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ARTICLE

Diet composition of Steller sea lions (*Eumetopias jubatus*) in Frederick Sound, southeast Alaska: a comparison of quantification methods using scats to describe temporal and spatial variabilities

D.J. Tollit, M.A. Wong, and A.W. Trites

Abstract: We compared eight dietary indices used to describe the diet of Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) from 2001 to 2004 in Frederick Sound, southeast Alaska. Remains (*n* = 9666 items) from 59+ species categories were identified from 1684 fecal samples (scats) from 14 collection periods. The most frequently occurring prey were walleye pollock (*Theragra chalcogramma* (Pallas, 1814) = *Gadus chalcogrammus* Pallas, 1814; 95%), Pacific herring (*Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847; 30%), Pacific hake (*Merluccius productus* (Ayres, 1855); 29%), and arrowtooth flounder (*Atheresthes stomias* (Jordan and Gilbert, 1880) = *Reinhardtius stomias* (Jordan and Gilbert, 1880); 21%). These species, along with Pacific salmon (genus *Oncorhynchus* Suckley, 1861) and skate (genus *Raja* L., 1758), accounted for 80%–90% of the reconstructed biomass and energy contribution, with pollock contributing 37%–60%. Overall, 80% of fish were 14–42 cm long and mainly pelagic, though 40% of scats contained benthic-associated prey. Steller sea lions switched from adult pollock to strong cohorts of juvenile pollock, and took advantage of spawning concentrations of salmon in autumn and herring in late spring and summer, as well as a climate-driven increase in hake availability. Observed temporal and site differences in diet confirm the need for robust long-term scat sampling protocols. All major indices similarly tracked key temporal changes, despite differences in occurrence and biomass-energy-based diet estimates linked to prey size and energy-density effects and the application of correction factors.

Key words: diet, scat, biomass reconstruction, hard remains, otoliths, Steller sea lion, dietary index.

Résumé : Nous avons comparé huit indices alimentaires utilisés pour décrire le régime d'otaries de Steller (*Eumetopias jubatus* (Schreber, 1776)) de 2001 à 2004, dans le détroit de Frederick (sud-est de l'Alaska). Les restes (*n* = 9666 pièces) de plus de 59 catégories d'espèces ont été identifiés dans 1684 échantillons fécaux (excréments) prélevés durant 14 périodes de collecte. Les proies les plus fréquentes étaient la goberge de l'Alaska (*Theragra chalcogramma* (Pallas, 1814) = *Gadus chalcogrammus* Pallas, 1814; 95 %), le hareng (*Clupea pallasii* Valenciennes dans Cuvier et Valenciennes, 1847; 30 %), le merlu du Pacifique nord (*Merluccius productus* (Ayres, 1855); 29 %) et la plie à grande bouche (*Atheresthes stomias* (Jordan et Gilbert, 1880) = *Reinhardtius stomias* (Jordan et Gilbert, 1880); 21 %). Ces espèces, ainsi que des saumons (le genre *Oncorhynchus* Suckley, 1861) et raies (le genre *Raja* L., 1758), représentaient de 80 % à 90 % de la biomasse et de la contribution énergétique reconstituées, la goberge en contribuant de 37 % à 60 %. Globalement, 80 % des poissons faisaient de 14 à 42 cm de longueur et étaient principalement pélagiques, même si 40 % des excréments contenaient des proies d'association benthique. Les otaries de Steller passaient de goberges adultes à de fortes cohortes de goberges juvéniles et tiraient profit des concentrations associées au frai de saumons à l'automne et de harengs à la fin du printemps et en été, ainsi que de l'augmentation d'origine climatique de la disponibilité de raies. Les variations temporelles et spatiales observées du régime alimentaire confirment la nécessité de protocoles robustes d'échantillonnage à long terme des excréments. Tous les principaux indices indiquent les mêmes variations temporelles importantes, malgré des variations reliées aux effets de la taille des proies et de la densité d'énergie des estimations du régime alimentaire reposant sur la présence et la biomasse-énergie, et bien que des facteurs de correction aient été appliqués. [Traduit par la Rédaction]

Mots-clés : régime alimentaire, excréments, reconstitution de la biomasse, restes durs, otolites, otarie de Steller, indice alimentaire.

Introduction

Quantifying diets and consumption by marine mammals is a central requirement to quantify trophic interactions, study foraging ecology, evaluate fisheries interactions, and develop conservation strategies. Given the limited opportunities for direct observation, diets of marine mammals have typically been described indirectly by identifying diagnostic prey remains recovered from stomachs, intestines, and faeces (also termed scats). Describing diet using occurrence of prey may be useful to make geographic and temporal comparisons; however, quantitative estimation of diet is best achieved using a biomass or ideally a bioenergetic approach (Hyslop 1980; Laake et al. 2002) with representative sampling and an assessment of biases and confidence levels (Trites and Joy 2005; Tollit et al. 2006). Captive feeding studies (Casper et al. 2006; Tollit et al. 2007; Phillips and Harvey 2009) and computer simulations (Joy et al. 2006) have shown that traditional occurrence indices can perform poorly compared with biomass reconstruction (BR)

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methods that combine techniques aimed at reducing the major limitations associated with using hard-part analysis, such as using multiple diagnostic prey structures rather than just fish otoliths and cephalopod beaks (Olesiuk et al. 1990; Cottrell and Trites 2002), the application of numerical correction factors (NCF) to account for interspecific differences in the proportion of prey remains surviving digestion (Tollit et al. 2003, 2007; Grellier and Hammond 2006; Phillips and Harvey 2009), and the application of digestion correction factors (DCF) to account for size reduction of hard remains due to acidic erosion (e.g., Tollit et al. 1997, 2004*a*; Phillips and Harvey 2009).

Until recently, no field study of pinniped diet has attempted to utilize all recovered prey structures to reconstruct the size, mass, and energetic contribution of prey after applying DCF and NCF. Consequently, no focused study has been able to compare diet quantified using such an all-inclusive method with more traditional indices. For otariids, such an approach is particularly important, because otoliths are not reliably recovered from scats, or may be damaged rendering taxonomic identification and quantification problematic. Furthermore, utilizing multiple prey structures can assist in understanding the potential biases of traditional otolith-based diet studies as previously highlighted (e.g., Hammond and Rothery 1996; Tollit and Thompson 1996; Laake et al. 2002; Hammond and Grellier 2005; Vollenweider et al. 2006).

The dramatic population decline of Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) in the Gulf of Alaska and Aleutian Islands in the 1970s and 1980s (Loughlin et al. 1992; Trites and Larkin 1996) prompted a listing of endangered in 1997 (for this western distinct population segment (DPS)) under the US *Endangered Species Act*. Conversely, the once threatened population in southeast Alaska (SEAK; part of the eastern DPS) increased in number since the mid-1950s to above historic levels (e.g., Pitcher et al. 2007) and since 2013 is no longer considered threatened. These divergent population trajectories may be linked to differences in prey quantity, quality, diversity, or availability caused by environmental changes and commercial fisheries (Merrick et al. 1997; DeMaster and Atkinson 2002; Trites and Donnelly 2003; Wolf and Mangel 2004; Sinclair et al. 2005; Trites et al. 2007*a*, 2007*b*), highlighting the necessity for robust comparative dietary and modeling studies that evaluate temporal dynamics and that assess levels of competitive and trophic interactions (York 1994; Winship et al. 2002; Sigler et al. 2009).

Traditional analyses of prey remnants in stomach samples and scats showed that Steller sea lions consume a wide range of prey, often targeting prey in spawning, overwintering, or migratory aggregations, with clear seasonal and regional differences in prey occurrence (Fiscus and Baines 1966; Pitcher 1981; Merrick et al. 1997; Sinclair and Zeppelin 2002; Womble and Sigler 2006; Trites et al. 2007*a*, 2007*b*; McKenzie and Wynne 2008; Sigler et al. 2009; Sinclair et al. 2013). Low summer diet diversity (and energy content) at rookeries in the 1990s have been linked with high rates of population decline (Merrick et al. 1997; Trites et al. 2007*a*). The haul-out sites around Frederick Sound in SEAK are used year-round and form an important metapopulation cluster (Raum-Suryan et al. 2004), representing >10% of the regional population following the breeding season (Womble et al. 2005) as animals return from the coastal rookery complexes (Raum-Suryan et al. 2004; Marcotte 2006). Consequently, this key area has been the focus of extensive research, including regular aerial counts (Womble et al. 2005), telemetry and behavioural studies (e.g., Raum-Suryan et al. 2004; Pitcher et al. 2005; Lea and Wilson 2006), and prey availability and quality assessments (Vollenweider 2004; Thedinga et al. 2006; Sigler et al. 2009). However, basic diet descriptions for the Frederick Sound metapopulation (as well as most other Steller sea lion diet studies) have been limited to reporting prey occurrence (e.g., Trites et al. 2007*a*).

The specific objectives of our study were to develop an inclusive approach to reconstructing the bioenergetic contribution of Steller sea lion prey in Frederick Sound, SEAK, using prey hard parts from scats collected systematically between 2001 and 2004, to test two overarching hypotheses: (1) biomass-based diet estimates differ from traditional occurrence-based indices and (2) Steller sea lion diet and foraging response varies temporally and geographically in response to prey availability.

Materials and methods

Estimating numbers and sizes of prey consumed

Scat samples were collected from the four largest haul-out sites in Frederick Sound (southwest Brothers Island, west Brothers Island, Sail Island, Sunset Island; 57.2°N–57.5°N, 133.5°W–133.9°W) located in the inside waters of SEAK. Southwest Brothers Island and west Brothers Island are separated by <2 nautical miles (1 nautical mile = 1.852 km) and were considered a single location (Brothers Islands). There were 14 collection trips across five periods (early spring: March; late spring: May; summer: June and July; autumn: September; winter: December and January) between May 2001 and March 2004 (March 2002 collection trip was excluded due to low sample size). We considered each year to extend from May of one year to March of the next year. Ten other supplementary scat collections were made prior to this main study period between autumn 1993 and summer 2000, providing a long-term retrospective data set that describes the occurrence of prey species.

Scat samples were washed through an elutriator and (or) 0.495 mm sieve. All hard remains (fish otoliths, bones, and scales, eye lenses, cephalopod beaks and pens, etc.) were recovered and identified by Pacific IDentifications Inc. (Victoria, British Columbia, Canada; PacificID) to the lowest taxon possible (typically species or related species groupings). Occasionally, prey were identified as a miscellaneous gadid or cephalopod. Miscellaneous gadids were apportioned into walleye pollock (*Theragra chalcogramma* (Pallas, 1814) = *Gadus chalcogrammus* Pallas, 1814; henceforth referred to as pollock), Pacific hake (*Merluccius productus* (Ayres, 1855); henceforth referred to as hake), or Pacific cod (*Gadus macrocephalus* Tilesius, 1810; henceforth referred to as cod), and cephalopods into squid or octopus based on the observed proportion in the scat sample or collection period.

Hard remains were first enumerated to determine the minimum number of individuals (MNI; Ringrose 1993) represented by each prey species within each scat sample using an all-structures approach (for details see Tollit et al. 2003). We previously confirmed otoliths alone were not found useful for counting prey, as they represented <15% of the individuals counted using the all-structures method, with the exception of pollock (<30%). In particular, otoliths only represented <0.5% of the skate (genus *Raja* L., 1758) and Pacific salmon (genus *Oncorhynchus* Suckley, 1861; henceforth referred to as salmon) enumerated using all structures. Experimentally derived species- or taxon-specific NCF values (or a proxy value for a similar species) were applied to account for interspecific differences in recovery, and for many species, applied NCF were also size-specific (Supplementary Table S1)[1] due to documented effects of fish size on recovery (Harvey 1989; Tollit et al. 1997; Bowen 2000).

A comparison reference collection was used by PacificID to assign most prey to a size-class category based on relative structure size and a subjective estimate of the level of digestion. To refine size estimates for the main prey categories (arrowtooth flounder,

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[1] Supplementary Tables S1, S2, and S3 and supplementary material are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2014-0292.

Atherestes stomias = *Reinhardtius stomias* (Jordan and Gilbert, 1880); Atka mackerel, *Pleurogrammus monopterygius* (Pallas, 1810); cephalopods, class Cephalopoda (octopus and squid); capelin, *Mallotus villosus* (Müller, 1776); eulachon, *Thaleichthys pacificus* (Richardson, 1836); Pacific herring, *Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847; Pacific cod; Pacific hake; salmon; Pacific sand lance, *Ammodytes hexapterus* Pallas, 1814; pollock; and skate), direct measurements (within 1 mm) were made of various prey structures for which allometric regressions were available (including 28 newly developed regression equations from eight different species detailed in Supplementary Table S2[1]). As elements can undergo a reduction in size during digestion (Harvey 1989), each was assigned a condition grade to categorize the level of digestion based on changes in the external morphological features (for methodology see Tollit et al. 1997, 2004*a*). Experimentally derived species and grade-specific DCF were applied to each element in good or fair condition (Supplementary Table S2).[1] Where DCF were unavailable, a representative proxy value was selected based on a related species or on similar skeletal fragility.

Fork length was calculated by applying an allometric regression (and converted from standard or total length where necessary) to the DCF-corrected element length (Supplementary Table S2).[1] For pollock, regression equations based on fish caught in concurrent local trawl surveys were used in preference to published regressions (Supplementary Table S2).[1] Given that the predictive power of some regressions was limited by size range and sample size (as well as potentially the use of a proxy DCF), we selected the PacificID size-class category median length when back-calculated fork length differed by >15% from the PacificID size-class category minimum or maximum.

Hard parts recovered from the scats that do not correlate with body size (e.g., gill rakers, teeth) or were in poor condition were not considered useful for estimating size (Tollit et al. 1997, 2004*a*). Thus, it was not always possible to measure any or all elements in each sample. In these cases, we systematically used the mean size estimate for the same size-class category from (*i*) the same sample, (*ii*) the same haul-out site and date, (*iii*) the same haul-out site within the same collection trip, or (*iv*) the nearest haul-out site within the same season. Finally, if size could not be approximated using these methods, the median of the PacificID size-class range was applied, with the exception of skate and cephalopods for which mean length and mass, respectively, were based on size estimates for all locations and dates. In the few cases where a size-class range was not available, we used a length proxy or a literature value (Supplementary Table S3).[1]

We calculated the mass of each fish by applying a second allometric regression equation (Supplementary Table S3)[1] to the fork-length estimate. Cephalopod mass was calculated from DCF-corrected beak or hood lengths. Regressions for salmon, squid, and octopus were based on mean values from two commonly occurring species (Supplementary Table S2).[1] The total mass of each prey category per sample was calculated by combining NCF-corrected MNI counts to the prey-mass estimates. Energetic contribution was calculated using energy-content values from prey collected locally in concurrent trawls, which allowed for interannual and seasonal (and age class for pollock) variations to be incorporated (Vollenweider 2004). For the remaining prey categories, literature or nearest species proxy values were used (Anthony et al. 2000; Logerwell and Schaufler 2005; J.J. Vollenweider, unpublished data).

Dietary indices

To compare and contrast different diet quantification methods, eight diet indices were calculated. The first two indices were commonly used occurrence indices: frequency of occurrence (FO) and split-sample frequency of occurrence (SSFO; Tollit et al. 2010). We converted FO to a modified frequency of occurrence (MFO; Bigg and Perez 1985), in which the sum of all prey categories equals 100%, which allowed a direct comparison with other models (Tollit et al. 2010). SSFO examines each scat sample individually, apportioning the contribution of each prey category to each scat depending on the number of other species present, and assumes that each prey category is consumed in equal quantities (Olesiuk et al. 1990). Finally, we calculated a fourth composite index, the index of relative importance (IRI; Pinkas et al. 1971), which is influenced by prey FO, but also incorporates the abundance (percent numbers) and mass of prey. Converting IRI to percent IRI (%IRI) allowed more comprehensive comparisons between indices.

The fifth and sixth dietary indices were variants of BR models (termed "variable" and "fixed"; sensu Laake et al. 2002). In the variable-biomass model (BR-V), each scat contributes a varying amount of prey biomass (depending on the estimated size and number of prey consumed). The model thus allows for variability in foraging success (meal size) between animals, while ignoring the potential impacts of animal age, sex, and size on digestion and scat deposition. The fixed-biomass model (BR-F) assumes the mean consumption of prey is equal across animals and meals, and therefore, the contribution of each scat is weighted equally or "fixed". The seventh and eighth indices consisted of two energetic contribution models (EC-V and EC-F) that were similarly calculated by integrating prey energy density data with BR estimates.

Pollock (as the clear dominant species) were separated into three ecologically relevant age classes (young of the year (YOY) < 20 cm; juvenile = 20–34 cm; adult ≥ 34 cm) that we termed "prey subcategories". We grouped infrequent species (FO < 0.5%) into functional categories such as flatfish or hexagrammids (Supplementary Table S3).[1] We also combined our data to ensure that each seasonal collection trip carried equal weighting (Laake et al. 2002; Trites et al. 2007*a*). This differs from the method used in Sigler et al. (2009) that weighted each collection trip to ensure consistency with comparative regional diet data sets (Vollenweider et al. 2006; Womble and Sigler 2006).

We estimated confidence intervals due to scat subsampling around BR and EC models using bootstrap resampling methodology (Manly 1997), which repeated the calculations 1000 times by choosing *n* scats at random with replacement from the original sample set of *n* scats. The 25th and 975th values of the sorted 1000 runs provided 95% confidence intervals. Captive-based diet studies suggest BR-V models may be marginally more preferable to BR-F models (Tollit et al. 2007; Phillips and Harvey 2009) and most biomass-based studies use the BR-V approach. Thus, overall we have focused on describing diet using variable-based bioenergetic indices, as well as FO (the descriptor that best describes number of animals utilizing each prey grouping, while highlighting the extent of major differences with other indices.

We calculated three diet diversity indices to compare with previous Steller sea lion studies (Supplementary material).[1] Shannon's index of species diversity (H) was calculated using only species with an overall FO ≥5% (sensu Womble and Sigler 2006), then using prey family FO data collapsed across multiple seasons (sensu Sinclair and Zeppelin 2002; H_f). Finally, we calculated a diet diversity index (DDI) based on Shannon's index (sensu Trites et al. 2007*a*) using the SSFO of eight major prey groupings (gadid, salmon, cephalopod, flatfish, forage fish, hexagrammid, rockfish (genus *Sebastes* Cuvier, 1829), and other).

Statistical and sensitivity analyses

We compared differences in the overall ranks of prey categories between diet indices using Spearman's rank-order correlations. Comparisons between the models were made for all prey categories and for prey categories contributing ≥1% FO and ≥5% FO (sensu Vollenweider et al. 2006).

Statistical analyses (Pearson's χ^2 test, $\alpha \leq 0.05$) were performed to test for differences in the FOs of the key prey species (FO ≥ 5%: pollock (overall and by each age class), herring, hake, arrowtooth

Table 1. Number of Steller sea lion (*Eumetopias jubatus*) scat samples collected, number of samples with remains, number of unique prey categories recovered, mean number of prey categories per scat sample, and the number of individual fish or cephalopods recovered and identified for each collection period, location, season, and year.

	Scat samples	Scat samples with remains	Unique prey categories	Prey categories/scat sample	Individuals recovered and identified
Overall	1684	1631	59	2.5	9666
Collection period					
Late spring 2001	145	143	18	1.9	489
Summer 2001	40	37	10	1.8	90
Autumn 2001	74	72	16	2.4	440
Winter 2001–2002	80	74	23	2.4	433
Late spring 2002	204	202	21	2.5	1174
Summer 2002	111	108	11	2.0	456
Autumn 2002	116	112	21	2.6	575
Winter 2002–2003	162	146	23	2.2	838
Early spring 2003	95	95	26	3.7	1138
Late spring 2003	181	179	22	2.2	814
Summer 2003	96	94	16	2.5	531
Autumn 2003	223	216	28	3.2	1633
Winter 2003–2004	82	80	18	2.6	516
Early spring 2004	75	73	18	2.9	539
Location					
Brothers Islands	682	647	48	2.4	3332
Sail Island	382	376	23	2.3	1912
Sunset Island	620	608	33	2.8	4422
Season					
Late spring	530	524	32	2.3	2477
Summer	247	239	16	2.1	1077
Autumn	413	400	34	2.9	2648
Winter	324	300	36	2.4	1787
Early spring	170	168	30	3.3	1677
Year					
Year one	339	326	35	2.1	1452
Year two	688	663	39	2.5	4181
Year three	657	642	37	2.7	4033

flounder, skates, salmon, cod, cephalopods, and rockfish). Additional analyses were then undertaken on FO, BR-V, and EC-V (using Friedman's rank-sum tests, nonparametric randomized block analysis of variance (ANOVA); Zar 1996) to test for trends across years, seasons, or haul-out sites. Scat collection protocols were thus assumed to be repeated measures and resulting data non-normally distributed. Differences in the size of prey consumed were tested (for sample sizes >25) across years, seasons, and sites using a Pearson's χ^2 analysis based on size-category frequencies (Tollit et al. 2004*b*).

Results

Diet composition summary

A total of 1631 scat samples with remains (n = 1684 total scats collected) were collected between May 2001 and March 2004 (Table 1). Sample sizes for each collection trip ranged from 40 to 223 samples (120 ± 55; mean ± SD). The supplementary collection trips (1993–2000) provided an additional 516 samples, averaging 52 ± 20 (range 32–98). A minimum of 59 prey species categories were identified between 2001 and 2004, comprising at least 9666 prey items (Table 1) and representing 2.6 tons of reconstructed prey biomass (mean prey biomass = 1.6 kg/scat, mean prey energy = 7.1 MJ/scat).

Energetically (EC-V) only seven prey species categories contributed ≥5% overall (Table 2). Pollock dominated the diet (37%), followed by arrowtooth flounder, herring, skate, salmon, hake, and cod; together, these species contributed 88% of the diet energetically. By occurrence, just nine key prey species categories occurred in ≥5% of scats. Pollock (especially juveniles) dominated numerically and by occurrence, followed by herring, hake, arrowtooth flounder, and cephalopods for both indices (Tables 2 and 3).

Dietary index comparisons and sensitivity analyses

Prey ranking did not differ between diet indices when all prey groupings or those 18 contributing ≥1% FO were compared (Table 3). When only the top nine (≥5% FO) key prey groupings were compared, all indices identified the same prey groupings, but with the clear exception of a lower ranking of cephalopods using biomass-based models. Rankings of the models were generally significantly correlated ($p < 0.03$), except BR-V was only correlated with EC-V ($r = 0.8$, $p = 0.03$) and EC-V was not correlated with either of the occurrence models ($r = 0.6$, $p = 0.10$). Noncorrelation was the result of up to twofold differences between occurrence indices and variable-based BR and EC indices (Tables 2 and 3). However, the absolute margin of difference between these indices was relatively small, averaging only 4.1% for key prey (range 0.6%–16.9%), with MFO and EC-V differing by a mean margin of 3.3% (range 0.6%–7.5%; Table 2). Furthermore, we found that observed temporal changes in diet were similarly tracked by all the major dietary index types (Fig. 1).

Differences between indices were explained mainly by prey-size effects (Fig. 2), followed by energetic density and also how data from each scat was averaged across sample sets (fixed versus variable). Occurrence and %IRI models provided higher estimates of small fish and lower estimates of large fish compared with BR- and EC-based models. For example, occurrence contributions of (small) herring and YOY pollock were ~2 times more than BR-V contributions, while conversely, the contributions of arrowtooth flounder,

Table 2. Key prey species consumed by Steller sea lions (*Eumetopias jubatus*) in Frederick Sound, southeast Alaska, from 2001 to 2004, based on percent number (*N*), frequency of occurrence (FO), modified frequency of occurrence (MFO), split-sample frequency of occurrence (SSFO), percent index of relative importance (%IRI), percent biomass reconstruction (fixed (BR-F) and variable (BR-V) models), and percent energy contributed (fixed (EC-F) and variable (EC-V) models), with 95% confidence intervals (CI) based on bootstrap resampling.

Prey	*N*	FO	MFO	SSFO	%IRI	BR-F	BR-F CI	BR-V	BR-V CI	EC-F	EC-F CI	EC-V	EC-V CI
Walleye pollock, *Theragra chalcogramma*	**63.9**	**95.4**	**38.4**	**53.8**	**85.0**	**59.8**	53.2–66.4	**43.1**	35.0–52.5	**56.2**	49.4–63.0	**36.9**	29.8–45.7
Arrowtooth flounder, *Atheresthes stomias*	**4.1**	**20.8**	**8.4**	**6.3**	**2.6**	**8.2**	5.0–11.8	**11.1**	6.5–16.6	**9.8**	6.0–13.9	**15.9**	9.7–27.8
Pacific herring, *Clupea pallasii*	**14.0**	**30.1**	**12.1**	**10.1**	**5.8**	**5.6**	3.4–8.2	5.6	3.1–8.8	**7.8**	5.0–11.0	**8.6**	4.9–13.4
Skate spp., genus *Raja*	2.6	12.3	4.9	3.2	**1.1**	4.1	2.0–6.7	**7.8**	3.9–12.1	4.2	2.0–6.9	**8.2**	4.2–12.7
Pacific salmon spp., genus *Oncorhynchus*	2.6	11.0	4.4	3.2	1.0	**4.5**	2.4–7.3	**6.7**	3.0–11.6	**4.3**	2.2–7.0	**6.6**	2.8–11.8
Pacific hake, *Merluccius productus*	**5.8**	**29.0**	**11.7**	**9.8**	**2.6**	**7.3**	4.7–10.4	6.5	4.3–9.2	**7.4**	4.8–10.4	6.5	4.4–9.0
Pacific cod, *Gadus macrocephalus*	2.9	12.6	5.1	3.6	1.0	4.5	2.1–7.4	**6.9**	3.0–11.4	4.1	1.8–6.8	5.7	2.5–9.4
Rockfish spp., genus *Sebastes*	0.9	4.5	1.8	1.2	0.1	1.2	0.3–2.6	2.9	0.5–6.5	1.4	0.3–3.0	3.6	0.6–7.6
Cephalopod spp., class Cephalopoda	**3.3**	**13.9**	**5.6**	**4.2**	0.5	1.7	0.8–3.0	1.7	0.7–3.3	1.7	0.8–2.9	1.5	0.6–2.8

Note: The top five prey species for each index are set in boldface type.

Table 3. Steller sea lion (*Eumetopias jubatus*) diet in Frederick Sound, southeast Alaska, from 2001 to 2004, for prey subcategories by percent frequency of occurrence (FO), modified frequency of occurrence (MFO), split-sample frequency of occurrence (SSFO), percent index of relative importance (%IRI), percent biomass reconstruction (fixed (BR-F) and variable (BR-V) models), and percent energy contributed (fixed (EC-F) and variable (EC-V) models).

Prey subcategories	FO	MFO	SSFO	%IRI	BR-F	BR-V	EC-F	EC-V
Juvenile walleye pollock, *Theragra chalcogramma*	**72.6 (1)**	**24.0 (1)**	**31.5 (1)**	**54.9 (1)**	**33.2 (1)**	**22.3 (1)**	**31.0 (1)**	**18.9 (1)**
Arrowtooth flounder, *Atheresthes stomias*	20.8 (6)	6.9 (6)	5.6 (6)	3.9 (6)	**8.2 (3)**	**11.1 (3)**	**9.8 (3)**	**15.9 (2)**
Adult walleye pollock	**45.3 (2)**	**15.0 (2)**	**18.4 (2)**	**13.7 (2)**	**21.5 (2)**	**17.7 (2)**	**20.6 (2)**	**15.6 (3)**
Pacific herring, *Clupea pallasii*	**30.1 (4)**	**9.9 (4)**	**8.6 (4)**	**8.6 (4)**	**5.6 (5)**	5.6 (8)	**7.8 (4)**	**8.6 (4)**
Skate spp., genus *Raja*	12.3 (9)	4.0 (9)	2.8 (9)	1.7 (7)	4.1 (9)	**7.8 (4)**	4.2 (8)	**8.2 (5)**
Pacific salmon spp., genus *Oncorhynchus*	11.0 (10)	3.6 (10)	2.8 (10)	1.5 (8)	4.5 (8)	6.7 (7)	4.3 (7)	6.6 (6)
Pacific hake, *Merluccius productus*	**29.0 (5)**	**9.6 (5)**	**8.4 (5)**	**3.9 (5)**	**7.3 (4)**	6.5 (6)	**7.4 (5)**	6.5 (7)
Pacific cod, *Gadus macrocephalus*	12.6 (8)	4.2 (8)	3.1 (8)	1.5 (9)	4.5 (7)	**6.9 (5)**	4.1 (9)	5.7 (8)
Rockfish spp., genus *Sebastes*	4.5 (11)	1.5 (11)	1.1 (11)	0.2 (11)	1.2 (11)	2.9 (10)	1.4 (11)	3.6 (9)
YOY walleye pollock	**32.2 (3)**	**10.6 (3)**	**10.0 (3)**	**9.0 (3)**	5.0 (6)	3.0 (9)	4.6 (6)	2.4 (10)
Cottidae	2.9 (13)	1.0 (13)	0.8 (13)	0.1 (12)	1.2 (12)	2.4 (12)	1.1 (12)	2.2 (11)
Cephalopod spp., class Cephalopoda	13.9 (7)	4.6 (7)	3.7 (7)	0.7 (10)	1.7 (10)	1.7 (13)	1.7 (10)	1.5 (12)
Lumpsucker spp., genus *Eumicrotremus*	1.0 (20)	0.3 (20)	0.2 (17)	0.1 (15)	0.3 (15)	2.5 (11)	0.2 (15)	1.1 (13)
Other deep fish	1.0 (19)	0.3 (19)	0.2 (19)	<0.1 (16)	0.3 (14)	0.9 (14)	0.3 (14)	1.1 (14)
Other flatfish	0.4 (24)	0.1 (24)	<0.1 (24)	<0.1 (20)	0.1 (18)	0.8 (15)	0.1 (18)	0.8 (15)
Gunnel spp.	1.0 (18)	0.3 (18)	0.2 (18)	<0.1 (18)	0.2 (16)	0.2 (16)	0.2 (16)	0.3 (16)
Hexagrammid	0.2 (26)	<0.1 (26)	<0.1 (26)	<0.1 (26)	<0.1 (20)	0.2 (17)	<0.1 (21)	0.2 (17)
Myctophid spp.	2.9 (14)	0.9 (14)	0.5 (14)	0.1 (14)	<0.1 (22)	<0.1 (23)	0.1 (19)	0.2 (18)
Capelin, *Mallotus villosus*	0.6 (22)	0.2 (22)	0.1 (21)	<0.1 (19)	0.1 (19)	0.2 (18)	0.1 (20)	0.1 (19)
Pacific sand lance, *Ammodytes hexapterus*	3.8 (12)	1.2 (12)	0.9 (12)	0.1 (13)	0.3 (13)	0.1 (21)	0.4 (13)	0.1 (20)
Rock sole, *Lepidopsetta bilineata* (Ayres, 1855)	1.1 (16)	0.4 (16)	0.3 (15)	<0.1 (22)	0.2 (17)	0.1 (19)	0.2 (17)	0.1 (21)
Pacific sandfish, *Trichodon trichodon* (Tilesius, 1813)	1.3 (15)	0.4 (15)	0.2 (16)	<0.1 (17)	<0.1 (21)	0.1 (20)	<0.1 (22)	0.1 (22)
Other-shallow fish	1.0 (17)	0.3 (17)	0.1 (22)	<0.1 (21)	<0.1 (24)	<0.1 (22)	<0.1 (24)	0.1 (23)
Snailfish spp., genus *Liparis* Scopoli, 1777	0.9 (21)	0.3 (21)	0.2 (20)	<0.1 (23)	<0.1 (23)	<0.1 (24)	<0.1 (24)	<0.1 (24)
Other forage fish	0.2 (25)	<0.1 (25)	<0.1 (25)	<0.1 (25)	<0.1 (25)	<0.1 (25)	<0.1 (25)	<0.1 (25)
Northern smoothtongue, *Leuroglossus schmidti* Rass, 1955	0.5 (23)	0.2 (23)	0.1 (23)	<0.1 (24)	<0.1 (26)	<0.1 (26)	<0.1 (26)	<0.1 (26)

Note: Walleye pollock contribution has been divided into three age classes (young of the year (YOY), juvenile, and adult). Rankings are shown in parentheses and the top five prey species for each index are set in boldface type.

salmon, and skate were ~2 times less (Table 3, Fig. 2). The occurrence of large fish in relatively few scats resulted in similar scale differences comparing BR-V with BR-F, with lower BR-V estimates for smaller fish (Fig. 2). Notably, the total energetic contribution of pollock to the diet increased from 37% to 56% when the EC-F model was applied instead of EC-V (Table 4). Similar increases were observed between MFO and SSFO, with pollock increasing in relative importance by 30% using SSFO (a fixed-type model).

We found that variable models are susceptible to outliers, highlighting the importance of assessing scat subsampling confidence intervals especially when using this model and collecting sufficient representative scat samples. For example, in early spring 2003, one scat sample contained 269 individual lumpsuckers (genus *Eumicrotremus* Gill, 1862), resulting in a trip BR-V of 32%, which was far higher than any other collection trip (range 0.2%–1.2%). Similarly, a high number of large skate was recovered during autumn 2003, which resulted in a strong seasonal peak in BR-V compared with BR-F (Fig. 1). Rockfish peaked in importance during summer 2001 and cephalopods during winter 2002–2003 when using the BR-V model, in both cases due to the recovery of one large individual (Fig. 1). These instances of course resulted in wide 95% confidence intervals (Fig. 1). Overall, the 95% confidence intervals (based on scat resampling protocols) differed from the point value by 50%, on average, (range 10%–100%) for the lower confidence interval and by 65%, on average, (range 10%–300%) for the upper confidence interval (EC-V; Fig. 1). The prey categories with the largest confidence intervals were those that were relatively large while occurring in relatively few scats (e.g., arrowtooth flounder, salmon, skate) or showed great variability in mass (e.g., cephalopods).

Conversion of biomass estimates to energy-based estimates resulted in an expected increased importance for high energy-content fish, such as herring and arrowtooth flounder, and lowered the importance of species such as pollock and cod (Table 3). Contributions of species with energetic densities close to the mean energy content of ~4.5 kJ/g, such as hake (4.5 kJ/g) and skate (4.7 kJ/g), remained similar (Fig. 1). Differences also reflected seasonal changes;

Fig. 1. Percent diet contribution using the split-sample frequency of occurrence (SSFO), the biomass reconstruction using the variable-biomass (BR-V) and fixed-biomass (BR-F) models, and the energy reconstruction using the variable-biomass (EC-V) model for the key prey species consumed by Steller sea lions (*Eumetopias jubatus*) in Frederick Sound, southeast Alaska, from 2001 to 2004. The 95% confidence intervals were calculated using bootstrap resampling. The key prey species were walleye pollock (*Theragra chalcogramma*; juvenile, adult, young of the year (YOY)), Pacific herring (*Clupea pallasii*), Pacific hake (*Merluccius productus*), arrowtooth flounder (*Atheresthes stomias*), cephalopod spp. (class Cephalopoda), Pacific cod (*Gadus macrocephalus*), skate spp. (genus *Raja*), Pacific salmon spp. (genus *Oncorhynchus*), and rockfish spp. (genus *Sebastes*). Figure appears in colour on the Web.

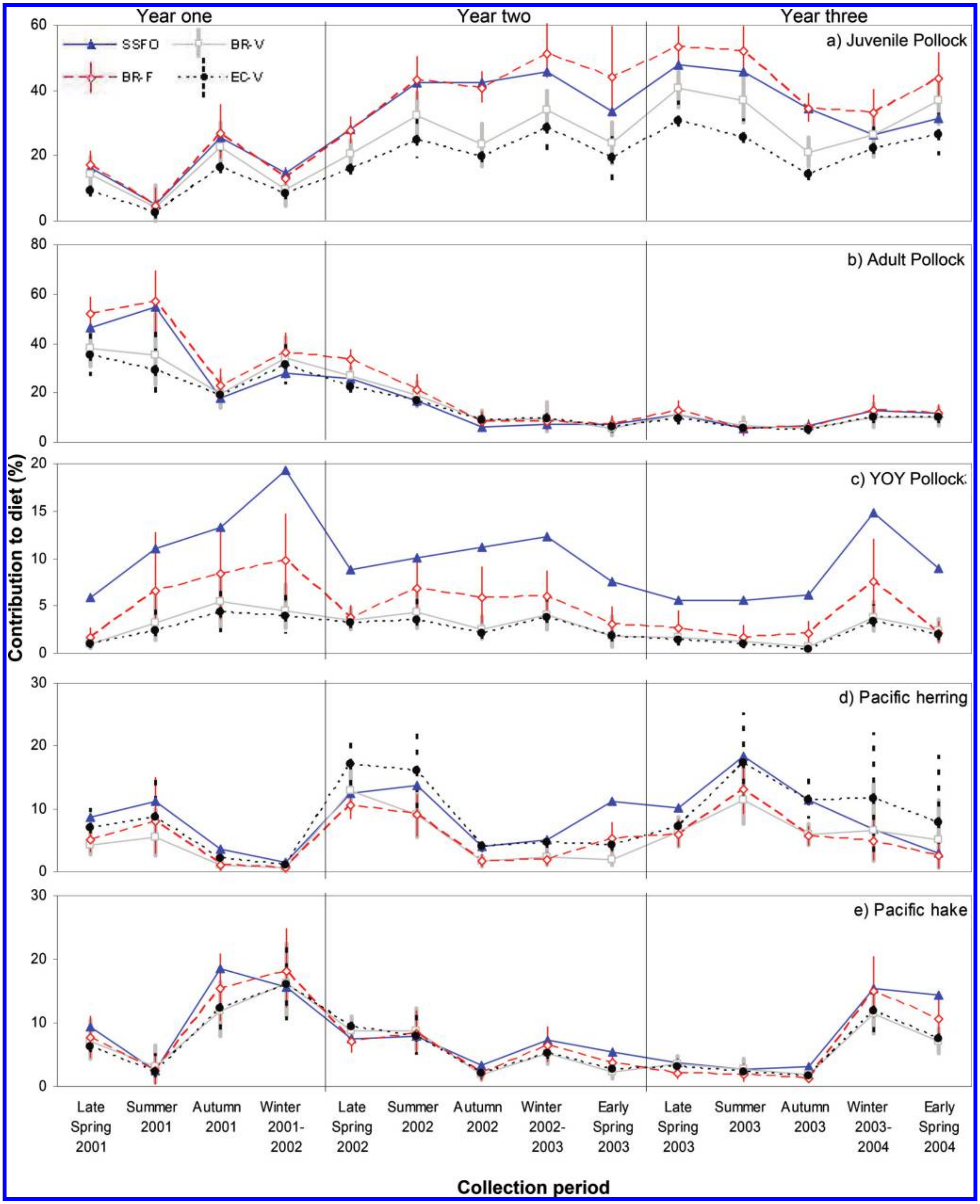


Fig. 1 (*concluded*).

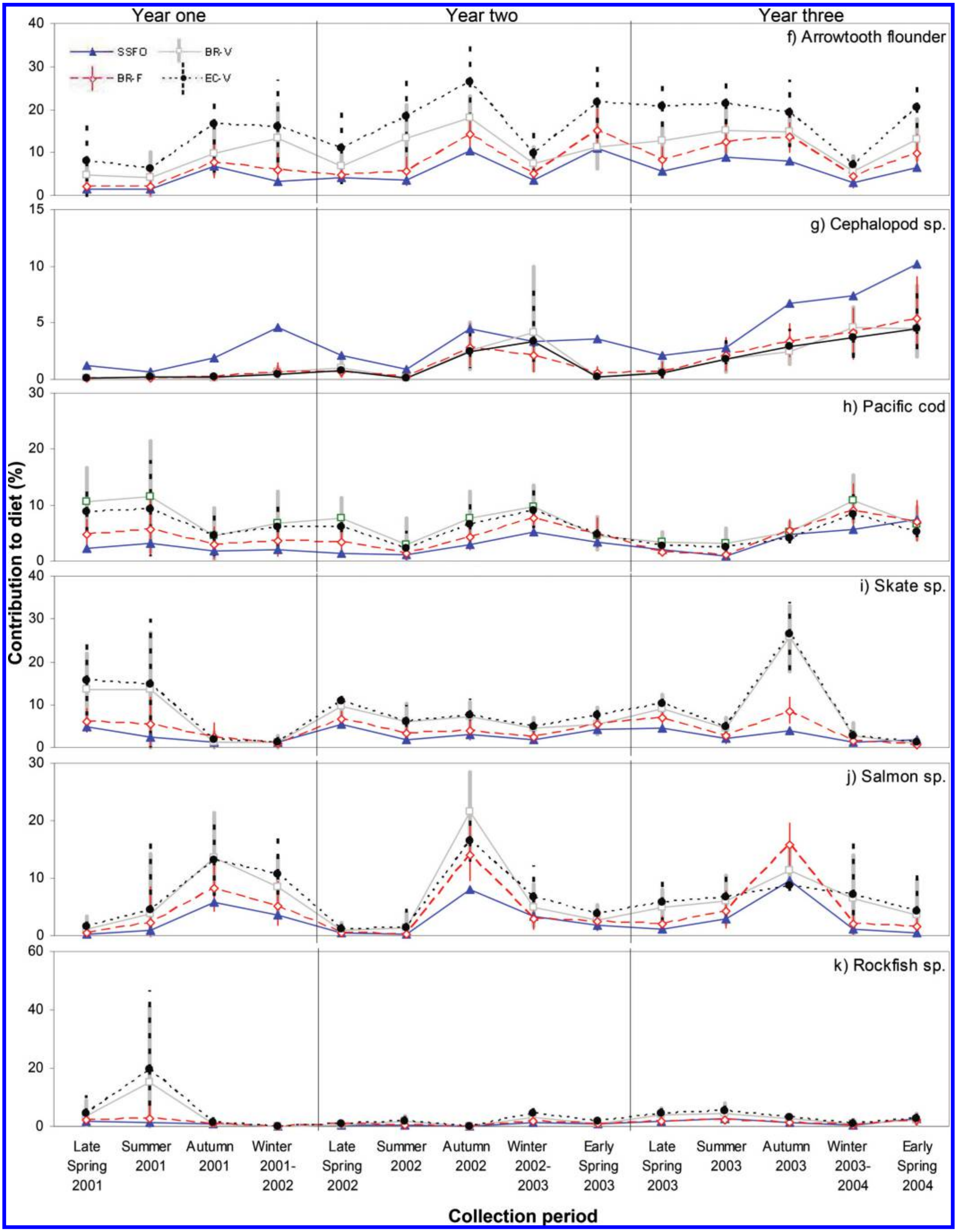
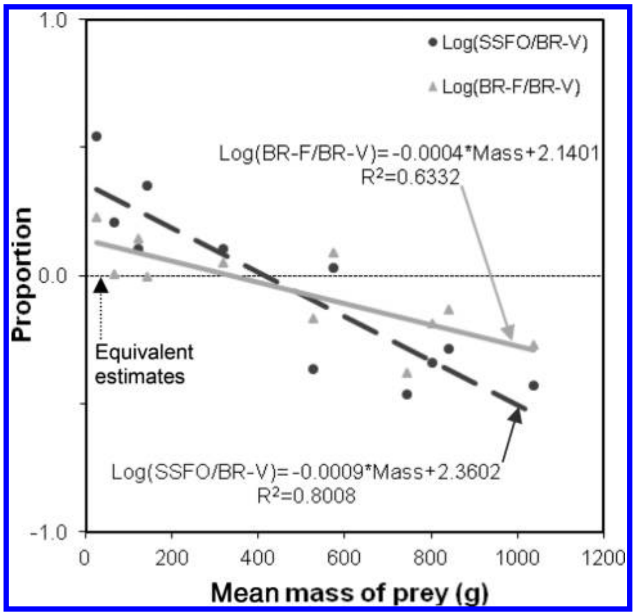


Fig. 2. Log ratio of the split-sample frequency of occurrence (SSFO) to the biomass reconstruction using the variable-biomass (BR-V) model, and log ratio of the biomass reconstruction using the fixed-biomass (BR-F) model to BR-V versus mean mass, calculated using the key categories of prey consumed by Steller sea lions (*Eumetopias jubatus*) in Frederick Sound, southeast Alaska, from 2001 to 2004. The horizontal line indicates where the ratio of the indices is equal to 1.



for example, the energy content of salmon was lowest during the autumn (Fig. 1).

Temporal and spatial variabilities in diet

Overall, key prey occurrence varied between years (χ^2 = 94.4, $p < 0.01$), seasons (χ^2 = 351.5, $p < 0.01$), and sites (χ^2 = 176.4, $p < 0.01$). Only pollock and arrowtooth flounder energetically contributed >10%, while herring contributed >5% in all seasons (Table 4). Pollock was the most important species in terms of occurrence (FO = 95%, MNI = 3.7 ± 5.0 (mean ± SD), range 1–85 fish), biomass, and energy across all collection trips, seasons, years, and haul-out sites, occurring in 2.7 times more scats and contributing at least three times the total mass and energy of any other species depending on the model used (Tables 3 and 4, Figs. 1 and 2). There were no significant seasonal, annual, or spatial differences in pollock occurrence (χ^2 = 0.1–0.4, p = 0.82–0.99), but when reassessed using our size subcategories, the FO of adult pollock was significantly highest in 2001, decreased in 2002, and was lowest in 2003 (Friedman's χ^2 = 6.0, $p < 0.05$). The opposite trend seen for juvenile pollock and YOY pollock was marginally insignificant (Friedman's χ^2 = 4.7, p = 0.10; Fig. 1).

Herring (MNI = 2.4 ± 3.9) and hake both occurred frequently, especially at Sunset Island where FO, BR-V, and EC-V were all highest (Friedman's χ^2 = 7.6–8.4, p = 0.02; Fig. 3), but seasonally, herring contributed least in winter and most in summer and late spring, while hake contributed most in winter (Table 4). The FO of herring was lowest during the first collection year (χ^2 = 6.5, p = 0.04), with hake also showing significant temporal differences in overall FO (season: χ^2 = 36.5, $p < 0.01$; years: χ^2 = 6.5, p = 0.04). Arrowtooth flounder FO and EC-V were consistently high in autumn and early spring (Table 4, Fig. 1). Both hake and arrowtooth flounder occurred mainly as single fish. Cephalopods (93% squid) occurred frequently (14%), but contributed <2% by mass or energy (Table 3). Single octopus and up to 10 small squid/scat were found most frequently in year three, mostly in winter, autumn, and early spring (Fig. 1) and at Sunset Island (Friedman's χ^2 = 5.0, p = 0.03; Fig. 3). Cod FO increased in successive collection years (Friedman's χ^2 = 6.0, p = 0.05) from 9% to 17%, with similar seasonal occurrence trends to cephalopods. Skate contributed most in late spring and autumn and least in winter (Table 4). Salmon contribution varied strongly by season, with a notably increased contribution in autumn (Table 4, Fig. 1). There was a significant decreasing trend in the BR-V and EC-V from autumn to winter with a low contribution in spring (Friedman's χ^2 = 9.0, p = 0.03). The FO was more than two times higher at Brothers Islands than at Sunset Island (Fig. 3). For both skate and salmon, usually only a single individual was recovered (100% and 87% of samples, respectively), reflecting the use of vertebrae and nonunique structures to estimate MNI. However, some scats in winter contained 5–11 smaller individuals of salmon (15–21 cm).

Supplementary data covering the period back to 1993 indicated the occurrence of pollock remained consistently high (mean (±SD) SSFO = 55% ± 8%; Fig. 4), with an FO > 85% in 23 of the 24 collection trips (outlier FO = 74% during summer 1999). The occurrence of herring peaked in 1996 and 2003 (mean (±SD) SSFO = 11% ± 6%) and was consistently higher in late spring and summer. In all of the seven collection periods between 1993 and 1999, hake occurrence was nonexistent or very insignificant. Hake then peaked during summer 1999 (FO = 63%, SSFO = 33%), resulting in the aforementioned reduction in pollock occurrence, and remained high in summer 2000, fluctuating at higher rates though seasonally thereafter. Cod showed a similar pattern to hake and was not recovered as frequently prior to 2001. In 1995 and 1996, the SSFO of salmon also peaked in autumn, but values were low (1%–2%) compared with the period of 2001–2004 (7%–11%).

Prey sizes

Vertebrae were the most useful element to identify, enumerate, and estimate size in herring (~75%), other forage fish, and salmon. Angulars, dentaries, otoliths, quadrates, and vertebrae were all useful for gadoids, and beaks for cephalopods (63%), but few (<18%) elements were available to estimate the size of arrowtooth flounder and skate (Fig. 5). Overall, half the prey had elements suitable for size estimation. It has been suggested that sea lions may tear off the head and only ingest the body of larger fish (Pitcher 1980), but we found only 1 of the 39 recovered fish that was larger than 60 cm was not identified using cranial bones.

Fish-length estimates ranged from a 3 cm myctophid to a 111 cm skate, but ~80% were within 14–42 cm, with an overall median length of 24 cm (Fig. 5). Pollock averaged 25 ± 9 cm and 172 ± 222 g (mean ± SD; range 2–3386 g), while herring averaged 18 ± 3 cm and 67 ± 37 g (range 1–539 g; Fig. 5), and thus are mostly ages 2 and 3. Hake and cod lengths were similar (cod: 38 ± 13 cm; hake: 37 ± 7 cm), representing both adults and subadults, but cod masses were greater than hake masses (cod: 802 ± 676 g (range 33–2351 g); hake: 317 ± 172 g (range 5–1390 g)). Arrowtooth flounder (43 ± 9 cm, 841 ± 503 g (range 30–3562 g)) and skate (48 ± 19 cm, 1038 ± 1998 g (range 61–8328 g)) were the largest key fish species recovered, while salmon appeared to be relatively small (31 ± 12 cm, 527 ± 675 g (range 17–3143 g)), though accurate size estimates for these species were hard to obtain. Cephalopod mass averaged 141 ± 334 g based on 187 beak measurements, but were as small as 1 g up to 600 g for squid (99 ± 110 g) and up to 4.9 kg for octopus (709 ± 1062 g).

Prey sizes varied seasonally and across years, as well as by site, for pollock and herring (Figs. 5 and 6). Pollock exhibited the largest variation. Confirming our subcategory FO analyses, adult-sized pollock dominated 2001, while smaller pollock were consumed more in 2002 and 2003. Cod and hake were also smaller in 2003, but arrowtooth flounder were larger. The opposing trends of adult and juvenile pollock found in scats were even more dramatic between 1993 and 2004, with numbers of adults peaking between 1996 and 2000. YOY pollock were recovered less frequently prior to 2001. Numbers of juvenile hake were consistently higher than adult hake in all years, with peaks in 1999 and 2003 (Fig. 7), and YOY hake being largely absent throughout. In general, more YOY

Table 4. Percent energy contribution (using variable (EC-V) and fixed (EC-F) models) for prey contributing ≥1% in any one season to the Steller sea lion (*Eumetopias jubatus*) diet in Frederick Sound, southeast Alaska, from 2001 to 2004 (prey contributing ≥10% are in boldface type).

		Season						
Model	Prey	Late spring	Summer	Autumn	Winter	Early spring	Overall	Confidence intervals
EC-V	Walleye pollock, *Theragra chalcogramma*	**42.9**	**37.1**	**30.1**	**40.2**	**32.8**	**36.9**	29.8–45.7
	Arrowtooth flounder, *Atheresthes stomias*	**13.3**	**15.2**	**20.6**	**11.0**	**20.9**	**15.9**	9.7–27.8
	Pacific herring, *Clupea pallasii*	**10.4**	**14.1**	5.9	5.8	6.0	8.6	4.9–13.4
	Skate spp., genus *Raja*	**12.2**	8.5	**11.9**	2.9	4.3	8.2	4.2–12.7
	Pacific salmon spp., genus *Oncorhynchus*	2.8	4.2	**12.7**	8.2	4.0	6.6	2.8–11.8
	Pacific hake, *Merluccius productus*	6.2	4.2	5.3	**11.0**	5.1	6.5	4.4–9.0
	Pacific cod, *Gadus macrocephalus*	5.9	4.7	5.0	7.8	4.9	5.7	2.5–9.4
	Rockfish spp., genus *Sebastes*	3.3	8.9	1.5	1.8	2.2	3.6	0.6–7.6
	Cottidae	0.1	—	1.5	6.7	2.6	2.2	0.2–5.0
	Cephalopod spp., class Cephalopoda	0.5	0.7	1.9	2.5	2.3	1.5	0.6–2.8
	Lumpsucker spp., genus *Eumicrotremus*	0.0	0.1	0.0	—	7.6	1.1	0–2.8
EC-F	Walleye pollock	**64.0**	**60.8**	**47.7**	**57.1**	**49.1**	**56.2**	49.4–63.0
	Arrowtooth flounder	6.5	8.1	**14.4**	6.0	**16.4**	9.8	6.0–13.9
	Pacific herring	9.3	**14.1**	5.2	3.7	6.0	7.8	5.0–11.0
	Skate spp.	7.0	3.9	5.0	1.7	3.2	4.2	2.0–6.9
	Pacific salmon spp.	1.1	2.3	**11.6**	3.8	2.0	4.3	2.2–7.0
	Pacific hake	5.5	3.9	6.5	**13.7**	7.7	7.4	4.8–10.4
	Pacific cod	2.9	2.4	3.9	6.3	5.4	4.1	1.8–6.8
	Rockfish spp.	1.7	1.9	1.0	0.8	1.8	1.4	0.3–3.0
	Cottidae	0.1	—	1.0	3.4	1.2	1.1	0.2–2.4
	Cephalopod spp.	0.4	0.9	2.5	2.1	3.1	1.7	0.8–2.9
	Lumpsucker spp.	0.0	0.0	0.0	—	1.3	0.2	0.0–0.5

Fig. 3. Percent frequency of occurrence (FO) of the key prey species (FO ≥ 5%) consumed by Steller sea lions (*Eumetopias jubatus*) in Frederick Sound, southeast Alaska, from 2001 to 2004, at each haul-out site (Brothers Islands, Sail Island, and Sunset Island). The asterisk indicates a significant trend across haul-out sites. The key prey species were walleye pollock (*Theragra chalcogramma*; overall, young of the year (YOY), juvenile, adult), Pacific herring (*Clupea pallasii*), Pacific hake (*Merluccius productus*), arrowtooth flounder (*Atheresthes stomias*), cephalopod spp. (class Cephalopoda), Pacific cod (*Gadus macrocephalus*), skate spp. (genus *Raja*), Pacific salmon spp. (genus *Oncorhynchus*), and rockfish spp. (genus *Sebastes*).

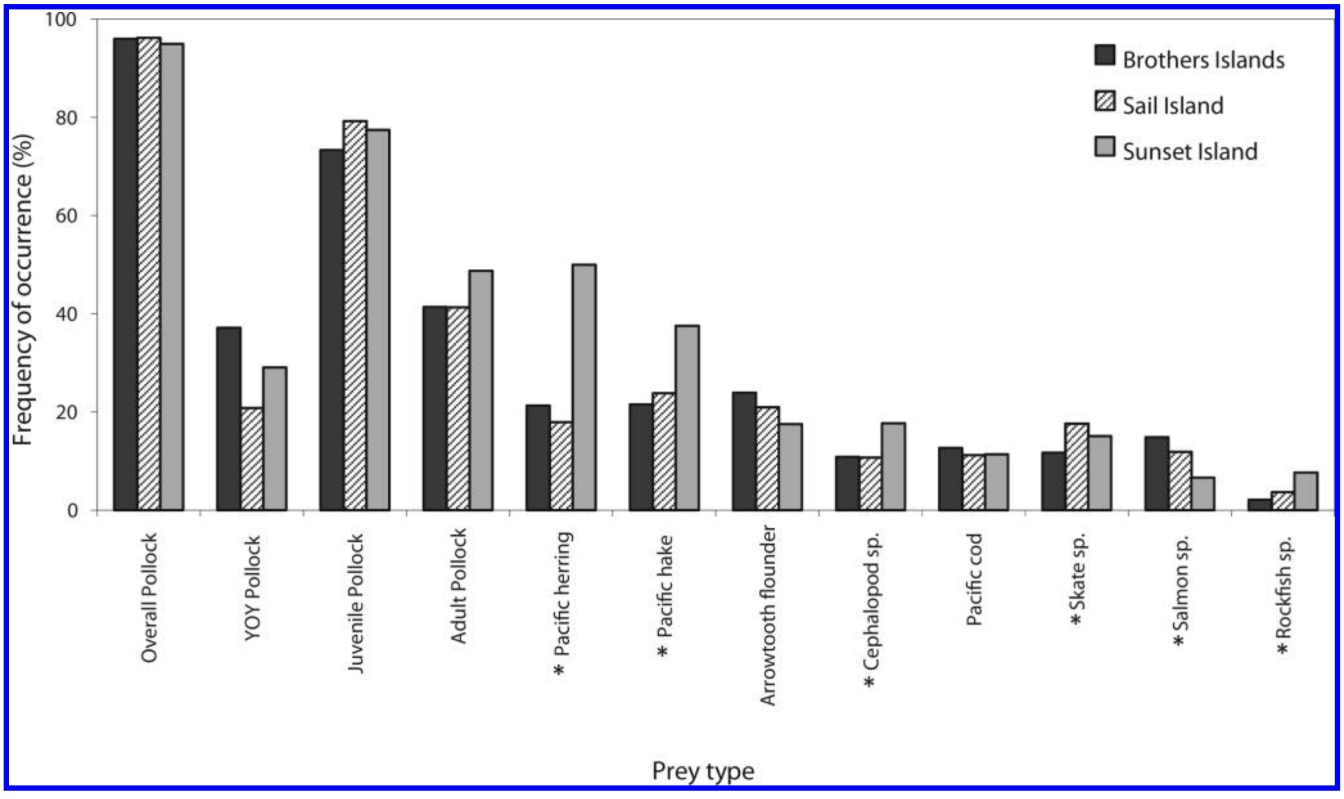
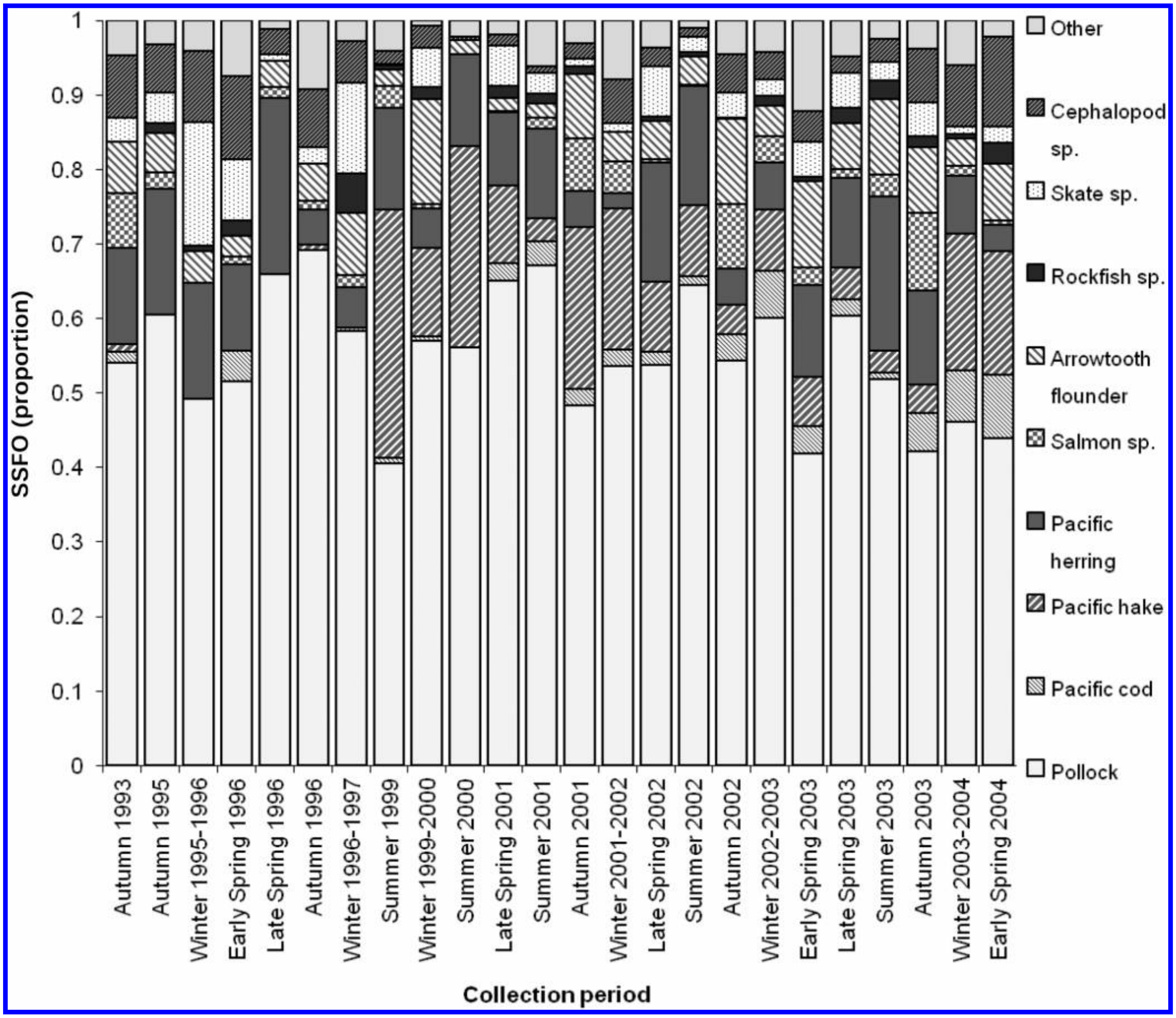


Fig. 4. Split-sample frequency of occurrence (SSFO) of the top prey categories consumed by Steller sea lions (*Eumetopias jubatus*) in Frederick Sound, southeast Alaska, over 24 collection periods between 1993 and 2004. The top prey species were walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific hake (*Merluccius productus*), Pacific herring (*Clupea pallasii*), Pacific salmon spp. (genus *Oncorhynchus*), arrowtooth flounder (*Atheresthes stomias*), rockfish spp. (genus *Sebastes*), skate spp. (genus *Raja*), cephalopod spp. (class Cephalopoda), and other.



pollock were consumed in winter, while more juvenile pollock were consumed in early spring and more juvenile and adult pollock were consumed in late spring and summer. A similar trend was seen for cod, where smaller fish were consumed in autumn than other seasons, progressing to a higher proportion of large fish in early spring and very large fish in late spring and summer. Pollock were smaller at Brothers Islands, which corresponded with our findings that YOY pollock occurred more frequently in the diet at Brothers Islands (Fig. 3). In general, herring were larger in late spring and at Sunset and Sail islands, but these size differences were small (<3 cm).

Diet diversity

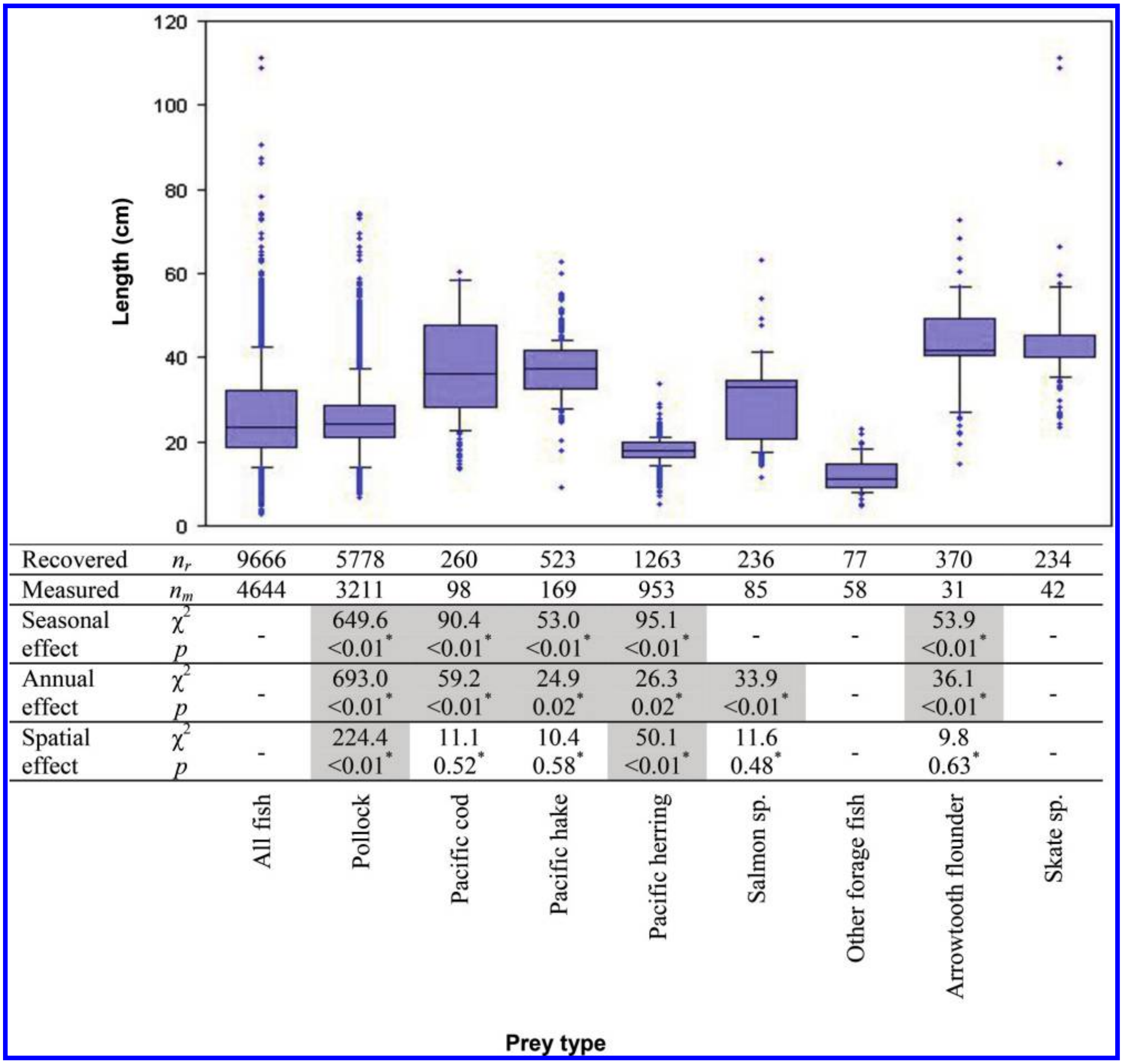
The mean (±SD) number of prey per sample was 2.5 ± 1.7 (range 1–14 species; Table 1). The only species that occurred alone in a large number of scat samples was pollock (30% of scats), followed by hake (3%). Pollock occurred with one other prey species in 27% of samples. Prey species associated with the benthos (e.g., flatfish, skate, cod) were found in at least 40% of scats.

Species diversity was 2.3 using Shannon's index of diversity (H) and 3.5 using the diet diversity index (DDI). The diversity was highest in early spring (H = 2.5, DDI = 4.1) and autumn (H = 2.4, DDI = 4.0) and lower in winter, late spring, and summer (H = 2.1, 2.0, 1.8 and DDI = 3.1, 3.0, 2.9, respectively; Fig. 6). Diet diversity increased from 2001 (H = 1.9, DDI = 2.9) to 2003 (H = 2.5, DDI = 4.0; Fig. 6), but did not vary appreciably by location (Brothers Islands: H = 2.2, DDI = 3.2; Sail Island: H = 2.2, DDI = 3.2; Sunset Island: H = 2.3, DDI = 3.8). Family-level diversity (H_f) was 2.3 in late spring through autumn and 2.6 in winter through early spring. Across collection trips, the mean energy per scat was positively correlated with diet diversity (H) and DDI (Spearman's rank correlation; H: $r = 0.9$, $p < 0.01$; DDI: $r = 0.8$, $p < 0.01$; Fig. 6).

Discussion

The growing population of Steller sea lions in SEAK has been the focus of intensive research, allowing comparison with other regions experiencing major population declines. Diet differences

Fig. 5. Box plots of the fork length (cm) of measured fish species consumed by Steller sea lions (*Eumetopias jubatus*) in Frederick Sound, southeast Alaska, from 2001 to 2004, showing the median and the 25th and 75th percentiles. Error bars represent the 10th and 90th percentiles, with outliers denoted as circles. The overall length distribution of all species is also shown. The number of fish recovered (n_r) and the number of fish measured (n_m) are shown below. Chi-squared analysis was used to test for differences in the size-class distribution of fish across seasons, years, and locations for prey categories with ≥5% frequency of occurrence (not including cephalopods) with sufficient sample size for comparison (significant differences are shaded). Fish species were walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific hake (*Merluccius productus*), Pacific herring (*Clupea pallasii*), Pacific salmon spp. (genus *Oncorhynchus*), arrowtooth flounder (*Atheresthes stomias*), and skate spp. (genus *Raja*). Figure appears in colour on the Web.



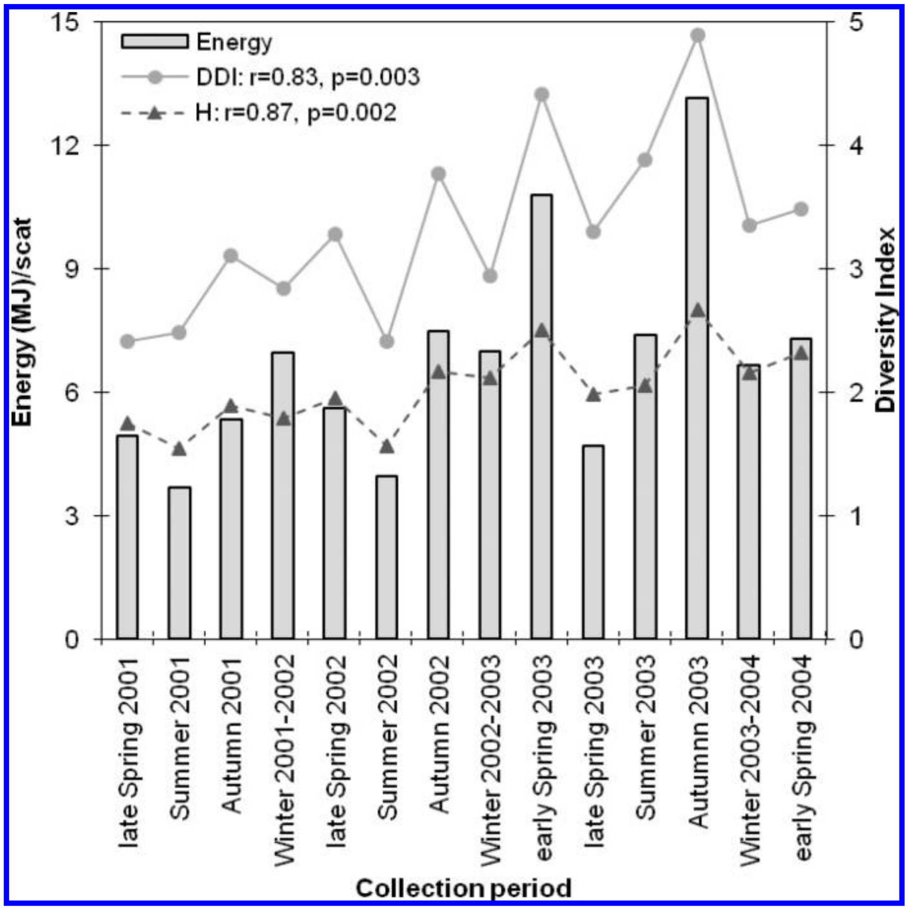
		All fish	Pollock	Pacific cod	Pacific hake	Pacific herring	Salmon sp.	Other forage fish	Arrowtooth flounder	Skate sp.
Recovered	n_r	9666	5778	260	523	1263	236	77	370	234
Measured	n_m	4644	3211	98	169	953	85	58	31	42
Seasonal effect	χ^2	-	649.6	90.4	53.0	95.1	-	-	53.9	-
	p		$<0.01^*$	$<0.01^*$	$<0.01^*$	$<0.01^*$			$<0.01^*$	
Annual effect	χ^2	-	693.0	59.2	24.9	26.3	33.9	-	36.1	-
	p		$<0.01^*$	$<0.01^*$	0.02^*	0.02^*	$<0.01^*$		$<0.01^*$	
Spatial effect	χ^2	-	224.4	11.1	10.4	50.1	11.6	-	9.8	-
	p		$<0.01^*$	0.52^*	0.58^*	$<0.01^*$	0.48^*		0.63^*	

can influence pinniped population trends (e.g., Merrick et al. 1997; Bowen et al. 2002; Trites and Donnelly 2003; Soto et al. 2006), yet systematic seasonal, multiyear Steller sea lion diet studies are sparse, especially biomass-based ones, which are considered the optimal approach, assuming key limitations are taken into account (Bowen 2000; Tollit et al. 2010). Consequently, our study uniquely integrated data from all-structure hard remains from 1631 scats with correction factors, regressions, and prey energetic densities to provide Steller sea lion diet (2001–2004) for a key region of SEAK, the cluster of haul-out sites around Frederick Sound. Both biomass- and occurrence-based dietary indices tracked major temporal and geographical differences, and overall, sea lions were documented to take advantage of widespread, abundant, and highly accessible prey like pollock, but also prey upon alternative pelagic or demersal prey.

Sea lion ecology

Pollock dominated the diet across all years, seasons, and locations, irrespective of the dietary index employed. The overall energetic contribution of pollock (mainly from juveniles) averaged 37% using EC-V and 56% using EC-F (Table 4), clearly exceeding the next most important species, arrowtooth flounder (10%–16%) and herring (8%–9%). Skates, salmon, hake, and cod were the only other notable species energetically, each with more seasonally focused

Fig. 6. Comparison of the mean energy of prey consumed per scat sample (MJ/scat) collected from Steller sea lions (*Eumetopias jubatus*) in Frederick Sound, southeast Alaska, from 2001 to 2004. Also shown are the Shannon's index of diversity (*H*) and the diet diversity index (DDI) per collection trip. Results of Spearman's rank correlation between energy per scat and each diversity index are shown in the legend.



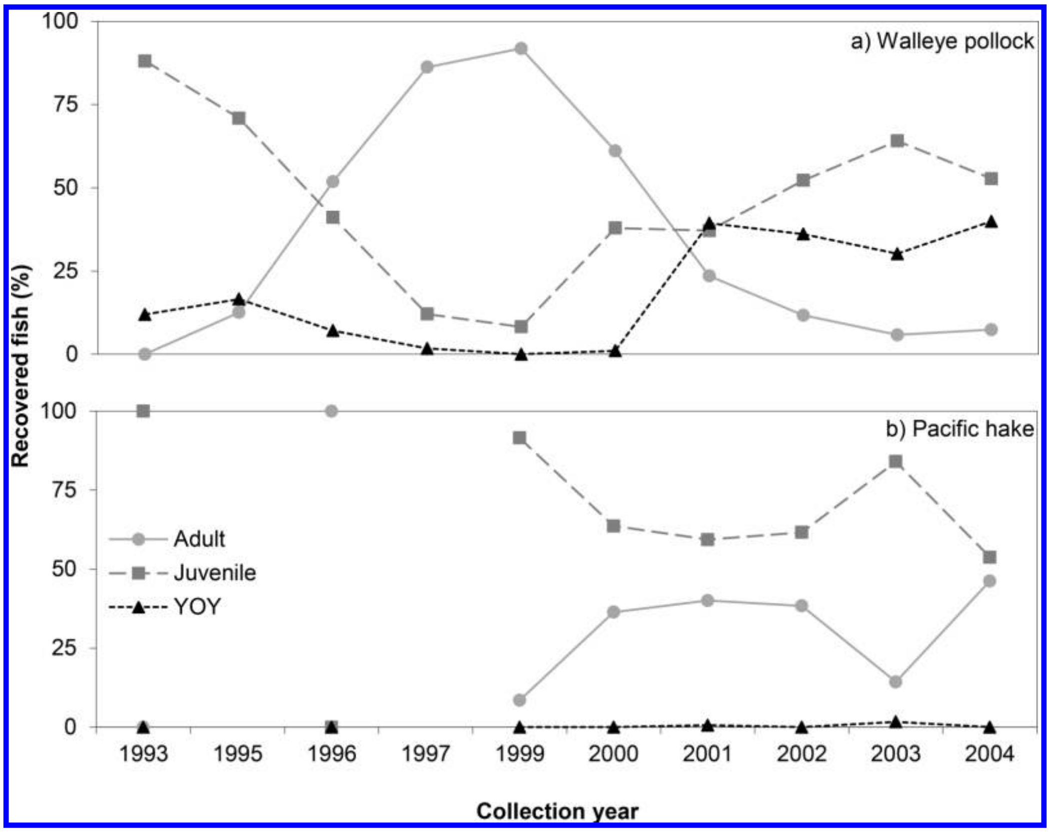
contributions. All these species have been noted previously as being important in the diet of Steller sea lions (e.g., Trites et al. 2007*a*, 2007*b*; Sigler et al. 2009; Sinclair et al. 2013). The prominence of pollock and large contributions from herring and arrowtooth flounder in the diet of Steller sea lions confirms earlier SEAK scat-based studies in the 1990s (Trites et al. 2007*a*). What is different is an increase in hake, which was negligible in the diet from the 1990s. Overall, Steller sea lions consumed fish from 3 to 111 cm, though ~80% of the fish recovered were juvenile or small adults between 14 and 42 cm. A majority of the scats contained pelagic prey (60%), with the remaining containing benthic-associated prey (40%).

Our study reiterates the considerable value of intense multi-season and long-term sampling protocols for accurately describing diet and investigating pinniped foraging ecology (e.g., Bailey and Ainley 1981–1982; Tollit and Thompson 1996). Across years, pollock was consistently important and occurred more frequently (>95%) than reported in previous Steller sea lion studies, which ranged from 7% to 91% (Trites et al. 2007*a*, 2007*b*; Sinclair et al. 2013). However, the relative importance of adult, juvenile, and YOY pollock varied dramatically between years and seasons (Figs. 1 and 7). For example, adult pollock dominated the diet in the late 1990s (Fig. 7; Tollit et al. 2004*b*), whereas juvenile (subadult) pollock dominated in the early 1990s and 2002–2004, with clear peaks of YOY fish observed in 2001 and 2004. Predation of small pollock was a result of targeting strong year-class cohorts as they moved from shallow-water habitats to pelagic habitats (Thedinga et al. 2006; Sigler et al. 2009). The dominance of pollock in the diet reflects their pelagic abundance (~75% by mass) and widespread availability (Sigler et al. 2009).

Our 10-year data set provides further evidence of sea lions opportunistically taking advantage of pelagic prey concentrations as they become available (e.g., Bailey and Ainley 1981–1982; Sinclair and Zeppelin 2002). For example, subadult and adult (Fig. 7; Bailey et al. 1982) hake became important prey after summer 1999, with a seasonal mean FO > 30% from 1999 to 2004, but occurred only sporadically in the diet from 1993 to 1997 (Fig. 4). This abrupt occurrence of hake in the diet was also noted at outer-coast rookeries of SEAK in 1998, but not in collections from previous years (A.W. Trites, unpublished data). Historically, hake migrate northwards in spring from Californian coastal waters to as far as central British Columbia, before returning south to spawn in winter (Bailey et al. 1982). Evidence to the contrary from both foraging sea lions in SEAK and from range-wide and local research pelagic surveys (our study; Benson et al. 2002; Sigler et al. 2009) indicate that hake have moved north of their traditional habitat following a strong El Niño–Southern Oscillation event in 1997–1998 and (or) after a putative regime shift to warmer conditions in 1989 (see Benson et al. 2002; Ressler et al. 2007). Since 1999, hake have become entrained in the Frederick Sound area, and consequently, have become a recent important source of food for Steller sea lions, especially in winter (Table 4), highlighting in particular their flexible foraging strategy and the need for long-term dietary monitoring in an unpredictable environment.

Energetic contribution of many species varied seasonally in our study (Table 4), notably salmon which peaked in autumn

Fig. 7. Percentage of fish recovered from Steller sea lion (*Eumetopias jubatus*) scats in Frederick Sound, southeast Alaska, from 1993 to 2004, estimated to be adult, juvenile, or young of the year (YOY) for (*a*) walleye pollock (*Theragra chalcogramma*) and (*b*) Pacific hake (*Merluccius productus*).



each year, coinciding with the return of spawning pink salmon (*Oncorhynchus gorbuscha* (Walbaum, 1792)) to the area (Heard 1991), hake in winter, and local spawning herring in late spring and summer (Skud 1960). Interestingly, seasonal fluctuations of herring and hake in the diet did not correspond with changes in their overall relative abundance based on local pelagic surveys (Sigler et al. 2009), perhaps as a result of the high surplus of pollock available, fine-scale prey patchiness, or access to alternate foraging areas. While both species were present year-round, skate were energetically most important in late spring and autumn, whereas cod were most important in winter (Table 4), as seen elsewhere (Sinclair and Zeppelin 2002). The occurrence of herring, hake, and salmon also exhibited strong site variability, presumably as result of animals taking advantage of local prey concentrations (see Womble et al. 2005). For example, sea lion numbers at Sunset Island peaked between April and June (Sigler et al. 2009), coincident with local spawning aggregations and the very high herring FO (~60%) noted in our study. Like most studies, our analysis assumed site scat collection success was related to the number of animals present. Sampling protocols, such as those we aimed for in our study, should try to ensure capturing a representative proportion of the population based on previous monitoring.

Estimating the importance of salmon to pinnipeds, a prey noted for fragile hard parts, has concerned many researchers (e.g., Pierce and Boyle 1991). Molecular genetic techniques can now identify prey in scats from soft prey tissue DNA remains and concurrent DNA comparisons with hard-part identifications indicated that hard parts had missed ~20% of recent meals (Tollit et al. 2009). These consisted mainly of salmonids, flatfish, elasmobranchs, and cephalopods, amounting to 10%–15% increases in the occurrence of individual species, which suggests that other sea lion diet studies that only use hard parts potentially underestimate the importance of these species. As such, dual methodologies are recommended (Tollit et al. 2010). This same study identified the salmon hard parts recovered in Frederick Sound during autumn (September) as mainly pink salmon. Local district (109 and 110) purse seiners landed a mean of 9 million pink salmon through our study period (mainly during mid-July through August; ADF & G Integrated Fisheries Database). The contribution of salmon to the year-round diet is thus potentially considerably higher than what we have documented, based on DNA results and the fact that our sampling dates missed the peak return of pink salmon. Increased rates of sampling may be required for a full description of key prey. Salmon were the most frequently occurring prey at SEAK rookeries (Trites et al. 2007*a*) and was the only species through the 1990s to seasonally contribute >20% FO in all four western DPS regions (Sinclair and Zeppelin 2002). Given their clear importance and strong interannual and regional density fluctuations, a more thorough review of which species are important, when they are important, and the extent to which they are energetically important is warranted. For example, the peak in sea lion abundance in Frederick Sound (July to October; Sigler et al. 2009) may represent animals returning from the coastal rookeries and following the adult salmon as they migrate inshore to spawning rivers. On a wider scale, potential influences of salmon on sea lions have been highlighted by Sinclair et al. (2005).

In Frederick Sound, sea lions take advantage of widespread, abundant, and highly accessible prey like pollock, but also find more profitable patches of alternative pelagic or demersal prey (as indicated by the 2.5 prey categories/scat). Optimal foraging theory (Stephens and Krebs 1986) applied to a central place forager such as the Steller sea lion predicts that an animal will attempt to minimize search (swimming and diving) and handling (capture, killing, eating, and digesting) time, while maximizing energetic return. Energetic return from a single prey item is largely dependent on its size, quality (energetic density), and encounter rates.

Prey associated with the benthos were found in 40% of scats, with abundant mid-sized species found at accessible depths apparently targeted by sea lions, especially arrowtooth flounder (Sigler et al. 2009). Arrowtooth flounder are among the most abundant demersal fish in Frederick Sound longline surveys (Sigler et al. 2009), are predators of pollock, and have relatively high energetic density in SEAK (Schaufler et al. 2006). Their energetic contribution peaked (~20%) in autumn and early spring (coinciding with autumn through winter batch spawning events), with a mean size range of around 43 cm, suggesting that both juvenile and adult fish were consumed. Previously, arrowtooth flounder have both been recorded as important prey in the Gulf of Alaska (Sinclair and Zeppelin 2002) and in British Columbia waters (Olesiuk et al. 1990).

Unlike the very diverse summer diet seen at coastal breeding rookeries in SEAK from 1990 to 1999 (DDI = 5.3; Trites et al. 2007*a*), the diet of nonbreeding sea lions using the protected inshore haul-out sites of Frederick Sound were least diverse in summer (DDI = 2.9), peaking instead in autumn and early spring (DDI = 4.0 and 4.1, respectively) when increases in arrowtooth flounder, cephalopods, cod, salmon (autumn only), and hake (early spring only) occurrence were apparent. The local regional differences in summer diet diversity were driven by more than sixfold higher rates of occurrence of salmon, sand lance, and rockfish in scats collected at the coastal rookery sites compared with our study. Diet diversity outside of summer was clearly lower ($H = 2.3$) than at an important seasonal haul-out site in the Lynn Canal region of northern SEAK (Benjamin Island, $H = 3.5$), where herring was the most frequently consumed prey (90% FO), together with pollock (88% FO; Womble and Sigler 2006) and 12 prey groupings exceeding 5% FO, including capelin, eulachon, and northern lampfish (*Stenobrachius leucopsarus* (Eigenmann and Eigenmann, 1890)). In contrast to Frederick Sound, research surveys at Benjamin Island from 2001 to 2004 detected dense, highly predictable year-to-year winter aggregations of herring, which overall represented 82% of the pelagic prey energy available (Gende and Sigler 2006). The importance of Benjamin Island as a seasonal haul-out site was further highlighted by the more than fourfold higher prey-derived energy per scat (mean energy content 30.4 MJ) compared with Frederick Sound (7.1 MJ). Overall, Steller sea lions thus appear to be opportunistic marine predators, with a flexible foraging strategy that select abundant, accessible prey and shift among seasonally available species.

The relationship between low diet diversity and population decline reported by Merrick et al. (1997) is well supported by rookery diet data from SEAK and British Columbia (Trites et al. 2007*a*; A.W. Trites and P.F. Olesiuk, unpublished data). Diversity of prey families in our study from May to September in 2001–2004 ($H_f = 2.3$) are fairly similar to the eastern Aleutians and western Gulf of Alaska in the 1990s ($H_f = 2.0$–2.1), but clearly higher than the central and western Aleutians ($H_f = 1.5$) where population declines are largest. Family diversity in Frederick Sound was notably higher from October through April ($H_f = 2.6$) than reported for any of the western DPS populations of Steller sea lions ($H_f = 1.8$–2.1; Sinclair and Zeppelin 2002), potentially indicating this time period may be of some importance to Steller sea lions.

The diversity indices (both DDI and H) that we derived for Frederick Sound appear to have captured seasonal changes in mean energy contributed by the different species recovered in the scats (Fig. 6), suggesting that further exploration with different suites of prey is warranted. An approach that integrates prey biomass and energetic content to estimate diet diversity would best allow for wider scale regional comparisons. A wider array of diet groupings would provide a clearer ecological assessment of diversity and allow for within-group energetic density disparities. Having said that, robust temporal comparisons with regional diet data sets collected prior to 1990s are difficult due to methodological differences, low sample sizes, and potential sex-ratio-related differences. Pollock dominated the relatively few stomach samples collected in the 1970s and 1980s (mainly collected in the winter from the Gulf of Alaska; e.g., Pitcher 1981). Diversity appeared low to moderate, also mirroring that seen in regional scat collections in the 1990s, providing few clues as to why population declines were so severe in the former time period.

Diet index performance

In addition to providing a valuable overall bioenergetic summary of Steller sea lion diet and investigate the causes of regional, interannual, and seasonal prey consumption patterns described, our study also aimed to contrast diet index performance. It is important to bear in mind, given the highlighted issues and effort of enumerating prey and estimating mass from morphometric relationships with prey remains, at the wider scale that occurrence indices can be used to highlight key prey species and track temporal or geographical differences. Secondly, it is clear that the percent diet composition for some top-ranking prey can vary by a factor of up to two or more, depending on the method used to estimate composition within each scat. However, the mean absolute margin of these differences was only ~4% and were only significant when comparing occurrence indices and variable-based BR and EC indices for key prey (i.e., unimportant prey groupings contributing <5% FO were excluded from the analysis). Observed differences appeared to be well correlated with prey size, with variable biomass-based models estimating the greatest contributions from large prey and SSFO estimating the greatest contributions from smaller prey (Figs. 1 and 2), a result also highlighted in previous pinniped diet index comparative studies (Laake et al. 2002; Vollenweider et al. 2006), as well as computer simulations (Olesiuk 1993; Joy et al. 2006). Thus, these two indices were most similar when prey were of moderate size (~400 g), such as hake and adult pollock. We could potentially conclude that estimated values for small prey should be considered upper limits and that values for large prey should be conversely considered lower limits if occurrence indices are used to describe diet.

Captive studies to date document biomass models perform better than occurrence models across a range of diet scenarios (Casper et al. 2006; Tollit et al. 2006; Phillips and Harvey 2009), with variable models providing marginally better predictions of actual mass fed than fixed models. The variable models attempt to capture the unpredictability of foraging and the apparent pulsed nature of hard-part recovery in scats. Thus, animals presumably foraging most successfully are given a higher weighting. This assumption may also have a tendency to bias towards larger animals and, as observed in our study, can sometimes inflate the contribution of particularly large or abundant prey found in only a few scats. We therefore strongly recommend generating confidence intervals (using resampling methods, e.g., Stenson and Hammill 2004) for biomass models (especially variable-based ones) to provide a measure of error and to allow the impact of any outliers to be critically assessed. Confidence intervals in our study averaged 50%–65% around EC-V, but often exceeded 200% and would have been higher still if we had included variability in NCF and prey size estimates. As a result, point values of prey proportions in a diet must be treated with appropriate caution, especially if they are subsequently used for calculating consumption estimates or used in ecosystem models.

Given the differences observed between fixed and variable methods (including SSFO versus MFO), further fine-scale foraging studies are needed to determine if meal size actually varies systematically with prey type and availability (justifying variable models). Overall, we recommend deriving diet composition estimates using both variable and fixed methods due to the plausible but largely untested assumption that reconstructed biomass of scats reflects variability in foraging success and meal size (consumption), as well as due to differences in digestion and subsequent deposition, and the probable inclusion of incomplete scat samples in most scat studies. MFO considers overall contribution of a species to be the same irrespective of the number of species within a scat, whereas SSFO makes an equal contribution assumption whereby the more prey species in a scat the less important each one is overall. SSFO seems to be the more reasonable assumption of the two and contributions generally match BR-F, but once again the extent of index differences will depend mainly on diet diversity and feeding patterns. For example, in our study, pollock occurred alone in 30% of scats, resulting in a higher contribution calculated using SSFO (54%) compared with MFO (38%; Table 2).

Numerous captive feeding studies have shown that differential erosion and passage rate of prey items in relation to their size and robustness is one of the major sources of error in the analysis of prey remains from scats (Harvey 1989; Tollit et al. 1997; Bowen 2000; Staniland 2002; Grellier and Hammond 2006). Numerical and digestion correction factors can theoretically account for these differences and this study has for the first time attempted to integrate both correction factor types with an all-structure diet assessment. However, we note that correction factors were not available for all species and that it was not always possible to apply robust species-specific regressions. Nevertheless, applying NCF did have a significant effect on key prey rankings (Spearman's $\rho = 0.81$, $p = 0.011$), reducing the importance of large gadids by approximately 30%–40% (though pollock still remained the predominant prey). It is clear that future biomass-based diet studies must continue to address digestion-related biases (Cottrell and Trites 2002; Tollit et al. 2003; Grellier and Hammond 2006). Secondary ingestion of prey and prey hard-part regurgitation are also potential biases that are difficult to quantify (Gudmundson et al. 2006, Tollit et al. 2010). The 20% of fish found that were less than 14 cm in length were mainly small YOY pollock, but also sand lance, myctophids, and gunnels. With the exception of YOY pollock, the energetic contribution of these small fish was small (~1%; Table 3), indicating secondary prey effects were likely small. Hard parts of large cephalopods and large fish may be regurgitated or discarded during ingestion leading to potential underestimation using scats alone (Tollit et al. 2003).

Overall, our study shows that Steller sea lions switched from adult pollock to strong cohorts of juvenile pollock, and took advantage of spawning concentrations of salmon in autumn and herring in late spring and summer, as well as a climate-driven increase in hake availability. Our findings point to the need for robust scat sampling protocols to capture temporal and spatial variabilities in prey selection. All of the major indices of diet that we applied tracked similar key temporal changes in diet. However, diet estimates derived from occurrence-based and biomass-energy-based methods, while differing by a mean of 4%, differed by as much as a factor of two, highlighting the effect that prey size, energy density, and numerical correction factors can have on the robustness of diet estimates.

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