DIET DIFFERENCES IN THE THRESHER SHARK (*ALOPIAS VULPINUS*) DURING TRANSITION FROM A WARM-WATER REGIME TO A COOL-WATER REGIME OFF CALIFORNIA-OREGON, 1998–2000

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ABSTRACT

The diet of thresher shark (*Alopias vulpinus*) during a cool-water oceanographic regime, July 1999 through May 2000, was compared to the diet during the previous warm-water/transitional period, August 1998 through January 1999. Stomach samples were collected from the U.S. Pacific Coast drift and set gill net fisheries. Of the samples examined from the cool-water period, only 8 prey taxa were found, revealing a narrower trophic spectrum than found during the previous warm-water/transitional period, when 20 prey taxa were identified. As in the warm-water/transitional period, northern anchovy (*Engraulis mordax*) was the most important overall prey, even more dominant than in the previous period. Additionally, market squid (*Loligo opalescens*) was second in importance and dramatically more prevalent in the cool-water period than in the warm-water/transitional period. Other important diet items in the cool-water period, in descending order of importance, were "unidentified teleosts"; Pacific sardine (*Sardinops sagax*); Pacific hake (*Merluccius productus*); and Pacific or chub mackerel (*Scomber japonicus*): these were also among the top six items in the previous warm-water/transitional period. As expected, pelagic red crab (*Pleuroncodes planipes*), relatively common in the diet during the warmer period, was absent from the diet during the cool-water period. It is suggested that during cool-water periods the thresher shark subsists on a narrow range of food items (such as anchovy and squid), but the diet becomes more diversified and opportunistic during less-productive warm-water El Niño periods.

INTRODUCTION

The thresher shark (*Alopias vulpinus*) is currently the most important commercial shark in California and is also sought by recreational anglers, especially in southern California (Holts et al. 1998). It is to be managed under the Pacific Fisheries Management Council's new U.S. West Coast Highly Migratory Species Fishery Management Plan (PFMC 2003), to be implemented in 2004. Patterns of observed catches and tagging studies indicate that thresher sharks migrate seasonally along the Mexico-U.S. west coast from near Clarion Island, Mexico (18°32'N, 117°42'W), north to Johnstone Strait (50°15'N, 126°00'W), moving northward up the coast in summer, returning to waters off northern and central Mexico in winter (Hart 1973; Hanan et al. 1993; Smith et al. in press). Its greatest apparent abundance in the North Pacific is reportedly within 40 miles offshore (Strasburg 1958).

This species was heavily targeted by the West Coast drift gill net fishery in 1977–89, when the population was depleted to an estimated one-third of its virgin biomass (Hanan et al. 1993; PFMC 2003). Since the early 1990s, coastal states implemented various seasonal and area closures, and fishery effort was redirected toward swordfish. The closures and shift in effort appear to have helped protect the adult portion of the stock. A preliminary assessment suggests that the stock has rebounded to almost 60% of virgin biomass and is maintaining a modest amount of positive population growth (PFMC 2003, chap. 3).

In the early 1990s, Bedford (1992) suggested that off California this species had a highly specialized diet composed primarily of northern anchovy, but he did not present supporting data. More recently, Preti et al. (2001) found a far more varied diet composed of 20 prey taxa. Although northern anchovy (*Engraulis mordax*) was the most important species, Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), market squid (*Loligo opalescens*), and pelagic red crab (*Pleuroncodes planipes*) were also important. The sampling was done while the California Current system was undergoing a change from warm-water El Niño conditions to cold-water La Niña conditions, with most samples collected during El Niño, before full transition into the cool-water period (Hayward et al. 1999). Preti et al. (2001) suspected that the oceanographic environment may have contributed to the great diversity of prey in the diet, but no comparative data were available.

Here we examine the results of new sampling during the following cool-water period to compare with the warm-water/transitional period. The purpose is to understand differences and flexibility in the diet of the thresher

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shark in the California Current region under differing oceanographic regimes.

METHODS

Stomach samples were collected during a warm-water/transitional period (August 1998–January 1999) as described by Preti et al. (2001), and during a cool-water oceanic regime (July 1999–May 2000). Sample processing and analyses were similar for both periods. National Marine Fisheries Service (NMFS) fishery observers collected the samples aboard commercial drift gill-net (84 trips) and setnet vessels (4 trips) off the U.S. West Coast within the Exclusive Economic Zone.

Stomach content data were pooled and analyzed by prey taxa for relative measures of prey quantity (RMPQs) as follows: numeric occurrence percentage (%*N*), weight percentage (%*W*), and frequency-of-occurrence percentage (%*F*) of food items. The value %*N* is the number of individuals of one prey taxon divided by the total number of all prey individuals times 100; %*W* is the weight of one prey taxon divided by the total weight of all prey times 100; %*F* is the number of stomachs containing prey of one taxon divided by the total number of stomachs that contained any prey items time 100 (Preti et al. 2001).

Empty stomachs, slurry, and detritus were not used in calculating percentages or indexes. We examined the differences in degree of prey digestion (ranked 1–5, from 'fresh' to digested as in Preti et al. 2001) by tallying the frequencies of each digestive state in the two periods and testing them using a 2 × 5 contingency table.

Authors of fish dietary studies have long emphasized that each of the commonly used measures of prey quantity has its limitations, each biased toward different aspects of the diet (Hyslop 1980; Cortés 1997). We thus chose the geometric index of importance (GII) (Assis 1996; Mohan and Sankaran 1988; Fernández and Oyarzun 2001), and the index of relative importance (IRI) (Pinkas et al. 1971) to rank prey and to graphically represent the relative measures of prey quantity. In comparing the two indexes, we used each method to examine only the difference in ranking of the suite of prey types, because individual index values were not comparable.

The GII, in its simplified form, may be calculated

$$\mathrm{GII}_j = \frac{\left(\sum_{i=1}^{n} V_i\right)_j}{\sqrt{n}} \tag{1}$$

Where GII_j = geometric index of importance for the *j*th prey category; V_i = the magnitude of the vector for the *i*th RMPQ of the *j*th prey category; n = the number of RMPQs used in the analysis. In our study this can be expressed as

$$\mathrm{GII}_j = \frac{(\%N_j + \%W_j + \%F_j)}{\sqrt{3}} \tag{2}$$

Where $\%N_j$ is the percentage number; $\%W_j$ is the percentage weight; $\%F_j$ is the percentage frequency of occurrence for the jth prey category.

The IRI is calculated as

$$\mathrm{IRI} = (\%N + \%W) \times \%F$$

In the area north of 34°00'N, to determine if we could pool drift gill-net and setnet samples for the 1999–2000 sampling period (where we supplemented drift-net samples with setnet samples collected in Monterey), we used the Fisher Exact Test to determine statistical difference in diet between samples collected in the nearshore set gill-net fishery and samples collected in the offshore drift gill-net fishery over the same fishing season and same general area. If the diet was found not to differ significantly, we pooled the results.

We examined differences in diet between northern and southern fishing areas, in thresher sharks caught early and late in the fishing season, and by size of shark. We chose 34°00'N latitude as a boundary dividing the sampling area because the area north of that latitude (which crosses the Santa Barbara Channel Islands and includes the area between Point Conception and San Miguel and Santa Rosa islands) often has cooler water (generated by seasonal coastal upwelling) than areas south of that latitude. The data were pooled into subgroups, and 2 × 5 contingency table analyses were carried out to determine whether consumption of the five leading diet items varied significantly in number among the subgroups. Only the numerical measure was considered for this exercise, since it is the only statistically valid RMPQ that can be entered into the chi-square table. Weight was not tested because of the extensive range of the measurement values (in grams) and general dependence of this RMPQ on digestive state. Frequency of occurrence was not used because the row and column sums do not represent any real quantity, which violates the assumptions of the chi-square test (Crow 1982).

The following subgroups were considered:

1. Sharks collected north of 34°00'N, and sharks collected south of 34°00'N, all seasons combined for both periods.
2. Adult sharks (> 159 cm fork length) female and male first maturity (Smith et al., in press) and juvenile sharks (≤ 159 cm fork length), all latitudes combined, both periods.

Cool-water and warm-water/transitional period diet differences were compared with two-way 10-cell contingency table analyses of the major diet items of each sampling period. We tested only the top five major iden-

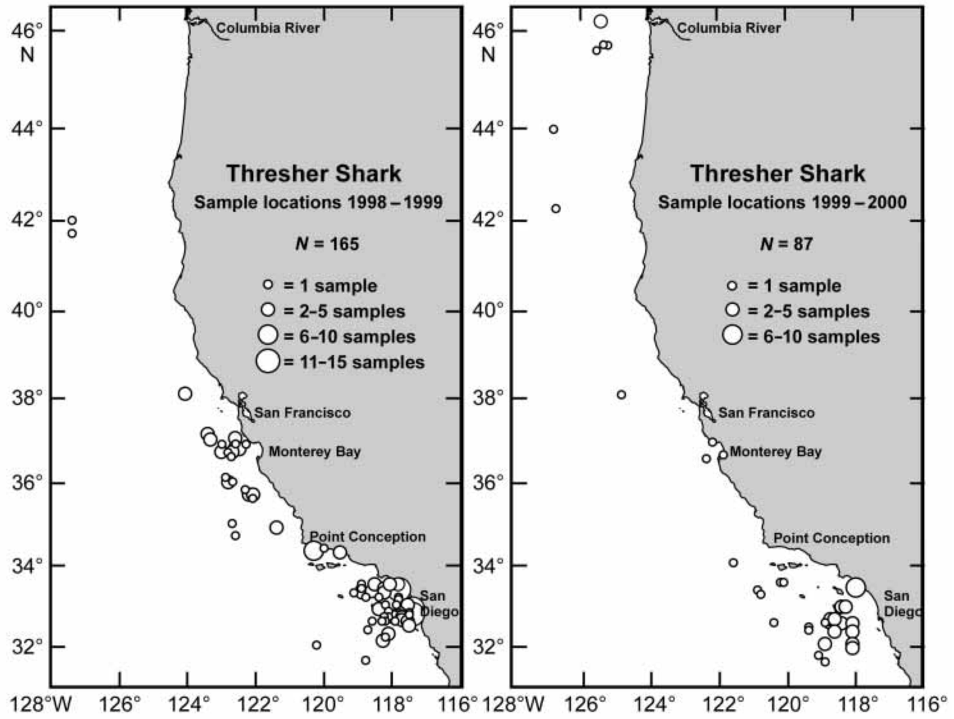

Figure 1. Collection locations for thresher shark (*Alopias vulpinus*) stomach samples, during warm-water/transitional period 1998-99 (*left*) and cool-water period 1999-2000 (*right*).

tifiable items in these analyses because the number values for others were too small to apply the test.

Randomized cumulative prey curves were constructed to examine trophic diversity and determine if sample sizes were sufficient to describe the full diet (Hurtubia 1973; Ferry et al. 1997; Gelsleichter et al. 1999; Yamaguchi and Taniuchi 2000). The order in which stomachs were analyzed was randomized 10 times, and the mean number of new prey types was cumulated consecutively in order of the stomachs obtained and plotted against the number of stomachs examined. In this type of sample-size analysis, the presence of an asymptotic relationship indicates that the number of stomachs analyzed is sufficient to represent the diet of a particular predator, and that the enlargement of the sample beyond the point of curve stabilization would cause little further increase in the measured trophic diversity (e.g., Gelsleichter et al. 1999).

The fork-length size composition of the samples in the two periods (data for 1998–99 from Preti et al. 2001) was compared by means of an unpaired Student's *t*-test to determine if the size composition was significantly different.

RESULTS

Vessel Operations and Sampling

Between 16 August 1998 and 24 January 1999, 165 stomach samples (107 with food) were collected aboard observed vessels on 48 trips operating from the California-Mexico border (31°37'36"N, 118°27'48"W) to the California-Oregon border (41°35'54"N, 127°13'48"W) over water depths from 27 to 2250 fm (49 to 4115 m). All vessels sampled during that period fished with drift gill nets (≥ 14-in. stretched mesh) set overnight and collected in the morning hours. Between 23 July 1999 and 17 May 2000, 87 stomach samples (67 with food) were collected aboard driftnet and set-net vessels on 40 observed trips operating from the California-Mexico border to southern Washington (46°25'30"N, 125°16'42"W) over water depths from 30 to 2,160 fm (55 to 3,950 m) (fig. 1). Most (94%) were collected during drift gill-net trips ($n = 36$) on overnight sets as before; five samples were collected from set gill-net vessels fishing in Monterey Bay ($n = 4$ trips; ≤ 12 in. stretched mesh), with average soak time of 26.4 hr (range: 21–45 hr), with net retrieval during morning hours.

Thresher sharks for both sampling periods were similar in size. The size compositions for the two periods were found not to be significantly different ($t = -1.37$, $d.f. = 246$, $p = 0.17$). Those collected during the warm-water/transitional period ranged from 79 cm to 237 cm fork length (FL) ($n = 163$) with 82.8% from 130 to 189 cm fork length (Preti et al. 2001). Those sampled during the cool-water period ranged from 70 cm to 262 cm fork length ($n = 85$) with 82.0 % from 130 cm to 189 cm fork length (fig 2).

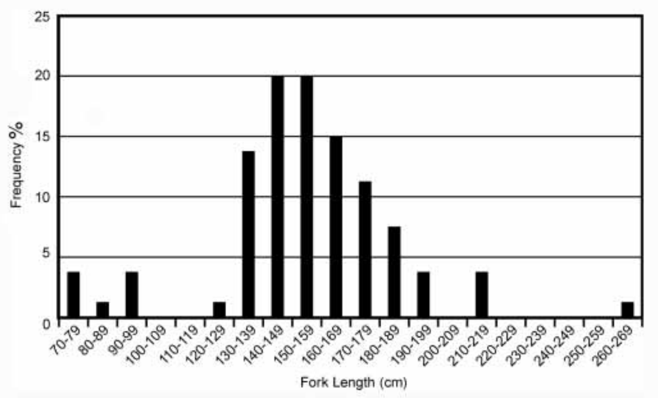

Figure 2. Length-frequency distribution of thresher sharks sampled during the July 1999–May 2000 cool-water period (n = 85 sharks). (For distribution during the August 1998–January 1999 warm-water/transitional period, see Preti et al. 2001.)

Analyses

Although range of values differed, ranking of prey items was the same with either GII or IRI (tab. 1, figs. 3 and 4). A two-way, 10-cell contingency table analysis of the five major identifiable diet items of fish captured during the two periods showed the diet to differ significantly for number ($\chi^2 = 219.4$, $d.f. = 4$, $\alpha < 0.05$). The variety of prey found during the cool-water period (only 8 taxa) was significantly less than that found during the previous warm-water/transitional period (20 taxa; Preti et al. 2001). During both fishing periods, northern anchovy was the most important identifiable prey. During the 1998–99 warm-water/transitional period, "unidentified teleost"[1] ranked first, but of identifiable taxa, northern anchovy had the highest indexes of importance (GII = 48.2, IRI = 1,332.1), followed by Pacific hake, Pacific mackerel, and Pacific sardine. Of invertebrate prey, pelagic red crab and market squid contributed to the diet in the warm-water/transitional period, the latter being of minor importance (GII and IRI = 2.0). Although northern anchovy was important overall during both periods, it was identified only in Southern California Bight samples, south of 34°00'N. During the warm-water/transitional period, Pacific hake was the most important food item north of 34°00'N, followed by unidentified teleosts and Teuthoidea. Rockfish (*Sebastes* spp.) and a variety of other species also contributed to the diet in the north, and occurred in the diet in both periods. Only two categories of rockfish were identified in our samples: *Sebastes jordani* and *Sebastes* spp. unidentified. The latter consisted of more highly digested (worn) otoliths that may have been *S. jordani*, but could not be identified beyond the generic level. During the cool-water period, all rockfish otoliths were identifiable to species as *S. jordani*. Of those examined during the warm

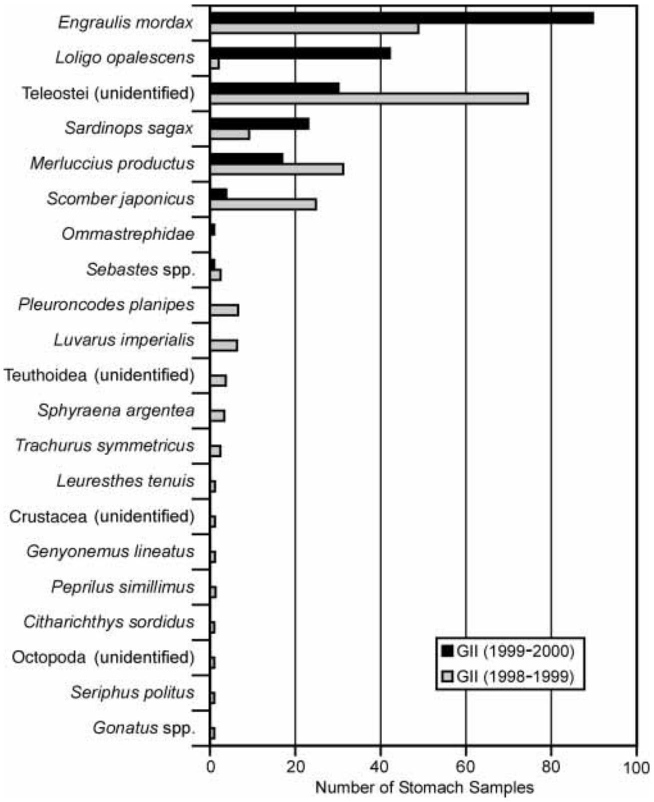

Figure 3. Geometric index of importance (GII) for prey taxa found in stomachs of thresher sharks during warm-water/transitional period 1998–99 and cool-water period 1999–2000. See also tab. 1.

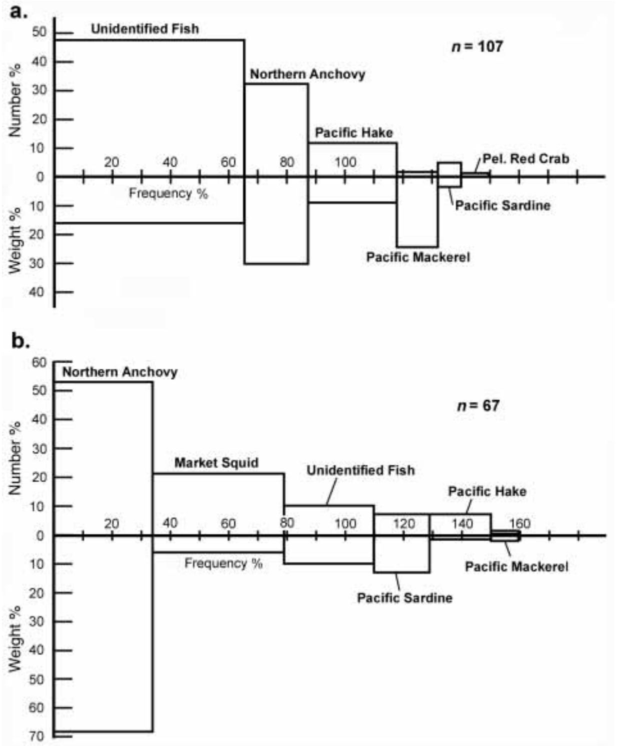

Figure 4. Graphical representation of index of relative importance (IRI) of major prey taxa found in stomachs of thresher sharks during (*a*) warm-water/transitional period 1998–99 and (*b*) cool-water period 1999–2000.

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[1] Bony fish remains that are highly digested or fragmented.

TABLE 1
Prey found in Stomachs of Thresher Shark (*Alopias vulpinus*) from the California-Oregon Coast

	1998–99 Warm-water/transitional period (n = 107 stomachs with food)[a]						1999–2000 Cool-water period (n = 67 stomachs with food)					
Prey species	%W	%N	%F	GII	IRI	Rank	%W	%N	%F	GII	IRI	Rank
Fishes												
Engraulis mordax (northern anchovy)	30.12	31.87	21.49	48.18	1,332.09	2	68.00	53.09	34.33	89.73	4,156.92	1
Teleostei (unidentified)	17.48	47.13	64.49	74.51	4,166.44	1	10.29	10.52	31.34	30.11	652.11	3
Sardinops sagax (Pacific sardine)	3.97	4.46	7.48	9.18	63.07	5	12.76	7.73	19.40	23.03	397.61	4
Merluccius productus (Pacific hake)	9.17	11.21	33.64	31.19	685.48	3	1.10	7.32	20.90	16.93	175.93	5
Scomber japonicus (Pacific mackerel)	24.73	1.42	16.82	24.81	439.86	4	1.79	0.31	4.48	3.80	9.4	6
Sebastes spp. (rockfishes)	0.01	0.54	3.74	2.46	2.06	11	<0.01	0.21	1.49	0.98	0.31	7[b]
Luvarus imperialis (louvar)	9.93	0.07	0.93	6.31	9.30	7	—	—	—	—	—	—
Sphyraena argentea (Calif. barracuda)	1.75	0.27	3.74	3.32	7.54	9	—	—	—	—	—	—
Trachurus symmetricus (jack mackerel)	2.17	0.14	1.87	2.41	4.30	10	—	—	—	—	—	—
Genyonemus lineatus (white croaker)	<0.01	0.14	1.87	1.16	0.26	13[b]	—	—	—	—	—	—
Leuresthes tenuis (Calif. grunion)	<0.01	0.14	1.87	1.16	0.25	13[b]	—	—	—	—	—	—
Peprilus simillimus (Pacific butterfish)	0.34	0.07	0.93	0.77	0.38	14	—	—	—	—	—	—
Seriphus politus (queenfish)	<0.01	0.07	0.93	0.58	0.06	15[b]	—	—	—	—	—	—
Citharichthys sordidus (Pacific sanddab)	<0.01	0.07	0.93	0.58	0.06	15[b]	—	—	—	—	—	—
Cephalopods												
Loligo opalescens (market squid)	0.12	0.61	2.80	2.04	2.03	12	6.06	20.62	46.27	42.12	1234.38	2
Ommastrephidae family	—	—	—	—	—	—	<0.01	0.21	1.49	0.98	0.31	7[b]
Teuthoidea (unidentified)	0.09	0.68	5.60	3.68	4.27	8	—	—	—	—	—	—
Gonatus sp.	<0.01	0.07	0.93	0.58	0.07	15[b]	—	—	—	—	—	—
Octopoda (unidentified)	<0.01	0.07	0.93	0.58	0.06	15[b]	—	—	—	—	—	—
Crustaceans							—	—	—	—	—	—
Pleuroncodes planipes (pelagic red crab)	0.13	0.95	10.28	6.55	11.01	6	—	—	—	—	—	—
Crustacea (unidentified)	<0.01	0.14	1.87	1.16	0.26	13[b]	—	—	—	—	—	—

Note: W = weight in grams; N = number; F = frequency of occurrence; GII = geometric index of importance; IRI = index of relative importance

[a] Preti et al. 2001.

[b] Tied ranks based on GII value.

period, 75% were *Sebastes* spp. unidentified; 25% were *S. jordani* (A. Preti, Southwest Fisheries Science Center, La Jolla, Calif., unpub. data).

Degrees of prey digestion were significantly different between the two periods. In the cool-water period prey items were less digested overall ($\chi^2 = 702$, *d.f.* = 4, $\alpha < 0.05$).

For the cool-water 1999–2000 period, the Fisher Exact Test showed that the diet of sharks sampled north of 34°00'N in the nearshore setnet fishery ($n = 5$) did not differ significantly from that of sharks collected from the offshore drift gill-net fishery ($n = 10$; $p = 0.801$), so we pooled these samples. Northern anchovy was the highest ranking in importance overall in the cool-water period (GII = 89.7; IRI = 4,156.9). Market squid, of minor importance in the warm-water/transitional period, advanced to second place (GII = 42.1, IRI = 1234.4), ranking first in frequency of occurrence. Other prey items in descending order of importance were unidentified teleosts, Pacific sardine, Pacific hake, Pacific mackerel, ommastrephid squids, and *Sebastes* spp. For the area north of 34°00'N, Pacific sardine was the most important identifiable food in the cool-water period, followed by market squid and Pacific hake, which were the only other identifiable prey.

Statistical differences in consumption of the top five diet items among the different groups were similar for both periods, even though diversity varied greatly. Numbers of the top five prey items consumed north ($n = 9$) versus south ($n = 58$) of 34°00'N during the cool-water period were significantly different ($\chi^2 = 92.4$, *d.f.* = 4, $\alpha < 0.05$), similar to results of the previous period (Preti et al. 2001). Diet differences (as measured by differences in numerical consumption of the top five items) were also significant between immature-sized thresher sharks (≤ 159 cm fork length, $n = 39$) and mature-sized sharks (> 159 cm fork length, $n = 27$) ($\chi^2 = 58.5$, *d.f.* = 4, $\alpha < 0.05$). During both periods, larger sharks ate greater numbers of prey.

Analyses of the randomized cumulative prey curves for both periods indicate that our sample sizes were large enough to adequately capture an accurate profile of at least the major diet items of *A. vulpinus*, as examined in various treatments (figs. 5 and 6). The prey curves for the cool-water period leveled off earlier and more dramatically than those constructed for diet samples observed in the warm-water/transitional period, reaching full asymptotic stabilization for small thresher sharks ≤ 159 cm FL (fig. 6). Large sharks and those sampled north of 34°00'N had the highest diversity and may need additional sampling to determine the full range of prey.

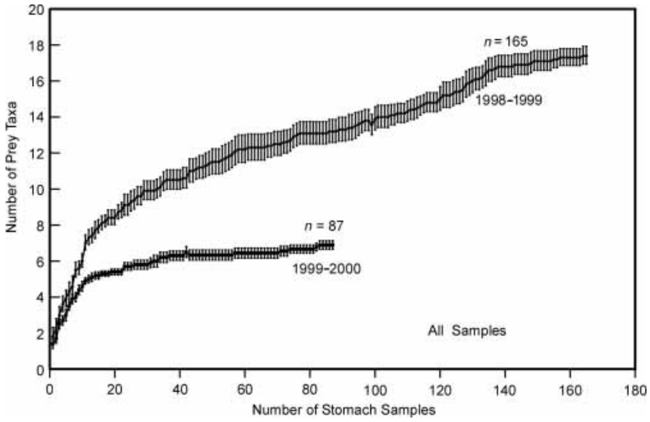

Figure 5. Randomized cumulative prey curve for thresher shark (*Alopias vulpinus*) diet samples. Mean values are plotted; error bars represent ±1 SE.

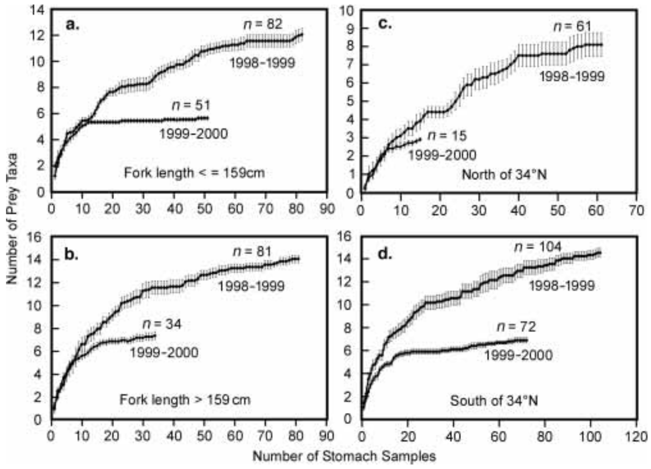

Figure 6. Randomized cumulative prey curves for thresher shark stomach samples for warm-water/transitional 1998–99 and cool-water 1999–2000 periods: (*a*) small sharks (≤ 159 cm fork length) and (*b*) adult sharks (> 159 cm fork length), (*c*) north of 34°00'N, and (*d*) south of 34°00'N. Mean values are plotted; error bars represent ±1 SE.

DISCUSSION

During the period spanned by this study, the California Current system made a full transition from warm El Niño to cool La Niña conditions (Hayward et al. 1999; Kahru and Mitchell 2000). A noticeable shift from El Niño conditions in 1997–98 to La Niña conditions is thought to have occurred around January 1999 after a period of intense El Niño conditions along the U.S. West Coast (Bograd and Lynn 2001; Chavez et al. 2003).

Our findings confirm the importance of northern anchovy in the diet of the thresher shark off southern California, where most juvenile and subadult thresher sharks in U.S. West Coast waters are found (PFMC 2003). Anchovy was the single most important prey during both periods, especially in the more recent cool-water period in the south. This small, schooling pelagic species tends to increase in abundance when cooler temperatures inhibit expansion of the sardine population along the U.S. West Coast, and has tended to decrease when the sardine population expands (Chavez et al. 2003).

The central stock of northern anchovy has its center of abundance in the Southern California Bight (PFMC

1998). Since 1980, sardine has greatly increased in abundance and expanded its range northward (Lluch-Belda et al. 1989). Anchovy was not identified in the diet north of Point Conception, where sardine was the most important identifiable prey in the cool period and hake the most important in the warmer period. Market squid changed from a minor diet item in the warm-water/transitional period to a major one in 1999–2000 (south of 34°00'N), mirroring its resurgence in fishery landings after a period of scarcity during the preceding El Niño regime (Rogers-Bennett 2001; Jackson and Domeier 2003).

In all, we found the trophic spectrum much narrower during the cool-water period, compared to the previous El Niño transition period. This is not likely due to differences in processing techniques or experience, because the same person processed both sets of stomach samples, and was probably more (rather than less) experienced in identifying stomach contents during examination of the 1999–2000 samples than in 1998–99, when there was a higher diversity of items. Mean digestive state was not higher for the cool-water period, which might have accounted for the low diversity of prey detected then (i.e., because so few diet items were identifiable). Analyses of the cumulative prey curves indicate that our sample sizes for both periods were sufficient to adequately capture an accurate profile of the major prey of *A. vulpinus* as examined, but more sampling may be needed for adult fish in northerly waters (north of 34°00'N). Although total sample prey diversity curves did not reach a complete asymptote in either sampling period, the leveling off was more pronounced and occurred at a smaller sample size in the cool-water period. Judging from the flat prey diversity curve of threshers ≤ 159 cm fork length, total prey diversity of small threshers might possibly have been captured by a sample size as small as 12 (Fig. 6). For prey items of primary and secondary importance, the statistical tests indicate a significant difference in individual number of the top five prey between the sampling periods.

Lower prey diversity during the cool-water period could have been partially due to the greater percentage of stomach samples collected south of 34°00'N (fig. 1), where northern anchovy dominated the diet in both periods. However, we believe that this low diversity, greater dominance of northern anchovy and squid and lack of the more tropical species in the diet were largely due to the biological oceanographic regime change that ushered in conditions more favorable for market squid and anchovy. These may be the two prey species most preferred by thresher sharks in this area (at least among subadults), but when conditions are less favorable, they may be forced to diversify their diet.

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