



# Through the stomach of a predator: Regional patterns of forage in the diet of albacore tuna in the California Current System and metrics needed for ecosystem-based management



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## ABSTRACT

Foraging habits of predators can reveal patterns in prey ecology and guide ecosystem-based management by informing species interactions. This study describes the diet habits of albacore tuna in three regions (north, central, south) of the California Current System (CCS) and estimates the total predation mortality imposed on twenty prey taxa. The northern CCS was defined by predation on decapods, euphausiids, anchovy and hake. The central CCS was defined by predation on squid, hake and Pacific saury. The southern CCS was defined by predation on anchovy. We estimate North Pacific albacore consumed each year, on average, 54,000 mt of decapods and euphausiids, 43,000 mt of cephalopods, 84,000 mt of juvenile hake, 1600 mt of myctophids, 21,000 mt of juvenile sardine, 10,000 mt of juvenile rockfishes, almost 43,000 mt of Pacific saury, and over 107,000 mt of juvenile anchovy. While variability in predation certainly exists, this and prior studies show that diet habits of albacore are fairly stable through time. The northern CCS appears to be a more significant source of energy for albacore. When designing ecosystem-based approaches to the management of CCS-based fisheries, we recommend that the forage contribution of saury, hake and anchovy to the albacore population be considered.

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## 1. Introduction

Foraging habits reveal important details not only about predator dynamics, but also about the ecology of their prey. Of course, stomach content analysis is a rough observation tool: prey patterns must be interpreted through the lens of the biological sampling unit (the predator), and that sampling is far from random. However, for a great many forage species in the California Current System (CCS), reliable estimates of mortality from predation are lacking. As marine community management adopts more tenets of ecosystem-based management (EBM), we need empirical estimates of predator–prey linkages, predation mortality, and spatial patterns of energy flow for guidance. The aim of this paper is to describe the foraging ecology of juvenile North Pacific albacore (*Thunnus alalunga*) in three regions of the CCS through patterns of diet habits at medium spatial scales and small taxonomic scales. Estimates of annual biomass consumption by albacore for twenty categories of forage are provided, and aspects of prey ecology are discussed.

The diet habits of North Pacific albacore in the CCS have been described by five quantitative studies since 1949 (Bernard et al., 1985; Glaser, 2010; Iversen, 1962; McHugh, 1952; Pinkas et al., 1971). These studies failed to report or analyze data at the scale of the individual predator. Albacore diet in the CCS is diverse, and studies have identified northern anchovy (*Engraulis mordax*), Pacific saury (*Cololabis saira*), Pacific hake (*Merluccius productus*), euphausiids, and various species of cephalopod as significant prey. Of these studies, only Iversen (1962), Pinkas et al. (1971), and Glaser (2010) describe diet habits at high taxonomic resolution.

Juvenile albacore (ages 2–4, of 52–100 cm in fork length; Suda, 1966) undergo Pacific-wide migrations, entering the CCS in late spring or early summer and leaving in late fall (Childers et al., 2011; Otsu and Uchida, 1962). The appearance of juvenile albacore in CCS waters corresponds to the development of the frontal boundaries of the transition zone (Laurs and Lynn, 1977), waters defined by sharp gradients in temperature and salinity that are home to diverse and abundant predators and prey (Polovina et al., 2001). The transition zone chlorophyll front (TZCF) acts as a highway connecting the western North Pacific and eastern North Pacific, and albacore, sea turtles, sharks, and other predators follow the TZCF as it shifts northward from winter to summer (Polovina et al., 2001). During this movement of the TZCF, juvenile albacore move from the open ocean waters of the central North Pacific gyre

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into the productive upwelling zone of the CCS (Childers et al., 2011) shortly after many important forage species have spawned. Given the aggregation of oceanic predators along the TZCF and the common use of frontal regions as foraging grounds (Kirby et al., 2000), a better understanding of albacore foraging will shed light on patterns of competition and niche overlap in these regions.

## 2. Material and methods

### 2.1. Data collection

Diet habits of albacore were quantified through gut content analysis. Albacore stomachs ( $n = 371$ ) were collected aboard recreational ( $n = 188$ ) and commercial ( $n = 183$ ) fishing vessels during June–September 2005 and 2006. Location, date and albacore fork length (to the nearest cm) were recorded for stomachs collected aboard recreational vessels. Location and date were recorded for stomachs collected aboard commercial vessels. Sampling was undertaken from the ports of San Diego (California), Morro Bay (California), Half Moon Bay (California), Crescent City (California), Newport (Oregon), Garibaldi (Oregon), and Bainbridge Island (Washington). Locations of stomach collection occurred between 27°N to 57°N and between 10 and 800 km off the West Coast of the United States. Immediately following removal from the albacore, stomachs and their contents were preserved in a chest of dry ice or blast frozen and later stored in the laboratory at  $-11$  °C. Each stomach was thawed, its volume and weight measured (to the nearest 0.1 ml or g, respectively), cut open, its contents retained on brass sieves with mesh size of 0.3 mm, and the volume and weight of the empty stomach measured. Contents were stored in jars of 95% ethanol until sorted and identified.

### 2.2. Gut content analysis and descriptive statistics

Visual inspection was the primary method of identifying prey items. All organisms were identified to the highest possible taxonomic resolution. Organisms that could not be identified, whether due to a lack of reference material or digestion beyond the ability to identify characteristics, were classified as ‘unknown’ (unk). If sufficient tissue was available from an unknown organism, a sample was retained for genetic sequencing. Prey size (see below) was measured with digital calipers. For prey categories with fewer than five specimens per stomach, all specimens were measured. For prey categories with five or more specimens, a random subsample of five was measured.

Fishes were identified based on vertebral characteristics (Clothier, 1950), otoliths (Harvey et al., 2000), skull bones, and occasionally whole bodies. The number of specimens in a stomach was determined either by halving the number of paired structures (e.g., eyeball lenses, otoliths, operculi for rockfish (*Sebastes*)) or counting the number of singular structures (e.g., vertebral column, parasphenoid for saury, urostyle and basioccipital bones for sardine (*Sardinops sagax*) and anchovy). Prey fish length was estimated from one or more of the following measurements: 1) body length (fork length or standard length, depending on the norm for the species), 2) vertebral column length (hereafter, vertebral length), or 3) otolith width. Only whole vertebral columns were measured. The latter two measurements were used to calculate body length. If the vertebral column was measured, it was scaled to body length according to a ratio of 1.1 for anchovy, 1.3 for sardine, and 1.2 for saury. These ratios were calculated by measuring the total and vertebral lengths for no more than five full specimens of each species. Lacking whole specimens as reference for other species, a conservative ratio of 1.1 was used. Otolith width was converted to body length according to Harvey et al. (2000), and body length (mm) was converted to reconstituted (pre-digestion) mass (g) using species-specific allometric relationships from the literature (Clarke, 1986; Clothier, 1950; Froese and Pauly, 2013; Harvey et al., 2000; Wolff, 1984).

Cephalopods were identified using beak morphology (Clarke, 1986; Pinkas et al., 1971; and a reference collection at the Santa Barbara Natural History Museum). Numbers of cephalopods were counted by pairing upper and lower beak halves and counting the greater number of individual upper or lower beaks. The length of the rostrum of the lower beak (LRL) was measured. Squid are easily distinguishable from octopi based on the shape of the beak rostrum (Clarke, 1986), and therefore this was the lowest resolution possible for beaks for which species-level identification was not possible. The LRL of four species of squid (*Abroliaopsis* sp., *Doryteuthis opalescens*, *Gonatus* sp., and *Onychoteuthis borealijaponica*) fell within the ranges appropriate for published length–weight regressions (Wolff, 1984). The mean weight calculated thereby was applied to the other species of squid and octopi for which allometric relationships did not exist for the LRL size ranges of prey.

Crustaceans were identified by carapace morphology or eyeball morphology. Numbers were determined by halving the total number of eyeballs (which were most likely to resist digestion), or counting the number of carapaces or telsons. In the case of *Phronima sedentaria*, the number of gnathopods (divided by two) was used. Even small degrees of digestion rendered crustacean appendages difficult to characterize, thus eliminating one of the more effective ways of identifying species. All crustaceans found inside albacore stomachs were of the class *Malacostraca*, and with the exception of a few species that could be identified easily (*Pleuroncodes planipes* and *P. sedentaria*), most specimens were classified as Decapoda, Euphausiacea, Amphipoda, or Isopoda. These categories permitted discrete tests to distinguish partially digested remains. Decapods were identified by having two elongated, stalked eyeballs and lacking thoracic gills. Euphausiids were identified by having two rounded, stalked eyeballs and gills at the base of their thoracic limbs. Hyperiid amphipods were identified by having one large compound eye. Isopods were identified by having a dorso-ventrally flattened body. If the presence or absence of gills was not definitive to identify euphausiids from decapods, the crustacean was classified as an unknown malacostracan. Crustacean length was measured as the length of the carapace and telson, not including the rostrum (Isaacs et al., 1969). Wet weight and volume (water displacement) were measured to the nearest 0.1 g or mL and values for whole organisms were used to calculate mass of whole organisms and estimate the mass of partial organisms.

In addition to these three major categories of prey (fishes, cephalopods, and crustaceans), a few additional organisms were found inside stomachs. Six *Thaliacea* were recorded. Tens of copepods were found inside stomachs, although the frequency of occurrence was low. Given the small size of copepods and based on conclusions of other researchers (Pinkas et al., 1971), these copepods were assumed to be secondary prey ingested simultaneously with other items, and were therefore excluded from analysis. Small nematodes were common, but these intestinal parasites also were not classified as prey. Finally, many fishing vessels used live bait (sardine, anchovy, and occasionally Pacific mackerel), and bait was counted and measured but excluded from analyses. Bait was easily identified because a record of the bait used on each boat was kept, bait was of a nearly-uniform length (much larger than the real prey; Glaser, 2010), and bait was  $\leq 5\%$  digested.

For all prey categories, the numeric abundance ( $N$ ) and percent numeric abundance ( $\%N$ ), the mass ( $M$ ) and percent mass ( $\%M$ ), and frequency of occurrence ( $FO$ ) and percent frequency of occurrence ( $\%FO$ ) were calculated.  $N$  was the count of individual organisms in a prey category.  $M$  was the reconstituted mass of all organisms in a prey category.  $N$  and  $M$  were calculated for all stomachs, and as an average for each region of the CCS.  $FO$  is a binary measure of prey presence or absence and was calculated for individual stomachs and for daily sampling units (described below).

### 2.3. Species accumulation curves

While 371 stomachs were analyzed for this study, over 700 stomachs were collected during 2005 and 2006. Gut content analysis

was halted based on the results of species accumulation curves showing the sample size needed to describe fully the diversity of prey the albacore consumed. The number of new prey species discovered for each additional stomach analyzed was plotted, and the sample size at which the curve became asymptotic described the needed sampling effort (Thompson and Withers, 2003). Curves are means derived from shuffling 100 times the order in which stomachs were analyzed and calculating a new curve with each iteration. Curves were sensitive to the level of taxonomic resolution, and therefore four levels of aggregation were explored. First, the highest resolution for all identifiable prey categories ( $n = 59$ ) was analyzed. Second, ten species of *Sebastes* were aggregated into one *Sebastes* spp. category. Such an aggregation was considered because this is the first study of albacore diet to identify juvenile *Sebastes* to the species level using genetic sequencing. Given that past studies have not identified *Sebastes* species, and anticipating future studies may not employ genetic identification, this species curve provides guidance for sample size needed at this resolution. Third, 17 of 59 prey categories were represented by only one specimen, and the next level of aggregation re-classified those rare prey. These categories were incorporated into the next lowest taxonomic grouping. For example, *Bathyagonus pentacanthus*, a fish that occurred one time, was consolidated into the 'unknown fishes' category. Fourth, only 20 prey categories occurred in 5% of stomachs or more. To estimate how many stomachs were necessary to identify the most common prey in albacore diet, the final aggregation subsumed rare taxa (<5 %FO) into higher categories. For example, the occurrence of 26 individual *Argonauta argo*, a pelagic octopus, was moved into the category 'Octopus.' This final taxonomic aggregation was carried through in some of the data analysis to overcome difficulties posed by zero-inflated matrices. To determine whether enough samples were analyzed, the slope of the least squares regression line resulting from the number of species identified in the final four stomachs was tested against a slope of zero (ordinary least squares with a Student's t-test of the slope, R Statistical Software).

#### 2.4. Variability between individual predators and daily sampling units

Stomachs were analyzed individually and aggregated according to the date and location from which the sample was drawn (the daily sampling unit or DSU). Samples collected on the same day and in the same location were grouped into one DSU. Thus, this study overcomes a statistical shortfall of many diet studies of large pelagic predators. Although an individual stomach cannot be considered an independent sample of the prey environment if multiple stomachs were collected at the same time and place, by grouping stomachs according to DSU there is an independent unit of analysis and each stomach is a replicate. DSUs that contained fewer than five stomachs were not included in analyses that used DSU as a treatment.

Individual stomachs and DSUs were compared using 1) the reconstituted (pre-digestion) mass of contents in a stomach (g), 2) the total energy of contents in a stomach (kJ), and 3) the total protein of contents in a stomach (g). These values for individual stomachs were calculated as

$$M_R = \sum_i N_i \times \bar{M}_i \quad (1)$$

$$\text{energy} = \sum_i N_i \times \bar{M}_i \times \bar{ED}_i \quad (2)$$

$$\text{protein} = \sum_i N_i \times \bar{M}_i \times \bar{p}\bar{r}\bar{o}_i \quad (3)$$

where, for prey category  $i$ ,  $M_R$  is the reconstituted mass of gut contents,  $N$  is the number of prey specimens,  $\bar{M}$  is the mean reconstituted mass (g) of one organism,  $\bar{ED}$  is the mean energy density ( $\text{kJ g}^{-1}$ ) of one organism, and  $\bar{p}\bar{r}\bar{o}$  is the mean percent protein content of one organism. Energy density and protein values were obtained from the literature

**Table 1**

Energy density and percent protein values used to estimate energy and protein content of prey items in albacore stomach contents.

|                             | Prey category                 | Energy density ( $\text{kJ g}^{-1}$ ) | % protein |      |
|-----------------------------|-------------------------------|---------------------------------------|-----------|------|
| Cephalopods                 | <i>Abraliopsis</i> sp.        | 4.4                                   | 17.4      |      |
|                             | <i>Octopoteuthis</i> sp.      | 4.5                                   | 17.4      |      |
|                             | <i>Gonatus</i> spp.           | 6.4                                   | 13.7      |      |
|                             | <i>Doryteuthis opalescens</i> | 3.5                                   | 16.6      |      |
|                             | <i>O. borealijaponicus</i>    | 5.6                                   | 12.8      |      |
|                             | <i>Japetella heathi</i>       | 2.8                                   | 13.8      |      |
|                             | Octopus unknown               | 2.8                                   | 13.8      |      |
|                             | Squid unknown                 | 4.4                                   | 15.7      |      |
|                             | Crustaceans                   | Amphipod                              | 2.5       | 12.9 |
|                             |                               | <i>Phronima sedentaria</i>            | 2.5       | 12.9 |
| Decapod                     |                               | 3.2                                   | 12.9      |      |
| Euphausiid                  |                               | 3.1                                   | 12.9      |      |
| <i>Malacostraca</i> unknown |                               | 3.2                                   | 12.9      |      |
| Fishes                      |                               | <i>Sardinops sagax</i>                | 7.3       | 21.4 |
|                             | <i>Engraulis mordax</i>       | 6.7                                   | 13.8      |      |
|                             | <i>Merluccius productus</i>   | 5.9                                   | 14.5      |      |
|                             | Myctophid                     | 7.1                                   | 11.6      |      |
|                             | <i>Cololabis saira</i>        | 7.5                                   | 20.0      |      |
|                             | <i>Sebastes</i> spp.          | 4.2                                   | 18.6      |      |
|                             | Fishes unknown                | 6.4                                   | 19.2      |      |

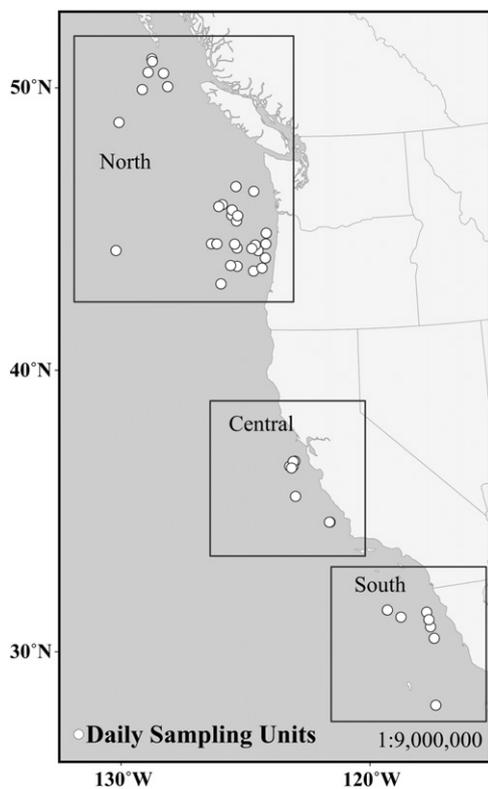
(Donnelly et al., 1993; Sidwell, 1980; see also Glaser, 2010) and are provided in Table 1.

The three metrics were compared univariately. For each of the 31 DSUs that contained five or more replicate stomachs, five stomachs were randomly chosen, resulting in 155 stomachs available for a balanced ANOVA using DSU as a treatment effect. The data do not meet assumptions of normality, therefore randomized ANOVAs were performed (Chippis and Garvey, 2007). First, an  $F$  statistic was calculated with data organized by DSU. Next, data were randomly shuffled between DSUs and a new, randomized  $F$  statistic was calculated. This randomization was performed 500 times, and the distribution of randomized  $F$  statistics was compared to the observed  $F$  statistic to assign a  $p$ -value.

#### 2.5. Spatial and temporal variability

Data collection fell into three well-defined regions in the CCS: a northern region, which included all stomachs collected north of 44° N latitude; a central region, which fell between 33° N and 43° N latitude (but which, practically, only included stomachs between 35° N and 38° N); and a southern region, which included all stomachs collected south of 33° N latitude (Fig. 1). These regions were opportunistic in that they were logical collection points from the ports of ship. Pinkas et al. (1971) used similar regional divisions of the CCS in their study of albacore diet during the late 1960s. These divisions also are relevant from a biogeographical standpoint insofar as the northern and southern regions have distinct biological communities and the central region is a transition zone (McGowan and Williams, 1973; Polovina et al., 2001). For eight select forage species, we mapped the distribution of foraging. The contribution (%) of a prey species to the total energy contents of a stomach was calculated for each stomach sampled, and those values were averaged across stomachs in a DSU.

A multivariate contingency analysis was performed on the numeric prey frequencies collected from all 371 stomachs to test for differences between prey categories and regions (Crow, 1981). To satisfy requirements of contingency analysis (no more than 20% of cells may contain an expected frequency of less than five), data were aggregated into categories defined by a cutoff of  $\geq 5$  %FO (as in the fourth level of aggregation outlined in the species accumulation curve section) with the added step of further aggregating *Japetella heathi* into the category 'Octopus.' These same aggregated categories (but disaggregating *J. heathi* from Octopus) were used to compare the biomass of prey categories consumed



**Fig. 1.** Distribution of Daily Sampling Units (DSUs) approximating albacore schools, where one DSU aggregates all albacore stomachs collected on the same day in the same location. Three sampling regions (north, central, south) are delineated.

in the three regions. Principal component analysis (PCA) tested for differences in reconstituted biomass of prey categories between regions, DSUs, and years.

## 2.6. Consumption of forage species

The bioenergetics model described in Glaser (2010) and Essington (2003) was used to calculate the daily energetic demand ( $\text{kJ kg}^{-1} \text{d}^{-1}$ ) of albacore ranging from 52 to 100 cm fork length. Briefly, daily energy demand was estimated from the sum of energy used in standard metabolism, active metabolism, reproduction, somatic growth, and that lost to assimilation. These values were estimated using, among others, parameters for average swimming speed, instantaneous mortality rates, length at age, and weight at age. Following the guidelines of Essington (2003), 90% confidence intervals for daily demand were estimated by 1000 Monte Carlo simulations that randomized the variables to which the model was sensitive (assimilation efficiency and parameters related to swimming speed and active metabolic rate). Observed energy intake (total energy value of gut contents) was calculated from stomach content data to compare with modeled values (Eq. (2)). Assuming stomach contents represented an eight-hour digestion period (Olson and Boggs, 1986), observed energy intake was multiplied by three to reflect feeding over a 24-hour period. Albacore weight (kg) was calculated from lengths of albacore collected in the field for diet analysis (Essington, 2003), and the total energetic content of a stomach was standardized by albacore weight.

Daily energy demand next was converted to a daily prey consumption rate (grams of prey per kg of albacore per day) by assuming a constant energy intake and multiplying demand by a weighted average energy density ( $6.2 \text{ kJ g}^{-1}$ ) of the prey consumed by albacore. Daily consumption rate was then multiplied by estimates of albacore biomass

in the CCS to calculate the biomass of forage species removed from the CCS. Monthly estimates of albacore biomass during 1966–2012 in the three regions of the CCS were calculated by the method outlined in Glaser (2011) but using updated stock assessment estimates of albacore numbers-at-age (ISC, 2014). Briefly,  $1^\circ \times 1^\circ \times \text{month}$  catch and effort data from voluntarily-submitted commercial logbooks (maintained by the Southwest Fisheries Science Center, NOAA) were standardized using a random forest regression tree (Breiman, 2001) to produce monthly estimates of catch-per-unit-effort (CPUE) in each region. The standardized CPUE time series was a relative index of abundance in the three regions in each month that albacore are present in the CCS. These standardized monthly indices were then applied to annual estimates of total juvenile albacore biomass in the North Pacific Ocean to produce regional, monthly estimates of the albacore population in the CCS.

Pacific-wide, annual estimates of numbers of albacore aged 2–4 were provided by the Albacore Working Group stock assessment (ISC, 2014); these numbers were then multiplied by the average age-specific weight of albacore to produce metric tons of albacore aged 2–4 in the North Pacific (age 2 = 3 kg, age 3 = 5.6 kg, age 4 = 8.7 kg). Because juvenile albacore are found either in the western or eastern North Pacific during summer and fall migrations, the Pacific-wide biomass of albacore was reduced to 40% of the total to reflect the proportion of the population in the CCS (Glaser, 2011). The estimates of albacore biomass were then multiplied by the number of days in the months April–November (244 total days). Note that this calculation does not mean one albacore spends 244 days per year in the CCS. Rather, the monthly CPUE indices already account for migration into and out of the CCS. A weighted daily consumption rate was estimated by calculating the daily consumption rates for albacore of ages 2, 3 and 4, then weighing the age-specific rate by the proportion of age-classes in the CCS (0.05, 0.65, and 0.30, respectively). Finally, the weighted daily consumption rate was multiplied by the daily biomass estimates of albacore to calculate a final estimate for the total prey biomass consumed by the juvenile albacore subpopulation in the CCS, in each of the three regions, over the period 1966–2012. See Glaser (2011) for a detailed accounting of methodology.

Consumption of forage species (mt) was estimated by multiplying the biomass consumed in a region by the proportion in the diet represented by a given forage species. In any given season, the biomass of a forage species consumed by albacore is not solely a function of the biomass of albacore, as assumed in these calculations. If the relative biomass of a forage species changes significantly, the proportion of that species in albacore diet also could change (*i.e.*, predator switching). However, for the vast majority of forage species considered here, estimates of biomass are not available. Furthermore, Glaser (2010) demonstrated that decadal variability in albacore diet is small (with Pacific hake being a notable exception). Thus, we assumed that the interannual variability in albacore biomass was one way to approximate the variability in predation mortality for a given prey species. Average annual consumption of a given forage species was therefore calculated over the period for which albacore biomass data were available (1966–2012).

Finally, estimates of diet diversity were made at the scale of a DSU. The number of different forage species in a given stomach was calculated (using no aggregation of categories), and this species richness metric was averaged over the stomachs in a DSU. GIS was used to count the number of different prey species in one square kilometer cells (to avoid overlap between DSUs) and spatially interpolate local values of unique prey species between DSUs. A natural neighbor interpolation method, which proportionally weighs overlapping regions of Voronoi polygons (Euclidean distance) based on centroids of DSUs, was used to maximize local support within sampling regions and in consideration of discrete, non-uniform sampling points (Bobach and Umlauf, 2006). Interpolation results were resampled to twenty kilometer cells to smooth the visualization surface. Prey species abundance was similarly

interpolated from normalized counts of prey per stomach averaged and aggregated by DSU ( $1 \leq x \leq 10$ ).

### 3. Results

The spatial and temporal distribution of sampling effort at the scale of DSU is shown in Fig. 1. During 2005, 17 DSUs and 106 individual albacore were sampled, and 29 DSUs and 265 albacore were sampled during 2006. From the northern region, 31 DSUs and 275 albacore were analyzed, eight DSUs and 45 albacore were analyzed from the central region, and seven DSUs and 51 albacore were analyzed from the southern region.

#### 3.1. Forage composition

Fifty-nine prey categories were discovered in 371 stomachs resulting in a total of 18,401 individual prey items and 21,367 g of reconstituted biomass (see Supplementary Table 1). Thirteen of the 20 prey categories that were found in 5% of stomachs or more were consumed in groups of fewer than 5 specimens per stomach (Table 2). Anchovy was the most commonly occurring prey species, occurring in 53% of all stomachs, followed by unknown squid (%FO = 29) and unknown malacostracans (%FO = 27). By mass, hake was the most consumed prey (%M = 30), followed by anchovy (%M = 23) and saury (%M = 20). Although significantly less numerically abundant than anchovy (%N = 27) or hake (%N = 19), saury (%N = 2) contributed high biomass because its mean weight (13 g) was much higher than other prey. Decapods were the third most numerically abundant category (%N = 13).

Fishes were the most abundant prey taxa. Anchovy was the most commonly consumed prey by number and frequency of occurrence (%N = 27, %FO = 53) and was consumed in all three regions. Pacific hake (%N = 19, %FO = 16) was confined to the northern and central regions. Pacific saury (%N = 2, %FO = 18) also was most commonly consumed in the northern region, although it was found occasionally in the central and southern regions. The family Myctophidae was represented by the species *Diaphus theta* (%N = 0.03, %FO = 1), *Stenobrachius leucopsaurus* (%N = 0.1, %FO = 3), and *Tarletonbeania crenularis* (%N = 0.02, %FO = 1). Unidentified myctophids (%N = 0.1, %FO = 6) were aggregated with these species, and were found

commonly in the northern region. This is the first study of albacore diet in the CCS to identify *Sebastes* (the genus of rockfishes) by species. All *Sebastes* were juveniles (mean length 14 mm), representing eight species and one species complex (*Sebastes wilsoni*, *Sebastes proriger*, and *Sebastes zacentrus*) identified by genetic sequencing. *Sebastes* were found throughout the three regions. Finally, sardine juveniles (%N = 3, %FO = 27) were commonly found in albacore stomachs also containing anchovy, although anchovy occurred in larger numbers. They were consumed throughout the three regions but were primarily in the southern region. Ten rarely-consumed fishes occurred in less than 5% of all stomachs. These categories (*B. pentacanthus*, *Anoptopterus nikparini*, *Atherinopsis californiensis*, *Trachurus symmetricus*, *Icichthys lockingtoni*, *Lestidiops ringens*, *Pleuronichthys decurrens* and *Pleuronichthys* sp., *Psychrolutidae*, *Scomber japonicus*, and *Syngnathus californiensis*) were included in the aggregate category 'unknown fishes' (%N = 2, %FO = 22) for statistical analysis.

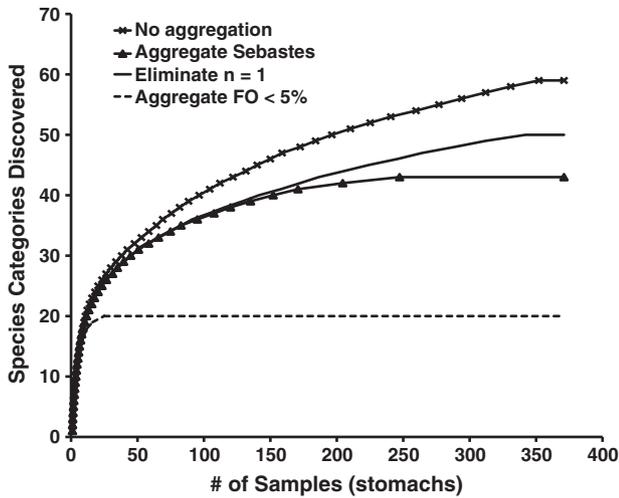
Crustaceans were abundant in number and commonly occurred as prey. Numerically, decapods (%N = 13, %FO = 14) and euphausiids (%N = 12, %FO = 20) were the third and fourth most commonly consumed prey across all taxa. However, when the mass of the organisms was taken into account (mean weight 0.1 g for decapods and euphausiids), their contribution to the total mass consumed dropped to 1.0%. While numerically abundant, the low mass and low energy density values of malacostracans make them insignificant contributors to overall albacore diet in near-shore CCS waters (Glaser, 2010). Decapods were found in four southern region stomachs but were absent entirely from the central region; they were significantly more common in the northern region. Similarly, while present in both the southern and central regions, euphausiids also were more commonly consumed in the northern region. Amphipods, including the species *P. sedentaria*, occurred frequently but in smaller numbers than decapods or euphausiids (%N = 1, %FO = 12.0 and %N = 1, %FO = 19, respectively). Finally, 1006 (%N = 5) unidentified malacostracans were found in 27% of all stomachs.

Of the squids, *Abraliopsis* sp. (either *Abraliopsis felis* or *Abraliopsis falco*) was by far the most commonly consumed prey (%N = 2, %FO = 26). This squid was also the smallest, with a mean reconstituted mass of 0.4 g. *Abraliopsis* was consumed throughout the three regions and in both years of sampling. *D. opalescens*, the commercially valuable California market squid, was the next most commonly consumed cephalopod (%N = 1, %FO = 9). Like all squid prey, this species was of juvenile sizes (7 g each). Although found in four stomachs in the northern region and once in the central region, *D. opalescens* was disproportionately consumed in the southern region. *Octopoteuthis* sp., the third most commonly consumed squid group (%N < 1, %FO = 12), is most likely *Octopoteuthis deletron* and not *Octopoteuthis sicula*, as described by Pinkas et al. (1971) (F. G. Hochberg, pers. comm.). Its consumption was distributed throughout all three regions. Gonatid squids, including the species *Gonatus pyro*, *Gonatus onyx*, *Gonatus californiensis*, and *Gonatopsis borealis*, were fairly common and distributed throughout the three sampling regions. *O. borealijaponica* (%N = 1, %FO = 19) was found in two stomachs in the southern region, but predominated in the northern region. Five remaining species of squid (*Vampyroteuthis infernalis*, *Moroteuthis robusta*, *Eucleoteuthis luminosa*, *Histioteuthis* sp., and *Mastigoteuthis dentata*) were aggregated for statistical analysis with 326 unknown individual squids.

Two species of octopus were identified: *J. heathi* (%N < 1, %FO = 7) and *A. argo* (%N < 1, %FO = 1). *J. heathi* was commonly found singly or in pairs inside stomachs, whereas *A. argo* was found in groups of between two and twelve. *J. heathi* was most commonly consumed in the northern region whereas *A. argo*, classified with unknown octopi for statistical analysis, were more evenly consumed across the three regions. In octopi, the lower rostral length is not a unit of measurement that can be converted to biomass (the rostrum angle is too blunt) but, subjectively, beaks were smaller than most squid beaks.

**Table 2**  
Average numbers of individual prey inside an albacore stomach.

|                      | Prey category               | Mean N per stomach         |     |
|----------------------|-----------------------------|----------------------------|-----|
| Cephalopods          | <i>Abraliopsis</i> sp.      | 4.6                        |     |
|                      | <i>Octopoteuthis</i> sp.    | 1.6                        |     |
|                      | <i>Gonatus</i> spp.         | 2.2                        |     |
|                      | <i>Loligo opalescens</i>    | 3.1                        |     |
|                      | <i>O. borealijaponica</i>   | 3.0                        |     |
|                      | <i>Japetella heathi</i>     | 1.5                        |     |
|                      | Octopus unknown             | 2.8                        |     |
|                      | Squid unknown               | 2.8                        |     |
|                      | Crustaceans                 | Amphipod                   | 2.6 |
|                      |                             | <i>Phronima sedentaria</i> | 3.5 |
| Decapod              |                             | 41.3                       |     |
| Euphausiid           |                             | 29.8                       |     |
| Malacostraca unknown |                             | 9.2                        |     |
| Fishes               | <i>Sardinops sagax</i>      | 6.2                        |     |
|                      | <i>Engraulis mordax</i>     | 25.3                       |     |
|                      | <i>Merluccius productus</i> | 57.9                       |     |
|                      | Myctophidae                 | 1.2                        |     |
|                      | <i>Cololabis saira</i>      | 5.0                        |     |
|                      | <i>Sebastes</i> spp.        | 6.3                        |     |
|                      | Fishes unknown              | 3.4                        |     |



**Fig. 2.** Species accumulation curves showing the necessary sample size needed to discover the number of species categories given different levels of aggregation. Data collected from juvenile albacore foraging in the CCS during 2005 and 2006.

### 3.2. Species accumulation curves

This study analyzed a sufficient sample size to describe diet habits at the lowest level of taxonomic aggregation or highest level of taxonomic resolution here analyzed (Fig. 2). With no taxonomic aggregation beyond that constrained by accurate identification, 59 prey categories were described by stomach sample #352 out of 371 (slope not significantly different from 0,  $p > 0.05$ ). The first level of aggregation, combining ten species of *Sebastes* into one category, did not dramatically decrease the number of stomachs needed to discover all prey categories (342 stomachs,  $p > 0.06$ ). When the prey categories represented by one specimen were aggregated into a higher taxon, the species accumulation curve reached an asymptote by stomach #247 ( $p > 0.2$ ). Finally, the curve with the highest level of aggregation (20 prey categories resulting from aggregating all categories with  $< 5\%$  FO) reached an asymptote by stomach #25 ( $p > 0.4$ ).

**Table 3**

The impact of analyzing frequency of occurrence of forage at scales of the individual predator ( $n = 371$ ) or an independently-sampled unit of analysis (daily sampling unit,  $n = 46$ ) for juvenile albacore in the CCS.

|             | Prey category                 | %FO Individual | %FO DSU |
|-------------|-------------------------------|----------------|---------|
| Cephalopods | <i>Abraliopsis</i> sp.        | 26.4           | 54.3    |
|             | <i>Octopoteuthis</i> sp.      | 11.6           | 47.8    |
|             | <i>Gonatus</i> spp.           | 12.1           | 54.3    |
|             | <i>Doryteuthis opalescens</i> | 8.9            | 26.1    |
|             | <i>O. borealijaponica</i>     | 19.1           | 56.5    |
|             | <i>Japetella heathi</i>       | 7.0            | 37.0    |
|             | Octopus unknown               | 10.0           | 34.8    |
|             | Squid unknown                 | 33.4           | 87.0    |
| Crustaceans | Amphipod                      | 11.9           | 47.8    |
|             | <i>Phronima sedentaria</i>    | 19.4           | 37.0    |
|             | Decapod                       | 15.1           | 45.7    |
|             | Euphausiid                    | 19.9           | 58.7    |
|             | Malacostraca unknown          | 27.8           | 60.9    |
| Fishes      | <i>Sardinops sagax</i>        | 26.7           | 73.9    |
|             | <i>Engraulis mordax</i>       | 52.8           | 73.9    |
|             | <i>Merluccius productus</i>   | 16.4           | 28.3    |
|             | Myctophidae                   | 11.3           | 47.8    |
|             | <i>Cololabis saira</i>        | 18.3           | 50.0    |
|             | <i>Sebastes</i> spp.          | 34.5           | 80.4    |
|             | Fishes unknown                | 29.1           | 80.4    |

### 3.3. Variability between individual albacore and DSUs

The prey items of albacore ranged in mean energy density from  $2.5 \text{ kJ g}^{-1}$  (crustaceans) to  $7.5 \text{ kJ g}^{-1}$  (saury) and protein content ranged from 12.9% (crustaceans) to 21.4% (sardine) (Table 1). Individual albacore stomachs contained, on average,  $62 \pm 72$  (SD) g of reconstituted prey biomass. Total energy content of stomachs ranged from 2 to 3021 kJ, with a mean value of  $307 \pm 353$  kJ. Total protein content ranged from 0.1 g to 74.5 g with a mean value of  $8.8 \pm 9.4$  g. All three metrics were significantly different between DSUs ( $F_{\text{biomass}} = 2.51$ ,  $F_{\text{energy}} = 2.32$ ,  $F_{\text{protein}} = 2.32$ ,  $df = 30$ ,  $p < 0.002$ ).

The frequency of occurrence (FO) of a species category in albacore diet was calculated according to presence in individual stomachs ( $n = 371$ ) or presence in a DSU ( $n = 46$ ). Table 3 compares the two methods of calculating %FO. The %FO by DSU is uniformly higher than that by individual. While saury was present in only 18.3% of individuals, 50% of all DSUs contained at least one. Furthermore, although anchovy appeared in 52.8% and 73.9% of individuals and DSUs, respectively, sardine occurred in only 26.7% of individuals but 73.9% of DSUs. By DSU, the most frequently occurring categories were unknown squid followed by unknown fishes and *Sebastes*. The smallest increase in %FO when scaling from individual to DSU was for hake, which occurred in 16.4% of individuals and 28.3% of DSUs.

### 3.4. Spatial and temporal variability

The regional distribution of prey consumption varied in 11 of 20 prey categories ( $\chi^2 = 53.4$ ,  $p < 0.05$ ). *Abraliopsis* sp., *Octopoteuthis* sp., *D. opalescens*, unknown squid, euphausiids, decapods, sardine, anchovy, hake, saury, and unknown fishes were distributed unevenly between the three regions, while remaining categories (*Gonatus* sp., *O. borealijaponica*, unknown octopi, amphipods, *P. sedentaria*, unknown malacostracans, myctophids, and *Sebastes* spp.) were distributed evenly. The spatial distribution of energy intake averaged over a DSU is shown in Fig. 3a for anchovy and Fig. 3b for *Sebastes*. Maps for the distribution of saury, myctophids, hake, euphausiids, market squid, and *O. borealijaponica* are provided in Supplementary Fig. 1a–f.

By biomass intake, the three regions were significantly different (Table 4). Forage in the northern region was comprised of decapods (%M = 26), anchovy (%M = 23), euphausiids (%M = 19), and hake (%M = 13). The central region was dominated by predation on hake (%M = 42) and saury (%M = 22). Prey in the southern region was dominated by just one species, anchovy (%M = 67), with the next most abundant species, sardine, comprising only 7.2% of biomass. PCA confirmed these patterns, isolating the pairings of the southern region with anchovy and the central region with hake (Fig. 4). Variability between DSUs was explained by predation on either anchovy, saury or hake. Diet preferences in 2005 versus 2006 did not vary significantly. Most prey categories were not a significant source of interannual variability. Again, differences in mass of hake, anchovy, and saury consumed explained the variability between years. Hake was more abundant in 2005, whereas saury and anchovy were more abundant in 2006, relative to other prey categories.

### 3.5. Consumption of forage species and diversity

The bioenergetics model estimated daily energetic demand of  $90\text{--}200 \text{ kJ kg}^{-1} \text{ d}^{-1}$  (Fig. 5). The discontinuity in daily energetic demand at albacore length 65 cm is a result of a change in age-specific mortality rates, and the jump in demand at length 92 cm is a result of investment in reproduction (Essington, 2003). Observed values ranged from 0.18 to  $1378.2 \text{ kJ kg}^{-1} \text{ d}^{-1}$  (mean  $141.7 \pm 193.1 \text{ kJ kg}^{-1} \text{ d}^{-1}$ ). There was no correlation between length of albacore and the observed energy value of stomach contents. The daily consumption rate of albacore was estimated at  $25.6 \text{ g kg}^{-1} \text{ d}^{-1}$  for a two-year-old albacore,  $20.3 \text{ g kg}^{-1} \text{ d}^{-1}$  for a three-year-old albacore, and  $18.0 \text{ g kg}^{-1} \text{ d}^{-1}$  for a four-year-old

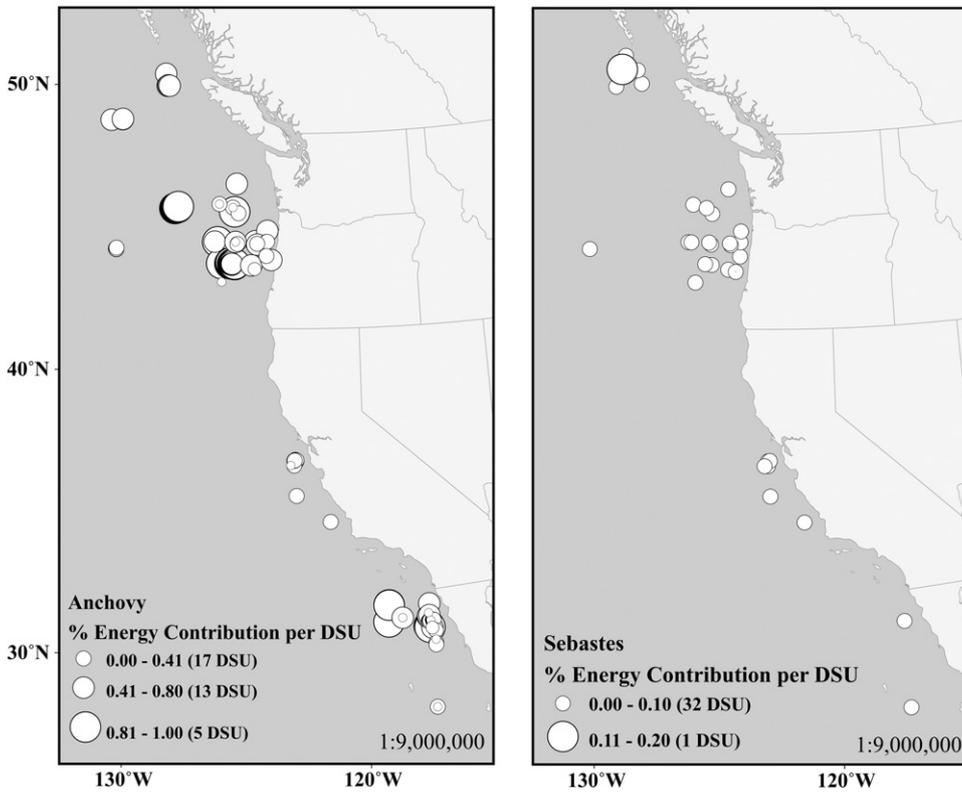


Fig. 3. Distribution of albacore foraging on a) *E. mordax* and b) the family *Sebastes* calculated as the percentage contribution to total energy intake averaged over a Daily Sampling Unit (DSU).

albacore. Weighted by the proportion of ages in the CCS, an albacore foraging in the CCS consumed on average  $19.7 \text{ g kg}^{-1} \text{ d}^{-1}$ . Estimates for average annual biomass consumption of twenty forage categories are given in Table 5. The southern region of the CCS appears to contribute less energy per DSU compared to the northern and central regions (Fig. 6). On average, one stomach contained only four unique categories of prey. Fig. 7 shows the diversity of prey in the water as sampled by albacore and the number of prey in an albacore stomach (shown as contours).

**Table 4**  
Percent mass (%M), energy (%E), and protein (%P) contributed by each of the 20 prey categories in 371 albacore stomachs in three regions of the California Current System. Mass was reconstituted to pre-digestion mass of an organism based on allometric relationships between length and weight.

| Prey category                 | North |      |      | Central |      |      | South |      |      |
|-------------------------------|-------|------|------|---------|------|------|-------|------|------|
|                               | %M    | %E   | %P   | %M      | %E   | %P   | %M    | %E   | %P   |
| <i>Abraliopsis</i> sp.        | 1.6   | 1.5  | 1.9  | 12.7    | 9.5  | 13.4 | 2.7   | 2.0  | 3.2  |
| <i>Octopoteuthis</i> sp.      | 0.2   | 0.2  | 0.2  | 1.6     | 1.2  | 1.7  | 0.2   | 0.1  | 0.2  |
| <i>Gonatus</i> sp.            | 0.4   | 0.5  | 0.4  | 0.3     | 0.3  | 0.2  | 0.8   | 0.8  | 0.7  |
| <i>Doryteuthis opalescens</i> | 0.0   | 0.0  | 0.0  | 0.0     | 0.0  | 0.0  | 4.3   | 2.5  | 4.7  |
| <i>O. borealijaponica</i>     | 1.2   | 1.5  | 1.1  | 6.7     | 6.4  | 5.2  | 0.3   | 0.3  | 0.3  |
| <i>Japetella heathi</i>       | 0.3   | 0.2  | 0.3  | 0.3     | 0.1  | 0.2  | 0.3   | 0.1  | 0.3  |
| Octopus unknown               | 0.3   | 0.2  | 0.3  | 0.5     | 0.3  | 0.4  | 1.8   | 0.8  | 1.7  |
| Squid unknown                 | 0.8   | 0.7  | 0.9  | 1.5     | 1.1  | 1.4  | 6.6   | 4.8  | 6.8  |
| Amphipod                      | 0.5   | 0.2  | 0.4  | 2.1     | 0.9  | 1.7  | 1.2   | 0.5  | 1.0  |
| <i>P. sedentaria</i>          | 0.9   | 0.5  | 0.9  | 0.7     | 0.3  | 0.5  | 0.0   | 0.0  | 0.0  |
| Decapod                       | 21.7  | 14.9 | 19.9 | 0.0     | 0.0  | 0.0  | 0.2   | 0.1  | 0.1  |
| Euphausiid                    | 21.2  | 14.1 | 19.4 | 0.8     | 0.4  | 0.6  | 0.2   | 0.1  | 0.1  |
| <i>Malacostraca</i> unknown   | 3.6   | 2.5  | 3.3  | 0.5     | 0.3  | 0.4  | 6.4   | 3.4  | 5.5  |
| <i>Sardinops sagax</i>        | 2.8   | 4.3  | 4.2  | 0.4     | 0.5  | 0.5  | 12.7  | 15.3 | 17.9 |
| <i>Engraulis mordax</i>       | 20.8  | 29.8 | 20.3 | 1.3     | 1.5  | 1.1  | 60.8  | 67.4 | 55.5 |
| <i>M. productus</i>           | 16.5  | 20.9 | 16.9 | 37.3    | 37.6 | 32.8 | 0.0   | 0.0  | 0.0  |
| Myctophid                     | 0.3   | 0.5  | 0.2  | 0.5     | 0.6  | 0.4  | 0.0   | 0.0  | 0.0  |
| <i>Cololabis saira</i>        | 0.5   | 0.7  | 0.6  | 23.8    | 30.5 | 29.0 | 0.3   | 0.4  | 0.4  |
| <i>Sebastes</i> spp.          | 4.7   | 4.3  | 6.2  | 3.9     | 2.8  | 4.4  | 0.0   | 0.0  | 0.0  |
| Fishes unknown                | 1.8   | 2.5  | 2.5  | 5.2     | 5.7  | 6.1  | 1.4   | 1.5  | 1.7  |

Small sample sizes in the southern and central regions result in less clear pattern. In the northern region, several prey diversity “hotspots” appear south of the Columbia River outflow.

4. Discussion

A typical juvenile albacore feeding in the California Current System in 2005 and 2006 consumed, at any given point in time, four unique categories of prey accounting for 60 g of biomass and providing 300 kJ of energy and 9 g of protein to the albacore. These estimates are within the confidence intervals predicted from a model describing daily energetic demand. Patterns of variability were revealed at the scales of

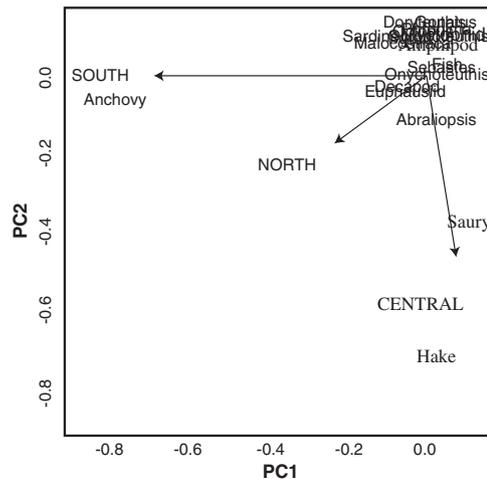
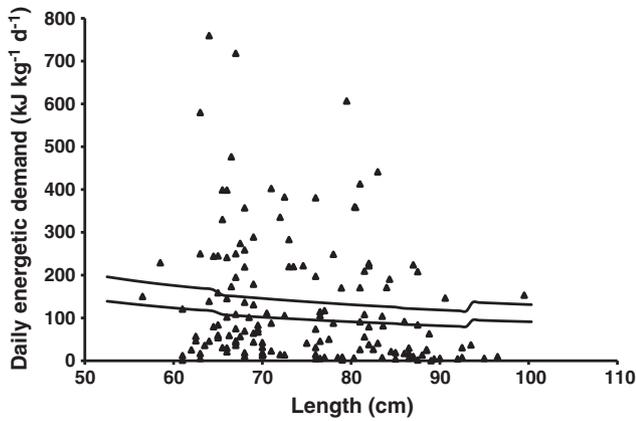


Fig. 4. Regional differences in dietary habits of albacore in the California Current System based on biomass of species consumed.



**Fig. 5.** Daily energetic demand of albacore calculated with a bioenergetics model developed by Essington (2003). The top and bottom lines represent the 90% confidence intervals calculated by 1000 Monte Carlo simulations. Individual triangles are the observed total energetic content (kJ per kg of albacore) found inside each stomach.

individual predators, DSUs, and regions in the CCS, but not between the two sampling years. Dominant prey patterns were strongly tied to region.

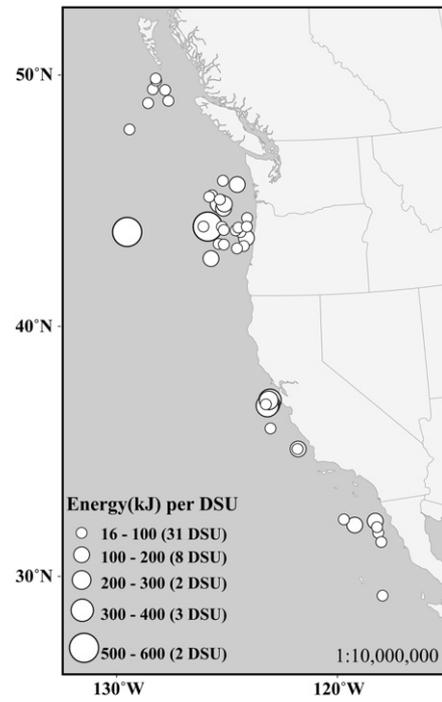
4.1. Prey ecology

4.1.1. Spatial distribution of prey

While the distributions of common (especially commercially important) species (e.g., anchovy, sardine, market squid) are well known, the distributions of less common species often are not documented, and diet data can inform here. Northern anchovy (although relatively less in the central and more in the southern region), gonatid squid, *J. heathi* and *Sebastes* were consumed throughout the CCS. Hake were not consumed in the south, while they had considerable (42% by mass) predation in the central region, and some (13% by mass) predation in the north. Myctophids also were not consumed in the south. In contrast, sardine were consumed almost exclusively in the south. Saury were consumed almost exclusively in the central CCS region. *D. opalescens*, the neritic California market squid, was consumed almost exclusively in the southern region of the CCS. In contrast, the distributions of *Onychoteuthis* and *Abraliopsis* appears to be concentrated in the central CCS.

**Table 5**  
Consumption (mt) by juvenile albacore of forage species in three regions in the CCS.

| Species/taxa               | Southern region |          | Central region |          | Northern region |          | Whole CCS       |                 |
|----------------------------|-----------------|----------|----------------|----------|-----------------|----------|-----------------|-----------------|
|                            | Average         | SD       | Average        | SD       | Average         | SD       | Sum of averages | Pooled variance |
| Crustaceans                |                 |          |                |          |                 |          |                 |                 |
| Amphipods                  | 435.6           | 99.6     | 1226.9         | 260.2    | 388.5           | 83.6     | 2051.0          | 7,803,411.3     |
| <i>P. sedentaria</i>       | 0.0             | 0.0      | 383.4          | 81.3     | 789.1           | 169.9    | 1172.5          | 84,716.9        |
| Decapods                   | 69.7            | 15.9     | 0.0            | 0.0      | 23,573.4        | 5075.3   | 23,643.1        | 76,362,571.6    |
| Euphausiids                | 67.5            | 15.4     | 570.5          | 121.0    | 22,295.4        | 4800.2   | 22,933.4        | 25,759,382.1    |
| <i>Malacostraca</i> unk.   | 2927.3          | 669.1    | 392.6          | 83.3     | 3947.1          | 849.8    | 7266.9          | 280,324,254.0   |
| Cephalopods                |                 |          |                |          |                 |          |                 |                 |
| <i>Abraliopsis</i> spp.    | 1725.0          | 394.3    | 12,821.0       | 2719.6   | 2329.0          | 501.4    | 16,874.9        | 23,056,637.3    |
| <i>D. opalescens</i>       | 2134.5          | 487.9    | 0.0            | 0.0      | 17.0            | 3.7      | 2151.5          | 3,464,602.7     |
| <i>Octopoteuthis</i>       | 98.0            | 22.4     | 1656.3         | 351.3    | 262.2           | 56.5     | 2016.6          | 65,031.1        |
| <i>Gonatus</i> spp.        | 697.0           | 159.3    | 392.6          | 83.3     | 839.1           | 180.7    | 1928.7          | 5276.5          |
| <i>O. borealijaponicus</i> | 243.9           | 55.8     | 8588.1         | 1821.7   | 2311.4          | 497.7    | 11,143.5        | 238,107.0       |
| Squid unk.                 | 4120.9          | 941.9    | 1484.5         | 314.9    | 1175.2          | 253.0    | 6780.6          | 1,176,828.3     |
| <i>J. heathi</i>           | 122.0           | 27.9     | 171.8          | 36.4     | 258.3           | 55.6     | 552.1           | 165,939,001.3   |
| Octopus unk.               | 731.8           | 167.3    | 343.5          | 72.9     | 271.9           | 58.5     | 1347.3          | 58,520.8        |
| Fishes                     |                 |          |                |          |                 |          |                 |                 |
| <i>M. productus</i>        | 0.0             | 0.0      | 50,670.2       | 10,748.4 | 32,977.7        | 7100.1   | 83,648.0        | 127,209.1       |
| <i>Myctophidae</i>         | 0.0             | 0.0      | 871.1          | 184.8    | 724.0           | 155.9    | 1595.1          | 36,795.8        |
| <i>S. sagax</i>            | 13,196.3        | 3016.2   | 671.7          | 142.5    | 6841.9          | 1473.1   | 20,709.9        | 3,569,595.8     |
| <i>Sebastes</i> spp.       | 0.0             | 0.0      | 3735.8         | 792.5    | 6751.0          | 1453.5   | 10,486.8        | 35,557.2        |
| <i>C. saira</i>            | 326.7           | 74.7     | 41,177.0       | 8734.6   | 1165.5          | 250.9    | 42,669.2        | 11,287,816.9    |
| <i>E. mordax</i>           | 58,225.5        | 13,308.3 | 2055.1         | 435.9    | 47,143.9        | 10,150.0 | 107,424.4       | 2,740,693.3     |
| Fishes unk.                | 1254.6          | 286.8    | 7655.7         | 1624.0   | 4009.1          | 863.2    | 12,919.4        | 1,050,406.3     |



**Fig. 6.** Distribution of energy content per albacore, averaged over a Daily Sampling Unit, derived from waters of the CCS.

Decapods and euphausiids were consumed primarily in the north in contrast to their known distribution: euphausiids and decapods comprise the second and fifth most abundant sources of carbon from zooplankton in the southern and central regions of the CCS (Lavaniegos and Ohman, 2007). Moreover, the central region has twice the zooplankton carbon biomass of the southern region (Lavaniegos and Ohman, 2007). However, euphausiids and decapods comprised <1.1% of total biomass consumed in these two regions. This is suggestive of a preference for prey other than mesozooplankton in the southern and central regions of the CCS.

4.1.2. Size and age during predation mortality

The vast majority of prey consumed by albacore were in the juvenile stage of growth; this information has important implications for

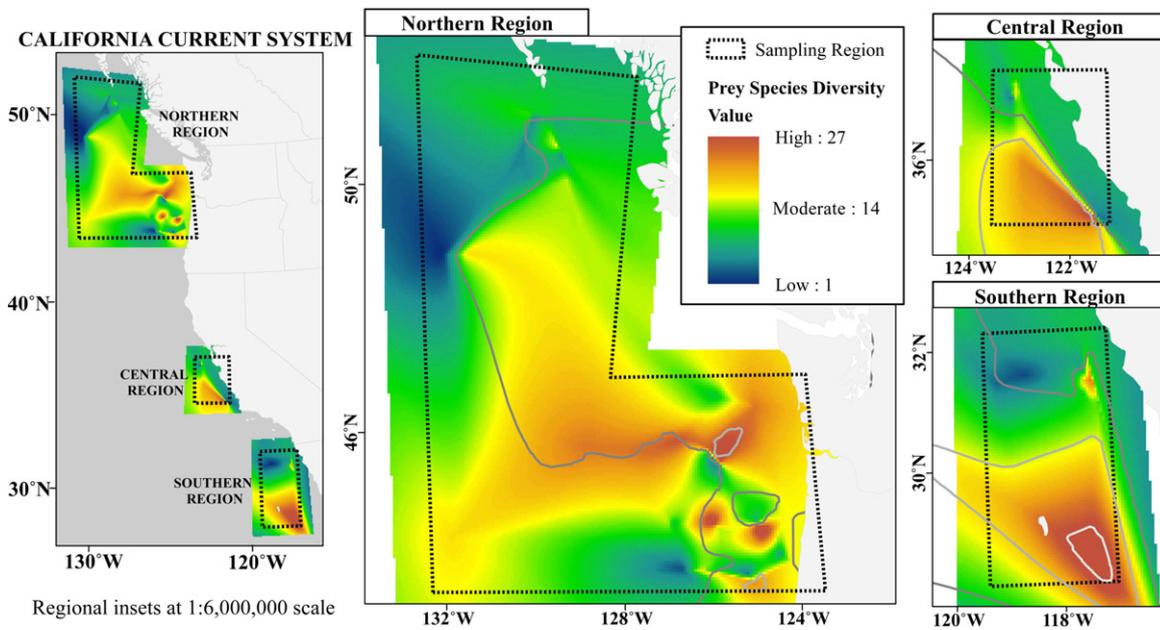


Fig. 7. Diversity of prey in albacore stomach contents in the CCS calculated by interpolating species richness using a nearest neighbor algorithm.

understanding species interactions and sources of mortality for the forage species. The anchovy consumed by albacore were juveniles of mean length 34.6 mm and likely were spawned in the early spring in inshore CCS waters (Smith, 1985). Albacore appear to consume juvenile hake in their spawning grounds (Agostini et al., 2006; Horne and Smith, 1997). Moreover, this is the first study in the CCS to find hake in significant quantities in albacore diet, suggesting albacore consumption of hake varies along with episodic spawning events (Horne and Smith, 1997; Lo et al., 1997). Although the mean saury length was 120 mm, the large standard deviation reflected two main length classes found in the sample: one with mean length approximately 60 mm (juveniles) and one with mean length approximately 180 mm (adults). *Sebastes* are inshore, demersal fishes as adults, but their larvae and juveniles swim in the upper water column at which point they are vulnerable to predation by fishes and birds (Ainley et al., 1993). The beak sizes of *Abraliopsis* sp., *D. opalescens*, *Octopoteuthis* spp., and gonatid squids found in albacore stomachs were all of juvenile sizes. Myctophids and crustaceans, which have smaller maximum sizes than the majority of other prey, were consumed in adult stages.

#### 4.1.3. Inference on prey aggregations

The number of prey of a given species consumed together allows some inference on whether they existed in the environment in large aggregations, in small groups, or singly. Such information is important for understanding spatial patchiness and potential predator encounter rates from the perspective of the prey. When a stomach contained decapods, euphausiids, anchovy, or hake, those prey existed in large numbers within one stomach, while other categories occurred in small groups of six or fewer (Table 2). Saury is known to occur in large schools; however, the saury consumed by albacore in this study mostly occurred in stomachs in groups of five. Smaller saury were usually found in small groups inside stomachs, whereas larger saury were usually found singly or in pairs. Hake were found in only 16% of all stomachs, but they occurred in the largest groupings of any species consumed (on average, 58 individuals per stomach), suggesting large schooling aggregations. Over half of the stomachs containing *Abraliopsis* had fewer than 3 beaks per stomach, suggesting that these prey are consumed singularly or in small groups. However, twelve stomachs contained between ten and 23 *A. felis* beaks, suggesting that they could be consumed in small aggregations. *Onychoteuthis* also was consumed in small groups (on average, three beaks per stomach).

The relative abundance of anchovy and sardine within a stomach sheds some light on their ecology. Sardine always co-occurred with anchovy, but anchovy frequently occurred without sardine. In the former case, similar degrees of digestion suggested predation on mixed schools that were predominantly anchovy with some sardine. It is possible that, within a school of juvenile forage fishes, the sardine were better able to evade predation than the anchovy, in which case the relative abundance in stomachs would be dictated by vulnerability and not relative abundance. However, anchovy and sardine were of the same size and therefore swimming speed (van der Lingen, 1995), and it is more plausible that anchovy outnumbered sardine in the immediate foraging environment as well as inside albacore stomachs.

#### 4.1.4. Rare prey

While ecosystem-based approaches to management should focus on biologically and commercially meaningful interactions, weak species interactions are known to be important stabilizers of food web dynamics (McCann et al., 1998). Moreover, the lack of interaction between a predator and common forage species also is important. Two common and commercially and biologically important coastal pelagic species, sardine and *S. japonicus*, were not significant components of albacore diet. Myctophids, of which three species were identified (*T. crenularis*, *S. leucopsaurus*, and *D. theta*), are presently overlooked in EBM approaches in the CCS, but their extraordinarily large biomass makes them an important species for which to count predators. This study is the first to identify *I. lockingtoni*, the medusafish, and *B. pentacanthus*, the bigeye poacher, as rare prey of albacore. Moreover, several fishes that previously had only been identified to genus were identified to species (*A. nikparini*, *P. decurrens*, and *S. californiensis*). The most commonly discovered species of amphipod, *P. sedentaria*, is a known parasitoid on salps and doliolids, and it may have been secondary prey that was consumed along with a host. Predation on gelatinous zooplankton is notoriously difficult to quantify, and evidence of this parasite might be a useful indicator.

Uncommon species of squid do not receive much attention in the literature. *A. argo* (a pelagic octopus), *M. dentata*, *Histioteuthis* sp., and *M. robusta* (all muscular pelagic squid), and *V. infernalis* (a meso- or bathypelagic squid) previously have been found in the diet of albacore (Pinkas et al., 1971). *E. luminosa*, a pelagic squid about which little is known, was newly identified in this study. *J. heathi*, another prey species first identified in this study, is a pelagic octopus that exists in the North

Pacific from Southern California (Young, 1972) to the Bering Sea (Pearcy, 1962).

#### 4.2. Patterns of variability in albacore diet

Albacore prey in this study did not vary between 2005 and 2006. Over longer time scales (decades), some temporal variability can be detected in diet habits (Glaser, 2010). Anchovy were not important prey during the 1950s, and this is the first study to demonstrate that hake can be important. Overall, however, diet habits of albacore seem fairly consistent from year to year and over decades (Glaser, 2010). Given the tendency of biological populations to display temporal autocorrelation (Steele and Henderson, 1984), we expect diet habits in adjacent years to be similar while distant years diverge. Rapid and widespread changes in the community structure of the CCS could change the suite of prey available to albacore (e.g., Hare and Mantua, 2000; McGowan et al., 2003). However, such potential changes were not detected in this study. Finally, the conventional wisdom from commercial and recreational fishers is that albacore diet can vary significantly from year to year. John Lagrange, former president of the American Fisherman's Research Foundation and a career commercial albacore fisher, notes that, in some years, squid are by far the most abundant prey in albacore stomachs rather than small fishes (J. Lagrange, personal communication). Interannual variability must be quantified with long-term, repeated sampling efforts.

Patterns of spatial variability were apparent at several scales: within one DSU, between DSUs, and between regions. High between-individual and within-DSU variabilities are evident in the patterns of %FO (Table 3). All prey categories occurred with greater frequency at the level of DSU compared to individuals. An opposite pattern could be possible: if stomachs within one DSU were homogenous, and variability between DSUs was high, %FO in stomachs could be greater than %FO in schools. Within any given DSU, a dominant prey (such as anchovy or hake) may be found in all stomachs within that unit, but each individual also contained several rare prey items, accounting for variability detected by PCA and contingency analysis.

The variability in reconstituted stomach contents, total energy and total protein between schools reflects regional variability in prey and prey energy density. Euphausiids and decapods, the third and fourth most abundant prey in the northern region, have much lower energy density values than most cephalopods and all species of fish. The central region was dominated by predation on hake, the lowest energy density of the major categories of fish. Saury, however, is the most energy dense of all the fishes and was the second most abundant prey in this region. The southern region is dominated by anchovy, a prey with average energy density. The significant differences between DSUs in biomass and energy reflected the low species diversity found in a given stomach. Given that each stomach contained only four unique prey types but overall 59 total categories were consumed, the between-individual variability should be high.

If we assume stomach contents represent one feeding event, and that albacore feed three times per day (Chancollon et al., 2006), the total energy content found in albacore matches that predicted by a bioenergetics model. Stomachs contained, on average, 60 g of prey biomass which contributed 306 kJ of energy and 9 g of protein to albacore metabolism. Roughly, these numbers confirm estimates of prey energy density used in tuna bioenergetics models (Essington, 2003; Olson and Boggs, 1986; Olson and Watters, 2003). These studies have assumed that the mean prey field available to tuna has an energy density of 5.0 kJ g<sup>-1</sup>, whereas this study estimates a mean prey field of 6.2 kJ g<sup>-1</sup>. Species-specific rates of digestion do not exist for albacore nor for most of their prey items (Chancollon et al., 2006; Consoli et al., 2008). While differential rates of digestion, particularly between cephalopods and fishes, pose a challenge to diet studies, these results suggest that model estimates and field observations may converge. Thus, despite longer gut retention time for cephalopod beaks, the fact that cephalopods make up a small energetic

contribution to albacore diet (Glaser, 2010) means approximations made herein are justifiable.

#### 4.3. Limitations of the study

Studies of diet habits of large marine predators face several concurrent challenges: collecting and processing a sufficient sample size, adequately sampling the geographic extent of the predator population, consistently resolving taxonomic categories, and handling differential digestion times of prey. Previous diet studies of juvenile albacore have described between 83 and 905 individuals. In studies of the North Pacific, samples sizes were 321 (McHugh, 1952), 155 (Iversen, 1962), 905 (Pinkas et al., 1971), 83 (Bernard et al., 1985), and 132 (Watanabe et al., 2004). In studies of the Mediterranean and Atlantic, samples sizes were 97 (Ortiz de Zarate, 1987), 78 (Pusineri et al., 2005), and 189 (Consoli et al., 2008). Only Pinkas et al. (1971) collected and analyzed more stomachs than this study.

The question of appropriate sample size is a matter of what questions are posed in the study and a matter of resources. We investigated the number of samples necessary to describe the prey diversity in the diet; in other words, how many samples are required to discover all the prey that are consumed by albacore? The answer is heavily dependent on the degree of taxonomic aggregation. At the highest taxonomic scale, the species accumulation curve reached an asymptote only 19 samples before the final. If all prey categories had been resolved to species, a greater number of samples would have been needed. The taxonomic resolution resolved in this study varied between orders and families of organisms. For example, ten species of *Sebastes* were identified, but only two species of decapod were distinguished. Likewise, the category Euphausiid certainly includes many *Euphausia pacifica*, but whether this category contains one, two, or ten other species of euphausiid is unknown. The inconsistency in taxonomic resolution between groups suggests that additional new species would continue to be found beyond sample #352.

The sample size analyzed here was sufficient to make medium-scale comparisons, as supported by the species accumulation curves that result from the highest degrees of aggregation. Combining categories represented by one individual reduced the required sample size from 352 to 247. This, too, was an artificial distinction because full identification of the 'unknown' categories would likely reduce the categories of prey represented by one specimen. Finally, aggregating taxa so that all categories occurred in at least 5% of individuals resulted in a dramatic decrease in sampling effort to only 25 stomachs. This level of aggregation is useful for understanding broad patterns in diet, identifying the dominant prey, and comparing regions. However, such a small sample size would be inaccurate at describing a fully realized food web structure or in quantifying weak predator-prey interactions (McCann et al., 1998). Nevertheless, this scale of taxonomic aggregation is useful for many of the multivariate statistical approaches used herein to describe patterns in diet habits.

One challenge in interpreting the dataset is the disproportionate number of samples from the northern region. Given the known differences in regional distribution and relative abundance of prey species (McGowan et al., 2003), this unequal sampling effort could lead to an inaccurate description of diet habits in the CCS as a whole. The cause of this uneven sampling distribution is partially a result of the commercial vessels contributing to this study. While recreational vessels were sampled more uniformly throughout the three regions, the commercial vessels were based in northern California and Puget Sound, WA and their fishing effort was concentrated in the northern region. Catch and effort time series show that the commercial albacore fleet, as a whole, concentrates effort (and has higher catch) in the northern region (ISC, 2014). This pattern of fishing may reflect higher catch rates (and, theoretically, more albacore) in the northern region, or it may be a function of the location of tuna canneries along the coast. Additionally, most samples were collected within 300 km of shore, whereas juvenile albacore

populations occur out to 800 and 1000 km from shore (Childers et al., 2011). In the northern region, sampling did extend to 800 km, but southern and central region sampling was closer. Offshore patterns of prey vary significantly and the distribution of sampling may underestimate offshore prey such as cephalopods (Okutani and McGowan, 1969).

Great care was taken to identify prey to the species level. Forty species-level, nine genera- or family-level, and ten order-level identifications were made in this study. When necessary, species identifications were made or confirmed using genetic sequencing. Sequencing was highly successful for fishes, identifying five species that otherwise would have been classified as ‘unknown fish,’ distinguishing nine species of *Sebastes* (Hyde and Vetter, 2007); identifying five species of cephalopod whose beaks lacked keys; and confirming the identification of five species of cephalopod whose beaks were not described for juvenile stages. Unidentified categories (326 squid, 11 octopus, 1006 malacostracans, and 413 fishes) numerically accounted for 9.5% of all prey specimens. If identifications for these categories had been possible, it is unlikely that mass-based results describing interannual, DSU, or regional variability, or principal component analyses, would have changed. Furthermore, estimates of stomach content mass and energy are unlikely to be impacted significantly by this source of uncertainty because mean values of mass and energy were applied to categories of unidentified prey.

Some researchers distinguish fresh prey from nonfresh prey, using degree of digestion to guide their choices (Chancollon et al., 2006; Pusineri et al., 2005). This may allow more precise estimates of daily intake because some hard parts (particularly cephalopod beaks) remain in the gut for longer periods of time, thus biasing stomach content estimates in favor of species with slower digestion or evacuation rates. This practice was not here followed for two reasons. First, the average degree of digestion for all prey in this study was approximately 75%, and few prey would have been considered fresh. Moreover, there was low variability in degree of digestion within a given stomach, suggesting that the prey had been consumed at the same time. The only exception to this was cephalopods: eight fully undigested specimens were found in the entire study, and most beaks were loose and had no remnant of flesh attached. The second rationale for not dividing prey items into fresh and nonfresh was based on early results. While cephalopods were found with high frequency in stomachs, they exist in small numbers and contribute only 11% of total mass to overall diet. Reliable estimates for differential rates of digestion in cephalopods versus fishes do not exist (Chancollon et al., 2006). Consequently, the exclusion of cephalopod beaks from analysis seemed arbitrary, and their inclusion only makes estimates of biomass consumed and total energy slightly more conservative than if cephalopod beaks were excluded.

#### 4.4. Implications for predation on CCS forage species

In general, the population of albacore tuna in the North Pacific Ocean is fairly stable with patterns of decadal variability (Glaser, 2011; ISC, 2014). Population fluctuations in albacore create a variable source of mortality for the dozens of forage species subject to predation. In order to calculate an instantaneous mortality rate for prey ( $M$ ), an estimate of the population size for the forage species also is needed. Unfortunately, for the vast majority of forage species considered here, those estimates are lacking. Nevertheless, the estimates of biomass consumed by albacore of these forage groups is a valuable starting point for expanding current fisheries management in the CCS to ecosystem-based approaches. For any given forage species, the predation mortality from all predators should be measured. Here, we provide an estimate for only one predator – a valuable starting point, but an incomplete picture of predation in the CCS. Future work should combine efforts of researchers whose focus on top predators can reveal new patterns and provide a top-down perspective on forage distribution and ecology in the CCS.

As EBM progresses, it is imperative to begin identifying which species interactions should be considered in an ecosystem context. *E. mordax*, the Northern anchovy, is the most important prey species of albacore based on multiple metrics: distribution (all three regions), numbers, and energetic contribution to albacore diet. The albacore-anchovy interaction should therefore be the first step in extending albacore management beyond a single-species approach. However, sufficient data are now available to go beyond the consideration of only one prey species. From the perspective of albacore, we recommend considering the three main forage species: Pacific saury, Northern anchovy, and Pacific hake. Currently, saury is not commercially fished in the CCS and there are not estimates of its population size. However, in the future it is conceivable that saury could become a viable commercial fishery (likely for fishmeal). In such a case, the importance of saury to albacore diet must be considered when setting fishing limits on saury. Furthermore, while fishing pressure on anchovy is currently relatively low, anchovy is a critical forage species for many predators in the CCS. An ecosystem-based approach to the management of anchovy must protect sufficient biomass for the predators that rely on this species. Finally, while hake was a critical forage species during 2005 and 2006, it has not been reported as prey in other years. Albacore appear able to survive on other forage species when hake are not present in large numbers (Glaser, 2010). During peaks in hake spawning, however, albacore may exert an important predation mortality. We conclude that the albacore-anchovy-hake-saury tetrad is a manageable ecosystem unit to consider in ecosystem-based management in the CCS.

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#### Appendix A. Supplementary data

The following supplementary material is available online: [Supplementary Table 1](#) listing all taxa consumed by albacore with related quantity and allometric statistics, and [Supplementary Fig. 1](#) showing spatial distribution of foraging on euphausiids, *Doryteuthis opalescens*, Myctophidae, *Cololabis saira*, *Merluccius productus*, and *Onychoteuthis borealijaponicus*.

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