# Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship

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**Abstract:** We examined the diet of Steller sea lions *(Eumetopias jubatus)* during June-August 1990-1993 from six areas in the Aleutian Islands and Gulf of Alaska and related these diets to sea lion population changes that occurred during the period. Seven general prey categories were identified, but either walleye pollock *(Theragra chalcogramma)* or Atka mackerel *(Pleurogrammus monopterygius)* dominated in every area. The diversity of prey consumed varied among sites. Only the eastern Aleutian Islands area had all seven categories in the diet, and there, walleye pollock and Atka mackerel each made up around 30% of the diet. The remainder was composed mostly of small schooling fish (e.g., Pacific herring *(Clupea pallasi)* and salmon *(Oncorhynchus* spp.)). The diet in the Gulf of Alaska included mostly walleye pollock whereas the central and western Aleutian diet was composed mostly of Atka mackerel. Populations in the six areas decreased up to 49% during 1990-1994. A strong positive correlation ($r$ = 0.949, $P$ = 0.004) was found between diet diversity and the amount of decline in an area: as diet diversity decreased, populations decreased. This suggests that sea lions need a variety of prey available, perhaps to buffer significant changes in abundance of any single prey.

**Résumé** : Nous avons examiné le régime alimentaire de l'otarie de Steller (*Eumetopias jubatus*) entre juin et août de 1990 à 1993 dans six régions des îles Aléoutiennes et du golfe de l'Alaska et relié ces régimes alimentaires aux changements de la population d'otaries observés durant cette période. Sept catégories générales de proies ont été observées, mais dans toutes les régions, les proies ont été dominées soit par la goberge de l'Alaska (*Theragra chalcogramma*) ou maquereau Atka (*Pleurogrammus monopterygius*). La diversité des proies consommées a varié d'un site à l'autre. Seules les otaries de la région des îles Aléoutiennes orientales comptaient les sept catégories dans le régime alimentaire, et à cet endroit, la goberge de l'Alaska et maquereau Atka constituaient chacun environ 30% du régime alimentaire. Le reste était constitué surtout de petits poissons vivant en bancs (p. ex., harengs du Pacifique (*Clupea pallasi*) et saumons (*Oncorhynchus* spp.). Dans le golfe de l'Alaska, le régime alimentaire était constitué surtout de goberges de l'Alaska, alors que dans les régions centrales et occidentales des Aléoutiennes, c'était maquereau Atka. Les populations dans les six régions ont diminué d'une valeur allant jusqu'à 49% au cours de la période 1990–1994. Une forte corrélation positive ($r$ = 0,949, $P$ = 0,004) a été observée entre la diversité du régime alimentaire et l'importance du déclin dans une région : lorsque la diversité du régime diminue, la population en fait autant. Cette constatation indique que l'otarie doit avoir à sa disposition une variété de proies, peut-être pour pouvoir absorber les variations importantes d'abondance qui touchent les proies individuelles.
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## Introduction

The cause(s) of the 68% decline in the U.S. population of Steller sea lions *(Eumetopias jubatus)* since the 1970s remains uncertain (National Marine Fisheries Service (NMFS) 1995); however, the consensus among researchers appears to be that the decline is a result of changes in the availability of preferred prey (Merrick et al. 1987; D. Calkins, Alaska Department of Fish and Game (ADF&G), 333 Raspberry Rd., Anchorage, AK 99502, unpublished data; Loughlin and Merrick 1989; Alverson 199 1; Springer 1992; Alaska Sea Grant 1993).

Examination of the health of individual animals *as* a means of evaluating the food limitation hypothesis has provided inconclusive results. Kodiak Island area sea lions were significantly shorter and lighter in 1985-1986 (during the decline) than they were in 1975-1978 (before the decline had begun) (D. Calkins, unpublished data). However, current studies of sea lion condition and health have found no significant differences between adult females and pups in summer in the Gulf of Alaska (a declining population) and southeast Alaska (an increasing population) (Castellini 1993; Davis et al. 1993; Rea et al. 1993; Spraker et al. 1993; Merrick et al. 1995; Rea 1995). Despite the apparent disappearance of thousands of sea lions each year, it has not been possible to evaluate the cause of the decline from beach-cast animals because few dead animals have been found.

An alternative approach to evaluating the food limitation hypothesis is to compare food habits between areas of the range with different population trajectories. To facilitate such analyses, the NMFS, ADF&G, and U.S. Fish and Wildlife Service (USF&WS) began a diet sampling program for Steller sea lions in 1990 that encompassed most of the region of decline in Alaska, from the Kenai Peninsula to the western Aleutian Islands. Declines continued in this region during the period, although the rates of change differed among areas (from +1 to -49%; Strick et al. 1997). Here, we present an

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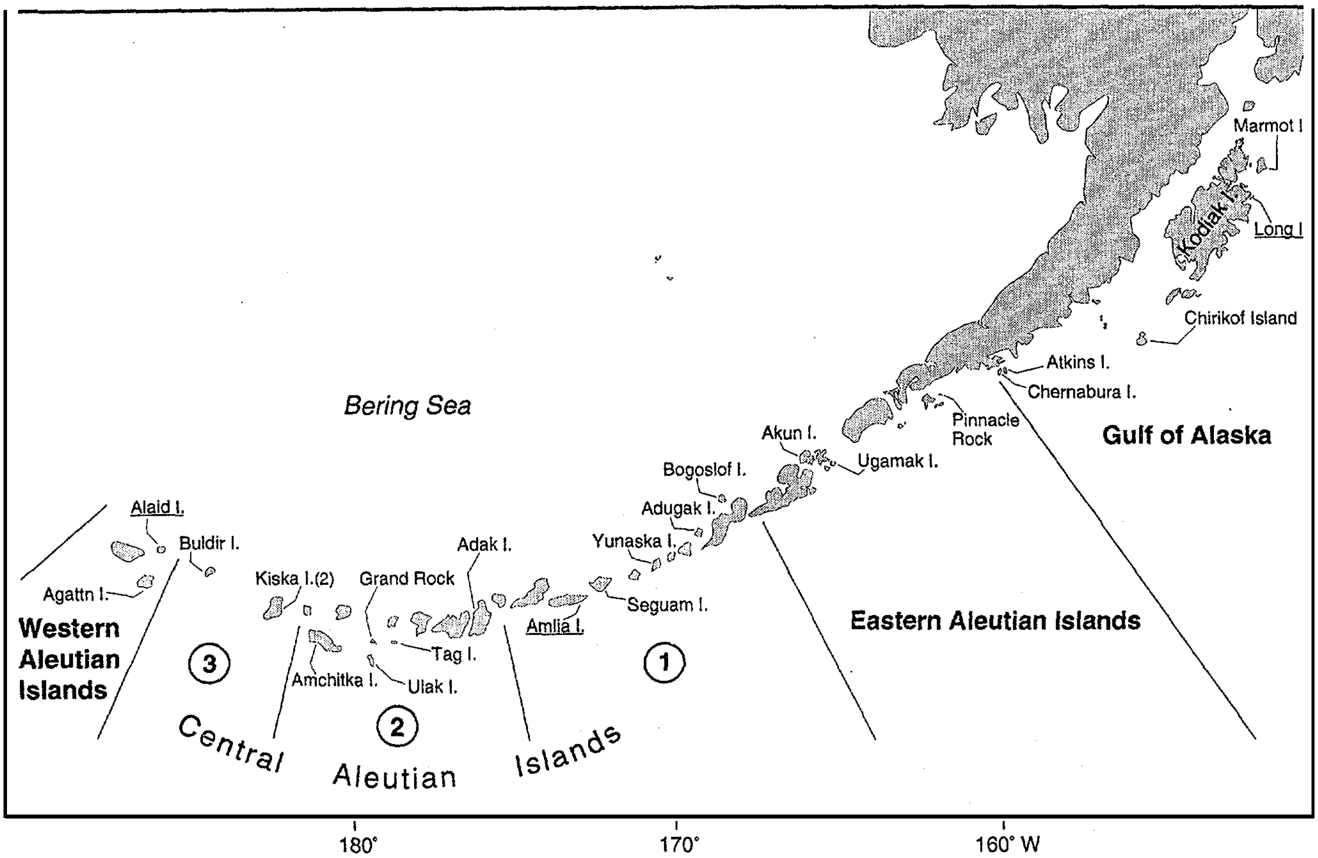
Fig. 1. Sites and diet analysis areas in Alaska where Steller sea lion fecal samples were collected for 1990-1993. Haul-outs are underlined and include Long, Amlia, and Alaid islands. All remaining sites are rookeries, with Kiska Island including two separate rookeries.




area-specific comparison between diet and population change. We initially tested a hypothesis of no difference in diets between areas (i.e., no relationship between diet and rates of declines). Differences were found; thus, we tested a second hypothesis that there was no relationship between diet and the amount of decline by area. Rejection of this hypothesis would then support a third hypothesis that diet and the decline were related.

## Materials and methods

### Collection and laboratory methods

Fecal samples ($n$ = 421) were collected at Steller sea lion haul-outs and rookeries during the last week of June and first week of July or the first week of August (western Aleutian Islands only) of 1990-1993. A total of 37 collections were made at 19 rookeries and three haul-outs in the area from the Kodiak Archipelago in the central Gulf of Alaska westward through the Near Islands in the western Aleutian Islands (Fig. 1). Most of the sea lions (other than pups) on the rookeries were adult females, so most of the scats collected came from adult females.

Biologists collected only fresh scats to ensure that remains were from recent feeding trips. Older scats are harder to process, and could result in damaged hard parts. A scat was only collected if it was obvious that it had come from one animal. Each scat was scooped into a separate gallon-sized plastic bag and frozen. Scats were processed at the National Marine Mammal Laboratory's food habits laboratory in Seattle, Wash.. Samples were thawed and allowed to soak for at least 24 h in an emulsification mixture (Treaty and Crawford 1981) until the scat had softened and formed a slurry at the bottom of the

The softened scat materials were either hand-washed through a series of three nested sieves (2, 1, and 0.5 mm) or passed through an automated washing device (an elutriator; Bigg and Olesiuk 1990) to separate the prey materials. Identifiable hard parts (otoliths, other intact bones, teeth, and beaks) were removed and stored dry in vials. Prey remains contained in each scat were identified by comparing them with reference materials. Most of this identification was performed by Pacific Identifications, Victoria, B.C. Prey were identified to the lowest taxonomic level possible (often species) using multiple structures. A detailed discussion of these methods is provided in Olesiuk et al. (1990). Of the original 421 scats, 364 contained identifiable fish or cephalopod remains (Merrick 1995), 39 contained only unidentifiable fish parts, and 18 contained no identifiable remains. Taxa identified from the 364 scats were grouped into the following categories: (1) gadids: walleye pollock *(Theragra chalcogramma),* Pacific cod *(Gadus macrocephalus),* Pacific hake *(Merluccius productus),* and unidentified gadids; (2) Pacific salmon *(Oncorhynchus* spp.); (3) small schooling fish: capelin *(Mallotus villosus),* Pacific herring *(Clupea pallasi),* eulachon *(Thaleichthys pacifius),* and Pacific sand lance *(Ammodytes hexapterus);* (4) flatfish: arrowtooth flounder *(Atheresthes stomias),* rock sole *(Pleuronectes bilineatus),* and other pleuronectids; (5) other demersal fish: sculpins (Cottidae), rockfish *(Sebastes* spp.), Stichaeidae, skates *(Raja* spp.), sharks, and lamprey *(Lampetra* sp.); (6) Atka mackerel *(Pleurogrammus monopterygius);* (7) cephalopods: squid and octopus. Species were grouped based on similarities in their behavior (e.g., schooling versus nonschooling), nutritional content, and patterns of abundance during the period (Merrick 1995). Analysis at a higher taxonomic level also reduces the effect of errors in the identification of prey.

### Analyses

Separate analysis of the 37 individual collections (a day and site combination) was generally inappropriate because of the small sample size and because of biases possible from site- and time-specific samples. We were concerned about sample sizes, from 1 to 22 scats per collection with a mean of 10, because unrepresentative small samples (e.g., a collection of one scat) could inadvertently skew the results. Thus, we dropped from analysis the nine collections with less than five scats (a total of 26 scats). This left 338 scats for analysis. Furthermore, we expected that because each collection only reflected what was available at the site on the collection day, individual collections were not accurate indices of the general diet of the site or area. Collections should probably be viewed as a sampling unit. Consequently, we decided that it would be more appropriate to use some aggregation of collections.

Adjacent sea lion rookeries have had similar population trends (York et al. 1996), suggesting that some shared environmental feature (e.g., a common food resource) might link sites together. Because our research focused on associating population change with dietary differences, an analysis structure that captured this spatial pattern of common population trends seemed appropriate. Therefore, we used a spatial structure developed from a cluster analysis of individual rookery population trends from 1989 to 1994 (York et al. 1996): (i) Gulf of Alaska (GOA); (ii) eastern Aleutian Islands (EAI); (iii) central Aleutian Islands Area 1 (CAI-1); (iv) central Aleutian Islands Area 2 (CAI-2); (v) central Aleutian Islands Area 3 (CAI-3); (vi) western Aleutian Islands (WAI). This geographical structure (Fig. 1) was used for the food habits analyses discussed here.

*Calculation of the frequency of occurrence of prey categories within the diet*

The relative importance of prey in the diet was measured using split-sample frequency of occurrence (Olesiuk et al. 1990). The split-sample frequency of occurrence of each prey category ($FO_{jk}$) for a collection was calculated as follows:

$$FO_{jk} = \sum_{i=1}^{n_j} (O_{ijk} / \sum_{k=1}^{7} O_{ijk}) / n_j$$

where i = scat sample within a collection, j = collection (each site and year combination), k = prey categories ($1 \geq k \geq 7$), and $O_{ijk}$= a binary variable for the presence of prey category k in the ith scat sample for area j. Thus, the frequency of occurrence ($FO_{jk}$) in the diet of the kth prey categories in the jth collection was estimated from the i = 1 to $n_j$ samples collected in that analysis area. The $FO_{ak}$ for a specific category (k) for an analysis area (a) was calculated as the sum of the weighted category FOs for all j collections from the area:

$$FO_{ak} = \sum_{j=1}^{n_a} [FO_{jk} \cdot (p_j / P_a)]$$

where $p$, = number of animals counted at the site around the time of the collection, $P_a$= total number of animals counted at all analysis area sites where collections occurred, and $n_a$ = number of collections in an analysis area. Population numbers used in the weighting were obtained from the NMFS aerial survey typically conducted 2-3 weeks prior to the date of the collection.

The split-sample approach assumes that remains in the sample represent a complete sample of all prey consumed in the most recent meal(s) and that individual prey taxa were consumed in the meal in equal volume. Olesiuk et al. (1990) assessed the degree to which these assumptions were violated using dietary information from the northem fur seal and found the amount of error to be relatively small. However, in viewing these results, one must remain aware that certain fish with small bony structures may be underrepresented. A volumetric approach would have been preferable; however, the requisite data for volumetric analyses (e.g., otoliths to estimate prey size) usually are not available from Steller sea lion scats.

*Diet diversity index (DDI)*

An index was developed using the Shannon-Wiener species diversity index (Ricklefs 1979) as a model to evaluate diet differences between analysis areas:

$$DDI_a = e^{-\sum_{k=1} FO_{ak} \ln FO_{ak}}$$

where $DDI_a$= diversity of the ath area. Potential values ranged from 1.0 (one taxon in the diet) to 7.0 (all seven categories equally represented). Analysis area $DDI_a$ were calculated from the mean $FO_{ak}$ values for all collections within the area.

*Analysis ofspatial and temporal differences*

Techniques for statistical comparisons of the split-sample FO values have not been rigorously developed. Therefore, we used a contingency table analysis of the numerical occurrence of prey categories in scats (Pearson $\chi^2$, $\alpha = 0.05$) to test for spatial differences.

Temporal differences were analyzed for two areas: the eastern Aleutian Islands and the Kodiak Island area of the Gulf of Alaska. For the eastern Aleutian Islands, diet samples were available from Bogoslof and Ugamak islands for 1985-1989 (40 scats) and 1990-1993 (52 scats). Comparisons in the Kodiak Island area were made between the June-July stomach collections from 1976-1978 (*n* = 28) and 1985-1986 (*n* = 20) and the 1990-1993 scat collections (*n* = 54) (Pitcher 1981; D. Calkins, unpublished data; Merrick and Calkins 1996). Because the Kodiak collections from the 1970s and 1980s were from stomachs with prey identified only from whole fish or from otoliths, it is likely that the results are not strictly comparable with the 1990-1993 scat analyses. To minimize the effect of these differences on comparisons, only the proportions of animals consuming a prey category group were compared (rather than attempting to calculate a split-sample frequency of occurrence). Contingency table (Pearson $\chi^2$, $\alpha = 0.05$) analysis was used to test the frequency of occurrence of each of the seven categories by time or area.

*Comparison between diets andpopulation change*

The DDI and FO (by category) were compared (correlation coefficients, a = 0.05) with the estimated population change of an analysis area's rookery population for the period from 1990 to 1994. Count data were obtained from the 1990 and 1994 NMFS Steller sea lion aerial surveys (Merrick et al. 1991; Strick et al. 1997). No survey occurred in 1993.

## Results

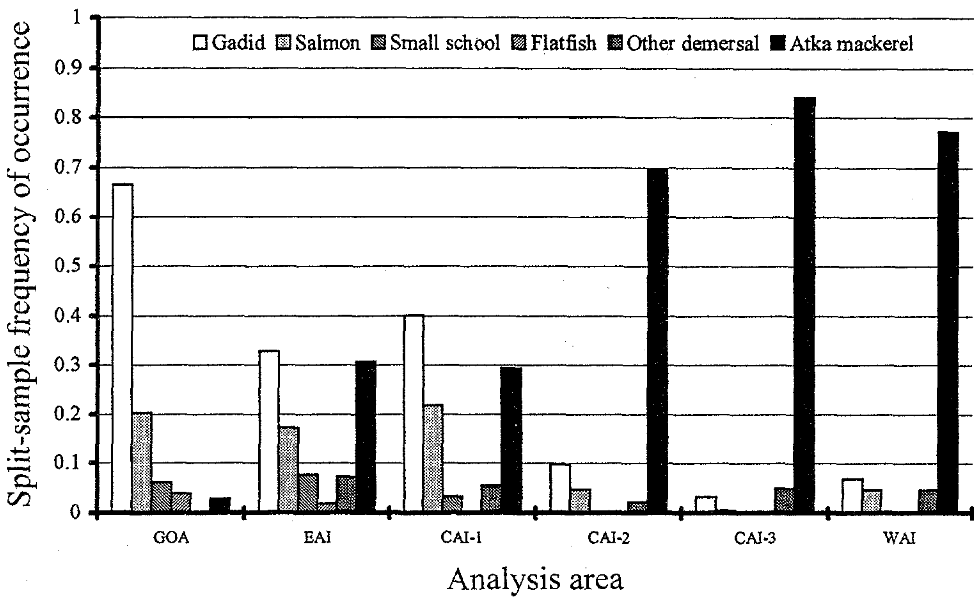
The 338 scats with identifiable contents contained the remains of 29 taxonomic groups, including 13 species (Merrick 1995). Atka mackerel was the most common prey category and species identified (209 occurrences in the 338 samples). Gadids, the second most common taxon (*n* = 145 scats), included 98 scats with walleye pollock, 95 with unidentified gadids (probably walleye pollock), six with Pacific cod, and five with Pacific hake. Salmon and cephalopods were the third (*n* = 66 scats) and fourth (*n* = 39 scats) most common prey. Cephalopods were always found in association with fish remains. Thirty samples included small schooling fish. In almost all cases, these scats contained only small schooling fish remains; therefore, they were not introduced from the guts of other larger fish (e.g., Pacific cod or walleye pollock). Most of the small schooling fish were Pacific herring (*n* = 16 scats) or Pacific sand lance (*n* = 11 scats), but capelin (*n* = 3 scats) and eulachon (*n* = 1 scat) were also found. Other demersal fish were found in 22 samples and included a variety of species. Flatfish was the least commonly found category (*n* = 11 scats).

**Table 1.** Steller sea lion's relative consumption of seven prey categories, DDI, and percent decline in rookery populations by area of Alaska (see Fig. 1 for analysis areas) for 1990-1993.

| Area | Sample size[a] | Gadids (%) | Salmon (%) | Small schooling (%) | Flatfish (%) | Other demersal (%) | Atka mackerel (%) | Squid or octopus (%) | DDI | Decline 1990-1994 (%) |
|---|---|---|---|---|---|---|---|---|---|---|
| Gulf of Alaska | 76 (8) | 66.5 | 20.3 | 6.1 | 3.9 | 0.0 | 0.3 | 2.9 | 2.8 | -35.7 |
| EAI | 67 (5) | 32.9 | 17.3 | 7.7 | 1.8 | 7.3 | 30.7 | 2.3 | 4.0 | 1.1 |
| CAI-1 | 33 (3) | 40.2 | 21.8 | 3.3 | 0.0 | 5.4 | 29.4 | 0.0 | 3.2 | -20.1 |
| CAI-2 | 54 (5) | 9.7 | 4.7 | 0.0 | 0.0 | 2.2 | 69.7 | 13.7 | 2.5 | -25.2 |
| CA13 | 80 (4) | 3.2 | 0.5 | 0.0 | 0.0 | 4.9 | 84.2 | 7.1 | 1.6 | -48.5 |
| WAI | 28 (2) | 6.9 | 4.6 | 0.0 | 0.0 | 4.6 | 77.3 | 6.7 | 2.0 | -40.9 |
| Area-wide | 338 (27) | 25.6 | 11.1 | 3.1 | 0.7 | 3.3 | 50.7 | 5.4 | 3.5 | -20.7 |
| Pearson $\chi^2$ | | 130.3 | 38.3 | 55.9 | 19.0 | 18.5 | 186.2 | 27.7 | | |
| P | | <0.001 | <0.001 | <0.001 | 0.002 | 0.002 | <0.001 | <0.001 | | |

**Note:** Pearson $\chi^2$ calculated from the number of scats with or without a prey.
[a]Number of collections in parentheses.

**Fig.** 2. Proportion of Steller sea lion diet attributable to six fish prey categories by Alaskan analysis area from 1990-1993 fecal samples.




### Spatial differences

All seven categories had different (Pearson $\chi^2$, $P < 0.01$) spatial consumption patterns (Table 1). Diet in each area was dominated by one or two categories (walleye pollock or Atka mackerel; Fig. 2); however, there was a distinct shift in the dominant taxon from east to west. The major prey of sea lions in the Gulf of Alaska was walleye pollock (FO = 0.665). The proportion of walleye pollock in the diet decreased to the west where it was replaced by Atka mackerel (Fig. 2). From Area 2 in the central Aleutian Islands westward the diet consisted mostly of Atka mackerel (FO = 0.647-0.842). Salmon, small schooling fish, and flatfish were found more commonly in the eastern areas. No spatial patterns were apparent for other demersal fish or cephalopods.

Only the eastern Aleutian Islands scats contained all seven categories (Table 1). Atka mackerel and walleye pollock made up roughly equal parts of the diet. This area had the highest proportion of small schooling fish and other demersal fish, and a moderately high proportion of salmon. Area 3 of the central Aleutian Islands represented the opposite dietary extreme. It had the highest proportion of Atka mackerel in the diet and the lowest proportions of gadids, salmon, small schooling fish, and flatfish in the diet.

Differences existed in diet diversity (DDI) among the six regions (Table 1). Diet diversity was greatest in the eastern Aleutian Islands (DDI = 4.0) and least diverse in Area 3 of the central Aleutian Islands (DDI = 1.6).

During 1990-1994, the adult and juvenile Steller sea lion population in Alaska decreased by 20.7% (Strick et al. 1997). Populations of adult and juvenile sea lions in specific study areas decreased up to 48.5% (Table 1). Diet diversity was negatively correlated (Pearson $r$ = -0.994, $P$ = 0.004) with population trends in the six areas (Fig. 3). The less diverse the diet the more an area's population declined. We also compared the FO values for each category with population change; small schooling fish were the only category with a significant correlation (Pearson $r$ = 0.8144, $P$ = *0.05).*

### Temporal differences

Scats collected from Bogoslof and Ugamak islands in the eastern

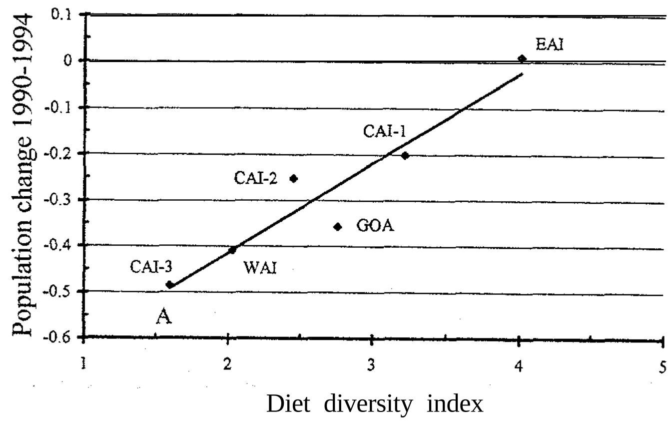
Aleutian Islands during the summers of 1985-1989 contained only three prey categories: gadids (*n* = 39, FO = 0.867), salmon, (*n* = 6, FO = 0.083), and cephalopods (*n* = 4, FO = 0.050). Gadid (mostly walleye pollock) consumption was less in 1990-1993 (FO = 0.372) than in 1985-1989 ($\chi^2$= 23.47, $P$ < 0.001). There was no difference between years (1990-1993) in the proportion of sea lions consuming flatfish (FO = 0.0), salmon (FO = 0.061), or cephalopods (FO = 0.088). All other prey were consumed more frequently in the 1990-1993 period: small schooling fish (FO = 0.037, $\chi^2$= 9.89, $P$ = 0.002), other demersal fish (FO = 0.079, $\chi^2$ = 7.54, $P$ = 0.006), and Atka mackerel (FO = 0.364, $\chi^2$= 26.61, $P$ < 0.001). The diet diversity index for the 1985-1989 collection was 1.6: and the 1989 population was 54.0% of the 1985 population (point "A" on Fig. 3).

Gadids were the most common summertime prey in the Kodiak Island area in the 1985-1986 and 1990-1993 collections, but not in the 1976-1978 collection (Table 2). Of 54 scats from 1990 to 1993 with identifiable remains, 46 (85.2%) contained gadids compared with 32.1% of stomachs in collections from 1976 to 1978 ($\chi^2$= 23.49, $P$ < 0.001) and 60.0% of stomachs in 1985-1986 ($\chi^2$= 5.46, $P$ = 0.019). Salmon and small schooling fish were the second most common prey in the 1990-1993 collection (18.5% of scats each). Salmon consumption did not differ from the earlier collections. Small schooling fish consumption was not different from that recorded in 1985-1986, but was less than in 1976-1978 (60.7% of stomachs; $\chi^2$= 14.86, $P$ < 0.001). At that time, small schooling fish (mostly capelin) were the most common prey in the summer Kodiak Island collections. The 1990-1993 collection included only one sample with capelin; the remainder were either Pacific sand lance (*n* = 4), Pacific herring (*n* = 4), or unidentifiable osmerids (*n* = 1). Flatfish were the fourth most common prey in 1990-1993 (13.0% of scats). This was greater than observed in either of the previous collections and was different ($\chi^2$ = 3.97, $P$ = 0.046) from 1976-1978 when no flatfish were found in the summer Kodiak Island area stomachs. The proportion of sea lions consuming cephalopods did not differ between periods. Atka mackerel and other demersal fish were not found in any of the Kodiak Island samples.

## Discussion

The high correlation between area-specific diet diversity and population change supports the hypothesis that diet is linked with the Steller sea lion population decline in Alaska. Additional support for this linkage comes from the increase in diet diversity observed in the eastern Aleutian Islands area between 1985-1989 (a period of large decline) and 1990-1993 (a period of stability). The Kodiak Island data also support this hypothesis. Pitcher (198 1) found that capelin and walleye pollock were common in the sea lion summer diet during the 1970s. Merrick and Calkins (1996) found that the 1985-1986 summer diet in the Kodiak Island area had increased its focus on walleye pollock (despite declines in juvenile walleye pollock abundance), and capelin was gone from the diet. They suggested that this may have contributed to the moderate population declines that occurred there between the 1970s and 1980s. The 1990-1993 diet indicated a further concentration of the diet on walleye pollock since the 1985-1986 period, and

**Fig. 3.** Steller sea lion DDI (based on scat analysis) compared with population declines experienced during 1990-1994 at rookeries in six areas. Point "A" is comparable data from the eastern Aleutian Islands collected during 1985-1989. The regression line was fit to the equation $y = 0.195x - 0.804$ ($r^2$ = 0.901, $P$ < 0.01) for the six areas' 1990-1993 DDIs *(x)* and 1990-1994 rookery population changes *(y)*.




the sea lion population has since gone through a severe decline (Strick et al. 1997).

The available data suggest that the Steller sea lion diet was different prior to the onset of the declines, which began in the eastern Aleutian Islands in the early 1970s and in the Gulf of Alaska in the early 1980s (Merrick et al. 1987). Fiscus and Baines (1966) found capelin in nine and Pacific sand lance in five of 14 sea lion stomachs collected in the eastern Aleutian Islands and Gulf of Alaska during 1960-1962. Walleye pollock and Atka mackerel were each found in one stomach. In a single summer's collection at Chemabura Island in 1960 (*n* = 74 stomachs with contents), 12 stomachs were found with "smelt" (perhaps capelin), 10 with "greenling" (perhaps Atka mackerel), seven with rockfish, five with sculpins, and 19 with cephalopods (Mathisen et al. 1962). No walleye pollock were found. Similarly, Pitcher (1981) found capelin in 61% of the stomachs of sea lions collected in the Kodiak Island area in the summers of 1975-1978. Subsequent studies, including this study, have failed to find capelin in significant numbers of stomachs. Of these predecline studies, only the 1975-1978 Kodiak Island collection included a substantial amount of walleye pollock (32% of stomachs).

No Steller sea lion food habits study has found a stable or increasing population maintained on a diet consisting mostly of either walleye pollock or Atka mackerel; it appears that at least two major prey need to be commonly available (e.g., walleye pollock and Atka mackerel in the eastern Aleutians in 1990-1993 and walleye pollock and capelin in the Kodiak area in 1975-1978). The eastern Aleutian Islands data further suggest that having secondary prey available stabilizes sea lion numbers. However, this apparent need for multiple prey is not necessarily due to differences in the energetic density of prey. Fadely et al. (1994) found that California sea lions *(Zalophus californianus)* maintained mass equally well on diets of either walleye pollock (4.6 kJ•g wet mass$^{-1}$) or herring (6.0 kJ•g wet mass$^{-1}$). This suggests that the advantage of using several prey is one of foraging efficiency. Diverse prey is easier to find

**Table 2.** Proportion of Steller sea lion stomachs and scats containing seven prey categories for summer Kodiak Island area collections made during 1976-1978, 1985-1986, and 1990-1993.

| Period | Sample size | Gadids (%) | Salmon (%) | Small schooling (%) | Flatfish (%) | Other demersal (%) | Atka mackerel (%) | Squid or octopus (%) |
|---|---|---|---|---|---|---|---|---|
| 1990-1993 | 54 | 85.2 | 18.5 | 18.5 | 13.0 | 0.0 | 0.0 | 11.1 |
| 1985-1986 | 20 | 60.0 | 5.0 | 20.0 | 5.0 | 0.0 | 0.0 | 20.0 |
| 1976-1978 | 28 | 32.1 | 17.9 | 60.7 | 0.0 | 0.0 | 0.0 | 0.0 |

(more prey patches), capture (patch densities are increased), and handle (prey size is correct).

**Source(s) of the diet differences**

The 1990-1993 diets appear to reflect a combination of the sea lions' preference for relatively small (< 30 cm) schooling mid-water fishes (Merrick and Calkins 1996) and changes in the diversity and abundance of prey species. In the Aleutian Islands region, Atka mackerel biomass increased significantly after the early 1980s (Lowe and Fritz 1994). Abundance of small walleye pollock on the eastern Bering Sea shelf was also high during 1989-1993 as a result of the strong 1989 year-class (Wespestad 1994). Thus, sea lions in the eastern Aleutian Islands may have benefitted from positive trends in prey abundance from both the Aleutian Islands and the eastern Bering Sea and had multiple abundant schooling prey available during 1990-1993.

Sea lions in most other areas generally consumed only one category of schooling prey, probably because of the low abundance of such prey. Walleye pollock abundance decreased through most of the central and western Aleutian Islands during the 1980s and 1990s while Atka mackerel populations were increasing (Lowe and Fritz 1994; Wespestad 1994). This restricted sea lions there to a diet composed largely of Atka mackerel. In the Gulf of Alaska, Atka mackerel biomass has remained very low since the early 1980s (1993 adult biomass = 21 600 t (metric tons); Lowe and Fritz 1994). Walleye pollock biomass was reduced and declining through 1993, but walleye pollock biomass remained much greater than that of Atka mackerel (1993 adult biomass = 1 062 000 t; Hollowed et al. 1994). However, most of the walleye pollock biomass in 1990-1993 consisted of large, older fish from the 1984-1985 year-classes. These fish were larger than those that sea lions normally consume (Merrick and Calkins 1996).

The other feature distinguishing the diet of eastern Aleutian Islands sea lions from other areas was the common consumption of other categories of prey. Salmon and small schooling fish constituted more than 10% of the diet. Salmon abundance was high in Alaska during 1990-1993 (Hare and Francis 1995) and they were relatively common in sea lion diets from almost all areas. However, the eastern Aleutian Islands area was the only area where small schooling fish (Pacific herring and Pacific sand lance) and other demersal fish made up a significant part of the diet. This suggests that these prey are more common in the area, but there is little research to document this. Prey surveys begun in 1994 by NMFS, USF&WS, and University of Alaska in the eastern Aleutian Islands to central Gulf of Alaska area suggest that pelagic and demersal fish abundance is highest in the eastern Aleutian Islands (NMFS, 7600 Sand Point Way, Seattle, Wash., unpublished data; B. Norcross, University of Alaska, Fairbanks, Alaska, personal communication). If availability of small schooling and demersal fish prey has increased in the eastern Aleutian Islands, it may be a result of recent declines in the abundance of piscivorous, adult walleye pollock (Wespestad 1994; Merrick 1996). Conversely, the recent record high abundance of piscivorous, adult arrowtooth flounder in the Gulf of Alaska could be partly responsible for the apparent low abundance of small fish prey there (Wilderbuer and Brown 1992; Merrick 1995).

In conclusion, it should be recognized that these results reflect only the diets of successfully foraging adult females in summer. Sea lions who do not find prey leave no record of their failure in scat analyses. However, we believe that these analyses still represent a reasonable index of the prey field sampled by foraging sea lions. This is because the collections integrate across a range of foraging successes, including sea lions who forage poorly but find some prey as well as those sea lions who forage quite well and maintain a rich diet. Still, the apparent relationship found between summer diets and the pattern of decline was unexpected because food limitation has been predicted to most heavily affect juvenile sea lions in winter (Loughlin and Merrick 1989). Juvenile sea lions appear to be less adept foragers than adults (Merrick et al. 1994; Merrick 1995) and juveniles have a more restricted diet than adults (Merrick and Calkins 1996). Prey densities are also lower in winter near sea lion haul-outs; many prey (e.g., Atka mackerel, salmon, capelin, and herring) are only found nearshore in summer during spawning, and in winter are only available offshore and in deeper water. Thus, any indication of scarcity seen in the summer adult diet could be magnified in winter, particularly for juvenile sea lions. Our results suggest that summer diets of adult females index the prey available to juvenile sea lions in winter. Perhaps this is due to the absence or presence of the small fish in both diets because the large size of adult walleye pollock and Atka mackerel may make these prey difficult for small sea lions to capture and consume. Insofar as juvenile survival is related to their foraging success, then increased diversity in the adult diet would correlate well with improved population trends.

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## References

Alaska Sea Grant. 1993. Is it food? Addressing marine mammal and seabird declines. Workshop summary. Alaska Sea Grant Rep. 93-01. University of Alaska, Fairbanks.

Alverson, D.L. 1991. Commercial fisheries and the Steller sea lion *(Eumetopias jubatus):* the conflict arena. Fisheries Research Institute, University of Washington, Seattle.

Bigg, M.A.., and Olesiuk, P.F. 1990. An enclosed elutriator for processing marine mammal scats. Mar. Mammal Sci. 6: 350-355.

Castellini, M.A. 1993. Physiological health status of Steller sea lions and other pinnipeds in Alaskan waters: program objectives. Abstr. Tenth Bienn. Conf. Biol. Mar. Mammals, 11-15 Nov. 1993, Galveston, Tex.

Davis, R.W., Brandon, E.A.A., Kanatous, S., Adams, T., Brandon, D.W., Williams, T.M., Castellini, M.A., Loughlin, T.R., Calkins, D.G., and Sease, J. 1993. Female reproductive effort and pup growth in Steller sea lions. Abstr. Tenth Bienn. Conf. Biol. Mar. Mammals, 11-15 Nov. 1993, Galveston, Tex.

Fadely, B.S., Zaligs, J.A., and Costa, D.P. 1994. Assimilation efficiencies and maintenance requirements of California sea lions *(Zalophus californianus)* fed walleye pollock *(Theragra chalcogramma)* and herring *(Clupea harengus)*. Final report to NMML, AFSC/NMFS, 7600 Sand Point Way NE, Seattle, WA 98115.

Fiscus, C.H., and Baines, G.A. 1966. Food and feeding behavior of Steller and California sea lions. J. Mammal. 47: 195-200.

Hare, S.R., and Francis, R.C. 1995. Climate change and salmon production in the Northeast Pacific Ocean. In Climate change and northern fish populations. Edited *by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 357-372.

Hollowed, A.B., Wilson, C., Brown, E., and Megrey, B. 1994. Walleye pollock. In Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1995. Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 995 10.

Loughlin, T.R., and Merrick, R.L. 1989. Comparison of commercial harvests of walleye pollock and northern sea lion abundance in the Bering Sea and Gulf of Alaska. *In* Proc. Int. Symp. Biol. Manage. Walleye Pollock. Alaska Sea Grant Rep. 89-l. University of Alaska, Fairbanks. pp. 679-700.

Lowe, S.A., and Fritz, L. 1994. Atka mackerel. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea and Aleutian Islands regions as projected for 1995. Bering Sea and Aleutian Islands Groundfish Plan Team, North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99510.

Mathisen, O.A., Baade, R.T., and Lopp, R.J. 1962. Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. J. Mammal. 43: 469-477.

Merrick, R.L. 1995. The relationship of the foraging ecology of Steller sea lions *(Eumetopias jubatus)* to their population decline in Alaska. Ph.D. thesis, University of Washington, Seattle.

Merrick, R.L. 1996. Current and historical roles of apex predators in the Bering Sea ecosystem. J. Northwest Atlantic Fish. Sci. In press.

Merrick, R.L., and Calkins, D.G. 1996. Importance of juvenile walleye pollock in the diet of Gulf of Alaska Steller sea lions. *In* Ecology of juvenile walleye pollock *(Theragra chalcogramma).* Edited *by* R.D. Brodeur, P.A. Livingston, T.R. Loughlin, and A.B. Hollowed. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 126.

Merrick, R.L., Loughlin, T.R., and Calkins, D.G. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus,* in Alaska, 195686. Fish. Bull. U.S. 85: 351-365.

Merrick, R.L., Ferm, L.M., Everitt, R.D., Ream, R.R., and Lessard, L.A. 199 1. Aerial and ship-based surveys of northern sea lions *(Eumetopias jubatus)* in the Gulf of Alaska and Aleutian Islands during June and July 1990. U.S. Dep. Commer. NOAA Tech. Memo. NMFS F/NWC-196.

Merrick, R.L., Loughlin, T.R., Antonelis, G.A., and Hill, R. 1994. Use of satellite-linked telemetry to study Steller sea lion and northem fur seal foraging. Pol. Res. 13: 105-114.

Merrick, R.L., Brown, R., Calkins, D.G., and Loughlin, T.R. 1995. Comparison of Steller sea lion *(Eumetopias jubatus)* pup masses from rookeries with decreasing and increasing populations, Fish. Bull. U.S. 93: 752-757.

NMFS. 1995. Status review of the United States Steller sea lion *(Eumetopias jubatus)* population. Prepared by NMML, AFSC, NMFS, Seattle, Wash.

Olesiuk, P.F., Bigg, M.A., Ellis, G.M., Crockford, S.J., and Wigen, R.J. 1990. An assessment of the feeding habits of harbour seals *(Phoca vitulina)* in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. No. 1730.

Pitcher, K.W. 1981. Prey of the Steller sea lion, *Eumetopias jubatus,* in the Gulf of Alaska. Fish. Bull. U.S. 79: 467-472.

Rea, L.D. 1995. Prolonged fasting in pinnipeds. Ph.D. thesis, University of Alaska, Fairbanks.

Rea, L.D., Castellini, M.A., and Merrick, R.L. 1993. Body condition and metabolic chemistry of Steller sea lion pups in the Aleutian Islands and Gulf of Alaska. Abstr. Tenth Bienn. Conf. Biol. Mar. Mammals, 11-15 Nov. 1993, Galveston, Tex.

Ricklefs, R.E. 1979. Ecology. Chiron Press, New York.

Spraker, T.R., Calkins, D.G., Bradley, D.J., Loughlin, T.R., and Merrick, R.L. 1993. Diseases found in Steller sea lions from the Gulf of Alaska and Bering Sea. Abstr. Tenth Bienn. Conf. Biol. Mar. Mammals, 11-15 Nov. 1993, Galveston, Tex.

Springer, A.M. 1992. A review: Walleye pollock in the North Pacific. How much difference do they really make? Fish. Oceanogr. 1: 80-96.

Strick, M., L. Fritz, Lewis, J.P., and McAllister, D.C. 1997. Aerial and ship-based surveys of Steller sea lions *(Eumetopias jubatus)* in Southeast Alaska, the Gulf of Alaska, and Aleutian Islands during June and July 1994. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-71.

Treaty, SD., and Crawford, T.W. 1981. Retrieval of otoliths and statoliths from the gastrointestinal contents and scats of marine mammals. J. Wildl. Manage. 45: 990-993.

Wespestad, V.G. 1994. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Island regions as projected for 1995. Bering Sea and Aleutian Island Plan Team, North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99510.

Wilderbuer, T.K., and Brown, E.S. 1992. Flatfish. *In* Stock assessment and fishery evaluation report for the 1993 Gulf of Alaska groundfish fishery. Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council , P.O. Box 103 136, Anchorage, AK 99510.

York, A.E., Merrick, R.L, and Loughlin, T.R. 1996. An analysis of the Steller sea lion metapopulation in Alaska. *In* Metapopulations and wildlife conservation. Chap. 12. *Edited by* D.R. McCullough Island Press, Covelo, Calif.