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ABSTRACT

Steller sea lions (*Eumetopias jubatus*) are listed as an endangered species in western Alaska due to a precipitous decline that occurred in the 1980s and 1990s. In 2000, cascading declines slowed or ceased and clusters of rookeries between the eastern Aleutian Islands and eastern Gulf of Alaska began to show signs of population growth. Reasons for the decline and for a range-wide failure to recover are unresolved, but reduction in the availability of prey due to commercial fishing or environmental perturbation has been hypothesized.

Discerning the diet and patterns of prey use by Steller sea lions (SSL) is fundamental to isolating the mechanisms driving population health. Here we evaluate the frequency of occurrence (FO) of prey species in 3,412 scats of adult female and juvenile SSL collected during 1999-2009, across the range of the U. S. Western Stock. Thirteen primary prey are identified based on their occurrence in ≥ 5% of total scats. We reduce the dimension of the diet profile of the 13 primary prey to two categorical groups through principal component analysis (PC). A hierarchical cluster analysis of PC scores on collection site locations describes four geographic regions of SSL diet (with Amak Island as an outlier) nearly identical to those identified in a previously published 1990-1998 (n = 3,762) dataset. Geographic regions of diet continue to correspond with regional population trends of SSL.

The species of primary prey consumed by SSL are analogous between 1990-1998 and 1999-2009. However, the rangewide FO of 7 of the 13 primary prey increased significantly ($p \leq 0.05$) during the latter decade. Only cephalopods (Gonatidae) and walleye pollock (*Theragra chalcogramma*) decreased significantly in FO in any season or region between decades. Generalized linear mixed models (GLMM) of seasonal prey FO determined that trends in the FO of primary prey between decades were locally driven by significant changes within one or more of the four diet regions and fishery conservation management areas (RCA). The most significant increases ($p = 0.001$) in FO during 1999-2009 were for commercial fishes: arrowtooth flounder (*Atheresthes* sp.), Atka mackerel (*Pleurogrammus monopterygius*), rock sole (*Lepidopsetta* sp.), and Pacific cod (*Gadus macrocephalus*); and one non-commercial fish species (Pacific sand lance, *Ammodytes hexapterus*) in diet Regions 2 and 3 (RCA zones 6 and 7) between the eastern Aleutian Islands and western Gulf of Alaska. Diversity scores (H') for primary prey were also highest in these regions compared to the previous decade, and are coincident with SSL population increases that began in the same area in 2000.

Atka mackerel continues to dominate SSL diet west of Samalga Pass, and walleye pollock continues to dominate SSL diet east of Samalga Pass (despite its decreased presence in diets in Regions 1-3 during 1999-2009). The results of generalized additive mixed models (GAMM) of annual trends (1990-2009) in summer prey FO on each rookery across the study area are consistent with the results of GLMM decadal comparisons.

The additional 11 years of data presented here support earlier conclusions that adult female and young juvenile SSL of the Western Stock collectively eat a wide variety of prey species, but demonstrate fidelity to prey types that are predictably available in seasonal concentrations over the continental shelf or other bathymetric structures, within close range of natal rookery sites. Foraging within close proximity to birth and breeding sites keeps adult females close to pups onshore and to young juveniles learning to forage. However, it also increases their vulnerability to potential nearshore environmental and anthropogenic interference which could ultimately influence their reproductive success.

It was not the objective of this study to define the relationship between SSL diet and population decline, or to identify the interactive mechanisms that drive diet change. However, coincident patterns emerged that suggest relationships between SSL diet, regional population patterns, climate and fisheries. Some of the patterns are worthy of discussion and future research: 1) the areas of greatest increases in the FO and diversity of prey (Regions 2 and 3) beginning in 1999, overlap with those of the strongest population growth since 1999; 2) the increase in primary prey FO and diversity since 1999 is coincident with increased restrictions on groundfish trawling within SSL Critical Habitat, enacted in 2000; and 3) the area of lowest prey diversity (Region 4) overlaps with those areas of continuing population declines, the most restricted foraging habitat (narrow continental shelf) and the lowest seasonal and temporal variability in sea surface temperature in all years of study.

CONTENTS

INTRODUCTION

Diet studies are essential to identifying factors that influence the population health of marine mammals. The most comprehensive overview of Western Stock Steller sea lion (SSL) (*Eumetopias jubatus*) diet and associated indications of foraging behavior was based on a seasonal and spatial analysis of prey remains in adult female and juvenile scats collected during 1990-1998 (Sinclair and Zeppelin 2002). That study was based on scat collected from the Gulf of Alaska (GOA) westward across the Aleutian Island (AI) chain and incorporated several hundred samples detailed in an earlier published account (Merrick et al. 1997). Here, we compare the Sinclair and Zeppelin (2002) findings with 11 years of additional data from scat collected during 1999-2009 in the same area. This 20-year collection of data confirms regional and seasonal specificity of primary prey and highlights positive trends in the frequency of prey occurrence in SSL diet across three quarters of the study area. A direct link between diet composition and population stability cannot be reconciled, in part, because we currently lack the tools required to assess the biomass of prey required for the reproductive health and survivability of free ranging SSL. Instead, in this study, we treat diet and change in diet as an indicator of the shifting state of SSL foraging habitat, with strong inference for the relationship between foraging conditions and population health.

The opportunity to compare long-term datasets collected systematically over extensive geographical areas is rare in diet studies of marine mammals, especially from such remote locations as western Alaska. Equally rare are the robust sample sizes in each decade of collection that are required to accurately identify seasonal and temporal range-wide trends in diet. The large sample sizes, extensive prey reference material and consistent methodologies in collection and analysis used across this long-term dataset allow us to reconstruct SSL diet patterns despite limitations in our ability to determine the amount and type of prey required for adequate nutrition of free ranging SSL during different stages of their life history.

Marine apex predators of the northern North Pacific and Bering Sea sustained extensive population declines beginning in the mid-1970s, that continue to variable degrees today (NRC 1996, Anderson and Piatt 1999, Hunt et al. 2002, NRC 2003, DeMaster et al. 2006, Byrd et al. 2008a, NMFS 2010). The mechanism(s) that initiated and continue to drive system-wide declines have yet to be identified, in part due to our limited understanding of marine ecosystem dynamics. However, because declines in pinniped and marine bird populations often parallel changes in diets (Alaska Sea Grant 1993, NRC 1996, Piatt and Anderson 1996, DeMaster and Atkinson 2002, Hunt et al. 2002, Sinclair et al. 2008), the commercial exploitation of fish and climate change are most often implicated as causative factors of decline due to their potential influence on prey availability (NRC 1996, Loughlin and York 2000, NRC 2003, DeMaster et al. 2006, Hennen 2006).

The precipitous population decline of SSL in western Alaska became apparent in the 1980s (Braham et al. 1980, Merrick et al. 1997). In 1990, the currently designated U. S. Western Stock, which ranges from the eastern GOA to the western AI, was estimated to be at just 20% of its former population level 30 years prior. In 1993, Critical Habitat (CH) was designated, based in part on the proximity of SSL rookeries and haul-outs to the projected availability of food. This habitat designation resulted in certain areas being reserved as ‘no-trawl’ zones at certain times, within 10-20 nautical miles (nmi) of rookeries and important haul outs. In 1997, the Western Stock (all haulouts and rookeries west of longitude 144°W) was listed as endangered (NMFS 1998). In 1998, a ban on commercial exploitation of forage fishes (small schooling fishes such as Pacific sand lance and juvenile walleye pollock) important as prey to marine apex predators including mammals, birds and larger commercial fishes was instituted. In 2000, an injunction against all groundfish trawling within SSL CH was established (NMFS 2010). The 2000 ruling has since been adjusted to allocate certain kinds of fishing on certain dates and locations within CH, but provides substantially greater buffer within critical foraging regions and within 20 nmi of SSL rookeries and haul-outs than that of the previous decade (NMFS 2010). The overall decline across the U. S. Western Stock reached its nadir in 2000. Regionally, the stock shows promising signs of population increase in the eastern and western GOA and eastern AI, but continues to decline in the central and western AI (NMFS 2010).

Our analysis of SSL diet is based on measures of the frequency with which identifiable skeletal remains of prey taxa occur (FO) in individual scats. FO measures both the presence or absence of prey species and indicates the percentage of the sampled population eating a particular prey species or group. It does not measure the number of prey (PN) consumed within each species or the number of prey individuals within a given scat. Ideally, PN is partnered with estimates of FO in diet studies, but due to digestive properties peculiar to the gastrointestinal constitution of SSL (Sinclair and Zeppelin 2002, Tollit et al. 2003, Tollit et al. 2007), paired skeletal structures such as fish earbones (otoliths) occur infrequently in scats and reduce our ability to count prey or accurately estimate prey biomass.

Every sample source (including scat) and method of analysis (including FO) in marine mammal diet studies have well-described characteristic biases (Fitch and Brownell 1968, Jobling and Brieby 1986, Harvey 1987, Olesiuk et al. 1990, Tollit et al. 2006, Bowen and Iverson 2012, Rosen and Tollit 2012). Scat is widely used and well accepted in dietary studies of free ranging pinnipeds (Bowen and Iverson 2012) as is the FO calculation of prey remains in scat (Tollit et al. 2006, Tollit et al. 2007). The FO metric allows for a broad brush interpretation of prey absence or presence in population-wide diets over time, and has proven informative in deciphering system-wide changes in prey distributions and consumption patterns for a wide variety of terrestrial and marine predators including birds, fish, and mammals (Stobberup et al. 2009). Overall, the successful application of FO as an ecological description of local, regional, and range-wide diet trends in Western Stock SSL studies is supported by metapopulation trends (York et al. 1996) and confirmed by recent comparative work in emerging fields including SSL genetics (O'Corry-Crowe et al. 2006), SSL prey genetics (Tollit et al. 2009), and stable isotope analysis (Kurle and Sinclair 2003, Kurle and Gudmundson 2007, Kurle et al. 2011).

MATERIALS AND METHODS

Sample Collection

Scat (fecal) samples were collected from summer (May-September) rookeries and winter (November-April) haulouts across the range of the U. S. Western Stock of Steller sea lions during 1999-2009 (Fig. 1). Some collection sites were visited during both summer and winter, but typically only once per season. Rookery collections are presumed to be primarily from adult females because adult males usually fast during the breeding season. Juveniles of both sexes are present on rookeries and are undoubtedly represented in scat samples, but to a much smaller degree than adult females. Scat collected on winter haul-outs may represent a greater cross-section of ages and sexes than those collected in summer, but older juvenile and adult males are thought to be largely transient during this time in pelagic areas of the northern North Pacific and along the ice edge in the Bering Sea (NMFS 2010). Therefore, we assume that the scat evaluated in this study primarily represents the diet of adult female and young juvenile SSL. In order to reduce the chance of repetitive sampling of single meals or individual animals, study protocol emphasized collection of scats that appeared to be whole samples recently deposited by an individual animal. Samples were stored dry upon collection then frozen prior to a warm water rinse through a series of nested sieves (minimum = 0.05 mm mesh) to recover prey remains. Prey were identified to the lowest taxonomic level possible based on comparison with reference libraries of skeletal and cartilaginous remains of fishes and cephalopods from the northern North Pacific Ocean and Bering Sea. Fish otoliths are poorly represented in SSL scat so fish prey identification relied on other skeletal features in addition to otoliths, such as skull structures and vertebrae that tend to survive the digestion process. This technique of using a mixed assemblage of bones and skeletal features (including otoliths, when available) to identify prey is currently referred to as an ‘all structures’ technique and increases species recovery rates in SSL up to four-fold (Tollit et al. 2007). Experimental studies (Tollit et al. 2006, Tollit et al. 2007) determined that the ‘all structures’ technique fully accounted for the presence of species (i.e., salmon, Salmonidae) whose otoliths typically occur infrequently in scat compared to other skeletal structures, as long as prey reference material is extensive (Tollit et al. 2006, Tollit et al. 2007) and specific to study locale (Sinclair 1994, Walker 1996). Cephalopod beaks (upper and lower rostra) were the most common hard parts used to identify squid and octopus, but statoliths (earbones), mouth raduli, gladii, and armhooks were also occasionally present and used for identification. Typically, 10% of scats collected from any given site are either empty or contain only unidentifiable prey remains. These were excluded from the total sum of scats collected and from any further analysis in this study.

Sample Analysis

Prey composition patterns -- seasonal and spatial

Each prey species (or lowest taxonomic level of prey type identified) was recorded as present or absent in each sampled scat and each scat was treated as an independent sample. The presence or absence of a prey species (or prey type) is termed prey frequency of occurrence (FO). Percent FO (PFO) represents the number of scats containing a prey type as a portion of the total number of scats containing identifiable prey. PFO reflects the percentage of the sampled predator population that consumed a specific prey species or type. The PFO for any particular prey taxon at site *j*, in season *k*, in year *l*, was calculated by dividing the number of scats containing a prey type by the total number of scats containing identifiable prey; that is,

$$PFO_{jkl} = \frac{\sum_{i=1}^{n_{jkl}} O_{ijkl}}{n_{jkl}},$$

where $O_{ijkl} = 1$ if the taxon is present in sample *i* in collection (*j*,*k*,*l*) and zero otherwise, n_{jkl} is the number of samples with any identifiable prey taxon. Frequency of occurrence (FO_{jkl}) is simply the numerator of the previous fraction.

Prey that were present at ≥ 5% FO in all data combined were selected for further statistical analyses. The ≥ 5% FO minimum was set to ensure representation of prey types that might be relatively insignificant range-wide, but important on local scales. Months of collection were categorized as summer or winter based on the SSL breeding/pupping cycle. Summer data were used to determine regional boundaries of diet because sampling was most consistent across the study area during this time. The 13 prey taxa identified as primary in the 1999-2009 dataset included 9 that were also considered primary at the ≥ 5% FO level in 1990-1998, as well as an additional 4 taxa that were present in lower PFO in 1990-1998 (Sinclair and Zeppelin 2002). For consistency, all 13 species were evaluated in comparative analyses of each decade.

We used Principal Components Analysis (PC) of summer data to reduce the dimension of FO data into categorical groups that accounted for most of the variance in the dataset. The prey that occurred in ≥ 5% of scats across all 1999-2009 collection sites in summer (n = 1,772) and winter (n = 1,640) were used as variables, and scat collection sites (n = 35) were used as observations.

Sinclair and Zeppelin (2002) used a hierarchical cluster analysis of principle component scores to define regional boundaries for spatial comparison. In order to assess whether these regions were still appropriate for both the 1990-1998 data (after the addition of four new taxa) and for the previously unanalyzed 1999-2009 data, we duplicated this procedure for decadal comparison of diet. First, PFO was calculated for each rookery within each time period. For this portion of the analysis, occurrences were aggregated over samples and years within periods (1990-1998 and 1999-2009) before normalizing to PFO. Principle components (PC) scores were calculated for each rookery from the 35 PFO profiles using the first two principle components. Separate PC analysis was conducted within each period to assess whether the addition of 4 new taxa would change the results of the Period 1 (1990-1998) analysis and to compare the Period 2 (1999-2009) data to Period 1.

As in Sinclair and Zeppelin (2002), cluster analysis was conducted on PC scores using squared Euclidian distance (Ludwig and Reynolds 1988) as a measure of similarity between scat collection sites with identified prey groupings, and Ward's (1963) method was used to compare cluster distances. The R statistical environment (v. 2.15.1; R Core Team, 2012) was used for all model analyses. Spatial breaks in the clusters were determined visually from output dendograms of the data from summer. Winter data was laid over these same breaks for comparison of seasonal diets within regions.

Prey composition patterns -- temporal and spatial

In order to examine changes in prey composition over time, we compared seasonal spatial divisions found from the cluster analysis of the 1999-2009 data with that described for 1990-1998 (Sinclair and Zeppelin 2002). Collection sites, sample handling, and data treatment were consistent between the two studies**.** Prey identification techniques are the same between decades of collection, with the exception of cases where we have gotten better at identifying prey remains to species specific levels as in the case of squid and fishes of the families Hexagrammidae and Stichaeidae (Table 1). Our enhanced ability to identify some taxa to species did not affect decadal comparisons because we standardized taxonomic level in quantitative comparison of datasets. In other words, current identification techniques allow us to identify most squid, for example, to the species level that in the 1990-1998 dataset were identified only to the level of cephalopoda. So while squid are tabularized to the lowest taxonomic level possible (Table 1), all quantitative comparisons of squid FO between decades are restricted to the level of 'cephalopods'.

Generalized linear mixed models (GLMM) fit by Laplace approximation (lme4 package for R) were applied to evaluate 1) temporal seasonal change in prey FO between Period 1 and Period 2, within regional diet boundaries first described in Sinclair and Zeppelin (2002) and confirmed in this study; and 2) temporal seasonal change in prey FO between Periods 1 and 2, within regional fisheries management boundaries (RCA) established in 2010. Finally, the FO data was analyzed on a spatio-temporally continuous basis using a Generalized Additive Mixed Model (GAMM; gamm4 package for R). The GAMM model uses smooth effects over longitude and years, in order to describe how summer prey FO trended over space and time outside of predefined regional divisions and temporal periods.

The basic model form for both analyses is given by

$$FO_{jkl} \sim Binomial(n_{jkl}, p_{jkl}),$$

where

- p_{jkl} is the probability of a sample containing the prey taxon in question,
- $\mathrm{logit}(p_{jkl}) = f_k(j,l) + e_{jkl}$,
- $f_k(j,l)$ is a function of site j and year l, and
- $e_{jkl} \sim N(0, V_k)$ is a normal error term with variance V_k.

Note that separate analyses were used for summer and winter seasons; there was no pooling of FO values over years and regions. The difference between the GLMM analysis and the GAMM analysis is the formulation of $f_k(j,l)$. In the GLMM analysis,

$$f_k(j,l) = b_{region}(j,l) + b_{period}(j,l),$$

where

- $b_{region}(j,l)$= baseline effect for the region containing site j for year l in period 1 and
- $b_{period}(j,l)$ is the *change* in regional effect for site j for year l in period 2.

Two analyses were conducted where regions were defined as the diet regions of Sinclair and Zeppelin (2002) and as the RCA management zones. For the GAMM analysis, $f_k(j,l) = s(j,l)$, where $s()$ is a smooth function over the longitude of site j and year l. The gamm4 package uses a penalized spline coupled with the Laplace approximation method of the lme4 package to fit this function with the error term.

We compared diet diversity between Period 1 and Period 2 with a Shannon – Weiner index of heterogeneity: $H' = - \sum (p_i \ln p_i)$ where p_i = the decimal fraction of individual prey species present in all scats combined (FO) for each season, within each diet and RCA region; and *ln* is the natural log. H' is a unit less measure that increases with increasing heterogeneity of the sample (Preston 1948, Cox 1996). We evaluate prey diversity because it is has been proposed as an influencing factor in the population health of otariids (Sinclair 1988, Sinclair et al. 1994, NRC 1996) and is associated with areas of population stability in SSL specifically (Merrick et al. 1997, Sinclair and Zeppelin 2002, Trites et al. 2007a).

Mean annual sea surface temperatures (SST) within diet regions were calculated for Period 1 and Period 2 as a measure of environmental conditions within the study area between decades. We selected SST over other measures because it is an oceanographic feature correlated with fish distribution (Hollowed et al. 2012) and the diet and foraging behavior of marine birds and sympatric northern fur seals (*Callorhinus ursinus*) in the Bering Sea (Ream et al. 2005, Byrd et al. 2008b, Sinclair et al. 2008, Renner et al. 2012). Also, cetacean distribution (Sinclair et al. 2005), SSL distribution (Call and Loughlin 2005), SSL regional diet and population patterns (Lander et al. 2009) and SSL diet and foraging behavior are correlated with SST in the GOA and along the AI (Fadely et al. 2005, Sinclair et al. 2005, Trites et al. 2007b, Lander et al. 2010).

We sourced mean SST values from the National Center for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) Reanalysis data. Reanalysis is a synthetic product that uses all available sources of meteorological and oceanographic information (including drifter buoys and satellite data) to provide long-term physical observations of ocean conditions (Kalnay et al. 1996). We defined the geographic boundaries for calculation of mean SST to include all sampled sites within each diet region. By proximity, these primarily include SST values to the south of the Aleutian chain and GOA, but in some instances also include recorded values from the nearshore Bering Sea. The boundaries of SST calculations within each diet region are:

Region 4: lat. 50.5°N-52.4°N, long. 172.5°E-168.7°W
Region 3: lat. 52.4°N-54.3°N, long. 168.7°W-163.1°W
Region 2: lat. 54.3°N-56.2°N, long. 163.1°W-159.4°W
Region 1 (central GOA): lat. 54.3°N-56.2° N, long. 159.4°W-153.7°W
Region 1 (eastern GOA): lat. 58.1°N-60.0°N, long. 153.7°W-146.2°W.

RESULTS

Summary of Findings

Eighty-seven prey taxa were identified in SSL scats in 1999-2009 (Table 1), 13 of which are considered primary because they occurred in frequencies ≥ 5% across the study area (Fig. 1) compared to 9 (of the 13 taxa) that were primary in the diet in 1990-1998. PC analysis reduced the 13-dimensional diet profile for each site in each decadal dataset down to 2 and defined four principal groups of sites that have similar diets based on PC loading scores of prey FO (Fig. 2). Cluster analysis of the four groups of sites identified four regions of diet (with Amak Island as an outlier) where SSL on rookeries and haulouts in close proximity to one another have similar diets with similar seasonal variation in primary prey FO (Figs. 3 and 4). The four regions of diet identified by PC and cluster analyses are identical between decades. The most definitive break between regions remains at the boundary (long. 170°W) between Region 4 and Regions 1-3 (Fig. 4) where Atka mackerel and walleye pollock, respectively, continue to dominate diet profiles.

The primary species of prey consumed by SSL remained the same and fell within the same regional boundaries between decades, despite significant shifts in prey FO values. This result suggests that overall prey assemblages did not change, and affirms our confidence that prey identification was consistent between periods. A quality check of prey identifications between Period 1 and 2 revealed that errors were typically random errors of omission rather than species mis-identification and were not biased toward any particular species. Most importantly, we found that our increased ability to identify prey to the species level did not have an appreciable effect on the FO of the most commonly occurring prey identified in this study, because their bones are highly recognizable and were as readily identified in the 1990s as they are now.

When all data are combined across regions and seasons, walleye pollock and cephalopods were the only primary prey that significantly ($p \leq 0.05$) decreased in FO between decades while all others increased (seven significantly). Decadal changes in species FO were regionally and seasonally specific and the most significant changes ($p = 0.001$) occurred in Regions 2 and 3 (RCA 6 and 7) during summer and winter (Tables 2a and 2b). Regions 2 and 3 are also the areas of highest prey diversity (H') during summer in both decades (Table 3). Mean SST were temporally and regionally consistent between decades, and all four regions of diet paralleled each other in annual increases and decreases in mean SST. Among all four regions, Region 1 in the eastern GOA demonstrated the most seasonal variation in mean SST, and Region 4 (western and central AI) demonstrated the least.

Prey Composition Patterns -- Spatial and Seasonal, 1999-2009

The threshold of ≥ 5% FO across the study area successfully captured prey signals that appeared unimportant over the whole Western Stock range, but occurred in high frequencies in certain areas or seasons. For instance, snailfish (Liparididae) are only 6% FO in all scats combined and have a trace presence in summer samples, but occur in 15% of scats collected in winter that cluster in Region 3 (Table 1, Fig. 1). Likewise, prey types that dominate overall FO are sometimes insignificantly represented outside of a single region or season. Atka mackerel is the highest ranking prey at 50% overall FO, and occurs at 93% FO in summer on rookeries in Region 4, yet is present in only 2% of scats collected during winter on haulouts in Regions 1 and 2 (Table 1, Fig. 1).

Seasonal fluctuation is a dominant pattern in the presence of several species range-wide (Table 1). Salmonids (*Onchorhyncus* sp.) occur at 28% FO across the range, but more frequently in summer diets (35% FO) than in winter (20% FO). Arrowtooth flounder (*Atheresthes* sp.) and Pacific cod (*Gadus macrocephalus*) are more important in SSL diets in winter (15% FO and 37% FO, respectively) compared to summer (8% FO and 16% FO, respectively). Seasonal variation in prey FO is even more apparent when considered within region. For example, in winter in Region 3, arrowtooth flounder and Pacific cod are 22% FO and 41% FO, respectively, compared to summer values in Region 3 of 5% FO and 8% FO (Table 1).

Prey Composition Patterns -- Spatial and Seasonal, Decadal

PC and cluster analysis demonstrate that the longitudinal breaks between prey species groupings are spatially and seasonally consistent between Period 1 (1990-1998, n = 3,676) and Period 2 (1999-2009, n = 3,412) (Figs. 3 and 4). The number of PC factors accounting for the majority of the variance in the dataset are the same between decades. There are some differences in the PC factor loadings for some taxa between datasets (Fig. 2), likely resulting from the addition of four species due to increased FO values and decrease in walleye pollock presence in Regions 1-3 in the second decade. In both periods, however, the factor loading score for Atka mackerel was large due to its increasing FO and singular dominance in Region 4.

Cluster analyses on PC scores in both decades demonstrate that the primary regional break in diet occurs east (Regions 1-3) and west (Region 4) of Samalga Pass (170°W), followed by finer breaks within Regions 1-3 and Amak Island (lat. 55°24'N, long. 163°10'W), which consistently stands as an outlier to all other regional patterns (Figs. 3 and 4). Atka mackerel and walleye pollock continue to dominate SSL diets west and east of Samalga Pass, respectively.

The GLMM of seasonal and spatial FO demonstrated that walleye pollock and cephalopods were the only primary prey taxa that decreased significantly ($p \leq 0.05$) in FO between decades in any diet Region, RCA or season (Tables 2a and 2b). Herring (*Clupea pallasii*), snailfish, salmonids, and Pacific sandfish (*Trichodon trichodon*) increased in overall FO between Periods 1 and 2, but not significantly. Rockfish (*Sebastes* spp.), arrowtooth, rock sole (*Lepidopsetta* sp.), Pacific cod, Irish lord (*Hemilepidotus* sp.), and Atka mackerel increased significantly ($p \leq 0.05$) in either summer or winter between periods in one or more RCA and in one or all of diet Regions 1-3 (Tables 2a and 2b). Pacific sand lance increased ($p \leq 0.05$) in both summer and winter in each of Regions 1-3, in summer in RCA 6 and 7, and winter in RCA 6, 7 and 9 during the second period of study (Table 1, Tables 2a and 2b, Fig. 5). Walleye pollock FO decreased in all four regions and all RCA during summer, but decreases were significant only in diet Regions 1 and 3 and RCA 6 and 7. During winter, walleye pollock consumption decreases were significant in RCA 9 only. The only significant increase in walleye pollock during Period 2 was in Region 4 during winter. Despite regional decreases in consumption that were enough to drive a 10% overall decline in walleye pollock FO between periods, it remains the second most highly ranked prey species in range-wide diets following Atka mackerel (Table 1, Tables 2a and 2b, Fig. 5).

The most significant ($p = 0.001$) changes in prey FO between decades were in diet Regions 2 and 3, in the western GOA and eastern AI, and all were positive except for walleye pollock. The greatest increases in summer FO were for Atka mackerel in Region 3, and Pacific cod and Pacific sand lance in Region 2. During winter, the greatest increases in FO were for arrowtooth flounder, rock sole, and Pacific sand lance in Region 3. The most significant ($p = .001$) decrease in walleye pollock occurrence was during summer in Region 3 (Table 2a, Fig. 5).

Some prey species that were important only in localized pockets of the range in Period 1 increased significantly in FO during Period 2 due to increases in FO within broader regions of diet, a "spreading out" in presence. Pacific sand lance demonstrated the most widespread increase in FO of all species with a stronger ($p \leq 0.05$) presence in both summer and winter in Regions 1-3. Regionally specific increases in Pacific sand lance drove the range-wide increase in FO of 22% in this study compared to 6% FO in the previous decade. Irish lord currently ranks 17% FO range-wide compared to earlier estimates of 8% FO, driven by a significantly increased ($p = 0.01$) winter presence in Region 3. The FO of Irish lord nearly doubled during summer in Region 2, but this change did not test as significant. Increases in Irish lord were significant in RCA 4 during summer and in RCA 6 during winter (Tables 2a and 2b, Fig. 5).

Regional areas of conservation (RCA) are defined by a matrix of an overlap between bottom trawl strata used in research surveys, and SSL rookeries that had similar trends in pup production, population, and diet. As such, RCA overlap fairly closely with diet regions (Fig. 1). GLMM analysis of diet within RCA boundaries are similar to those within diet regions during both decades. Significant ($p = 0.001$) increases in FO in summer were in RCA 6 (Pacific sand lance) and 7 (Pacific cod), and in winter in RCA 6 (arrowtooth flounder, Atka mackerel, Irish lord, rock sole, Pacific sand lance) which overlay diet Regions 2 and 3 (Table 2b). It should be noted that summer values represent results based on RCA 1-9 (spanning all four diet regions), but sample restrictions limited the analysis of winter patterns to those within RCA 5-9 (spanning diet Regions 1-3, and part of Region 4) (Fig. 1).

The GAMM results for annual (1990-2009) trends in summer prey FO at each collection site (n = 3,874) reflect point estimates of west to east patterns in annual prey consumption across the two decades. Annual patterns for those prey that changed significantly ($p \leq 0.05$) during summer (Fig. 6) confirm GLMM findings of decadal FO changes in diet regions and RCA during summer across the study area.

Prey diversity increased ($p \leq 0.08$) during summer in Regions 1 and 2 and during winter in Region 3 in the second decade of study. Region 4 is significantly lower in overall prey diversity compared to all other regions and showed no change in prey diversity between decades (Table 3). For all but Region 2, H' is higher in winter than in summer in both decades. The two single highest measures of diversity are for Region 2 in summer in both decades and Region 3 in winter during 1999-2009. If seasons are combined as a measure of the year-round foraging canvas a female would find in one region vs. another, the increase in diversity is greatest for Region 1 in Period 2 ($p = 0.02$).

All regions are synchronous in temporal patterns of increase or decrease in mean SST, but they vary from each other by as much as 9 °C (Fig. 7). Region 1 in the eastern GOA always has the coldest temperatures during winter relative to all other regions and generally the warmest temperatures during summer making it the area of greatest seasonal variation in SST across all years (7 °C). In contrast, Region 4 generally has the warmest temperatures in winter and coldest in summer so the average seasonal variation in SST in this area across all years is small (3 °C) relative to Region 1 in the eastern GOA and central GOA (5 °C), Region 2 (5 °C) and Region 3 (4 °C).

There is no variation in seasonal averages of SST between decades, but there are more temperature extremes in the 1999-2009 dataset (highest highs 2003; lowest lows, 2007 and 2008). In summer, the warmest temperature peaks were during 2005, followed by those of 1997. Coldest summer temperatures were in 2008 and 2009 for most regions, and in 1999 for all regions.

DISCUSSION

There was little change in the species of prey or in the seasonal and regional patterns of prey consumption among adult female and juvenile SSL of the U. S. Western Stock between 1990-1998 and 1999-2009. However, the FO of most primary prey increased during the past decade along with prey diversity, suggesting that prey are more available through distribution or abundance to a greater proportion of the SSL population. Biases that might falsely impart the appearance of greater prey availability were accounted for as follows: 1) sample sizes were large and similar between decades and seasons; 2) data was collected and analyzed uniformly between decades; and 3) we confirmed that our current enhanced ability to identify prey did not inflate relative values for the simple presence or absence of a prey item in a scat.

Despite significant changes in prey FO values, the regional boundaries in diet remained consistent over time, again portraying adult female and young juvenile SSL as highly localized in the longitudinal extent of their foraging range, during both winter and summer (Sinclair and

Zeppelin 2002). Our nominal understanding of the seasonal distribution of the primary species of prey indicates that adult female and young juvenile SSL of the Western Stock are also localized in the latitudinal extent of their foraging. Seasonal and regional diets indicate that prey species are selected when they are most abundant and highly concentrated within definitive SSL foraging corridors over the continental shelf.

Adult Female SSL -- Localized, Nearshore Foragers

The life history and age-related distribution of fish and cephalopod prey are good indicators of the location and depth in which their predators feed. Prey concentrate in oceanographic boundary areas created by eddies, cold pools, frontal zones (Nishiyama et al. 1986, Decker and Hunt 1994, Hollowed et al. 2012) and around bathymetric structures (Pearcy 1992b, Love et al. 2002). Concentrations of prey in turn influence predator foraging locations (Goebel et al. 1991, Antonelis et al. 1997, Robson et al. 2004, Fadely et al. 2005, Ream et al. 2005, Zeppelin and Ream 2006, Sterling and Ream 2004, Trites et al. 2007b, Hunt et al. 2008, Call and Ream 2012), and presumably even more so if concentrations are stable or at least temporally predictable. In the case of otariid pinnipeds, dense predictably available prey concentrations may even be required for foraging success (Sinclair 1988, Sinclair et al. 1994, Antonelis et al. 1997, Fadely et al. 2005, Sigler et al. 2012).

Adult female and young juvenile SSL of the Western Stock consume a wide variety of prey from the nearshore epipelagic, semi-demersal and demersal zones. However, the most frequently occurring prey share a number of characteristics (Eschmeyer et al. 1983), one being that at some point in their life history they live on or over the continental shelf (Hay and McCarter 1997, Witherell 2000, Mueter and Norcross 2002, Hollowed et al. 2012) on at least a seasonal basis, and it is during this time that they are consumed by SSL (Sinclair and Zeppelin 2002).

The primary regional break in cluster analysis occurs between Region 4 and Regions 1-3 where respectively, Atka mackerel and walleye pollock serve as year-round staples in SSL diet during both decades (Figs. 4 and 5). Atka mackerel and walleye pollock are distributed over age-associated depths of the continental shelf as both juveniles and adults in variable densities throughout the year (Smith 1981, Nishiyama et al. 1986, Livingston 1993, Lauth et al. 2007), and both dominate SSL diet as juveniles and adults (Zeppelin et al. 2004) year-round.

The secondary regional breaks associated by cluster analysis (breakdown between Regions 1, 2 and 3; Fig. 4) are linked with diets that depict both resident and seasonal members of the demersal fish community. Resident groundfish are thought to occur in highest biomass in areas with relatively broad continental shelves and to concentrate most densely near the continental shelf edge (Mueter and Norcross 2002). Other seasonal or ontogenetic migrants move onto and off of the continental shelf, either coming from or going to continental slope and pelagic waters (Spies et al. 2012). The timing of offshore-onshore movements of fish and cephalopods are predictable and these species are eaten by SSL when they pass through Regions 1-3 in greatest age-related densities. For example, the remains of Pacific cod represent those of adult-size fish (Sinclair and Zeppelin 2002) and they are eaten predominantly in winter in Region 2, during the time and area of well-described aggregated spawning movements of cod from the EBS into the submarine canyons of the GOA (Shimada and Kimura 1994).

Other species of the prey matrix of Regions 1-3 move permanently onto the nearshore continental shelf as they reach maturity, where they form large aggregations over and in sandy/muddy substrate (Pacific sand lance) (Blackburn and Anderson 1997), and establish territory over rocky outcroppings and within kelp beds (rockfish) (Pearcy 1992a, Love et al. 2002). Based on the size of bony remains from these taxa, it is during this nearshore stage that they are eaten by SSL.

Other primary prey that appear to be eaten over the continental shelf are seasonally transient migrants moving from nearshore to pelagic waters as juveniles and back to nearshore waters as adults en route to spawning grounds (Salmonidae, Pearcy 1992b; and herring, Grosse 1988). Others aggregate in predictable seasonal pulses over the nearshore continental shelf or shelf edge where they spawn and die (cephalopods, Roper and Young 1975, Hochberg and Fields 1980, Sinclair et al. 1999). In the latter case, the young of these same species develop in nursery zones over the continental shelf where they are eaten as juveniles prior to ontogenetic migration to midwater and demersal zones offshore (gonatid squid) (Roper and Young 1975, Sinclair et al. 1999, Beamish et al. 1999) or into deeper waters over the continental slope (Nesis 1987).

Prey species that are strictly pelagic in distribution and undergo densely aggregated diurnal vertical migrations offshore in the water column (i.e., Myctophidae) are also eaten, but not by a high proportion of the population in this study. If pelagic species were regularly eaten during SSL female foraging bouts of 2-3 days, their remains should show up in higher frequencies than currently observed, especially in areas with a narrow continental shelf (Region 4). Capelin and salmon (similar in light bone structure to Myctophidae) are represented in SSL scats from meals consumed up to 144 hours earlier in captive experiments with animals that are retained in a physically active environment (Tollit et al. 2007). Region 4 SSL could feed pelagically and still remain in close proximity to island haul-outs and rookeries where the remains of their pelagic prey should be found. However, neither endemic members of the pelagic zone, such as Myctophidae, nor those that have strong seasonal pulses in the nearshore pelagic (i.e., *Leuroglossus stilbius*) (Sinclair and Stabeno 2002) are common in the diet in Region 4 or any other area in this study (Table 1). While some offshore feeding occurs and females are likely utilizing oceanographic boundary zones nearshore and at the edge of the continental shelf, their diet suggests that adult females and young juveniles of Western Stock SSL feed primarily over the nearshore continental shelf year-round.

In a comparative study of diet based on scat, stable isotope analysis, and fatty acid analysis with foraging location determined by satellite telemetry, Waite et al. (2012) concluded that adult female SSL of the Asian stock forage primarily in the nearshore benthic within 4 km of rookeries. The Waite et al. (2012) study was conducted in an area with a very narrow continental shelf, much like that in our diet Region 4, and adult females confined themselves to this area, while sympatric northern fur seals focused foraging primarily in the pelagic zone.

Satellite telemetry studies have been published on just four adult female SSL (Merrick and Loughlin 1997) and on a large number of immature SSL in the GOA and Aleutian Islands (Raum-Suyan et al. 2004, Merrick and Loughlin 1997, Loughlin et al. 2003, Fadely et al. 2005). Most individuals foraged nearshore, but a smaller percentage of tagged animals including two adult females traveled offshelf into pelagic waters (Merrick and Loughlin 1997, Fadely et al. 2005). Individuals that traveled offshore were typically associated with bathymetric features such as submarine ridges and seamounts (Merrick and Loughlin 1997, Fadely et al. 2005). Since immature SSL sometimes forage with their mothers beyond 2 years of age, records of offshore feeding among juveniles could include accompaniment by adult females (Fadely et al. 2005), depending on juvenile age and possibly sex. Adult male and female northern fur seals eat different sized prey that are consumed in different areas or depths of the water column (Call and Ream 2012) and this also appears to be true of SSL. Additional age-based telemetry studies will indicate at what point a juvenile male SSL diverges from prey selection typical of adult females towards that of adult male SSL. Additional studies on adult female SSL will confirm or refute the patterns indicated by diet alone, that most feeding by adult females of the Western Stock occurs over the continental shelf and nearshore waters associated with oceanographic fronts and bathymetric features of the nearshore benthic year-round (Sinclair and Zeppelin 2002).

Adult Female SSL -- Indicators of Prey Availability

Regional patterns in SSL diet reflect the distribution patterns of high concentrations of their prey (Call and Loughlin 2005, Fadely et al. 2005, Lander 2010). One clear example of this is at the primary break in cluster analysis between Regions 1-3 and Region 4 at Samalga Pass (long. 170°W) (Fig. 3). The diet of SSL between these regions reflects the abrupt change in the distribution and abundance of the zooplankton, seabird, cetacean, and fish communities that occur there (Stabeno et al. 2005). Moving westward across the Aleutian chain, the system switches at Samalga Pass from a pollock-based guild to Atka mackerel (Loggerwell et al. 2005), and likewise, SSL crossover from a walleye pollock- to an Atka mackerel-based diet (Sinclair et al. 2005). Also reflected in SSL diet at the boundary between Regions 1-3 and Region 4 is the large decline in the number and diversity of fish species distributed over the narrow shelf in the oceanic, low productivity (Mordy et al. 2005) waters west of Samalga Pass compared to the broad-shelf productive coastal waters to the east (Loggerwell et al. 2005, Mordy et al. 2005; Fig. 4). Samalga Pass is the primary biophysical transition point that occurs longitudinally between the GOA and western AI and is the most definitive boundary zone differentiating SSL diet profiles across the Aleutians.

Changes in the FO of primary prey during 1999-2009 likely reflect in situ changes in prey availability over the continental shelf, but whether increased availability is due to changes in the distribution, schooling behavior, and/ or increased abundance of prey cannot be evaluated from our data. In a wide variety of marine mammal diet studies, FO has been shown to be closely associated with measures of the amount of prey consumed such as prey number (PN), whereby as FO increases, PN increases as well (Antonelis et al. 1997, Sinclair 1992, Sinclair 1994, Walker 1996, Trites et al. 2007a). If this is the case with SSL diet, increases in FO could indicate that prey are more available within foraging range due to increased abundance. Some general trends in fish abundance, such as the increase in walleye pollock that occurred between the late 1970s and early 1980s (Conners et al. 2002, Mueter and Norcross 2002), are reflected in an increased presence in SSL diet relative to historical studies (Sinclair and Zeppelin 2002). Likewise, the increase in arrowtooth flounder population in the GOA during the period of this study (Mueter and Norcross 2002; Spies et al. 2012) may be the basis for the increasing FO of this species in SSL diet. Diet studies of eastern stock SSL have demonstrated a strong relationship between foraging behavior, haul-out locations, and known concentrations, or “hot spots”, of prey abundance (Womble et al. 2005, Gende and Sigler 2006, Sigler et al. 2009).

The greatest increases in prey FO between decades in both winter and summer were for Pacific sand lance in Regions 1-3. This species of fish has also become more frequent and more numerous in diets of other marine apex predators in the Bering Sea since the 1990s (Sinclair et al. 2008). However, whether this reflects an increased abundance or just increased availability is unknown since the burrowing behavior of Pacific sand lance makes them challenging to survey with standard research trawls (Arimitsu et al. 2005). The relationship between prey abundance in the water column and its FO pattern in SSL diets is likely specific to prey type, area, and time of collection and requires further study and analysis of fisheries research surveys within specific SSL diet regions.

Adult Female SSL – Risks and Rewards of Localized, Nearshore Foraging

Animals hauled out on islands in close proximity to one another are genetically related (O'Corry-Crowe et al. 2006), have similar diets (Sinclair and Zeppelin 2002, this study) and have similar population trends (York et al. 1996, Sinclair and Zeppelin 2002, Call and Loughlin 2005). The consistent regional overlay of diet, genetics, and population between decades supports suggestions that the boundaries of foraging regions are dictated by proximity to natal rookeries, and that SSL may develop foraging skills specific to the regions of their birth (Sinclair and Zeppelin 2002, O'Corry-Crowe et al. 2006).

Adult females of Western Stock SSL appear to maintain close proximity to natal site rookeries year round (Sinclair and Zeppelin 2002, York et al. 2008), which for most areas translates to year-round fidelity to specific foraging locale over the continental shelf. In Region 4, females could forage offshelf and still remain in close proximity to rookeries, but diet findings are most indicative of onshelf feeding year-round. Area-centric movements that rely on the temporal and spatial predictability of prey save energy during lactation and when traveling with young at sea. Womble et al. (2005) concluded that in summer, it is critical that seasonal prey important in the diet of eastern stock SSL is not too far from central breeding/pupping areas in order to increase chances of reproductive success. In our study, adult female SSL of the Western Stock appear to implement a strategy that reduces the amount of time away from the rookery, and at-sea with young, by focusing on prey species that are predictable seasonal migrants into defined foraging regions. We suggest that this foraging strategy is one that also makes SSL vulnerable to localized changes in prey resources, and to disturbance in general over the continental shelf.

Prey Availability and Population Success

The areas of greatest increases in prey FO and greatest diversity in diet (diet Regions 2 and 3; RCA 6 and 7) beginning in 1999, overlay those of the greatest increase in population numbers beginning in 2000. Prey diversity was also highest in Regions 2 and 3 compared to all other areas during Period 1 (Sinclair and Zeppelin 2002). Prey diversity also tracks this area of population increase when evaluated using different subsets of the SSL diet database 1990-1993 (Merrick et al. 1997) and 1990-2001 (Sinclair et al. 2005). The areas of greatest population increase and continuing high prey diversity during Period 2 follow York et al. (1996) predictions that a 6 rookery complex contained in Regions 2 and 3 (including Amak Island) demonstrated persistently stable or increasing populations and would remain viable, even in the face of extinction of all other rookery sites.

The regions of greatest increases in population in the eastern AI and western GOA are flanked by continuing population declines to the west (Region 4) and static patterns in population growth directly to the east, in diet Region 1 (RCA 8 and 9) in the central GOA. Population counts further east, still within diet Region 1 (RCA 10) in the eastern GOA, show promising signs of growth. Overall, Western Stock SSL population counts appear to be rebounding in the center of their historical range (NMFS 2010) where calculations of prey diversity have always been highest (Merrick et al. 1997, Sinclair and Zeppelin 2002) and particularly so since 1999.

The inherent complexity and intricate association of environmental and anthropogenic influences means that there may not be (or we may not detect) a single direct cause of system-wide change in SSL population as it relates to diet (nutrition) specifically. However, at the very least, increased prey diversity and higher FO in areas of population increase since 1999 implies that there has been a greater release of prey (in terms of abundance or availability) within manageable foraging distances for adult females maintaining close proximity to pups on the rookery, or traveling with young juveniles at sea.

Environmental Influence on Prey Availability

The high degree of coherence in SST patterns across all regions suggests that in very broad terms, the physical feedback from climate influences along the continental shelf is similar between the eastern GOA and the western AI. However, the extreme range of temperatures between regions also implies that the biological impact of climate influences could be quite variable between regions. While temporal patterns of increases and decreases in SST are parallel between regions, the effect of a 2 °C decrease in mean SST on the prey field in Region 1, for instance, could be dramatically different than in Region 4, in large part due to the extent of the continental shelf. The population success of herring, for instance, is thought to be limited by the width of continental shelf habitat available at various life stages (Hay and McCarter 1997). While each region has a signature range and pattern of temporal change in SST, Regions 1 and 4 both have the most extreme temperatures between seasons so it can be seen how similar climate influences could have different effects on the prey field and on prey movements in areas with strongly contrasting bathymetry and hydrography.

There was no variation in average SST between decades in either summer or winter, even though the highest and lowest temperature peaks occurred from the late 1990s forward. Despite synchronous patterns in interannual temperature variability between all regions, Region 4 had an extremely narrow range of temperature between summer and winter across all years. Region-wide physical changes in the study area that occurred in response to a shift in the Aleutian Low in 1999 (Rodionov et al. 2008) were not apparent in our narrow nearshore SST data by region in 1990-2009. However, biological changes are often more responsive to subtle changes in temperature (Overland et al. 2012) than physics can forecast, and could be reflected in the observed increases in FO of demersal fishes in SSL diet during 1999-2009. While these results do not speak directly to regional influences on diet change, they are compelling and worthy of additional research particularly as to how they may interact with anthropogenic influences over the continental shelf.

Anthropogenic Influence on Prey Availability

The increase in the FO of primary prey in SSL diet across the study area during 1999-2009 (including walleye pollock in Region 4), is coincident with establishment of restrictive trawl exclusion zones (NMFS 2010) put in place over the continental shelf and within important foraging zones in 2000. Since the expansion of no-trawl protection zones there has been a concomitant increase in the FO of most all SSL prey that are directly targeted (i.e., Atka mackerel, Pacific cod, sole, and arrowtooth flounder), indirectly caught as bycatch (i.e., Pacific sand lance, greenlings, poachers, eelpouts, snailfish, squid) or typically dispersed by habitat destruction or disturbance by bottom trawls (rockfish). Whether or not the time and areas of trawl restrictions directly relate to the regions of greatest increase in FO and the most positive trends in SSL population since 2000 (Regions 2 and 3, RCA 6 and 7) requires additional study. However, two concurrent studies of Atka mackerel distribution and abundance within and outside of trawl exclusion zones (TEZ) in Region 4 concluded that TEZ are effective in preserving an increased biomass of prey for SSL consumption (McDermott et al. 2005, Cooper and McDermott 2011, Lauth et al. 2007), and that TEZ create default marine reserves (Cooper and McDermott 2011).

In areas of heavy trawling, Atka mackerel, rockfish, and behaviorally related species are unable to maintain nesting sites (Cooper and McDermott 2011) or the large aggregations (Love et al. 2002) in which SSL tend to forage, and the habitat that is essential to the occupation of these species is disrupted or destroyed by trawling (Collie et al. 1997, Pauly et al. 1988, Witherell and Coon 2000, Lauth et al. 2007, Pauly 2007, Watling and Norse 2008, Cooper and McDermott 2011,). Numerous studies have demonstrated that the exclusion of fishing activity within nearshore marine habitats results in increases in the abundance and size of many marine species within a very short period of time (*see* MPA 2008). Also, species cross into and out of protected areas during specific life stages, which eventually enhances their fisheries potential outside of TEZ (Lauth et al. 2007, MPA 2008, Cooper and McDermott 2011).

The extent of overlap between the size of fish eaten by SSL and taken by walleye pollock and Atka mackerel trawl fisheries could result in direct competition between fisheries and foraging sea lions (Zeppelin et al. 2004). Indirect competition for a 'shared' foraging field could be problematic for SSL as well. Hennen (2006) concluded that reduction in fishing activities has been successful in moderating localized effects of fishing activity around some rookeries more than others. The Hennen (2006) findings of localized variability in population response to restrictions in TEZ speaks to the potential for multiplicative effects of fish distribution, climate and anthropogenic activity that could influence one area differently than another. Theoretically, TEZ together with the 'right' climactic conditions within diet regions could positively influence increased forage success of SSL. This could be especially true in an area like Region 4, with its limited continental shelf and comparatively depauperate biota compared to regions east of Samalga Pass (Stabeno et al. 2005) where SSL are stable and increasing.

Climate and Fisheries -- Interrelated Influences on Prey Availability

Identifying the links between climate, fishery activity, and prey availability to SSL is challenging because we do not understand the dimensionality of the marine system. Each influence likely has multiplicative effects regarding how removal of one prey type affects the abundance or availability of another. Extended limits placed on fishing activity within 20 nmi of rookeries and haulouts may have a positive direct or indirect effect on population growth of fish, and subsequently SSL abundance, because protections are region-wide rather than species-specific, and thus protect complex relationships within the system that we are not able to identify (Fowler and McCluskey 2011).

A scenario can be envisioned where the positive effects of no-trawl zones on groundfish could be negated by years of aberrant temperature conditions that affect cold-loving walleye pollock differently than warm-loving Pacific herring and Pacific sand lance (Arimitsu et al. 2005), with compounded variable effects in different areas of their distribution over a broad versus a narrow continental shelf. The interrelationship between ocean conditions and anthropogenic activities within SSL Critical Habitat has not been evaluated. The potential for their combined effect on SSL diet and population is considerable and deserving of additional study.

The additional years of data here describe a change point in diet that might be overlooked using other methods of analyses. Other emerging methods of marine mammal diet analysis using stable isotopes (Hobson 1999), quantitative fatty acids (Iverson et al. 2004, Bowen and Iverson 2012), and prey genetics (Tollit et al. 2009) are promising, and comparative studies using these techniques demonstrate agreement with findings based on FO (Goebel 2002, Kurle and Sinclair 2003, Hobson et al. 2004, Kurle and Gudmundson 2007, York et al. 2008, Tollit et al. 2009, Zeppelin and Orr 2010, Kurle et al. 2011). However, these alternative methods are not yet stand-alone tools for describing specifics of the wild diet of SSL across their range (Rosen and Tollit 2012). The best application of stable isotope, fatty acid, and prey genetic analyses of pinniped diet is in conjunction with FO analysis, and additional reduction of bias in diet interpretation can be achieved by employing two or more sample schemes at once, such as collecting both scats and spews whenever possible (*see* Sinclair et al. 1996, Gudmundson et al. 2006, Tollit et al. 2006, Bowen and Iverson 2012, Rosen and Tollit 2012). The broad brush of the FO of prey over 20 years of data collection across the range helps to coalesce our understanding of the relationship between diet patterns, foraging conditions, and population health of SSL.

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APPENDIX

Prey Notes – False Negatives and Secondary Introduction

One prey species likely missing in scat sign in this study, or a ‘false negative’ as referred to by Bowen and Iverson (2012), is the adult giant octopus (*Octopus dofleini*) which has been documented as important prey in other studies of SSL diet based on stomach collections (Pitcher 1981). This species reaches sizes up to 250 kg (Hochberg and Fields 1980) and beaks from 20 kg individuals have been observed in large quantities in individual stomachs of SSL collected in the North Pacific, and in adult male and older juvenile male SSL collected in the nearshore pelagic during winter in the Bering Sea (P. Gearin, W.A. Walker, pers. comm., NMML, Seattle, WA). Based on the volume and size of individuals in stomachs, *O. dofleini* is likely eaten during inshore spawning movements (Greene 1973) and could represent an important winter prey to adult females as well. Due to their large size, the beaks of adult *O. dofleini* would be unlikely to travel through the gastrointestinal system of SSL intact, and are most likely regurgitated as are the greater percentage of moderately sized beaks from other cephalopods eaten by sympatric northern fur seals (Gudmundson et al. 2006).

Cephalopods also represent the potential for ‘false positives’ as a secondary prey source. Prey size was not formally evaluated in this study, but the small size of *Gonatid* squid and octopods eaten in Region 4 may indicate secondary introduction to SSL through consumption of salmon or walleye pollock (in winter). It is noteworthy, however, that SSL consumption of walleye pollock increased in Region 4 during Period 2, while the FO of cephalopods decreased. Also noteworthy is that directly consumed cephalopods and walleye pollock have been shown to have opposite trends in the diet of northern fur seals and thick-billed murres in the Bering Sea (Sinclair et al. 2008). The contrasting pattern of increase and decrease of walleye pollock and cephalopod FO in Region 4 may indicate that cephalopods were eaten directly by SSL, despite their small size. It is possible that very small, post-larval gonatid squid are eaten by SSL, and perhaps particularly by juvenile SSL when they occur in seasonal shoals over the continental shelf.

Additional potential 'false positives' in this study include polychaete worms that spend a portion of their life history partially buried in nearshore sediments (Eschemeyer et al. 1983, Allen and Smith 1988, Arimitsu et al. 2005). Most other sediment spawners identified as prey in this study (i.e. gunnels, Pacific sand lance) also spend time shoaled nearshore prior to settling into a demersal stage, and they are probably eaten by SSL while in shoaling aggregations. Polychaete worms, on the other hand, form large calcified mats that SSL are less likely to directly feed upon, but that serve to shield other more mobile species (rock sole). They are also known to be an important food source for juvenile rock sole in the GOA (Love et al. 2002), and so could reflect secondary introduction in this study. Polychaetes occurred in large frequencies in scats from both decades in this study and are increasingly frequent in scats from northern fur seals in the Bering Sea as well **(**NMML, unpubl. data). We assume their presence in SSL diet is due to secondary introduction from rock sole, or from inadvertent consumption while pursuing other prey. So despite their high FO, polychaetes are listed (Table 1) but, were not included in further analysis.

Prey that are secondarily introduced to SSL diets are relevant to understanding foraging behavior whether or not they contribute directly to SSL nutrition. Prey items may be intentionally consumed by juvenile SSL that are playing, practicing feeding, or lack a proper food source due to their mother's absence. Based on diet studies of other pinnipeds, juveniles appear to do a lot of 'poke-and-search' feeding, particularly in environments with complex strata containing layered microcosms of prey (Sinclair 1994). Ongoing research on the intra-specific size of prey species consumed by SSL as well as seasonal and ontogenetic migration of prey will enhance our continuing ability to differentiate between primary and secondary consumption.

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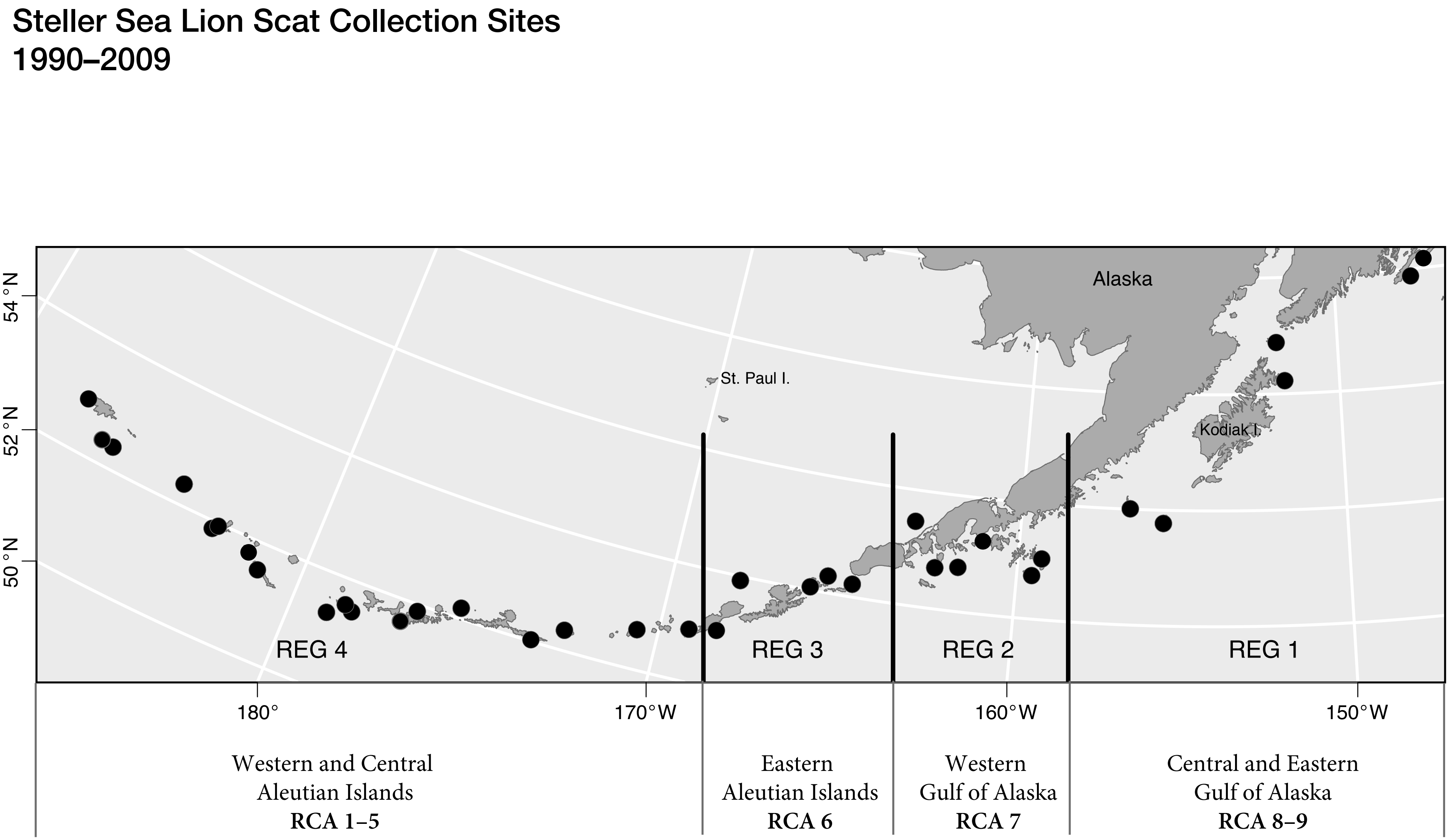
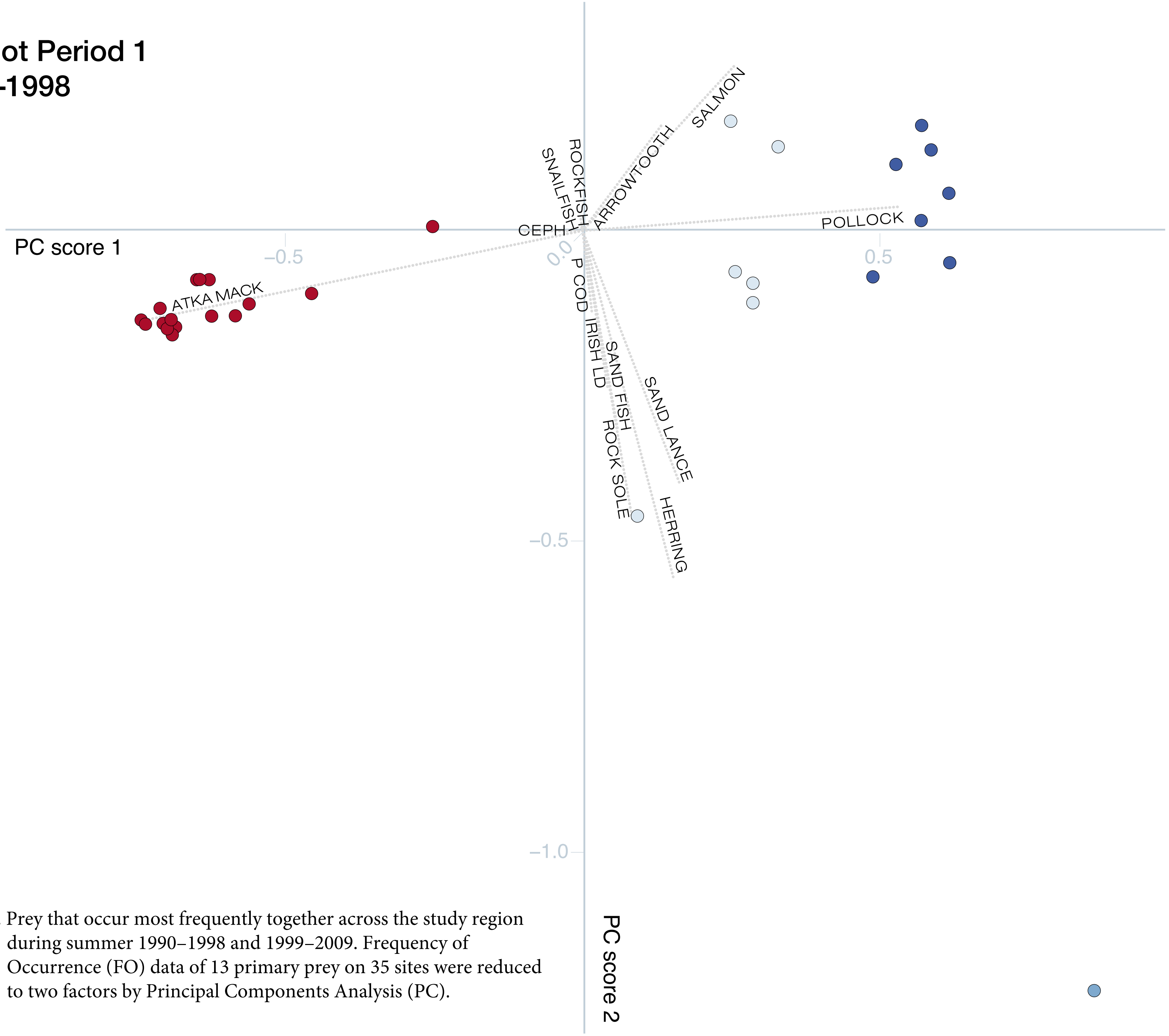


Figure 1. Island sites of Steller sea lion (*Eumetopias jubatus*) scat collections 1990–2009 with diet Regions (REG) 1–4 and regional areas of fishery conservation zones (RCA) 1–9. Diet regions were first defined based on 1990–1998 scat collections (Sinclair and Zeppelin 2002) and confirmed with 1999–2009 comparative scat data in this study.



PC Plot Period 1
1990–1998

Figure 2. Prey that occur most frequently together across the study region during summer 1990–1998 and 1999–2009. Frequency of Occurrence (FO) data of 13 primary prey on 35 sites were reduced to two factors by Principal Components Analysis (PC).

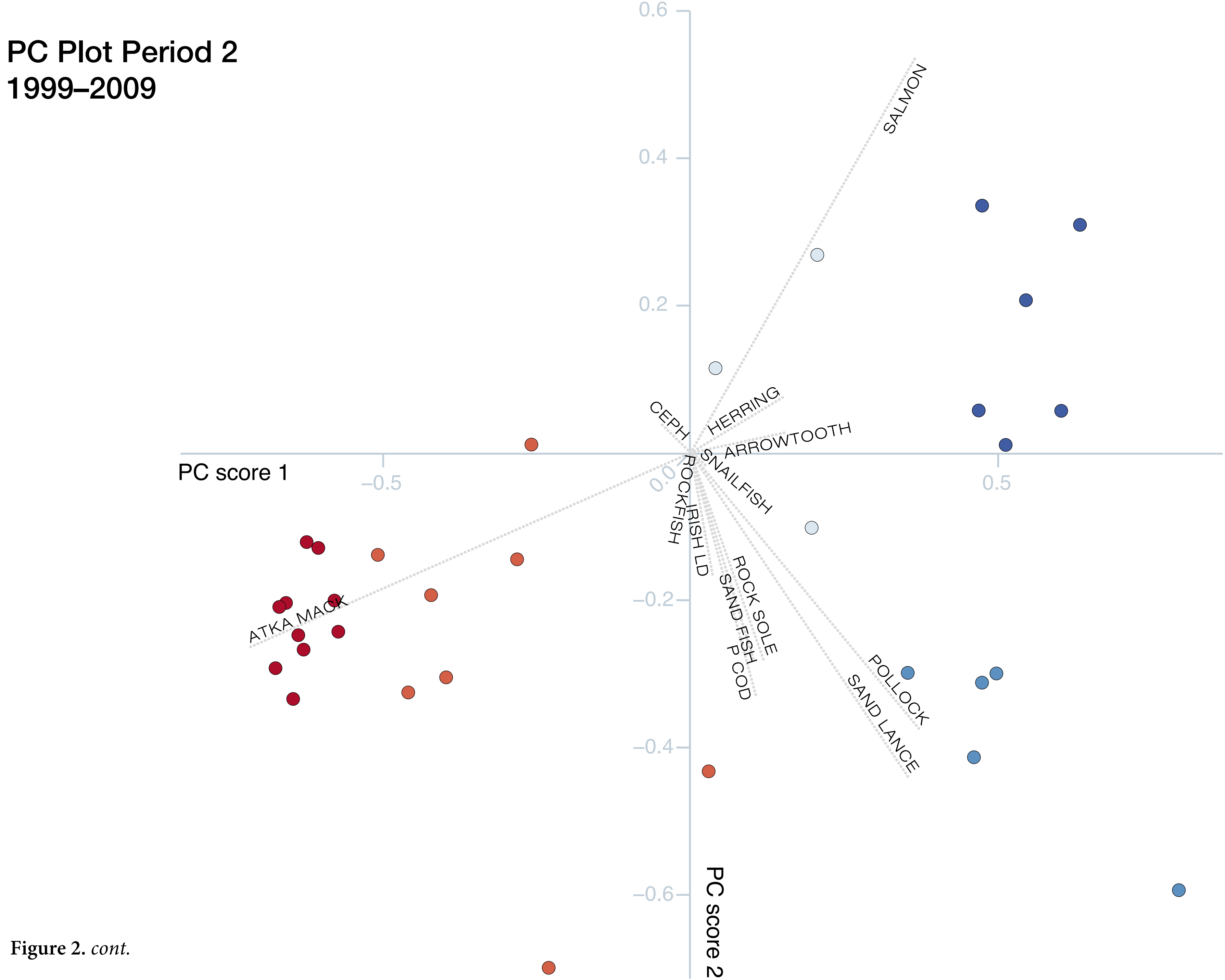


Figure 2. *cont.*

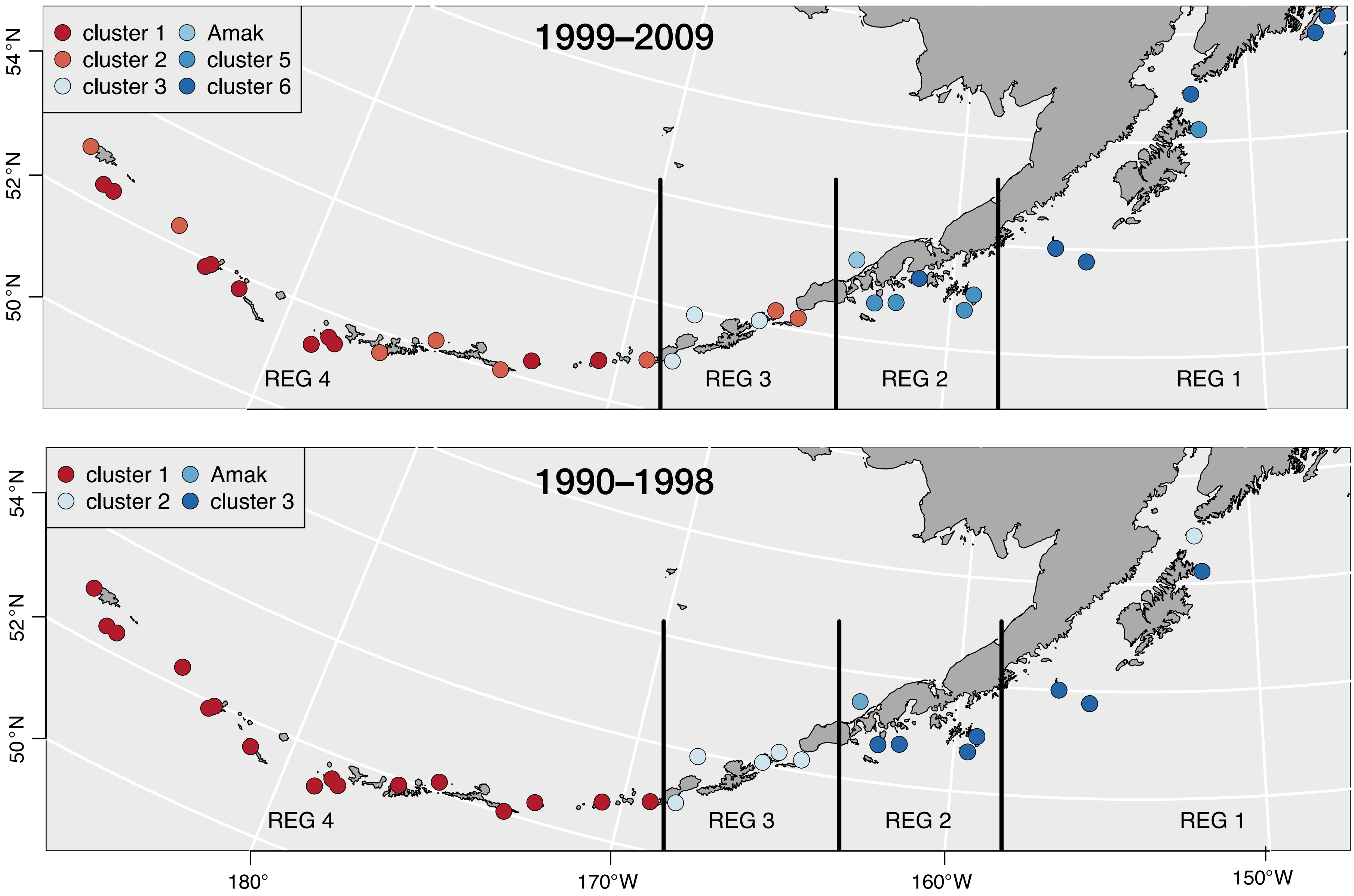


Figure 3. Regional patterns of prey group clusters at Steller sea lion (*Eumetopias jubatus*) scat collection sites during: summer, 1999–2009 and 1990–1998 (adapted from Sinclair and Zeppelin 2002). Boundary zones between each diet region during both decades are identical for winter.

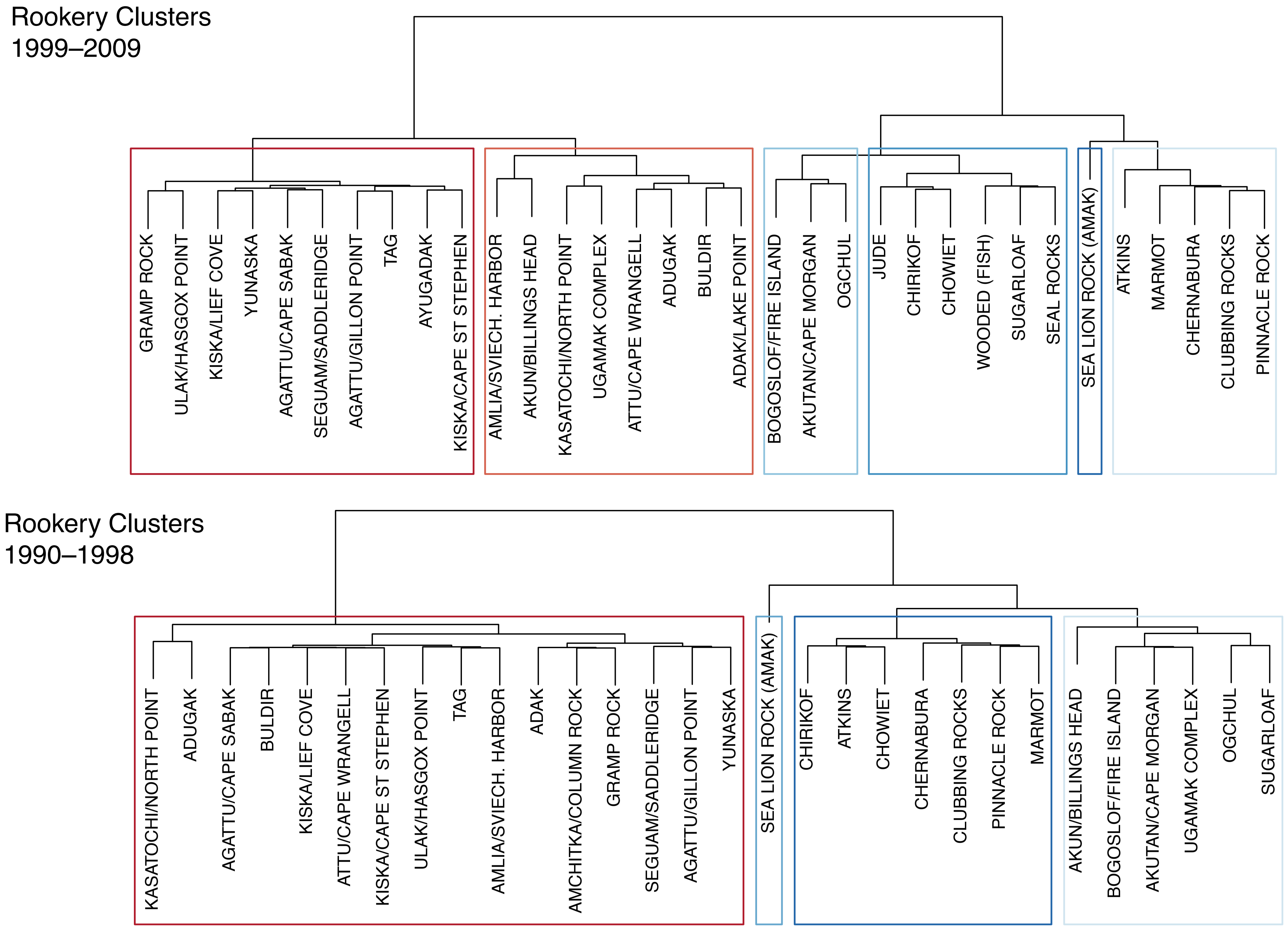


Figure 4. Dendograms from a hierarchical cluster analysis of Principal Component scores on the frequency of occurrence of prey in Steller sea lion diet. Groupings show sites that cluster together most closely based on similarity in prey identified from scats collected on those sites.

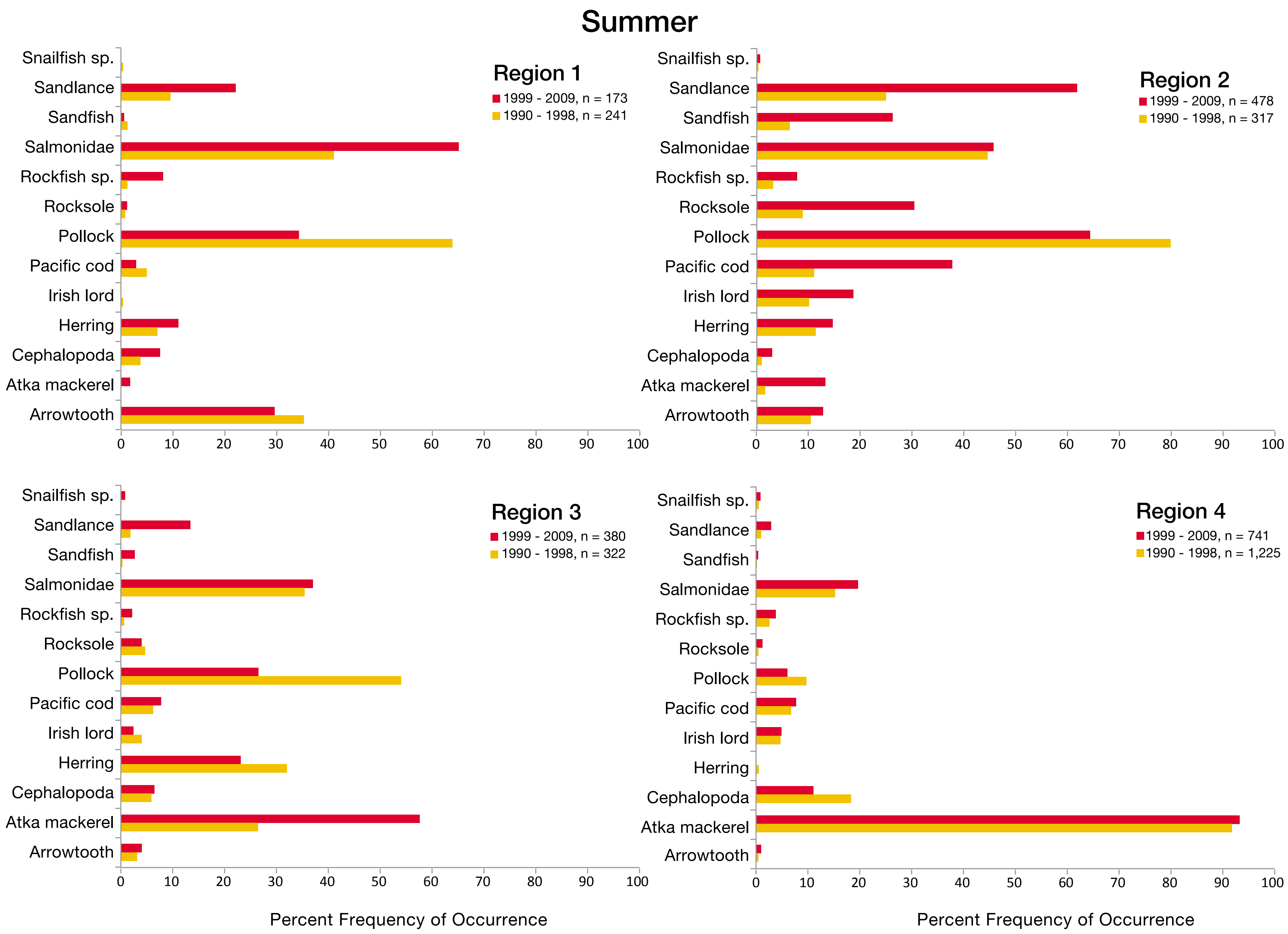


Figure 5. The seasonal frequency of occurrence (FO) of Steller sea lion (*Eumetopias jubatus*) primary prey species based on scat collected within diet Regions 1–4 during 1990–1998 and 1999–2009.

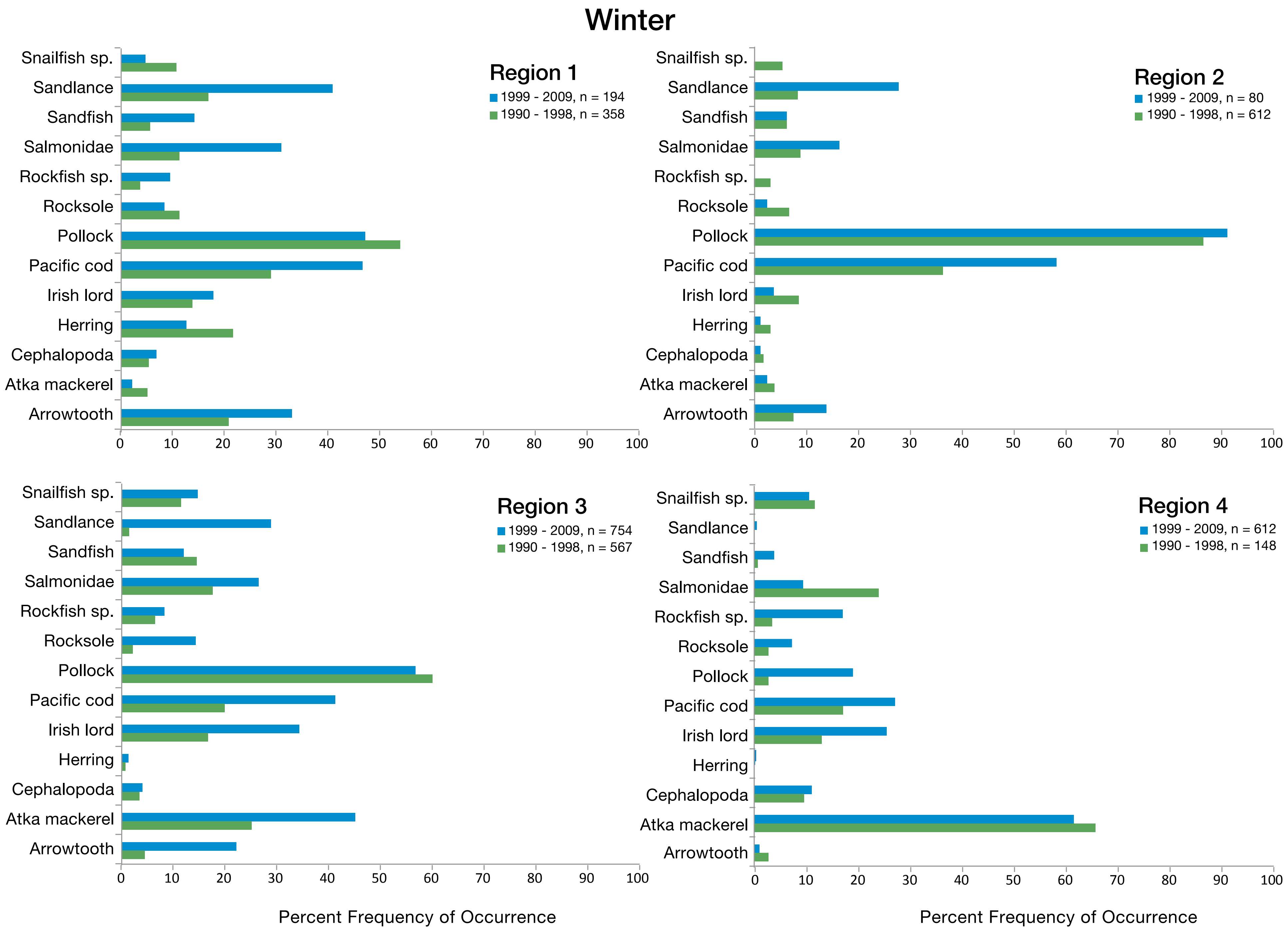


Figure 5. *cont.*

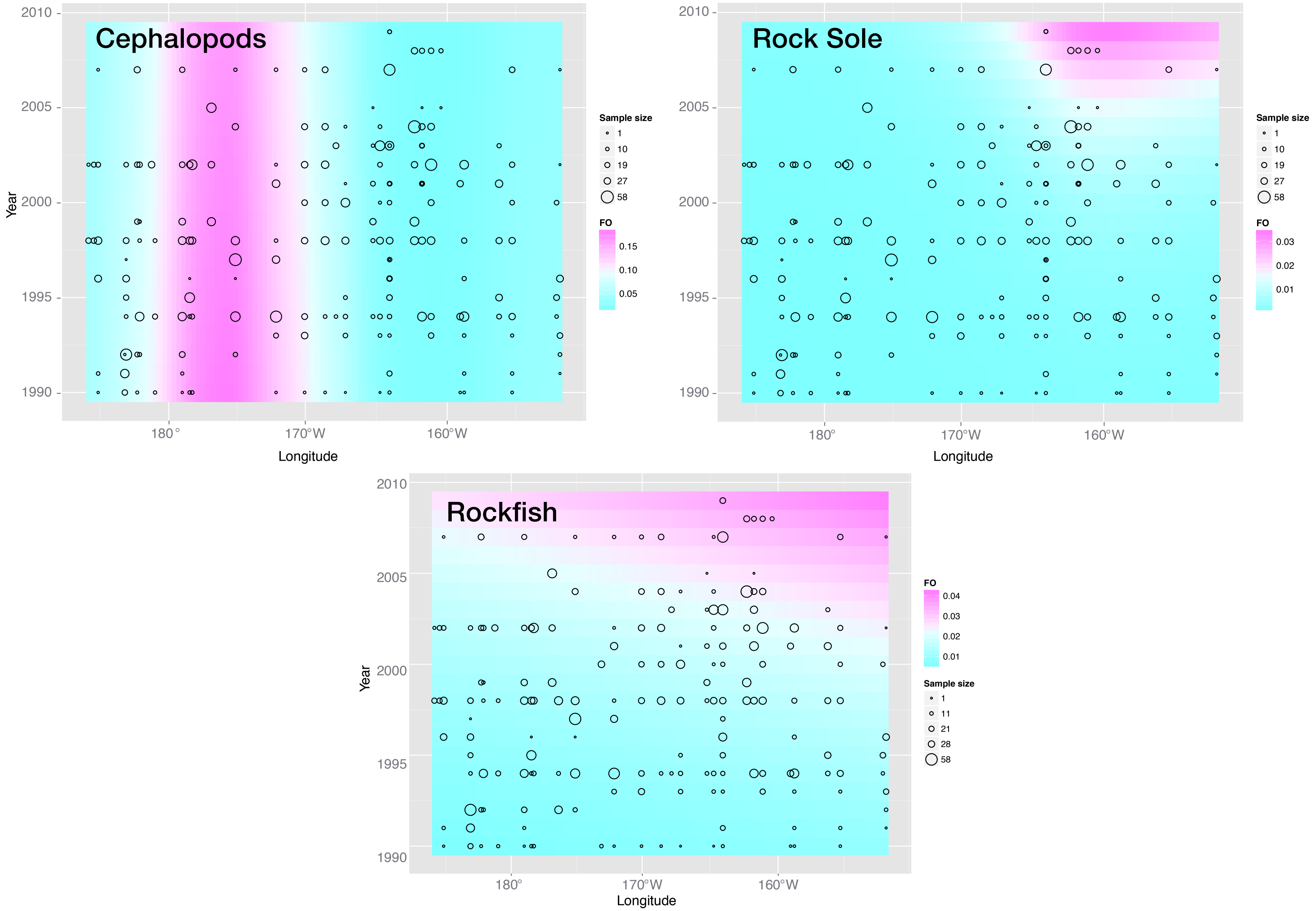


Figure 6. Generalized Additive Model (GAMM) fit showing annual W-E longitudinal trends in Steller sea lion (*Eumetopias jubatus*) summer diet 1990–2009. Prey shown here are those whose FO increased or decreased most significantly (p=0.001) in one or more Regions between 1990-1998 and 1999-2009 datasets.

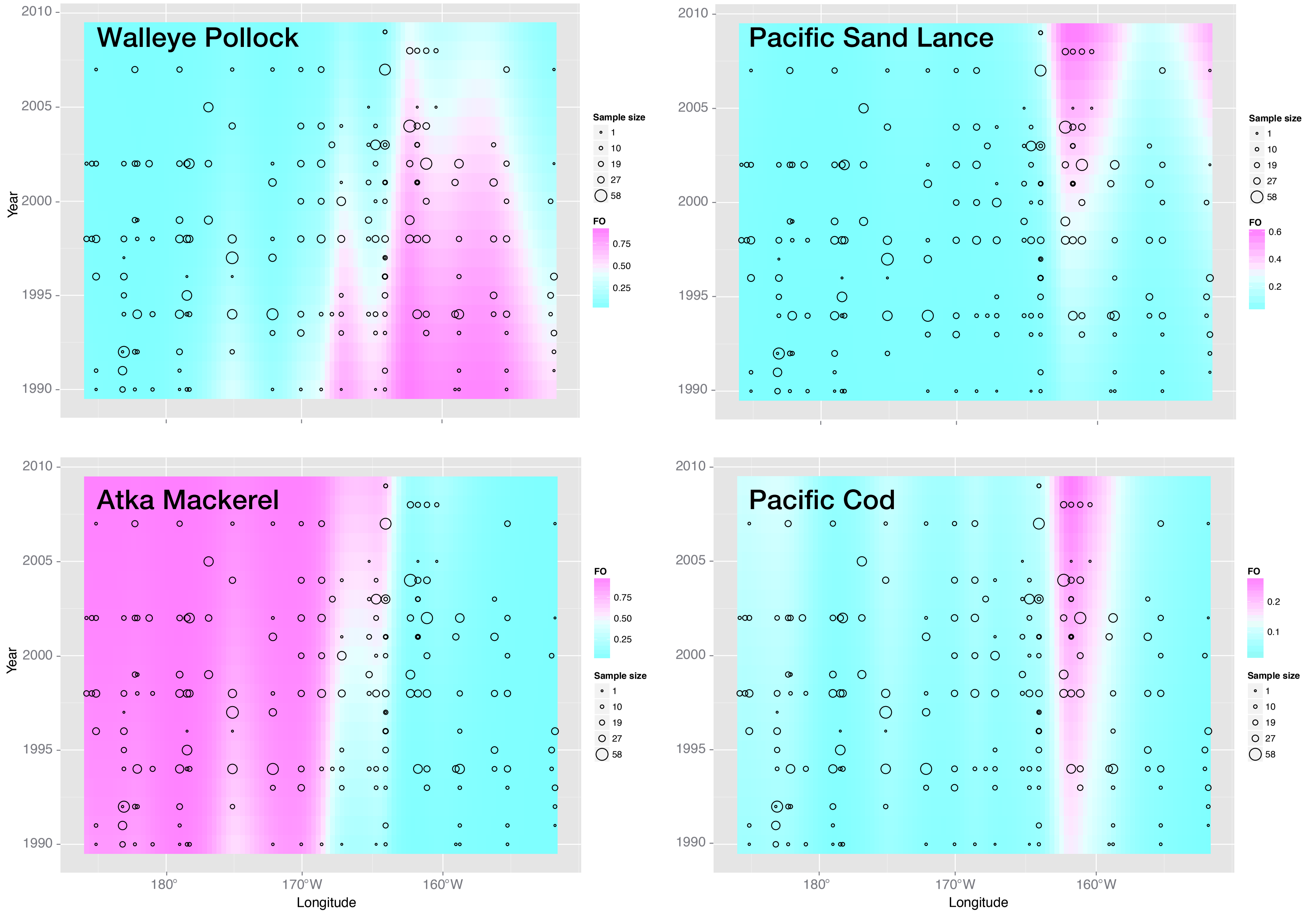


Figure 6. *cont.*

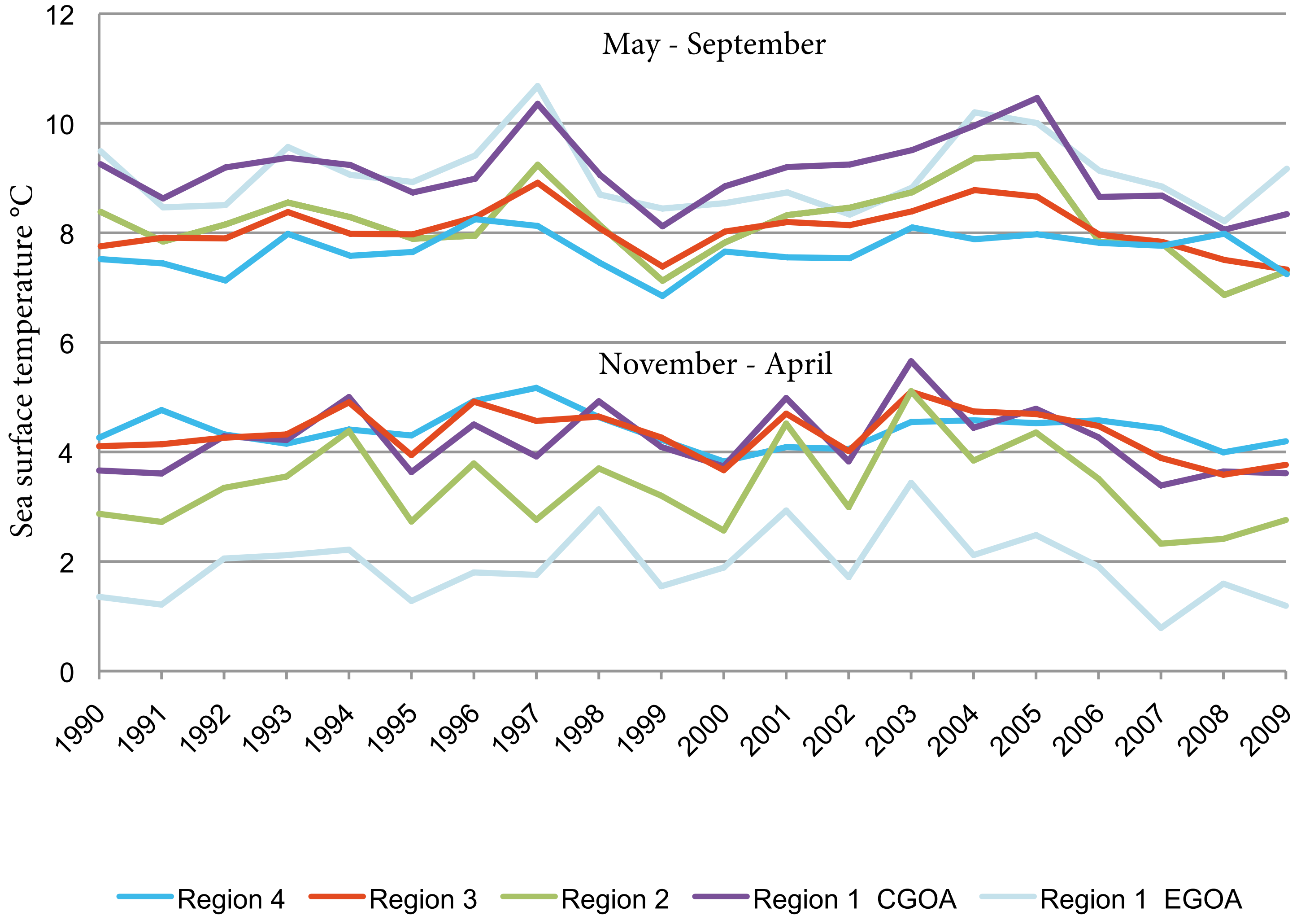


Figure 7. Mean sea surface temperatures (SST) in Steller sea lion diet Regions 1–4, 1990-2009.

Table 1. Frequency of occurrence of all prey identified from remains in Steller sea lion *(Eumetopias jubatus)* scat collected during summer and winter, 1999-2009, across the range of the U.S. western stock. Prey frequencies are summarized for each of four diet Regions first described in Sinclair and Zeppelin (2002) and confirmed in this study. The thirteen primary prey taxa (≥ 5% FO) are highlighted.

	All Seasons	Summer (May-September)				Winter (December-April)			
	Rangewide	Reg-1	Reg-2	Reg-3	Reg-4	Reg-1	Reg-2	Reg-3	Reg-4
Total number scats containing identifiable prey	3,412	173	478	380	741	194	80	754	612
Cods: Gadidae									
Pacific cod (*Gadus macrocephalus*)	887	5	180	31	65	89	46	307	164
Walleye pollock (*Theragra chalcogramma*)	1,220	59	307	101	53	90	72	423	115
Pacific hake (*Merluccius productus*)	1	0	0	0	0	0	0	0	1
Saffron cod (*Eleginus gracilis*)	4	0	0	0	0	3	0	1	0
Unidentified gadid spp.*	57	7	9	8	5	3	0	16	9
Flatfishes: Pleuronectiformes									
Arrowtooth flounder (*Atheresthes stomias*)	380	51	61	17	7	63	11	164	6
Rock sole (*Lepidopsetta bilineata*)	340	2	145	15	9	16	2	107	44
Yellowfin sole (*Limanda aspera*)	4	0	3	0	0	0	0	1	0
Pacific halibut (*Hippoglossus stenolepis*)	126	5	14	2	2	25	2	74	2
Starry flounder (*Platichthys stellatus*)	19	0	15	0	0	1	2	1	0
Sand sole (*Psettichthys melanostictus*)	3	0	0	0	0	1	0	2	0
Butter sole (*Isopsetta isolepis*)	1	0	0	0	0	0	0	1	0
Rex sole (*Glyptocephalus zachirus*)	5	0	0	0	0	0	0	5	0
Flathead sole (*Hippoglossoides elassodon*)	32	0	15	0	0	3	1	13	0
Bering flounder (*Hippoglossoides robustus*)	5	0	1	0	0	0	0	4	0
Dover sole (*Microstomus pacificus*)	13	2	5	0	0	1	0	5	0
English sole (*Parophrys vetulus*)	3	0	0	0	0	0	0	3	0
Alaska plaice (*Pleuronectes quadritubercul*)	3	0	3	0	0	0	0	0	0
Longhead dab (*Limanda proboscidea*)	1	0	1	0	0	0	0	0	0
Unidentified flatfish spp.* (*Pleuronectidae*)	66	7	26	1	5	3	0	13	12
Greenlings: Hexagrammidae									
Atka mackerel (*Pleurogrammus monopterygius*)	1688	3	63	217	691	4	2	336	372
Rock greenling (*Hexagrammos lagocephalus*)	122	0	3	2	14	10	1	47	45
Masked greenling (*Hexagrammos octogrammus*)	6	0	0	0	1	2	0	2	0
Kelp greenling (*Hexagrammos decagrammus*)	16	0	3	0	0	1	1	6	5
W-S greenling (*Hexagrammos stelleri*)	1	1	0	0	0	0	0	0	0
unidentified Hexagrammidae sp.*	2	0	1	0	0	0	0	0	1
unidentified Hexagrammos spp.*	64	2	11	3	4	8	0	23	13
Herring: Clupeidae									
Pacific herring (*Clupea pallasi*)	211	19	70	92	0	24	1	4	1
American shad (*Alosa sapidissima*)	2	0	0	0	0	0	0	2	0
Sardine (*Sardinops sagax*)	3	0	0	0	0	2	0	0	1
Salmon: Salmonidae									
Pacific salmon (*Oncorhynchus* spp.)	940	112	218	143	145	59	13	193	57
Sandfishes: Trichodontidae									
Pacific sandfish (*Trichodon trichodon*)	8.4	0.58	26.2	2.6	0.94	13.9	6.3	11.9	3.8
Sand Lances: Ammodytidae									
Pacific sand lance (*Ammodytes hexapterus*)	738	38	295	50	36	78	22	216	3
Sculpins: Cottidae									

* Unidentified species were included in analyses only if they did not co-occur with identifiable species from the same family group. Scat containing only unidentifiable prey were not included in analyses.

Table 1. *cont.*	All Seasons	Summer (May-September)				Winter (December-April)			
	Rangewide	Reg-1	Reg-2	Reg-3	Reg-4	Reg-1	Reg-2	Reg-3	Reg-4
Irish lord sp. (*Hemilepidotus* sp.)	588	0	89	9	42	34	3	257	154
Crested sculpin (*Blepsias bilobus*)	2	0	0	0	0	0	0	0	2
Great sculpin (*Myoxocephalus polyacanthocephalus*)	1	0	1	0	0	0	0	0	0
Shorthorn sculpin (*Myxocephalus scorpius*)	1	0	0	1	0	0	0	0	0
Warty sculpin (*Myoxocephalus verrucosus*)	1	0	1	0	0	0	0	0	0
Tidepool sculpin (*Oligocottus maculosus*)	8	0	1	0	0	2	0	4	1
Prickly sculpin (*Cottus asper*)	1	0	0	0	0	0	0	1	0
Shortmast sculpin (*Nautichthys robustus*)	1	0	0	1	0	0	0	0	0
Northern sculpin (*Icelinus borealis*)	2	0	0	0	0	1	0	1	0
Blacknose sculpin (*Icelus canaliculatus*)	2	0	0	0	0	1	0	1	0
Threaded sculpin (*Gymnocanthus pistilliger*)	5	0	0	0	0	0	0	2	3
Warty sculpin (*Myoxocephalus verrucosus*)	1	0	1	0	0	0	0	0	0
Gymnocanthus sp.	7	0	2	0	0	1	0	2	2
unidentified sculpin spp.*	26	0	1	0	2	6	2	7	8
Sculpins:Hemitripteridae									
Sea raven (*Hemitripterus villosus*)	2	1	0	0	0	0	0	1	0
Snailfishes: Liparididae	196	0	3	3	7	9	0	110	64
Smelts: Osmeridae									
Capelin (*Mallotus villosus*)	47	17	14	0	0	8	0	4	4
Eulachon (*Thaleichthys pacificus*)	19	1	8	1	0	8	0	1	0
unidentified smelt spp.*	2	1	1	0	0	0	0	0	0
Cartilaginous fishes: Chondrichthyes									
Dogfish (*Squalus acanthias*)		0	0	0	0	2	0	0	0
Skates (*Raja* sp.)	139	3	59	1	8	8	1	4	55
Cat sharks: Scylinorhinidae	15	0	1	0	0	4	1	8	1
unidentified shark spp.*	1	0	1	0	0	0	0	0	0
Rockfishes and scorpionfish: Scorpaenidae									
Rockfish (*Sebastes* sp.)	269	14	37	8	27	18	0	62	103
Gunnels: Pholididae									
Penpoint gunnel (*Apodichthys flavidus*)	2	0	0	0	0	0	0	2	0
Crescent gunnel (*Pholis laeta*)	9	0	1	0	0	2	0	6	0
unidentified gunnel spp.*	22	0	4	0	3	1	0	10	4
Poachers: Agonidae									
Sturgeon poacher (*Podothecus acipenserinus*)	1	0	1	0	0	0	0	0	0
unidentified poacher spp.*	56	0	49	0	2	0	0	5	0
Eelpouts: Zoarcidae									
Marbled eelpout (*Lycodes raridens*)	1	0	0	0	0	0	0	1	0
eelpout spp.*	1	0	1	0	0	0	0	0	0
Ronquils: Bathymasteridae									
Ronquil sp. (*Bathymaster signatus*)	8	0	0	0	0	2	0	4	2
Ronquil sp. (*Ronquilus jordani*)	5	0	0	0	0	0	0	4	1
unientified ronquil spp.*	12	0	1	0	0	1	0	8	2
Prickleback: Stichaeidae/Cottidae									
Black prickleback (*Xiphister atropurpures*)	6	0	3	0	0	0	0	3	0
High cockscomb (*Anoplarchus purpurescens*)	15	0	0	0	2	1	0	8	4
Rock prickleback (*Xiphister mucosus*)	1	0	0	0	0	0	0	1	0
Arctic shanny (*Stichaeus punctatus*)	2	0	1	0	1	0	0	0	0

* Unidentified species were included in analyses only if they did not co-occur with identifiable species from the same family group. Scat containing only unidentifiable prey were not included in analyses.

Table 1. *cont.*	All Seasons	Summer (May-September)				Winter (December-April)			
	Rangewide	Reg-1	Reg-2	Reg-3	Reg-4	Reg-1	Reg-2	Reg-3	Reg-4
Decorated warbonnet (*Chirolophis decoratus*)	1	0	0	0	0	1	0	0	0
Shortspine thornyhead (*Sebastolobus alascanus*)	1	0	0	0	0	0	0	0	1
Snake prickleback (*Lumpenus sagitta*)	1	0	0	0	0	0	0	1	0
Slender eelblenny (*Lumpenus fabricii*)	2	0	0	0	0	0	0	0	2
Stone cockscomb (*Alectrias alectrolophus*)	1	0	0	0	0	0	0	0	1
unidentified prickleback spp.*	21	0	0	0	2	0	0	16	3
Tubesnouts: Aulorhynchidae									
Tubesnout (*Aulorhynchus flavidus*)	2	0	0	0	1	0	0	1	0
Lampreys: Petromyzontidae									
Lamprey (*Lampetra* spp.)	7	0	1	3	0	0	0	1	2
Lanternfishes: Myctophidae									
Northern lampfish (*Stenobrachius leucopsarus*)	29	0	0	2	2	2	0	2	21
(Stenobrachius sp.)	4	0	0	0	4	0	0	0	0
Northern flashlight fish (*Protomyctophum thompsoni*)	1	0	0	1	0	0	0	0	0
unidentified myctophid spp.*	10	0	0	2	6	0	0	0	2
Prowfishes: Zaproridae									
Prowfish (*Zaprora silensus*)	7	0	0	0	7	0	0	0	0
Sablefishes: Anoplopomatidae									
Sablefish (*Anopoploma fimbria*)	12	0	1	0	1	5	0	3	2
Wolffishes: Anarhichadidae									
Bering wolffish (*Anarhichas orientalis*)	1	0	0	0	0	0	0	1	0
Wolf eel (*Anarrichthys ocellatus*)	1	0	0	0	0	0	0	0	1
wolffish sp.*	3	0	2	0	0	0	0	1	0
Lancetfishes: Alepisauridae									
Longnose lancet (*Alepisaurus ferox*)	1	0	0	0	0	0	0	1	0
Sticklebacks: Gasterosteidae									
Threespine stickleback (*Gasterosteus aculeatus*)	48	0	43	0	0	0	0	4	1
Lumpfishes: cyclopteridae									
Smooth lumpsucker (*Aptocyclus ventricosus*)	164	0	2	3	1	6	1	79	72
Eumicrotremus sp.	3	0	0	0	0	0	0	0	3
Deep sea smelts: Bathylagidae									
Northern smoothtongue (*Leuroglossus schmidti*)	15	0	0	7	2	1	0	2	3
Codling: Moridae									
codling sp.*	2	0	0	0	0	0	0	0	2
Squid and Octopus: Cephalopoda									
(*Rossia pacifica*)	3	0	0	0	0	2	0	0	1
(*Enteroctopus dofleini*)	33	7	8	2	5	4	0	4	3
(*Japatella diaphana*)	10	1	0	0	5	0	0	2	2
(*Chiroteuthis calyx*)	1	0	0	0	0	0	0	0	1
Gonatidae sp.	141	3	0	15	65	3	0	13	42
Octopus sp.	25	3	2	0	4	5	0	3	8
Squid sp.	26	0	2	3	9	0	0	2	10
unidentified cephalopod	30	1	4	4	1	1	1	9	9
Bird/Mammal	4	0	0	0	1	1	0	2	0
Polychaete	302	0	59	32	75	10	2	61	53

* Unidentified species were included in analyses only if they did not co-occur with identifiable species from the same family group. Scat containing only unidentifiable prey were not included in analyses.

Table 2a. Significance of seasonal Frequency of Occurrence (FO) values of primary prey in Steller sea lion *(Eumetopias jubatus)* diets between decades within diet Regions 1 – 4. The thirteen primary prey were those that occurred in ≥ 5% of all scats collected at any location or season.

		Summer Percent Frequency of Occurrence (FO)													
		Years	Arrowtooth flounder	Atka mackerel	Cephalopods	Irish Lord	Pacific cod	Pacific herring	Pacific sand lance	Pacific sandfish	Rock sole	Rockfish	Salmon	Snailfish	Walleye pollock
Area	Diet Region 1	1990 - 1998	35.27	0	3.73	0.41	4.98	7.05	9.54	1.24	0.83	1.24	41.08	0.41	63.9
		1999 - 2009	29.65	1.74	7.56	0	2.91	11.05	22.09	0.58	1.16	8.14	65.12	0	34.3
		p =	*1*	*1*	*1*	*1*	*1*	*1*	*0.05*	*1*	*1*	*0.1*	*0.1*	*1*	*0.05*
	Diet Region 2	1990 - 1998	10.41	1.58	0.95	10.09	11.04	11.36	24.92	6.31	8.83	3.15	44.48	0.32	79.81
		1999 - 2009	12.76	13.18	2.93	18.62	37.66	14.64	61.72	26.15	30.33	7.74	45.61	0.63	64.23
		p =	*1*	*0.01*	*1*	*0.1*	*0.001*	*1*	*0.001*	*0.1*	*0.01*	*1*	*1*	*1*	*0.1*
	Diet Region 3	1990 - 1998	3.11	26.4	5.91	4.04	6.21	31.99	1.86	0.31	4.66	0.61	35.4	0	54.04
		1999 - 2009	4.47	57.64	6.43	2.41	7.77	23.06	13.4	2.68	4.02	2.14	37	0.8	26.54
		p =	1	0.001	1	1	1	1	0.01	1	1	1	1	1	0.001
	Diet Region 4	1990 - 1998	0.45	91.88	18.34	4.7	6.78	0.54	0.99	0.18	0.45	2.62	15.27	0.54	9.76
		1999 - 2009	0.94	93.26	11.1	4.92	7.72	0	2.95	0.84	1.26	3.79	19.66	0.84	6.04
		p =	1	1	0.05	1	1	1	1	1	1	1	1	1	1

		Winter percent Frequency of Occurrence (FO)													
		Years	Arrowtooth flounder	Atka mackerel	Cephalopods	Irish Lord	Pacific cod	Pacific herring	Pacific sand lance	Pacific sandfish	Rock sole	Rockfish	Salmon	Snailfish	Walleye pollock
Area	Diet Region 1	1990 - 1998	20.44	4.97	5.25	13.53	28.45	21.27	16.57	5.52	11.05	3.59	11.05	10.5	53.04
		1999 - 2009	32.47	2.06	6.7	17.53	45.88	12.37	40.21	13.92	8.25	9.28	30.41	4.64	46.39
		p =	*0.1*	*1*	*1*	*1*	*0.05*	*1*	*0.01*	*1*	*1*	*1*	*1*	*1*	*1*
	Diet Region 2	1990 - 1998	7.52	3.92	1.8	8.5	35.95	3.1	8.33	6.21	6.7	3.1	8.82	5.39	85.46
		1999 - 2009	13.75	2.5	1.25	3.75	57.5	1.25	27.5	6.25	2.5	0	16.25	0	90
		p =	*0.1*	*1*	*1*	*1*	*0.01*	*1*	*0.01*	*1*	*1*	*1*	*1*	*1*	*1*
	Diet Region 3	1990 - 1998	4.41	24.69	3.35	16.4	19.58	0.71	1.41	14.29	2.12	6.35	17.28	11.29	59.08
		1999 - 2009	21.81	44.42	3.94	33.78	40.6	1.31	28.38	11.83	14.06	8.14	26.02	14.45	55.85
		p =	*0.001*	*0.01*	*1*	*0.01*	*0.01*	*1*	*0.001*	*1*	*0.001*	*1*	*1*	*1*	*1*
	Diet Region 4	1990 - 1998	2.7	64.86	9.46	12.84	16.89	0	0	0.68	2.7	3.38	23.65	11.49	2.7
		1999 - 2009	0.98	60.78	10.95	25.16	26.8	0.16	0.49	3.76	7.19	16.83	9.31	10.46	18.79
		p =	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*0.1*	*1*	*1*	*0.05*

Table 2b. Significance of seasonal Frequency of Occurrence (FO) values of primary prey in Steller sea lion *(Eumetopias jubatus)* diets between decades within areas of fishery conservation (RCA) zones 1 – 9. The thirteen primary prey were those that occurred in ≥ 5% of all scats collected at any location or season

Summer Percent Frequency of Occurrence (FO)														
Area	Years	**Arrowtooth flounder**	**Atka mackerel**	**Cephalopods**	**Irish Lord**	**Pacific cod**	**Pacific herring**	**Pacific sand lance**	**Pacific sandfish**	**Rock sole**	**Rockfish**	**Salmon**	**Snailfish**	**Walleye pollock**
RCA 9	1990 - 1998	41.18	0	5.88	0.98	2.94	12.75	15.69	1.96	0.98	1.96	43.14	0.98	50.98
	1999 - 2009	55.15	1.21	2.12	11.21	26.67	38.18	53.64	13.33	19.39	5.15	18.18	1.21	41.52
	p =	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
RCA 8	1990 - 1998	30.56	0	2.78	0	6.25	2.78	4.86	0.69	0.69	0.69	38.19	0	73.61
	1999 - 2009	48.77	1.64	5.74	13.11	20.08	10.25	33.2	8.61	22.95	5.74	27.46	1.23	43.03
	p =	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*0.1*	*1*	*1*	*1*
RCA 7	1990 - 1998	11	1.78	0.71	6.38	9.93	3.19	18.44	0.71	1.42	3.55	45.74	0.36	80.14
	1999 - 2009	15.45	15.87	2.92	15.45	31.32	3.13	51.36	5.85	12.53	9.81	46.56	0	54.7
	p =	*1*	*0.001*	*1*	*1*	*0.001*	*1*	*0.05*	*1*	*0.05*	*0.1*	*1*	*1*	*0.05*
RCA 6	1990 - 1998	2.94	30.64	5.89	6.62	7.35	33.09	8.09	4.66	9.56	1.47	34.07	0	50.49
	1999 - 2009	8.54	48.39	4.2	18.65	24.19	12.28	32.13	15.96	18.35	7.12	29.36	1.8	35.66
	p =	*0.1*	*0.05*	*1*	*1*	*0.01*	*1*	*0.001*	*1*	*0.1*	*1*	*1*	*1*	*0.05*
RCA 5	1990 - 1998	0	91.39	15.31	2.87	4.31	0	1.44	0	2.39	0.48	10.05	0	10.53
	1999 - 2009	1.08	98.39	11.29	4.84	9.68	0	9.14	2.15	0.54	1.08	7.53	1.08	12.9
	p =	*1*	*0.05*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
RCA 4	1990 - 1998	0.83	83.33	23.33	2.08	7.08	0	1.25	0.83	0	4.17	39.17	1.67	27.92
	1999 - 2009	0.71	90.78	14.18	11.35	6.38	0	1.42	0.71	3.55	4.97	41.13	2.84	8.51
	p =	*1*	*1*	*1*	*0.05*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*0.1*
RCA 3	1990 - 1998	1.14	98.86	31.06	2.65	3.03	0.38	0	0	0	2.65	9.85	0	6.06
	1999 - 2009	0	99.29	21.99	2.13	2.13	0	0.71	0	0	0	23.4	0	0.71
	p =	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*0.1*
RCA 2	1990 - 1998	0	94.8	13.29	5.2	13.87	0	1.16	0	0	1.73	14.45	1.16	0
	1999 - 2009	0	87.9	4.03	3.23	5.65	0	0.81	0	0	2.42	6.45	0	0
	p =	*1*	*1*	*0.1*	*1*	*0.1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
RCA 1	1990 - 1998	0	94.86	10.29	9.71	7.14	0	1.14	0	0	1.14	5.43	0.29	2.86
	1999 - 2009	3.08	90.77	4.62	3.08	13.85	0	3.08	0	1.54	13.85	9.23	0	1.54
	p =	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*0.05*	*1*	*1*	*1*

Table 2b. *cont.*

		Winter percent Frequency of Occurrence (FO)												
Area	Years	**Arrowtooth flounder**	**Atka mackerel**	**Cephalopods**	**Irish Lord**	**Pacific cod**	**Pacific herring**	**Pacific sand lance**	**Pacific sandfish**	**Rock sole**	**Rockfish**	**Salmon**	**Snailfish**	**Walleye pollock**
RCA 9	1990 - 1998	24.44	1.85	4.82	12.22	31.48	19.63	18.52	5.91	4.82	2.96	12.22	10.74	57.04
	1999 - 2009	33.95	2.47	6.79	19.75	51.85	14.81	46.91	16.05	8.64	9.88	36.42	5.56	36.42
	p =	*1*	*1*	*1*	*0.1*	*0.1*	*1*	*0.01*	*1*	*1*	*0.1*	*1*	*1*	*0.05*
RCA 8	1990 - 1998	18.42	7.9	9.21	19.74	44.74	14.47	7.9	0	2.63	17.11	15.79	10.53	82.89
	1999 - 2009	25	0	6.25	6.25	15.63	0	6.25	3.13	6.25	6.25	0	0	96.88
	p =	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
RCA 7	1990 - 1998	7.55	3.54	1.18	8.49	34.91	2.12	8.49	2.12	6.37	1.42	8.96	3.54	83.49
	1999 - 2009	13.75	2.5	1.25	3.75	57.5	1.25	27.5	6.25	2.5	0	16.25	0	90
	p =	*0.1*	*1*	*1*	*1*	*0.01*	*1*	*0.01*	*1*	*1*	*1*	*1*	*1*	*1*
RCA 6	1990 - 1998	3.5	21.74	3.22	13.45	21.43	0.56	2.38	15.41	3.5	5.32	17.51	10.36	62.75
	1999 - 2009	21.75	44.56	3.98	34.08	40.72	0.53	28.65	11.94	14.19	8.22	25.6	14.59	56.1
	p =	*0.001*	*0.001*	*1*	*0.001*	*0.01*	*1*	*0.001*	*1*	*0.001*	*1*	*1*	*0.1*	*1*
RCA 5	1990 - 1998	6	64.18	7.46	19.4	17.91	0	0	1.5	4.48	2.99	8.96	22.39	2.99
	1999 - 2009	1.44	79.5	14.39	19.42	12.23	0	0.36	4.68	2.85	6.12	6.84	9.35	6.84
	p =	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*

* due to samples size restrictions, GLM calculations of the significance of winter prey FO changes between decades within the narrow zones of RCA 1 - 4 are unavailable.

Table 3. Shannon-Weiner diversity (H') scores and students t-test significance of seasonal Frequency of Occurrence (FO) values of 13 primary prey in Steller sea lion *(Eumetopias jubatus)* diet. Diversity was compared within diet Regions 1 – 4, between 1990 – 1998 and 1999 - 2009, across the study area.

	Summer					**Winter**				
	1990 - 1998	N	1999 - 2009	N	T-TEST, *p*	1990 - 1998	N	1999 - 2009	N	T-TEST
Region 1	1.897	241	2.238	173	0.01	3.223	358	3.475	194	0.5
Region 2	2.469	317	3.478	478	0.07	2.253	612	1.926	80*	0.00*
Region 3	2.259	322	2.586	380	0.6	2.702	567	3.654	754	0.08
Region 4	1.487	1225	1.536	741	0.9	2.098	148	2.71	612	0.3

*low sample size limited a meaningful comparison of diversity between periods for winter in Region 2

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