Abstract—Prey-size selectivity by Steller sea lions (*Eumetopias jubatus*) is relevant for understanding the foraging behavior of this declining predator, but studies have been problematic because of the absence and erosion of otoliths usually used to estimate fish length. Therefore, we developed regression formulae to estimate fish length from seven diagnostic cranial structures of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*). For both species, all structure measurements were related with fork length of prey (r^2 range: 0.78–0.99). Fork length (FL) of walleye pollock and Atka mackerel consumed by Steller sea lions was estimated by applying these regression models to cranial structures recovered from scats (feces) collected between 1998 and 2000 across the range of the Alaskan western stock of Steller sea lions. Experimentally derived digestion correction factors were applied to take into account loss of size due to digestion. Fork lengths of walleye pollock consumed by Steller sea lions ranged from 3.7 to 70.8 cm (mean=39.3 cm, SD=14.3 cm, n=666) and Atka mackerel ranged from 15.3 to 49.6 cm (mean=32.3 cm, SD= 5.9 cm, n=1685). Although sample sizes were limited, a greater proportion of juvenile (≤20 cm) walleye pollock were found in samples collected during the summer (June–September) on haul-out sites (64% juveniles, n=11 scats) than on summer rookeries (9% juveniles, n=132 scats) or winter (February–March) haul-out sites (3% juveniles, n=69 scats). Annual changes in the size of Atka mackerel consumed by Steller sea lions corresponded to changes in the length distribution of Atka mackerel resulting from exceptionally strong year classes. Considerable overlap (>51%) in the size of walleye pollock and Atka mackerel taken by Steller sea lions and the sizes of these species caught by the commercial trawl fishery were demonstrated.

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

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The western stock of Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska and the Bering Sea has experienced dramatic and continued declines since the mid-1970s (Loughlin et al., 1992; Loughlin and York, 2000). It is likely that changes in prey availability linked to commercial fisheries and large-scale oceanographic changes are among the reasons for the continued decline (Loughlin and Merrick, 1989; NRC, 1996). The diet of the western stock of Steller sea lions has been recently assessed (Sinclair and Zeppelin, 2002), but discrete selection of prey by size has not been described. The size of prey is relevant for understanding the foraging behavior of the predator as well as the ecological role of the prey (e.g., mortality at a given life history stage). In the case of the Steller sea lion, prey-size selectivity is particularly important for understanding spatial and temporal changes in

diet and is needed for making fishery management decisions.

Size of fish prey consumed by marine mammals has been estimated by using sagittal otoliths recovered from stomach and more recently scat samples (Pitcher, 1981; Frost and Lowry, 1986; Browne et al., 2002). Significant relationships have been demonstrated between fish fork length (FL) and otolith length (Templeman and Squires, 1956; Frost and Lowry, 1981; Harvey et al., 2000). The use of otoliths to describe the size of prey taken by Steller sea lions has proved useful in data collected from stomach samples (e.g., Pitcher, 1981; Calkins and Goodwin[1]). However, few

[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 Road, Anchorage, Alaska, 99518-1599.

otoliths are recovered from Steller sea lion scat, and measurements of otoliths recovered from scats likely underestimate prey size because of partial erosion from digestion (Prime and Hammond, 1987; Dellinger and Trillmich, 1988; Harvey, 1989). Because of the impracticality of collecting stomachs and the low number and poor quality of otoliths found in scats, alternative methods are needed to accurately describe the size of prey consumed by Steller sea lions.
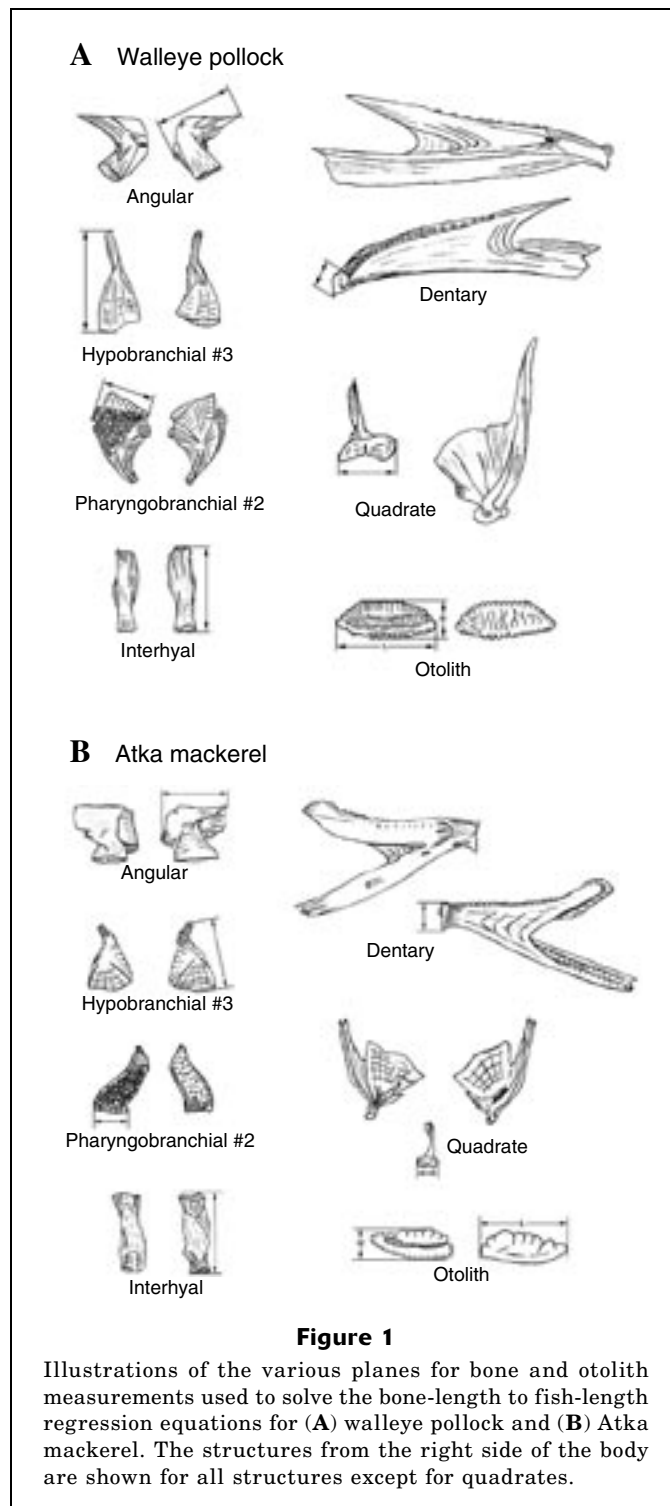
Archaeological studies routinely use skeletal structures other than otoliths to estimate either fish length or mass (Keys, 1928; Casteel, 1976; Owen and Merrick, 1994; Desse and Desse-Berset, 1996). Wise (1980) used a regression of fish length on vertebrae length to estimate prey size from scat samples of otters (*Lutra lutra*) and mink (*Mustela vison*). The regression approach relies on the assumption that the overall size of a given fish and the size of skeletal structures are highly correlated. This assumption has been substantiated for cranial and skeletal structures other than otoliths in various North Pacific fish species (Orchard, 2001). Thus, the use of cranial structures appear to be a viable alternative to the use of otoliths for studying prey size of Steller sea lions.

Walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) rank among the top prey items of Steller sea lions (Sinclair and Zeppelin, 2002) as well as being valuable in the U.S. commercial fishery (NMFS, 2003). We estimated fork length for these two primary prey species from scats collected between 1998 and 2000 across the range of the Alaskan western stock of sea lions. Fish length was estimated by using regression formulae relating bone or otolith measurement to fork length for seven cranial structures found in sufficient quantities and in good and fair condition in scat samples. Experimentally derived digestion correction factors (Tollit et al., 2004b, this issue) were applied to bone and otolith measurements to account for loss of size due to erosion. The methods developed here proved to be an effective tool to estimate size of prey selected by Steller sea lions and are applicable for other marine mammal diet studies particularly where otoliths are highly eroded.

Materials and methods

Development of regression formulae

Fork-length to bone and otolith-length regression equations were developed for seven cranial structures from walleye pollock and Atka mackerel. Bones and otoliths were selected according to species-specific features, predictability in condition, and prevalence in scats. Bones included the angular (ANG), quadrate (QUAD), interhyal (INTE), dentary (DENT), pharyngobranchial 2 (PHAR), and hypobranchial 3 (HYPO)

Figure 1

Illustrations of the various planes for bone and otolith measurements used to solve the bone-length to fish-length regression equations for (**A**) walleye pollock and (**B**) Atka mackerel. The structures from the right side of the body are shown for all structures except for quadrates.

(Fig. 1). Fork length regressions were developed for sagittal otolith length (OTOL), as well as for width (OTOW) measurements. All selected cranial structures were paired (having a left and right side) which allowed for enumeration of prey species. Only right-sided bones and otoliths were used to develop the regression equations.

In symmetrical fishes such as walleye pollock and Atka mackerel the left and right otoliths are mirror images of each other (Härkönen, 1986). We compared the left and right-sided measurements for all seven structures using a subsample of the structures used to develop the regression equations. There was no significant difference for either walleye pollock (paired *t*-test, *P*<0.05, *n*=13 for HYPO, 15 for QUAD, and 14 for all other structures) or Atka mackerel (paired *t*-test, *P*<0.05, *n*=14 for OTOS and 17 for all other structures).

Fish specimens used for regressions were collected from the Gulf of Alaska and Bering Sea. Standard length (SL) was converted to fork length for walleye pollock (when fork length was not available for a small number of otoliths included in the regressions) by using the following equation: $FL = 0.40+1.07(SL)$ (Wilson[2]). We chose to use FL over SL for the regressions because all fish were in good condition, thus allowing for accurate measurements. Additionally, FL is the standard used for commercial fishery and survey data by the National Marine Fisheries Service for direct comparisons. A partial analysis of these data was previously reported in Orchard (2001). We expanded the data set reported in Orchard (2001) to reflect the size range of bones found in Steller sea lion scats and included only fish specimens collected within our study area.

Linear regression models were fitted for most cranial structures by using the following equation:

$$Y = \alpha + \beta X,$$

where Y = the fork length of the fish;
X = the measurement of the cranial structure; and
α and β are constants that define the regression formula.

However, some cranial structures provided a better fit with the following quadratic regression equation:

$$Y = \alpha + \beta X + \beta X^2.$$

The strength of the relationship of the regression models was assessed by using a coefficient of determination (r^2).

Erosion is a potential source of bias when estimating prey body size from digested otoliths (Prime and Hammond, 1987; Dellinger and Trillmich, 1988; Harvey, 1989). We used condition-specific digestion correction factors (DCFs) developed by Tollit et al. (2004b, this issue) to correct for the high degree of variation in the erosion of cranial structures. DCFs were obtained from feeding experiments on captive juvenile Steller sea lions by using a subsample of fish collected for the regression analysis (Tollit et al., 2004b, this issue). Selected cranial structures from three size groups of pollock

(28.5–45.0 cm FL) and one size group of Atka mackerel (30–36 cm FL) were used to develop the DCFs.

Estimation of size of walleye pollock and Atka mackerel consumed by Steller sea lions in the Bering Sea and Gulf of Alaska

Steller sea lion scats were collected from 1998 to 2000 along most of the U.S. range of the Alaskan western stock. Scats were collected from rookery (breeding) and haul-out (nonbreeding) sites in summer (June–September) and haul-out sites in winter (February–March). We assumed that scats collected on summer rookery sites primarily represent the diet of adult females because adult males present on rookeries usually fast during this time. Juveniles of both sexes come ashore on rookeries during summer and undoubtedly are represented in the data, but to a lesser degree than adult females. Scats from juvenile Steller sea lions are more likely to be sampled on haul-out sites during summer, where juveniles make up the greatest proportion of individuals. Scats collected on summer haul-out sites or any winter site presumably represent a greater cross-section of ages and sexes than collections from rookeries during summer.

Scats were rinsed through nested sieves of 4.8-, 1.4-, 0.7-, and 0.5-mm mesh. Bones and otoliths were identified to the lowest possible taxon by using reference collection specimens. All recovered otoliths and selected bones identified as either walleye pollock or Atka mackerel were given a condition grade based on the degree of erosion (Tollit et al., 2004b, this issue). In general, cranial structures considered in "good" condition had little or no erosion, "fair" were moderately eroded (generally up to about 20%), and "poor" were heavily digested (Tollit et al., 2004b, this issue). All structures that were given a condition grade of "good" or "fair" were identified as being from the left or right side and measured to the nearest 0.01 mm with digital calipers. Cranial structures graded as "poor" were not measured and excluded from further analyses because of high observed intraspecific variation (Tollit et al., 1997; Tollit et al., 2004b, this issue).

Fork-length estimates with and without DCFs applied were calculated for each cranial structure and for all structures combined. Otoliths were treated separately because most diet studies currently rely on otolith length to estimate fish fork length. Ninety-five percent confidence intervals around all mean size estimates were calculated by using parametric bootstrapping procedures (Manly, 1997) in which error associated with the regression equation and resampling error resulting from variability within correction factors, and variability in scats were taken into account. Full details of the bootstrapping procedure are presented in Tollit et al. (2004b, this issue).

The same fish may be represented by multiple cranial structures within a scat; therefore, in order to avoid pseudoreplication, we selected a minimum number of individuals (MNI; Ringrose, 1993) for each scat sample.

Table 1

Relationship between bone measurement and fish fork length (FL) in millimeters. For each equation the number of bones measured (*n*), coefficient of determination (r^2), standard error of the regression coefficient (SE and SE_x^2 for quadratic regression coefficients), range of fish lengths and mean of fork lengths are given. All measurements are given in millimeters.

Species	Structure code	Regression	r^2	n	SE, SE_x^2	Range of FL	Mean FL
Walleye pollock	INTE	FL = 49.78*x* + 5.12	0.98	49	1.12	83–477	201.61
	HYPO	FL = 43.14*x* + 14.12	0.99	49	0.78	83–477	231.58
	PHAR	FL = 80.19*x* + 19.43	0.95	51	2.58	83–477	204.37
	ANGU	FL = 59.25*x* +15.27	0.96	44	1.82	83–477	208.75
	QUAD	FL = 89.47*x* + 6.77	0.99	59	1.32	83–477	203.92
	DENT	FL = 108.46*x* − 1.52	0.99	60	1.75	83–477	206.61
	OTOL	FL = 0.50*x*^{2} + 15.74*x* + 13.3	0.99	504	0.68, 0.34	49–530	187.35
	OTOW	FL = 2.32*x*^{2} + 44.74*x* + 3.73	0.99	508	1.54, 0.19	49–530	188.66
Atka mackerel	INTE	FL = 57.38*x* + 95.57	0.86	106	2.26	185–500	355.37
	HYPO	FL = 38.58*x* 80.64	0.95	105	0.85	185–500	355.62
	PHAR	FL = 81.32*x* + 70.40	0.91	107	2.48	185–500	354.90
	ANGU	FL = 58.38*x* + 73.86	0.91	105	1.85	185–500	355.34
	QUAD	FL = -8.90*x*^{2} + 129.38*x* + 9.16	0.96	108	7.07, 0.96	185–500	354.69
	DENT	FL = −7.10*x*^{2} + 115.83*x* −21.68	0.94	108	7.08, 0.73	185–500	354.69
	OTOL	FL = 62.54*x* +24.24	0.83	165	2.19	185–500	349.82
	OTOW	FL = 188.19*x* − 77.71	0.78	170	7.71	185–500	350.09

Minimum number of individuals for each species in each scat was estimated by counting species-specific sided elements and choosing the greatest number of left or right elements. If more than one structure had the same number, the structure with the highest r^2 value in its regression on fork length (Table 1) was selected as a representative length estimate for that fish. If an equal number of left and right bones were present, right bones were selected.

Temporal variation in size of walleye pollock and Atka mackerel consumed by Steller sea lions

Temporal differences were assessed by grouping fish into stage-class categories. Stage-class categories were defined for pollock as follows: juvenile or 1-year-old fish (≤20 cm FL), adolescent (20.1–34 cm FL), subadult (34.1–45 cm FL), and adult (>45.1 cm FL; Dorn et al., 2001; Smith, 1981; Walline, 1983). Walleye pollock sub-adults are likely 3–4 years old, of which ~50% have matured and recruited into the fishery, whereas adults are sexually mature fish, likely 5 years or older. Stage-class categories for Atka mackeral were defined as follows: juvenile up to 2-year-old fish (≤30 cm), adolescent or 3-year-old fish (30.1–35.2 cm), subadult or 4-year-old fish (35.3–45 cm), and adults (>45.1 cm; Lowe et al., 2001; McDermott and Lowe, 1997). Atka mackerel adolescents are ~50% sexually mature and adult-size fish are fully mature.

A chi-squared contingency test was used to test for differences in the proportion of fish stage-classes occur-ring in scats among rookeries and haul-out sites, years, and seasons by using corrected fork-length estimates from all cranial structures (S-PLUS 2000, Mathsoft, Inc., Cambridge, MA). To avoid pseudoreplication, we used presence or absence of cranial elements of a stage class in a scat particilarily because multiple elements from the same stage-class within a sample may not be independent (Hunt et al., 1996). By using presence-absence data we also avoided the problems associated with the variability in passage and recovery rates of different size structures (Tollit et al., 1997). Because sample sizes were small, juvenile and adolescent wall-eye pollock stage classes and recruiting adult and adult Atka mackerel stage classes were combined for seasonal comparisons among years. Fisher's exact test was used for comparisons when samples sizes for any stage class were less than 5 (S-PLUS 2000, Mathsoft, Inc., Cambridge, MA).

We obtained size composition data from commercial bottom trawls of walleye pollock and Atka mackerel from the NMFS North Pacific Groundfish Observer Program. Data were divided into winter (January–April) and fall (August–November) seasons and compared with our seasonal scat data (February–March and June–September). The percentage of overlap in sizes of fish caught by the commercial groundfish fishery with sizes of fish consumed by Steller sea lions was calculated by comparing size-frequency distributions. Two-cm size bins were used for the overlap calculation and Steller sea lion prey-size data were rounded to the nearest integer to be consistent with the fishery data.

Results

Regression formulae

A total of 517 pollock and 191 Atka mackerel samples were used to develop the regression equations of bone and otolith measurement to fork length. The sample size and range of fish lengths used for the regressions varied between species and cranial structures (Table 1). No clear indications of sample size required for regression analysis are currently provided in the literature; however, Owen and Merrick (1994) recommend a minimum sample size of 30–40. Sample sizes used to develop equations presented here ranged from 44 to 508.

In general, linear models were used for regression equations; however, several cranial structures were best fitted with a quadratic model. For both species, all structures were strongly related to fork length (r^2 range: 0.78–0.99; Table 1). The regressions encompassed the majority of sizes of bones and otoliths found in Steller sea lion scat samples for this study. However, a small proportion of walleye pollock bones from scats were larger than those used to develop the regressions.

Frost and Lowry (1981) developed otolith linear regression equations for walleye pollock from the Bering Sea using a double-regression approach that produced an inflection point at 10 mm. We examined the double regression approach but found a higher degree of correlation using a quadratic regression model. We compared the results of our model with Frost and Lowry's (1981) model and found that estimated fork lengths of walleye pollock differed less than 2 cm across the length range in our samples.

Estimation of size of walleye pollock and Atka mackerel consumed by Steller sea lions in the Bering Sea and Gulf of Alaska

A total of 714 scats from 39 sites contained 3646 selected cranial elements from either walleye pollock or Atka mackerel. Of those, 212 scats contained 666 walleye pollock cranial elements with a condition grade of either "good" (n=236) or "fair" (n=430). The minimum number of individual pollock per scat ranged from 1 to 18 with a mean of 1.6 (SD=1.7). For Atka mackerel, 379 scats contained 1685 skeletal elements with condition grade of either "good" (n=755) or "fair" (n=930). The minimum number of individual Atka mackerel per scat ranged from 1 to 14 with a mean of 1.9 (SD=1.6).

The mean fork length of walleye pollock consumed by Steller sea lions in the Bering Sea and Gulf of Alaska estimated from uncorrected otoliths found in scats was 23.7 cm (SD=12.0; n=88). Application of the DCF increased the mean estimate to 28.4 cm (SD=14.75; n=88). The size distribution estimated from corrected otoliths had three modes: a major mode around 32 cm and minor modes around 5 cm and 13 cm (Fig. 2A). Confidence intervals for all grade-corrected estimates can be found in Table 1.

The mean fork length of walleye pollock estimated from all seven structures was 39.8% greater than the mean estimated from otoliths alone. The uncorrected mean was 33.1 cm. Applying the DCF increased the mean length of walleye pollock by 18.7% to 39.3 cm (paired t test, t_{665}=37.9, P<0.001). Mean grade-corrected size estimates for cranial structures other than otoliths ranged from 34.5 cm (PHAR) to 47.2 cm (HYPO) and 95% confidence intervals ranged from 25.2 to 50.6 cm (Table 2). The condition-specific DCFs increased length estimates between 6.8% (HYPO) and 28.3% (DENT). The size distribution estimated from all grade-corrected structures had three modes: a major mode around 44 cm and minor modes around 5 cm and 15 cm (Fig. 2A).
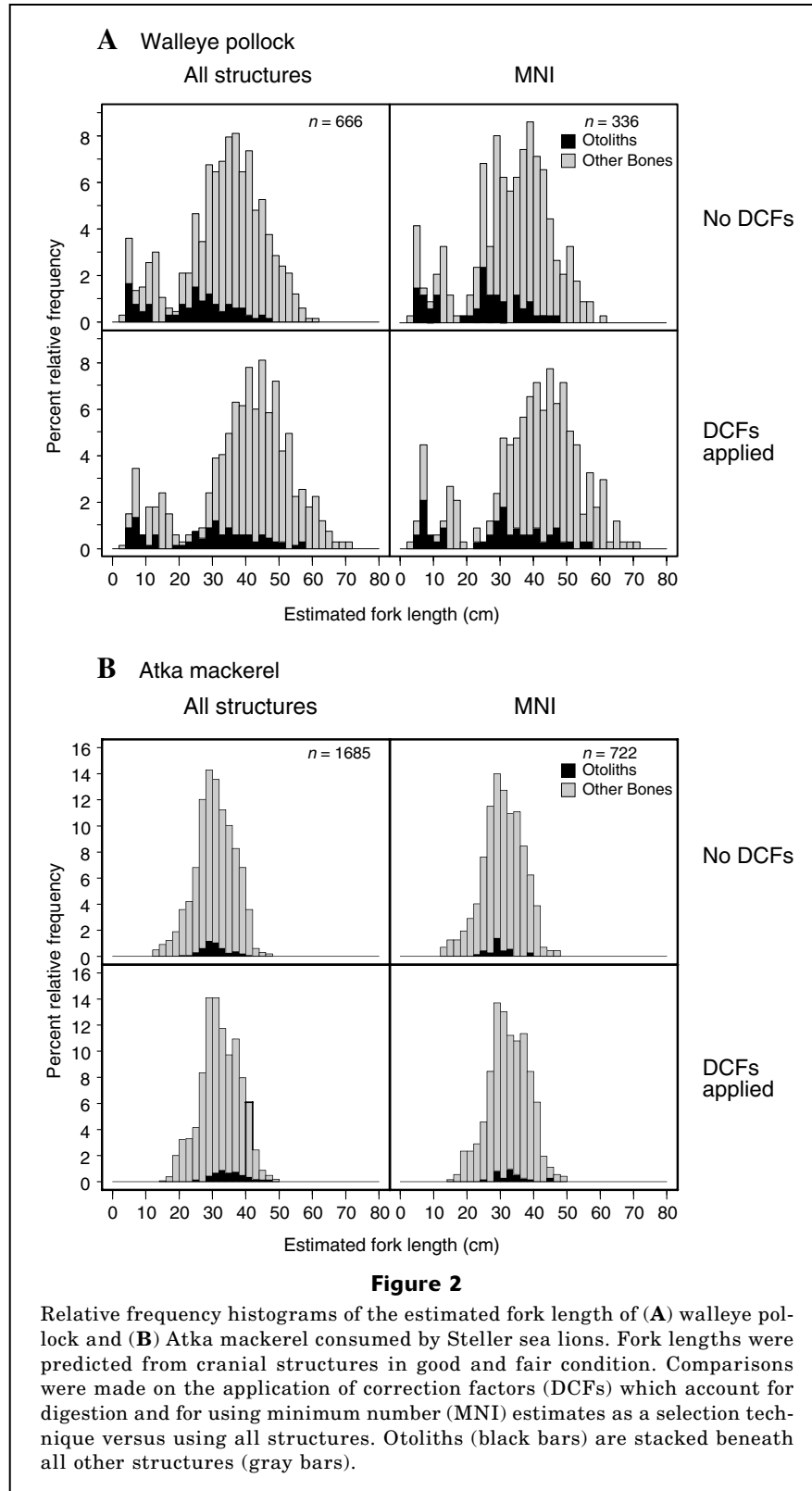
The mean fork length of Atka mackerel consumed by Steller sea lions in the Bering Sea and Gulf of Alaska estimated from uncorrected otoliths was 30.3 cm (SD=4.0; n=117). Application of the DCF increased the mean estimate to 34.7 (SD=4.8; n=117).

The mean fork length of Atka mackerel estimated from all structures (30.7 cm; SD=5.9 cm, corrected 32.3 cm; SD=5.9 cm, n=1685, paired t test, t_{1684}=39.1, P<0.001) was similar to the mean estimated from otoliths (6.9% less without a DCF and 1.3% less with a DCF; Fig. 2B). Mean grade-corrected size estimates for structures other than otoliths ranged from 26.6 cm (QUAD) to 34.2 cm (INTE) and 95% confidence intervals ranged from 24.0 cm (DENT) to 35.0 cm (INTE; Table 2). Use of the condition-specific DCFs increased length estimates between 2.1% (INTE) and 24.0% (DENT). Fork length estimates for all structures did not include PHAR because too few were recovered in scats in the feeding studies of captive Steller sea lions to develop a correction factor.

When mean prey size was calculated by using MNI, the mean corrected and uncorrected size estimate of both walleye pollock and Atka mackerel differed by less than 0.2 cm from estimates derived by using all structures. There was little difference in the standard deviations or distributions when MNI estimates were used compared with all structures (Table 2). Unsurprisingly, the use of MNI estimates did substantially reduce the sample size (336/666 for walleye pollock and 722/1685 for Atka mackerel).

Spatial and temporal variation in size of pollock and Atka mackerel consumed by Steller sea lions

No statistical difference was found in the proportion of pollock stage classes among years on summer rookery sites (P=0.29, χ^2=4.9, df=3) or winter haul-out sites (P=0.10; Fisher's exact test). Scats were collected only on summer haul-out sites during 2000. Although sample sizes were limited, we found significant differences in the proportion of pollock stage classes between summer rookery and haul-out scats (P=0.02; Fisher's exact test) and between summer and winter haul-out sites (P=0.018; Fisher's exact test) for year 2000. A greater proportion of juvenile pollock were found on summer haul-outs (64% juveniles, n=11 scats) than on summer rookeries (9% juveniles, n=132 scats) or winter haul-out sites (3% juveniles, n=69 scats, Fig. 3). No statistical difference

Figure 2

Relative frequency histograms of the estimated fork length of (**A**) walleye pol-
lock and (**B**) Atka mackerel consumed by Steller sea lions. Fork lengths were
predicted from cranial structures in good and fair condition. Comparisons
were made on the application of correction factors (DCFs) which account for
digestion and for using minimum number (MNI) estimates as a selection tech-
nique versus using all structures. Otoliths (black bars) are stacked beneath
all other structures (gray bars).

was found in the proportion of stage classes between
summer rookery (9.09% juvenile; 20.45% adolescent;
53.03% subadult; 65.15% adult) and winter haul-out

(2.90% juvenile; 21.74% adolescent; 57.97% subadult;
46.38% adult) sites for all years combined (P=0.32,
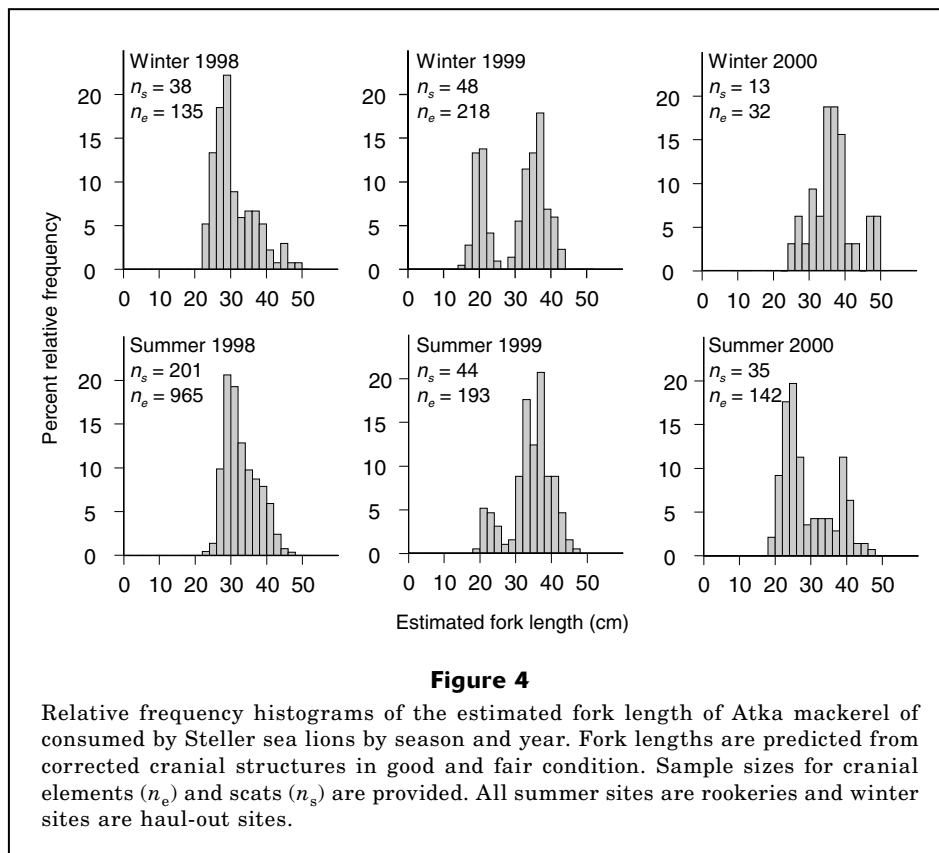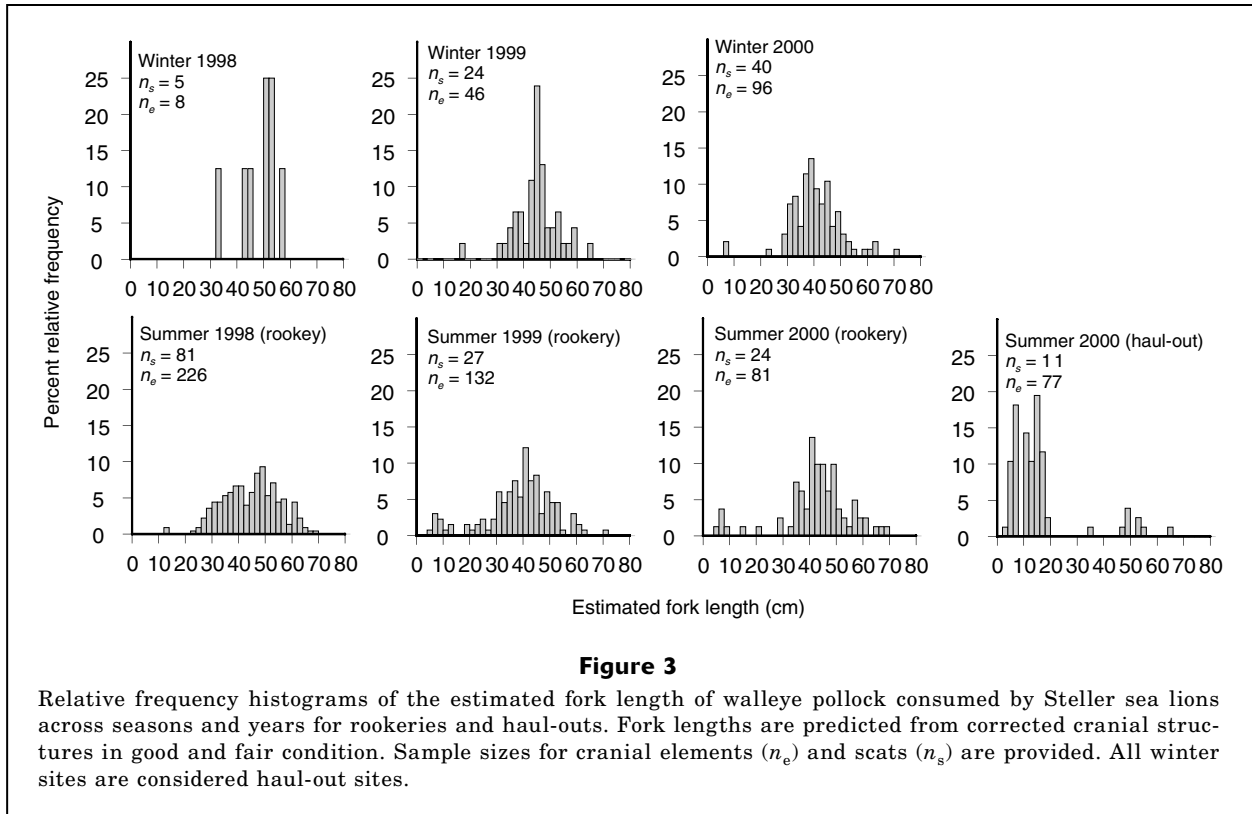χ^2=2.3, df=2).

Table 2

Estimated mean fork length of walleye pollock and Atka mackerel consumed by Steller sea lions based on selected structures with or without application of condition-specific digestion correction factors (DCFs). Data sets exclude all structures graded as heavily digested. Remaining total sample sizes of elements (n^e) are given along with proportion of grade "good" structures (n^g). For data sets where DCFs were applied, 95% confidence intervals (95% CI) were estimated by using bootstrap resampling procedures (Tollit et al., 2004b, this issue).
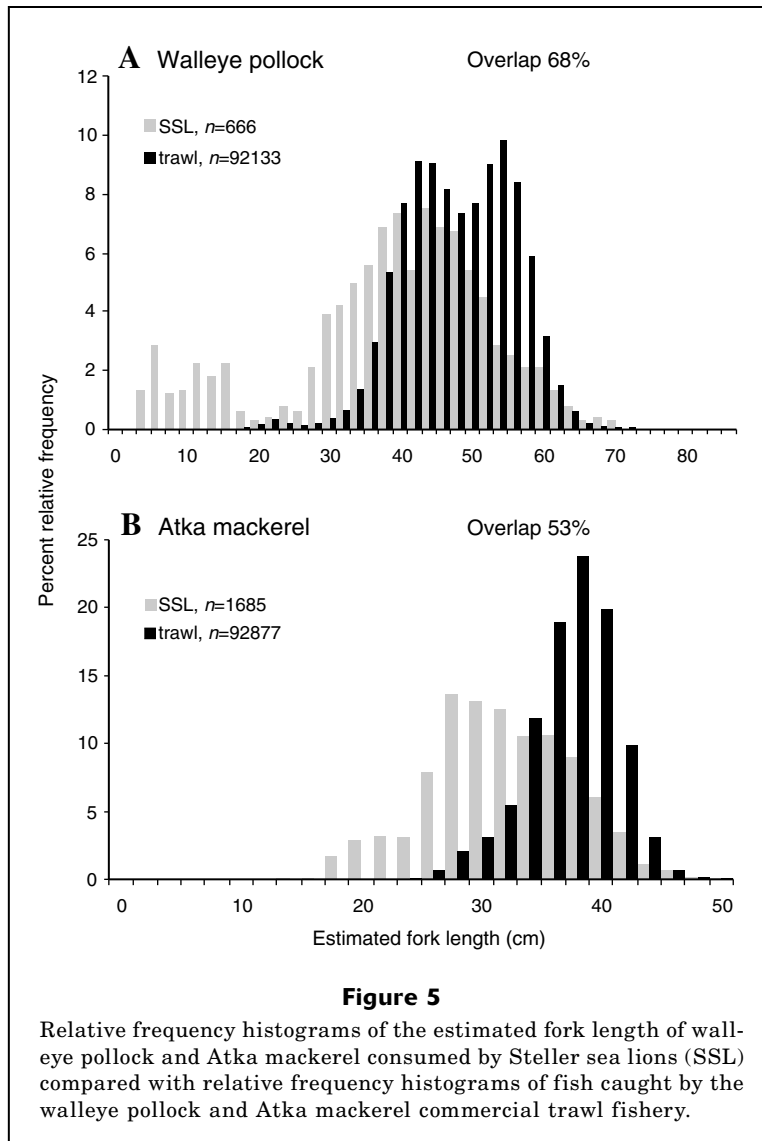
Species	Structure code	DCF	n^e	n^g	Mean FL (cm)	SD (cm)	Range (cm)	95% CI
Walleye pollock	INTE	No	60	0.45	43.7	8.0	16.7–59.4	
		Yes	60	0.45	47.0	8.5	16.7–65.9	44.9–49.8
	HYPO	No	38	0.55	44.2	7.2	30.5–60.4	
		Yes	38	0.55	47.2	7.8	34.9–62.7	44.5–50.6
	PHAR	No	23	0.61	32.2	14.3	9.7–53.1	
		Yes	23	0.61	34.5	14.8	10.9–53.1	25.2–44.5
	ANGU	No	136	0.40	36.1	8.4	10.6–55.3	
		Yes	136	0.40	40.2	9.0	10.6–60.6	38.5–42.4
	QUAD	No	134	0.34	35.1	12.0	9.4–57.8	
		Yes	134	0.34	44.5	15.3	11.9–70.8	38.8–49.6
	DENT	No	187	0.37	28.6	11.8	3.1–57.2	
		Yes	187	0.37	36.7	15.1	3.7–70.2	30.3–42.4
	OTOL	No	88	0.03	23.7	12.0	4.6–46.8	
		Yes	88	0.03	28.4	14.8	4.6–57.1	17.0–32.4
	All	No	666	0.35	33.1	12.4	3.1–60.4	
		Yes	666	0.35	39.3	14.3	3.7–70.8	35.9–42.4
Atka mackerel	INTE	No	601	0.58	33.5	5.0	19.5–46.8	
		Yes	601	0.58	34.2	5.1	19.5–49.6	33.4–35.0
	HYPO	No	238	0.42	31.1	4.8	18.8–46.2	
		Yes	238	0.42	32.9	5.5	19.3–48.3	32.4–34.6
	ANGU	No	488	0.45	30.2	4.7	17.3–43.0	
		Yes	488	0.45	31.8	5.1	17.3–46.1	31.7–33.3
	QUAD	No	161	0.37	25.3	5.4	14.8–40.6	
		Yes	161	0.37	26.6	5.6	15.3–41.4	25.1–28.4
	DENT	No	80	0.28	22.5	7.7	13.0–38.7	
		Yes	80	0.28	27.9	8.0	17.7–44.1	24.0–33.0
	OTOL	No	117	0.06	30.3	4.0	21.2–40.6	
		Yes	117	0.06	34.7	4.8	21.2–47.0	33.5–35.8
	All	No	1685	0.45	30.7	5.9	13.0–46.9	
		Yes	1685	0.45	32.3	5.9	15.3–49.6	31.7–33.4

Significant differences were found in the proportion of Atka mackerel stage classes between 1998 and 1999 on summer rookery sites (P=0.05, χ^2 =6.0, df=2) and winter haul-out sites (P=0.01, χ^2=9.9, df=2) and between 1998 and 2000 winter haul-out sites (P=<0.01, Fisher's exact test). Significant seasonal differences were found only in 1998 (P=0.03, χ^2=7.1, df=2) which may be the result of the small sample size in winter 2000. In summer and winter, annual differences in size of Atka mackerel consumed by Steller sea lions corresponded to changes in the length distribution of Atka mackerel resulting from exceptionally strong year classes in 1995 and 1998 (Lowe et al., 2001). The 1995 year class is represented as a mode around 30 cm in 1998 (3-year-old fish), 35 cm in 1999 and >40 cm in

2000 (Fig. 4). The 1998 year class is represented most clearly as 2 year olds (mode 20–25 cm) in summer 2000 (Fig. 4). Strong annual modes found in our data match those recorded in surveys of Atka mackerel in the Bering Sea and Gulf of Alaska (Lowe et al., 2001).

For walleye pollock and Atka mackerel there was no difference in the mean size of fish caught by the commercial fishery among years (P>0.4, one-way ANOVA). There was a significant difference (P<0.05, one-way ANOVA) in the size of fish caught between seasons. This difference is likely due to aggregations of spawning adult fish caught during the roe fishery. In the winter there is a 56% overlap between the size of fish caught in the commercial pollock fishery and those taken by sea lions and a 54% overlap in the size taken by the Atka

Figure 3

Relative frequency histograms of the estimated fork length of walleye pollock consumed by Steller sea lions across seasons and years for rookeries and haul-outs. Fork lengths are predicted from corrected cranial structures in good and fair condition. Sample sizes for cranial elements (n_e) and scats (n_s) are provided. All winter sites are considered haul-out sites.

Figure 4

Relative frequency histograms of the estimated fork length of Atka mackerel of consumed by Steller sea lions by season and year. Fork lengths are predicted from corrected cranial structures in good and fair condition. Sample sizes for cranial elements (n_e) and scats (n_s) are provided. All summer sites are rookeries and winter sites are haul-out sites.

Figure 5

Relative frequency histograms of the estimated fork length of walleye pollock and Atka mackerel consumed by Steller sea lions (SSL) compared with relative frequency histograms of fish caught by the walleye pollock and Atka mackerel commercial trawl fishery.

mackerel fishery. In the summer the overlap in size of fish consumed by sea lions and the size of fish caught in the pollock fishery is 67% and there is a 51% overlap in the size of fish caught in the Atka mackerel fishery. When seasonal data were pooled, overlap between the size of fish caught in the commercial fishery and the size of fish consumed by sea lions was 68% for walleye pollock (Fig. 5A) and 53% for Atka mackerel (Fig. 5B).

Discussion

Regression formulae

Regressions of cranial structure measurement on fish fork length with the use of multiple structures was an effective tool for estimating size of fish consumed by Steller sea lions. Sample sizes of measurable prey remains from scats were enhanced by using a number of cranial structures in addition to otoliths. Body size estimates of only 13.2% of the pollock and 6.9% of the Atka mackerel prey in this study were based on otoliths alone. Fork-length estimates can be considered accurate regardless of which structure was used in the estimate because all r^2 values were high (range: 0.78–0.99). Likewise errors associated with the application of DCFs were consistent across structures (Tollit et al., 2004b, this issue). Confidence intervals around size estimates generally overlapped across structures; however, it was not surprising that different structures yielded slightly different mean sizes because different bones can originate from different scats.

The use of multiple cranial structures may also reduce bias resulting from variability in recovery and passage rates of structures from different species or sizes of fish (Pierce and Boyle, 1991; Browne et al.,

2002; Tollit et al., 2003). Even after applying a DCF, the estimated mean size of walleye pollock based on otoliths was 10.9 cm smaller than the mean size estimated by using all cranial structures. Because walleye pollock otoliths are relatively large and have a different composition than other cranial structures, the larger otoliths may be regurgitated, fully digested, or crushed by rocks in the stomach and not pass through in scat as readily as smaller otoliths or other cranial structures, thereby reducing their occurrence in scat and use in generating prey-size estimates. Atka mackerel otoliths are much smaller at older ages in relation to walleye pollock, which may explain why the size of prey estimated from otoliths was similar to the size estimated from other cranial structures.

The use of DCFs for all structures, including otoliths, to account for erosion increased mean size estimates for both walleye pollock (33.1 vs. 39.3 cm FL) and Atka mackerel (30.7 vs. 32.3 cm FL). The relatively small increase in the corrected size of Atka mackerel reflects that the structures from this species were found in better condition than those from pollock (Table 2), as well as that correction factors were found to be species-, structure-, and condition-specific (Tollit et al., 2004b, this issue). Overall, our results emphasize the importance of using appropriate condition-specific DCFs. Other studies with captive sea lions have also demonstrated that grade-specific DCFs can reduce systematic error and increase precision of body mass estimates (Tollit et al. 1997). For walleye pollock, there was no significant difference in the degree of erosion across the three size ranges for each structure within each condition category (Tollit et al., 2004b, this issue). We assume the DCFs can be used for fish outside of this size range because the relative shape, structure, and proportion of the morphological features are consistent for both smaller and larger fish (Tollit et al., 2004b, this issue). Further research is necessary to test whether there are differences across the size range for Atka mackerel.

Size of walleye pollock and Atka mackerel consumed by Steller sea lions in the Bering Sea and Gulf of Alaska

In general, Steller sea lions on summer rookery and winter haul-out sites consumed primarily subadult and adult-size walleye pollock and Atka mackerel year-round in 1998–2000. Steller sea lions typically forage near shore, in shallow water (<50 m) and at night (Raum-Suryan et al., 2002; Loughlin et al., 2003). Likewise, adult walleye pollock migrate vertically to shallower depths during the night (Smith, 1981). Adult-size Atka mackerel also are commonly found in nearshore coastal areas during their spawning season (Zolotov, 1993).

Juvenile walleye pollock were found in relatively high numbers only in scats collected on summer haul-out sites. Scats collected from summer haul-out sites likely represent a larger proportion of juvenile Steller sea lions than those collected on summer rookery or winter haul-out sites. Previous studies indicate that juvenile

sea lions (<4 years old) consume smaller walleye pollock than adult sea lions (Pitcher, 1981; Frost and Lowry, 1986; Merrick and Calkins, 1996). Juvenile walleye pollock are often found at shallow depths in bays and near shore habitat (Smith, 1981). Likewise, Loughlin et al. (2003) reported that juvenile Steller sea lions are typically shallow divers and frequently make short range foraging trips (<15 km). Additional scat collections on summer haul-out sites are necessary to determine more conclusively prey-size selectivity for juvenile Steller sea lions.

Annual changes in the size-frequency distribution of Atka mackerel consumed by Steller sea lions followed changes in the size distribution of Atka mackerel resulting from exceptionally strong year classes. Merrick and Calkins (1996) also showed that the size of prey consumed by Steller sea lions can reflect the size distribution of the fish population. From the mid-1990s on, only 1999 was a strong recruitment year for walleye pollock in the Gulf of Alaska (Dorn et al., 2001), but we did not find a significantly greater proportion of juvenile fish eaten by Steller sea lions in 2000 than in 1999 or 1998 perhaps because sufficient numbers of larger size fish were available in regions where walleye pollock were consumed.

Historical studies of Steller sea lion prey size have primarily been based on measurements of walleye pollock otoliths found in stomach samples but often without application of correction factors for erosion (Pitcher, 1981; Merrick and Calkins, 1996; Calkins, 1998). Prey-size estimates based on stomach contents will likely differ from estimates derived from scats because of differences in digestion rates and breakage (Jobling and Breiby, 1986). However, results of studies examining the variability in prey size with sample type are variable. Sinclair et al. (1996) suggested that in northern fur seals (*Callorhinus ursinus*), another otariid, small otoliths tend to flush through the digestive system more quickly than larger ones, resulting in a possible bias in scats towards smaller otoliths. In contrast, experiments with captive sea lions have shown that smaller otoliths are recovered in lower relative frequencies than are larger ones (Tollit et al., 1997). Frost and Lowry (1980) found no significant difference between the size of otoliths obtained from stomach and intestines of ribbon seals. Overall, we believe useful comparisons of prey size consumed by Steller sea lions can be made between our study and earlier studies.

Steller sea lions have been reported to consume a wide size range of walleye pollock. However, in most prior studies a larger proportion of juvenile fish were found than what we estimated from scats. Otoliths from stomach samples collected from 1975 to 1978 in the Gulf of Alaska contained primarily juvenile age pollock (mean FL=29.8cm; SD= 11.6; Pitcher, 1981). Undigested otoliths from stomach samples collected between 1975 and 1981 in the Bering Sea also contained mostly juvenile fish (mean FL=29.3 cm) but had a distinct mode of adult-size pollock (48 cm FL; Frost and Lowry, 1986). Likewise, 43 stomach samples collected between 1985

and 1986 in the central Gulf of Alaska contained primarily juveniles (mean FL=25.4 cm; SD=12.4) and had a weak mode of adult-size fish (39–43 cm; Merrick and Calkins, 1996; Calkins and Goodwin[1]). Mostly adult-size fish were found in stomachs recovered from Steller sea lions caught in trawl nets in the central Gulf of Alaska (1983–84; Loughlin and Nelson, 1986) and in stomach samples collected from 1994 to 1995 in Japanese waters (Goto and Shimazaki, 1998). However, in both these studies the samples of prey size may have been biased by the selectivity of the fishing gear for larger fish.

Using identical methods to those of our study, Tollit et al. (2004a, this issue) estimated the size of walleye pollock consumed by the eastern stock of Steller sea lions between 1994 and 1999. The average size of walleye pollock consumed, estimated from all grade-corrected structures (mean=42.4 cm; SD=11.6), was similar to the average size found in our study of the western stock of Steller sea lions. Furthermore, Tollit et al. (2004a, this issue) also found a greater occurrence of adult pollock in scats collected on rookery sites than from scats collected on haul-out sites. However, Steller sea lions from the western stock consumed a greater proportion of juvenile and adolescent fish and less adult fish than those from the eastern stock during summer (June–July) and similar-size fish were consumed on haul-out sites in winter (March) in both regions. Neither study indicated the high occurrence of juvenile walleye pollock reported in the 1970s and 1980s. The greater occurrence of juvenile walleye pollock in historical studies may be a result of prey availability or differences in sampling methods.

By examining the relative size-frequency distributions of prey selected by Steller sea lions and those taken in the commercial trawl fishery, we found considerable overlap (68% walleye pollock and 53% Atka mackerel). Likewise, high levels of potential overlap in size were found between walleye pollock selected by Steller sea lions from the eastern stock and caught by the small commercial fishery bordering Southeast Alaska (Tollit et al., 2004a, this issue). The extent of overlap throughout the range of Steller sea lions between the size of prey consumed by sea lions and the size of fish targeted and taken by the pollock and Atka mackerel trawl fisheries could result in competition between fisheries and foraging sea lions if resources are limited.

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