comprise the majority of fur seals wintering in the Bering Sea, the average body mass of these fur seals during winter months was estimated to be 70 kg.

Food consumption by northern fur seals is described by Kajimura (1984) and Perez and Bigg (1986). The diet consists of 67% fish and 33% squid (Table 2). The dominant fish species eaten by northern fur seals in the eastern Bering Sea is walleye pollock, Theragra chalcogramma (Table 2).

Northern Sea Lion

The northern sea lion is found in continental shelf waters from the Sea of Japan, northern Honshu Island, and the Korean peninsula northward to the Okhotsk Sea, Kuril Islands and Commander Islands; through the Aleutian Islands into the *Bering Sea, including the Pribilof Islands; eastward throughout and around the Gulf of Alaska; and southward along the coast to California (Schusterman 1981; Loughlin et al. 1984). Northern sea lions range in all coastal waters seaward as far as the continental shelf break (Kajimura and Laughlin 1988); they utilize well-defined locations on shore to haul out and rest, and reproduce (Calkins and Pitcher 1982). Northern sea lions do not migrate, but some disperse broadly throughout the Bering Sea and Gulf of Alaska during fall and winter (Calkins and Pitcher 1982).

Table 2.--Estimated diet composition (percent) for pinnipeds in the eastern Bering Sea and Aleutian Islands region.

Prey species	Northern fur seal	Northern sea lion	Harbor seal	Spotted seal	Ringed seal	Ribbon seal	Bearded seal	Pacific walrus
Fishes								
Pacific herring	6	3	5	8	1	-	-	-
Salmon (*Oncorhynchus* spp.)	2	1	1	-	-	-	-	-
Capelin	16	5	5	15	<1	2	<1	-
Eulachon (*Thaleichthys pacificus*) and smelts (Osmeridae)	<1	1	4	1	1	-	-	-
Deep-sea smelts and lanternfishes	4	-	-	-	-	-	-	-
Walleye pollock	34	33	12	19	<1	16	<1	-
Pacific cod	<1	7	8	1	-	<1	-	-
Saffron cod	-	1	3	8	33	9	4	-
Arctic cod	-	-	<1	12	45	12	3	-
Rockfishes (Scorpaenidae)	<1	4	1	-	-	-	<1	-
Sablefish	1	-	-	-	-	-	-	-
Atka mackerel	2	<1	9	-	-	-	-	-
Greenlings (Hexagrammidae)	-	-	8	-	-	-	-	-
Sculpins	<1	6	9	12	4	1	12	-
Pacific sand lance	1	4	4	4	1	-	<1	-
Eelpouts	-	1	1	12	<1	9	<1	-
Flatfishes	1[a]	9	3	1	<1	4	4	-
Other fish[b]	<1	2	2	3	<1	1	-	<1
Subtotal (fish)	67	76	75	96	85	54	23	<1
Invertebrates								
Squid	33	3	4	<1	-	1	-	-
Octopus	<1	18	15	2	-	5	<1	1
Shrimp	-	1	2	1	10	28	32	2
Crab	-	2	2	<1	-	10	33	3
Gastropods	-	<1	-	-	-	-	7	6
Clams	-	<1	-	-	-	-	4	67
Other invertebrates[c]	-	<1	2	1	5	2	1	18
Subtotal (invertebrates)	33	24	25	4	15	46	77	97

Table 2.--Continued.

Prey species	Northern fur seal	Northern sea lion	Harbor seal	Spotted seal	Ringed seal	Ribbon seal	Bearded seal	Pacific walrus
Miscellaneous								
Pinnipeds	-	<1	-	-	-	-	-	3
Total	100	100	100	100	100	100	100	100
Data sources[d]	1, 2	3, 4, 5, 6, 7, 8, 9, 10	8, 11, 12, 13, 14, 15	8, 16, 17	8, 18, 19, 20, 21	8, 22, 23, 24	8, 18, 20, 25, 27	8, 28, 29, 30, 31

[a] Flatfishes eaten by northern fur seals during 1958-74 consisted primarily of Greenland turbot, *Reinhardtius hippoglossoides*.

[b] Other fish species eaten by some pinnipeds include Pacific sandfish, *Trichodon trichodon*; searcher, *Bathymaster signatus*; lumpsuckers and snailfishes, Cyclopteridae; poachers, Agonidae; pricklebacks, Stichaeidae; sticklebacks, Gasterosteidae; gobies, Gobiidae; and lampreys, Petromyzontidae.

[c] Other invertebrates eaten by some pinnipeds include euphausiids, amphipods, mysids, polychaetes, annelids, and echinoderms.

[d] Data sources: (1) Kajimura 1984; (2) Perez and Bigg 1986; (3) Wilke and Kenyon 1952; (4) Mathisen et al. 1962; (5) Thorsteinson and Lensink 1962; (6) Fiscus and Baines 1966; (7) Pitcher 1981; (8) Lowry et al. 1982; (9) Gearin 1985; (10) Gearin 1986; (11) Wilke 1957; (12) Kenyon 1965; (13) Pitcher 1980a; (14) Pitcher 1980b; (15) Burns and Gol'tsev 1984; (16) Ognev 1935; (17) Bukhtiyarov et al. 1984; (18) Kenyon 1962; (19) Lowry et al. 1978; (20) Lowry et al. 1980a; (21) Lowry et al. 1981; (22) Shustov 1965; (23) Frost and Lowry 1980; (24) Burns 1986; (25) Kosygin 1966; (26) Kosygin 1971; (27) Lowry et al. 1980b; (28) Fay et al. 1977; (29) Fay et al. 1984; (30) Fay and Stoker 1982; (31) Lowry and Fay 1984.

Loughlin et al. (1984) estimated the worldwide population in 1980 at 245,000 to 290,000, of which 200,000 animals were resident in Alaska. Recently, there have been significant declines in the number of northern sea lions in the eastern Aleutian Islands and the Pribilof Islands (Braham et al. 1980, Loughlin et al. 1984). Data obtained during 1984-86 indicate that the adult population counted on land at rookeries in the Bering Sea and western Gulf of Alaska has declined about 50%, from approximately 140,000 animals during 1959-60 to approximately 68,000 in 1985 (Merrick et al. 1987). Data from 1989 indicate that the decline has continued, with a drop of 63% since 1985 (Loughlin et al. 1990). Northern sea lion populations in all regions of Alaska have declined, with the greatest loss of animals in the eastern Aleutian Islands and the lowest decline in the central Aleutian Islands. Northern sea lions were listed as a threatened species pursuant to the Endangered Species Act on 5 April 1990.

The Bering Sea population of adult and juvenile northern sea lions (including animals on all of the Aleutian Islands and Bering Sea rookeries) was estimated to number at least 21,000 animals based on count data during 1989 (Loughlin et al. 1990; National Marine Mammal Laboratory, Alaska Fisheries Science Center, NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, unpubl. data). Calkins and Pitcher (1982) calculate the total number of sea lions of all ages present at the end of the pupping season in Alaska to average about 4.5 times the number of pups born. Based on this average and 1985 count data, pup production during 1989 was estimated at 4,000 for the Bering Sea. The estimated population levels were based on the number of animals counted on land during the breeding season. I increased these totals by

one-third (compared with previous estimates of 23% by Bigg (1985) and 3-21% by Loughlin et al. (1984)) to account for missed animals and animals away from land, yielding an estimate of 32,000 animals for the total eastern Bering Sea and Aleutian Islands population of northern sea lions during all months (Table 1). This assumes that there is no winter migration out of the region.

The average body mass of northern sea lions from all age classes, including pups, is estimated by McAlister (1987) at 212 kg (Table 1) based on life table data in Fiscus (1961) and Calkins and Pitcher (1982).

There are limited data in the literature on the diet of the northern sea lion in the Bering Sea. The estimated diet composition shown in Table 2 was based on data from the Gulf of Alaska (Pitcher 1981) and from studies in the Bering Sea and Aleutian Islands (Wilke and Kenyon 1952; Mathisen et al. 1962; Thorsteinson and Lensink 1962; Fiscus and Baines 1966; Lowry et al. 1982; and Gearin 1985, 1986). These data were averaged, giving equal weight to both the Gulf of Alaska and the Bering Sea, to represent the percentage of fish in the diet. The relative proportions of individual prey species were assumed to be similar throughout the eastern Bering Sea and Aleutian Islands region.

Pacific Harbor Seal

The Pacific harbor seal, usually found in inshore waters less than 55 m in depth, is a common resident of the Bering Sea and Aleutian Islands (Everitt and Braham 1980). The population in Bristol Bay, the north side of the Alaska Peninsula, and the eastern Aleutian Islands has been estimated at 30,000 animals (Everitt and Braham 1980; Lowry

and Frost 1981). The population of the central and western Aleutian Islands has been estimated to number at least 15,000 (Fiscus et al. 1981), and the total Aleutian Islands population of Pacific harbor seals may be as high as 85,000 (Lowry and Frost 1981; Pitcher 1985). There are no population estimates for Pacific harbor seals in the western Bering Sea. In the Gulf of Alaska, the Pacific harbor seal population has been declining in recent years (Calkins 1987); there are no available data on recent population trends for harbor seals in the Bering Sea. I estimated the number of harbor seals in the eastern Bering Sea and Aleutian Islands at 45,000 during all months (Table 1).

The average body mass of Pacific harbor seals of all age classes, including pups, in the Bering Sea is estimated by McAlister (1987) at 49 kg (Table 1) based on life table data in Bigg (1969) and Pitcher (1977) and body mass data from Burns and Gol'tsev (1984).

The percentage composition of prey species in the diet of Pacific harbor seals listed in Table 2 was based on data in Wilke (1957), Kenyon (1965), Pitcher (1980a, 1980b), Lowry et al. (1982), and Burns and Gol'tsev (1984). The percentage of fish in the diet was estimated by averaging data for the Aleutian Islands, Commander Islands, eastern Bering Sea, and Gulf of Alaska. The percentage composition of fish (76%) and invertebrate (24%) species in the diet of harbor seals (Table 2) was based on an average of data for the Aleutian Islands and eastern Bering Sea areas; diet composition, in this report, accounts for the relative abundance of the Pacific harbor seal population in both areas.

Spotted Seal

The range of the spotted seal is primarily restricted to the Okhotsk, Bering, and Chukchi Seas. A few spotted seals have been recorded in the Beaufort Sea and some probably range into the East Siberian Sea. The seasonal distribution of spotted seals is associated with sea ice for pupping, breeding, and molting (Lowry and Frost 1981; Lowry 1985a; Burns 1986). In late winter and early spring, the entire Bering-Chukchi spotted seal population is concentrated in or near the ice-front, close to open water on the smaller and more dispersed floes of the southern front and fringe of the pack ice (Lowry 1985a; Burns 1986). During April, spotted seals are found along all areas of the front, with highest densities in Bristol Bay near the Alaskan coast and Karaginski Bay on the Siberian coast (Burns 1986). As the sea ice recedes northward and disintegrates in late spring, spotted seals generally move northward and toward the coast. Adults and pups are concentrated among remnants of seasonal ice in May and June; subadults appear to have already moved to coastal waters by that time (Lowry and Frost 1981). During summer and autumn they are widely distributed along the coasts from northern Bristol Bay to the western Beaufort Sea; few spotted seals are associated with ice at this time (Burns 1986). As the sea ice forms in late autumn, spotted seals move southward into the Bering Sea away from the coast and become associated with the front of the southward advancing ice cover (Burns 1986).

The population of spotted seals in the Bering-Chukchi region has been estimated at 280,000 to 330,000 animals, of which 80,000 comprise the Karaginski Bay stock; the remaining 200,000 to 250,000 spotted seals inhabit the ice-front zone of the northern and

eastern Bering Sea during February-April (Lowry and Frost 1981; Lowry 1985a; Burns 1986). Based on the lower population estimate (200,000) and relative abundance data by location in the Bering Sea during April (Braham et al. 1984), I estimated that 70% of the total population, or 140,000 spotted seals, are present in the eastern Bering Sea during November-April (Table 1). Ten percent of the population (14,000 seals) were estimated to remain in the region during May-October.

The average body mass of spotted seals of all age classes, including pups, is estimated by McAlister (1987) at 72 kg (Table 1) based on body mass and age-related mortality data in Popov (1982) and Bums (1986).

Spotted seals feed primarily on fish; some spotted seals, especially young individuals, also eat amphipods, shrimps, euphausiids, crabs, mysids, and octopuses (Lowry and Frost 1981; Lowry et al. 1982; Bukhtiyarov et al. 1984). Major prey species are capelin, Pacific herring, and walleye pollock in the southeastern Bering Sea; walleye pollock and eelpouts ***(Zoarcidae*** spp.) in the central Bering Sea; and capelin and saffron cod ***(Eleginus gracilis)*** in the northern Bering Sea (Lowry and Frost 1981; Bukhtiyarov et al. 1984). The estimated diet composition (Table 2) of spotted seals in the eastern Bering Sea was based on data from Lowry et al. (1982) and Bukhtiyarov et al. (1984); diet composition, in this report, accounts for the relative seasonal abundance of the spotted seal population in the eastern Bering Sea.

Ringed Seal

The ringed seal has a circumpolar distribution and is the most abundant pinniped species in the ice-covered regions of the Northern Hemisphere (Frost and Lowry 1981a;

Lowry and Frost 1981). The distribution of ringed seals in Alaskan waters is strongly correlated with that of sea ice (Burns 1970; Fay 1974). The seals occur seasonally in the Bering Sea, appearing with the formation of seasonal shore-fast ice in November and leaving when the ice disintegrates in May and June. Few are present in summer or fall.

Ringed seals of the Bering, Chukchi, and Beaufort Seas appear to constitute a single population estimated to number 1-1.5 million (Lowry and Frost 1981). Lowry et al. (1982) and Frost (1985) estimate that at least 250,000 ringed seals occur on the shorefast ice in the Bering Sea. Based on the lower total population estimate of one million and relative abundance data by location in the Bering Sea during April (Braham et al. 1984), I estimated that 60% of the total population, or 600,000 ringed seals, are present in the eastern Bering Sea during November-April (Table 1). Less than 1% of the population (1,000 ringed seals) were estimated to occur in the northeastern Bering Sea during May-October.

The average body mass of ringed seals of all age classes, including pups, is estimated by McAlister (1987) at 34 kg (Table 1) based on body mass and age-related mortality data in Fedoseev (1965), Frost and Lowry (1981a), Popov (1982), and Burns (1986).

Ringed seals feed primarily on Arctic cod ***(Boreogadus saida)*** and saffron cod, but their diet varies markedly by season and geographical area; they also feed on shrimps, euphausiids, amphipods, and mysids (Frost and Lowry 1981a; Lowry and Frost 1981; Burns 1986). Young ringed seals eat a significant amount of crustaceans (Frost and Lowry 1981a). The estimated diet composition (Table 2) of ringed seals in the eastern

Bering Sea region was based on data from Kenyon (1962) and Lowry et al. (1978, 1980a, 1981, 1982); diet composition, in this report, accounts for the relative seasonal abundance of the ringed seal population in the eastern Bering Sea.

Ribbon Seal

The ribbon seal inhabits the seasonally ice-covered regions of the Okhotsk, Bering, and Chukchi Seas and the bays and straits contiguous with them, but the animals may sometimes be found in the Bering Sea south to the Aleutian Islands and west to Kamchatka and the Kuril Islands (Burns 1981a). The range of the ribbon seal is in part dependent on seasonal conditions. The formation of extensive ice in the Bering Sea may result in the occurrence of large numbers of ribbon seals further south than they normally occur; the reverse is also true (Burns 1981a). Ribbon seals are associated with sea ice during the late winter, spring, and early summer, but their distribution and activities during the late summer and fall are not well known. These seals may become pelagic in the central Bering Sea near the edge of the continental shelf during the months when ice is not present; some ribbon seals have been sighted in this area during summer (Burns 1981a).

The population of ribbon seals in the Bering Sea has been estimated at 100,000-110,000 (Burns 1981a; Lowry and Frost 1981; Lowry 1985b). Based on relative abundance data by location in the Bering Sea in Braham et al. (1984), about 60% of the population, or 66,000 ribbon seals (Table 1) have been estimated to be in the eastern Bering Sea during November-April. Ribbon seals are pelagic in the Bering Sea during the ice-free months in summer (Burns 1981a), and 66,000 ribbon seals (Table 1) were

also estimated to be present during May-October in the eastern Bering Sea. The relative distribution of ribbon seals between the western and eastern Bering Seas was assumed to be similar throughout the year.

The average body mass of ribbon seals of all age classes, including pups, is estimated by McAlister (1987) at 46 kg (Table 1) based on body mass and age-related mortality data in Shustov (1969), Bums (1981a), and Popov (1982).

Ribbon seals in the Bering Sea feed during spring on crabs, shrimps, fish, mysids, and squid (Shustov 1965; Bums 1981a). Young ribbon seals feed mainly on crustaceans (Popov 1982). Shustov (1965) states that the diet of the ribbon seal is intermediate between that of ringed and bearded seals. Thus, the percentage of fish (54%) in the diet was estimated as the average of values for ringed and bearded seals (Table 2). Prey species composition for fish and invertebrate taxonomic subgroups (Table 2) was based on data in Shustov (1965), Frost and Lowry (1980), and Lowry et al. (1982).

Bearded Seal

The bearded seal has a circumpolar range and is associated with sea ice. Bearded seals avoid regions of thick, continuous shore-fast ice; they utilize areas of shallow water where the ice is in constant motion and produces leads, polynya, and other openings (Burns 1981b). Most of the population of bearded seals moves south through the Bering Strait in late fall and early winter, and during the winter and early spring bearded seals are widely distributed throughout the drifting ice of the Bering Sea (Burns 1981b). The northward spring migration through the Bering Strait into the Chukchi Sea occurs from mid-April to June (Burns 1981b). Some bearded seals, particularly juveniles, occur in

the open sea of the Bering-Chukchi region during summer (Burns 1981b). Areas of greatest abundance have been reported south of Bering Strait near St. Lawrence Island and in the Gulf of Anadyr (Kosygin 1966).

Bearded seals in the Bering and Chukchi Seas are considered to be a single population numbering about 300,000 (Burns 1981b; Lowry and Frost 1981; Nelson et al. 1985). Based on relative abundance data by location in the Bering Sea in Braham et al. (1984), I estimated the population of bearded seals to be 150,000 (Table 1) in the eastern Bering Sea during November-April. Burns (1981b) states that some juvenile bearded seals remain in the Bering Sea during summer months; less than 5% of the population, about 5,000 animals (Table 2), was estimated to be present in the eastern Bering Sea during May-October.

The average body mass of bearded seals of all age classes, including pups, is estimated by McAlister (1987) at 243 kg in winter and 172 kg (for bearded seals of ages l-5 years only) in summer (Table 1) based on body mass and age-related mortality data in Burns and Frost (1979) and Burns (1981b).

Bearded seals feed primarily on benthic prey found in waters less than 200 m in depth (less than 130 m in the southeastern Bering Sea) (Burns 1981b; Popov 1982). Crabs, shrimps, octopuses, snails, clams, polychaetes, and echinoderms constitute the bulk of the diet of bearded seals (77%, Table 2); some demersal fish are eaten, but they are of little importance to the diet of bearded seals (Burns 1981b; Lowry and Frost 1981). The estimated percentage composition of the bearded seal diet in Table 2 was based on data in Kenyon (1962), Kosygin (1966, 1971), and Lowry et al. (1980b, 1981,

1982); diet composition, in this report, accounts for the relative seasonal abundance of the bearded seal population in the eastern Bering Sea.

Pacific Walrus

The Pacific walrus is found seasonally in the Bering Sea, with the southern part of the winter range extending into Bristol Bay (Fay 1982, 1985). Walruses principally inhabit the moving pack ice over the shallow waters of the continental shelf (Fay 1981). Most walruses migrate southward with the advancing ice in autumn and northward as the ice recedes in spring (Fay 1982). Walruses are found mainly on the pack ice of the northcentral and southeastern Bering Sea during December-March. They migrate northward through the Bering Strait in April-June, occur along the ice edge in the Chukchi Sea during July-September, and return to the Bering Sea again in autumn (Fay 1981). However, several thousand male walruses remain in the Bering Sea throughout the summer, utilizing small islands in Bristol Bay and the Gulf of Anadyr as hauling grounds.

The population of Pacific walruses in the Bering-Chukchi Seas is estimated to number from 270,000 to 290,000 animals (Lowry and Frost 1981; Lowry 1985c). Based on relative abundance data by location in the Bering Sea in Braham et al. (1984), the Pacific walrus population in the eastern Bering Sea during November-April was estimated at 200,000 (Table 1). As some walruses haul out on beaches in the Bristol Bay area and western Alaska (Lowry and Frost 1981; Lowry et al. 1982), I estimated that 5% of the population (10,000 individuals; Table 1) are present in the eastern Bering Sea during May-October.

Walruses are among the largest of the pinnipeds. The adults are sexually dimorphic; males are about 20% longer and 50% heavier than females (Fay 1981). The average adult body mass is about 1,200 kg for males and 800 kg for females (Fay 1981, 1982). Fay et al. (1977) estimates the body mass of an average Pacific walrus at 900 kg (Table 1).

The walrus primarily feeds on benthic invertebrates (97%, Table 2), and fish are rarely consumed (Fay et al. 1977; Fay 1981, 1982, 1985; Lowry et al. 1982; Fay et al. 1984). Fay and Stoker (1982) report an incidental ingestion rate of 0.4% for fish in the diet of Pacific walruses taken near Nome, Alaska, and even this low percentage is considered high for the population. Male walruses have long been reported to eat seals occasionally, ostensibly when benthic foods are unavailable. There has been an increase in recent years of predation on pinnipeds by walruses in the Chukchi and northern Bering Seas, although such predation accounts for less than 3% of the walrus diet (Lowry and Fay 1984). Pinnipeds killed by walruses for food include spotted, ringed, and bearded seals (Lowry and Fay 1984). Walruses may also eat the carcasses of cetaceans and other animals (Ognev 1935).

Other Marine Carnivores

Sea Otter

The sea otter is found in coastal waters within the 75 m depth contour of the Bering Sea throughout the Aleutian Islands area and along the north side of the Alaskan Peninsula (Kenyon 1981; Calkins and Schneider 1985). Sea ice limits the northern

border of the permanent range of sea otters at about lat. 57° N (Estes 1980). The formation of sea ice in Bristol Bay precludes sea otter distribution there during winter (Lowry et al. 1982). Based on data in Calkins and Schneider (1985) the eastern Bering Sea population of sea otters was estimated at 79,000 (range 66,800 to 90,900) during all months of the year.

Adult female sea otters attain body mass values up to 32.5 kg with an average range from 16 to 27 kg, and adult males weigh up to 45.4 kg with a range from 27 to 38.6 kg (Estes 1980; Kenyon 1981). I estimated the body mass of an average sea otter, including juveniles, at 20 kg.

Sea otters feed primarily on invertebrates, and they form a significant element in the ecosystem of the Aleutian Islands. Using data in Kenyon (1969; 1981) and Lowry et al. (1982), I estimated that the sea otter's diet consists of 82% invertebrates (50% sea urchins; 18% bivalves and mussels; 6% crabs; and 8% other invertebrates, e.g., snails and octopuses) and 18% fish. However, sluggish, epibenthic fishes may be the most important prey in sea otter populations near equilibrium density (Estes 1980). Fish eaten by sea otters (and estimated importance in the diet) include lumpsuckers (Cyclopteridae; 9%); sculpins (Cottidae; 5%); rock greenling ***(Hexagrammos lagocephalus;*** 3%); and the seldom eaten (<1%) but commercially important Atka mackerel ***(Pleurogrammus monopterygius);*** rockfishes ***(Sebastes*** spp.); sablefish ***(Anoplopoma fimbria);*** Pacific cod ***(Gadus macrocephalus);*** and walleye pollock (Barabash-Nikiforov 1947; Kenyon 1969; Lowry et. al. 1982).

Polar Bear

The polar bear, ***Ursus maritimus,*** has a circumpolar distribution (DeMaster and Stirling 1981). The southern limits of their range are determined by the distribution of pack ice and annual landfast ice during winter. About 5,700 to 9,500 polar bears have been estimated in the Alaskan population (Lentfer 1985). Based on harvest data reported by Lowry et al. (1982), less than 8% may enter the northern Bering Sea, and then only seasonally. Polar bears usually occur in very low numbers at St. Lawrence Island during winter, but during years of extensive ice cover in the northern Bering Sea they may occur as far south as Nunivak Island at lat. 60°N (Burns 1981b).

The polar bear consumes primarily ringed seals, and secondarily, bearded seals on and near the edge of the pack ice. Polar bears also eat the carcasses of belukha whale ***(Delphinapterus leucas),*** bowhead whale ***(Balaena mysticetus),*** walrus, and seals (DeMaster and Stirling 1981; Frost and Lowry 1981b; Lentfer 1985).

Because polar bears are top trophic level consumers, feeding mainly on marine mammals (Lentfer 1985) and not significantly on either fish or invertebrates, they will not be discussed further in this study.

Cetaceans

Twelve cetacean species occur seasonally in the Bering Sea. Five of these are baleen whales (suborder Mysticeti): the gray whale ***(Eschrichtius robustus),*** the minke whale ***(Balaenoptera acutorostrata),*** the fin whale ***(Balaenoptera physalus),*** the humpback whale ***(Megaptera novaeangliae),*** and the bowhead whale; and seven species are toothed whales (suborder Odontoceti): the killer whale ***(Orcinus orca),*** the harbor porpoise

(Phocoena phocoena), the Dall's porpoise ***(Phocoenoides dalli),*** the belukha whale, the sperm whale ***(Physeter macrocephalus),*** the North Pacific giant bottlenose whale ***(Berardius bairdii),*** and the Bering Sea beaked whale. In contrast to the relatively large amount of data available for pinnipeds, information on the abundance, distribution, biomass, and feeding habits of cetaceans in the Bering Sea and Aleutian Islands region is limited. Only five cetacean species (gray whale, minke whale, sperm whale, belukha whale, and Dall's porpoise) occur in the Bering Sea in large numbers (more than 1,000 animals per species).

Gray Whale

Most gray whales migrate annually between their summer feeding grounds in the Chukchi, western Beaufort, and northern Bering Seas and their winter breeding grounds off Mexico (Rice and Wolman 1971; Bogoslovskaya et al. 1981, 1982; Rice et al. 1984). In October and November, gray whales begin leaving the Chukchi Sea, exiting the Bering Sea through Unimak Pass, Alaska, mainly in November and December; they then migrate southward near shore along the coast of North America to Baja California, Mexico (Braham 1984a; Rice et al. 1984; Wolman 1985). The northbound migration begins in mid-February, and by April, when the sea ice degenerates, whales begin showing up in the southern Bering Sea (Rice and Wolman 1971; Rice et al. 1984). They are apparently restricted by feeding habits to shallow waters of the continental shelf, generally in areas of high benthic biomass (Braham 1984a; Wolman 1985) and have not been found in deep waters of the southwestern Bering Sea.

The eastern North Pacific stock of gray whales is estimated to number 13,450-19,201 (Braham 1984b; Rice et al. 1984). Rugh (1984) estimates that 17,000 gray whales leave the Bering Sea through Unimak Pass during migration each fall. Berzin (1984) estimates that approximately 25% of these gray whales summer as residents in the northwest and northern Bering Sea, and perhaps 7% in the eastern Bering Sea. Based on these data, I estimated a May-October feeding population of 5,000 (Table 3). The average body mass of gray whales is about 18,000 kg (Table 3), based on the length-mass relationship in Rice and Wolman (1971) for an average length of 12 m, although adult body mass ranges between 16,000 and 45,000 kg (Rice and Wolman 1971; Rice et al. 1984).

Nerini (1984) summarizes gray whale feeding ecology in the Bering and Chukchi Seas. Amphipod crustaceans comprise approximately 95% of the diet of gray whales (Zimushko and Lenskaya 1970; Zimushko and Ivashin 1980; Bogoslovskaya et al. 1981, 1982). Although 43 species of amphipods have been identified from stomachs, one of seven species ***(Pontoporeia femorata, P. affinis, Anonyx nugax, Ampelisca macrocephala, A. eschrichti, Nototropis brueggeni,*** or ***N. ekmani),*** depending on the area, is usually dominant in the diet (Zimushko and Ivashin 1980; Rice et al. 1984). Gray whales also consume other large and small benthic invertebrates, epifaunal invertebrates in kelp forests and along rocky shores, and zooplankton (Oliver et al. 1983) such as shrimp, crabs, polychaetes, snails, clams, and isopods. Fish, such as Pacific sand lance ***(Ammodytes hexapterus),*** and fish larvae may be ingested incidentally with benthos (Zimushko and

Table 3.--Estimated cetacean abundance in the North Pacific Ocean, average feeding abundance in the eastern Bering Sea and Aleutian Islands region by season and average body mass.

Species	Abundance			Body mass (kg)	Data sources[a]
	North Pacific	Eastern Bering Sea and Aleutian Islands			
		May-Oct.	Nov.-April		
Baleen whales					
Gray whale	13,450-19,201	5,000	-	18,000	1, 2, 3, 4, 5
Minke whale	>21,000	3,000	800	6,000	6, 7, 8, 9, 10, 11
Fin whale	14,620-18,630	1,000	-	49,000	3, 8, 10, 12, 13, 14, 15
Humpback whale	<1,200	150	-	30,000	3, 8, 10, 12, 13, 14, 16
Bowhead whale	4,800-9,600	200	1600	46,000	17, 18, 19, 20
Toothed whales					
Killer whale	N.E.	700	300	4,000	21, 22, 23
Harbor porpoise	N.E.	1,000	500	50	24, 25, 26, 27
Dall's porpoise	741,000	85,500	42,700	95	28, 29, 30, 31, 32, 33
Belukha whale	25,000	3,500	18,000	800	34, 35, 36, 37
Sperm whale	274,000	15,000	-	36,000	3, 8, 10, 13, 25, 38, 39, 40

Table 3.--Continued.

Species	Abundance: North Pacific	Abundance: Eastern Bering Sea and Aleutian Islands: May-Oct.	Abundance: Eastern Bering Sea and Aleutian Islands: Nov.-April	Body mass (kg)	Data sources[a]
North Pacific giant bottlenose whale	N.E.	500	-	8,000	25, 41, 42, 43
Bering Sea beaked whale	N.E.	200	200	2,000	41, 43, 44, 45, 46, 47

[a] Data sources: (1) Rice and Wolman 1971; (2) Berzin 1984; (3) Braham 1984b; (4) Rice et al. 1984; (5) Rugh 1984; (6) Masaki 1979; (7) Ohsumi 1979; (8) Wada 1980; (9) Lockyer 1981; (10) Wada 1981; (11) Kasamatsu and Hata 1985; (12) Berzin and Rovnin 1966; (13) Lockyer 1976; (14) Votrogov and Ivashin 1980; (15) Mizroch et al. 1984; (16) Johnson and Wolman 1984; (17) International Whaling Commission 1988; (18) Brodie 1981; (19) Braham 1984c; (20) Reeves and Leatherwood 1985; (21) Dahlheim 1981; (22) Braham and Dahlheim 1982; (23) Brueggeman et al. 1984; (24) Gaskin et al. 1974; (25) Lowry et al. 1982; (26) Gaskin 1984; (27) Jones 1984; (28) Scheffer 1953; (29) Loeb 1972; (30) Kajimura et al. 1980b; (31) Bouchet and Haines 1985; (32) Bouchet et al. 1986; (33) Turnock 1987; (34) Sergeant and Brodie 1969; (35) Burns and Seaman 1985; (36) Lowry 1985d; (37) Seaman et al. 1985; (38) Ohsumi 1966; (39) Ohsumi et al. 1977; (40) Gosho et al. 1984; (41) Tomilin 1957; (42) Kasuya and Ohsumi 1984; (43) Rice 1986b; (44) Kenyon 1961; (45) Nishiwaki 1972; (46) Loughlin et al. 1982; (47) Loughlin and Perez 1985.

Lenskaya 1970; Bogoslovskaya et al. 1981; Rice et al. 1984). Table 4 lists the estimated diet composition of gray whales in the eastern Bering Sea.

Minke Whale

The minke whale has a wide distribution in both hemispheres and occurs throughout the North Pacific Ocean from Japan to California, north to the Bering and Chukchi Seas (Tomilin 1957; Stewart and Leatherwood 1985). Minke whales occur in the Bering Sea mainly during spring and summer months, especially in May and June; however, some of these whales are found in the Bering Sea throughout the year (Tomilin 1957; Ivashin and Votrogov 1981a; Lowry et al. 1982; Kasamatsu and Hata 1985).

The Okhotsk Sea-West Pacific stock of minke whales is estimated to number at least 21,000 animals, and some of these whales can occur in the Bering Sea (Kasamatsu and Hata 1985). There are no population estimates for the eastern North Pacific stock of minke whales, and some of these animals may range into the Bering Sea. Based on relative density data and subregional differences in the density of these whales at sea (Wada 1980, 1981; Kasamatsu and Hata 1985), I estimated a total summer population of 3,000 and a winter population of 800 minke whales in the eastern Bering Sea (Table 3).

The minke whale is the smallest of the rorquals (Stewart and Leatherwood 1985). Minke whales become physically mature at about 8 m in length (Tomilin 1957; Masaki 1979). Based on the length-mass relationship in Ohsumi (1979) and data in Lockyer (1981) I estimated 6,000 kg as the average body mass of adult minke whales (Table 3).

Table 4.--Estimated diet composition (percent) for cetaceans in the eastern Bering Sea and Aleutian islands region.[a]

Prey species	Gray whale	Minke whale	Fin whale	Humpback whale	Bowhead whale	Killer whale	Harbor porpoise	Dall's porpoise	Belukha whale	Sperm whale	North Pacific giant bottlenose whale	Bering Sea beaked whale
Fishes	Trace	60	16	29	Trace	65	95	50	93	18	10	10
Cephalopods	-	1	2	1	-	20	1	50	2	82	90	90
Euphausiids	-	30	55	69	45	<1	-	<1	3	<1	-	-
Amphipods	95	-	-	<1	27	<1	<1	-	1	-	-	-
Copepods	-	9	27	1	24	<1	-	-	-	-	-	-
Other invertebrates[b]	5	-	-	<1	4	<1	4	<1	1	<1	-	-
Mammals	-	-	-	-	-	15	-	-	-	Trace	-	-
Total	100	100	100	100	100	100	100	100	100	100	100	100
Data sources[c]	1, 2, 3, 4, 5	6, 7, 8, 9, 10, 11	7, 8, 9, 12	7, 8, 9, 12	13	14, 15, 16, 17, 18, 19	20, 21, 22, 23	24, 25, 26	27, 28, 29, 30	31, 32, 33, 34	22, 35, 36	35, 37

[a] Where data were unavailable for the Bering Sea, diet information from other regions was used as an estimate.

[b] Other invertebrates eaten by some cetaceans include pteropods, gastropods, clams, crabs, shrimp, mysids, isopods, and polychaetes.

[c] Data sources: (1) Zimushko and Lenskaya 1970; (2) Zimushko and Ivashin 1980; (3) Bogoslovskaya et al. 1981; (4) Bogoslovskaya et al. 1982; (5) Nerini 1984; (6) Omura and Sakiura 1956; (7) Nemoto 1959; (8) Nemoto 1970; (9) Kawamura 1980; (10) Jonsgaard 1982; (11) Kasamatsu and Hata 1985; (12) Nemoto 1957; (13) Lowry and Frost 1984; (14) Nishiwaki and Handa 1958; (15) Ivanova 1961; (16) Rice 1968; (17) Mikhalev et al. 1981; (18) Braham and Dahlheim 1982; (19) Berzin and Vladimirov 1983; (20) Gaskin et al. 1974; (21) Prescott and Fiorelli 1980; (22) Frost and Lowry 1981b; (23) Lowry et al. 1982; (24) Loeb 1972; (25) Kajimura et al. 1980b; (26) Crawford 1981; (27) Kleinenberg et al. 1964; (28) Seaman et al. 1982; (29) Frost et al. 1984; (30) Lowry et al. 1985; (31) Berzin 1959; (32) Okutani and Nemoto 1964; (33) Tarasevich 1968a; (34) Kawakami 1980; (35) Tomilin 1957; (36) Rice 1986b; (37) Loughlin and Perez 1985.

Trace = incidental ingestion reported in the literature

The diet of minke whales in the North Pacific consists mainly of fish and euphausiids. Of the baleen whales, the minke whale is most adapted to feed on fish. Near Attu and Atka Islands, minke whales mainly preyed on euphausiids, but they also ate some fish (Kasamatsu and Hata 1985). Fish constitute about 43% of the diet of minke whales off Japan (Omura and Sakiura 1956; Kawamura 1980); in the North Atlantic fish comprised 55% of the diet of minke whales (Jonsgaard 1982). Minke whales in the Sea of Okhotsk have been observed to feed almost exclusively on walleye pollock and Pacific herring (Kawamura 1980). The stomach of a minke whale stranded on Unalaska Island in the eastern Aleutian Islands contained only walleye pollock (Frost and Lowry 1981b, 1986). Other fishes eaten by minke whales include capelin, Arctic cod, saffron cod, and Pacific sand lance (Omura and Sakiura 1956; Tomilin 1957; Kasamatsu and Hata 1985). Pelagic squids and copepods are of lesser importance in the diet of minke whales in the North Pacific (Nemoto 1959, 1970; Kawamura 1980). The estimated diet composition of minke whales in the eastern Bering Sea is given in Table 4.

Fin Whale

Fin whales are distributed worldwide. They breed and calve in temperate and subtropical waters during winter then migrate poleward to feed during summer (Mizroch et al. 1984; Gambell 1985). In the eastern North Pacific Ocean, fin whales range from the Chukchi Sea southward to California and beyond. They are frequently seen in waters south of the Pribilof Islands and north of Unalaska Island in the southeastern Bering Sea, near the Aleutian Islands, and in the northern Bering Sea (Berzin and Rovnin 1966; Votrogov and Ivashin 1980; Lowry et al. 1982). Northward migration

begins in spring, and fin whales arrive in the eastern Aleutians and Gulf of Alaska during April-June. They feed throughout the Bering and Chukchi Seas from late June to October. Southward migration out of the Chukchi and Bering Seas occurs during September-October (Lowry et al. 1982).

The North Pacific Ocean population of fin whales is estimated at 14,620-18,630 animals (Braham 1984b; Mizroch et al. 1984), but no population estimate is available for the Bering Sea. In addition, data are not available on migration movement patterns related to abundance for fin whales in the Bering Sea. I assumed that fin whales may have a spring and fall migration abundance pattern similar to that of gray whales (the only baleen whale species in the Bering Sea for which this type of data is available) with the population peak during August. Using relative abundance and distribution data for fin whales in Berzin and Rovnin (1966) and Wada (1980, 1981), I estimated that there is a seasonal average of 1,000 fin whales in the eastern Bering Sea and Aleutian Islands area during May-October (Table 3).

Fin whales in the Bering Strait and Chukchi Sea average 20-21 m in length (Votrogov and Ivashin 1980). The average body mass is 49,000 kg (Table 3), based on the length-mass relationship in Lockyer (1976). The fin whale is the second largest whale, exceeded only by the blue whale (Gambell 1985).

Fin whales feed primarily on euphausiids and copepods. When euphausiids and copepods are not abundant in the Bering and Chukchi Seas, fishes or squid may become of major importance in the diet of fin whales (Nemoto 1957, 1959, 1970; Tomilin 1957; Kawamura 1980). The most important fish species eaten by fin whales are Pacific

herring, capelin, and walleye pollock. Smelts (Osmeridae), Pacific salmon (Oncorhynchus spp.), Pacific cod, Arctic cod, saffron cod, Pacific sand lance, rockfishes, and Atka mackerel may also be consumed (Tomilin 1957; Frost and Lowry 1981c; Lowry et al. 1982). Table 4 lists the estimated diet composition of fin whales in the eastern Bering Sea.

Humpback Whale

The humpback whale is distributed in low numbers in both hemispheres. Like most baleen whales, humpback whales spend the summer on high-latitude feeding grounds and migrate long distances to low-latitude winter grounds where mating and calving occur (Johnson and Wolman 1984; Winn and Reichley 1985). Humpback whales arrive in the Gulf of Alaska and Aleutian Islands during April-June, appear at Bristol Bay and around Cape Newenham in July, and enter the Chukchi Sea during July-September (Tomilin 1957; Lowry et al. 1982). They begin their southward migration in October.

The North Pacific Ocean population of humpback whales is estimated to number less than 1,200 animals (Braham 1984b; Johnson and Wolman 1984); their abundance in the Bering Sea is unknown, although they occur seasonally in low numbers. I followed the same procedure I adopted for fin whales using relative abundance and distribution data for humpback whales in Berzin and Rovnin (1966) and Wada (1980, 1981) and the seasonal migration abundance trend of gray whales (Rugh 1984) to determine the number of humpback whales in the eastern Bering Sea. I estimated that there may be

an average of 150 humpback whales in the eastern Bering Sea and Aleutian Islands during June-October (Table 3).

Humpback whales in the Bering Strait average about 13 m in length (Votrogov and Ivashin 1980). The average body mass is about 30,000 kg (Table 3) based on the length-mass relationship in Lockyer (1976), although body mass changes considerably due to varying blubber thickness throughout the year (Winn and Reichley 1985).

The diet of humpback whales in the North Pacific and Bering Sea consists primarily of euphausiids and fish (Nemoto 1957, 1959, 1970; Tomilin 1957; Kawamura 1980). Squids, pteropod mollusks, shrimps, amphipods, and copepods are eaten infrequently (Nemoto 1957, 1959). Fish consumed by humpback whales include Pacific herring, juvenile salmon, capelin, smelts, walleye pollock, Arctic cod, saffron cod, Pacific sand lance, rockfishes, and Atka mackerel (Tomilin 1957; Nemoto 1959; Frost and Lowry 1981b, 1981c; Lowry et al. 1982). The estimated diet composition of humpback whales in the eastern Bering Sea is given in Table 4.

Bowhead Whale

The bowhead whale is the only baleen whale which spends its entire life in and around Arctic waters; a few bowheads also reside in the Sea of Okhotsk (Braham 1984c). Bowhead whales migrate from their wintering grounds in the western and northern Bering Sea to their summering grounds in the Amundsen Gulf (Northwest Territories of Canada) and the Beaufort and Chukchi Seas in association with the seasonal movement of Arctic pack ice (Braham 1984c; Reeves and Leatherwood 1985). These whales feed primarily during the summer months and fast during the winter (Brodie 1981; Braham

1984c), although some bowhead whales feed during the northward migration during May in the Bering Sea (Lowry and Frost 1984). The western Arctic population of bowhead whales is estimated at 7,200 & 2,400 animals (International Whaling Commission 1988). Based on the distribution of these whales discussed by Braham (1984c), I assumed that about 10% of the total population (700 bowheads) occur in mid-winter in the northeastern Bering Sea and 50% of the total population migrates through the northeastern Bering Sea from the western Bering Sea into the Bering Strait. Therefore, I estimated the mean winter population of bowhead whales in the eastern Bering Sea at about 1,600 (Table 3). Also, because some whales may be found in the Bering Sea during migration in May and October (Reeves and Leatherwood 1985), I estimated an average summer population of 200 bowheads present only during these two months (Table 3).

Female bowhead whales reach sexual maturity by 14 m in length; there are no data for males (Nerini et al. 1984). Reeves and Leather-wood (1985) suggest that adult bowhead whales may have an average body mass near 70,000 kg, whereas Brodie (1981) estimates the body mass of the average bowhead whale (13.7 m in length) at 46,000 kg.

Bowhead whales feed mainly on euphausiids, amphipods, and copepods, occasionally ingesting other invertebrates, such as pteropods, crabs, shrimps, isopods, and mysids (Tomilin 1957; Johnson et al. 1966; Lowry and Frost 1984). Fish species infrequently and incidentally consumed by bowhead whales include Arctic cod and sculpins (Lowry and Frost 1984). Hazard and Lowry (1984) report that a bowhead whale from the northern Bering Sea in May had fed principally on benthic amphipods. I

assumed that bowhead whales feed in the eastern Bering Sea during an average of 1 month in both the spring and fall migration periods (April-May and October-November) through the northeastern Bering Sea. Table 4 lists the estimated diet composition of bowhead whales in the eastern Bering Sea.

Killer Whale

The killer whale has a cosmopolitan distribution limited by seasonal pack ice (Tomilin 1957; Frost and Lowry 1981b; Dahlheim 1981) and is found throughout the North Pacific Ocean, including the Bering, Chukchi, and Beaufort Seas. In the Chukchi and northern Bering Seas, killer whales move south with the advancing ice pack; however, some year-round residents have been sighted in the northwestern Bering Sea during December (Ivashin and Votrogov 1981b; Braham and Dahlheim 1982). Killer whales have been observed primarily in waters over the continental shelf and slope, where they seem to concentrate near the 200 m depth contour in the southeastern Bering Sea (Braham and Dahlheim 1982). In most geographical regions, killer whale movements appear to be related primarily to movements in their food supply (Nishiwaki and Handa 1958; Rice 1968; Dahlheim 1981).

Estimates of killer whale abundance are not available for the North Pacific Ocean or Bering Sea. Killer whales appear to be abundant off the Pribilof Islands and the Aleutian Islands chain, especially north of Unimak Pass (Dahlheim 1981; Braham and Dahlheim 1982). Brueggeman et al. (1984) estimate the density per area of killer whales in the Navarin Basin of the north Bering Sea during May-November. Using their data, and the approximate area of the continental slope (3×10^5 km^2; Hood and Kelley 1974),

I estimated that about 700 killer whales are present in the eastern Bering Sea during May-October (Table 3). I assumed that nearly half of the summer population may be resident during winter.

Adult male killer whales attain an average length of 8.2 m and weigh about 8,000 kg; adult female killer whales attain an average length of 7.0 m and weigh about 4,000 kg (Dahlheim 1981). Lengths at sexual maturity are reported to be 4.9 m for females and 6.7 m for males (Dahlheim 1981). The average body mass of eight captive killer whales of both sexes at ages 4-18 years was 3,500 kg (Hinga 1979; Perez et al. 1990). The average body mass of an adult killer whale in the Bering Sea was estimated at 4000 kg (Table 3).

Killer whales are opportunistic feeders, and their diet varies from one region to another or within a specific locality (Dahlheim 1981). They primarily eat fish (Sleptsov 1961a), but also prey on pinnipeds, cetaceans, seabirds, and squids (Nishiwaki and Handa 1958; Braham and Dahlheim 1982). Killer whales may switch their diet to marine mammals only when fish are less abundant or not available (Tomilin 1957; Braham and Dahlheim 1982). Fishes eaten by killer whales in parts of their range in the North Pacific region include Pacific herring, salmon, capelin, smelts, Pacific cod, Arctic cod, saffron cod, Atka mackerel, Pacific halibut ***(Hippoglossus stenolepis),*** other flatfishes (Pleuronectiformes), sharks (Squaliformes), and skates (Rajidae) (Tomilin 1957; Nishiwaki and Handa 1958; Rice 1968; Lowry et al. 1982). Killer whales are known to eat northern fur seals; northern sea lions; harbor, ringed, and bearded seals; walruses; sea otters; gray, minke, fin, humpback, and bowhead whales; harbor and Dall's porpoises;

belukhas; and North Pacific giant bottlenose whales (Tomilin 1957; Nishiwaki and Handa 1958; Rice 1968; Braham and Dahlheim 1982).

There are no data on the feeding habits of killer whales in the Bering Sea or Aleutian Islands region. Off Japan, Nishiwaki and Handa (1958) report that the relative rank order of prey in the diet of killer whales, from greatest to least quantity eaten, is fishes, squids, and marine mammals. The proportion of marine mammals in the diet of killer whales varies regionally: off the Kuril Islands, killer whales were found to have eaten only fish and cephalopods (Ivanova 1961); off the west coast of North America, two-thirds of the killer whale diet consisted of marine mammals (Rice 1968). In the South Atlantic, the importance of marine mammals to killer whales varies by latitude (Mikhalev et al. 1981); and in the Antarctic, Ivashin (1981) reports that killer whales eat 67% fishes, 27% marine mammals, and 6% squids. Berzin and Vladimirov (1983) report that killer whales off Antarctica consume either fish or marine mammals almost exclusively. Killer whales seem to eat fish and squid in the ratio of at least 2 to 1 (Nishiwaki and Handa 1958). Because killer whales primarily eat fish when available, rather than marine mammals (Sleptsov 1961a), I reduced in half the percentage of marine mammals in the diet and added the difference to the fish estimate. Therefore, I estimated that killer whales in the Bering Sea will have an average annual diet consisting of 65% fish, 20% squid, 15% marine mammals, and less than 1% other invertebrates, such as shrimp (Table 4).

Harbor Porpoise

The harbor porpoise is a coastal species confined to the Northern Hemisphere, with a more or less circumpolar distribution in temperate regions (Tomilin 1957; Gaskin et al. 1974). In the North Pacific, it occurs from the Chukchi Sea southward to the southern coasts of Japan and Mexico (Frost and Lowry 1981b; Gaskin 1984). Harbor porpoises regularly occur along the mainland coast in the Bering Sea, including Bristol Bay, the Yukon-Kuskokwim Delta, and Norton Sound; they have been recorded from the Aleutian and Pribilof Islands (Leatherwood et al. 1982; Lowry et al. 1982; Jones 1984). Formation of seasonal sea ice in the Chukchi and Bering Seas could affect harbor porpoise distribution (Lowry et al. 1982; Gaskin 1984). Harbor porpoises which occur in the Chukchi Sea during summer probably winter in the Bering Sea; however, some of the southern Bering Sea summer population may leave the Bering Sea in winter (Gaskin 1984).

Although there is a widely distributed population in the eastern Bering Sea, at least from early summer through autumn (Gaskin 1984), there are no estimates of harbor porpoise populations for the Bering Sea or North Pacific. Harbor porpoises and Dall's porpoises overlap in distribution to a significant degree, although harbor porpoises are generally regarded as inhabitants of more inshore and shallower water (Leatherwood et al. 1982). Jones (1984) presents data showing that in the western Bering Sea and North Pacific Ocean harbor porpoises occur 0.2-5.0% as frequently as Dall's porpoises in the incidental catch of the Japanese salmon driftnet fisheries. I assumed that these data may indicate the relative proportion of the populations of the two cetacean species to

each other in the eastern Bering Sea, but there are no data to verify this assumption. I estimated a population of 1,000 harbor porpoises in the eastern Bering Sea during May-October (Table 3). I also estimated that half of this population is resident in the region during November-April near the Aleutian Islands.

The average body mass of an adult harbor porpoise is 45-60 kg; the recorded maximum is 90 kg (Gaskin et al. 1974). Lowry et al. (1982) report that a female taken near Nome, Alaska, had a body mass of 52.7 kg. I used 50 kg as the estimated average body mass of harbor porpoises in the Bering Sea (Table 3).

The harbor porpoise forages on a wide variety of schooling, soft-rayed fishes, and on some invertebrates such as squid and shrimp (Gaskin et al. 1974; Prescott and Fiorelli 1980; Frost and Lowry 1981b). Fish species eaten by harbor porpoises include Pacific herring, salmon, capelin, Arctic cod, saffron cod, sablefish, sand lance, sculpins, and flatfishes (Tomilin 1957; Frost and Lowry 1981b; Lowry et al. 1982). Lowry et al. (1982) summarizes the only data on diet for these animals in the Bering Sea, specifically in Norton Sound. In the Northwest Atlantic, clupeoid (50%) and gadoid (30%) fishes comprise the major elements of their diet (Smith and Gaskin 1974). Based on the data in these studies, I estimated that fishes comprise 95% of the diet of harbor porpoises in the Bering Sea (Table 4).

Dall's Porpoise

The Dall's porpoise ranges throughout the North Pacific Ocean from Baja California north along the coast of North America, to the Aleutian Islands and Bering Sea, and westward to the Sea of Okhotsk and Japan (Frost and Lowry 1981b;

Leatherwood and Reeves 1986). Its usual distribution appears to extend to the Pribilof Islands, and in summer it may reach the Bering Strait; Dall's porpoises are abundant in outer Bristol Bay and throughout the southern Bering Sea from the Pribilof Islands to Unimak Pass, and near the Aleutian Islands (Lowry et al. 1982; Leatherwood and Reeves 1986). They have been observed during winter in ice-free regions of the Bering Sea, but the distribution shifts southward during winter, with some animals leaving the Bering Sea (Fiscus 1980).

The Dall's porpoise population in the North Pacific has been estimated to number 741,000 (Turnock 1987). In the eastern Bering Sea the population has been estimated to number between 66,500 and 121,700 animals (Bouchet and Haines 1985; Bouchet et al. 1986), or an average population of 85,500 Dall's porpoises in this region. There are no data for winter abundance. I have estimated that half (42,700 animals) of the population winters in the southern ice-free portion of the eastern Bering Sea (Table 3). This was assumed on the basis that 50% of the eastern Bering Sea is covered by ice during winter (Brower et al. 1977; Niebauer 1980), which would probably exclude half of the Dall's porpoise population from the region.

I estimated the body mass of the average Dall's porpoise at 95 kg (Table 3) based on data in Scheffer (1953); Tomilin (1957); Loeb (1972); and Kajimura et al. (1980b).

The diet of the Dall's porpoise is principally oceanic cephalopods and fishes, but also some crustaceans such as shrimps and euphausiids (Tomilin 1957; Loeb 1972; Crawford 1981; Frost and Lowry 1981b). Fishes eaten by Dall's porpoises include Pacific herring, salmon, capelin, deep-sea smelts (Bathylagidae), lanternfishes (Myctophidae),

walleye pollock, Arctic cod, eelpouts, Pacific sand lance, rockfishes, sablefish, Atka mackerel, and flatfishes (Tomilin 1957; Frost and Lowry 1981b; Stroud et al. 1981; Lowry et al. 1982). Loeb (1972) reports that Dall's porpoises off California consumed 80% fish and 20% cephalopods, whereas Crawford (1981) reports that porpoises taken in the Japanese salmon driftnet fisheries in the North Pacific ate 90% squid and 10% fish. Kajimura et al. (1980b) present data for seven animals taken in the Bering Sea and Unimak Pass whose stomach contents consisted of 57% fish and 43% squid. I estimated that Dall's porpoises in the eastern Bering Sea throughout the year consume fish and squid about equally in the diet, and that crustaceans are relatively insignificant prey to these cetaceans in this region (Table 4).

Belukha Whale

The belukha whale is circumpolar in distribution, occurring off North America, Europe, and Asia (Kleinenberg et al. 1964). In the Pacific, belukhas are distributed along Alaska as far south as Bristol Bay, and a small but apparently separate stock occurs in Cook Inlet (Seaman and Burns 1981). Most Alaskan belukhas range seasonally throughout the Bering, Chukchi, Beaufort, and at least parts of the East Siberian Seas; these animals may occur during some part of the year in the Bering Sea (Lowry et al. 1982; Seaman et al. 1985). In general, belukhas spend the winter in ice-covered offshore waters. During winter and early spring they are also found in outer Bristol Bay and the southeastern Bering Sea (Seaman et al. 1985). During spring and early summer, they move to coastal regions of the eastern Bering and Chukchi Seas, including inner Bristol Bay and the Norton Sound area. At this time they are especially abundant in shallow

bays or estuaries of large rivers, where they spend most of the summer. They may also travel many miles up these rivers. In late summer to late autumn they move away from the coast, ahead of or with advancing pack ice (Kleinenberg et al. 1964; Seaman et al. 1985).

Seaman et al. (1985) and Lowry (1985d) estimate that a minimum of 2,000-3,500 belukhas summer in Alaskan waters south of Bering Strait. Approximately 1,000-1,500 belukhas are in Bristol Bay and the North Aleutian Basin at this time, and at least 1,000-2,000 belukhas utilize the coastal waters of the eastern Bering Sea from Bering Strait to Kuskokwim Bay during the summer. The total winter population of belukha whales in the Bering Sea was estimated at 13,500-18,000 (Table 3), but may be in excess of 25,000 (Seaman et al. 1985).

Burns and Seaman (1985) report that average lengths of male and female belukha whales are 4.03 m and 3.51 m, respectively. Assuming a 1:1 sex ratio (Seaman and Burns 1981; Burns and Seaman 1985) and using the length-mass relationship given by Sergeant and Brodie (1969), the average body mass of adult belukhas is about 800 kg (Frost and Lowry 1984; Frost et al. 1984).

Over 100 species have been identified in the diet of belukha whales worldwide (Kleinenberg et al. 1964). Belukhas eat primarily pelagic and semidemersal fishes, but also cephalopods and crustaceans, especially shrimp (Kleinenberg et al. 1964; Frost and Lowry 1981b). In coastal areas of the northern Bering and Chukchi Seas, summer foods were Pacific herring, capelin, smelt, saffron cod, eelpouts, sculpins, shrimps, squids, and octopuses; in Bristol Bay primary foods during spring and summer were salmon and

smelt. No diet samples are available from autumn or winter (Frost and Lowry 1981b; Lowry et al. 1982, 1985; Seaman et al. 1982; Frost et al. 1984). During autumn and winter, it is probable that walleye pollock is a major prey in the southcentral Bering Sea, while Arctic cod and saffron cod are major foods in more northern areas (Lowry et al. 1985). The estimated diet composition of belukha whales in the Bering Sea is given in Table 4.

Sperm Whale

The sperm whale is distributed worldwide in all oceans, usually in offshore waters deeper than 300 m, from the edges of the north and south ice pack to the equator (Tomilin 1957; Berzin 1971; Gosho et al. 1984). In the North Pacific, sperm whales are found from equatorial waters northward to the Gulf of Alaska and northern Bering Sea, at least as far as Cape Navarin, but not to the Bering Strait (Berzin and Rovnin 1966; Ohsumi et al. 1977; Wada 1980, 1981). In the spring, they migrate poleward from their wintering grounds (off the Philippines and coast of Japan in the western Pacific, and California in the eastern Pacific) to the Kuril Islands and Kamchatka, the Aleutian Islands, the Gulf of Alaska, and into the Bering Sea (Ohsumi 1966; Gosho et al. 1984; Rice 1986a). Females are rarely found north of lat. 45° N (Tomilin 1957; Berzin and Rovnin 1966; Ohsumi and Masaki 1977). Generally, only male sperm whales occur in the Bering Sea east of long. 180° during May-September (Ohsumi and Masaki 1977), usually in deep waters north of the Aleutian Islands eastward to Unimak Pass (Lowry et al. 1982). They usually appear off the Aleutian Islands during April and May and leave by September-November (Tomilin 1957; Berzin and Rovnin 1966; Ohsumi et al.

1977). In the Bering Sea, sperm whales are common along the shelf break between the Pribilof Islands and Cape Navarin, south of the Pribilof Islands, and north of Atka Island (Berzin 1971; Lowry et al. 1982).

There may be more than two stocks of sperm whales in the North Pacific. Geographic boundaries have not been defined and adult males of all North Pacific sperm whale stocks presumably intermingle in the Bering Sea (Ohsumi and Masaki 1977; Gosho et al. 1984). There are currently an estimated 198,100 adult sperm whales in the western North Pacific and 274,000 adult sperm whales in the eastern North Pacific (Braham 1984b); 172,400 of these animals are sexually mature males older than 11 years (Gosho et al. 1984). Ohsumi (1966) states that 40-60% of the sexually mature male sperm whales migrate to high latitudes in the North Pacific Ocean, including the Bering Sea and Aleutian Islands region. Based on these population estimates and data on distribution of sperm whales in the North Pacific from Ohsumi et al. (1977) and Wada (1980, 1981), I estimated that there are approximately 15,000 adult male sperm whales in the eastern Bering Sea and Aleutian Islands region during a 3-month period in summer (Table 3).

Male sperm whales become sexually mature when they reach 10-12 m in length; however, they do not become socially mature until they reach about 13-14 m (Lockyer 1976; Lowry et al. 1982; Gosho et al. 1984). Males become physically mature at about 16 m and grow to a maximum length of 20 m (Tomilin 1957; Berzin 1971), but males larger than 18 m are rare (Gosho et al. 1984). Based on the length-mass relationship in Lockyer (1976) and an average length of 15.5 m for adult males (Lowry et al. 1982;

Gosho et al. 1984), I estimated an average body mass of 36,000 kg for sperm whales in the Bering Sea (Table 3).

Sperm whales consume mainly medium-sized and large mesopelagic squid, but also octopus, other invertebrates, and fish (Tomilin 1957; Tarasevich 1968a; Berzin 1971). Fishes are generally less important than cephalopods in the diet of sperm whales; however, they may be locally important in the eastern Bering Sea along the shelf break (Berzin 1959, 1971; Okutani and Nemoto 1964; Lowry et al. 1982). The diet of sperm whales in areas near the Pribilof Islands is similar to that of sperm whales near the Aleutian Islands (Tarasevich 1968b). Fish eaten by sperm whales in the North Pacific include salmon, lanternfishes, lancetfish (Alepisauridae), Pacific cod, walleye pollock, saffron cod, rockfishes, sablefish, Atka mackerel, sculpins, lumpsuckers (Cyclopteridae), lamprey (Petromyzontidae), skates, and rattails (Macrouridae) (Tomilin 1957; Kawakami 1980; Rice 1986a). Pinnipeds have been reported as incidentally ingested food of sperm whales near Norway (Tomilin 1957). Based on data from Berzin (1959), Okutani and Nemoto (1964), Tarasevich (1968a), and Kawakami (1980), I estimated that the diet of sperm whales in the Bering Sea consists of 82% cephalopods (mostly squid) and 18% fish, with trace ingestion of euphausiids, shrimp, crabs, other invertebrates, and marine mammals (Table 4).

North Pacific Giant Bottlenose Whale

The North Pacific giant bottlenose whale is an oceanic species found only in the North Pacific Ocean from the coast of Japan in the west and southern California in the east, north to St. Matthew Island in the northeastern Bering Sea (Tomilin 1957; Rice

1986b), and possibly into the Chukchi Sea (Sleptsov 1961b). This species may be restricted to waters over the continental slope (Rice 1986b). The whales apparently arrive in the Bering Sea during April and May, and return south to the North Pacific during October and November (Tomilin 1957; Frost and Lowry 1981b).

Population estimates are not available for the North Pacific giant bottlenose whale. The species is uncommon, but not rare. Kasuya and Ohsumi (1984) presented subregional density data on the sightings of this species in the North Pacific. Based on the relative abundance of these whales per 3.43×10^4 km^2 in the North Pacific as discussed by Kasuya and Ohsumi (1984) and the approximate area of the entire Bering Sea (2.3×10^6 km^2; Lowry et al. 1982), I estimated that there are at least 500 bottlenose whales in the Bering Sea during a 5-month feeding period from mid-May to mid-October (Table 3).

Adult females average 10.1-12.8 m in length; the males are slightly smaller at 9.8-11.9 m (Tomilin 1957; Rice 1986b). The body mass of a female giant bottlenose whale about 10.8 m in length was 7.5 metric tons (t) (Tomilin 1957). I used 8,000 kg as an estimate of the average body mass of giant bottlenose whales (Table 3).

The food habits of the North Pacific giant bottlenose whale are largely uninvestigated, but appear to parallel those of the sperm whale (Frost and Lowry 1981b). They feed primarily on medium-sized squid, but occasionally consume fish, octopus, and crustaceans (Tomilin 1957; Lowry et al. 1982; Rice 1986b). Fish eaten by the North Pacific giant bottlenose whale include Pacific herring, bathypelagic fishes (e.g., lanternfishes), saffron cod, rockfishes, and rays (Order Rajiformes) (Tomilin 1957; Frost

and Lowry 1981b; Rice 1986b). I have estimated the diet of the North Pacific giant bottlenose whale in the Bering Sea to be 90% cephalopods and 10% fish (Table 4).

Bering Sea Beaked Whale

The Bering Sea beaked whale is rarely seen and its distribution has generally been inferred from stranded specimens. The infrequency of sightings of this species may be a result of their rarity, behavioral characteristics of the animals, or their similarity to other species (Laughlin et al. 1982); however, the Bering Sea beaked whale is the most frequently encountered ***Mesoplodon*** species (Rice 1986b). It is endemic to the cold-temperate waters of the North Pacific Ocean, the Sea of Japan, the Gulf of Alaska, and the deep waters of the southwest Bering Sea (Loughlin and Perez 1985). It has been found in the Bering Sea from the Aleutian Islands north to the Pribilof Islands and Bristol Bay, and west to the Commander Islands (Tomilin 1957; Rice 1986b).

There are no population estimates for these whales, although they likely occur in low numbers (Loughlin and Perez 1985). Loughlin et al. (1982) reported that 52 animals of the genus ***Mesoplodon,*** presumably Bering Sea beaked whales, were sighted during June and July 1979 in waters ranging in depth from 730 to 1,560 m over the slope of the central Aleutian Islands. I have estimated a minimum resident year-round population of 200 based on observations of these animals at sea, assuming that less than 25% of the population was sighted (Table 3).

No body-mass data for the Bering Sea beaked whale exist. Of the beaked whales, ***Mesoplodon*** is most closely related to ***Hyperoodon,*** and more distantly related to ***Ziphius*** and ***Berardius*** (Moore 1968). A 6.6 m specimen of the North Atlantic bottlenose whale,

Hyperoodon ampullatus, had a body mass of 2,200 kg (Nishiwaki 1972); a 6.6 m goosebeak whale ***(Ziphius cavirostris)*** had a body mass of 2,953 kg (Kenyon 1961); and a 10.8 m specimen of the North Pacific giant bottlenose whale had a body mass of 7,500 kg (Tomilin 1957). Beaked whales of the genus ***Mesoplodon*** generally average about 3.6-5.5 m in length (Rice 1986b). Based on the relative size of these four genera, I estimated 2,000 kg as the average body mass of the Bering Sea beaked whale (Table 3).

The primary food of the Bering Sea beaked whale is probably squid; they may also feed on some fish such as salmon (Tomilin 1957; Loughlin and Perez 1985). If the diet of the Bering Sea beaked whale is basically similar to that of the North Pacific giant bottlenose whale, then Bering Sea beaked whales should consume prey consisting of approximately 90% cephalopods and 10% fishes (Table 4).

Other Cetaceans

The blue whale ***(Balaenoptera*** musculus), sei whale ***(Balaenoptera borealis),*** right whale ***(Balaena glacialis),*** Pacific white-sided dolphin ***(Lagenorhynchs obliquidens),*** narwhal ***(Monodon monoceros),*** and goosebeak whale may infrequently be found in the Bering Sea. Because these species are rare in this region, I have not included them in this discussion.

ENERGY VALUE OF DIET

The average energy value of the diet (Table 5) of each marine mammal species discussed in this paper was calculated based on the estimated energy equivalents of important prey species (Appendix Table 1) and the diet composition for each species in

Table 5.--Estimated energy value of the total diet of marine mammal species in the eastern Bering Sea and Aleutian Islands region.

Species	Estimated energy value of total diet (kcal/g)[a]
Pinnipeds	
Northern fur seal	1.3 S 1.4 W
Northern sea lion	1.3
Harbor seal	1.4
Spotted seal	1.3 S 1.4 W
Ringed seal	1.2
Ribbon seal	1.2
Bearded seal	1.2
Walrus	1.3
Cetaceans	
Gray whale	1.0
Minke whale	1.7 S 1.8 W
Fin whale	2.0
Humpback whale	1.8
Bowhead whale	1.8
Killer whale	1.8
Harbor porpoise	1.7 S 1.8 W
Dall's porpoise	1.3 S 1.4 W
Belukha whale	1.3
Sperm whale	1.2

Table 5.--Continued.

Species	Estimated energy value of total diet (kcal/g)[a]
North Pacific giant bottlenose whale	1.2
Bering Sea beaked whale	1.2
Mustelids	
Sea otter	0.9

[a] Based on diet composition data in Tables 2 and 4, except for sea otter (see text), and estimates of the caloric equivalents of their prey species in Appendix Table 1.

Tables 2 and 4. The average of the caloric data for the marine mammal species listed in Appendix Table 1 was used as an approximation of the energy value of marine mammals in the diet of killer whales.

The content of fat in the flesh and other parts of the body of some fish species (e.g., Pacific herring, capelin, Atka mackerel, rockfishes, flatfishes) changes significantly during the year between spawning (summer) and foraging (winter) periods (Kizevetter et al. 1965; Kizevetter 1971; Jangaard 1974; Bigg et al. 1978). Fat content also varies by age, body mass, or migration of the fish (e.g., salmon, sablefish) (Kizevetter 1971). For many other fishes (e.g., walleye pollock, other gadids, sculpins), the fat content of the body does not vary appreciably during the year (Kizevetter 1971). Seasonal values were given where a significant portion of the diet consisted of either Pacific herring or capelin, the only two species for which data on seasonal averages in energy content were available.

The average energy value of a diet (based on the comparative caloric content values of prey species in Appendix Table 1 and the relative importance of these prey species in the diets listed in Tables 2 and 4) was estimated to range from 1.2 to 1.4 kcal/g for pinniped species (Table 5) and 1.0 to 2.0 kcal/g for cetacean species (Table 5). Until further data become available, these average diet values and the average values for population abundance and body mass discussed earlier may be used as input parameters in future studies involving conceptual analyses (e.g., McAlister and Perez 1977) or ecosystem models (e.g., Laevastu and Larkins 1971) to assess the trophodynamic relationships of marine mammals and fish in the eastern Bering Sea.

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APPENDIX

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Appendix Table I.--Estimated comparative energy values (wet mass) of various marine mammal prey species occurring in the Bering Sea.

Prey species	Energy value (kcal/g)[a]	Analysis and tissue[b]	Data sources[c]	Estimated comparative energy value (kcal/g)[d, e]
Fishes				
Capelin (*Mallotus villosus*)	1.81	P, whole	1	1.57 S 2.05 W
Arctic cod (*Boreogadus saida*)	1.15	P, whole	2	1.15
Pacific cod (*Gadus macrocephalus*)	1.04	R, whole	2	1.04
Saffron cod (*Eleginus gracilis*)	1.14	R, whole	2	1.14
Eelpouts (Zoarcidae)	0.91	R, whole	2	0.91
Flatfishes (Bothidae and Pleuronectidae)	1.52[f]	R, whole	2, 3	1.52
Greenling (*Hexagrammos* spp.)	1.73	R, whole	2	1.73
Pacific herring (*Clupea harengus pallasi*)	2.17	P, whole	4, 5	2.05 S 2.29 W
Lampreys (Petromyzontidae)	2.84	P, R, whole	2, 6	2.84
Lanternfishes (Myctophidae)	1.63	P, whole	7	1.63
Lumpfishes (Cyclopteridae)	0.98	P, muscle	6	1.08
Atka mackerel (*Pleurogrammus monopterygius*)	1.86	R, whole	2	1.86
Walleye pollock (*Theragra chalcogramma*)	1.25	C, P, R, whole	2, 3, 6, 8, 9	1.25
Rockfish (Scorpaenidae)	1.75	P, R, whole	2, 3, 10	1.75
Sablefish (*Anoplopoma fimbria*)	2.24	R, whole	2, 3	2.24
Salmon (Salmonidae)	1.61[g]	P, whole	2, 6	1.61
Sand lance (*Ammodytes* spp.)	1.49	P, muscle	2, 6	1.64
Sculpins (Cottidae)	1.33	C, whole	11	1.33
Dogfish shark (Squalidae)	1.75	P, muscle	2, 6	1.93
Skate (Rajidae)	1.26	P, muscle	2, 6	1.39
Rainbow smelt (*Osmerus mordax*)	1.28	P, whole	6, 12	1.28
Deep-sea smelts (Bathylagidae)	0.77	P, whole	7	0.77

Appendix Table 1.--Continued.

Prey species	Energy value (kcal/g)[a]	Analysis and tissue[b]	Data sources[c]	Estimated comparative energy value (kcal/g)[d, e]
Invertebrates				
Squid	1.14	C, P, whole	6, 8, 13, 14, 15	1.14
Octopus	1.03	P, muscle	6	1.03
Pteropods	0.46	C, whole	16	0.46
Snails (Gastropoda)	1.37	P, whole	6	1.37
Clams and mussels (Pelecypoda)	0.34	P, whole	17	1.37[h]
Crab	1.48	P, muscle	6	1.48
Shrimp	1.11	C, whole	18	1.11
Euphausiids	1.98	C, whole	16	1.98
Amphipods	0.99[i]	C, whole	16	0.99
Copepods	2.52	C, whole	16	2.52
Isopods	0.37	C, whole	16	0.37
Mysids	0.99	C, whole	18	0.99
Polychaetes	0.72	C, whole	17	0.72
Sea cucumbers	0.54	P, muscle	6	0.54
Sea urchins	0.51[j]	C, whole	19	0.51
Mammals				
Northern fur seal	2.50	P, whole	20	2.50
Northern sea lion	1.54	P, muscle	20	2.31
Ringed seal	3.55	C, whole[k]	21	3.55
Porpoise (unspecified)	1.89	P, muscle	20	4.73
North Pacific giant bottlenose whale	1.64	P, muscle	22	4.10
Whale (unspecified)	2.21	P, muscle	6	5.53

[a] The values given in column 1 represent the average of range values obtained from the data in the cited references. Values based on proximate composition data, including estimates calculated from relative proportions of total body mass represented by different body parts, were calculated with the following energy factors (representing heats of combustion) derived from Watt and Merrill (1963): 9.50, 5.65, and 4.20 kcal/g respectively for fat, protein, and carbohydrate.

Appendix Table l.--Continued.

[b] Analysis: C = bomb calorimetry combustion value; P = proximate composition data averaged (to the extent possible) over the seasonal range of values for the percentage of protein, fat and carbohydrate in the tissue sample; R = value estimated from data on the relative proportions of body parts and their respective energy value based on proximate composition data. Tissue: muscle = raw flesh material only; whole = raw material from entire specimen. Data for the Bering Sea and North Pacific were used where possible; otherwise, data from other regions of the world were used.

[c] Data sources: (1) Jangaard 1974; (2) Kizevetter 1971; (3) Kizevetter et al. 1965; (4) McBride et al. 1959; (5) Bigg et al. 1978; (6) Sidwell 1981; (7) Childress and Nygaard 1973; (8) Miller 1978; (9) Ashwell-Erickson and Elsner 1981; (10) Thurston 1961; (11) Krzynowek and Murphy 1987; (12) Geraci 1975; (13) Croxall and Prince 1982; (14) Vlieg 1984; (15) Perez and Bigg 1986; (16) Percy and Fife 1980; (17) Fay et al. 1977; (18) Lowry et al. 1980a; (19) Costa 1978; (20) Stansby 1976; (21) Stirling and McEwan 1975; (22) Tomilin 1957.

[d] Where data were not available for whole specimens, the comparative energy value of edible whole fish was estimated at 1.1 times the muscle tissue value; this correction factor was based on data for capelii, herring, walleye pollock, and smelt in Sidwell (1981). For mammals, the comparative energy value of whole specimens was estimated at 1.5 times the muscle tissue value for pinnipeds and 2.5 times the muscle tissue value for cetaceans; these correction factors ***were*** based on data in Stansby (1976) and Tomilin (1957). No correction was made for octopus, crab or sea cucumbers.

[e] Data were not available to make estimates of energy value by season except for capelin and Pacific herring.

[f] Weighted by the relative biomass of flatfish species in the Bering Sea based on data in Bakkala and Balsiger (1987), Sample and Wolotira (1985), Walters et al. (1988), and Long et al. (1988). Greenland turbot, ***Reinhardtius hippoglossoides;*** Pacific halibut, ***Hippoglossus stenolepis,*** and arrowtooth flounder, ***Atheresthes stomias,*** were estimated, as a group, to have an average energy value of 1.96 kcal/g; other flatfishes ***(e.g.,*** yellowfin sole, ***Limanda aspera;*** Alaska plaice, ***Pleuronectes quadrituberculatus;*** flathead sole, ***Hippoglossoides elassodon;*** rock sole, ***Lepidopsetta bilineata)*** were estimated, as a group, to have an average energy value of 1.47 kcal/g. Diet information for marine mammals in the Bering Sea are insufficient to identify relative importance of specific flatfish species as prey.

[g] Based on the average of data from whole chum salmon, ***Oncorhynchus keta,*** and sockeye salmon, O. ***nerka.***

[h] The edible portion of bivalves, excluding the shell, was estimated at 4 times the whole specimen energy value based on data in Fay et al. (1977).

[i] Based on the average of values for hyperiid and gammarid amphipods.

[j] Based ***on values*** for ***Strongylocentrotus*** spp.

[k] Includes blubber.

S = May-October
W = November-April.

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