DIET OF NORTHERN FUR SEALS, *CALLORHINUS URSINUS*, OFF WESTERN NORTH AMERICA

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ABSTRACT

Data recorded from the stomach contents of 18,404 northern fur seals, *Callorhinus ursinus*, mostly females aged ≥3 years collected off western North America during 1958-74, were analyzed to determine the relative importance of each prey species by region, subregion, and month. When weighted for energy content, the primary food species were small schooling fishes. Between western Alaska and California from December to August the most significant prey species were northern anchovy, *Engraulis mordax* (20%); Pacific herring, *Clupea harengus pallasi* (19%); capelin, *Mallotus villosus* (8%); Pacific sand lance, *Ammodytes hexapterus* (8%); Pacific whiting, *Merluccius productus* (7%); salmon, *Oncorhynchus* spp. (6%); Pacific saury, *Cololabis saira* (4%); and rockfishes, *Sebastes* spp. (4%). Other food species eaten in this area consisted of a wide variety of squids (17%) and other fishes (7%). In the eastern Bering Sea the main prey species from June to October were juvenile walleye pollock, *Theragra chalcogramma* (35%); capelin (16%); Pacific herring (11%); and squids, *Berryteuthis magister* and *Gonatopsis borealis*, which comprise most (30%) of the remaining diet of northern fur seals in this region. In all areas off western North America, fishes were the main food species of these pinnipeds in neritic waters, while squids were the most important prey in oceanic waters. Typically three prey species comprised 80% of their diet in any one area, although the composition of the diet varied in type and importance by region and month.

The northern fur seal, *Callorhinus ursinus*, is found in the Bering Sea, Sea of Okhotsk, and throughout the North Pacific Ocean, north of approximately lat. 32°N off western North America and lat. 36°N off Asia (Baker et al. 1970; Fiscus 1978). Although its pelagic distribution is extensive, the main concentrations lie over the continental shelf. There are three main stocks of this species. The largest stock breeds on the Pribilof Islands in the eastern Bering Sea and migrates primarily to coastal waters between the Gulf of Alaska and California. The other two stocks breed on the Commander Islands in the western Bering Sea and on Robben Island off northern Japan. Both stocks migrate primarily along the Asian coast. To determine the diet of the Pribilof Islands population, the United States and Canada, under the auspices of the North Pacific Fur Seal Commission, conducted annual pelagic studies during 1958-74 to collect stomach contents and other biological information.

The results of research on the diet of northern fur seals by the United States and Canada during 1958-74 have been presented in many annual and 2-6 yr summaries submitted by each country to the North Pacific Fur Seal Commission. Kajimura (1984) cited most of these reports. Spalding (1964), Stroud et al. (1981), and Kajimura (1985) also published reports on diet collected since 1958. Studies on the food habits of the northern fur seal prior to 1958 include Lucas (1899), Clemens and Wilby (1933), Clemens et al. (1936), Schultz and Rafn (1936), May (1937), Wilke and Kenyon (1952, 1954, 1957), Taylor et al. (1955), and Kenyon (1956).

Investigations to date have reported that northern fur seals eat a wide variety of fishes and squids. However, the relative importance of each prey species has remained uncertain because substantial differences often existed between values of relative importance derived by volumetric measure and those derived by frequency of occurrence. For example, squids were important (averaging 39%) in the diet using frequency of occurrence but not significant (15%) using volume (Bigg and Fawcett 1985; Perez and Bigg[3]). The long-suspected reason for this difference was that squid beaks accumulated

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[3]Perez, M. A., and M. A. Bigg. 1980. Interim report on the feeding habits of the northern fur seal in the eastern North Pacific Ocean and eastern Bering Sea. *In* H. Kajimura, R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg. Further analysis of pelagic fur seal data collected by the United States and Canada during 1958-74, Part 2, p. 4-172. Unpubl. rep. Northwest and Alaska Fisheries Center, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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in stomachs of seals thereby inflating the importance of squid (Scheffer 1950; Spalding 1964; Bigg and Fawcett 1985). Recent experimental studies confirmed that squid beaks accumulate in fur seal stomachs (Bigg and Fawcett 1985).

To date, no reports have been published on the diet of northern fur seals that take this bias into account. However, Bigg and Perez (1985) suggested a method, called modified volume, which reduces the bias and also accounts for differences in digestion rates between fish and squid. In this method, evidence of diet based on trace remains, such as squid beaks and fish bones, is omitted in the analyses, and a combination of the frequency of occurrence and volumetric methods is used to establish the relative importance of individual prey species.

We use the modified volume method in this report to analyze data from the stomach contents collected by the United States and Canada during 1958-74. We will describe the annual diet of northern fur seals in the eastern North Pacific and eastern Bering Sea by region and subregion. We also incorporate the energy content of important prey species to determine whether this might affect relative importance, a procedure not tried previously with this seal.

METHODS

Lander (1980) and Kajimura (1984, 1985) described the methods used to take northern fur seals at sea during 1958-74 and to identify and measure the prey items found in their stomachs by volume and frequency of occurrence. A total of 18,404 stomachs were collected of which 7,373 contained food and an additional 3,326 had only trace remains. Perez and Bigg (fn. 3) summarized the data on volume and frequency of occurrence for all species of northern fur seal prey by month and region.

Perez and Bigg[4] and Bigg and Perez (1985) gave a detailed discussion of the procedure used to calculate modified volume values. First, prey species represented in any stomach only by trace amounts (≤10 cc) were omitted. Second, the proportions of total fish and total squid in the diet by subregion, region, and month were then determined by nontrace frequency of occurrence. Third, the ratio of each species within only the fish category and within only the squid category was determined by volume. The taxonomic groupings recorded in the original data which overlapped each other were either pooled with higher taxa or were proportionally divided among component species depending upon which level of taxa had the most data. This prevented food groupings from being partially compared against themselves. Next, the volumetric ratios for individual fish and squid species were adjusted to sum, respectively, to the total proportion of fish and squid in the diet. Finally, all values were readjusted to total 100%.

The relative importance of prey species has been presented in this report in two ways: 1) modified volume values for each region by month, and for each subregion with data from all months pooled; and 2) modified volume values for each region based on combined months data which were weighted for

[4]Perez, M. A., and M. A. Bigg. 1981. Modified volume: a two-step frequency-volume method for ranking food types found in stomachs of northern fur seals. Unpubl. rep., 25 p. Northwest and Alaska Fisheries Center, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

TABLE 1.—Estimated energy values (wet mass) for important northern fur seal prey. C = bomb calorimetry combustion value; P = proximate analysis value[1]; muscle = edible portion only of raw material; whole = raw material from entire specimen.

Prey	Energy value (kcal/g)	Analysis and tissue	Reference
American shad	2.08	P, muscle	Sidwell (1981)
Pacific herring	2.17	P, whole	Sidwell (1981); Bigg et al. (1978)
Northern anchovy	1.79	P, whole	Sidwell (1981)
Salmonids	2.01	P, muscle	Sidwell (1981)
Capelin	1.31	C, whole	Miller[2]
Eulachon	1.41	P, muscle	Stansby (1976)
Deep-sea smelts	0.76	P, whole	Childress and Nygaard (1973)
Myctophiform fishes	1.58	P, whole	Childress and Nygaard (1973)[3]
Pacific saury	2.20	P, muscle	Sidwell (1981)
Jacksmelt	1.24	P, muscle	Watt and Merrill (1963)
Pacific cod	1.00	P, muscle	Sidwell (1981)
Pacific whiting	1.17	P, whole	Sidwell (1981)
Walleye pollock	1.41	C, whole	Miller[2]
Threespine stickleback	1.15	C, whole	Wootton (1976)
Jack mackerel	1.24	P, whole	Sidwell (1981)
Rockfishes	1.17	P, muscle	Sidwell et al. (1974)
Sablefish	2.17	P, muscle	Sidwell (1981)
Atka mackerel	1.58	P, muscle	Kizevetter (1971)
Pacific sand lance	1.22	P, muscle	Sidwell (1981)
Flounders	1.20	P, muscle	Sidwell (1981)[4]
Market squid	1.15	P, muscle	Sidwell (1981)
Onychoteuthid squids	1.29		Perez[5]
Gonatid squids	1.27		Perez[5]

[1]Values were calculated with the following energy factors derived from Watt and Merrill (1963): 9.50, 5.65 and 4.00 kcal/g respectively for fat, protein and carbohydrate.

[2]Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. U.S. Mar. Mammal Comm. Rep. MMC-75/08, 27 p.

[3]Myctophidae and Paralepididae.

[4]Pleuronectidae.

[5]Perez, M. A., Natl. Mar. Mammal Lab., Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, unpubl. data, 1984.

the energy value of prey. Data from all years of collection were pooled. We assumed that the importance of a prey species to northern fur seals depended, at least in part, on its energy content. Table 1 lists the estimated caloric values for prey species consumed most often. These estimates are provisional because little is known about changes in energy content within each species by season. Energy values for squids tend to be lower than those for fishes, although large variability exists among fish species.

No attempt was made to describe diet by age, sex, and reproductive condition. In our sample, 88% of the northern fur seals were females aged ≥3 yr, of which 53% were pregnant and 29% were nonpregnant. Thus, the diet described is primarily that for pregnant and nonpregnant females aged ≥3 yr.

The eastern North Pacific Ocean and eastern Bering Sea were divided into 7 regions and 21 subregions (Fig. 1). The boundaries for the seven regions were those which have been traditionally

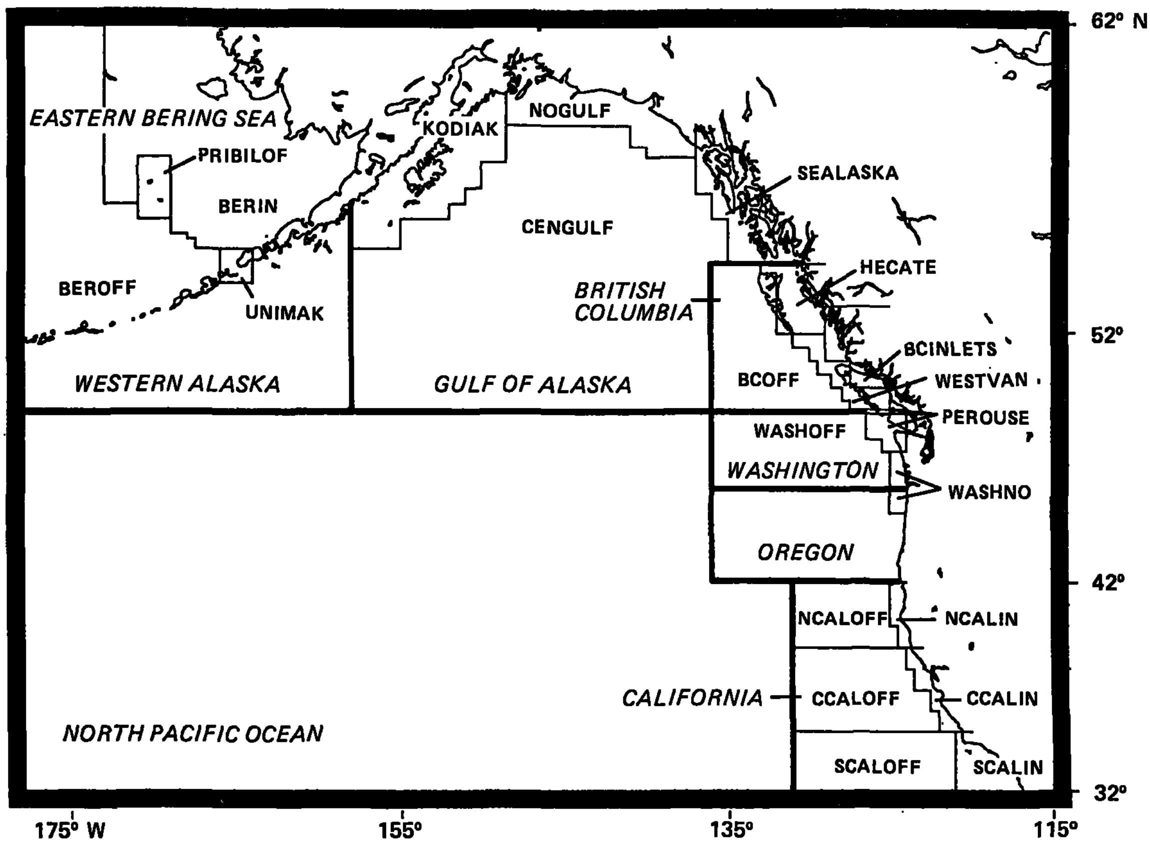

FIGURE 1.—Seven regions (denoted by darker lines) and 21 subregions used in the northern fur seal analyses: 1) California comprised of subregions SCALIN (southern California, inshore), SCALOFF (southern California, offshore), CCALIN (central California, inshore), CCALOFF (central California, offshore), NCALIN (northern California, inshore), and NCALOFF (northern California, offshore); 2) Oregon which includes half of subregion WASHNO (southern Washington and northern Oregon, inshore); 3) Washington which includes subregions PEROUSE (area west of Juan de Fuca Strait from Barkley Sound to Cape Flattery, including La Perouse Bank and Swiftsure Bank; inshore), WASHOFF (Washington, offshore), and half of WASHNO; 4) British Columbia which includes subregions BCINLETS (inside passages and inlets of B.C., inshore), WESTVAN (area west of Vancouver Island and Queen Charlotte Strait, inshore), HECATE (Hecate Strait area, inshore), and BCOFF (British Columbia, offshore); 5) the Gulf of Alaska which includes subregions SEALASKA (southeast Alaska, inshore), NOGULF (northern Gulf of Alaska, including Fairweather Bank; inshore), KODIAK (area around Kodiak Island, including Portlock Bank and Albatross Bank; inshore), and CENGULF (oceanic region of the Gulf of Alaska, offshore); 6) western Alaska which includes part of subregion UNIMAK (Unimak Pass area); and 7) the eastern Bering Sea comprised of subregions BERIN (Bering Sea shelf, inshore) and BEROFF (Bering Sea basin, offshore), and also includes subregions PRIBILOF (area around the Pribilof Islands) and most of UNIMAK. Subregions in which ≥50% of the area is ≤100 fathoms are noted as inshore; the remainder are noted as offshore.

used in analyses of pelagic data for northern fur seals. The subregions were selected to compare diet between inshore (neritic) and offshore (oceanic) areas and to indicate diet in certain localities where collection effort was relatively high. Inshore areas were defined as those generally occurring on the continental shelf (depths up to 100 fathoms) and offshore areas as those beyond the continental shelf.

RESULTS

The cruise tracks (Fig. 2) taken by research vessels of the United States and Canada for the collection of northern fur seals during 1958-74 indicate the relative distribution of research effort. Most collections were made in the coastal areas between California and British Columbia, off Kodiak Island, and in the eastern Bering Sea between Unimak Pass and the Pribilof Islands. Few specimens were taken more than 160 km from shore.

Diet by Region and Month

An examination of the number of prey species that made up the diet indicates that at least nine species may be consumed within any one subregion. However, typically only three prey species made up about 80% of the diet (Fig. 3). Thus, relatively few species of food are of primary importance in any one locality. As will be made clear in the following regional and subregional accounts, the primary food species can change among localities.

Our interpretation of Figures 4-11 which follow requires clarification. These figures show modified volume values only for those individual species that we felt were important and that had sufficient sample sizes to be reliable. Thus, we arbitrarily presented only those species that were of ≥5% in importance for samples with at least 20 stomachs containing food. Species of less importance were pooled either as miscellaneous fishes or squids. Also, be-

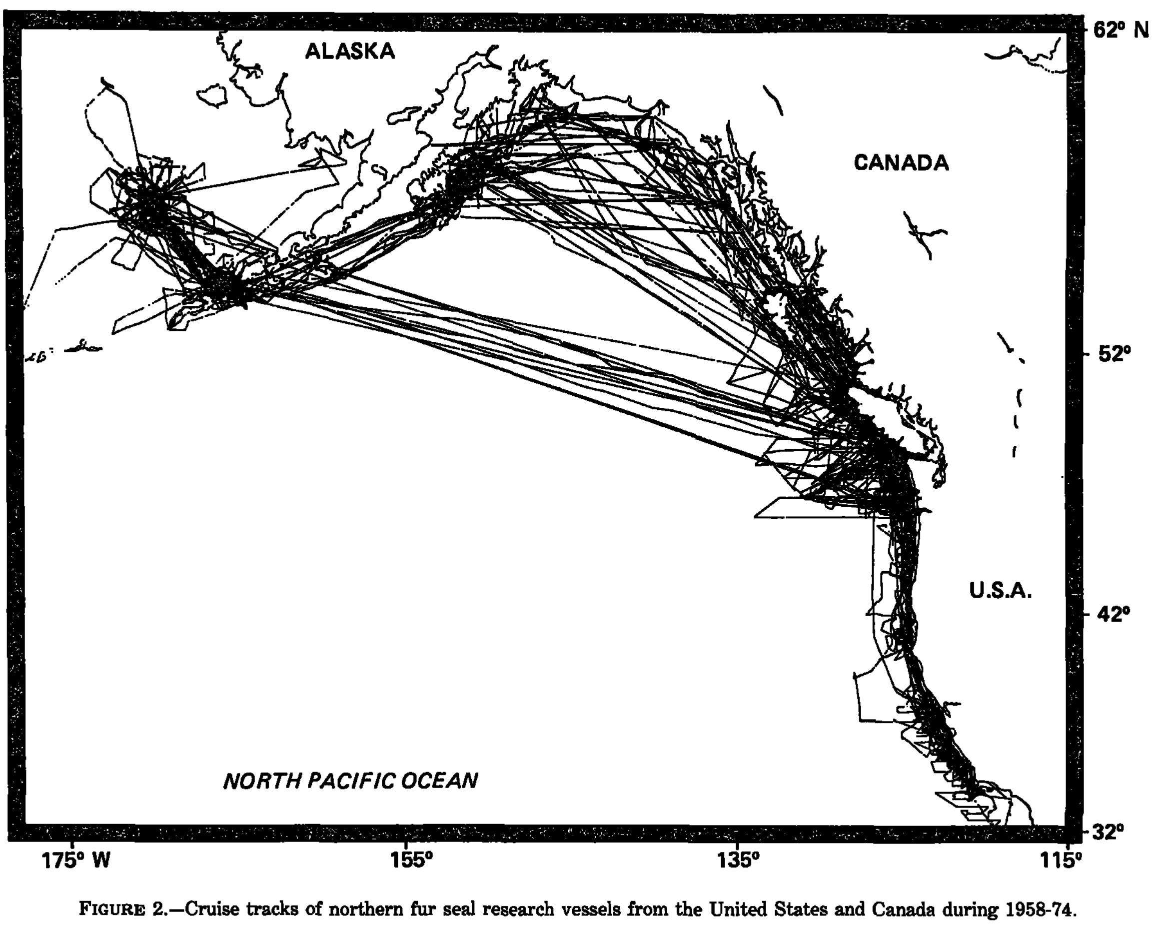

FIGURE 2.—Cruise tracks of northern fur seal research vessels from the United States and Canada during 1958-74.

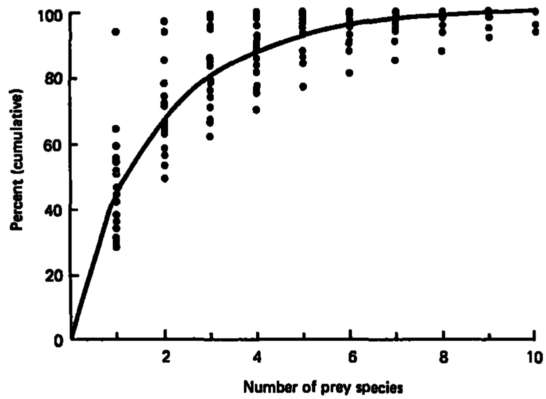

FIGURE 3.—The cumulative percentage distribution of the number of prey species eaten in the total diet of northern fur seals taken during 1958-74. Data for each of the 21 subregions are plotted, although only the average relationship is graphed.

cause the prey consumed by month within subregions were not presented here, we take these data from Perez and Bigg[5] in our interpretation of subregional data.

California

Northern anchovy, *Engraulis mordax*, was the most important food eaten by the northern fur seals off California (Fig. 4A) whether its energy content was considered or not. However, it was more important when its caloric value was taken into account. Northern anchovy was eaten mainly during January to March in inshore and offshore waters of central and southern California (Fig. 4B, C). Pacific whiting, *Merluccius productus*, was second in importance (Fig. 4A) and was preyed upon in all areas of California, although primarily during April and May (Fig. 4B, C). Market squid, *Loligo opalescens*, was eaten from January to June, but only in neritic locations (Fig. 4B, C). Onychoteuthid squids (Onychoteuthidae) were eaten offshore and were the more important squid species consumed in the southern areas off California (Fig. 4C). Other prey types were of relatively minor importance, although some were locally significant, such as Pacific saury, *Cololabis saira*, mainly in oceanic areas off northern and central California (Fig. 4A, B, C).

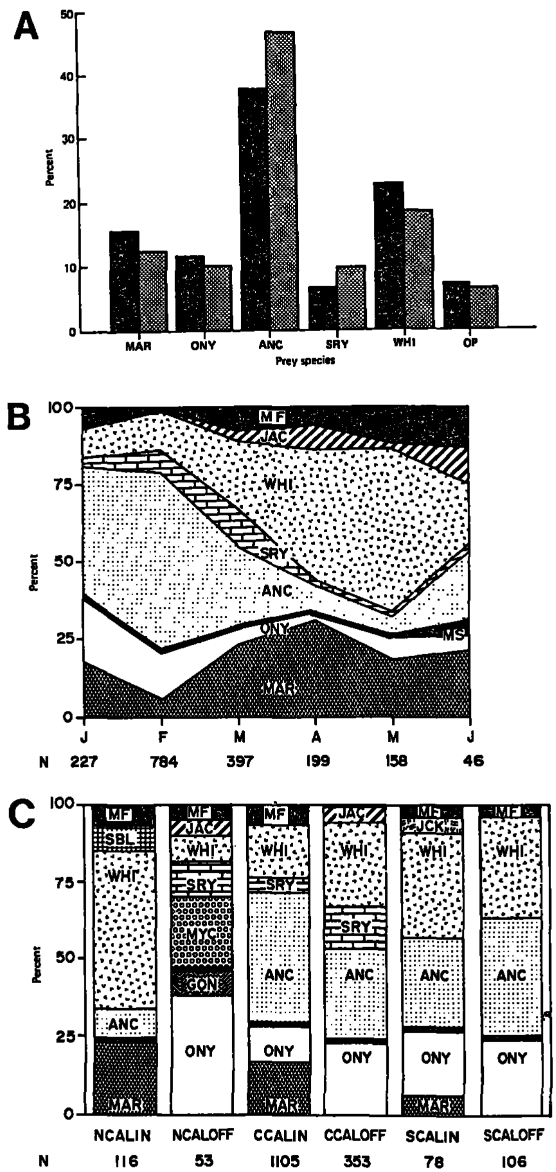

FIGURE 4.—Composition (percent) of diet of northern fur seals by prey species off California during 1958-74 (A) for pooled January-June samples (N = 1,811), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion with pooled January-June samples using modified volume. A dark line separates squid and fish categories in the latter two figures. Key: ANC = northern anchovy; GON = gonatid squids; JAC = jack mackerel; JCK = jacksmelt; MAR = market squid; MF = miscellaneous fish species; MS = miscellaneous squid species; MYC = myctophiform fishes; ONY = onychoteuthid squids; OP = other prey; SBL = sablefish; SRY = Pacific saury; WHI = Pacific whiting.

[5]Perez, M. A., and M. A. Bigg. 1981. An assessment of the feeding habits of the northern fur seal in the eastern North Pacific Ocean and eastern Bering Sea. Unpubl. draft rep., 146 p. Northwest and Alaska Fisheries Center, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Oregon

Only 69 northern fur seals with food in their stomachs were collected in Oregon between January and May during 1958-74, with 58 of these taken during April. Thus, diet could not be determined by month or by inshore and offshore areas. As in California, the main food was northern anchovy (Fig. 5). Other important prey were market squid, onychoteuthid squids, Pacific whiting, and rockfishes (*Sebastes* spp.).

Washington

Pacific herring, *Clupea harengus pallasi*, was the most important food for northern fur seals off Washington, particularly when energy content was considered (Fig. 6A). It was only slightly more significant than rockfishes, salmonids (Salmonidae, primarily *Oncorhynchus* spp.), and northern anchovy when caloric values were not incorporated. Pacific herring was eaten from December to June but only

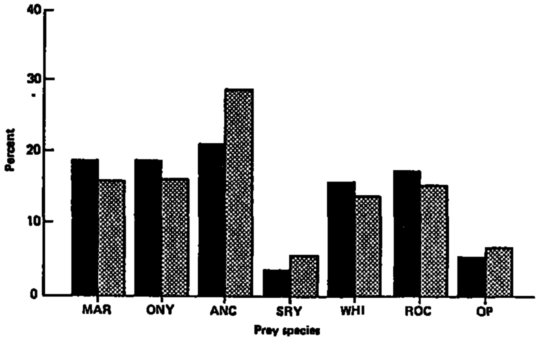

FIGURE 5.—Composition (percent) of diet of northern fur seals by prey species off Oregon during 1958-74 for pooled January-June samples (N = 69), using modified volume (dark bars) and energy-adjusted modified volume. Key: ANC = northern anchovy; MAR = market squid; ONY = onychoteuthid squids; OP = other prey; ROC = rockfishes; SRY = Pacific saury; WHI = Pacific whiting.

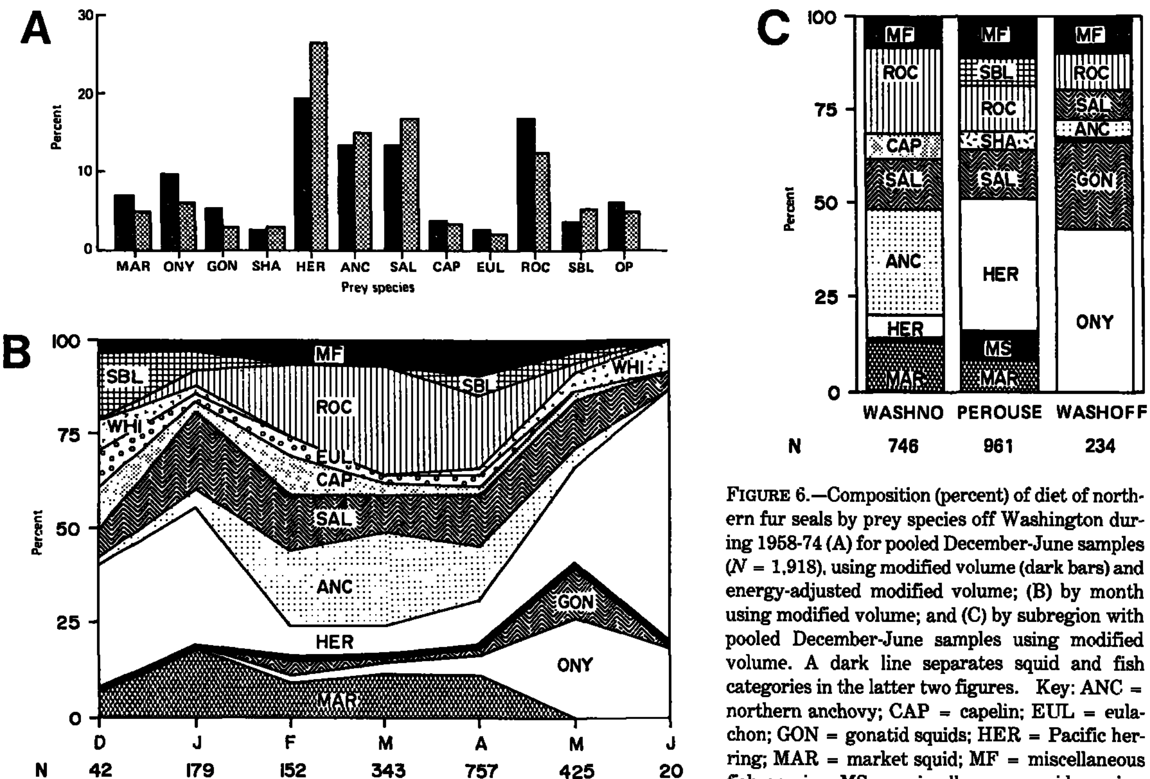

FIGURE 6.—Composition (percent) of diet of northern fur seals by prey species off Washington during 1958-74 (A) for pooled December-June samples (N = 1,918), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion with pooled December-June samples using modified volume. A dark line separates squid and fish categories in the latter two figures. Key: ANC = northern anchovy; CAP = capelin; EUL = eulachon; GON = gonatid squids; HER = Pacific herring; MAR = market squid; MF = miscellaneous fish species; MS = miscellaneous squid species; ONY = onychoteuthid squids; OP = other prey; ROC = rockfishes; SAL = salmonids; SBL = sablefish; SHA = American shad; WHI = Pacific whiting.

in neritic areas (Fig. 6B, C). Rockfishes, salmonids, and northern anchovy were also consumed by seals during this time, both inshore and offshore. Northern anchovy was primarily important in the southern area of the region (Fig. 6C). The main food in oceanic waters consisted of two families of squids, Onychoteuthidae and Gonatidae (Fig. 6C). Market squid was the primary squid species preyed upon in neritic areas.

British Columbia

As in Washington, Pacific herring was the primary food of the northern fur seals from February to June in most inshore areas, particularly when energy content was taken into account (Fig. 7A, B, C). It was mainly consumed by northern fur seals off the west coast of Vancouver Island and in Hecate Strait. In coastal inlets, market squid was important, but not significantly for the region as a whole. The diet of northern fur seals in oceanic waters during May and June was almost exclusively onychoteuthid squids and salmonids (Fig. 7B, C). Other prey species were relatively insignificant (Fig. 7A). However, because the coastline of British Columbia is complex, and sample sizes were small, additional local differences in diet may exist in inshore areas (Fig. 7C).

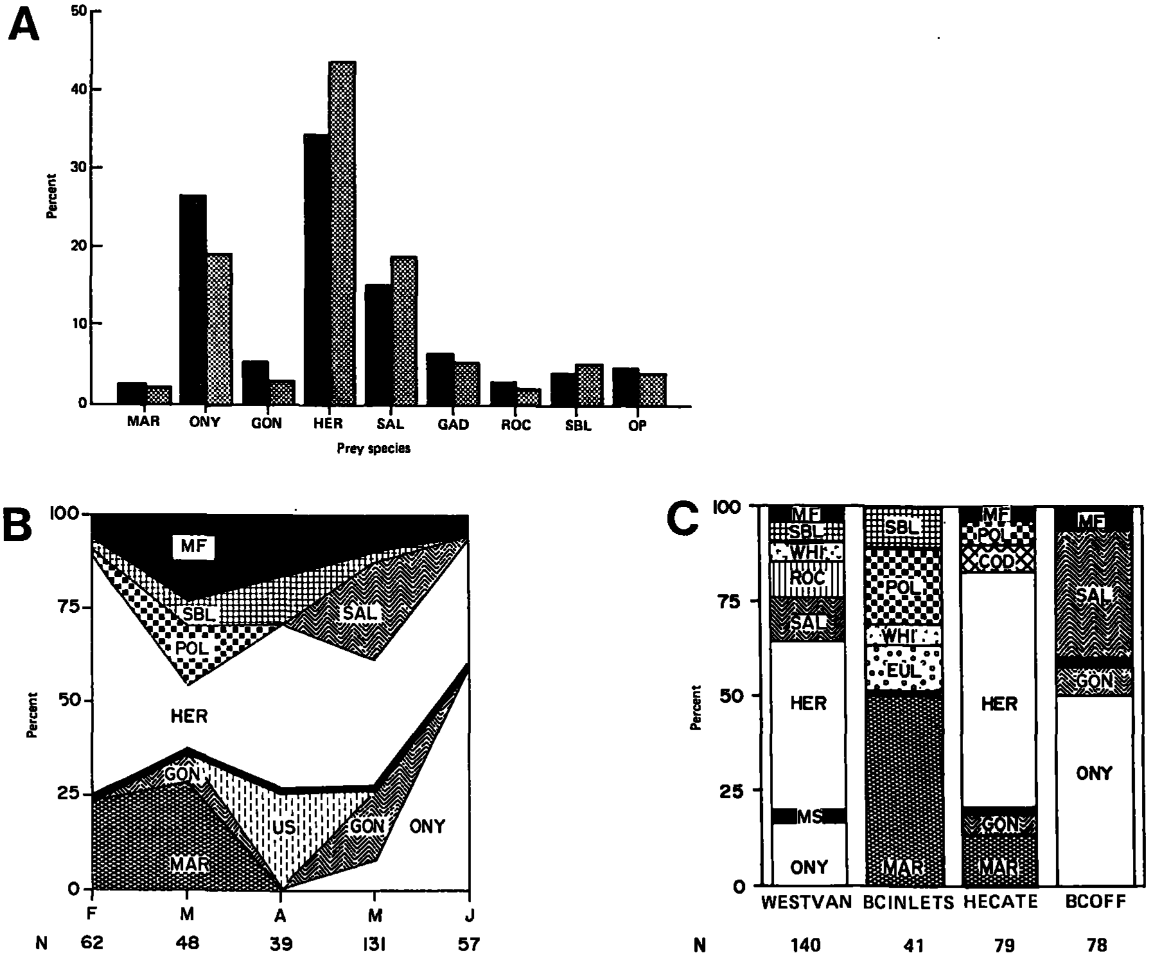

FIGURE 7.—Composition (percent) of diet of northern fur seals by prey species off British Columbia during 1958-74 (A) for pooled January-June samples ($N = 354$), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion with pooled January-June samples using modified volume. A dark line separates squid and fish categories in the latter two figures. Key: COD = Pacific cod; EUL = eulachon; GAD = gadid fishes; GON = gonatid squids; HER = Pacific herring; MAR = market squid; MF = miscellaneous fish species; ONY = onychoteuthid squids; OP = other prey; POL = walleye pollock; ROC = rockfishes; SAL = salmonids; SBL = sablefish; US = unidentified squid; WHI = Pacific whiting.

Gulf of Alaska

Based on all samples collected in the Gulf of Alaska, the main diet of northern fur seals was Pacific herring when energy content was considered, but Pacific sand lance, *Ammodytes hexapterus*, was most important when caloric values were not considered (Fig. 8A). However, there were subregional differences in diet. Off southeastern Alaska, collections were made in Sitka Sound during February and March where the diet was almost exclusively Pacific herring (Fig. 8B, C). In the northernmost area of the region the diet consisted chiefly of capelin, *Mallotus villosus*, but also to a lesser degree of both walleye pollock, *Theragra chalcogramma*, and Pacific sand lance (Fig. 8C). Off Kodiak Island during April to July, the diet was mainly Pacific sand lance and capelin (Fig. 8B, C). Gonatid squids (Gonatidae) were the primary foods of northern fur seals in oceanic waters of this region from April to June. Rockfishes and salmonids were also eaten by northern fur seals in offshore and northern inshore areas of the region (Fig. 8C).

Western Alaska

Of the 309 stomachs with food collected in this region from May to October 1958-74, 239 were taken during June, with most of these collected south of Unimak Pass. The main foods of the northern fur seals were Pacific sand lance and capelin, as off Kodiak Island, with the energy content of each having little effect on their relative importance (Fig. 9). Other important prey were Atka mackerel, *Pleurogrammus monopterygius*, salmonids, walleye pollock, and the squid *Berryteuthis magister*. Sablefish, *Anoplopoma fimbria*, and Pacific herring were also eaten by northern fur seals south of Unimak Pass during summer months.

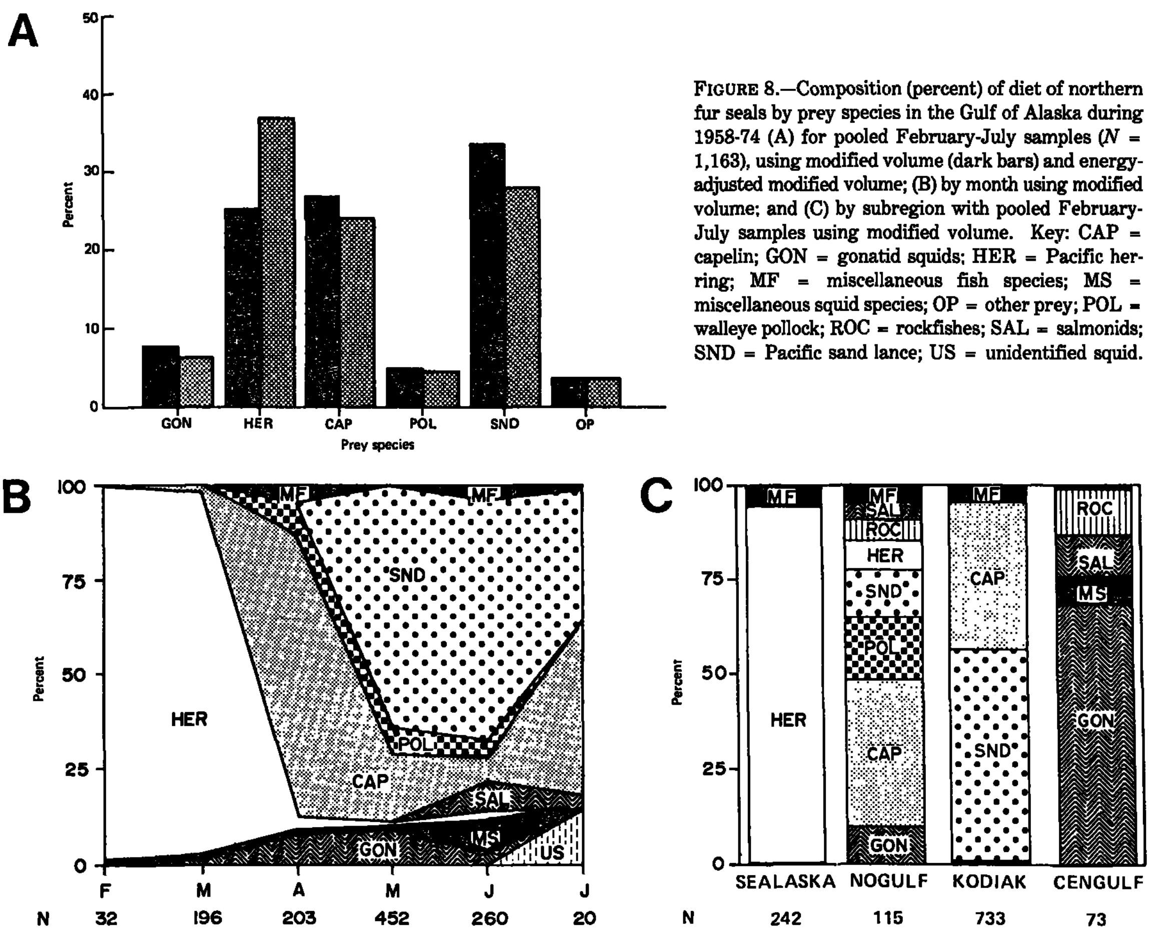

FIGURE 8.—Composition (percent) of diet of northern fur seals by prey species in the Gulf of Alaska during 1958-74 (A) for pooled February-July samples (*N* = 1,163), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion with pooled February-July samples using modified volume. Key: CAP = capelin; GON = gonatid squids; HER = Pacific herring; MF = miscellaneous fish species; MS = miscellaneous squid species; OP = other prey; POL = walleye pollock; ROC = rockfishes; SAL = salmonids; SND = Pacific sand lance; US = unidentified squid.

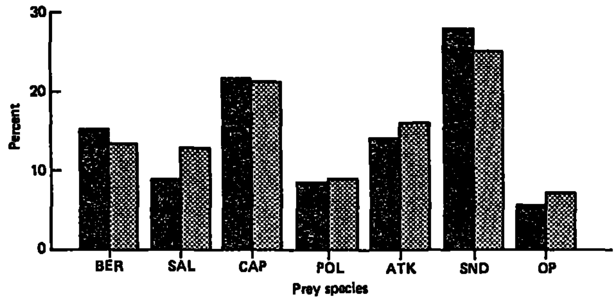

FIGURE 9.—Composition (percent) of diet of northern fur seals by prey species in western Alaska during 1958-74 for pooled May-October samples (N = 309), using modified volume (dark bars) and energy-adjusted modified volume. Key: ATK = Atka mackerel; BER = *Berryteuthis magister*; CAP = capelin; OP = other prey; POL = walleye pollock; SAL = salmonids; SND = Pacific sand lance.

Eastern North Pacific

Northern anchovy (20%) and Pacific herring (19%) were the main species eaten by the northern fur seals in the eastern North Pacific when data from all regions and months were pooled (Fig. 10). These prey were the most important whether energy content was considered or not, although importance increased when the caloric values were included. Salmonids (6%), capelin (8%), Pacific whiting (7%), walleye pollock (2%), Pacific sand lance (8%), and rockfishes (4%) were also commonly eaten. The remaining diet was made up of a wide variety of squids (mainly market squid, 6%; onychoteuthid squids, 6%; and gonatid squids, 5%) and other fishes (mainly Pacific saury, 4%; sablefish, 2%; and Atka mackerel, 2%). Squids were the primary food species in oceanic waters between California and the Gulf of Alaska, and fishes were the main prey in the neritic areas. Although not eaten in large amounts, salmonids and rockfishes were the main fishes consumed in oceanic areas between Washington and the Gulf of Alaska (Figs. 6C, 7C, 8C).

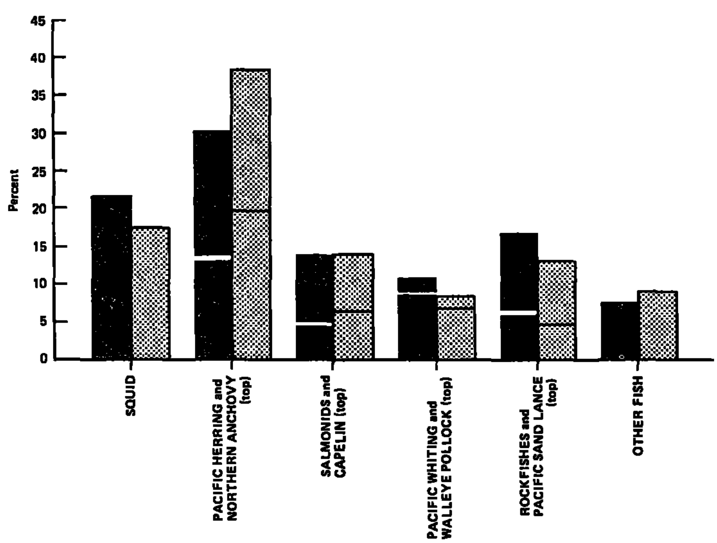

FIGURE 10.—Composition (percent) of diet of northern fur seals by prey species in the eastern North Pacific (excluding the Bering Sea) during 1958-74 using modified volume (dark bars) and energy-adjusted modified volume. Data from all months and years were pooled (N = 5,624).

Eastern Bering Sea

Walleye pollock was the most important food for northern fur seals in the eastern Bering Sea, particularly around the Pribilof Islands and in other inshore waters during July to September (Fig. 11A, B, C). Capelin was the main food near Unimak Pass during June to October. The squids, *Berryteuthis magister* and *Gonatopsis borealis*, were the primary prey species of fur seals in the oceanic areas (Fig. 11C). Deep-sea smelts (Bathylagidae) were eaten offshore, mainly in association with squid. The relative importance of each prey species was not markedly affected by the energy content adjustments (Fig. 11A).

Effect of Energy Value of Prey

In general, the ranking of prey species in the diet of northern fur seals was similar when using either modified volume or modified volume weighted for the energy content of prey. However, caloric values affected relative importance in regions where high energy foods (e.g., Pacific herring, northern anchovy, salmonids), or where low energy foods (e.g., market squid, Pacific whiting) were commonly eaten. In such cases, the adjustment shifted importance of a prey species in the same direction as the relative value of their caloric content compared with other prey in the diet. A species with high energy content increased in importance, but this caused others to decrease because the relative values of prey species in the diet all totaled 100%.

DISCUSSION

The results of earlier investigations on the diet of northern fur seals indicated that basically the

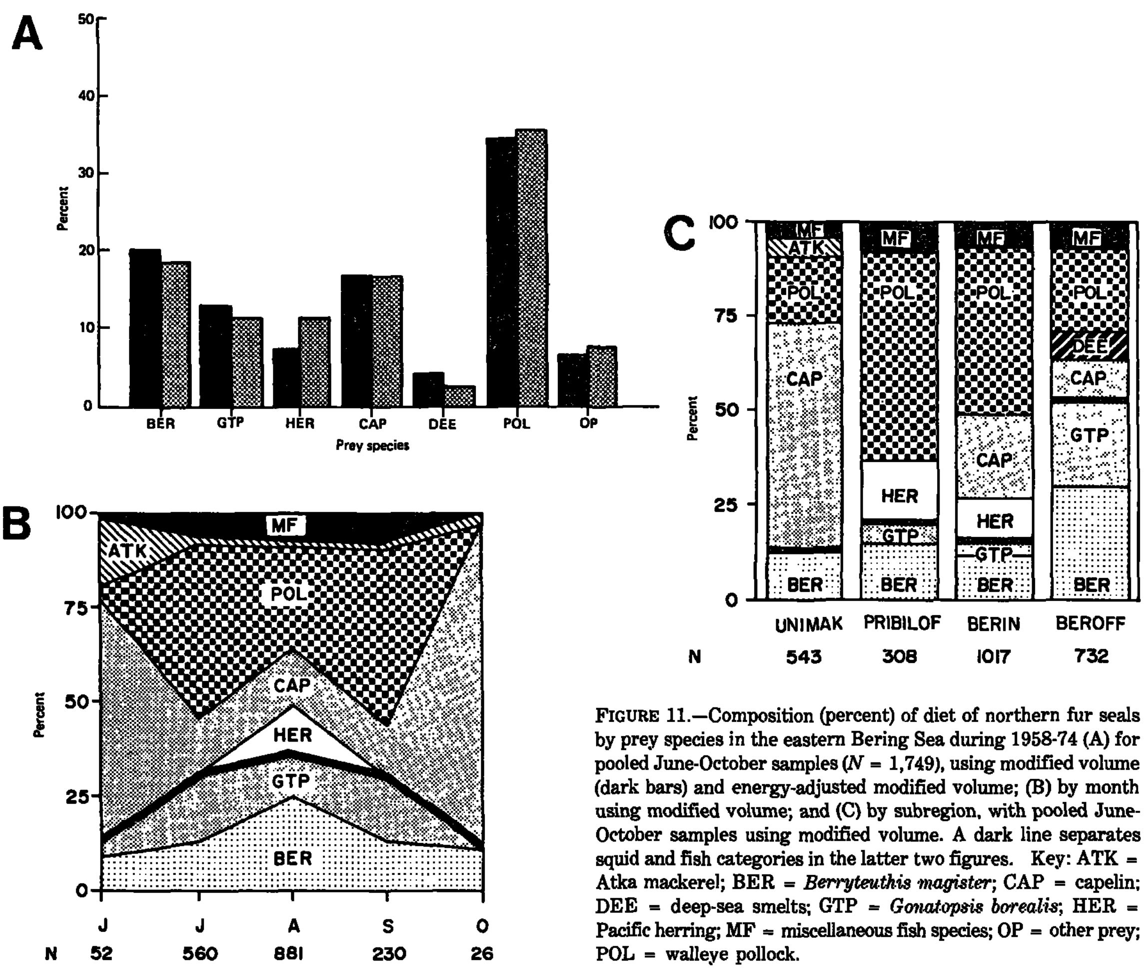

FIGURE 11.—Composition (percent) of diet of northern fur seals by prey species in the eastern Bering Sea during 1958-74 (A) for pooled June-October samples (*N* = 1,749), using modified volume (dark bars) and energy-adjusted modified volume; (B) by month using modified volume; and (C) by subregion, with pooled June-October samples using modified volume. A dark line separates squid and fish categories in the latter two figures. Key: ATK = Atka mackerel; BER = *Berryteuthis magister*; CAP = capelin; DEE = deep-sea smelts; GTP = *Gonatopsis borealis*; HER = Pacific herring; MF = miscellaneous fish species; OP = other prey; POL = walleye pollock.

same species of prey were important by region and month as reported in the current study. This was true for the numerous annual and intermittent summary reports prepared by the United States and Canada for the North Pacific Fur Seal Commission during 1958-74. However, they are not reviewed here because they typically described diet for a particular year or 2-6 yr period and were based on subsets of the samples that we used. In other studies, Stroud et al. (1981) and Kajimura (1984, 1985) mentioned, although did not demonstrate, that squids were the main food species in offshore areas, whereas fishes were the most important inshore. This observation was confirmed in our findings. The phenomenon appears to exist throughout the feeding range of northern fur seals off western North America.

Also, as found in our study, Taylor et al. (1955) and Kajimura (1985) reported that the main food for the northern fur seal off California was northern anchovy. Similarly, Clemens and Wilby (1933), Clemens et al. (1936), Schultz and Rafn (1936), May (1937), Wilke and Kenyon (1952), Spalding (1964), and Kajimura (1985) all indicated that Pacific herring was the primary prey between Washington and southeastern Alaska. Taylor et al. (1955) and Kajimura (1985) found that capelin was prominent in the diet off Kodiak Island; and Lucas (1899), Wilke and Kenyon (1952), and Kajimura (1985) found that walleye pollock was the most significant species in the eastern Bering Sea; and Wilke and Kenyon (1957) reported that capelin was important to northern fur seals near Unimak Pass.

However, there were some differences between the results of earlier research and the current analysis. Taylor et al. (1955) stated that 1) jacksmelt, *Atherinopsis californiensis*, was second in importance for northern fur seals off California rather than insignificant as we reported; 2) salmon was the main food off Oregon rather than a minor diet item; 3) walleye pollock was more important than Pacific herring off Washington; and 4) Pacific sand lance was rarely foraged off Kodiak Island rather than eaten almost as frequently as capelin. Kenyon (1956) found Pacific sandfish, *Trichodon trichodon*, to be the most commonly consumed food of seals which were taken on rookeries of the Pribilof Islands, whereas the current study found that it was rarely eaten. Most of these differences probably resulted from small sample sizes of earlier studies or dissimilar measures of importance. Also, some differences in diet will result from interannual variability in prey abundance and movement patterns owing to environmental conditions or other factors.

Factors other than just the relative importance by region and month must be taken into account when determining the significance of each prey species to the seal. Robbins (1983) stated that the nutritional value of food should also be considered. For example, food species with high caloric values will be more important than those with low caloric values because the amount of food required for metabolic functions depends to some extent upon the energy content of that food. However, high energy foods are more valuable only when they are not more difficult to capture and do not contain more indigestible or toxic substances than lower energy content species. These detrimental factors do not appear to be involved when considering the most important foods eaten by northern fur seals in the eastern North Pacific Ocean. Northern anchovy and Pacific herring were already the most important prey species even without accounting for their energy content. But because they also had relatively high energy values, their importance increased in the seal's diet. Thus, relative importance with an adjustment for energy content appears to be a better measure of diet than when energy content is not incorporated.

Another factor to consider is the proportion of the year that the northern fur seal population spends in each locality. Each prey species in the total annual diet should be weighted by the importance of each subregion and region where the prey is eaten. This weighting requires understanding the route and timing of migration, and the changes in local seasonal abundance of northern fur seals. The general pattern of migration for the Pribilof Islands stock is well known (Baker et al. 1970; Fiscus 1978; Bigg 1982[6]). Essentially all population components, except most 1-2 yr-olds, are thought to occur in the eastern Bering Sea during June-July to October where they pup, mate, nurse, and rest on the Pribilof Islands. Most 1-2 yr-olds remain in the North Pacific Ocean during this time. The stock leaves the eastern Bering Sea in November-December and travels mainly to the coastal areas between southeastern Alaska and California, with the largest number apparently going to California by January. Most males remain in Alaskan waters, and seals aged 1-2 yr remain offshore. The return migration starts in March-April with most seals arriving in the northern Gulf of Alaska by May. However, while this general pat-

[6]Bigg, M. A. 1982. Migration of northern fur seals in the eastern North Pacific and eastern Bering Sea: an analysis using effort and population composition data. Unpubl. rep., 77 p. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia V9R 5K6, Canada.

tern of migration is known, no estimates have been made of the seasonal abundance of seals by region, and thus total diet cannot be weighted by the significance of each locality.

Nonetheless, we are of the opinion that the lack of estimates of local abundance of northern fur seals may not be a major bias in our descriptions of diet for the large coastal regions of the eastern North Pacific (Fig. 10) and the eastern Bering Sea (Fig. 11). We reason that the sampling effort in the eastern North Pacific was extensive from December to June, as indicated by the size of samples collected by month and region (Figs. 4-9; see also Figure 2), and may have largely reflected the seasonal changes in relative abundance of seals during their coastal migration. For the eastern Bering Sea, essentially all samples were taken during July-October, which was the time most seals resided there.

The most general conclusion to be made about the diet of coastal northern fur seals is that it consists primarily of small schooling fish. Previous studies have made the point that the diet consists of small schooling fish and squid (Spalding 1964; Kajimura 1985; others). However, our findings suggest that squid are no more important in the overall diet to the seal than are the larger sized fish. In the coastal regions of the eastern North Pacific the northern fur seal's diet consists of 60% small schooling fish, 23% other fish, and 17% squid. When northern fur seals arrive off the coast of southeastern Alaska to California during winter, they feed on northern anchovy, Pacific herring, capelin, and Pacific saury. When most northern fur seals arrive along the coast of the Gulf of Alaska in spring, they eat capelin and Pacific sand lance. These are fish <30 cm in length (Table 2). Typically they are eaten whole whereas larger fish are first broken into small pieces (Spalding 1964). Walleye pollock is the primary food in the eastern Bering Sea. It is a large fish as an adult (Smith 1981), and these fish school. However, northern fur seals feed mainly upon the juvenile stages, i.e., <20 cm (McAlister and Perez[7]). Thus, the diet in this region consists up to 64% small schooling fish, 6% other fish, and 30% squid.

On the Asian coast the diet of northern fur seals also includes small schooling fishes such as myctophiform fishes (lanternfishes), Pacific saury, Pacific sand lance, and the Japanese anchovy, *Engraulis japonicus*, in addition to walleye pollock and squid (Taylor et al. 1955; Lander and Kajimura 1980). Of interest is the fact that in recent years the Japanese sardine, *Sardinops melanosticta*, has become more important in the diet of northern fur seals off Asia (Yoshida et al.[8,9]; Yoshida and Baba[10,11]). This sardine was depleted during the 1930's and 1940's and

TABLE 2.—Summary of the size range and general habitat of northern fur seal prey.[1] A = anadromous; BC = British Columbia; BER = eastern Bering Sea; CAL = California; GULF = Gulf of Alaska; I = inshore; NS = near surface; O = offshore; ORE = Oregon; S = schooling fish; WASH = Washington; WEST = western Alaska.

Prey	Average adult size (cm)	Size range (cm) of specimens in fur seal stomachs (sample size in parentheses)[2]	General habitat
Pacific herring	<20-30	10-25 (11,>27)	Pelagic (I,S)
Northern anchovy	<18	9-18 (7,27)	Pelagic (I-O,S)
Salmonids[3]	<80	15-41 (22,>26)	Pelagic (I-O,A)
Capelin	22	7-14 (7,64)	Pelagic (I,S)
Eulachon	23-30	12-21 (3,11)	Pelagic (I,S,A)
Deep-sea smelts	2-18	8-12 (6,986)	Pelagic (O,S)
Myctophiform fishes	13-20	—	Pelagic (O,S)
Pacific saury	10-32	25 (1,4)	Pelagic (O,S)
Pacific whiting	66-76	15 (1,2)	Pelagic and semidemersal (I-O,S)
Walleye pollock	<90	4-40 (71,1721)	Pelagic and semidemersal (I-O,S)
Rockfishes	30-53	11-31 (6,>19)	Demersal (I-O,S)
Sablefish	57-60	20-31 (3,>3)	Pelagic and semidemersal (I-O,S)
Atka mackerel	<120	15-23 (5,>5)	Pelagic and semidemersal (I,S)
Pacific sand lance	20	—	Demersal (I,S)
Market squid	14-17	7-15 (6,43)	Pelagic (I)
Onychoteuthid squids[4]	10-37	14-22 (3,>3)	Pelagic (I-O)
Gonatid squid	12-32	5-24 (10,>59)	Pelagic (I-O)

[1]Data on average lengths of prey and ecology were compiled from Akimushkin (1963), Bakkala et al. (1981), Baxter (1967), Baxter and Duffy (1974), Carl (1964), Childress and Nygaard (1973), Childress et al. (1980), Fields (1965), Fitch (1974), Fitch and Lavenberg (1968, 1971, 1975), Hart (1973), Inada (1981), Miller and Lea (1976), Naito et al. (1977), Niggol (1982), Pearcy (1965), Pearcy et al. (1979), Smith (1981), Taka et al. (1980), and Wespestad and Barton (1981).

[2]Total length for fish and dorsal mantle length for squid. The first number in parentheses is the number of fur seal stomachs examined, and the second number in parentheses is the number of prey specimens measured. These data were derived from an analysis of the original unpublished 1958-74 data.

[3]Maximum size of salmonids found at sea. Adults in freshwater are larger (to 147 cm) depending upon species.

[4]Does not include size range of *Moroteuthis* (<140 cm) which has been taken by northern fur seals, but rarely off North America.

[7]McAlister, W. B., and M. A. Perez. 1977. Ecosystem dynamics—birds and marine mammals. Part 1: preliminary estimates of pinniped-finfish relationships in the Bering Sea (final report). *In* Environmental assessment of the Alaskan continental shelf, Annual Report 12, p. 342-371. U.S. Department of Commerce, Environmental Research Laboratory, Boulder, CO.

[8]Yoshida, K., N. Okumoto, and N. Baba. 1979. Japanese pelagic investigation on fur seals, 1978. Far Seas Fish. Res. Lab., Shimizu, Jpn., Fur Seal Resour. Sect., Contrib. No. 41-9, 66 p.

recovered only recently (Kondo 1980). The northern fur seal appears to have reacted to this recovery by eating more sardines. A similar change in diet may have taken place off California during the past 50 years. The Pacific sardine, *Sardinops sagax*, was once the most abundant small, schooling fish off California, whereas now northern anchovy is (Murphy 1966; Smith 1972; Mais 1974). The Pacific sardine population was drastically reduced during the 1940's mainly because of fishing pressure and has remained at a relatively low level since, while the northern anchovy increased in abundance during the 1950's and the 1960's (Vrooman and Smith 1971; Hart 1973; Wolf and Smith 1985). The Pacific sardine may undergo long-term periodic fluctuations in population size (Thompson 1921), and it may now once again be increasing in biomass (Wolf and Smith 1985). Northern fur seals have not eaten Pacific sardine in recent years, but perhaps they fed on this species prior to the 1940's. The seal may have changed its diet from largely Pacific sardine to northern anchovy. Unfortunately, the stomach contents of only two northern fur seals were collected from California prior to the 1950's (Scheffer 1950). Clemens and Wilby (1933) gave the only evidence that sardines were once consumed by these seals in the eastern North Pacific Ocean. They found that sardines were commonly eaten during 1931 off southwestern Vancouver Island.

An interesting speculation regarding the significance of small schooling fish to northern fur seals is the relationship between diet and the migration route of the seal. Small schooling fish could be important just because they are abundant and lie along the coastal migration path of northern fur seals. Kajimura (1985) argued for this possibility. He suggested that the migration pattern of northern fur seals is genetically established and that the seal feeds opportunistically upon whatever prey species are most abundant in its path. He believes that, although food is not a major factor in determing the migration route of northern fur seals, the movements of prey species can still alter the local distribution of fur seals. An alternative possibility is that the seals learn the location of the main foods and then selects its migration route to include them. Baker (1978) argued for this alternative. He proposed that, while some inherited factors may be involved in migration, northern fur seals could mainly search the North Pacific Ocean for the most preferred or abundant food, and thereafter establish the migration route. Such being the case, perhaps inexperience explains why 1-2 yr-old seals are rarely seen inshore feeding with older seals. Also, perhaps squid is not a preferred or sufficiently available food for northern fur seals offshore, because most seals older than 1-2 yr feed inshore on fish. However, at this stage, not enough is known about the factors that control migration of the northern fur seal to establish which alternative is true. As Kajimura (1985) has pointed out, factors other than diet are no doubt involved as indicated by the fact that males do not migrate as far south as females.

[9]Yoshida, K., N. Okumoto, and N. Baba. 1981. Japanese pelagic investigation on fur seals, 1979-1980. Far Seas Fish. Res. Lab., Shimizu, Jpn., Fur Seal Resour. Sect., Contrib. No. 41-10, 150 p.

[10]Yoshida, K., and N. Baba. 1983. Japanese pelagic investigation on fur seals, 1981-1982. Far Seas Fish. Res. Lab., Shimizu, Jpn., Fur Seal Resour. Sect., Contrib. No. 41-11, 118 p.

[11]Yoshida, K., and N. Baba. 1984. Japanese pelagic investigation on fur seals, 1983. Far Seas Fish. Res. Lab., Shimizu, Jpn., Fur Seal Resour. Sect., Contrib. No. 41-12, 67 p.

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