UNIVERSITY OF CALIFORNIA, SAN DIEGO

Foraging ecology of North Pacific albacore in the California Current System.

A dissertation submitted in partial satisfaction of the
requirements for the degree of Doctor of Philosophy

in

Oceanography

by

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The Dissertation of Sarah M. Glaser is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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DEDICATION

For his passion to understand the ocean and the creatures who swim within, this dissertation is dedicated to John Lagrange and the memory of his wife, Linda. Without Mr. Lagrange, I might never have decided to study albacore, a powerful and beautiful fish that has taught me an incredible amount. Thank you, John, for your insight and your guidance, for the support of the American Fisherman's Research Foundation and the commercial albacore industry, and for prioritizing the role of scientific inquiry in management while reminding us of our limitations.

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ABSTRACT OF THE DISSERTATION

Foraging ecology of North Pacific albacore in the California Current System.

by

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Doctor of Philosophy in Oceanography

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Professor David M. Checkley, Jr., Chair

The aims of this dissertation are to identify critical interactions between juvenile North Pacific albacore (*Thunnus alalunga*) and their prey in the California Current System (CCS), classify the foraging strategy of albacore, and examine the potential for top-down effects of albacore predation. Predator-prey interactions are the fundamental component of food webs, and quantifying variability in strengths of interactions is critical for predicting how ecosystems will respond to changing environments. Stomachs from 371 juvenile albacore were collected in the CCS during summer and fall 2005 and 2006. Interdecadal variability was examined by comparing these samples to four studies conducted during 1949-1983. I hypothesized that, given significant changes to communities in the CCS, albacore diet would reflect these changes. However, diet has been stable, and despite a recent resurgence of Pacific sardine, only Northern anchovy and Pacific saury consistently have been important prey. These results support theoretical predictions of optimal foraging models that albacore prefer cold, near-shore waters containing anchovy and saury while minimizing time in warmer, offshore habitat of sardine. Albacore derived 68-97% of nutrition from juvenile fishes, 3-30% from juvenile cephalopods, and the remainder from crustaceans. In the northern CCS, decapods, euphausiids, and anchovy dominated biomass of prey; in the central CCS, hake and saury dominated; and in the southern CCS, anchovy were the sole significant prey. Using graphical approaches examining foraging strategy, I demonstrated that albacore are not true generalists, as commonly thought, but rather employ a mixed-feeding strategy that includes specialization on anchovy, variable predation on localized prey such as hake, saury, or decapods, and generalized (but rare) predation on over 50 additional species. Given the importance of anchovy to albacore diet, I investigated the impact of predation mortality on young-of-year anchovy. Albacore removed between 0.1% - 5% of anchovy recruitment biomass annually. Results demonstrated that albacore are attracted to regions of abundant anchovy and suggest that albacore predation exerts top-down influences. Based on historical importance, widespread patterns of consumption, specialization on anchovy, and potential top-down impacts of predation, I conclude that albacore and anchovy interact strongly and populations may be sensitive to changes in the other.

Chapter 1. Introduction to the Dissertation

The aims of this dissertation are to identify the critical interactions between juvenile North Pacific albacore (*Thunnus alalunga*) and their prey in the California Current System (CCS), to classify the foraging strategy of albacore, and to measure the potential for top-down effects of albacore predation. The intial motivation for my research was the observation that four albacore diet studies conducted in the CCS between 1949-1983 found significant quantities of Northern anchovy (*Engraulis mordax*) and Pacific saury (*Cololabis saira*) in albacore diet, but never Pacific sardine (*Sardinops sagax*) (McHugh 1952, Iversen 1962, Pinkas et al. 1971, Bernard et al. 1985). These studies were conducted during periods of high anchovy and low sardine abundance (Schwartzlose et al. 1999, Chavez et al. 2003). Recently, populations of these pelagic fishes have reversed, and sardine outnumber anchovy in the CCS (Hill et al. 2007).

Consequently, I was curious whether albacore would respond to changes in relative abundance of these biologically-similar forage fishes. A two-year diet study of juvenile albacore in the CCS was undertaken to answer this question. The CCS has undergone significant changes in the physical environment and its biological communities over the past half-century (*e.g.*, Roemmich & McGowan 1995a,b, McGowan et al. 1998, Hare & Mantua 2000, Minobe 2002, McGowan et al. 2003, Lavaniegos & Ohman 2007). Given the high degree of functional redundancy in marine food webs (Link 2007), changes in relative abundance of common prey (Brodeur et al. 2005), and the commonality of generalist foraging strategies (Roughgarden 1974), variability in predator diet is expected.

1.1. Theoretical foundation

Spatial and temporal variability in the strengths of predator-prey interactions has important implications for ecosystem-based modeling of marine environments. Many multispecies models have shown promise in quantifying the impact of variable fishing effort on marine communities, estimating recruitment and natural mortality, and describing climate impacts on food webs (*e.g.*, Cox et al. 2002, Latour et al. 2003, Christensen & Walters 2004, Watters et al. 2003, Field et al. 2006). On the other hand, the complexity inherent in these models obscures individual components (species), making them difficult to isolate. Independently quantifying predator-prey interactions is an important means of verifying hypotheses posed by multispecies models. Diet studies are especially useful in open, poorly-observed systems such as the pelagic marine environment, where interaction strengths and coefficients in predator-prey models are difficult to quantify (Wootton 1997).

Predation can be variable in time and space given environmental gradients of productivity (MacArther & Pianka 1966), absolute and relative abundances of prey (Holling 1959, Ivlev 1961, Roughgarden 1974), ontogenetic changes in the predator (Werner & Gilliam 1984), the caloric value of prey (Emlen 1966), or differential costs to the predator of pursuit (Charnov 1976, Dall & Cuthill 1997). The foraging strategy of a predator can provide insight into the cost-benefit analysis applied to how, when, and where to focus hunting effort (Emlen 1966, Roughgarden 1974, Stephens & Krebs 1986, Kirby et al. 2000). Such tradeoffs ultimately create evolutionary pressures that, in the long-term, affect predator growth rates and life history strategies (Roughgarden 1974).

Predator foraging strategies can be classified as generalist or specialist. Generalists consume a high diversity of prey, frequently in direct proportion to the relative abundance of prey in the environment (Stephens & Krebs 1986), while specialists consume a low diversity of prey, frequently focusing hunting effort on one or two species. Predators may exhibit generalist or specialist foraging strategies, or a combination of both, and the strategy employed can have implications for a predator's response to changing environments and availability of prey (Holling 1959, MacArthur & Pianka 1966, Stephens & Krebs 1986).

While foraging strategy describes the importance of hunting to the predator, diet studies also elucidate the impact of foraging on prey populations. Density-independent factors, such as temperature (Fiedler 1983) and turbulence (Lasker 1981), and density-dependent factors, such as food availability (Cushing 1974) and predation (Connolly & Roughgarden 1999), affect the mortality rates of prey populations. For prey fishes, over 99% of total mortality will occur during their egg, larval, and juvenile stages (Jennings et al. 2001); therefore, understanding sources and variability of predation mortality is critical to estimating adult abundance and predicting changes in stock structure.

Predation mortality has been shown to play an important role in structuring marine communities (Hunter & Price 1992, Roughgarden et al. 1994, Menge 2000, Cury et al. 2000, Shurin et al. 2002, Munch et al. 2005). The top-down effects of predation can alter the diversity (Paine 1974), realized niches (Connell 1961), and abundances of species (Dayton 1971). Pronounced top-down effects can cause cascades in which species at all trophic levels in a food chain are impacted (Estes et al. 1998). Bottom-up effects of environmental factors, nutrient availability and prey abundance also can impact the productivity, size-structure, growth rates, and abundance of predators (Cury et al. 2000, Shurin et al. 2002, Munch et al. 2005). The relative importance of top-down versus bottom-up regulation depends on a host of interrelated factors and can vary in time (Hunter & Price 1992, Roughgarden et al. 1994, Munch et al. 2005). Observational diet studies coupled with bioenergetic and demographic models (Williams et al. 2004, Hunsicker & Essington 2008), while neither as elegant nor as conclusive as experimental manipulation, have demonstrated correlative relationships between pelagic predators and their prey, highlighting the potential for top-down impacts by migratory predators in open ecosystems.

1.2. Biology of North Pacific albacore

North Pacific albacore, *Thunnus alalunga*, are highly migratory predators that account for 60,000 – 100,000 metric tons of commercial fish landings annually (ISC 2006). Adults reach 12 - 14 years of age and up to 120 cm in length. The North Pacific population of albacore is a distinct stock from populations in other ocean basins. Adults spawn in the western-central North Pacific and juveniles (ages 0-4) occupy the productive California and Kuroshio Current regions (Laurs 1977). Juvenile albacore migrate into CCS waters in the late spring and reside there until late fall. Some juveniles over-winter at the southern end of the CCS along the Baja continental shelf, while some migrate across the Pacific, turning up in the central North Pacific and the Kuroshio system (Kimura et al. 1997). Albacore complete over 90% of total growth by age five (Ortiz de Zarate & Restrepo 2001); given the residence time of juveniles in the CCS, then, their diet habits in this region are of considerable importance to the overall production of their population.

The appearance of juvenile albacore in CCS waters corresponds to the development of the frontal boundaries of the transition zone (Laurs & 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 gyre into the productive upwelling zone of the CCS 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, a better understanding of albacore niche width and foraging strategy may shed light on patterns of interspecies competition and niche overlap in these regions.

Diet habits of juvenile albacore in the CCS have been quantified in four studies: McHugh (1952), Iversen 1962 (in conjunction with Graham (1959)), Pinkas et al. (1971), and Bernard et al. (1985). Data collected by Pinkas et al., in particular, are widely used in ecosystem models to describe albacore diet (Kitchell et al. 1999, Olson & Watters 2004, Field et al. 2006). These four historical diet studies never have been analyzed in concert, but they conclude that juvenile albacore are generalists whose diet relies upon *Cololabis saira* (Pacific saury), *Engraulis mordax* (Northern anchovy), cephalopods and euphausiids.

1.3. Outline of the dissertation

The diet data presented in this dissertation are used to investigate albacore foraging ecology in three complimentary ways. In Chapter 2, I present newly collected diet data in the context of four historical studies to investigate the hypothesis that albacore diet has changed over time to reflect an increase in sardine in the environment. I reanalyze historical diet studies, originally framed by traditional metrics of diet habits (numeric abundance and frequency of occurrence), using the more contemporary approach of bioenergetics. When analyzed according to energetic contribution, the diet habits of albacore in the CCS are more narrow than previously described. The majority of albacore diet is comprised of saury and anchovy, and recently hake (*Merluccius productus*) have become important. Sardine never have been found in significant amounts in albacore diet, contrary to expectations. I argue that, although albacore are opportunistic predators, thermal optimization confines them to certain water masses even in the face of abundant prey elsewhere, and I suggest that albacore do not occupy the same waters as sardine.

Chapter 3 describes the foraging ecology of albacore through patterns of variability in diet habits at medium spatial and temporal scales, and small scales of taxonomic resolution. I present the detailed results of gut content analysis of 371 albacore collected in 2005 and 2006, making regional comparisons of prey diversity and quantifying the daily consumption rates of albacore. First, I describe species-level patterns of albacore diet habits in the CCS and discuss prey ecology. Second, I compare individuals and aggregations of foraging albacore to describe differences in energy content, biomass consumed, and prey aggregations. Third, I compare prey consumed in three different regions of the CCS (north, central, and south). Finally, I classify albacore foraging strategy using graphical means of comparing individual prey diversity to population prey diversity. Based on the results of Chapter 2, I hypothesize and demonstrate that albacore are not true generalists; rather, they display foraging strategies more closely approximating transitory specialists or a mixed-feeding strategy based on specialization on one or two prey with a broad supplement of more rare prey.

Chapter 4 investigates the predation impact of albacore on their most important prey, Northern anchovy. First, I estimate the abundance of juvenile North Pacific albacore in the CCS from 1966-2005. Second, I quantify the annual consumption of the central stock of Northern anchovy by albacore. Finally, given the large population of albacore (ISC 2006) and the significant fraction of their diet comprised by anchovy (Chapters 2 and 3), I hypothesize that albacore exert top-down pressure on anchovy. Borrowing generalizations gleaned from experiments in intertidal zones, I expect an inverse relationship between albacore abundance and anchovy abundance. I demonstrate that albacore consume between 1 – 5% of anchovy recruitment biomass annually. Furthermore, changes in albacore population abundance in the southern CCS are negatively correlated with changes in anchovy recruitment biomass the following year, suggesting the potential for top-down effects on anchovy.

Chapter 5 presents concluding remarks. This dissertation is the first to quantify interdecadal variability in diet habits of an important marine predator, and the findings have implications for marine ecosystems. Albacore diet has been surprisingly stable despite significant changes in the marine communities in the CCS. Contrary to expectations, albacore do not consume Pacific sardine, and their niche width is more narrow than previously assumed. Northern anchovy are a critical prey species for albacore, and models containing albacore or anchovy could be improved by focusing on this key interaction. Although conventional wisdom classifies albacore as generalists, their mixed-approach to foraging means they may be more sensitive to dramatic changes in important prey species, especially Northern anchovy. Finally, the role of albacore in the CCS, while transitory, appears to be sufficient to impact at least one population of prey.

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Chapter 2. Quantifying interdecadal variability in diet habits, prey energetics, and consumption rates of North Pacific albacore in the California Current System.

Abstract

Predator-prey interactions are critical components of any multispecies model, and most attempts to quantify these interactions in pelagic marine environments rely on observational diet studies. North Pacific albacore (*Thunnus alalunga*) are important predators in the California Current System (CCS), and diet habits of juvenile albacore have been quantified in four previous studies spanning 1949 - 1983. The aims of this new diet study are 1) to identify decadal patterns of predator-prey interactions for juvenile North Pacific albacore in the CCS, and 2) to quantify variability in prey energetics and predator consumption rates. Stomachs from juvenile albacore were collected in 2005 and 2006 and are compared to past studies (total n = 1766). A bioenergetics model is used to calculate daily and annual consumption rates. Estimates of biomass consumed can be sensitive to the choice of prey energy density values; consequently, I calculated the energetic contribution of prey items to albacore diet as a means of comparing studies. Albacore derive 68-97% of nutrition from fishes, 3-30% from cephalopods, and the remainder from crustaceans. Their prey is comprised of small individuals, primarily young-of-year fishes (~2.5 g) and cephalopods (~4 g). Diet habits of juvenile albacore in the CCS are stable through time as a result of low variability in species consumed and the high energy density of prey, translating into stable consumption to biomass ratios ($Q:B$). Despite a resurgence in abundance of Pacific sardine (*Sardinops sagax*) in the CCS, only Northern anchovy (*Engraulis mordax*) and Pacific saury (*Cololabis saira*) consistently have been important to albacore diet. These

results support theoretical predictions of optimal foraging models that albacore will prefer hunting in cold, near-shore waters containing anchovy and saury and minimize time spent in the warmer, offshore waters of sardine habitat.

Introduction

The aims of this study are to identify the critical relationships between juvenile North Pacific albacore and their prey in the California Current System (CCS), and to quantify variability in diet and consumption rates. This research is motivated by the recognition that diet studies are a mere snapshot of the habits of marine predators. Given the extraordinary changes to the CCS over the past half-century (e.g., Roemmich & McGowan 1995a,b, Mantua et al. 1997, McGowan et al. 1998, Hare & Mantua 2000, Minobe 2002, McGowan et al. 2003, Lavaniegos & Ohman 2007), we should not assume diet habits quantified in past decades will remain static. In fact, given the high degree of functional redundancy in marine food webs (Link 2007), changes in relative abundance of common prey (Brodeur et al. 2005), and the commonality of generalist foraging strategies (Roughgarden 1974), variability in predator diet is expected. These observations have important implications for ecosystem-based management of marine resources.

Fisheries science underwent a paradigm shift 30 years ago that led to the current focus on ecosystem approaches to modeling and management (Brown et al. 1976). The recognized interconnectedness of marine organisms with each other and the environment called in to question single-species approaches to management, and multispecies models have moved to the fore of marine ecosystem research (Larkin 1996). Many multispecies models have shown promise in quantifying the impact of variable fishing effort on marine communities, estimating recruitment and natural mortality, and describing climate impacts on food webs (e.g., Cox et al. 2002, Latour et al. 2003, Christensen & Walters 2004, Watters et al. 2003, Field et al. 2006). On the other hand, the complexity inherent in these models obscures individual components (species), making them difficult to isolate. The degree of aggregation necessary to make ecosystem models tractable inhibits long-term forecasting (Hollowed et al. 2000). The poor health of the world's marine ecosystems underscores the urgency implicit in the move towards more comprehensive approaches to protecting and using marine resources (Pauly et al. 2002, Myers & Worm 2003, Worm et al. 2006). This juxtaposition – the need to develop and implement ecosystem-based management in the face of model uncertainty – partly explains why, despite decades of research on multispecies models and many viable options, fisheries managers have not converged on a standard multispecies model for developing policy guidelines (Christensen & Walters 2004).

Predator-prey interactions are a critical component of any multispecies model, and most empirical attempts to quantify the strengths of these interactions rely upon diet studies or observed feeding events. Ecopath, a common food web model, utilizes diet data to structure the trophic relationships modeled through mass balance equations (e.g., Polovina 1985, Cox et al. 2002, Olson & Watters 2003, Christensen & Walters 2004, Field et al. 2006). Diet studies are especially useful in open, poorly-observed systems such as the pelagic marine environment, where interaction strengths and coefficients in predator-prey models are difficult to quantify (Wootton 1997). Thus, for pelagic predators, gut content studies remain one of the only methods for quantifying food web linkages. Additionally, quantifying variability in diet and diet-derived parameters, such as consumption rates or the consumption to biomass ratio ($Q{:}B$), is a critical next step for improving ecosystem-based models (Christensen & Walters 2004).

North Pacific albacore, *Thunnus alalunga*, are highly migratory predators that account for 60,000 – 100,000 metric tons of commercial fish landings annually (ISC 2006). Adults reach 12 - 14 years of age and up to 120 cm in length. The North Pacific population of albacore is a distinct stock from populations in other ocean basins. Adults spawn in the western-central North Pacific and juveniles (ages 0-4) occupy the productive California and Kuroshio Current regions (Laurs 1977). Juvenile albacore migrate into CCS waters in the late spring and reside there until late fall. Some juveniles over-winter at the southern end of the CCS along the Baja continental shelf, while some migrate across the Pacific, turning up in the central North Pacific and the Kuroshio system (Kimura et al. 1997). Albacore complete over 90% of total growth by age five (de Zarate & Restrepo 2001); given the residence time of juveniles in the CCS, then, their diet habits in this region are of considerable importance to the overall production of their population.

Diet habits of juvenile albacore in the CCS have been quantified in four studies: McHugh (1952), Iversen 1962 (in conjunction with Graham (1959)), Pinkas et al. (1971), and Bernard et al. (1985). Data collected by Pinkas et al., in particular, are widely used in ecosystem models to describe albacore diet (Kitchell et al. 1999, Olson & Watters 2004, Field et al. 2006). These four historical diet studies never have been analyzed in concert, but they generally conclude that the diet of juvenile albacore includes *Cololabis saira* (Pacific saury), *Engraulis mordax* (Northern anchovy), cephalopods and euphausiids. Given the physical and biological changes in the CCS over the past few decades (e.g., McGowan et al. 1998, Hare and Mantua 2000), and the widespread presumption that albacore are opportunistic predators, an updated diet study is warranted.

In particular, significant fluctuations in two forage fishes, *Sardinops sagax* (Pacific sardine) and *E. mordax* (Northern anchovy) (Schwartzlose et al. 1999), motivate a specific hypothesis. Past studies have failed to find sardine in significant quantities in albacore diet. However, those studies were conducted during periods of high anchovy and low sardine abundance (Jacobson et al. 1995, Hill et al. 2007). Recently, the relative abundance of these small pelagic fishes has reversed, and sardine currently outnumber anchovy in the CCS (Hill et al. 2007). Thus, I hypothesize that, in response to the rise of the sardine, juvenile albacore have increased predation on sardine and decreased predation on anchovy.

In this study, I present new data quantifying diet habits of juvenile albacore in the CCS and, in the context of four prior studies, investigate changes in diet habits over time. I reanalyze historical albacore diet studies, originally framed by traditional metrics of diet habits (numeric abundance and frequency of occurrence), using the more contemporary approach of bioenergetics. When analyzed according to energetic contribution, the diet habits of albacore in the CCS are more narrow than previously described. The majority of albacore diet is comprised of saury and anchovy, and recently hake (*Merluccius productus*) have become important. Sardine never have been found in significant amounts in albacore diet, contrary to expectations. I argue that, although albacore are opportunistic predators, thermal optimization confines them to certain water masses even in the face of abundant prey elsewhere, and I suggest that albacore do not occupy the same waters as sardine at mesoscales.

Methods

Data collection – present study

Stomachs from 371 juvenile North Pacific albacore were collected during June – September 2005 and 2006. Sampling locations extended from central Baja California to the southern Gulf of Alaska (Figure 2.1e). Stomachs were collected on recreational charter boats (*n* = 188) and from two commercial boats (*n* = 183). The author collected stomachs from recreational vessels. These boats used troll gear and fishing poles; vessels in southern Californian and Mexican waters frequently used live bait (sardine and anchovy), and vessels in northern California and Oregon used unbaited poles. Date, time, location, type of bait (if any), and length of albacore were recorded. Most stomachs were removed on deck from fish minutes after death and frozen in dry ice; a small percentage (~10%) were collected at docks from vessels returning from day trips. Captain and crew collected stomachs on commercial vessels. These boats used troll gear and hand lines, and did not use live bait. Stomachs were removed on deck and frozen in the vessel blast freezer, and date and location were recorded.

In the laboratory, stomachs were thawed, and full and empty stomach volume and weight were measured. Stomach contents were identified visually, primarily utilizing fish vertebrae (Clothier 1952), fish otoliths (Harvey et al. 2000), cephalopod beaks (Pinkas et al. 1971, Clarke 1986), and crustacean body and eyeball morphology to identify species to the lowest taxonomic level possible. Unidentifiable remains, tissue from *Sebastes*, and voucher specimens of juvenile cephalopods were sequenced for genetic identification. Lengths of individual prey items were measured to reconstruct original (pre-digestion) prey weights; at most, five randomly chosen specimens of each species in a stomach were measured. Reconstructions of weight from published allometric relationships were based on vertebral length or otolith width for fishes (Frose & Pauly 2008, Harvey et al. 2000), lower beak rostral length for cephalopods (Wolff

1984, Clarke 1986), and carapace length for crustaceans (Isaacs et al. 1969).

Data collection – past studies

The first quantitative investigation of albacore diet in the CCS was McHugh (1952). Stomachs (*n* = 321, 20 empty) were collected during the summers of 1949 and 1950 using unbaited pole and line jigs. Sampling locations extended from central Baja California to Oregon (Figure 2.1a, based on McHugh Figure 1). Albacore lengths were not given. McHugh reported mean volumes of select prey: *Cololabis saira* (14.1 cc), *Pleuroncodes planipes* (2.6 cc), squid (1.9 cc), *Vincinguerria lucetia* (0.9 cc), *Engraulis mordax* (0.4 cc), amphipods (0.4 cc), and euphausiids (0.1 cc). Young and larval *Merluccius productus, Trachurus symmetricus, Sebastes,* paralepids, *Sardinops sagax,* and *Scomber japonicus* were found in small quantities, as well as adult myctophids. McHugh reported frequency of occurrence and total volume of prey consumed, but not numbers of prey.

Graham (1959) and Iversen (1962) reported separate results from a study undertaken by the Fisheries Biological Laboratory in Honolulu. Graham detailed stomach contents from one cruise (cruise 36) and Iversen reported the balance. Data are combined here. Investigators collected over 500 albacore stomachs between 1950 and 1957 and results were separated according to gear type (longline, gill net, and troll). Of these, I analyze here only those collected by troll gear (*n* = 155). Other sampling methods are not comparable: longline captured albacore were significantly larger (hence older) and collected most frequently in the central North Pacific, and gill net captured albacore tended to have smaller stomach volume due to regurgitation in the net. Trolling occurred primarily in the CCS, but some (*n* = 38) were collected further west (Figure

2.1b, based on Iversen Table 1). These samples outside the CCS could not be excluded from the gear-aggregated results. The troll-sampled albacore were 53 – 85 cm fork length (mean ~ 67 cm; Figure 2.2). Sampling for these specimens occurred during fall/winters 1954, 1955, and 1956 and summers 1955, 1956, and 1957. Iversen (1962) reported frequency of occurrence, number of prey items, and volume of prey items while Graham (1959) reported numeric data only. Prey size data were not reported.

Pinkas et al. (1971) collected 905 (78 empty or bait only) albacore from commercial vessels using troll gear. Sampling took place during July – November 1968 and July – September 1969, from central Baja California to the southern Gulf of Alaska (Figure 2.2c, based on their Figure 4). Fork length of albacore ranged from 52.2 – 93.2 cm, with “the majority in age groups II and III” (52 – 76 cm, Figure 2.2). Anchovy prey were 30 – 40 mm in length, but there was no further discussion of prey size. They reported frequency of occurrence, volume, and number of prey items for each of three regions (southern, central, and northern CCS). Data from the three regions were combined, and the aggregated data are analyzed here.

Bernard et al. (1985) conducted the most recent diet study of North Pacific albacore prior to the present study. Their sample size was limited: 94 stomachs (nine empty) were collected during one cruise off Southern California during August 1983 (Figure 2.2d, from their Figure 1). They collected with unbaited pole and line jigs; mean albacore fork length was 69.3 ± 8 SD cm (Figure 2.2). Anchovy prey ranged in length from 20 – 45 mm, but no other prey size data were reported. Anchovy were the only fish identified to species, and the remainder were aggregated into an ‘other fishes’ category. This impedes comparison with the other four studies, and the limited spatial and temporal scale make the study informative but interpretation must be cautious.

With the exception of 38 stomachs collected in the central North Pacific (Iversen 1962), these four studies, in conjunction with the present study, describe diet habits of 1766 juvenile albacore in the CCS at various points during a period of 52 years. Albacore were caught using the same gear (troll or pole and line), bait were identified and excluded from all studies, and size ranges of both predator and prey are comparable between studies (when reported). The CCS is inhabited by a juvenile subpopulation of the larger North Pacific albacore stock (Laurs 1977, Laurs 1991), and these five diet studies sample the same age-classes as those harvested by the commercial troll fleet based in the Eastern North Pacific Ocean (Figure 2.2). This collection of studies presents an opportunity to investigate temporal changes in albacore diet habits.

Data analysis

The taxonomic resolution of prey identification in these five studies varies. I analyze any prey category (species or species group) that occurred in at least ten albacore stomachs in any of the five studies. Ideally, all studies would report the number of prey, the weight or volume of prey, and the frequency with which prey occurred (number of stomachs containing that category). The critical information is contained in the weight or volume of prey consumed. The degree of digestion of prey was not reported by any of the four historical studies, complicating comparison of volumetric data. To overcome this, numbers of prey (presented in Iversen (1962), Pinkas et al. (1971), Bernard et al. (1985), and the present study) were converted to pre-digested weight using mean weights calculated from the 371 stomachs collected in 2005 and 2006. McHugh (1952) presented only volume and frequency of occurrence data, thus percentage volume was used directly.

Weights of prey prior to digestion were reconstituted as follows. Allometric length-weight relationships were used for all species of fish. For example, the measured length-frequency distribution for *Engraulis mordax* (Figure 2.3) was applied to the total number of anchovy consumed in each historical study. This length distribution was then transformed into wet weight (Harvey et al. 2000, Froese & Pauly 2008). For seven categories of crustaceans, direct measurements of length and weight were used. For cephalopods, measurements of beak lower rostral length were used to calculate wet weight. The lower rostral lengths measured from cephalopod beaks found in this study ranged from 0.2 – 2.0 mm. Allometric equations relating lower rostral length to total body mass for this range of beak sizes exist for *Loligo opalescens, Gonatus* sp., *Onychoteuthis borealijaponica*, and *Abraliopsis* sp. (Wolff 1984). Body mass was calculated for these four species of cephalopod, and the mean body size was used for species lacking allometric relationships.

To compare diet studies, I calculated the energetic contribution (%E) of prey to the diet of juvenile albacore:

$$\%E_i = W_i \times X_i \tag{2.3}$$

where W_i is the reconstituted wet weight (g) and X_i is the energy density (kJ g^{-1}) of species i. Energetic values are the most accurate way to quantify the importance of a prey item to the growth of the predator (Wallace 1981, Probst et al. 1984, Pope et al. 2001). Numerous indices can be used to quantify diet habits, such as the Index of Relative Importance (Pinkas et al. 1971), the Geometric Importance Index (Assis 1996), mean stomach fullness (Pope et al. 2001), and simple metrics of number, volume, or frequency of occurrence of prey. Energetic contribution avoids over-emphasizing small but numerous prey (e.g., euphausiids) or prey that occur regularly but in small numbers, and is also a biologically meaningful quantity.

A bioenergetics model of albacore, developed by Essington (2003), was used to calculate daily consumption rates (J kg^{-1} d^{-1}). Following the convention of Olson & Boggs (1986) and the model structure presented in Essington (2003), daily consumption rate (C) is calculated as:

$$C = AL + SMR + AMR + REP + G \tag{2.1}$$

where AL are losses from energy assimilation, SMR is standard metabolic rate, AMR is active metabolic rate, REP is energy dedicated to reproduction, and G is somatic growth. Here, AL describes the loss of energy, as a percentage of energy intake, due to feces (10%), excretion (10%), and specific dynamic action (15%) (Olson & Boggs 1986, Essington 2003). All components have units of J kg^{-1} d^{-1}. The model is size- and age-based, accounts for swimming speed (Dotson 1976), lift, sex ratio (1:1), age of reproductive maturity (5 years), and variable mortality (M) rates (ages 0-5 M = 0.2 yr^{-1}; age 6 M = 0.3 yr^{-1}; age 7 M = 0.4 yr^{-1}; ages > 7 M = 0.5 yr^{-1}). Parameter values were taken directly from Essington (2003) and references contained therein. To quantify the biomass (in grams) of prey consumed daily by a predator (C_B), consumption rate (C) is multiplied by ED^{-1}, the energy density of the prey (kJ g^{-1}). Finally, to calculate the annual $Q:B$, C_B is multiplied by 365.25 days per year.

Uncertainty in model parameters and calculated variables was quantified by running 10,000 Monte Carlo simulations of the bioenergetics model. Essington performed sensitivity analysis of his model and found $Q:B$ was sensitive to 10% perturbations of AL, swimming speed (x_{swim}), the slope of the line relating AMR to swimming speed (x_{AMR}), and ED. In the simulation, I varied AL, x_{swim} and x_{AMR} by 10%. Noting that ED values have never been quantified for albacore, Essington chose a mean ED value of 5.0 kJ g^{-1}, representative of energetic values for tuna prey in general (Olson

& Boggs 1986). Although Essington made no explicit assumption about the range of ED values of prey, in the case of albacore, ED values vary by more than 10% (Table 2.2). The equation demonstrates the geometric nature of the relationship: $C_B = C \times \mathrm{ED}^{-1}$ such that for every x increase in ED, C_B decreases by $1/x$. Thus, the sensitivity of the model to ED values depends on the magnitude of ED.

To investigate the impact of variable prey ED on albacore consumption rates, I collected published values of prey energy density (kJ g^{-1}) and proximate composition (Table 2.2 and Appendix 2.1). The ED values used in the bioenergetics model were sampled from a distribution determined by the mean and standard deviation of values reported in the literature. Any prey category that occurred in ten or more stomachs in any one of the five diet studies was included in analysis. While ten is arbitrary, this eliminated rare species while maintaining a large enough sample size to assess thoroughly the range of ED values albacore consume. Only ‘whole body’ values reported as wet weight were used, to the exclusion of data on muscle or other partial body values. If ED data for a species were not available, the next highest taxonomic level (same genus or family) in common with the species was used. In some cases, when ED data from a given family were not available, the nearest ecologically similar family was used. For example, values for *Paralepis atlantica* were unavailable; instead, values for the family Myctophidae were used because both taxa occupy deep water and are assumed to have similar body composition.

The four historial diet studies do not have consistent taxonomic resolution of prey categories. In cases where species were aggregated in diet metrics, the ED value used in the bioenergetics model was also aggregated. While six species of cephalopods were found in notable quantities in Pinkas et al. (1971) and this study (Table 2.1), the other three studies did not identify species of cephalopods, and therefore a mean ED value was applied to the cephalopod category in the model. Mean ED values were calculated directly. The standard deviations (SD) of the data were more complicated to compile. For crustaceans, true SDs were computed from the data points or were provided in the literature. For cephalopods, the SD is of the mean of nine species of cephalopods consumed by albacore. Finally, for fishes, a uniform percentage was applied to all categories (SD was 8% of the mean). This was based on the degree of variability found in ED of juvenile anchovy (Tirelli et al. 2006). The particular decision rule applied to any species or species category is given in detail in Appendix 2.1.

The bioenergetics model was evolved through time by varying diet habits according to the historical studies and by changing the age distribution of albacore in the CCS. The energy a predator consumes is a weighted combination of the ED of a prey item and the proportion that prey item comprises of total volumetric intake. Knowing the percentage weight a species group contributed to albacore diet, I calculated an ensemble energy density value (ED_n) for each study (simply a weighted mean). To calculate ED_n for any non-study year *x*, I used a weighting function that accounted for the distance of year *x* from the two studies flanking *x* in time (*i* and *i*+1) , such that

$$ED_{nx} = \left[1 - \left(\frac{t_x - t_i}{t_{i+1} - t_i}\right)\right] \times ED_{ni} + \left[1 - \left(\frac{t_{i+1} - t_x}{t_{i+1} - t_i}\right)\right] \times ED_{ni+1} \qquad (2.2)$$

where *t* is the year of study *i* or the non-study year *x*. C_B is a function of age, therefore I used the age-distribution of Eastern North Pacific albacore landed by North American commercial troll fisheries to represent albacore sampled by the diet studies (Figure 2.2). Data were provided by the Southwest Fisheries Science Center, NOAA (ISC 2006). This age-distribution comes from annual catch data during 1966-2005 and describes between

345,074 (1989) and 4,510,329 (1971) albacore each year, providing a large data set from which to sample. Two diet studies (McHugh 1952 and Iversen 1962) relied on data collected earlier than the beginning of the age distribution data set. To extrapolate for the time period 1949-1966, I used the mean age distribution for all years (1966-2005). In each iteration of the simulation, the following variables were randomly sampled from the distributions described above: AL, x_{AMR}, x_{swim}, ED, and predator age. $\mathrm{ED_n}$, C_B and $Q{:}B$ were calculated along with estimates of uncertainty.

Results

The five diet studies examined here sample juvenile albacore, primarily between 50-70 cm in fork length and occupying the 2-3 year age groups (Figure 2.2). Albacore sampled in 2005 and 2006 were 75.4 ± 9 (SD) cm. This is representative of the overall population of juvenile albacore that inhabit the Eastern North Pacific Ocean, as described by commercial catch data. Albacore of this size and age are not yet reproductively mature, and they allocate approximately 10% of energetic intake to growth, 20 – 25% to active metabolism (swimming), 40% to standard metabolism, and the balance is lost (Essington 2003 and values calculated here).

Considering the CCS over the past 50 years, juvenile albacore eat primarily young-of-year (YOY) fishes and cephalopods with minimal intake of adult zooplankton (Table 2.1). Despite the ability to ingest larger prey, as reflected in the few saury 100 - 200 mm in length and the size of bait ingested (Figure 2.3 and Table 2.1), their natural prey are small, recently spawned fishes 30 - 40 mm in length and cephalopods weighing approximately 4 g. *Cololabis saira*, the Pacific saury, is notable for its larger mean size (13.0 ± 20 g) associated with considerable variability. In comparison, *Engraulis mordax*, the Northern anchovy, were consistently of juvenile lengths and weights (34.7 ± 10.0 mm and 1.1 ± 1.3 g). Large (12.5 g) *Trachurus symmetricus* (Jack mackerel) were consumed as well, though not in significant numbers. The remainder of fishes were juveniles 14 - 60 mm in length, except myctophids, which, while small (50.1 ± 15.8 mm), were adults. Juvenile *Sebastes* (mean length 14.5 ± 4.5 mm) were a common prey item and were the smallest fish, as a group, regularly consumed by albacore. Cephalopods, both octopus and squid, were all juvenile sizes, while crustaceans (amphipods, decapods, and euphausiids) were adult sizes. Thus, while bait boats harvest anchovy and sardine 15 – 20 cm in length for fishing vessels to use, the natural prey of albacore are considerably smaller.

Table 2.2 summarizes ED values chosen from the literature and reports the means and standard deviations used for defining a distribution sampled in the bioenergetics model. Crustaceans and cephalopods were significantly lower in energy content than fishes, although some individual species of squid are more comparable to the mean values of fishes. Of the prey consumed by albacore, crustaceans range from 2.5 - 3.2 kJ g^{-1}, cephalopods from 3.0 - 6.7 kJ g^{-1}, and fishes from 3.5 - 7.9 kJ g^{-1} (see Appendix 2.1 for detailed accounting of species-level values).

Depending on the ensemble ED value consumed by albacore, daily consumption rates could range from 100-750 grams of prey per average-sized age-3 albacore (Figure 2.4). Prey consumed by albacore range in ED from 2 – 8 kJ g^{-1}. Given the high proportion of fish in albacore diets, the five studies lie along the flat portion of the curve relating consumption rates to prey energy density, and ED_n values for the five studies are not significantly different.

Two species of fish are consistently the most important prey items: *C. saira* and

E. mordax (Table 2.3). The energetic contribution (*%E*) of saury ranges from 24.1% - 85.1% in four of the five studies (excluding Bernard et al. (1985), because only anchovy were identified to species). It is plausible—but impossible to verify—that saury comprised a significant portion of the 'other fishes' category reported in Bernard et al (1985). Anchovy, in comparison, were not found in significant quantities in albacore diet until the 1968-1969 study, after which they have comprised 23-32% of *%E*. *Merluccius productus* (Pacific hake) is comparable in *%E* to saury in the 2005-2006 study (28.7%), but is not significant in any other study. No other category of fish comprises greater than 4% of *%E*. It is notable that, although *Sardinops sagax* can be abundant in the CCS and is regularly used as bait for albacore, it has not been a significant contributor to albacore diet in these five studies.

The Monte Carlo simulations quantified several key food web model parameters and the associated uncertainty. ED_n estimated for the five diet studies was similar, ranging from 6.0 – 7.0 kJ g^{-1}, with low variability (SDs ranging from 0.6 – 0.9 kJ g^{-1}). According to the model, a reproductively immature albacore feeding in the CCS consumes between 0.018 and 0.021 grams of prey per gram of body mass per day (C_B). Using an age-3 albacore (5.9 kg) as a example, this estimate of C_B translates into a steady-state energetic intake of between 105.7 – 124.5 grams per albacore per day.

Fishes represented the vast majority (68 – 92%) of *%E*, while cephalopods contributed between 3 and 30% *%E* (Figure 2.5). Except for Pinkas et al. (1971) and the present data set, other studies failed to resolve cephalopod prey into quantifiable species categories. Thus, I maintained that aggregation for comparison. Crustaceans, although numerically common in diet, contribute at most 10.5% (and more commonly < 5%) of albacore nutritional intake.

The annual *Q:B* calculated here is fairly stable through time and ranges from 6.7 – 8.0 year^{-1}. The greatest variability occurs early in the time series when three diet studies were relatively close in time. The studies in the late 1960s, mid-1980s, and mid-2000s have similar ED_n and the *Q:B* line is relatively flat through this period. Given the wide temporal spacing between studies, it is impossible to know whether changes in diet (and hence changes in *Q:B*) are gradual or sudden; the weighting function used here assumes the former. If the study by Bernard et al. (1985) had an ED_n significantly different from the two flanking studies, the small sample size of that study would cast doubt on including the study in analysis because the time series would be adjusted to a new ED_n value in 1983. However, given the similar values, omitting the 1983 study from the data analysis would have virtually no effect on the calculated *Q:B* time series.

Discussion

This study presents strong observational evidence that only two or three species of fish are important prey items for juvenile albacore in the California Current System. Albacore obtain greater than 60% (either singly or combined) of their total energetic intake from two species of coastal pelagic fish: Northern anchovy (*Engraulis mordax*) and Pacific saury (*Cololabis saira*). These results have been consistent over 50 years. In 2005 and 2006 (but potentially beginning earlier), Pacific hake (also called Pacific whiting, *Merluccius productus*) became energetically important, comprising 29% of albacore nutrition. Whether this species will continue to play an important role remains to be seen, and whether it was an important prey item in the past is unknowable from available data. The CCS is dominated by five species of forage fish: anchovy, saury, hake, Pacific sardine (*Sardinops sagax*), and Pacific mackerel (*Scomber japonicus*)

(Agostini et al. 2006). Of these, sardine and mackerel never have been found in significant quantities as prey of albacore. These results call into question the conventional wisdom that albacore are true generalists and suggest that albacore have diet preferences. Without concurrently quantifying prey relative abundance, it cannot be demonstrated that albacore are selectively consuming anchovy, saury, and hake over sardine and mackerel.

Continuous long-term time series of abundance of YOY fishes are available only for hake and mackerel (1966-present and 1929-present, respectively). Sardine time series have a gap from 1964-1981, anchovy data span 1963-1994 only, and saury have no associated time series because they are not commercially harvested in the CCS (Figure 2.7). Consequently, the two primary prey species are too data-poor to make conclusive statements about preference or selectivity. However, Figure 2.7 does support some observations. At any given time, YOY Pacific mackerel are considerably less abundant than sardine, anchovy, or hake, and they do not appear in albacore diet. During the 1968-1969 study (Pinkas et al. 1971), YOY anchovy and hake were in similar abundance in the CCS; sardine were not assessed and are assumed to have been far less abundant than anchovy or hake during this time (Jacobson & Macall 1995). While anchovy were significant prey in the 1968-1969 study, it is curious that hake were not also present. The 1983 study (Bernard et al. 1985) occurred during a similar period (low sardine, high anchovy and hake). However, due to the low taxonomic resolution of that study, it is impossible to know what species comprised the 60% of ‘other fishes’. Finally, by the 2005-2006 study, anchovy assessments were no longer carried out. Sardine recruitment has been high over the past two decades, and YOY sardine are more abundant than YOY hake. Additionally, it is assumed that sardine were more abundant than anchovy during

2005 and 2006 (Hill et al. 2007). Thus, one might expect sardine to be more commonly found in diet in the 2005-2006 study, rather than anchovy and hake, if relative abundance were the dominant predictor of diet habits.

Even during periods of relatively high abundance of sardine in the CCS, albacore do not appear to prey on this species. Optimal foraging theory provides several possible explanations for why albacore consume anchovy, saury, and (recently) hake instead (MacArthur & Pianka 1966, Charnov 1976, Kirby et al. 2000). First, sardine could be faster swimmers than other species and therefore more costly to chase. However, at the size consumed by albacore during summer and fall months, there is little to no difference in swimming speed of sardine and anchovy (van der Lingen 1995). Second, sardine could be of inferior energetic quality (Emlen 1966); however, sardine are considerably higher in ED than hake, slightly higher than anchovy, and only slightly lower than saury (Table 2.2). Third, albacore may not co-exist with sardine at mesoscales.

The latter seems the most plausible explanation. Adult sardine live further offshore than anchovy, saury, or juvenile hake, and the species have distinct spawning regions (Checkley et al. 2000, Reiss et al. 2008). Sardine spawn in warmer (13˚- 25˚C) offshore waters (Lluch-Belda et al. 1991) that are subject to weaker, slower rates of curl-driven upwelling (Rykaczewski & Checkley 2008), whereas anchovy and saury spawn in colder nearshore waters with stronger coastal upwelling (anchovy: 11.5˚- 16.5˚C (Lluch-Belda et al. 1991); saury 13˚ - 18˚C (Kurita 2006)). Newly spawned hake are also found in nearshore waters during spring and summer (Saunders & Macfarlane 1997). The optimal thermal range for albacore is 16-19˚C (Kirby et al. 2000), and optimal foraging models of tuna predict albacore will forage in waters just warmer than the threshold at which thermal stress accumulates. A foraging model developed by Kirby et al. (2000)

that includes prey relative abundance, water temperature, energy density of prey, and tuna bioenergetics demonstrates that, *ceteris paribus*, albacore occupy cold, nearshore waters to the exclusion of warmer, offshore waters. Under more realistic scenarios of variable prey abundance and energy density, albacore occupy warmer offshore waters when satiated, but the majority of daylight hours are spent in colder nearshore waters for foraging. Thus, I suspect that juvenile albacore prefer the habitat of YOY anchovy, saury, and hake to that of sardine even during periods of high sardine abundance.

It is possible that field data collection did not adequately sample sardine habitat, especially given sardine live further offshore than anchovy, and fishing vessels have economic incentives to stay as close to shore as possible. I overlayed sampling locations with the spatial extent of sardine and anchovy habitat described by egg distributions (see Checkley et al. 2000) in the southern CCS, and egg, larval, and adult distributions in the northern CCS (Emmett et al. 2005). Only southern egg distribution maps were available for the years concurrent with sampling (2005 and 2006). Northern distributions were from 1999-2004, but these were the only maps of sardine habitat available. Stomach sampling did occur in sardine habitat, although sampling was more frequent in anchovy habitat (Appendix 2.2).

These results raise an interesting question regarding sardine and anchovy population dynamics. Over the past century, the populations of these two coastal pelagic species have fluctuated asynchronously (Soutar & Isaacs 1974, Klyashtorin 1998, Schwartzlose et al. 1999, Lluch-Belda et al. 2001). While many explanations have been advanced, environmental factors may be the root cause (Chavez et al. 2003, Rykaczewski & Checkley 2008). If sardine and anchovy do not occupy the same water masses (Checkley et al. 2000), do not eat the same prey (van der Lingen 1995), and do not have the same predators, can the two species be considered competitors? More likely, these two coastal pelagic species have uncoupled dynamics.

The absence of hake from all but one diet study can be explained by the episodic nature of hake spawning and recruitment (Horne & Smith 1997, Lo et al. 1997). Hake have the highest degree of spatial patchiness in egg and larval distribution of any fish in the CCS (Lo et al. 1997). The geographic center of hake spawning in the CCS can move annually, likely in response to changes in temperature (Horne & Smith 1997). Hake abundance is also highly patchy in time, with outstanding years of recruitment 3 – 10 times greater than in an average year (Horne & Smith 1997, Helser et al. 2006). None of the major spikes in hake recruitment co-occurred with the four historical diet studies, and this could explain the failure to find large numbers of hake in diet. If a diet study had been conducted during 1980, the largest recruitment spike for hake on record (Horne & Smith 1997), hake may have been found in significant quantities. Although hake abundance during the 1968-1969 study was on par with abundance of anchovy (Figure 2.7), the absence of hake in the diet study could be due to a temporal mis-match in hake spawning and albacore predation in the CCS, a temporal or spatial mis-match in hake presence and stomach sampling, or a difference in relative abundance of hake to itself. That is, there may be some threshold abundance of hake above which albacore consume significant quantities but below which albacore focus on anchovy and saury for prey.

This study reconceptualizes four historical diet studies by translating numeric gut content data into the currency of energetics. Consequently, the diet habits of albacore appear less diverse than presumed in the past. For example, Pinkas et al. (1971) emphasize the importance of crustaceans, in particular euphausiids, to albacore diet. However, when ED is taken into account, crustaceans are insignificant: only one of five studies found *%E* greater than 3%. Likewise, cephalopods were 30% of energetic intake during the 1968-1969 study, but elsewhere cephalopods contributed less than 12%. This new view of albacore diet habits suggests that their classification as generalist predators may be unwarranted. Undoubtedly albacore ‘eat what they see,’ a characteristic of opportunists. However, what they see may be confined to a particular environment, in this case, to that favoring juvenile anchovy, saury, and hake. Therefore, the scale at which predation is viewed becomes critical. If one conceptualizes of the CCS as an aggregated food web, albacore do not appear to consume some species of fish (namely, sardine) in proportion to their abundance in the environment. However, when smaller spatial scales are considered, albacore consume prey they have the opportunity to encounter, possibly in proportion to their relative encounter rates.

Underlining findings of many others (Stewart & Binkowski 1986 and following references), this study emphasizes the potential importance of variable ED of prey to accurate modeling of predator consumption rates (Stewart & Binkowski 1986). Interspecific variability in ED has been recognized as a significant cause of feeding variability in marine mammals (Lawson et al. 1998a, Laidre et al. 2002). Some studies have demonstrated that ED values can differ significantly within a species, depending primarily on prey reproductive status (Kitts 2004) and size (Cianelli et al. 2002, van de Putte et al. 2006). However, other studies have shown weak or no relationships between size and energy density (Payne et al. 1999, Eder & Lewis 2005). In the case of North Pacific albacore, prey spawning status is uniform (reproductively immature) and the size distribution of prey is narrowly confined to YOY sizes. Thus, the most relevant evidence on this point comes from studies that focus on juvenile fishes (e.g., Arrhenius & Hansson 1996 (Baltic sea sprat), Cianelli et al. 2002 (Bering Sea pollock), Tirelli et al. 2006

(Adriatic sea anchovy)). These studies find that, among juvenile fishes, ED increases linearly throughout a season with growth, but the intraspecies variability at any given time is low. Thus, when focusing on a sub-population of predators in a given region and season, the effects on predation of intraspecies ED variability attributable to differences in size or spawning status are less important than interspecies variability.

The choice of ED_n used in a bioenergetics model can have a significant impact on calculated consumption rates for certain types of predators (Figure 2.4). There is a geometrically decreasing relationship between the biomass a predator must consume to maintain stable energetic intake and the ensemble energy density consumed by the predator. The steepest portion of the curve in Figure 2.4 demonstrates the importance of calculating a weighted mean for ED values used in bioenegetics or mass balance food web models. For example, if albacore diet were 75% *Pleuroncodes planipes* (a pelagic decapod) and 25% *E. mordax*, ED_n would be 3.9 kJ g^{-1} and an age-3 albacore would need to consume 190.5 grams per day, or 3.2% of its body weight, to maintain stable energetic intake. However, if diet were 25% *P. planipes* and 75% *E. mordax*, ED_n would be 5.8 kJ g^{-1} and that albacore would need to consume only 128.8 grams, or 2.2% of body weight, per day. Furthermore, the arithmetic mean of the individual ED values (3.0 and 6.7 kJ g^{-1}, respectively) of 4.8 kJ g^{-1}, corresponding to consumption of 154.8 grams per day, is an inaccurate estimate. When scaled to the population level, as in most ecosystem models, these inaccuracies become significant. Thus, unless prey are consumed in uniform proportions, an ensemble ED must be calculated as a weighted mean.

Although the three main prey items of albacore vary in ED, the range of values lies on the asymptotic portion of the curve in Figure 2.4 and thus tradeoffs between prey items may be of small consequence to daily consumption rates. Hypothetically, if diet was 100% hake (ED = 5.9 kJ g^{-1}), an average-sized age-3 albacore (5.9 kg) would have a daily biomass demand of 125.9 g, whereas daily demand for 100% anchovy (6.7 kJ g^{-1}) would be 110.9 g and for saury (7.5 kJ g^{-1}) demand would be 99.1 g. A 25% difference in daily demand between saury and hake might ultimately impact albacore growth rates. However, given the mix of several important species in albacore diet, the ensemble energy density values are strikingly similar (Figure 2.6). This suggests that albacore have a stable base of prey, from an energetics standpoint.

However, this is not to neglect the possibility of detrimental shifts in the future, nor to discount the importance of variable ED_n in other types of predators. Changes in relative energy density can explain predator preferences in prey (Mohn & Bowen 1996, Stenson et al. 1997) and declines in ED_n have been linked to declining predator populations (Lawson et al. 1998a). For example, declines in Stellar sea lions in the Gulf of Alaska have been tied to increases in pollock (lower ED) concurrent with decreases in cod (higher ED) (Kitts 2004). If the suite of prey available to albacore in the CCS were to change significantly, and in particular, if anchovy and saury were replaced by lower energy prey, albacore would either switch prey, increase daily consumption rates, or face declining growth rates. Moreover, and in general, the type of predator is a critical consideration when assessing variable energy densities of prey. For predators that consume primarily crustaceans or other low energy density prey, interspecies variability can lead to dramatic differences in daily consumption rates. However, for piscivores or predators that consume high energy density prey, the interspecies differences may contribute much less to overall variability in growth rates or population dynamics.

The low variability in ED_n consumed by albacore translates into equally stable *Q:B* ratios over decades. *Q:B* is a measure of the relative predation rates of albacore, and this study suggests the amount of biomass consumed by juvenile albacore, on a per-weight basis, has remained stable through time. The variability in *Q:B* is driven by changes in the ED_n calculated for each study year and by which the bioenergetics model was weighted. The value for *Q:B* calculated here (mean 7.3) is lower than the 13.4 calculated by Essington (2003). Essington used a mean ED value of 5.0, and his calculation applied to the full age-structure of albacore and not a subpopulation; adults significantly increase the ratio. Consequently, for any given ecosystem model that is spatially defined (e.g., Field et al. 2006) and contains a predator population with age-structure, a regional *Q:B* is needed. Finally, while these *Q:B* ratios are specific to juvenile North Pacific albacore in the CCS, the estimates of uncertainty can be used to guide input to models of other species and systems.

Diet data from periods over the past fifty years should offer some reassurance that consumption rates and ensemble energy density values are stable, even during periods of widespread change in the physical and biological components of the CCS (such as those in 1976-1977; e.g., Roemmich & McGowan 1995, Mantua et al. 1997, McGowan et al. 1998, Hare & Mantua 2000, Minobe 2002, McGowan et al. 2003). These findings are analogous to those of Lavaniegos & Ohman (2007), who showed carbon biomass of zooplankton in the CCS has remained stable throughout the oceanic changes evident during 1976-1977. Despite changes in species composition of CCS zooplankton since the mid-1950s (Ohman & Venrick 2003), the aggregated biomass of zooplankton has remained stable (except for pelagic tunicates which are found extremely rarely in albacore diet). Although zooplankton are not a major source of energy to albacore, stable carbon biomass estimates of these lower trophic levels suggest that the overall food web has redundancies at the level of species.

This study supports recent calls (Link 2007) to expand data collection for species of fish that are not currently monitored or assessed. Heavy fishing pressure has been linked to serial depletion of top predators: when one commercial species is fished to low population abundances, fisheries have economic incentives to switch to a different species (Pauly et al. 2002, Link 2007). For example, Link (2007) recently demonstrated in Georges Bank that previously unfished groundfishes are subject to new and increasing levels of fishing mortality, and changes throughout the food web have resulted. One of the most alarming aspects of serial depletion is newly fished species are rarely as well studied as traditionally profitable fisheries (Pauly et al. 2002). This scenario has a likelihood of being repeated in the CCS. The dearth of data describing saury in the CCS, and the short time series of anchovy biomass, mean we cannot be sure if the recent increase in hake in albacore diet is a result of fewer anchovy or saury in the environment. We can say for certain that if the ED_n available to albacore declines to the steep portion of the curve in Figure 2.4, the productivity of their juvenile population will also decline, and this will ultimately translate to the North Pacific-wide population and into the commercial fishery for albacore. Human catch of anchovy and saury are low and zero, respectively, suggesting albacore are not directly competing with humans for their most important prey items. However, humans already have expanded fisheries into previously unharvested species, and the trend will most likely continue to sustain world protein demand (Pauly et al. 2002). Collection of more thorough biological data on saury and resumption of stock assessments of anchovy may be a prudent undertaking now, before these stocks face new or increasing fishing pressure. Failure to understand and document long-term changes in these critical prey species may one day inhibit our study of the population dynamics of a commercially-important marine predator.

Conclusions

The results presented in this study should be useful for developers and users of ecosystem models. First, I demonstrate that, even over 50 years of variable environmental conditions (Mantua et al. 1997, McGowan et al. 1998, Minobe 2002) and changes in the biological community in the CCS (e.g., Roemmich & McGowan 1995, Hare & Mantua 2000, McGowan et al. 2003, Brodeur et al. 2005), the diet habits of an important predator have not changed substantially, except recently to incorporate a third major prey item. We should not ignore prey items that make up a small component of diet. Weak interactions are important for the topological stabilization of food web models (McCann 1998) and pressure on rarely consumed species, such as *Sebastes*, may scale to be a significant source of predation. However, from the perspective of the predator, understanding of predator-prey dynamics could be greatly enhanced by focusing research efforts on a few key prey species.

Second, I demonstrate that while ensemble ED can significantly affect daily consumption rates, the nonlinear relationship demonstrated in Figure 2.4 is of varying significance depending on the type of predator in question. For predators whose diet is largely comprised of crustaceans and cephalopods, or who have a diet that is bi-modal in terms of ensemble ED (half crustacean-half fish), changes in prey availability may have large impacts on consumption rates (Probst et al. 1984). For piscivores in general, because they are feeding at the asymptotic portion of the consumption curve, the exact nature of species composition of available prey suites may have less of an impact on growth rates than other factors.

Third, I demonstrate that it is possible to quantify variability in critical model parameters such as *Q:B* in a given region and for a particular population of predator. As ecosystem models begin to incorporate measurements of uncertainty, field-verified data are increasingly needed (Christensen & Walters 2004). If these parameters are robust, and if the critical rates can be identified and correctly measured, there is promise for successful forecasting with large multispecies models.

Table 2.1. Measured lengths and calculated weights of prey categories in common to five studies of albacore diet. Measurements were made from stomach contents collected in 2005-2006 (this study). Mass values were applied to numeric data from past studies to reconstruct the pre-digestion wet weights of prey.

	Length *n*	Length (mm) Mean (SD)	Weight *n*	Weight[1] (g) Mean (SD)
Crustaceans				
Amphipods	47	11.7[2] (6.5)	8	0.04 (0)
Pleuroncodes planipes	2	33.8[2] (2.5)	1	2.0
Euphausiids	30	23.0[2] (4.8)	8	0.1
Malacostracans	24	26.3[2] (8.4)	1	0.1
Cephalopods	181	0.8[3,6] (0.2)	181	3.8[6] (4.0)
Fishes				
Cololabis saira	87	119.1[4] (68.3)	87	13.0 (20.0)
Engraulis mordax	421	34.7[4] (10.0)	421	1.1 (1.3)
Sardinops sagax	128	49.21[4] (16.9)	128	1.8 (3.6)
Sebastes spp.	29	14.5[4] (4.5)	29	0.1 (0.1)
Merluccius productus	232	60.9[5] (15.3)	232	2.1 (2.0)
Trachurus symmetricus	7	64.7[5] (39.3)	7	12.5 (17.6)
Myctophidae	16	50.1[5] (15.8)	16	1.9 (1.4)
Fishes (other)	942	49.7[6] (34.9)	942	2.5 (7.3)[6]
Engraulis mordax bait	29	100.0[4] (22.8)	29	13.6 (7.0)
Sardinops sagax bait	39	145.5[4] (16.2)	39	33.0 (12.9)
Scomber japonicus bait	8	227.7[5] (36.1)	8	60.9 (21.5)

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[1] Wet weight (g)
[2] Tip of rostrum to end of telson (mm)
[3] Beak lower rostral length (mm)
[4] Standard length (mm)
[5] Total length (mm)
[6] Taxonomic mean

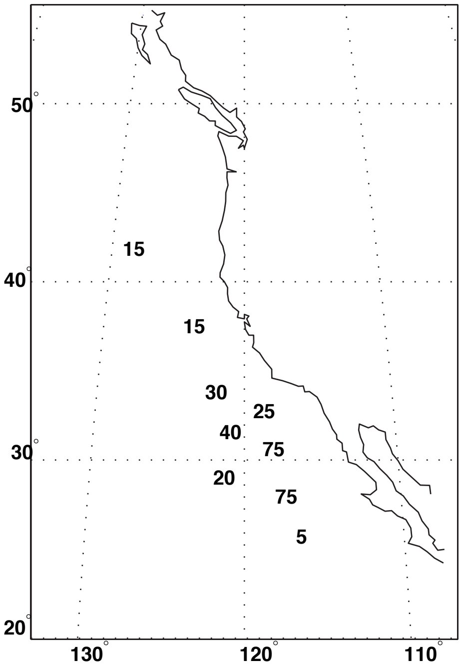
Table 2.2. Energy density values (kJ g^{-1}) of prey common to five studies of albacore diet.

Species Category	mean ED	SD ED
Amphipods	2.5	0.9
Pleuroncodes planipes	3.0	1.3
Euphausiids	3.1	1.1
Crustaceans (other)	3.2	1.1
Cephalopods	4.4	0.5
Cololabis saira	7.5	1.0
Engraulis mordax	6.6	0.5
Sardinops sagax	7.3	0.6
Sebastes spp.	4.2	0.3
Merluccius productus	5.9	1.3
Trachurus symmetricus	6.4	0.5
Myctophidae	7.1	0.6
Paralepididae	7.1	0.6
Vinciguerria lucetia	5.2	0.4
Fishes (other)	6.6	0.6

Table 2.3. Energetic contribution (*%E*) of prey to diet of juvenile albacore in the California Current. Studies are: McHugh 1952, Iversen 1962, Pinkas et al. 1971, Bernard et al. 1985, and Glaser (this study). Columns are years data were collected. Species categories represent taxa in common to the five studies, in general distinguishing any species category accounting for ≥ 1% of *%E*. The ensemble ED is the weighted mean energy density value. Consumption rate and daily demand are calculated using a bioenergetics model (Essington 2003) for an age-3 albacore of mean weight (5.9 kg).

Species Category	1949-1950	1954-1957	1968-1969	1983	2005-2006
Amphipods	0.8	0.1	0.1	0.0	0.0
Pleuroncodes planipes	5.5	0.0	0.2	0.1	0.0
Euphausiids	3.6	0.4	0.8	0.4	0.4
Malacostracans	0.5	0.0	0.7	0.0	0.6
Cephalopods	8.8	10.3	30.4	2.8	12.4
Cololabis saira	57.6	85.1	37.4	0.0	24.1
Engraulis mordax	4.5	0.0	22.8	31.9	24.9
Sardinops sagax	0.0	0.0	0.0	0.0	5.2
Sebastes spp.	0.7	0.0	0.5	0.0	0.0
Merluccius productus	3.0	0.0	0.0	0.0	28.7
Trachurus symmetricus	3.2	0.0	0.0	0.0	0.9
Myctophidae	1.2	1.1	3.8	0.0	0.5
Paralepididae	3.6	0.0	0.1	0.0	0.0
Vinciguerria lucetia	2.6	0.0	0.0	0.0	0.0
Fishes (other)	4.4	3.0	3.3	64.8	2.2
Ensemble ED (kJ g^{-1})	6.0	7.0	6.2	6.5	6.2
Standard deviation	0.9	0.9	0.7	0.6	0.9
Consumption rate (g g^{-1} d^{-1})	0.021	0.018	0.020	0.019	0.020
Standard deviation	0.0047	0.0035	0.0044	0.0044	0.0042
Daily demand (g $fish^{-1}$ d^{-1})	124.5	105.7	120.4	115.4	119.6
Standard deviation	28.8	20.9	26.0	25.9	24.7

a) collected during 1949-1950



b) collected during 1954-1958

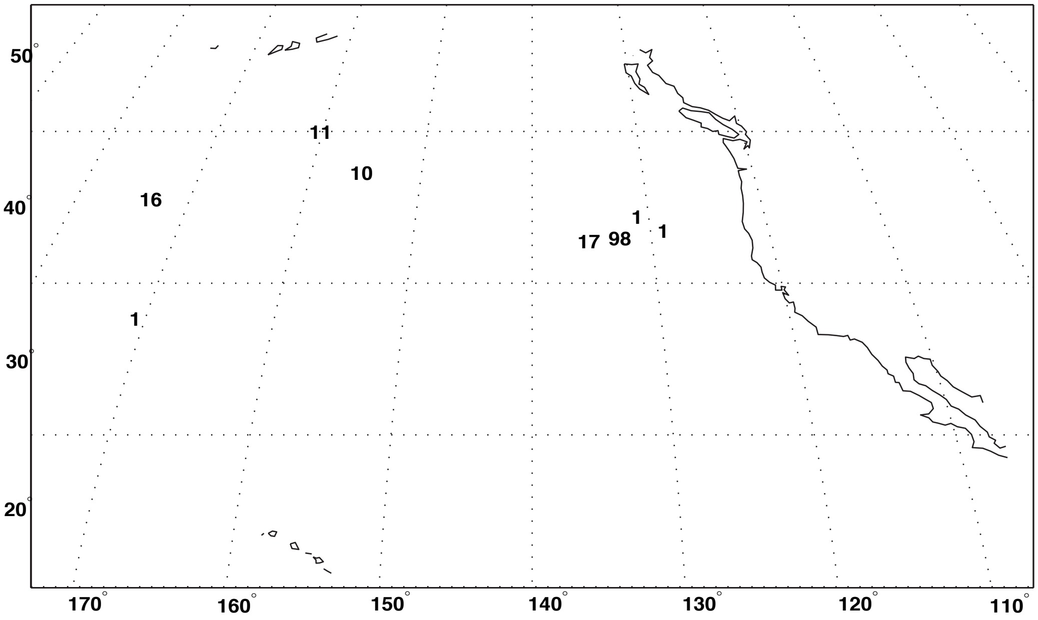
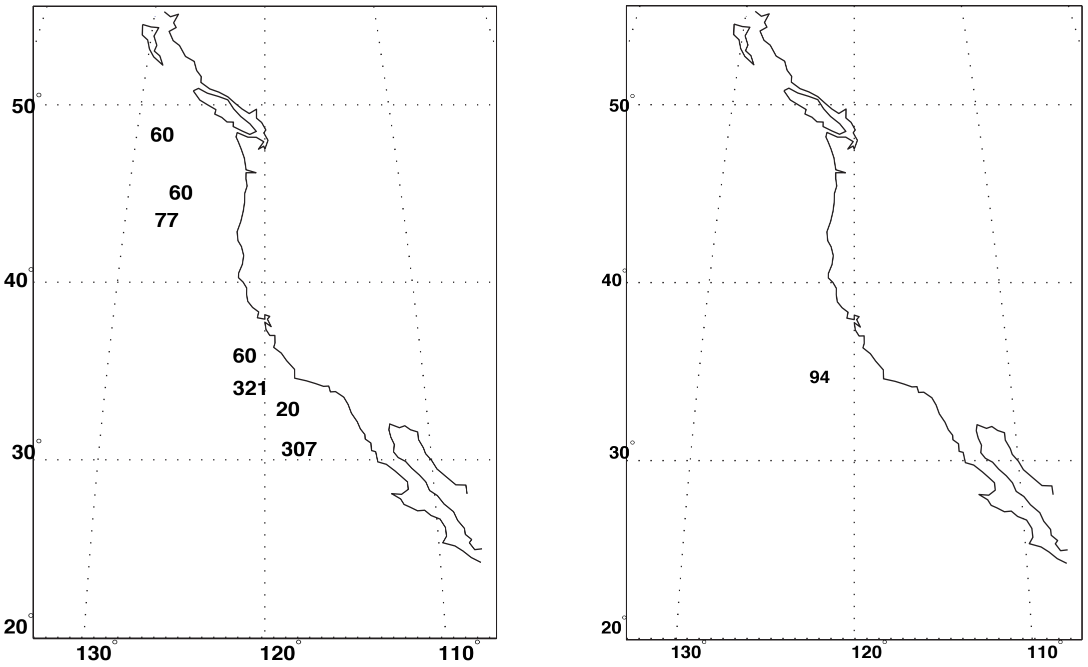
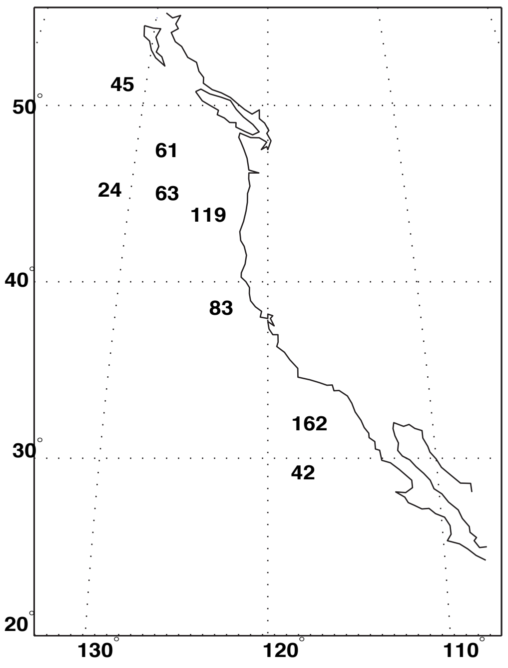


Figure 2.1. Distribution of sampling effort for five albacore diet habits studies. a) McHugh 1952, b) Graham 1959 and Iversen 1962, c) Pinkas et al. 1971, d) Bernard et al. 1985, e) this study.



c) collected during 1968 - 1969

d) collected during 1983



e) collected during 2005 - 2006

Figure 2.1. Distribution of sampling effort for five albacore diet habits studies. a) McHugh 1952, b) Graham 1959 and Iversen 1962, c) Pinkas et al. 1971, d) Bernard et al. 1985, e) this study. Continued.

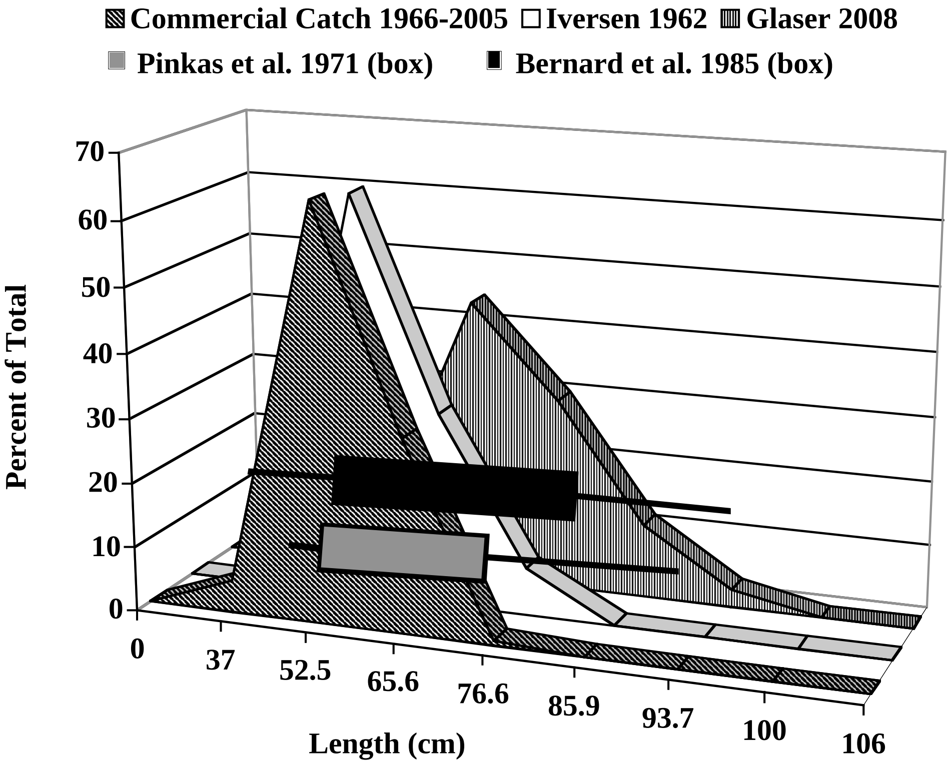


Figure 2.2. Length-frequency distribution of albacore from 4 of 5 diet studies, and from commercial logbooks of Eastern North Pacific troll fisheries. Albacore length data were not reported for McHugh (1952).

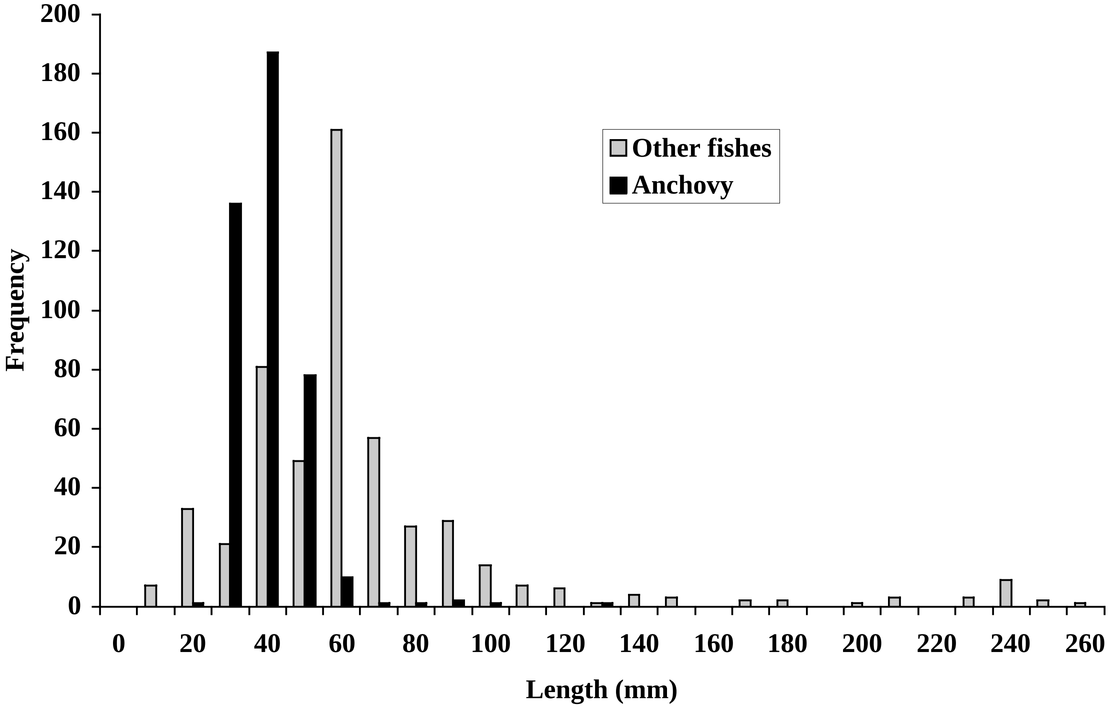


Figure 2.3. Length-frequency distribution of fish prey (*n* = 942) found in juvenile albacore, 2005-2006 (this study). Bait are excluded. Length distribution of anchovy (*n* = 421) is singled out.

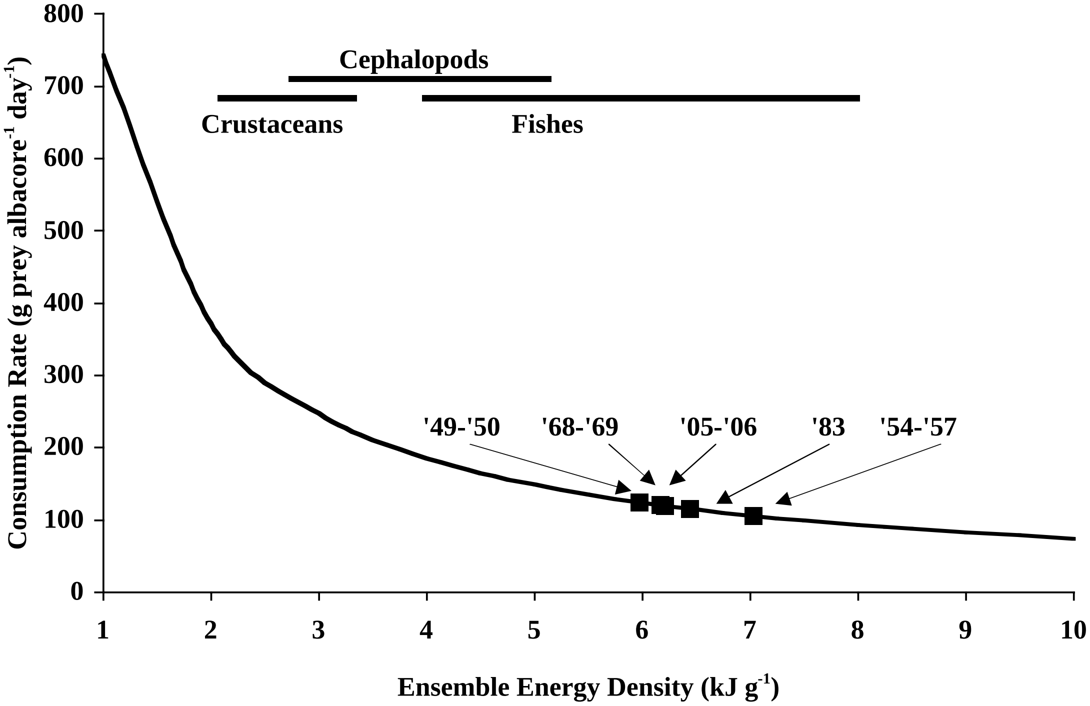


Figure 2.4. Influence of prey energy density on daily consumption rates of albacore. Consumption rates were calculated according to Essington (2003) for age-3 albacore (mean weight 5.9 kg). The ensemble energy density (a weighted mean, ED_n) calculated for five albacore diet studies is marked. The range of ED values for prey species found in albacore diet is shown for reference.

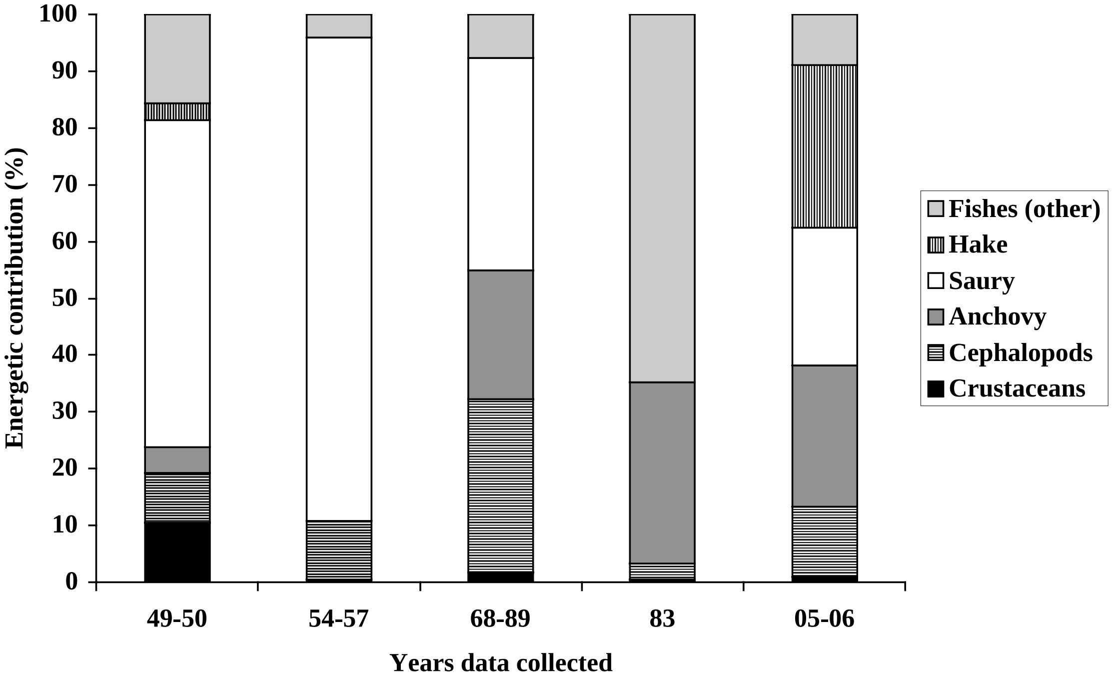


Figure 2.5. Energetic contribution of common prey items to juvenile albacore diet in the California Current System. Energetic contribution is calculated as the percent total weight (g) × energy density (kJ g^{-1}) for a given prey category.

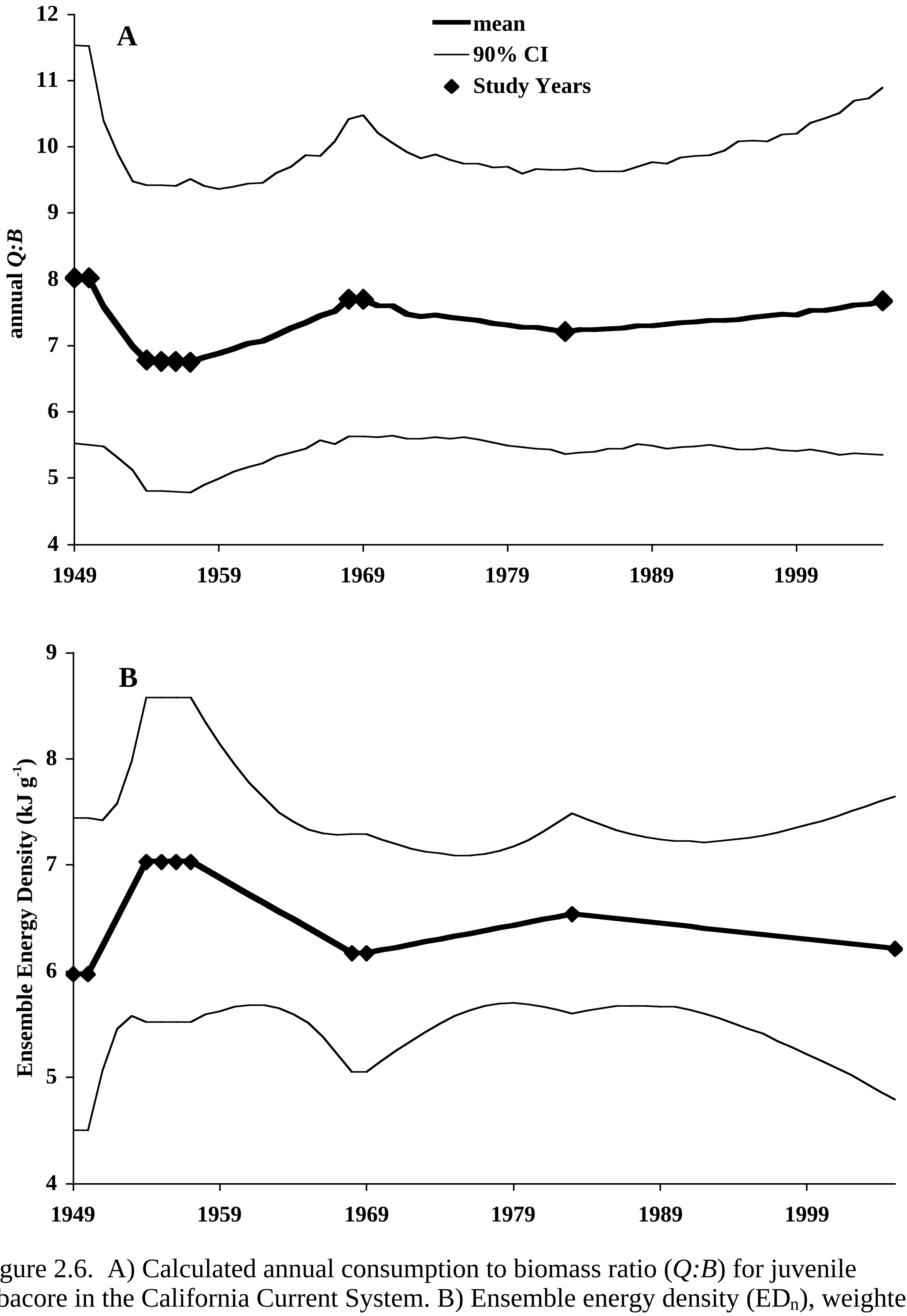


Figure 2.6. A) Calculated annual consumption to biomass ratio ($Q:B$) for juvenile albacore in the California Current System. B) Ensemble energy density (ED_n), weighted according to proximity from two flanking diet studies. Diet studies denoted by diamonds.

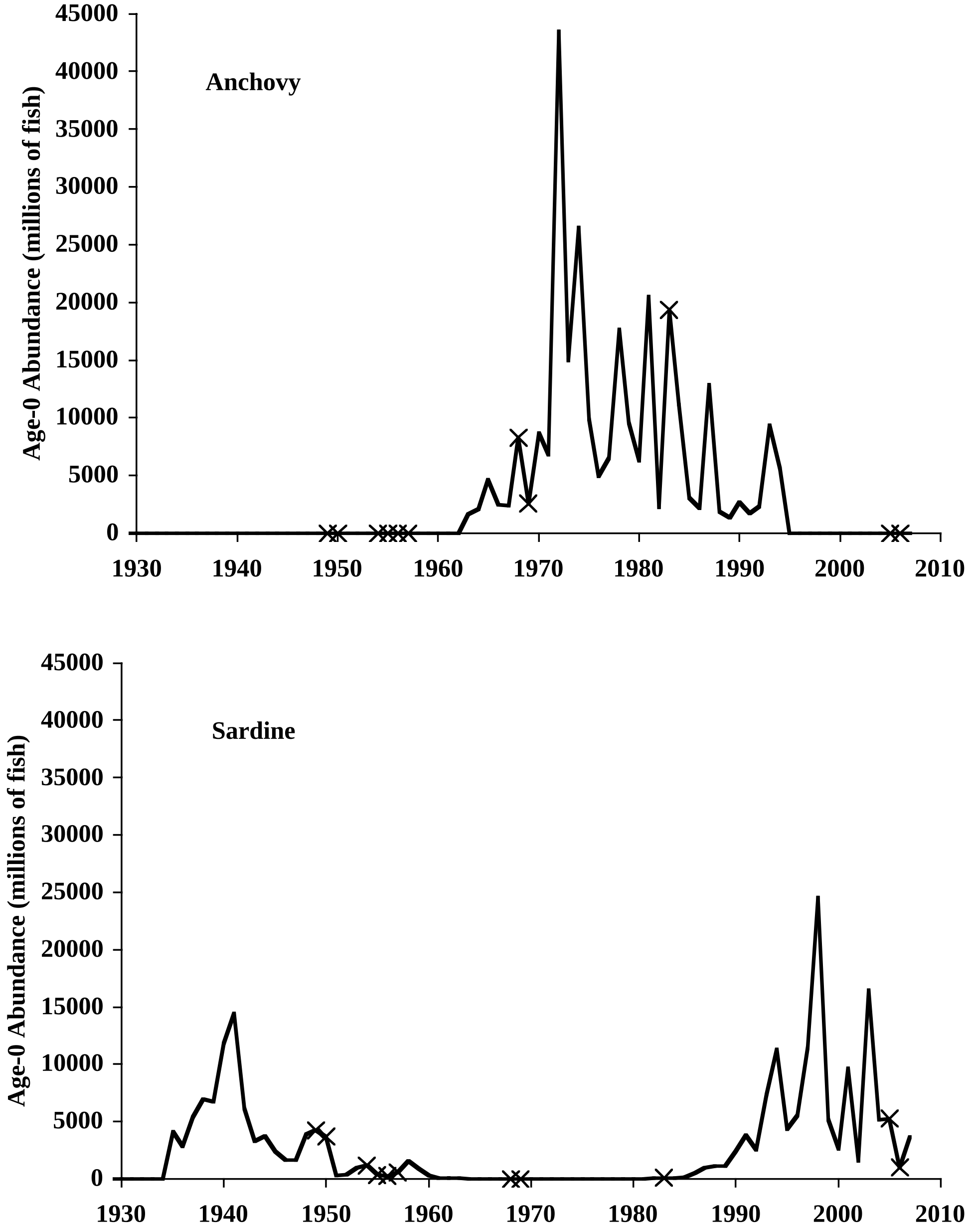
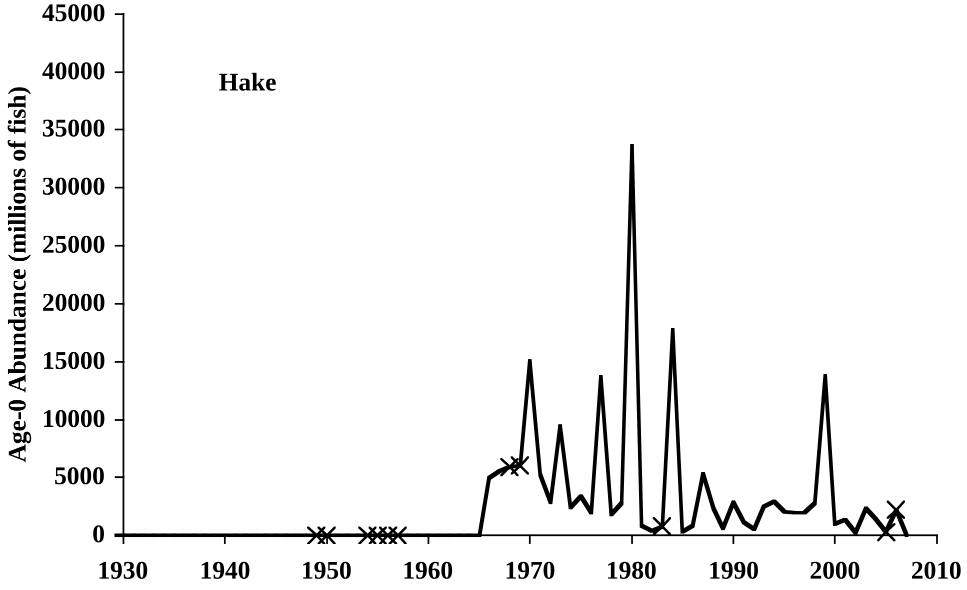


Figure 2.7. Time series of abundance for age-0 (recruitment) anchovy (Jacobson et al. 1995), sardine (Jacobson & MacCall 1995, Hill et al. 2007), hake (Helser et al. 2006), and Pacific mackerel (Hill & Crone 2005). Diet study years are marked. Note the different *y*-axis for mackerel.



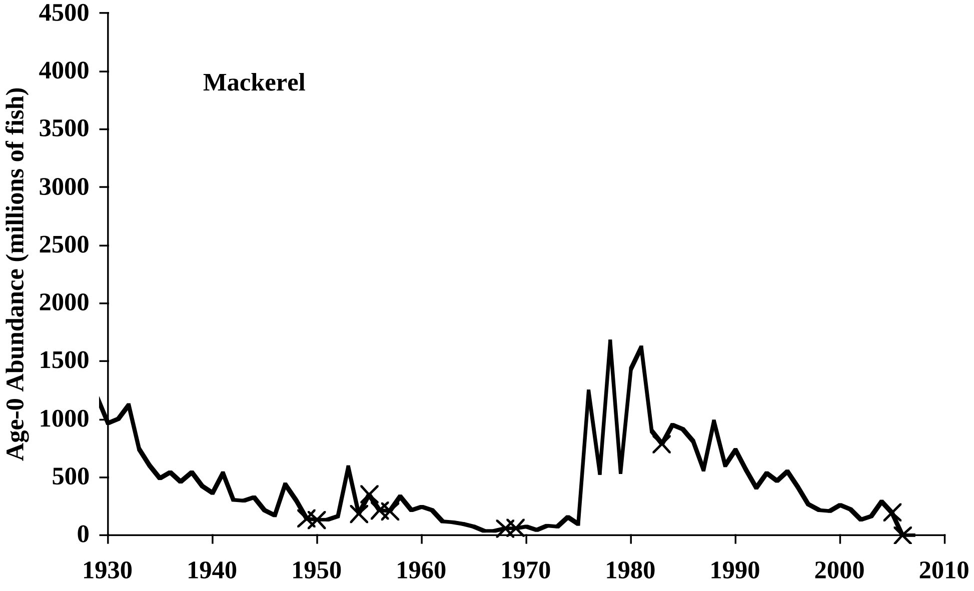


Figure 2.7. Time series of abundance for age-0 (recruitment) anchovy (Jacobson et al. 1995), sardine (Jacobson & MacCall 1995, Hill et al. 2007), hake (Helser et al. 2006), and Pacific mackerel (Hill & Crone 2005). Diet study years are marked. Note the different *y*-axis for mackerel. Continued.

Appendix 2.1. Variability in prey energy density values.

Variability in intra- and interspecies energy density (kJ g^{-1}) was assessed from values reported in the literature (Table A2.1). Taxonomic aggregation was based on species categories used in Chapter 2, and represent those categories that occurred in ten or more stomachs in any of four historical studies (McHugh 1952, Iversen 1962, Pinkas et al. 1971, Bernard et al. 1985) or the present study. For many prey consumed by albacore, species-specific energetic values were available. However, for others, closely related or ecologically similar species were used. Furthermore, the taxonomic resolution of diet categories often necessitated aggregation of species values. For crustaceans, mean and standard deviation (SD) was available for *Pleuroncodes planipes*; otherwise, values were reported as taxonomic aggregations (amphipods and euphausiids) and I averaged values reported for 25 species of decapods and mysids for the ‘Crustaceans (other)’ category. In the case of cephalopods, I used values for four species that are consumed by albacore, three species in the same family as species consumed by albacore, and two values that were reported for the categories Octopoda and Decapoda, generally. The SD was calculated for cephalopods using these nine values, some of which were means themselves.

Finally, for fishes, values were available for most species, unless otherwise noted in Table A2.1. The SD used for all categories of fishes was based on data from Tirelli et al. (2006). They found low SDs (8% of the mean) for *Engraulis encrasicolus* ranging from 40 – 59 mm in length, the size range of fish prey found in albacore diet. As most studies that calculate *ED* report, the greatest degree of intraspecies variability occurs in adults at spawning. Therefore, I assumed similarly low levels of ED variability for the other juvenile fish species. Values for *Vinciguerria lucetia* were unavailable; instead, I used the mean value calculated for five categories of Myctophidae, because the similarities between ecological niches (vertically migrating mesopelagic fishes) suggests similar body chemistry. The SD for the category 'Fishes (other)' is the SD of the values collected from the literature for all fishes.

The following studies are referenced in Table A2.1:

a) Sidwell 1981

b) Abitia-Cardenas et al. 1997

c) Davis et al. 1998

d) Donnelly et al. 1993

e) Lawson et al. 1998b

f) Eder & Lewis 2005

g) Perez 1994

h) Osako et al. 2002

i) Riis-Vestergaard et al. 2000

j) Hunt et al. 2000

k) Payne et al. 1999

l) Childress & Nygaard 1973

m) Peterson 1979

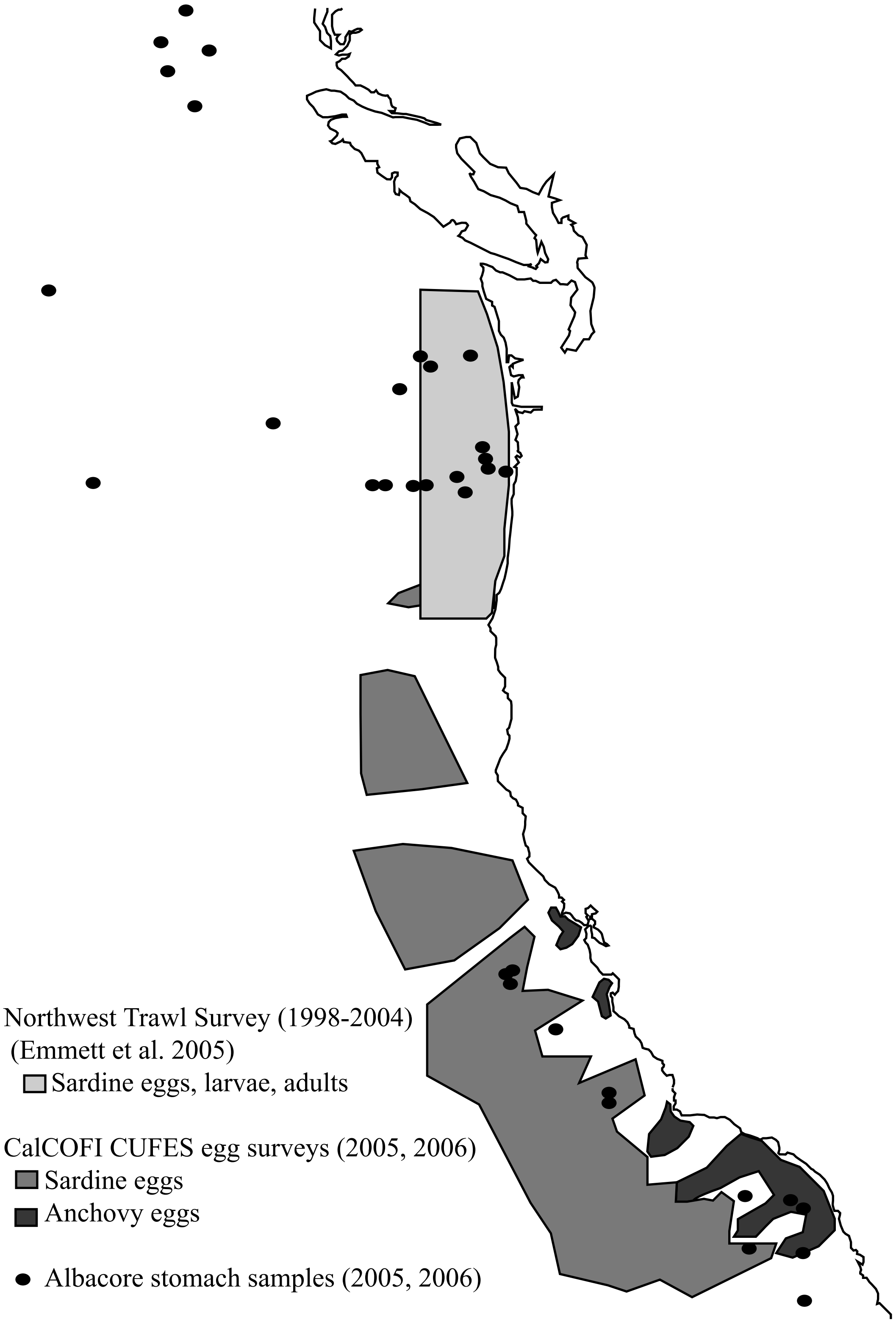
n) Bunce 2001

o) Childress et al. 1980

Table A2.1. Energy density values used to calculate distributions for parameters in an albacore bioenergetics model.

Species category	Mean ED	ED values from literature	Notes on means	SD	Notes on SDs
Amphipods	2.5	2.5c		0.9	literature
Pleuroncodes planipes	3	2.09a, 3.93b		1.3	two studies
Euphausiids	3.1	3.1c		1.1	literature
Malacostracans	3.2	3.2d	Mean of 25 species decapods and mysids	1.1	literature
Cephalopods	4.4	3a, 6.72e, 3.51a, 5.64f, 3.29a, 3.85g, 3.8g, 4.69g, 5.4g	Octopoda, *Gonatus fabricii*, *Loligo opalescens*, *Moroteuthis ingens*, Decapoda, *Berryteuthis magister*, *Berryteuthis* sp., *Gonatopsis borealis*, *Onychoteuthis borealijaponica*	0.47	mean of 9 categories cephalopods
Cololabis saira	7.5	7.92a, 7.0j		1.04	8% of mean
Engraulis mordax	6.6	6.7a		0.54	8% of mean
Sardinops sagax	7.3	8.6n, 7.4b, 5.9o		0.58	8% of mean
Sebastes spp.	4.2	3.75a, 3.95a, 4.39a, 3.87a, 3.99a, 4.37a, 4.79a, 4.43a, 3.7a, 5.12f, 3.95a, 4.18a, 3.75a, 3.21a, 3.95a, 5.21e, 4.65a	*Sebastes alascanus*, *S. aleutianus*, *S. crameri*, *S. elongatus*, *S. flavidus*, *S. inermis*, *S. iracundus*, *S. matsubarae*, *S. melanops*, *S. oculatus*, *S. paucispinus*, *S. pinniger*, *S. rosaceus*, *S. ruberrimus*, *S. rubivinctus*, *S. spp.*, *S. goodei*	0.34	8% of mean
Merluccius productus	5.9	5.9i	Regression equation: mean ED calculated from hake size-frequency in this diet study	1.3	8% of mean
Trachurus symmetricus	6.4	6.4h	Value for *Trachurus japonicus*	0.51	8% of mean
Myctophidae	7.1	9.8a, 7.6k, 7.6l, 7.3l, 3.5a	*Diaphus theta*, Lanternfish, *Stenobrachius leucopsaurus*, *Triphoturus mexicanus*, *Tarletonbeania crenularis*	0.57	8% of mean
Paralepididae	7.1	7.1	Value for Myctophidae	0.57	8% of mean
Vinciguerria lucetia	5.2	5.2m		0.42	8% of mean
Fishes (other)		6.6	Mean value of all 9 fish categories here	0.6	mean of 9 categories fishes

Appendix 2.2. Sampling in relation to sardine habitat.



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Chapter 3. The foraging ecology of North Pacific albacore in the California Current System.

Abstract

The aim of this study is to describe the foraging ecology of albacore through patterns of variability in diet habits at medium spatial and temporal scales, and small scales of taxonomic resolution. Specifically, I investigate whether albacore are strict generalists, and I hypothesize that their foraging behavior will involve a mixed approach. Stomachs from 371 juvenile albacore were collected from throughout the California Current System (CCS) during summer and fall 2005 and 2006. Numeric, biomass, and frequency of occurrence data were collected along with prey length and weight. Variability was calculated between individuals, between daily aggregations of albacore, between regional divisions of the CCS, and between years. Daily ration was calculated from a bioenergetics model and compared to the observed energetic content of prey inside each stomach. 59 prey categories were identified and, on average, each stomach contained only four unique prey categories. Anchovy were the most numerous and most frequent prey, and hake comprised the greatest biomass. Multivariate analysis showed prey varied between daily sampling units and between regions. In the northern CCS, decapods, euphausiids, and anchovy dominated the biomass of prey; in the central CCS, hake and saury dominated; and in the southern CCS, anchovy were the sole significant prey. Interannual variability was not detected. Total energetic intake calculated from observed stomach contents (141 ± 193 kJ kg^{-1} d^{-1}) was comparable to demand calculated by the bioenergetics model. Graphical approaches to examining foraging strategy

demonstrated that albacore are not true generalists, as commonly thought, but rather employ a mixed-feeding strategy that includes specialization on anchovy, high between-predator variability in second-tier prey such as hake and saury, and generalized, but rare, predation on over 50 additional species of prey.

Introduction

Foraging theory predicts that a suite of interacting variables will dictate the feeding preferences of a predator. A model of predator response to prey was formalized by Holling (1959), in which the number of predator attacks on a species of prey was related to prey density, encounter rate, search time and handling time. However, foraging strategies are even more complex in highly variable environments (Dall & Cuthill 1997). Predation can be variable in time and space given environmental gradients of productivity (MacArther & Pianka 1966), absolute and relative abundances of prey (Ivlev 1961, Roughgarden 1974), ontogenetic changes in the predator (*e.g.*, increases in speed or gape size with predator size) (Werner & Gilliam 1984), the caloric value of prey (Emlen 1966), or the cost to the predator of pursuit (Charnov 1976).

The foraging strategy of a predator can provide insight into the cost-benefit analysis applied to how, when, and where to focus hunting effort (Emlen 1966, Roughgarden 1974, Stephens & Krebs 1986, Kirby et al. 2000). Such tradeoffs ultimately create evolutionary pressures that, in the long-term, affect predator growth rates and life history strategies (Roughgarden 1974). Predator foraging strategies can be classified as generalist or specialist, and the diversity of prey species consumed is dubbed the predator’s niche width. Generalists consume a high diversity of prey, frequently in direct proportion to the relative abundance of prey in the environment (Stephens & Krebs 1986). This is not a condition of generalism, however, as predator preferences for certain species of prey could result in disproportionate consumption of some species, while the niche width of the population of predators remains wide. Specialists consume a low diversity of prey, frequently focusing hunting effort on one or two species. This narrow niche width could be a result of allometric constraints, such as jaw size, or preferences in prey habitat or caloric value (Emlen 1966). However, categorization of foraging strategies can be plastic.

A population of predators may exhibit generalist or specialist foraging strategies, or a combination of both. A thorough understanding of niche width is essential to properly categorizing foraging strategies (Tokeshi 1991, Bridcut & Giller 1995, de Billy de Crespin 2000). The total niche width of a population of predators has two components: the within-phenotype component, describing prey diversity for one individual, and the between-phenotype component, describing prey diversity for the population (Roughgarden 1974). A predator may be a specialist in a given habitat or during a particular life history stage while broadening its niche width under different conditions (MacArthur & Pianka 1966, Werner & Gilliam 1984). Similarly, a predator that is a generalist early in life may become a specialist; for example, meroplanktonic organisms spend their larval stages in the upper water column and may consume a diversity of plankton, but diet specializes upon settlement. Furthermore, at any given time and place a population of predators may contain some individuals that are specializing while others are generalizing. Consequently, a full understanding of predator foraging strategy and niche width must be analyzed at the scale of individual predators.

While population-level analysis of diet habits is important for parameterizing multispecies models and describing large-scale patterns such as interdecadal variability, small and medium-scale patterns should be described by analysis at the scale of individual fish (de Billy de Crespin et al. 2000). If predators are sampled in replicate from various aggregations, the unit of analysis should also include that scale. Analyses resolved at the species-level for prey and individual- or aggregation-based levels for predators offer insights into the feeding ecology of predators in many respects. First, niche width can only be calculated from diet data of individual predators (Bridcut & Giller 1995, de Billy de Crespin 2000). Second, spatial variability in prey distribution may exist for highly mobile predators, and regional analyses are needed to describe predator-prey relationships driven by variability in prey abundance (MacArthur & Pianka 1966, Stephens & Krebs 1986). Third, seasonal or annual variations in predation require more frequent sampling rates. Fourth, between-predator variability in prey consumption also reveals patterns in the ecology of prey. For example, individually-resolved foraging habits suggest whether prey occur as solitary individuals or whether (and how extensively) they exist as schools when vulnerable to predation.

The diet habits of North Pacific albacore, *Thunnus alalunga,* have been described for the California Current System (CCS) by four quantitative studies since 1949 (McHugh 1952, Iversen 1952, Pinkas et al. 1971, Bernard et al. 1985). These studies failed to report data at the scale of the individual predator and no study has investigated foraging strategy of albacore in the CCS. Albacore in the CCS consume a wide diversity of prey items, and studies have identified *Engraulis mordax, Cololabis saira, Euphausia pacifica, Pleuroncodes planipes,* and various species of cephalopod as significant prey. Of these studies, only Iversen (1962) and Pinkas et al. (1971) describe diet habits at high taxonomic resolution. Both conclude that albacore are strict generalists, consuming up to 60 species of prey. However, relying on numeric abundance or the mass of digested prey remains, as these studies do, can lead to erroneous conclusions about prey importance. Chapter 2 re-examined these studies and concluded that, energetically-speaking, only a few species were important to albacore diet in the CCS. In particular, two species of fish (*E. mordax, C. saira*) appear to be key prey items of juvenile albacore. Consequently, the characterization of albacore as foraging generalists may be inaccurate. I hypothesize that albacore are not true generalists. Rather, they display foraging strategies more closely approximating transitory specialists or a mixed-feeding strategy based on specialization on one or two prey with a broad diet of more rare prey.

Juvenile albacore undergo Pacific-wide migrations whereby they enter the CCS in late spring to early summer (Otsu & Uchida 1962) and leave in late fall. The appearance of juvenile albacore in CCS waters corresponds to the development of the frontal boundaries of the transition zone (Laurs & 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 gyre into the productive upwelling zone of the CCS 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, a better understanding of albacore niche width and foraging strategy may shed light on patterns of interspecies competition and niche overlap in these regions.

The aim of Chapter 3 is to describe the foraging ecology of albacore through patterns of variability in diet habits at medium spatial and temporal scales, and small scales of taxonomic resolution. Specifically, I investigate whether albacore are strict generalists, and I hypothesize that their foraging behavior will involve a mixed approach. First, I describe species-level patterns of albacore diet habits in the CCS and discuss prey ecology. Second, I compare individuals and aggregations of foraging albacore to describe differences in energy content, biomass consumed, and prey aggregations. Third, I compare prey consumed in three different regions of the CCS (north, central, and south). Finally, I use these metrics to describe albacore foraging ecology using graphical approaches that distinguish generalists from specialists.

Methods

Data collection

Diet habits of albacore were quantified through species-level 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. The author collected stomachs aboard recreational vessels. Location, date, and albacore length were recorded at the time of stomach collection. Stomachs collected aboard commercial vessels were obtained by the vessel captain and crew. Date and location, but not albacore length, were recorded for each commercially-obtained stomach. 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 within 27°N to 57°N and between the West Coast of North America to 10-800 km offshore (Figure 3.1).

Immediately following removal from the albacore, stomachs and their contents were preserved in a chest of dry ice and later stored in the laboratory at -11˚C. Each stomach was thawed, its volume and weight measured, 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. The difference between empty and full stomach weights is the weight of stomach contents subjected to digestion. Contents were stored in jars of 95% ethanol until sorted and identified.

Gut content analysis

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.’ 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 (especially for *Merluccius productus*), operculi for *Sebastes*) or counting the number of singular structures (*e.g.*, vertebral column, parasphenoid for *Cololabis saira*, urostyle and basioccipital bones for *Sardinops sagax* and *Engraulis mordax*). 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), and/or 3) otolith width. 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 *E. mordax*, 1.3 for *S. sagax*, and 1.2 for *C. saira*. These ratios were calculated by measuring the total and vertebral lengths for several full specimens of each species in the laboratory. For other species of fish, a ratio of 1.1 was used. Otolith width was converted to body length according to Harvey et al. (2000), and body length (mm) was translated to reconstituted (pre-digestion) mass (g) using species-specific allometric relationships from the literature (Clothier 1950, Wolff 1984, Clark 1986, Harvey et al. 2000, Froese & Pauly 2008).

Cephalopods were identified using beak morphology (Pinkas et al. 1971, Clark 1986, and reference collections). Numbers of cephalopods were counted by pairing upper and lower beak halves and counting the larger 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 (Clark 1986), and therefore this was the lowest resolution possible for unidentifiable beaks. The LRL of four species of squid (*Abraliopsis* sp., *Loligo 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, 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 *Phronima 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. These distinctions did not always uniquely identify one Order, in which case 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 and values for whole organisms were used to calculate mass.

In addition to these three major categories of prey (fishes, cephalopods, and malacostracans), 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), I assumed these copepods were secondary prey ingested simultaneous with other items, and I therefore excluded them 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 comparative diet analyses.

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 simply 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 samples, and 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).

Species accumulation curves

While 371 stomachs were analyzed for this study, over 700 total stomachs were collected during 2005 and 2006. I stopped laboratory analysis based partly on the results of species accumulation curves. Species accumulation curves calculate the sample size needed to fully describe the diversity of prey species a predator consumes. The number of new prey species discovered for each additional stomach analyzed was plotted, and the sample size at which the curve asymptoted described the needed effort (Thompson & 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, 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: genetic sequencing of tissue was necessary. Given past studies that have not identified *Sebastes* species, and anticipating future studies that 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 ‘other fishes’ category. Fourth, only 20 prey categories occurred in ≥ 5% of stomachs. To estimate how many stomachs are necessary to identify the most common prey in albacore diet, the final aggregation subsumed rare taxa (< 5 *%FO*) into larger categories. For example, the occurrence of 26 individual specimens of *Argonauto argo*, a pelagic octopus, were 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.

Variability between individuals and daily sampling units

Stomachs were analyzed individually and aggregated according to the date and location from which the sample was drawn (hereafter, the daily sampling unit or DSU). DSUs were assigned based on data recorded during collection: samples that were collected on the same day and in the same location were grouped into one DSU. Thus, this study overcomes a shortfall of many diet studies of large pelagic predators regarding statistical analysis. Although an individual stomach cannot be considered an independent sample 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 analysis that used DSU as a treatment.

Individual stomachs and DSUs were compared using five metrics: 1) the mass of an empty (contents removed) stomach (g), 2) the mass of the partially digested contents inside a stomach (g), 3) the reconstituted (pre-digestion) mass of contents (g), 4) the total energy of contents (kJ), and 5) the total protein of contents (g). The first two metrics were measured directly. For metrics three, four, and five, the value for an individual stomach was calculated as

$$M_R = \sum_i N_i \times \overline{M_i} \tag{3.1}$$

$$energy = \sum_i N_i \times \overline{M_i} \times \overline{ED_i} \tag{3.2}$$

$$protein = \sum_i N_i \times \overline{M_i} \times \overline{pro_i} \tag{3.3}$$

where, for prey category i, M_R is the reconstituted mass of gut contents, N is the number of prey specimens, $\overline{M}$ is the mean reconstituted mass (g) of one organism, $\overline{ED}$ is the mean energy density (kJ g^{-1}) of one organism, and $\overline{pro}$ is the mean percent protein content of one organism. Energy density and protein values were obtained from the literature (Sidwell 1981, Donnelly et al. 1993; see Appendix 2.1).

The five metrics describing individuals were compared univariately. For each of 31 DSUs that contained five or more replicate stomachs, five stomachs were randomly chosen, resulting in 155 stomachs available for ANOVA using DSU as a treatment effect. The data do not meet assumptions of normality, therefore randomized ANOVAs were performed (Chipps & 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.

Spatial and temporal variability

Collections fell into three well-defined regions in the California Current System: 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. 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 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 & Williams 1973, Polovina et al. 2001).

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). One requirement of contingency analysis is no more than 20% of cells may contain an expected frequency of less than five. By aggregating prey categories according to a cutoff of ≥ 5 *%FO* (as in the fourth level of aggregation outlined in the species accumulation curves), this requirement was met, with the exception of further aggregating *Japatella heathi* into the category ‘Octopus.’

These same aggregated categories (but disaggregating *J. heathi* from Octopus) were used to compare the (reconstituted) mass of prey consumed in the three regions. Principal component analysis (PCA) was performed on three arrangements of the data. First, the effect of region (n = 3) was tested on reconstituted mass consumed of a given prey category (n = 20). Second, the effect of reconstituted mass of prey categories on DSU (n = 31) was tested. Third, the effect of interannual variability (2005 versus 2006) was tested on reconstituted mass of prey categories. A PCA generates orthogonal linear combinations of independent variables that maximize the differences between dependent variables. These linear combinations, the principal components (e.g., PC1, PC2), quantify the amount of variability (loadings) explained by the combinations of independent variables and can identify correlated independent variables that have similar effects on the dependent variable.

Daily ration and energetic demand

The bioenergetics model described in Chapter 2 was used to calculate the daily energetic demand (J kg^{-1} d^{-1}) of albacore ranging from 52-100 cm fork length. Following the guidelines of Chapter 2 and Essington (2003), I calculated 90% confidence intervals by running 1000 Monte Carlo simulations and randomizing the variables to which the model was sensitive (assimilation efficiency and parameters related to swimming speed and active metabolic rate). Observed estimates of energetic intake (energy value of gut contents) were calculated (equation 3.2) from stomach content data to compare with modeled values. Assuming stomach contents represented an eight-hour digestion period (Olson & Boggs 1986), I multiplied all observed energy values by three to reflect feeding events in a 24-hour period. Albacore weight (kg) was calculated from lengths (Essington 2003) of albacore collected in the field for diet analysis. The total energetic content of a stomach was standardized by albacore weight.

Niche width and foraging strategy

Niche width and foraging strategy were quantified as diversity of prey consumed by individuals and by subpopulations. The number of unique prey categories found in any given stomach was calculated for all individuals. Costello (1990) developed a plot useful for classifying foraging behavior as specialist or generalist, and for identifying important prey. The percent frequency of occurrence (*%FO*) in stomachs was plotted against prey specific abundance (P_i), calculated as

$$P_i = \left(\sum S_i / \sum S_{ti}\right) \times 100 \qquad 3.4$$

where P_i can have units of numbers, mass, or volume, S_i is the abundance of prey i in a stomach and S_{it} is the abundance of all prey in stomachs that contain prey i (Chipps & Garvey 2007). Here, I used numeric abundance for the calculation of P_i. The plot is divided evenly into quadrants: specialist foraging (high P_i, low *%FO*), generalist foraging (low P_i, high *%FO*), dominant prey (high P_i, high *%FO*), and rare prey (low P_i, low *%FO*).

Standard diversity indices also describe foraging strategies. Following Bridcut & Giller (1995), the reciprocal of Simpson's diversity index (D) was used to quantify prey diversity within a subpopulation of albacore (between-phenotype) and prey diversity of individual albacore (within-phenotype), calculated as

$$D = {}^{1}\!\Big/\!\sum p_i^{\,2} \quad . \qquad 3.5$$

Subpopulations were defined by CCS region (north, central, south) and sampling year (2005, 2006) resulting in six subpopulations. To calculate subpopulation diversity, p_i was the numeric abundance of prey category i divided by the numeric abundance of all prey consumed in a given subpopulation. To calculate individual diversity, p_i was the numeric abundance of prey category i consumed by an individual albacore divided by the numeric abundance of all prey consumed by that albacore. Mean individual diversity was plotted against subpopulation diversity for the six subpopulations (Tokeshi 1991). On such a plot, generalist foraging strategies correspond to high subpopulation diversity and either high or low individual diversity, while specialist foraging strategies correspond to low subpopulation and low individual diversity. Bridcut & Giller (1995) defined D = 5.0 as the dividing line between high and low diversity. Finally, individual diversity was plotted against the number of prey consumed by each albacore (Bridcut & Giller 1995). This plot defines generalist foraging as high individual diversity with high (>5 per stomach) prey numbers, and specialist foraging as low individual diversity with high prey numbers.

Results

The spatial and temporal distribution of sampling effort is shown in Figure 3.1. The central region received the least amount of coverage. This was due to the preponderance of individual, non-charter fishing vessels in the central California region as opposed to large, recreational charter vessels available in southern California and Oregon, the latter of which collected more fish per trip. Furthermore, the majority of sampling done by commercial boats was in the northern region. During 2005, 17 DSUs and 106 individuals were sampled, and 29 DSUs and 265 individuals were sampled during 2006. From the northern region, 31 DSUs and 275 individuals were analyzed, eight DSUs and 45 individuals were analyzed from the central region, and seven DSUs and 51 individuals were analyzed from the southern region. The geographic distributions of stomachs containing the twenty aggregated prey categories are mapped in Appendix 3.1, Figures A3.1.1 - A3.1.20.

Diet composition

Fifty-nine prey categories were discovered in 371 stomachs (Table 3.1) resulting in a total of 18,401 individual prey items and 21,367 g of reconstituted biomass.

Numeric totals ranged from one occurrence (five species of squid and four species of fish) to thousands (euphausiids, decapods, *Merluccius productus* (Pacific hake), and *Engraulis mordax* (Northern anchovy)). Anchovy was the most commonly found 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).

Of the squids, *Abraliopsis* sp. (either *A. felis* or *A. 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 (Figure A3.1.1). *Loligo opalescens*, a valuable commercial species, was the next most commonly consumed prey (*%N* = 1, *%FO* = 9). Like all squid prey, this species was of juvenile sizes (7 g). Although found in four stomachs in the northern region and once in the central region, *L. opalescens* was disproportionately consumed in the southern region (Figure A3.1.2). *Octopoteuthis* sp., the third most commonly consumed squid (*%N* < 1, *%FO* = 12), is most likely *O. deletron* and not *O. sicula* (a Western Pacific species), as described by Pinkas et al. (1971) (F. G. Hochberg, pers. comm.). Its consumption was distributed throughout all three regions (Figure A3.1.3). Gonatid squids, including the species *Gonatus pyro, G. onyx, G. californiensis*, and *Gonatopsis borealis*, were fairly common and distributed throughout the three sampling regions (Figure A3.1.4). *Onychoteuthis borealijaponica*

(*%N* = 1, *%FO* = 19) was found in two stomachs in the southern region, but predominated in the northern region (Figure A3.1.5). Five remaining species of squid (*Vampyroteuthis infernalis, Moroteuthis robusta, Eucleoteuthis luminosa, Histioteuthis* sp., and *Mastigoteuthis dentata*) were aggregated for analysis with 326 unknown individual squids (Figure A3.1.6).

Only two species of octopus were identified: *Japatella heathi* (*%N* < 1, *%FO* = 7) and *Argonauta 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 (although it was found in two southern and one central stomachs; Figure A3.1.7) whereas *A. argo,* classified with unknown octopi for statistical analysis, were more evenly consumed (Figure A3.1.8). 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.

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 item of albacore. However, when the mass of the organisms were taken into account (mean weight 0.1 g for both categories), their contribution to the total mass consumed dropped to 1.0%. Results presented in Chapter 2 confirm that, 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. 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 (Figure A3.1.9). Similarly, while present in both the southern and central regions, euphausiids were more commonly consumed in the northern region (Figure A3.1.10). Amphipods, including the species *Phronima sedentaria*, occurred frequently but in smaller numbers than decapods or euphausiids (*%N* = 1, *%FO* = 12.0 and *%N* = 1, *%FO* = 19, respectively) (Figures A3.1.11 and A3.1.12). Finally, 1006 (*%N* = 5) unidentified malacostracans were found in 27% of all stomachs (Figure A3.1.13).

Fishes were the most abundant prey of albacore. *Engraulis mordax* was the most commonly consumed prey by number and frequency of occurrence (*%N* = 27, *%FO* = 53) and was consumed in all three regions (Figure A3.1.14). *Merluccius productus* (*%N* = 19, *%FO* = 16) was found in one stomach in the central region but otherwise was confined to the northern region (Figure A3.1.15). *Cololabis saira* (*%N* = 2, *%FO* = 18), was also most commonly consumed in the northern region, although it was found occasionally in the central and southern regions (Figure A3.1.16). 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 (Figure A3.1.17). 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), and eight species and one species complex (*S. wilsoni, S. proriger,* and *S. zacentrus*) were identified by genetic sequencing. *Sebastes* were found throughout the three regions, but were most common in the northern region (Figure A3.1.18). Finally, *Sardinops sagax* juveniles (*%N* = 3, *%FO*

= 27) were commonly found in albacore stomachs also containing *E. mordax,* although anchovy occurred in larger numbers. Like anchovy, they were consumed throughout the three regions (Figure A3.1.19). Ten rarely-consumed prey categories occurred in less than 5% of all stomachs. These categories (*Bathyagonus 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 'fishes' (*%N* = 2, *%FO* = 22) (Figure A3.1.20).

Species accumulation curves

This study analyzed a sufficient sample size to describe diet habits at the lowest level of taxonomic aggregation/highest level of taxonomic resolution here analyzed (Figure 3.2). With no taxonomic aggregation beyond that constrained by accurate identification, 59 prey categories were described by stomach sample #352 out of 371. 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). When the prey categories represented by one specimen were aggregated, the species accumulation curve asymptoted by stomach #247. Finally, the curve with the highest level of aggregation (20 prey categories resulting from aggregating < 5 *%FO*) asymptoted rapidly by stomach #25.

Variability between individuals and DSUs

The prey items of albacore ranged in mean energy density from 2.5 kJ g^{-1} (crustaceans) to 7.5 kJ g^{-1} (*Cololabis saira*) (Table 3.2). Protein content ranged from 12.9% (crustaceans) to 21.4% (*Sardinops sagax*) (Table 3.2). Individual stomachs contained, on average, 62 ± 72 (SD) g of reconstituted prey mass (Figure 3.3). Most stomachs contained between 30-40 g prey biomass. Total energy values of stomachs ranged from 2 to 3021 kJ, with a mean value of 307 ± 353 kJ (Figure 3.4). Total protein content ranged from 0.1 g to 74.5 g with a mean value of 8.8 ± 9.4 g (Figure 3.5). Empty stomachs ranged from 32.9 – 164.2 g (mean 82.3 ± 8.8 g). The mass of empty stomachs (after prey were removed) was explained by the size (fork length in cm) of the albacore (R^2=0.62, $p < 0.001$). Means of these metrics differed significantly between DSUs (randomized ANOVA, ($p < 0.002$) (Table 3.3)). Results were robust to removing outliers. In all analyses, the observed *F* statistic was higher than the largest randomized *F* statistic making the level of significance achieved < 0.002 (1/500).

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 3.4 compares the two ways 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 *M. productus*, which occurred in 16.4% of individuals and 28.3% of DSUs.

Spatial and temporal variability

The regional distribution of prey consumption varied in 11 of 20 prey categories ($\chi^2 = 53.4$, $p < 0.05$; Table 3.5). *Abraliopsis* sp., *Octopoteuthis* sp., *Loligo 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*, Octopus, Amphipod, *P. sedentaria*, malacostraca, Myctophidae, and *Sebastes* spp.) were distributed evenly.

By mass of prey category consumed, the three regions were significantly different (Table 3.6). Prey in the northern region were 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 were 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 (Figure 3.6). Variability between DSUs was explained by predation on either anchovy, saury or hake (Figure 3.7). Diet preferences in 2005 versus 2006 did not vary significantly (Figure 3.8). PC 1 explained 95% of the variance, with strong positive loadings on both 2005 and 2006. 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.

Daily ration and energetic demand

The bioenergetics model estimated daily energetic demand of 90 - 200 kJ kg^{-1} d^{-1} (Figure 3.9). The discontinuity 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 reaching reproductive maturity. Observed values ranged from 0.18 – 1378.2 kJ kg^{-1} d^{-1} (mean 141.7 ± 193.1 kJ kg^{-1} d^{-1}). There was no correlation between length of albacore and the total energy value of stomach contents.

Niche width and foraging strategy

Prey diversity, on a per-stomach basis, was low; on average, each stomach contained four unique species categories (Figure 3.10). Figure 3.11 reveals some of the foraging strategy of albacore. According to Costello (1990), Amundsen et al. (1996) and Chipps & Garvey (2007), the top right quadrant of the graph represents dominant prey while the bottom left quadrant represents rare prey. The bottom right quadrant represents high variability within individual predators while the top left quadrant represents high between-predator variability, effectively describing niche width. Finally, the top mid-section of the plot represents a specialist diet while the bottom mid-section of the plot represents a generalist strategy. According to this rubric, anchovy was the clear dominant prey type. The presence of decapods in significant numbers was highly variable between individual albacore. The remaining prey items fell within the ‘rare prey’ quadrant. Furthermore, all prey categories except anchovy fell in the ‘generalist’ section of the plot. No species fell along the niche width axis, demonstrating the tendency for this graph to describe niche width poorly (Bridcut & Giller 1995).

Individual prey diversity was low; that is, for any given albacore, prey diversity in one stomach was low (Figures 3.12 and 3.13). Subpopulation diversity was low for samples collected in 2005 (< 5.0), falling into the ‘specialist’ section of the plot, and medium (< 6.0) for samples collected in 2006. The slightly higher subpopulation diversity for 2006 samples placed them in the ‘generalist’ section of the plot. Based on the plots of Bridcut & Giller (1995), almost all individuals were classified as specialists given the low individual diversity (Figure 3.13). Individuals with fewer than five prey specimens do not accurately represent diet preferences, thus the section of the plot to the left of the vertical line were not considered.

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

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 – 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. 2005). 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. I 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 (or beyond sample #342, the result when *Sebastes* were aggregated). However, the leveling off of the species accumulation curve confirmed that the rate of finding new species was slowing.

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. Nevertheless, this scale of taxonomic aggregation is useful for many of the multivariate statistical approaches used herein to describe patterns in diet habits.

One shortfall of the field sampling effort was 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 2006). 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 (ISC 2006). 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 & 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 ‘unknown fish;’ distinguishing nine species of *Sebastes* (Hyde & 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 by this source of uncertainty because mean values of mass and energy were applied to categories of unidentified prey. The species accumulation curves and the number of prey categories per stomach would change if all unknown specimens could have been identified at higher resolution.

Some researchers distinguish fresh prey from nonfresh prey, using degree of digestion to guide their choices (Pusineri et al. 2005, Chancollon et al. 2006). 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. I did not follow this practice for two reasons. First, the average degree of digestion for all prey in my 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 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.

Prey ecology

Cephalopods

The most abundant cephalopod prey is a species of *Abraliopsis*. While Pinkas et al. (1971) described *A. felis* as prey of albacore, genetic sequencing of tissue samples identified *A. falco*. Both species are small as adults (mantle lengths up to 30-40 mm). *Abraliopsis* consumed by albacore were juveniles (Wolff 1984). *Abraliopsis felis* is likely endemic to the California Current System and occupies surface waters in all seasons of the year (Okutani & McGowan 1969). *A. felis* paralarvae are most abundant in May-July throughout the CCS, although they tend to be more abundant in the northern and central regions (Okutani & McGowan 1969). The patterns of albacore consumption support the observed geographical distributions of *A. felis*. *A. felis* is also found in the Western Pacific in the Kuroshio-Oyashio transition zone and is known to occur at night in the top 50 m of surface waters (Tsuchiya 2000). Over half of the stomachs containing *Abraliopsis* had fewer than 3 beaks per stomach, suggesting these prey are consumed singularly or in small groups. However, twelve stomachs contained between ten and 23 *A. felis* beaks, suggesting they could be consumed in small aggregations.

Onychoteuthis borealijaponica, a member of the oceanic clubhook squid family (so named by two rows of hooks on their tentacles), is abundant throughout the North Pacific from the Gulf of Alaska to Baja California, throughout the central gyre, and in the Western Pacific Kuroshio region. The species was identified based on beak morphology (Pinkas et al. 1971) and genetic sequencing. However, the known geographic distribution of this species, in comparison to distributions of *O. banskii* (Okutani & McGowan 1969, Bigelow 1994) and an undescribed species of *Onychoteuthis* (Bigelow 1994), suggests beaks found in albacore stomachs may be either *O. borealijaponica* or *O. banksii*. Both species have cosmopolitan distributions and range from southern Baja to the southern Bering Sea. *O. borealijaponica* is known to reproduce continuously throughout the year and grow to over 350 mm mantle length (Bigelow 1994). One in five stomachs contained, on average, three beaks of this species at juvenile sizes.

Loligo opalescens, the neritic California market squid, was consumed almost exclusively in the southern region of the CCS. This muscular squid is most commonly found in surface waters. Adults of this species range throughout the CCS, and spawning follows a general south-to-north progression beginning in southern Baja in winter. However, paralarvae can be found at all times of year throughout the range (Okutani &

McGowan 1969). Market squid grow rapidly and reach full size in only six to eight months after hatching (Jackson & Domeier 2003). The size of squid found in albacore stomachs suggests they are consuming squid that were recently hatched. *L. opalescens* is subject to commercial fishing pressure and episodic spawning events. During spawning, adults produce tens of thousands of demersal egg cases in inshore waters. *L. opalescens* was not a major prey item of albacore in 2005 and 2006, occurring in only 10% of all stomachs and comprising less than 1% of total prey biomass.

Octopoteuthis sp. is most likely *O. deletron*. The beaks identified and described by Pinkas et al. (1971) were misidentified as *Octopodoteuthis sicula*, a species that does not occur in the North Pacific (F. G. Hochberg, personal communication). Furthermore, since the description by Okutani & McGowan (1969) of *Octopodoteuthopsis* sp., the systematics has been updated so that the genus *Octopoteuthis* subsumes these species (Young & Vecchione 2008). *O. deletron* can grow to 170 mm mantle length (Young 1972); the prey consumed by albacore were juveniles approximately 30 mm in mantle length. The species occurs in the Eastern Pacific ocean from Baja to Alaska, and consumption by albacore was more frequent in the central region (Table 3.6).

Four species of the family Gonatidae were consumed by albacore, the most frequent category being unidentified species of *Gonatus.* The systematics of Gonatidae are frequently reorganized; specimens identified by Okutani & McGowan (1969) and Pinkas et al. (1971) as *Gonatus fabricii* are likely one of the three species identified here by genetics (*G. californiensis, G. onyx,* or *G. pyro*) given the currently accepted confinement of *G. fabricii* to the Atlantic Ocean (Vecchione & Young 2006). Gonatids are pelagic squid that are known to occur from the surface to 1000 m depth and in the

North Pacific from the tropics to the arctic (Kubodera et al. 2006). Gonatids consumed by albacore were juveniles (mantle lengths up to 30 mm (Okutani & McGowan 1969)) and there were no regional patterns to their consumption.

The remaining species of cephalopod were consumed rarely. *Argonauta argo* (a pelagic octopus), *Mastigoteuthis dentata*, *Histioteuthis* sp., and *Moroteuthis robusta* (all muscular pelagic squid), and *Vampyroteuthis infernalis* (a meso- or bathypelagic squid) previously have been found in the diet of albacore (Pinkas et al. 1971). *Eucleoteuthis luminosa*, a pelagic squid about which little is known, was newly identified in this study. *Japatella heathi*, another newly-identified prey species, is a pelagic octopus that exists in the North Pacific from Southern California (Young 1972) to the Bering Sea (Pearcy 1962).

Crustaceans

Malacostracans belonging to the orders Decapoda and Euphausiacea comprised a significant proportion of biomass consumed by albacore in the northern region of the CCS (25.6% and 19.3%, respectively). The most common species of euphausiid in the northern CCS is *Euphausia pacifica*, and genetic analysis identified this species (Brinton & Townsend 2003). *Thysanoessa spinifera* is also abundant in northern waters (Reese et al. 2005). Decapods were not positively identified genetically; based on trawl surveys, the decapods could be *Cancer magister*, the most abundant decapod in those waters (Reese et al. 2005). A few *Sergestes similis* from a northern stomach and four *Pleuroncodes planipes* from two southern stomachs were identified visually. After copepods (which are not prey of albacore), euphausiids and decapods comprise the second and fifth most abundant source of carbon from zooplankton in the southern and central regions of the CCS (Lavaniegos & Ohman 2007). Moreover, the central region has twice the zooplankton carbon biomass of the southern region (Lavaniegos & Ohman 2007). However, euphausiids and decapods comprised < 1.1% of total biomass consumed in these two regions.

Studies have documented species-level patterns in distribution of euphausiids and decapods that range from inshore to offshore. Species-level zooplankton community structure may change over time in response to changing environmental conditions (Peterson & Schwing 2003). However, the total biomass of zooplankton carbon has not responded to environmental changes (Lavaniegos & Ohman 2007); thus, while the prey species that are available to albacore may vary from year to year, the overall biomass of zooplankton appears to be a steady source of energy in northern waters. Amphipods contributed only a minor fraction to albacore diet and regional differences were not detected. The most commonly discovered species of amphipod, *Phronima sedentaria*, is a known parasitoid on salps and doliolids, and it may have been secondary prey that was consumed along with a host. Six undigested Thaliacea were discovered in stomachs, and the rapid digestion of gelatinous versus chitinous tissue could explain finding more *P. sedentaria* than Thaliacea.

Fishes

Engraulis mordax, the Northern anchovy, is the most important prey species of albacore based on multiple metrics. First, they are consumed in all three regions of the CCS, although relatively less in the central and more in the southern region. Second, they are consumed in greater numbers than any other prey species. Third, although hake make up a greater portion of the total biomass consumed based on their larger individual size, the greater energy density of anchovy causes the two species to contribute equally, in terms of energy, to the diet of albacore (Chapter 2). Finally, the Costello plot identifies anchovy as the dominant prey (Figure 3.11). Anchovy are small (maximum standard length = 248 mm), grow rapidly, school, and are the forage of many types of predators (see Schwartzlose et al. 1999 for a review). They vary in abundance on the scale of decades (Soutar & Isaacs 1974, Baumgartner et al. 1992). The anchovy consumed by albacore were juveniles (mean length 34.6 mm) and likely were spawned in the early spring in inshore CCS waters (Smith 1985). Anchovy are planktivores and their primary habitat is cold, high-salinity, upwelled waters (Lluch-Belda et al. 1991, Checkley et al. 2000).

Pacific hake, *Merluccius productus*, is a pelagic fish that can grow to nearly one meter in length (Froese & Pauly 2008) and migrates annually throughout the CCS (Agostini et al. 2006). Adults spawn in the southern California Bight and north of Point Conception in the late winter, and juveniles move in large schools northward during the summer (Horne & Smith 1997, Agostini et al. 2006). Albacore appear to consume juveniles in northern spawning grounds: consumption patterns showed no hake predation in the south, considerable (42% by mass) predation in the central region, and some (13% by mass) predation in the north. Hake were found in 16% of all stomachs, but when present, they occurred in the largest groupings of any species consumed (mean 58 individuals per stomach), suggesting large schooling aggregations. This is the first study in the CCS to find hake in significant quantities, suggesting that albacore consumption of hake varies along with episodic spawning events (Horne & Smith 1997, Lo et al. 1997).

Pacific saury, *Cololabis saira*, is known to fishers as ‘albacore smelt’, reflecting the common appearance of this forage fish in albacore diet. This study differs from past studies in the magnitude of saury predation relative to other species of forage fishes. Studies from the late 1940s (McHugh 1952) and mid-1950s (Iversen 1962) found saury comprised between 46-82% of biomass consumed, whereas this study is more similar to diet habits in the late 1960s in which saury accounted for 30% of diet by mass (Pinkas et al. 1971). Here, saury accounted for only 20% of biomass consumed, and its high energy density raised its energetic contribution to 24% (Chapter 2). Unlike anchovy and hake, saury appeared in stomachs, on average, in groups of five. Although the mean length was 120 mm, the large standard distribution reflected two main length classes found in the sample: one with mean length approximately 60 mm and one with mean length approximately 180 mm. Smaller saury were usually found in small groups inside stomachs, whereas larger saury were usually found singly or in pairs. Saury were consumed almost exclusively in the central CCS region.

Additional species of fish comprised 6.5% of the remaining biomass, not including biomass of unidentified fishes (1.8%). Two common and commercially and biologically important coastal pelagic species, *Sardinops sagax* and *Scomber japonicus*, were not significant components of albacore diet. Myctophids, of which three species were identified (*Tarletonbeania crenularis*, *Stenobrachius leucopsaurus*, and *Diaphus theta*), are small mesopelagic fishes that can live up to 3000 m deep, but are more common between 400m – 1000 m. Albacore likely consumed myctophids that migrated to the surface at night to feed (Ahlstrom 1969). The family of rockfishes, *Sebastes*, are inshore, demersal fishes as adults, but their larvae and juveniles swim in the upper water column and are vulnerable to predation by fishes and birds (Ainley et al. 1993). Over 50 species of rockfish are found in the CCS, and predation by albacore on *Sebastes* occurred in all three regions. All other fishes consumed by albacore during this study occurred rarely. In addition to identifying nine species of *Sebastes* in the diet of albacore, this study is the first to identify *Icichthys lockingtoni*, the medusafish, and *Bathyagonus pentacanthus*, the bigeye poacher, as rare prey. Moreover, several fishes that previously had only been identified to genus were identified to species (*Anopterus nikparini*, *Pleuronichthys decurrens*, and *Syngnathus californiensis*). Past studies of albacore diet habits in the CCS have identified *Vincinguerria lucetia* as a common prey item, but this study did not replicate those findings.

Sources of variability

Albacore prey in this study did not vary between 2005 and 2006. Over longer time scales (decades), temporal variability can be detected in diet habits (Chapter 2). Anchovy were not important prey during the 1950s, and this is the first study to demonstrate that hake can be important. Given the tendency of biological populations to display temporal autocorrelation (Steele & 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 & 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, 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 variability is evident in the mean number of unique prey categories per stomach and patterns of *%FO* (Table 3.4). 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, ANOVA, and graphs depicting foraging strategy.

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. The category ‘malacostraca’ is uninformative in this context because an unknown crustacean was categorized as malacostraca only when it could not be identified more precisely. Thus, in stomachs with large numbers of malacostracans, a more precise identification was likely due to the greater opportunity of finding an intact individual. Ignoring, then, the category malacostraca, the remaining prey categories occurred in groups of six or fewer in any given stomach. 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 environment as well as inside albacore stomachs. 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.

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.

Daily ration and energetic demand

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 (Olson & Boggs 1986, Olson & Watters 2003, Essington 2003). These studies have assumed the mean prey field available to tuna has an energy density of 5.0 kJ g^{-1}. 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 (Chapter 2) means approximations made herein are justifiable.

Niche width and foraging strategy

Albacore long have been considered generalists (McHugh 1952, Iversen 1962, Pinkas et al. 1971, Bernard et al. 1985, Pusineri et al. 2005, Catalan et al. 2007) but this study indicates that they have a mixed-approach to foraging. The Costello plot (Figure 3.11) demonstrates that *Engraulis mordax* stands alone as a dominant source of prey, whereas all others fall into the ‘rare prey’ section of the plot. Costello’s method, comparing *%FO* to the relative abundance of prey in diet, was better at distinguishing dominant from rare prey than in distinguishing specialist from generalist foraging strategies. This method functions at the level of the albacore population and does not reveal within-phenotype niche width.

Consoli et al. (2008) found similar results using the Costello approach for juvenile albacore in the Mediterranean, although species of paralepids were the dominant prey rather than anchovy. They remarked on the narrow niche width of Mediterranean albacore but stopped short of eschewing the term ‘generalist’. Specialization on or preference for one prey species is impossible to prove without data on relative abundances of prey in the environment (MacArthur & Pianka 1966, Emslen 1966). In the case of Mediterranean albacore, consumption of paralepids likely reflected the high biomass of these pelagic fishes compared to other sources of prey (Consoli et al. 2008). In the case of CCS albacore, anchovy have been a dominant prey item since the late 1960s (Pinkas et al. 1971, Bernard et al. 1985, this study). Before that, however, anchovy were not found in albacore diet, and saury were the dominant prey (McHugh 1952, Iversen 1962). Thus, at times, saury replaces anchovy in albacore diet. Nevertheless, the results of this study and those found by Consoli et al. (2008) are strong evidence that albacore specialize on one prey item (saury, anchovy or paralepids, in these cases) and supplement with variable feeding on more rare prey. In the CCS, the supplemental species include hake, cephalopods, and malacostracans, depending on the region. That specialization could change from year to year or decade to decade, depending on which prey species is dominant in the environment.

If Consoli et al. (2008) had utilized individual-based graphical approaches to assessing foraging behavior, they may have concluded, like this study, that albacore are not generalists. The Tokeshi plot (Figure 3.12) appears to separate 2005 from 2006. However, 2006 had a much higher sample size and, based on the results from the species accumulation curves, the sample size in 2005 did not fully describe all categories of prey that could have been consumed. Nevertheless, the low individual diversity in both years suggests that, in the time frame of one feeding event, albacore are fairly targeted in their foraging. Furthermore, the subpopulation diversity, even including 2006 samples, was low to medium (1.3 – 5.6), further strengthening the theory of a mixed foraging strategy. For reference, salmonids studied by Bridcut & Giller (1995) had subpopulation diversities of up to 10, and those subpopulations were classified as generalists. Results for albacore are strengthened by PCA that found a strong regional component to prey diversity. Finally, the Bridcut & Giller plots (Figure 3.13) describe virtually all individuals as specialists. Discounting individuals that had fewer than five prey items in their stomach, the consistently low individual diversity at both low and high numbers of prey consumed places most of the 371 individuals studied here in the 'specialist' section of the plot.

These three graphical approaches to describing foraging strategy of albacore are not cut and dry, but they do have consistent elements. An individual albacore feeding in the CCS is not a strict generalist, nor is it a strict specialist. Rather, a mixed-feeding strategy is employed to maximize foraging efficiency (Stephens & Krebs 1986). Anchovy appear to be the main prey species throughout the CCS, and I hypothesize in Chapter 2 that this is due to thermal preferences of albacore for juvenile anchovy habitat. That same habitat is home to juvenile hake, saury, decapods and euphausiids. While feeding on large aggregations of small pelagic fishes, albacore also encounter a high diversity of more rare, and singly occurring, species of cephalopods and other fish. While this understanding of albacore diet is not radically different from past interpretations of data, the importance in classifying albacore as less-than pure generalists is important from an ecological perspective.

Decadal variability in diet habits (Chapter 2) and differences in foraging strategy may be explained by evolutionary pressures, *i.e.*, the school-mix hypothesis (Bakun 2001). [Although, to be clear, the example given by Bakun of albacore selecting on sardine is not borne out by the actual diet of albacore. Anchovy illustrate the same point]. According to this theory, albacore encounter abundant schools of forage fishes during migrations and 'remember' the location during future migrations. The anchovy, conversely, learn over time to avoid the regions in which albacore predation is high. Although many generations must pass, eventually the anchovy and albacore do not overlap, and the anchovy are released for some time from predation by albacore. Eventually, however, the memory of albacore predation is lost to the anchovy population as new generations, unfamiliar with albacore, begin expanding territorial ranges. Albacore re-encounter anchovy, and the cycle is repeated. While this study offers no direct support of the school-mix hypothesis, the interdecadal patterns of anchovy appearance in diet do not contradict it.

Conclusions

Characterizing albacore foraging strategy as mixed, rather than generalist, has important implications for understanding the CCS as a whole. First, if albacore niche width is more narrow than previously assumed, albacore should experience less direct competition from other predators if niche overlap is minimized (Roughgarden 1974, Stouffer et al. 2005). Juvenile albacore compete with medium-sized predators such as salmon (Brodeur 1991), seabirds (Hunt 2000), and bonito (Pinkas et al. 1971), but not larger predators such as bluefin or yellowfin tuna (Pinkas et al. 1971), sharks (Preti et al.

2001), or marine mammals (Hunt 2000). Second, the narrow niche width may be a contributing factor to the relatively high and stable abundances of albacore in the CCS (Sugihara et al. 2003). Third, if albacore rely on a small diversity of prey for a significant portion of energy, changes to that base of prey could have more drastic impacts on albacore than if they were true generalists (Bellwood et al. 2003). Finally, in the context of multispecies and ecosystem-based models, the linkages between albacore and a few key species are worthy of closer scrutiny, and results here call into question the practice of model simplification through functional groupings of prey species.

Table 3.1. Metrics describing species of prey found in 371 albacore stomachs collected in 2005 and 2006. *N* is numeric abundance. *M* is reconstituted mass. *FO* is the frequency of occurrence (presence) in stomachs. For all categories except cephalopods, length is body length. For cephalopods, length is lower rostral length.

Order/Family	**Prey Category**	**N**	**%N**	**FO**	**%FO**	**Total Mass (g)**	**%M**	**Mean Length (cm)**	**Std Length (cm)**	**Mean Wt (g)**	**Std Wt (g)**
CEPHALOPODS											
Argonauatidae	*Argonauta argo*	26	0	4	1	98.8	0.4	0.0	0.00	3.8	4.00
Bolitaenidae	*Japatella heathi*	38	0	26	7	144.4	0.6	0.0	0.00	3.8	4.00
Chiroteuthidae	*Mastigoteuthis dentata*	10	0	4	1	38.0	0.2	0.0	0.00	3.8	4.00
Enoploteuthidae	*Abraliopsis* sp.	452	2	98	26	176.3	0.7	0.005	0.016	0.4	0.50
	Octopoteuthis sp.	70	0	43	12	266.0	1.0	0.009	0.035	3.8	4.00
Gonatidae	*Gonatopsis borealis*	1	0	1	0	3.8	0.0	0.0	0.00	3.8	4.00
	Gonatus californiensis	1	0	1	0	1.6	0.0	0.012	0.00	1.6	0.00
	Gonatus onyx	9	0	2	1	22.9	0.0	0.015	0.029	2.5	1.10
	Gonatus pyro	5	0	1	0	29.4	0.1	0.0	0.00	5.9	0.95
	Gonatus spp.	84	0	41	11	360.4	1.5	0.018	0.065	4.3	3.07
Histioteuthidae	*Histioteuthis* sp.	1	0	1	0	3.8	0.0	0.018	0.00	3.8	4.00
Loliginidae	*Loligo opalescens*	102	1	33	9	808.9	3.3	0.006	0.024	7.9	4.67
Ommastrephidae	*Eucleoteuthis luminosa*	1	0	1	0	3.8	0.0	0.0	0.00	3.8	4.00
Onychoteuthidae	*Moroteuthis robusta*	21	0	11	3	79.8	0.3	0.010	0.020	3.8	4.00
	O. borealijaponica	211	1	71	19	810.2	3.3	0.008	0.024	3.8	2.83
	Onychoteuthidae	17	0	1	0	64.6	0.3	0.0	0.00	3.8	4.00
Watasellidae	*Vampyroteuthis infernalis*	1	0	1	0	3.8	0.0	0.028	0.00	3.8	4.00
Decapoda	Squid unknown	326	2	109	29	1238.8	5.0	0.012	0.042	3.8	4.00
Octopoda	Octopus unknown	11	0	5	1	41.8	0.2	0.0	0.00	3.8	4.00
	Octopus C	71	0	29	8	71.0	0.3	0.0	0.00	1.0	0.00

Table 3.1. Metrics describing species of prey found in 371 albacore stomachs collected in 2005 and 2006. Continued.

Order/Family	**Prey Category**	**N**	**%N**	**FO**	**%FO**	**Total Mass (g)**	**%M**	**Mean Length (cm)**	**Std Length (cm)**	**Mean Wt (g)**	**Std Wt (g)**
CRUSTACEA											
Amphipoda	*Phronima sedentaria*	249	1	72	19	12.5	0.0	22.0	6.36	0.1	0.00
	Amphipod unknown	129	1	44	12	5.2	0.0	9.2	6.51	0.0	0.00
Decapoda	*Pleuroncodes planipes*	4	0	2	1	8.0	0.0	33.8	2.47	2.0	0.00
	Sergestes similis	14	0	1	0	1.4	0.0	36.0	0.00	0.1	0.00
	Decapod unknown	2416	13	53	14	241.6	1.0	31.5	4.31	0.1	0.00
Euphausiacea	Euphausiid	2202	12	74	20	176.2	1.0	23.0	4.83	0.1	0.00
Isopoda	Isopod	13	0	5	1	0.7	0.0	5.9	0.17	0.1	0.00
Malacostraca	Malacostraca unknown	1006	5	99	27	100.6	0.4	15.8	6.16	0.1	0.00
FISHES											
Agonidae	*Bathyagonus pentacanthus*	1	0	1	0	0.0	0.0	0	0	0	0
Anotopteridae	*Anotopterus nikparini*	2	0	2	1	0.0	0.0	0	0	0	0
Atherinopsidae	*Atherinopsis californiensis*	1	0	1	0	6.9	0.0	94.6	0.00	6.9	0.00
Carangidae	*Trachurus symmetricus*	20	0	15	4	238.0	1.0	64.7	36.35	11.9	16.37
Centrolophidae	*Icichthys lockingtoni*	6	0	5	1	0.0	0.0	0.0	0.00	0.0	0.00
Clupeidae	*Sardinops sagax*	612	3	99	27	1077.1	4.0	49.2	16.93	1.8	3.58
Engraulidae	*Engraulis mordax*	5011	27	196	53	5612.3	23.0	34.7	9.97	1.1	1.30
Gadidae	*Merluccius productus*	3530	19	61	16	7342.4	30.0	60.9	15.30	2.1	2.03
Myctophidae	*Diaphus theta*	6	0	5	1	16.5	0.1	66.0	0.00	2.8	0.00
	Stenobrachius leucopsarus	19	0	12	3	36.5	0.2	59.8	15.74	1.9	1.63
	Tarletonbeania crenularis	3	0	3	1	10.9	0.0	74.8	0.00	3.6	0.00
	Myctophid unknown	29	0	24	6	49.4	0.2	53.2	17.15	1.7	1.35
Paralepididae	*Lestidiops ringens*	36	0	16	4	0.0	0.0	0.0	0.00	0.0	0.00
Pleuronectidae	*Pleuronichthys* spp.	3	0	3	1	0.5	0.0	21.0	3.61	0.2	0.08
	Pleuronichthys decurrens	6	0	2	1	0.5	0.0	18	1.41	0.09	0.02

Table 3.1. Metrics describing species of prey found in 371 albacore stomachs collected in 2005 and 2006. Continued.

Order/Family	Prey Category	N	%N	FO	%FO	Total Mass (g)	%M	Mean Length (cm)	Std Length (cm)	Mean Wt (g)	Std Wt (g)
Psychrolutidae	Psychrolutidae	1	0	1	0	0.0	0.0	8.7	0.00	0.0	0.00
Scomberesocidae	*Cololabis saira*	374	2	68	18	4854.5	20.0	119.1	68.33	13.0	19.97
Sebastidae	*Sebastes aleutianus*	6	0	1	0	0.2	0.0	11.8	0.00	0.0	0.00
	Sebastes brevispinus	9	0	4	1	0.3	0.0	12.5	2.85	0.0	0.02
	Sebastes diploproa	38	0	4	1	3.0	0.0	16.8	2.58	0.1	0.04
	Sebastes helvomaculatus	7	0	1	0	0.0	0.0	0	0	0	0
	Sebastes maliger	1	0	1	0	0.0	0.0	11	0	0.02	0
	Sebastes miniatus	33	0	1	0	0.5	0.0	9.9	1.5556	0.02	0.01
	Sebastes proriger	8	0	3	1	0.4	0.0	14.4	1.98	0.0	0.02
	Sebastes wilsoni complex	16	0	4	1	0.8	0.0	13.0	7.07	0.1	0.06
	Sebastes zacentrus	43	0	1	0	5.0	0.0	19.3	0.6	0.12	0.01
	Sebastes unknown	664	4	110	30	44.0	0.0	14.4	5.0	0.1	0.08
Syngnathidae	*Syngnathus californiensis*	4	0	4	1	0.0	0.0	0	0	0	0
Fishes unknown		413	2	81	22	384.1	2.0	40.1	16.4	0.9	0.81
THALIACEA		6	0	4	1	12.0	0.0	0.0	0.00	2.0	0.00
Sum		**18401**		**371**		**24511**					

Table 3.2. Energy density and percent protein values used to compare stomach contents.

	Aggregated Prey Category	**Energy Density (kJ g^{-1})**	**% Protein**
Cephalopods	*Abraliopsis* sp.	4.4	17.4
	Octopoteuthis sp.	4.5	17.4
	Gonatus spp.	6.4	13.7
	Loligo opalescens	3.5	16.6
	O. borealijaponicus	5.6	12.8
	Japatella heathi	2.8	13.8
	Octopus	2.8	13.8
	Squid	4.4	15.7
Crustaceans	Amphipod	2.5	12.9
	Phronima sedentaria	2.5	12.9
	Decapod	3.2	12.9
	Euphausiid	3.1	12.9
	Malacostraca	3.2	12.9
Fishes	*Sardinops sagax*	7.3	21.4
	Engraulis mordax	6.7	13.8
	Merluccius productus	5.9	14.5
	Myctophid	7.1	11.6
	Cololabis saira	7.5	20.0
	Sebastes spp.	4.2	18.6
	Fish unknown	6.4	19.2

Table 3.3: Results of randomized ANOVA in which treatment effect was independent daily sampling units (DSU).

Variable	**Effect**	**df**	**SS**	**Mean Sq**	***F***	**Rand *F***	***p***
Empty Stomach	DSU	27	71295.0	2640.6	9.7	1.57	<0.002
Weight (g)	Error	112	30503.7	272.4			
Raw Stomach	DSU	27	68530.6	2538.2	1.95	1.55	<0.002
Contents (g)	Error	112	145952.6	1303.2			
Reconstituted	DSU	30	525529.4	17517.6	2.51	1.58	<0.002
Contents (g)	Error	124	865792.7	6982.2			
Total Energy (kJ)	DSU	30	2.3×10^7	780491.1	2.32	1.53	<0.002
	Error	124	4.2×10^7	335926.4			
Total Protein (g)	School	30	15922.7	530.8	2.32	1.53	<0.002
	Error	124	28314.3	228.3			

Table 3.4. Percent frequency of occurrence (*%FO*) of 20 aggregated prey categories in each of 46 DSUs versus all 371 individuals, and mean number of prey category in one stomach.

	Aggregated Prey Category	***%FO* Individual**	***%FO* DSU**	**Mean *N* per Stomach**
Cephalopods	*Abraliopsis* sp.	26.4	54.3	4.6
	Octopoteuthis sp.	11.6	47.8	1.6
	Gonatus spp.	12.1	54.3	2.2
	Loligo opalescens	8.9	26.1	3.1
	O. borealijaponica	19.1	56.5	3.0
	Japatella heathi	7.0	37.0	1.5
	Octopus	10.0	34.8	2.8
	Squid	33.4	87.0	2.8
Crustaceans	Amphipod	11.9	47.8	2.6
	Phronima sedentaria	19.4	37.0	3.5
	Decapod	15.1	45.7	41.3
	Euphausiid	19.9	58.7	29.8
	Malacostraca	27.8	60.9	9.2
Fishes	*Sardinops sagax*	26.7	73.9	6.2
	Engraulis mordax	52.8	73.9	25.3
	Merluccius productus	16.4	28.3	57.9
	Myctophidae	11.3	47.8	1.2
	Cololabis saira	18.3	50.0	5.0
	Sebastes spp.	34.5	80.4	6.3
	Fish	29.1	80.4	3.4

Table 3.5. Numeric abundance of prey aggregated into 20 categories in each of three regions. Asterisks in the Sum row and column denote species or regions that are significantly different (df = 38, $\chi^2 = 53.36$, $p < 0.05$).

	Aggregated Prey Category	**North**	**Central**	**South**	**Sum**
Cephalopods	*Abraliopsis* sp.	82	48	24	154*
	Octopoteuthis sp.	14	13	1	28*
	Gonatus sp.	22	5	9	36
	Loligo opalescens	1	0	19	20*
	O. borealijaponica	57	16	3	76
	Octopus + *Japatella heathi*	28	4	9	41
	Squid	34	12	44	90*
Crustaceans	Amphipod	35	15	8	58
	Phronima sedentaria	101	5	0	106
	Decapod	1790	0	1	1791*
	Euphausiid	1347	6	8	1361*
	Malacostraca	278	13	39	330
Fishes	*Sardinops sagax*	162	1	52	215*
	Engraulis mordax	1631	7	481	2119*
	Merluccius productus	934	280	0	1214*
	Myctophidae	23	3	0	26
	Cololabis saira	33	144	1	178*
	Sebastes spp.	309	39	13	361
	Fishes	103	56	10	169*
	Sum	6984*	667*	722*	8373*

Table 3.6. Percent mass (*%M*), energy (*%E*), and protein (*%P*) contributed by each of 20 aggregated 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.

	North			**Central**			**South**		
Prey Category	**%M**	**%E**	**%P**	**%M**	**%E**	**%P**	**%M**	**%E**	**%P**
Abraliopsis sp.	1.6	1.5	1.9	12.7	9.5	13.4	2.7	2.0	3.2
Octopoteuthis sp.	0.2	0.2	0.2	1.6	1.2	1.7	0.2	0.1	0.2
Gonatus sp.	0.4	0.5	0.4	0.3	0.3	0.2	0.8	0.8	0.7
Loligo opalescens	0.0	0.0	0.0	0.0	0.0	0.0	4.3	2.5	4.7
O. borealijaponica	1.2	1.5	1.1	6.7	6.4	5.2	0.3	0.3	0.3
Japatella heathi	0.3	0.2	0.3	0.3	0.1	0.2	0.3	0.1	0.3
Octopus	0.3	0.2	0.3	0.5	0.3	0.4	1.8	0.8	1.7
Squid	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
P. sedentaria	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
Malacostraca	3.6	2.5	3.3	0.5	0.3	0.4	6.4	3.4	5.5
Sardinops sagax	2.8	4.3	4.2	0.4	0.5	0.5	12.7	15.3	17.9
Engraulis mordax	20.8	29.8	20.3	1.3	1.5	1.1	60.8	67.4	55.5
M. productus	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
Cololabis saira	0.5	0.7	0.6	23.8	30.5	29.0	0.3	0.4	0.4
Sebastes spp.	4.7	4.3	6.2	3.9	2.8	4.4	0.0	0.0	0.0
Fishes	1.8	2.5	2.5	5.2	5.7	6.1	1.4	1.5	1.7

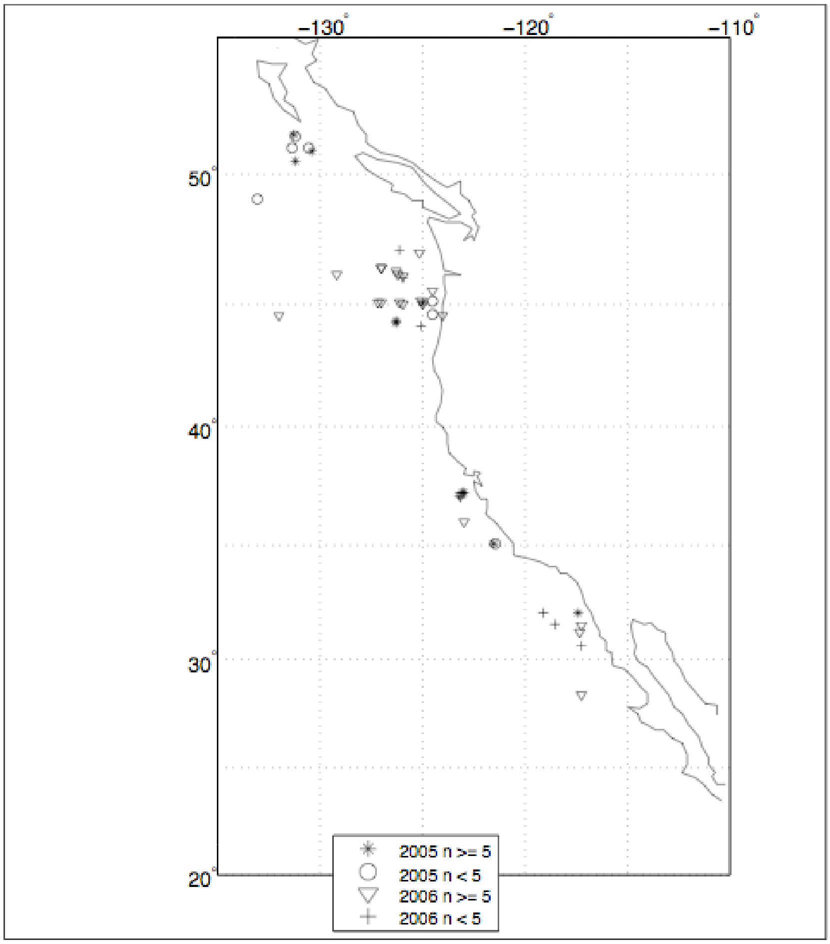


Figure 3.1. Distribution of sample collection in summer-fall 2005 and 2006, aggregated by albacore daily sampling unit.

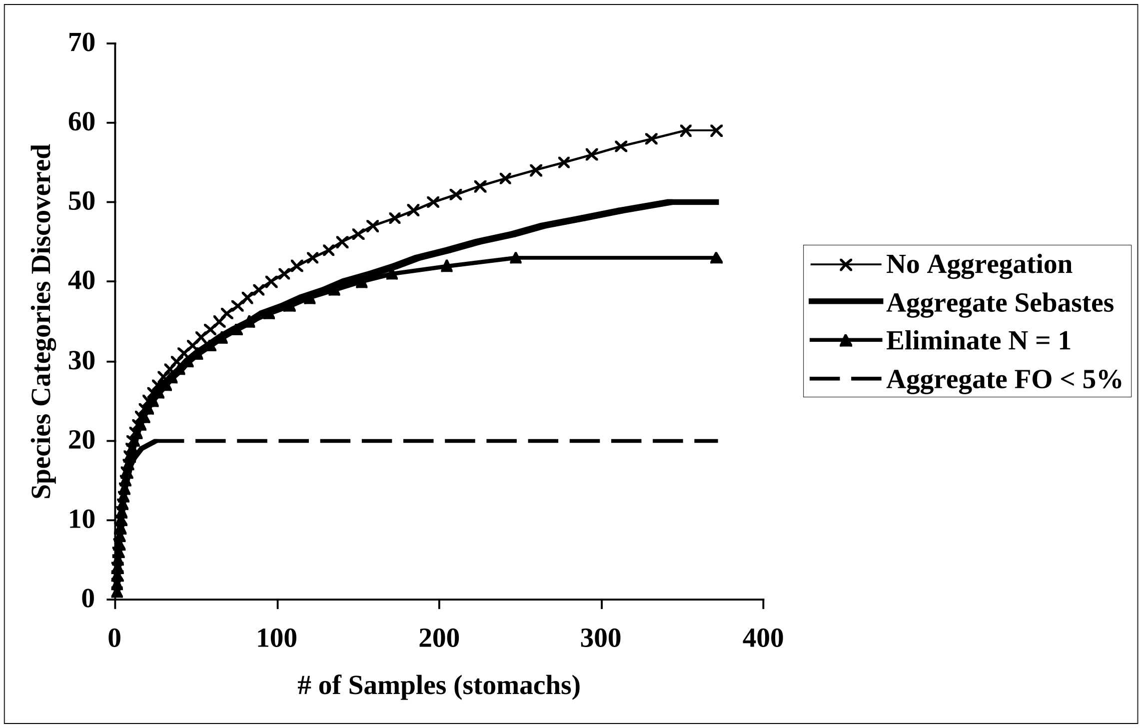


Figure 3.2. Species accumulation curves showing the necessary sample size needed to discover the number of species categories given different levels of aggregation.

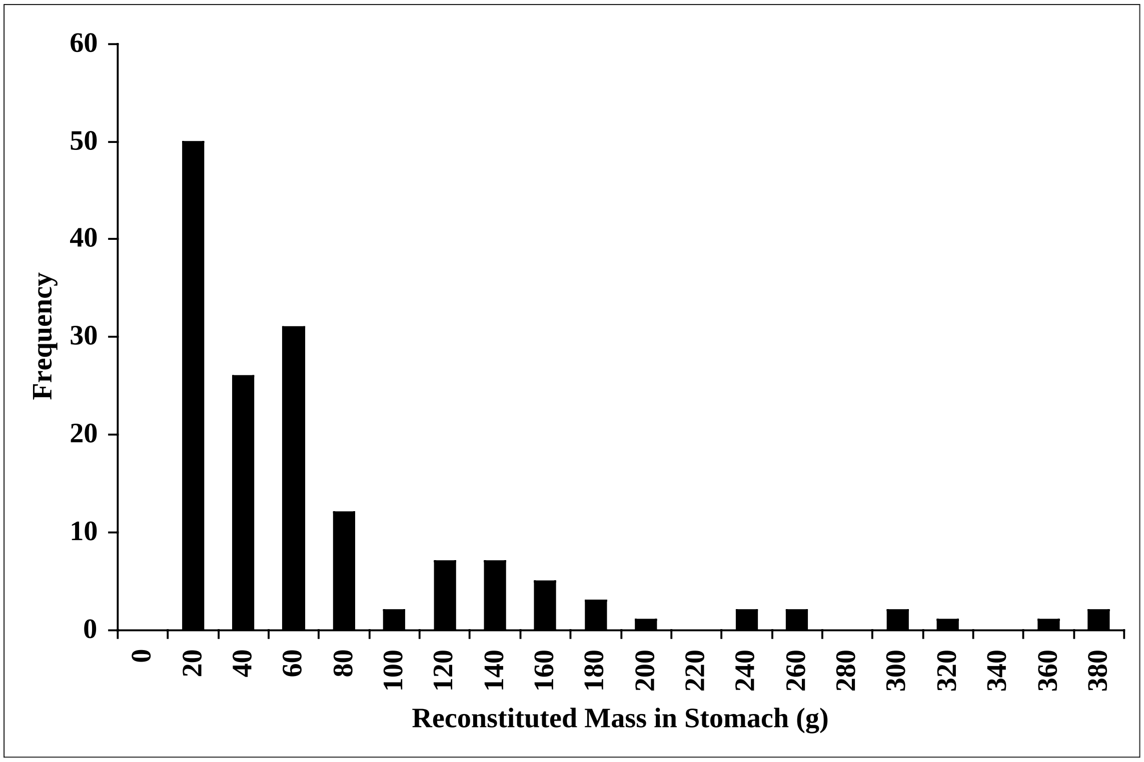


Figure 3.3. Total reconstituted mass as a snapshot in time in an albacore stomach.

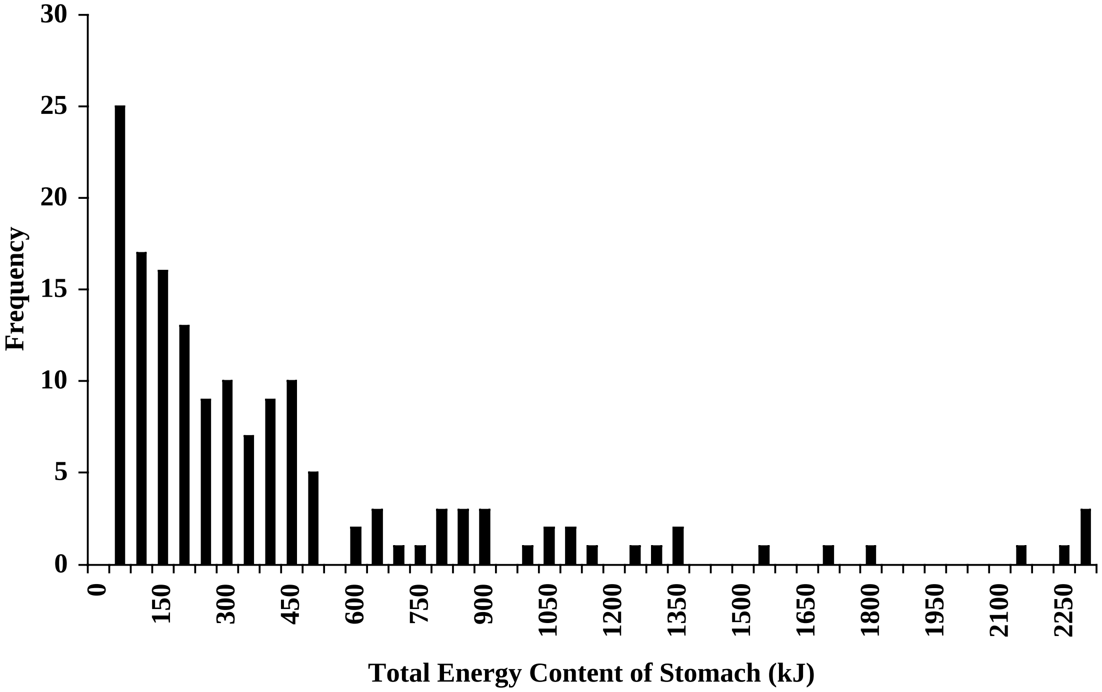


Figure 3.4. Total energy content as a snapshot in time in an albacore stomach.

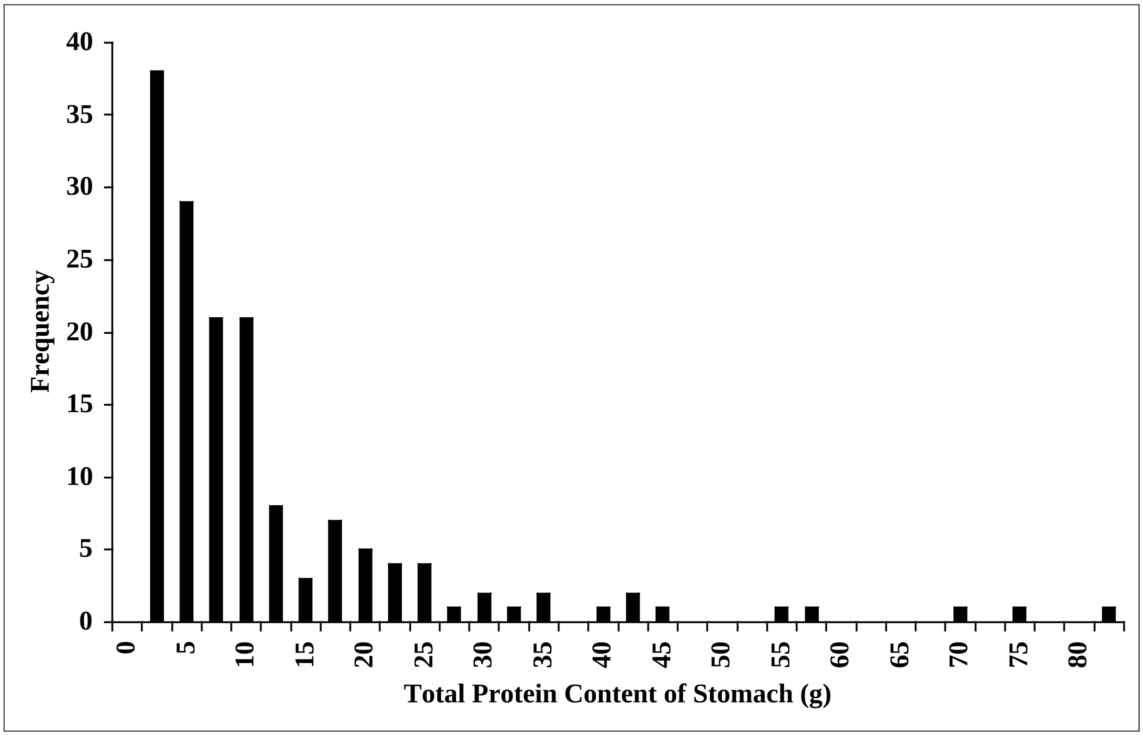


Figure 3.5. Total protein content as a snapshot in time in an albacore stomach.

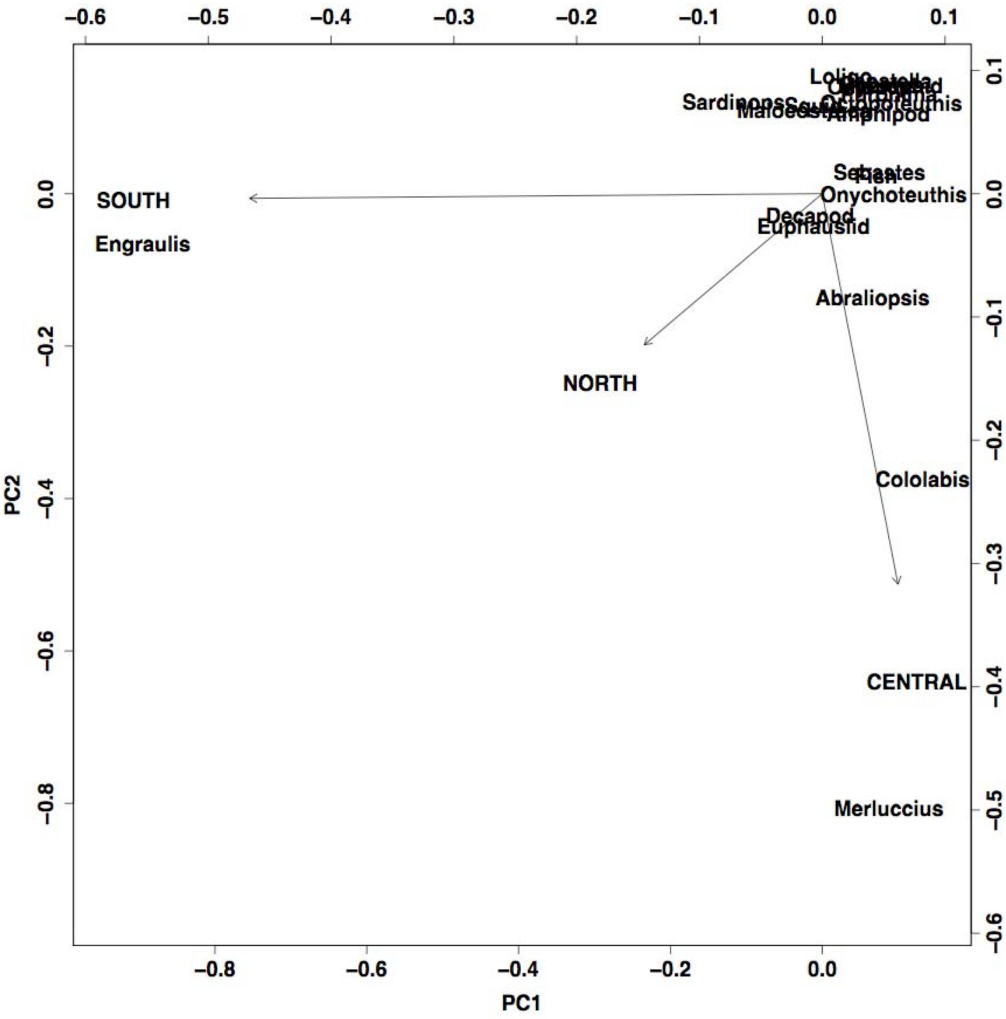


Figure 3.6. Regional differences in dietary preferences of albacore in the California Current System.

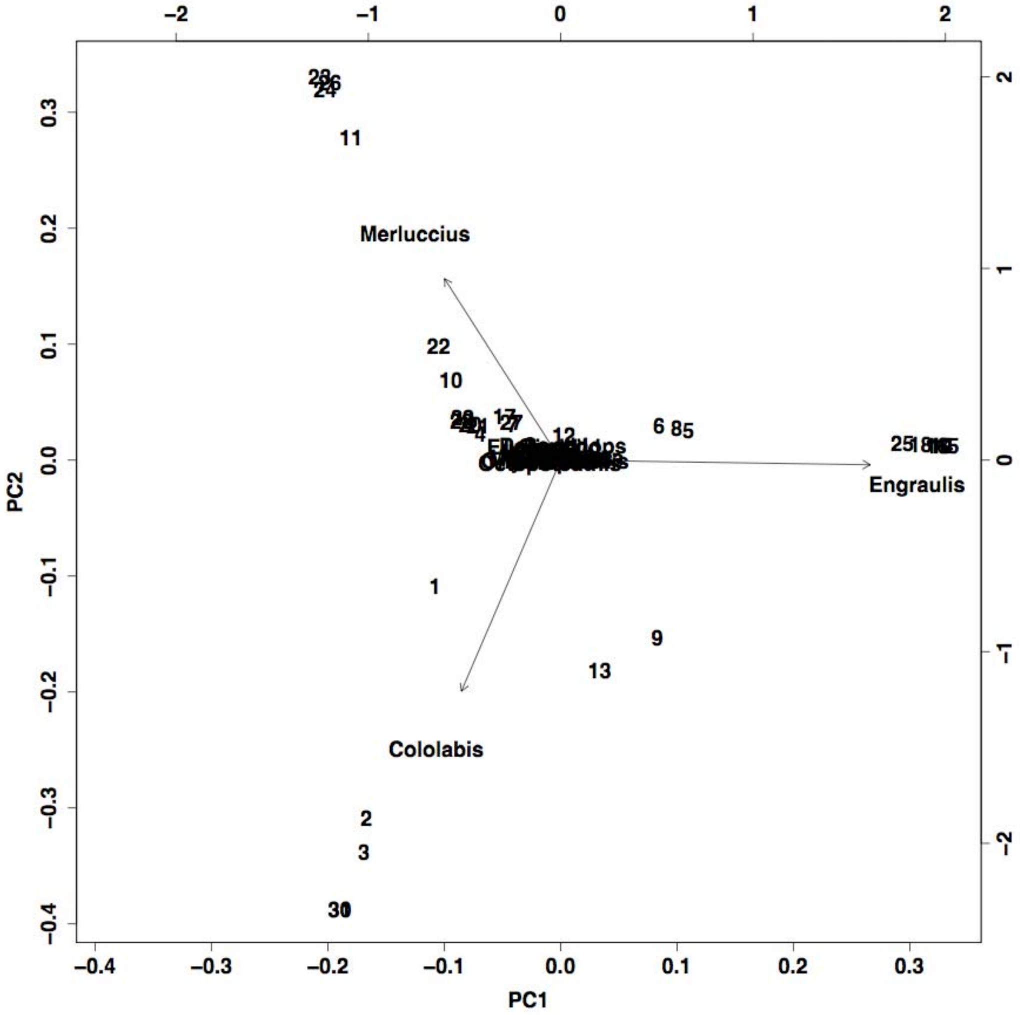


Figure 3.7. Dietary preferences of albacore grouped as 31 independent daily sampling units.

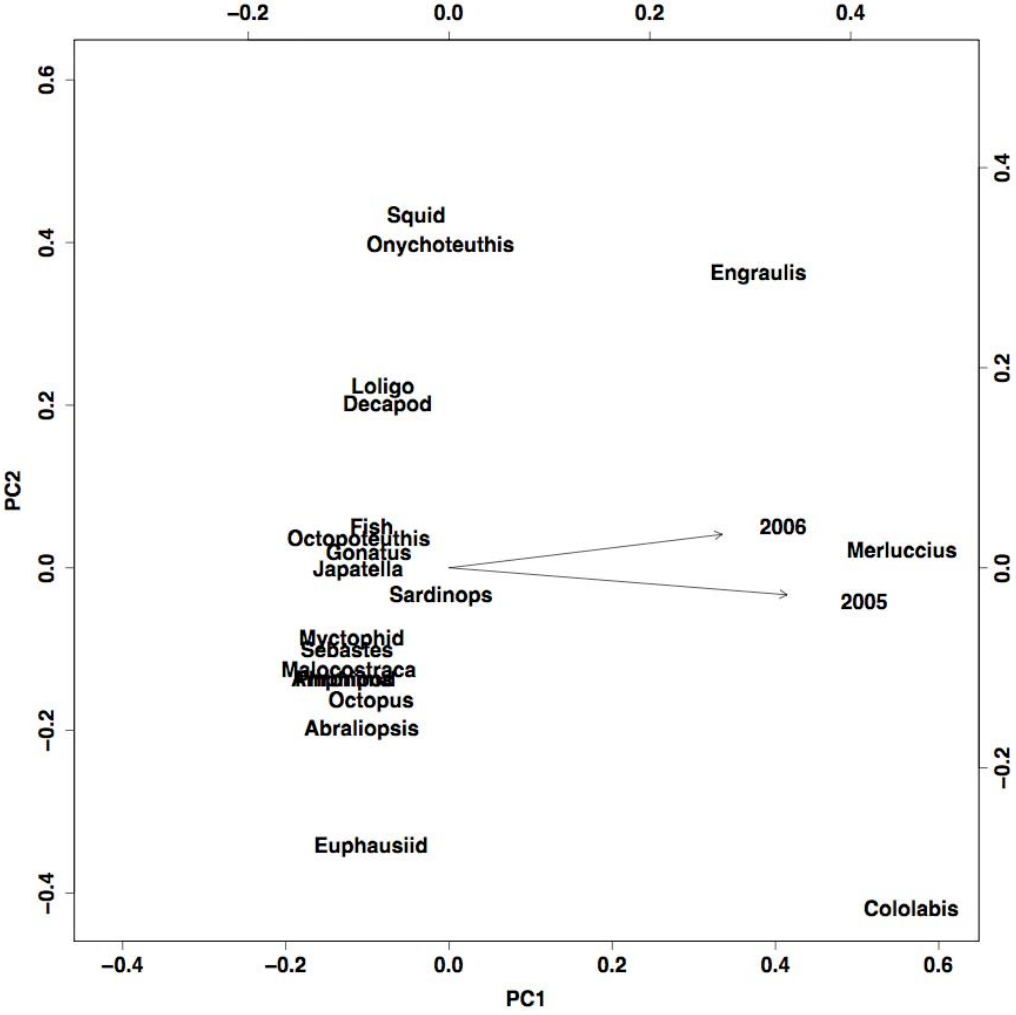


Figure 3.8. Interannual dietary preferences of albacore for 20 species categories of prey.

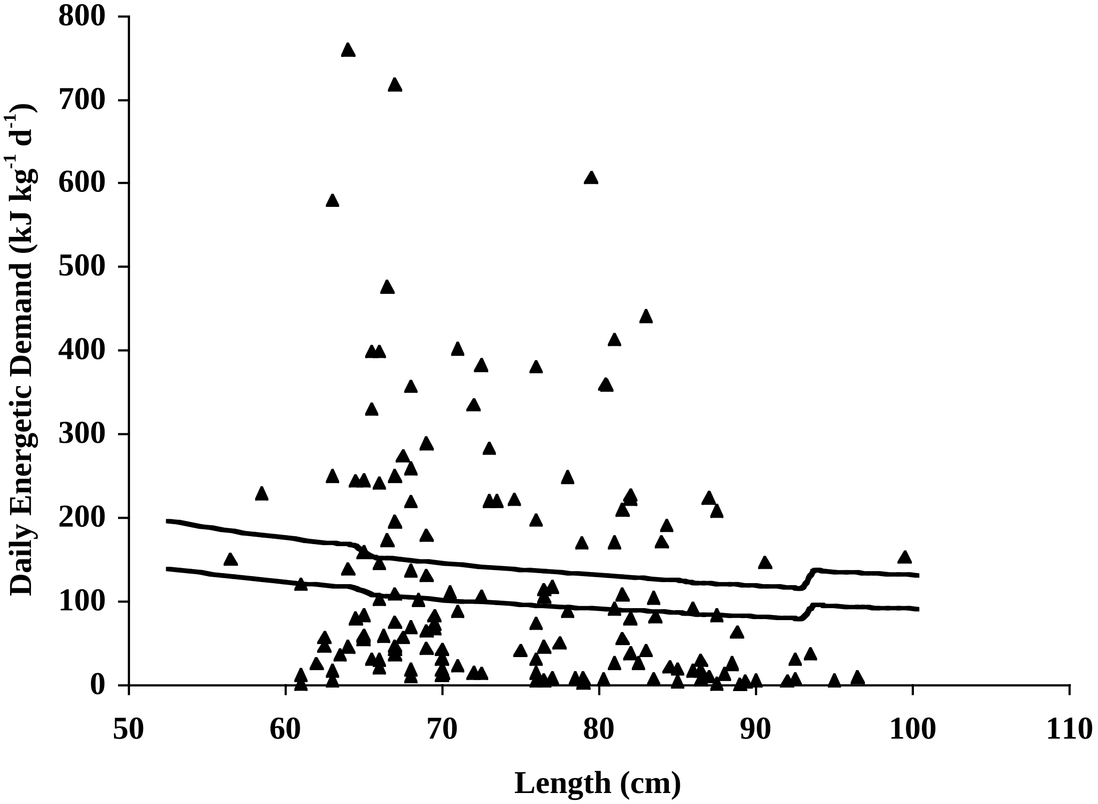


Figure 3.9. Daily energetic demand for albacore calculated with a bioenergetics model developed by Essington (2003). The top and bottom lines represent the 90% confidence intervals calculated by 1000 Monte Carlo simulations. Individual triangles are the observed total energetic content (kJ per kg of albacore) found inside each stomach.

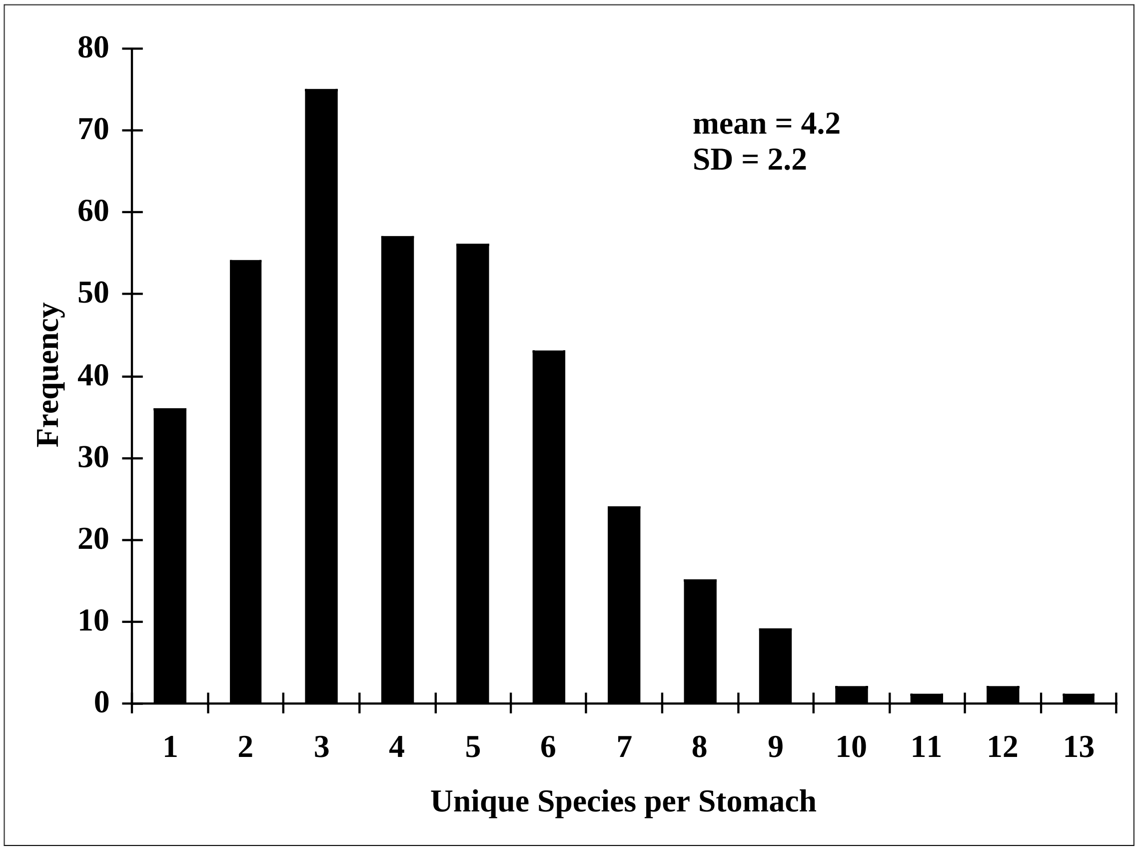


Figure 3.10. Number of unique prey species categories (unaggregated, *n* = 59) found in a stomach.

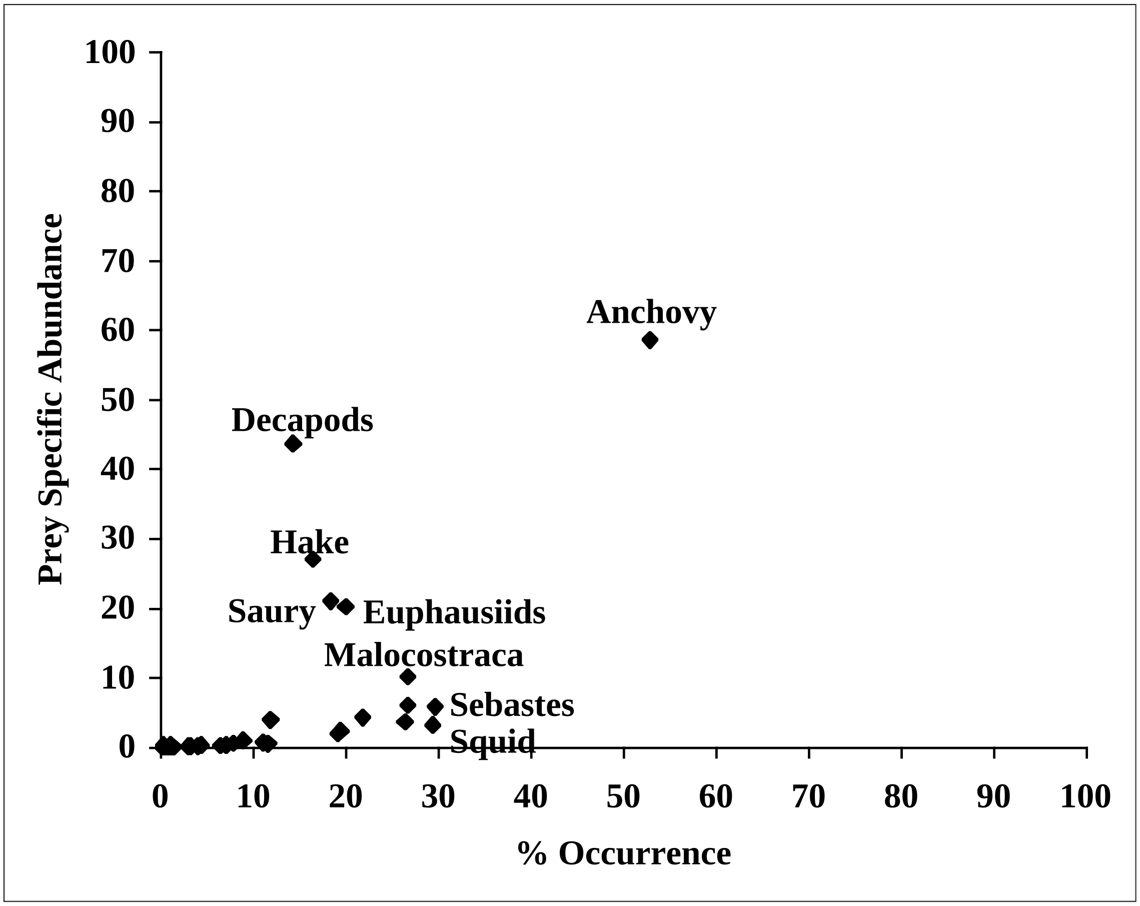


Figure 3.11. Foraging strategy of and prey importance to albacore, after Costello (1990).

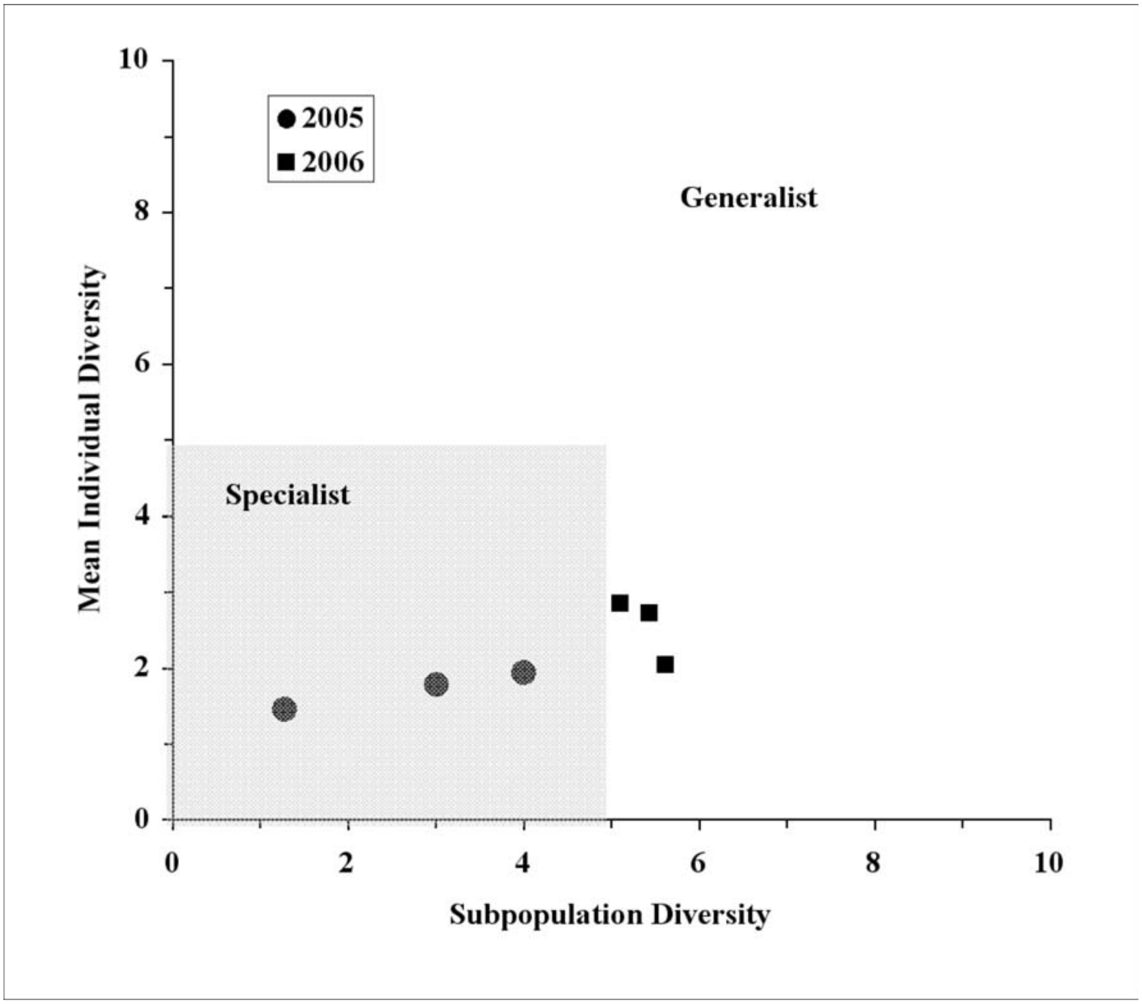
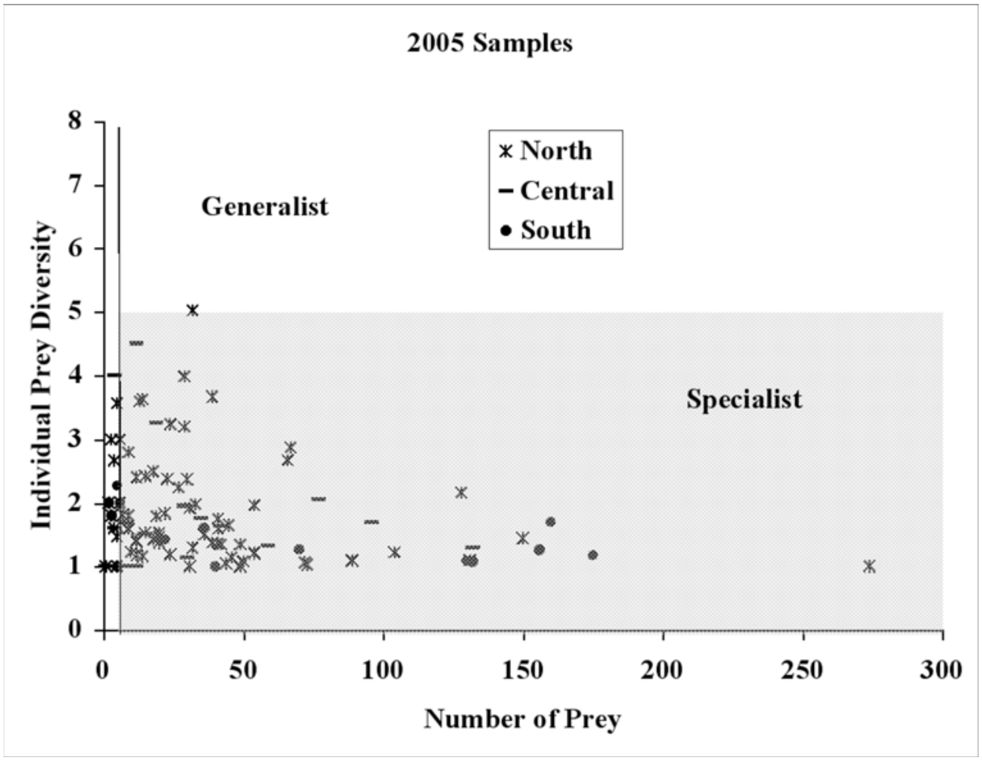


Figure 3.12. Classification of albacore foraging strategy according to Tokeshi (1991). Each point is one of six subregions (North, Central, or South for 2005 and 2006).



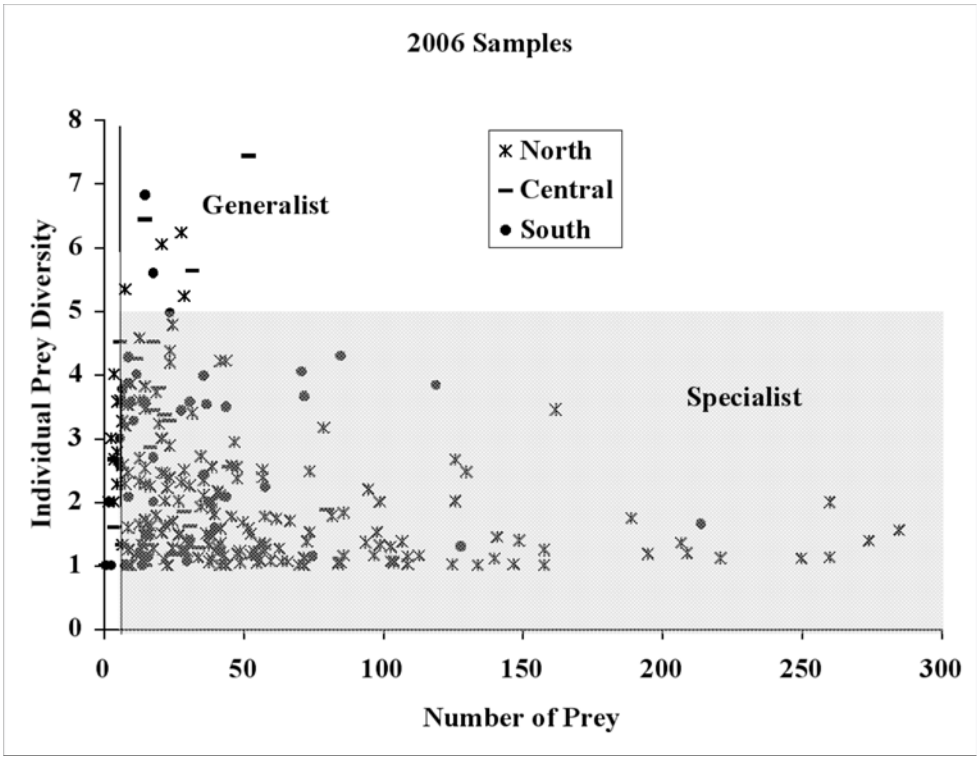


Figure 3.13. Classification of albacore foraging strategy according to Bridcut and Giller (1995). Each point is an individual stomach from a designated region.

Appendix 3.1. Distribution maps of prey consumed by albacore.

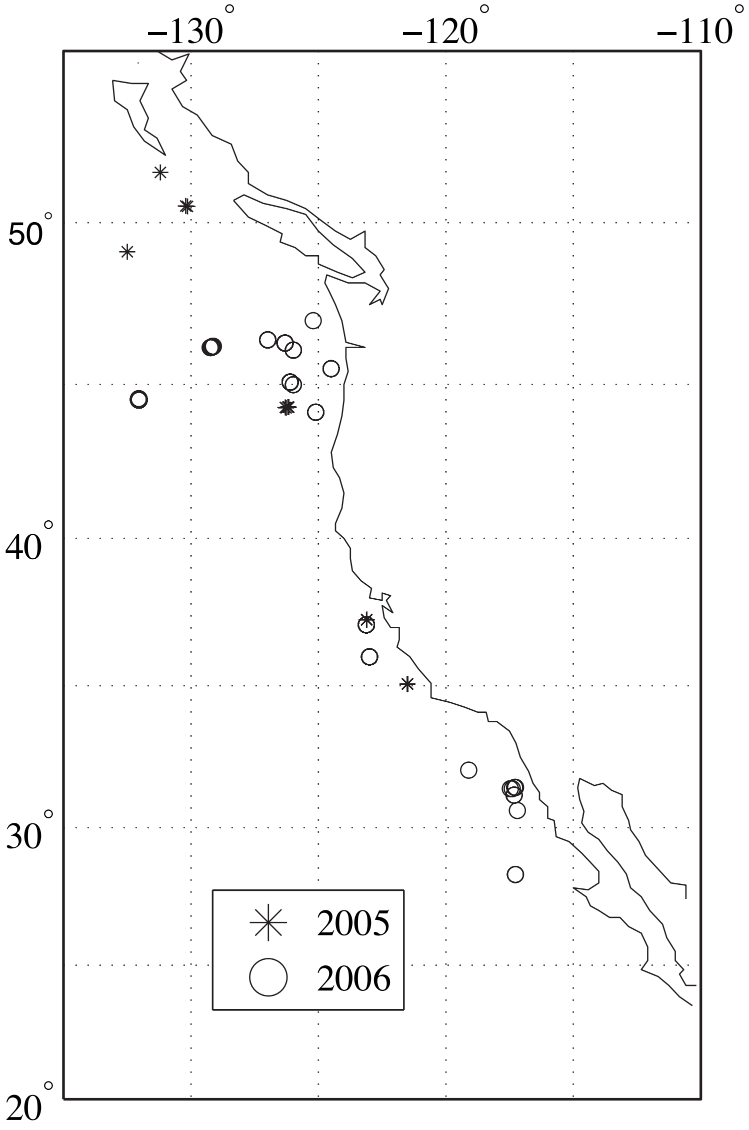


Figure A3.1.1. Stomachs containing *Abraliopsis* sp.

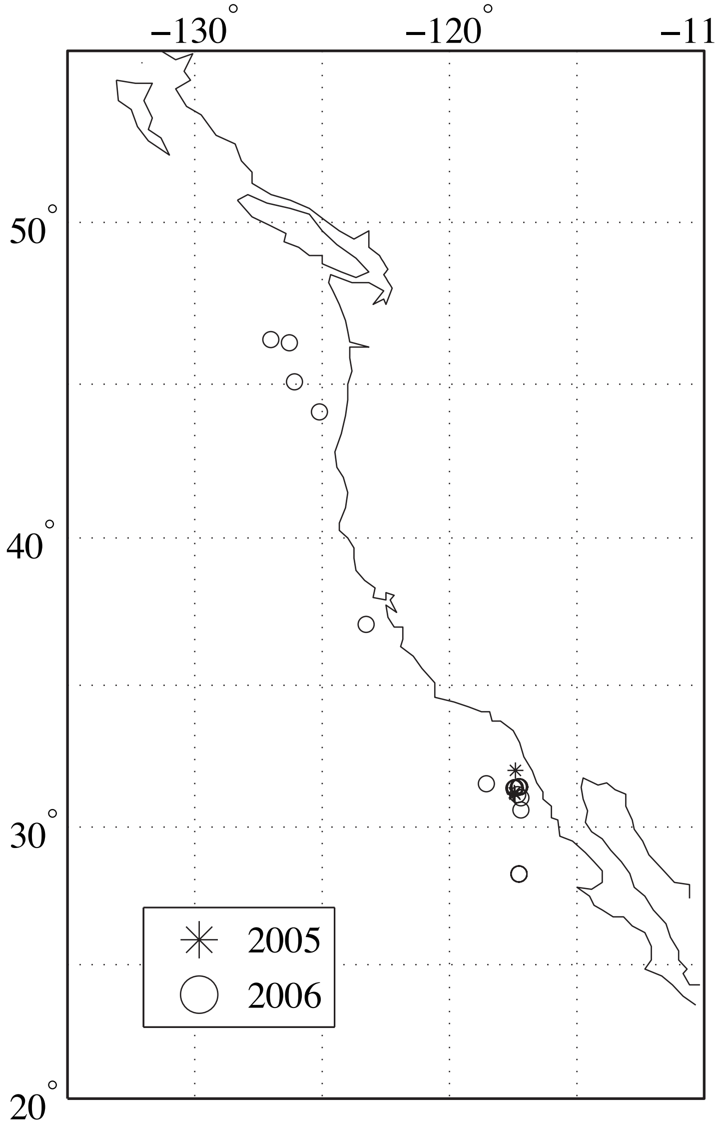


Figure A3.1.2. Stomachs containing *Loligo opalescens*.

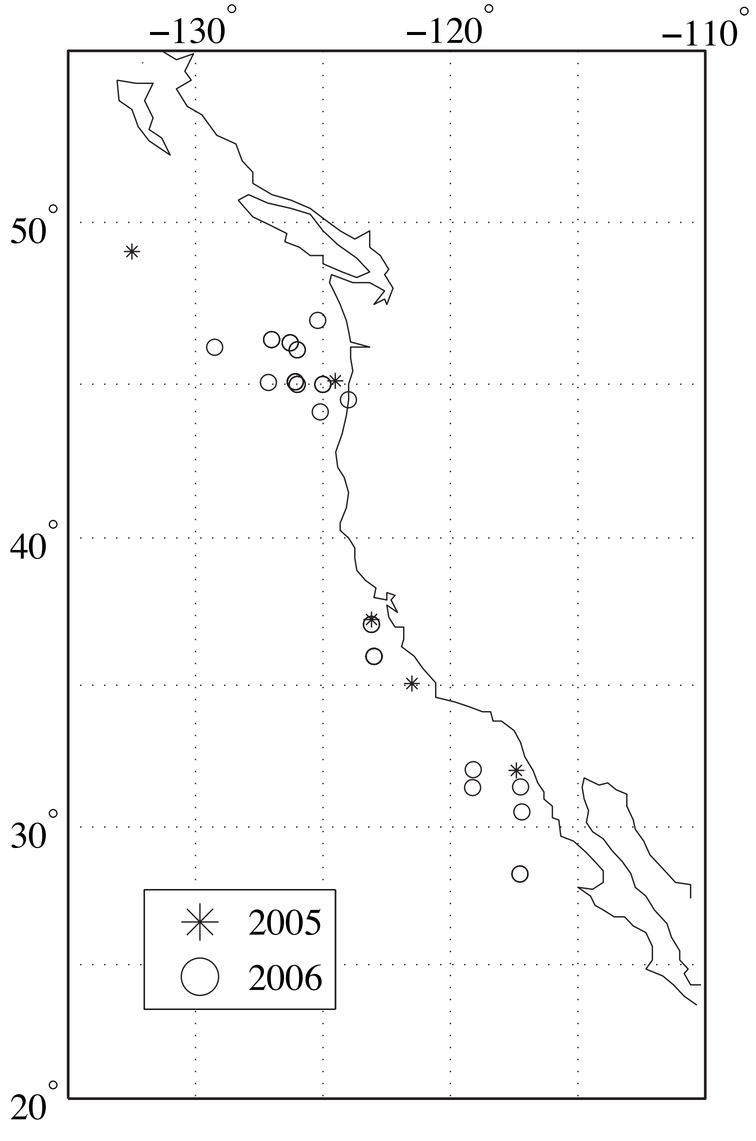


Figure A3.1.3. Stomachs containing *Octopoteuthis* sp.

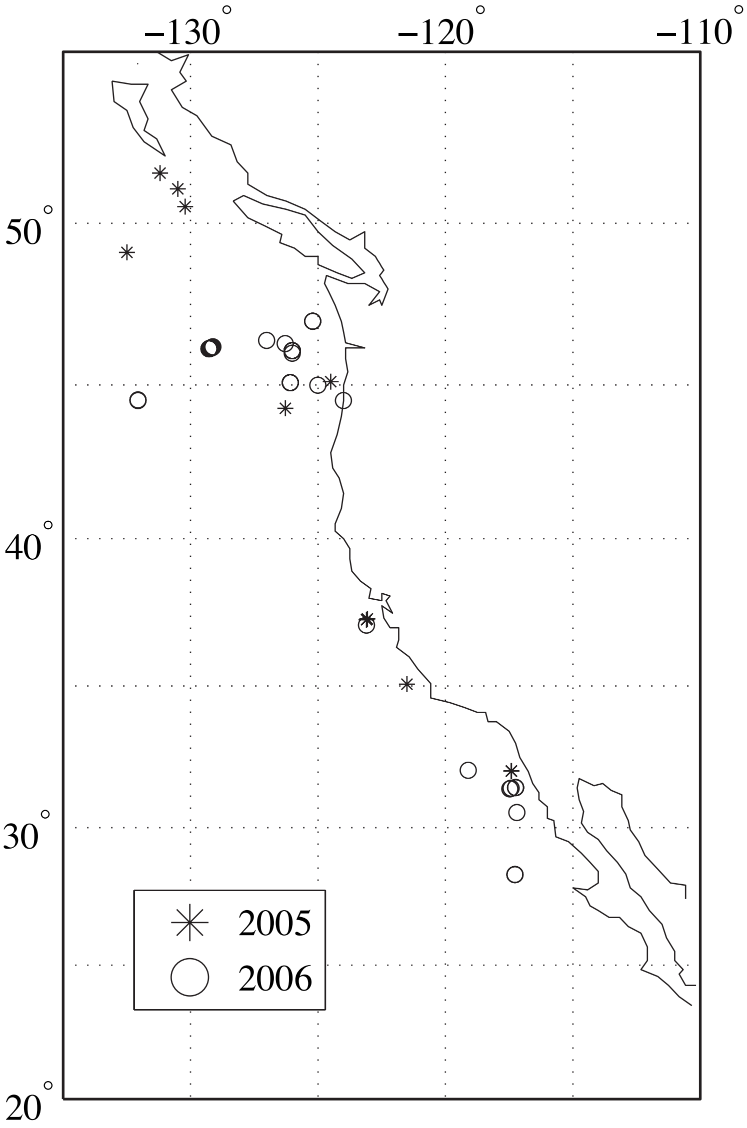


Figure A3.1.4. Stomachs containing *Gonatus* spp.

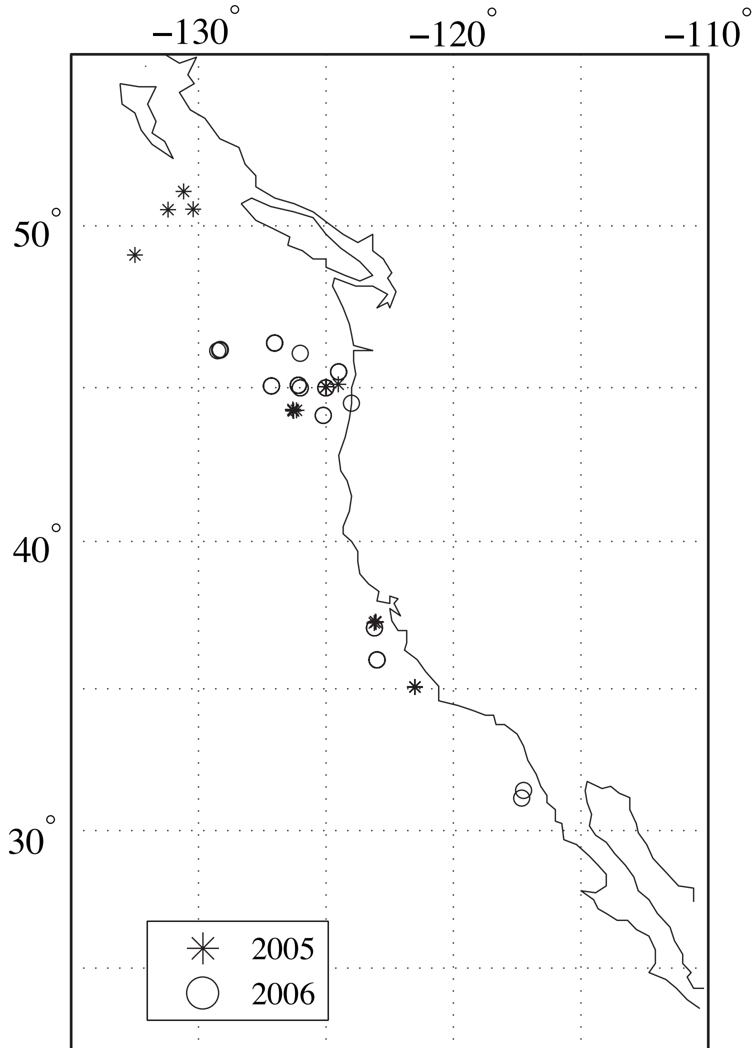


Figure A3.1.5. Stomachs containing *Onychoteuthis borealijaponica*

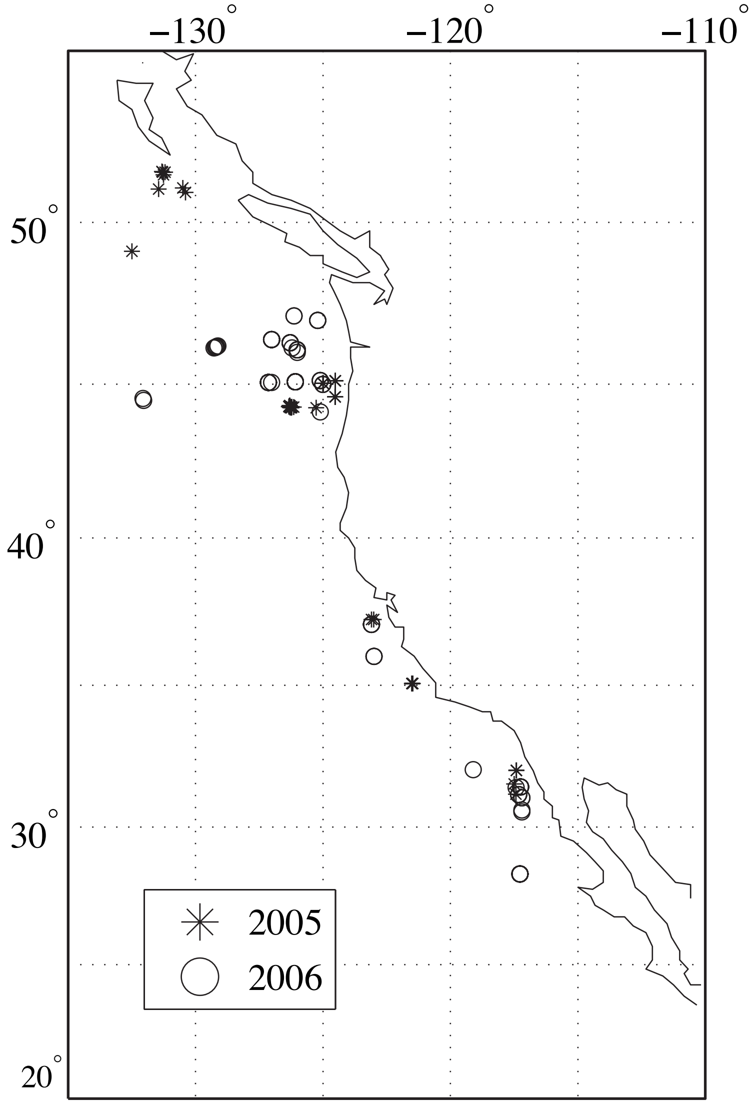


Figure A3.1.6. Stomachs containing squid (other and unidentified).

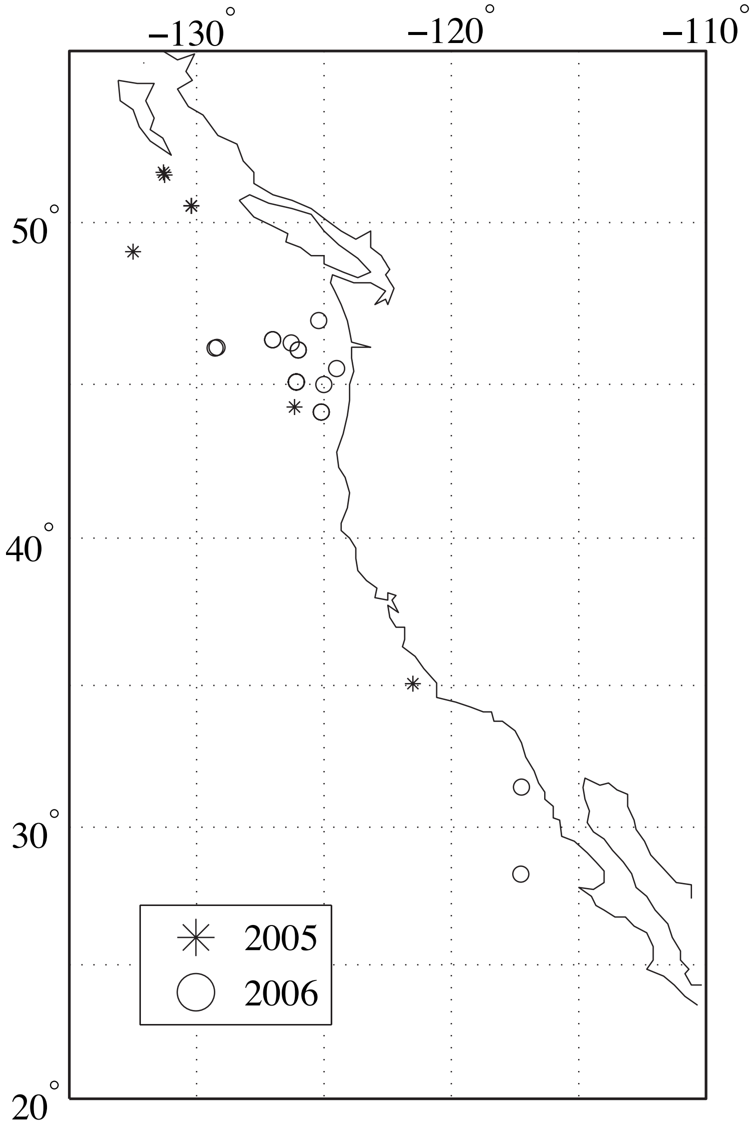


Figure A3.1.7. Stomachs containing *Japatella heathii.*

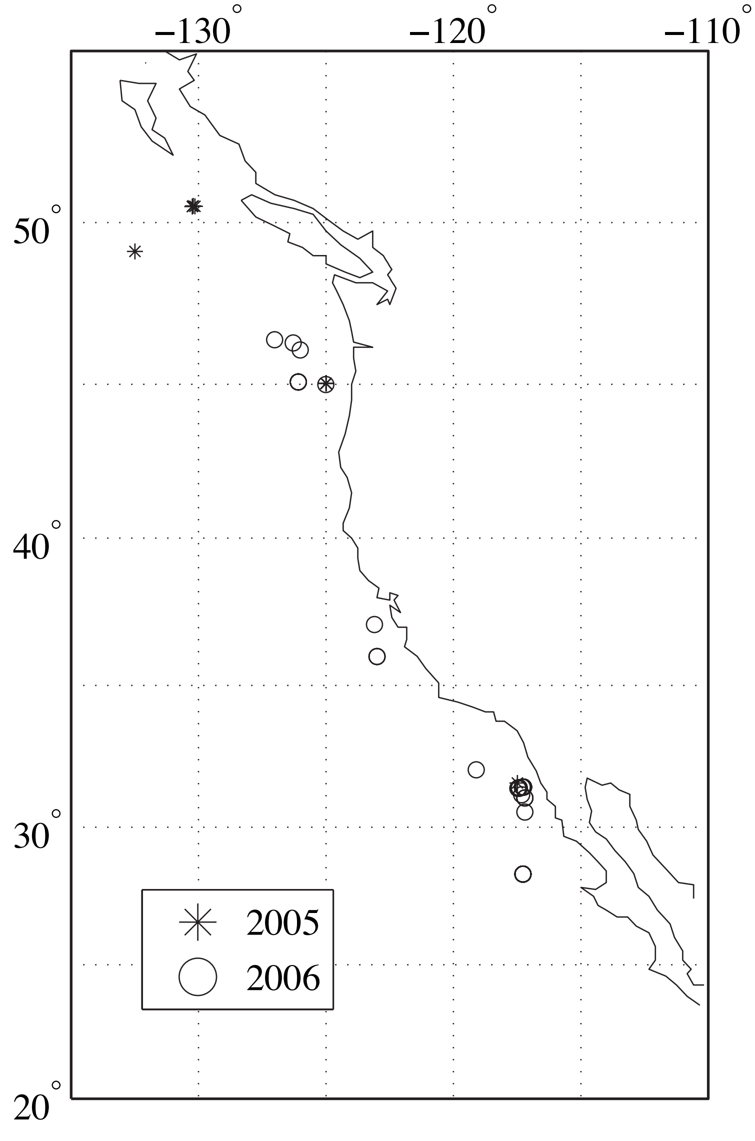


Figure A3.1.8. Stomachs containing Octopus (other and unidentified).

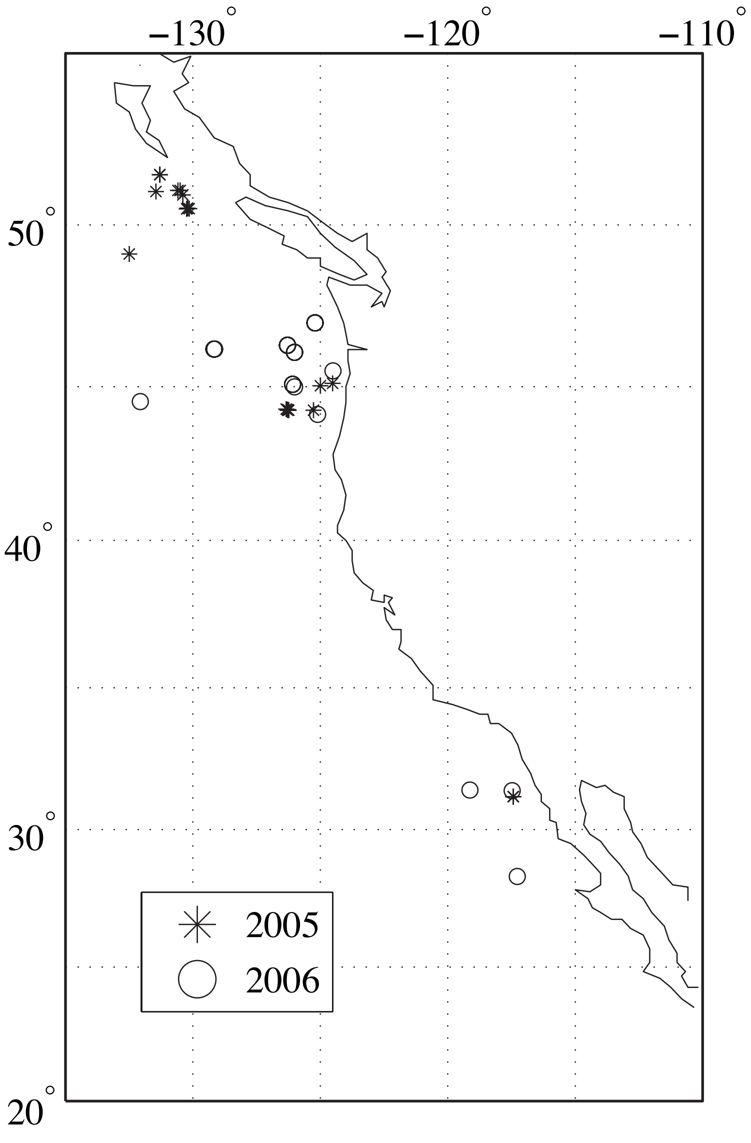


Figure A3.1.9. Stomachs containing decapods.

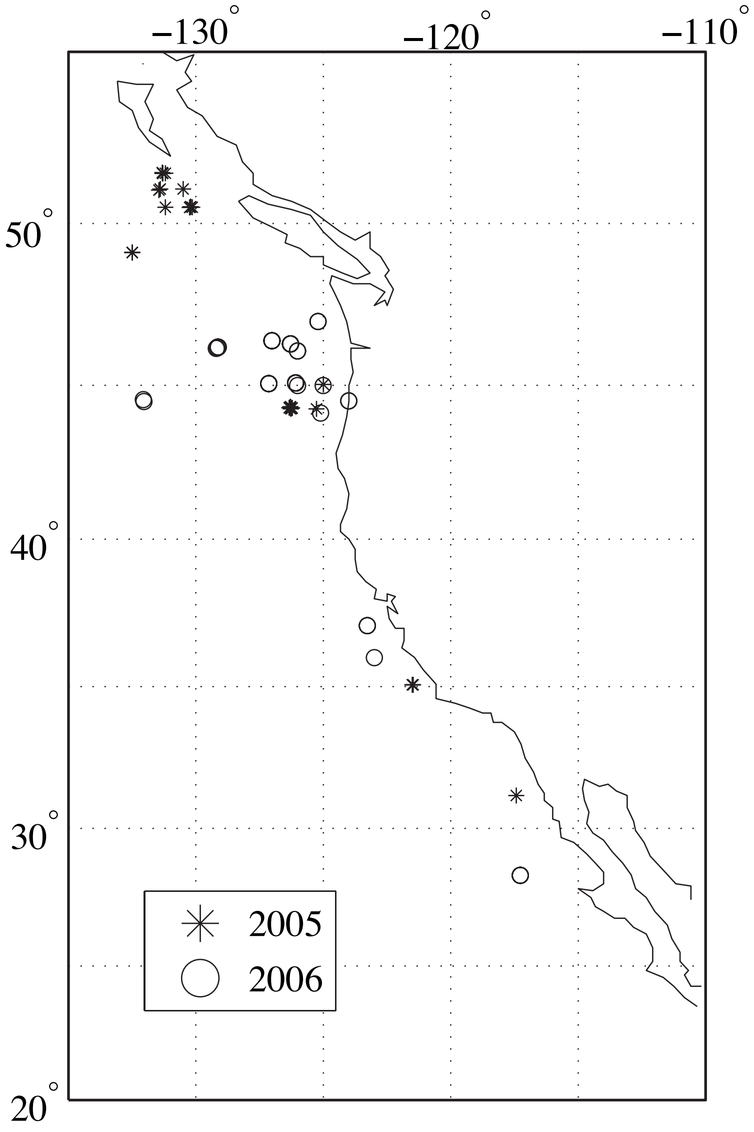


Figure A3.1.10. Stomachs containing euphausiids.

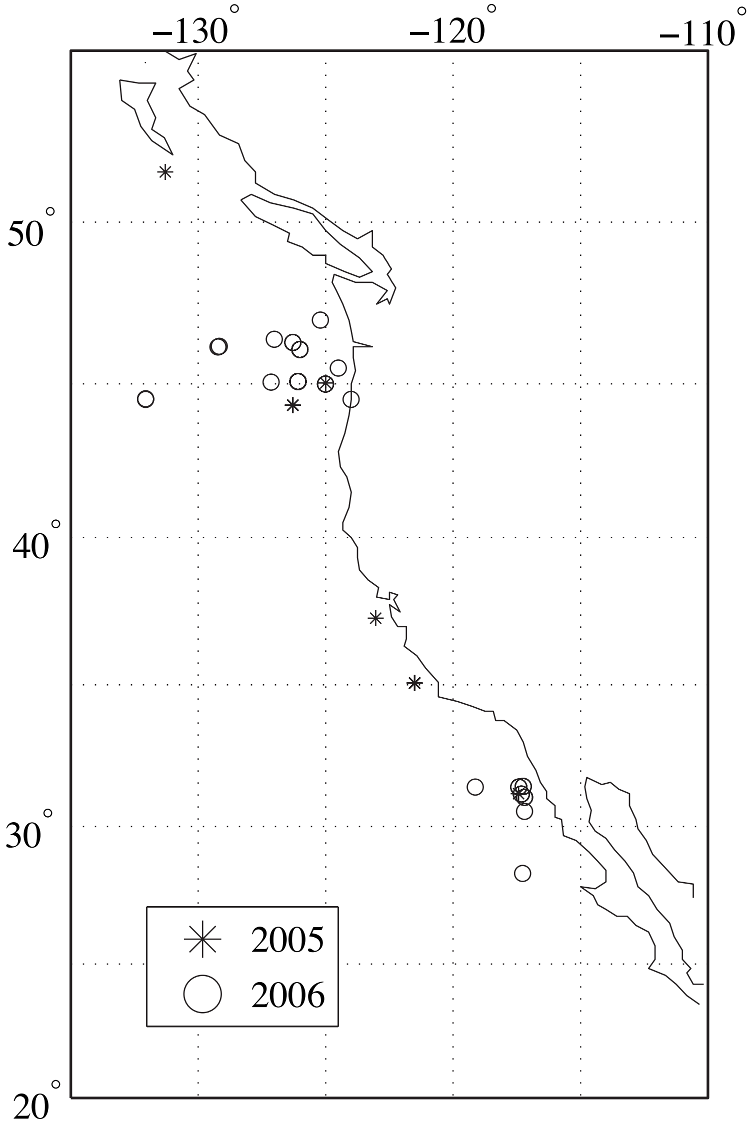


Figure A3.1.11. Stomachs containing amphipods.

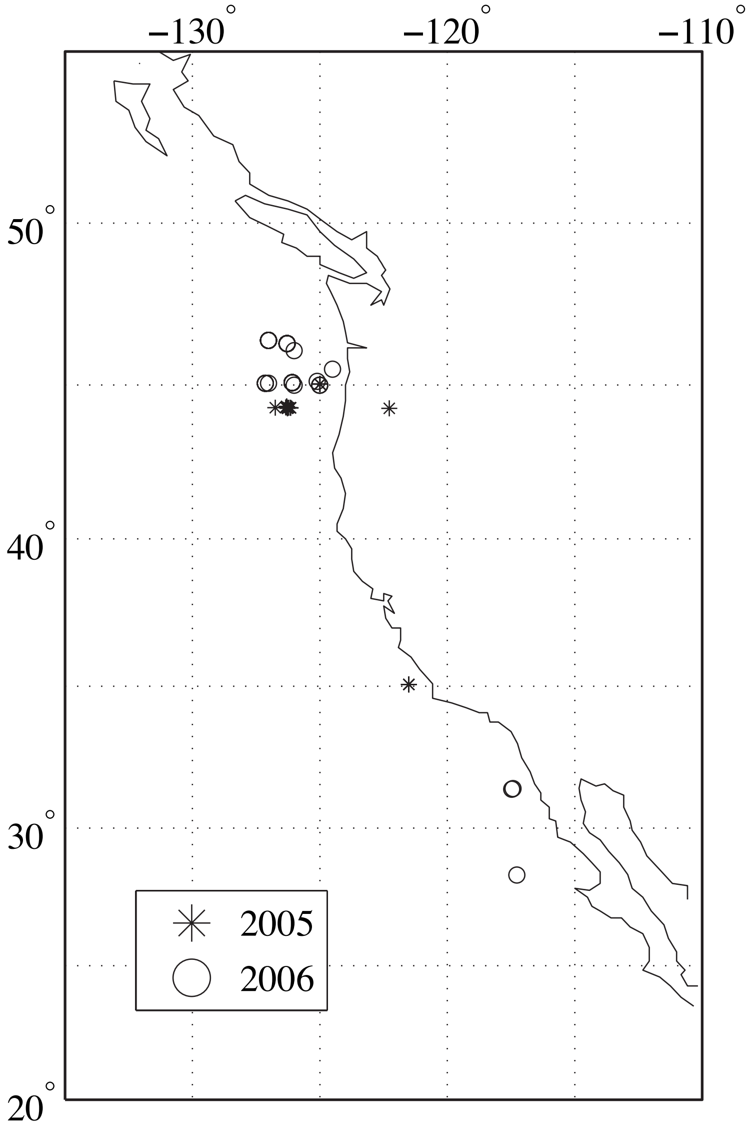


Figure A3.1.12. Stomachs containing *Phronima sedentaria.*

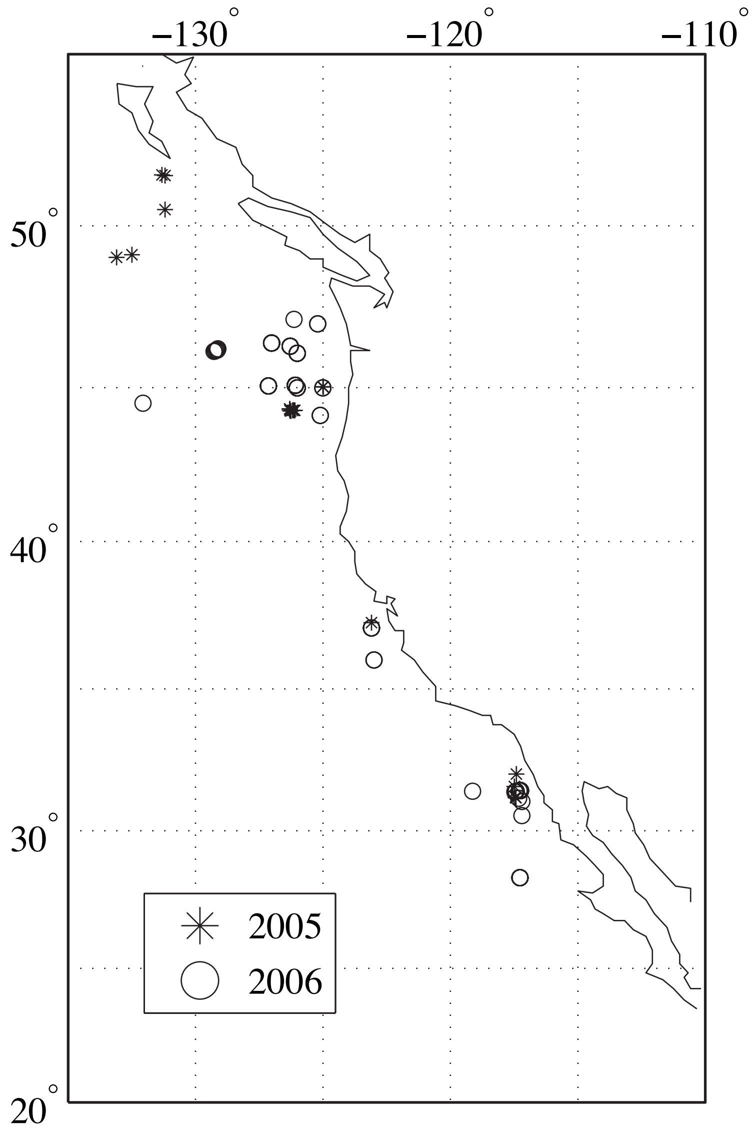


Figure A3.1.13. Stomachs containing Malacostraca.

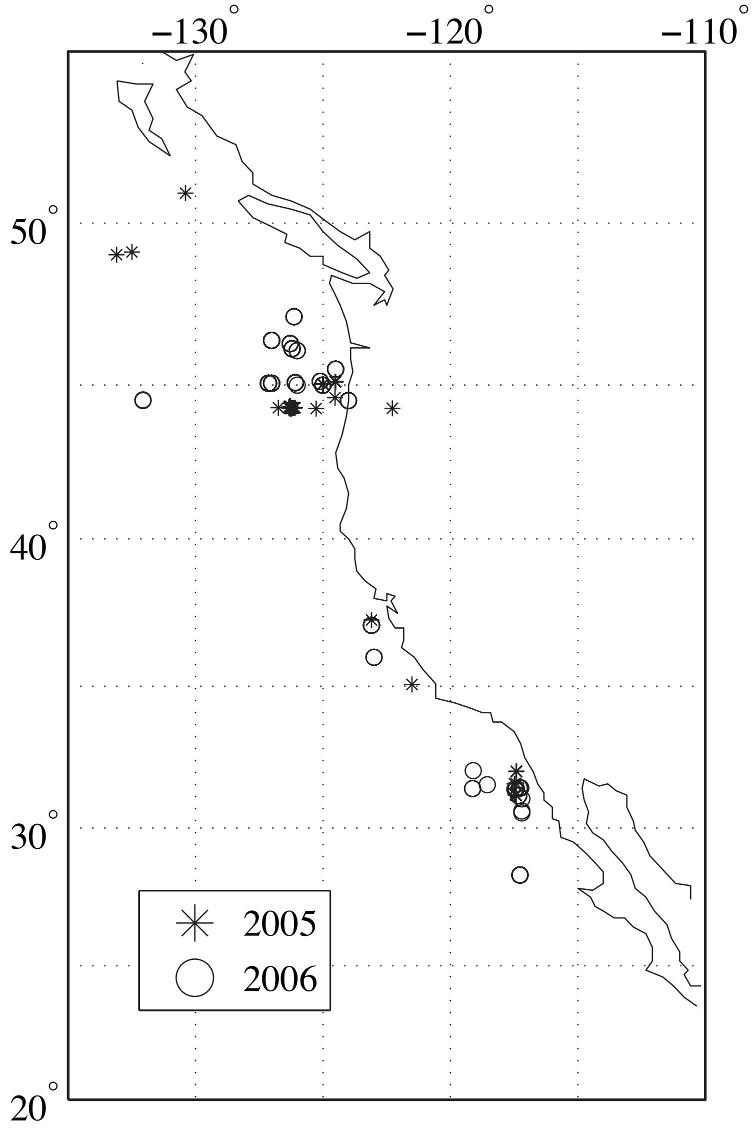


Figure A3.1.14. Stomachs containing *Engraulis mordax*.

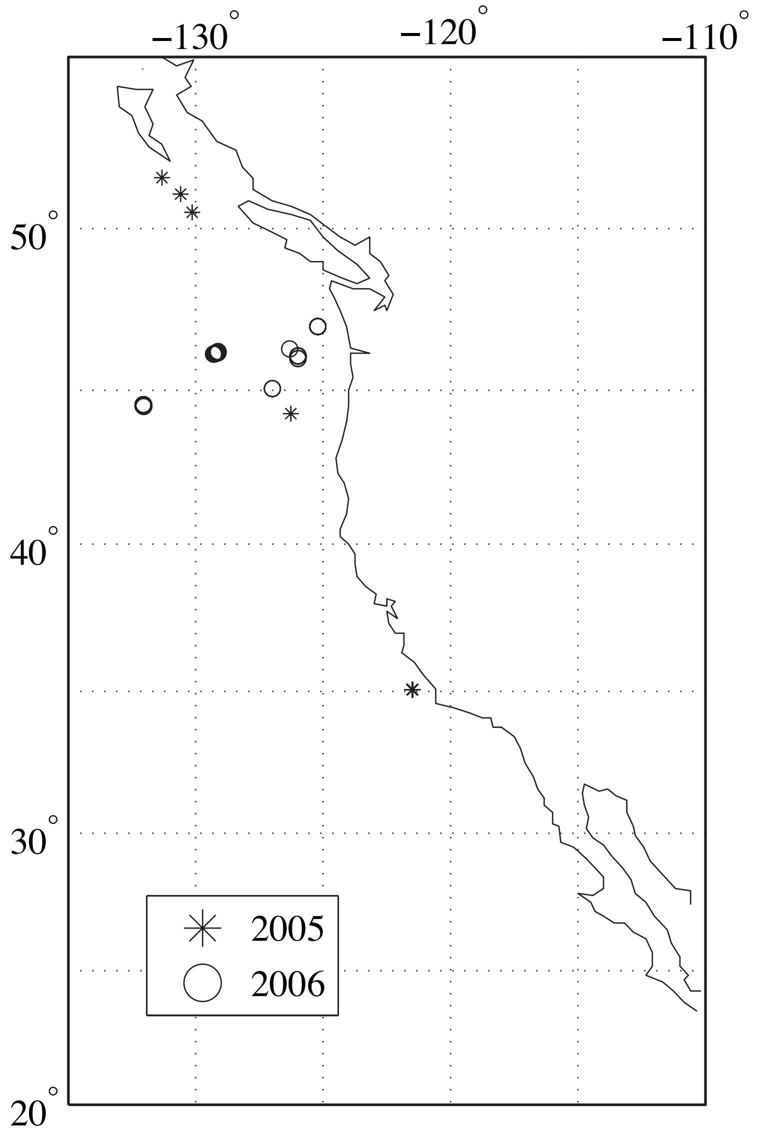


Figure A3.1.15. Stomachs containing *Merluccius productus.*

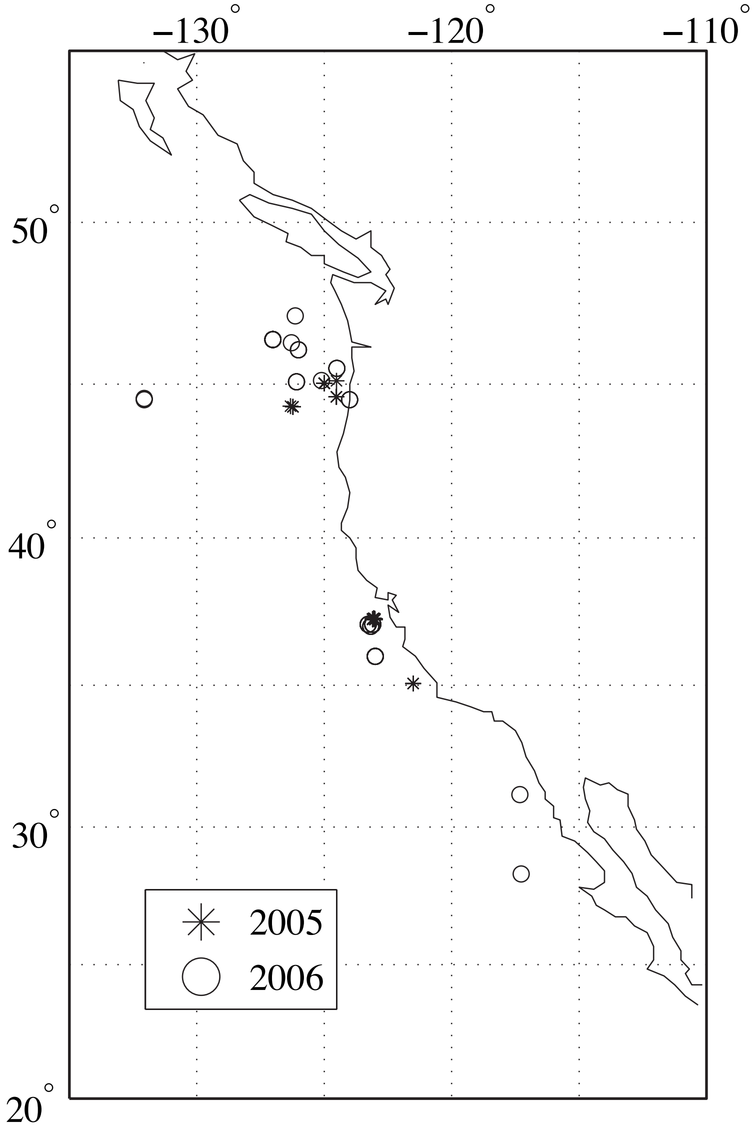


Figure A3.1.16. Stomachs containing *Cololabis saira.*

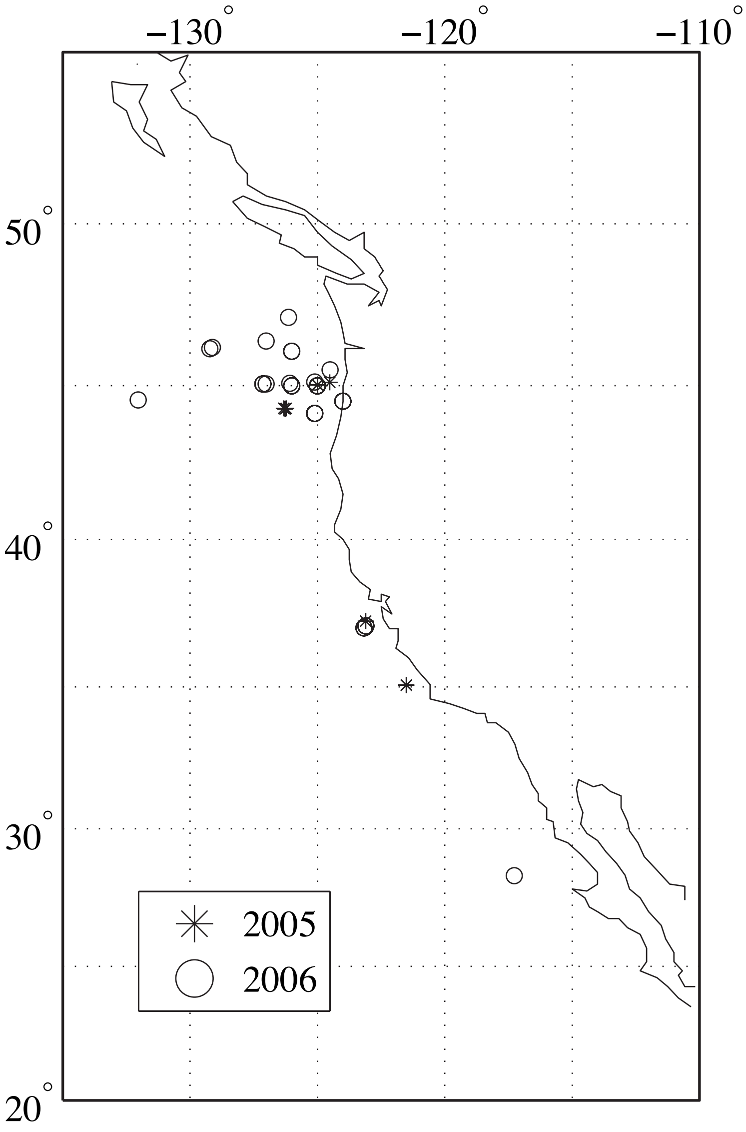


Figure A3.1.17. Stomachs containing Myctophids.

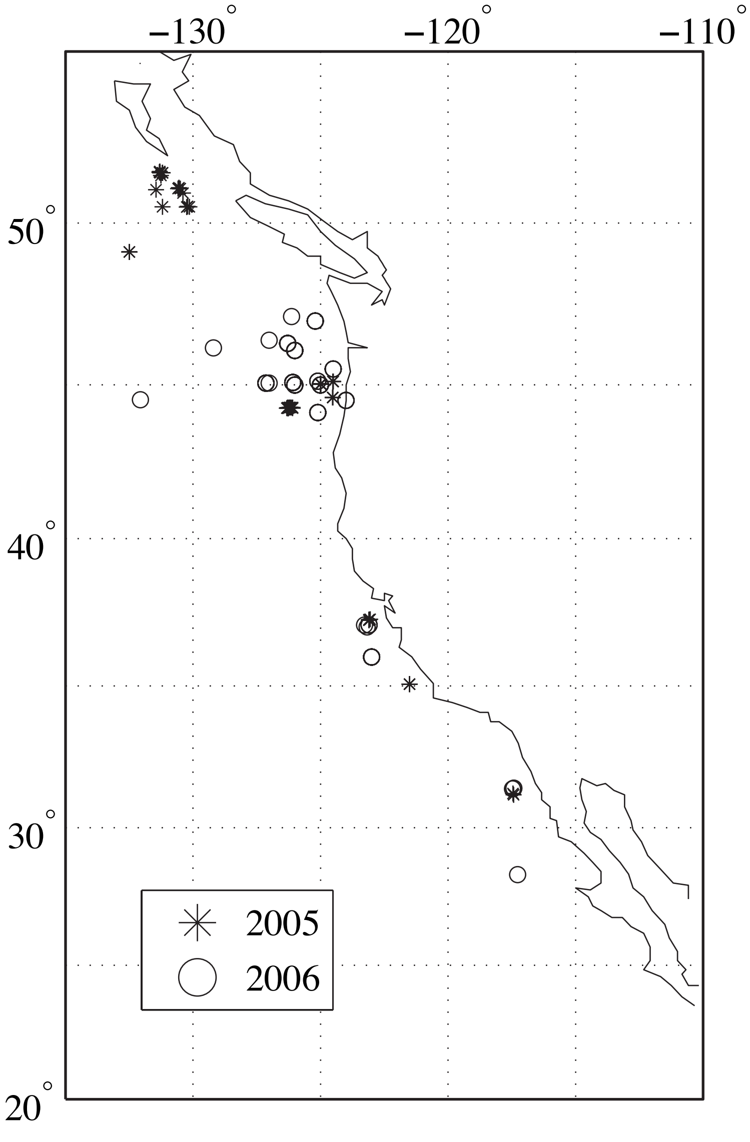


Figure A3.1.18. Stomachs containing *Sebastes* spp.

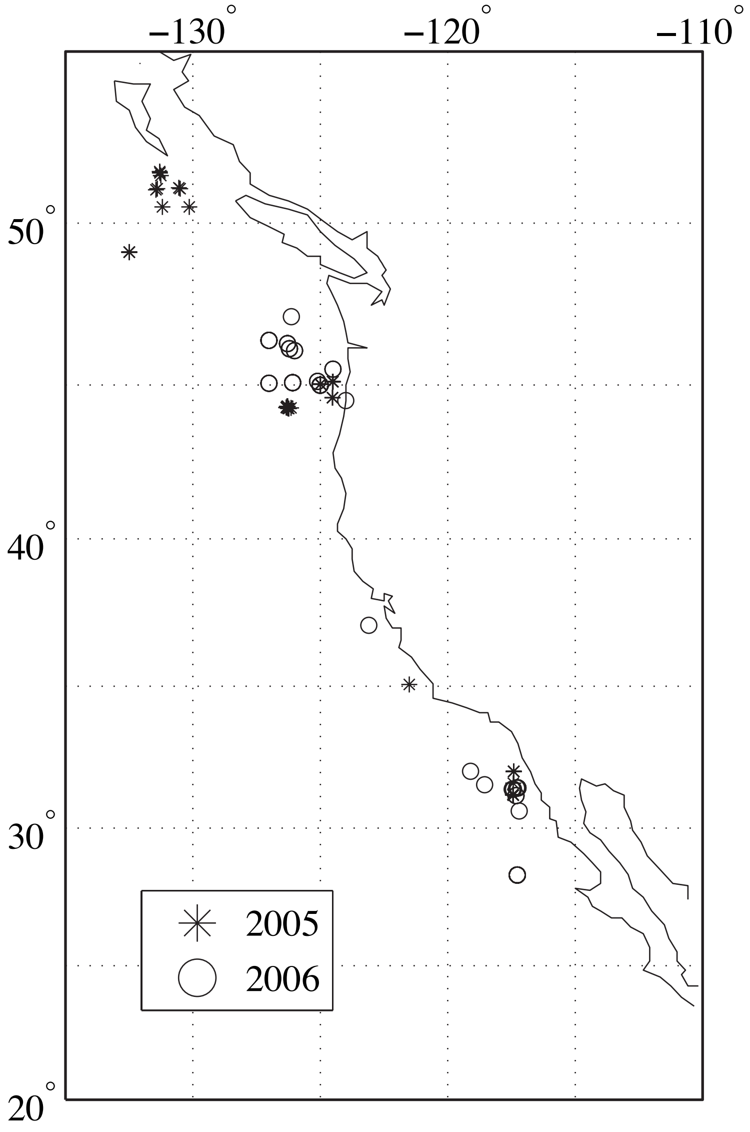


Figure A3.1.19. Stomachs containing *Sardinops sagax*.

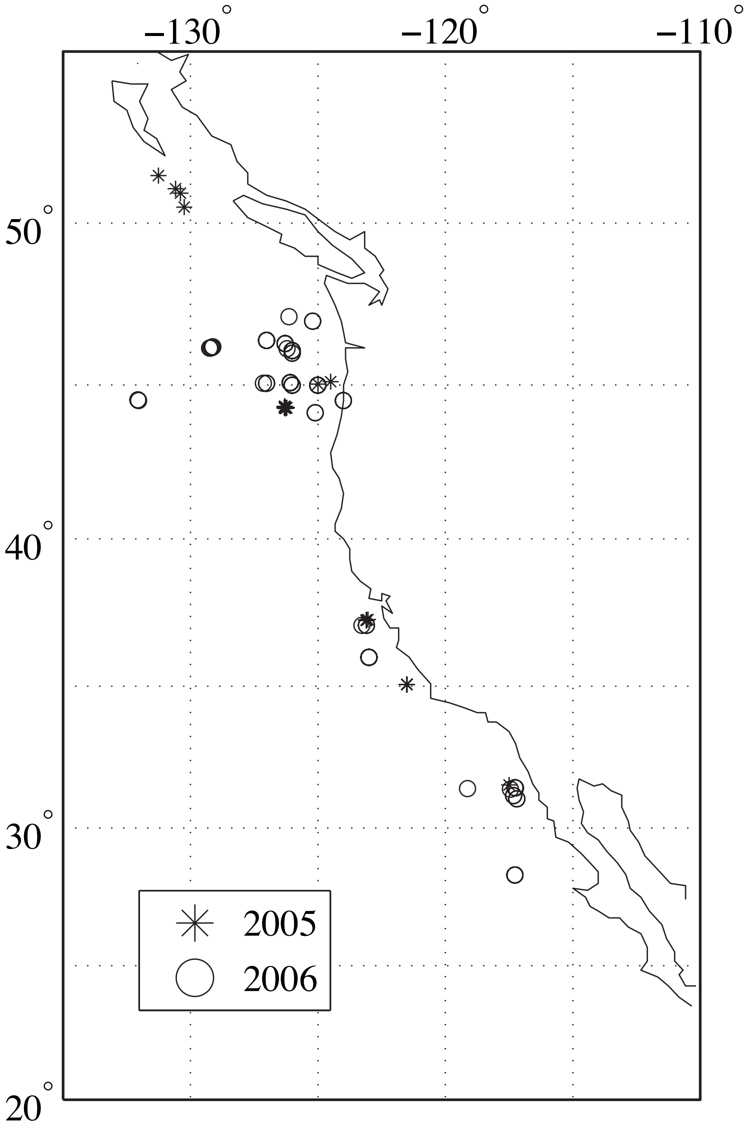


Figure A3.1.20. Stomachs containing fishes (other and unidentified).

Appendix 3.2. Genetic sequencing of visually-unidentifiable prey.

Certain prey were identified using genetic sequencing. In the beginning stages of laboratory identification of prey, genetics were used to verify visual identifications. Voucher specimens of cephalopods were analyzed because most available reference guides (e.g., Pinkas et al. 1971, Wolff 1984) are for adults. *Sebastes* could not be identified to species based on available morphology, therefore samples with sufficient tissue were analyzed. Finally, some crustaceans were analyzed for species identifications; however, early difficulties obtaining clean DNA and the decision to limit crustacean identification to orders resulted in few such identifications. Tissue to be sequenced was removed from prey using forceps, rinsed with 100% ethanol, and stored in capped vials in 100% ethanol until sequencing.

Genetic sequencing

Extraction

Unpigmented, fleshy tissue was selected when available. Excess ethanol was removed by blotting with a paper towel and a small (1mm x 1mm) piece of tissue was cut for processing. Samples were placed in aliquots containing 150 μL of 10% chelex solution for chelating DNA. Samples were processed in the MJ Research PTC-200 thermocycler for 20 minutes at 60°C followed by 25 minutes at 103°C.

Polymerase Chain Reaction

Fishes

For each sample, 2 μL of extracted DNA was added to a mix containing: 3.125 μL water, 0.375 μL Bovine Serum Albumin (BSA) (20mg/ml), 1.0 μL of either forward or reverse primer (10 μM), and 7.5 μL of master mix. Universal primers for the mitochondrial cytochrome c oxidase gene had the following sequences (Hyde 2007):

Fishcox1R
5' - TAR ACT TCW GGG TGR CCR AAG AAT CA - 3'
Fishcox1F
5' - TCW ACC AAC CAC AAA GAY ATY GGC AC - 3'
PCR was completed on the thermocycler as:
40 cycles of
1) 92°C (2.5 minutes)
2) 94°C (30 seconds)
3) 55°C (1 minute)
4) 72°C (1 minute)

PCR contained a blank negative control to monitor for possible DNA contamination. Products were electrophoresed through a 2 % (w/v) agarose gel in 1 X Tris-Borate-EDTA buffer, stained with ethidium bromide and visualized via an UV-transilluminator to assess amplification success.

Cephalopods

Primers were designed by combining cytochrome c oxidase subunit 1 sequences from GenBank for a variety of cephalopod taxa, using a representative mix of species in order to design universal primers. The sequences were combined in Sequencher (Gencodes). The primer sequences were:

Cephcox1F

5' TCCACWAAYCATAAAGATATTGGMAC

Cephcox1R

5' TAMACTTCTGGGTGYCCAAARAAYCA

Bases that were not standard ACGT (e.g., W, M, Y, R) were degenerate nucleotide sites at which a variety of bases were inserted (i.e., Y = C or T) to increase primer effectiveness.

For each sample, 2 μL of extracted DNA was added to a mix containing: 3.125 μL water, 0.375 μL Bovine Serum Albumin (BSA) (20mg/ml), 1.0 μL of either forward or reverse primer (10 μM), and 7.5 μL of master mix. The PCR thermocycler was programmed for the first run as follows:

40 cycles of:

1) 92°C (2.5 minutes), first cycle only

2) 94°C (30 seconds)

3) 55°C (1 minute)

4) 72°C (1 minute)

The second PCR thermocycle conditions were 40 cycles of:

1) 92°C (2.5minutes), first cycle only

2) 92°C (30 seconds), Denature

3) 48°C (1.5 minute), Anneal

4) 70°C (1.5 minute), Extend

PCR included a blank negative control to monitor for possible DNA contamination. Products were electrophoresed through a 2 % (w/v) agarose gel in 1 X Tris-Borate-EDTA buffer, stained with ethidium bromide and visualized via an UV-transilluminator to assess amplification success.

Sequencing

Reactions were digested using ExoSAP-IT (USB Corp.) to remove unincorporated primers and deoxynucleotides prior to cycle sequencing. 5 μL of PCR product were mixed with 2 μL of enzyme mix. The ExoSap thermocycler program was 15 minutes at 37°C followed by 15 minutes at 80°C.

DNA strands were individually cycled using BigDye v.3.1 Dye Terminator mix. The reaction mixture was: 1 μL big dye terminator mix, 2 μL buffer, 0.4 μL of primer, 4.6 μL water, and 4 μL PCR product. Cycle Sequencing was programmed for 30 cycles of:

1) 94 degrees (10 sec)
2) 50 degrees (10 sec)
3) 60 degrees (4 min)

Sequence products were analyzed by automatic sequencing on an ABI 3130XL automated capillary sequencer (Applied Biosystems). Sequencher (Gencodes) was used to edit the sequences. Reverse and forward sequences were combined into one sequence, a ‘contig’, using an algorithm that required a minimum base match of 80%. Ambiguities in base pair sequence were resolved by comparing the forward and reverse chromatograms.

Database Comparison

Edited sequences were compared with sequences in the GenBank BLAST database and the Barcode of Life database (BOLD). Samples with a 99% or higher maximum identification match in the BLAST database were considered reliable matches. Those receiving lower scores were analyzed in the BOLD, providing a specimen similarity score based on a distance algorithm. Similarity scores were given for the top 20 most related individuals in the database. For our purposes, only specimens having 99% or higher similarity scores were considered positive species identifications. BOLD reports placement probabilities by comparing the unknown with duplicate reference sequences for each species. In order to award a 100% probability of placement, there must be 5 reference sequences in the database. Many of the cephalopods in this study had 1 or 2 reference barcodes only. Therefore, specimen similarity score was the best available information provided by BOLD for cephalopods.

Results

For all specimens combined, PCR successfully amplified approximately 50% of DNA samples. Contaminated DNA product was the most likely cause of PCR failure. Species identifications are reported in Table A.3.2. The *Sebastes wilsoni* complex was DNA from *S. wilsoni, S. zacentrus*, or *S. proriger*, but sequences were insufficient to distinguish these three species from each other.

Table A3.2. Genetic identifications of albacore gut contents, unidentifiable prey.

Visual ID	Identification	% Similarity
Fish	*Sardinops sagax*	
Fish	*Cololabis saira*	97.34
Fish	*Engraulis mordax*	100
Fish	Family Myctophidae	
Fish	Family Psychrolutidae	
Fish	*Merluccius productus*	99.22
Sebastes	*Pleuronichthys decurrens*	100
Fish	*Scomber japonicus*	99.18
Sebastes	*Sebastes aleutianus*	98.6
Sebastes	*Sebastes brevispinis*	99.22
Sebastes	*Sebastes diploproa*	100
Sebastes	*Sebastes proriger*	100
Fish	*Sebastes wilsoni* complex	
Fish	*Stenobrachius leucopsarus*	99.85
Fish	*Trachurus symmetricus*	
Octopus	*Argonauta argo*	100
Squid	*Erosaria ocellata*	83.24
Squid	*Eucleoteuthis luminosa*	98
Squid	*Gonatopsis borealis*	98.39
Squid	*Gonatus californiensis*	99.32
Squid	*Gonatus onyx*	99.34
Squid	*Gonatus pyros*	88.62
Octopus	*Japatella heathi*	99.85
Squid	*Leachia atlantica*	83.33
Squid	*Loligo opalescens*	99.68
Squid	*Moroteuthis robusta*	99.24
Squid	*Octopoteuthis sicula*	99
Squid	*Onychoteuthis borealijaponica*	99.67
Squid	*Vampyroteuthis infernalis*	98.06
Euphausiid	*Euphausia pacifica*	

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Dr. John Hyde, Dr. Russ Vetter, Nicole Mehaffie, Dr. Kristen Gruenthal and Mitch Degeusus contributed substantially to the genetic sequencing of prey. Hyde directed all laboratory work and provided considerable knowledge and resources. We used the laboratory of Vetter, including his instruments and supplies. Mehaffie conducted the analysis, under the direction of Hyde, for all but the first 30 samples. Degeusus analyzed the first 30 samples, which were repeated and verified by Gruenthal in the laboratory of Dr. Ron Burton.

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Chapter 4: Do albacore exert top-down pressure on Northern anchovy? Estimating mortality of juvenile anchovy as a result of predation by North Pacific albacore.

Abstract

Quantifying mortality of juvenile fishes is an important component of understanding spawner-recruit relationships, predicting year-class strength, and improving fishery stock assessment models. There is increasing evidence that pelagic predators, despite being highly migratory, can exert top-down influence on species of prey, especially during critical larval and juvenile stages. The aims of this study are three-fold. First, I estimate the abundance of juvenile North Pacific albacore in the California Current System (CCS) from 1966-2005 based on Pacific-wide estimates. Second, I quantify the biomass of Northern anchovy (central stock) annually consumed by albacore. Third, given the importance of anchovy to albacore diet, I attempt to demonstrate that albacore exert top-down influence on cohorts of juvenile anchovy. Albacore abundance (1966-2005) in three regions of the CCS is estimated using stock assessments and spatially explicit catch-per-unit-effort time series. Anchovy abundance (1966-1993), both recruitment and total biomass, also is obtained from a stock assessment model. Annual rates of anchovy consumption by albacore are calculated using diet studies of albacore in the CCS, an age-structured bioenergetics model, and regional estimates of albacore abundance. Two estimates of albacore abundance are made: a low estimate, based solely on landings, and a high estimate, based on an age-adjusted stock assessment model. Albacore remove between 7 and 66,000 mt of anchovy annually, an estimate exceeded by fisheries landings during periods of high catch and corresponding to 0.1% - 5% of anchovy annual recruitment biomass. I find a positive relationship between albacore biomass in year *X* and anchovy recruitment in year *X*, and a negative relationship between albacore in year *X* and anchovy recruitment in year *X*+1. These findings suggest that albacore are attracted to areas of high anchovy abundance, and predation on pre-recruit juveniles is evident in the recruitment biomass the following year. This study is the first to quantify a specific source of mortality on juvenile anchovy and to demonstrate top-down effects of predation on anchovy.

Introduction

The seminal observation by Hjort (1914) that mortality in the early life stages of marine fishes significantly impacts the strength of cohorts has guided the studies of marine ecology, fisheries science, and resource management. Density-independent factors, such as temperature (Fiedler 1983) and turbulence (Lasker 1981), and density-dependent factors, such as food availability (Cushing 1974) and predation (Connolly & Roughgarden 1999), affect the mortality rates of larval and juvenile fishes. Over 99% of total mortality will occur during the egg, larval, and juvenile stages of marine fish life history (Jennings et al. 2001); therefore, understanding sources and variability of mortality is critical to estimating adult abundance and predicting changes in stock structure. The relationship between the number of recruits in a population and the size of the reproductive (spawning) stock is a crucial theoretical construct and, while the relationship is often difficult to observe, the implications of compensation and depensation (increased and decreased recruitment at low levels of spawner abundance) are profound (Beverton & Holt 1957, Quinn & Deriso 1999).

Related to spawner-recruit relationships is the concept of top-down and bottom-up regulation of populations within the context of a food web. In diverse marine ecosystems around the globe, research has demonstrated that both top-down and bottom-up forces are important in structuring communities (Hunter & Price 1992, Roughgarden et al. 1994, Menge 2000, Cury et al. 2000, Shurin et al. 2002, Munch et al. 2005). The top-down effects of predation can alter the diversity (Paine 1974), realized niches (Connell 1961), and abundance of species (Dayton 1971). Pronounced top-down effects can cause cascades in which species at all trophic levels in a food chain are impacted (Estes et al. 1998). Bottom-up effects of environmental factors, nutrient availability and prey abundance can impact the productivity, size-structure, growth rates, and abundance of predators. The relative importance of top-down versus bottom-up regulation depends on a host of interrelated factors and can vary in time (Hunter & Price 1992, Roughgarden et al. 1994, Munch et al. 2005).

The majority of our understanding of regulation in marine communities has been generated from studies in intertidal zones because the open nature of the pelagic zone renders it more challenging to sample and observe (Roughgarden et al. 1994, Williams et al. 2004). The most elegant and conclusive studies simultaneously manipulate predator and prey abundances (*e.g.*, Dayton 1971, Paine 1974), but such experiments on highly mobile animals are difficult. As a result, pelagic ecology rapidly has moved towards ecosystem-based models that trace flows of mass and energy as a means of quantifying species interactions (*e.g.*, McCann et al. 1998, Cury et al. 2001, Christensen & Walters 2004). These models are important tools by which researchers investigate ecosystem responses to fishing pressure and natural mortality, changes in species diversity and abundance, and changes in productivity through scenario-based model runns. However, the large (thousands) of parameters involved in these models can make individual interactions more opaque, and isolating just one predator-prey relationship in such a model can be suspect (Cox et al. 2002).

Given the limitations imposed by working in pelagic ecosystems, the majority of studies that investigate predator-prey relationships in this zone are observational in nature. Recently, an approach combining bioenergetic modeling, demographic models, and diet analysis has been used to demonstrate top-down effects of large, migratory oceanic predators. Williams et al. (2004) demonstrated that killer whale predation on Stellar sea lions and sea otters had the potential to cause dramatic declines in prey abundance. Hunsicker and Essington (2008) provided estimates of predation by *Loligo pealeii* on juvenile fishes that suggested an impact on recruitment biomass. In both cases, alternate causes of mortality could not be ruled out. However, as evidence mounts that predation may shape the structure and function of pelagic communities, there are increased calls for quantifying isolated predator-prey interactions in order to verify the hypotheses generated by complex, highly parameterized ecosystem models.

In this chapter, I investigate the relationship between North Pacific albacore and one of its most important prey species, Northern anchovy (*Engraulis mordax*). Anchovy occupy nearshore waters of the California Current System (CCS), and juvenile albacore prey on anchovy during the summer and fall months. The aims of this study are three-fold. First, I estimate the abundance of juvenile North Pacific albacore in the CCS from 1966-2005. Second, I quantify the annual consumption of the central stock of Northern anchovy by albacore. Finally, given the large population of albacore (ISC 2006) and the significant fraction of their diet comprised by anchovy (Chapters 2 and 3), I test the hypothesis that albacore exert top-down pressure on anchovy. Borrowing generalizations gleaned from experiments in intertidal zones, I expect an inverse relationship between albacore abundance and anchovy abundance.

Predator and prey biology

North Pacific albacore comprise an isolated population that occupies oceanic waters from the subtropics to the subpolar regions, and from the Eastern boundary current to the far Western North Pacific. Although the population is managed as one stock, there is evidence that subpopulations exist with varying growth rates (Laurs 1983), migration patterns (Otsu & Uchida 1959, Laurs & Lynn 1991, Kimura et al. 1997), and feeding habits (Pinkas et al. 1971, this study). Adult albacore (ages five and older) spawn in the tropical and subtropical central North Pacific (Otsu & Uchida 1959) and are distributed throughout the central gyre where they are harvested by distant-water longline fisheries (Stocker 2005). Albacore aged two years appear in CCS waters in late spring, at which point they recruit into the commercial and recreational troll and pole fisheries of the Eastern Pacific (Otsu & Uchida 1962, Laurs & Lynn 1977). In the late fall, juveniles in the CCS either migrate to the Western North Pacific, in which they might be harvested by the pole and line, gillnet, and longline fisheries of Japan, Korea, and Taiwan, or they migrate south into coastal waters of central Mexico (Otsu & Uchida 1962, Laurs & Lynn 1991, Kimura et al. 1997, Kohin et al. 2008). There is a tendency for the older juveniles (ages four and five) to migrate across the Pacific while the younger juveniles (ages two and three) remain off the coast of North America. Juveniles that migrate south return to the CCS the following summer, while most juveniles that migrate to the West North

Pacific remain there. While there is some documentation of juvenile albacore migrating from the West North Pacific back into the East North Pacific, the bulk of migration is a one-way movement from east to west (Otsu & Uchida 1962, Kimura et al. 1997). Once mature, albacore join the adult population in the central gyre and rarely are found in coastal waters.

Northern anchovy are commercially harvested, schooling, small pelagic fish that live within the boundaries of the CCS and have been the most important prey item of juvenile albacore in the CCS during the past 40 years (Pinkas et al. 1971, Bernard et al. 1985, this study). Adult anchovy spawn in cold, high-productivity upwelling zones in near-shore coastal waters (Fiedler 1983, Lluch-Belda et al. 1991). Four stocks of anchovy are recognized: a northern stock, extending from British Columbia to central California; a central stock, extending from the Southern California Bight to central Baja; a southern stock, off the coast of Baja; and a stock confined to the Gulf of California (Schwartzlose et al. 1999). Their populations undergo large swings in abundance; over the past century, anchovy have fluctuated asynchronously with another pelagic forage species, Pacific sardine (Soutar & Isaacs 1974, Baumgartner et al. 1992). The modes of variability are on the order of decades, and several mechanisms have been identified: temperature (Lluch-Belda et al. 1991, Chavez et al. 2003), atmospheric circulation (Klyashtorin 1998), patterns of oceanic circulation (Schwartzlose et al. 1999), and food availability (Schwartzlose et al. 1999). Such bottom-up processes have been the focus of most studies on anchovy population fluctuations. In one study of potential top-down regulation, Methot (1989) hypothesized that predation by Pacific mackerel (*Scomber japonicus*) would impact mortality rates of anchovy in the CCS. However, his model failed to find evidence for such an effect. Consequently, there is a need for further studies examining the role of top-down influences on Northern anchovy.

Methods

Data

Catch and effort data for the North Pacific population of albacore were obtained from Paul Crone and Al Coan at the Southwest Fisheries Science Center, NOAA. Data were collected from logbooks, voluntarily contributed by U.S. commercial fishing vessels. Data were aggregated to 1° x 1° x month cells, of which 10,209 were nonzero. While data were available beginning in 1961, the most reliable data sets begin in 1966 (ISC 2006). For this study, I used data from 1966-2005. Data were pre-processed by Al Coan; any cell containing fewer than three fishing vessels was excluded. Total annual commercial catch data for all North Pacific albacore fisheries were obtained from Paul Crone.

Population estimates for North Pacific albacore were obtained from a stock assessment model produced by the International Scientific Committee Albacore Working Group (ISC 2006). Age-structured estimates were made using virtual population analysis (model scenario D1). This model used catch-at-age data and indices of abundance from several fisheries from 1966-2005.

Anchovy abundance estimates are available only for the central stock of Northern anchovy during 1963-1994 (Jacobson et al. 1995). Jacobson et al. (1994) used stock assessment models employing indices of abundance (including daily egg production and catch data) to estimate the abundance of year-0 anchovy (recruitment biomass), spawning stock biomass, and total stock biomass.

Albacore diet data were obtained from 371 stomachs collected in the CCS during 2005 and 2006. These data were used to calculate size of anchovy consumed by albacore (Chapters 2 and 3).

Estimating albacore abundance in the CCS

Two data sets were used to estimate the biomass of albacore in the CCS. The first data set, metric tons of albacore landed by the U.S. commercial troll fishery, represents the lowest possible count of albacore in the CCS (hereafter, low estimate). The second data set, Pacific-wide, age-structured estimates of albacore population as estimated by a stock assessment model (ISC 2006), represents a high estimate of albacore population (hereafter, high estimate). The low estimate is self-evident: I assume all albacore residing in the CCS were caught.

The high estimate relies on two assumptions, supported by catch and effort data. First, two fisheries account for a majority of all juvenile (ages 4 and under, Otsu & Uchida1959) albacore landings: the U.S. troll fishery, and the Japanese pole and line fishery (Figure 4.1). The U.S. fishery contains primarily ages two, three and four, while the Japanese fishery contains ages one through six. I am interested in the albacore present in CCS waters, therefore I can narrow my scope of inquiry to albacore of ages two – four. Combined, these two fisheries account for 80 - 90% of all two, three, and four year old albacore caught by fisheries. Second, the migration patterns of juveniles, described above, show juvenile albacore in the CCS during spring, summer and fall months followed either by migration into the Southern Baja coastal region or trans-

Pacific movement into the Kuroshio current where they are harvested by the Japanese pole and line fishery during the winter and spring (Kimura et al. 1997). It is unknown what proportion of albacore migrate to the Western North Pacific versus remain in the Eastern North Pacific. Although the units of effort are different in the two fisheries, their standardized catch-per-unit-effort time series, an index of relative abundance, have strong temporal correlation (Figure 4.2). This coherence suggests the subpopulations have corresponding fluctuations. I therefore assume that patterns of catch and effort on all juvenile albacore can be accounted for by combining data from the U.S. troll and Japanese pole and line fisheries. For the high estimate of albacore abundance in the CCS, I use abundances of ages two, three and four calculated by the ISC stock assessment model. This high estimate represents the upper bounds of abundance by assuming that, for any given season, all juveniles aged two, three or four are present in the CCS.

Given these two estimates (high and low) of albacore in the CCS annually, I further divide the subpopulation into three regions: northern (44° - 50° N latitude), central (35° - 43° N latitude), and southern (25° - 34° N latitude). Each region extends 10 degrees from shore (Figure 4.3), approximating the mean boundaries of the CCS (Hickey 1998) and, together, fully covering the extent of the Northern anchovy population. The relative abundance of albacore in these three regions was calculated by comparing regional standardized catch-per-unit-effort time series. The standardized index was treated as a proportion and the number of albacore found in each of the three regions was calculated by partitioning total albacore biomass in the CCS accordingly.

Standardizing catch-per-unit-effort time series

Catch (number of albacore) and effort (number of boat-days) in each 1° x 1° x month cell were used to calculate a standardized annual time series of catch-per-unit-effort (CPUE). CPUE, also referred to as catch rate, reflects relative changes in mean fish abundance over a given fishing period if catch and effort are proportional. However, factors other than fish abundance may affect catch rates (Harley et al. 2001, Maunder and Punt 2004). For example, differences in types of fishing gear, behavior of fishing vessels such as clustering or use of locator technology, or environmental variables such as sea surface temperature may influence catch rates and are exogenous to fish abundance (Quinn & Deriso 1999). Methods of standardization attempt to remove the effects of these external variables.

Several methods for standardizing CPUE data are available, the most common being general linear models (GLMs). This technique has certain drawbacks, especially for large data sets. First, GLMs only estimate linear relationships between response variables (here, CPUE) and predictor variables. Second, these models frequently result in hundreds of estimated parameters, complicating interpretation. Finally, high-order interactions between predictor variables can confound the indices of abundance. To avoid these problems, I use a regression tree (Breiman et al. 1984), a technique that is less frequently used than GLMs but has been shown to be more parsimonious, result in significantly fewer parameters, and account for nonlinear relationships between variables (Watters & Deriso 2000).

Regression trees model CPUE by estimating the time effect of a collection of predictor variables. The model selects one predictor that best divides the response variable into two groups, maximizing the sum of squares difference between the two groups while minimizing the difference within groups. The process is repeated on each sub-group until further splitting fails to increase the goodness of fit of the model. The final tree is used to calculate the value of the response variable (as a mean of the data in each group) associated with a given combination of predictor variables.

The random forest technique (Breiman 2001) is a randomized regression tree approach. In standard regression tree analysis, the response variable is modeled using all predictor variables. In the random forest approach, response variables are calculated repeatedly by randomly sampling the vectors of predictor variables, without replacement. In this way, measures of standard error can be calculated and the final tree is less sensitive to changes in predictors (Breiman 2001).

Random forest was employed using the R statistics program and the library randomForest. The modeled response variable was square root transformed catch divided by effort, and the predictor variables were year (1966-2005), month (January – December), latitude, and distance from shore (km). Initial analysis demonstrated that model fit was higher, for all three regions, when transformed catch/effort was used. 500 randomizations were run for each of three regions and the mean square error for the final tree was calculated. The effects of the predictor variables were calculated using the function partialPlot. The annual standardized CPUE time series was the effect that the variable ‘year’ had on catch/effort. The effect of ‘month’ on CPUE was used to apportion the albacore population into the three regions on a monthly basis. The highest monthly index was treated as 100% of estimated annual abundance, and other monthly estimates were scaled down proportionally.

Estimating albacore consumption of anchovy

A bioenergetics model (Essington 2003, Chapter 2) was used to calculate albacore consumption rates of anchovy on a daily basis. Albacore daily consumption was estimated using a mean prey energy density of 6.2 kJ g^{-1}, the mean ensemble energy density value calculated for albacore diet in studies done in 1968-1969 (Pinkas et al. 1971) and 2005-2006 (Chapter 2). Consumption rate is a function of albacore age; therefore, the consumption rate was further refined by the age-structure of the subpopulation in the CCS (Figure 4.1). Mean daily consumption rate was weighted by the proportion of albacore at various ages (age 2 = 5.8%, age 3 = 64.2%, age 4 = 30.0%). The biomass of anchovy consumed by albacore annually was calculated as:

$$B_a = \sum_{region=1}^{3} \sum_{month=1}^{12} B_{A,r,m} \times C \times \%diet_r \times days_m \tag{4.1}$$

where B_a is biomass of anchovy (mt), B_A is biomass of albacore (mt), C is daily consumption rate of albacore (g kg^{-1} d^{-1}), $\%diet_r$ is the percentage that anchovy comprised of albacore diet in a given region, and $days_m$ is the number of days in a given month.

The percentage of diet comprised by anchovy varied between two diet studies that spanned the CPUE time series (Pinkas et al. 1971, this study) and between the three regions. The percentage of anchovy in diet was linearly weighted based on the proximity in time to the two diet studies using the values calculated in the study as anchor points. Diet data were collected in 1968, 1969, 2005, and 2006. From 1968/1969 to 2005/2006, anchovy in albacore diet varied from 74.2 - 23% in the northern region, from 3.8 – 1% in the central region, and from 28.5 – 67% in the southern region.

Albacore consume juvenile anchovy but not adult anchovy (Bernard et al. 1985, this study). Monthly variability in length of anchovy consumed was analyzed using measurements from albacore gut contents collected in 2005 and 2006 (n = 421). Specimens were separated according to the month in which they were collected, and a one-tailed ANOVA was run to test for differences in mean length.

Estimating anchovy population size and predation mortality

Abundance estimates for anchovy recruitment, spawning stock, and total population size from 1963-1994 were taken from Jacobson et al. (1995). Estimates were made using a forward simulation, hybrid surplus production and age-structured model (Jacobson et al. 1994). Recruitment biomass was independent from spawning stock biomass and estimated as a parameter in the model. Jacobson et al. (1995) analyzed the central stock of Northern anchovy only, which coincides with the southern region of albacore distribution. Using estimates of albacore abundance and consumption in the southern region, I calculated the proportion of anchovy recruitment consumed annually. I estimated the contribution of predation to anchovy mortality according to

$$M_t = {}^{(Z \times B_{c,t})}\big/_{B_t \times (1 - e^{-Z})} \qquad (4.2)$$

where M_t is the mortality at time t imposed by albacore, Z is total mortality (here, assumed to be 0.8 yr^{-1} after Jacobson et al. 1994), $B_{c,t}$ is the biomass of anchovy consumed by albacore at time t, and B_t is the total biomass of anchovy. Here, because predation is exclusively on juveniles, I use estimates of recruitment biomass for B_t.

Finally, to test the hypothesis that albacore predation exerts top-down influence on anchovy, I calculated simple, linear correlations between albacore population size in the southern CCS and anchovy recruitment in the central stock, and between albacore and anchovy total stock biomass. Time series were first differenced ($x_t - x_{t-1}$) to remove temporal autocorrelation. Thus, the analysis tests for correlation between timing and direction of population changes. To test for effects on anchovy recruitment biomass, I analyzed time series with no lag and with a lag of one year. To test for possible effects in the adult population, I lagged the anchovy time series by 1, 2, and 3 years. If predation on recruitment biomass has a pronounced impact on anchovy population, I expect to see an effect on the adult population in the future, as the cohorts age.

Results

Two estimates of albacore population size in the California Current System were made. The low estimate, equal to total landings by the U.S. commercial troll fishery, ranged from 2000 mt (in 1991) to 32,000 mt (in 1972) (Figure 4.4). Periods of high catch existed during the 1970s and 1990s, while the 1980s had much lower catch. The high estimate, derived from stock assessment models of age groups two through four, displays the same temporal patterns of highs and lows. The high estimate is one order of magnitude higher than albacore landings. These two time series provide an abundance envelope, between which the true CCS-based population size lies.

From 1966-2005, albacore were more numerous in the northern region and least numerous in the southern region (Figure 4.5). The standardized indices of abundance for the three regions demonstrate the same patterns as the total abundance estimates: higher abundance in the 1970s followed by a period of lower abundance. However, the low period of abundance persisted longer, into the mid-1990s, than the low period illustrated by total abundances. The CPUE for the southern region is fairly stable through time, while the northern region has pronounced changes beginning in the early 1970s and around 2001. The regression tree model produced good fits to data (Southern region R^2 = 0.43, Central region R^2 = 0.37, Northern region R^2 = 0.37).

The standardized annual CPUE indices were translated into estimates of abundance in the three regions (Figure 4.6). According to the low estimate, in any given year the southern region contained between 487 and 8022 mt of albacore, the central region contained between 595 and 10,120 mt, and the northern region contained between 909 and 14,677 mt. According to the high estimate, the southern region contained between 24,435 and 86,662 mt, the central region contained between 31,169 and 106,118 mt, and the northern region contained between 47,155 and 165,880 mt of albacore. Albacore began to appear in the CCS in April in all three regions and peak catch rates occurred during August (Figure 4.7). In the southern region, albacore catch rates rapidly dropped off beginning in September, whereas catch rates in the central and northern regions remained high until November. During December through March, albacore catch rates in the CCS were zero.

Annual consumption of anchovy in the three regions of the CCS ranged from 7 mt (central region, low estimate) to 56,871 mt (northern region, high estimate) (Table 4.1). Altogether, albacore removed between 365 mt and 65,654 mt of anchovy annually from the CCS ecosystem (Figure 8). Human catch of anchovy (FAO landings data) since 1966 has ranged from 1450 mt (1998) to 149,000 mt (1975). From the mid-1960s to the mid-1980s, human extraction of anchovy exceeded that of albacore. However, since 1983, human landings have been far less and lie between the low and high estimates of albacore predation (Figure 4.8).

Albacore consistently preyed on young anchovy, even as the season progressed (Figure 4.9). Mean size of anchovy prey ranged from 24 – 50 mm standard length, with monthly mean values between 30 and 39 mm. Anchovy consumed in August were significantly smaller than those consumed in June, July, or September ($p < 0.001$). There was no significant trend in monthly data.

Abundance of age-0 anchovy in the central stock is reproduced here from Jacobson et al. (1995) (Figure 4.10). Recruitment biomass peaked in 1972 at 4,348,000 mt and had a low of 88,000 mt in 1989. Based on Jacobson's model, albacore annually consumed between 0.01% and 5% of central stock anchovy recruitment biomass (Figure 4.11). These levels of consumption translate into instantaneous rates of mortality ranging from 0.001 – 0.03 yr^{-1} for the low estimate of albacore consumption, and from 0.02 – 0.26 yr^{-1} for the high estimate of consumption (Figure 4.12). Assuming a total mortality rate (not including fishing) of 0.8 yr^{-1} (Methot 1989), albacore predation can account for less than 1% of juvenile natural mortality, up to 33%.

Correlation analysis revealed three significant relationships between changes in CCS albacore population and changes in the central stock of the anchovy population (Table 4.2). Statistically significant relationships were found only when analyzing the low estimate (landings) of albacore population. First, there was a positive relationship between changes in albacore abundance and changes in anchovy recruitment abundance in the same year ($p = 0.0003$, Figure 4.13). Second, there was a negative relationship between changes in albacore abundance in year X and changes in anchovy recruitment in year *X*+1 ($p = 0.0454$). Third, there was a positive relationship between changes in albacore population in year *X* and changes in total anchovy population in year *X*+1 ($p = 0.0005$). Additional time lags in anchovy population did not result in significant relationships.

Discussion

Estimates of changes in albacore population size and changes in anchovy population size are consistent with the hypothesis that albacore exert top-down pressure on anchovy. The full context of this study is important for the interpretation of the correlation analysis. The anchovy stock assessment model estimates recruitment biomass on July 1 of a given fishing season, and assumes anchovy recruit to the fishery at 0.5 years of age. The anchovy consumed by albacore in the CCS are pre-recruits. At a mean length of 30-37 mm, these anchovy are between 40 and 80 days old and thus the age-class estimated for recruitment by Jacobson et al's (1995) model does not include these anchovy. The model estimates adult (year-1 and older) biomass on February 15 of each fishing season. Therefore, anchovy consumed in year *X* during July-October (as in this study) will be represented in the model in year *X*+1 as recruits. The statistically significant negative relationship between albacore in year *X* and anchovy recruitment in year *X*+1 suggest that periods of growth in albacore abundance in the southern CCS are followed by a decline in anchovy recruitment the following year.

This finding is consistent with density-dependent predictions of standard predator-prey models; in fact, time delays in models with few species is one mechanism by which stability is conferred on such models (May 1974). The finding that the relationship breaks down beyond a one-year time lag is consistent with predictions from top-down models (Munch et al. 2005). They demonstrate that bottom-up forcing is best observed in adult populations and over longer periods of observation. However, the effects of top-down pressure will be most visible in early life history stages and will impact recruitment for short time periods. Observational studies of pelagic ecosystems rely on correlations between time series to make conclusions about top-down and bottom-up effects (Cury et al. 2001). While correlations never prove causation, these results are consistent with predictions of theoretical models (Munch et al. 2005), support the observational findings of other studies on pelagic predator-prey interactions (Williams et al. 2004, Hunsicker & Essington 2008), and agree with hypotheses of anchovy specialists (Smith 1985, Methot 1989, Jacobson et al. 1995).

The positive relationship between albacore abundance and anchovy recruitment, in the same year and region, suggests one of two possibilities. First, juvenile albacore abundance in the southern CCS and juvenile anchovy in the central stock could respond similarly to environmental conditions, in which case both populations would respond similarly to bottom-up forces (Connolly & Roughgarden 1999). However, given the fact that juvenile albacore are spawned thousands of miles to the West, and that the population migrates in and out of the CCS, this explanation is both difficult to test and less plausible than the second possibility. Second, albacore could simply be attracted to areas of high forage biomass (MacArthur & Pianka 1966, Polovina et al. 2001, Bakun 2001). These results support observations that albacore catch rates are high in areas with high anchovy abundance, and they suggest that recruitment biomass of anchovy helps aggregate albacore, even if albacore are preying on younger fishes.

Finally, the relationship between albacore and the full anchovy population suggests that the effects of predation are limited to juvenile anchovy. One year after an increase in albacore abundance, the anchovy population (total biomass) experiences an increase. This is likely unrelated to albacore, but rather reflects an increase in the total stock size after a large recruitment year. By age 1, the proportion of reproductively mature anchovy is a function of sea surface temperature, but by age 2, the full cohort is mature (Jacobson et al. 1994). Anchovy fecundity is strongly tied to age and size, and the majority of spawning biomass is in anchovy ages 2 and 3 (Jacobson et al. 1994). For top-down effects at the pre-recruit stage to be observed in the adult population, a lag of several years is required. However, Munch et al. (2005) demonstrate that, at such lags, the effects of earlier top-down factors will be swamped by bottom-up forces acting on the adult population. These observations documented here are consistent with their finding.

High mortality rates in juvenile anchovy could significantly impact recruitment biomass (Smith 1985), and estimates of consumption and contribution to total mortality suggest albacore may impose levels of mortality on juvenile anchovy sufficient for such an impact. The low and high estimates of albacore consumption provide bounds to the possible level of consumption. If the true level is the arithmetic mean of these two estimates, albacore account for mortality of between 0.02 and 0.16 yr^{-1}, or between 3 and 20% of total mortality (assuming $Z = 0.8\ yr^{-1}$, Methot 1989). Predation mortality is focused on a specific cohort of anchovy, those between 40 and 80 days old. This knife-edge selection on pre-recruits means significant mortality is imposed during a short period of life.

Sources of uncertainty in estimates of abundance affect the estimates of annual consumption rates. Observation error exists in the catch and effort data for both species and in the diet data, and process error exists in the stock assessment models and the bioenergetics model used to calculate consumption rates. The first source of observation error is assumed to be relatively low: U.S. fisheries have strong incentives to accurately record catch and effort data. Diet composition was calculated based on two studies that flank the anchovy time series: Pinkas et al. (1971) collected stomachs in 1968 and 1969, and this study collected stomachs in 2005 and 2006. Both studies repeatedly sampled the southern CCS region and diet data were aggregated based on regional divisions congruent with those used here to divide the CCS. If more diet studies were available during the time of anchovy assessments, it may be possible to address whether albacore exhibit prey switching in the face of reduced anchovy populations. Instead, the working assumption of this paper is that diet proportion changes linearly through time.

The stock assessment model used to estimate abundance of albacore has been tested rigorously on an annual basis. Data are submitted by six nations, the quality of data is evaluated in annual meetings, and final data sets are maintained by the Southwest Fisheries Science Center. Fifteen different scenarios, each with different combinations of indices of abundance, spatial extent, and catch-at-age data, are compared using goodness-of-fit criteria. Scenario D1, used in this study, was recommended by the Albacore Working Group based on statistical goodness-of-fit and because it used all available data (ISC 2006). The greatest uncertainty in the model lies with age-1 albacore, an age-group not represented in the consumption calculations here because they are not sampled by Eastern North Pacific surface fisheries in the CCS.

The error and uncertainty associated with the anchovy model is thoroughly documented in Jacobson et al. (1994). The bias analysis by Jacobson et al. (1994) revealed consistent bias, which was removed, and negligible retrospective bias. There is greater uncertainty in recruitment estimates than total biomass estimates because recruitment was an estimated parameter whereas total biomass was adjusted to five observed indices of abundance (Jacobson et al. 1994). However, the independence of recruitment biomass from total biomass within the model removes possible interactions in the correlation analysis. If recruitment biomass were simply estimated from adult stock size, as in virtual population analyses, the relationships between albacore and recruitment biomass, and albacore and total anchovy biomass, would be confounded. Finally, the estimates for recruitment are a function of sea surface temperature (SST), a variable strongly associated with anchovy egg production (Methot 1989). While the albacore stock assessment model does not involve environmental variables, the inclusion of SST in the anchovy model increases its realism (Jacobson et al. 1994).

A final source of uncertainty is the relationship between CPUE and true population abundance of albacore. Harley et al. (2001) found that CPUE frequently underestimates population depletion, such that CPUE indices remain stable while true abundance declines. Fishery-dependent data may commonly overestimate abundance because skilled fishers efficiently exploit areas of high predator density. If these same rates are extrapolated into areas of low density, where fishing may not occur, the ratio of catch to effort will be overly high (Quinn & Deriso 1999, Maunder & Starr 2003). However, the use of CPUE indices in this study is extremely conservative and not used as a mere proxy for abundance. Rather, the regional CPUE indices are subsets of a larger, uniform data set (U.S. commercial troll data) collected in a standard way, by many of the same vessels, and with the same gear (and thus uniform vulnerabilities). Consequently, the indices are used only in a comparative manner to apportion abundance, which is estimated from more complicated models that include biological data, estimates of total abundance, and adjust for differing catchabilities and gear types. Insofar as the data have been uniformly collected since 1966 (ISC 2006), these indices represent a faithful application of CPUE within one species of fish.

The regression tree model produced a fairly good fit to the data, comparable to other regression tree models (Watters & Deriso 2000) and within the range of R^2 values for most CPUE models (as reported by Watters & Deriso (2000)). Analysis of CPUE indices used by the ISC stock assessment model demonstrated that creating regional indices from the global data set improved goodness of fit of models, and the working group recommended the exploration of regional (rather than Pacific-wide) indices. Consequently, the use of regionally-specific indices, as done here, can be justified and in fact be more reliable. The model developed here could be criticized for omitting sea surface temperature, a variable shown to have a strong influence on albacore movement patterns (Laurs et al. 1984, Zainuddin et al. 1996). However, Watters & Deriso (2000) demonstrated that when space and time variables were included in a regression tree analysis, environmental variables were frequently superfluous. The resolution of space and time variables used here matches that of most commonly available environmental variables (such as COADs sea surface temperature or wind data), and thus any interaction between space and time variables accounts for interactions that may arise from environmental variables.

Despite these varied sources of uncertainty in estimates of albacore and anchovy abundance, the simple correlation analysis was able to detect significant relationships between the time series. I attribute the ability to detect a signal amidst considerable noise to the use of first-differenced time series in analysis. First, this removes the demand that the stock assessment models be accurate in estimating the absolute size of the predator and prey populations. Rather, the models need only be accurate in estimating timing and direction of annual fluctuations in populations. Second, because autocorrelation is removed, the ability to find correlation is more rigorous and thus significant relationships are more believable. Finally, the fact that significance was only found when analyzing the low estimate of albacore abundance does not mean that landings are a more accurate proxy for albacore abundance. Rather, it implies the landings time series more accurately represents fluctuations in abundance. This is a reasonable assumption because the catch data were limited to the CCS and are assumed to have low error.

Conclusions

This study is the first to quantify mortality imposed on juvenile Northern anchovy by a specific predator. Additionally, it is the first to document, although far from the first to suggest, that levels of predation on juvenile anchovy have top-down impacts on recruitment biomass. However, this is neither conclusive nor final word on the matter; quite the contrary, these results are merely the opening salvo. In the words of Mohn and Bowen (1996), "ecological models…may be viewed as a serial process that builds on each previous step by adding some new information to form the next." Thus, results from this study, in particular estimates of predation pressure and size-specific mortality, are an important first step in laying the foundation for a more thorough understanding of albacore-anchovy dynamics.

These findings have important implications for the management of both albacore and anchovy. Currently, neither species has an active management plan that restricts catch or effort by fisheries. At times, during periods of high catch (1970-1980), human landings of adult anchovy exceeded the biomass of juveniles removed by albacore. Anchovy are currently harvested at very low levels, and the population of albacore appears to be relatively stable (ISC 2006). However, if history can be a guide, the dramatic population fluctuations of sardine and anchovy in the CCS could lead to changes in demand for anchovy in the future. Furthermore, if albacore stocks mimic the dramatic declines evident in more heavily harvested tuna species, such as bluefin, there is reason to be mindful of the health of the species. If albacore appreciably impact anchovy, then fewer albacore might result in an increase in anchovy. Conversely, although this study does not address the reverse trophic pathway, decreases in anchovy could result in declines in albacore, at least in the CCS (Cury et al. 2000, Navarette et al. 2000). Isolating and quantifying individual predator-prey relationships will aid in the development and application of decision-based management models that are designed to address such questions.

Table 4.1. Annual consumption of anchovy (mt) by albacore in the CCS. ‘Low estimate’ assumes albacore biomass equal to landings; ‘high estimate’ assumes biomass from stock assessments. Regions are divisions of the CCS based on albacore distribution.

	Low Est			**High Est**		
Year	**Northern**	**Central**	**Southern**	**Northern**	**Central**	**Southern**
1966	3366	126	390	36734	1380	4256
1967	4667	169	416	37902	1372	3380
1968	5496	202	523	44246	1626	4214
1969	4655	180	446	45026	1736	4318
1970	4632	222	548	48570	2331	5750
1971	4007	199	679	42764	2120	7244
1972	5866	196	873	52644	1758	7836
1973	3525	115	539	45274	1475	6922
1974	5083	155	630	56871	1735	7049
1975	4250	136	564	50471	1611	6695
1976	2871	132	613	38705	1773	8271
1977	1689	81	386	32683	1567	7461
1978	2632	128	513	37615	1823	7337
1979	1077	45	274	27827	1150	7087
1980	1063	50	316	25550	1205	7584
1981	1703	82	530	18242	876	5676
1982	889	42	296	23183	1105	7725
1983	1226	58	411	23444	1101	7864
1984	1278	62	568	20778	1006	9228
1985	1033	51	360	14564	719	5071
1986	678	25	201	23960	898	7116
1987	407	13	116	17332	564	4940
1988	674	20	187	15946	463	4412
1989	266	9	90	12331	413	4185
1990	358	12	127	23831	770	8476
1991	223	7	87	22437	738	8756
1992	552	17	210	25487	806	9691
1993	709	23	309	21571	703	9407
1994	1317	41	645	22274	689	10907
1995	914	30	533	24546	817	14307
1996	1812	59	1164	16410	536	10547
1997	1373	55	1028	23216	926	17386
1998	1622	50	1172	16266	506	11754
1999	1077	43	1126	13017	525	13614
2000	1178	39	951	18197	597	14688
2001	1313	41	1004	17872	560	13672
2002	1358	37	968	19708	532	14046
2003	1846	36	1198	24500	476	15910
2004	1737	34	1168	13002	253	8746
2005	1002	23	997	14692	338	14605

Table 4.2. Pearson sample correlation coefficients between anchovy and albacore biomass in the CCS. Temporal autocorrelation was removed from time series by first differencing. Two albacore parameters (high and low estimates of albacore biomass) and two anchovy parameters (recruitment only and total population biomass) were tested. The anchovy parameter was tested at various annual lags.

Albacore	**Anchovy**	**Lag**	***r***	***p***
Low Estimate	Recruitment	0	0.6780	0.0001*
		1	-0.4880	0.0454*
	Population	1	0.6254	0.0005*
		2	-0.1309	0.5239
		3	0.1933	0.3545
High Estimate	Recruitment	0	0.0225	0.9093
		1	0.2558	0.1978
	Population	1	0.0363	0.8572
		2	0.3254	0.1048
		3	0.0708	0.7367

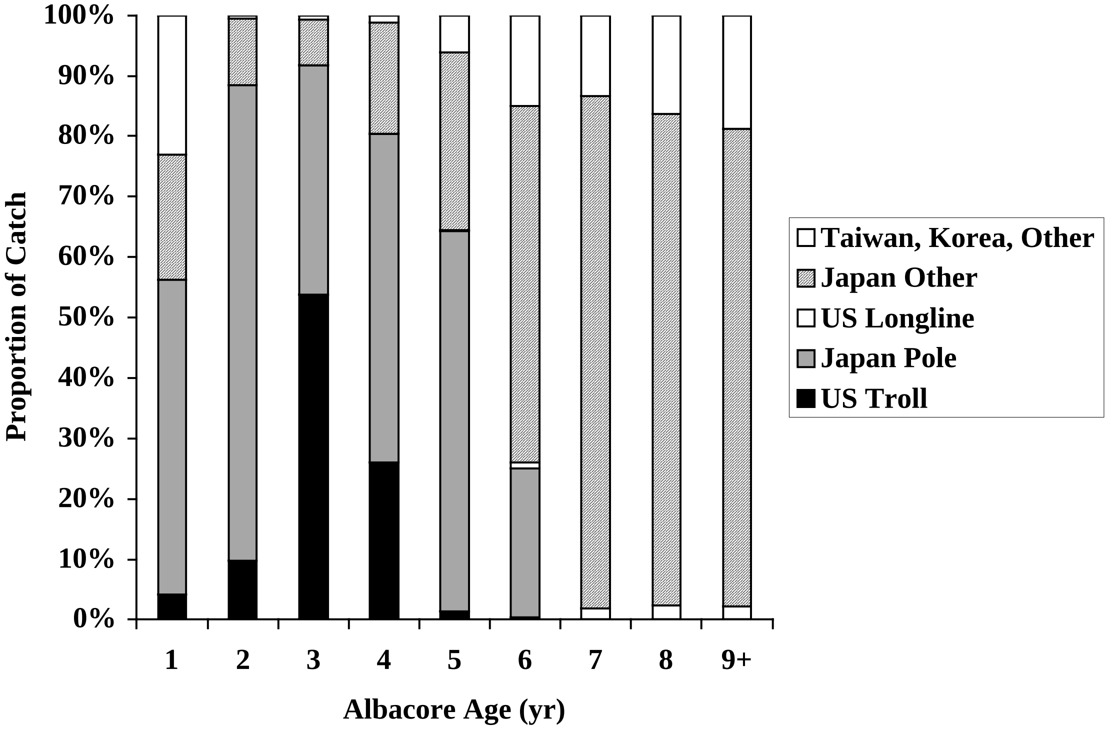


Figure 4.1. Age composition of landings in major fisheries for albacore in the North Pacific Ocean. The Japanese pole fishery and U.S. troll fishery harvest the majority of juvenile (≤ 4 years of age) albacore that are landed. Data are aggregated from 1966-2005 for all fisheries that report data to the ISC.

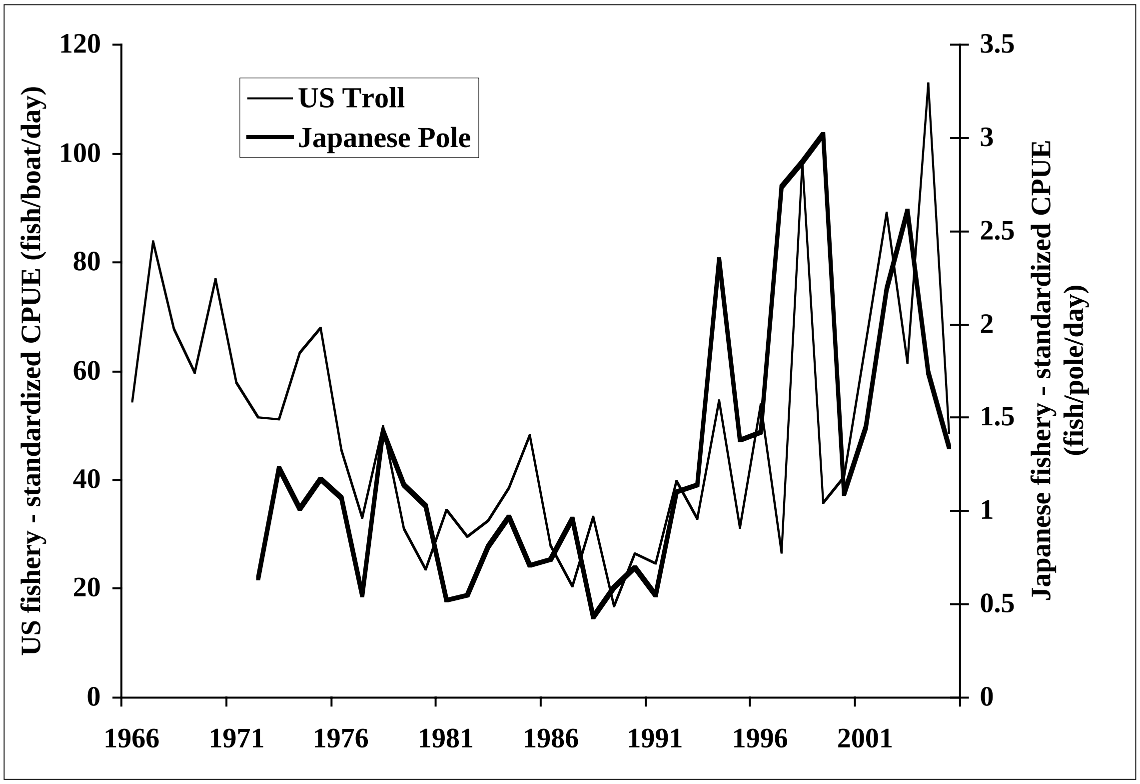


Figure 4.2. Indices of relative abundance of albacore caught by two major fisheries. Units are not directly comparable, but time series are correlated through time (Pearson sample correlation coefficient, *r* = 0.486, p < 0.005).

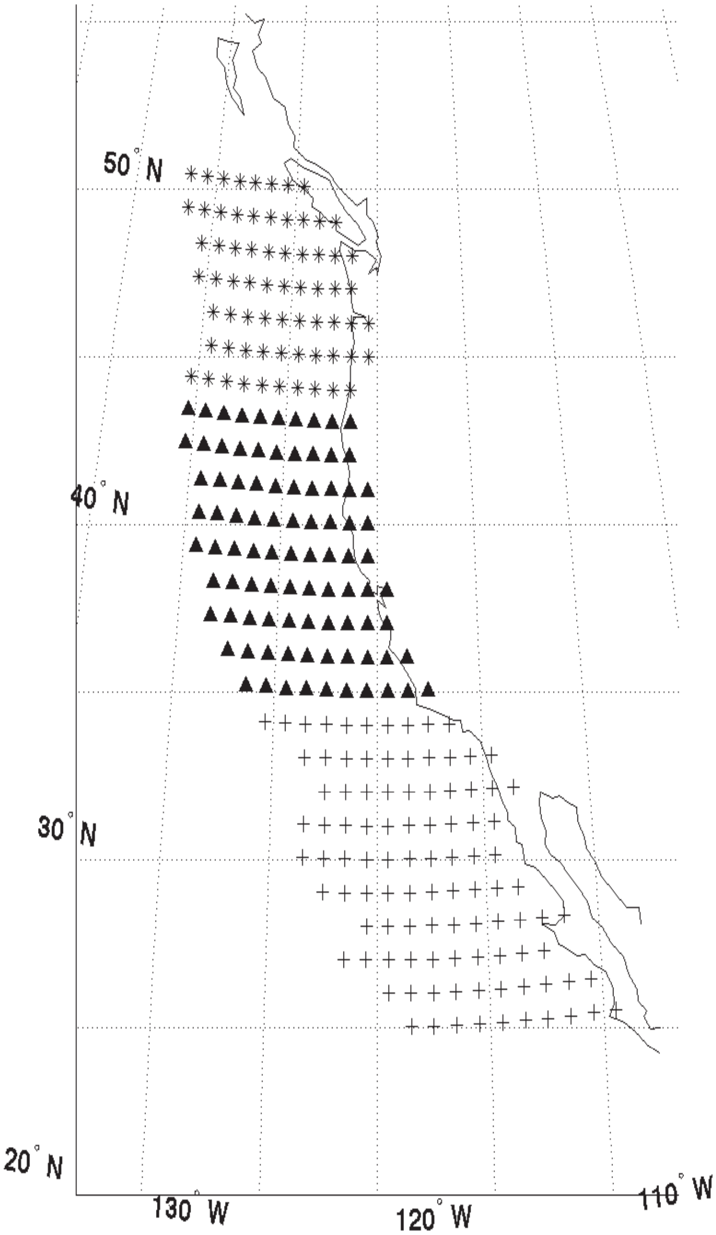


Figure 4.3. 1 degree x 1 degree cells used to estimate albacore abundance in the California Current System. Each cell has an associated catch and effort value, monthly. Three regions (north, central, south) are shown in different shapes.

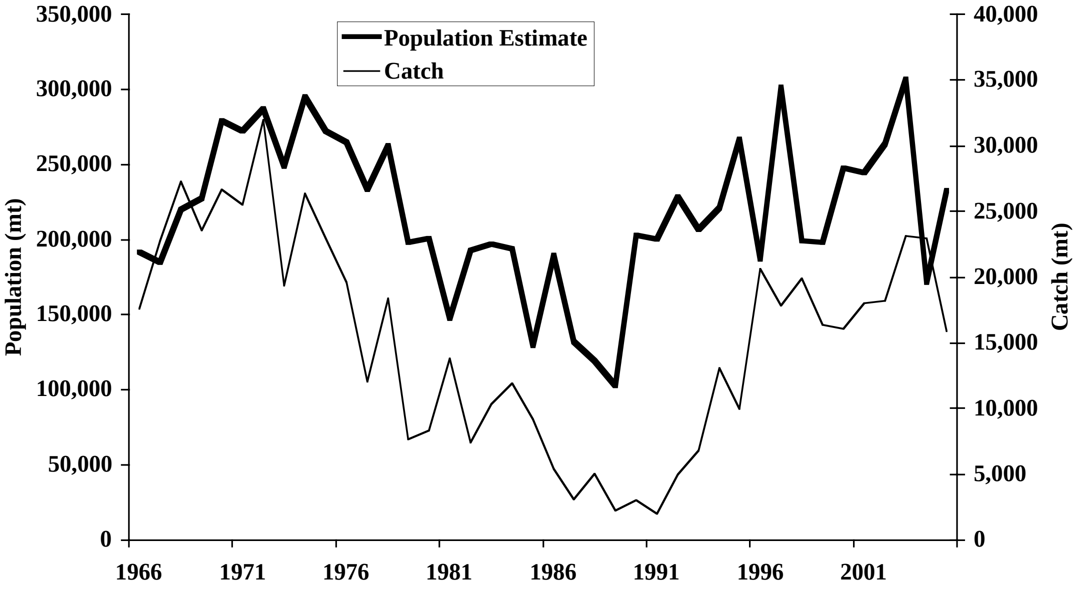


Figure 4.4. Estimates of albacore biomass in the California Current System. The low estimate is the total catch by the U.S. and Canada troll fisheries operating in the Eastern Pacific Ocean which lands albacore ages 2 - 4 (see Figure 4.1). The high estimate is the biomass of all albacore ages 2 - 4 estimated from a Pacific-wide stock assessment model (ISC 2006).

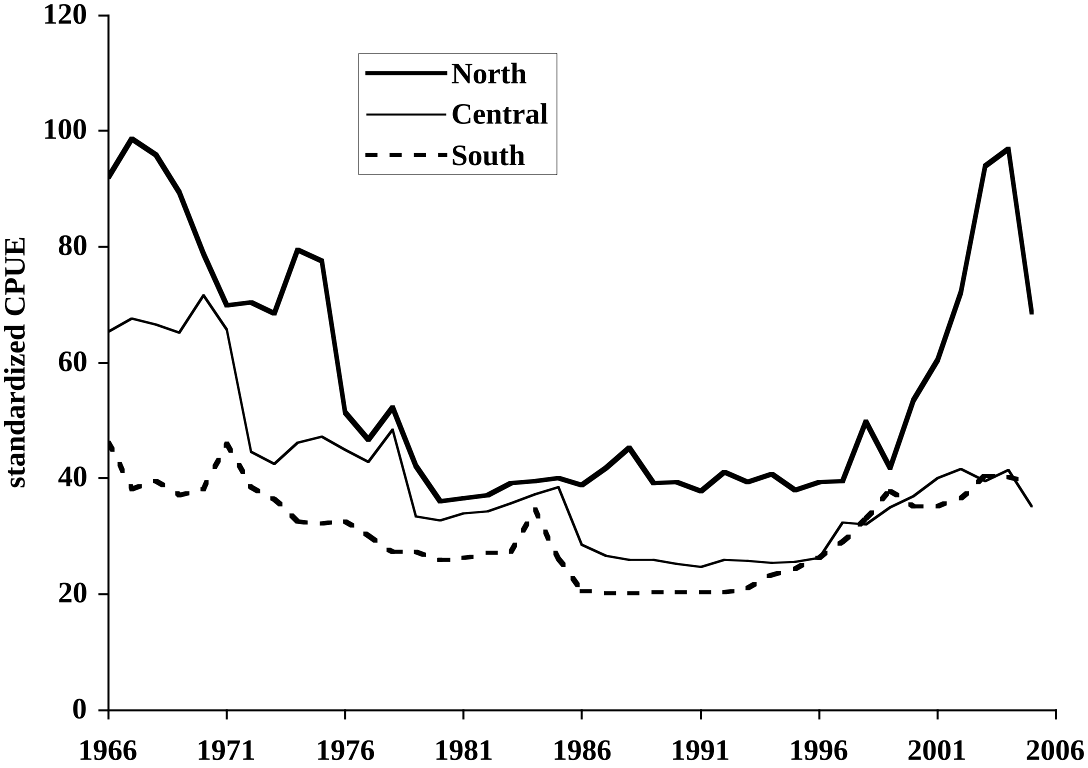
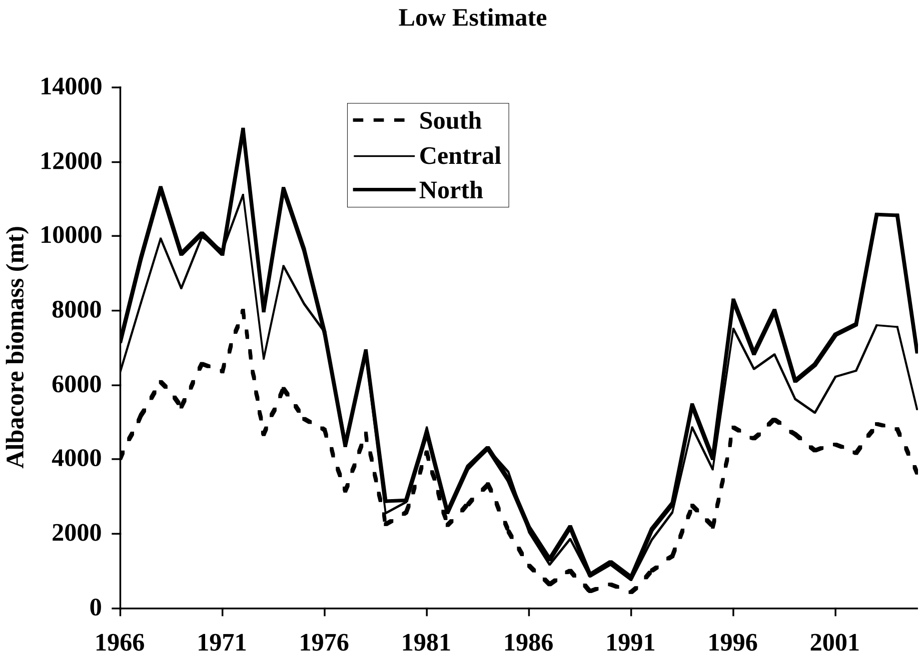


Figure 4.5. Index of relative abundance of albacore in the California Current System in three regions.



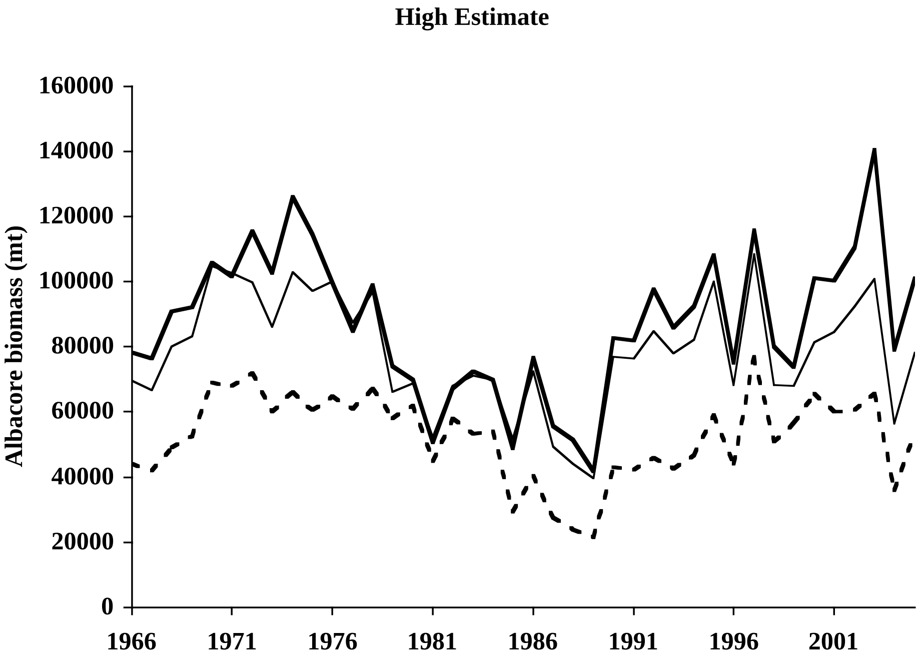


Figure 4.6. Estimates of albacore biomass in three regions of the CCS. Low estimate is based on landings data alone. High estimate is based on a stock assessment model.

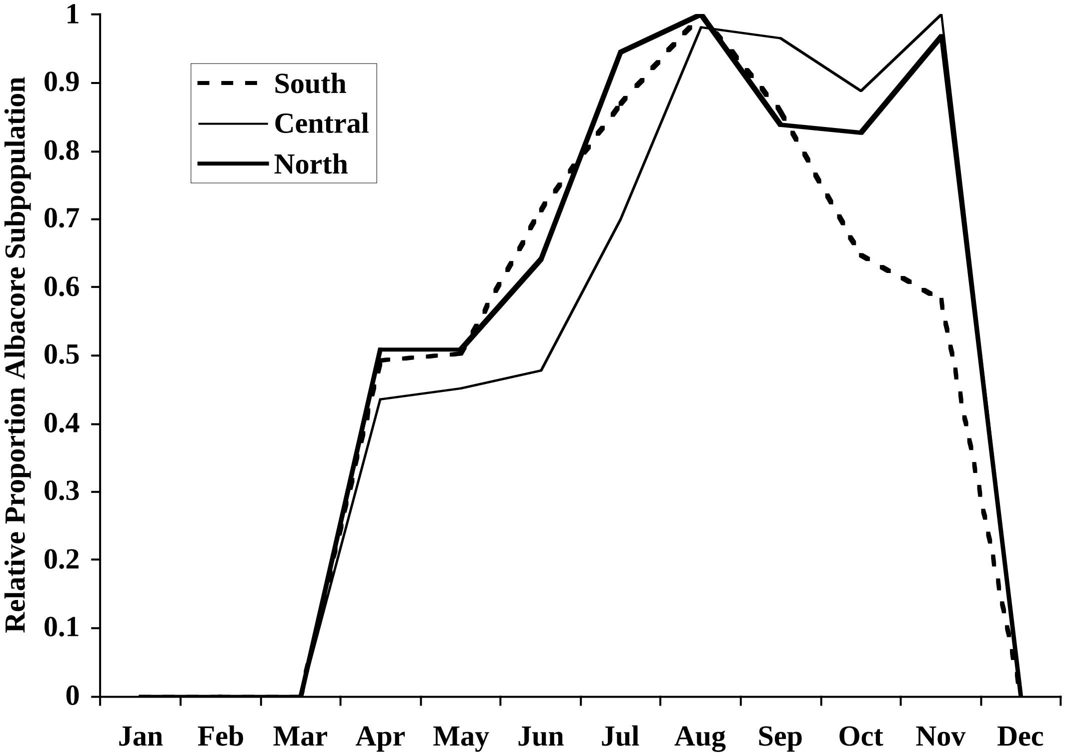


Figure 4.7. Seasonal distribution of albacore in the CCS from standardized CPUE data.

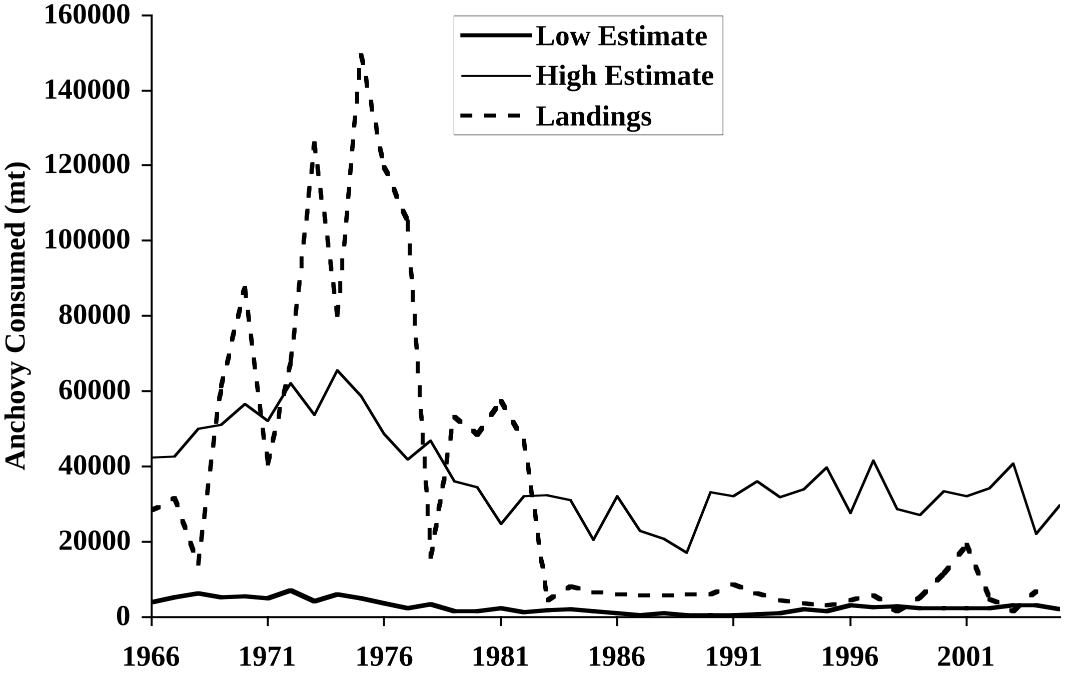


Figure 4.8. Total annual albacore consumption of anchovy in the California Current System and human landings.

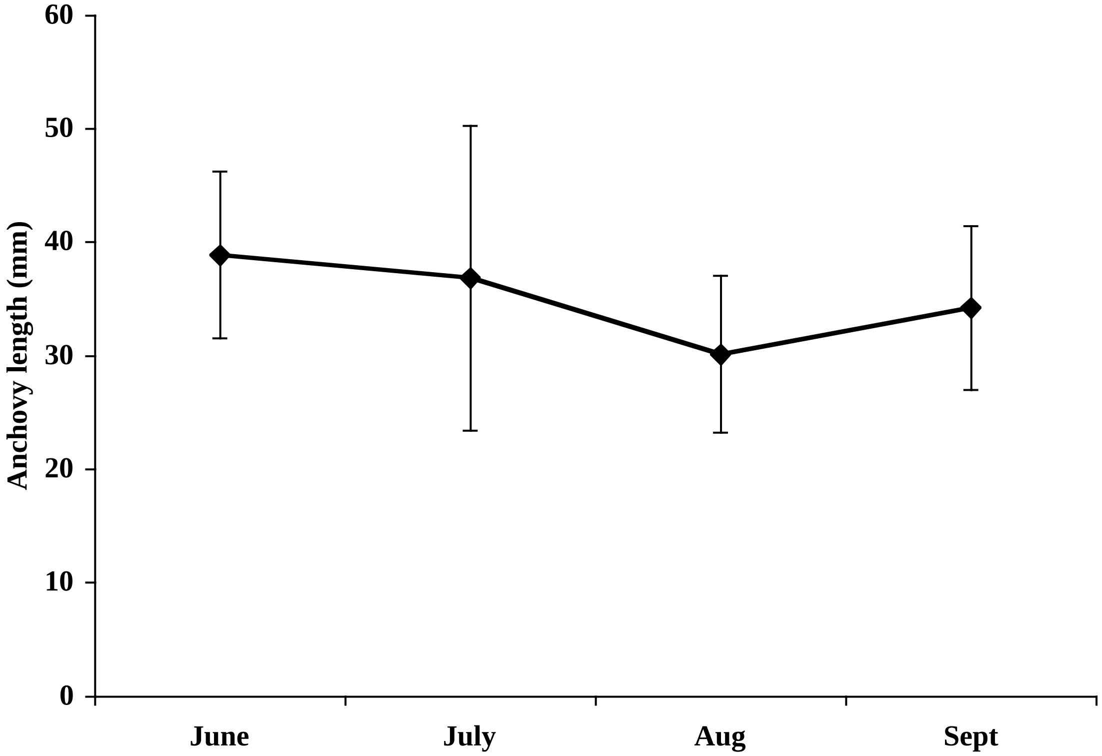


Figure 4.9. Size of anchovy found in albacore stomachs by month, collected in 2005 and 2006. One-tailed ANOVA $F = 11.998$, df = 3, $p < 0.001$. Bars are one standard deviation.

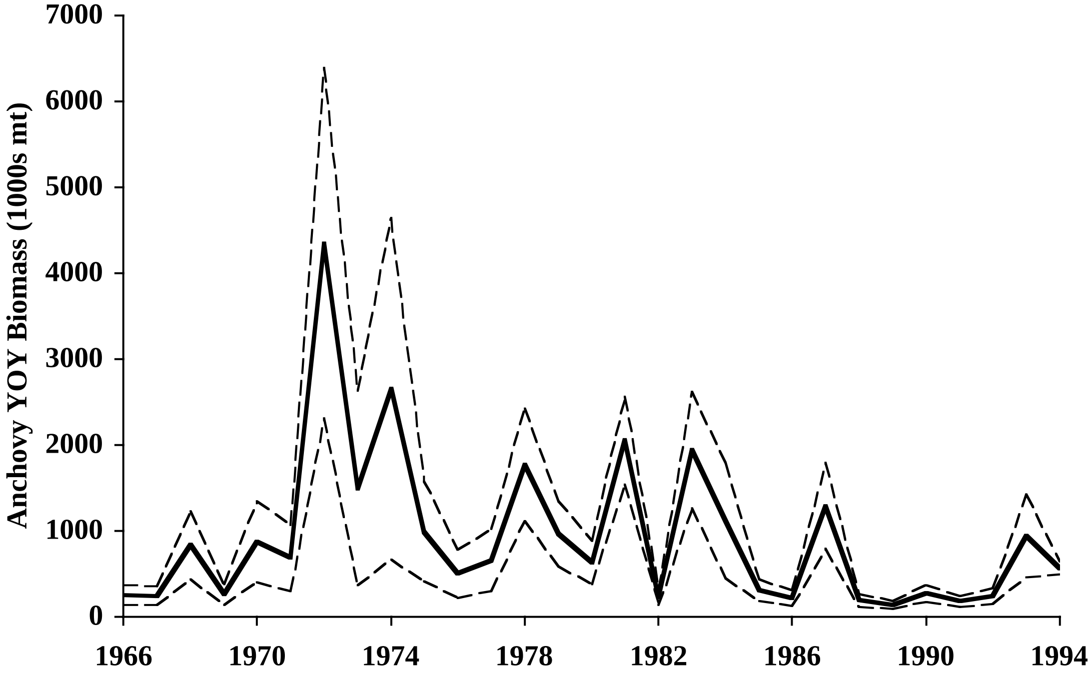


Figure 4.10. Calculated biomass of anchovy recruitment (young of year fish) for the central Northern anchovy stock in the CCS. Dashed lines are +/- the CV. Data from Jacobson et al. (1995).

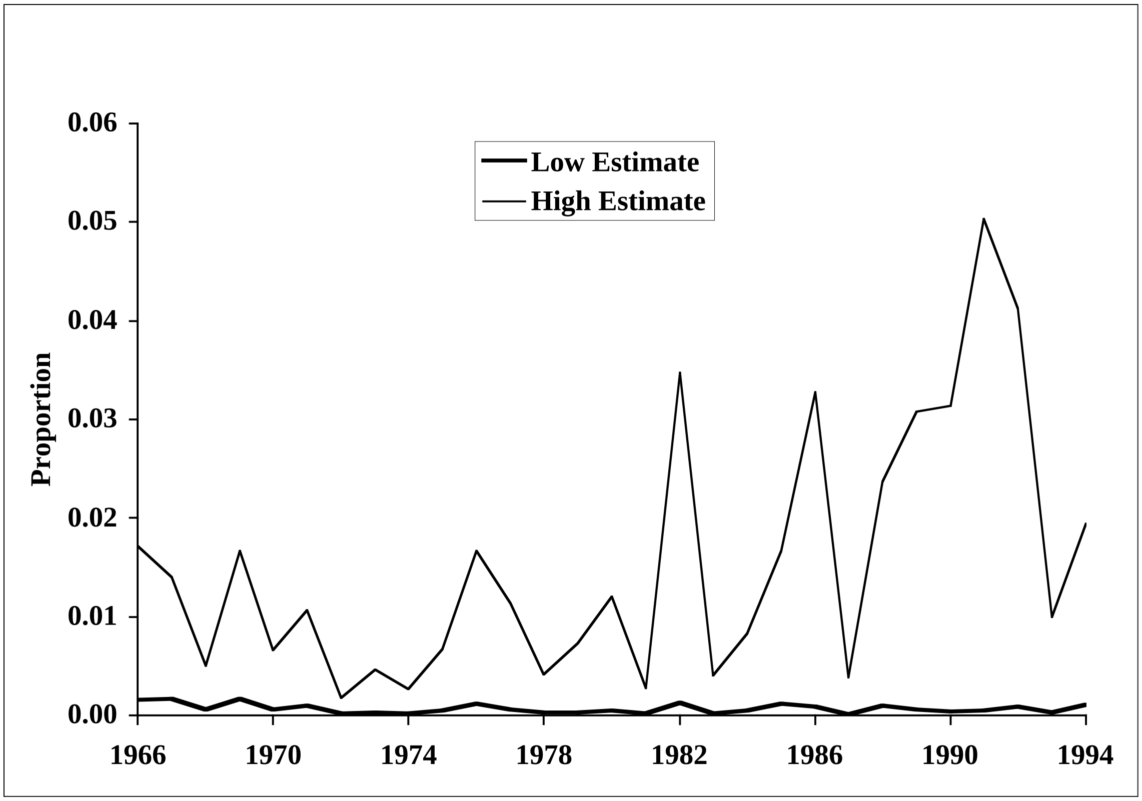


Figure 4.11. Proportion of young of year Northern anchovy in the central stock consumed by albacore.

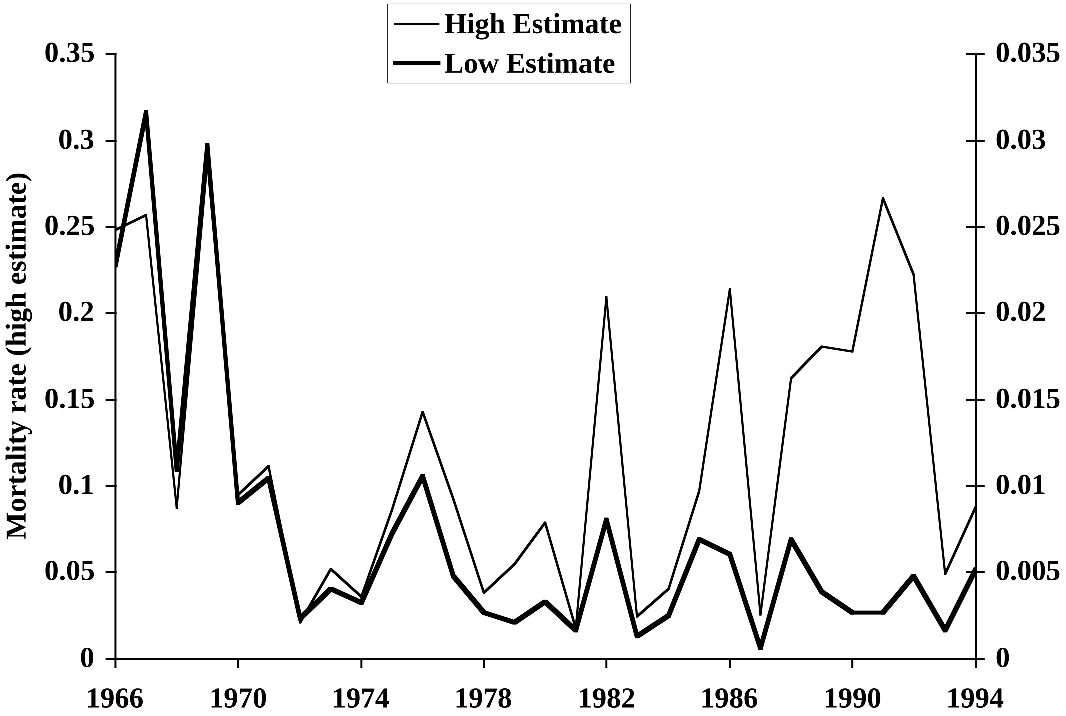


Figure 4.12. Instantaneous mortality rate on juvenile anchovy imposed by albacore predation.

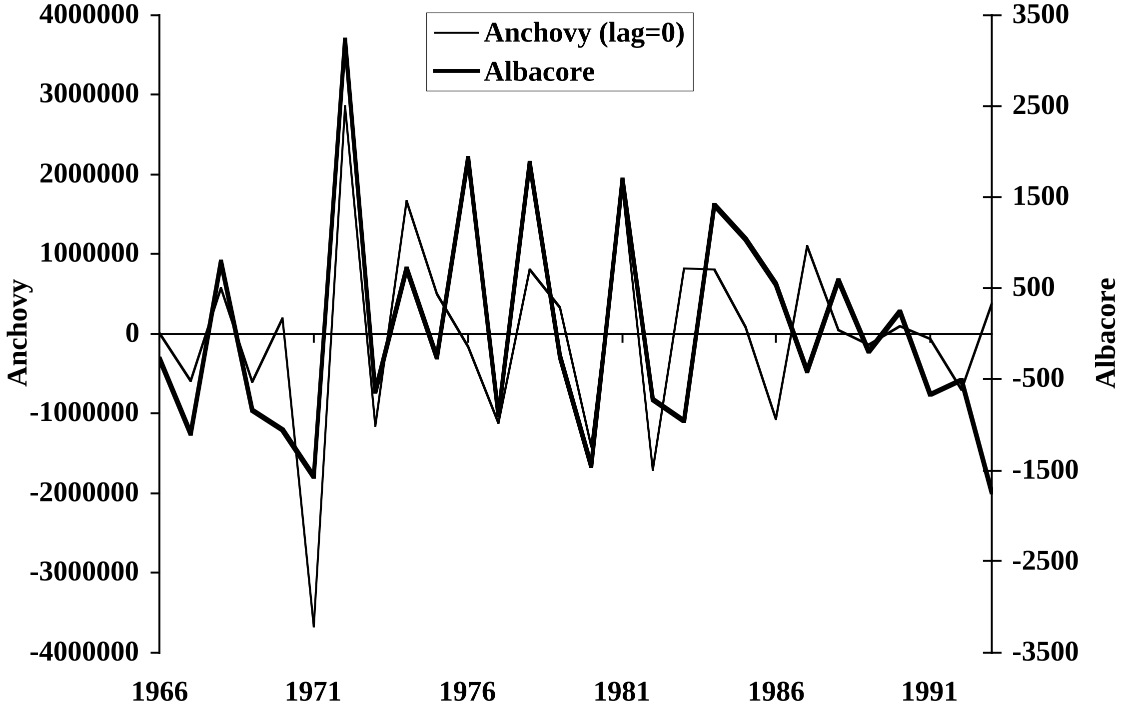


Figure 4.13. Temporal correlation between albacore biomass and anchovy recruitment. Data were first differenced to remove autocorrelation. (*r* = 0.678, *p* = 0.0001).

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Chapter 5. Conclusions.

This dissertation is the first to quantify interdecadal variability in diet habits of an important pelagic marine predator, and the findings have implications for marine ecosystems. Albacore diet has been stable despite significant changes in the marine communities in the CCS. Contrary to expectations, albacore do not consume Pacific sardine, and their niche width is more narrow than previously assumed. Northern anchovy are a critical prey species for albacore, and models containing albacore or anchovy could be improved by focusing on this key interaction. Although conventional wisdom classifies albacore as generalists, their mixed-approach to foraging means they may be more sensitive to dramatic changes in important prey species, especially Northern anchovy. Finally, the role of albacore in the CCS, while transitory, appears to be sufficient to impact at least one population of prey.

The results presented in this study should be useful for developers and users of ecosystem models. First, I demonstrated that, even over 50 years of variable environmental conditions (Mantua et al. 1997, McGowan et al. 1998, Minobe 2002) and changes in the biological community in the CCS (e.g., Roemmich & McGowan 1995a,b, Hare & Mantua 2000, McGowan et al. 2003, Brodeur et al. 2005, Lavaniegos & Ohman 2007), the diet habits of an important predator have not changed substantially, except recently to incorporate a third major prey item. This is not to say that we should ignore prey items that make up a small component of diet. Weak interactions are important for the topological stabilization of food web models (McCann 1998) and pressure on rarely consumed species, such as *Sebastes*, may scale to be a significant source of predation.

However, from the perspective of the predator, understanding of predator-prey dynamics could be greatly enhanced by focusing research efforts on a few key prey species.

Characterizing albacore foraging strategy as mixed, rather than generalist, has important implications for understanding the CCS as a whole. First, if albacore niche width is more narrow than previously assumed, albacore should experience less direct competition from other predators if niche overlap is minimized (Roughgarden 1974, Stouffer et al. 2005). Juvenile albacore compete with medium-sized predators such as salmon (Brodeur 1991), seabirds (Hunt 2000), and bonito (Pinkas et al. 1971), but not larger predators such as bluefin or yellowfin tuna (Pinkas et al. 1971), sharks (Preti et al. 2001), or marine mammals (Hunt 2000). Second, the narrow niche width may be a contributing factor to the relatively high and stable abundances of albacore in the CCS (Sugihara et al. 2003). Third, if albacore rely on a small diversity of prey for a significant portion of energy, changes to that base of prey could have more drastic impacts on albacore than if they were true generalists (Bellwood et al. 2003). Finally, in the context of multispecies and ecosystem-based models, the linkages between albacore and a few key species are worthy of closer scrutiny, and results here call into question the practice of model simplification through functional groupings of prey species.

This study is the first to quantify mortality imposed on juvenile Northern anchovy by a specific predator. Additionally, it is the first to document, although far from the first to suggest, that levels of predation on juvenile anchovy have top-down impacts on recruitment biomass. However, this is neither conclusive nor final word on the matter; quite the contrary, these results are merely the opening salvo. In the words of Mohn and Bowen (1996), “ecological models…may be viewed as a serial process that builds on each previous step by adding some new information to form the next." Thus, results from this study, in particular estimates of predation pressure and size-specific mortality, are an important first step in laying the foundation for a more thorough understanding of albacore-anchovy dynamics.

These findings have important implications for the management of both albacore and anchovy. Currently, neither species has an active management plan that restricts catch or effort by fisheries. At times, during periods of high catch (1970-1980), human landings of adult anchovy exceeded the biomass of juveniles removed by albacore. Anchovy are currently harvested at very low levels, and the population of albacore appears to be relatively stable (ISC 2006). However, if history can be a guide, the dramatic population fluctuations of sardine and anchovy in the CCS could lead to changes in demand for anchovy in the future. Furthermore, if albacore stocks mimic the dramatic declines evident in more heavily harvested tuna species, such as bluefin, there is reason to be mindful of the health of the species. If albacore appreciably impact anchovy, then fewer albacore might result in an increase in anchovy. Conversely, although this study does not address the reverse trophic pathway, decreases in anchovy could result in declines in albacore, at least in the CCS (Cury et al. 2000, Navarette et al. 2000). Isolating and quantifying individual predator-prey relationships will aid in the development and application of decision-based management models that are designed to address such questions.

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