MARKET SQUID (*LOLIGO OPALESCENS*) IN THE DIET OF CALIFORNIA SEA LIONS (*ZALOPHUS CALIFORNIANUS*) IN SOUTHERN CALIFORNIA (1981–1995)

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ABSTRACT

California sea lion (*Zalophus californianus*) scat and spewing samples collected at three rookeries in southern California during 1981–95 were used to determine how sea lions utilized the market squid (*Loligo opalescens*) resource. The samples revealed that market squid is one of the most important prey of sea lions in southern California, occurring in 35% to 44% of scat samples from San Nicolas Island (SNI), San Clemente Island (SCI), and Santa Barbara Island (SBI). It is eaten by sea lions throughout the year, but most often during fall and winter, and patterns suggest periods of high and low consumption associated with prevailing oceanographic conditions and, possibly, with squid abundance and movements. Percent frequency of occurrence values for market squid in scat samples collected seasonally from SNI were positively correlated with those from SCI ($r = 0.78$), and samples collected during summer at SBI were positively correlated with summer samples from SCI ($r = 0.82$) and SNI ($r = 0.85$). Landings of market squid at ports in southern California and percent occurrence values of market squid in scat samples collected seasonally were positively correlated for SNI ($r = 0.66$) and SCI ($r = 0.74$), but not for summer samples from SBI ($r = 0.25$). Sea lions eat squid with dorsal mantle lengths from 10 to 235 mm (mean = 127 mm). Significant seasonal, annual, and interisland differences ($P < 0.001$) were found in the size of squid consumed by sea lions. Significant differences ($P < 0.001$) were found in size of squid between scats and spewings, and between individual samples.

INTRODUCTION

Market squid (*Loligo opalescens*) is one of the most common prey species for California sea lions (*Zalophus californianus*) in southern California (Antonelis et al. 1984; Lowry et al. 1990, 1991). Sea lions eat squid throughout the year, but predominantly during autumn and winter, and its presence in their diet varies from year to year (Lowry et al. 1990, 1991). A spring and summer study at San Miguel Island showed that sea lions eat squid with a dorsal mantle length of 62 to 185 mm (mean = 127 mm; Antonelis et al. 1984).

In 1995, the sea lion population along the U.S. Pacific coast was estimated at 167,000 to 188,000 individuals, with an average annual growth rate of 8.3% since 1983 (Barlow et al. 1997). Sea lions are also found in western Mexico from the U.S.–Mexico border to central Mexico, and in the Gulf of California (Le Boeuf et al. 1983), but there is no current abundance estimate for sea lions south of the U.S.–Mexico border.

Numbers of sea lions in southern California fluctuate during the year. More are present at rookeries (fig. 1) during the summer breeding season, and fewer during autumn and winter. Adult females generally remain in the area throughout the year to nurse their pups, and juveniles either remain near rookeries or travel north or south along the coast (Bartholomew 1967; Huber 1991). After the summer breeding season, subadult and adult males from U.S. rookeries migrate north (some as far as British Columbia, Canada) and those from western Baja California, Mexico, migrate into and through southern California (Bartholomew 1967; Bigg 1988).

Studies at San Miguel Island have shown that adult female sea lions forage between 10 and 100 km (mean = 54.2 km, SD = 32.4 km, $n = 9$) from the rookery (Antonelis et al. 1990), and dive to average depths of 31.1 to 98.2 m, with maximum dives between 196 and 274 m (Feldkamp et al. 1991). Laboratory studies indicated that sea lions travel at an estimated speed of 10.8 km/hr (Feldkamp 1985), and that one- and two-year-old sea lions have an initial defecation time averaging 4.2 hours (Helm 1984). Adult females spend 1.6–1.9 days on land and 1.7–4.7 days at sea (Heath et al. 1991). Feeding experiments on California sea lions that were fed market squid revealed that (1) 80% of squid beaks (i.e., mandibles) pass through the gastrointestinal tract within 48 hours and 95% within 96 hours; (2) squid remains may be spewed within 20 to 48 hours; and (3) all beaks are not regurgitated when squid remains are spewed—some pass through the gastrointestinal tract (Hawes 1983; Orr 1998). It is reasonable to assume, therefore, that scat and spewing samples collected at haul-outs represent a sample of feeding within 100 km of the haul-out site.

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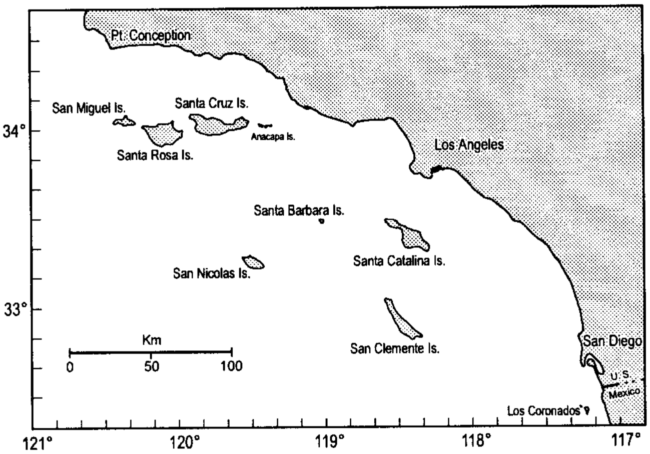

Figure 1. Map of Southern California Bight. California sea lion (*Zalophus californianus*) rookeries are located at Santa Barbara, San Clemente, San Miguel, and San Nicolas Islands.

Sea lions haul out of the water to rest, pup, and mate. While on shore, they eliminate waste in the form of scats (feces) and spewings (vomitus), which can be used to study their diet. Squid are identified from beaks, and fish from otoliths (earbones) recovered from scats and spewings collected at haul-out sites. Although fish otoliths are susceptible to erosion during digestion, chitinous beaks of squid are highly resistant to digestion (Hawes 1983).

Because market squid are one of the sea lion's most important prey items, it is apparent that the sea lion population and the squid fishery compete for the same resource. The California market squid fishery was the state's most valuable fishery in 1996, with ex-vessel revenues of $30 million (Yaremko 1997). Southern California fishermen accounted for 93% of 80,360 metric tons of market squid landed statewide in 1996, with most landings in autumn and winter.

Although sea lions consume a variety of fish and squid (Antonelis et al. 1984; Lowry et al. 1990, 1991), we will only report on market squid for three of four rookeries in southern California during 1981–95. Data on this and other prey species from San Clemente Island (SCI) and San Nicolas Island (SNI) during 1981–86 were published by Lowry et al. (1990, 1991). Long-term studies of sea lion diet provide information that may help to quantify how one of the top-level predators in the ecosystem affects the squid and fish resource. We investigate whether sea lion scat and spewing samples might be useful sources of information about trends in abundance or availability of market squid. We describe seasonal, annual, and interisland differences of market squid in sea lion scat samples, relationships with El Niño, and the size of market squid eaten by sea lions; we also compare the frequency of occurrence of market squid in scat samples to market squid landings (which may be a crude measure of abundance) by the southern California fishery.

METHODS

Sample Collection

Scat and spewing samples from sea lions were collected at Santa Barbara Island (SBI), SCI, and SNI during 1981–95 (fig. 1). As the population of sea lions increased during the study period, the number of haul-out sites at SBI and SCI remained the same, but in the late 1980s sea lions began to occupy additional sites along the southeastern shoreline of SNI. No samples were collected from new haul-out sites at SNI. Samples were collected from (1) the Southeast Rookery at SBI, (2) Mail Point and its vicinity along the western shoreline of SCI, and (3) three areas of coastline at SNI approximately 3.6–4.8 km, 5 km, and 6.5–7 km along the southern shoreline from Vizcaino Point (i.e., the westernmost point on the island). Samples from the 5 km site at SNI (added in 1992) were collected only in July, when subadult and adult males were separated from adult females. All other collecting sites were occupied year-round by adult females, but other age and sex classes were also present during various times of the year.

Samples were collected opportunistically at intervals ranging from two weeks to three months during 1981–87 at SCI and at intervals ranging from two weeks to nine months during 1981–90 at SNI. A quarterly sampling design was established in 1988 at SCI and in 1991 at SNI, and approximately fifty samples were collected (whenever possible) at each collection site during January, April, July, and October. Samples at SBI were collected only during summer (mostly in July). In 1981–82, samples at SBI were collected opportunistically; thereafter approximately fifty samples were collected each year.

Samples were grouped by season into winter (December–February), spring (March–May), summer (June–August), and autumn (September–November; table 1). Fresh and dry samples from monitored sites were collected at SCI in 1981–87 and at SNI in 1981–90, but thereafter only fresh samples were collected. At SBI, only fresh samples were collected. We estimated that fresh samples represented the diet within the last 3–4 days of the collection date, and dry samples represented the time since the last collection.

Sample Processing

Each sample was washed through a 2.8 mm^2 mesh sieve placed atop a 0.710 mm^2 mesh sieve (sometimes a 1.5 mm^2 mesh sieve was placed between the two sieves). Fish otoliths, cephalopod beaks, teeth from jawless and cartilaginous fishes, and crustacean exoskeletal remains were collected from all sieves and used to identify prey remains to the lowest possible taxonomic level. Market squid beaks were identified from museum voucher spec-

TABLE 1
Number of California Sea Lion (*Zalophus californianus*) Scats and Spewings (in Parentheses) Collected at Sites in Southern California, 1981–95

Year	San Clemente Island				San Nicolas Island				Santa Barbara Island
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Summer
1981				41			24(2)	18	76
1982	3	107	143	54(1)	12	15	68	13	50
1983	59(12)	110(1)	77	78	4	42	150	55(1)	31
1984	144(1)	101	89(1)	53	75	35	107	93(1)	50
1985	16	12	60	26	62	77(7)	64	63	44
1986		44	65	22	35	24	80	124	52
1987	6(2)	30	50	34(1)			25		57
1988	49(1)	57	43	12(2)	18	26	49		51
1989	25(43)	55	51(1)	68(11)	23	36	31		56
1990	37(33)	50	55	50		49			56
1991	51(8)	52	55	55	49(3)	52(1)	110	99(2)	51
1992	50(1)	51	52	50	102(3)	97	149	101	51
1993	50	50(2)	51	49(1)	102(9)	96(5)	152	99(2)	52
1994			49(1)	45(5)			98	99	50
1995	46(4)	51(5)	41(9)		99(1)	98(4)	147	102	49

imens and from a pictorial guide (Iverson and Pinkas 1971). Although several species of squid have been identified as prey of California sea lions (see Antonelis et al. 1984; Lowry et al. 1990, 1991), the distinctive shape and coloration of market squid beaks make them easy to distinguish from other species even when degraded by digestion.

Sample Analysis

Percent frequency of occurrence in scat samples was used as a seasonal index of consumption for each prey taxon, to rank prey, and to examine seasonal and annual changes. Percent frequency of occurrence is the percentage of samples containing either a prey taxon or unidentified fish otoliths, cephalopod beaks, teeth from jawless and cartilaginous fishes, or crustacean exoskeletal remains. We smoothed the time series of percent occurrence index values with a distance-weighted least squares (DWLS) smoother with the tension set at 0.25 (Systat 6.0 for Windows; Anonymous 1996a) to examine multiyear cycles of market squid in scat samples for the three rookeries. Percent frequency of occurrence index values for each season were arcsine-transformed.

We used correlation analysis to compare transformed index values among the three islands to test the hypothesis that market squid appears in the diet of sea lions from different islands in equal proportions. We also used correlation analysis to compare transformed index values from each island to seasonal market squid landings in southern California (landings data provided by Bill Jacobson, NMFS, Southwest Region, pers. comm., March 21, 1997) to test the hypothesis that squid in the diet of sea lions reflects abundance (assuming that landings are a crude measure of abundance).

Estimation of Squid Length

We estimated dorsal mantle length (DML) of market squid eaten by sea lions by measuring the rostral width of upper beaks recovered from scat and spewing samples. We used upper rostral width (URW) because it resists digestion better than other beak dimensions. Beaks were measured with a micrometer in the eyepiece of a dissecting microscope. Samples included beaks collected at SBI (1989–95), SNI (1987–95), and SCI (1981–95; table 2). We used the regression equation developed by Kashiwada et al. (1979) to estimate dorsal mantle length from each rostral width measurement. Measurements of URW were used for statistical analysis, and DML estimates from URW measurements were used for graphic presentations.

Analysis of Squid Size

A missing cells design means-model ANOVA (Systat 6.0 for Windows; Milliken and Johnson 1984; Anonymous 1996b) was used to compare URW measurements between islands, years, and seasons because not all seasons were sampled during 1981–95 (table 1) and because not all beaks found in samples were measured (table 2). We tested the null hypothesis that there was no difference (at $\alpha = 0.05$) in URW of market squid between season, year, and island for samples collected at SCI and SNI during 1988–95 (samples from SBI were not included because all seasons were not represented). We performed this analysis on URWs from beaks found in scats and, separately, scats and spewings combined. We also used the means-model ANOVA to compare URWs of beaks found in scats to those in spewings when both sample types were collected at SCI during 1988–95 and, separately, at SNI during 1991–95.

TABLE 2
Number of Beaks Measured from Scats and Spewings (in Parentheses) for Estimating Dorsal Mantle Length of Market Squid (*Loligo opalescens*) Consumed by California Sea Lions, 1981–95

	San Clemente Island				San Nicolas Island				Santa Barbara Island
Year	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Summer
1981				127					
1982		39	434	16					
1983	54(98)	3	70	40					
1984		1	1						
1985			47	4					
1986	74(22)	317	27						
1987		13	42	42			10		
1988	152	13	25	87	19	6	62		
1989	443	53	181	216	96	2	78		434
1990	442	167	23	159		250			335
1991	371	112	31	171	408	221(83)	748	995	163
1992	274(3)	10	10	91	627	11	120	1,332	10
1993	274	1(34)	51	235	718	133(4)	400	899	35
1994			56(38)	247			31	446	88
1995	736	145	154		1,048	671	702	556	95

TABLE 3
Frequency of Occurrence of Common Prey Found in California Sea Lion Scat Collected Seasonally at San Clemente (n = 2,543) and San Nicolas Islands (n = 2,980), and in Summer at Santa Barbara Island (n = 736), 1981–95

		San Clemente Island		San Nicolas Island		Santa Barbara Island	
Scientific name	Common name	n	%	n	%	n	%
Engraulis mordax	Northern anchovy	1,155	45.4	897	29.4	360	48.9
Loligo opalescens	Market squid	895	35.1	1,323	44.3	315	42.7
Merluccius productus	Pacific whiting	631	24.8	931	31.2	290	39.4
Trachurus symmetricus	Jack mackerel	631	24.8	659	22.1	147	19.9
Sebastes jordani	Shortbelly rockfish	328	12.8	423	14.1	100	13.5
Pleuroncodes planipes	Pelagic red crab	301	11.8	244	8.1	72	9.7
Scomber japonicus	Pacific mackerel	264	10.3	463	15.5	59	8.0
Sardinops sagax	Pacific sardine	122	4.7	371	12.4	73	9.9

We examined size of squid within individual scat and spewing samples to see if scat and spewing samples had beaks from similar-sized squid. We assigned a unique sample code number to each scat and spewing sample. There were insufficient spewing samples from most collections for this analysis (table 1), but seven collections had an adequate number of spewing samples: (1) winter 1989 at SCI, (2) autumn 1989 at SCI, (3) winter 1990 at SCI, (4) winter 1991 at SCI, (5) autumn 1994 at SCI, (6) summer 1995 at SCI, and (7) winter 1993 at SNI. We used a nested ANOVA for each collection to test the hypothesis that there was no difference (at $\alpha = 0.05$) in URW of squid found between sample types (i.e., scats and spewings) and individual samples (sample was nested within sample type). Graphic representations of these comparisons were chosen for two of the seven collections (autumn 1989 at SCI and winter 1990 at SCI).

RESULTS

Market Squid in the Diet of California Sea Lions

Market squid was found in 35.1% to 44.3% of scat samples, and represented the most common or second most common prey taxon found at three southern California rookeries during 1981–95 (table 3). Other common prey of sea lions were northern anchovy (*Engraulis mordax*); Pacific whiting (*Merluccius productus*); jack mackerel (*Trachurus symmetricus*); shortbelly rockfish (*Sebastes jordani*); Pacific mackerel (*Scomber japonicus*); Pacific sardine (*Sardinops sagax*); and pelagic red crab (*Pleuroncodes planipes*, consumed only during El Niño periods). Sea lions ate market squid year-round, but predominantly during autumn and winter (table 4).

Smoothed seasonal percent occurrence index data indicated fewer squid in sea lions' diet during and immediately after moderate and severe El Niño episodes (1983–84 and 1992–93) and more squid in 1989–90 and 1995 (fig. 2). The sharpest decline occurred in 1984 and the first half of 1985, during or just after the 1983–84 El Niño period in California. We found market squid in scat samples of sea lions from different rookeries in similar proportions. Percent frequency of occurrence values for market squid in scat samples from SCI were positively correlated with those from SNI (r = 0.78) and SBI (r = 0.82), and samples from SNI were positively correlated with samples from SBI (r = 0.85). Seasonal

TABLE 4
Seasonal Frequency of Occurrence Indices for Market Squid Found in California Sea Lion Scat, and Metric Tons of Market Squid Landed in Southern California Ports, 1981–95

Year	Season	Percent frequency of occurrence[a] SBI	SCI	SNI	Landings (t)
1981	Summer	36.7	—	18.0	3.8
	Autumn	—	42.4	56.0	1,483.4
1982	Winter	—	66.6	92.0	7,737.1
	Spring	—	17.5	50.0	1,537.0
	Summer	40.4	26.4	12.0	337.0
	Autumn	—	19.6	53.8	2.3
1983	Winter	—	28.2	25.0	895.0
	Spring	—	8.4	14.3	9.0
	Summer	38.7	22.2	17.1	4.0
	Autumn	—	25.6	27.3	0.9
1984	Winter	—	5.5	7.1	0.5
	Spring	—	3.4	6.9	64.0
	Summer	0	1.1	13.5	11.0
	Autumn	—	0	7.4	0.1
1985	Winter	—	0	13.0	347.4
	Spring	—	0	4.5	800.1
	Summer	28.2	23.6	13.3	322.1
	Autumn	—	20.8	41.8	1,824.1
1986	Winter	—	—	19.4	6,475.2
	Spring	—	35.1	0	957.2
	Summer	31.2	23.4	17.8	349.7
	Autumn	—	0	58.6	5,640.4
1987	Winter	—	50.0	—	8,589.9
	Spring	—	63.3	—	2,437.7
	Summer	35.4	26.0	4.0	14.1
	Autumn	—	46.8	—	3,839.2
1988	Winter	—	35.4	60.0	9,651.2
	Spring	—	19.6	26.9	4,749.2
	Summer	58.3	36.8	45.6	1,836.4
	Autumn	—	72.7	—	11,540.9
1989	Winter	—	80.9	91.3	20,855.7
	Spring	—	50.9	11.4	3,101.3
	Summer	83.0	63.0	73.3	618.6
	Autumn	—	67.7	—	10,825.3
1990	Winter	—	94.5	—	10,212.4
	Spring	—	57.4	64.5	137.9
	Summer	69.2	47.2	—	1.4
	Autumn	—	71.1	—	9,275.7
1991	Winter	—	76.0	89.1	11,984.6
	Spring	—	38.0	51.0	19.8
	Summer	72.5	31.2	63.0	500.2
	Autumn	—	63.4	76.5	17,099.8
1992	Winter	—	70.8	69.4	9,292.7
	Spring	—	12.8	11.7	35.4
	Summer	20.4	12.2	23.0	0
	Autumn	—	50.0	65.9	751.4
1993	Winter	—	46.9	71.4	7,681.4
	Spring	—	6.1	40.7	86.2
	Summer	33.3	45.0	40.7	2,201.7
	Autumn	—	81.2	88.6	17,258.4
1994	Winter	—	—	—	22,187.8
	Spring	—	—	—	600.4
	Summer	29.1	34.1	25.9	1,193.8
	Autumn	—	53.6	55.2	16,283.7
1995	Winter	—	97.7	73.9	21,708.9
	Spring	—	70.7	75.5	1,808.3
	Summer	60.4	50.0	64.0	5,708.8
	Autumn	—	—	75.7	28,500.1

Note: No samples were collected where dashes appear.
[a]SBI = Santa Barbara Island; SCI = San Clemente Island; and SNI = San Nicolas Island.

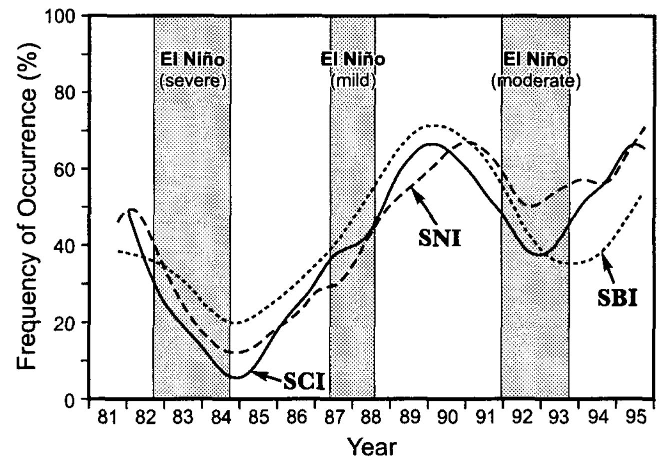

Figure 2. Distance-weighted least squares (DWLS) smoothed seasonal percent frequency of occurrence indices of market squid (*Loligo opalescens*) in California sea lion (*Zalophus californianus*) scat samples collected from Santa Barbara (SBI), San Clemente (SCI), and San Nicolas (SNI) Islands, California, 1981–95.

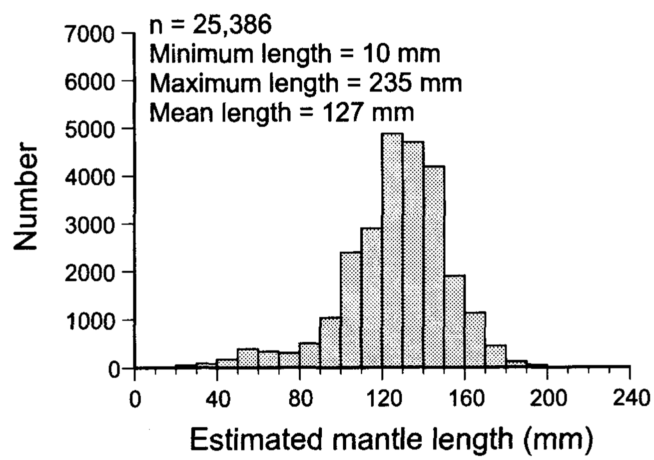

Figure 3. Size structure of all dorsal mantle length estimates of market squid (*Loligo opalescens*) derived from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples collected at Santa Barbara, San Clemente, and San Nicolas Islands, California, 1981–95.

landings of market squid in southern California ports correlated positively with seasonal frequency of occurrence values for SCI ($r = 0.74$) and SNI ($r = 0.66$), but did not correlate well with summer samples from SBI ($r = 0.25$).

Squid Length

Squid lengths from scats and spewings collected from 1981 through 1995 were combined into one data set to provide information on squid consumed by sea lions in the study area. Measurements of 25,386 squid beaks recovered from scats and spewings showed that sea lions ate market squid with a DML between 10 mm and 235 mm, with a mean length of 127 mm (fig. 3).

Seasonal, Annual, and Island Differences in Squid Length

The null hypothesis that there was no difference in size between seasons, years, and islands was rejected with the means model ANOVA ($P < 0.001$; table 5). The average size of squid (combining data from three rookeries) was 118 mm in spring, 109 mm in summer, 128 mm in autumn, and 137 mm in winter. Squid size was more variable between years in summer (fig. 4). Average squid size was 62–85 mm in El Niño summers and 109–128 mm in other summers (fig. 5). El Niño periods had smaller squid than non–El Niño periods (nested ANOVA: df = 3, F = 1204.174, $P < 0.001$). Sea lions at SCI ate larger squid than sea lions at SNI during winter (nested ANOVA: df = 6, F = 139.190, $P < 0.001$).

Size of Squid in Scats and Spewings

The mean upper rostral width of squid found in scats was significantly smaller than that in spewings at SCI (df = 1, F = 82.182, $P < 0.001$) and SNI (df = 1, F = 5.406, P = 0.020). Although squid represented in spewings were larger than squid in scats, overlapping distributions of seasonal samples indicated that no distinct size

TABLE 5
Means Model ANOVA for Upper Rostral Width Measurements of Market Squid Beaks Found in California Sea Lion Scat and Spewing Samples at San Clemente and San Nicolas Islands, 1988–95

	Scat samples			Scat and spewing samples		
Factor	df	F	P-value	df	F	P-value
Island	1	6.759	0.009	1	13.339	<0.001
Year	5	138.435	<0.001	5	184.812	<0.001
Season	4	418.133	<0.001	4	526.191	<0.001
Island*year	15	30.142	<0.001	15	37.950	<0.001
Island*season	16	44.389	<0.001	22	62.882	<0.001
Year*season	22	118.058	<0.001	22	185.164	<0.001

Note: Upper rostral width measurements were used to estimate dorsal mantle length.

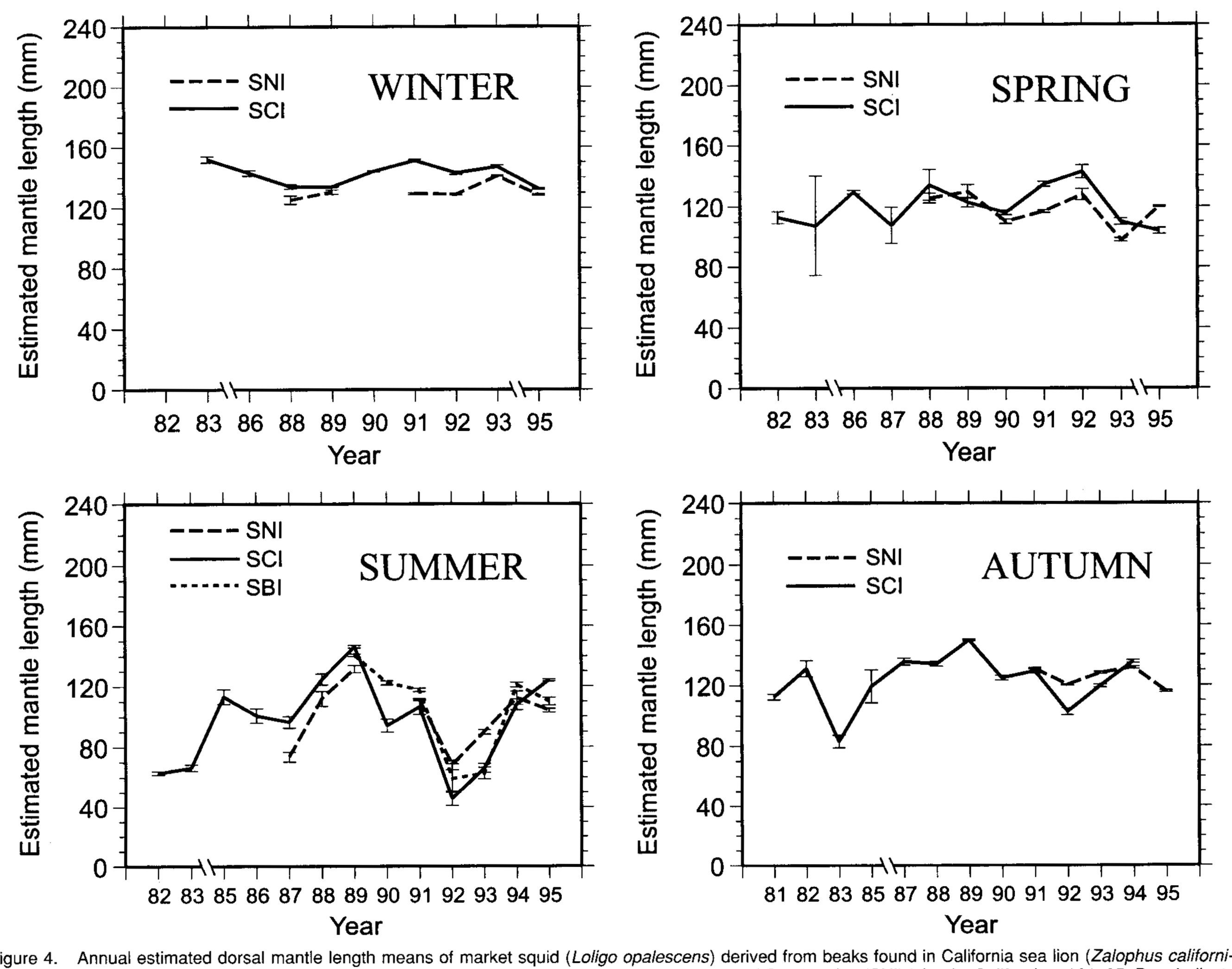

Figure 4. Annual estimated dorsal mantle length means of market squid (*Loligo opalescens*) derived from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples for each season at Santa Barbara (SBI), San Clemente (SCI), and San Nicolas (SNI) Islands, California, 1981–95. Bars indicate standard error of each mean.

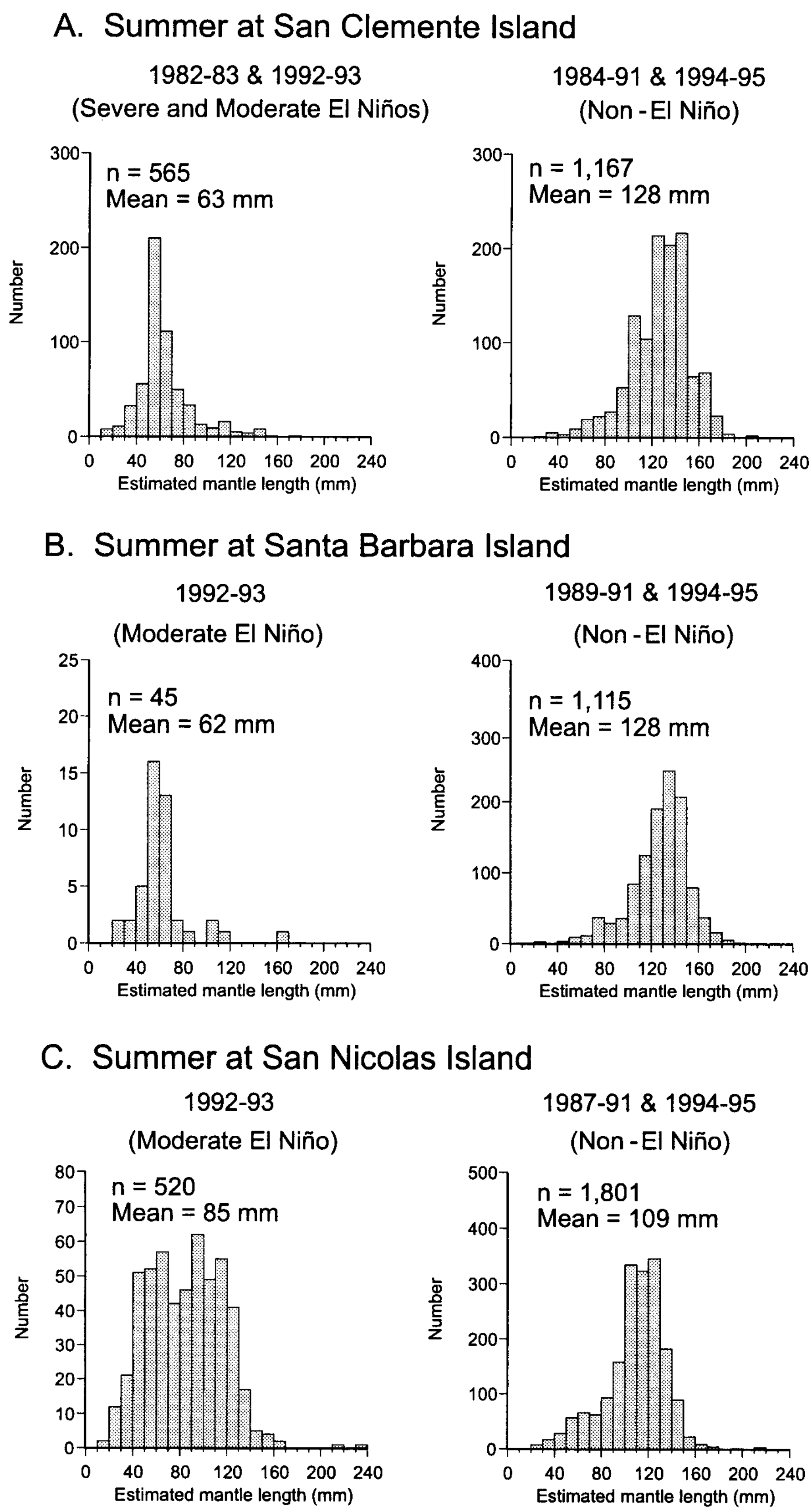

Figure 5. Comparison of size structure of dorsal mantle length estimates for market squid (*Loligo opalescens*) derived from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples collected during summer at (A) San Clemente Island, (B) Santa Barbara Island, and (C) San Nicolas Island during El Niño and non–El Niño years.

class was present in either sample type (figs. 6 and 7). Examination of individual collections (table 6) showed that squid size did not always differ ($P > 0.063$) between scat and spewing samples.

Size of Squid in Individual Samples

Size of squid in individual scat and spewing samples was significantly different for all seven collections examined (table 6). Although average size of squid varied, there was considerable overlap in distributions of size between samples (fig. 8).

DISCUSSION

Market squid is one of the most important prey of sea lions in southern California. Consumption of market squid by sea lions (inferred from the percent occurrence index) from three rookeries in southern California was synchronous; samples from the rookeries displayed similar seasonal and annual frequency of occurrence index values. Squid consumption was highly variable over shorter time periods: seasonal and annual data revealed periods when sea lions did not eat any market squid, and other periods when more than 90% of sea lions included it in their diet. The average size of squid consumed by sea lions had a DML of 127 mm, with a range from 10 mm to 235 mm. Although the average DML of squid in the Antonelis et al. (1984) study was similar to that in this study, the larger sample size of this study (25,386 vs. 76) showed that sea lions eat smaller and larger squid than previously reported.

Changes in oceanographic conditions within southern California, such as El Niño episodes, were reflected by dietary changes in sea lions (Lowry et al. 1990, 1991). During the 1981–95 period, oceanic waters off southern California were affected by three El Niño episodes of varying intensity: 1983–84 (severe), 1988 (mild), and 1992–93 (moderate). The sea lions ate fewer squid during moderate and severe El Niño episodes. These multiyear consumption cycles reflect the availability of market squid in southern California to sea lions, and may indicate the recovery rate of the squid population following moderate and severe El Niño episodes.

At San Clemente and Santa Barbara Islands, the average size of squid eaten during El Niño summers was half of that eaten during non–El Niño summers. This difference may be due to a lack of larger squid in the waters surrounding these two rookeries during El Niño summers, as evidenced by the paucity of larger squid in the samples. In contrast, at San Nicolas Island, both small and large size classes of squid were eaten during the 1992–93 El Niño summer, and the distribution of size classes is almost bimodal. The waters surrounding SNI

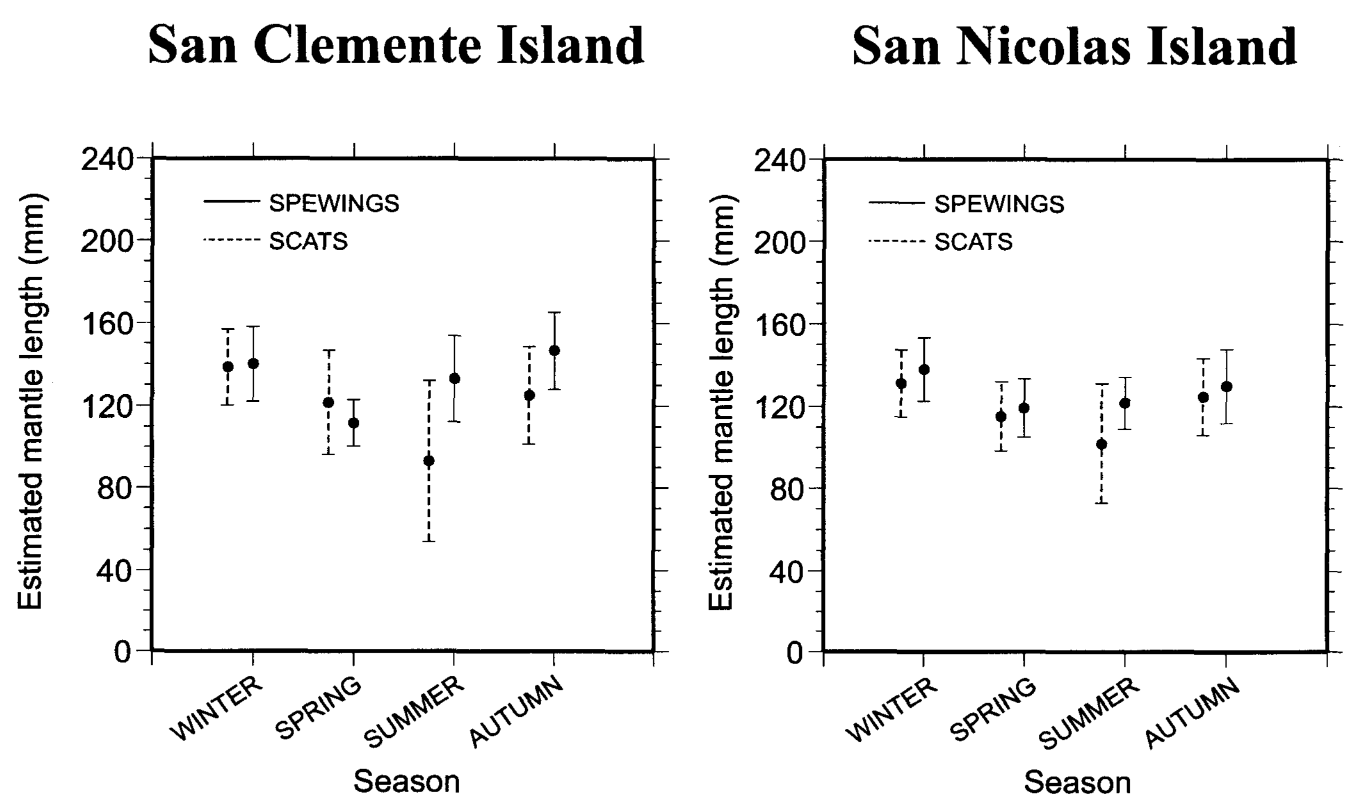

Figure 6. Mean dorsal mantle length of market squid (*Loligo opalescens*) estimated from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples collected seasonally at San Clemente and San Nicolas Islands, California. Bars indicate one standard deviation from each mean.

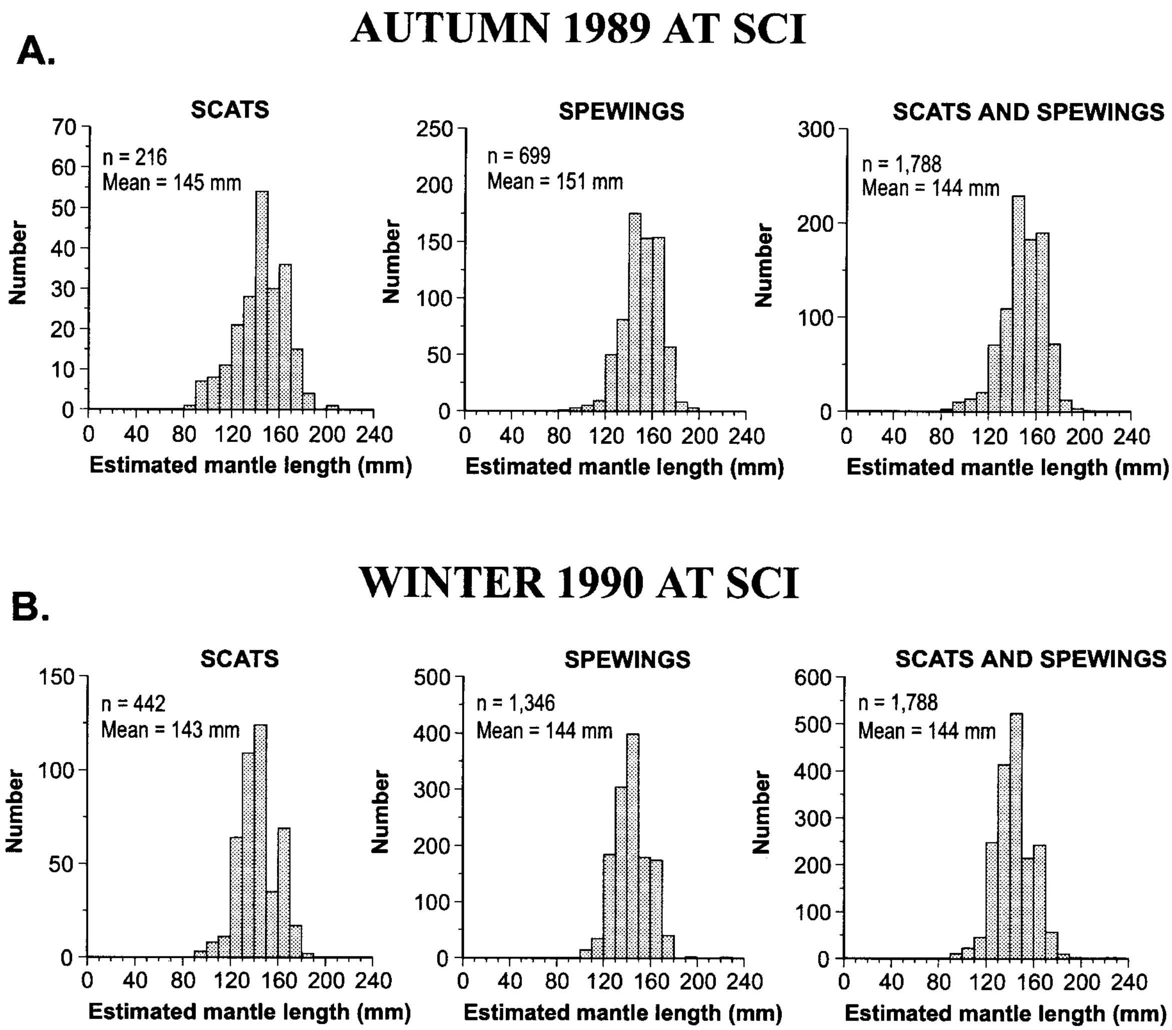

Figure 7. Size structure of dorsal mantle length estimates of market squid derived from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples collected at San Clemente Island, California, during (*A*) autumn 1989 and (*B*) winter 1990.

TABLE 6
Results of ANOVA Tests on Upper Rostral Width Measurements of Market Squid Beaks Recovered from Individual California Sea Lion Scat and Spewing Samples at San Clemente Island (SCI) and San Nicolas Island (SNI)

Source of variation	SS	df	MS	*F*-ratio	*P*-value
Winter 1989 at SCI					
Type[a]	0.631		0.631	23.908	<0.001
Sample[b] (type)	3.457	37	0.093	3.542	<0.001
Error	72.083	2,733	0.026		
Autumn 1989 at SCI					
Type	0.796		0.796	30.355	<0.001
Sample (type)	4.531	33	0.137	5.238	<0.001
Error	23.068	880	0.026		
Winter 1990 at SCI					
Type	0.028		0.028	1.108	0.293
Sample (type)	2.584	53	0.049	1.951	<0.001
Error	43.320	1,733	0.025		
Winter 1991 at SCI					
Type	0.003		0.003	0.080	0.777
Sample (type)	1.845	22	0.084	2.679	<0.001
Error	20.883	667	0.031		
Winter 1993 at SNI					
Type	0.139		0.139	5.262	0.022
Sample (type)	3.894	47	0.083	3.126	<0.001
Error	29.758	1,123	0.026		
Autumn 1994 at SCI					
Type	0.648		0.648	20.478	<0.001
Sample (type)	1.300	17	0.076	2.416	<0.001
Error	10.577	334	0.032		
Summer 1995 at SCI					
Type	0.082		0.082	3.464	0.063
Sample (type)	1.432	22	0.065	2.744	<0.001
Error	10.817	456	0.024		

[a]Scats and spewings.
[b]Individual samples (nested within scats and spewings).

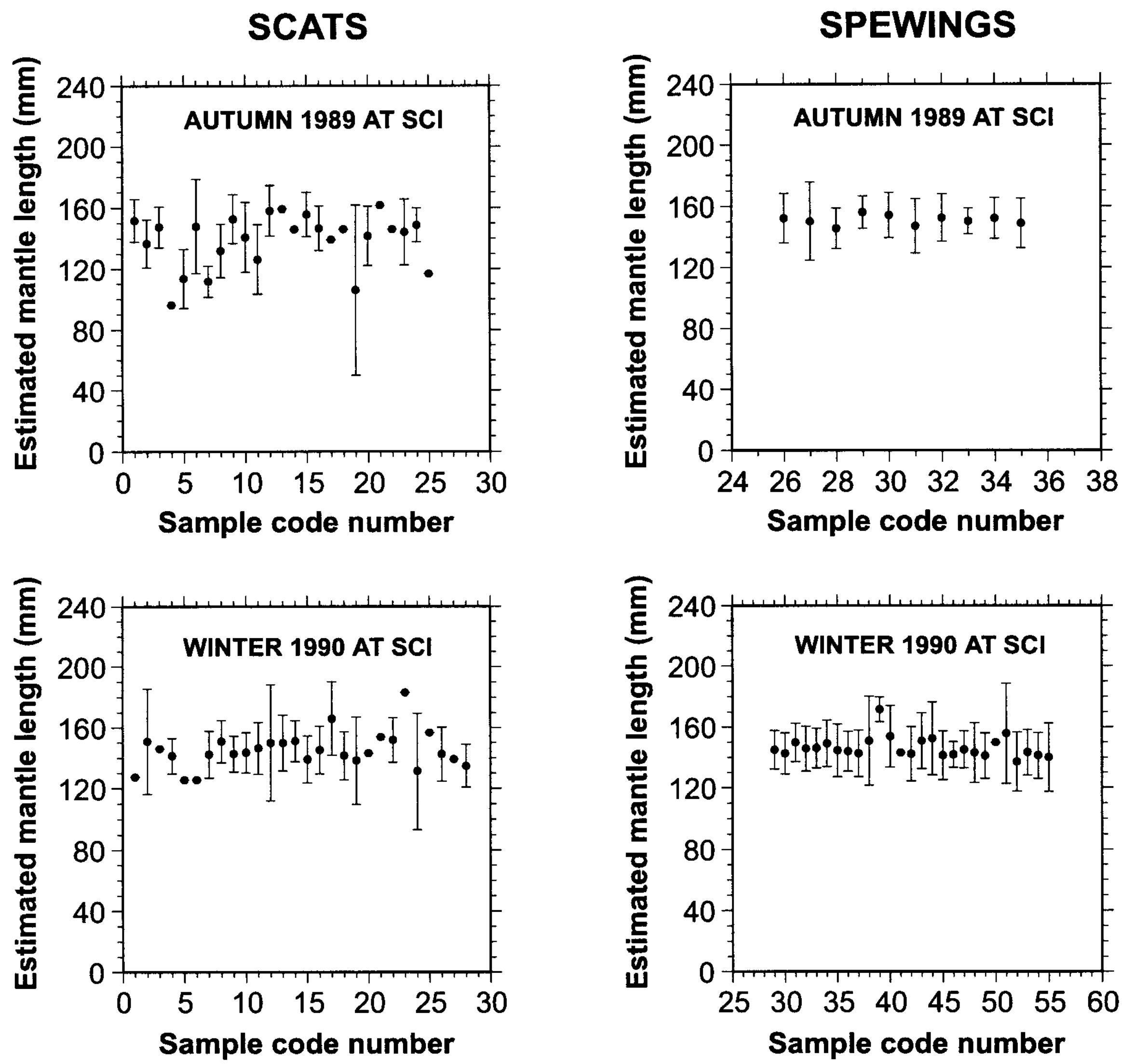

Figure 8. Mean dorsal mantle length of market squid (*Loligo opalescens*) estimated from beaks found in individual California sea lion (*Zalophus californianus*) scat and spewing samples collected at San Clemente Island (SCI), California, during autumn 1989 and winter 1990. Bars indicate one standard deviation from each mean.

were relatively cooler and more productive than the waters around SBI and SCI during summer 1992 and 1993 (Hayward et al. 1994), and it is possible that larger market squid moved to more productive waters in response to El Niño. Shifts in the distribution of pelagic forage species in response to El Niño episodes, and the negative effects of these prey shifts on sea lion populations have been well documented (Costa et al. 1991; DeLong et al. 1991; Feldkamp et al. 1991; Francis and Heath 1991).

The fact that small size classes were also consumed at San Nicolas Island during the 1992–93 El Niño may reflect a need for sea lions to augment their diet with smaller sizes of prey (and alternative species) that would be ignored during years of plentiful prey. Alternative hypotheses that may partially explain the smaller size classes of market squid eaten during El Niño summers are (1) oceanographic changes associated with El Niño result in a temporal shift (delay) in the spawning cycle of market squid; and (2) growth rates are slowed as a result of nutritional stress caused by declines in prey forage of market squid.

The percentage of scat samples with market squid yields the frequency of occurrence index which depicts sea lion consumption and the availability of squid to sea lions. The close correlation of this index to market squid landings in southern California (a crude measure of abundance) implies that the index may indicate market squid abundance. Spewings are not included in this index because the same animal may have deposited both sample types on the collection grounds. A better occurrence index might include lenses and squid pens (i.e., gladius) with beaks, because beaks are sometimes absent in scat samples (Bigg and Fawcett 1985).

Length-composition data showed significant differences between size of squid found in scats and in spewings. These differences were very small and were probably detected because of the large sample size and high statistical power. Differences in average size of squid found in these samples are likely to have little or no biological importance. Therefore, we derived the size structure of the market squid consumed by sea lions from beaks collected from both scats and spewings.

We have not attempted to estimate the biomass of market squid or other species eaten by California sea lions. Estimating biomass consumption by sea lions in southern California would be difficult for several reasons. (1) The population of sea lions fluctuates throughout the year. (2) The percentage of market squid in the diet of sea lions is highly variable through time. (3) Although timing, length, and distance of foraging trips are known for adult female sea lions (Feldkamp et al. 1989; Heath et al. 1991), they are not known for juveniles or subadult and adult males. (4) Consumption by age and sex is not documented. (5) Although beaks have been found to resist digestion (Hawes 1983), degradation rates of hard parts for other prey species must be determined. Once this information is known, models can be developed for estimating consumption of market squid and other species of commercial value that are preyed on by sea lions for a given region.

There are problems with using California sea lions to sample prey populations that commonly occur in their diet. First, presence-absence data (i.e., percent frequency of occurrence) is not a good index of abundance because it cannot go beyond 100% due to nonlinearity. Special modeling approaches to estimate population abundance, such as that used for sardine by Mangel and Smith (1990), would have to be developed for sea lion scat presence-absence data to index abundance of fish and squid. Second, scat and spewing samples have to be independent if they are to be used to predict size structure of squid and fish populations. There is no way to determine from scat and spewing samples if a sea lion, or a group of sea lions, fed on the same school of squid (or fish) or on multiple schools during a foraging trip, nor is it possible to determine where they foraged. The difference in sizes of squid in individual scat and spewing samples suggests that scat and spewing samples are independent. Also, time differences in deposition of samples and their location at the rookery may reflect sea lions' foraging on different schools.

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