FEEDING HABITS OF THE COMMON THRESHER SHARK (*ALOPIAS VULPINUS*) SAMPLED FROM THE CALIFORNIA-BASED DRIFT GILL NET FISHERY, 1998–1999

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ABSTRACT

The diet of common thresher shark (*Alopias vulpinus*) from U.S. Pacific Coast waters was investigated by means of frequency of occurrence, gravimetric and numerical methods, and calculating the geometric index of importance (GII) of prey taxa taken from stomachs collected by fishery observers from the California-based drift gill net fishery. Sampling was done from 16 August 1998 to 24 January 1999, a time when the California Current was undergoing rapid change from El Niño to La Niña conditions. Of the 165 stomachs examined, 107 contained food representing a total of 20 taxa, revealing a broader trophic spectrum than previously reported for this species. Of the identifiable items, northern anchovy (*Engraulis mordax*) was the most important in the diet (GII = 48.2), followed by Pacific hake (*Merluccius productus*; GII = 31.2), Pacific mackerel (*Scomber japonicus*; GII = 24.8), and Pacific sardine (*Sardinops sagax*; GII = 9.2). Of the invertebrates, squid (Teuthoidea, including *Loligo opalescens*; GII = 6.3), and pelagic red crab (*Pleuroncodes planipes*; GII = 6.6), were also important, especially numerically. For sharks collected north of 34°N latitude, hake was the most important identifiable species in the diet; northern anchovy was most important in the south, but was not identified in stomachs collected north of Point Conception.

INTRODUCTION

The Pacific Fishery Management Council recently included the common thresher shark (*Alopias vulpinus*) as a management unit species within the U.S. West Coast Highly Migratory Species Fishery Management Plan, now under development. This has prompted the need for biological information on life history, stock structure, feeding ecology, and essential habitat of this species to better assess stock status and harvest impacts. To date, little has been documented on its habitat requirements, and only anecdotal accounts are available on its feeding ecology off the U.S. West Coast.

The common thresher shark is a large, active, and strong-swimming shark that occurs in neritic and oceanic waters in subtropical and temperate seas worldwide (Compagno 1984). It is epipelagic, gregarious, and cosmopolitan, and in the northeastern Pacific seems to be most abundant within 40 miles of shore (Strasburg 1958). Its known range extends from Clarion Island, Mexico, north to British Columbia; it is common seasonally from mid–Baja California, Mexico, to Washington state.[1] It is the leading commercial shark taken in California, where it is highly valued in the fresh fish trade (Holts et al. 1998). It is also sought by recreational anglers for its fighting ability as well as food value, especially in southern California. Patterns of observed catches and results of limited tagging suggest that it undertakes a seasonal north–south migration along the Mexico–U.S. West Coast, moving northward in summer, then returning to waters off Mexico in winter (Hanan et al. 1993).

Anecdotal accounts identifying prey items of this shark are scattered throughout the literature, but no comprehensive study of food habits has been undertaken. In California, as in other parts of the world (e.g., Spain; Moreno et al. 1989), *A. vulpinus* frequently occur in association with large schools of small fishes, and feed on them near the surface, often slashing the water with their whiplike tails, presumably to herd or disorient their prey. According to Compagno (1984), this shark also feeds on mackerels, bluefishes, clupeids, needlefishes, lancetfishes, and lanternfishes, as well as squids, octopuses, pelagic crustaceans, and (rarely) seabirds. Although he provided no supporting data, Bedford (1992) reported that, unlike other pelagic shark species off California, the common thresher shark does not appear to be an opportunistic feeder, but rather feeds almost exclusively on northern anchovy (*Engraulis mordax*). California fishermen have reported finding salmon in the stomachs of large individuals (W. Rendernick, Monterey, Calif., pers. comm. 2/28/98). In the eastern North Atlantic, Pascoe (1986) examined teleost otoliths from the stomach of a 264 kg female, and concluded that the stomach had originally contained at least 28 scad (*Trachurus trachurus*), 6 whiting (*Merlangius merlangus*), and a single mackerel (*Scomber scombrus*).

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[1]Smith, S. E., R. C. Rasmussen, D. A. Ramon, and G. M. Cailliet. Biology and ecology of thresher sharks (family:Alopiidae). *In* Sharks of the open ocean, E. Pikitch and M. Camhi, eds. MS submitted to Blackwell Scientific Publications.

We examined and analyzed the stomach contents of common thresher shark collected by drift gill net observers off California, and compared diets between size/age classes, seasons, and general catch locations.

MATERIALS AND METHODS

Sampling at Sea

Stomach samples were collected from three common thresher shark size groups by federal fishery observers aboard commercial drift gill net vessels operating off California and southern Oregon during the 1998–99 August through January fishing season. Because sampling time and freezer space are limited aboard these vessels, and to maximize sampling for small fish in the undersampled inshore areas, observers were instructed to collect stomachs according to the following protocol:

1. size group = <100 cm fork length (up to ~200 cm total length, or young-of-year), up to 10 stomachs per trip;[2]
2. size group 101–160 cm FL (200–300 cm TL, or juveniles/subadults), up to 5 stomachs per trip; and
3. size group >160 cm FL (over about 300 cm TL, or adults/large subadults), up to 5 stomachs per trip.

Samples were excised at sea; esophageal and pyloric ends were secured with plastic cinch ties; and the stomachs were bagged, labeled, and frozen. Data on set and haul time, water depth, sea-surface water temperature, location, fish size, sex, and maturity state were recorded.

Processing in the Laboratory

Stomach samples were thawed, tamped with absorbent paper to remove excess water, and weighed full. Contents were then removed, and the empty stomach was weighed to determine the overall weight of the contents. Materials and slurry were rinsed and sorted with a series of screen sieves with mesh sizes 9.5 mm, 1.4 mm, and 0.5 mm for ease in rinsing midsized food boluses without losing some of the smallest items, such as fish otoliths. Percentage of stomach fullness (0–100%) was estimated visually as a broad gauge of relative fullness. The degree of prey digestion was estimated as follows:

1. Fresh: head, body, skin, and most fins intact, although some individuals may be in pieces (i.e., bitten on capture);
2. Intermediate: body and most flesh intact; fins, scales, and some or all skin may be digested;
3. Intact: skeleton from head to hypural plate or body/mantle/carapace intact, or easily reconstructed to obtain standard length measurements;
4. Unmeasurable body parts only: parts cannot be reconstructed to obtain standard measurements, but higher taxon or species group still identifiable;
5. Digested: identifiable only to a very general high-level taxon; and
6. Fully digested: unidentifiable material; slurry.

Prey items were then separated, identified to lowest possible taxonomic level, and enumerated, measured (to nearest mm, standard length) and weighed (to the nearest 0.1 g), when possible. Fish otoliths and squid beaks were counted in pairs, with the highest count representing the minimum number present. Weights were recorded by taxon groups (not individually), while lengths of all intact individuals within a taxon were measured.

Content data were pooled for all stomachs (all strata combined) and analyzed by prey taxa for relative measures of prey quantity (RMPQs) as follows: percent numeric occurrence (%N), percent weight (%W), and percent frequency of occurrence (%F) of food items. The value %N = the number of individuals of one prey taxon divided by the total number of all prey individuals $\times$ 100; %W = weight of one prey taxon divided by total weight of all prey $\times$ 100; and %F = number of stomachs containing prey of one taxon divided by total number of stomachs that contained any prey items $\times$ 100. Empty stomachs and certain small incidentally ingested organisms, slurry, and detritus were not used in calculating percentages or indices.

Cumulative prey curves were constructed to determine whether an adequate number of specimens overall or in subsamples had been collected to describe diet (e.g., Hurtubia 1973; Cailliet et al. 1986; 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 species was cumulated consecutively in order of the stomachs examined. In this type of sample-size analysis, presence of an asymptotic relationship indicates that the number of stomachs analyzed is sufficient to represent the diet of a particular predator, and that enlargement of the sample beyond the point of curve stabilization would cause no further increase in trophic diversity (Hurtubia 1973).

Measure of prey quantity (RMPQ) values were used to calculate the geometric index of importance (GII), as developed by Assis (1996). The GII is based on a multivariate and multidimensional approach similar to principles used by Mohan and Sankaran (1988) for defining their two-dimensional diet indices. Summarizing Assis (1996), the degree to which a predator consumes each prey category is represented by vectors (V_i) along orthogonal axes in space, where i = 1 to n, as many orthogonal axes as the number of RMPQs used. The magnitude of each vector is the value of each RMPQ.

[2]Young sharks in this size group are usually taken only in certain areas and not in association with larger thresher sharks.

Any number of measures of prey quantity can be used (e.g., three RMPQs would occupy a cubic space; if $n > 3$, the space would be hypercubic). For a given prey category j, the GII is found by calculating a resultant vector $\boldsymbol{P}$ of magnitude $|P|$ that essentially unites all RMPQ vectors, where

$$|P_j| = \left(\sqrt{\sum_{i=1}^{n}(V_i)^2}\right)_j \quad (1)$$

A reference vector $\boldsymbol{D}$ is defined to represent maximum prey utilization (e.g., 100% V, 100% F, 100% N), where its magnitude $|D|$ would then be defined as

$$|D| = 100 \times \sqrt{n} \quad (2)$$

For prey type j, the GII is defined as the component of $\boldsymbol{P}$ along $\boldsymbol{D}$. Thus it measures the degree of approach to complete utilization of that prey type, reducing the n dimensional space to one dimension, and originating a natural ranking of prey according to the magnitude of the projected prey vectors. After certain algebraic steps (Assis 1996), this component is found as

$$\mathrm{GII}_j = \frac{\left(\sum_{i=1}^{n} V_i\right)_j}{\sqrt{n}} \quad (3)$$

where GII_j = index value for the jth prey category; V_i = the vector for the ith RMPQ of the jth prey category; and n = the number of RMPQs used in the analysis.

To examine differences in diet between mature- and immature-sized fish, northern and southern fishing areas, and fish caught early and late in the fishing season, the data were pooled into the following subgroups, and 2 × 5 contingency table analyses were carried out to determine whether consumption of the leading five diet items varied significantly in frequency and number among the subgroups. Only these two RMPQs were considered for this exercise; weight was not tested because of the extensive range of measurement values (in grams) and because of its general dependence on digestive state.

1. Sharks collected north of latitude 34°N, and sharks collected south of 34°N, all seasons combined.
2. Sharks collected August–October, and sharks collected November–January, all latitudes combined.
3. Presumed adult sharks >159 cm FL, and juvenile sharks ≤159 cm FL, all seasons and latitudes combined.

Finally, we compared results of our overall GII analysis with an analysis of the same RMPQ values using the index of relative importance (IRI, Pinkas et al. 1971). The IRI can be calculated as

IRI = (% number + % weight) × % frequency of occurrence.

In comparing the two indices, we examined only the difference in relative ranking of the suite of prey types for each method, not the individual magnitude of index values, which is not comparable. To better graph and visually compare these proportional differences, we divided the IRI arbitrarily by 60 to equalize the vertical scale of the two indices.

RESULTS

A total of 165 stomach samples was collected from 48 trips by drift gill net vessels fishing between 16 August 1998 and 24 January 1999, from the California-Mexico

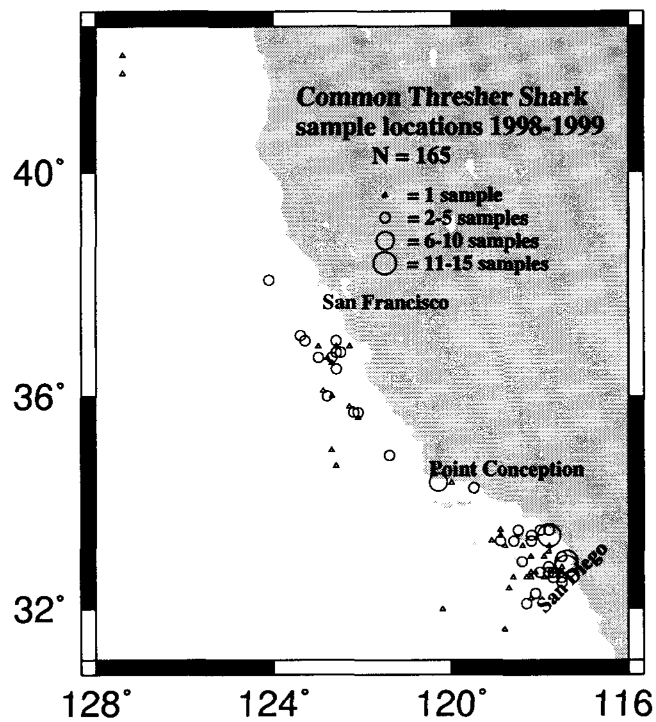

Figure 1. Collection locations for common thresher shark stomach samples, 1998–99.

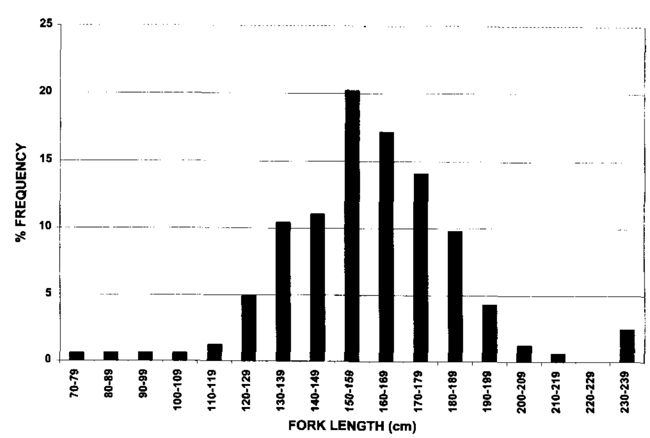

Figure 2. Length-frequency distribution of common thresher sharks sampled in the diet study.

TABLE 1
Qualitative and Quantitative Prey Composition of the Common Thresher Shark (*Alopias vulpinus*) along the California-Oregon Coast

Prey species	W	%W	N	%N	F	%F	GII	IRI
Unidentified Teleostei	3,139.1	17.48	698	47.13	69	64.49	74.51	4,166.44
Northern anchovy, *Engraulis mordax*	5,409.7	30.12	472	31.87	23	21.49	48.18	1,332.09
Pacific hake, *Merluccius productus*	1,646.9	9.17	166	11.21	36	33.64	31.19	685.48
Pacific mackerel, *Scomber japonicus*	4,442.8	24.73	21	1.42	18	16.82	24.81	439.86
Pacific sardine, *Sardinops sagax*	714.0	3.97	66	4.46	8	7.48	9.18	63.07
Pelagic red crab, *Pleuroncodes planipes*	22.6	0.13	14	0.95	11	10.28	6.55	11.01
Louvar, *Luvarus imperialis*	1,784.3	9.93	1	0.07	1	0.93	6.31	9.30
Unidentified Teuthoidea	15.7	0.09	10	0.68	6	5.60	3.68	4.27
California barracuda, *Sphyraena argentea*	313.8	1.75	4	0.27	4	3.74	3.32	7.54
Sebastes spp.	1.2	0.01	8	0.54	4	3.80	2.46	2.09
Jack mackerel, *Trachurus symmetricus*	389.0	2.17	2	0.14	2	2.80	2.41	6.44
Market squid, *Loligo opalescens*	21.2	0.12	9	0.61	3	1.87	2.04	1.36
White croaker, *Genyonemus lineatus*	0.3	0.00	2	0.14	2	1.87	1.16	0.26
Unidentified Crustacea	0.3	0.00	2	0.14	2	1.87	1.16	0.26
California grunion, *Leuresthes tenuis*	0.2	0.00	2	0.14	2	1.87	1.16	0.25
Pacific butterfish, *Peprilus simillimus*	61.0	0.34	1	0.07	1	1.87	0.77	0.76
Gonatus sp.	0.5	0.00	1	0.07	1	0.93	0.58	0.07
Queenfish, *Seriphus politus*	0.2	0.00	1	0.07	1	0.93	0.58	0.06
Unidentified Octopoda	0.1	0.00	1	0.07	1	0.93	0.58	0.06
Pacific sanddab, *Citharichthys sordidus*	0.1	0.00	1	0.07	1	0.93	0.58	0.06

W = weight in grams; N = number; F = frequency; GII = geometric index of importance; IRI = index of relative importance. A total of 107 stomachs containing food and 58 without food were examined.

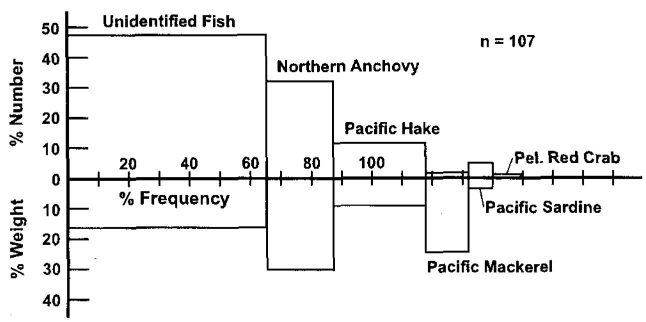

Figure 3. Graphical representation of diet using RMPQ values % weight, % frequency of occurrence, and % number of the six major prey items (IRI diagram).

border north to off the California-Oregon border (fig. 1) over water depths 27 to 2,250 fm (49 to 4,115 m). All specimens were collected in the morning hours from nets set overnight, which is the general practice of the drift gill net fishery.

Sampled sharks ranged in size from 79 cm to 237 cm FL (lengths were available for 163 sharks out of 165) with 82.8% between 130 and 189 cm FL (fig. 2).

Of the 165 stomachs examined, 107 contained food representing a total of 20 taxa (table 1), indicating a broader trophic spectrum than previously assumed for this species. The category "unidentified teleost" was the most important in number, frequency, and weight (table 1, fig. 3), with a GII value of 74.5 (fig. 4). Most of the food items (82%) were in advanced digestive states 5 and 6.

Overall, of the food items identified below the phylum level, northern anchovy (*Engraulis mordax*; GII = 48.2) was the chief prey, followed by Pacific hake (*Merluccius productus*; GII = 31.2), Pacific mackerel (*Scomber japonicus*; GII = 24.8), and Pacific sardine (*Sardinops sagax*; GII = 9.2; fig. 4). Of pelagic invertebrate prey, market squid (*Loligo opalescens*) and pelagic red crab (*Pleuroncodes planipes*) also contributed to the diet.

The distribution of the stomach collection locations for major diet items revealed certain patterns (fig. 5). Northern anchovy was important overall, especially in the Southern California Bight. North of 34°, Pacific hake appeared to be the most important food item, followed by unidentified teleosts, unidentified squid, and northern anchovy. Rockfishes (*Sebastes* spp.) and a variety of other species also contributed to the diet in the north. Anchovy, sardine, and pelagic red crab were not identified in the diet of fish collected north of Point Conception (34°27'N, 120°28'W).

Cumulative prey curves all described a general asymptotic relationship (figs. 6 and 7), but only two reached full asymptotic stabilization (fig. 7A, D). Thus our sample sizes may not have been sufficient to describe the overall trophic diversity of this predator's diet, but are adequate to describe the main prey items, since all curves exhibited a pronounced "knee," leveling off at about 40–70 samples.

Two-way, 10-cell contingency table analyses of the five major identifiable diet items of fish captured north of 34°N ($N = 28$) versus those captured south of that latitude ($N = 119$) showed the diet to differ significantly for frequency (chi-square = 12.1; d.f. = 4; $p < 0.05$) and also for number (chi-square = 43.8; d.f. = 4; $p < 0.05$).

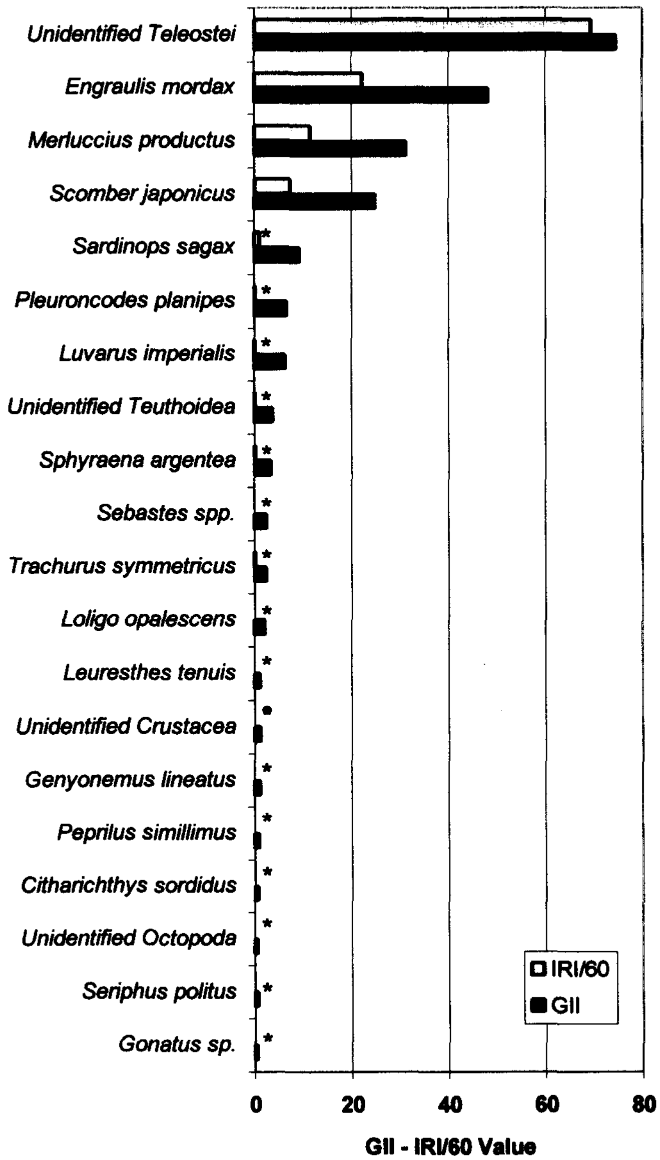

Figure 4. Results of geometric index of importance (GII) and index of relative importance (IRI) analyses for the 20 prey categories (N = 107 sharks). The IRI is divided by 60 to equalize vertical scale. * denotes positive values. See also table 1.

Diet differences in samples collected during the first half of the fishing season (Aug.–Oct., $N = 88$) and the second half of the season (Nov.–Jan., $N = 61$) were also statistically significant for frequency (chi-square = 16.3; d.f. = 4; $p < 0.05$) and for number (chi-square = 260.0; d.f. = 4; $p < 0.05$).

For the diet/predator size analysis, insufficient samples were available to partition the data into the three initially targeted size groups, so the data were lumped into two size categories: immature-sized sharks (≤159 cm FL, $N = 59$) and mature-sized sharks (>159 cm FL, $N = 46$). No significant overall diet differences were observed between the two size categories for frequency of occurrence of the top diet items (chi-square = 2.48; d.f. = 4; $p > 0.05$), but there was a statistically significant difference in total numbers consumed (chi-square = 14.9; d.f. = 4; $p < 0.05$). Although anchovy was important in number for both groups, it ranked far higher for juvenile fish (<159 cm FL, ~0–5 yrs old), which consumed fewer hake and Pacific mackerel than did adults (≥159 cm FL; 5 years and older).

Comparison between the GII and IRI analyses (table 1 and fig. 4) showed the order of ranking to be very similar, but secondary- and tertiary-ranked diet items were proportionately more important in the vector-based GII analysis than in the IRI analysis.

DISCUSSION

The samples were taken during a transitional period when the physical and ecosystem structure of the California Current region was changing rapidly from El Niño to La Niña conditions. According to Hayward et al. (1999), winter and spring of 1998 were periods of strong El Niño conditions. Indeed, the presence of pelagic red crab in the diet seemed to indicate lingering warm-water conditions, since this species is normally found to the south, off Baja California, Mexico. But by fall of 1998, El Niño effects had waned, finally changing to cool-water conditions during the winter–spring of 1998–99 (Hayward et al. 1999).

Our findings confirm the importance of northern anchovy in the diet of the common thresher shark off southern California, but also suggest that the diet may be more varied and opportunistic than previously reported for California waters (Bedford 1992). Warm-water conditions, especially during the first part of the season (Hayward et al. 1999), may have been a contributing factor in the greater diversity of prey items, but we have not yet analyzed comparative data from a more "typical" year. Higher than average water temperatures throughout the 1990s have been implicated in a concurrent decline in anchovy abundance off California, just as the recent transition to La Niña conditions has been associated with a subsequent increase in anchovy numbers (Hayward et al. 1999). But although northern anchovy appears to be a preferred prey, especially among juveniles, our study indicates that the common thresher shark can also consume a diverse diet. Pacific hake is important north of the Channel Islands and Point Conception, where larger and older thresher shark individuals are thought to migrate or congregate in spring and early summer (Bedford 1992). Because Pacific hake also migrate northward in spring (Saunders and McFarlane 1997), it is possible that these two migrations could coincide.

We recognize that diet differences with size, season, and area were complicated by fleet dynamics during the sampling period, which imposed an overlying pattern

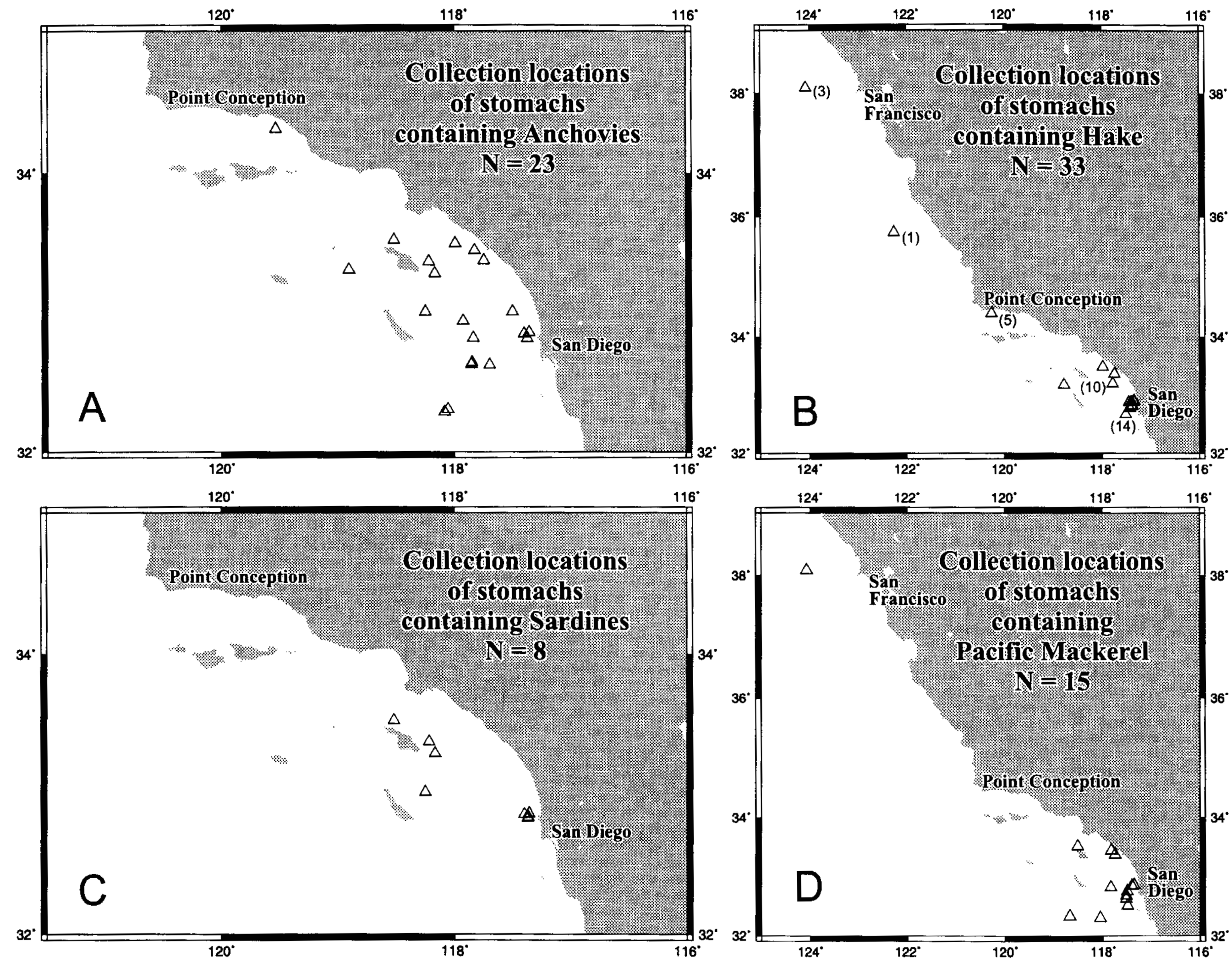

Figure 5. Distribution of the four major diet items by sampling location: *A*, northern anchovy, *B*, Pacific hake, *C*, Pacific sardine, and *D*, Pacific mackerel. (No anchovy or sardine were found in stomachs north of Point Conception: 34°27'N, 120°28'W.)

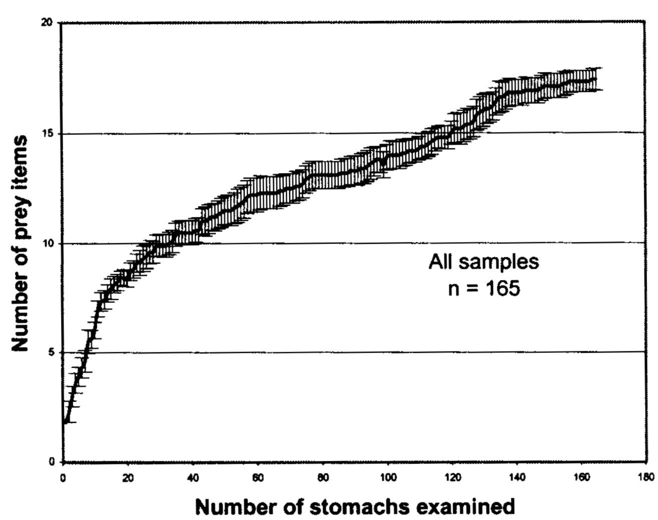

Figure 6. Randomized cumulative prey curve for overall *Alopias vulpinus* diet sample. Mean values are plotted; error bars represent ±SE.

of collection times and areas. According to L. Enriquez (NMFS Drift Net Observer Program, Long Beach, Calif., pers. comm., 9/2000), in the 1998–99 fishing season, most samples from the August–October period were taken after the large boat fleet (boats most likely to accommodate observers) had shifted north of Point Conception. Most samples taken in the second half of the season (November–January) were collected south of Point Conception after the fleet moved south to the Southern California Bight. Thus, early season samples were collected mostly in the north, and late season samples primarily in the south. Nonetheless, diet differences for fish caught in the north early in the season and fish caught in the south later in the season appear to be real. And analyses of the cumulative prey curves 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 the various treatments.

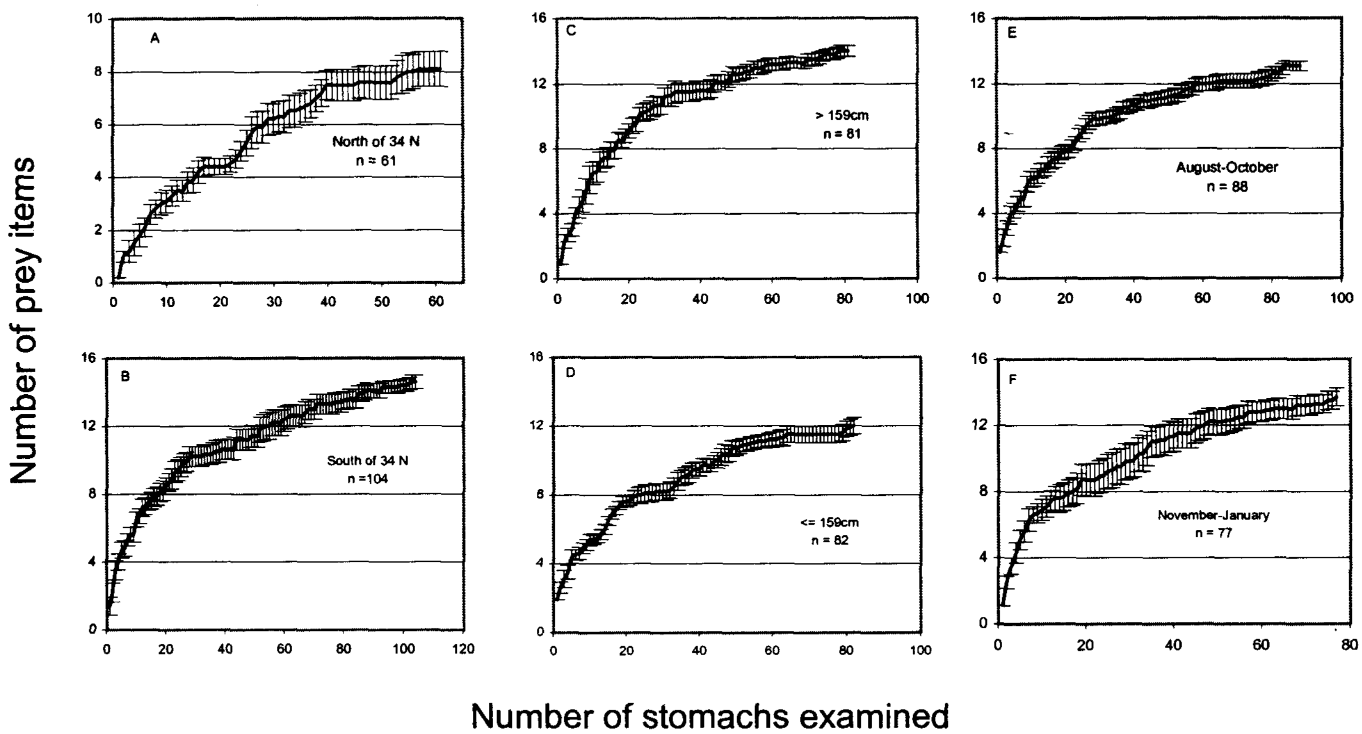

Figure 7. Randomized cumulative prey curves for analyses by area, predator size, and season: *A*, north and *B*, south of 34°N; *C*, large (>159 cm FL) and *D*, small (≤159 cm FL) *A. vulpinus*; *E*, Aug.–Oct. and *F*, Nov.–Jan. collection periods. Mean values are plotted; error bars represent ±SE.

No conclusions can be drawn about diel feeding, because the period of time fish spent in the net before being sampled is unknown. That 82% of food was in an advanced state of digestion was not too surprising, considering the overnight duration of the sets.

This study applies a relatively new methodology (Assis 1996) for interpreting the overall relative importance of various diet items. Another recent example of its application is the work of Duarte and Garcia (1999), who used the GII to describe the diet of the mutton snapper (*Lutjanus analis*). Authors of fish dietary studies have long emphasized that each of the commonly used measures of prey quantity has limitations, each biased toward different aspects of the diet (Hyslop 1980; Cortés 1997). As Cortés (1997) points out, for this reason, many have chosen to use a simple compound index to rank prey, combined with some graphic representation of the relative measures of prey quantity. An example is the IRI developed by Pinkas et al. (1971). However, as Assis (1996) contends, these indices tend to be heterogeneous and produce results difficult to compare. Additionally, we feel that their logic and meaning are unclear, making interpretation of results difficult.

On the other hand, the GII analysis treats each measure of prey importance as a distinct orthogonal vector, combines them into a resultant vector, and then solves for its component along a reference diagonal that represents maximum prey utilization. From the resulting geometry, the GII can be directly related to the degree of specialization in feeding on a particular prey type. Although technically this aspect is best expressed by the % GII (Assis 1996, eq. 8), the absolute GII itself (as presented in this paper and in eq. 7 of Assis 1996) differs only by a constant, thus the same relative ranking of importance or specialization among prey types (the most important feature) is found with either calculation. Although development of the GII is a welcome improvement, we also stress that any study of fish feeding should always include basic data summaries of all measures of prey quantities, because these data are crucial for application to ecosystem models and comparative diet studies.

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