Importance of Walleye Pollock, *Theragra chalcogramma*, in the Diet of Phocid Seals in the Bering Sea and Northwestern Pacific Ocean

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ABSTRACT

In the Bering Sea and northwestern Pacific Ocean all species of phocid seals feed on walleye pollock. Pollock has been one of the most important foods of harbor seals sampled at the Pribilof Islands, in Bristol Bay, and in the eastern Aleutian Islands. Ice-associated seals, particularly spotted and ribbon seals, feed on pollock in the winter and spring when they inhabit the drifting ice of the Bering Sea. In the Sea of Okhotsk pollock is a significant food for spotted and ribbon seals. The distribution of ringed seals is more coastal and northern, but they regularly feed on small gadid fishes and probably eat pollock when their ranges overlap. Bearded seals feed mostly on invertebrates and bottom fishes, but pollock have been found in their stomachs. Bearded seals consume more pollock in the southern part of the Sea of Okhotsk than in the north. In the eastern Bering Sea, harbor seals eat a wide range of sizes of pollock, but the other species eat mostly small pollock. Data from the Sea of Okhotsk suggest that younger seals eat mostly small pollock, whereas older seals also eat larger fishes. All species of seals also feed on other demersal and schooling fishes, and invertebrates. Overall, pollock is of most importance in the diets of harbor seals, spotted seals, and ribbon seals, and of little importance to bearded and ringed seals. Although some estimates have been made of the total amount of pollock consumed by seals, many of those estimates are based on old and incomplete data and are probably not reliable. Seal predation may affect pollock stocks, and pollock fishing may influence seal populations, but the possible interactions are complex and poorly understood.

Introduction

Five species of seals of the family Phocidae inhabit waters of the Bering Sea and northwestern Pacific Ocean: harbor seal, *Phoca vitulina*; spotted (or larga) seal, *P. largha*; ribbon seal, *P. fasciata*; ringed seal, *P. hispida*; and bearded seal, *Erignathus barbatus*. Harbor seals occur principally in coastal areas south of the normal extent of seasonal sea ice, including the Gulf of Alaska, Bristol Bay, the Aleutian Islands, the Pribilof Islands, the Commander Islands, the Kuril Islands, and the Sea of Japan (Bigg, 1981). Within this broad geographical

Lowry, L. F., V. N. Burkanov, and K. J. Frost. 1996. Importance of walleye pollock, *Theragra chalcogramma*, in the diet of phocid seals in the Bering Sea and northwestern Pacific Ocean, p. 141–151. *In* U.S. Dep. Commer. NOAA Tech. Rep. NMFS 126.

range there may be two subspecies—*P. v. richardsi*, occurring along the coast of western North America, and *P. v. stejnegeri*, in eastern Asia (Shaughnessy and Fay, 1977). The closely related spotted seal spends summer months in more northern coastal waters, and moves to the drifting sea ice in winter and spring (Shaughnessy and Fay, 1977; Lowry et al., 1994). Ribbon seals also associate with drifting sea ice in spring, and are largely pelagic during other times of year (Burns, 1981a). Bearded seals and ringed seals are closely associated with sea ice throughout most of the year. During winter–spring, bearded seals occur principally in moving pack ice (Burns, 1981b) while ringed seals prefer stable, shorefast ice (Frost and Lowry, 1981a).

American, Russian, and Japanese investigators have devoted considerable research effort to the biology of these seal species in the North Pacific Ocean and the Bering Sea. Studies of natural history and biology often produced information on diet composition. The purpose of this paper is to review available information on the foods eaten by phocid seals in this region, with emphasis on the dietary importance of walleye pollock, *Theragra chalcogramma*.

Methods and Materials

Studies on foods of phocid seals in the region of concern have used a variety of sources for specimen material and various techniques for analyzing samples and data. Samples collected in Alaska have come principally from animals taken for subsistence by coastal Eskimos, and from animals collected for scientific research. Most of the samples in Russian and Japanese studies have come from scientific studies conducted in conjunction with commercial seal harvesting.

Diet has generally been analyzed by examining and identifying the material taken from stomachs or intestines. In cases where food was well digested, identifications have usually been based on characteristic hard parts. The sagittal otoliths of walleye pollock are relatively robust and easy to identify (Frost, 1981). Regression equations have been published and used to estimate the sizes of pollock consumed from otolith measurements (Frost and Lowry, 1986). For this paper, pollock lengths were estimated from otolith lengths by means of the formulas in Frost and Lowry (1981b) as follows:

for otoliths ≤10 mm long, fish fork length (cm) = 2.246 (otolith length [mm]) – 0.51

for otoliths >10 mm long, fish fork length (cm) = 3.175 (otolith length [mm]) - 9.77

There are many methods for quantifying diet composition (see review by Pierce and Boyle, 1991). The most straightforward are the apparent number of prey eaten (based on counts of whole items or unique parts) and the percent frequency of occurrence (number of samples in which a prey occurred, divided by the total number of samples examined, times 100). When stomachs with substantial contents are analyzed, the percent of total volume made up by a particular prey type can be calculated. All of these measures are biased because of differences in detectability and digestibility of prey. Various techniques have been used to correct for bias and produce more realistic estimates of the actual amounts of different prey species that were consumed (Pierce and Boyle, 1991). Most of the results presented in this paper will be given as number of prey eaten, percent frequency of occurrence, or percent volume.

Results and Discussion _

Occurrence of Pollock in Seal Diets

Harbor Seals—The most comprehensive study of harbor seal foods was conducted in the Gulf of Alaska by Pitcher (1980), who examined 269 stomachs containing food. Overall, pollock was the most important prey, occurring in 21% of the samples and constituting 21% of the total volume. When analyzed by geographical subarea, pollock ranked number 1 in the northeastern gulf, Prince William Sound, and along the Kenai coast; number 2 along the Alaska Peninsula; and number 3 around Kodiak Island.

For other areas in the northwestern Pacific Ocean and Bering Sea, relatively few harbor seals have been collected and examined (see review in Lowry et al.¹). In eight seals collected at Otter Island (central Bering Sea) during April 1979, fish made up 64% of the stomach contents; 44% of the identified fishes were pollock. Pollock have been recorded as prey in seals sampled at Port Moller and Port Heiden in Bristol Bay, and at Akun, Unalaska, and Amchitka Islands in the Aleutians, but sample sizes were too small to evaluate their relative importance. Harbor seals in the Commander and Kuril Islands have been reported to feed on cephalopods and bottom fishes, but the species of fishes were not identified (Burdin²).

Pollock were found in harbor seal stomach samples collected in southeast Hokkaido in 1982–83, but were not one of the top 20 foods in terms of volume or frequency of occurrence (Wada et al., 1992).

¹ Lowry, L. F., K. J. Frost, D. G. Calkins, G. L. Swartzman, and S. Hills. 1982. Feeding habits, food requirements, and status of Bering Sea marine mammals. Council Doc. #19. North Pacific Fishery Management Council, Anchorage, AK, 292 p.

² Burdin, A. Kamchatka Institute of Ecology and Nature Management, Petropavlovsk-Kamchatsky, Russia. Unpubl. data.

Spotted Seals—Bukhtiyarov et al. (1984) presented data on foods of spotted seals collected in the Bering Sea in March–June 1972–78. Pollock were the most important prey in the central Bering Sea (88% of the identified fishes in 4 of 5 seals with stomach contents). Pollock occurred less frequently in seals from the southeastern Bering Sea (6 of 14) and the northern Bering Sea (1 of 12). Other studies (reviewed in Lowry et al.¹) also indicate that pollock are not important in the diet of spotted seals in the northern Bering Sea. Lowry et al.³ found pollock in all 12 spotted seals collected in the central Bering Sea in March 1985, and pollock made up 58% of all identified fishes. Lowry et al. also reported pollock in 1 of 3 seals collected in the western Bering Sea in April 1985.

Most of the information on foods of spotted seals in the western Bering Sea and Sea of Okhotsk comes from Russian studies that harvested seals from vessels operating in the pack ice during spring and early summer. In the western Bering Sea (Gulf of Anadyr and Karaginskiy Gulf) during the late 1960's, pollock occurred in 9% of the spotted seal stomachs examined, and octopus was the most commonly occurring food (Gol'tsev, 1971). Bukhtiyarov (1983) reported that pollock made up 5% of the diet in the Gulf of Anadyr. During the early 1980's, Trukhin et al. (1991), like Gol'tsev, found that octopus was the most important food in the Gulf of Anadyr and that saffron cod (Eleginus gracilis), followed by pollock, were the most commonly eaten fishes. In Karaginskiy Gulf, Trukhin et al. (1991) found that fish occurred in 75% of stomachs with food but that pollock were found in only 7%. Bukhtiyarov (1983) reported that pollock made up 35% of the overall spotted seal diet in Karaginskiy Gulf. Bukhtiyarov (1986) estimated that 24% of the diet of spotted seals in the Bering Sea consisted of pollock.

In the western Bering Sea, young seals beginning to feed independently ate mostly small pollock and other schooling fishes such as sand lance, *Ammodytes* sp., and saffron cod (Trukhin, 1986).

In the Sea of Okhotsk, pollock made up 83% of the total volume of stomach contents from 19 spotted seals collected in the pack ice off northern Hokkaido in April (Wilke, 1954). Pollock also occurred in spotted seal stomach samples collected in northeastern Hokkaido during the fall of 1992 and 1993, but was not one of the top 20 foods in terms of volume or frequency of occurrence (Wada et al., 1992).

In the southwestern Sea of Okhotsk, including the Gulfs of Aniva and Terpeniy near Sakhalin Island,

Bukhtiyarov (1990) identified 24 species of prey in 222 stomachs with food collected during spring 1974–77. The most important foods were saffron cod and sand lance; pollock were found in only 5% of the stomachs. In the central and northern Sea of Okhotsk the most important food was pollock (65–91% frequency of occurrence). The measured amount of pollock in individual stomachs ranged from 100 to 4,000 g (Fedoseev and Bukhtiyarov, 1972; Popov and Bukhtiyarov, 1975).

In summer, stomachs were examined from spotted seals taken in scientific collections in coastal areas of the northern and eastern part of the Sea of Okhotsk, and the frequency of occurrence of pollock was 6–9% (Bukhtiyarov, 1984; Burkanov, 1990). Near the Kamchatka coast in the eastern part of the Sea of Okhotsk, the most important foods during summer were salmon, *Oncorhynchus* spp., and arctic char, *Salvelinus alpinus*. In the southeastern Sea of Okhotsk near the Kuril Islands, Panina (1966) found pollock in 10% of the stomachs she examined.

Information from the Sea of Okhotsk shows clear seasonal variation in the importance of pollock in the spotted seal diet. Pollock is most important in spring, particularly in the northern part. The picture is less clear for the southern Sea of Okhotsk, where pollock made up most of the contents in samples from the late 1940's and only a small portion of samples from the mid-1970's. In summer, pollock is much less important in the diet in the northern Sea of Okhotsk. In the southeastern area during summer, salmonids, rather than pollock, make up most of the spotted seal diet. Overall, Bukhtiyarov (1986) estimated that pollock made up 30% of the total mass of food eaten by spotted seals in the Sea of Okhotsk.

In the northern part of the Sea of Japan (Tartar Strait) the frequency of occurrence of pollock was 85% (Gol'tsev, 1971; Kosygin and Gol'tsev, 1971). In Peter the Great Gulf, pollock was not found in the spotted seal diet (Gol'tsev, 1971).

Ribbon Seals—Frost and Lowry (1980) reported on the diet of ribbon seals in the Bering Sea from samples collected during March–June 1976–79. Pollock was the most important prey item in the south central and central regions (89% of the total number of fishes and 50% of the total corrected weight, in 9 seal stomachs with food in the south central Bering Sea; 55% by number and 28% by weight, in 12 seals with food in the central Bering Sea). Pollock occurred in only one of seven seals with food collected in the northern Bering Sea. In contrast, Shustov (1965) did not find pollock to be an important food in the ribbon seals he examined from the central Bering Sea in 1961–63 (32 with food).

Trukhin et al. (1991) collected samples from ribbon seals in Karaginskiy Gulf during spring 1982 and found pollock in 4 of 18 stomachs with food. In the Gulf of

³ Lowry, L. F., K. J. Frost, and J. J. Burns. 1986. Assessment of marine mammal-fishery interactions in the western Gulf of Alaska and Bering Sea: consumption of commercially important fishes by Bering Sea pinnipeds. Final Rep. to NMFS, Contract NA-85-ABH-00029, 26 p.

Anadyr, pollock was reported to be the second most important food based on frequency of occurrence, but no figures were given. Overall, Bukhtiyarov (1986) estimated that pollock made up 13% of the total mass of food eaten by ribbon seals in the Bering Sea.

Arsen'ev (1941) examined stomachs with food from 54 ribbon seals collected in the ice of the southwestern Sea of Okhotsk during April–June and found that pollock was the major prey in all three months. Wilke (1954) reported that pollock made up 60% of the total volume of stomach contents in two ribbon seals he examined from the southern Sea of Okhotsk in April 1949. Bukhtiyarov (1990) examined stomachs of ribbon seals collected in the southern Sea of Okhotsk in 1974–77. Pollock was one of 13 identified species of prey and occurred in 12 of 50 stomachs with food. For young seals (1– 2 years old) small pollock were the most important food.

Pollock was also a very important component in the diet of ribbon seals in the northern Sea of Okhotsk. In 1970–71, 42 of 48 stomachs examined contained pollock (Fedoseev and Bukhtiyarov, 1972) and in 1972–73 pollock occurred in 66 of 94 stomachs (Bukhtiyarov, 1978). Overall, Bukhtiyarov (1986) estimated that pollock made up 69% of the total mass of food eaten by ribbon seals in the Sea of Okhotsk.

Ringed Seals—Pollock have not been reported from stomachs of ringed seals collected in the Bering Sea (see review in Lowry et al.¹). Other small gadids (saffron cod, and arctic cod, *Boreogadus saida*) are often very important in ringed seal diets (Lowry et al., 1980b), so pollock may be eaten in areas where their ranges overlap.

Pollock is not very important in the diet of ringed seals in the Sea of Okhotsk (Pikharev, 1946; Fedoseev, 1965; Kosygin et al., 1984; Trukhin et al., 1991). Bukhtiyarov (1984, 1990) examined the stomachs of more than 125 ringed seals collected in the Sea of Okhotsk in spring and found that pollock occurred at a frequency of about 1%. In summer and fall he examined 20 stomachs and found no pollock. Bearded Seals-In general, bearded seals feed on invertebrates and benthic fishes (Lowry et al., 1980a). A few pollock were recorded in stomachs of 15 bearded seals taken north of the Pribilof Islands and near Nunivak Island in 1975-77.¹ Antonelis et al. (1994) found pollock in the stomachs of 7 of 74 bearded seals collected near St. Matthew Island in March-April 1981. In spring samples taken in the northern and eastern Bering Sea during 1963-65, Kosygin (1966, 1971) found pollock in only 1 of 152 stomachs examined. Lowry et al.¹ found no pollock in the stomachs of 173 bearded seals taken in the northern Bering Sea during 1975-79. Trukhin et al. (1991) found pollock in 3 of 31 bearded seals collected in April-May 1982 in Karaginskiy and Anadyr Gulfs. Trukhin et al. stated, however, that pollock play an important role in the diet of bearded seals in the western Bering Sea.

In the southern Sea of Okhotsk during spring 1974– 77, Bukhtiyarov (1990) found pollock in 5% of the stomachs examined (n=63). He stated that pollock play a more important role in the bearded seal diet in the southern Sea of Okhotsk than they do in other regions. Pollock were not found in samples from the northern Sea of Okhotsk in spring (n=72) and summer (n=128) (Fedoseev and Bukhtiyarov, 1972; Bukhtiyarov, 1984).

Sizes of Pollock Consumed

Pitcher (1981) measured otoliths from stomachs of 94 harbor seals collected in the Gulf of Alaska during 1973–78 (Table 1). He reported that the average length of pollock eaten by harbor seals was 19.2 cm, and noted that this was significantly smaller than the pollock eaten by Steller sea lions, *Eumetopias jubatus*, collected in the same regions and years (mean 29.8 cm).

Information on sizes of pollock consumed by seals in other areas is based on relatively few otoliths retrieved from seal stomachs and intestines (Table 1). Frost and

Table 1 Sizes of pollock eaten by phocid seals in the Gulf of Alaska, Bering Sea, and Sea of Okhotsk.						
Species	Location	Number of seals	Number of otoliths	Fork length (cm)		······································
				Mean	Range	Source
Harbor seal	Gulf of Alaska	94	2,030	19.2	4.2-53.2	Pitcher, 1981
	Bering Sea	5	35	24.5	8.2-56.3	Frost and Lowry, 1986
Ribbon seal	Bering Sea	19	468	11.2	6.5-34.4	Frost and Lowry, 1986
Spotted seal	Bering Sea	2	21	10.9	8.0-15.0	Frost and Lowry, 1986
	Sea of Okhotsk	10	26	15.9	2.0-39.1	Burkanov, unpubl. data
Bearded seal	Bering Sea	5	56	11.8	6.9-14.3	Antonelis et al., 1994

Lowry (1986) summarized available data on sizes of pollock eaten by pinnipeds in the Bering Sea. Their data showed that ribbon seals and spotted seals ate almost entirely small pollock, while harbor seals ate all sizes (Fig. 1–3). Data from spotted seals collected in the Okhotsk Sea (Fig. 2) showed a wider range in sizes of pollock eaten (Burkanov, unpubl. data). Antonelis et al. (1994) reported that bearded seals collected in the central Bering Sea had eaten only small pollock (mean length 11.8 cm). Bukhtiyarov (1984, 1990) stated that all the pollock found in ringed seals collected in the Sea of Okhotsk in spring were small.

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This information suggests that most phocid seals eat predominantly small pollock. Harbor seals, which eat all sizes of pollock, are the principal exception. Because of the exponential relation between pollock length and weight, however, the few larger fishes that are eaten may be of considerable nutritional significance. We used the formula in Frost and Lowry (1981b) to estimate the weights of pollock eaten by harbor seals in the central Bering Sea in April 1979. Although only 11 of the 23 pollock eaten were estimated to be over 30 cm long, those fishes contributed 84% of the estimated biomass consumed.

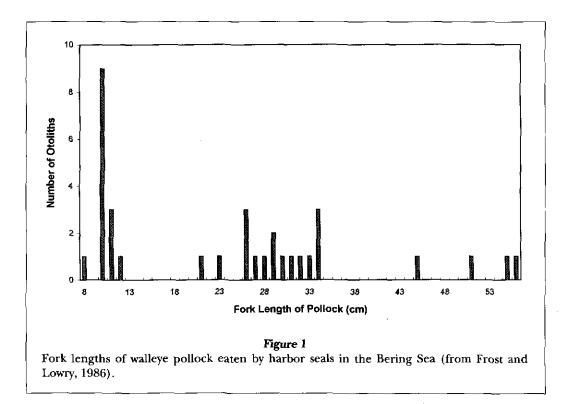
Quantities of Pollock Consumed

Simple calculations of the amount of food consumed by pinnipeds are often based on estimates of population sizes and daily food consumption rates. More detailed studies may take into account the size structure of the pinniped population, metabolic requirements, and caloric values of various prey (e.g., Perez and McAlister, 1993). Information on diet composition can then be used to estimate the amount of a particular prey that is eaten annually.

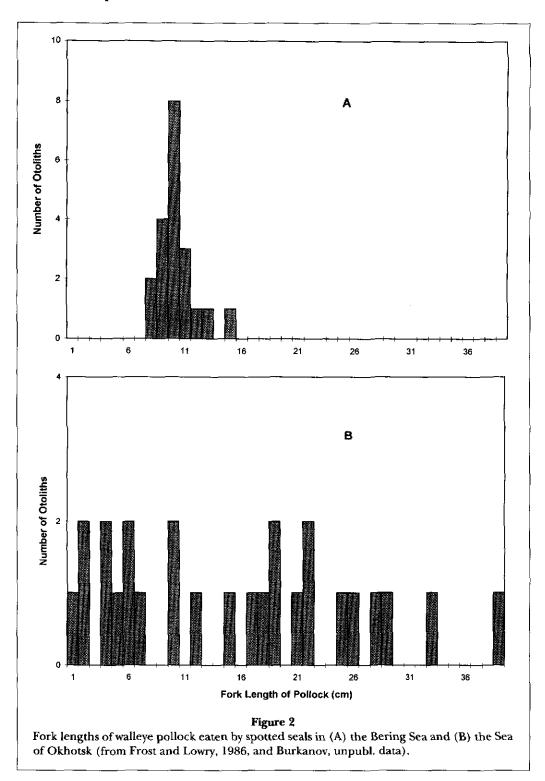
The only estimate of the amount of pollock eaten by harbor seals in the Gulf of Alaska is that by Lowry et al. (1989), who estimated that 72,800 metric tons (t) were consumed annually. Their calculations were based on population size and diet data from the late 1970's provided in Calkins (1986) and Pitcher (1980), and may not reflect the current consumption level.

Ashwell-Erickson and Elsner (1981) used energy-flow models to estimate that harbor seals consumed 34,700 t of pollock in the Bering Sea each year, and that spotted seals consumed 46,900 t (Table 2). Frost and Lowry (1980) used diet composition, daily ration, and population size to estimate that ribbon seals could consume 55,000 t of pollock per year in the Bering Sea. Lowry et al. (1989) produced estimates of pollock consumed by ribbon seals that were much lower than Frost and Lowry's (1980) estimates, partly because Lowry et al. included only the eastern section of the Bering Sea.

Bukhtiyarov (1986) estimated that the average amount of pollock eaten by a ribbon seal each day in the Bering Sea was 1.1 kg, and in the Sea of Okhotsk 7.4 kg. Corresponding estimates for spotted seals were 4.2 and

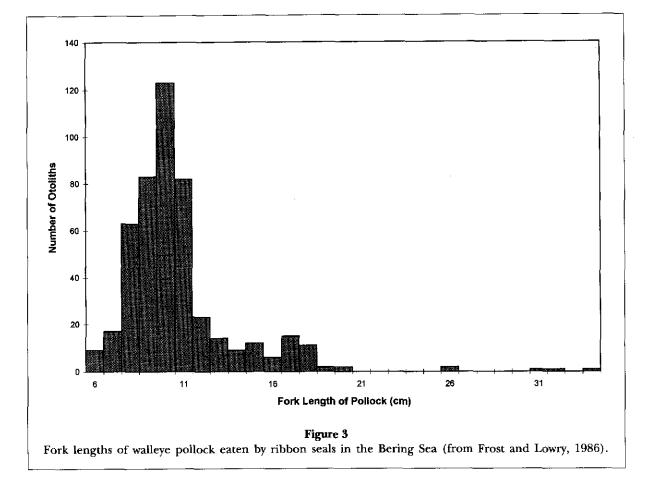






2.2 kg. These figures were used to extrapolate to the annual amounts eaten by the seal populations in each area (Table 2). For the Bering Sea his estimate for spotted seal consumption was nearly twice that derived by Ashwell-Erickson and Elsner (1981), while his ribbon seal estimate was less than that of Frost and Lowry (1980).

The consumption estimates made by Bukhtiyarov (1983) indicated that over 900,000 t of pollock were eaten by seals in the Sea of Okhotsk. Of this, 128,000 t was attributed to spotted seals and 772,000 t to ribbon seals. In another set of calculations, Bukhtiyarov (1990) estimated that during April–June ribbon seals in the



Sea of Okhotsk would eat more than 100,000 t of pollock. Sobolevsky (1983) estimated the total amount of fish eaten each year in that region by spotted seals as 164,000 t and by ribbon seals as 171,000-239,000 t. These estimates are much less than would be expected from the pollock consumption calculated by Bukhtiyarov (1983). For ribbon seals, this may largely be due to the high value that Bukhtiyarov used for per capita food consumption. Applying his estimate of 7.4 kg pollock per day to a diet consisting of 69% pollock results in a total daily food intake of 10.7 kg. We do not consider this a realistic average consumption for a seal whose body weight averages less than 100 kg (Fedoseev, 1973; Burns, 1981a), because maintenance requirements for similar phocids are generally 3-6% of body weight per day (e.g., Markussen et al., 1990).

The variation in estimates of the amount of pollock consumed by phocid seals is largely due to differing assumptions about individual energy requirements, overall diet composition, and population sizes. From the information presented in previous sections it is evident that the dietary data available are fragmentary, and most come from samples collected before the mid-1980's. The situation is similar for population sizes. Most estimates are derived from information collected

Table	2
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Estimates of the amount (metric tons \times 1000) of pollock consumed by phocid seals in the Gulf of Alaska, the Sea of Okhotsk, and the Bering Sea.

Species	Gulf of Alaska	Sea of Okhotsk	Bering Sea	Source
Harbor seal			34.7	Ashwell-Erickson and Elsner, 1981
	72.8		5.3	Lowry et al., 1989*
Spotted seal		127.6	85.9	Bukhtiyarov, 1983
•			46.9	Ashwell-Erickson and Elsner, 1981
			19.2	Lowry et al., 1989*
Ribbon seal		799.2	39.6	Bukhtiyarov, 1983
			55.0	Frost and Lowry, 1980
			11.4	Lowry et al., 1989*

in the 1970's, and in nearly all cases the surveys they come from were not adequately designed or conducted (see reviews in Lowry et al.¹ and Lentfer, 1988). Rea-

sonably good information on relative numbers of harbor seals comes from counts of hauled-out animals (e.g., Pitcher, 1990; Loughlin⁴), but those figures are not population estimates because they do not account for animals not hauled out during surveys. Thus the data needed to generate current estimates of the quantities of pollock being consumed by phocid seals are not available, and we consider that previous estimates are of unknown reliability.

Potential Interactions with Pollock Fisheries

In the late 1970's, pollock was an important food for harbor seals in the Gulf of Alaska. The commercial trawl fishery targeting on pollock developed in the late 1970's, peaked in the early 1980's, and has declined since then. Harbor seal numbers at index areas at Tugidak Island and Prince William Sound have shown a major decline in the 1980's (Pitcher, 1990; Frost et al., 1994). It is not known whether the pollock fishery has been a factor in the harbor seal decline.

The 1993 estimate of the exploitable biomass of pollock in the Gulf of Alaska was 1,062,000 t (Hollowed et al.⁵). The estimate of pollock consumption by harbor seals in Lowry et al. (1989) would represent a significant fraction of that pollock stock. However, that consumption estimate was based on diet and population size data collected during the 1970's, and the amount currently consumed may be much less.

Estimates of the amount of pollock eaten by seals in the Bering Sea are also based on relatively old data on diets and population sizes (Lowry et al., 1989). Harbor seal numbers may be stable in that region,⁴ and the population status of ribbon and spotted seals is not known. Nonetheless, if pinnipeds still consume about 150,000 t of pollock in the Bering Sea annually, that should have little impact on the pollock stock, which had an estimated 1993 exploitable biomass of about 6,700,000 t (Wespestad⁶). In recent years, commercial fisheries have harvested approximately 4 million metric tons of pollock in the Bering Sea annually, and stock abundance has fluctuated largely as a result of variable year-class strengths (Springer, 1992). Because the phocid seals discussed in this paper eat principally small pollock, fisheries should not have a major effect on seal nutrition unless the

Sobolevsky (1983) compared the amount of pollock eaten annually by all species of pinnipeds (including Steller sea lions and fur seals, *Callorhinus ursinus*) in the Sea of Okhotsk (240,000–280,000 t) to estimates of the biomass of pollock (4.0–4.5 million t) and concluded that pinnipeds ate about 6–7% of the total biomass. If the higher estimate of pollock consumption produced by Bukhtiyarov (1983) is used, this figure would be 21– 23% for phocid seals alone.

fisheries affect recruitment or survival of young fishes.

In the Sea of Okhotsk, pollock are very important in the ribbon seal diet and are subject to major commercial fisheries. Nonetheless, during the period from 1981 to 1988 the ribbon seal population in the region is thought to have doubled from 250,000 to 500,000 (Bukhtiyarov, 1990).

Conclusions

Available data allow a general description of the foods eaten by phocid seals in most regions of the northwestern Pacific Ocean and Bering Sea (Table 3). Of the five species discussed in this paper, pollock are of greatest significance in the diets of harbor seals, spotted seals, and ribbon seals. Bearded seals feed mostly on benthic invertebrates and fishes, while ringed seals eat mostly Arctic cod, saffron cod, and crustaceans. For most species, our understanding of the diet is based on irregular and incomplete sampling. We have only limited information to evaluate seasonal, annual, geographical, or sex/age-related variation in pollock consumption.

Available samples make it evident that prerecruit pollock are eaten by all species of seals. Harbor seals and spotted seals also eat larger pollock, while ribbon seals, ringed seals, and bearded seals may eat only small pollock. For most species and areas, few otoliths have been measured, and quantitative data are very limited.

Estimates of the amount of pollock consumed by seals have been calculated with various techniques that have produced quite different results. The estimators mostly used data that are 10–20 years old, and the estimates therefore cannot be considered reliable measures of current pollock consumption.

Phocid seals (and other marine mammals) consume large amounts of prerecruit and older pollock in the northwestern Pacific Ocean and Bering Sea. It is not clear whether or how this predation may affect pollock stocks and their ability to withstand fishery harvests.

⁴ Loughlin, T. R. 1992. Abundance and distribution of harbor seals (*Phoca vitulina richardsi*) in Bristol Bay, Prince William Sound, and Copper River delta during 1991. Unpubl. Annu. Rep. NMFS Population Assessment Program, Nat'l. Marine Mammal Lab., Alaska Fish. Sci. Cent., NMFS/NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070, 26 p.

⁵ Hollowed, A. B., B. A. Megrey, and E. Brown. 1993. Walleye pollock. In Stock assessment and fishery evaluation report for groundfish resources of the Gulf of Alaska as projected for 1994, p. 1–54. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

⁶ Wespestad, V. G. 1993. Walleye pollock. *In* Stock assessment and fishery evaluation report for groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1994, p. 1–26. North Pacific Fishery Management Council, Anchorage, AK.

Table 3

Principal foods of seals in the Gulf of Alaska, the Bering Sea, and the Sea of Okhotsk, listed in approximate order of overall importance. From Pitcher (1980), Lowry et al.,¹ Bukhtiyarov (1984, 1986, 1990), and Trukhin et al. (1991).

Species	Gulf of Alaska	Eastern Bering Sea	Western Bering Sea	Northern Bering Sea	Sea of Okhotsk
Harbor seal	Pollock Octopus Capelin Eulachon Herring	Pollock Octopus Pacific cod Sculpins Sand lance	Octopus Squid Rockfishes		
Spotted seal		Pollock Capelin Herring Eelpout Sculpins	Pollock Arctic cod Sand lance Saffron cod Herring	Arctic cod Capelin Saffron cod Sculpins Herring	Pollock Saffron cod Sand lance Shrimps Octopus
Ribbon seal		Pollock Eelpout Capelin Shrimp Flatfish	Pollock Squid Saffron cod Shrimp	Arctic cod Saffron cod Sculpins Pollock	Pollock Saffron cod Shrimps Squid
Ringed seal		Saffron cod Mysids Sculpins Shrimp	Capelin Sand lance Saffron cod Amphipods Shrimp	Arctic cod Saffron cod Shrimp Mysids Amphipods	Euphausiids Shrímp Saffron cod Pollock
Bearded seal		Shrimp Crabs Sculpins Isopods Pollock	Shrimp Crabs Octopus Clams Saffron cod	Shrimp Clams Crabs Sculpins Arctic cod	Crabs Shrimp Clams Saffron cod Pollock

Conversely, without a detailed understanding of how pollock fisheries affect the availability of pollock for foraging seals, it is not possible to assess whether fishing has had or may have an impact on seal populations.

Acknowledgments ____

We thank the many people who helped with the collection and analysis of seal foods. Many of the samples collected by U.S. investigators were obtained as part of the NOAA Outer Continental Shelf Environmental Assessment Program. International collaboration in the preparation of this paper was aided by the U.S.-Russia Agreement on Environmental Protection Project V.6. and the U. S. Department of State. Two anonymous reviewers made helpful comments on the draft manuscript.

Literature Cited _

Antonelis, G. A., S. R. Melin, and Y. A. Bukhtiyarov.

1994. Early spring feeding habits of bearded seals (*Erignathus barbatus*) in the central Bering Sea, 1981. Arctic 47:74–79.

Arsen'ev, V. A.

1941. Feeding of the ribbon seal. Izv. TINRO 20:121–127. [In Russ.]

Ashwell-Erickson, S., and R. Elsner.

1981. The energy cost of free existence for Bering Sea harbor and spotted seals. In D. W. Hood and J. A. Calder, (eds.), The eastern Bering Sea shelf: oceanography and resources. Vol. II, p. 869–899. Univ. Washington Press, Seattle.

Bigg, M. A.

1981. Harbor seal. In S. H. Ridgway and R. J. Harrison (eds.), Handbook of marine mammals, vol. 2. Seals, p. 1–27. Academic Press, Lond.

Bukhtiyarov, Y. A.

- 1978. Some data about feeding of ribbon and spotted seal in the seas of the north part of the Pacific Ocean. *In* Tez. dokl. 7-go Vses. sov. Moskva, p. 52–54. [In Russ.]
- 1983. Feeding of true seals in the Sea of Okhotsk and Bering Sea. Otchet NIR "Sostoyanie zapasov, rasprostranenie i biologiya lastonogikh i kalana" Mo TINRO, Magadan, 113 p. [In Russ.]
- 1984. Feeding of seals in the northern part of the Sea of Okhotsk in summer and fall. *In* Morskie mlekopitaushchie Dalnego Vostoka, p. 23-31. TINRO, Vladivostok. [In Russ.]
- 1986. Diet of true seals in the Sea of Okhotsk and Bering Sea. In Tez. dokl. 9-go Vses. sovesch. po izuch., okhrane i raz. ispolz. mor. mlek., Arkhangelsk, 9–11 Sent. 1986, p. 67–68. [In Russ.]
- 1990. Feeding of seals in the south part of the Sea of Okhotsk. Izv. TINRO 112:96-101. [In Russ.]

Bukhtiyarov, Y. A., K. J. Frost, and L. F. Lowry.

- 1984. New information on foods of the spotted seal, *Phoca* largha, in the Bering Sea in spring. In F. H. Fay and G. A. Fedoseev (eds.), Soviet-American cooperative research on marine mammals, vol. I—Pinnipeds, p. 55–59. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12.
- Burkanov, V. N.
 - 1990. Data on feeding of spotted seals (*Phoca larga* Pal.) in summer and fall near the western coast of Kamchatka. *In* Morskie mlekopitaushchie, p. 49–56. VNIRO, Moskva. [In Russ.]
- Burns, J. J.
 - 1981a. Ribbon seal. In S. H. Ridgway and R. J. Harrison (eds.), Handbook of marine mammals, vol. 2. Seals, p. 89– 109. Academic Press, Lond.
 - 1981b. Bearded seal. In S. H. Ridgway and R. J. Harrison (eds.), Handbook of marine mammals, vol. 2. Seals, p. 145– 170. Academic Press, Lond.
- Calkins, D. G.
 - 1986. Marine mammals. In D. W. Hood and S. T. Zimmerman (eds.), The Gulf of Alaska: physical environment and biological resources, p. 527–558. Minerals Manage. Serv. Publ. OCS, MMS 86-0095. (Available from Nat. Tech. Info. Service as PB87-103230, U.S. Dep. Commer., Springfield, VA 22161).

Fedoseev, G. A.

- 1965. Nutrition of the ringed seal. Izv. TINRO 59:216–223. [In Russ.]
- 1973. Morphological-ecological characteristics of ribbon seal populations and factors affecting the conservation of usable stocks. Izv. TINRO 86:158-177. [In Russ.]
- Fedoseev, G. A., and Y. A. Bukhtiyarov.
 - 1972. Food of seals of the Okhotsk Sea. In Tez. dokl. 5-go Vses. sovesch. po izuch. mor. mlekop., Chast. 1., Makhachkala, USSR, p. 110–112. [In Russ.]

- 1981. Descriptive key to the otoliths of gadid fishes of the Bering, Chukchi, and Beaufort Seas. Arctic 34:55-59.
- Frost, K. J., and L. F. Lowry.
 - 1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Can. J. Zool. 58:1601-1607.
 - 1981a. Ringed, Caspian, and Baikal seals. In S. H. Ridgway and R. J. Harrison (eds.), Handbook of marine mammals, vol. 2. Seals, p. 29-54. Academic Press, Lond.
 - 1981b. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fish Bull. 79:187-192.
 - 1986. Sizes of walleye pollock, *Theragra chalcogramma*, consumed by marine mammals in the Bering Sea. Fish Bull. 84:192-197.
- Frost, K. J., L. F. Lowry, E. H. Sinclair, J. VerHoef, and
 - D. C. McAllister.
 - 1994. Impacts on distribution, abundance and productivity of harbor seals. In T. R. Loughlin (ed.), Marine mammals and the Exxon Valdez, p. 97–118. Academic Press, N.Y.
- Gol'tsev, V. N.
- 1971. Feeding of spotted seals. Ecologiya 2:62-70. [In Russ.] Kosygin, G. M.
 - 1966. Some data on feeding of bearded seals in the Bering Sea in spring and summer. Izv. TINRO 58:153-158. [In Russ.]
 - 1971. Feeding of bearded seals, *Erignathus barbatus nauticus* (Pallas), in the Bering Sea in spring and summer. Izv. TINRO 75:144-151. [In Russ.]

Kosygin, G. M., and V. N. Gol'tsev.

1971. Data on the morphology and ecology of spotted seals

in Tatarsky Strait. In Issledovaniya morskikh mlekopitaushchih, p. 238-251. Kaliningrad. [In Russ.]

- Kosygin, G. M., S. I. Lagerev, and A. M. Trukhin.
 - 1984. Data on the biology of pinnipeds in the Bering Sea (ZRS Zybovo 1982). In NIR po morskim mlekopitaushchim Severnoi chasti Tikhogo Okeana v 1982/83 g, p.42– 46. VNIRO, Moskva. [In Russ.]
- Lentfer, J. W. (ed.).
 - 1988. Selected marine mammals of Alaska. Species accounts with research and management recommendations. U.S. Marine Mammal Commission, Washington, DC, 275 p.
- Lowry, L. F., K. J. Frost, and J. J. Burns.
 - 1980a. Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. Arctic 33:330-342.
 - 1980b. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Can. J. Fish. Aquat. Sci. 37:2254-2261.
- Lowry, L. F., K. J. Frost, R. Davis, R. S. Suydam, and D. P. DeMaster. 1994. Movements and behavior of satellite-tagged spotted seals (*Phoca largha*) in the Bering and Chukchi Seas. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-38, 71 p.

Lowry, L. F., K. J. Frost, and T. R. Loughlin.

1989. Importance of walleye pollock in the diets of marine mammals in the Gulf of Alaska and Bering Sea, and implications for fishery management. *In* Proc. Int. Symp. Biol. Manage. Walleye Pollock, p. 701-726. Alaska Sea Grant Rep. 84-1.

Markussen, N. H., M. Ryg, and N. A. Oritsland.

- 1990. Energy requirements for maintenance and growth of captive harbor seals, *Phoca vitulina*. Can. J. Zool. 68:423– 426.
- Panina, G. K.
 - 1966. Nutrition of sea lion and seals on Kuril Islands. Izv. TINRO 58:235-236. [In Russ.]
- Perez, M. A., and W. B. McAlister.
 - 1993. Estimates of food consumption by marine mammals in the eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-14, 36 p.
- Pierce, G. J., and P. R. Boyle.
 - 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanogr. Mar. Biol. Annu. Rev. 29:409– 486.
- Pikharev, G. A.
 - 1946. Nutrition of ringed seal. Izv. TINRO 22:259–261. [In Russ.]

Pitcher, K. W.

- 1980. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Fish. Bull. 78:544-549.
- 1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull. 79:467-472.
- 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. Mar. Mamm. Sci. 6:121-134.

Popov, V. N., and Y. A. Bukhtiyarov.

- 1975. Age related changes in feeding and helminth fauna of spotted seals in the Sea of Okhotsk. *In* Morskie mkekopitaushchie: Mat. 6-go Vses. soveschaniya, p. 62-64. Kiev. [In Russ.]
- Shaughnessey, P. D., and F. H. Fay.
 - 1977. A review of the taxonomy and nomenclature of North Pacific harbour seals. J. Zool. (Lond.) 182:385-419.
- Shustov, A. P.
- 1965. The food of ribbon seals in the Bering Sea. Izv. TINRO 59:178–183.

Sobolevsky, E. I.

1983. Marine mammals of the Sea of Okhotsk; distribution,

Frost, K. J.

Lowry et al.: Importance of Walleye Pollock in the Diet of Phocid Seals in the Bering Sea and Northwestern Pacific Ocean 151

numbers, and their importance as predators. Biologiya Morya 5:13-20. [In Russ.]

Springer, A. M.

· · · · · ·

1992. A review: walleye pollock in the North Pacific—how much difference do they really make? Fish. Oceanogr. 1:80–96. Trukhin, A. M.

1986. Information on the feeding of young spotted seals. In Tez. dokl. 9-go Vses. sovesch. po izuch., okhrane i raz. ispolz. mor. mlek., Arkhangelsk, 9–11 Sent. 1986, p. 398–399. [In Russ.]

Trukhin, A. M., A. I. Makhnyr', and V. A. Pavluchkov.

1991. Feeding of true seals in the Bering Sea in spring and summer. *In* Biologiya ryb i bespozvonochnykh severnoi chasti tikhogo okeana, p. 128–142. Vladivostok. [In Russ.]

Wada, K., T. Hamanaka, T. Nakaoka, and K Tanahashi.

1992. Food and feeding of Kuril and Largha seals in southeastern Hokkaido. Mammalia 56:555–566.

Wilke, F.

1954. Seals of northern Hokkaido. J. Mammal. 35:218-224.