Comparative feeding ecology of shortfin mako, blue and thresher sharks in the California Current

**Antonella Preti · Candan U. Soykan ·
Heidi Dewar · R. J. David Wells · Natalie Spear ·
Suzanne Kohin**

Abstract This study describes the feeding ecology of three pelagic shark species in the California Current: shortfin mako (*Isurus oxyrinchus*); blue (*Prionace glauca*); and thresher (*Alopias vulpinus*) sharks. Stomach contents of sharks collected from 2002 to 2008 were identified to the lowest taxonomic level and analyzed using univariate and multivariate methods. Of 330 mako sharks sampled (53 to 248 cm fork length [FL]), 238 stomachs contained 42 prey taxa, with jumbo squid (*Dosidicus gigas*) and Pacific saury (*Cololabis saira*) representing the most important prey based on the geometric index of importance (GII). In addition, 158 blue sharks were sampled (76 to 248 cm FL) and 114 stomachs contained 38 prey taxa, with jumbo and *Gonatus* spp. squids representing the most important prey. Lastly, 225 thresher sharks were sampled (108 to 228 cm FL) and 157 stomachs contained 18 prey taxa with northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) identified as the most important prey. Overall, mako sharks had the most diverse diet based upon Simpson's diversity index (1/D) (8.43 ± 1.16), feeding on many species of teleosts and cephalopods, followed by blue sharks (6.20 ± 2.11) which consumed a wide range of prey (primarily cephalopods), while thresher sharks were most specialized (2.62 ± 0.34), feeding primarily on coastal pelagic teleosts. Dietary overlap was lowest between blue and thresher sharks (Sørensen similarity index=0.321 and Simplified Morisita Horn index= 0.006), and seasonal variability in diet was greatest for blue sharks (Simplified Morisita Horn index= 0.260, Analysis of Similarity (ANOSIM) $p < 0.001$). In addition, size class, and subregion were significant factors that affected diet of each species differently (ANOSIM $p < 0.001$). Despite similarities in life history characteristics and spatial and temporal overlap in habitat, diets of these three common shark species are distinct in the California Current.

A. Preti (✉) · C. U. Soykan · H. Dewar · R. J. D. Wells ·
N. Spear · S. Kohin
Fisheries Resources Division, Southwest Fisheries Science
Center, National Marine Fisheries Service, National
Oceanic and Atmospheric Administration,
8604 La Jolla Shores Drive,
La Jolla, CA 92037-1508, USA
e-mail: Antonella.Preti@noaa.gov

Introduction

Shortfin mako (*Isurus oxyrinchus*, hereafter mako), blue (*Prionace glauca*) and thresher sharks (*Alopias vulpinus*) are found worldwide in temperate and tropical waters (Casey and Kohler 1992; Compagno 2001; Kohler et al. 2002). Mako and blue sharks are more

oceanic while thresher sharks are more frequently found in coastal areas (Compagno 2001); however, these three species co-occur in the California Current Large Marine Ecosystem (CCLME). Inshore areas of the CCLME, between Point Conception, California to the north and Sebastián Vizcaíno Bay, Baja California, Mexico to the south comprise important nursery habitat for all three species (Taylor and Bedford 2001; Smith and Aseltine-Neilson 2001; Holts et al. 2001; Cartamil 2009; Cartamil et al. 2010).

These pelagic shark species are commonly taken in both U.S. and Mexican fisheries throughout the CCLME. In the U.S. they are caught in the pelagic drift gillnet (DGN) fishery that targets swordfish and operates from the U.S.-Mexico border to 48°N latitude within the U.S. west coast Exclusive Economic Zone (EEZ). While not the primary target of the DGN fishery, mako and thresher sharks are marketed and provide significant revenue (combined ex-vessel revenue of $240 000 in 2008; PFMC 2009a). Blue sharks, also caught in large numbers, are not marketable due to inferior quality of the meat and are therefore discarded from the U.S. DGN fishery, but they are targeted and retained in Mexico and elsewhere. Recreational fishing for mako and thresher sharks, two species prized for their energetic fights, has grown in popularity off Southern California over the past 20 years (Holts et al. 1998). Given their interactions with local fisheries, federal management of mako, blue and thresher sharks was implemented in 2004 under the Pacific Fisheries Management Council's U.S. West Coast Highly Migratory Species Fishery Management Plan (PFMC 2003) with harvest guidelines set for mako and thresher sharks.

The removal of sharks by fisheries affects the sharks directly and can cause dramatic changes in the ecosystem (Stevens et al. 2000; Myers et al. 2007; Heithaus et al. 2008; Baum and Worm 2009). Given their life history characteristics (late maturity, low fecundity), sharks are more susceptible to overfishing than most teleosts (Stevens et al. 2000; Smith et al. 2008). A reduction in the California thresher shark population followed the opening of the DGN fishery in 1977 and necessitated restrictions, imposed by the mid 1980s, to reduce their take (Bedford 1987; PFMC 2003). Reductions in shark populations can cause trophic cascades through top-down control mechanisms (Heithaus et al. 2008). For example, a decline in large-bodied shark populations resulted in an increase in cownose ray (*Rhinoptera bonasus*) populations which subsequently decimated local

scallop resources (Myers et al. 2007). On the other hand, bottom up effects stemming from changes in abundance of mid-trophic level species may cause changes in top predator abundance. Mid-trophic level control may be more likely in highly productive upwelling systems, such as the CCLME, where only a few mid-trophic level species tend to dominate (Cury et al. 2000; Bakun 2006). In such systems, changes in the forage base resulting from heavy exploitation or environmental change has had dramatic effects on populations of predatory fish and birds (Cury et al. 2000), although the specific effects on shark populations are rarely studied.

Despite the importance of sharks for marine ecosystems and the local economy, and a shift towards ecosystem-based management, the feeding habits of these three locally abundant shark species are not well documented in the CCLME. Some information on their diets is available from a few published studies; however, results for each species often differ across time and space. Makos in the CCLME are known to feed on mackerel, bonito, anchovy, sardine, saury, tuna, other sharks, and squid (Mearns et al. 1981; Hanan et al. 1993; Sepulveda et al. 2004), while billfish and marine mammals have been found in the stomachs of larger specimens (PFMC 2003). Like many of their oceanic relatives, makos are thought to be opportunistic feeders that eat locally abundant prey (Taylor and Bedford 2001). Since its recent range expansion northward in the CCLME (Field et al. 2007; Zeidberg and Robison 2007), jumbo squid (*Dosidicus gigas*) now appears to be an important component of the mako diet (Vetter et al. 2008). Previous studies in the CCLME reported that blue sharks feed on northern anchovy (*Engraulis mordax*), jack mackerel (*Trachurus symmetricus*), Pacific hake (*Merluccius productus*), Pacific herring (*Clupea pallasii*), flatfishes, spiny dogfish (*Squalus acanthias*), various species of cephalopods and pelagic crustaceans including euphausiids (Tricas 1979; Mearns et al. 1981; Brodeur et al. 1987; Harvey 1989; Markaida and Sosa-Nishizaki 2010). Prey importance varied considerably among studies, suggesting opportunistic feeding by blue sharks on spatio-temporally abundant food resources. A few studies have found that anchovy is the most important prey item for thresher sharks, while their diet also includes other coastal pelagic species such as Pacific sardine (*Sardinops sagax*), Pacific hake, Pacific mackerel (*Scomber japonicus*) and the market squid (*Loligo opalescens*) (Mearns et al. 1981; Preti et al. 2001; Preti et al. 2004).

Although valuable, the previous feeding studies did not provide quantitative information on the diet compositions of these three shark species concurrently and within a single ecoregion. Indeed, they suggested considerable diet variation between regions and years, underscoring the need for a more comprehensive study. As such, the overall goal of this study was to better understand the feeding ecology of these species in the CCLME during a seven-year study period. Specific objectives were to describe and analyze the relative importance of different prey types, prey diversity and the degree of dietary overlap among mako, blue and thresher sharks. We also examined diet variation within each species by fishing season, size, subregion, and sex, and put our results into an ecological context based on how these species may impact food web dynamics in the CCLME.

Materials and methods

Sampling at sea

Stomachs were collected from mako, blue and thresher sharks by federal fishery observers aboard DGN vessels during the 2002–2008 fishing seasons. The DGN vessels operate within the U.S. EEZ from the U.S.-Mexico border (31° 20′N) to as far north as Washington state (48° 03′N) between August 15th and January 31st. In recent years, the majority of the fishery has operated in the Southern California Bight (SCB) between Point Conception, California and the U.S.-Mexico border. Sets are conducted using 1.8 km (1,000 fathom [fm]) long drift gillnets extending from roughly 11 m to 100 m below the surface. Onboard the vessels, stomachs were collected as in Preti et al. (2001). At sea, data recorded included set and haul-back times, water depth, sea surface temperature (SST), location, fish size, sex, and maturity state. When fork length (FL; cm) was not measured, it was estimated from the alternate length (AL; cm), the straight line measurement from the anterior origins (leading edge) of the first and second dorsal fins using the following equations derived from measurements of sharks taken in this fishery; mako shark, FL=2.4054 × AL+9.8035 (R^2=0.9596, n=3,246); blue shark, FL=2.7507 × AL+11.627 (R^2=0.9442, n=9,494); thresher shark, FL=2.3471 × AL+17.725 (R^2=0.9123, n=3,013).

Processing in the laboratory

Stomach samples were processed as described in Preti et al. (2001). Percent stomach fullness (0–100%) was estimated visually to obtain a general, qualitative estimate of relative fullness. Degree of prey digestion was estimated on a relative scale between 1 and 6 as in Preti et al. (2001). Prey items were then separated, identified to lowest possible taxonomic level using taxonomic keys, enumerated, measured when intact (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 of pairs representing the minimum number present. Weights of all remains by species were recorded. Partial remains representing only large chunks (i.e. fist size or greater) or pieces of fish both in digestive state 1 and 2 were considered the result of sharks feeding on prey caught in the driftnet and therefore were discarded from the analysis. Genetic analyses were used to identify diet items that could not be identified visually.

Data analysis

A wide range of quantitative metrics were used to describe different aspects of the diet. The 14 methods included three relative measures of prey quantity (RMPQs) and two combined indices of prey importance based on the RMPQs, an analysis of sample size sufficiency, two univariate measures of diet diversity, two measures of diet similarity between species, and four multivariate methods for comparing diets. Consideration of all the different metrics provided a more comprehensive understanding of each shark's diet than could have been achieved with only one or a few metrics. Moreover, the results from one metric often inform the interpretation of results from other metrics.

Relative measures of prey quantities and indices of prey importance

Importance of prey type was analyzed by three RMPQs: percent frequency of occurrence (%F); percent composition by number (%N); and percent composition by weight (%W) (Bowen 1996; Preti et al. 2001). Empty stomachs, slurry, and detritus were not considered when calculating percentages. We used both the geometric index of importance (GII; Assis

1996) and the index of relative importance (IRI; Pinkas et al. 1971) as combined indices to rank prey importance, since these measures take into account both numerical and weight-based importance to the diet. We used each method to examine only the relative difference in ranking of prey types, because the two combined index values are not directly comparable.

The GII, in its simplified form, is calculated as:

$$GII_j = \frac{\left(\sum\limits_{i=1}^{n} V_i\right)_j}{\sqrt{n}} \tag{1}$$

where GII_j = index value for the j-th prey category; V_i = the magnitude of the vector for the i-th RMPQ of the j-th prey category; and n = the number of RMPQs used in the analysis.

The IRI for the j-th prey category is calculated as:

$$IRI_j = \left(\%N_j + \%W_j\right) * \%F_j \tag{2}$$

The IRI value was converted to a percentage in order to facilitate comparisons among studies (Cortés 1997).

Sample size sufficiency

Randomized cumulative prey curves for each shark species were constructed using the vegan package (Oksanen et al. 2010) of the R statistical software (R Development Core Team 2010) to determine if the sample size was sufficient to describe the full diet (Hurtubia 1973; Ferry and Cailliet 1996; Ferry et al. 1997; Gelsleichter et al. 1999; Yamaguchi and Taniuchi 2000). For this analysis, the order in which stomach contents were analyzed was randomized 100 times and the mean (± 2 standard deviations) number of new prey observed was plotted for each consecutive stomach. A curve approaching an asymptote with low variability indicates that the number of stomachs examined is sufficient to characterize the diet (Hurtubia 1973). To complement this visual approach, we also used the method proposed by Bizzarro et al. (2007) to objectively assess whether the curve had reached an asymptote or not. Specifically, we fit a straight line to the last 4 points from the species accumulation curve and compared the slope of the line with a line of slope zero. If the two lines did not differ significantly in slope, then the species accumulation curve was deemed to have reached an asymptote. However,

unlike Bizzarro et al. (2007), who lumped prey into higher-level taxonomic categories (e.g., crustaceans, teleosts, polychaetes), we used the lowest taxonomic level to which prey had been identified for constructing cumulative prey curves, making it much less likely that the curves would reach an asymptote. For comparative purposes, we also constructed species accumulation curves using 1) prey identified down to the family level (similar to, but still to lower taxonomic levels than was done by Bizzarro et al. 2007) and 2) excluding prey items that occurred in only one stomach.

Univariate measures of diet diversity

Diet composition was compared among species and within species classified by fishing season, size class, subregion, and sex. Two indices of diet diversity were calculated using EstimateS software (Colwell 2009): rarefied richness and Simpson diversity. Rarefied richness is the number of prey found relative to the number of shark stomachs sampled, while Simpson diversity incorporates both the number of prey and the relative abundance of each prey type. For each of the two indices described below (along with the two similarity indices described in the following section), no index value was estimated if the sample size was less than ten (since small samples are known to produce biased values; Magurran 2004). Confidence intervals were generated for rarefied richness and for the Simpson diversity index by bootstrapping (sampling with replacement) from the diet matrix 100 times. The number of prey taxa consumed by each species was estimated using sample-based rarefied richness to account for differences in the number of stomach samples collected for each shark species (Colwell et al. 2004). Diet evenness of each shark species was calculated using the reciprocal form of the Simpson index of diversity (Magurran 2004):

$$\frac{1}{D} = \frac{1}{\sum\limits_{j=1}^{n} p_j^2} \tag{3}$$

where D = Simpson's index of diversity; p_j = proportion of individuals belonging to prey taxon j; n = total number of prey taxa. We used the reciprocal form of the Simpson index ($1/D$) because greater values

correspond with greater evenness, matching the format of the other indices used in this study.

Univariate measures of diet similarity

EstimateS software (Colwell 2009) was also used to calculate similarity in prey taxa among shark species. However, unlike the diversity indices described above, confidence intervals could not be calculated for the two similarity indices that were selected, the Sørensen similarity index and the simplified Morisita-Horn index (SMH). The Sørensen similarity index measures overlap in prey taxa between pairs of consumers (A and B), irrespective of the number of prey items of each taxon consumed (Magurran 2004):

$$S_s = \frac{2a}{2a + b + c} \quad (4)$$

where S_s = Sørensen's similarity index; a = number of taxa in the diets of both species A and B (joint occurrences); b = number of taxa in the diet of species B but not in the diet of species A; c = number of taxa in the diet of species A but not in the diet of species B.

In contrast, the SMH index quantitatively assesses diet similarity in prey numbers between two species (i.e., the Sørensen index considers similarity in prey taxa, whereas the SMH index considers similarity in number of prey of a given taxon; Magurran 2004):

$$C_H = \frac{2 \sum\limits_{i=1}^{n} p_{iA} p_{iB}}{\sum\limits_{i=1}^{n} p_{iA}^2 + \sum\limits_{i=1}^{n} p_{iB}^2} \quad (5)$$

where C_H = Simplified Morisita-Horn index of diet overlap; p_{iA} = proportion in number consumed of taxon i to the total number of prey consumed by shark species A; p_{iB} = proportion in number consumed of taxon i to the total number of prey consumed by shark species B; n = total number of prey taxa.

Multivariate methods

Diet composition was additionally evaluated using multivariate techniques including analysis of similarity (ANOSIM), non-metric multidimensional scaling (MDS) plots, Bio-Environmental step-wise (BVSTEP) analysis, and multivariate regression trees. The former three methods were done using Plymouth Routines in

Multivariate Ecological Research (PRIMER-E) software (Clarke and Gorley 2006), while the latter was done using the R software package rpart (Therneau and Atkinson 2004). By reducing the dimensionality of the data with minimal distortion, MDS plots provide a method for visualizing shark diet. They are similar, in this regard, to PCA plots but differ in being non-parametric (they have fewer restrictive assumptions). Likewise, ANOSIM provides a non-parametric complement to ANOVA, allowing for an assessment of differences in diet among categories selected by the analyst (i.e., among species, size classes within species). BVSTEP analysis complements the aforementioned approaches by using a stepwise procedure to identify the group of prey taxa that contributed 90% of the overall variability in diets among categories. Finally, multivariate regression trees constitute a non-parametric method for identifying the relationships between a set of predictor variables and a multivariate response variable (in this case, how traits such as size, sex, fishing season and location of collection affect shark diet). For the regression trees, diet data from all stomachs were examined by number and with prey classified to the lowest taxonomic level or grouped to the family level.

Within-species comparisons

The aforementioned methods were also done as nested analyses within species. Thus, we compared diet within a species by fishing season, size class, subregion, and sex. A fishing season was labeled for the year in which the season started, for example season 2003 represents August 2003 through January 2004. Diet was compared among different size classes for all species. For mako and blue sharks, we examined differences in diet between small (up to 109 cm FL), medium (110–149 cm FL) and large (150 cm FL and up) specimens. Although not strictly conforming to any specific maturity stages, we divided individuals into these categories based on sample size constraints. For thresher sharks we analyzed the diet differences between large juveniles/subadults (up to 166 cm FL) and adults (167 cm FL and up), since neonates and small juveniles were not present in our sample. Stomachs collected east and west of 120° 30′W were put into subregions generally classified as "within SCB" and "beyond SCB". This line of longitude approximately separates the waters in the SCB where the

northward flowing California Counter Current influences nearshore oceanography and the more offshore waters are affected by the California Current as it moves southward.

Results

A total of 713 (330 mako, 158 blue, 225 thresher) shark stomachs were collected during 151 observed trips throughout the CCLME (Fig. 1). SST at the time of collection ranged from 11.6 to 22.4°C (mean 17.7°C). Mako sharks ranged in size from 53 to 248 cm FL (Fig. 2); 184 were males and 143 females. Fork lengths were not determined for three of the mako sharks. Of the 330 mako stomachs examined, 238 contained food representing a total of 42 taxa. Ninety-one percent of the food items were in an advanced state of digestion (defined as states 4 and 5; Preti et al. 2001). Blue sharks ranged in size from 76 to 248 cm FL (Fig. 2); 102 were males and 54 females. Fork lengths were not determined for two of the blue sharks. Of the 158 blue shark stomachs examined, 114 contained food representing a total of 38 taxa. Ninety-three percent of the food items were in an advanced state of digestion. Thresher sharks ranged in size

from 108 to 228 cm (Fig. 2); 101 were males and 124 females. Of the 225 thresher stomachs examined, 157 contained food representing a total of 18 taxa. Ninety-two percent of the food items were in an advanced state of digestion.

Cumulative prey curves (when analyzed with all taxa identified to the lowest possible level) did not reach an asymptote for any of the three species (Fig. 3a). The terminal portions of all three curves had slopes that differed significantly from zero (mako: $p=0.007$; blue: $p=0.005$; thresher: $p=0.010$). If analyzed at the family level, curves for mako and blue sharks did not reach an asymptote, although the curve for threshers did (Fig. S1). When excluding prey that was found in only one stomach for each species, all three curves reached an asymptote ($p>0.05$ for all 3 species; Fig. 3b).

Tables 1, 2, and 3 list each of the RMPQs for all prey found, as well as the calculated GII and IRI values. For all three shark species, rankings based on GII and IRI were nearly identical. For the mako shark, jumbo squid was the most important prey item by frequency of occurrence, weight and the combined indices. Pacific saury (*Cololabis saira*) was the second most important prey item by GII and IRI, but the most abundant by number. Other dominant teleost prey included Pacific sardine, Pacific mackerel, jack
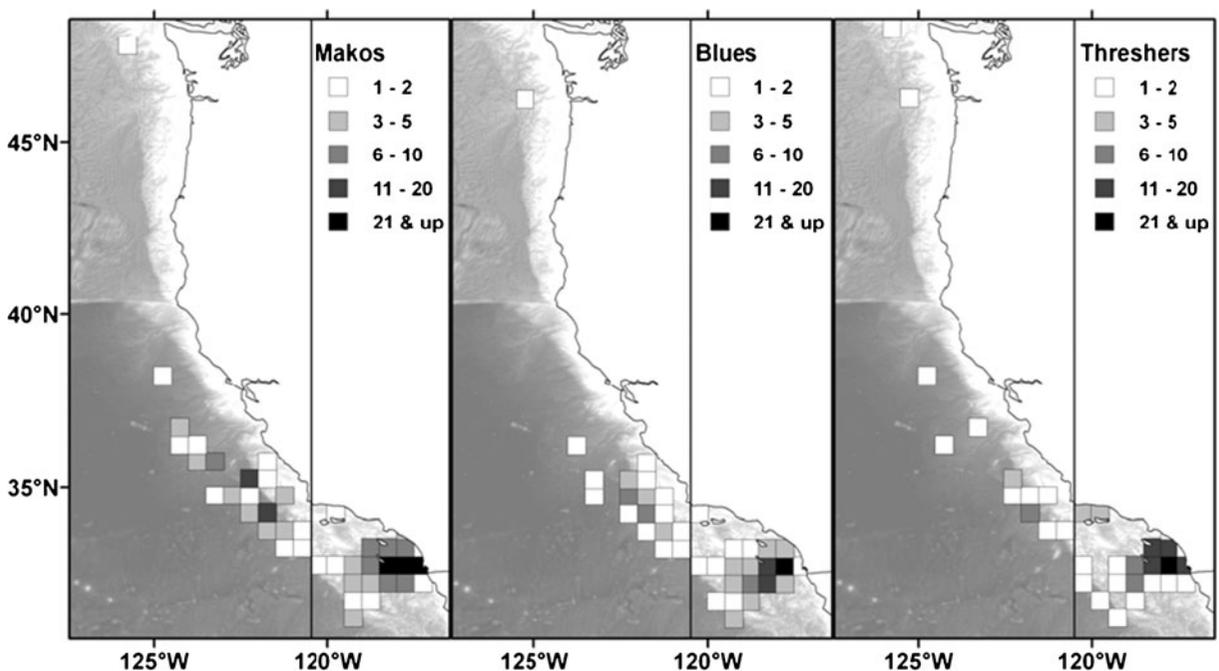

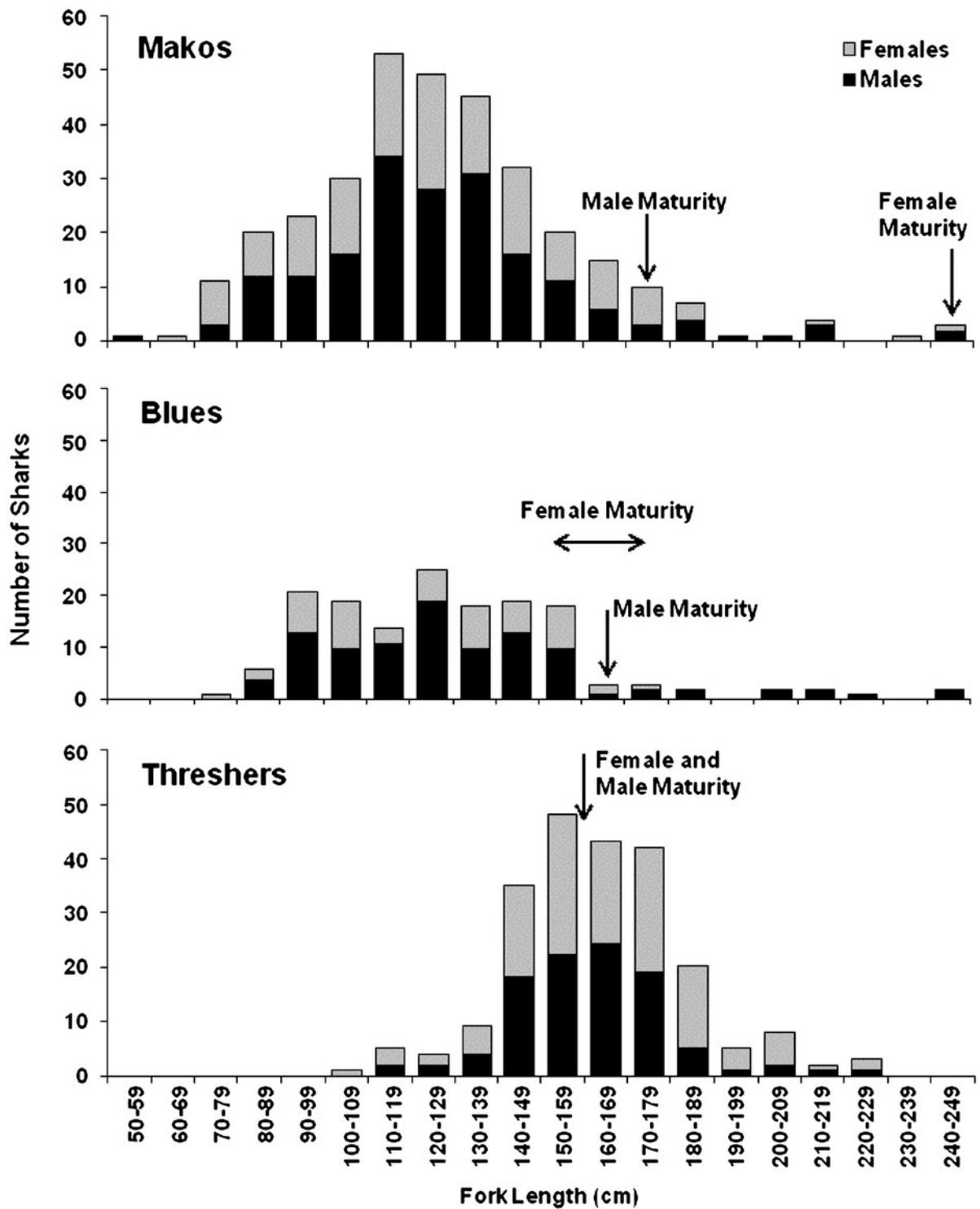Fig. 1 Collection areas of all mako, blue and thresher shark samples from 2002 to 2008 used for diet analysis

Fig. 2 Length-frequency distribution of mako (*N*=327), blue (*N*=156) and thresher (*N*=225) sampled in the diet study. *Arrows* indicate size at maturity for mako (Stevens 1983), blue (Nakano 1994) and thresher (Smith et al. 2008)
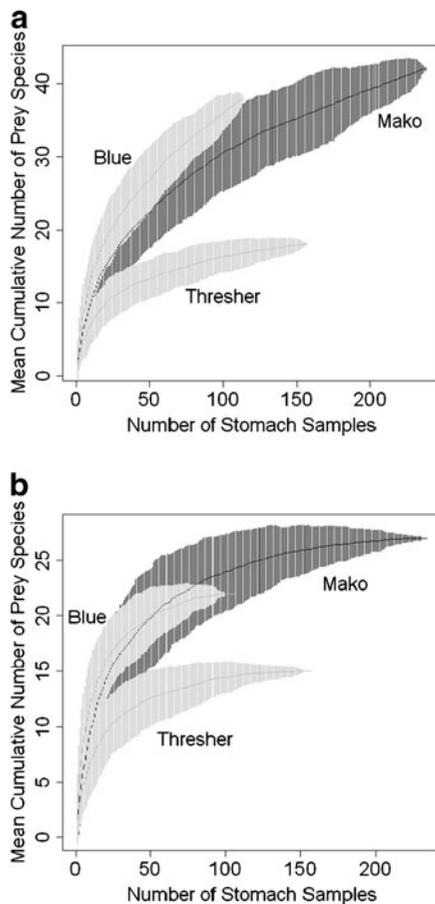
Fig. 3 **a** Cumulative prey curve for mako, blue and thresher sharks (prey identified to the lowest possible taxonomic level). **b** Cumulative prey curve for mako, blue and thresher sharks (prey items consumed on more than one occasion)

mackerel and striped mullet (*Mugil cephalus*). Three makos also had preyed on elasmobranchs or marine mammals; blue sharks were found in two mako stomachs and one mako fed on a short-beaked common dolphin (*Delphinus delphis*).

Jumbo squid also ranked first by GII, IRI and weight for the blue shark. Squids of the genus *Gonatus* ranked second, but they were the most important in terms of number and frequency of occurrence. Other dominant prey included octopuses of the genus *Argonauta* and the flowervase jewell squid (*Histioteuthis dofleini*). Three blue sharks also fed on elasmobranchs (spiny dogfish, and soupfin shark, *Galeorhinus galeus*), one fed on an unidentified cetacean, and one ingested a bird (common tern, *Sterna hirundo*). A small fraction of the blue shark prey items (4.3% by number) were bitten in chunks and were found in a

fresh state of digestion (states 1 and 2) which were interpreted as prey caught in the net. Indeed, one blue shark stomach contained a skipjack tuna head with a piece of net in its mouth. Other net-fed prey taxa included scombridae ($F=31$), broadbill swordfish (*Xiphias gladius*) ($F=3$), unidentified elasmobranchs ($F=2$), Pacific pomfret (*Brama japonica*) ($F=1$), an unidentified bird ($F=1$), and 21 pork steaks wrapped in paper that were likely discarded at sea ($F=1$). Similar fresh chunks were observed in only one mako shark and no thresher sharks.

For the thresher shark, northern anchovy ranked first in both the GII and IRI and had the highest number and frequency of occurrence. Pacific sardine ranked second in both the GII and IRI and had the highest weight. Other dominant teleosts included Pacific hake and Pacific mackerel. Only two cephalopod species were present: market squid was the most important cephalopod and ranked 6th overall while jumbo squid was found in only one stomach. Jack mackerel, Pacific saury, short-belly rockfish (*Sebastes jordani*) and fishes of the family Paralepididae were each found in at least 6 stomachs.

Across-species comparisons

Across species, rarefied diet richness was greatest in blue sharks, followed by mako and thresher (Table S1); however, the differences in diet richness among species were not statistically significant ($p>0.05$). Diet evenness of mako sharks was significantly greater than that of thresher sharks ($p<0.05$; Table S1). For the blue shark, the diet evenness was similar to that of the mako shark and although greater than for the thresher, this difference was not significant ($p>0.05$).

The similarity indices differed somewhat in their rankings. Sørensen similarity results suggested that mako and blue shark diets were more similar than mako and thresher shark diets, whereas blue and thresher shark diets were least similar (Table S2). SMH results, on the other hand, suggested that mako and thresher diets were most similar, followed by mako and blue, with blue and thresher again being the least similar (Table S2).

ANOSIM results indicated significant differences in diet among species (Table 4). Likewise, species was identified as the most important variable in regression tree analyses (Fig. 4). The differences among species are illustrated by a MDS plot of shark diet by species (Fig. 5). BVSTEP analyses suggest that the

differences were driven by 11 diet items belonging to 11 different families or higher orders. These include *Argonauta* sp., flowervase jewell squid, *Gonatus* spp., jack mackerel, jumbo squid, northern anchovy, octopus squid (*Octopoteuthis* sp.), Pacific mackerel, Pacific sardine, Pacific saury and striped mullet.

Within-species comparisons

Results by fishing season

The differences between fishing seasons were not significant for either of the diversity indices (Table S1) although some patterns were apparent in the similarity indices (Table S2). The average fishing season Sørensen similarity was highest for threshers (mean=0.657), followed by blues (mean=0.572), and makos (mean=0.568). In contrast, average fishing season SMH similarity was highest for makos (mean=0.654), followed by threshers (mean=0.519), and then blue sharks (mean=0.260). ANOSIM results indicate significant differences in diet among fishing seasons for each of the three species ($p<0.001$) (Table 4); however, fishing season did not emerge as an important variable in the regression tree analyses (Fig. 4). We did not calculate indices of prey importance by season due to low sample sizes.

Results by size

Some differences with body size were apparent across species. GII results by size for the mako shark revealed that for the smallest sharks, Pacific sardine was the most important prey item followed by Pacific mackerel, Pacific saury, and jumbo squid (Table S3). Pacific saury ranked first in importance for medium sized makos, followed by jumbo squid and striped mullet (Table S4). One specimen (137 cm FL) in this size category fed on a short-beaked common dolphin, demonstrating that medium sized makos are capable of consuming marine mammals. Jumbo squid ranked first in importance for large makos, followed by Pacific mackerel and Pacific saury (Table S5). Two mako specimens in this group fed on blue sharks. The number of taxa consumed increased with body size, demonstrating an ontogenetic expansion of diet rather than a shift in prey types. GII results by size for the blue shark revealed that for the smallest sharks, euphausiids were the most important prey item (although this result is biased due to a large number of this prey

found in a single stomach) followed by *Argonauta* sp. and *Gonatus* spp. (Table S6). *Gonatus* spp. ranked first in importance for medium blue sharks, followed by jumbo squid and *Argonauta* sp. (Table S7). Jumbo squid ranked first for large blues, followed by *Gonatus* spp. and pelagic red crab (*Pleuroncodes planipes*) (Table S8). One large specimen fed on an unidentified cetacean. Similar to makos, the number of taxa consumed increased with body size. GII results by size for the thresher shark indicated that medium and large threshers had similar diets consisting primarily of northern anchovy followed by Pacific sardine (Tables S9 and S10).

Although the diversity statistics were not significantly different among size classes, some patterns were apparent. For both mako and blue sharks, rarefied diet richness tended to be greater for large and medium size classes than for small individuals (Table S1). Likewise, for threshers, rarefied diet richness tended to be greater for the large versus the medium size class. A similar pattern held for Simpson diversity values for mako and blue sharks, but not for threshers (Table S1). Diet similarity between size classes for makos was lowest between small and large individuals for both indices (Table S2). With blue sharks, however, the pattern was reversed, being highest between small and large individuals and lowest between small and medium individuals (though the variation in similarity values for these comparisons is very small: range=0.640–0.708). Thresher sharks had high diet similarity between the two size classes. ANOSIM results indicated significant differences in diet among size classes for each of the three species (Table 4). Size class also emerged as an important variable in some of the regression tree analyses (data not shown).

Results by subregion

A comparison of the GII results by subregion revealed some differences in diet. For the mako shark, striped mullet and Pacific sardine were important within the SCB (Table S11), whereas Pacific saury, and Pacific pomfret ranked higher beyond the SCB (Table S12). In contrast, jumbo squid and jack mackerel were important prey items in both areas. GII data for the blue shark revealed that within the SCB the most important prey was *Argonauta* sp. followed by *Gonatus* spp. and jumbo squid (Table S13). Beyond the SCB, jumbo squid was the most important prey item followed by

Table 1 Quantitative prey composition of the shortfin mako (*Isurus oxyrinchus*) in the California Current. A total of 238 stomachs containing food and 92 without food were examined.

Prey items are shown by decreasing GII value. See methods for descriptions of the measured values. Two unidentified species in the genus *Onychoteuthis* are indicated with (1) and (2)

Prey Species	W	%W	N	%N	F	%F	GII	IRI	%IRI
Jumbo squid, *Dosidicus gigas*	29411.0	38.97	106	12.60	67	28.15	46.03	1451.93	49.92
Pacific saury, *Cololabis saira*	5203.1	6.89	201	23.90	32	13.45	25.54	414.05	14.24
Pacific sardine, *Sardinops sagax*	1593.9	2.11	128	15.22	30	12.61	17.28	218.47	7.51
Pacific mackerel, *Scomber japonicus*	3086.7	4.09	89	10.58	36	15.13	17.20	221.94	7.63
Jack mackerel, *Trachurus symmetricus*	11803.4	15.64	29	3.45	23	9.66	16.60	184.47	6.34
Striped mullet, *Mugil cephalus*	9401.6	12.46	28	3.33	25	10.50	15.18	165.83	5.70
Unidentified Teleostei	2494.9	3.31	41	4.88	30	12.61	12.90	121.46	4.18
Gonatus spp.	1.6	<0.01	34	4.04	22	9.24	7.67	37.39	1.29
Flowervase jewell squid, *Histioteuthis dofleini*	20.9	0.03	25	2.97	19	7.98	6.34	23.95	0.82
Pacific pomfret, *Brama japonica*	3601.7	4.77	8	0.95	7	2.94	5.00	16.83	0.58
Unidentified Teuthoidea	358.7	0.48	21	2.50	13	5.46	4.87	16.24	0.56
Octopoteuthis sp.	2.6	<0.01	13	1.55	9	3.78	3.08	5.86	0.20
Histioteuthis spp.	16.4	0.02	12	1.43	9	3.78	3.02	5.48	0.19
Market squid, *Loligo opalescens*	1.0	<0.01	11	1.31	8	3.36	2.70	4.40	0.15
Blue shark, *Prionace glauca*	2627.6	3.48	2	0.24	2	0.84	2.63	3.13	0.11
Duckbill barracudina, *Magnisudis atlantica*	171.7	0.23	19	2.26	4	1.68	2.41	4.18	0.14
Northern anchovy, *Engraulis mordax*	72.3	0.10	11	1.31	5	2.10	2.02	2.95	0.10
Short-beaked common dolphin, *Delphinus delphis*	2173.0	2.88	1	0.12	1	0.42	1.97	1.26	0.04
Skipjack tuna, *Katsuwonus pelamis*	743.9	0.99	3	0.36	3	1.26	1.50	1.69	0.06
Argonauta sp.	0.1	<0.01	13	1.55	2	0.84	1.38	1.30	0.04
Cock-eyed squid, *Histioteuthis heteropsis*	0.1	<0.01	4	0.48	4	1.68	1.25	0.80	0.03
Barracudinas, Paralepididae	105.7	0.14	5	0.59	3	1.26	1.15	0.93	0.03
Shortbelly rockfish, *Sebastes jordani*	593.0	0.79	6	0.71	1	0.42	1.11	0.63	0.02
Boreopacific gonate squid, *Gonatopsis borealis*	0.8	<0.01	4	0.48	3	1.26	1.00	0.60	0.02
Bullet mackerel, *Auxis rochei*	743.3	0.98	2	0.24	1	0.42	0.95	0.51	0.02
Pacific grenadier, *Coryphaenoides acrolepis*	288.1	0.38	2	0.24	2	0.84	0.84	0.52	0.02
Pacific Bonito, *Sarda chiliensis*	732.7	0.97	4	0.48	3	1.26	0.66	0.25	0.01
Sebastes spp.	33.7	0.04	2	0.24	2	0.84	0.65	0.24	0.01
Coryphaenoides sp.	0.7	<0.01	2	0.24	2	0.84	0.62	0.20	0.01
Japetella sp.	<0.1	<0.01	2	0.24	2	0.84	0.62	0.20	0.01
Onychoteuthis sp. (1)	<0.1	<0.01	2	0.24	1	0.42	0.38	0.10	<0.01
Chilipepper, *Sebastes goodei*	84.6	0.11	1	0.12	1	0.42	0.38	0.10	<0.01
Scombridae	58.9	0.08	1	0.12	1	0.42	0.36	0.08	<0.01
Unidentified Aves	24.1	0.03	1	0.12	1	0.42	0.33	0.06	<0.01
Unidentified Cephalopoda	13.2	0.02	1	0.12	1	0.42	0.32	0.06	<0.01
Halfmoon, *Medialuna californiensis*	1.0	<0.01	1	0.12	1	0.42	0.31	0.05	<0.01
Unidentified Invertebrate	0.5	<0.01	1	0.12	1	0.42	0.31	0.05	<0.01
Robust clubhook squid, *Onykia robusta*	0.3	<0.01	1	0.12	1	0.42	0.31	0.05	<0.01
Spotted cusk-eel, *Chilara taylori*	<0.1	<0.01	1	0.12	1	0.42	0.31	0.05	<0.01
Pacific sanddab, *Citharichthys sordidus*	<0.1	<0.01	1	0.12	1	0.42	0.31	0.05	<0.01
Abraliopsis sp.	<0.1	<0.01	1	0.12	1	0.42	0.31	0.05	<0.01
Onychoteuthis sp. (2)	<0.1	<0.01	1	0.12	1	0.42	0.31	0.05	<0.01

Table 2 Quantitative prey composition of the blue shark (*Prionace glauca*) in the California Current. A total of 114 stomachs containing food and 44 without food were examined. Prey items are shown by decreasing GII value. See methods for descriptions of the measured values

Prey Species	W (g)	%W	N	%N	F	%F	GII	IRI	%IRI
Jumbo squid, *Dosidicus gigas*	5678.0	38.73	30	3.25	19	16.67	33.86	699.73	28.06
Gonatus spp.	117.8	0.80	108	11.71	52	45.61	33.56	570.97	22.90
Argonauta sp.	409.8	2.80	130	14.10	34	29.82	26.97	503.89	20.21
Flowervase jewell squid, *Histioteuthis dofleini*	2.2	0.01	82	8.89	33	28.95	21.86	257.88	10.34
Unidentified Euphausiidae	219.9	1.50	300	32.54	1	0.88	20.16	29.86	1.20
Ocean sunfish, *Mola mola*	2194.7	14.97	5	0.54	5	4.39	11.49	68.04	2.73
Octopoteuthis sp.	3.2	0.02	45	4.88	17	14.91	11.44	73.11	2.93
Histioteuthis spp.	0.7	<0.01	41	4.45	16	14.04	10.67	62.48	2.51
Pelagic red crab, *Pleuroncodes planipes*	660.1	4.50	58	6.29	7	6.14	9.78	66.27	2.66
Unidentified Teuthoidea	27.3	0.19	22	2.39	15	13.16	9.08	33.84	1.36
Skipjack tuna, *Katsuwonus pelamis*	1760.2	12.01	2	0.22	2	1.75	8.07	21.44	0.86
Unidentified Teleostei	221.7	1.51	11	1.19	10	8.77	6.63	23.73	0.95
Seven-arm octopus, *Haliphron atlanticus*	0.4	<0.01	14	1.52	11	9.65	6.45	14.68	0.59
Market squid, *Loligo opalescens*	0.2	<0.01	13	1.41	10	8.77	5.88	12.38	0.50
Vampire squid, *Vampyroteuthis infernalis*	19.6	0.13	10	1.08	8	7.02	4.76	8.55	0.34
Japetella sp.	0.1	<0.01	8	0.87	8	7.02	4.55	6.09	0.24
Pacific mackerel, *Scomber japonicus*	418.2	2.85	7	0.76	4	3.51	4.11	12.67	0.51
Spiny dogfish, *Squalus acanthias*	839.5	5.73	1	0.11	1	0.88	3.88	5.12	0.21
Soupfin shark, *Galeorhinus galeus*	497.3	3.39	2	0.22	2	1.75	3.10	6.33	0.25
Unidentified Cetacea	392.4	2.68	1	0.11	1	0.88	2.11	2.44	0.10
Luvar, *Luvarus imperialis*	366.9	2.50	1	0.11	1	0.88	2.01	2.29	0.09
Boreopacific gonate squid, *Gonatopsis borealis*	4.8	0.03	5	0.54	3	2.63	1.85	1.51	0.06
Unidentified Elasmobranchii	126.1	0.86	2	0.22	2	1.75	1.63	1.89	0.08
Pacific saury, *Cololabis saira*	74.8	0.51	5	0.54	2	1.75	1.62	1.85	0.07
Jack mackerel, *Trachurus symmetricus*	41.1	0.28	2	0.22	2	1.75	1.30	0.87	0.03
Opah, *Lampris guttatus*	175.4	1.20	1	0.11	1	0.88	1.26	1.14	0.05
Unidentified Invertebrate	21.6	0.15	2	0.22	2	1.75	1.22	0.64	0.03
Pacific sardine, *Sardinops sagax*	74.1	0.51	3	0.33	1	0.88	0.99	0.73	0.03
Sebastes spp.	102.8	0.70	1	0.11	1	0.88	0.97	0.71	0.03
Striped mullet, *Mugil cephalus*	100.0	0.68	1	0.11	1	0.88	0.96	0.69	0.03
Albacore tuna, *Thunnus alalunga*	44.8	0.31	1	0.11	1	0.88	0.75	0.36	0.01
Common tern, *Sterna hirundo*	36.6	0.25	1	0.11	1	0.88	0.71	0.31	0.01
Unidentified Cephalopoda	18.2	0.12	1	0.11	1	0.88	0.64	0.20	0.01
Pacific hake, *Merluccius productus*	0.01	<0.01	2	0.22	1	0.88	0.63	0.19	0.01
Bocaccio, *Sebastes paucispinis*	9.7	0.07	1	0.11	1	0.88	0.61	0.15	0.01
Abraliopsis sp.	0.1	<0.01	1	0.11	1	0.88	0.57	0.10	<0.01
Opisthoteuthis sp.	0.01	<0.01	1	0.11	1	0.88	0.57	0.10	<0.01
Onychoteuthis sp.	0.01	<0.01	1	0.11	1	0.88	0.57	0.10	<0.01

Gonatus spp. and octopus squid (*Octopoteuthis* sp.; Table S14). Thresher sharks were most concentrated within the SCB (93%), precluding robust diet comparisons between subregions. However, regardless of capture location, diet was dominated by the coastal pelagic species, northern anchovy and Pacific

Table 3 Quantitative prey composition of the thresher shark (*Alopias vulpinus*) in the California Current. A total of 157 stomachs containing food and 68 without food were examined.

Prey items are shown by decreasing GII value. See methods for descriptions of the measured values

Prey species	W (g)	%W	N	%N	F	%F	GII	IRI	%IRI
Nothern anchovy, *Engraulis mordax*	7596.8	25.74	1310	55.16	59	37.58	68.40	3040.14	58.49
Pacific sardine, *Sardinops sagax*	9262.2	31.38	614	25.85	42	26.75	48.49	1531.17	29.46
Pacific hake, *Merluccius productus*	6427.0	21.78	168	7.07	21	13.38	24.38	385.90	7.42
Pacific mackerel, *Scomber japonicus*	2314.8	7.84	57	2.40	20	12.74	13.27	130.49	2.51
Jack mackerel, *Trachurus symmetricus*	1795.5	6.08	13	0.55	9	5.73	7.14	38.01	0.73
Market squid, *Loligo opalescens*	30.2	0.10	45	1.89	13	8.28	5.93	16.53	0.32
Pacific saury, *Cololabis saira*	619.3	2.10	71	2.99	8	5.10	5.88	25.93	0.50
Unidentified Teleostei	115.2	0.39	18	0.76	14	8.92	5.81	10.24	0.20
Duckbill barracudina, *Magnisudis atlantica*	58.4	0.20	14	0.59	11	7.01	4.50	5.52	0.11
Shortbelly rockfish, *Sebastes jordani*	160.0	0.54	39	1.64	6	3.82	3.47	8.35	0.16
Scombridae	518.6	1.76	2	0.08	2	1.27	1.80	2.35	0.05
Pacific sanddab, *Citharichthys sordidus*	3.6	0.01	13	0.55	3	1.91	1.43	1.07	0.02
Pacific bonito, *Sarda chiliensis*	444.4	1.51	1	0.04	1	0.64	1.26	0.99	0.02
Barracudinas, Paralepididae	76.9	0.26	4	0.17	2	1.27	0.98	0.55	0.01
Topsmelt, *Atherinops affinis*	63.2	0.21	2	0.08	2	1.27	0.91	0.38	0.01
Unidentified Teuthoidea	26.4	0.09	2	0.08	2	1.27	0.84	0.22	<0.01
Jumbo squid, *Dosidicus gigas*	0.1	<0.01	1	0.04	1	0.64	0.39	0.03	<0.01
Unidentified Crustacea	0.1	<0.01	1	0.04	1	0.64	0.39	0.03	<0.01

sardine (Tables S15 and S16). Although the differences between subregions were not significant for either of the diversity indices, several trends were apparent (Table S1). Rarefied diet richness tended to be greater within the SCB for all three species (Table S1). The same held true for Simpson diversity for mako and thresher sharks. Blue sharks, on the other hand, had higher Simpson diversity beyond the SCB. Sørensen similarity in diets between subregions was highest for blue sharks, followed by mako, then thresher (Table S2). In contrast, SMH similarity exhibited the opposite pattern, being highest for thresher sharks, followed by mako, then blue (Table S2). ANOSIM results indicate significant differences in diet between subregions for each of the three species (Table 4). Likewise, longitude, which could be considered a proxy for a distinction between nearshore and offshore subregions, emerged as an important variable in the regression tree analysis (Fig. 4).

Results by sex

Comparisons between sexes were not statistically significant for any of the diversity indices. Sørensen

similarity in diets between the sexes was highest for threshers, followed by makos, then blues, although all values were similar in magnitude (Table S2). SMH similarity between sexes was high for both mako and thresher, but relatively low for blue sharks. ANOSIM results also indicated a lack of significant differences in diet between the sexes (p=0.131) (Table 4). None of the regression trees selected sex as an important variable structuring shark diet. Given these results, we did not calculate by-sex indices of prey importance.

Discussion

Our findings for the mako shark are generally consistent with the brief report by Hanan et al. (1993) and results from the Atlantic that found coastal teleosts and squid dominated mako diets (Stillwell and Kohler 1982). While larger mako sharks may occasionally feed on marine mammals (PFMC 2003), in this study a relatively small mako (137 cm FL) fed on a short-beaked common dolphin. For blue sharks, our results provide a more detailed and different view of their diets in the CCLME. In previous studies, cephalopods were

Table 4 ANOSIM results (using a square-root transformed Bray-Curtis matrix) comparing diet among species, size classes, fishing seasons, subregions, and sexes. These results are based on number of prey taxa and include all possible prey categories

Variable	Comparison	R-value	p-value
Among species	Among all 3 species	0.14	<0.001
	Mako-Blue	0.082	<0.001
	Mako-Thresher	0.12	<0.001
	Blue-Thresher	0.278	<0.001
Among fishing seasons	Averaged over all 3 species	0.086	0.001
	Blue	0.224	< 0.001
	Mako	0.022	0.013
	Thresher	0.148	<0.001
Among size classes	Averaged over all 3 species	0.03	<0.001
	Blue	0.028	<0.001
	Mako	0.033	<0.001
	Thresher	0.023	0.054
Between subregions	Averaged over all 3 species	0.07	<0.001
	Blue	0.14	0.002
	Mako	0.031	0.037
	Thresher	0.112	0.024
Between sexes	Averaged over all 3 species	0.006	0.131
	Blue	−0.003	0.509
	Mako	0.013	0.018
	Thresher	−0.005	0.645

Fig. 4 Regression tree based on all prey items by number

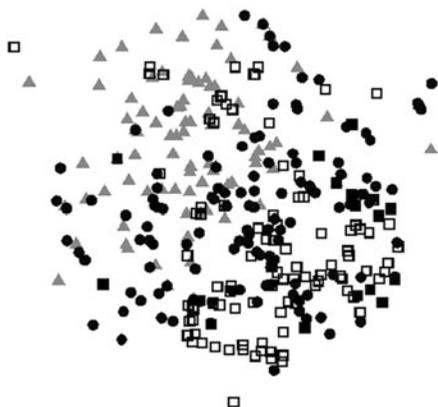Error : 0.875 CV Error : 0.898 SE : 0.0176
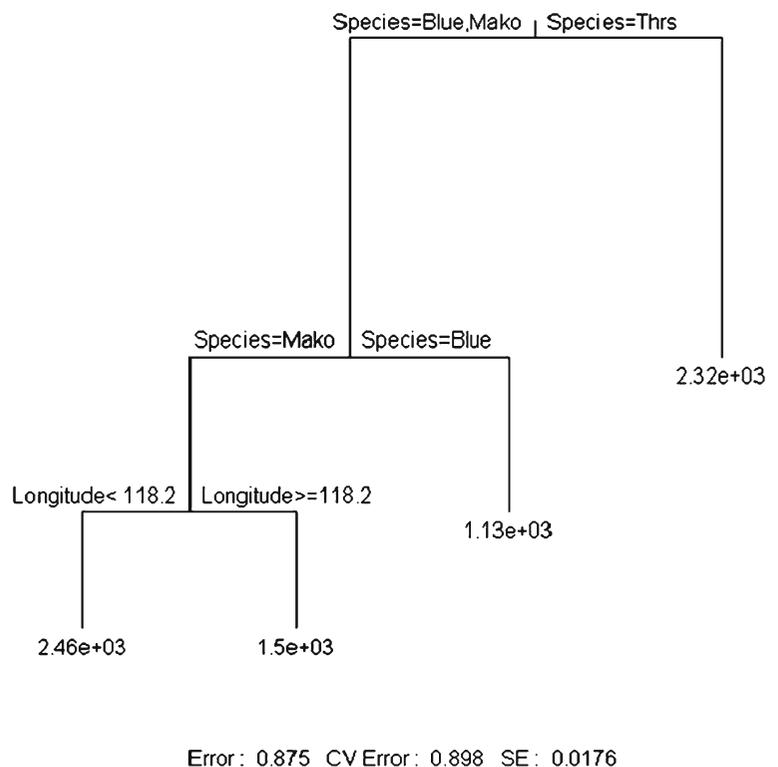
Fig. 5 MDS plot for diet by species. Mako sharks are represented by *black dots*, blue sharks by *grey triangles*, thresher sharks by *white squares*. The stress level for the 2-D ordination was 0.01

present but teleosts and crustaceans were consistently more important (Tricas 1979; Brodeur et al. 1987; Harvey 1989). Northern anchovy, an important prey item in past studies, was not detected in this study and only a single anchovy was found in blue sharks sampled off northern Baja California, Mexico from 1995 to 1997 (Markaida and Sosa-Nishizaki 2010). Differences may be attributed to higher numbers of anchovy available to sharks in the California Current prior to 1990 (Barange et al. 2009). For the present study, both euphausiids and pelagic red crabs had relatively high rankings for both GII and IRI in blue shark diets because of the high number of prey; frequency of occurrence, however, was relatively low, suggesting that these species are likely consumed opportunistically and not a consistent part of the diet. Results for thresher sharks are similar to those of previous studies from the same area (Mearns et al. 1981; Preti et al. 2001; Preti et al. 2004) showing a predominance of northern anchovy, Pacific sardine and market squid. The consistency in diet composition across years and studies highlights the importance of coastal pelagic species to thresher shark diets in the CCLME.

An important difference between this and previous studies was the significance of jumbo squid in the diet of both blue and mako sharks. Jumbo squid was rare or of minimal importance in previous blue shark diet studies in California Current waters (Tricas 1979; Harvey 1989; Markaida and Sosa-Nishizaki 2010). Likewise, jumbo squid has not been reported in mako shark diets, excluding the study of Vetter et al. (2008) on predatory interactions between mako sharks and jumbo squid, which was based in part on a subset of these same stomachs.

The increase in importance of jumbo squid as prey for blue and mako sharks is likely linked to its recent range expansion in the CCLME (Field et al. 2007; Zeidberg and Robison 2007) that has potentially caused other significant changes in the local food web. While jumbo squid is clearly an important prey item for blue and mako sharks, it may also compete with these and other large pelagic species for resources. Analysis of jumbo squid stomach contents revealed a range of prey items including Pacific hake, northern anchovy and Pacific sardine (Field et al. 2007), which are particularly important in the diet of the thresher sharks as well as other pelagic fishes in the SCB (Mearns et al. 1981).

The combination of uni- and multivariate analyses points to a number of significant differences in diet among these three species. The ANOSIM and regression tree analyses indicated that species was the most significant factor distinguishing stomach samples. Additionally, MDS plots show a clear separation among the three species. BVSTEP analysis provided insights into which prey taxa contributed most to the overall variability in shark diets. The distinguishing combination of major prey for blue sharks included jumbo squid, *Argonauta* sp., flowervase jewell squid, and *Gonatus* spp. For mako sharks, a combination of jumbo squid, Pacific saury, Pacific mackerel, jack mackerel, Pacific sardine, and striped mullet contributed to the variability among species. For thresher sharks, the distinguishing prey included northern anchovy, Pacific sardine and Pacific mackerel. Despite the fact that all three sharks inhabit the same area and are captured simultaneously in the same fishery, they are apparently utilizing different resources and exhibiting niche separation.

Some insights into the niche separation among mako, blue, and thresher sharks can be gained through an examination of their vertical movement patterns. Electronic tagging data for sharks in the CCLME suggest that vertical movement patterns differ somewhat among these three species (Tricas 1979; Holts and Bedford 1993; Klimley et al. 2002; Sepulveda et al. 2004; Weng et al. 2005; Baquero 2006; Cartamil et al. 2010) and may help explain differences in their diets. Sepulveda et al. (2004) studied both vertical movement patterns and feeding events of juvenile mako sharks in the SCB and found this species primarily occupied (80% of time recorded) upper mixed layer waters (<12 m) with occasional dives to below 100 m during the day. One mako preyed upon Pacific

saury at depth and several fed on epipelagic Pacific sardine (Sepulveda et al. 2004). Interestingly, Pacific saury and Pacific sardine accounted for the second and third most important prey of makos in the present study based on the GII. Diet data for blue sharks reveals the importance of cephalopods, many of which are associated with the deep scattering layer (DSL), including jumbo squid, *Gonatus* spp. and *Histioteuthis* spp. Foraging within the DSL is consistent with the vertical movement patterns of blue sharks (Tricas 1979; Carey and Scharold 1990; Weng et al. 2005). During the day when the DSL is at greater depths, blue sharks make regular vertical excursions to a depth consistent with the DSL before returning to the surface, presumably to thermally recharge in warmer surface waters (Carey and Scharold 1990; Weng et al. 2005). Similar to the vertically migrating DSL, some blue sharks occupy shallower depths during the night (Sciarrotta and Nelson 1977; Carey and Scharold 1990; Weng et al. 2005). For thresher sharks, the diet consists primarily of small schooling epipelagic fish, in addition to species that are found in midwater or demersal habitats, such as Pacific hake, or fish species associated with the DSL (Barracudinas). Tracking studies conducted in the CCLME (Baquero 2006; Cartamil 2009) suggest that foraging occurs during the day and reveal a range of daytime vertical movement patterns for subadult and adult thresher sharks. On some days, animals remained primarily above the thermocline, while on others the majority of the day was spent below the thermocline. Although vertical movement patterns and diet among all three species overlap to some degree, information presented here suggests differences in habitat use reflect the differential feeding ecology of mako, blue, and thresher sharks.

Horizontal movement patterns may also help to explain some of the distinctions in diets among mako, blue and thresher sharks. Regional prey availability may vary depending upon a number of factors, including distance from shore, proximity to islands, sea mounts or other bathymetric features, as well as local biological or physical conditions such as chlorophyll-*a* levels, water clarity and thermocline depth. A number of studies have examined the movement patterns of mako (Holts and Bedford 1993; Klimley et al. 2002; Sepulveda et al. 2004; Vetter et al. 2008), blue (Sciarrotta and Nelson 1977; Carey and Scharold 1990; Klimley et al. 2002) and thresher sharks (Baquero 2006; Cartamil 2009; Cartamil et al. 2010) in the SCB. For mako and blue

sharks, horizontal movements include both onshore-offshore and alongshore movements (Klimley et al. 2002; Weng et al. 2005; Vetter et al. 2008) and short-distance tracks remaining within the SCB (Sciarrotta and Nelson 1977; Holts and Bedford 1993; Sepulveda et al. 2004). Many pelagic shark species, including mako and blue sharks, exhibit different vertical behavior and may encounter different prey types in offshore relative to nearshore habitats (Boustany et al. 2002; Weng et al. 2005; Vetter et al. 2008; Stevens et al. 2010). Thresher sharks, on the other hand, remain more coastally oriented and their movements are predominately alongshore (Baquero 2006; Cartamil 2009; Cartamil et al. 2010). Even though broad-scale movement patterns show some differences among the three species, samples collected in the present study overlapped in space (Fig. 1), suggesting that the horizontal distribution alone cannot explain dietary differences among species. Within-species comparisons for mako and blue sharks, however, revealed significant subregional differences in diet. Important prey items for mako sharks beyond the SCB included offshore species such as Pacific pomfret and Pacific saury, whereas coastal species like Pacific sardine and striped mullet were more important in diets of mako sharks collected within the SCB. A study of blue sharks in the North Atlantic detected more cephalopods in sharks caught offshore, while bluefish (*Pomatomus saltatrix*), clupeids and gadids were more common in stomachs collected nearshore (Kohler 1988). Similarly, we found jumbo squid, *Gonatus* spp., and octopus squid (*Octopoteuthis* spp.) were most important for blue sharks collected offshore. Neonate and small juvenile thresher sharks (<120 cm FL) primarily occupy habitat over the continental shelf while subadults and adults preferentially inhabit waters off the shelf (Cartamil 2009; Cartamil et al. 2010). Unfortunately, the lack of small threshers and the low sample sizes of thresher sharks from beyond the SCB in this study precluded a subregional comparison.

Temporal variation in diets was also apparent for each species investigated. The fluctuations among fishing seasons may reflect oceanographically-driven variation in prey availability. Thresher shark diet has been shown previously to vary with oceanographic conditions, with higher diversity during El Niño in contrast with La Niña conditions (Preti et al. 2004). Within a season, temporal patterns in prey occurrence may also be reflected in the diets of these opportunistic predators. For example, 85% of the striped mullet in

mako stomachs occurred in samples collected during October and November. This is the time of year when striped mullet undertake fall spawning migrations, leaving coastal and estuarine habitats for open waters (Eschmeyer et al. 1983). Providing support for this idea was the occurrence of a gravid striped mullet in a mako stomach collected during the fall. Inferences based on this study, however, are limited by modest sample sizes by fishing season limiting robust quantitative analyses between or within seasons.

Ontogenetic feeding shifts in mako and blue sharks showed that smaller sharks had lower diet richness and evenness relative to larger individuals, suggesting that diet breadth expanded with size for both species. Similarly, for studies in the North Atlantic, Stillwell and Kohler (1982) found that mako shark diet expanded with size, although Kohler (1988) found no ontogenetic dietary shift for blue sharks. Size is known to be a key factor in diet diversity for a number of other shark species (Klimley 1985; Ebert 2002; Bethea et al. 2004), and the observed increase in diet richness is likely linked to a number of factors, including an increase in absolute swimming speed and mouth size as well as both an expansion of their vertical and geographic range (Lowe et al. 1996). Additional samples collected over a broader range of sizes will improve interpretation of ontogenetic shifts in diet across these species. In contrast, diets of the two different size classes of thresher sharks were similar. This may be an artifact of the smaller range of sizes for sampled thresher sharks with no representation of neonates or small juveniles, or it may be due to the specialized feeding mode of threshers. Other types of pelagic prey that are solitary or form looser schools may be more difficult to stun with their tail than the anchovy, sardine, hake and market squid that dominate their diet.

Management implications

Results of this study provide a detailed, quantitative evaluation of the diets of these three shark species in the CCLME. This new information on predator–prey relationships will aid researchers as assessment approaches shift from single species to ecosystems, especially for species of commercial importance. The more holistic approach associated with ecosystem-based fishery management is complex and has multiple elements, including understanding both top-down and bottom-up effects on food webs, better defining

essential habitat, and identifying the impacts of climate change on populations in order to more effectively aid in the management of both predators and prey (EPAP 1999; Levin et al. 2009).

There are a number of prey species found in the sharks' diets that are actively managed or monitored in the CCLME (PFMC 2009b). Pacific sardine, Pacific mackerel, northern anchovy and market squid were four important prey types identified in this study and they account for a large percentage of landings (by weight) and market value in California (CDFG 2009) with the majority of landings and revenue supported by sardine and market squid, respectively (PFMC 2009b). In managing coastal pelagic species (CPS) there is an increased effort to consider the importance of these commercially important fish and cephalopods as forage base to a range of predators including those that do not support fisheries, such as birds and mammals (PFMC 2009b). Currently there is a minimum biomass threshold of 150,000 mt for sardine and 18 200 mt for Pacific mackerel below which fishing is not allowed. The decision rule to terminate fishing at the threshold biomass is linked to the importance of these species as forage (PFMC 2009b). There is currently no minimum biomass threshold for the most valuable CPS, market squid. While market squid were not highly ranked as a diet item for any individual species, they were found in the stomachs of all three sharks, and the cumulative consumption may need to be considered if a threshold is considered for this species. Better data on the relative importance of forage species will advance efforts to determine minimum biomass thresholds and has recently been identified as a research need in the CPS management plan (PFMC 2009b).

As key predators, sharks exert top-down control with strong potential to affect marine ecosystems. The focus of the majority of research on top-down effects with sharks in recent years has been on the cascading effects of reductions in shark populations (Ferretti et al. 2010). Within the CCLME specifically, a reduction in top predators has been suggested to have contributed to the expansion of the jumbo squid (Zeidberg and Robison 2007), although there is some controversy about whether this is the case (Watters et al. 2008). Additional data are needed to determine the importance of top-down effects of mako and blue sharks on the jumbo squid range expansion. For commercially important prey species, the thresher

shark is the most likely to exert top-down control. Thresher shark populations in the CCLME appear to be increasing after overfishing-induced declines in the early 1980s, and consequently their ecological impact on their prey may be increasing (PFMC 2003). Information on trophic interactions may therefore help elucidate how predator populations affect their prey.

In addition to providing insight into trophic interactions, diet data provide an improved understanding of essential fish habitat. Essential fish habitat is defined as those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity (Benaka 1999). An improved understanding of essential fish habitat can help identify temporal and spatial patterns in predator distribution linked to bottom-up effects. For example, the DSL appears to be more important to the blue shark than either the mako or thresher shark based both on diet and on vertical movement patterns. Based on data collected over the past 57 years, the oxygen minimum zone in the SCB appears to be shoaling (Vetter et al. 2008; McClatchie et al. 2010). While many DSL-associated organisms, including jumbo squid, are hypoxia-tolerant (Childress 1971; Sanders and Childress 1990; Gilly et al. 2006), low oxygen concentrations can restrict the movements of active predators (Carey and Robison 1981; Prince and Goodyear 2006). Consequently, a shallow oxygen minimum zone may reduce forage opportunities for blue sharks more than those for the other two species which have a stronger reliance on species linked to the mixed layer.

A better understanding of trophic webs will also advance efforts to predict the impact of climate change in the CCLME. The CCLME is subject to considerable environmental variability over temporal scales from a few years (El Niño Southern Oscillation, ENSO) to decades (Pacific Decadal Oscillation, PDO), and climate-linked population variability differs among the commercially important CPS species (Chavez et al. 2003; PFMC 2009b). For example, anchovy and market squid landings have shown marked declines during El Niño periods while sardine and mackerel have not. In comparison to during El Niño, the PDO has the opposite effect on sardine and anchovies, although less well defined. During the positive PDO when temperatures are warmer, sardine landings increase while anchovy landings decrease (Chavez et al. 2003; Takasuka et al.

2008). Changes in prey abundance may have serious impacts on foraging success for specialists such as the thresher sharks relative to other generalists such as the blue and mako shark. In El Niño years for example, thresher sharks would likely be more impacted by the overall reduction in anchovy. Correspondingly, we found that during the latter phase of the 1998 El Niño, thresher sharks fed on a larger number of prey taxa than during the 1999 La Niña event (Preti et al. 2004). The broader implications of these changes in diet remain to be determined but may indicate that sharks must travel farther to forage or may target less desirable prey. Better information is needed on the diets of all species over longer time periods, particularly during large-scale climactic conditions such as ENSO or PDO events.

A major source of fishing mortality for blue sharks in the CCLME is incidental bycatch in the California DGN Fishery, which targets swordfish (Hanan et al. 1993). The ratio of blue shark to swordfish catch was estimated to average approximately 1.1:1 for the years 1990 to 1994, and the majority of sharks are discarded dead (Holts et al. 1998). Whereas DGN gear is typically considered passive gear, the fish and sharks trapped early during a set may actually attract additional sharks to the nets where they ultimately become entangled in the process of feeding. The occurrence of fresh chunks in 37 blue shark stomachs, including a piece of net in the mouth of a skipjack tuna, suggests that blue sharks are feeding on prey in the nets. This appears to be less of a concern for mako and thresher sharks; only one mako stomach contained obvious evidence of net-feeding. Opportunistic foraging by blue sharks on entangled prey may contribute to their high bycatch rates in this fishery. Understanding the shark's behavior in relation to the nets may help to develop measures to reduce their bycatch.

Information on foraging ecology is critical to ecosystem-based management. This study is a good first step to better understanding the diets and niche overlap of blue, mako and thresher sharks in the CCLME, however there is always a need for additional information as climatic changes occur and/or different species or size classes move into an area. Feeding studies provide a window into the lives of marine predators that are nearly impossible to observe and should be considered integral to long-term, ecosystem sampling programs.

References

Assis CA (1996) A generalized index for stomach contents analysis in fish. Sci Mar 60(2–3):385–389

Bakun A (2006) Wasp-waist populations and marine ecosystem dynamics: navigating the 'predator pit' topographies. Prog Oceanogr 68:271–288

Baquero AB (2006) Horizontal and vertical movements of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. Dissertation. University of San Diego

Barange M, Coetzee J, Takasuka A, Hill K, Gutierrez M, Oozeki Y, Lingen CVD, Agostini V (2009) Habitat expansion and contraction in anchovy and sardine populations. Prog Oceanogr 83(1–4):251–260

Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. J Anim Ecol 78:699–714

Bedford DW (1987) Shark management: a case history of the California pelagic shark and swordfish fishery. In: Cook S (ed) Sharks: an inquiry into biology, behavior, fisheries, and use. Oregon State University Extension Service, Corvallis, pp 161–171

Benaka LR (1999) Fish habitat: essential fish habitat and rehabilitation, American fisheries society symposium 22, Bethesda

Bethea DM, Buckel JA, Carlson JK (2004) Foraging ecology of the early life stages of four sympatric shark species. Mar Ecol Prog Ser 268:245–264

Bizzarro JJ, Robinson HJ, Rinewalt CS, Ebert DA (2007) Comparative feeding ecology of four sympatric skate species off central California, USA. Environ Biol Fish 80:197–220

Boustany AM, Davis SF, Pyle P, Anderson SD, LeBoeuf BJ, Block BA (2002) Expanded niche for white sharks. Nature 415:35–36

Bowen SH (1996) Quantitative description of the diet. In: Murphy BR, Willis DW (eds) Fisheries techniques. American Fisheries Society, Bethesda, pp 513–532

Brodeur RD, Lorz HV, Pearcy WG (1987). Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979-1984. NOAA Tech Rep NMFS 57

Carey FG, Robison BH (1981) Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fish Bull 79:277–292

Carey FG, Scharold JV (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. Mar Biol 106:329–342

Cartamil D (2009) Movement patterns, habitat preferences, and fisheries biology of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. Dissertation, University of California

Cartamil D, Wegner NC, Aalbers S, Sepulveda CA, Baquero A, Graham JB (2010) Diel movement patterns and habitat preferences of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. Mar Freshwat Res 61:596–604

Casey JG, Kohler NE (1992) Tagging studies on the shortfin mako (*Isurus oxyrinchus*) in the Western North Atlantic. Aus J Mar Freshwat Res 43:45–60

CDFG (2009) California commercial landings data for 2000–2008. http://www.dfg.ca.gov/marine/research.asp. Accessed 8/1/10KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth

Chavez FP, Ryan J, Lluch-Cota SE, Niquen M (2003) From anchovies to sardine and back: multidecadal change in the Pacific Ocean. Science 299:217–221

Childress J (1971) Respiratory adaptations to the oxygen minimum layer in the bathypelagic mysid *Gnathophausia ingens*. Biol Bull 141:109–121

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Colwell RK (2009) EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. user's guide and application published at: http://purl.oclc.org/estimates

Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85:2717–2727

Compagno LJV (2001) Sharks of the world: an annotated and illustrated catalogue of sharks species known to date. Bullhead, mackerel and carpet sharks. Heterodontiformes, lamniformes and orectolobiformes. Food and Agriculture Organization species catalogue, Vol 2. FAO, Rome

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can J Fish Aquat Sci 54:76–738

Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon LJ, Verheye HM (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J Mar Sci 57:603–618

Ebert DA (2002) Ontogenetic changes in the diet of the sevengill shark (*Notorynchus cepedianus*). Mar Freshwat Res 53:517–523

EPAP (1999) Ecosystem-based fishery management: a report to Congress by the Ecosystem Principles Advisory Panel US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Washington DC

Eschmeyer WN, Herald ES, Hammann H (1983) A field guide to Pacific coast fishes of North America. Houghton Mifflin, Boston

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns in ecosystem consequences of shark declines in the ocean. Ecol Lett 13:1055–1071

Ferry LA, Cailliet GM (1996) Sample size and data analysis: are we characterizing and comparing diet properly? In: MacKinley D, Shearer K (eds) Feeding ecology and nutrition in

fish. International Congress of the Biology of Fishes, American Fisheries Society, San Francisco, CA, 14–18th July 1996, pp 71–80

Ferry LA, Clark SL, Cailliet GM (1997) Food habits of spotted sand bass (*Paralabrax maculofasciatus*, Serranidae) from Bahia de Los Angeles, Baja California. Bull South Calif Acad Sci 96(1):1–21

Field JC, Baltz K, Phillips AJ, Walker WA (2007) Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. Calif Coop Oceanic Fish Invest Rep 48:131–146

Gelsleichter J, Musick JA, Nichols S (1999) Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Carcharhinus obscurus* Atlantic sharp-nose shark, *Rhizoprionodon terranovae* and the sand tiger, *Carcharias taurus*, from the Northeast Atlantic Ocean. Environ Biol Fish 54:205–217

Gilly WF, Markaida U, Baxter CH, Block BA, Boustany A, Zeidberg L, Reisenbichler K, Robison B, Bazzino G, Salinas C (2006) Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. Mar Ecol Prog Ser 324:1–17

Hanan DA, Holts DB, Coan AL Jr (1993) The California drift gill net fishery for sharks and swordfish, 1981–1982 through 1990–91. Calif Dep Fish Game Fish Bull 175:1–95

Harvey JT (1989) Food habits, seasonal abundance, size, and sex of the blue shark, *Prionace glauca*, in Monterey Bay, California. Calif Fish Game 75(1):33–44

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23(4):202–210

Holts DB, Bedford DW (1993) Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the Southern California Bight. Aust J Mar Freshwat Res 44:901–909

Holts DB, Julian A, Sosa-Nishizaki O, Bartoo NW (1998) Pelagic shark fisheries along the west coast of the United States and Baja California, Mexico. Fish Res 39:115–125

Holts DB, Wilson C, Lowe CG (2001) Blue Shark. In: Leet SW, Dewees CM, Klingbeil R, Larson EJ (eds) California's Living Marine Resources: A Status Report. University of California Agriculture and Natural Resources, Davis, pp 342–344

Hurtubia J (1973) Trophic diversity measurement in sympatric predatory species. Ecology 54(4):885–890

Klimley AP (1985) The aerial distribution and autecology of the white shark (*Carcharodon carcharias*), off the west coast of North America. Mem South Calif Acad Sci 9:15–40

Klimley AP, Beavers SC, Curtis TH, Jorgensen SJ (2002) Movements and swimming behavior of 3 species of sharks in La Jolla Canyon, California. Environ Biol Fish 63:117–135

Kohler NE (1988) Aspects of the feeding ecology of the blue shark, *Prionace glauca* in the Western North Atlantic. Dissertation, University of Rhode Island

Kohler NE, Turner PA, Hoey JJ, Natanson LJ, Briggs R (2002) Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. Int Comm Conserv Atl Tunas 54(4):1231–1260

Levin PS, Fogarty MJ, Murawski SA, Fluharty D (2009) Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. PLoS Biol 7(1):e1000014. doi:10.1371/journal.pbio.1000014

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environ Biol Fish 47:203–211

Magurran AE (2004) Measuring biological diversity. In: Blackwell, Oxford

Markaida U, Sosa-Nishizaki O (2010) Food and feeding habits of the blue shark *Prionace glauca* caught off Ensenada, Baja California, Mexico, with a review on its feeding. J Mar Biol Assoc UK 90:977–994

McClatchie S, Goericke R, Cosgrove R, Auad G, Vetter R (2010) Oxygen in the Southern California Bight: multi-decadal trends and implications for demersal fisheries. Geophys Res Lett 37:L19602

Mearns AJ, Young DR, Olson RJ, Schafer HA (1981) Trophic structure and the cesium-potassium ratio in pelagic ecosystems. Calif Coop Oceanic Fish Invest Rep 22:99–110

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846–1850

Nakano H (1994) Age, reproduction and migration of blue shark in the North Pacific Ocean. Bull Natl Res Inst Far Seas Fish 31:141–256

Oksanen J, Blanchet F, Kindt R, Legendre P, O'Hara RG, Simpson G, Solymos P, Stevens MH, Wagner H (2010) Vegan: community ecology package. R package version 1.17-0 Accessible online: http://CRAN.R-project.org/package=vegan

PFMC (2003) Fishery management plan and environmental impact statement for U.S. West Coast fisheries for highly migratory species. NOAA award No. NA03NMF4410067. Pacific Fishery Management Council, Portland

PFMC (2009a) Status of the U.S. West Coast fisheries for highly migratory species through 2008. Stock assessment and fishery evaluation

PFMC (2009b) Status of the Pacific coast coastal pelagic species fishery and recommended acceptable biological catches: stock assessment and fishery evaluation 2009

Pinkas L, Oliphant MS, Iverson ILK (1971) Food habits of albacore, bluefin tuna, and bonito in California waters. Calif Dep Fish Game Fish Bull 152:1–105

Preti A, Smith SE, Ramon DA (2001) Feeding habits of the common thresher (*Alopias vulpinus*) sampled from the California-based drift gill net fishery, 1998–99. Calif Coop Oceanic Fish Invest Rep 42:145–152

Preti A, Smith SE, Ramon DA (2004) 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. Calif Coop Oceanic Fish Invest Rep 45:118–125

Prince ED, Goodyear PC (2006) Hypoxia-based habitat compression of tropical pelagic fishes. Fish Oceanogr 15:451–464

R Development Core Team (2010) R: a language and environment for statistical computing. R foundation for statistical computing. Vienna, Austria. http://www.R-project.org

Sanders NK, Childress JJ (1990) Adaptations to the deep-sea oxygen minimum layer: oxygen binding by the hemocyanin of the bathypelagic mysid, *Gnathophausia ingens* Dohrn. Biol Bull 178:286–294

Sciarrotta TC, Nelson DR (1977) Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. Fish Bull 75(3):519–528

Sepulveda CA, Kohin S, Chan C, Vetter R, Graham JB (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. Mar Biol 145:191–199

Smith SE, Aseltine-Neilson D (2001) Thresher Shark. In: Leet SW, Dewees CM, Klingbeil R, Larson EJ (eds) California's Living Marine Resources: A Status Report. University of California Agriculture and Natural Resources, Davis, pp 339–341

Smith SE, Rassmussen RC, Ramon DA, Cailliet GM (2008) Biology and ecology of thresher sharks (family: Alopiidae). In: Pikitch E, Camhi M (eds) Sharks of the open ocean. Blackwell Publishing Ltd., Oxford, pp 60–68

Stevens JD (1983) Observations on reproduction on the shortfin mako, *Isurus oxyrinchus*. Copeia 1983:126–130

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476–494

Stevens JD, Bradford RW, West GJ (2010) Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks off eastern Australia: depth behaviour, temperature experience and movements. Mar Biol 157:575–591

Stillwell CE, Kohler NE (1982) Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the Northwest Atlantic. Can J Fish Aquat Sci 39:407–414

Takasuka A, Oozeki Y, Kubota H, Lluch-Cota SE (2008) Contrasting spawning temperature optima: why are anchovy and sardine regime shifts synchronous across the North Pacific? Prog Oceanogr 77:225–232

Taylor VB, Bedford DW (2001) Shortfin Mako Shark. In: Leet SW, Dewees CM, Klingbeil R, Larson EJ (eds) California's Living Marine Resources: A Status Report. University of California Agriculture and Natural Resources, Davis, pp 336–338

Therneau TM, Atkinson EJ (2004) The RPART package. Mayo Clinic, Section of Statistics, Rochester

Tricas TC (1979) Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. Fish Bull 77(1):175–182

Vetter R, Kohin S, Preti A, McClatchie S, Dewar H (2008) Predatory interactions and niche overlap between mako shark, *Isurus oxyrinchus*, and jumbo squid, *Dosidicus gigas*, in the California Current. Calif Coop Oceanic Fish Invest Rep 49:142–156

Watters GM, Olson RJ, Field JC, Essington TE (2008) Range expansion of the Humboldt squid was not caused by tuna fishing. Proc Natl Acad Sci USA 105:E5

Weng KC, Castilho PC, Morrissette JM, Landiera A, Holts DB, Schallert RJ, Goldman KJ, Block BA (2005) Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. Science 310:104–106

Yamaguchi A, Taniuchi T (2000) Food variation and ontogenetic dietary shifts of the star spotted dogfish *Mustelus manazo* at five locations in Japan and Taiwan. Fish Sci 66:1039–1048

Zeidberg LD, Robison BH (2007) Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. Proc Natl Acad Sci USA 104:12948–12950