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ABSTRACT

One important aspect of the management of commercial fisheries in an ecosystem context involves understanding the diet and consumption rates of fish species by their natural predators. Such knowledge allows for comparison of commercial fish catches with consumption through predation by species groups such as marine mammals. For the Bering Sea, the limited data available only allows a preliminary assessment of food consumption by marine mammals. Estimates of food consumption for this study were based on marine mammal population and diet data reported in the literature. Where direct consumption data were not available, consumption was estimated from population data and energy requirements. Food consumption by marine mammals (except walrus) in the eastern Bering Sea and Aleutian Islands region was estimated at 3.21×10^6 metric tons (t) per year. Fish comprised 42% of food consumed, an estimated 1.34×10^6 t of fish eaten per year. Pinnipeds ate 65% of the estimated annual consumption of fish. Marine mammals ate an estimated 3.2% of the standing stock of all fish species occurring in the eastern Bering Sea and Aleutian Islands region. Accounting for variations in population size over time of marine mammals in the Bering Sea, the estimated historical consumption of fish by all marine mammals was 0.44×10^6 t to 3.04×10^6 t, which represents 1.0% to 7.3% of the standing stock of all fish species. Commercial groundfish fisheries during the period 1988-90 caught about 7.1% (1.79×10^6 t) of the stock of commercially important groundfish species each year, whereas, at present, marine mammals annually consume an estimated 2.0% (0.45×10^6 t) of the standing stock of those fish species. This is 75% lower than the average commercial catch.

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INTRODUCTION

Fish stocks and marine mammals are recognized as interacting components of the marine ecosystem. For the commercially valuable species, knowledge about the degree of competition between fisheries and marine mammal predators is of vital importance. This is of particular importance in view of the potential impacts of fisheries on marine mammal populations, and vice versa, through reduction of their food supply. The literature on marine mammal-fish relationships indicate that fish are the dominant prey of many of the most abundant marine mammal species in the Bering Sea (Perez 1990). The present study uses available data on marine mammal diets and feeding rates to estimate food consumption by marine mammals. The biomass of fish consumed annually by marine mammals in the Eastern Bering Sea also is estimated for comparison with commercial fish catches.

The Bering Sea (Fig. 1) has an approximate surface area of 2.3 x 10^6 km^2, of which 44% is continental shelf (depth <200 m) (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 ice-free. During winter and early spring, part of the shelf is covered with ice, sometimes to the continental slope in the southeastern Bering Sea. During the year, this seasonal movement of sea ice significantly affects the distribution and abundance of marine mammals in the Bering Sea (Tikhomirov 1964; Burns 1970; Fay 1974). The study region in this report is the Eastern Bering Sea, including the shelf area surrounding the Aleutian Islands (Fig. 1).

Twenty-eight marine mammal species are found in the Eastern Bering Sea, of which 21 species (8 pinnipeds, 12 cetaceans, and 1 mustelid; Table 1) are abundant and usual constituents of the Bering Sea ecosystem (Lowry et al. 1982; Lowry and Frost 1985; Perez and Loughlin 1986). Only five cetacean species (gray whale, *Eschrichtius robustus;* minke whale, ***Balaenoptera acutorostrata;*** Dall's porpoise, *Phocoenoides dalli;* belukha whale, *Delphinapterus*

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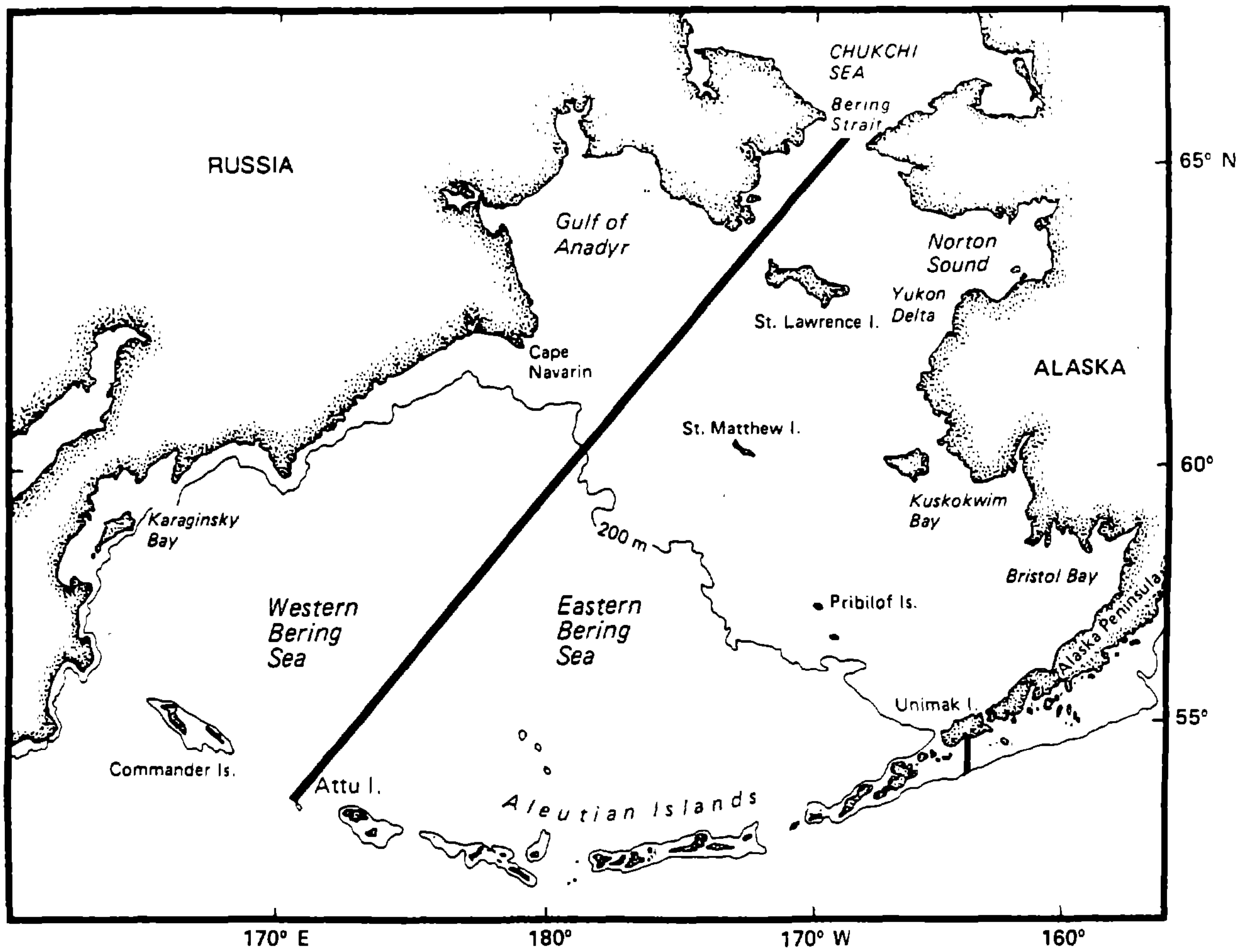

Figure 1 .--The Bering Sea region. A line (from the Bering Strait to the North Pacific Ocean) separates the western and eastern Bering Sea areas, and a shorter line (at Unimak Pass, 164° W long,) denotes the eastern boundary of the Aleutian Islands area in the Gulf of Alaska. The Aleutian Islands shelf area (depth <200 m) is the southernmost boundary of the region. These boundaries were chosen arbitrarily to include all of the Aleutian Islands and U.S. territorial waters, but exclude most international waters. The 200 m depth contour is indicated.

leucas; and sperm whale, *Physeter macrocephalus)* occur in the Bering Sea in large numbers (more than 1,000 animals per species; Table 1). Additional important cetacean species in the Bering Sea are fin whale, *Balaenoptera physalus;* humpback whale, *Megaptera novaeangliae;* bowhead whale, *Balaena mysticetus;* killer whale, *Orcinus orca;* harbor porpoise, *Phocoena phocoena;* giant bottlenose whale, *Berardius bairdii;* and Stejneger's beaked whale, *Mesoplodon stejnegeri* (Table 1). Other cetaceans that occur infrequently in the Eastern Bering Sea have not been included in this study.

The quantity and quality of data available on distribution, diet, abundance, and biomass of marine mammals in the Bering Sea vary widely (Loughlin and Jones 1984; Lowry 1984). Estimates of abundance are available for most pinniped species (Lowry et al. 1982), but not for most cetaceans. In addition, data are not current for many species (e.g., spotted seals, *Phoca largha;* ringed seals, *Phoca hispida;* ribbon seals, *Phoca fasciata;* bearded seals, *Erignathus barbatus)* in the Bering Sea. Apart from northern fur seal *(Callorhinus ursinus)* data, diet and prey availability information, especially by season, are incomplete. However, in view of the importance of the issue involved in fishery management and marine mammal predation it is important to use the available data.

Nearly all studies on food consumption by marine mammals in the Bering Sea have focused on a single species. However, Laevastu and Larkins (1981) estimated prey consumption by all marine mammals in the Eastern Bering Sea using the PROBUB and DYNUMES ecosystem models. Lowry et al. (1982) reviewed the literature through 1982 on prey consumption by marine mammals in the Eastern Bering Sea.

Lowry (1982, 1984) Lowry et al. (1982) Kajimura and Fowler (1984) Loughlin and Jones (1984) Perez and Loughlin (1986), and Lowry et al. (1988) have discussed the relationships of marine mammals to their fish prey and commercial fisheries in the Bering Sea. Fowler (1982), Swartzman and Haar (1983), and Livingston (1989) specifically addressed interactions of northern fur seals. Loughlin and Merrick (1988) and Alverson (1992) have discussed the issue of impacts of commercial fisheries on the northern sea lion *(Eumetopias*

Table 1 .--Estimated total population in the Alaska area and average pelagic abundance of marine mammal species in the Eastern Bering Sea by semiannual period (modified from Perez 1990).

Species	Estimated total population in the Alaska area [a]		Estimated average pelagic abundance in the Eastern Bering Sea [b] May-Oct.	Nov.-April	Data sources [c]
Pinnipeds:					
Otariids:					
Northern fur seal (*Callorhinus ursinus*)	871,000		399,500	40,000	1, 2, 3, 4, 5
Northern sea lion (*Eumetopias jubatus*)	>39,396		32,000	32,000	5, 6, 7
Phocids:					
Harbor seal (*Phoca vitulina richardii*)	<150,000		45,000	45,000	5, 8, 9, 10
Spotted seal (*Phoca largha*)	>200,000		14,000	140,000	5, 11, 12
Ringed seal (*Phoca hispida*)	1-1.5 million		1,000	600,000	11, 13
Ribbon seal (*Phoca fasciata*)	100,000-110,000		66,000	66,000	11, 14
Bearded seal (*Erignathus barbatus*)	>300,000		5,000	150,000	11, 15
Odobenids:					
Walrus (*Odobenus rosmarus*)	200,000		15,000	150,000	11, 16, 17, 18
Cetaceans:					
Mysticetes:					
Gray whale (*Eschrichtius robustus*)	19,737-22,489	d	5,000	-	5, 19, 20
Minke whale (*Balaenoptera acutorostrata*)	>21,000	d	3,000	800	21, 22, 23
Fin whale (*Balaenoptera physalus*)	14,620-18,630	d	1,000	-	21, 22, 24, 25
Humpback whale (*Megaptera novaeangliae*)	1,398-2,040	d	150	-	5, 21, 22, 25
Bowhead whale (*Balaena mysticetus*)	6,400-9,200	d	200	1600	5, 26, 27
Odontocetes:					
Killer whale (*Orcinus orca*)	N.E.		700	300	5, 28
Harbor porpoise (*Phocoena phocoena*)	N.E.		1,000	500	5, 29
Dall's porpoise (*Phocoenoides dalli*)	741,000	d	85,500	42,700	30, 31
Belukha whale (*Delphinapterus leucas*)	25,000	d	3,500	18,000	32, 33
Sperm whale (*Physeter macrocephalus*)	274,000	d	15,000	-	21, 22, 24, 34
North Pacific giant bottlenose whale (*Berardius bairdii*)	N.E.		500	-	35
Stejneger's beaked whale (*Mesoplodon stejnegeri*)	N.E.		200	200	36
Mustelids:					
Sea otter (*Enhydra lutris*)	66,800-90,900	e	79,000	79,000	37

[a] This column is for reference purposes only to indicate the current status of the population size. These estimates include animals not present in the eastern Berring Sea study area as delined in Figure I, N.E. = no estimate.

Table 1 .--Continued

[b] Estimated pelagic abundance refers IO the average number of animals feeding at sea during each semiannual period, accounting for seasonal migration out of the eastern Bering Sea region and excluding animals for time on land or ice fasting for several months.

[c] Details concerning the estimates in this table were discussed by Perez (1990). Data sources: (1) Kajimura et al. 1979; (2) Kajimura et al. 1980; (3) Lander 1980; (4) North Pacific Fur Seal Commission 1984; (5) Low 1991; (6) Merrick et al. 1987; (7) Loughlin et al. 1990; (8) Everitt and Braham 1980; (9) Fiscus et al. 1981; (10) Pitcher 1985; (11) Braham et al. 1984; (12) Lowry 1985a; (13) Frost 1985; (14) Lowry 1985b; (15) Nelson et al. 1985; (16) Fay et al. 1989; (17) Gilbert 1989; (18) Fay and Kelly(l990); (19) Berzin 1984; (20) Rugh 1984; (21) Wada 1980; (22) Wada 1981; (23) Kasamatsu and Hata 1985; (24) Braham 1984a; (25) Berzin and Rovnin 1966; (26) International Whaling Commission 1988; (27) Braham 1984b; (28) Brueggeman et al. 1984; (29) Jones 1984; (30) Bouchet and Haines 1985; (31) Tumock 1987; (32) Lowry 1985c; (33) Seaman et al, 1985; (34) Ohsumi et al. 1977; (35) Kasuya and Ohsumi 1984; (36) Loughlin et al. 1982; (37) Calkins and Schneider 1985.

[d] Estimate for the entire North Pacific region; data for only the Alaska area are not available.

[e] Alaska Peninsula, Eastern Bering Sea, and Aleutian Islands only.

jubatus) in the Bering Sea and North Pacific Ocean. Lowry et al. (1988) have suggested that removal of marine mammal prey resources by commercial fisheries may affect the abundance of marine mammal populations.

The purpose of the present study was to estimate the total amount of food consumed by all marine mammal populations in the Bering Sea. The range of food consumption by marine mammals based on historical marine mammal population sizes also was estimated. In particular, the estimated total consumption of fish by marine mammals was compared with the current and potential commercial catch.

Finally, estimated consumption of fish, especially commercially important species of fish, by marine mammals in the eastern Bering Sea and Aleutian Islands region was compared with estimates of biomass of fish stocks based on catch statistics and the ecosystem simulation models of Laevastu and Larkins (1981). Estimates of food consumption for walruses (Odobenus *rosmarus)* were not reported because they feed nearly exclusively on benthic invertebrates (e.g., mollusks and echinoderms) which consist of shell or other exoskeleton that must be considered when estimating total biomass consumption (Fay et al. 1977).

METHODS

Total food consumption (F) for marine mammal species in the Eastern Bering Sea ecosystem (study area defined in Fig. 1) was based on the following expression:

$$F = (E \times N \times T) / K ,$$

where *E* is the estimated daily energy requirements (kcal/d) per average biomass of an individual, N is the number of individuals in the population, *T* is the time period in days, and K is the estimated energy density (kcal/g) of the diet. Individual daily energy requirements for active (i.e., animals in states of behavior such as swimming, feeding, etc.) marine mammals were calculated using body mass/energy consumption relationships for each species group (Table 2; Perez et al. 1990).

Table 2.--Estimated coefficients (a) for the feeding rates of marine mammals approximated to the allometric relationship, $E=aM^{0.75}$, where E is energy consumption (kcal/d) and M is body mass (kg).

Taxonomic group	Estimated coefficient *a*	Estimation method and references
Otariids	372	Geometric mean regression line for data cited by Perez et al. (1990)
Phocids	200	Average of values from 1) the feeding rate equation coefficients (weighted by sample size) in Innes et al. (1987) using average body mass of the species in this study, and 2) data in Perez et al. (1990)
Mysticetes	192	Average of oxygen consumption data from Wahrenbrock et al. (1974) and Sumich (1983)
Odontocetes	**317**	Geometric mean regression line for data cited by Perez et al. (1990)
Sea otter	520	Based on data in Costa (1978, 1982)

Perez (1990) lists the sources used to estimate-average body mass in this study. Length-mass relationships were used to estimate average body mass for most cetacean species (Perez 1990). For pinnipeds, estimates of average body mass during summer and winter were based on the average age/sex distribution in the region by season. For northern fur seals, we included an estimated amount of increased food consumption due to the energy requirements of lactation for females, The average body mass of lactating females has been estimated at 35.3 kg and the increased rate of ingestion was estimated at 1.6 times the feeding rate for nonlactating females (Perez and Mooney 1986). Lactation requirements were calculated for July-October (122 days). For all other species, lactation was accounted for by including pup mass in the average body mass.

Perez (1990) provides estimates for the average pelagic abundance of marine mammals in the Eastern Bering Sea (Table 1). These estimates refer to the average number of animals feeding at sea during each semiannual period, accounting for the seasonal migration of animals out of the eastern Bering Sea region and excluding animals for the time spent on land or ice fasting for several months (when they feed later in the year outside the Eastern Bering Sea) using data in Braham et al. (1984). For some species, it was necessary to estimate the pelagic abundance of the Bering Sea population using published data of seasonal distribution and observed counts of these species in adjacent areas of the North Pacific Ocean.

Total annual food consumption by all marine mammals was calculated as the sum of consumption for two semiannual (182 days) periods, May-October (summer) and November-April (winter), by each marine mammal species. However, based on published data regarding migration, four species were estimated to have shorter semiannual feeding periods in the Eastern Bering Sea: 1) humpback whales were estimated to feed in the Bering Sea only during 5 months (152 days) from June to October, 2) bowhead whales were estimated to feed in the Bering Sea only during 30 days of each semiannual period in this region, 3) sperm whales were estimated to feed in the Bering Sea only during a 3-month period (92 days) in summer, and

4) North Pacific giant bottlenose whales were estimated to feed in the Bering Sea only during a 5-month period (152 days) from mid-May to mid-October.

The food consumption estimates were based on data averaged over the year. Seasonal or interannual differences in diet have not been considered (data were not available for this purpose). Perez (1990) lists the sources used to estimate the energy value of the diet and average diet composition for each marine mammal species:

Estimates for the percentage of groundfish in the total diet were based on known fish species eaten and the total percentage of fish in the diet (Perez 1990). For taxonomic groups of marine mammals, these diet estimates were weighted by the relative abundance, energy requirements, and total food consumption of the individual marine mammal species. Groundfish species in the Bering Sea region consist of the following commercially important fishes: walleye pollock, *Theragra chalcogramma;* Pacific cod, *Gadus macrocephalus;* Pacific ocean perch, *Sebastes alutus* and other rockfishes; sablefish, *Anoplopoma fimbria;* Atka mackerel, *Pleurogrammus monopterygius;* and yellowfin sole, *Pleuronectes asper,* turbots, and other flatfishes of the family Pleuronectidae (Bakkala 1988; Low 1991). Other gadoid species were not included.

Lavigne et al. (I 986) suggest that the daily maintenance requirements of seals are about two times the basal metabolic rate. Therefore, lower level estimates of the food consumption rate range were calculated at twice the basal metabolic rate of Kleiber (1961), $70M^{0.75}$. However, lower level estimates for the sea otter *(Enhydra lutris)* were calculated at twice their observed basal metabolic rate, $233M^{0.75}$, based on the arguments discussed by Costa (1982).

Estimates of the minimum population size were based on actual count data when available (for northern fur seals, northern sea lions, harbor seals *(Phoca vitulina richardii),* sea otters, gray whales, Dall's porpoises, and belukha whales); otherwise they were arbitrarily calculated as one-half the current estimate of the population size. An upper population range level was based on maximum estimates from actual count data for ringed seals, sea otters, and gray whales (species in the Bering Sea area estimated to be at or near carrying capacity; Calkins and Schneider

1985; Frost 1985; Low 1991). However, many marine mammal populations in the Bering Sea are below historically high abundance levels (e.g., northern fur seal, North Pacific Fur Seal Commission 1984; northern sea lion, Merrick et al. 1987; harbor seal, Low 1991). In these cases, the upper abundance estimates were based on 1) former population sizes during the 1950s for northern fur seals (Briggs and Fowler 1984) and northern sea lions (for the latter, four times the current population size based on population decline data in Met-rick et al. 1987 and Laughlin et al. 1990); 2) population estimates during the 1970s for harbor seals (Pitcher 1985); and 3) estimated precommercial whaling population sizes for fin whales, humpback whales, bowhead whales, and sperm whales (Braham *1984a).* For other species the upper abundance level was arbitrarily calculated as 150% of the current population estimate. Current seasonal distribution patterns, population age/sex structures, and diets of marine mammals in the Bering Sea were used to determine estimates of lower and upper population size and food consumption for all species.

RESULTS

Currently (early 1990s), pinnipeds (excluding walruses) consume an estimated 1.34×10^6 t of food (all prey species) annually in the Eastern Bering Sea (Table 3). Cetaceans consume an estimated 1.71×10^6 t of food (all prey species) annually (Table 3). Consumption by the sea otter population is estimated to be 0.16×10^6 t of prey per year (Table 3). Each year, marine mammals collectively consume an estimated 3.21×10^6 t of food in the eastern Bering Sea region.

The lower and upper estimates of total food consumption by all marine mammals (except walruses) in the eastern Bering Sea and Aleutian Islands region were 1.08×10^6 t and 6.79×10^6 t, respectively. Fish represented 42% (range 41-45%) of the annual food consumption (Table 4).

Presently, marine mammals in the Eastern Bering Sea consume an estimated 1.34×10^6 t of fish per year (Table 3). Pinnipeds account for 65% of the annual consumption of fish

Table 3.--Estimates of average body mass, daily energy requirements per animal, energy value of diet, percent fish in the diet, and annual food consumption by population for marine mammal species in the Eastern Bering Sea.

Species	Estimated average body mass (kg) [a]	Estimated daily energy requirements (10^3 kcal)	Estimated energy value of diet (kcal/g) [b]	Estimated percent fish in diet [a]	Estimated annual food consumption by population: Total (10^3 t)	Fish (10^3 t)
Pinnipeds:						
Northern fur seal	43	6.2	1.3 summer 1.4 winter	67	432.4	289.7
Northern sea lion	212	20.7	1.3	76	185.2	140.7
Harbor seal	49	3.7	1.4	75	43.3	32.5
Spotted seal	62	4.4	1.3 summer 1.4 winter	96	89.1	85.5
Ringed seal	34	2.8	1.2	85	256.7	218.2
Ribbon seal	46	3.5	1.2	54	70.7	38.2
Bearded seal	241	12.2	1.3	23	265.2	61.0
Subtotal (pinnipeds)	-	-	-	-	1,342.6	865.8
Cetaceans:						
Gray whale	18,000	298.4	1.0	Trace	271.5	Trace
Minke whale	6,000	130.9	1.7 summer 1.8 winter	60	52.6	31.6
Fin whale	49,000	632.3	2.0	16	57.5	9.2
Humpback whale	30,000	437.7	1.8	29	5.5	1.6
Bowhead whale	46,000	603.1	1.8	Trace	18.1	Trace
Killer whale	4,000	159.4	1.8	65	16.1	10.5
Harbor porpoise	50	6.0	1.6 summer 1.7 winter	85	1.0	0.8
Dall's porpoise	95	9.6	1.3 summer 1.4 winter	50	169.0	84.5
Belukha whale	800	47.7	1.3	93	143.3	133.5
Sperm whale	36,000	828.5	1.2	18	952.8	171.5
North Pacific giant bottlenose whale	8,000	268.2	1.2	10	17.0	1.7
Stejneger's beaked whale	2,000	94.8	1.2	10	5.8	0.6
Subtotal (cetaceans)	-	-	-	-	1,710.4	445.5
Mustelids:						
Sea otter	20	4.9	0.9	18	157.1	28.3
Total (all species)	-	-	-	-	3,210.1	1,339.6

Table 3.--Continued.

[a] Based on references cited by Perez (I 990).

[b] Based on diet composition data for marine mammal species in the Bering Sea and estimates of the caloric equivalents of their prey species discussed by Perez (1990).

Table 4.-Estimated average pelagic abundance of feeding marine mammals and their estimated total annual consumption of fish in the Eastern Bering Sea.

Marine mammal species group	Estimated average pelagic abundance of feeding animals				Estimated annual fish consumption (10^3t)	
	May-October		November-April			
	current	Range	Current	Range	current	Range
Northern fur seal	399,500	340,000 - 998,800	40,000	34,000 - 99,900	290	93 - 833
Northern sea lion	32,000	23,000 - 128,000	32,000	23,000 - 128,000	141	38 - 639
Phocids	131,000	73,000 - 245,000	1,001,000	508,000 - 1,549,000	436	161 - 795
Mysticetes	9,350	5,675 - 24,500	2,400	1,200 - 5,200	42	15 - 105
Odontocetes	106,400	77,200 - 154,150	61,700	47,250 - 92,550	403	112 - 624
Sea otter	79,000	66,800 - 90,900	79,000	66,800 - 90,900	28	23 - 40
Total	757,250	585,675 - 1,641,350	1,216,100	680,250 - 1,965,550	1,340	442 - 3,036

(Table 3). As a group, the otariids (northern fur seals and northern sea lions) have been the major fish consumers among the pinnipeds in **Alaska** (McAlister and Perez 1977). At the present time, they consume an estimated 0.43 x 10^6 t of fish per year. However, northern fur seal and northern sea lion populations in the Bering Sea have declined significantly in recent decades (Merrick et al. 1987; York 1987; Loughlin et al. 1990), and estimated annual consumption has likewise declined. By comparison, the phocids, with their larger populations, currently consume collectively an estimated 0.44 x 10^6 t of fish per year (Table 4). Cetaceans accounted for about 33% of the estimated annual fish consumption by marine mammals of the eastern Bering Sea region; sea otters accounted for the remaining 2% (Table 3). The lower and upper estimates of fish consumption by all marine mammals in **the** eastern Bering Sea and Aleutian Islands region were 0.44 x 10^6 t and 3.04 x 10^6 t, respectively (Table 4).

DISCUSSION

Accuracy and Reliability of Results

Reliable feeding or energy data for active large cetaceans are very limited. Estimates of energy use were given for gray whales by Sumich (1983) (on the basis of observed respiration) and Wahrenbrock et al. (1974) (feeding studies and observed respiration). There is a larger uncertainty about food consumption rates in baleen whales than in smaller cetaceans. Except for minke whales, the impact of this uncertainty on the estimates of fish consumption will probably not be great because baleen whales do not generally prey on fish, or fish accounts for less than 30% of the diet.

Energy consumption was estimated to be uniform throughout the year. Those marine mammal species that fast during winter will consume at a higher rate during summer to meet average annual food consumption rates. No corrections in feeding rates were made to account for increased seasonal energy demands due to fasting periods

Feeding rates of captive animals may not correctly estimate feeding rates of free-ranging animals. Commonly cited reasons are reduced activity levels for larger animals because of aquarium size and differences in food between aquarium feeding and wild feeding. Whereas limitations on activity may generally reduce food consumption, there is a balancing tendency to overfeed captive marine mammals (Innes et al. 1987). Some animals in captivity are often obese indicating overfeeding and inactivity.

The accuracy of the results reported here is not adequate for purposes of constructing cause-effect models. However, the results provide a basis for estimating fish consumption by various marine mammal groups.

Marine mammal-fish interactions have been studied for many years, and many of the elements of the interactions are known, but the difficulties of obtaining adequate field observations, imposed by the natural variability of the ecosystem, make it unlikely that direct observations with a high accuracy will be available in the foreseeable future. Indirect methods of estimating food consumption will continue to be used out of necessity.

Use of Mean Body Mass and Pooled Ages

Other than for not-them fur seals, no attempt has been made to quantify consumption by age, especially by juveniles, or for stressful periods such as lactation or pregnancy. In this respect the estimates are probably conservative.

Juvenile marine mammals feed at a higher rate per body mass than do adult marine mammals. Innes et al. (1987) reported that juvenile consumption rates for otariids and phocids is 1.4 to 1.8 times the rates of adult seals.

The feeding rates in Table 2 are nonlinear with respect to body mass; use of a mean value for the biomass of a given species will slightly overestimate the energy consumption. The inclusion in the biomass, without correction, ofjuveniles which consume at a higher rate than adults will result in an energy consumption value (determined from the feeding rates in Table 2) which slightly underestimates the actual energy consumption, Since these two errors are largely compensating and since the net error is small in comparison with uncertainties in both the population size and diet data, no correction has been made.

Effects of Energy Value of Diet

Estimated energy values of the average diet of each marine mammal species (Table 3) do not take into account intraannual changes in the energy content of prey species (except for Pacific herring, *Clupea pallasi,* and capelin, *Mallotus villosus)* because data were not available to make seasonal averages of estimated energy content. Fat content of some fish species (e.g., Pacific herring, capelin) changes significantly between spawning (summer) and foraging (winter) periods. For many other fishes (e.g., walleye pollock), fat content does not vary appreciably during the year (Kizevetter 1971).

Food consumption estimates based on average daily energy requirements for marine mammals (e.g., sea otter, walrus) that feed extensively on benthic invertebrates may underestimate the true biomass of mollusks and echinoderms which are preyed on by these mammals. This is because the mass of shell or other exoskeleton of these invertebrates cannot be estimated by this method. Only consumption on fish stocks was considered in this paper. The magnitude of predation on standing stocks of invertebrates eaten by marine mammals was not assessed.

Consumption Estimates from Other Studies

Our estimates of food consumption for northern fur seals are about 20% lower than values reported by McAlister and Perez (1977) (Table 5). This difference is largely due to a decline in the population of northern fur seals during the 1970s and 1980s and also reflects a difference in feeding rates used between the two studies. The data in Table 5 for northern fur seals from Perez and Mooney (1986) is for 3 months only, and only includes adult females. Their estimated consumption value is consistent with the data reported here. It should be noted, however, that the studies reported in Table 5 refer to Bering Sea regions defined by each particular investigation. They are similar, but not identical to the eastern Bering Sea area as defined here (Fig. 1).

The estimates of food consumption reported by Ashwell-Erickson and Elsner (1981) for harbor seals and spotted seals are 2.3 and 1.3 times higher, respectively, than values reported here (Table 5). The difference is primarily a result of population estimates for both species used in this study (based on current data) that were one-half to one-third those used by Ashwell-Erickson and Elsner (1981).

Our estimate for gray whales was about half the lower end of the range reported by Nerini (1984) (Table 5). Nerini, however, estimated an effective feeding population in the Bering Sea 53% higher than the value used here (Table 1). The difference is largely because Nerini estimated food consumption for gray whales for the entire Bering Sea, including the Gulf of Anadyr, whereas the present study limited the area of concern to the eastern Bering Sea and Aleutian Islands areas. Estimated food consumption of gray whales by Frost and Lowry (198 1) was for the Bering and Chukchi Sea areas, and was based on more than twice the number of feeding days used by Nerini (1984).

Several ecosystem models of the Bering Sea, based on fisheries data, have been developed (Laevastu et al. 1976; Laevastu and Favorite 1977; Laevastu and Larkins 1981). In these simulation models, marine mammal food consumption rates typically appear as input parameters; commercial fisheries, marine mammals, and birds are considered to be apex predators. For their models, Laevastu and Larkins (198 1) generated marine mammal population and feeding rate distributions based on literature sources. Population estimates and feeding rates used in the simulation model of Laevastu and Larkins (198 1) were higher than those used here. Computations using spatially gridded ecosystem models reported by Laevastu and Larkins (198 1) produced an estimate of 2.67 $x10^6$ t for total fish consumption by marine mammals in the eastern Bering Sea and Aleutian Islands region, or 1.77 x 10^6 t for only the Bering Sea (Table 5). Their research area was somewhat larger than that used in this study (see data sources in Laevastu et al. 1980a, 1980b). Approximately one-half of the Aleutian Islands area considered by Laevastu and

Table 5.-Representative estimates of total annual food and fish consumption by marine mammal populations of the Bering Sea region previously reported in the literature.

Taxonomic group and data source	Estimated annual food consumption by population (10^3t)	Estimated annual fish consumption by population (10^3t)
Northern fur seal:		
McAlister and Perez (1977):		
Bering Sea and Aleutian Islands	540	439
Bering Sea only	447	375
Perez and Mooney (1986) [a]	190	126
Present study	432	290
Harbor seal:		
Ashwell-Erickson and Elsner (1981)	98	79
Present study	43	32
Spotted seal:		
Ashwell-Erickson and Elsner (1981)	118	92
Present study	89	86
Gray whale:		
Zimushko and Lenskaya (1970)[b]	850	-
Frost and Lowry (1981)[b]	2,700 - 3,240	-
Nerini (1984)	571 - 1,674	-
Present study	272	-
Marine Mammals (all species combined):		
Laevastu and Larkins (1981):		
Bering Sea and Aleutian Islands [c]	11,504 (10,124)	2,666 (2,346)
Bering Sea only [c]	7,333 (6,453)	1,773 (1,560)
Present study	3,210	1,340

[a] Estimates are for the adult female population during July-September only.

[b] Estimates include food biomass eaten by animals in the Chukchi Sea.

[c] Laevastu and Larkins (1981) stated that these estimated maximum consumption values should be reduced by 12% to attain equilibrium of calculations in their ecosystem simulation models. The lower equilibrium consumption estimates are shown in parentheses.

Larkins (198 1) lies south of the Aleutian Islands in the North Pacific Ocean, and they also included most of the Gulf of Anadyr as part of the Eastern Bering Sea.

Laevastu and Larkins (198 1) defined their food and fish consumption estimates as "plausible maximum values" because "simulation results indicate that the Bering Sea and Aleutian ecosystems cannot accommodate such a high consumption unless their carrying capacity is greater than that estimated in the model" (Laevastu and Larkins 1981). Equilibrium results were only obtained in the model when marine mammal inputs were reduced by a minimum of 12%. Operating inputs were 1.56 x 10^6 t per year of fish consumption by marine mammals in the Eastern Bering Sea **and** 2.35 x 10^6 t per year of fish consumption by marine mammals in both the eastern Bering Sea and Aleutian Islands areas combined (Table 5).

Although the total fish consumption by marine mammals predicted by the simulation model (Laevastu and Larkins 1981) was only about 15% higher than total fish consumption reported here (Table 5) the allocation of food consumption among individual marine mammal species in the model is quite different from the food consumption by species distribution obtained here. Because the model uses only total fish consumption by apex predators, the model will function as long as the totals are correct without regard to allocation among apex predators. The ecosystem model of Laevastu and Larkins (198 1) also defines feeding rates for marine mammals as percentage of **body** mass per day, and does not account for varying energy densities of prey.

The allocation of food consumption among marine mammal species is arbitrary in these models, and although generally done to conform to realistic values, no allocation is either predicted or confirmed **by** such simulation models, In using these models, care must be taken in interpreting consumption estimates because the models can generate essentially similar equilibrium states with a wide variety of marine mammal population and feeding rate inputs. It is the total fish consumption **by** apex predators and the distribution of prey consumption which drives these models, not the allocation among apex predators.

Utilization of Fishery Standing Stocks

Groundfish in the Eastern Bering Sea and the adjacent Aleutian Islands area have been exploited commercially for many years, Management programs for species of commercial interest have developed stock estimates for these species (Bakkala 1984; Low 1984; Low 1991) which have been used in ecosystem models (Laevastu and Larkins 1981). Standing stock estimates from resource assessment surveys also exist for demersal species (Sample and Wolotira 1985; Bakkala et al. 1992; Harrison 1993) (Table 6). Standing stock estimates were given by Laevastu and Larkins (1981) for all fish species, including pelagic species (Table 6). Their estimates were essentially the values required to operate the PROBUB and DYNUMES models in an equilibrium condition given fixed apex predation (fishery catch and marine mammal inputs).

The estimated catch and standing stock values for all fish species (Laevastu and Larkins 1981) and for groundfish stocks (Bakkala 1988; Low 1991) cover similar, but not identical, areas to those used in this study. Their "eastern Bering Sea and Aleutian Islands region" includes part of the North Pacific Ocean to the south of the Aleutian Islands (EAI, expanded Aleutian Islands area; stock estimates given in column 4 of Table 6, section A) and also deletes the area adjacent and north of the Aleutian Islands in their definition of the Eastern Bering Sea (RBS, reduced Bering Sea; stock estimates given in column 3 of Table 6, section A). Accordingly, percent of standing biomass of fish consumed (Table 7) has been calculated with both sets of catch and standing stock data. The range minimum was taken from the analyses for both the RBS and EAI areas combined compared to the probable lower estimate of fish consumption by marine mammal species in Table 4. The range maximum has been taken from the RBS analysis only compared to the probable upper level estimate of marine mammal fish consumption in Table 4. The mean value is the average of estimates calculated for the combined RBS and EAI areas and only the RBS area compared to the current estimates of marine mammal fish consumption.

Commercially important groundfish species comprised 99% of the fish caught during 1988-90 in the combined domestic and joint venture groundfish fisheries (Low 1991). These

Table 6.--Estimates of the standing stock (thousands of metric tons) of important fish species in the eastern Bering Sea and Aleutian Islands region based on trawl survey estimates[a], midwater acoustic surveys [a], and ecosystem model computations [b]. Species of commercial importance are denoted by an asterisk.

Taxa	Eastern Bering Sea	Norton Sound	Eastern Bering Sea and Norton Sound (combined)	Aleutian Islands and southern Bering Sea	Total Region
(A) By species:					
● Walleye pollock (Theragra chalcogramma)					
Total stock	11,581.2	0.8	11,582.0	3,901.0	15,483.0
Demersal stock only	7,052.9	0.4	7,053.3	264.8	7,318.1
Midwater stock only[c]	4,528.3	0.4	4,528.7	280.7	4,809.4
Pelagic stock only[d]	-	-	-	3,355.5	3,355.5
● Pacific cod *(Gadus macrocephallus)*	968.9	-	968.9	183.8	1,152.7
● Rockfishes *(Scorpaenidae)*	44.4	-	44.4	637.5	681.9
● Sablefish *(Anoplopoma fimbria)*	30.8	-	30.8	21.1	51.9
● Atka mackerel *(Pleurogrammus monopeirygius)*	-	-	-	688.2	688.2
● Flatlishes *(Pleuroneclidae)*	6,847.5	11.9	6,859.4	167.0	7,026.4
● Pacific herring *(Clupea pallasi)*					
Semidemersal stock only	164.4	0.1	164.5	0.6	165.1
Other fish species [e]	875.1	66.6	941.7	74.2	1,015.9
Total	20,512.3	79.4	20,591.7	5,673.4	26,265.1
(B) By subgroup:					
Commercial fish species/					
(Survey estimate)	19,637.2	12.8	19,650.0	5,599.2	25,249.2
Commercial fish species [b,g]					
(Ecosystem model estimate)	-	-	23,646.0	8,842.0	32,488.0
Noncommercial fish species[b,g]					
(Ecosystem model estimate)	-	-	12,700.0	3,800.0	16,500.0
Total standing stock [b,g]					
(Ecosystem model estimate)	-	-	36,346.0	12,642.0	48,988.0

[a] Based on data in Sample and Wolotira (1985) and Bakkala et al. (1992) for the Eastern Bering Sea and Norton Sound; and data in Harrison (1993) for the Aleutian Islands and southern Bering Sea area.

[b] Based on data in Laevastu and Larkins (1981).

[c] Midwater walleye pollock has not been surveyed in Nothern Sound and the Aleutian islands areas. The biomass of midwater pollock for these two areas was estimated using the average ratio of midwater 10 demersal pollock flocks observed in 4 years of biennial bonom trawl and hydroacoustic **(midwater) surveys in** the **rcmalning Eastern Bering** Sea (1.06. 1; Bakkala et al. 1992).

[d] Based on data in Okada (1986).

Table 6.--Continued.

[e] These values were based on trawl survey estimates, and are not representative of the abundance of other fish species, especially pelagic stocks (including pelagic stocks of Pacific herring).

[f] Based on the data above in Section A of this table, excluding other fish species

[g] All stocks (pelagic, demersal, etc.) of fish species in their respective subgroups are included in these estimates.

Table 7.--Estimated percent of standing stock biomass of fish consumed annually by marine mammals and commercial fisheries in the Eastern Bering Sea. The numbers in parentheses are possible range values.

			Estimated percent of standing biomass of fish consumed annually in the Eastern Bering Sea		
Predator	Estimated annual fish consumption (10^3t)	Estimated percent commercial groundfish species [a]	All fish species [b]	Commercial groundfish species [c]	Other fish species [b]
Northern fur seal	289.7	56 (38)	0.7 (0.2 - 2.0)	0.7 (0.2 - 2.1)	0.9 (0.3 - 2.6)
Northern sea lion	140.7	69 (52)	0.3 (0.1 - 1.5)	0.4 (0.1 - 2.0)	0.3 (0.1 - 1.4)
Other pinnipeds	435.4	13 (8)	1.1 (0.4 - 1.9)	0.3 (0.1 - 0.6)	2.6 (0.9 - 4.7)
Subtotal (pinnipeds)	865.8	37 (24)	2.1 (0.7 - 5.4)	1.4 (0.4 - 4.7)	3.8 (1.3 - 8.7)
Mysticetes	42.4	34 (4)	0.1 (0.0 - 0.3)	0.1 (0.0 - 0.2)	0.2 (0.1 - 0.5)
Odontocetes	403.1	28 (9)	0.9 (0.3 - 1.5)	0.5 (0.2 - 0.8)	2.0 (0.6 - 3.1)
Subtotal (cetaceans)	445.5	28 (7)	1.0 (0.3 - 1.8)	0.6 (0.2 - 1.0)	2.2 (0.7 - 3.6)
Sea otter	28.3	8 (1)	0.1 (0.0 - 0.1)	Trace	0.2 (0.1 - 0.2)
Total (marine mammals)	1,339.6	33 (14)	3.2 (1.0 - 7.3)	2.0 (0.6 - 5.7)	6.2 (2.1 - 12.5)
Commercial fisheries [d]	1,800.5	99	3.7 (5.8)	7.1 (11.3)	Trace

d Expressed as a percentage of the value in column 1; the numbers in parentheses refer to the estimated percentage of groundfish in the total diet

[b] Based on the total standing stock values (ecosystem model estimates; Laevastu and Larkins 1981) from Table 6.

[c] Based on the biomass estimates (survey estimates) for commercial fish species from Table 6

[d] Based on data in Low (1991).

species represent only an estimated 30-40% of the total biomass of fish eaten by marine mammals in the same area. For the eastern Bering Sea and Aleutian Islands region, marine mammals consume 3.2% (1.0-7.3%) annually of the standing biomass of all fish stocks; 2.0% (0.6-5.7%) of commercially important groundfish stocks; and 6.2% (2.1-12.5%) of all other fish stocks (Table 7). Groundfish fisheries during 1988-90 took an average of 3.7% of all fish biomass and 7.1% of commercial groundfish stocks annually (Table 7). Based on full utilization of the long-term potential yield (2.84 $x10^6$ t per year) for all groundfish resources in the Bering Sea (Low 1991), commercial groundfish fisheries could take annually up to 5.8% of the standing biomass of all fish stocks and 11.3% of commercially important groundfish stocks in the Eastern Bering Sea. The combined annual harvest by various groundfish fisheries and marine mammal consumption was estimated at 6.9% (13.1% potential total take) for all fish species and 9.1% (17.0% potential total take) for commercially important groundfish stocks (Table 7).

Although marine mammals and commercial fisheries take fish from the same stocks, they generally take different sizes of fish. Marine mammals usually consume fish smaller than 30 cm, although larger fish are sometimes eaten (Nemoto 1957, 1959; Crawford 1981; Frost and Lowry 1981, 1986; Seaman et al. 1982; Bukhtiyarov et al. 1984; Perez and Bigg 1986). The commercial fisheries predominantly catch larger fish (Bakkala 1988). Walleye pollock comprised 74% of fish caught in joint venture and domestic groundfish fisheries during 1988-90 (Low 1991). Frost and Lowry (1986) reported data on the size and age groups of walleye pollock eaten by six marine mammal species. Only northern sea lions and harbor seals forage significantly on walleye pollock older than age 3 (about 16% of pollock consumption), whereas 66% of walleye pollock caught in fisheries were older than age 3 (Bakkala 1988). Based on the estimated fish consumption data in Tables 3 and 4 and on the diet data summarized in Perez (1990), annual consumption of walleye pollock by marine mammals in the eastern Bering Sea and Aleutian Islands areas was estimated at 0.30×10^6 t. This accounts for 2% of the total standing biomass (Table 6) of walleye pollock; 45% of this estimate were fish 1 year old and 46% were fish 2-3 years old. The commercial fisheries catch (average take of pollock during 1988-90 was 1.33×10^6 t per year; Low 1991) accounts for 9% of the estimated standing biomass of walleye pollock in the region; few fish were younger than 2 years in age, and 34% of this take were fish 2-3.years old (Bakkala 1988). Overlap in predation between marine mammals and commercial fisheries for the walleye pollock resource occurs primarily on age-2 fish, with the fisheries taking about twice as much as marine mammals.

In the case of the northern fur seal, Livingston (1989) stated that its greatest competition for age-l pollock as food came from the cannibalistic adult walleye pollock. Assuming that no other predators increase their consumption of walleye pollock, the short-term effect of the fishery is to increase the amount of age-l pollock available to fur seals (Livingston 1989). This result is in agreement with the modeling exercises of Laevastu et al. (1980b). Livingston (1989) also suggested that Eastern Bering Sea fisheries may have an indirect beneficial effect on the food supply of northern fur seals by removing the other predator.

In the absence of data on prey preference or data on costs of shifts in prey composition of the diet, no definitive statements can be made on the noncommercial stock take. The stock biomass estimates used in this paper, proposed by Laevastu and Larkins (198 1), for noncommercial stock levels are consistent with the consumption values derived here. Also, if the relative importance of fish to the diet of marine mammals should vary appreciably from the values used in this study, then the level of marine mammal predation on the standing stocks of fish in the Eastern Bering Sea also would change.

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