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SEASONAL AND SPATIAL DIFFERENCES IN DIET IN THE WESTERN
STOCK OF STELLER SEA LIONS (*EUMETOPIAS JUBATUS*)

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ABSTRACT

Prey remains identified from 3,762 scats (feces) collected 1990-1998, on summer and winter

island sites across the range of the U.S. western stock of Steller sea lions depict walleye pollock

(*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) as the two

dominant prey species, followed by Pacific salmon (Salmonidae) and Pacific cod (*Gadus

macrocephalus*). Other primary prey species included Arrowtooth flounder (*Atheresthes

stomias*), Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), Irish lord

(*Hemilepidotus sp.*), and cephalopods (squid and octopus). Species that occurred among the top

three prey items on select islands included: snailfish (Liparididae), rock greenling (*Hexagrammos

lagocephalus*), kelp greenling *(Hexagrammos decagrammus)*, sandfish (*Trichodon trichodon*),

rock sole (*Lepidopsetta bilineata*), northern smoothtongue (*Leuroglossus schmidti*), skate

(Rajidae), and smelt (Osmeridae). Capelin (*Mallotus villosus*) occurred in very low frequencies

in this study despite their predominance in Steller sea lion diet prior to the 1980s.

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Regions of diet similarity as defined by Principal Components and Agglomerative Hierarchical Cluster Analyses suggest area specific foraging strategies, with significantly strong seasonal patterns in consumption of most species based on Chi square analysis. An exception is walleye pollock which is a staple in Steller sea lion diet both winter and summer from the Gulf of Alaska up to the central Aleutian Islands area.

The seasonal and regional patterns in prey consumption, as well as known geographic distributions and estimated body size of their primary prey, indicate that Steller sea lions target prey when they are densely schooled in spawning or migratory aggregations nearshore (over or near the continental shelf) or along oceanographic boundary zones. This is true in summer when collected scats are primarily from adult females, and in winter when scats are presumably from some increased proportion of juveniles and adult males as well as females. Based on the close parallel of these data with those of metapopulation patterns of decline and the tendency for site tenacity among the Otariidae, we suggest that regional diet patterns among the western stock reflect regional foraging strategies learned at or near the natal rookery site on seasonally dense prey patches characteristic of that area.

Key Words: diet, food, foraging, Otariid, prey, sea lions, Steller sea lions

INTRODUCTION

Since the 1970's, Steller sea lion (*Eumetopias jubatus*) numbers have declined precipitously (over

80%) throughout the western portion of their range across the North Pacific Rim (Kenyon and

Rice 1961; Loughlin et al. 1992). In 1990, these declines resulted in listing Steller sea lions as

threatened under the U.S. Endangered Species Act. In 1997, Steller sea lions were classified as 2

distinct populations or stocks, at which time the newly defined western stock (west of 144°W in

the Gulf of Alaska) (Bickham et al. 1996; Loughlin 1997) was listed as endangered. The cause of

this and similar declines among other North Pacific apex predators are thought to be due to

decreased reproductivity and increased mortality associated with diet or foraging restrictions

stemming from a combination of natural and anthropogenic influences (NRC 1996). Recently,

commercial fisheries have been implicated as playing a role in jeopardizing the population health

and recovery of Steller sea lions through resource alteration and competition (NMFS 2000).

These recent events underscore the importance of understanding Steller sea lion diet and foraging

behavior.

While the potential mechanisms driving Steller sea lion population declines have been

extensively studied over the past 2 decades, until now data has been insufficient to define

seasonal and regional differences in prey consumption. Lack of adequate data is in part due to

the remoteness and relative inaccessibility of sea lion habitat and the requirement of large sample

sizes and long time series required to adequately interpret diet patterns.

Steller sea lions breed, bear and nurse their young on remote island sites called rookeries which

are occupied variably during summer months (May-September) by territorial adult males, adult

females, and pups of the year. Pups of the previous year and older juveniles are also present on

rookeries, but to a lesser extent. After breakup of summer reproductive structure on the rookeries

in July, adult bulls disperse from the islands while females and their pups remain or move to and between other islands referred to as haul-outs. As of August, all islands where sea lions are present are classified as haul-outs, even though some may serve as rookeries during the summer breeding season. After September, haul-outs are composed of a full matrix of ages and sexes. It is during their occupation of rookery and haul-out sites that Steller sea lions are accessible to researchers.

This study is based on scat (fecal) material collected throughout the 1990's on rookeries and haulouts across the range of the U.S. western stock of Steller sea lions (Fig. 1). It is the first study to evaluate long-term regional trends in Steller sea lion diet and long-term diet trends during winter months, a time of enhanced sensitivity for juvenile survival.

MATERIALS AND METHODS

Field and Laboratory.- Steller sea lion scats were collected (1990-1998) across the U.S. range of the western stock resulting in 2,340 samples from 31 sites (rookeries) in summer (May-September), and 1,843 samples from 31 sites (haul-outs) in winter (December-April) (Fig. 1; Table 1). Some sites were visited during both winter and summer, but typically, sites were visited no more than once per season with a target collection of 60 scats per site.

Only scats considered to be a whole sample from an individual animal were collected. Scats were initially stored dry in plastic bags then frozen prior to processing in the laboratory. Each bagged sample was thawed separately in soapy water before being either hand-washed through nested sieves of 4.8, 1.4, 0.7 and 0.5 mm mesh, or passed from an elutriator (Bigg and Olesiuk 1990) into nested sieves of 0.7 and 0.5 mm mesh. All prey remains (e.g.,lenses, scales, bones including fish earbones (otoliths), and cephalopod rostra or beaks) were recovered from the sieves and

stored for later analysis. Beaks and lenses were stored in 50% isopropyl alcohol, scales and bones were stored dry in glass vials. This diet analysis is based on beaks, bones, scales, and otoliths identified to the lowest possible taxon using reference collection specimens.

We assume summer collections primarily represent the diet of adult females since adult males usually fast during the breeding season. However, partially weaned juveniles of both sexes do haul out on rookeries during the summer and are undoubtedly represented to some degree in the dataset. Conversely, winter collection sites are all considered haul-outs with breakdown of the summer breeding structure. Therefore, winter scat collections presumably represent a greater cross-section of variable ages and sexes than summer collections.

Analysis.- The relative 'importance' of each prey species was based on the frequency with which it occurred in scats, where each scat was treated as an independent sample. The percent frequency of occurrence (*FO*) of individual prey species was calculated by dividing the number of scats in which a prey item occurred by the total number of scats that contained identifiable prey remains. This technique allows interpretation of trends in prey species composition and provides an index of the proportion of the predator population consuming a particular prey item. *FO* does not provide the number of each prey species consumed, a current limitation particular to Steller sea lion diet studies based on scat, due to the efficient digestive capacity of Steller sea lion stomachs. The large sample sizes in this study most likely overwhelm potential bias introduced by this limitation; an assumption supported by a wide range of marine mammal diet studies (examples: Antonelis et al. 1997; Kajimura 1984; Sinclair 1992, 1994; Sinclair et al. 1994, 1996; Walker 1996) where prey rank based on frequency of occurrence vs. number is interchangeable.

In order to determine site specific differences in Steller sea lion diet, *FO* values were compared on a site-by-site basis for summer and winter, all years combined. Collection sites for summer scats were then grouped in order to describe areal diet patterns and to make seasonal comparisons (since not all sites were visited in both seasons). Sites were grouped based on similarities between the *FO* of prey species, using principal components analysis (*PCA*) and an agglomerative hierarchical cluster analysis (Ludwig and Reynolds 1988).

PCA was used first to reduce the data into representative prey species that accounted for the majority of the variance in the data set. *PCA* was calculated on a correlation matrix using prey species as variables and 31 sites as observations. In order to minimize zeros in the analysis, only prey that occurred in greater than 5% of the scats across all sites were included as variables in the *PCA*. Cluster analysis was then conducted on the *PCA* factors using squared Euclidian distance (Ludwig and Reynolds 1988) as a measure of similarity between sites, and Wards (1963) method to compare cluster distances. Logical spatial breaks in the clusters were determined from output dendograms (SPSS Inc. 1999) and used to group sites into regions. Although *PCA* and cluster analyses were done for both summer and winter data, only summer data was used fro grouping sites into regions since it encompasses a broader range of sites and presumably has less variability in age and sex of the animals than winter data.

Chi-square (Splus 2000) was used to test the hypothesis that there was no difference in the proportion of scats containing a particular prey item (*FO*) within each of the regions (island groupings as defined by *PCA* and cluster analysis) between winter and summer. For purposes of this analysis, it was assumed that all species within a scat were independent of each other, and data were limited to prey items occurring in greater than 5% of scats across all regions and seasons. A 2x2 contingency table was used to compare the proportion of scats containing a

particular prey item between the summer and winter. Since Chi-square is based on large cell counts (observed values), statistics were not calculated for prey species with any cell count less than or equal to 5 (Ramsey and Schafer 1997). Sample sizes were large overall, so significance was determined at the 0.01 level.

Diet diversity was calculated for each region using Shannon's index of diversity, *H*, where p_i is the proportion of the *i*th family in the sample (Ludwig and Reynolds 1988).

$$H = \sum_{i=1}^{n} p_i \ln p_i$$

Prey identified to family rather than species were used for the diet diversity analysis in order to include all data on an equivalent taxonomic level. Exceptions to this were flatfish and cephalopods which we were unable to breakdown into family groups.

RESULTS

Of the 4,183 scats collected, a total of 3,762 contained identifiable prey items in summer (*n* = 2,102) and winter (*n* = 1,660). Frequency of occurrence values combined across years, seasons, and sites depict walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) as the two dominant prey species overall, followed by Pacific salmon (*Oncorhynchus* spp.) and Pacific cod (*Gadus macrocephalus*) (Table 2). Based on comparison with prey reference collections, remains recovered from these primary prey were predominantly from late stage juvenile and adult sized fish (> 25cm) (Zeppelin et al. unpub. data). In addition to the dominant species, those occurring at frequencies of 5% or greater that were included in *PCA* and cluster analysis were: Arrowtooth flounder (*Atheresthes stomias*), Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), Irish lord (*Hemilepidotus* sp.), and cephalopods (squid and octopus) (Table 2).

Island comparisons.- In general, collections from island rookeries in close proximity to one another had similar prey matrices (the same prey species of similar rank). However, inter-island comparisons of diet on a seasonal basis demonstrate that some prey species, when averaged throughout the year, have a low FO, but have consistently high FO values within a particular season on particular islands (Table 3). It is only when *FO* values are averaged across sites that these species lose rank as primary prey (Table 2). Examples of fish species occurring among the top three prey items on select islands during winter only include: snailfish (Liparididae) on Perl, Kodiak, Atkins, Unalaska (Bishop Point), and Seguam Islands; rock greenling (*Hexagrammos lagocephalus*) on Ulak and Attu Islands; kelp greenling *(Hexagrammos decagrammus*) on Adugak Island; sandfish (*Trichodon trichodon*) on Amak Rocks and Ugamak Island; and rock sole (*Lepidopsetta bilineata*) on Amak (Sea Lion Rock) and Clubbing Island. Species occurring among the top 3 prey on specific islands during summer months only include: northern smoothtongue (*Leuroglossus schmidti*) on Bogoslof Island[2], skate (Rajidae) on Semisopochnoi Island, and smelt (Osmeridae) on Sugarloaf Island. A comparison of relative *FO* values among the primary prey species also demonstrates wide variation in relative importance between islands. Pacific cod, for instance, is a significant prey item across the western range during winter months only, however percent *FO* values range as low as 0 and as high as 62 between rookeries located in the same region for the same time period.

PCA and Cluster Regional Divisions.- The majority of the variance (67.7%) in the diet data was explained by two principle components. *PCA* Axis One accounted for 43.6% of the variance and *PCA* Axis Two accounted for 23.1%. The remaining components had variance of 9.5% or less, and were not considered useful in determining site divisions based on prey. A plot

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[2] Collections on Bogoslof Island occurred only during summer

of Component One against Component Two shows 3 groups of prey which are related based on

similar loading scores (Fig. 2). Likewise, 3 logical spatial breaks were evident from the cluster

analysis with the exception of one outlier, a Bering Sea rookery (Sea Lion Rock near Amak

Island). Cluster 1 had negative values for Component One and generally positive values for

Component Two, meaning these sites were characterized by relatively high occurrences of Atka

mackerel and cephalopods. Cluster 2 had positive values for Component One and negative

values for Component Two, and these sites were characterized by relatively high values of

pollock, salmon, and arrowtooth flounder. Cluster 3 had positive values for Components One and

Two. Although sites within Cluster 3 had significant occurrences of pollock, salmon and Atka

mackerel, the relatively high occurrence of sand lance, herring, Pacific cod, and Irish lord

differentiated Cluster 3 from the others.

Plotting cluster analysis results by location shows that sites in each cluster were generally

separated spatially (Fig. 3). One site in Cluster 2 (Ogchul Island) fell out far west of the other

sites, possibly due to low sample sizes. There was also some spatial overlap between Clusters 2

and 3. For the purposes of this analysis 4 regions were defined based on the spatial distribution

of the Cluster assignments for each site; 3 regions where diets were clearly distinctive and 1

region (Region 2) where diet overlap occurred (Fig. 3).

Regional comparisons.- Patterns in prey composition by region (island group) illustrate

changing foraging patterns moving east to west across the western range (Table 2; Fig. 3). In

general, among the primary prey, there is a shift in regional diet dominance from pollock to Atka

mackerel and cephalopods moving west from Region 3 to Region 4. The general profile of

Regions 1, 2, and 3 are similar in that they are all most strongly defined by the high *FO* of

walleye pollock during both winter (Region-1, 56%; Region-2, 86%; Region-3, 59%) and

summer (Region-1, 64%; Region-2, 80%; Region-3, 54%), and high *FO* values for salmon in the summer (Region-1, 41%; Region-2, 45%; Region-3, 35%). Region 1 differs from all others in that it is characterized by a consistently high *FO* of arrowtooth flounder in both winter (21%) and summer (35%). The *FO* of Irish lord and forage fishes, Pacific sand lance and Pacific herring, are also highest in Regions 2 and 3. Region 2 has the highest *FO* levels of Pacific cod consumption in both winter (36%) and summer (11%) compared to all other regions. Region 4 is generally distinguished by low frequencies of all prey except for cephalopods and Atka mackerel.

Seasonal comparisons.- Several trends were apparent when examining prey *FO* seasonally within regions (Fig. 4). Pollock *FO* was not significantly different between seasons in Regions 1, 2, and 3 and not statistically comparable due to low values in Region 4. Likewise, cephalopod *FO* was not significantly different between seasons in any region. Otherwise, the seasonal shifts in prey between regions were highly significant by Chi-square analysis (Table 4). Pacific cod *FO* was significantly larger in winter in every region. Salmon *FO* was significantly lower during winter in Regions 1-3 and higher in Region 4. In Region 1, where arrowtooth flounder is most abundant in scats and well represented year-round, its *FO* was significantly lower in winter. Atka mackerel was significantly lower in the winter in Region 4 where it was the dominant prey species year-round. Herring is significantly higher in the winter in Region 1, lower in Region 2 and appears to be higher but is not statistically comparable in Region 3. Conversely, Pacific sand lance *FO* was significantly higher during winter in Region 1 and lower in Region 2. Irish lord *FO* was generally higher in winter than in summer. Though rarely occurring during summer and not included in Chi-square analysis, sandfish and snailfish had relatively high occurrences during the winter across all regions.

Diversity.- In all regions except Region 2, diversity values were higher in winter than in

summer. During the summer, diet diversity was highest in Region 2 ($H = 2.1$) and Region 3 ($H = 2.0$), and lowest in Region 4 ($H = 1.5$) where the diet was made up almost entirely of Atka mackerel and cephalopods. In winter, highest diversity was in Region 1 ($H = 2.1$) and Region 3 ($H = 2.1$), and lowest in Region 2 ($H = 1.8$).

DISCUSSION

Seasonal and regional (island group) patterns in prey composition in this study are strongly defined and provide a detailed illustration of the foraging behavior of Steller sea lions. Based on seasonal diet data presented here, and records of prey distribution on and offshore, we suggest that Steller sea lions target prey when they are nearshore and densely schooled in spawning aggregation or highly concentrated migratory movements, alleviating the need to travel far from land. Further, we suggest that the strong regional fidelity in summer diet patterns of adult females demonstrated here, reflect regional foraging strategies learned at or near the rookery site where females were born. In otherwords, as adults, females forage close to shore near their natal rookery, on seasonally dense prey patches characteristic of that area. Essentially, depending upon the stability of prey resources in a specific locale, future reproductive success of the Steller population may, in this way, be closely tied to the location of the natal rookery of female pups.

Indications that Steller sea lions typically forage over or near the continental shelf, or on nearshore oceanographic or bathymetric structures, are supported by several factors including: prey size (fish consumed by Steller sea lions are primarily adults and late stage juveniles, as approximated by comparison with reference collection specimens), relative seasonal frequencies of occurrence and regional specificity of prey in Steller diet, along with known seasonal distributions of these prey. Based on comparison with reference collection specimens, the

remains of the primary fish prey recovered in this study were from adults and late stage juveniles (Zeppelin and Call unpub. data). Most of these fish species are migratory with seasonal nearshore and offshore (offshelf) schooling habits depending upon season and age. The known seasonal and spatial distribution of their spawning aggregations parallel their highest seasonal and regional frequencies of occurrence in Steller sea lion diet. For instance, Pacific cod congregate in high densities during winter along the continental shelf of the Gulf of Alaska and Aleutian Islands, dispersing away from the area during the rest of the year (Shimada and Kimura 1994), and Pacific cod were eaten by Steller sea lions nearly exclusively during winter in this study. The few additional records of Pacific cod in previous studies of Steller sea lion diet within this study area were based on stomach contents collected during the winter (Calkins 1998; Pitcher 1981). Salmon were consumed by Steller sea lions in this study mostly at late juvenile to adult sizes, and mostly during summer except in Region 4 where winter consumption values were significantly higher than summer. Most North Pacific salmon species live pelagically as juveniles for 1-3 years, making spring/summer high density alongshore migrations to breeding streams as adults (Pearcy 1992). Adult salmon movements to the spawning grounds are rapid and the timing is precise (Pearcy 1992), conceivably allowing some level of prediction for predators. Region 4 is within the projected fall/winter migratory corridor for Bristol Bay salmon stocks that have spent their first summer in the Bering Sea and are heading south to the open Pacific for their pelagic phase (Pearcy 1992), and Region 4 was the single area where salmon consumption was higher in winter than in summer. Similarly to salmon, herring are pelagic in distribution except during spring and summer when they migrate in dense shoals alongshore towards coastal embayments where they spawn (Grosse 1988). Herring are often associated with dense congregations of sand lance in spring and summer, that are otherwise thought to remain nearshore but, burrowed in the substrate during winter (Blackburn and Anderson 1997). Frequencies of consumption of both herring and sand lance were highest in summer in all regions where they occurred except Region

1 where winter consumption was significantly higher. Walleye pollock and Atka mackerel (EFHT 1998) are available nearshore year-round in the areas where they are consumed as a year-round staple of Steller sea lions. Atka mackerel consumption by sea lions was, however, significantly higher in summer than winter, possibly related to nest guarding by males or dense aggregations of adults and juveniles that gather outside the nesting region during summer.

Strong patterns of seasonal consumption by Steller sea lions holds true for those prey species less predominant in the diet overall, but dominating diet at particular island sites. Sculpins spawn nearshore during winter months where nests are guarded by males (Eschmeyer et al. 1983) and sculpin (Irish lord) consumption by Steller sea lions is 3 times higher in winter than summer when averaged across sites. This is not the case however at all islands where Irish lord is consumed. At Sea Lion Rock for instance, summer consumption of Irish lord averages 40% *FO*, but the species is entirely absent from the diet in winter. The consistent consumption of prey at particular islands that are of otherwise minor importance rangewide, and the broader regional patterns of consumption of primary prey species are indicative of strong site fidelity in feeding. Results of cluster analysis on winter data were not presented here due to uncertainty in the effect of small sample sizes, but it is noteworthy that patterns in regional diet specificity with few exceptions, appeared to be identical to summer.

During seasons of low occurrence in Steller sea lion diet, these migratory prey fish are more highly dispersed, but still distributed in pelagic areas that remain within the foraging range (Loughlin et al. 1998; Merrick and Loughlin 1997) of adult Steller sea lions. Fishes consumed pelagically during their offshelf distribution phase should be detected in scat if sea lions are returning to haul out between feeding bouts (within 72 hrs). Yet, they appear to be absent from the diet, indicating that either the prey are not eaten during their high dispersal phase away from

rookery regions, or that some portion of the Steller sea lion population may be eating them away

from rookeries, and not returning to the islands with any regularity.

There is evidence that more animals are represented on rookeries and haul-outs in summer

compared to winter (Calkins 1998; Sease, unpub. data), but the degree of transience is unknown

and may be sex specific. Calkins (1998) randomly collected 110 sea lions hauled out along the

seasonal ice edge in the central and western Bering Sea in winter (March-April), and reported that

no females or young of the year were collected or sighted in the study area. Gearin (unpub. data

1985) reports on collections of 19 Steller sea lions randomly collected from the central Bering

Sea in late March, 1985, all male. Similarly, historical reports on distribution patterns of Steller

sea lions on haul-outs along the Russian Commander Islands detail sites that were occupied

nearly entirely by large groups of males in winter (October-April) and only by single juvenile

males in summer (Barabash-Nikiforov 1938; Tikhomirov 1964). Females have been tracked

offshore in winter, but not to the degree observed among males. Satellite telemetry has shown

that 3 of 5 adult females tagged in winter fed near the island on which they were tagged, while

the other two moved immediately offshore to the Patton Seamount area where they remained until

their return to the islands near the end of the sampling period (Merrick and Loughlin 1997).

Mean trip distances in summer were 17 km (Merrick and Loughlin 1997) and 20 km (Loughlin et

al. 1998). Based on mitochondrial DNA haplotype distinction, Bickham et al (1998) concluded

that 36 male and female Steller sea lions collected during winter and summer from the Gulf of

Alaska in 1976-1978 were probably from Gulf of Alaska rookeries. Whether winter dispersal

away from rookeries and haul-outs is typical of a significant portion of the population or

primarily of adult males is uncertain. But, based on a close relationship between diet clusters and

clusters of population decline patterns in Steller sea lions (Fig. 5) during both winter and summer,

we suggest this study represents typical year-round diet and foraging behavior for the majority of

the population, and that most animals, or at least most adult females are regional feeders with

strong site specificity in their diet.

Regional summer diet divisions closely parallel those defined by population decline patterns of

females and their pups (York et al. 1996) (Fig. 5), suggesting that diet and decline are linked

either directly, or by a third mechanism. York et al. (1996) modeled metapopulation breaks of

western stock Steller sea lions based on trends in summer population counts (1976-1994) of adult

females and pups. The results of their work determined that rookeries in close proximity to one

another demonstrated similar trends in patterns of population change just as our results show that

scat collections from rookeries in close proximity to one another demonstrate similar patterns in

diet. York et al. (1996) drew boundaries around the rookery clusters (metapopulations) defined

by these population trends which are nearly identical to those clustered in this study by diet (Fig.

5). The strong site fidelity in feeding patterns shown here (Fig. 3), support breeding site fidelity

theory suggested (Kenyon and Wilke 1953) and demonstrated for northern fur seals (*Callorhinus*

ursinus) (Baker et al. 1995), another otariid pinniped, as well as suggestions by York et al. (1996)

that dispersal by adult breeding females away from natal rookeries (in summer) is low. We take

this argument further by suggesting that widespread dispersal from the region of natal rookeries is

low for the lifetime of females, as evidenced by the summer and winter site specific diet patterns

demonstrated here, and female summer site specific decline patterns shown by York et al. (1996).

We propose that genetic diversity in the western stock, as evidenced by Bickham et al. (1996) is

maintained primarily by males that disperse and breed away from the birth rookery. Considering

the strong prey selection patterns by rookery, region, and possibly rookery cohort, we suggest

that the rookery of birth may be more definitive of diet pattern and future reproductive success

than individual variation in diet. Thus, due to strong regional selection, prey species that form a

minor part of the diet rangewide may play a very important role in the foraging success of

regional populations of Steller sea lions and their young, particularly in terms of diet diversity.

Reduced prey diversity has been proposed as a potential factor in widespread declines of

pinnipeds (Merrick et al. 1997; Sinclair et al. 1994) and seabirds (Sinclair et al. 1994) in the

Bering Sea and North Pacific ecosystem since the mid-1970's. A diversity of prey resources may

be important to Steller sea lions less for nutritional reasons than for the continual availability of

prey. In theory, reduced availability of primary prey is more readily tolerated by a predator

population if other resources are predictably available (Sinclair et al. 1994). While predator

reliance on 1 or 2 primary prey may work well when fish year class is strong, such specialization

would be disastrous in years following poor recruitment and larval survival. On the other hand,

regions of high prey diversity may simply reflect an environment of generally high productivity

and/or strong habitat diversity. The Unimak Pass area in general is considered an

oceanographically dynamic, highly productive region that supports large numbers of apex

predators and possibly nursery stocks of critical prey (Sinclair and Stabeno in press). The

Unimak Pass area as well as Sea Lion Rock (Amak Island) on the continental shelf just eastward

of the pass (Fig. 1) encompassed the regions of highest prey diversity in this study. In the midst

of precipitous population declines rangewide among the western stock (Loughlin et al. 1992),

Amak Island was among 5 other rookeries identified by York et al. (1996) that demonstrated

persistently stable or increasing population counts: Amak, Akun, Akutan, Chernabura, Clubbing,

Ugamak. The York et al. (1996) temporal model for extinction of the western stock predicted

that in the face of extinction of all other sites, these six would remain viable. All of these sites

fall within Regions 2 and 3 as defined in this study, regions of highest diversity and greatest

overlap in prey matrices between regions in this study (Fig. 5). Implications of the importance of

diversity in otariid diet (Merrick et al. 1997; Sinclair et al. 1994), though difficult to measure,

should be further addressed, with special attention given to the dynamics of physical and bottom-

up processes that influence nearshore habitat of rookery regions and ultimately, the population
stability of Steller sea lions.

Diet, dive depth capacities (Loughlin et al. 1998; Merrick and Loughlin 1997), and prey
distributions suggest that when Steller sea lions feed deeply, it is at or close to the bottom over
relatively shallow water near landforms. The deepest dives are probably made in pursuit of
nearshore demersal and semi-demersal species in the submarine canyons and crevices that define
the bathymetry along the continental shelf of the Aleutian arc, as opposed to feeding deeply
offshore during the high dispersal phase of these same prey. The results of this study are very
similar to historical studies in terms of indicated foraging patterns on demersal (flatfish), semi
demersal (greenlings), and epipelagic (herring) prey groups, but the species of prey consumed
differ significantly from studies conducted in the same area prior to the mid-1970's.

In terms of the species of fish eaten by Steller sea lions, this study compares most closely with
those conducted since the mid-1970's. In studies conducted along the range of the western stock
between 1958 and 1969 pollock were completely absent from Steller diet (Fiscus and Baines
1966; Mathisen et al., 1962; Perlov 1975; Thorsteinson and Lensink 1962; Tikhomirov 1964).
The high occurrence of pollock in this study is comparable to diet studies conducted since 1975
(Calkins 1998; Frost and Lowry 1986; Merrick et al. 1997[3]; Pitcher 1981) and possibly prior to
the 1950s' when Imler and Sarber (1947) reported pollock in 2 stomachs collected near Kodiak
Island in 1945-1946. This study also highlights the importance of Pacific cod in Steller diet
during the winter months. Prior to this work, relatively few papers have focused on winter diet,
so it is difficult to assess whether this is a recent trend. Pacific cod was a top prey item in Calkins

[3]Merrick et al. 1997 was based on portions of the 1990-1993 dataset incorporated into this
study.

(1998) Bering Sea winter collections, and in stomachs collected in the Gulf of Alaska 1973 - 1975 (Pitcher 1981). Although some of the stomachs were collected in winter (Pitcher 1981) it is unclear whether these were the stomachs that contained cod. Overall, the most common prey items in studies prior to the mid-1970's included: capelin (*Mallotus villosus*), sand lance, cephalopods, herring, greenlings (Hexagrammidae), rockfishes, and smelts. Capelin, which were important in Steller diet through the 1970's (Fiscus and Baines 1966; Pitcher 1981) do not have an occurrence greater than 5% in this study. Salmon were present in early studies, but, not at the frequencies found across the western range during the summer in this study. The occurrence of flatfish, especially Arrowtooth flounder, in the Gulf of Alaska is substantially higher in this study than any previous studies. Cephalopods were among the top prey items found in Steller sea lion stomachs in many early studies (Mathisen et al. 1962; Pitcher 1981; Thorsteinson and Lensink 1962), sometimes ranking as the most frequently occurring prey item (Fiscus and Baines 1966). Cephalopod occurrence in this study was primarily limited to the central and western Aleutian Islands of Region 4 and highest during the summer months, but never reached the high frequencies of the 1960's.

Most differences between this and earlier studies reflect true changes in diet. But, some are related to study methodology and biases inherent in study technique. Historically, diet studies on marine mammals were based on the remains of prey in the stomach contents of the predator. Comparatively, scats are a more accessible indicator of diet, and a valuable tool for quantifying seasonal and temporal trends in predator diets, without the need to euthenize the predator. However, hard parts from very large prey are most likely regurgitated or retained in the stomach, never passing through to scat. In addition, small otoliths tend to flush through the digestive system more quickly than larger ones remaining intact and more abundant in scats than stomachs. Therefore, the adult and late juvenile size fish identified in this study probably represent the

minimum sizes consumed, and the largest prey species may never be detected at all in scats.   For

example, the difference in cephalopod values between this and stomach based diet studies may be

due to differences in representation of cephalopod beaks in stomachs vs. scats. Adults of the

octopod species (*Octopus dofleini*); historically and currently present in quantity in stomach

collections of Steller sea lions across their Alaskan range (Calkins 1981; Gearin unpub. data

1986; Springer unpub. data) were not found in this study. The cephalopod beaks that were

present were very small and few in number, probably representing secondary digestion through

consumption of *O. dofleini*, or Atka mackerel (Yang 1999) as the primary prey. With exception

of prey such as *O. dofleini* that are only consumed at large body sizes, stomach and scat

techniques are comparable in terms of determining trends in the species of prey consumed by

Steller sea lions.

The current foraging behavior of Steller sea lions has not changed substantially since the mid-

1970's, in that they specialize feeding throughout the water column (epipelagic to demersal), but

diet composition has changed in ways that reflect a markedly different ecosystem than that of the

1950's and 1960's. Similar diet shifts are now well documented for other apex predators in the

North Pacific and Bering Sea ecosystem during this time period including: northern fur seals

(*Callorhinus ursinus*) (Sinclair et al. 1994), piscivorous birds (Decker et al. 1995; Hunt et al.

1996; Piatt and Anderson 1996)**,** and fish (Alaska Sea Grant 1997). Changes in prey availability

and resultant shifts in apex predator diet in the mid-1970's are indirectly attributed to the effects

of climate change (Hunt et al. 1996; Hunt and Byrd 1999; NRC 1996). Continued depression of

prey availability and predator recovery is attributed to anthropogenic influences including

commercial fishing (NMFS 2000; NRC 1996).

The results of this study and previous observations (Fiscus and Baines 1966; Pitcher 1981)

suggest Steller sea lions are predators that capitalize on precise timing of high density, seasonal,

nearshore migrations of their prey. In this sense, they are not opportunistic, but would seem

adapted to capitalize on changing prey conditions, compared with other apex predators in the

northern North Pacific ecosystem (northern fur seals, Dall's porpoise (*Phocoenoides dalli*) that

specialize feeding in one or two ecological zones (Antonelis et al. 1997; Beamish et al. 1999;

Sinclair et al. 1996). The capacity to feed on predictably occurring resources throughout the

water column in protected waters near the island of their birth should theoretically provide Steller

sea lions with some choice of prey year-round. However, this may be less of a foraging strategy

than a requirement, in that Steller sea lions may depend upon the presence of large, dense prey

patches bound by bathymetric or temperature boundaries in order to successfully detect or capture

prey, and may encounter reduced foraging success if prey school structure is disrupted or

marginilized and local prey resources are depleted (NMFS 2000). The prey base described here

depicts 2 kinds of predatory strategies. The first and dominant pattern is of a predator that herds

its prey (herring, salmon, sand lance, pollock, cod), a strategy requiring, or enhanced by,

cooperative or group feeding behavior and large densities of available prey. The second pattern

suggests a foraging pattern of poking and searching for presumably single cryptic prey items

most commonly eaten during winter. Fiscus and Baines (1966) describe similar patterns they

term 'massing' behavior in Steller sea lions: groups of up to 50 animals foraging on schooling

fishes and squids, reduced to 1-5 animals in the absence of large prey schools. The 2 foraging

patterns indicated in this study may also reflect the difference between adult and juvenile feeding,

just as winter feeding patterns may reflect a higher number of scats from juveniles.

For the dominant pattern of group feeding to be successful for a population, prey must have

predictability in occurrence, be accessible in sufficient patch densities, and be physically

contained by bathymetric boundary zones or temperature/salinity gradients (Nishiyama et al.

1986; Sinclair et al. 1994) all of which are interelated factors. Together with indications of high

site fidelity in feeding patterns - at least for females, consistently compromised fish school

structures due to climate or anthropogenic factors could conceivably be a driving mechanism in

either a decrease in survival, or the breakdown of intra-island, or intra-region reproductive

success.

ACKNOWLEDGMENTS

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FIGURE LEGENDS

Figure 1. Scat collection sites on island rookeries and haulouts of western stock of Steller sea lions. Refer to Table 1 for site names.

Figure 2. Principal Components Analysis Plot of Principal Component one against Principal Component two representing prey species that account for the majority of variance in Steller sea lion diet across the study area.

Figure 3. Regional variation in Steller sea lion diet patterns as depicted by Principal Components Analysis and Hierarchical Cluster Analysis.

Figure 4. Seasonal variation in Steller sea lion diet patterns by region tested for significance by Chi-square analysis.

Figure 5. Diet divisions in relation to population trends from York et al. 1996. Colors represent sites clustered together based on patterns of decline between 1976 - 1994. Descriptive interpretation of the rates of decline within these clusters are for the years 1989 - 2000.
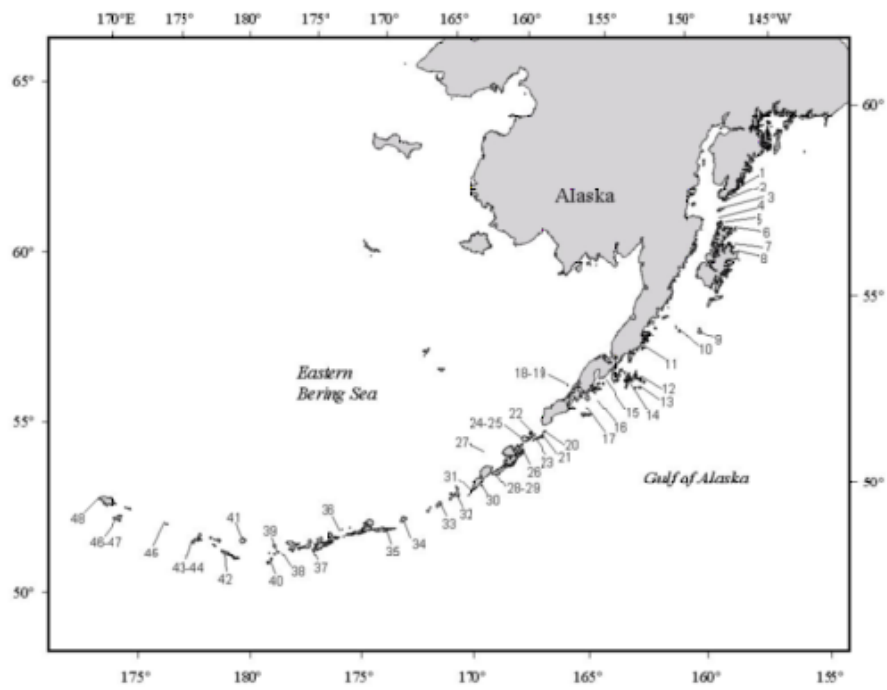
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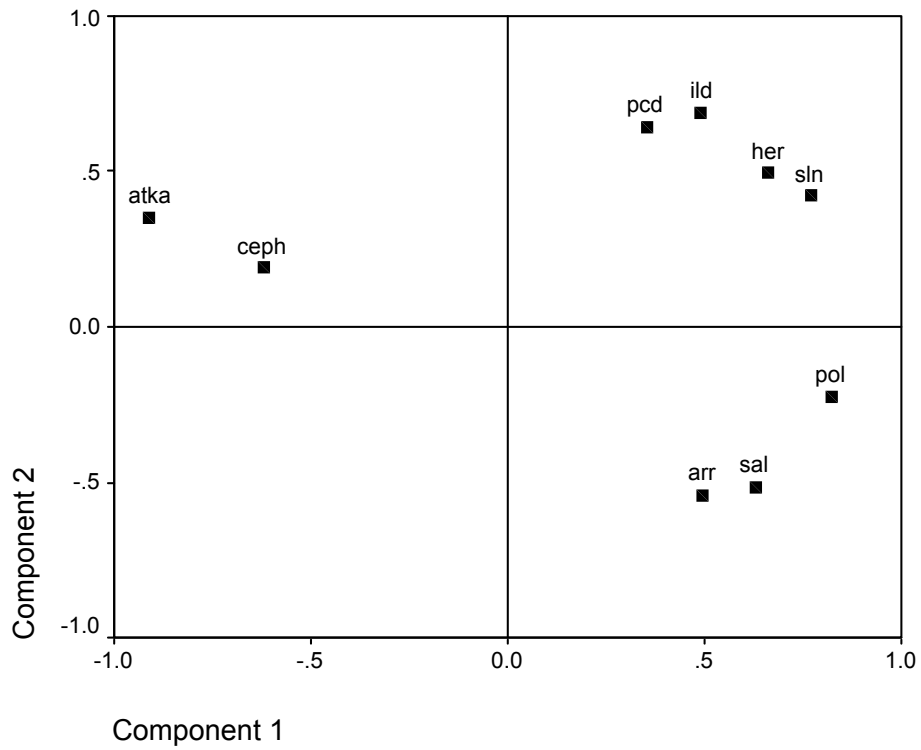
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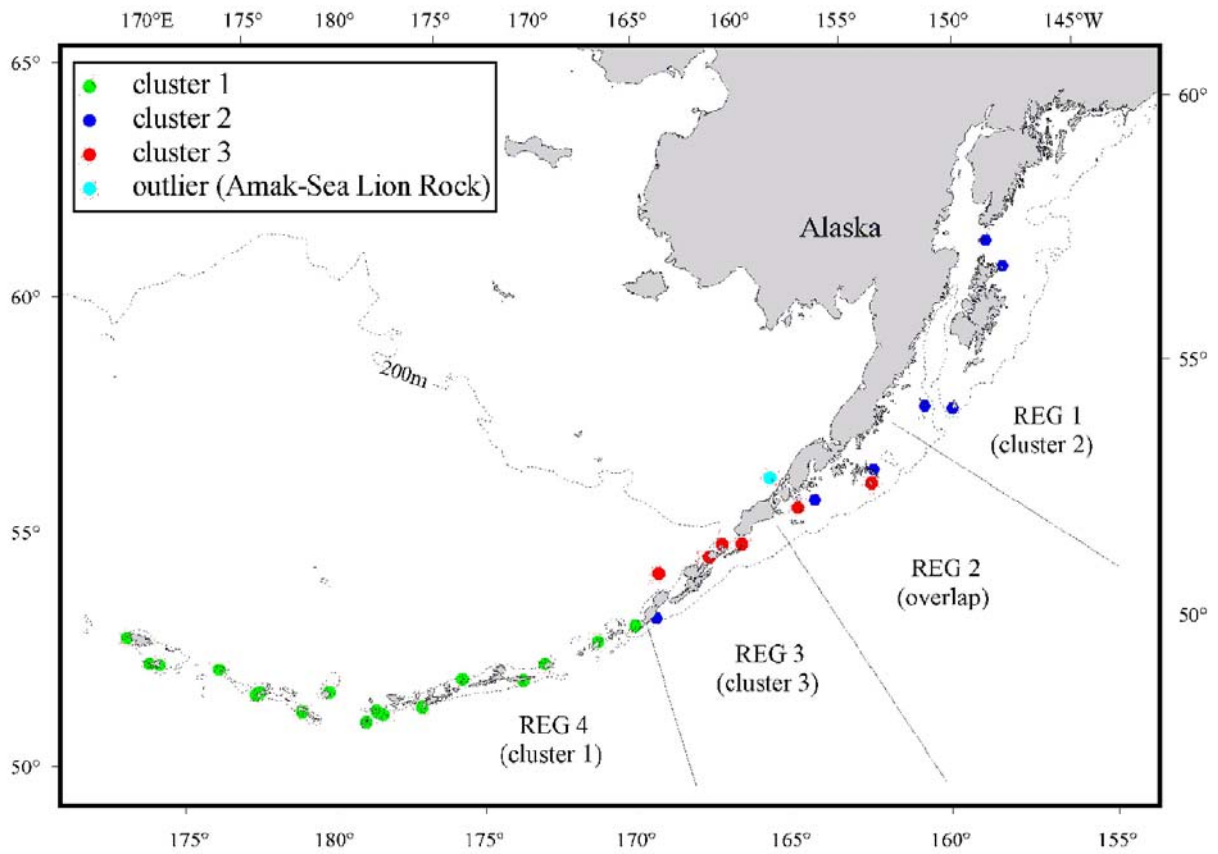
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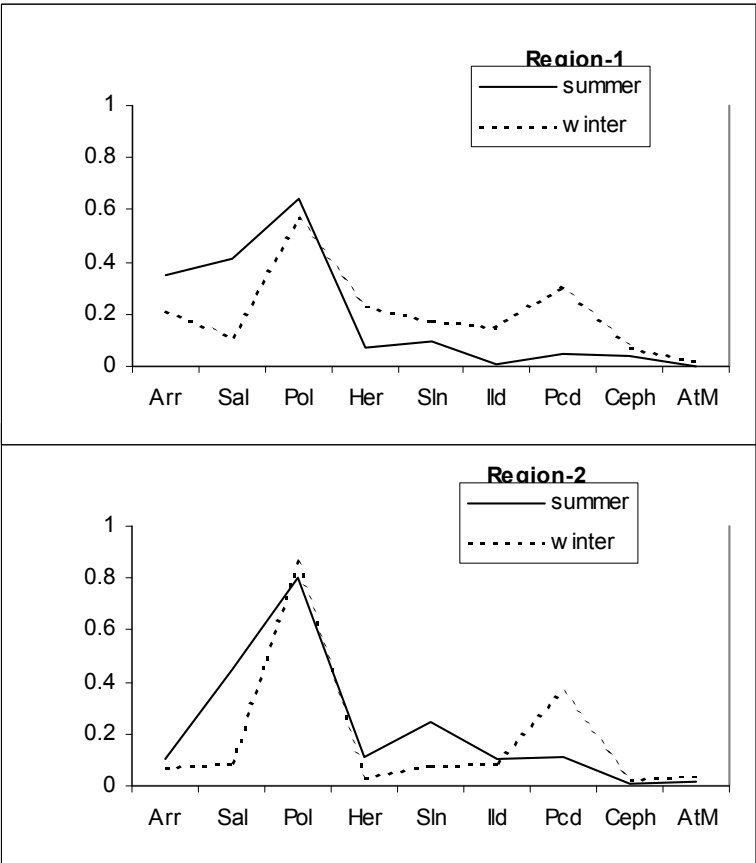
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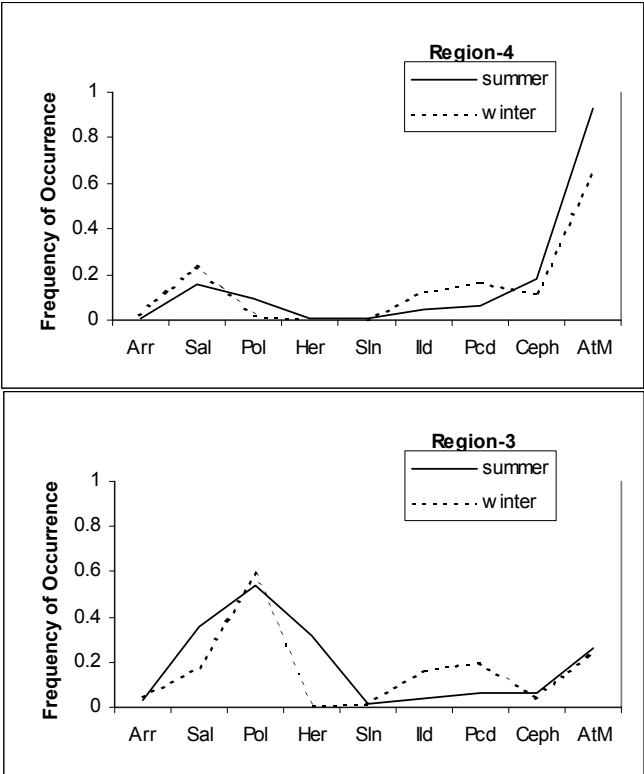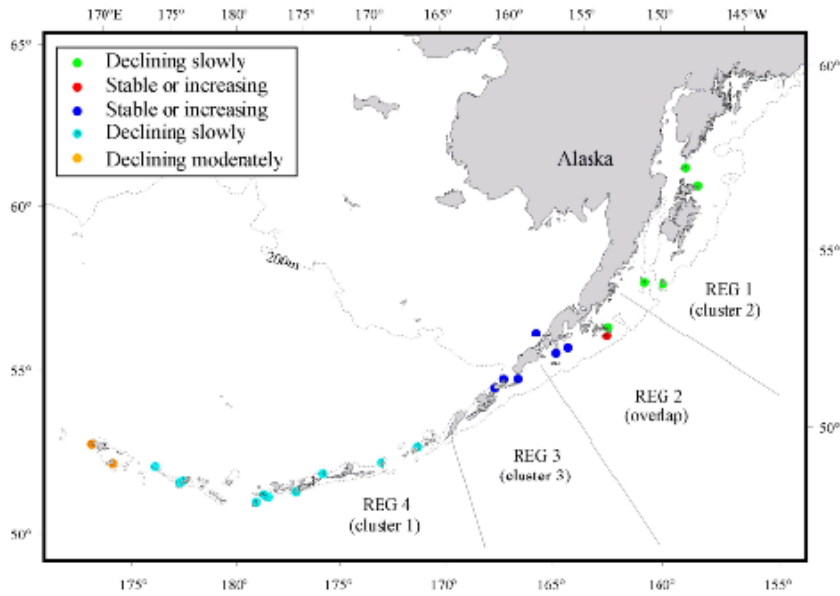
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Table 1. Number of scats collected at each site with identifiable prey remains.

site#	site	May-Sept scats(yrs collected)	Dec-April scats(yrs collected)
1	Flat		31 (97)
2	Perl		23 (97)
3	Sugarloaf	33 (94,95)	
4	Latax Rocks		21 (94,97)
5	Sea Otter		87 (93,94,95,97)
6	Marmot	64 (91,92,93,96)	49 (94,96)
7	Long		97 (93,94,95,96,97)
8	Kodiak/C. Chiniak		16 (94)
9	Chrikof	74 (90,91,93,94,98)	9 (90)
10	Chowiet	70 (94,95,98)	
11	Mitrofania		67 (96,97)
12	Atkins	101 (90,91,93,94, 96, 98)	21(97)
13	Chernabura	32 (90,94)	30 (94,96)
14	The Whaleback		89 (94, 96,97)
15	Jude		85 (96,97)
16	Pinnacle Rocks	79 (93,94,98)	81 (94,96,97)
17	Clubbing Rocks	70 (94, 98)	118 (94,95,96,97)
18	Amak/Rocks		70 (96,97)
19	Amak/Sea Lion Rk	35 (98)	51 (94,95)
20	Aiktak		113 (95,96,97)
21	Ugamak	155 (90,91,93,94,95,96,97,98)	112 (94,97,98)
22	Akun/Billings Hd	58(90,93,94, 98)	35 (94,95,97)
23	Basalt Rock		24 (97)
24	Akutan/C. Morgan	25 (94,98)	
25	Akutan/Reef-Lava		9 (94)
26	Old Man Rocks		94 (95,96,97)
27	Bogoslof	74(90,93,94,95,98)	
28	Unalaska/Bishop Pt		82 (94,96,97)
29	Unalaska/C. Izigan		59 (94,96)
30	Ogchul	10 (94)	39 (96)
31	Adugak	51 (90,94,98)	26 (96)
32	Chuginadak		32 (98)
33	Yunaska	81 (90,93,94,98)	
34	Seguam	117 (90,93,94,97,98)	35 (98)
35	Amlia	11(90)	
36	Kasatouchi/N. Point	153 (92,94,97,98)	
37	Adak/C. Yakak-Lk Pt.	86(92,94,98)	
38	Gramp Rk.	59 (90,94,98)	
39	Tag	99 (90,94,95,96,98)	
40	Ulak/Hasgox Pt.	105 (90,91,92,94,98)	31 (98)

41	Semisopochnoi	21 (96)	
42	Amchitka/C. Rock	40 (90,94,98)	
43	Kiska/C. St. Stephen	24 (90,92)	24 (98)
44	Kiska/Lief Cove	62 (92,94,98)	
45	Buldir	197 (90,91,92,94,95,96,98)	
46	Agattu/C. Sebak	74 (90,91,96,98)	
47	Agattu/Gillion Pt.	21 (98)	
48	Attu/C. Wrangell	21 (98)	

Table 2. Percent FO of all Steller sea lion prey recovered from scats. Highlighted species are those that were included in the cluster analysis.

	All Seasons	(May - September)					(Dec - April)				
	RANGE	REG-1	REG-2	REG-3	REG-4	RANGE	REG-1	REG-2	REG-3	REG-4	RANGE
scats containing identifiable prey items	3762	241	317	322	1222	2102	333	612	567	148	1660
scats containing only undentifiable prey items	254	22	21	33	48	124	36	37	43	14	130
empty scats	168	17	16	35	47	115	17	21	12	3	53
Cods: Family Gadidae											
Pacific cod (*Gadus macrocephalus*)	16.1	5.0	11.0	6.2	6.5	6.9	30.9	35.9	19.6	16.9	27.7
Walleye pollock (*Theragra chalcogramma*)	46.4	63.9	79.8	54.0	9.6	33.2	56.2	85.5	59.1	2.7	63.2
Pacific hake (*Merluccius productus*)	<1	1.2	<1	<1	<1	<1	<1	-	-	-	<1
unidentified Gadid spp.*	4.5	5.4	6.0	5.0	2.3	3.6	11.7	3.6	5.3	1.4	5.6
Flatfishes: Order Pleuronectiformes											
Arrowtooth flounder (*Atheresthes stomias*)	7.4	35.3	10.4	3.1	<1	6.3	21.3	7.5	4.4	2.7	8.8
Rock Sole (*Lepidopsetta bilineata*)	3.6	<1	8.8	4.7	<1	2.4	8.4	6.7	2.1	2.7	5.1
Yellowfin sole (*Limanda aspera*)	<1	-	1.9	-	-	<1	-	<1	-	-	<1
Pacific halibut (*Hippoglossus stenolepis*)	1.2	1.7	<1	2.5	<1	<1	<1	<1	3.5	<1	1.6
Starry flounder (*Platichthys stellatus*)	<1	-	1.6	-	-	<1	2.1	1.0	<1	-	<1
Rex sole (*Glyptocephalus zachirus*)	<1	-	-	-	-	-	-	-	<1	-	<1
Flathead sole (*Hippoglossoides elassodon*)	<1	-	-	-	-	-	-	-	<1	-	<1
Dover sole (*Microstomus pacificus*)	<1	1.2	-	-	-	<1	-	-	-	-	-
unidentified Flatfish spp.*	3.7	2.1	2.2	2.5	<1	1.4	5.7	9.0	5.1	3.4	6.5
Greenlings: Family Hexagrammidae											
Atka Mackerel (*Pleurogrammus monopterygius*)	39.6	-	1.6	26.4	92.6	58.1	2.1	3.9	24.7	64.9	16.1
Rock greenling (*Hexagrammos lagocephalus*)	1.5	-	1.9	<1	<1	<1	-	-	1.4	21.6	2.4
Lingcod (*Ophiodon elongatus*)	<1	<1	-	<1	-	<1	-	-	-	-	-
Masked greenling (*Hexagrammos octogrammus*)	<1	-	-	-	<1	<1	-	-	-	-	-
Kelp greenling (*Hexagrammos decagrammus*)	<1	-	<1	<1	<1	<1	-	-	2.8	4.1	1.3
unidentified Greenling spp.*	1.4	-	2.8	<1	<1	<1	<1	1.6	3.5	3.4	2.2
Herrings: Family Clupeidae											
Pacific herring (*Clupea pallasi*)	6.9	7.1	11.4	32.0	<1	7.7	22.8	3.1	<1	-	6.0
Salmon: Family Salmonidae											
Pacific salmon (*Oncorhynchus* sp.)	20.4	41.1	44.5	35.4	15.5	25.9	10.8	8.8	17.3	23.6	13.4
Sandfishes: Family Trichodontidae											

Pacific Sandfish (*Trichodon trichodon*)	4.4	1.2	6.3	<1	<1	1.2	6.0	6.2	14.3	<1	8.4
Sand Lances: Family Ammodytidae											
Pacific sand lance (*Ammodytes hexapterus*)	6.3	9.5	24.9	1.9	1.0	5.7	17.7	8.3	1.4	-	7.1
Sculpins: Family Cottidae											
Irish Lord sp. (*Hemilepidotus sp.*)	8.3	<1	10.1	4.0	4.5	4.8	14.7	8.5	16.4	12.8	12.8
Pacific staghorn sculpin (*Leptocottus armatus*)	<1	-	-	-	<1	<1	-	-	<1	-	<1
Great sculpin (*Myoxocephalus polyacanthocephalus*)	<1	-	<1	-	-	<1	-	<1	-	-	<1
Tidepool sculpin (*Oligocottus maculosus*)	<1	-	-	-	<1	<1	<1	-	-	-	<1
Cabezon (*Scorpaenichthys marmoratus*)	<1	-	-	-	-	-	-	<1	-	-	<1
Prickly sculpin (*Cottus asper*)	<1	-	-	-	-	-	-	<1	-	-	<1
Scalyhead sculpin (*Artedius harringtoni*)	<1	-	-	-	-	-	-	-	<1	-	<1
Threaded sculpin (*Gymnocanthus pistilliger*)	<1	-	<1	-	-	<1	-	-	-	-	-
Icelinus spp.	<1	-	-	-	-	-	-	-	<1	-	<1
Triglops spp.	<1	-	-	-	-	-	-	<1	-	-	<1
Gymnocanthus sp.	<1	-	-	-	-	-	<1	<1	<1	-	<1
unidentified Cottidae spp.*	<1	-	-	1.9	<1	<1	1.8	<1	2.1	1.4	1.4
Snailfishes: Family Liparididae	4.3	<1	<1	-	<1	<1	11.4	5.4	11.3	11.5	9.2
Smelts: Family Osmeridae											
Capelin (*Mallotus villosus*)	<1	2.9	3.2	<1	-	<1	<1	-	<1	-	<1
Eulachon (*Thaleichthys pacificus*)	<1	<1	<1	-	-	<1	<1	<1	-	-	<1
unidentified Osmeridae spp.*	<1	7.1	0.9	0.6	-	1.0	0.9	1.1	<1	-	<1
Squid & Octopus: Class Cephalopods	8.8	3.7	<1	6.2	18.2	12.1	7.2	2.5	3.9	11.5	4.7
Cartilaginous Fishes											
Dogfish: Family Squalidae	<1	-	-	-	<1	<1	-	-	-	-	-
Skates: Family Rajidae	1.0	1.3	3.2	1.9	<1	1.2	1.8	<1	<1	1.4	<1
Cat Sharks: Family Scyliorhinidae	<1	-	-	<1	-	<1	<1	-	-	-	<1
unidentified Shark spp.*	<1	-	-	-	<1	<1	-	-	-	-	-
unidentifed cartilaginous fish*	<1	-	-	<1	-	<1	<1	-	<1	-	<1
Rockfishes: Family Scorpaenidae	3.0	1.2	3.2	<1	2.4	2.1	2.7	3.1	6.3	3.4	4.2
Gunnels: Family Pholididae											
Penpoint gunnel (*Apodichthys flavidus*)	<1	-	1.3	-	-	<1	-	<1	<1	-	<1
unidentified Gunnel spp.*	<1	-	1.3	-	-	<2	1.8	1.1	<1	2.7	1.2
Poachers: Family Agonidae											

Strugeon poacher (*Podothecus acipenserinus*)	<1		-	-	5.4	-	<1	<1	<1	-	-	<1
unidentified Poacher spp.*	<1		-	2.2	-	<1	<1	<1	1.5	-	-	<1
Eelpouts: Family Zoarcidae	<1		-	-	-	<1	<1	-	<1	-	-	<1
Ronquils: Family Bathymasteridae	<1		-	<1	-	<1	<1	-	<1	<1	-	<1
Prickleback: Family Stichaeidae												
Daubed shanny (*Lumpenus maculatus*)	<1		-	2.2	<1	-	<1	-	-	-	-	-
Black prickleback (*Xiphister atropurpures*)	<1		-	-	-	-	-	-	-	<1	-	<1
High cockscomb (*Anoplarchus purpurescens*)	<1		-	-	-	-	-	-	-	<1	-	<1
Longsnout prickleback (*Lumpenella longirostris*)	<1		-	-	-	-	-	<1	-	-	-	<1
unidentified Stichaeidae spp.*	<1		-	-	<1	<1	<1	<1	<1	<1	-	<1
Wrymouths: Family Cryptacanthodidae	<1		-	-	-	-	-	-	-	-	<1	<1
Tubesnouts: Family Aulorhynchidae	<1		-	-	-	-	-	<1	<1	-	-	<1
Lampreys: Family Petromyzontidae	<1		-	<1	2.2	<1	<1	-	-	<1	-	<1
Lanternfishes: Family Myctophidae	<1		<1	-	-	<1	<1	<1	<1	<1	2.0	<1
Sablefishes: Family Anoplopomatidae	<1		2.5	<1	-	-	<1	-	-	<1	-	<1
Wolffishes: Family Anarhichadidae	<1		-	-	<1	-	<1	-	-	-	-	-
Lancetfishes: Family Alepisauridae	<1		-	-	-	-	-	-	-	<1	-	<1
Sticklebacks: Family Gasterosteidae												
Threespine stickleback (*Gasterosteus aculeatus*)	<1		-	-	-	<1	<1	<1	<1	-	-	<1
Lumpfishes: Family Cyclopteridae												
Smooth lumpsucker (*Aptocyclus ventricosus*)	1.4		-	-	-	1.0	<1	-	<1	5.8	2.7	2.5
Deep sea smelts: Family Bathylagidae												
Northern smoothtongue (*Leuroglossus*)	<1		-	-	4.3	1.5	1.5	-	<1	<1	-	<1
Bird/Mammal	<1		-	<1	-	<1	<1	-	<1	1.4	-	<1

* Unidentified species were included only if they did not co-occcur with identifiable species from the same family group

Table 3. X-square test for difference in prey frequency of occurrence between the winter and summer seasons.

Prey	REG 1			REG 2			REG 3			REG 4		
	X-square	df	p-value	X-square	df	p-value	X-square	df	p-value	X-square	df	p-value
Atka Mackerel	*			3.79	1	0.0514	0.32	1	0.5793	109.58	1	<0.0001
Arrowtooth flounder	13.74	1	0.0002	2.25	1	0.1338	0.92	1	0.3368	*		
Walleye pollock	3.48	1	0.0622	4.84	1	0.0278	2.14	1	0.1438	*		
Cephalopods	3.11	1	0.0777	*			2.48	1	0.1154	4.09	1	0.0431
Irish lord	*			0.65	1	0.4207	29.90	1	<0.0001	17.96	1	0.0001
Pacific herring	25.61	1	<0.0001	25.53	1	<0.0001	*			*		
Pacific sandlance	7.63	1	0.0057	47.74	1	<0.0001	0.27	1	0.6025	*		
Pacific cod	58.78	1	<0.0001	65.05	1	<0.0001	29.20	1	<0.0001	20.46	1	<0.0001
Salmon	71.21	1	<0.0001	160.09	1	<0.0001	37.13	1	<0.0001	6.31	1	0.012

* If all observed values in the contingency table were not >5 test was not run