

A re-examination of the relationship between Steller sea lion (*Eumetopias jubatus*) diet and population trend using data from the Aleutian Islands

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Abstract: Prey diversity and energy density have been linked to each other and to population trends in many studies of bird and mammal diets. We re-examined these relationships in Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) using data collected from the Aleutian Islands, where there has been a strong longitudinal gradient in population trend. Diet diversity and energy density metrics were similar in the western Aleutians, where sea lion counts declined consistently, and in the easternmost Aleutian area, where population trends improved significantly. We compared traditional deterministic diet diversity metrics with diversity scores based on an occupancy model that accounts for differences in sample size and uncertainty in prey group detection. This analysis indicated that there was no significant change in diet diversity over the 23-year study period or any significant differences across the Aleutian Islands. These results are consistent with prey abundance data from nine groundfish bottom trawl surveys conducted over the same period. While diet studies detail what Steller sea lions eat and provide an estimate of their energy intake, they provide only limited information on the energy expended to obtain their food or the consequences of their diet and foraging ecology on individual or population fitness.

Key words: Steller sea lion, *Eumetopias jubatus*, diet, diet diversity, diet energy density, population dynamics, Aleutian Islands.

Résumé : La diversité des proies et la densité énergétique ont été reliées l'une à l'autre et à des tendances démographiques dans de nombreuses études sur les régimes alimentaires d'oiseaux et de mammifères. Nous avons réexaminé ces relations chez les otaries de Steller (*Eumetopias jubatus* (Schreber, 1776)) en utilisant des données recueillies dans les îles Aléoutiennes, où la tendance démographique définit un important gradient longitudinal. Les mesures de la diversité du régime alimentaire et de la densité énergétique étaient similaires dans l'ouest des Aléoutiennes, où le nombre d'otaries avait uniformément diminué, et dans l'extrême est de l'archipel, où les tendances démographiques s'étaient significativement améliorées. Nous avons comparé des mesures déterministes traditionnelles de la diversité des régimes alimentaires à des notes de diversité reposant sur un modèle d'occupation qui tient compte des variations de la taille des échantillons et de l'incertitude associée à la détection des groupes de proies. L'analyse indique qu'il n'y a pas eu de changement significatif de la diversité des régimes alimentaires au cours des 23 années de l'étude, ou de variations spatiales significatives à l'échelle des îles Aléoutiennes. Ces résultats concordent avec des données sur l'abondance de proies de neuf évaluations des poissons démersaux au chalut de fond menées durant la même période. Si les études des régimes alimentaires décrivent ce que les otaries de Steller mangent et fournissent une estimation de leur apport énergétique, elles ne fournissent qu'une information limitée sur l'énergie qu'elles dépensent pour obtenir leur nourriture ou les conséquences de leur régime alimentaire et de l'écologie de leur approvisionnement sur l'aptitude individuelle ou de la population. [Traduit par la Rédaction]

Mots-clés : otarie de Steller, *Eumetopias jubatus*, régime alimentaire, diversité des régimes alimentaires, densité énergétique du régime alimentaire, dynamique des populations, îles Aléoutiennes.

Introduction

Diversity is a commonly calculated index in diet studies of free-ranging predators. It has been related to population performance in both negative and positive ways depending on the circumstances. Diet diversity and fledging success of Montagu's Harriers (*Circus pygargus* (Linnaeus, 1758)) were negatively correlated: when hares (*Lepus granatensis* Rosenhauer, 1856), their preferred prey, were less abundant, nest failures were more common as parents expended greater energy to find a wider variety of prey to feed

their young (Arroyo and Garcia 2006). When specialists are forced to diversify their diets, this often results in diets with lower overall energy densities than if they primarily consumed their preferred prey (Bose and Guidali 2001). Therefore, diet diversity may be a less important correlate for population performance than diet energy density (Winship and Trites 2003; Gomez et al. 2016). However, switching to a diverse, lower energy diet can provide some specialists with enough nutrition to survive periods when preferred prey is scarce, a strategy used by maned wolves (*Chrysocyon*

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cyon *brachyurus* (Illiger, 1815)) during wet seasons when they eat more fruits and insects to withstand periods of low availability of small mammals (Bueno and Motta-Junior 2006).

By definition, an opportunist has a more flexible foraging strategy than a specialist, presumably developed in response to changes in the availability of prey during annual migratory and reproductive cycles, as well as interannual changes in prey availability over the course of its lifetime. As such, it could be expected that opportunist populations (as well as individual fitness) may be buffered more from changes in prey availability than specialists (Merrick et al. 1997; Trites et al. 2007a). Temporal and spatial variation in diet diversity and energy density may be the norm as individuals react to ever-changing prey fields, reflecting variability in lower trophic level recruitment and the biogeography of prey species.

Diet diversity has also been used to delineate specialists from opportunists and to describe variation in diet related to habitat or along spatial-temporal gradients in response to environmental or anthropogenic changes. For a feeding specialist, a predator that consistently consumes only a few preferred species, diet diversity overall would be expected to be low but would increase as the availability or abundance of preferred species declined (Futuyma and Moreno 1988; Diaz-Ruiz et al. 2013). An opportunist is a predator that consumes suitable prey largely in proportion to their encounter probabilities or abundances. The diversity of an opportunist's diet across its range reflects the diversity of the various prey fields and would be expected to decrease in habitats where a few suitable prey species were highly abundant. Conversely, diet diversity of an opportunist would be expected to increase if the availability of an abundant suitable prey dropped (in the absence of another abundant species). Therefore, for both specialists and opportunists, diet diversity would be expected to increase as the availability of the preferred or most abundant prey species declined, respectively. Given that the expected response to changes in the prey field is the same, diet diversity indices alone may have limited ability to delineate foraging strategies.

Diets of migratory opportunistic predators reflect the prey available to them as they occupy different habitats throughout the year; thus, diversity indices calculated at any single point may have little association with population performance. Diets of Pribilof Islands northern fur seals (*Callorhinus ursinus* (Linnaeus, 1758)) reflect the numerous prey fields that they encounter along their >20 000 km annual migration from summer Bering Sea breeding grounds around the North Pacific Ocean in the fall, winter, and spring (Kajimura 1984; Ream et al. 2005). The diversity of their diets is low when they concentrate on locally aggregated (but relatively energy dense) prey available at certain times and places during their migration. This includes, for example, overwintering and pre-spawning Pacific herring (*Clupea pallasii pallasii* Valenciennes, 1847) in January to April off the Washington–British Columbia coast or pre-spawning Pacific sand lance (*Ammodytes hexapterus* Pallas, 1814) in May to June in the Gulf of Alaska (Kajimura 1984). Diet diversity increases in the summer when they feed in the eastern Bering Sea, one of the most productive marine ecosystems in the world (Loughlin et al. 1999).

The relationship between diet diversity and regional population trends of the Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)),¹ an opportunistic predator, has been the subject of two previous studies in Alaska. The first, Merrick et al. (1997), found a positive relationship between summer (June–August) diet diversity (based on seven prey groups) and overall population changes

in a 5-year period in six Alaska areas spanning the Aleutian Islands through the central Gulf of Alaska (Kodiak archipelago). Populations declined between 20% and 50% overall in five of the six regions and were essentially stable in the sixth (Merrick et al. 1997). The second study, Trites et al. (2007a), built upon Merrick et al. (1997) by adding a seventh analysis area (southeast Alaska), where sea lions were increasing, and an eighth prey group and by using a different definition of diversity. This study also found a positive relationship between population change and diet diversity but also limited the scope to the summer diet. Merrick et al. (1997) hypothesized that high diet diversity led to improved Steller sea lion population performance because of increased foraging efficiency rather than higher energy density: “diverse prey is easier to find (more prey patches), capture (patch densities are increased), and handle (prey size is correct).” Trites et al. (2007a) supported this conclusion but also, along with Winship and Trites (2003), more directly linked diversity, “quality” (energy density), and population performance. Diverse diets composed of a suite of species with both low and high energy densities could make sea lions less sensitive to changes in overall prey abundance or availability, enable them to satisfy their energy requirements more easily, and spend less time foraging (which would decrease their vulnerability to predation). However, a serious limitation of these studies is the lack of consideration of the non-summer diet, which represents approximately two-thirds of the year and is arguably the most energetically expensive given the reproductive life history of Steller sea lions and the challenging sub-Arctic weather in Alaska that occurs during this time of the year (Winship et al. 2002; Winship and Trites 2003; Rodionov et al. 2005; Williams 2005).

As with northern fur seal diets along their migratory route, Steller sea lion diets across their vast breeding range reflect local prey fields and the biogeography of fish and cephalopods (Sinclair and Zeppelin 2002; Sinclair et al. 2013). An issue not considered by Merrick et al. (1997) or Trites et al. (2007a) was the diversity and composition of prey communities across the ~4000 km of southern Alaska in which they studied sea lion diets. In general, numbers of fish species decrease from east to west across the Gulf of Alaska and the Aleutian Islands (Mueter and Norcross 2002; Logerwell et al. 2005), and the trend in Steller sea lion diet diversity was the same across that range. Therefore, given the underlying longitudinal trends in fish community structure, are diet diversity and population trend in Steller sea lions actually related?

In this study, we re-examine the relationship between Steller sea lion diet (based on analyses of hard parts sieved from almost 3000 scats collected over a 23-year period) and population trend in the Aleutian Islands (Alaska) west of Samalga Pass (Fig. 1). We also include an examination of the underlying fish community structure. The limitations of dietary quantifications by the hard parts in pinniped scat are well described (Pierce and Boyle 1991) and we therefore confined core analyses (related to diet and trend) to high-level prey occurrence results in subsets of sufficient sample size. Samalga Pass is a major biogeographical boundary delineating the eastern boundary of the Aleutian marine ecosystem (Logerwell et al. 2005), which is less productive and diverse than that of the Gulf of Alaska to the east (Mueter and Norcross 2002). For Steller sea lions, Samalga Pass also separates “stocks” on the basis of mtDNA haplotype frequencies (O’Corry-Crowe et al. 2014) and diets (Sinclair and Zeppelin 2002; Sinclair et al. 2013). Within the Aleutian Islands, however, there is a strong longitudinal gradient in Steller sea lion population trends, with steep declines in

¹There are two stocks, or distinct population segments, of the Steller sea lion: eastern (*Eumetopias jubatus monteriensis*; Phillips et al. 2009), which breeds on rookeries east of 144°W in the United States (southeast Alaska, Washington, Oregon, and California) and Canada (British Columbia), and western (*Eumetopias jubatus jubatus*), which is defined as the population west of 144°W in the United States (southern and western Alaska, including the Aleutian Islands) and Russia (National Marine Fisheries Service (NMFS) 2008; Fig. 1).

Fig. 1. (A) Distribution of terrestrial breeding sites (rookeries; Fritz et al. 2015) and at-sea habitat (cross-hatched area; Fritz et al. 2014) of the western distinct population segment (DPS) of Steller sea lion (*Eumetopias jubatus*) in Alaska and Russia. The study area in the Aleutian Islands is circled and the eastern boundary (Samalga Pass) is labeled. The boundary between the western and eastern DPSs is 144°W. (B) Detail of Aleutian Islands showing areas (1–5) used in the analysis of Steller sea lion diet and population trend; the eastern, central, and western bottom trawl survey (prey community) regions; locations of terrestrial haul-out and rookery sites where scats were collected during this study; and the 300 m isobath. (C) Estimated non-pup counts (with 95% credible intervals) by year (1990–2015) and area.

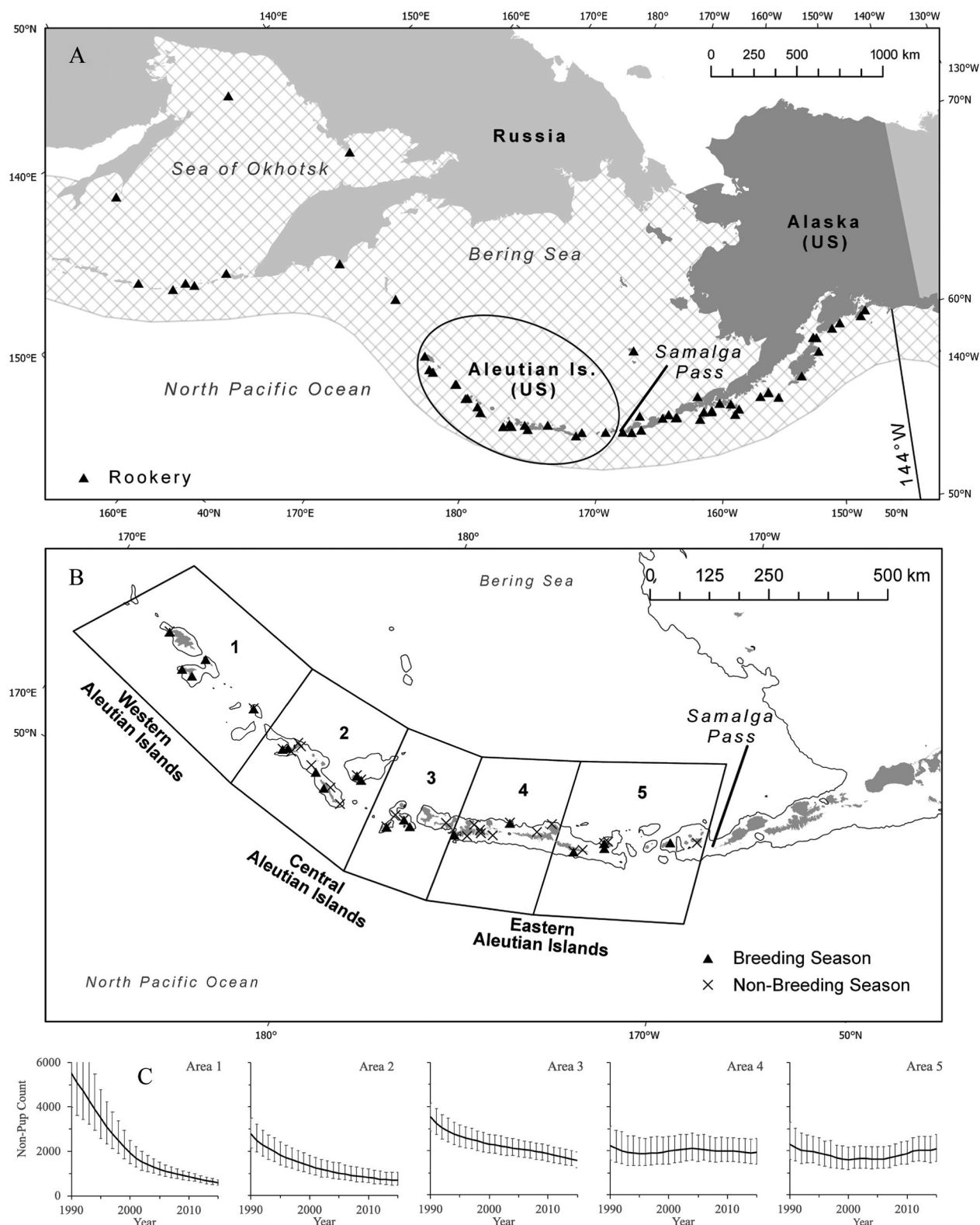


Table 1. Number of scats used in the analysis ($n = 2913$) out of the total number collected ($n = 3109$) at Steller sea lion (*Eumetopias jubatus*) terrestrial sites by decade, season, and area in the Aleutian Islands, 1990–2012.

| Decade | Season | Area | | | | | Total |
|--------|--------------|---------|---------|---------|---------|---------|-----------|
| | | 1 | 2 | 3 | 4 | 5 | |
| 1990s | Breeding | 342/364 | 183/201 | 280/287 | 267/282 | 201/221 | 1273/1355 |
| | Non-Breeding | 2/2 | 85/104 | 42/45 | 36/41 | 109/114 | 274/306 |
| 2000s | Breeding | 69/78 | 106/115 | 136/138 | 105/109 | 166/170 | 582/610 |
| | Non-Breeding | 23/23 | 73/80 | 98/109 | 284/303 | 306/323 | 784/838 |

Note: Decades: 1990s, 1990–1999; 2000s, 2000–2012.

the western Aleutians to recent positive trajectories in the eastern-central Aleutians (Fritz et al. 2016b). Thus, we chose to re-examine the relationship between annual (not solely summer) Steller sea lion diet and population trends in the Aleutian Islands as all necessary analytical components are contained within a single ecosystem, thus avoiding the confounding multi-ecosystem approach used by both Merrick et al. (1997) and Trites et al. (2007a).

There has been considerable recent research into the link between diet and the persistent (since at least the 1980s) decline in abundance of the Aleutian Island Steller sea lion population (Sinclair and Zeppelin 2002; Winship et al. 2002; Sease and York 2003; Winship and Trites 2003; Fadely et al. 2005; Lander et al. 2009, 2010; National Marine Fisheries Service (NMFS) 2010; Sinclair et al. 2013; Sweeney et al. 2016, 2017; Tollit et al. 2017). This study complements and builds in particular upon those of Sinclair and Zeppelin (2002), Sinclair et al. (2013), and Tollit et al. (2017) as all four used many of the same sea lion diet samples.

Materials and methods

We took a multipronged approach to examining the diet of Steller sea lions in the Aleutian Islands and its relationship to population trend. First, we determined prey prevalence in the diet samples and described seasonal, decadal, and regional diets through traditional deterministic metrics (frequency of occurrence, principal components analysis, hierarchical cluster analysis, and diversity; Merrick et al. 1997; Sinclair and Zeppelin 2002). Second, we developed new deterministic diet metrics to examine spatial and temporal patterns in diet energy density and Steller sea lion foraging strategies based on the number of unique combinations of prey items in the diet. Third, we developed a novel stochastic approach to estimate diet diversity using occupancy models (Mackenzie et al. 2002; Tyre et al. 2003) that accounted for prey detection uncertainty and scat sampling inequities. Fourth, we examined the temporal and spatial structure of the Steller sea lion prey community by analyzing data collected in the Aleutian Islands during groundfish bottom trawl surveys. Finally, Steller sea lion abundance data (counts of adults and juveniles, or non-pups, during the breeding season) were analyzed to test the hypothesis that there is no relationship between diet and population trend.

Steller sea lion diet was analyzed by examination of prey hard parts found in scats collected on land in the Aleutian Islands (from the Islands of Four Mountains at $\sim 170^\circ\text{W}$ through Attu Island at $\sim 173^\circ\text{E}$) between 1990 and 2012 (Table 1 and Fig. 1B; $n = 3109$). All methods for sample processing and prey identification were identical to those used by Sinclair and Zeppelin (2002). Individual scats were rinsed through nested sieves, and all retained hard parts were identified to the lowest possible taxonomic group based on diagnostic morphological criteria developed by Pacific IDentifications Inc. (scats collected through early 2008) or by the Marine Mammal Laboratory (scats collected in late 2008 through 2012, plus fish otoliths and cephalopod beaks from all years), both using comprehensive comparative reference skeletons (e.g., see Olesiuk et al. 1990). Scat samples with no prey remains and spew samples

collected concurrently with scat samples were not included in this study. Birds and mammals (11 occurrences) and polychaetes (219 occurrences) were never the sole hard parts found in any scats. These were treated as secondary prey or incidentally collected items and excluded from further dietary analysis following standard recommendations for scat reporting and bias limitation (Pierce and Boyle 1991; Tollit et al. 2010).

Seasons, decades, and areas were identified and used to classify diet and population trends for spatial-temporal analysis. Seasons were identified based on the Steller sea lion reproductive cycle (Pitcher and Calkins 1981). The breeding season (pupping and mating) of Steller sea lions is relatively short and synchronous, likely due to the strong seasonality of the environment in the Bering Sea and North Pacific Ocean and the need to balance aggregation for reproductive purposes with dispersion to avoid intraspecific competition for food resources (Bartholomew 1970). Adult males establish breeding territories on rookeries beginning in mid- to late May, followed shortly by the arrival of adult females. Parturition usually occurs within days of arrival at the rookery (between late May and mid-July), with the mean birth dates varying between 9 and 11 June within the Aleutian and Commander islands that “bookend” the longitudinal range of this study (170°W – 172°E ; Pitcher et al. 2001; Kuhn et al. 2017). We defined the breeding season as May–August, and the non-breeding season as September–April. We placed September in the non-breeding season because, by this time, the rookery structure has clearly dissolved and adult females have begun to take longer foraging trips, including relocating to different terrestrial sites with their young-of-the-year (Fadely et al. 2005). These definitions differ from those of Sinclair et al. (2013), who defined “summer” as May–September and “winter” as November–April, but only in which season September occurs. Regardless, $<2\%$ ($N = 54$) of all scats with identifiable prey analyzed in this study were collected in September.

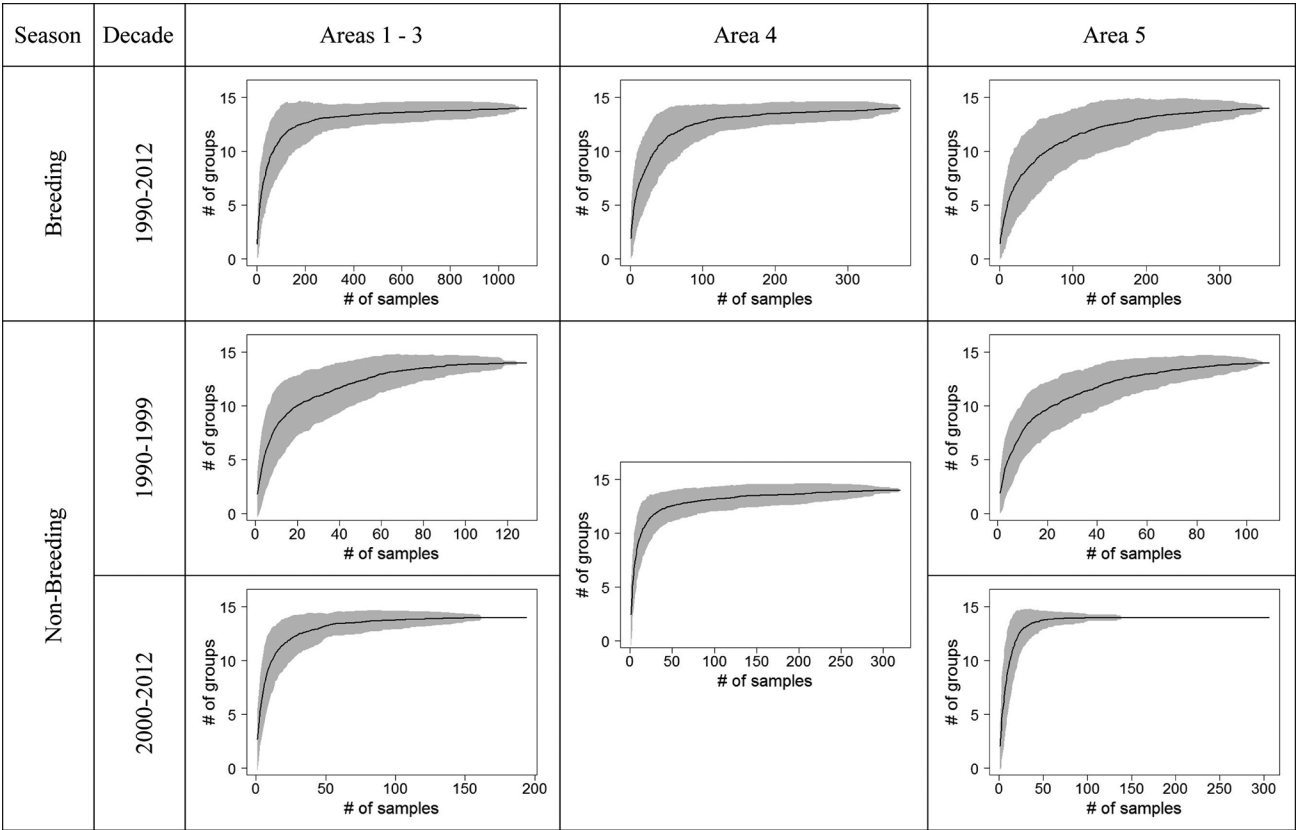
Decades were defined as 1990s (1990–1999) and 2000s (2000–2012). As with season, our decadal definitions differ slightly from those of Sinclair et al. (2013), who defined two “decades” as 1990–1998 and 1999–2008 to allow comparison of the latter period with the previous as summarized by Sinclair and Zeppelin (2002).

Areas in the Aleutian Islands were defined based on observed similarities in Steller sea lion population trends (Fig. 1B; Fritz et al. 2016b):

1. Aleutian Islands between 172°E and 177°E (Buldir Island and the Near Islands);
2. Aleutian Islands between 180° and 177°E (Rat Islands);
3. Aleutian Islands between 177°W and 180° (Kanaga, Tanaga, and the Delarof islands);
4. Aleutian Islands between 174°W and 177°W (Atka and Adak islands);
5. Aleutian Islands between $\sim 170^\circ\text{W}$ (Samalga Pass) and 174°W (Yunaska, Seguam, and Amlia islands).

The following basic statistics were derived from the prey identifications from scats:

Fig. 2. Accumulation curves (solid line \pm 2 standard deviations) of 14 Steller sea lion (*Eumetopias jubatus*) prey groups by season, decade, and area (1–3, 4, and 5). All years (1990–2012) were combined for the breeding season in each area and for the non-breeding season in area 4. Non-breeding season diets were analyzed separately by decade in areas 1–3 and 5.



(a) Frequency of occurrence (FO) for prey group O (prey groups are defined in Results) in area or site j in season k in decade l was calculated by dividing the number of scats containing a prey group by the total number of scats containing identified prey n_{jkl} :

$$FO_{jkl} = \left[\sum_{i=1}^{n_{jkl}} O_{ijkl} \right] / n_{jkl} \times 100$$

where O_{ijkl} is 1 if the group is present in sample i in collection (j, k, l) and 0 otherwise. Site, season, decade, or any combination could be omitted in the summation process to obtain FO across all sites for a season and decade, for both seasons in a decade, etc. FO values (expressed as a percentage) for a sampling unit will sum to a value different from 100 because some scats will contain more than one prey group.

- (b) Modified FO (MFO) is the FO for prey group O divided by the sum of FO for all prey groups in area or site j in season k in decade l (multiplied by 100). This provided a set of standardized FO values that summed to 100 for each sampling unit (e.g., area–season–decade combination) for statistical analysis, diversity index, and energy density calculations.
- (c) Diet diversity index for each area, season, and decade was calculated as the anti-log of the Shannon–Wiener index of heterogeneity $H' = -\sum (p_i \ln p_i)$, where p_i is the decimal MFO for each prey group. H' is a unitless measure that increases with increasing heterogeneity (e.g., diversity) of the sample (Preston 1948; Spellerberg and Fedor 2003). The anti-log of H' ($e^{H'}$) ranges from 0 to T , where T is the number of prey groups considered in the analysis (eight using Trites et al. (2007a) classifications and 14 in this study). An evenness

index (E , ranges from 0 to 1) for the diet in each area, season, and decade was calculated as H' divided by $\ln T$, which yields a unitless proportion of the maximum possible value for H' for each sample unit.

- (d) Foraging strategy diversity index (FSDI) was calculated for each area, season, decade, and overall by determining the number of unique combinations of prey groups and dividing it by the number of scats analyzed. This index ranges from 0 to 1 and is the proportion of all scats that had unique combinations of prey.

PERMANOVA was used to detect differences in the prevalence of each prey group in the diet by season, decade, and area. PERMANOVA is a nonparametric statistical test for comparing groups of multivariate data (Anderson 2001), and the vegan package (Oksanen et al. 2017) in R version 3.3.2 (R Core Team 2016) was used. The test is analogous to multivariate ANOVA but can be used with distance metrics commonly used in ecology (e.g., Bray–Curtis) and does not assume an underlying distribution for the data (e.g., multivariate normality). Data were FO values by area pooled by season, decade, or both.

Prey group accumulation curves by area, season, and decade (to test for sample size adequacy) were calculated using the vegan package (Oksanen et al. 2017) in R version 3.3.2 (R Core Team 2016; Fig. 2). For each dataset, sample order was randomized 100 times and the mean number of new prey groups (± 2 standard deviations) was plotted for each added sample. Sample size was deemed to be sufficient if the prey curve appeared to approach an asymptote and the variability decreased over the curve.

Seasonal energy density data for each prey group were obtained from R. Heintz (NMFS Alaska Fisheries Science Center, Auke Bay Laboratory; personal communication), Perez (1994), and Rosen and

Trites (2013; for Atka mackerel only) (Supplementary Table S1²). Energy density information was available for some species on a seasonal basis, but only for the Aleutian Islands region as a whole and not separately by decade. An energy density index was calculated for each diet by area (areas 1–3 combined, 4, and 5), season, and decade (except area 4 non-breeding season for which both decades were pooled) using energy density ($\text{kJ}\cdot\text{g}^{-1}$ dry mass) and MFOs of each prey taxon. Energy densities and MFOs of prominent members of the sculpin (Irish lords, genus *Hemilepidotus* Cuvier, 1829), flatfish (rock sole, *Lepidopsetta bilineata* (Ayres, 1855)), forage (each species considered separately), and snailfish–lumpsuckers (smooth lumpsucker, *Aptocyclus ventriosus* (Pallas, 1769)) groups were considered separately when developing the energy index. Annual energy density indices were calculated by weighting the non-breeding season twice the breeding season based on duration (8 months vs. 4 months, respectively).

Steller sea lion population trends by area were calculated using the method of Johnson and Fritz (2014) and counts of adult and juvenile Steller sea lions (non-pups) during the breeding season obtained through 2017 (Fig. 1C; Fritz et al. 2016a, 2016b; Sweeney et al. 2016, 2017).

Sinclair and Zeppelin (2002) and Sinclair et al. (2013) used a hierarchical cluster (HC) analysis of principal components (PC) scores to define regional boundaries that defined similar diets across most of southern Alaska. Within that broad spatial context, the entire Aleutian Islands fell out as a region distinct from areas to the east in Alaska. Our PC and HC analyses looked for similarities in diet within seasons and decades within the Aleutian Islands. The FO values for 14 prey groups for each collection were used as variables, regional groups of scat collection sites (to ensure a minimum of 30 scats per group) were used as observations (Supplementary Table S2),² and the data were pooled within site groups by season and decade as follows: (1) breeding season 1990–2012, (2) non-breeding season 1990–1999, and (3) non-breeding season 2000–2012. As in Sinclair and Zeppelin (2002), HC analysis was conducted on PC scores using squared Euclidian distance (Ludwig and Reynolds 1988) as a measure of similarity between scat collection sites (by season and decade) with 14 identified prey groups, and Ward's (1963) method was used to compare cluster distances. The R version 3.3.2 (R Core Team 2016) was used for all model analyses.

Estimates of biodiversity can be biased when not all species in a community are equally detectable or identifiable (Boulinier et al. 1998; Buckland et al. 2011; Colwell et al. 2012). When comparing diversity among sites, unbalanced sampling effort can also cause bias because additional surveys or samples translate to increased opportunity for detection (Colwell et al. 2012). Reliable estimates of Steller sea lion diet diversity require methods that address both issues. For example, cephalopods have few hard parts and are thus more difficult to detect after digestion than boney fish such as Atka mackerel (*Pleurogrammus monopterygius* (Pallas, 1810)) (Tollit et al. 2009, 2017). The number of sea lion scats collected within a year also varied by more than fivefold across areas. Although rarefaction and extrapolation have been used to address unequal sample sizes in diversity calculations (Colwell et al. 2012; Chao et al. 2014), these techniques do not account for imperfect detection.

We resolve issues related to imperfect detection and unbalanced sampling effort using a class of binomial mixture models referred to as “occupancy” models (Mackenzie et al. 2002; Tyre et al. 2003). Occupancy models rely on repeat sampling to estimate the true but partially unobserved occurrence of a species while controlling for the detrimental effect of imperfect detection. The approach further allows for unbalanced sampling effort because detections are modeled as a binomial random variable

(Appendix A); that is, the model describes the number of observed occurrences given the number of opportunities to detect a species (e.g., number of scat samples collected) and the probability of detection. Although occupancy models were originally developed for a single species, they have been updated to estimate the occurrence of multiple species simultaneously (Dorazio and Royle 2005; Dorazio et al. 2006). Moreover, estimation of species diversity (e.g., richness and Shannon's index) has been incorporated into the multispecies occupancy modeling framework, thus providing a unified approach to obtain diversity metrics that are free of bias from imperfect detection and unbalanced sampling effort (Dorazio and Royle 2005; Broms et al. 2015), issues that are not addressed by the traditional deterministic diet metrics above. In our analysis, multiple scat samples collected at the same site and within the same year and season serve as the replicates necessary to quantify Steller sea lion diet diversity while explicitly accommodating imperfect detection within the multispecies occupancy modeling framework.

We modeled species-specific occupancy (φ) as a function of season, region, and their interaction. Occupancy status must not change among replicate samples to ensure that probabilities of detection and occurrence are both uniquely identifiable (i.e., closure; Mackenzie et al. 2002). Although this is a reasonable assertion in many occupancy analyses, in our particular application, closure requires scat samples to contain the same prey items, an unlikely proposition given individual preferences for prey items and regional, yearly, and seasonal differences in prey availability. Consequently, the observation process in our analysis is related not only to species-specific detection probability, but also to Steller sea lion prey selection (i.e., the product of detection and selection probabilities). We denote this product of probabilities as π , which we let vary by species (to allow for differences in detection), as well as covariates affecting selection, namely year, season, region, and the interactive effects of year and season and year and region. See Appendix A for additional details concerning the multispecies occupancy model, including a full model specification and occupancy-based diversity calculations (Broms et al. 2015).

To characterize spatial and temporal patterns of Steller sea lion prey communities in the Aleutian Islands, we analyzed the results of nine summer bottom trawl surveys conducted between 1991 and 2012 (e.g., Zenger 2004; Rooper 2008; Rooper and Wilkins 2008; von Szalay et al. 2011). An average of ~400 stations were completed in each survey, and catch data from a total of 3591 successful hauls at stations < 301 m deep were included in the analysis. A total of 21 taxa (15 fish species, five fish groups, and one squid genus) were chosen from the Aleutian Islands groundfish survey catches to represent the potential SSL prey community found in these trawl hauls (Supplementary Table S3).² Eight taxa (Atka mackerel, *P. monopterygius*; Pacific cod, *Gadus macrocephalus* Tilesius, 1810; Pacific halibut, *Hippoglossus stenolepis* Schmidt, 1904; arrowtooth flounder, *Atheresthes stomias* (Jordan and Gilbert, 1880); rock sole (combined *L. bilineata* and northern rock sole, *Lepidopsetta polyxystra* Orr and Matarese, 2000); Pacific ocean perch, *Sebastes alutus* (Gilbert, 1890); northern rockfish, *Sebastes polyspinis* (Tarantetz and Moiseev, 1933); and walleye pollock, *Gadus chalcogrammus* Pallas, 1814) perennially dominated catches, corporately comprising 80%–90% of the total biomass within each area.

Regions used for prey community analysis reflect the stratified-random design of the bottom trawl survey and are not the same as areas 1–5 used to analyze Steller sea lion diet and trend. From west to east, bottom trawl survey regions consisted of the western Aleutian Islands (WAI, identical to area 1), the central Aleutian Islands (CAI, combined areas 2 and 3), and the eastern Aleutian Islands (EAI, combined areas 4 and 5; Fig. 1B). While this does not

²Supplementary tables and figure are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0329>.

permit area-by-area comparison of sea lion diet and fish community structure, the longitudinal structure is essentially the same, and regions with declining sea lion population trend (WAI and CAI) are considered separately from those with stable or increasing trends (EAI). There is no comparable time series of trawl survey data collected in the winter.

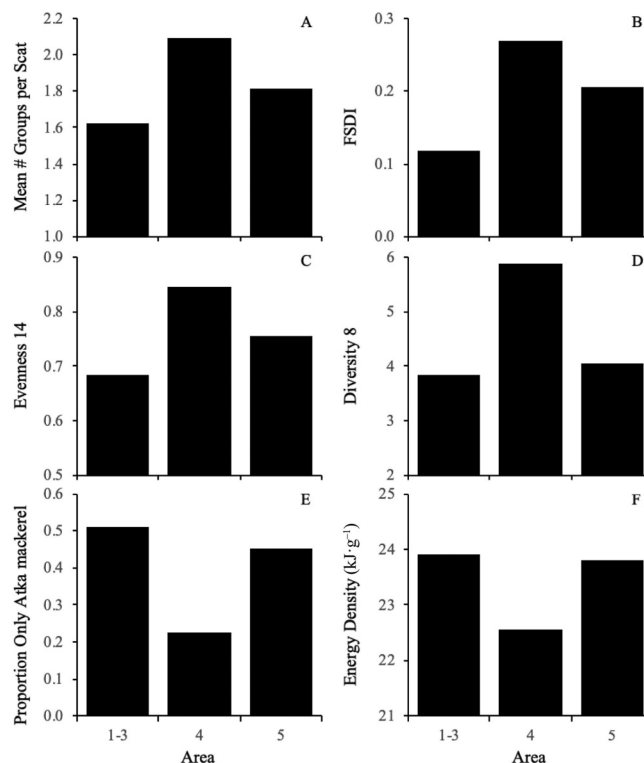
Prey presence and abundance data from bottom trawl surveys were analyzed using the vegan package in R (Oksanen et al. 2017). Nonmetric multidimensional scaling (nMDS; Faith et al. 1987; Minchin 1987) of Wisconsin double-standardized and square-root-transformed mean catch per unit effort (kilograms per area swept by the trawl) was used to quantify the Bray–Curtis similarity (Krebs 1989) between annual communities within trawl survey regions using the metaMDS function from the vegan package. Results of the nMDS are presented graphically as two-dimensional plots in ordination space in which the distance between annual community scores indicates their degree of similarity. A measure of the goodness of fit or stress (S) to the two-dimensional ordination was also calculated. Stress decreases as the rank-order agreement between distances and dissimilarities in the nMDS improves so that lower stress levels indicate better fit models. A nonparametric analysis of similarity (ANOSIM; Clarke 1993; Warton et al. 2012) was applied to the rank similarity matrix of untransformed station-level taxon presence and abundance data underlying the nMDS ordination to test the significance of the similarities among the annual communities within trawl survey regions. The ANOSIM test statistic (R) provides an absolute measure of compositional differences among groups (Bonelli and Patzkowski 2008) and usually ranges from 0 (indicating that the groups are indistinguishable) to 1 (indicating that the similarities within groups are distinct). Clarke and Gorely (2006) give the following thresholds for interpreting R : $R > 0.5$ indicates overlapping but clearly different groups; $R > 0.25$ indicates strongly overlapping groups; and $R < 0.25$ indicates groups that are barely distinguishable. Clarke and Warwick (2001) indicate that with a high number of samples, a very small R value can be significantly different from zero ($p \leq 0.05$) and still indicate that the separation between communities is not significantly different from random. An evenness statistic to estimate community diversity was also calculated for groundfish trawl survey data using the 21 prey taxa; means (\pm standard error (SE)) by decade and survey region are reported.

Results

Scat sample collection

Scats were collected during the months of February through September, but 96% were collected in March, April, June, July, and August. Frequency of occurrence (FO) of prey taxa in scat ($n = 3109$) was tabulated. A total of 77 prey taxa were identified: 35 to species, 14 to genus, 21 to family, three to order or super order, and four to class (Supplementary Table S3).² Prey taxa were grouped to allow for spatial-temporal analyses and comparisons with previous studies of Steller sea lion diet in Alaska. This resulted in 14 prey groups (Supplementary Table S3)² that consisted of three individual species (Atka mackerel, Pacific cod, and walleye pollock), one genus (rockfish *Sebastes*), one “forage” group (Pacific sand lance and Pacific sandfish, *Trichodon trichodon* (Tilesius, 1813)), and nine families or higher taxa (flatfish, Pleuronectiformes; lanternfish, Myctophidae; octopus, Octopoda; other greenlings, Hexagrammidae; salmon, Salmonidae; sculpins, Cottidae and Hemitriptidae; skates, Rajidae; combined snailfish, Liparidae, and lumpfishes, Cyclopteridae; and squid, Decapodiformes). Of the 5604 prey occurrences identified, 93% were in one of the 14 groups. Occurrences of unidentified bony fish and other trace (FO < 1%) fish or cephalopod taxa were excluded from the data analyzed (Supplementary Table S3).² Unidentified Gadidae (61 occurrences; FO = 2%) were likely either Pacific cod or walleye pollock and were excluded to avoid the potential for overcounting gadid presence

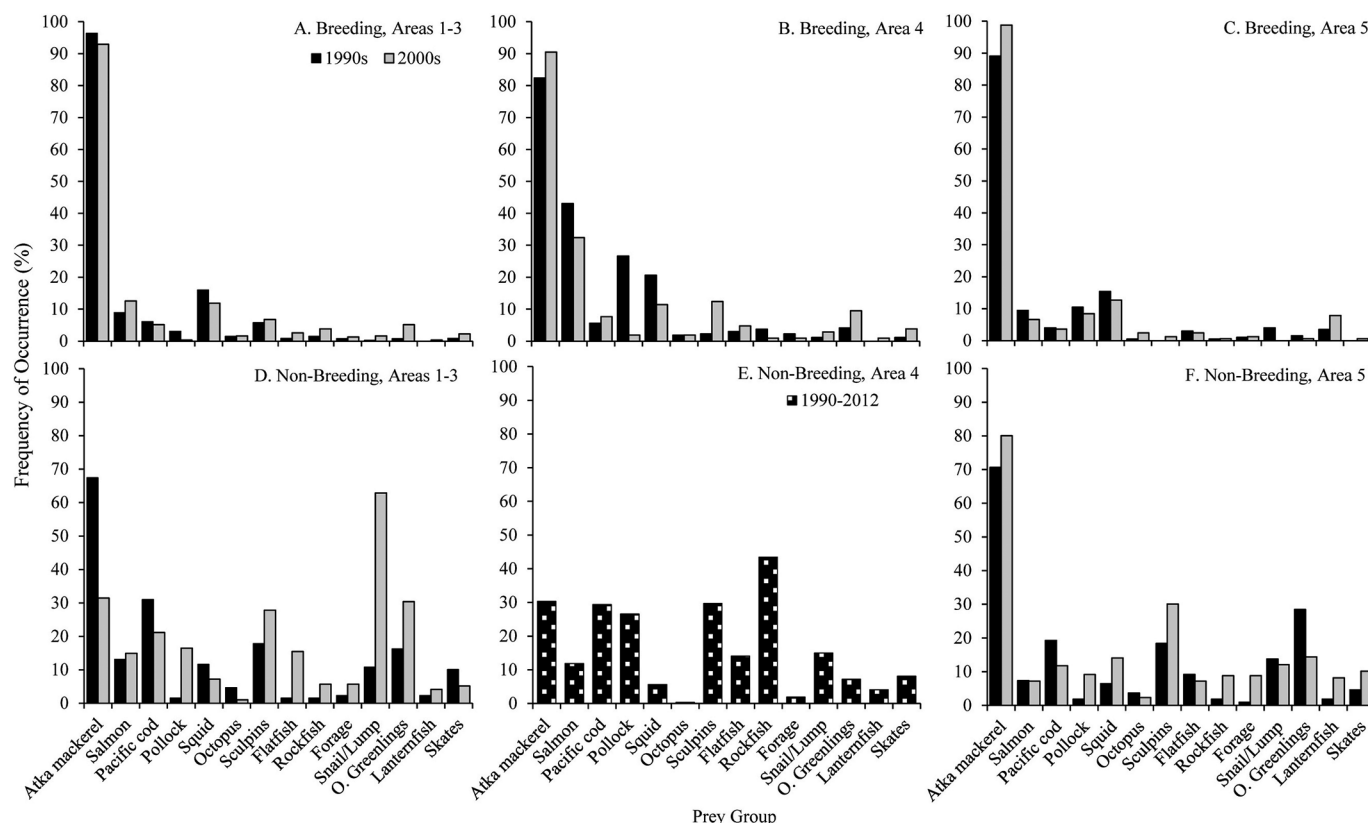
Fig. 3. Steller sea lion (*Eumetopias jubatus*) diet diversity indices by area in the Aleutian Islands, both seasons, 1990–2012: (A) mean number of prey groups per scat (maximum of 14); (B) foraging strategy diversity index; (C) evenness based on 14 prey taxa; (D) diversity based on eight prey taxa; (E) proportion of scats that contained only Atka mackerel; and (F) energy density index ($\text{kJ} \cdot \text{g}^{-1}$ dry mass). The x axes in E and F apply to A–B and C–D, respectively.



in those scats that contained unidentified Gadidae and one or both of the two primary species ($n = 19$ scats). Only those scats ($n = 2913$ or 94%) that contained prey identified to one or more of the 14 groups were retained for analysis. This standardized high-level approach was considered optimal given this study's main comparative goals. Evidence of more than one individual of the same prey group within a single scat was treated as a single occurrence. Taxa were also grouped using classification criteria developed by Trites et al. (2007a; eight groups): Cephalopoda, Pleuronectiformes, forage fish, Gadidae, Hexagrammidae, *Sebastes* sp., Salmonidae, and Other.

Examination of initial species accumulation curves indicated that data from areas 1–3 should be pooled for breeding and non-breeding seasons within each decade. Counts of Steller sea lions in areas 1–3 declined throughout the course of the study, so pooling data collected in these areas is consistent with study objectives. Sample size in area 4 during the 1990s non-breeding season was small ($n = 36$) and collected in 1999; hence all non-breeding season data from area 4 were pooled. In addition, results of PERMANOVA indicated that breeding season diets for areas 1–3, 4, and 5 were not significantly different ($p > 0.05$) between the 1990s and 2000s but that non-breeding season diets were different ($p < 0.05$) between decades (for areas 1–3 and 5) and from breeding season diets (Fig. 3). As a result, eight area-season-decade cells were used for analysis of diet and trend using deterministic methods: breeding season diets for 1990–2012 in areas 1–3, 4, and 5; non-breeding season diets for the 1990s and 2000s in areas 1–3 and 5; and non-breeding season diet for 1990–2012 in area 4 (Fig. 2). Pooling diet data by area and decade could have obscured the importance of some prey that had limited spatial or temporal usage by sea lions but was either necessary because of the relatively small sample

Fig. 4. Percent frequency of occurrence of 14 Steller sea lion (*Eumetopias jubatus*) prey groups by season (A–C, breeding; D–F, non-breeding), area (A and D, areas 1–3; B and E, area 4; C and F, area 5), and decade in the Aleutian Islands. Legend in A also applies to B–D and F. In E, data from 1990–2012 were pooled. The x axes in D–F also apply to A–C. Snail/Lump, snailfish and lumpfishes; O. Greenlings, other greenlings; Pollock, walleye pollock (*Gadus chalcogrammus*).



sizes of some time–area cells or efficient because there were no statistically significant differences between the diets.

Overall diet by area and general relationship to population trend

Using deterministic diet metrics, area 4 had the highest overall diversity indices (mean number of taxa per scat, FSDI, evenness based on 14 taxa, and diversity based on eight taxa) when all data (1990–2012) were pooled (Fig. 3). Areas 1–3 and 5 had diets with greater proportions of scats that contained only Atka mackerel and higher energy density indices than area 4. Thus, overall, Steller sea lions appeared to rely more on Atka mackerel and had diets with greater energy density and lower diversity in areas 1–3 (declining abundance) and 5 (stable abundance but improving trend) compared with area 4 (stable abundance and trend; Fig. 1C).

Temporal-spatial diet patterns

Atka mackerel was the most prevalent taxon in Steller sea lion diets throughout the Aleutian Islands during the breeding season and more prevalent in areas 1–3 and 5 (overall pooled FO of 95%) than in area 4 (overall pooled FO of 85%; Fig. 4). The only other taxa that had FO > 10% during the breeding season were squid, salmon, walleye pollock, and sculpins (varied by area and decade).

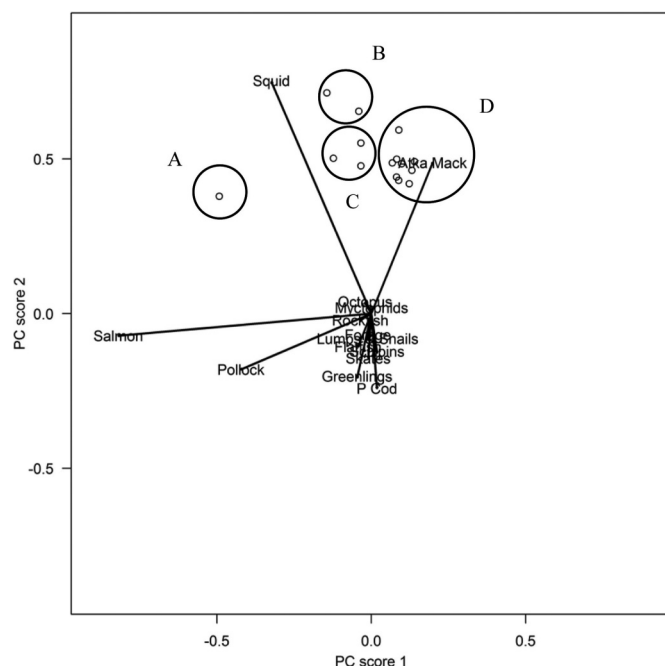
Diets at breeding season site groups separated primarily (PC 1; 57% of total variance) along an Atka mackerel and combined salmon – walleye pollock axis and secondarily (PC 2; 17% of total variance) along a combined squid – Atka mackerel and all other prey axis (Fig. 5). Clusters were tightly grouped, indicating high Atka mackerel and squid. A cumulative proportion of the total variance that exceeded 95% was achieved by PC 5 for breeding season PC analysis, and the average Euclidean distance between

all site groups was 0.21. Of the 15 pooled (1990–2012) breeding season PC–HC site groups, Atka mackerel was the sole dominant prey in nine groups (pooled FO = 92%); no other prey group had a pooled FO > 10%. This “Atka mackerel” cluster included site groups in all areas except area 4 (Fig. 5). A second cluster consisted of a single site in area 4, where the diet was the least dominated by Atka mackerel (FO = 75%) and supplemented with salmon (54%), walleye pollock (31%), and squid (22%). The third and fourth site clusters in areas 2–5 had high FOs (>90%) of Atka mackerel and moderate FOs (10%–27%) of salmon, squid, and walleye pollock.

During the non-breeding season, Atka mackerel was less prevalent in scat in all areas than during the breeding season, there were more taxa with FOs > 10%, and there were differences between decades, particularly in areas 1–3 (Fig. 4). From the 1990s to the 2000s, in areas 1–3, Atka mackerel FO dropped from 67% to 31%, while snailfish–lumpfishes FO increased from 11% to 63%. The increase in consumption of snailfish–lumpfishes in the non-breeding season was limited to areas 1–3 and due almost entirely to an increase in smooth lumpfishes in the diet. Pacific cod, sculpins, other greenlings, and salmon each had FOs > 10% in both decades in areas 1–3. In area 4, rockfish were the most prevalent prey during the non-breeding season, followed by seven taxa with FO > 10%. Atka mackerel was the most prevalent non-breeding season prey in area 5 in the 1990s and 2000s and was more prevalent here than in any other Aleutian area.

Diets at non-breeding season site groups separated primarily (PC 1; 37% of total variance) along an Atka mackerel and combined walleye pollock and rockfish axis and secondarily (PC 2; 24% of total variance) along a combined walleye pollock and rockfish–walleye and combined snailfish–lumpfishes and other green-

Fig. 5. Results of hierarchical cluster analysis (plot of principal component (PC) 2 vs. PC 1) of Steller sea lion (*Eumetopias jubatus*) diets in the breeding season in the Aleutian Islands (pooled 1990–2012 data). Prey groups are vectors and site groups (Supplementary Table S2²) are points; site groups with similar diets are encircled and have the same letter code as in Supplementary Fig. S1 (top).² Atka Mack, Atka mackerel (*Pleurogrammus monopterygius*); Greenlings, other greenlings; Lumps & Snails, snailfish and lumpsuckers; Myctophids, lanternfish; Pollock, walleye pollock (*Gadus chalcogrammus*); P Cod, Pacific cod (*Gadus macrocephalus*).

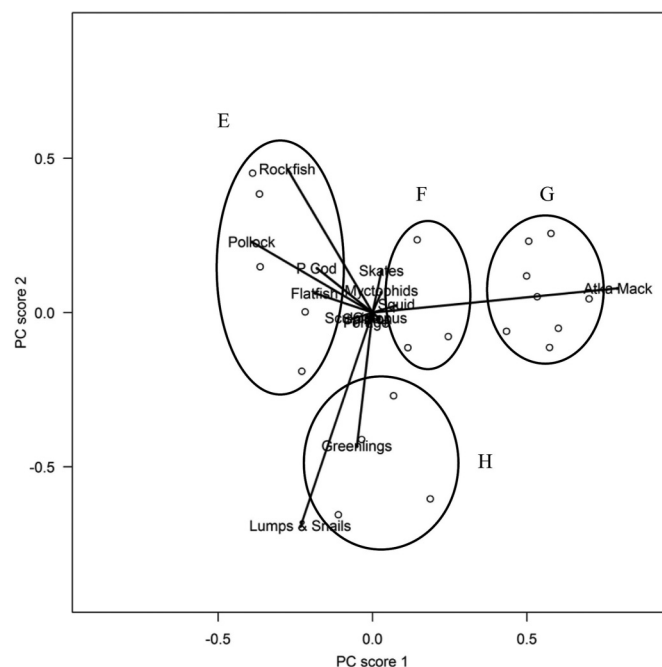


lings axis (Fig. 6). Clusters were more loosely grouped across PC 1 and PC 2 than during the breeding season, indicating a greater mix of prey at generally more intermediate FOs. A cumulative proportion of the total variance exceeding 95% was achieved by PC 8 for non-breeding season PC analysis, and the average Euclidean distance between all site groups was almost three times larger than during the breeding season (0.60). Of the 20 non-breeding season site groups (six from the 1990s and 14 from the 2000s), Atka mackerel was the dominant prey in eight groups. Site groups in the “Atka mackerel” cluster were located in each of the five areas but were dominated by area 5 (Fig. 6).

Deterministic diversity metrics were lower during the breeding season in all areas and generally lower in areas 1–3 and 5 compared with area 4 throughout the year (Fig. 7). Breeding season diets in areas 1–3 and 5 were highly dominated by Atka mackerel, had the lowest mean number of taxa per scat, FSDI, evenness, and diversity values, and had the highest proportion of Atka mackerel only scats. The breeding season diet in area 4 was more diverse in all metrics than in areas 1–3 and 5 but lower in energy density by $\sim 1 \text{ kJ} \cdot \text{g}^{-1}$.

Diet energy densities in areas 1–3 and 5 were similar in the breeding season and in the 1990s non-breeding season despite large differences in diversity metrics and Atka mackerel dominance (Fig. 7). In addition, diet energy density was greater in both seasons in areas 1–3 and 5 than in area 4. While diet indices in the 2000s non-breeding season in areas 1–3 indicated that it was one of the most diverse, it had the lowest energy density. The decline in diet energy density in the non-breeding season between the 1990s and 2000s in areas 1–3 was due to a large drop in FO of Atka mackerel and large increase in snailfish–lumpsuckers (Fig. 6). Diet energy density was highest overall in area 5 in the non-breeding

Fig. 6. Results of hierarchical cluster analysis (plot of principal component (PC) 2 vs. PC 1) of Steller sea lion (*Eumetopias jubatus*) diets in the non-breeding season in the Aleutian Islands (1990s and 2000s considered separately). Prey groups are vectors and site–decade groups (Supplementary Table S2²) are points; site–decade groups with similar diets are encircled and have the same letter code as in Supplementary Fig. S1 (bottom).² Atka Mack, Atka mackerel (*Pleurogrammus monopterygius*); Greenlings, other greenlings; Lumps & Snails, snailfish and lumpsuckers; Myctophids, lanternfish; Pollock, walleye pollock (*Gadus chalcogrammus*); P Cod, Pacific cod (*Gadus macrocephalus*).



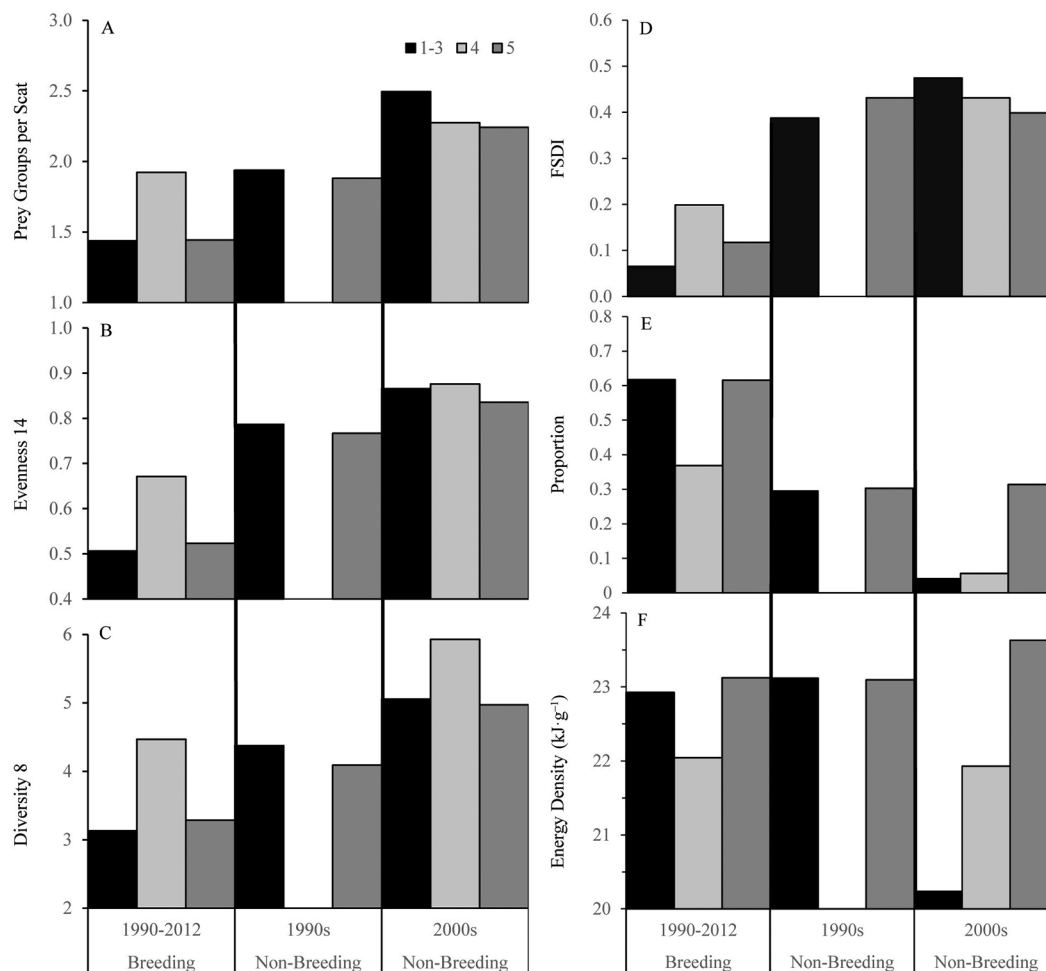
season in the 2000s, and the increase from the 1990s in the area was associated with increases in three diversity metrics (mean number of taxa per scat, evenness, and diversity).

Relationship between diet diversity and population trend

The relatively wide confidence bounds on modeled diet diversity indices (Fig. 8) indicate the importance of considering sample sizes and prey detection probabilities when computing these metrics and using them to make inferences about their relationship to other population metrics. If diet diversity is directly related to abundance trends, then abundance (Fig. 1) and rates of change (Fig. 8) should increase as diversity increases, and vice versa. In areas 1–3, abundance declined in each area from 1990 to 2012, but the rate of decline in the pooled areas slowed with time. In area 4, abundance declined in the early 1990s and then essentially stabilized through 2012, with rates of change increasing in the early 1990s, stabilizing at slightly above zero through the mid-2000s, and then declining through 2012. In area 5, abundance declined through the 1990s followed by increases through 2012, with rates of change generally increasing through the 1990s to 0, followed by positive and increasing rates through 2012.

During the breeding season, there was no change in modeled diversity with time within each analytical area (Fig. 8). As with the deterministic analyses (Figs. 3 and 7), modeled breeding season diversity was similar in areas 1–3 (annual medians between 6.3 and 8.4, with minimum and maximum 95% credible interval (CI) values of 3.5 and 11.1, respectively) and area 5 (median range, 7.3 to 9.8; CI range, 3.9 to 11.5) and greatest in area 4 (median range, 8.2 to 12.5; CI range, 5.0 to 13.9). However, there was no consistent relationship between breeding season diversity and abundance or

Fig. 7. Steller sea lion (*Eumetopias jubatus*) diet diversity, foraging strategy diversity, and diet energy density indices by area (1–3, 4, and 5), season, and decade in the Aleutian Islands 1990–2012: (A) mean number of prey groups per scat (maximum of 14 groups); (B) evenness based on 14 prey groups; (C) diversity based on eight prey groups; (D) foraging strategy diversity index (FSDI); (E) proportion of scats that contained only Atka mackerel (*Pleurogrammus monopterygius*); and (F) diet energy density index ($\text{kJ} \cdot \text{g}^{-1}$ dry mass). Legend in A (areas) applies to all. The x axes in C and F (season and decade) apply to A, B, D, and E. Pooled 1990–2012 data for area 4 during the non-breeding season are plotted with the 2000s because that is when 89% of the samples were collected.



rates of change in abundance. Breeding season diversities were similar and had no temporal trend in areas 1–3 and 5, yet abundance trends were different. Abundance declined continuously in areas 1–3 (but at slower rates through the time), while in area 5, abundance increased through most of the 2000s. Area 4 had the highest diversity, yet abundance was essentially stable.

Modeled diet diversity was generally greater in the non-breeding season than in the breeding season in areas 1–3 and 5 but not in area 4 (Fig. 8). During the non-breeding season, modeled diversity indices generally increased with time in areas 1–3 (medians ranged from 7.6 to 10.9 in the 1990s and from 10.6 to 12.5 in the 2000s) but generally decreased or were stable in areas 4 and 5 (Fig. 8). These results are similar to the deterministic results for areas 1–3; for area 5, however, the deterministic results showed greater diversity in the 2000s than in the 1990s (Fig. 7). In areas 1–3 and 4, trends in modeled non-breeding season diversity and rates of change in abundance were in general agreement (Fig. 8). In areas 1–3, both diversity and rates of abundance change increased, though rates remained negative. In area 4, both non-breeding season diet diversity and rates of abundance change declined from 1999 to 2012. These results suggest that a direct relationship between non-breeding season diet diversity and population trend might exist. However, in area 5, there was no direct relationship: non-breeding season diet diversity was stable or declined slightly

from 1998 to 2012, yet rates of change in abundance markedly increased.

Groundfish trawl surveys

There were no consistent patterns or trends in the annual (summer) prey community scores within survey regions (Fig. 9). Goodness of fit (S) of the nMDS ordinations regressions indicated that the two-dimensional solution ordination provided an adequate representation of the underlying data ($S \leq 0.1$ indicates a reasonable fit; Clarke and Warwick 2001). Annual prey communities from Aleutian Islands groundfish trawl hauls were similar in the EAI (areas 4 and 5) and WAI (area 1). ANOSIM did not detect any significant differences among annual communities within survey regions ($R = 0.05$ in the EAI and $R = 0.03$ in both the CAI and WAI), indicating that annual prey communities as described by groundfish trawl hauls within each region were indistinguishable from a random assemblage of community components. Temporally, survey catch evenness was generally higher overall in the 1990s than in the 2000s (Fig. 10); however, evenness was not significantly different between decades in the CAI (areas 2 and 3) and EAI (areas 4 and 5) but was higher in the 1990s than in the 2000s in the WAI (area 1). There was no consistent longitudinal trend in evenness in either decade.

Fig. 8. Modeled Steller sea lion (*Eumetopias jubatus*) diet diversity (median \pm 95% credible interval based on 14 prey groups) and annual abundance trend by area (left, areas 1–3 pooled; center, area 4; right, area 5) and year (x axis in all plots) in the Aleutian Islands. Top three panels show breeding (solid squares and solid simple linear trend line) and non-breeding season (open triangles and dashed simple linear trend line) diversity. Bottom three panels show estimated annual rate of change in counts of adult and juvenile Steller sea lions; dotted lines are simple linear trends over the same time period as non-breeding season diversity in each area.

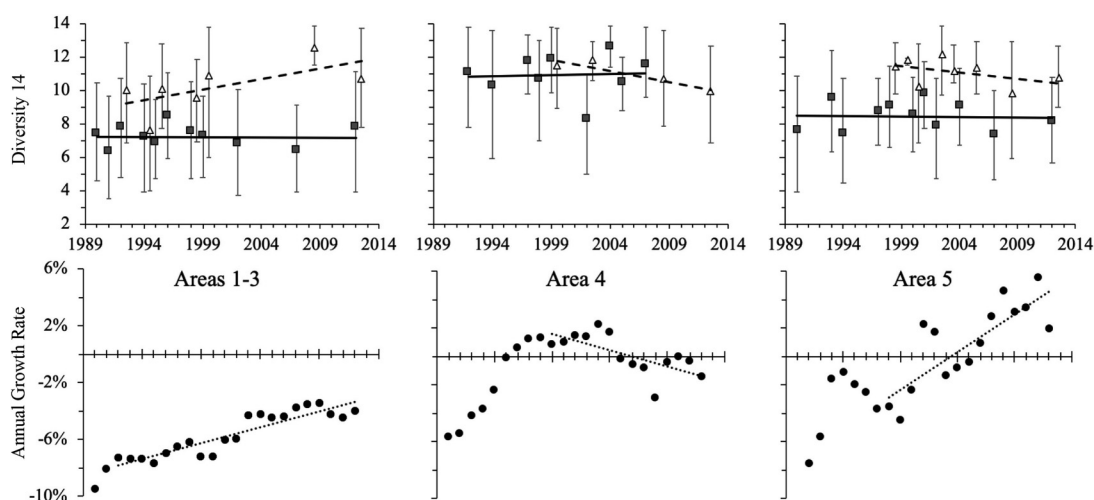


Fig. 9. Nonmetric multidimensional scaling (nMDS) of Wisconsin double-standardized and square-root-transformed mean annual biomass estimates (catch per unit effort) for 21 Steller sea lion (*Eumetopias jubatus*) prey taxa collected during nine Aleutian Islands bottom trawl surveys (indicated by year within each plot) by region (A, western; B, central; C, eastern). Goodness of fit (S) of the nMDS regressions are shown for each region.

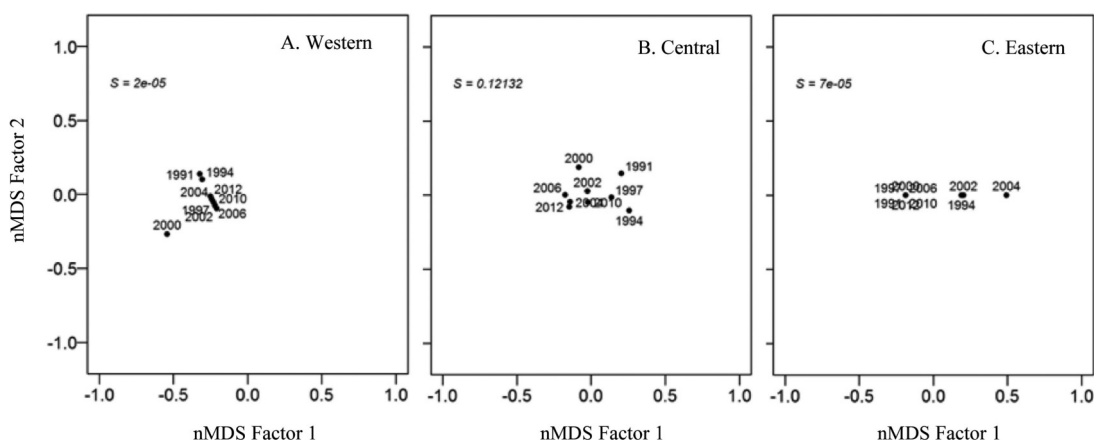
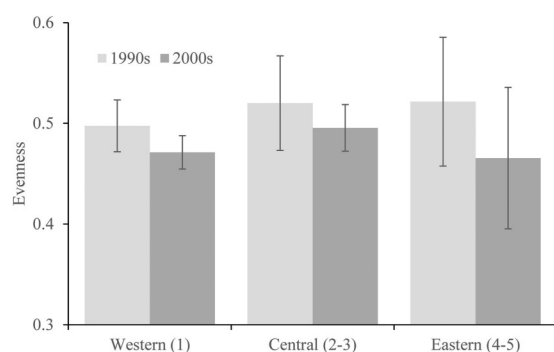


Fig. 10. Evenness indices by decade and region (western, central, and eastern) for Steller sea lion (*Eumetopias jubatus*) prey taxa caught in groundfish bottom trawl surveys in the Aleutian Islands, 1991–2012. Corresponding Steller sea lion analysis areas are shown in parentheses.



Discussion

A re-examination of the relationship between Steller sea lion diet diversity and population trend in the Aleutian Islands is warranted given the additional data on trend and diet available since Merrick et al. (1997). For instance, diet diversity in the four Aleutian areas of Merrick et al. (1997) was estimated using a total of only 195 scats (an average of fewer than 50 per area) collected only during the breeding season. As our results have shown, as well as those of Sinclair and Zeppelin (2002) and Sinclair et al. (2013), breeding and non-breeding season diets of Steller sea lions in the Aleutian Islands are different, with more prey groups consumed in the non-breeding season than in the breeding season. In this study, we developed new diversity metrics using larger sample sizes than Merrick et al. (1997), a minimum of 105 in each time-area cell (exceeding the 94 scats recommended by Trites and Joy (2005) to compare FO over time or between areas with moderate effect size); examined both breeding and non-breeding season diets; and developed an occupancy model that accounts for unequal sample sizes and uncertainty in prey group detection (Merrick et al. 1997; Mackenzie et al. 2002; Tyre et al. 2003; Trites

et al. 2007a). In general, our more regionally focused single ecosystem study showed that the relationship between Steller sea lion diet metrics and population trends in the Aleutian Islands over a 22-year period (1990–2012) is inconsistent, but it could also be described as nonexistent.

While occupancy models (Mackenzie et al. 2002; Tyre et al. 2003) account for some of the biases associated with diversity calculations, they will not overcome the potential to miss prey that Steller sea lions may focus on for brief periods of time or in small areas. These are issues that plague all studies that have attempted to summarize Steller sea lion diets (Merrick et al. 1997; Sinclair and Zeppelin 2002; Waite and Burkanov 2006; Trites et al. 2007a; McKenzie and Wynne 2008; Sinclair et al. 2013), largely because sea lions haul out, breed, and defecate on hundreds of remote locations spread across 1000s of kilometres of coastline in Alaska, which are expensive and time-consuming to reach throughout the year. Studies that have had a smaller temporal and areal focus (Sigler et al. 2004, 2017; Womble et al. 2005; Gende and Sigler 2006; Womble and Sigler 2006) have shown the importance of one or two prey species for limited periods of time. This may be how Steller sea lions feed throughout much of their range, particularly during the non-breeding season, switching prey as their availability changes. Our study, however, was designed to address a much broader question: do the available diet data collected in the Aleutian Islands over a 23-year period support the hypothesis that there is no relationship between diet diversity and population trend? As such, we conducted the analysis at spatial and temporal scales to discern broad patterns and acknowledge that gaps in our understanding of the diet of Steller sea lions in the Aleutian Islands remain.

Diet diversity by itself is a difficult metric to interpret in an ecological context. Merrick et al. (1997) and Trites et al. (2007a) hypothesized that Steller sea lion diet diversity was a healthy sign because, in their studies, it was directly associated with population trend. Merrick et al. (1997) noted two features of diverse prey fields that could increase sea lion foraging efficiency: prey may be easier to find (more and different kinds of prey patches) and capture (patch densities could be greater). Prey “quality” (energy density) may be less important to sea lions than ease and predictability of finding and capturing prey, an idea supported by the results of Sigler et al. (2009, 2017) and Womble et al. (2009). Diversity, energy density, and availability, however, may be linked (Trites et al. 2007a; Sigler et al. 2009; Womble et al. 2009) because sea lions may require high energy prey to be available at certain times and places to thrive, particularly in the winter when prey is generally less aggregated and when sea lion energetic expenditures may be the greatest (Winship et al. 2002). Thus, even when Steller sea lions have diverse diets (non-breeding season) and appear to be opportunists, they may have periods when they specialize on one or two aggregated prey, which in the Aleutian Islands could be Atka mackerel, Pacific cod, rockfish, walleye pollock, or possibly smooth lumpfish (as opposed to eulachon, *Thaleichthys pacificus* (Richardson, 1836), and Pacific herring identified in areas to the east by Sigler et al. (2004), Womble et al. (2005), Gende and Sigler (2006), Womble and Sigler (2006), and Sigler et al. (2017)).

Our results also indicate that the diversity and energy density of what Steller sea lions consumed had little correlation with each other and inconsistent relationships at best with population performance. For instance, deterministic diversity was lower in the breeding season (when they appear to specialize on Atka mackerel) than in the non-breeding season, yet energy densities were generally similar. There was one notable exception to this result — areas 1–3 in 2000s non-breeding season — where and when the diet had the highest diversity and lowest energy density (largely reflecting a mix of lumpfish, greenling, sculpins, and gadids). Areas 1–3 and 5, with the one exception, had similar deterministic diet metrics yet different population trends, while

area 4 had the highest deterministic diet diversity metrics and the lowest diet energy density (on an annualized basis), yet a stable population. Relationships between diet diversity as estimated by the occupancy model and population trends by region were also inconsistent.

Hard parts sieved from scats do not provide an unbiased, comprehensive description of pinniped diets, and we recognize a number of concerns and limitations. Firstly, while the number of scats analyzed is considerable for the region, relatively small sample sizes, most notably in the non-breeding season in area 1 (both decades) and areas 3 and 4 (1990s), require us to temper our conclusions. We cannot rule out that in certain areas or times of years, ephemeral prey may contribute to the diet (e.g., Sigler et al. 2004, 2017; Womble et al. 2005; Gende and Sigler 2006; Womble and Sigler 2006) and were not sampled during our study. We have therefore attempted to standardize our analyses and focus on higher level dietary results. There are also concerns associated with the sole use of frequency of occurrence of hard parts in pooled collections based on presence-absence (Tollit et al. 2010; Bowen and Iverson 2013). First, scats are an incomplete representation of prey that have few resilient hard parts (e.g., of squid and octopus), have soft, small, or fragile bones that do not withstand the digestive process (e.g., salmon, smooth lumpfish), or are too large to be ingested whole, which reduces the likelihood of recovery of diagnostic skeletal elements (e.g., Pacific octopus, *Enteroctopus dofleini* (Wülker, 1910), and Pacific cod). These concerns can be addressed somewhat by analyzing prey DNA in the soft matrix of each scat as a complement to the analysis of hard parts (Tollit et al. 2009, 2017). Second, passage rates of skeletal elements differ among prey species (Tollit et al. 2003). This leads to evidence from a single meal composed of one or more species being spread among one or more successive scats, which would artificially inflate FO values at different rates for different species. Because of the wide variability in passage rates even for a single species, no corrections have been applied here (nor are they generally applied in these studies), and it is assumed that they equally affect all collections. Therefore, if statistical differences in FO or MFO resulted from comparisons between areas or time periods, then these differences are thought to reflect actual differences in diet, but FO or MFO values by themselves should not be used to infer actual diet proportions. Third, there is uncertainty in the number and size of each species consumed, which precludes estimation of the actual contribution that each species provides to the entire diet. Tollit et al. (2017) used information on number, size, and energy density to reconstruct the diet of Steller sea lions during the non-breeding season (March and April) throughout the Aleutian Islands based on the 2008 and 2012 collections included in this analysis. Adding prey DNA analyses augmented detections of certain taxa, particularly Pacific cod, smooth lumpfish, and cephalopods (primarily Pacific octopus; Tollit et al. 2017). Fourth, scats reflect only prey consumed within several days (perhaps up to 3 days) of returning to shore to haul out and defecate. Prey consumed and digested at sea would not be represented in our results. Foraging trip durations of adult female Steller sea lions are longer, on average, during the non-breeding season than in the breeding season (Merrick and Loughlin 1997; Andrews et al. 2002). This is due to both the older age of any dependent offspring that they may have at this time (which enables them to be separated from them for longer periods between nursing bouts) and the apparent drop in availability of Atka mackerel. Thus, our results are likely to under-represent the contribution that pelagic species distributed off the continental shelf and slopes (e.g., lanternfish, squid, salmon) make to the Aleutian Steller sea lion diet, and this bias is likely to be stronger in the non-breeding season than in the breeding season. Last, and perhaps most important, FO of prey hard parts or DNA in sea lion scats is not the same as the proportion that each prey taxa provides to the diet or caloric intake of Steller sea lions. The energy density, mass, and number

of each taxa consumed must also be considered. For instance, [Tollit et al. \(2017\)](#) reported that Pacific cod and cephalopods (primarily giant Pacific octopus) together accounted for ~40% of the energy intake of Steller sea lions in the Aleutian Islands in the non-breeding season in 2008 and 2012, yet had combined percent MFOs of only ~10%.

Bottom trawls used in groundfish surveys are consistent samplers of demersal and semi-demersal Steller sea lion prey species (e.g., Atka mackerel, Pacific cod, pollock, rockfish, sculpins, flatfish, and skates) but are not well suited to assessing changes in pelagic or small-bodied prey (e.g., salmon, snailfish–lumpsuckers, the “forage” group, lanternfish, other greenlings, and squid) or those that primarily reside “in” the bottom (e.g., octopus; [Zenger 2004](#); [Rooper 2008](#); [Rooper and Wilkins 2008](#); [von Szalay et al. 2011](#)). Demersal and semi-demersal fish not only comprised the bulk of the diet of Steller sea lions in the Aleutian Islands, but they also reside in the region year-round, changing their depth–area distributions seasonally depending on their reproductive cycles ([Logerwell et al. 2005](#); [Barbeaux et al. 2015](#); [Thompson and Palsson 2015](#); [Lowe et al. 2017](#)). In addition, data from these surveys were used in stock assessments to set annual catch quotas for fisheries that operate year-round (e.g., [Barbeaux et al. 2015](#); [Thompson and Palsson 2015](#); [Lowe et al. 2017](#)). Consequently, the series of summer bottom trawl surveys adequately described annual changes in abundance and the community structure of most of the important Steller sea lion prey taxa over the 1991–2012 period but did a poor job with salmon, squid, smooth lumpsuckers, and octopus (see [Tollit et al. 2017](#)).

In general, groundfish trawl survey catches indicated little temporal variability within regions, as well as a similarity in the community structure between the WAI (area 1) and the EAI (which includes area 5), both of which are reflected in sea lion diets. [Logerwell et al. \(2005\)](#) reported that the number of fish species caught in survey bottom trawls decreased from east to west in the Aleutian Islands: 43 at Samalga Pass (~170°W); 28–29 at Amukta (~172°W), Tanaga (~178°W), and Amchitka (180°) passes; and 19 at Buldir Pass (~175°E; [Fig. 1B](#)). Our analysis of Steller sea lion diets in the Aleutian Islands did not reveal a similar longitudinal drop in diversity, possibly because we limited it to the most frequently consumed taxa and lumped prey to the family level (where appropriate) to investigate temporal–spatial differences in foraging strategies rather than consumption of individual species. While there were no systematic surveys of the Aleutian Island fish community prior to 1980, it is reasonable to assume that the cline in diversity reported by [Logerwell et al. \(2005\)](#) reflects the evolution of fish communities in the Aleutian Islands since at least the last ice retreat (~10 000 years BP).

Diet energy density estimates reported here for Steller sea lions in the Aleutian Islands are higher than those estimated by [Winship and Trites \(2003\)](#), largely because of the higher values used here for Atka mackerel. [Winship and Trites \(2003\)](#) had limited data for hexagrammids, mostly from juveniles, to use in their model, and they used a range of 3.5–6 kJ·g⁻¹ wet mass. We used energy densities of 24.37 and 29.47 kJ·g⁻¹ dry mass for the breeding and non-breeding seasons ([Rosen and Trites 2013](#)), respectively, which are equivalent to 6.76 and 9.78 kJ·g⁻¹ wet mass, respectively. These data were not available to [Winship and Trites \(2003\)](#) and are greater than those reported in [Logerwell and Schaufler \(2005\)](#) but indicate that Atka mackerel can be almost three times more energy-dense for two-thirds of the year (non-breeding season) than [Winship and Trites \(2003\)](#) assumed. Substituting these updated Atka mackerel seasonal energy densities into their model might reduce the estimated per capita prey consumption and might change their conclusions regarding the relationship between consumption and population performance ([Winship and Trites 2003](#), their fig. 6).

Seasonal changes in Steller sea lion diets in the Aleutian Islands reflect the seasonal changes in foraging strategies necessitated by

their reproductive life history. In this study, scat collections during the breeding season are thought to largely reflect the diets of adult females (4+ years old) as the vast majority of samples were collected at rookeries, where there are generally few juveniles and adult males rarely leave their breeding territories on land ([Pitcher and Calkins 1981](#); [Sinclair and Zeppelin 2002](#); [Sinclair et al. 2013](#)). During the non-breeding season, scats reflect the diets of adult females and juveniles (females 1–3 years old and males 1–7 years old; [Sinclair and Zeppelin 2002](#); [Sease and York 2003](#); [Raum-Suryan et al. 2004](#); [Fadely et al. 2005](#); [Sinclair et al. 2013](#)), because adult males vacate the Aleutian Islands at this time of year and likely move to the northern Bering Sea ([Jemison et al. 2013](#)).

There was no consistent relationship between breeding season diet metrics and population trends by area in the Aleutian Islands. Breeding season diets within each area were dominated by Atka mackerel, exhibited little or no temporal change, had low diversity, and were very similar in areas 1–3 and 5 despite their different population trends. Area 4 (stable population) had the most diverse breeding season diet, with a high prevalence of Atka mackerel supplemented by salmon, walleye pollock, and squid. Breeding season diet energy densities were generally higher in areas 1–3 and 5 than in area 4 because of the greater prevalence of Atka mackerel, which has the second highest breeding season energy density of any prey item (~4 kJ·g⁻¹ dry mass greater than salmon, walleye pollock, or squid). The limited data available on at-sea habitat use of breeding season adult females in the Aleutian Islands (three animals instrumented in June 1997 in area 5; [Andrews et al. 2002](#)) are consistent with a diet dominated by Atka mackerel. Adult female foraging trips were short (<0.5 days) and generally consisted of a single bout of frequent and shallow dives (<150 m) with a short period of time until first prey ingestion (as measured by a stomach temperature pill; [Andrews et al. 2002](#)). During the summer, Atka mackerel inhabit shallow, nearshore waters in areas of high current (e.g., island passes) to spawn and guard egg masses until they hatch in late summer and fall ([Zolotov 1993](#); [Fritz and Lowe 1998](#); [Cooper and McDermott 2011](#)), making them highly available to foraging Steller sea lions. Atka mackerel also undertake diurnal vertical migrations, coming off the bottom during the day ([Nichol and Somerton 2002](#)). High prevalence of Atka mackerel and low breeding season FSDI and other diet diversity metrics suggest that Steller sea lions almost exclusively target semi-demersal, schooling prey during the breeding season in areas 1–3 and 5, with only a slight modification in area 4 ([Sinclair and Zeppelin 2002](#); [Sinclair et al. 2013](#)). Atka mackerel in areas 1–3 are smaller-at-age than in area 5 ([Lowe et al. 2017](#)), which could decrease the foraging efficiency of Steller sea lions in areas 1–3 compared with area 5, which, in turn, could have contributed to the poorer population performance. However, it is not known whether a difference in primary prey size alone, without drops in availability or abundance, could cause such a large difference in population performance.

Non-breeding season diets had much greater spatial and temporal variability than breeding season diets, yet also had no consistent relationship with population trend. Based on a biomass reconstruction, [Tollit et al. \(2017\)](#) found that Atka mackerel provided almost half the energy consumed in area 5 in the 2000s non-breeding season, but <15% in each of areas 1–3 and 4 where octopus, smooth lumpsucker, and Pacific cod together accounted for ~50% of the energy consumed. Our results are in agreement, as we found that non-breeding season hard part diversity metrics were generally lower in area 5, with its non-breeding season diet dominated by a single species, than in either areas 1–3 or 4. Overall greater diversity metrics in winter may reflect (i) the more challenging foraging environment for sea lions because they consume more non-aggregated prey (e.g., sculpins) at this time and (ii) the diets of both adult female and juvenile sea lions, which have different foraging capabilities ([Richmond et al. 2006](#)). Atka mackerel remained the dominant non-breeding season prey in area 5

throughout the study and in areas 1–3 in the 1990s but was ranked second in area 4 (entire study) and in areas 1–3 in the 2000s. Even where Atka mackerel FO remained high (area 5), a wider variety of foraging strategies appear to have been used in winter than in the summer. After their eggs hatch in the fall, Atka mackerel move to deeper offshore waters (Zolotov 1993; Fritz and Lowe 1998; Cooper and McDermott 2011), which likely reduces their availability to foraging sea lions. The seasonal decline in Atka mackerel availability was evident in each area, but the least in area 5, where perhaps the largest aggregation of Atka mackerel exists in the Aleutian Islands (Seguam Pass; McDermott et al. 2005). Two of the species consumed more often in winter than in summer (walleye pollock and Pacific cod) aggregate to spawn in winter, which increases their availability (Sinclair and Zeppelin 2002; Sinclair et al. 2013) but likely only to sea lions hauled out near the aggregations (Marine Mammal Laboratory, unpublished data).

Prey availability in winter is thought to be a key factor in the energy budgets of Steller sea lions, particularly for pregnant adult females who may have a dependent pup born in the previous summer (NMFS 2010). For adult females, foraging trip duration, home range, and mean dive depth are each greater in winter than in summer (Merrick and Loughlin 1997). At-sea habitat use by adult females in the Aleutian Islands (and elsewhere) shows large individual variation during the non-breeding season, with some exclusively using shallow (<100 m) areas within 10s of kilometres of the shore on short (1–2 days) trips, while others take longer (6–8 days, 100s of kilometres) trips to shelf-break (~200+ m depth and diving to the seafloor) and pelagic (>1000 m depth and foraging in the upper water column) habitats (Merrick and Loughlin 1997; Marine Mammal Laboratory, unpublished data). There is evidence that juveniles have a similar wide variety of foraging strategies, but the sample size of weaned, independent animals is small for the Aleutian Islands (Fadely et al. 2005; Lander et al. 2009, 2010). Consequently, there is considerable individual and regional variability in foraging strategies used by Steller sea lions during the non-breeding season that is reflected in greater diet diversity. In most cases, diet energy density within an area was similar between winter and summer, which initially might lead one to conclude that winter diets were inadequate given the likely greater energy expenditures at this time to find more dispersed prey and maintain body temperature. Given the population trends throughout most of the Aleutian Islands, this may be a valid conclusion, but it also reflects the limitations of using only data on what Steller sea lions consumed to infer something about individual condition and population performance with only limited information on energy expenditures during extended foraging trips and diving (e.g., Malavaer 2002; Winship and Trites 2003; Fahlman et al. 2008).

Most (56%) of the scats analyzed by Tollit et al. (2017) were collected in area 4, which had the lowest overall non-breeding season FO of Atka mackerel. Furthermore, all were collected in the 2000s, which had a lower Atka mackerel FO during the non-breeding season than in the 1990s throughout most of the Aleutian Islands (areas 1–4). Based on a diet reconstruction using DNA and hard part prey detections along with species- and season-specific energy densities, Tollit et al. (2017) estimated that Atka mackerel and Pacific cod each contributed approximately 25% of the energy ingested by Steller sea lions in the Aleutian Islands in the non-breeding season. Thus, even though hard part diversity metrics increased from breeding season to non-breeding season, relatively few species contributed most of the energy. Given the Atka mackerel FO differences between the 1990s and 2000s non-breeding seasons in areas 1–3, Atka mackerel may have contributed twice as much energy to the non-breeding season Steller sea lion diet in the 1990s compared with the 2000s in areas where sea lion abundance continues to decline; area 5 shows no such decline.

Where data were available (areas 1–3 and 5), deterministic diversity metrics tended to be greater in the 2000s non-breeding season than in the 1990s, which is not reflected in the trawl survey data. However, trawl survey data are collected in the summer, so they may be poor metrics of non-breeding season prey community structure. In general, there were no differences between seasons in diet energy density within an area, but there were two notable exceptions. Where sea lions continue to decline (areas 1–3), Atka mackerel prevalence dropped considerably in the non-breeding season from the 1990s to the 2000s, and this was associated with some of the highest deterministic diversity metrics (number of prey groups per scat and FSDI) and the lowest energy density of any time–area estimated, largely due to the increased prevalence of smooth lumpsuckers and other greenlings, which have relatively low energy densities. In area 5, Atka mackerel prevalence was higher in the 2000s than in the 1990s and was the highest of all areas during the non-breeding season, likely because of the large population of Atka mackerel in Seguam Pass (McDermott et al. 2005). Diversity metrics in area 5 were higher in the 2000s than in 1990s non-breeding season, as was energy density because of the increased prevalence of Atka mackerel.

The regime shift (Mantua et al. 1997) – nutritional stress hypothesis (Trites and Donnelly 2003; Fritz and Hinckley 2005; Trites et al. 2007b) for the decline in abundance of western Steller sea lions posits that sea lions have been unable to consume enough energy to survive and reproduce at rates sufficient to maintain stable populations because of an environmentally induced change to the prey fields in the North Pacific Ocean. Prey fields were hypothesized to have changed from a diverse assemblage dominated by high-energy species (e.g., Pacific herring, capelin (*Mallotus villosus* (Müller, 1776)), and eulachon) to near monocultures of low-energy gadids (walleye pollock and Pacific cod) and hexagrammids (Atka mackerel, which were thought to have low energy density at the time). Western Steller sea lions supposedly had an abundance of prey biomass to eat, but because of its low energy density and the limited digestive capacities of juveniles, they could not thrive (Winship and Trites 2003; Rosen and Trites 2004). Increasing Steller sea lion populations (principally in southeastern Alaska, part of the eastern stock) had more diverse summer diets that were hypothesized to buffer them from shortages of any single prey (Trites et al. 2007a). Our results in the Aleutian Islands reveal that the relationship between diet diversity, energy density, and population performance of the Steller sea lion is less direct and that the associations are more uncertain than proposed in the regime shift – nutritional stress hypothesis. First, there is no evidence that the prey communities in the Aleutian Islands changed as a result of the 1977 regime shift, the effects of which were hardly noticeable in the Aleutian Islands (Rodionov et al. 2005). Species such as Pacific herring, capelin, and eulachon currently have only modest abundances in the Aleutian Islands, and there is no evidence to suggest that they were more abundant in the past. Thus, prey communities composed of the same mix of species and largely in much the same range of proportions (given recruitment variability) that have been observed since the 1990s supported Steller sea lion populations in the past that were 50 times greater (e.g., in the 1970s) than currently exist in some areas (e.g., area 1). Second, Atka mackerel is not a low-energy food, but instead is one of the highest in the North Pacific Ocean (Logerwell and Schaufler 2005; Rosen and Trites 2013). Consequently, if nutrition is the primary driver of current Steller sea lion demography in the Aleutian Islands, then it appears that what sea lions are eating — the diversity, species mix, and energy density of ingested prey — may not be the most important concern.

What is not considered in the regime shift – nutritional stress hypothesis is the potential for changes in the availability of the typical suite of prey species (rather than the loss of a single high-energy species), even by as little as 15% (Malavaer 2002), to have strong demographic consequences for Steller sea lions. Adult fe-

male otariids do not have large blubber stores and require a ready supply of prey nearby terrestrial rookeries and haul-outs to feed themselves, allow for fetal development, and supply milk to dependent pups or juveniles (Boyd 2000; Malavaer 2002; Winship and Trites 2002; Williams 2005). Prey species (e.g., Atka mackerel, Pacific cod, and walleye pollock) are likely to have lower overall abundance, less predictable spatial distributions, and altered demographics in fished versus unfished habitats (Hsieh et al. 2006; Barbeaux et al. 2013), which could result in increases in energy expenditures by Steller sea lions associated with finding and capturing prey. Predictability of prey aggregations in space and time appear to be more important factors as attractants to Steller sea lions and other central place foragers than the size of the aggregation (Benoit-Bird et al. 2013; Sigler et al. 2017). Therefore, Steller sea lions could be characterized as foraging risk minimizers, returning to successful foraging locations on subsequent days rather than seeking the largest aggregations that exist. They do not have perfect knowledge of the prey distributions in their nearby environment, but they do remember where they successfully foraged in the past (Sigler et al. 2017).

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Appendix A. Additional details concerning the multispecies occupancy model

1. Model statement

We estimated the true occurrence of prey species in Steller sea lion scats using a multispecies occupancy model that accounts for imperfect detection and unbalanced sampling effort (Dorazio and Royle 2005; Royle and Dorazio 2008). We fit the model using a Markov chain Monte Carlo (MCMC) algorithm written in R (R Core Team 2016).

Let y_{ijt} represent the number of detections (in J_{jt} scat samples) for species i ($i = 1, \dots, n$) at site j ($j = 1, \dots, R$) during time t ($t = 1, \dots, T$). In the context of our analysis, t denotes some year and season combination. We denote the latent occupancy state as z_{ijt} , where $z_{ijt} = 1$ indicates that the sample truly contains species i and $z_{ijt} = 0$ indicates that it does not. The full multispecies occupancy model statement is

$$\begin{aligned} y_{ijt} &\sim \begin{cases} \text{Binom}(J_{jt}, p_{ijt}), & z_{ijt} = 1 \\ 0, & z_{ijt} = 0 \end{cases} \\ z_{ijt} &\sim \begin{cases} 0, & v_{ijt} \leq 1 \\ 1, & v_{ijt} > 0 \end{cases} \\ v_{ijt} &\sim \mathcal{N}(\mathbf{x}'_{jt}\boldsymbol{\beta}_i, 1) \\ p_{ijt} &= \text{logit}^{-1}(\mathbf{w}'_{jt}\boldsymbol{\alpha}_i) \\ \boldsymbol{\beta}_i &\sim \mathcal{N}(\boldsymbol{\mu}_\beta, \sigma_\beta^2 \mathbf{I}) \\ \boldsymbol{\alpha}_i &\sim \mathcal{N}(\boldsymbol{\mu}_\alpha, \sigma_\alpha^2 \mathbf{I}) \\ \boldsymbol{\mu}_\beta &\sim \mathcal{N}(\mathbf{0}, \sigma_{\mu_\beta}^2 \mathbf{I}) \\ \boldsymbol{\mu}_\alpha &\sim \mathcal{N}(\mathbf{0}, \sigma_{\mu_\alpha}^2 \mathbf{I}) \\ \sigma_\beta^2 &\sim \text{IG}(r, q) \\ \sigma_\alpha^2 &\sim \text{IG}(r, q) \end{aligned}$$

where v_{ijt} is a continuous, latent version of the binary occupancy process (Albert and Chib 1993); \mathbf{x}_{jt} and \mathbf{w}_{jt} are vectors of covariates affecting occupancy and detection probability (p_{ijt}); $\boldsymbol{\alpha}_i$ and $\boldsymbol{\beta}_i$ are vectors of species-specific coefficients associated with detection and occupancy; and $\boldsymbol{\mu}_\alpha$ and $\boldsymbol{\mu}_\beta$ are vectors of population-level effects. The parameters r and q are the scale and shape parameters of the inverse gamma distribution, respectively. Following Broms et al. (2015), we estimated the Shannon diversity within the occupancy modeling framework using

$$\Delta^1_{\text{occu}} = \exp \left(- \sum_{i=1}^N \frac{\psi_{ijt}}{\sum_{s=1}^N \psi_{sjt}} \log \frac{\psi_{ijt}}{\sum_{s=1}^N \psi_{sjt}} \right)$$

where $\psi_{ijt} = \Phi(\mathbf{x}'_{jt}\boldsymbol{\beta}_i)$ is the occupancy probability and Φ is the standard normal cumulative distribution function.

2. Full-conditional distributions

A Bayesian analysis using MCMC estimates the joint posterior distribution by sampling iteratively from the full-conditional distributions (Hobbs and Hooten 2015). In the full-conditional distributions below, we use bracket notation to denote a probability distribution. For example, $[x]$ indicates the probability distribution of x . Similarly, $[x|y]$ indicates the probability distribution of x

given the parameter y . The notation “.” represents the data and other parameters in the model.

2.1. Occupancy state (z_{ijt})

$$\begin{aligned} [z_{ijt}|\cdot] &\propto [y_{ijt}|p_{ijt}, z_{ijt}][z_{ijt}|v_{ijt}] \\ &\propto \text{Binom}(y_{ijt}|J_{jt}, p_{ijt})^{z_{ijt}} \mathbf{1}_{\{y_{ijt}=0\}} \text{Bern}(z_{ijt}|v_{ijt}) \\ &\propto (p_{ijt}^{y_{ijt}}(1-p_{ijt})^{J_{jt}-y_{ijt}})^{z_{ijt}} (1-p_{ijt})^{1-z_{ijt}} \psi_{ijt}^{z_{ijt}} (1-\psi_{ijt})^{1-z_{ijt}} \\ &\propto (\psi_{ijt} p_{ijt}^{y_{ijt}} (1-p_{ijt})^{J_{jt}-y_{ijt}})^{z_{ijt}} ((1-\psi_{ijt}) \mathbf{1}_{\{y_{ijt}=0\}})^{1-z_{ijt}} \\ &= \text{Bern}(\psi_{ijt}) \end{aligned}$$

where

$$\psi_{ijt} = \frac{\psi_{ijt} p_{ijt}^{y_{ijt}} (1-p_{ijt})^{J_{jt}-y_{ijt}}}{\psi_{ijt} p_{ijt}^{y_{ijt}} (1-p_{ijt})^{J_{jt}-y_{ijt}} + (1-\psi_{ijt}) \mathbf{1}_{\{y_{ijt}=0\}}}$$

and

$$\psi_{ijt} = \Phi(\mathbf{x}'_{jt} \boldsymbol{\beta}_i)$$

2.2. Occupancy-state auxiliary variable (v_{ijt})

$$\begin{aligned} [v_{ijt}|\cdot] &\propto [z_{ijt}|v_{ijt}][v_{ijt}|\boldsymbol{\beta}_i] \\ &\propto (\mathbf{1}_{\{z_{ijt}=0\}} \mathbf{1}_{\{v_{ijt} \leq 0\}} + \mathbf{1}_{\{z_{ijt}=1\}} \mathbf{1}_{\{v_{ijt} > 0\}}) \times \mathcal{N}(v_{ijt}|\mathbf{x}'_{jt} \boldsymbol{\beta}_i, 1) \\ &= \begin{cases} \mathcal{TN}(\mathbf{x}'_{jt} \boldsymbol{\beta}_i, 1)_{-\infty}^0, & z_{ijt} = 0 \\ \mathcal{TN}(\mathbf{x}'_{jt} \boldsymbol{\beta}_i, 1)_{0}^{\infty}, & z_{ijt} = 1 \end{cases} \end{aligned}$$

2.3. Occupancy coefficients ($\boldsymbol{\beta}_i$)

$$\begin{aligned} [\boldsymbol{\beta}_i|\cdot] &\propto [\mathbf{v}_i|\boldsymbol{\beta}_i][\boldsymbol{\beta}_i|\boldsymbol{\mu}_\beta, \sigma_\beta^2] \\ &\propto \mathcal{N}(\mathbf{v}_i|\mathbf{X}\boldsymbol{\beta}_i, \mathbf{I}) \mathcal{N}(\boldsymbol{\beta}_i|\boldsymbol{\mu}_\beta, \sigma_\beta^2 \mathbf{I}) \\ &\propto \exp\left\{-\frac{1}{2}(\mathbf{v}_i - \mathbf{X}\boldsymbol{\beta}_i)'(\mathbf{v}_i - \mathbf{X}\boldsymbol{\beta}_i)\right\} \exp\left\{-\frac{1}{2}(\boldsymbol{\beta}_i - \boldsymbol{\mu}_\beta)'(\sigma_\beta^2 \mathbf{I})^{-1}(\boldsymbol{\beta}_i - \boldsymbol{\mu}_\beta)\right\} \\ &\propto \exp\left\{-\frac{1}{2}(-2\mathbf{v}_i' \mathbf{X}\boldsymbol{\beta}_i + \boldsymbol{\beta}_i' \mathbf{X}' \mathbf{X} \boldsymbol{\beta}_i)\right\} \exp\left\{-\frac{1}{2}(-2(\boldsymbol{\mu}_\beta' (\sigma_\beta^2 \mathbf{I})^{-1}) \boldsymbol{\beta}_i + \boldsymbol{\beta}_i' (\sigma_\beta^2 \mathbf{I})^{-1} \boldsymbol{\beta}_i)\right\} \\ &\propto \exp\left\{-\frac{1}{2}(-2(\mathbf{v}_i' \mathbf{X} + \boldsymbol{\mu}_\beta' (\sigma_\beta^2 \mathbf{I})^{-1}) \boldsymbol{\beta}_i + \boldsymbol{\beta}_i' (\mathbf{X}' \mathbf{X} + (\sigma_\beta^2 \mathbf{I})^{-1}) \boldsymbol{\beta}_i)\right\} \\ &= \mathcal{N}(\mathbf{A}^{-1} \mathbf{b}, \mathbf{A}^{-1}) \end{aligned}$$

where $\mathbf{A} = \mathbf{X}' \mathbf{X} + (\sigma_\beta^2 \mathbf{I})^{-1}$, $\mathbf{b}' = \mathbf{v}_i' \mathbf{X} + \boldsymbol{\mu}_\beta' (\sigma_\beta^2 \mathbf{I})^{-1}$, $\mathbf{v}_i' = \{v_{ijt}, \forall j, t\}$, and $\mathbf{X} = \{\mathbf{x}'_{jt}, \forall j, t\}$.

2.4. Detection coefficients (α_i)

$$\begin{aligned} [\alpha_i|\cdot] &\propto \prod_{j=1}^R \prod_{t=1}^{T_j} [y_{ijt}|p_{ijt}, z_{ijt}][\alpha_i|\boldsymbol{\mu}_\alpha, \sigma_\alpha^2] \\ &\propto \prod_{j=1}^R \prod_{t=1}^{T_j} \text{Binom}(y_{ijt}|J_{jt}, p_{ijt})^{z_{ijt}} \mathcal{N}(\alpha_i|\boldsymbol{\mu}_\alpha, \sigma_\alpha^2) \end{aligned}$$

The update for α_i proceeds using a Metropolis–Hastings algorithm. Note that the product over j and t only includes instances of j and t such that $z_{ijt} = 1$.

2.5. Mean of occupancy coefficients ($\boldsymbol{\mu}_\beta$)

$$\begin{aligned} [\boldsymbol{\mu}_\beta|\cdot] &\propto \prod_{i=1}^n [\boldsymbol{\beta}_i|\boldsymbol{\mu}_\beta, \sigma_\beta^2][\boldsymbol{\mu}_\beta] \\ &\propto \prod_{i=1}^n \mathcal{N}(\boldsymbol{\beta}_i|\boldsymbol{\mu}_\beta, \sigma_\beta^2 \mathbf{I}) \mathcal{N}(\boldsymbol{\mu}_\beta|\mathbf{0}, \sigma_{\mu_\beta}^2 \mathbf{I}) \\ &\propto \exp\left\{\sum_{i=1}^n \left(-\frac{1}{2}(\boldsymbol{\beta}_i - \boldsymbol{\mu}_\beta)'(\sigma_\beta^2 \mathbf{I})^{-1}(\boldsymbol{\beta}_i - \boldsymbol{\mu}_\beta)\right)\right\} \exp\left\{-\frac{1}{2}(\boldsymbol{\mu}_\beta - \mathbf{0})'(\sigma_{\mu_\beta}^2 \mathbf{I})^{-1}(\boldsymbol{\mu}_\beta - \mathbf{0})\right\} \\ &\propto \exp\left\{-\frac{1}{2}\left(-2\left(\sum_{i=1}^n \boldsymbol{\beta}_i' (\sigma_\beta^2 \mathbf{I})^{-1}\right) \boldsymbol{\mu}_\beta + \boldsymbol{\mu}_\beta' (n(\sigma_\beta^2 \mathbf{I})^{-1}) \boldsymbol{\mu}_\beta\right)\right\} \exp\left\{-\frac{1}{2}(\boldsymbol{\mu}_\beta' (\sigma_{\mu_\beta}^2 \mathbf{I})^{-1} \boldsymbol{\mu}_\beta)\right\} \\ &\propto \exp\left\{-\frac{1}{2}\left(-2\left(\sum_{i=1}^n \boldsymbol{\beta}_i' (\sigma_\beta^2 \mathbf{I})^{-1}\right) \boldsymbol{\mu}_\beta + \boldsymbol{\mu}_\beta' (n(\sigma_\beta^2 \mathbf{I})^{-1} + (\sigma_{\mu_\beta}^2 \mathbf{I})^{-1}) \boldsymbol{\mu}_\beta\right)\right\} \\ &= \mathcal{N}(\mathbf{A}^{-1} \mathbf{b}, \mathbf{A}^{-1}) \end{aligned}$$

where $\mathbf{A} = n(\sigma_\beta^2 \mathbf{I})^{-1} + (\sigma_{\mu_\beta}^2 \mathbf{I})^{-1}$, $\mathbf{b}' = \boldsymbol{\beta}' (\sigma_\beta^2 \mathbf{I})^{-1}$, and $\boldsymbol{\beta}$ is the vector sum $\sum_{i=1}^n \boldsymbol{\beta}_i$.

2.6. Mean of detection coefficients (μ_α)

$$\begin{aligned} [\mu_\alpha | \cdot] &\propto \prod_{i=1}^n [\alpha_i | \mu_\alpha, \sigma_\alpha^2] [\mu_\alpha] \\ &\propto \prod_{i=1}^n \mathcal{N}(\alpha_i | \mu_\alpha, \sigma_\alpha^2 \mathbf{I}) \mathcal{N}(\mu_\alpha | \mathbf{0}, \sigma_{\mu_\alpha}^2 \mathbf{I}) \\ &= \mathcal{N}(\mathbf{A}^{-1} \mathbf{b}, \mathbf{A}^{-1}) \end{aligned}$$

where $\mathbf{A} = n(\sigma_\alpha^2 \mathbf{I})^{-1} + (\sigma_{\mu_\alpha}^2 \mathbf{I})^{-1}$, $\mathbf{b}' = \alpha'(\sigma_\alpha^2 \mathbf{I})^{-1}$, and α is the vector sum $\sum_{i=1}^n \alpha_i$.

2.7. Variance of occupancy coefficients (σ_β^2)

$$\begin{aligned} [\sigma_\beta^2 | \cdot] &\propto \prod_{i=1}^n [\beta_i | \mu_\beta, \sigma_\beta^2] [\sigma_\beta^2] \\ &\propto \prod_{i=1}^n \mathcal{N}(\beta_i | \mu_\beta, \sigma_\beta^2 \mathbf{I}) \text{IG}(\sigma_\beta^2 | r, q) \\ &\propto \prod_{i=1}^n |\sigma_\beta^2 \mathbf{I}|^{-1/2} \exp\left\{-\frac{1}{2}((\beta_i - \mu_\beta)'(\sigma_\beta^2 \mathbf{I})^{-1}(\beta_i - \mu_\beta))\right\} (\sigma_\beta^2)^{-(q+1)} \exp\left\{-\frac{1}{r\sigma_\beta^2}\right\} \\ &\propto (\sigma_\beta^2)^{-(qXn)/2} \exp\left\{\sum_{i=1}^n \left(-\frac{1}{2\sigma_\beta^2}(\beta_i - \mu_\beta)'(\beta_i - \mu_\beta)\right)\right\} (\sigma_\beta^2)^{-(q+1)} \exp\left\{-\frac{1}{r\sigma_\beta^2}\right\} \\ &\propto (\sigma_\beta^2)^{-((qXn)/2 + q + 1)} \exp\left\{-\frac{1}{\sigma_\beta^2} \left(\frac{\sum_{i=1}^n (\beta_i - \mu_\beta)'(\beta_i - \mu_\beta)}{2} + \frac{1}{r}\right)\right\} \\ &= \text{IG}\left(\left(\frac{\sum_{i=1}^n (\beta_i - \mu_\beta)'(\beta_i - \mu_\beta)}{2} + \frac{1}{r}\right)^{-1}, \frac{qX \times n}{2} + q\right) \end{aligned}$$

where qX is the column dimension of \mathbf{X} (or length of β_i).

2.8. Variance of detection coefficients (σ_α^2)

$$\begin{aligned} [\sigma_\alpha^2 | \cdot] &\propto \prod_{i=1}^n [\alpha_i | \mu_\alpha, \sigma_\alpha^2] [\sigma_\alpha^2] \\ &\propto \prod_{i=1}^n \mathcal{N}(\alpha_i | \mu_\alpha, \sigma_\alpha^2 \mathbf{I}) \text{IG}(\sigma_\alpha^2 | r, q) \\ &= \text{IG}\left(\left(\frac{\sum_{i=1}^n (\alpha_i - \mu_\alpha)'(\alpha_i - \mu_\alpha)}{2} + \frac{1}{r}\right)^{-1}, \frac{qW \times n}{2} + q\right) \end{aligned}$$

where qW is the column dimension of \mathbf{W} (or length of α_i).

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