

Abstract.— Gastrointestinal tract contents were evaluated from 73 female and juvenile male northern fur seals (*Callorhinus ursinus*) for analysis of their diet in the Bering Sea. Fur seals were collected from August to October of 1981, 1982, and 1985. Juvenile walleye pollock (*Theragra chalcogramma*) and gonatid squid were the primary prey. Pacific herring (*Clupea pallasii*) and capelin (*Mallotus villosus*), considered important fur seal prey in previous reports, were absent from the diet. Prey species and size varied among years and between near-shore and pelagic sample locations. Interannual variation in the importance of pollock in the diet of fur seals was positively related to year-class strength of pollock. Midwater ($n=23$) and bottom ($n=116$) trawls were conducted at the location of fur seal collections to determine availability of fish and squid relative to prey species eaten by fur seals. The species and size composition of prey taken by fur seals was similar to midwater trawl collections, but differed from bottom trawl catches. Contrary to earlier conclusions that northern fur seals are opportunistic in their feeding habits, we conclude that fur seals are size-selective mid-water feeders during the summer and fall in the eastern Bering Sea.

Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea

Elizabeth Sinclair

Thomas Loughlin

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

William Percy

College of Oceanography, Oregon State University
Oceanography Administration Building 104
Corvallis, Oregon 97331

The Pribilof Island population (St. George and St. Paul Islands) of northern fur seals (*Callorhinus ursinus*) represents approximately 75% of the total species breeding population. Between 1975 and 1981, the Pribilof Island population declined from 1.2 million to an estimated 800,000 animals (York and Hartley, 1981; Fowler, 1985). Abundance levels on St. Paul Island appear to have stabilized (York and Kozloff, 1987) at a level 60–70% below estimates of the 1940's and 1950's, and at one-half the estimated carrying capacity (Fowler and Siniff, 1992). The number of animals continues to decline on St. George Island (York, 1990).

The objectives of this study were to determine the species and size of prey eaten by northern fur seals in the eastern Bering Sea, to compare the seals' present diet with that prior to the population decline, and to examine the seals' consumption of prey relative to prey availability. Previous studies on the feeding habits of northern fur seals in the eastern Bering Sea (Scheffer, 1950a; Wilke and Kenyon, 1952; Wilke and Kenyon, 1957; North Pacific Fur Seal Commission Reports 1962,¹ 1975,² and 1980³; Fiscus et al., 1964; Fiscus et al., 1965; Fiscus and Kajimura, 1965)

were conducted prior to the 1975–81 population decline and prior to the 1970's development of a commercial walleye pollock (*Theragra chalcogramma*) fishery in the Bering Sea. Neither the size of fur seal prey, nor fur seal selection of prey relative to real-time availability have been previously examined in detail.

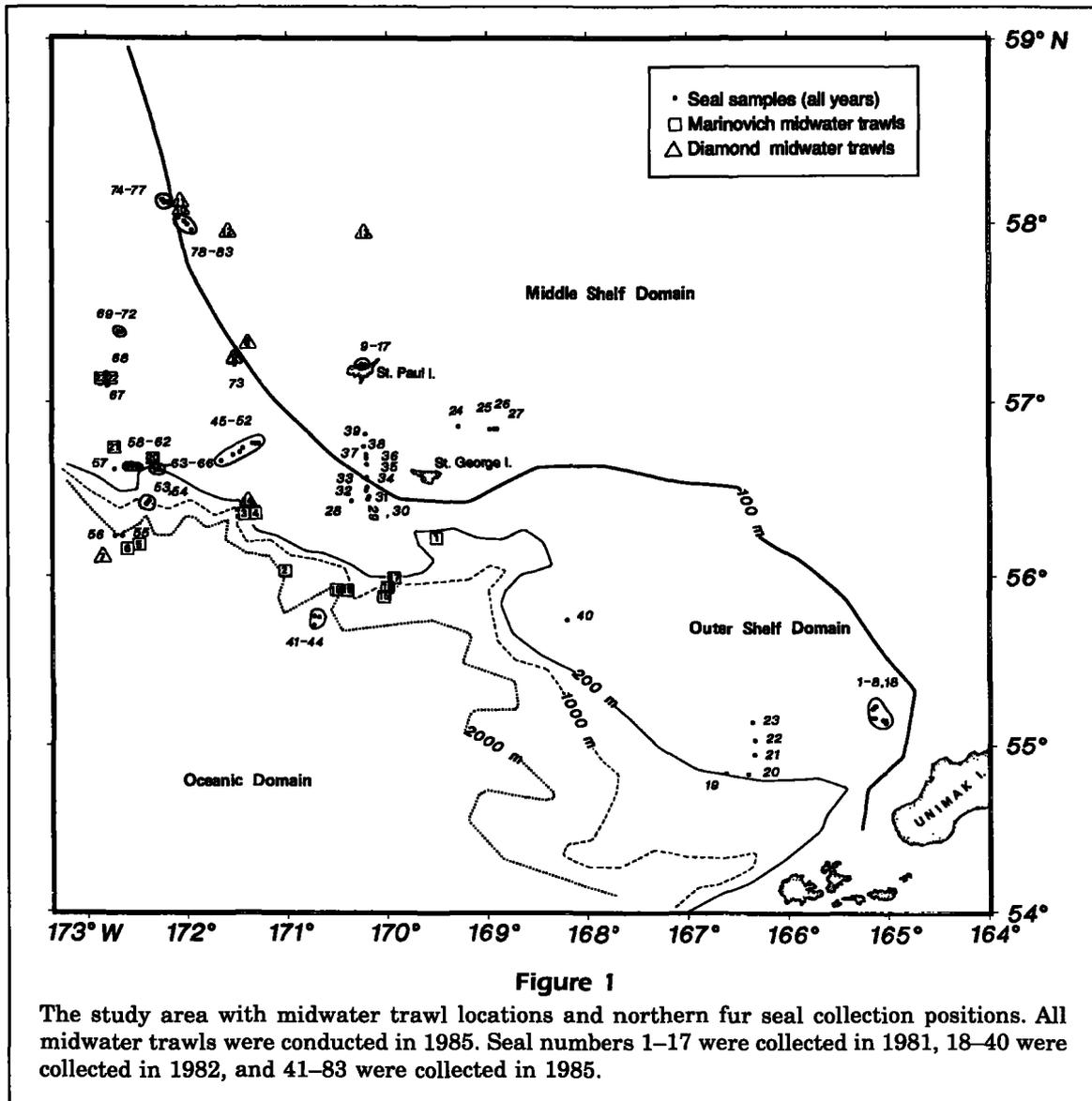
Methods

Northern fur seals were collected from 17 to 28 October 1981; from 24 September through 6 October

¹ North Pacific Fur Seal Commission Report on Investigations from 1958 to 1961: Presented to the North Pacific Fur Seal Commission by the Standing Scientific Committee on 26 November 1962, 183 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

² North Pacific Fur Seal Commission Report on Investigations from 1967 through 1972: Issued from the headquarters of the Commission, Washington, D.C., June 1975, 212 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

³ North Pacific Fur Seal Commission Report on Investigations during 1973–76: Issued from the headquarters of the Commission, Washington, D.C., February 1980, 197 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.



1982; and from 6 to 16 August 1985. Collections were made within 185 km of the Pribilof Islands over the continental shelf, continental slope, and oceanic domain of the eastern Bering Sea (Fig. 1).

Seals were shot from a small craft and returned to the NOAA ship *Miller Freeman* (65-m stern trawler) for examination within 1.5 hours of collection. The esophagus of each seal was checked for food as an indication of regurgitation, and the gastrointestinal (GI) tract was removed and frozen. Gastrointestinal tract contents were later thawed and gently rinsed through a series of graded sieves (0.71, 1.00 or 1.40, and 4.75 mm in 1981 and 1982; 0.50, 1.00, 1.40, and 4.75 mm in 1985). Fleishy remains were preserved in 10% formalin. Fish otoliths and bones were stored dry. Cephalopod rostra and

statoliths were preserved in 70% isopropyl alcohol.

Prey identification was based on all remains, including otoliths. Otoliths were not used for fish identification in earlier fur seal diet studies because stomach samples were stored in formalin, which dissolves otoliths. Techniques and references for the identification of prey based on otoliths include Fitch and Brownell (1968), Morrow (1979), Frost and Lowry (1981), and otolith reference collections (see Acknowledgments). References for cephalopod beak and statolith identification include Clarke (1962), Young (1972), Roper and Young (1975), Clarke (1986), and beak and statolith reference collections (see Acknowledgments). A tooth was collected from each fur seal that was shot and ages were derived from direct readings of canine tooth sections follow-

ing Scheffer (1950b). In the analysis of data, males and females of all ages were treated as one group because of small sample sizes.

The highest number of either upper or lower cephalopod beaks and left or right otoliths was recorded as the maximum number of each species present. If deterioration made some left and right otoliths of a species indistinguishable, they were counted and the total was divided by 2. The frequency of occurrence and number of individuals from each prey taxon was calculated for each seal.

The fork length (FL) of pollock and dorsal mantle length (DML) of squid was measured directly when whole prey were present in the stomachs. In the absence of whole prey, body size was estimated by measurement of otoliths and beaks. The maximum length of pollock otoliths and lower rostral length (LRL) of gonatid squid beaks were measured to the nearest 0.05 mm with vernier calipers. Squid DML's were estimated by comparison of LRL measurements to the LRL/DML relationship of 51 gonatid squid caught in trawls conducted in the vicinity of seal collections. Walleye pollock fork lengths were estimated by regression against otolith length (Frost and Lowry, 1981). For otoliths measuring:

$$> 10.0\text{mm, (FL) } Y = 3.175X - 9.770 \quad (R = 0.968)$$

$$\leq 10.0\text{mm, (FL) } Y = 2.246X - 0.510 \quad (R = 0.981).$$

Walleye pollock ages were estimated from these lengths based on length-age relation described by Smith (1981) and Walline (1983) for walleye pollock from the Bering Sea.

Otoliths may dissolve or erode to varying degrees depending on their size and duration in fur seal stomachs. We evaluated the bias introduced in FL estimates due to eroded otoliths by assigning otoliths to four condition categories (excellent, good, fair, and poor) based on amount of wear. After quality categorization, the maximum lengths of otoliths (except those in "poor" condition) were measured for estimation of body length by regression, and length frequencies of each category were determined independently.

Cephalopod beaks are more resistant to digestion than otoliths and were typically identifiable. Beaks with chipped, worn, or broken rostra were rare and were not measured. Cephalopod beaks were identified to species when possible, but most were categorized into two groups referred to as *Gonatopsis borealis-Berryteuthis magister* or *Gonatus madokai-Gonatus middendorffi*. The two individual species within each group can be separated based on their external morphology and statolith structure, but

cannot presently be separated based on beak structure alone (Clarke, 1986).

Trawl collections of potential seal prey

Trawls were conducted throughout the study area from the *Miller Freeman* between 1900 and 0600 hours within the vicinity of seal collections (Fig. 1). Both bottom and midwater trawls were conducted to provide a relative measure of the availability and size of potential fur seal prey species. Bottom trawls were made at 52–498 m (\bar{x} =139 m) depths with an 83/112 Eastern bottom trawl (17-m width, 2.3-m height mouth opening; 3.2-cm codend liner mesh; 360-mesh circumference; 200-mesh depth; 30-m bridle). Thirty-nine bottom trawls were conducted in 1981 (14 October–4 November), 51 in 1982 (24 September–8 October), and 26 in 1985 (5 August–22 August). Seven 1985 trawls were made beyond maximum recorded dive depths of adult female seals (257 m; Ponganis et al., 1992). They were included in analyses because the species and size of fish and squid caught were consistent with those caught by bottom trawl within seal dive depths.

Collection and sorting methods and calculation of bottom trawl catch per unit of effort (CPUE) values followed Smith and Bakkala (1982). The total bottom trawl catch was randomly split into a sample of about 2500 kg. Individual species of fishes were identified and weighed (wet) and CPUE (no./ha) was estimated based on distance trawled. In 1981 and 1982, cephalopods were classified as squid or octopus and discarded. In 1985, all cephalopods were identified, sexed, weighed, and frozen whole. Beaks were extracted and stored in 70% isopropyl alcohol.

Sex and age determination and body length measurements were made on a subsample of up to 200 walleye pollock from each trawl. Fork lengths were measured to the nearest centimeter. Saccular otoliths were collected for age determination (Smith and Bakkala, 1982) and stored in 70% isopropyl alcohol. Walleye pollock CPUE was calculated by age and body length. For purposes of this study, age-length frequencies for male and female walleye pollock were combined for each of the three years.

Midwater trawls were made in 1985 with a Diamond midwater net ($n=8$) (10–16 fm mouth opening; 3.2-cm codend liner mesh; 354-mesh circumference; and 160-mesh depth with 2-m bridles) and a Marinovich herring trawl ($n=15$) (6.1-m width, 6.1-m height mouth opening; 1-cm codend liner mesh; 150-mesh circumference; and 350-mesh depth with 10-m bridles). Specific trawling positions were chosen within the vicinity of northern fur seal collection areas based on the presence of fish or squid as

indicated on 38 kHz echosounders and a chromoscope. Midwater towing depths measured by an attached transducer ranged from 22 to 340 m ($x=143$ m).

All species of fish and cephalopods collected in midwater trawls were identified and counted. The CPUE and frequency of occurrence of each species, LRL and sex of gonatid squid, and walleye pollock frequency of occurrence by age and length were calculated separately for each trawl type.

Comparison of seal diet and trawl collections

The Odds Ratio (Fleiss, 1981) was used to compare prey availability (as determined by midwater and bottom trawls) with selection of prey by fur seals for each sample year:

$$O = \frac{p^1 q^2}{p^2 q^1},$$

where $p1$ = % of diet comprised by a given prey taxon,

$q1$ = % of diet comprised by all other prey taxon,

$p2$ = % of food complex in environment comprised by a taxa, and

$q2$ = % of food complex in environment comprised by all other taxa.

Values were calculated for number of each prey species and percent frequency of occurrence among seals, and CPUE values (no./ha) for each trawl type. Values for $p2$ and $q2$ were also calculated for the trawl types combined in order to provide a comprehensive description of the water column. The natural log of the calculated Odds Ratio represents either positive or negative selection. The Odds Ratio was chosen because, unlike other electivity indices, the significance of the distance of calculated values from zero (null hypothesis that prey were consumed non-selectively) can be tested with the Z -statistic (Gabriel, 1978).

In order to quantify the degree of overlap in the composition of bottom trawls, midwater trawls and fur seal GI contents, percent similarity (PS) values (Langton, 1982) were calculated:

$$PS = 100 - 0.5 \sum a - b,$$

where a = % number of a given prey for seals, and
 b = % number of the same prey for trawls.

Results

Fur seal diet

Eighty-three fur seals were collected. Ten of the 17 GI tracts collected in 1981 were empty and were

excluded from the analysis. Of the 73 animals included in the analysis, 13 were juvenile males, 3 were juvenile females and 57 were adult females. Most fur seals were collected over depths less than 200 m within the outer shelf domain (Fig. 1).

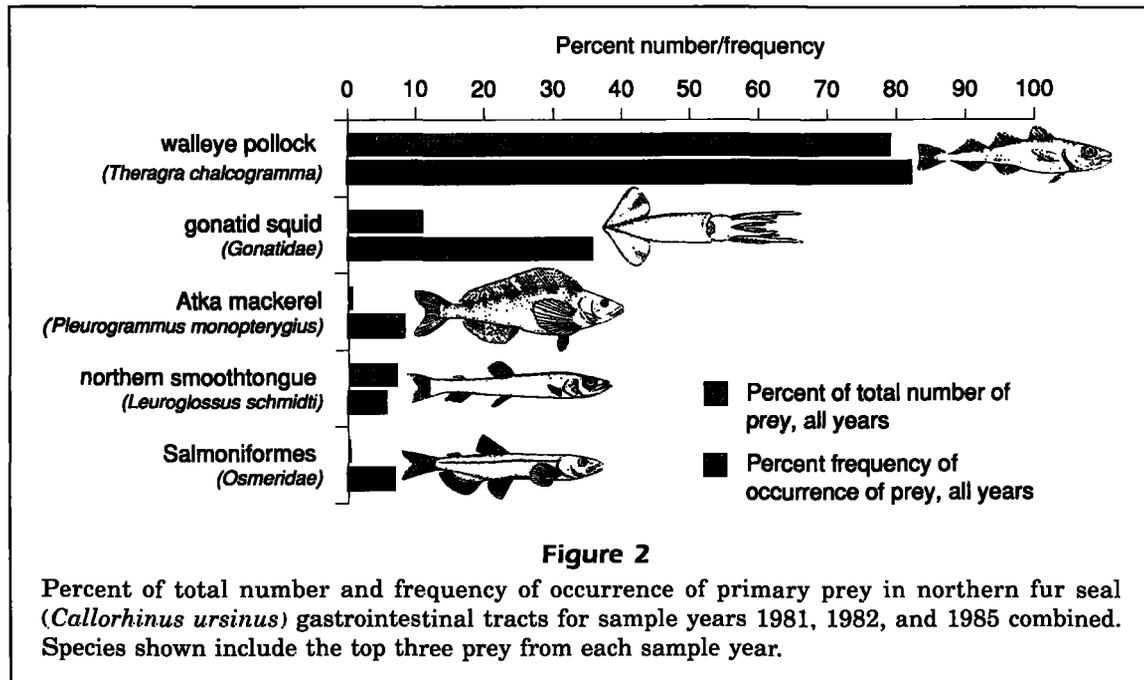
Fish represented 89% and cephalopods 11% of prey numbers for all three sample years combined. One-hundred percent of the GI tracts had fish remains and 82% of all samples contained walleye pollock. A total of 2,658 walleye pollock otoliths were measured. In all years combined, juvenile walleye pollock (3–20 cm FL) were the most numerous and frequently occurring prey species. Sixty-five percent of prey walleye pollock were from the 0-age group (3–13 cm FL) and 31% were from age group 1 (13–20 cm FL). Only 4% of prey pollock were from age group 2 (20+ cm FL) and older.

Gonatid squids occurred in 36% of the samples, but in comparison with pollock, they were not consumed in large numbers (Fig. 2). *Gonatus madokai*-*G. middendorffi* and *Gonatopsis borealis*-*Beryteuthis magister* were the second most frequently occurring prey in all years combined. Seventy-nine percent of the 389 beaks measured were from squid 5–12 cm DML.

Northern smoothtongue (*Leuroglossus schmidti*), a bathylagid deepsea smelt, was the second most numerous fish prey overall (Fig. 2) even though it was found only in 1985 (Table 1). Northern smoothtongue composed a higher percentage of the total number of fish than walleye pollock ≥ 2 years old for all sample years combined. Atka mackerel (*Pleurogrammus monopterygius*) composed 23.9% of the 1981 prey sample and was present in five of seven stomachs collected in 1981 that had prey remains, but the species was identified from the prey remains of only one other individual among the six collected in the same area in 1982 (Table 1).

Although walleye pollock were eaten by fur seals in all 3 years, marked differences in age and body size were found between years (Table 1; Fig. 3). In 1981, the few walleye pollock otoliths found were from fish 3–4 years of age. Fur seal GI tracts contained primarily age-0 pollock in 1982 and age-1 pollock in 1985. Exclusion of otoliths that were in fair condition caused a downward shift in modal FL frequencies of 1 to 2 cm, but did not change our estimation of the age categories of pollock eaten by fur seals.

The species of forage fishes and squids consumed by fur seals varied between samples taken on and off the continental shelf (200 m) (Fig. 4). The GI tracts of fur seals collected over oceanic and continental slope regions contained primarily northern smoothtongue and squids, especially *Gonatopsis*



borealis-Berryteuthis magister. Seals collected over the continental shelf contained the remains of walleye pollock of all ages and squids, especially *Gonatus madokai*-*G. middendorffi*. Adult walleye pollock, although rare in stomach contents, were found in greatest frequency in fur seals collected from the outer domain of the continental shelf. Juvenile walleye pollock were consumed primarily over the midshelf and outer domain. Atka mackerel was found only in samples collected over the outer shelf domain north of Unimak Island.

Comparisons with trawl samples

Of the five top-ranked species collected in bottom trawls, only walleye pollock was found in fur seal GI contents (Figs. 2 and 5). Walleye pollock from bottom trawls ranged from 1 to over 12 years of age and had mean body lengths of 38.9 cm (3–4 years old) in 1981, 39.7 cm (4–5 years old) in 1982, and 44 cm (5–6 years old) in 1985 (Fig. 6). All but four of the cephalopods caught in 1985 bottom trawls were *Berryteuthis magister* ranging from 17.5 to 31.2 cm DML (\bar{x} =21.6). As in the seal samples, *B. magister* was collected in trawls conducted over the outer continental shelf domain along the 200-m contour, or over the continental slope between 200 and 1000 m. Otherwise, the bottom trawl catch for all three years was so dissimilar to the midwater trawl catch (Figs. 5 and 6) and fur seal GI contents (Fig. 2) that electivity computations were not meaningful (Odds Ratio=0).

Calculation of the Odds Ratio and Z-statistic on 1985 data with midwater and bottom trawl catch combined showed statistically significant positive selection by fur seals for age-0 pollock ($P=0.0002$), age-1 pollock ($P<0.0001$), northern smoothtongue ($P<0.0001$), and gonatid squid ($P=0.02$). Negative selection for adult walleye pollock was suggested but was not statistically significant ($P=0.13$).

A similarity index of 81% was calculated for species composition and prey size in the 1985 GI samples and midwater trawls. Fur seals fed on three of the four top-ranked species caught in midwater trawls (Figs. 2 and 5). Midwater trawls and seals caught predominantly juvenile walleye pollock. Gonatid squids (*Gonatus madokai*, *G. middendorffi*, and *Gonatopsis borealis*) had low CPUE values but were second in frequency of occurrence in both fur seal GI tracts and midwater trawls. The modal length of walleye pollock and gonatid squids was 5–20 cm in both midwater trawl and GI samples in 1985. Few adult walleye pollock and no large squid were collected in midwater trawls or seal GI samples.

Seals and midwater trawls caught the same prey species at the same general locations on and off the continental shelf (Fig. 4). As in GI contents, age-0 and age-1 walleye pollock were collected in midwater trawls made on the middle and outer shelf and near the continental slope. *Gonatopsis borealis* were found on the continental slope and near-slope. *Gonatus madokai* and *G. middendorffi* were found throughout the sampling area, but primarily on the outer continental shelf and near-slope sampling areas.

Table 1

Gastrointestinal contents of 73 northern fur seals (*Callorhinus ursinus*) collected from the Bering Sea in 1981 (n=7), 1982 (n=23), and 1985 (n=43). Tentative identifications are designated as (t).

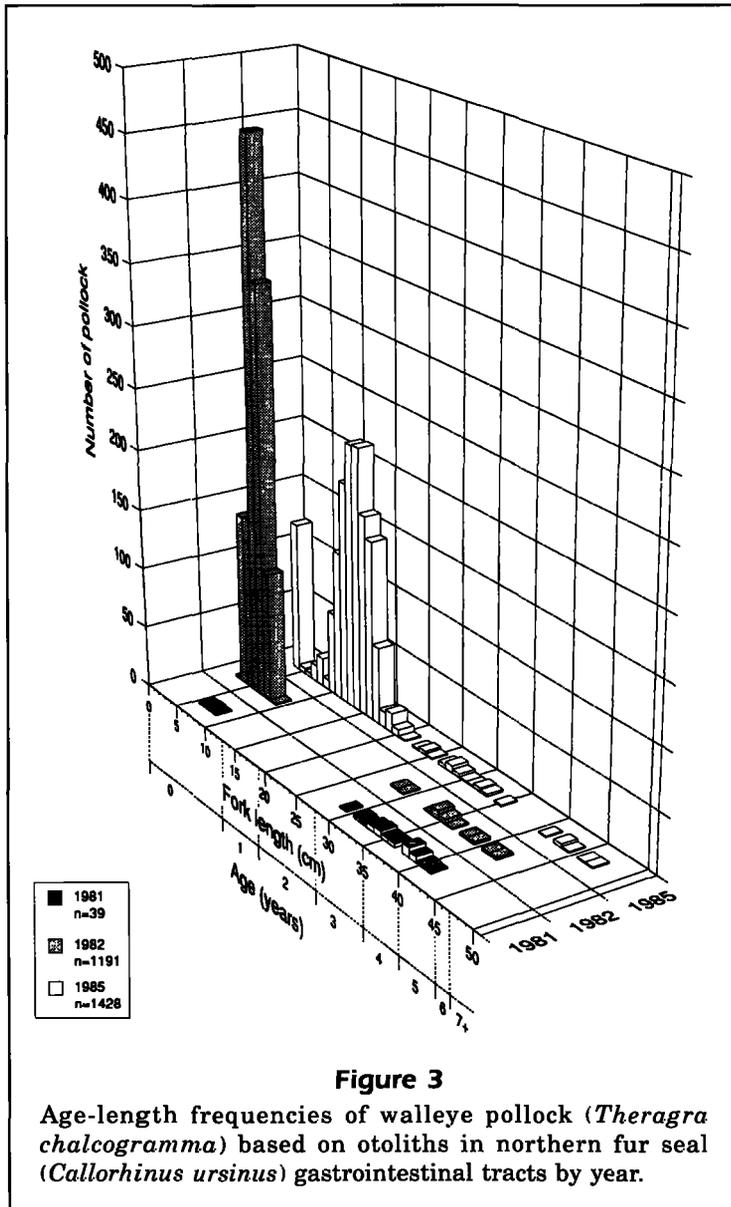
Prey species	% number in each year			% frequency occurrence		
	1981	1982	1985	1981	1982	1985
Fish						
<i>Clupea pallasii</i>	—	0.1	—	—	4.4	—
Osmeridae (t)	8.7	—	—	42.9	—	—
Salmonidae	5.4	—	—	42.9	—	—
<i>Leuroglossus schmidti</i>	—	—	12.7	—	—	9.3
<i>Gadus macrocephalus</i> (t)	—	—	0.1	—	—	7.0
<i>Theragra chalcogramma</i>	54.4	87.3	74.1	100	95.7	72.1
3–5cm fork length	—	(8.8)	(5.7)	—	—	—
5–10cm fork length	(4.3)	(63.9)	(2.3)	—	—	—
10–20cm fork length	—	—	(55.6)	—	—	—
>20cm fork length	(38.0)	(1.4)	(1.7)	—	—	—
<i>T. chalcogramma</i> (t)	—	0.1	0.1	—	8.7	4.7
unidentified Gadidae	—	—	0.9	—	—	20.9
<i>Lycodes</i> sp.	1.1	—	0.5	14.3	—	—
<i>Pleurogrammus monopterygius</i>	23.9	0.1	—	71.4	4.4	—
<i>P. monopterygius</i> (t)	—	0.1	—	—	4.4	—
unidentified percoid	1.1	—	—	14.3	—	—
unidentified fish	5.4	0.4	0.5	14.3	13.0	25.6
Squid						
<i>Gonatus berryi</i>	—	—	0.1	—	—	2.3
<i>G. pyros</i>	—	—	0.1	—	—	2.3
<i>G. tinro</i>	—	—	0.1	—	—	2.3
<i>G. tinro</i> (t)	—	—	0.1	—	—	2.3
<i>Gonatus madokai-middendorffi</i>	—	0.1	4.8	—	4.4	34.9
<i>Gonatus</i> sp.	—	—	0.1	—	—	2.3
<i>Berryteuthis magister</i>	—	0.6	—	—	8.7	—
<i>Gonatopsis borealis-B. magister</i>	—	10.2	6.4	—	17.4	20.9
unidentified Gonatidae	—	—	0.1	—	—	7.0
unidentified squid	—	1.0	—	—	34.8	—
Total number prey	92	1638	2189			
Total number fish	92	1445	1936	100	100	100
Total number squid	0	193	253	0	52.2	46.5

Discussion

The modal size distribution of walleye pollock in GI contents of female and juvenile male fur seals reflected year-class strength projections of walleye pollock (Fig. 7). Walleye pollock have highly variable recruitment rates (Smith, 1981), and year-class strength varied five-fold between 1977 and 1982 (Bakkala et al., 1987). Population estimates based on bottom trawl and midwater acoustic surveys in the eastern Bering Sea indicated that the 1980 year class (age 1 in 1981) was about half the average year-class size; the 1981 year class (age 0 in 1981) was the weakest observed prior to 1983; and the 1978 year class (age 3 in 1981) was the strongest observed. The 1982 and 1984 year classes were

strong and the 1985 year class was considered average (Bakkala et al., 1987). Similarly, walleye pollock as prey in 1981 were primarily adults 3 and 4 years of age (from the 1977 and 1978 year class); in 1982, seals ate age-0 pollock exclusively; and in 1985, prey pollock were primarily from the 1984 year class. The concordance of pollock recruitment and fur seal GI content analysis indicates that the variable recruitment of walleye pollock affects prey consumption by northern fur seals.

The three basic dive patterns described for adult females in the Bering Sea are shallow, pelagic nighttime diving (most commonly to 50–60 m); deep day-and-night diving over the continental shelf (most commonly to 175 m); and some combination of both, including shallow diving over the continental shelf



and both shallow and deep diving along the continental slope. Dive pattern information is based on time-depth recordings (Gentry et al., 1986; Loughlin et al., 1987; Goebel et al., 1991), radio telemetry (Loughlin et al., 1987), stomach volume estimates (Mead, 1953; Taylor et al., 1955⁴; Spalding, 1964; Wada, 1971; Kajimura, 1984), and stomach clearance studies (Miller, 1978⁵; Bigg, 1981⁶; Bigg and Fawcett, 1985; Murie and Lavigne, 1985).

⁴ Taylor, F. H. C., M. Fuginaga, and F. Wilke. 1955. Distribution and food habits of the fur seals of the North Pacific Ocean. Rept. of Coop. Invest. by the Govts. of Can., Japan, and the U.S.A. Feb.-July, 86 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115-0070.

Based on fur seal and trawl collections in this study and on distributional information of prey (Smith, 1981; Dunn, 1983; Kubodera and Jefferts, 1984; Lynde, 1984), shallow diving fur seals over the continental shelf concentrated on juvenile walleye pollock and juvenile gonatid squid (*Gonatus madokai*-*G. middendorffi*), while shallow divers off-shelf targeted juvenile gonatid squid (*Berryteuthis magister*-*Gonatopsis borealis*) and bathylagid smelt. Daytime deep diving over the continental shelf would be advantageous to seals concentrating on prey (i.e., adult walleye pollock) that tend to school at depth during daytime hours and disperse as they rise in the water column at night. Adult gonatid squid probably occur in schools at the bottom on the continental shelf and remain deep along the shelf edge during both day and night. The location and degree of concentration of prey may be closely associated with the hydrography of the foraging region. The hydrography of the foraging region may have the most direct influence on the diving patterns of fur seals.

Hydrographic characteristics of the Bering Sea continental shelf, include a two-layered midshelf and a three-layered outer shelf domain that may stratify and concentrate prey by species and age in a vertical plane. Nishiyama et al. (1986) proposed that vertical stratification within the eastern Bering Sea shelf serves as a "nursery layer" to confine young-of-the-year pollock in the upper 40 m of the water column within the boundary region between the upper and lower layers. Copepod nauplii are also concentrated in this area, providing a ready source of food for larval walleye pollock (Bailey et al., 1986). Wada (1971) determined that primary foods of fur seals off the Sanriku Coast in Japan consisted of migrating species closely related to boundary regions, especially transition zone regions. The horizontal temperature and salinity structures that occur on either side of frontal regions within our study area (Kinder and Schumacher, 1981) may

⁵ Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Final Rep. to U.S. Mar. Mamm. Comm. MMC-75/08, 27p.

⁶ Bigg, M. A. 1981. Digestion rates of herring (*Clupea harengus pallasii*) and squid (*Loligo opalescens*) in northern fur seals. Submitted to the 24th Annual Meeting of the Standing Sci. Comm., N. Pac. Fur Seal Comm., 6-10 April, Tokyo, Japan, Available: Alaska Fish. Sci. Cent., 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115-0070.

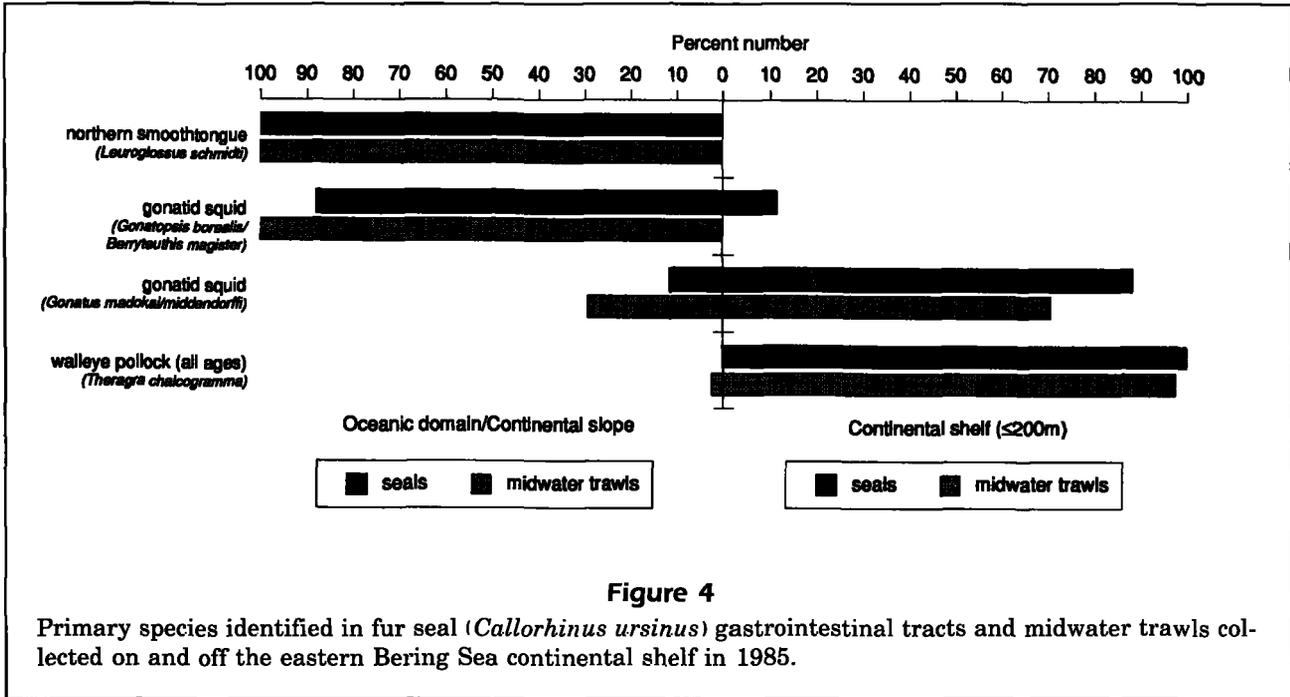


Figure 4

Primary species identified in fur seal (*Callorhinus ursinus*) gastrointestinal tracts and midwater trawls collected on and off the eastern Bering Sea continental shelf in 1985.

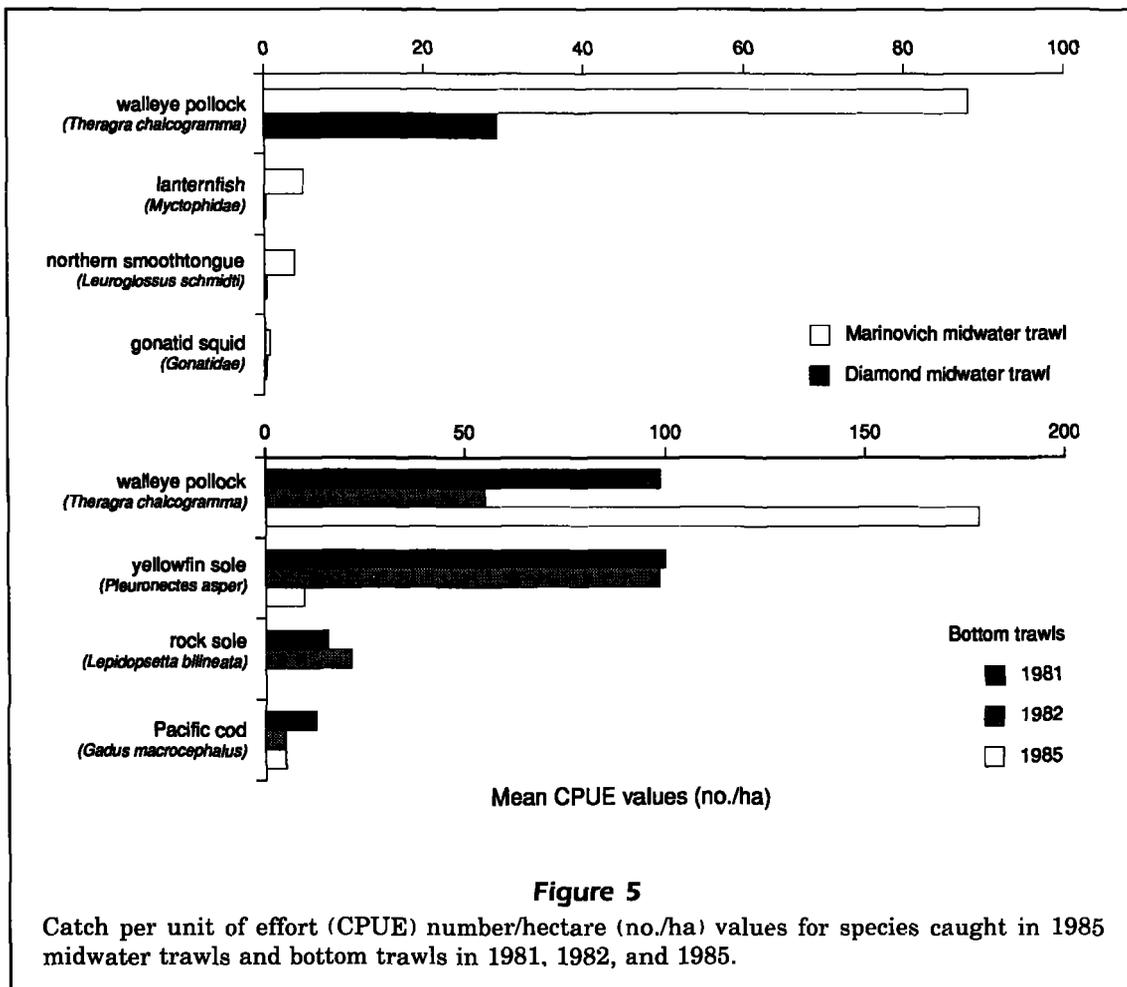
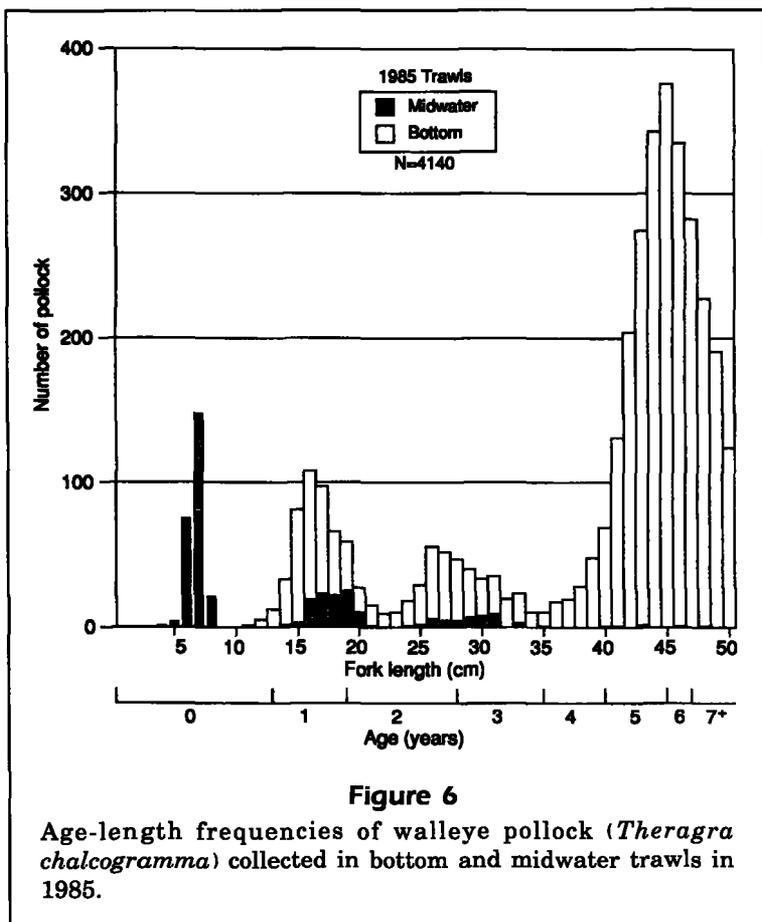


Figure 5

Catch per unit of effort (CPUE) number/hectare (no./ha) values for species caught in 1985 midwater trawls and bottom trawls in 1981, 1982, and 1985.



also form boundaries that concentrate prey. Diving depths of 175 m coincide with the depth break of the outer continental shelf. Diving depths of 50–60 m coincide with the depth break of the frontal systems between the midshelf and inner shelf.

Previous analyses of fur seal diet in the eastern Bering Sea were based primarily on a sample of 3,530 stomachs collected pelagically in 1960, 1962–64, 1968, 1973, and 1974 (North Pacific Fur Seal Commission Reports 1962,¹ 1975,² and 1980³; Fiscus et al. 1964; Fiscus et al. 1965; Fiscus and Kajimura 1965). Reviews of the pelagic data cite walleye pollock (Kajimura, 1985; Perez and Bigg, 1986), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), Atka mackerel, gonatid squids (*Gonatopsis* spp., *Berryteuthis magister* and *Gonatopsis borealis*), and intermittently, northern smoothtongue (Kajimura, 1984) as principal fur seal prey in the eastern Bering Sea. Published reports and reviews of fur seal feeding habits prior to the pelagic collections (1892–1950's) also described walleye pollock, capelin, gonatid squid, and bathylagid smelt as primary prey in seal spewings or stomachs (Scheffer, 1950a; Wilke and Kenyon, 1952; Wilke and Kenyon, 1957).

In terms of prey species composition, the summer diet of female and juvenile male northern fur seals does not appear to have changed dramatically since the turn of the century. Pollock and gonatid squid are still the predominant prey of northern fur seals in the eastern Bering Sea. More subtle changes, such as a decrease in pollock size may have occurred (Smith, 1981; Swartzman and Haar, 1983) and could play a critical role in foraging success of northern fur seals. Unfortunately, records of prey size in historical fur seal diet studies are incomplete.

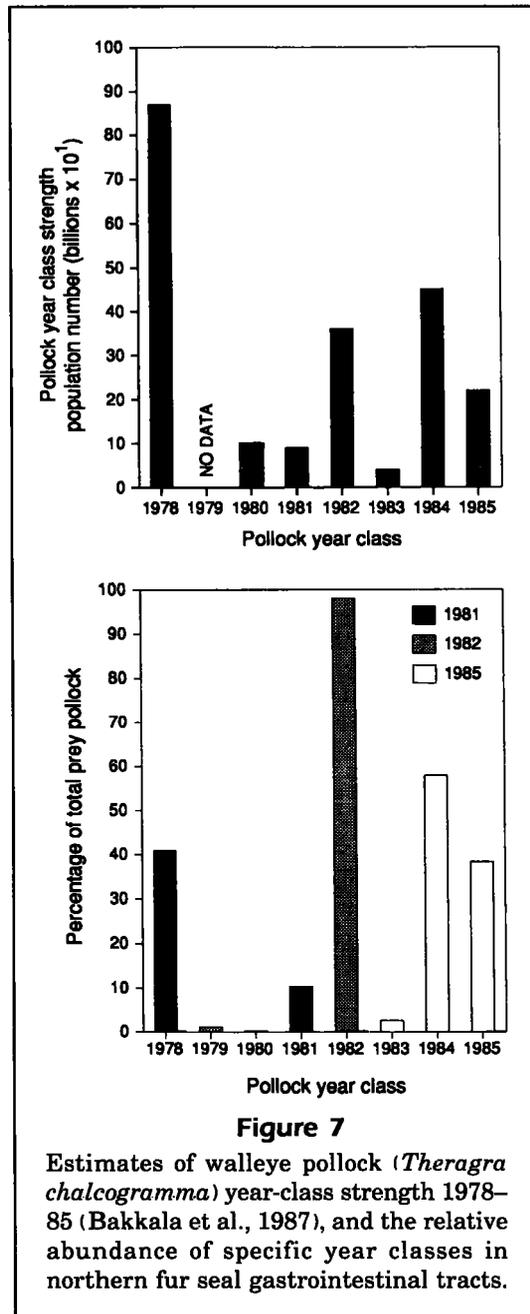
It should be noted that Pacific herring and capelin were absent from fur seal diets in this study, despite collections in areas where they occurred as important prey in the past. Fluctuation in the population status of Pacific herring and capelin in the Bering Sea has been attributed to the sporadic and localized nature of their abundance (Turner, 1886; Meek, 1916; Favorite et al. 1977⁷; Lowe 1991⁸), overharvesting and displacement by walleye pollock (Wespestad and Barton, 1981; Swartzman and Haar, 1983; Wespestad and Fried, 1983; Bakkala et al., 1987), and/or environmental change such as the pronounced warming in the Gulf of Alaska and Bering Sea over the past decade (Royer, 1989). The

absence of these previously important prey may be critical to seals during successive years of weak walleye pollock year-class abundance.

Fur seals select juvenile walleye pollock as prey despite a wide availability of other prey types within their dive range. Fur seals may select their prey by size and schooling behavior, whether the prey are myctophids in oceanic waters off Japan (Wada, 1971); Pacific herring, capelin, market squid (*Loligo opalescens*) and Pacific whiting (=Pacific hake, *Merluccius productus*) in the eastern North Pacific (Kajimura, 1984; Perez and Bigg, 1986); or walleye pollock in the eastern Bering Sea (Kajimura, 1984). The most consistent prey characteristic between feeding studies across the northern fur seal range

⁷ Favorite, F., T. Laevastu, and R. R. Straty. 1977. Oceanography of the northeastern Pacific Ocean and eastern Bering Sea, and relations to various living marine resources. NWAFC Proc. Rep. 280p. Alaska Fish. Sci. Cent., NMFS, NOAA, 7600 Sand Point Way NE., Bin C15700, Seattle, WA 98115-0070, 280p.

⁸ Lowe, S. A. 1991. Atka mackerel. In Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1992, p. 11–2 to 11–40. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.



is size and the tendency to form dense schools. In this sense, a “juvenation” of walleye pollock in the Bering Sea (Swartzman and Haar, 1983) may have provided fur seals with a newly abundant but unstable resource, due to large fluctuations in the annual year-class strength of walleye pollock and due to potential displacement of other prey species (Pacific herring and capelin). During years of low pollock recruitment, fur seals may switch to other prey such as capelin and Pacific herring, and experience food limitation only if these alternate prey resources have been displaced or depleted. Histori-

cal records of northern fur seal diet are inadequate to either support or refute an “alternate prey” argument. However, we suggest that when juvenile walleye pollock are unavailable, such as in our 1981 sampling season, female and juvenile fur seals select other specific prey of the same size and eat adult walleye pollock only if these other preferred prey are not available.

During their summer breeding season, northern fur seals consume the most abundant and available fish and squid in the eastern Bering Sea. Walleye pollock make up an estimated 50% of the ground-fish biomass in the eastern Bering Sea and Aleutian Islands area (Walters et al., 1988) and dense aggregations of 0-age pollock occur off the Pribilof Islands June through mid-August (Smith, 1981). Kubodera and Jefferts (1984) suggested gonatids are the major pelagic cephalopod group in the Bering Sea, where large increases in abundances of larval and postlarval gonatid squid occur in early June. Among Bering Sea gonatids, *Gonatopsis borealis* and *Berryteuthis magister* are considered to be among the most numerically dominant (Jefferts, 1983; Kubodera and Jefferts, 1984).

Selection by northern fur seals of a wide variety of numerically dominant prey species throughout their migratory range has led to the general conclusion that they are non-specific, opportunistic feeders (Kajimura, 1985). Northern fur seals are flexible in their feeding habits, as indicated by the variation in GI contents of seals collected between California and Alaska. Nonetheless, fur seals concentrate on an average of three primary species within each oceanographic subregion (Perez and Bigg, 1986). In addition, fur seal consumption of walleye pollock, gonatid squid, and bathylagid smelt in the eastern Bering Sea is consistent throughout historical records, despite the wide variety of prey available to fur seals within their diving range. Based on this study, we conclude that female and young male fur seals select juvenile and small-sized fish and squid, despite the availability of larger prey types within their diving range. This study demonstrates that female and young male fur seals are size-selective midwater shelf and mesopelagic feeders, at least during the breeding and haul-out season in the eastern Bering Sea.

Acknowledgments

Otolith identifications for the 1981 samples were made by the late J. Fitch. Otolith identifications for 1982 and 1985 were based on the otolith reference collections at the National Marine Mammal Labo-

ratory (NMML) and Los Angeles County Museum (LACM). Cephalopod identifications were based on the reference collections of the NMML and Oregon State University (OSU). Voucher specimens of prey material (statoliths, beaks, otoliths, teeth, and bones) are archived at the NMML. Identifications of squid and squid beaks were confirmed by C. Fiscus (NMML, retired), K. Jefferts (OSU), and W. Walker (LACM). Identification of fish otoliths and bones were confirmed by G. Antonelis Jr. (NMML) and J. Dunn (University of Washington) respectively. Voucher samples of juvenile pollock otoliths were confirmed by A. Brown (Alaska Fisheries Science Center [AFSC]), K. Frost (Alaska Department of Fish and Game [ADF&G]), and L. Lowry [ADF&G]). Gary Walters (AFSC) helped interpret bottom trawl values, and W. Carlson and C. Leap of the AFSC Graphics Unit helped produce the figures.

The following individuals contributed to the quality and content of this manuscript: G. Antonelis Jr., J. Baker, L. Fritz, R. Gentry, P. Livingston, and two anonymous reviewers. These data were first presented in part as a Northwest and Alaska Fisheries Center Processed Report (Hacker and Antonelis, 1986⁹) and in full as a Masters Thesis from Oregon State University (Sinclair, 1988).

Literature cited

- Bailey, K., R. Francis, and J. Schumacher.**
1986. Recent information on the causes of variability in recruitment of Alaska pollock in the eastern Bering Sea: physical conditions and biological interactions. *Int. North Pac. Comm. Bull.* 47:155-165.
- Bakkala, R. G., V. G. Wespestad, and J. J. Traynor.**
1987. Walleye pollock. *In* R. G. Bakkala and J. W. Balsiger (eds.), Condition of groundfish resources of the eastern Bering Sea and Aleutian Islands region in 1986, p. 11-29. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-117.
- Bigg, M. A., and I. Fawcett.**
1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). *In* J. R. H. Beddington, R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 284-299. George Allen and Unwin Ltd., London.
- Clarke, M. R.**
1962. The identification of cephalopod "beaks" and the relationship between beak size and total body weight. *Bull. Br. Mus. (Nat. Hist.) Zool.* 8:419-480.
- Clarke, M. R. (ed.)**
1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford, 273 p.
- Dunn, J. R.**
1983. Development and distribution of the young of northern smoothtongue, *Leuroglossus schmidti* (Bathylagidae), in the Northeast Pacific, with comments on the systematics of the genus *Leuroglossus* Gilbert. *Fish. Bull.* 81(1):23-40.
- Fiscus, C. H., and H. Kajimura.**
1965. Pelagic fur seal investigations, 1964. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. No. 522, 47 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE, BINC15700, Seattle, WA 98115-00700.
- Fiscus, C. H., G. A. Baines, and F. Wilke.**
1964. Pelagic fur seal investigations, Alaska waters, 1962. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. No. 475, 59 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BINC15700, Seattle, WA 98115-0070.
- Fiscus, C. H., G. A. Baines, and H. Kajimura.**
1965. Pelagic fur seal investigations, Alaska, 1963. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. No. 489, 33 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BINC15700, Seattle, WA 98115-0070.
- Fitch, J. E., and R. L. Brownell Jr.**
1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. *J. Fish. Res. Board Can.* 25(12):2561-2574.
- Fleiss, J. L.**
1981. Statistical methods for rates and proportions, 2nd ed. John Wiley & Sons, 321 p.
- Fowler, C. W.**
1985. An evaluation of the role of entanglement in the population dynamics of northern fur seals on the Pribilof Islands. *In* R. S. Shomura and H. W. Yoshida (eds.), Proceedings of the workshop on the fate and impact of marine debris; 27-29 November 1984, Honolulu, HI., p. 291-307. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-54.
- Fowler, C. W., and D. B. Siniff.**
1992. Determining population status and the use of biological indices for the management of marine mammals. *In* D. R. McCullough and R. H. Reginald (eds.), Wildlife 2001: populations, p. 1051-1061. Elsevier Science Publishers, London, England.
- Frost, K. J., and L. F. Lowry.**
1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. *Fish. Bull.* 79(1):187-192.

⁹ Hacker, E. S., and G. A. Antonelis Jr. 1986. Pelagic food habits of northern fur seals. *In* T. R. Loughlin and P. Livingston (eds.), Summary of joint research on the diets of northern fur seals and fish in the Bering Sea during 1985, p. 5-22. NWAFC Proc. Rep. 86-19, Alaska Fish. Sci. Cent., NMFS, NOAA, 7600 Sand Point Way NE., BINC15700, Seattle, WA 98115-0070.

- Gabriel, W. L.**
 1978. Statistics of selectivity. In S. J. Lipovsky and C. A. Simenstad (eds.), Gutshop '78, p. 62-66. Wash. Sea Grant Publ. WSG-WO-77-2, Univ. Washington, Seattle, WA.
- Gentry, R. L., G. L. Kooyman, and M. E. Goebel.**
 1986. Feeding and diving behavior of northern fur seals. In R. L. Gentry and G. L. Kooyman (eds.), Fur seals: maternal strategies on land and at sea, p. 61-78. Princeton Univ. Press, Princeton, NJ.
- Goebel, M. E., J. L. Bengtson, R. L. DeLong, R. L. Gentry, and T. R. Loughlin.**
 1991. Diving patterns and foraging locations of female northern fur seals. Fish. Bull. 89:171-179.
- Jefferts, K.**
 1983. Zoography and systematics of cephalopods of the northeastern Pacific Ocean. Ph.D. diss., Oregon State University, Corvallis, OR, 291 p.
- Kajimura, H.**
 1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-779, 49 p.
 1985. Opportunistic feeding by the northern fur seal, (*Callorhinus ursinus*). In J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 300-318. George Allen and Unwin Ltd., London.
- Kinder, T. H., and J. D. Schumacher.**
 1981. Hydrographic structure over the continental shelf of the southeastern Bering Sea. In D. W. Hood, and J. A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources, Vol. I, p. 31-52. Office of Mar. Poll. Assessment of NOAA.
- Kubodera, T., and K. Jefferts.**
 1984. Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the northern North Pacific (Part I and II). Bull. Nat. Sci. Mus. (Tokyo) Ser. A, 10(3 and 4):91-193.
- Langton R. W.**
 1982. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish. Fish. Bull. 80(4):745-759.
- Loughlin, T. R., J. L. Bengtson, and R. L. Merrick.**
 1987. Characteristics of feeding trips of female northern fur seals. Can. J. Zool. 65(8):2079-2084.
- Lynde, C. M.**
 1984. Juvenile and adult walleye pollock of the eastern Bering Sea. In D. Ito (ed.), Proceedings of the workshop on walleye pollock and its ecosystem in the eastern Bering Sea, p. 43-108. U. S. Dep. Commer., NOAA Tech. Memo NMFS F/NWC-62.
- Mead Jr., G. W.**
 1953. The food habits of the North Pacific fur seal in Japanese waters. Ph.D. diss., Stanford Univ., Palo Alto, CA, 138 p.
- Meek, A.**
 1916. The migrations of fish. Edward Arnold, London, 427 p.
- Morrow, J. E.**
 1979. Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea. U.S. Dep. Commer. NOAA Tech. Rep. NMFS Circ. 420, 33 p.
- Murie, D. J., and D. M. Lavigne.**
 1985. Interpretation of otoliths in stomach content analyses of phocid seals: quantifying fish consumption. Can. J. Zool. 64:1152-1157.
- Nishiyama, T., K. Hirano, and T. Haryu.**
 1986. The early life history and feeding habits of larval walleye pollock, *Theragra chalcogramma* (Pallas), in the southeast Bering Sea. Int. North Pac. Fish. Comm. Bull. 45:177-227.
- Perez, M. A., and M. A. Bigg.**
 1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fish. Bull. 84(4):957-971.
- Ponganis, P. J., R. L. Gentry, E. P. Ponganis, and K. V. Ponganis.**
 1992. Analysis of swim velocities during deep and shallow dives of two northern fur seals, *Callorhinus ursinus*. Mar. Mammal Sci. 8(1):69-75.
- Roper, C. F. E., and R. E. Young.**
 1975. Vertical distribution of pelagic cephalopods. Smithson. Contrib. Zool. 209, 51 p.
- Royer, T. C.**
 1989. Upper ocean temperature variability in the northeast Pacific Ocean: is it an indicator of global warming? J. Geophys. Res. 94(C12):18,175-18,183.
- Scheffer, V. B.**
 1950a. The food of the Alaska fur seal. Transactions of the fifteenth North American Wildlife Conference, p. 410-420. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115-0070.
 1950b. Growth layers on the teeth of Pinnipedia as an indication of age. Science 112:309-311.
- Sinclair, E. H.**
 1988. Feeding habits of northern fur seals in the eastern Bering Sea. M.S. thesis, College of Oceanography, Oregon State Univ., 1988, Corvallis, OR, 94 p.
- Smith, G. B.**
 1981. The biology of walleye pollock. In D. W. Hood and J. A. Calder (eds.), The eastern Bering Sea Shelf: oceanography and resources, Vol. I, p. 527-552, Office of Mar. Poll. Assessment of NOAA, 625 p.
- Smith, G. B., and R. G. Bakkala.**
 1982. Demersal fish resources of the Eastern Bering Sea: spring 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-754, 129 p.
- Spalding, D. J.**
 1964. Comparative feeding habits of the fur seal, sea lion, and harbour seal on the British Columbia Coast. Fish. Res. Board Can. Bull. 146, 52 p.
- Swartzman, G. L., and R. T. Haar.**
 1983. Interactions between fur seal populations

and fisheries in the Bering Sea. *Fish. Bull.* 81(1): 121-132.

Turner, L. M.

1886. *Researches in Alaska. Pt. IV: Fishes. Contributions to the natural history of Alaska: results of investigations made chiefly in the Yukon district and the Aleutian Islands; conducted under the auspices of the Signal Service, U.S. Army, extending from May 1874, to August 1881, p. 87-113. No. II, Arctic Series of Publs., issued in connection with the Signal Service, U.S. Army Gov. Print. Off., Washington DC.*

Wada, K.

1971. Food and feeding habit of northern fur seals along the coast of Sanriku. *Bull. Tokai Reg. Fish. Res. Lab* 64, Jan., p. 1-37.

Walline, P. D.

1983. Growth of larval and juvenile walleye pollock related to year-class strength. Ph.D. diss., Univ. Washington, Seattle, WA, 144 p.

Walters, G. E., K. Teshima, J. J. Traynor, R. G.

Bakkala, J. A. Sassano, K. L. Halliday, W. A.

Karp, K. Mito, N. J. Williamson, and

D. M. Smith.

1988. Distribution, abundance, and biological characteristics of groundfish in the eastern Bering Sea based on results of the U.S.-Japan triennial bottom trawl and hydroacoustic surveys during May-September, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-154, 400 p.

Wespestad, V. G., and L. H. Barton.

1981. Distribution, migration, and status of Pacific herring. *In* D. W. Hood and J. A. Calder (eds.), *The eastern Bering Sea Shelf: oceanography and*

resources, Vol. I, p. 509-525. Office of Mar. Poll. Assessment of NOAA, 625 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115-0070.

Wespestad, V. G., and S. M. Fried.

1983. Review of the biology and abundance trends of Pacific herring (*Clupea harengus pallasii*). *In* W. S. Wooster (ed.), *From year to year*, p. 17-29. Univ. Washington, Seattle, WA. Sea Grant Prog. Publ. WSG-WO-83-3.

Wilke, F., and K. W. Kenyon.

1952. Notes on the food of fur seal, sea-lion, and harbor porpoise. *J. Wildl. Manage.* 16(3):396-397.

1957. The food of fur seals in the eastern Bering Sea. *J. Wildl. Manage.* 21(2):237-238.

York, A. E.

1990. Trends in numbers of pups born on St. Paul and St. George Islands 1973-88. *In* H. Kajimura (ed.), *Fur seal investigations, 1987-88*, p. 31-37. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-180.

York, A. E., and J. R. Hartley.

1981. Pup production following harvest of female northern fur seals. *Can. J. Fish. Aquat. Sci.* 38:84-90.

York, A. E., and P. Kozloff.

1987. On the estimation of numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island, 1980-1986. *Fish. Bull.* 85(2):367-375.

Young R. E.

1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. *Smithson. Contrib. Zool.* (97), 159 p.