Abstract—Lengths of walleye pollock (*Theragra chalcogramma*) consumed by Steller sea lions (*Eumetopias jubatus*) were estimated by using allometric regressions applied to seven diagnostic cranial structures recovered from 531 scats collected in Southeast Alaska between 1994 and 1999. Only elements in good and fair condition were selected. Selected structural measurements were corrected for loss of size due to erosion by using experimentally derived condition-specific digestion correction factors. Correcting for digestion increased the estimated length of fish consumed by 23%, and the average mass of fish consumed by 88%. Mean corrected fork length (FL) of pollock consumed was 42.4 ±11.6 cm (range=10.0–78.1 cm, *n*=909). Adult pollock (FL>45.0 cm) occurred more frequently in scats collected from rookeries along the open ocean coastline of Southeast Alaska during June and July (74% adults, mean FL=48.4 cm) than they did in scats from haulouts located in inside waters between October and May (51% adults, mean FL=38.4 cm). Overall, the contribution of juvenile pollock (≤20 cm) to the sea lion diet was insignificant; whereas adults contributed 44% to the diet by number and 74% by mass. On average, larger pollock were eaten in summer at rookeries throughout Southeast Alaska than at rookeries in the Gulf of Alaska and the Bering Sea. Overall it appears that Steller sea lions are capable of consuming a wide size range of pollock, and the bulk of fish fall between 20 and 60 cm. The use of cranial hard parts other than otoliths and the application of digestion correction factors are fundamental to correctly estimating the sizes of prey consumed by sea lions and determining the extent that these sizes overlap with the sizes of pollock caught by commercial fisheries.

Sizes of walleye pollock (*Theragra chalcogramma*) consumed by the eastern stock of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska from 1994 to 1999

Dominic J. Tollit

Susan G. Heaslip

Andrew W. Trites

Marine Mammal Research Unit, Fisheries Centre
University of British Columbia
Room 18, Hut B-3, 6248 Biological Sciences Road
Vancouver, British Columbia, Canada, V6T 1Z4
E-mail (for D. J Tollit): tollit@zoology.ubc.ca

The dramatic decline of the western population of Steller sea lions (*Eumetopias jubatus*) in the 1980s (Loughlin et al., 1992; Trites and Larkin, 1996) prompted a number of studies to determine what they eat and the extent of overlap of the fish consumed by Steller sea lions and fish caught by commercial fisheries. The eastern population of sea lions (east of longitude 144°) located mainly in Southeast Alaska and British Columbia gradually increased as the western population declined (e.g., Calkins et al., 1999), permitting insightful comparative studies to be undertaken (e.g., Merrick et al., 1995; Milette and Trites, 2003). Possible explanations for the different population trends include ocean climate, competition with fisheries, predation, and the amount or the sizes of pollock in the diets of sea lions in the two regions (Loughlin and York, 2000; Benson and Trites, 2002; NRC, 2003; Trites and Donnelly, 2003; Calkins and Goodwin[1]; Loughlin and Merrick[2]).

Reliable estimates of prey size are important not only to investigate prey selectivity and the extent of overlap in size of prey with size of the same species caught by commercial fisheries and by other marine piscivores but are also vital for accurately assessing prey numbers, biomass, and total consumption (Beverton, 1985; Ringrose, 1993; Laake et al., 2002). One means of estimating prey size is to measure hard parts recovered from fecal remains and to apply allometric regressions relating fork length to the size of otoliths (Frost and Lowry, 1981) and other bones (Zeppelin et al., 2004, this issue). However, the extent of digestion incurred by both otoliths and bones as they pass through the digestive tract must be accounted for to ensure that prey size is not underestimated (Tollit et al., 2004, this issue). Application of these two steps is integral to correctly estimate the size of prey consumed by Steller sea lions and other pinnipeds.

The goal of our study was to estimate the size of walleye pollock (*Theragra chalcogramma*) consumed by Steller sea lions in Southeast Alaska between 1994 and 1999 by using new methods outlined by Tollit et al. (2004, this issue) and Zeppelin et al. (2004, this issue). Previous size estimates for this region of Alaska are based on the analysis of only eight stomachs collected in 1986 (Calkins

[1] Calkins, D. G., and E. Goodwin. 1988. Unpubl. report. Investigation of the declining sea lion population in the Gulf of Alaska, 76 p. Alaska Department of Fish and Game, 333 Raspberry Rd, Anchorage, AK 99518.

[2] Loughlin, T. R., and R.L. Merrick. 1989. Comparison of commercial harvest of walleye pollock and northern sea lion abundance in the Bering Sea and Gulf of Alaska. *In* Proceedings of the international symposium on the biology and management of walleye pollock, Nov. 14–16, 1988, Anchorage, AK, p. 679–700. Alaska Sea Grant Rep. 89-01, Univ. Alaska Fairbanks, Fairbanks, AK.
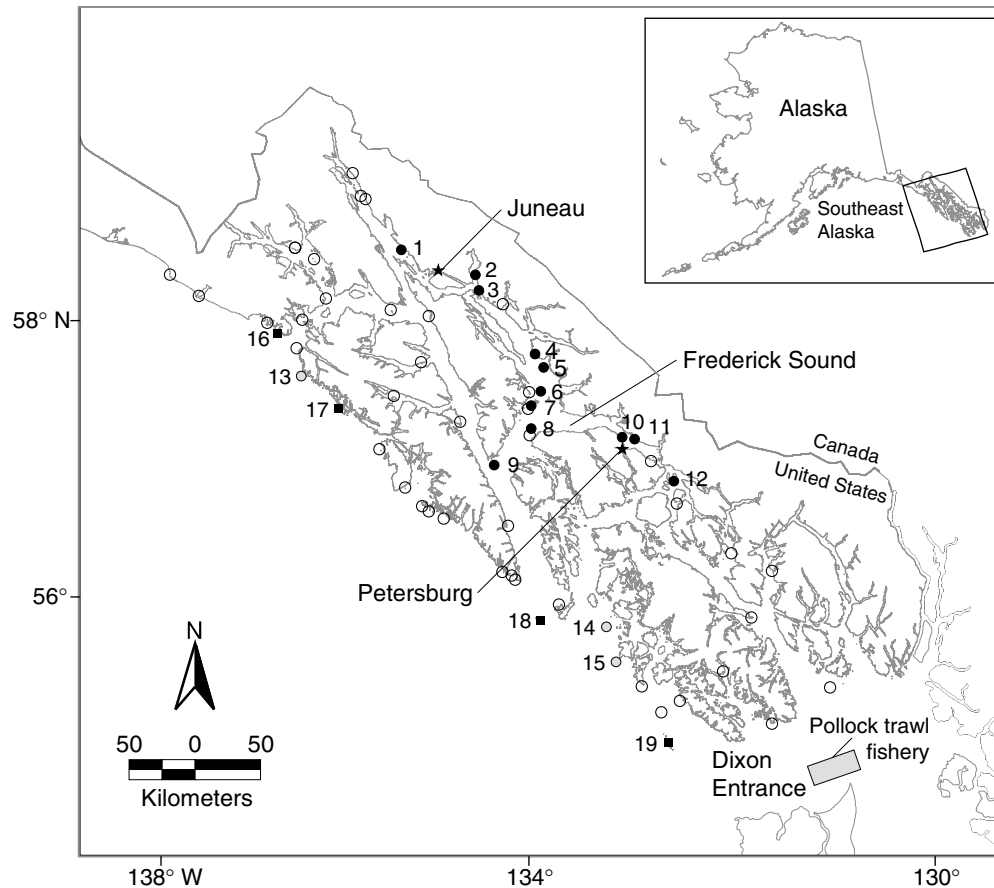
Figure 1

Location of Steller sea lion (*Eumetopias jubatus*) haul-outs and rookeries visited during 1994–99 to collect scats containing pollock hard remains. Symbols: haul-outs in inside waters (●), haul-outs in outside waters (◉), haul-outs where scats were not collected or sites at which no pollock hard remains were found (○), rookeries (■), and cities (★).

and Goodwin[1]). We sought to compare the sizes of pollock consumed in the 1990s with these earlier samples, as well as with the sizes consumed by the declining population of sea lions in the Gulf of Alaska and Bering Sea during the 1970s and 1980s (e.g., Pitcher, 1981; Merrick and Calkins, 1996) and between 1998 and 2000 (Zeppelin et al., 2004, this issue). We also wanted to evaluate the use of digestion correction factors (DCFs) and skeletal structures other than otoliths to estimate prey size, and to compare the different size estimates for fish consumed by sea lions in Southeast Alaska with sizes of fish caught by a nearby commercial trawl fishery.

Materials and methods

Estimating sizes of pollock consumed

Scats that contained pollock hard remains were collected from four rookeries and 16 haul-outs from both inside and outside waters of Southeast Alaska between 1994

and 1999 (Fig. 1 and Table 1). Scats from three haul-outs and four rookeries in outside waters were collected from May through October 1994–99, but most were collected from June and July. Scats from inside waters were collected at 13 haul-outs located in the straits and sounds between Juneau and Petersburg, Alaska (56.8–58.6°N, 132.8–134.9°W) (Fig. 1). The majority of these "inside" scats were collected from Frederick Sound (Fig. 1) between October 1995 and February 1997. Most were collected in the winter and spring, but some were collected in the summer of 1999 (Trites et al.[3]). In general, the haul-out sites visited to collect scats were those with relatively high numbers of animals across Southeast Alaska (Calkins et al., 1999; Sease et al., 2001).

Scats were washed and sieved (0.5 mm) and hard remains were identified by Pacific IDentifications Inc. (Univ. of Victoria, Victoria, B.C.). Seven commonly

---

[3] Trites, A. W., D. G. Calkins, and A. J. Winship. 2003. Unpubl. data. Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Room 18, Hut B-3, 6248 Biological Sciences Rd., Vancouver, B.C., Canada, V6T 1Z4.

Table 1

Steller sea lion scat collection sites in Southeast Alaska, as illustrated in Figure 1, giving details of the type (HO=haul-out), fish element sample size (n_f), and the estimated corrected mean fork length (mean FL, cm) of walleye pollock, based on seven cranial structures found in scats at each site.

Region	Site no.	Site name	Type	n_f	Mean FL	SD
Inside waters	1	Benjamin Island	HO	11	39.7	13.9
	2	Dorothy Island	HO	3	38.6	13.6
	3	Circle Point	HO	31	45.1	13.7
	4	Point League	HO	37	42.9	9.9
	5	Sunset Point	HO	196	37.4	10.3
	6	Sail Island	HO	36	35.5	10.0
	7a	W Brother Island	HO	8	40.9	14.7
	7b	SW Brother Island	HO	152	37.1	9.9
	8	Turnabout Island	HO	34	47.8	11.0
	9	Yasha Island	HO	19	44.8	5.3
	10	Sukoi Islets	HO	14	26.9	7.8
	11	Horn Cliffs	HO	19	44.3	12.7
	12	Liesnoi Island	HO	7	31.8	10.2
Outside waters	13	Cape Cross	HO	7	45.3	3.0
	14	Timbered Island	HO	5	39.3	8.7
	15	Point Addington	HO	1	53.5	—
	16	Graves Rock	Rookery	49	42.9	7.7
	17	White Sisters	Rookery	33	43.4	9.6
	18	Hazy Islands	Rookery	54	45.4	8.7
	19	Forrester Islands	Rookery	193	51.4	10.0

occurring, robust, and diagnostic pollock structures were removed from all scats containing pollock (see Tollit et al., 2004, this issue). All were from the cranium region (see Zeppelin et al., 2004, this issue) and included the sagittal otolith (OTO), as well as the interhyal (INTE), hypobranchial 3 (HYPO), pharyngobranchial 2 (PHAR), angular (ANGU), quadrate (QUAD), and the dentary (DENT). Each individual fish element was assigned one of three condition categories (good, fair, or poor) and was measured three times (±0.01 mm) at a specific location to calculate a mean estimate (see Tollit et al., 2004, this issue).

Fork lengths of pollock eaten by Steller sea lions in Southeast Alaska were first estimated by applying allometric regressions (Zeppelin et al., 2004, this issue) to otolith lengths (OTOL) without correcting for partial digestion (see Pitcher, 1981; Merrick and Calkins, 1996). We also measured and substituted otolith width (OTOW) when otoliths were broken lengthwise. We then applied appropriate DCFs and regression formulae to otoliths assigned in good and fair condition (Tollit et al., 2004, this issue). Finally, we applied allometric regressions (Zeppelin et al., 2004, this issue) to all elements of the remaining six cranial structures (bones) assigned to good or fair condition categories to provide estimates of fish size across structures both with and without applying the appropriate DCFs (Tollit et al., 2004, this issue). Structures in poor condition were excluded because of large intraspecific size variation noted from feeding experiments with captive sea lions (see also Sinclair et al., 1994; Tollit et al., 1997; Tollit et al., 2004, this issue).

To incorporate the major sources of error in our method, we calculated confidence intervals (95%) for fork-length estimates. First, we applied a random bootstrapped regression equation, followed by a bootstrapped correction factor applicable to each selected structure (see Tollit et al., 2004, this issue). For the five structures (INTE, HYPO, PHAR, ANGU, and OTO) in good condition for which Tollit et al. (this issue) recommended a DCF of 1.0 (no correction), we drew bootstrapped values from a discrete declining triangular probability distribution (◹) ranging from 1.0 to 1.05 (to simulate a limited degree of digestion). Finally, we bootstrapped individual scats at random, by selecting n scats with replacement from the original sample size n (to account for resampling variability across scats) and included only selected elements within those randomly bootstrapped scats. Bootstrap randomizations for these steps were done 1000 times and 95% confidence intervals were taken as the 25th and 975th values of the sorted bootstrapped values.

Finally, consideration was also given to whether an individual fish might be represented by different structures within a single scat. We therefore compared length estimates using all structures with those esti-

mated with the minimum number of individuals (MNI) technique (Ringrose, 1993; Browne et al., 2002). This technique is used to select structures within each scat that preclude pseudoreplication or double counting of fish. Within each scat, the structure with the greatest MNI was selected, and right-sided structures were selected over left-sided structures if both sides were found in equal number because right-sided structures are used in regression formulae. If two structures had the same MNI estimate, then selection was made on the structure with the larger regression determination coefficient, r^2 (OTO-W>OTO-L>QUAD>DENT>HYPO>INTER>ANGU>PHAR).

Geographical and temporal variation in sizes of prey consumed

All elements from the seven cranial structures in good or fair condition were used to compare size of pollock consumed by Steller sea lions in Southeast Alaska between regions (inside haul-outs versus outside rookeries), across years and across rookeries (with rookery data collected in June and July), and across months (with data collected from inside haul-outs). Biologically meaningful differences in FL of pollock were assessed by grouping corrected lengths into stage-class categories (juvenile or 1-year-old fish FL≤20 cm; adolescent 20<FL≤34 cm; subadult 34<FL≤45 cm; and adult FL>45 cm) (Smith, 1981; Walline, 1983; Dorn et al., 2001). Adults were considered to be mature fish ≥5 years old and targeted by fisheries (Smith, 1981). Subadults were likely 3 or 4 years old, of which only a proportion had matured or were targeted by the fishery. To avoid the possibility of pseudoreplication in our chi-squared comparisons, we used only the presence or absence of structures of each stage class in a scat because individual fish eaten by a sea lion may have come from an age-specific school and were therefore not independent (Hunt et al., 1996). Presence-absence data was chosen over MNI data because the former greatly reduces potential concerns regarding size-dependent recovery of cranial structures (Tollit et al., 1997). With the exception of our regional comparison, data from juvenile and adolescent stage-classes were pooled because of the low sample sizes of juvenile fish. A Fisher's exact test was used as an alternative test to chi-square comparisons when counts for a stage-class grouping were <5 (S-PLUS 2000, Mathsoft Inc., Seattle, WA).

Overlap of prey size with size of fish caught by fisheries

To assess the impact of using the new methods described and to compare the size of pollock consumed by sea lions with the size of pollock typically caught by fisheries, we obtained randomly subsampled size-frequency landing data from the Canadian commercial pollock fishery in Dixon Entrance (1993–1999) (Saunders[4]). This area is

---

[4] Saunders, M. 2002. Unpubl. data. Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, B.C., Canada, V9T 6N7.

115–135 km SE of the Forrester Island rookery on the southern border of Southeast Alaska (Fig. 1).

Results

Sizes of pollock consumed

The traditional method of estimating prey size from otoliths alone was not satisfactory because most otoliths were in poor condition (86%, n=247) or were broken lengthwise (>89%) (or were both broken and in poor condition). Cranial bones, on the other hand, occurred in higher numbers than otoliths and were therefore more useful for estimating prey size (Table 2).

Sixty-one percent of scats (1215 of 1987) collected from Southeast Alaska (1994–99) contained pollock remains, with an average MNI of 1.57 ±1.66 individual pollock per scat (range: 1–37 individuals). Many scats contained hard parts that were not useful for estimating prey size (e.g., gill rakers), leaving 531 scats (26%) with measurable selected structures. Of these, 303 scats contained 1746 elements in good (n=225), fair (n=684), and poor condition (n=837).

Applying digestion correction factors had a considerable effect on the estimated length and mass of fish consumed, and on the proportion that were deemed to be adults (Fig. 2). The estimated lengths of pollock calculated from all structures graded in good or fair condition (without accounting for digestion) was 34.4 ±9.7 cm (n=909, modal range: 32–40) (Table 2, Fig. 2). Lengths increased by 23% on average when appropriate DCFs were applied to each structure to account for the observed degree of digestion (mean FL=42.4 ±11.6 cm, modal range: 44–52, 95% CI=41.0–43.9) (paired t-test, t_{908}=67.1, P<0.001). A DCF of 1.0 (no correction required to account for digestion) was applied to 62 elements in good condition, resulting in a mean fork length of 39.6 ±11.9 cm estimated from those bones.

The size-frequency distribution of pollock consumed by sea lions also varied significantly following the application of DCFs (Kolmogorov-Smirnov, KS=176.2, P<0.001) and led to an increase in the proportion of fish thought to have been adult (>45 cm FL) from 16% to 44%. This result in turn reduced the proportion of fish thought to have been subadults (29%), adolescents (25%), and juveniles (<2%, ≤20 cm FL) (Fig. 2). The size range of pollock eaten ranged widely regardless of whether DCFs were applied (10–78 cm) or not (10–64 cm). When we calculated fork lengths using only elements selected according to MNI criteria, the means increased by just 0.5 cm for corrected and by just 0.3 cm for uncorrected lengths, with near identical standard deviations and distributions (Fig. 2) (Kolmogorov-Smirnov, uncorrected KS=0.33, P=0.89, corrected KS=0.032, P=0.91).

The use of all otoliths regardless of digestion state resulted in a mean fork length that was only about half of that derived by using all structures corrected for digestion (Table 2). Excluding otoliths in poor condition significantly reduced sample size (Table 2) but

Table 2

Estimated mean fork length (mean FL, cm) of walleye pollock consumed by Steller sea lions. Values were determined by using selected cranial structures with or without the application of condition-specific digestion correction factors (DCFs). Data sets exclude all structures graded in poor condition (with the exception of data sets marked with an asterisk). Fish element sample sizes (n_f) are given along with proportion of elements assigned condition category good (n^g). When DCFs were applied, 95% confidence intervals (95% CI) were estimated by using bootstrap resampling (see "Materials and methods").

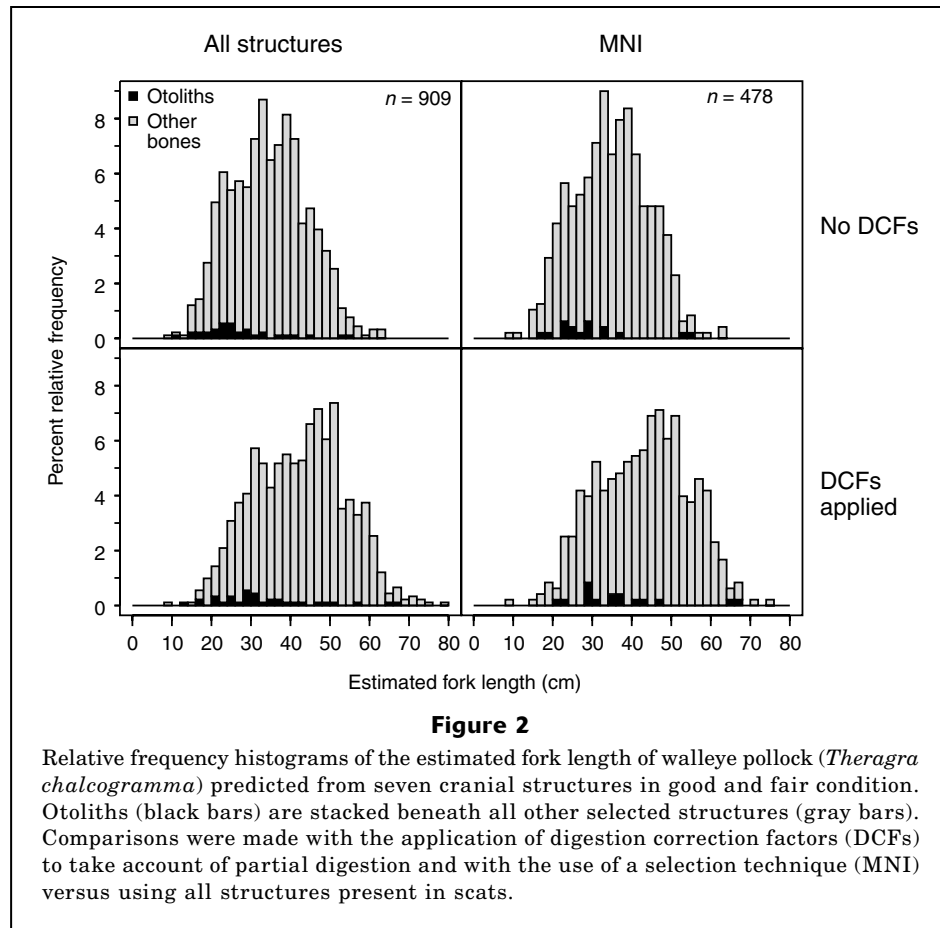| Structure code	DCF	n	n^g	Mean FL	SD	Range	95% CI
INTE	No	37	0.35	44.0	8.0	28.0–54.5	—
	Yes	37	0.35	48.0	9.3	31.9–62.2	45.0–52.2
HYPO	No	47	0.19	35.3	8.9	19.0–52.0	—
	Yes	47	0.19	39.8	10.1	19.0–60.4	36.7–43.6
PHAR	No	20	0.25	38.1	8.5	20.4–50.3	—
	Yes	20	0.25	43.7	9.5	20.4–56.1	39.9–48.4
ANGU	No	207	0.16	34.0	10.2	10.0–62.8	—
	Yes	207	0.16	39.4	11.4	10.0–63.2	37.4–41.5
QUAD	No	238	0.36	33.1	10.4	14.0–63.8	—
	Yes	238	0.36	41.9	13.2	17.3–78.1	39.5–44.7
DENT	No	326	0.24	34.9	8.1	11.0–63.0	—
	Yes	326	0.24	45.1	9.8	14.7–75.3	43.3–46.8
OTOL	No	10	0.10	30.6	13.8	14.2–54.8	—
	Yes	10	0.10	36.6	17.6	16.7–67.2	27.0–51.1
OTOL or OTOW	No	34	0.03	27.2	16.1	10.8–54.8	—
	Yes	34	0.03	33.7	12.8	13.3–67.2	29.5–39.5
All structures	No	909	0.25	34.4	9.7	9.8–63.8	—
	Yes	909	0.25	42.4	11.6	10.0–78.1	41.0–43.9
OTOL*	No	27	0.04	23.3	11.9	7.9–54.8	—
OTOL or OTOW*	No	247	<0.01	20.2	9.7	5.0–58.0	—

increased our estimate of fork length by approximately 33%. Applying grade-specific DCFs increased these estimates by another 19% (to 36.6 cm) for otolith length and by 24% (to 33.7 cm) for a combination of otolith length and width (Table 2). All six remaining structures in good or fair condition provided larger corrected mean length estimates than did otoliths alone, but 95% confidence intervals derived from otoliths did overlap with other structures (Table 2). The smaller estimate provided by otoliths may reflect that >83% of grade corrected otoliths ($n=34$) came from the inside haul-out sites, where animals seem to eat smaller fish (see following section). On the other hand, large pollock otoliths were observed to have been regurgitated in feeding studies on captive sea lions and also may be more easily crushed by rocks often found in the stomachs of Steller sea lions (Tollit et al., 2003). Regression formulae used in our study to predict pollock FL from otolith length were similar to those of Frost and Lowry (1981) for juvenile fish (<10 mm otolith length) but led to smaller fish size estimates (~1–1.7 cm) over the range of 30–50 cm.

The lengths of the biggest fish (corrected mean FL=48.0 cm) were estimated from measurements of INTE (Table 2), the structure with the lowest DCF. Dentary bones (the most abundant structure recov-

ered) predicted mean (Table 2) and modes (FL 44–50 cm) similar to those predicted from all structures. Applying DCFs increased our length estimates by between 9% (INTE) and 29% (DENT) (paired t-tests, all $P<0.001$). Overall, corrected fork length estimates from elements in good condition were similar to those from elements in fair condition (Mann-Whitney U, $P=0.47$), but multiple comparisons indicated a significant difference ($P<0.05$) between condition categories for INTE and DENT (lengths were estimated to be longer from elements graded in fair condition).

Repeat measurements of individual elements were all within 0.04 mm of the mean, and 88.9–99.5% were within 0.02 mm. The highest variability was associated with ANGU, HYPO, and PHAR with 88.9%, 91.7%, and 94.9% of their respective measurements falling within 0.02 mm. A 0.02-mm measurement difference corresponded to only a 0.1–0.2 cm difference in fish length, depending on the structure used.

Small differences in estimates of fork lengths can have large effects on estimated body mass (given the exponential mass-length relationship, see Tollit et al., 2004, this issue) and can increase the mean mass of fish by more than sixfold depending on which method is used to estimate body length (all otoliths and no correction versus condition-corrected structures). The ap-

Figure 2

Relative frequency histograms of the estimated fork length of walleye pollock (*Theragra chalcogramma*) predicted from seven cranial structures in good and fair condition. Otoliths (black bars) are stacked beneath all other selected structures (gray bars). Comparisons were made with the application of digestion correction factors (DCFs) to take account of partial digestion and with the use of a selection technique (MNI) versus using all structures present in scats.
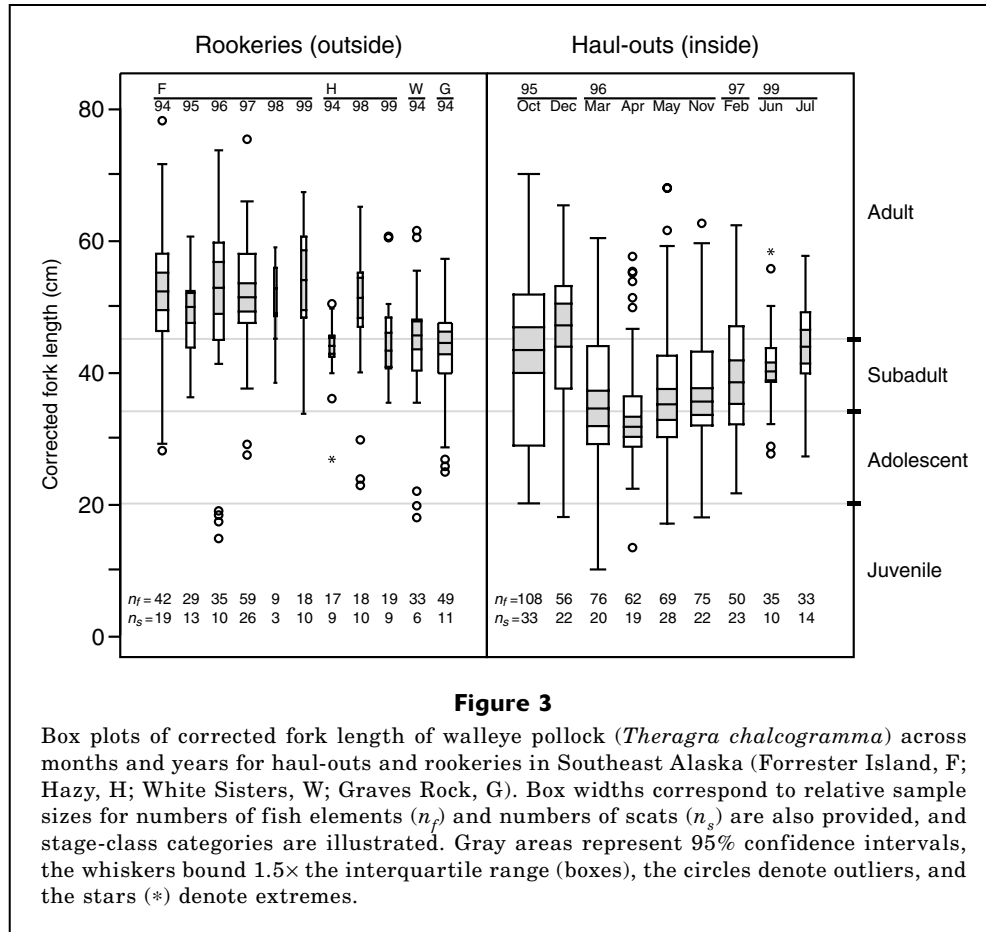
plication of our DCFs to all structures in good and fair condition increased the estimated mean mass of pollock consumed by 88% (from a mean of 388 g to 731 g). Thus, although we estimate that 44% of the number of pollock eaten by Steller sea lions were adults, based on length, their contribution, based on weight, increased to 74%. In contrast, the contribution of juvenile fish (in terms of mass) dropped to <0.1% (compared to <2% by number).

Geographical and temporal variation in sizes of pollock consumed

More pollock elements in good and fair condition were recovered from inside haul-outs (n=567) than from sites on the outside coastline (n=342) (Table 1). Upon investigation, we found the size of pollock consumed by Steller sea lions varied over time and across regions (Fig. 3). In particular, the frequency of occurrence of pollock stage classes differed significantly in the scats of sea lions resting at rookeries on the outside coastline of Southeast Alaska in summer (mean FL=48.4 cm, n=328, modal range: 44–50 cm, 95% CI=46.5–50.2, n_s=126 scats) compared to those collected between October and May at haul-outs in the waters of the inside passages (mean FL=38.4 cm, n=499, modal range; 30–34 cm,

95% CI=36.9–40.3, n_s=168 scats) (χ^2=45.2, P<0.001). Scats from these inside haul-outs contained a greater diversity of stage classes, and there was an equal probability of any given scat containing adults (51.2%), subadults (47.6%), and adolescents (53.0%), but a far less probability of containing juveniles (6.5%). In contrast, the pollock found in scats from the outside rookeries contained mostly adults (73.8%) and fewer occurrences of the remaining three stage classes (38.1%, 9.5%, and 3.2%, respectively). Notably, the stage-class comparison of summer 1999 with scats from inside versus outside waters was not significant (Fishers exact test, P=0.11).

Similar proportions of each pollock stage class were found in scats collected between years (Forrester, Fisher's exact test, P=0.54; Hazy, Fisher's exact test, P=0.16), and between rookeries (1994 only, Fisher's exact test, P=0.57; all years, Fisher's exact test, P=0.22). Scats from inside haul-outs collected in spring 1996 contained comparatively smaller fish than in other months and years examined (Fig. 3). However, there were no significant monthly differences in the proportions of age classes from October 1995 to February 1997 (χ^2=16.52, P=0.28) or when all monthly data (June and July 1999) were included from inside haul-outs (χ^2=23.4, P=0.10).

Figure 3

Box plots of corrected fork length of walleye pollock (*Theragra chalcogramma*) across months and years for haul-outs and rookeries in Southeast Alaska (Forrester Island, F; Hazy, H; White Sisters, W; Graves Rock, G). Box widths correspond to relative sample sizes for numbers of fish elements (n_f) and numbers of scats (n_s) are also provided, and stage-class categories are illustrated. Gray areas represent 95% confidence intervals, the whiskers bound 1.5× the interquartile range (boxes), the circles denote outliers, and the stars (*) denote extremes.

Overlap of size of pollock consumed by Steller sea lions with size of pollock caught by the fisheries

The Canadian commercial pollock trawl fishery in Dixon Entrance between 1993 and 1999 landed mostly (93%) adult fish (mean FL=52.2 ±5.9 cm, n=2103, modal range: 48–54 cm). The majority (79%) of scats containing pollock from the Forrester Island rookery in June and July also contained remains of adult pollock (mean corrected FL=51.4 ±10 cm, n=192, modal range: 46–52 cm, n_s=81 scats). Percentage overlap based on a comparison of size-frequency distributions totaled 75.1% for those fish eaten around Forrester Island and 52.1% for all fish eaten. However, the estimated overlap would have been assumed incorrectly to be half these values if DCFs had not been applied to the selected digested otoliths and bones (i.e., 36.7% overlap at Forrester and 24.1% for all areas combined). Clearly overlap levels would have been further underestimated if structures in poor condition had been included in our analyses.

Discussion

Only 57% of the scats (303 of 531) that contained suitable pollock remains had structures that were in good enough condition to be measured reliably. Numbers of elements in good or fair condition (n=909) averaged three per scat, and a very small fraction of these consisted of otoliths (<4%). The most numerous structures were DENT, QUAD, and ANGU (Table 1). This finding is inconsistent with feeding trials with captive Steller sea lions where otoliths were found to be the most commonly occurring structure (Cottrell and Trites, 2002; Tollit et al., 2003).

Different structures yielded somewhat different mean sizes of pollock, although 95% confidence intervals generally overlapped, ranging between 37 and 52 cm for bones (Table 2). Such discrepancy is not surprising given that different bones originate from different scats and possibly different fish (even within a single scat). Our comparison of estimates with all structures versus MNI selections indicates that the potential effect of double counting (and measuring) fish within a single scat is likely negligible with large sample sizes (Fig. 2). Although the use of all-structure data to estimate fish length results in a greatly increased sample size, there remains an underlying assumption that all structures are affected equally by digestion. Tollit et al. (2004, this issue) found no significant difference in the degree of erosion across the three size ranges (28.5–45.0 cm FL) for each structure within each condition category.

They also found that the relative shape, structure, and proportion of the morphological features used to estimate erosion were consistent for both smaller and larger fish. We therefore assumed that the DCFs in that study could be used reliably for the fish in our study outside of the experimental size range in which they were considered.

Applying DCFs increased mean fork length estimates by 23% (from 34.4 to 42.4 cm) on average and resulted in adult fish contributing 44% to the sea lion diet by number and 74% by mass. The contribution of juvenile fish was insignificant. Applying valid correction factors clearly provides better insights into prey-size selection and consequently niche overlap. It should also lead to more precise estimates of mass of prey consumed and the number of prey within a scat (Ringrose, 1993; Tollit et al., 1997; Laake et al., 2002).

Over 61 species of prey were identified in the diet of Steller sea lions in Southeast Alaska from 1993 to 1999 (Trites et al.[3]). The most common prey were walleye pollock, Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), salmon (*Oncorhynchus* spp.), arrowtooth flounder (*Reinhardtius stomias*), rockfish (*Sebastes* spp.), skates (*Raja* spp.), and cephalopods. During summer, gadids (most of which were pollock) made up 27% of the diet, and increased to 49–62% of the diet at other times of the year (Trites et al.[3]), confirming that pollock are a significant component of the diet.

Steller sea lions consumed a wide size range of pollock in Southeast Alaska; the bulk of fish fell between 20 and 60 cm and peaked between 44 and 52 cm (Fig. 2). The contribution of juvenile fish (≤20 cm) was insignificant. The only historical data to compare with these results are those from the stomach samples of eight Steller sea lions collected from Southeast Alaska in 1986 (Calkins and Goodwin[1]). Pollock lengths backcalculated from all otoliths found in the stomachs were generally shorter (mean FL=25.5 ±10.4 cm, range; 4.8–55.7cm, *n*=80) than our estimates from multiple structures found in scats collected during the 1990s (mean FL=42.4 ±11.6 cm, range: 10.0–78.1 cm, *n*=909). It should be noted that we derived our estimates after removing heavily eroded structures and applying DCFs, whereas Calkins and Goodwin[1] did not account for partial digestion. However our estimates of pollock length would have been similar to those of Calkins and Goodwin[1] if we had used only otoliths and had not corrected for digestion (Table 2). Although Frost and Lowry (1980) found no significant difference between the size of otoliths obtained from stomachs and intestines of ribbon seals, underestimates of fish size determined from otoliths from stomach samples will depend on the time since ingestion (i.e., on the extent of digestion).

One possible explanation for the virtual absence of juvenile pollock in the scats we examined is that the relatively smaller structures of smaller fish were more likely to be completely digested, and were therefore underrepresented in the scats (Tollit et al., 1997; Bowen, 2000). However, juvenile pollock otoliths and bones were found in large numbers in a number of scats collected from

the western stock (Zeppelin et al., 2004, this issue). Clearly, the potential for underestimating smaller fish depends heavily on the balance between relative recovery rates and the number of different size fish consumed in a meal. For example, if an animal needs to eat 5 kg a day, then it would have to consume 195 15.5-cm pollock, but less than ten 41-cm pollock. Given that large pollock bones are at least three times more likely than small bones to pass through the digestive tract (Tollit et al., 2003; D. J. Tollit, unpubl. data), the sheer numbers of small pollock in this example would lead to a conclusion that smaller fish were more important numerically, when in fact they were equally important. Conversely, the relative proportion of large fish is likely to be overestimated if ten large and ten small pollock are consumed together. The generally low number of structures per scat provides little information to assess this balance. Hence we must assume that our results are representative and unbiased.

Steller sea lions in Southeast Alaska did not seem to eat fish over 65 cm. Whether or not sea lions do not target large fish, or whether large fish are harder to catch and handle, or are encountered at a lower rate is not known. However, large fish could be under-represented in scats if large fish cannot be swallowed whole, and head skeletal parts are lost while the fish is torn apart on the surface (Olesiuk et al., 1990; Wazenbock, 1995) or if bone regurgitation is size specific.

Regional, geographical, and temporal variation in sizes of pollock consumed

Stomach samples collected in 1975–78 and 1985–86 in the Gulf of Alaska contained substantial numbers of juvenile pollock, as well as larger fish (mode: 39–43 cm). In 1985, the distribution of sizes consumed by sea lions around Kodiak Island appeared to mimic that of the pollock population (Merrick and Calkins, 1996). However, juvenile sea lions ate significantly smaller and relatively more juvenile pollock than adult sea lions. Stomachs from the Gulf of Alaska contained an average of 49 pollock (1975–78) and 72 pollock (1985) compared with 1.6 pollock per scat in Southeast Alaska. In the Bering Sea, 90 stomachs were examined between 1975 and 1981 by using only non-eroded otoliths, and these also contained mainly (76%) juvenile pollock (mean FL=29.3 cm), but also some adult fish (Frost and Lowry, 1986).

Between 1998 and 2000, Steller sea lions across the range of the western population in Alaska consumed pollock averaging 39.3 ±14.3 cm (range: 3.7–70.8 cm, Zeppelin et al., 2004, this issue). This finding suggests that sea lions may have been less reliant on juvenile pollock than they were during the 1970s and 1980s. Apparent differences may reflect differences in pollock year-class strength, and thus differences in the dominant size classes that were available to be consumed. However, Zeppelin et al. (2004, this issue) reported that the size distribution of walleye pollock consumed by Steller sea lions between 1998 and 2000 did not appear to fluctuate with year-class strength, unlike the

sizes of Atka mackerel (*Pleurogrammus monopterygius*) consumed in western Alaska.

Comparing samples collected at rookeries from the eastern and western populations reveals that sea lions in the western stock ate significantly greater numbers of smaller pollock and fewer adults in summer than sea lions in Southeast Alaska (Zeppelin et al., 2004, this issue; and our study). However, both eastern and western stock sea lions using haul-outs in March (winter) ate similar size pollock. Adult pollock occurred more frequently in scats collected from rookeries along the open ocean coastline of Southeast Alaska during June and July (74% adults) than they did in scats from haul-outs located in inside waters between October and May (51% adults). Scats collected at rookeries can be considered to be from adult female sea lions and to a lesser extent from adult males, whereas those collected at haul-outs during other times of the year contain a more diverse mix of age groups, including greater numbers of younger sea lions. Thus it is uncertain whether observed size differences in pollock between these two groups are seasonal or due more to size preferences of different aged animals. Limited support for the former comes from the similar size pollock observed in the scats between the two groups in June and July of 1999. Overall, however, it is unknown whether the consumption patterns observed are a result of an actual size selection of prey or if they result from coincidental distributions of sea lions and prey-size classes. Some pinnipeds may select prey of particular sizes (Sinclair et al., 1994) and may encounter difficulties if they cannot switch to other sizes or species if the abundance of preferred prey is reduced. Fine-scale studies are now being undertaken to address such uncertainties.

There are few assessments of pollock stock size for the 1990s in Southeast Alaska (Martin, 1997). However the biomass is believed to have been low compared to other regions of Alaska. Juvenile pollock are known to congregate in the shallow inside waters of Southeast Alaska during winter (Sigler[5]) but are also known to occur in significant numbers in the summer in waters shallower than 200 meters on the outer coastline (Martin, 1997). Recruitment of 1-year-old fish was found to be high during acoustic studies in 1994 and 1999 in the Gulf of Alaska (Guttormsen et al., 2003).

Steller sea lions using rookeries in Southeast Alaska consumed mainly adult pollock between 1994 and 1999 and showed no evidence of tracking any abundant age class of pollock. However, the trend in increasing length estimates for inside haul-outs after 1995 (Fig. 3) does suggest that sea lions might be tracking a particular age class of prey. Certainly a greater range of age classes were consumed at these haul-outs (Fig. 3).

Scientific trawls in 1996 indicated that the larger pollock on the outside coastline occurred generally in waters 201–300 m deep during daylight hours (Martin,

1997) and that smaller pollock were present in shallower depths. Larger pollock tend to disperse and move to shallow waters to feed at night (Smith, 1981). Thus, the observed crepuscular and nighttime foraging by lactating Steller sea lions (Higgins et al., 1988; Trites and Porter, 2002) would be a logical foraging strategy to capture adult pollock. Other important factors, in addition to depth, that likely influence size selection include prey density and spatial distribution in relation to rookeries and haul-outs. Given both the greater mass and energy content of adults compared with juveniles (Perez, 1994; Anthony et al., 2000), the selection of adults would be an energy efficient strategy—all other things being equal.

Overlap in sizes of pollock consumed by Steller sea lions and sizes of pollock caught by fisheries

There was no commercial fishery for pollock in Southeast Alaska during the 1990s. However, a small fishery occurred in nearby Dixon Entrance, B.C., that might indicate sizes that could have been caught in Southeast Alaska if a fishery had occurred. Overlap in sizes of pollock caught by the B.C. fishery with those taken by Steller sea lions further north (our study) more than doubled after applying digestion correction factors (from 24% to 52%). Similarly, high levels of overlap were also found between the sizes of pollock consumed by the western stock (1998–2000) and those caught in the same region by fisheries (after our DCFs were applied to structures recovered from scats—Zeppelin et al., 2004, this issue). A high degree of overlap in size highlights a potential conflict between fisheries and sea lions, but this overlap cannot be considered indicative of competition unless the resource that fisheries and sea lions seek is limited across the space and time in question (Krebs and Davies, 1991).

Conclusions

Our study provides the first substantial description of the size of pollock eaten by Steller sea lions in Southeast Alaska. It also shows the benefits of using bones other than otoliths to estimate the sizes of prey eaten by Steller sea lions, and the importance of correcting for degree of digestion. Accurately reconstructing the sizes of bones and otoliths recovered from scats has a significant bearing, in turn, on accurately determining the mass of prey consumed, and on the extent of overlap of sizes of prey consumed and sizes of the same resource caught in commercial fisheries.

We found that Steller sea lions in Southeast Alaska consumed a large proportion of adult pollock and few juveniles between 1994 and 1999. Although greater proportions of juvenile and adolescent pollock were consumed over the same period, during the summer in the Gulf of Alaska and Bering Sea, larger size fish still were the most abundant prey item in the diet of sea lions. A comparison of these estimates with the lengths of pollock consumed during the 1970s and 1980s shows that

---

[5] Sigler, M. F.   2003.   Unpubl. data.   Auke Bay Lab, National Marine Fisheries Service, 11305 Glacier Highway, Juneau, AK 99801.

Steller sea lions can consume a wide range of different size pollock (4–78 cm). Whether or not these differences in sizes of pollock consumed between regions and decades reflect differences in availability, size preferences, or year-class strength is not known and requires further study primarily with fine-scale data from scientific surveys and concurrent scat collections.

Acknowledgments

Literature cited

Anthony, J. A., D. D. Roby, and K. R. Turco.
2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Exp. Mar. Biol. Ecol. 248:53–78.

Benson, A. J., and A. W. Trites.
2002. A review of the effects of regime shifts on the production domains in the eastern North Pacific Ocean. Fish and Fisheries 3:95–113.

Beverton, R. J. H.
1985. Analysis of marine mammal-fisheries interaction. *In* Marine mammals and fisheries (J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne eds.), p. 3–33. George Allen & Unwin, Boston, MA.

Bowen, W. D.
2000. Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. Can. J. Fish. Aquat. Sci. 57:898–905.

Browne, P., J. L. Laake, and R. L. DeLong.
2002. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. Fish. Bull. 100:423–433.

Calkins, D. G., D. C. McAllister, K. W. Pitcher, and G. W. Pendleton.
1999. Steller sea lion status and trend in Southeast Alaska: 1979–1977. Mar. Mamm. Sci. 15(2):462–477.

Cottrell, P. E., and A. W. Trites.
2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci. 18:525–539.

Dorn, M., A. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn.
2001. Assessment of the walleye pollock stock in the Gulf of Alaska. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, 90 p. Prepared by the Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council, W 4th Avenue, Suite 306, Anchorage, AK 99501.

Frost, K. J., and L. F. Lowry.
1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Can. J. Zool. 58:1601–1607.

1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fish. Bull. 79:187–192.

1986. Sizes of walleye pollock, *Theragra chalcogramma*, consumed by marine mammals in the Bering Sea. Fish. Bull. 84:192–197.

Guttormsen, M. A., C. D. Wilson, and S. Stienessen.
2003. Results of the February and March 2003 echo integration-trawl surveys of walleye pollock (*Theragra chalcogramma*) conducted in the gulf of Alaska, cruises MF2003-01 and MF2003-05. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, August 2003, 45 p. Prepared by the Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

Higgins, L. V., D. P. Costa, A. C. Huntley, and B. J. Le Boeuf.
1988. Behavioral and physiological measurements of maternal investment in the Steller sea lion, *Eumetopias jubatus*. Mar. Mamm. Sci. 4:44–58.

Hunt, G. L., Jr., A. S. Kitaysky, M. B. Decker, D. E. Dragoo, and A. M. Springer.
1996. Changes in the distribution and size of juvenile walleye pollock, *Theragra chalcogramma*, as indicated by seabird diets at the Pribilof Islands and by bottom trawl surveys in the Eastern Bering Sea, 1975 to 1993. *In* Ecology of juvenile walleye pollock, *Theragra chalcogramma*. Papers from the workshop "The importance of prerecruit walleye pollock to the Bering Sea and North Pacific ecosystems" Seattle, WA, October 28–30, 1993 (R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed, eds.), p. 125–139. NOAA Tech. Rep. NMFS 126. [NTIS no. PB97-155188.]

Krebs, J. R., and N. B. Davies.
1991. Behavioral ecology: an evolutionary approach, 3rd ed., 483 p. Blackwell Scientific, Boston, MA.

Laake, J. L., P. Browne, R. L. DeLong, and H. R. Huber.
2002. Pinniped diet composition: a comparison of estimation models. Fish. Bull. 100:434–477.

Loughlin, T. R., A. S. Perlov, and V. A. Vladimirov.
1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. Mar. Mamm. Sci. 8:220–239.

Loughlin, T. R., and A. E. York.
2000. An accounting of the sources of Steller sea lion mortality. Mar. Fish. Rev. 62(4):40–45.

Martin, M. H.
1997. Data report: 1996 Gulf of Alaska bottom trawl survey. NOAA Tech. Memo. NMFS-AFSC-82, 235 p. [NTIS no. PB98-103930.]

Merrick, R. L., R. Brown, D. G. Calkins, and T. R. Loughlin.
1995. A comparison of Steller sea lion, *Eumetopias jubatus*, pup masses between rookeries with increasing and decreasing populations. Fish. Bull. 93(4):753–758.

Merrick, R. L., and D. G. Calkins.
1996. Importance of juvenile walleye pollock, *Theragra chalcogramma*, in the diet of Gulf of Alaska Steller sea lions, *Eumetopias jubatus*. *In* Ecology of juvenile walleye pollock, *Theragra chalcogramma*. Papers from the workshop "The importance of prerecruit walleye pollock to the Bering Sea and North Pacific ecosystems" Seattle, WA, October 28–30, 1993 (R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed, eds.), p. 153–166. NOAA Tech. Rep. NMFS 126. [NTIS no. PB97-155188.]

Milette, L. L., and A.W. Trites.
    2003. Maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) from stable and declining populations in Alaska. Can. J. Zool. 81: 340–348.

NRC (National Research Council)
    2003. Decline of the Steller sea lion in Alaskan waters: untangling food webs and fishing nets, 204 p. Prepared by the Committee on the Alaska Groundfish Fishery and Steller sea lions. National Academies Press, Washington, DC.

Olesiuk, P. F., M. A. Bigg, G. M. Ellis, S. J. Crockford, and R. J. Wigen.
    1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730, 135 p.

Perez, M. A.
    1994. Calorimetry measurements of energy value of some Alaskan fishes and squids. NOAA Tech. Memo. NMFS-AFSC-32, 32 p. [NTIS no. PB94-152907.]

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

Ringrose, T. J.
    1993. Bone counts and statistics: a critique. J. Archaeol. Sci. 20:121–157.

Sease, J. L., W. P. Taylor, T. R. Loughlin, and K. W. Pitcher.
    2001. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1999 and 2000. NOAA Tech. Mem. NMFS-ASFC-122, 52 p.

Sinclair, E. H., T. Loughlin, and W. Pearcy.
    1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fish. Bull. 92: 144–156.

Smith, G. B.
    1981. The biology of walleye pollock. *In* The eastern Bering Sea Shelf: oceanography and resources (D. W. Hood and J. A. Calder eds.), vol. 1, p. 527–551. Univ. Washington Press, Seattle, WA.

Tollit, D. J., S. G. Heaslip, T. K. Zeppelin, R. Joy, K. A. Call, and A. W. Trites.
    2004. A method to improve size estimates of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by pinnipeds: digestion correction factors applied to bones and otoliths recovered in scats. Fish. Bull. 102:498–508.

Tollit, D. J., M. J. Steward, P. M. Thompson, G. J. Pierce, M. B. Santos, and S. Hughes.
    1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. Can. J. Fish. Aquat. Sci. 54:105–119.

Tollit, D. J., M. Wong, A. J. Winship, D. A. S. Rosen, and A. W. Trites.
    2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of the Steller sea lion (*Eumetopias jubatus*). Mar. Mamm. Sci. 19(4):724–744.

Trites, A. W., and L. P. Donnelly.
    2003. The decline of Steller sea lions in Alaska: a review of the nutritional stress hypothesis. Mamm. Rev. 33:3–28.

Trites, A. W., and P. A. Larkin.
    1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? Aquat. Mamm. 22:153–166.

Trites, A. W., and B. T. Porter.
    2002. Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. J. Zool. (Lond.) 256:547–556.

Walline, P. D.
    1983. Growth of larval and juvenile walleye pollock related to year-class strength. Ph.D. diss., 144 p. Univ. Washington, Seattle, WA.

Wazenbock, J.
    1995. Changing handling times during feeding and consequences for prey size selection of 0+ zooplanktivorous fish. Oecologia (Heidelb.) 104:372–586.

Zeppelin, T. K., D. J. Tollit, K. A. Call, T. J. Orchard, and C. J. Gudmundson.
    2004. Sizes of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1998 to 2000. Fish. Bull. 102:509–521.