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Importance of Walleye Pollock in the Diets of Marine Mammals in the Gulf of Alaska and Bering Sea, and Implications for Fishery Management

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Abstract

Approximately 31 species of marine mammals occur at least seasonally in portions of the Gulf of Alaska and Bering Sea. Walleye pollock are eaten to some degree by euryphagous baleen whales, including fin, minke, humpback, and sei whales, and have been found in the stomachs of sperm whales and Dall's porpoise. Pollock may be a seasonally important food for belukha whales, harbor porpoises, and killer whales. Pollock are the most important food (35% of total energy intake) of northern fur seals in the eastern Bering Sea in summer and are also eaten in the Gulf of Alaska. Pollock composed 58% of the stomach contents of Steller sea lions and 21% of the stomach contents of harbor seals collected in the Gulf of Alaska, and are also important prey in the Bering Sea. Pollock are important foods for spotted and ribbon seals when they are associated with the Bering Sea ice front during March-June, and are sometimes eaten by bearded seals.

Foraging activities of marine mammals may affect walleye pollock populations by: (1) influencing abundance of certain size/age classes directly through predation; (2) influencing the productivity of pollock populations by feeding on the same prey base (e.g., copepods, euphausiids, and forage fishes); and (3) preying on species that are competitors or predators of pollock. Conversely, pollock fisheries may affect marine mammals by altering the abundance and age-class structures of pollock stocks and incidentally killing marine mammals during fishing activities. Available data are not adequate to accurately model or monitor interactions between marine mammals, pollock populations, and pollock fisheries. Clearly both fisheries and marine mammals remove large amounts of pollock from a complex and dynamic ecosystem. Changes in population status of marine mammals, whether or not they are directly caused by fishing activities, may have major consequences for fishery management.

Introduction

Approximately 31 species of marine mammals, including 8 species of baleen whales, 11 species of toothed whales, dolphins, and porpoises, 10 species of pinnipeds, and 2 species of marine carnivores occur in the Gulf of Alaska and Bering Sea (Lowry et al. 1982; Calkins 1986). Of those, 15 species are known or thought to feed to some extent on walleye pollock, *Theragra chalcogramma* (Table 1). Some of those species are year-round residents, while others occur in the region only seasonally. Most baleen whales winter in temperate or tropical waters and move northward into the Gulf of Alaska and Bering Sea to feed during the spring and summer months (Frost and Lowry 1981a; Calkins 1986). In the Bering Sea, the occurrence of seasonal sea ice greatly affects marine mammal distribution by providing habitat for some species and excluding others (Fay 1974). While most marine mammal species occur in both regions, ice-associated pinnipeds occur in the Bering Sea but not in the Gulf.

In this paper we will not attempt a complete review of the feeding ecology of all marine mammal species in the Gulf of Alaska and Bering Sea. Rather, we will focus on those species for which pollock may be an important dietary component. We will review previously published food habits data and present some recently collected information, then discuss the possible ecological interactions between marine mammals and pollock stocks in light of what we presently understand and what we need to know.

Information Sources

In order to assess the relationships between marine mammal feeding and fish stocks, we need information on composition of the marine mammal diets, and their food requirements. For a number of reasons, briefly discussed below, this information is difficult to obtain and is subject to considerable uncertainty and possible bias.

Information on diet composition may be obtained through direct observations of food being consumed or by examination of prey remains in gastrointestinal tracts, feces, or vomitus. Direct observation is possible only in limited circumstances and is not applicable to predation on walleye pollock, which are usually consumed below the surface. Our information therefore comes from examination and quantification of prey remains. In rare cases, stomach contents may be in such fresh condition that whole fish may be separated, identified and measured, providing reliable data on the type and quantities of prey consumed. Usually prey are more or less digested or the sample may consist only of hard parts such as otoliths. Pollock otoliths are readily identifiable (Frost 1981) and otolith length measurements may be used to estimate the sizes of fishes consumed (Frost and Lowry 1981b). If similar information is available for all species eaten it may be possible to back-calculate the composition of the diet (e.g., Frost and Lowry 1980).

Differential rates of digestion and passage of food remains through the gastrointestinal tract are a real problem in marine mammal food habits studies (Bigg and Fawcett 1985; Murie and Lavigne 1986). This

Table 1. Marine mammals that occur in the Gulf of Alaska and Bering Sea and are known or thought to feed on walleye pollock (adapted from Lowry et al. 1982 and Calkins 1986).

Species	Gulf of Alaska	Bering Sea
BALEEN WHALES		
Fin whale - *Balaenoptera physalus*	mostly spring-summer	mostly summer
Sei whale - *B. borealis*	mostly spring-summer	mostly summer
Minke whale - *B. acutorostrata*	resident (?)	resident (?) and migratory
Humpback whale - *Megaptera novaeangliae*	mostly spring-fall	mostly summer
TOOTHED WHALES		
Sperm whale - *Physeter macrocephalus*	spring-fall	mostly summer
Killer whale - *Orcinus orca*	resident	resident (?) and migratory
Belukha whale - *Delphinapterus leucas*	resident	resident and migratory
Dall's porpoise - *Phocoenoides dalli*	resident	resident and migratory
Harbor porpoise - *Phocoena phocoena*	resident	resident and migratory
PINNIPEDS		
Northern fur seal - *Callorhinus ursinus*	resident and migratory	resident and migratory
Steller sea lion - *Eumetopias jubatus*	resident	resident
Harbor seal - *Phoca vitulina*	resident	resident
Spotted seal - *Phoca largha*	-	resident and migratory
Ribbon seal - *Phoca fasciata*	-	resident and migratory
Bearded seal - *Erignathus barbatus*	-	mostly winter-spring

may cause erroneous results whether they are expressed as prey composition by number, by volume, or by frequency of occurrence (number of animals containing a specific prey divided by the total number of animals in the sample). Also, for at least some species, digestion of otoliths may greatly affect the apparent size distribution of prey consumed (da Silva and Neilsen 1985). However, walleye pollock otoliths are robust and appear relatively resistant to digestion during passage through the gastrointestinal tract. Frost and Lowry (1980) found no significant difference in lengths of intact walleye pollock otoliths recovered from stomachs and intestines of ribbon seals, and Antonelis et al. (1986) found a similar range of otolith sizes in stomachs and feces of northern fur seals. There was no significant difference in the frequency of occurrence of pollock based on analysis of stomach contents versus feces for harbor seals (Pitcher 1980a) or northern fur seals (Antonelis et al. 1986). Therefore, while we recognize that the information that has been collected on occurrence and relative importance of pollock in marine mammal diets is not definitive, we think it can be used for a general assessment of the dietary importance of pollock.

Interpretations of food habits data may be misleading unless accompanied by information on food availability. For example, the absence of pollock in an animal's stomach may only mean that pollock were not present when it fed, and not necessarily that pollock are not a preferred or important food for that species. The same problem occurs when considering the sizes of prey consumed (see Frost and Lowry 1986). Studies that concurrently sample marine mammal foods and prey availability are of particular value (e.g., Hacker and Antonelis 1986).

Food requirements of marine mammal populations are usually derived from independent estimates of individual food (or energy) requirements and population size. Food requirements may be estimated from feeding of captive animals (Sergeant 1969; Keyes 1968), bioenergetic models (e.g., Ashwell-Erickson and Elsner 1981), or metabolic rate studies (Huntley et al. 1987). Consideration must be given to the influence of age, sex, reproductive status, and season on energy needs, as well as to variations in nutritional and caloric value of prey. Estimates of population sizes for marine mammals in the Gulf of Alaska and Bering Sea are often based on very limited data and are of questionable accuracy (see Lowry et al. 1982; Calkins 1986).

Importance of Walleye Pollock in Marine Mammal Diets

Baleen whales

Fin whales in the North Pacific consume pelagic crustaceans, primarily euphausiids and copepods, along with a variety of schooling fishes and sometimes squid. Based on samples from Japanese whalers fishes, primarily herring (*Clupea harengus*), capelin (*Mallotus villosus*) and walleye pollock, were eaten most commonly in years when euphausiids and copepods are not abundant (Nemoto 1959). Pollock were of greatest importance in animals taken along the Bering Sea continental shelf between 58°N and 61°N latitude, but were also eaten by whales taken near the Commander and Kuril islands (Klumov 1963). The length of pollock eaten never exceeded 30 cm (Nemoto 1959). Pollock did not occur in the stomachs of fin whales taken in the Gulf of Alaska and western North Pacific Ocean (Kawamura 1982).

Sei whales taken by Japanese whalers in the North Pacific had eaten primarily copepods and lesser amounts of euphausiids, fishes, and squid (Kawamura 1982). According to Nemoto (1959) sei whales are surface feeders and would therefore be expected to consume only those species of fish that occur near the surface. Klumov (1963) lists several species of fish, including pollock, as prey items of sei whales. Tomilin (1957) indicated that pollock were eaten by sei whales near the Commander Islands.

Minke whales eat mostly euphausiids and schooling fishes, with squid and copepods of lesser importance in the diet (Nemoto 1959). Pollock were found to be a major food of minke whales taken in the Kuril Islands and off Japan (Omura and Sakiura 1956; Nemoto 1959). The stomach of a minke whale stranded at Unalaska Island in the Aleutians contained only remains of walleye pollock (Frost and Lowry 1981a). The fork length of fishes consumed averaged 14.5 cm with a range of 11.8-17.5 cm (Frost and Lowry 1986).

Humpback whales, which are common in the continental shelf waters of the Gulf of Alaska and Bering Sea, eat primarily euphausiids and fishes. According to Nemoto (1959) they are "famous for their fish feeding." He noted that their favorite food in the Aleutians was Atka mackerel (Pleurogrammus monopterygius) 15-30 cm long, and that two whales he examined had fed on adult walleye pollock. Klumov (1963) stated that the distribution of humpback whales near the Commander Islands and southern Kamchatka is closely connected with the distribution of spawning aggregations of pollock.

Toothed whales, dolphins, and porpoises

Sperm whales have been harvested extensively over deep waters of the North Pacific Ocean, and their diet has been reasonably well described. Their principal foods are deep-water squids, but they also eat sharks, skates, and some bony fishes (Tomilin 1957; Kawakami 1980). Pollock do not appear to be a major food in any area, but they have occurred in whales taken in the northwestern Pacific (Kawakami 1980).

Small odontocete cetaceans have generally not been commercially exploited and are rarely collected for scientific purposes. Therefore there are few data available on their food habits. The information that has been collected has come mostly from strandings, animals caught in fishing gear, and those taken in subsistence harvests.

Killer whales range throughout the Gulf of Alaska and Bering Sea. Their diet is quite diverse (Frost and Lowry 1981a) and though they are best known for predation on other marine mammals, they also feed on schooling fishes (Tomilin 1957). Walleye pollock have not been specifically identified as a component of the diet, but killer whales are common in areas where pollock are abundant, and we consider that they may sometimes eat them.

Belukha whales in western Alaska eat mostly pelagic and semi-demersal fishes. Fishes in the cod family (arctic cod, Boreogadus saida, and saffron cod, Eleginus gracilis) are particularly important foods (Seaman et al. 1982). Fishes eaten ranged from 5 to 50 cm long.

Pollock have not been found in belukha stomachs, however available stomach samples have been collected only from nearshore waters mostly in the northern Bering and Chukchi seas where pollock do not usually occur. Seaman et al. (1982) speculated that pollock may be an important food for belukhas in their wintering area in the central Bering Sea. The same may be true for the Cook Inlet stock of belukhas which probably winters in lower Cook Inlet (Calkins 1986).

Dall's porpoises caught incidentally in the Japanese high seas gillnet fishery in the North Pacific Ocean had eaten mostly squid and fishes. Pollock occurred in 8 of 185 stomachs examined from 1978 and 0 of 87 from 1979 (Crawford 1981). No measurements were given for pollock, but the lengths of fishes eaten were mostly 4-15 cm. Overall, squids are the most important food of Dall's porpoise (Tomilin 1957; Crawford 1981).

Very few data are available on foods of harbor porpoise in Alaska. Five animals caught in fishing nets in Norton Sound had eaten saffron cod ranging in length from 16.5 to 36.5 cm and some herring (Lowry and Frost, unpublished data). In eastern Canada they feed on several species of pelagic and semi-demersal fishes (Smith and Gaskin 1974). Based on their known foods we conclude that walleye pollock may be eaten in some areas in Alaska.

Pinnipeds

A considerable amount of data is available on food habits of pinnipeds, as a result of commercial and subsistence harvests and research collections. The following information focuses on samples in which pollock occurred, and is presented in summary form. Readers should consult review articles for general dietary information, and original references for detailed results.

Ribbon seals are found associated with seasonal sea ice in the Bering Sea in winter and spring, and are thought to be pelagic during the rest of the year. All food habits information comes from the winter-spring period. Burns (1981) reported pollock in 1 of 2 seals taken at Saint Lawrence Island in February. Frost and Lowry (1980) reported on food remains in 61 ribbon seals collected in the Bering Sea, March-June 1976-79. Walleye pollock was the primary food in the south-central Bering Sea (89% of the number of identified fishes and 50% of the estimated weight of food consumed) and was one of the 2 most important prey in the central Bering Sea (55% of the number of identified fishes and 28% of the estimated weight of food consumed). Pollock eaten were mainly 1-year-old fishes, 8-12 cm long, and were similar in size to those caught in otter trawls taken nearby. Frost and Lowry (1980) estimated that ribbon seals could consume 55,000 mt of pollock per year in the Bering Sea.

Spotted seals are also associated with sea ice in winter and spring, but, unlike ribbon seals, they move to coastal waters during summer and autumn. Throughout the year they feed primarily on a variety of fishes and shrimps (Lowry et al. 1982). Most food habits information comes from animals taken on the sea ice in spring. Goltsev (1971) indicated that pollock was the 6th ranked prey (based on frequency of occurrence) in seals collected in the Gulf of Anadyr. Bukhtiyarov et al. (1984) found that pollock was the most important food of spotted seals collected in March-June 1972-78 in the central Bering Sea (88% of the number of identified fishes eaten) and was also a component of the diet in the southeastern and northern Bering Sea (5% and 2% of identified fishes), and the Gulf an Anadyr (14% of the weight of stomach contents). The estimated length of pollock eaten ranged from 8 to 15 cm with a mean of 10.9 cm.

Lowry et al. (1986) reported the stomach contents of spotted seals collected in March-April 1985. Walleye pollock was the most commonly eaten prey both in the area southwest of Saint Matthew Island (58% of the number of identified fishes) and southwest of Cape Navarin (83% of the number of identified fishes). Based on measurable otoliths, seals had eaten 1 large pollock, 39.3 cm long, and 115 small pollock averaging 10.8 cm long (range 8.5-14.3 cm).

Ashwell-Erickson and Elsner (1981) estimated that spotted seals in the Bering Sea consume 46,900 mt of pollock per year.

The primary foods of bearded seals in the northern Bering and Chukchi seas are crabs, clams, and shrimps, although demersal fishes are sometimes eaten (Lowry et al. 1980). Antonelis et al. (in prep) reported on stomach contents of 74 bearded seals collected near St. Matthew Island in March-April 1981. Fishes occurred in 67 of the stomachs and pollock remains were found in six. Pollock averaged 11.8 cm long with a range from 6.9-14.3 cm.

Harbor seals are widely distributed in nearshore waters of the southeastern Bering Sea, Aleutian Islands, and Gulf of Alaska. Harbor seals eat a variety of fishes, cephalopods, and shrimps. The volume of stomach contents of seals collected at Otter Island in April 1979 consisted of 63.5% fishes, 28.7% octopus, and 7.8% other items; 44% of the total number of fishes eaten were pollock, ranging in length from 10.3 to 56.3 cm with a mean of 31.8 cm (Lowry and Frost 1981; Frost and Lowry 1986). Lowry et al. (1982) reported that pollock occurred in stomachs of harbor seals collected at 3 of 5 locations sampled in the southeastern Bering Sea in October 1981. Pollock was the second most important food at Port Moller, third in importance at Akun Island, and ranked fourth at Port Heiden. Pollock eaten at Port Heiden were all less than 12.6 cm long, with a mean length of 10.6 cm (Frost and Lowry 1986). Lowry et al. (1986) reported on the stomach contents of harbor seals collected in May-June 1985 at 5 locations along the Alaska Peninsula. Pollock were found only in seals taken at Nelson Lagoon where they accounted for 5% of the total number of fishes eaten. Sample sizes in all these studies were very small, with 1 to 8 stomachs with food from each locality.

Similarly small samples have been examined from several locations in the Aleutians. Wilke (1957) found pollock in the stomach of 1 of 7 harbor seals collected at Amchitka Island, March 1954. Three seals collected at Unalaska Island in April 1972 had all eaten large numbers of pollock (Lowry et al. 1979).

Ashwell-Erickson and Elsner (1981) estimated that harbor seals in the Bering Sea consume 34,700 mt of pollock per year.

Pitcher (1980b) conducted a comprehensive study of harbor seals in the Gulf of Alaska, in which he examined 269 stomachs containing food. Overall, pollock was the most important prey, occurring in 20.8% of all stomachs with food and comprising 21.4% of the volume of contents. Pollock was the number 1 ranked prey in 3 geographical subareas (northeastern Gulf, Prince William Sound, and Kenai coast), ranked second along the Alaska Peninsula, and ranked third in the Kodiak Island area. In the Kodiak area and Prince William Sound, where seasonal samples were available, pollock was an important food throughout the year. Lengths of pollock eaten ranged from 4.2 to 53.2 cm with a mean of 19.2 cm (Pitcher 1981).

Most northern fur seals migrate through the Gulf of Alaska and spend summer months in the Bering Sea where they pup and breed on the Pribilof Islands. The diet of northern fur seals has been the subject of numerous studies and reports; data from 7,373 seals collected 1958-74 were most recently summarized by Perez and Bigg (1986). Fur seals eat mostly small schooling fishes and squids. Overall in the Gulf of Alaska, pollock comprised about 5% of the fur seal diet; the importance of pollock was greatest in the north Gulf subregion (about 15% of the diet). In the Bering Sea as a whole, pollock was the most important food for fur seals comprising about 33% of the diet. Pollock were particularly important near the Pribilof Islands and on the continental shelf of the southeastern Bering Sea. Pollock eaten ranged in length from 4 to 40 cm.

Loughlin (unpublished) examined stomach contents of fur seals collected in the southeastern Bering Sea in 1981 and 1982. Pollock occurred in 14 of 33 stomachs examined. The mean length of pollock consumed was 30.4 cm, which was considerably smaller than fish caught in otter trawls taken nearby (mean length 38.3 cm).

Hacker and Antonelis (1986) reported on the examination of 43 stomachs from fur seals collected in the southeastern Bering Sea in August 1985, of which 35 contained identifiable food remains. Walleye pollock occurred in 29 stomachs and accounted for 77% of the total number of fishes consumed. Most of the pollock eaten were 10-18 cm long. Many large pollock, 35-55 cm in length, were caught in midwater trawls taken near where fur seals were collected, but very few large fishes occurred in seal stomachs. Examination of scats, and of colons from seals harvested on the Pribilofs, confirmed that walleye pollock was the species of fish most commonly eaten by fur seals in the Bering Sea in 1985 (Antonelis et al. 1986).

Perez (1986) estimated the amount of walleye pollock consumed by fur seals in the eastern Bering Sea in 1985. The estimated consumption was 132,500 tons, based on a population of 459,000 animals feeding in the area for 122 days. Most of the total was accounted for by lactating females.

Steller (or northern) sea lions occur throughout the southeastern Bering Sea, Aleutian Islands, and Gulf of Alaska. Sea lions eat mostly a wide variety of fishes but also consume some octopus and squid. Small samples of sea lions collected in the Bering Sea in 1951 and 1962 indicated that pollock was the fourth-ranked prey species (Wilke and Kenyon 1952; Fiscus and Baines 1966). Pollock was the predominant prey in 4 sea lions collected in March-April 1976, accounting for 97% of the food volume and 95% of the number of prey consumed (Lowry et al. 1982). Pollock eaten ranged from 34 to 57 cm in length. Pollock otoliths occurred in the stomach of a sea lion collected at Otter Island in April 1979 (Frost and Lowry unpublished).

In March-April 1981, 110 Steller sea lions were collected and examined in the central and western Bering Sea as part of a joint U.S.-Soviet research project. Of 86 stomachs containing food, pollock occurred in 79 and was the dominant component in 67 (Donald Calkins, ADF&G, Anchorage, personal communication). The lengths of pollock consumed ranged from 8.3 to 64.2 cm with a mean of 25.2 cm (Frost and Lowry 1986). Young sea lions ($\leq$ 4 years) ate considerably smaller pollock than did older animals (mean length 22.4 cm vs 26.9 cm), and fishes eaten by sea lions in the central Bering were larger than those eaten to the west, near Kamchatka (26.8 cm vs 23.5 cm).

The National Marine Mammal Laboratory has continued to collect information on foods of sea lions in the Bering Sea whenever possible (Loughlin, unpublished). Pollock occurred in the stomachs of 3 of 10 sea lions collected in the eastern Aleutians in October-November 1981-82. The length of pollock eaten averaged 29.9 cm with a range of from 1.7 to 42.7 cm. Pollock caught in trawls nearby averaged 25.5 cm long. Ten of 13 animals collected near Saint Matthew Island in March 1985 had eaten pollock ranging in length from 10.3 to 51.6 cm (mean 21.8 cm). Pollock composed 16.4% of the estimated total volume of food consumed and was ranked as the third most important prey item. Pollock occurred in stomachs of 2 of 10 sea lions found dead on the beach at Saint Paul Island during winter and early spring 1985. Fishes averaged 33.5 cm long and ranged from 20.8 to 44.5 cm.

Pitcher (1981) studied the foods of Steller sea lions in the Gulf of Alaska based on 250 animals collected in 1975-78. Walleye pollock was by far the dominant food item accounting for 58.3% of the volume of stomach contents and occurring in 102 of the 153 stomachs with food remains. Pollock eaten ranged from 5.6 to 62.9 cm long with a mean length of 29.3 cm. Pitcher noted that the only previous study that indicated pollock as an important food of sea lions in the Gulf was that of Imler and Sarber (1947). They examined stomachs of 23 sea lions collected in 1945-46; pollock was the principal item in 8 animals from southeastern Alaska, and 5 from the northern Gulf of Alaska.

Calkins and Goodwin (1988) reported the stomach contents of 88 sea lions collected in southeastern Alaska and the area around Kodiak Island in 1985-86. Pollock was the most frequently consumed prey in southeastern Alaska, occurring in 8 of 14 stomachs containing prey remains. Pollock composed 31.9% of the volume of contents and was ranked second in importance by volume. In the Kodiak area pollock was the most important prey both by frequency of occurrence (occurred in 43 of 74 stomachs with food) and volume (42.4% of the total food). Fork length averaged 25.5 cm in southeastern Alaska (range 4.8-55.7 cm) and 25.4 cm in the Kodiak area (range 7.9-54.2 cm).

Effects of Marine Mammals on Pollock Stocks

Foraging activities of marine mammals may affect pollock stocks in several ways: (1) they may compete with pollock and reduce pollock production by preying on similar food organisms; (2) they may enhance pollock productivity and/or survival by preying on pollock predators or competitors; and (3) they may influence the abundance of certain size or age classes of pollock directly through predation. Since most species of marine mammals have relatively diverse diets, they may produce more than one of these effects, and their overall impact on pollock stocks is very hard to evaluate.

Copepods and euphausiids are the major foods of pollock, especially smaller size classes. They are also major foods of almost all species of baleen whales (Frost and Lowry 1981a). Until the 1960's, several species of baleen whales were abundant in the North Pacific Ocean and adjacent seas. However, stocks of all species, with the probable exception of minke whales, have been greatly depleted by commercial whaling (Gambell 1976). The removal of many thousands of whales from the North Pacific Ocean undoubtedly resulted in major changes in trophic relationships in the ecosystem. Reduced competition from baleen whales may have encouraged development of the large stocks of pollock and other finfishes. Whales are no longer being harvested commercially and their numbers may increase in coming years.

Walleye pollock are the most abundant forage fishes in the Gulf of Alaska and Bering Sea and therefore provide food for and compete with many other species (Smith et al. 1984). Virtually all marine mammals feed to some extent on species that prey on pollock and/or compete with them for food. Baleen whales and most pinnipeds feed on schooling fishes such as smelt, capelin, and herring, which use the same foods as do pollock. Squids eaten by fur seals and Dall's porpoises, and demersal fishes eaten by sea lions and seals, are known predators of young pollock. Any analysis of effects of this type would be completely speculative, and, in any event, it is likely that such indirect effects would be overshadowed by effects of direct predation on pollock.

Marine mammals consume large amounts of walleye pollock, but data inadequacies limit the accuracy of quantitative estimates (see Lowry et al. 1982). Perez and McAlister (1988) provided information on food requirements and diet composition of marine mammals in the eastern Bering Sea. Estimates of pollock consumption based on those data (Table 2) suggest that pinnipeds alone consume in excess of 300,000 mt per year. Perez and McAlister (1988) estimated that cetaceans annually consume 480,000 mt of finfish, including pollock and herring, capelin, and other species. Similar calculations based on food requirement estimates from Calkins (1986) and diet composition studies reviewed in this paper suggest that, during the 1970's, about 400,000 mt of pollock may have been consumed annually by pinnipeds in the Gulf of Alaska (Table 3). Most of the pollock are eaten by Steller sea lions and northern fur seals. Population sizes of fur seals, sea lions, and to a lesser extent harbor seals have decreased in recent years, and current levels of pollock consumption may be less than indicated in Tables 2 and 3.

Table 2. Estimates of the annual amount of walleye pollock consumed by pinnipeds in the eastern Bering Sea region, adapted from Perez and McAlister (1988).

Species	Amount of food consumed (10^3 mt)	% pollock in diet	Amount of pollock consumed (10^3 mt)
Northern fur seal	431	34	146.5[1]
Steller sea lion	375	33	123.8
Harbor seal	44	12	5.3[2]
Ribbon seal	71	16	11.4[3]
Spotted seal	101	19	19.2[4]
TOTAL			306.2

[1] estimated as 132.5 x 10^3 mt by Perez (1986)
[2] estimated as 34.7 x 10^3 mt by Ashwell-Erickson et al. (1981)
[3] estimated as 55.0 x 10^3 mt by Frost and Lowry (1980)
[4] estimated as 46.9 x 10^3 mt by Ashwell-Erickson et al. (1981)

Table 3. Estimates of the annual amount of walleye pollock consumed by pinnipeds in the Gulf of Alaska.

Species	Amount of food consumed (10^3 mt)[1]	% pollock in diet	Amount of pollock consumed (10^3 mt)
Northern fur seal	142	5.0[2]	7.1
Steller sea lion	548	58.3[3]	319.5
Harbor seal	340	21.4[4]	72.8
TOTAL			399.4

[1] Calkins 1986; based on abundance estimates made during the 1970's, and including the Aleutian Islands
[2] Perez and Bigg 1986
[3] Pitcher 1981
[4] Pitcher 1980b

The sizes of fish consumed by marine mammal predators are also of significance in evaluating possible impacts on pollock stocks. Data presented in Frost and Lowry (1986) and reviewed in this paper indicate that Steller sea lions eat mostly medium and large pollock. Medium and large pollock are sometimes eaten by humpback whales, harbor seals, spotted seals, and fur seals, while other marine mammals mainly eat small pollock. Steller sea lions are the major direct competitor with the fishery, removing large quantities of fishes of the same size range as those being caught by the fishing fleets. Predation by other marine mammals is mostly on fishes smaller than those taken in the fishery, and their influence is therefore mostly on juvenile survival and year-class strength. The amounts of small pollock being consumed by marine mammals in the Bering Sea are generally similar to the amounts consumed by fishes (Livingston and Dwyer 1986).

The possible effects of marine mammal predation will depend on characteristics of the pollock stocks, especially stock size. Sissenwine et al. (1984) point out that effects of marine mammal predation are analogous to effects of fishing, and can be either compensatory or depensatory. If marine mammals switch to other foods when a target species becomes reduced, then there will be a compensatory effect that will tend to allow the fish population to recover. However, if the marine mammals continue to prey on a species at a nearly constant rate regardless of its overall abundance, then the effect will be depensatory. This is possible when prey are highly aggregated, occurring in dense schools even when reduced in overall abundance. The latter type of situation may have been responsible for the virtual elimination of the Georges Bank herring population (Sissenwine et al. 1984), and may be a concern with regard to Steller sea lion predation on pollock in the Gulf of Alaska as will be discussed in a later section.

Effects of Pollock Fisheries on Marine Mammals

Pollock fisheries may affect marine mammals directly through mortality incidental to fishing operations or indirectly by influencing their food supply.

Several species of marine mammals are occasionally caught in trawl gear used to fish for pollock, but the only one caught in substantial numbers is the Steller sea lion. Loughlin et al. (1983) estimated that the groundfish fishery (which targets mostly on pollock but includes other species) in the North Pacific Ocean and Bering Sea caught and killed an average of 724 Steller sea lions per year in 1978-81. In the 1982 joint venture fishery for pollock in Shelikof Strait an estimated 1,436 sea lions were caught and killed; the estimated mortality dropped to 324 in 1983 and 355 in 1984 (Loughlin and Nelson 1986). About two-thirds of the animals taken were females and most (79%) of those were old enough to be sexually mature.

Another direct source of mortality comes from entanglement in lost or discarded fishing gear. The few data available on this subject suggest it is not a major mortality factor for Steller sea lions (e.g., Loughlin et al. 1986). However, Fowler (1982) considers that entanglement may account for a 5.5% annual mortality in northern fur seals, and may be an important factor contributing to a decline in the Pribilof Islands population. Most of the fur seal entanglement results from discarded trawl web fragments.

Possible indirect effects of the pollock fishery on marine mammals depend on whether or not populations are food limited, characteristics of prey consumed by marine mammals, and how fisheries affect the abundance of various size classes of pollock.

DeMaster (1984) considered that most species of cetaceans and some species of pinnipeds are food limited. Some species of pinnipeds may be space limited since density-dependent parameters respond when rookeries become crowded. However, populations of rookery-breeding pinnipeds in the Gulf of Alaska and Bering Sea, northern fur seals and Steller sea lions, are reduced well below historic levels and there is empty space on the rookeries. Other factors such as human harvest or disease can also keep species at population levels below their carrying capacity in terms of food. With the exception of entanglement of fur seals and incidental take of sea lions discussed above, such factors do not now seem important in the population dynamics of the species under consideration.

Effects of pollock fisheries on pollock stocks are unclear. If there is a close relationship between the number of adults and recruitment (spawner-recruit effect) then a fishery targeting on adults would be expected to influence availability of food to marine mammals that prey on small size classes. Available data indicate that recruitment is not closely correlated with size of the spawning stock (Wespestad and Traynor 1987) and that year class strength is probably controlled by environmental conditions (Bakkala et al. 1987). Therefore, provided that stock sizes are not reduced below the level required for adequate recruitment, fisheries would not be expected to have a major influence on availability of food to most marine mammals since, with the exception of Steller sea lions, they feed mostly on small size classes. However, because of the exponential nature of the relationship between fish length and fish weight, we do not discount the possible energetic significance of large pollock to species such as harbor seals and fur seals, which can and sometimes do eat large fishes.

Interactions between Steller Sea Lions and Pollock Fisheries

It is clear from the data reviewed in this paper that Steller sea lions eat primarily medium- and large-sized pollock (Table 4). Comparative data indicate that this does not merely result from distributional patterns, but is the result of actual selection for larger fishes. For example, Pitcher (1981) compared the lengths of pollock eaten by sea lions and harbor seals collected over the same years in the same general areas of the Gulf of Alaska, and found that sea lions ate significantly larger fishes (29.8 cm) than did harbor seals (19.2 cm). Presumably, when given the opportunity marine mammals select the size range of prey that provides the maximum net energetic benefit. Sea lions are clearly capable of catching and entirely consuming very large pollock since otoliths representing fishes over 64 cm long have been found in their stomachs.

There have been substantial changes in the abundance of medium- and large-sized pollock in recent years. Based on cohort analysis, the exploitable biomass (ages 2-9) in the Bering Sea increased in the 1960's, peaked in the early 1970's, then declined in the mid-1970's. Part of the cause of this decline was "the accumulative removals by the fishery in 1970-75 (which totalled 9.6 million t)" (Bakkala et al. 1987). The catch-per-unit-effort in the fishery and by research vessels dropped by a factor of more than 3 from the late 1960's to the

Table 4. Mean lengths and weights of walleye pollock consumed by Steller sea lions in the Gulf of Alaska and Bering Sea. Weights are estimated from equations in Frost and Lowry (1981b).

Collection	Mean length (cm)	Mean weight (g)
Pribilof Islands 1976-79[1]	46.9	553
Central Bering Sea 1981[1]	26.8	109
off Kamchatka 1981[1]	23.5	74
eastern Aleutians 1981-82[2]	29.9	150
Saint Paul Island 1985[2]	33.5	208
near Saint Matthew Island 1985[2]	21.8	60
Gulf of Alaska 1975-78[3]	29.3	141
near Kodiak Island 1985-86[4]	25.4	93
southeastern Alaska 1985-86[4]	25.5	94

[1] Frost and Lowry 1986
[2] Loughlin, unpublished
[3] Pitcher 1981
[4] Calkins and Goodwin 1988

mid-1970's, and the average length of pollock caught dropped from 42-44 cm to 35 cm (Pereyra et al. 1976). Based on this change in lengths, the projected mean weight of fishes would have declined by about 45%. Similar changes probably occurred in the numbers and sizes of pollock caught by sea lions, which could have had a deleterious impact on their nutrition.

There has been a major decline in the abundance of sea lions in the Pribilof Islands (Loughlin et al. 1984). At the rookery on Walrus Island abundance declined from 7,000-8,000 in 1960 (including 3,000 pups) to 1,529 in 1975, and 1,172 in 1981 (including 292 pups). The estimated number of sea lions occurring in the eastern Aleutian Islands has declined from 52,530 in 1960 to slightly over 20,000 in 1975-77 and approximately 10,000 in 1984-85 (Merrick et al. 1987). Sea lions that haul out in the eastern Aleutian Islands may feed either in the Bering Sea or Gulf of Alaska.

Stock assessment model estimates of exploitable biomass (age 3-10) of pollock in the Gulf of Alaska indicate that abundance increased from 0.9 million t in 1976 to a peak of 2.4 million t in 1981 and has declined to 0.4 million t in 1986 (Megrey 1987). Although much of this variation is thought to be due to recruitment, it seems reasonable to assume that removals by the fishery, which totalled in excess of 1.1 million t from 1981 to 1985, had some effect on the stock size. The stock was heavily harvested in 1985 when removals by the fishery (285,000 mt) were equal to 41% of the estimated total exploitable biomass (687,000 mt). Based on a comparison of samples collected in the Gulf of Alaska in 1975-78 and the Kodiak area in 1985-86, there were changes in the characteristics of pollock eaten by sea lions (Calkins and Goodwin 1988). The percentage of the volume of stomach contents which consisted of pollock dropped from 58.3% to 42.4%, and the average length of fishes consumed declined from 29.8 cm to 25.4 cm. The change in length was statistically significant. The projected average weight of a pollock eaten in 1984-85 was 37% less than in 1975-78 (Table 4).

There have been major declines in the abundance of Steller sea lions in the eastern Aleutian Islands and western and central Gulf of Alaska, an area which corresponds to the Shumagin, Chirikof, and Kodiak fishery management areas. From the late 1960's to the mid-1980's, overall numbers declined by 79% in the eastern Aleutians, 73% in the western Gulf, and 31% in the central Gulf (Merrick et al. 1987). The decline in the eastern Aleutians and western Gulf may have begun in the 1970's, while most of the decline in the central Gulf occurred some time between 1977 and 1985.

Calkins and Goodwin (1988) presented data on sizes, blood values, and reproductive parameters of sea lions collected in the Gulf of Alaska in 1985-86 as compared to 1975-78. The recent samples indicated that sea lions were smaller, and blood values and reproductive rates were lower (Table 5). These results indicate that during the 1980's the sea lions have been under nutritional stress, which has resulted in slower growth rates, poorer fitness, and lowered productivity.

Table 5. Comparison of biological parameters of female Steller sea lions collected in the Gulf of Alaska, 1975-78 and 1985-86. Adapted from Calkins and Goodwin (1988).

	1975-78	1985-86
Mean standard length(cm)		
ages 1-5	205.7	196.4
ages 6-10	228.8	226.1
Mean girth (cm)		
ages 1-5	130.9	118.2
ages 6-10	148.4	141.5
Mean weight (kg)		
ages 1-5	185.0	143.3
ages 6-10	256.9	239.1
Mean packed cell volume	45.8	44.8
Mean hemoglobin concentration	16.9	15.4
Near term pregnancy rate	67%	60%
Projected birth rate	63%	55%

A comparison of growth rates by Calkins and Goodwin (1988) indicated overlap in mean sizes of female sea lions more than 10 years old collected in 1985-86 and 1975-78, but animals 10 years old and younger were smaller in the recent collections. The size differences were most marked in younger animals (Table 5; Figure 1). Sea lions 1-5 years old were 4.5% shorter and 22.5% lighter in 1985-86 than 1975-78, as compared to 1.2% shorter and 6.9% lighter for animals 6-10 years old. A comparison between the ratio of weight to length (0.90 in 1975-78 versus 0.78 in 1985-86) confirms that sea lions 1-5 years old were not just smaller in 1985-86, they were much leaner. The differences between young and old sea lions may be due to the fact that older animals encountered better feeding conditions during their early growth period in the late 1970's, while younger animals have experienced significant food limitation in the mid-1980's. Alternatively, older animals may, to some degree, have compensated for reduced early growth, perhaps by forgoing reproduction during the first years of potential sexual maturity. To examine this latter possibility we compared the reproductive activity of 3- to 5-year-old female Steller sea lions collected in 1975-78 (Pitcher and Calkins 1981) and 1985-86 (Calkins and Goodwin 1988). Both ovulation rate (26/45 versus 2/6; λ^2=1.278, 0.50>p>0.25) and pregnancy rate (15/37 versus 0/6; λ^2=3.736, 0.10>p>0.05) were lower in the 1985-86 sample.

Steller sea lions and commercial fisheries target on the same sizes of pollock in the same general areas, and their effects on pollock stocks should be generally similar. We have estimated the amount of pollock eaten by Steller sea lions in the area from Umnak Island to Cook Inlet, taking into account declines in population size (Merrick et al. 1987), and the change in the proportion of pollock in the diet (Calkins and Goodwin 1988) which was assumed to be linear over time.

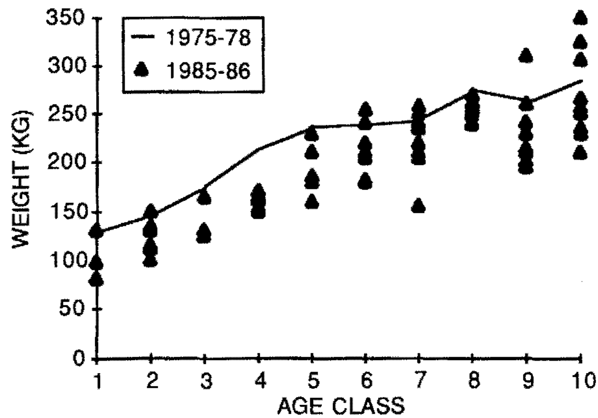

Figure 1. Mean weights of female Steller sea lions collected in 1975-78 compared to individual weights of animals collected in 1985-86.

Total daily food consumption was assumed to average 14.3 kg (Calkins 1986). The estimated amount of pollock consumed declined from 187,000 mt in 1976 to 76,000 mt in 1986. The catch in commercial fisheries increased from 86,500 mt in 1976 to 306,700 mt in 1984 and then declined to 72,800 mt in 1986 (Megrey 1987; Alton et al. 1987). Estimates of sea lion predation, along with total catch by fisheries, are shown in Figure 2.

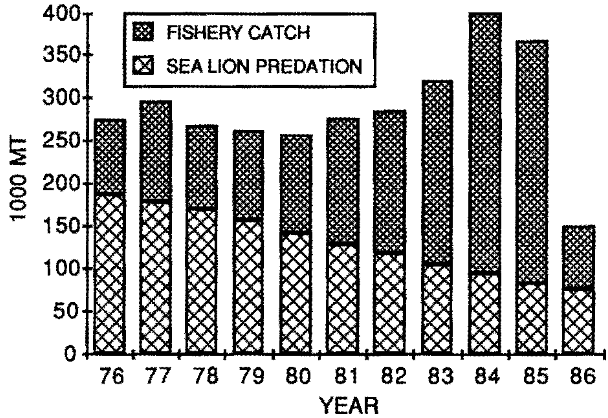

Figure 2. Amounts of walleye pollock eaten by Steller sea lions and removed by commercial fisheries in the Gulf of Alaska, 1976-86.

Removals of pollock due to sea lion predation and commercial catches are shown as a percentage of total exploitable biomass in Figure 3. Estimates of exploitable biomass used are from age-structured analysis which generally correspond well with hydroacoustic surveys that have been conducted at intervals since 1981 (Megrey 1987). The estimates for 1980 and before cannot be entirely verified but several sources of information point to an increase in pollock abundance in the late 1970's, mostly due to a succession of strong year classes in 1975-79 (Alton et al. 1987). Total percent removals were high in 1976-77 but declined greatly for the period 1979-82, due in part to reduced sea lion predation, but mostly to the large increase in biomass. Percentage removals increased greatly in 1983-86 due to increased commercial catches and declining stock size, and in spite of reduced sea lion predation. Total removals in 1985 (367,000 mt) were equal to 53% of the estimated total exploitable biomass (687,000 mt). Percentage removal was still high in 1986 (40%) in spite of absolute reductions in predation and fishery catches. In 1986, the estimated amount of pollock consumed by sea lions (76,000 mt) exceeded the catch by fisheries (73,000 mt). These data suggest that the decline in the Gulf of Alaska pollock stock was due not only to weak age classes in 1980-82 (Megrey 1987), but also to excessive harvests by the fisheries, and a depensatory effect of sea lion predation.

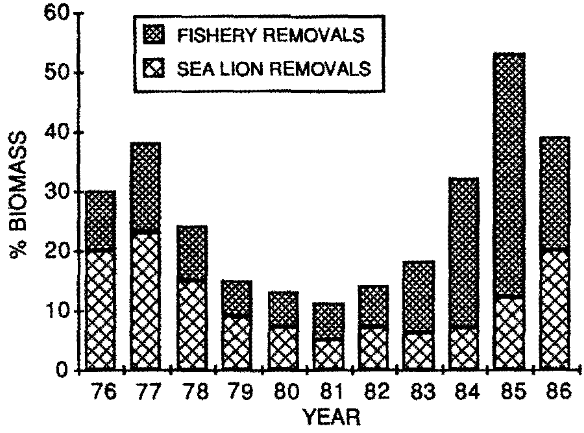

Figure 3. Amounts of walleye pollock eaten by Steller sea lions and removed by commercial fisheries in the Gulf of Alaska, 1976-86, expressed as percent of the estimated exploitable biomass.

Sea lions in the Gulf of Alaska are now less robust (Table 5), they have declined in overall abundance (Merrick et al. 1987), and pup production is greatly reduced on rookeries such as Marmot Island (Calkins and Goodwin 1988; Loughlin unpublished data) which is near Shelikof Strait where recent catches of pollock have been greatest. We recognize that changes in sea lion numbers do not correlate perfectly with apparent changes in pollock abundance. In particular we cannot say what food resources supported the large sea lion population that existed in the 1950's and 1960's if pollock stocks were small. Factors other than commercial fishing may have contributed to the sea lion population decline (Merrick et al. 1987). However, recent studies suggest that the cause is related to nutrition and largely discount effects of disease (Calkins and Goodwin 1988). Regardless of what importance various factors have had in the population decline, with reduced growth rates and lowered productivity the sea lion stock is more likely to continue its decline than to increase in abundance, because it is at, or above, its current carrying capacity level in terms of food. Furthermore, the present pollock stock is far from adequate to support the number of sea lions that occurred in the central and western Gulf of Alaska in the mid-1950's. We estimate that, if pollock composed 50% of their diet, the number of sea lions that occurred in the area at that time (about 118,000) would eat about 308,000 mt, which is almost equal to the current total exploitable biomass. Such a level of predation would obviously not be sustainable.

Conclusions

The data that are available allow a general consideration of the importance of pollock in marine mammal diets. A review of these data indicates that walleye pollock are generally of minor importance to cetaceans, but can be a major component of the diet of pinnipeds, especially Steller sea lions, northern fur seals, and harbor seals. Harbor seals and fur seals eat mostly small pollock, while sea lions eat mostly medium- and large-sized fishes. We note that data on diet composition are limited in many areas and seasons, and there is almost no information on prey selection (by species or size), or the energetic consequences of variations in prey availability.

The fisheries for pollock in the Bering Sea and the Gulf of Alaska have developed rapidly in recent years. Over the same period of time there have been population declines in northern fur seals (Fowler 1982), Steller sea lions (Merrick et al. 1987), and harbor seals (Pitcher 1986, and in prep.) in these areas. It is difficult to correlate changes in marine mammal populations with pollock fisheries for several reasons. First of all, both the Gulf of Alaska and Bering Sea are complex ecosystems, with large and diverse assemblages of fishes, marine mammals, and seabirds. Considerable annual variation occurs in the size of invertebrate and vertebrate populations, as well as in meteorologic and oceanographic processes. Possible correlations may be masked by simultaneous changes occurring in several ecosystem components. Marine mammals show a certain degree of dietary plasticity and may be able to compensate to some extent for a decline in one prey species by shifting to another. However, the limits on such switching and the possible long-term effects are unknown. Marine mammals are long-lived species that can store a substantial amount of energy in the form of blubber. We do not know how physical measurements and vital parameters will respond to food limitations, and responses may sometimes be obscured by time lags. The data we have on fish and marine mammal populations are limited and sometimes of unknown reliability. Estimates of the size of pollock stocks in the 1960's and early to mid-1970's are based on very limited trawl data and model projections. There are virtually no data available on the biology of sea lions in the Bering Sea, and the 2 significant studies conducted in the Gulf of Alaska were done 7 years apart, during which time the pollock stock increased, peaked, and then declined. Finally, the data we have and try to use may not be of the appropriate scale. For example, it may be of little or no significance to fur seals or sea lions that the total biomass of pollock is large if the density and size distribution of fishes near the locations where they feed are not adequate.

We think that the data reviewed in this paper are adequate to conclude that there has been a significant interaction between Steller sea lions and commercial fisheries for walleye pollock at least in the Gulf of Alaska. A reduction in availability of pollock, particularly medium- and large-sized fishes, has caused nutritional stress in sea lions, resulting in lower growth rates, delayed maturation, and reduced pup production. In the Gulf of Alaska the combined removals by predators and the fisheries appear to have exceeded the sustainable yield, and there is reason to think that sea lion predation may now be having a depensatory effect on the pollock stock. Since sea lions and the fisheries remove similar size classes of pollock, we suggest that, rather than considering sea lion predation as a component of natural mortality, models used for management should treat sea lion predation in the same manner as removals by fishing. This type of approach has been suggested by Sissenwine et al. (1984) and Beverton (1985).

Although walleye pollock make up a substantial portion of the diet of harbor seals and northern fur seals, it is less likely that their population declines have been directly caused by the pollock fishery. However, since several of their main dietary items are commercially exploited, fisheries, in aggregate, may affect their populations. Even if pollock fisheries do not directly impact these species, fisheries that harvest pollock stocks at or near maximum sustainable yield levels may retard or prevent population recovery. A population must not be food limited in order for the density-dependent responses (i.e., increased growth and survival, decreased age of sexual maturity and mortality) required for population growth to occur.

A final consideration in regard to interactions between marine mammals and pollock fisheries involves administrative and legal constraints imposed by policies and provisions of the Marine Mammal Protection Act (MMPA). The MMPA encourages resource management based on ecosystem principles. This has yet to become a reality since most fisheries are managed on single species considerations, with no explicit provisions for maintaining adequate food supplies for other consumers. Perhaps of more proximate concern is the MMPA requirement that marine mammals be maintained within what is called the optimum sustainable population range. Populations that drop below this range are classified as depleted; the Pribilof Islands population of northern fur seals was listed as depleted in May 1988. While the MMPA allows agencies to permit the taking of marine mammals incidental to commercial fisheries, such taking is not allowed if the population is depleted. Therefore, reduced populations of marine mammals may impact operations of commercial fisheries, whether or not fisheries were the cause of the decline.

The interrelationships among marine mammals and fisheries are complex, and a myriad of possible biological and administrative problems are obvious. This issue has not received adequate attention in past years, and there is a need for continued and comprehensive research programs. There is also a need to develop and implement comprehensive conservation and management plans for marine mammals that include biological sound population objectives, and realistic mechanisms to measure and monitor population status. Where marine mammals interact significantly with commercial fisheries, as is the case with Steller sea lions, management plans for the mammals and the fisheries should be closely integrated.

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