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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

Sarah M. Glaser [a,*], Katrina E. Waechter [b], Nicole C. Bransome [c,1]

[a] Joseph S. Korbel School of International Studies, University of Denver, 2201 S. Gaylord Street, Denver, CO 80210, USA
[b] Department of Geography, University of Denver, 2199 S. University Blvd, Denver, CO 80208, USA
[c] Scripps Institution of Oceanography, University of California, 9500 Gilman Road, La Jolla, CA 92093, USA

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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.

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

* Corresponding author. Tel.: +1 303 871 3778; fax: +1 303 871 2124.
E-mail addresses: sarah.glaser@du.edu (S.M. Glaser), kewaechter@gmail.com (K.E. Waechter), ncbransome@gmail.com (N.C. Bransome).
[1] Present address: Pew Charitable Trusts, 901 E Street NW, 10th Floor, Washington, DC 20004, USA.

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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 (*Abraliopsis* 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 simultaneous 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 ≤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