Interdecadal variability in predator–prey interactions of juvenile North Pacific albacore in the California Current System

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ABSTRACT: Predator–prey interactions are critical components of multispecies models, and most attempts to quantify these interactions in pelagic marine environments rely on observational diet studies. In conjunction with 3 historical studies, a new diet study quantifies decadal patterns of predator–prey interactions for juvenile North Pacific albacore *Thunnus alalunga* in the California Current System (CCS). Juvenile albacore in the CCS eat young-of-year prey and derive 68 to 89% of nutrition from fishes, 9 to 30% from cephalopods, and the remainder from crustaceans. Despite resurgence in abundance of Pacific sardine *Sardinops sagax* in the CCS, only Northern anchovy *Engraulis mordax*, Pacific saury *Cololabis saira*, and cephalopods have consistently 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 while minimizing foraging in warmer, offshore waters of sardine habitat. A bioenergetics model is used to calculate daily and annual consumption rates. The importance of calculating an ensemble prey energy density (ED_n) value for steady-state consumption models is demonstrated, and the relationship between ED_n and consumption rates is generalized to other marine predators. Low variability in ED_n consumed by juvenile albacore translates into equally stable consumption to biomass ($Q{:}B$) ratios over decades.

KEY WORDS: *Thunnus alalunga* · Predator–prey interaction · Bioenergetics · Ensemble energy density · Diet · Trophic ecology · Pelagic food web · California Current

INTRODUCTION

The aims of this study were to identify critical relationships between juvenile North Pacific albacore and their prey in the California Current System (CCS), and to quantify decadal variability in diet and consumption rates. Diet studies are a snapshot of the habits of marine predators. In light of significant ecological changes in the CCS over the past half-century (e.g. Hare & Mantua 2000, McGowan et al. 2003, Brodeur et al. 2005, Lavaniegos & Ohman 2007), and given functional redundancy in marine food webs (Link 2007) and the commonality of generalist foraging strategies (Roughgarden 1974), variability in diet is expected.

North Pacific albacore *Thunnus alalunga* are highly migratory predators that produce 60 000 to 100 000 t of commercial landings annually (ISC 2006). Adults spawn in the western-central North Pacific and juveniles (ages 0 to 4) occupy the productive California and Kuroshio Current regions (Laurs & Lynn 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 North Pacific to the Kuroshio system (Kimura et al. 1997). Albacore complete 90% of growth before reproductive maturity (de Zarate & Restrepo 2001); given

the residence time of juveniles in the CCS, their diet in this region is important to the production of the population.

Diet habits of juvenile albacore in the CCS have been described in a host of studies (Hart et al. 1948, Pearcy 1973, Bernard et al. 1985). Three notable studies (McHugh 1952, Iversen 1962 [in conjunction with Graham 1959], Pinkas et al. 1971) are sufficient in scope for interdecadal comparisons. Data collected by Pinkas et al. (1971), in particular, are widely used to parameterize ecosystem models (Kitchell et al. 1999, Olson & Watters 2003, Field et al. 2006). These 3 historical diet studies have never been analyzed in concert. Given the widespread presumption that albacore are opportunistic predators (Pinkas et al. 1971, Watanabe et al. 2004, Consoli et al. 2008), an updated diet study is warranted.

Significant fluctuations in population sizes of 2 forage fishes, *Sardinops sagax* (Pacific sardine) and *Engraulis mordax* (Northern anchovy), have occurred asynchronously over the past century (Soutar & Isaacs 1974, Schwartzlose et al. 1999, Baumgartner et al. 1992, Chavez et al. 2003). Past studies (McHugh 1952, Iversen 1962, Pinkas et al. 1971, Bernard et al. 1985) have identified anchovy, but not sardine, in significant quantities in juvenile 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 (Hill et al. 2007). Given the biological similarities between these forage species, it is reasonable to hypothesize that juvenile albacore have increased predation on sardine and decreased predation on anchovy.

Predator–prey interactions are critical components of multispecies models, and empirical attempts to quantify interaction strengths rely upon diet studies or field observations of predation. Diet studies are especially useful in poorly observed systems, such as the pelagic environment, where interaction strengths are difficult to quantify (Wootton 1997). For pelagic predators, gut content studies remain the primary method for measuring food web linkages. Estimating variability in diet-derived parameters is a critical step in improving multispecies and ecosystem-based models (Christensen & Walters 2004).

Multispecies models have shown great promise for estimating recruitment and natural mortality, quantifying fishing impact on community structure, and describing climate effects on food webs (e.g. Cox et al. 2002, Watters et al. 2003, Christensen & Walters 2004, Field et al. 2006). However, the complexity inherent in these models obscures more finely resolved components, such as species-level dynamics (Hollowed et al. 2000). Species-specific parameters in ecosystem-scale

models, such as the consumption to biomass ratio (*Q:B*), can be calculated within the models themselves, but it is important also to validate estimates empirically.

Q:B quantifies prey biomass consumed per unit biomass of a predator population on an annual basis (Pauly 1989). This parameter can be used, among other things, to estimate the predation pressure exerted on prey populations and to predict how a predator population may be affected by changes in prey abundance. The potential for sudden and unexpected fluctuations in marine populations, especially fisheries, underscores the importance of predicting community responses to changing climate and fishing pressure (Hare & Mantua 2000, Pauly et al. 2002, Hsieh et al. 2005). Thus, estimates of *Q:B* that are empirically derived for a given species are important for informing adaptive ecosystem-based management.

This study presents new data quantifying diet habits of juvenile albacore in the CCS, and, in the context of 3 prior studies, investigates changes over time. Historical studies are re-analyzed using a contemporary bioenergetics approach, and estimates of energetic demand are used to calculate *Q:B* for juvenile albacore. This is the first study to quantify empirically, for albacore, the suite of prey energy density (*ED*) values consumed and the impacts of variable prey on consumption rates. Results demonstrate that juvenile albacore rely on few species of prey to meet energetic requirements in the CCS.

MATERIALS AND METHODS

Data collection (present study). Stomachs from 371 juvenile North Pacific albacore were collected during June to September 2005 and 2006 (Fig. 1). Stomachs were collected by the author on recreational boats (n = 188) and by captains and crew on 2 commercial boats (n = 183). All boats used troll gear, poles, or hand lines. In all cases, date and location were recorded. Time of day and albacore length were recorded on recreational vessels. Stomachs were removed on deck from fish minutes after death and frozen with dry ice or in a blast freezer; a small percentage (~10%) were collected at docks from vessels returning from day trips.

Contents were identified visually by the author exclusively, 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* spp. (rockfishes), and voucher specimens of juvenile cephalopods were sequenced for genetic identification. Lengths of individual prey items
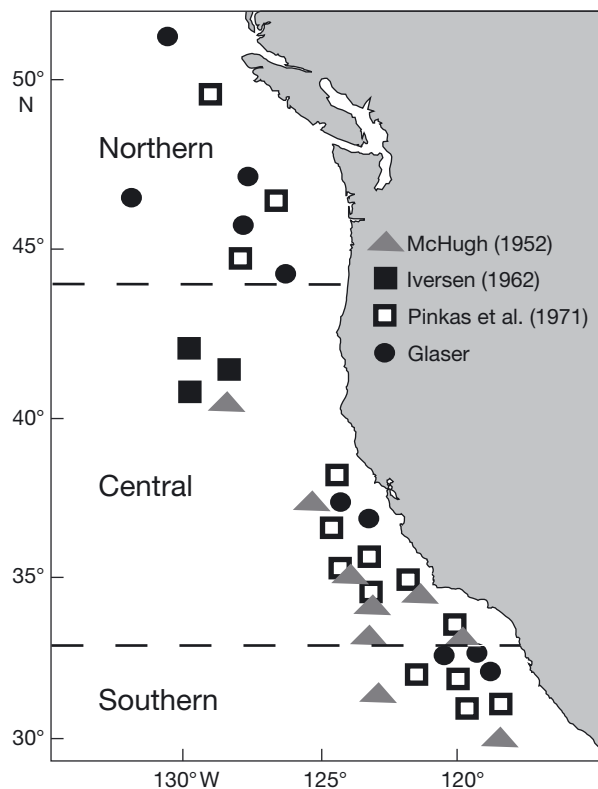
Fig. 1. Distribution of sampling effort for 4 studies of juvenile albacore diet in the California Current System

were measured to reconstruct original (pre-digestion) weights. If a stomach contained a large number of one species, 5 randomly chosen representatives per stomach were measured.

Data collection (historical studies). McHugh (1952) collected 321 stomachs during the summers of 1949 and 1950 using unbaited poles (Fig. 1, based on McHugh Fig. 1). Albacore lengths were not provided. McHugh reported mean volumes of individual prey, total volume of species consumed, and frequency of occurrence, but not numbers consumed.

Graham (1959) and Iversen (1962) reported independent results from one study and data are combined here (hereafter, jointly referred to as Iversen 1962). Investigators collected stomachs between 1950 and 1957 using longline, gill net, and troll gear. Only those collected by troll gear (n = 155 and starting in 1954) are analyzed here. Other sampling methods are not comparable due to location or gear bias. Trolling occurred primarily in the CCS, but some (n = 38) were collected further west (Fig. 1, based on Iversen Table 1) and could not be excluded from the gear-aggregated results. Sampling occurred during fall and winter 1954, 1955, and 1956 and summer 1955, 1956, and 1957. Iversen reported frequency of occurrence, number, and volume of prey items while Graham reported numeric data only.

Pinkas et al. (1971) collected 905 albacore from commercial vessels using troll gear. Sampling took place during July to November 1968 and July to September 1969 (Fig. 1, based on their Fig. 4). They reported frequency of occurrence, number, and volume of prey for each of 3 regions (southern, central, and northern CCS).

Data analysis. Stomachs were assigned to one of 3 regions in the California Current based on the regional divisions established by Pinkas et al. (1971). Regions were designated northern (north of 44° N latitude, inclusive), central (between 33° and 44° N latitude) and southern (south of 33° N latitude, exclusive). The northern region lacks data from McHugh (1952) and Iversen (1962) and the southern region lacks data from Iversen (1962).

The energetic contribution (E) of prey to the diet of juvenile albacore is $E_i = W_i \times ED_i$ where W_i is wet weight (g) and ED_i is energy density (kJ g^{-1}) of species i. Published values of prey ED and proximate composition were collected. Only 'whole body' values reported as wet weight were used. If ED for a species was unavailable, the next highest taxonomic level was used (see supplement at www.int-res.com/articles/suppl/m414p209_supp.pdf for details).

The taxonomic resolution of prey and diet metrics in the 4 studies varied. Any prey category that occurred in at least 10 stomachs in any of the 4 studies was analyzed. The degree of digestion was not reported in the historical studies, complicating comparisons of mass data. Therefore, numbers of prey were converted to pre-digested weight using published allometric length–weight relationships. The mean length of prey from 2005–2006 was applied to historical studies. This was justified by the similarity in prey sizes described (see Discussion). For McHugh (1952), percent volume was used directly because numeric data were not reported.

Pre-digested weight was reconstituted as follows. Allometric length-weight relationships were used for all species of fish (Harvey et al. 2000, Froese & Pauly 2008). For crustaceans, measurements of carapace length and wet weight were used (Isaacs et al. 1969). For cephalopods, measurements of beak lower rostral length (LRL) were used to calculate wet weight. The LRL of cephalopod beaks in this study ranged from 0.2 to 2.0 mm. LRL–weight relationships for this range of beak sizes exist for *Loligo opalescens*, *Gonatus* sp., *Onychoteuthis borealijaponica*, and *Abraliopsis* sp. (Wolff 1984, Clarke 1986). Body masses were calculated for these 4 species, and the overall mean was applied to remaining cephalopod species.

A bioenergetics model of albacore (Essington 2003) was used to calculate daily consumption rates. Daily consumption (C) is $C = AL + SMR + AMR + REP + G,$

where *AL* is loss from assimilation, *SMR* is standard metabolic rate, *AMR* is active metabolic rate, *REP* is reproduction, and *G* is somatic growth. Here, *AL* describes the loss of energy due to feces (10%), excretion (10%), and specific dynamic action (15%) (Olson & Boggs 1986). All components have units of J kg^{-1} d^{-1}. The model is size- and age-explicit, and includes swimming speed, lift, sex ratio (1:1), and age of reproductive maturity. To quantify the steady-state biomass (g kg^{-1} d^{-1}) of prey consumed (*C*$_B$), *C* was multiplied by prey *ED*$^{-1}$. Finally, to calculate annual *Q:B*, *C*$_B$ was multiplied over the year.

Parameter uncertainty was quantified by running 10 000 Monte Carlo simulations of the model. Essington (2003) found *Q:B* 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, *AL*, *x*$_{swim}$ and *x*$_{AMR}$ varied by 10% and *ED* varied according to the distributions in the literature.

The bioenergetics model was given a temporal component by varying diet according to the historical studies and by sampling from the age distribution of albacore in the CCS. The energy consumed is a weighted combination of the *ED* of prey and the proportion that prey comprises of total intake. Using the percentage weight a taxon contributed to albacore diet, an ensemble energy density value (*ED*$_n$) was calculated for each study (simply, a weighted mean). To calculate *ED*$_n$ for any non-study year *x*, a weighting function accounted for the distance of year *x* from the 2 studies flanking *x* in time (*i* and *i*+1), such that

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

where *t* is the year of study *i* or the non-study year *x. C* and *C*$_B$ are functions of albacore age, therefore the age-distribution of juvenile North Pacific albacore landed by the North American commercial troll fishery from 1966 to 2005 was used to create a distribution from which the simulation sampled. This fishery operates primarily in the CCS and targets juveniles (ISC 2006). To extrapolate for the time period 1949 to 1965, overall age distribution was used. In each iteration, the following variables were randomly sampled from their distributions: *AL*, *x*$_{AMR}$, *x*$_{swim}$, *ED*, and albacore size/age. *ED*$_n$, *C*$_B$ and *Q:B* were calculated along with estimates of uncertainty.

RESULTS

The 4 studies describe diet habits of 1672 juvenile albacore in the CCS at various points during a period spanning 55 yr. Albacore were between 52 and 105 cm in fork length (Table 1), corresponding to age groups of

2 to 3 yr old (Suda 1966). Albacore of this size allocate approximately 10% of energetic intake to growth, 20 to 25% to active metabolism (swimming), 40% to standard metabolism, and the balance is lost (Essington 2003 and values calculated here).

In the CCS, juvenile albacore consumed young-of-year (YOY) fishes, juvenile cephalopods, and adult zooplankton (Table 2). Juvenile albacore were capable of consuming adult-sized small pelagic fishes, evidenced by the size of bait in stomachs (Table 2). However, excluding bait and saury *Cololabis saira*, their mean prey was recently spawned fishes 15 to 65 mm in length and cephalopods weighing 4 g. The Pacific saury was notable because it was relatively larger than other prey (119.1 ± 68.3 mm, 13.0 ± 20 g, mean ± SD) and the large SD indicated both juvenile and adult saury were eaten. In comparison, anchovy *Engraulis mordax* were consistently of juvenile sizes (34.7 ± 10.0 mm, 1.1 ± 1.3 g). The remainder of fishes were also juveniles except myctophids, which, while small (50.1 ± 15.8 mm), were adults. Juvenile rockfish *Sebastes* spp. (14.5 ± 4.5 mm) were a common prey item and were the smallest fish regularly consumed by albacore. Cephalopods were juvenile sizes, and crustaceans (amphipods, decapods, and euphausiids) were adult sizes. While bait boats harvested anchovy and sardine *Sardinops sagax* 15 to 20 cm in length for fishing vessels, the natural prey of albacore were considerably smaller.

Table 3 summarizes prey *ED* values synthesized from the literature and used in the bioenergetics model. Crustaceans and cephalopods were significantly lower in energy content than fishes, although some species of squid were more comparable to fishes. Of the species consumed by albacore, crustaceans ranged from 2.5 to 3.2 kJ g^{-1}, cephalopods from 3.0 to 6.7 kJ g^{-1}, and fishes from 3.5 to 7.9 kJ g^{-1} (see supplement for detailed values).

Depending on the *ED*$_n$ of the albacore prey, daily consumption rates could range from 0.02 to 0.12 g g^{-1} d^{-1} for an age-3 albacore (mean length 65 cm) (Fig. 2). The relationship between biomass consumed and *ED*$_n$

Table 1. *Thunnus alalunga.* Collection years, and fork lengths of juvenile albacore (parentheses: SD) examined in 4 diet studies and from commercial catch (ISC 2006)

Collection years	Mean length (cm)	Range (cm)	Source
1949–1950	n/a	n/a	McHugh (1952)
1954–1958	~ 67	53–85	Iversen (1962)
1968–1969	n/a	52–93	Pinkas et al. (1971)
2005–2006	75.6 (8.9)	54–99	Glaser (this study)
1966–2005	68.4 (6.5)	37–105	ISC (2006)

Table 2. *Thunnus alalunga.* Measured lengths and calculated weights of prey categories common to 4 studies of juvenile albacore diet, mean (SD). Measurements were made from stomach contents collected in 2005–2006 (this study). Mass values from length–weight relationships were applied to numeric data from historical studies to reconstruct the pre-digestion wet weights of prey. n is the number of specimens measured

Prey category	n	Length (mm)	n	Weight[a] (g)
Crustaceans				
Amphipods	47	11.7[b] (6.5)	8	0.04 (0)
Pleuroncodes planipes	2	33.8[b] (2.5)	1	2.0
Euphausiids	30	23.0[b] (4.8)	8	0.1
Malacostracans	24	26.3[b] (8.4)	1	0.1
Cephalopods	181	0.8[c,f] (0.2)	181	3.8[f] (4.0)
Fishes				
Cololabis saira	87	119.1[d] (68.3)	87	13.0 (20.0)
Engraulis mordax	421	34.7[d] (10.0)	421	1.1 (1.3)
Sardinops sagax	128	49.2[d] (16.9)	128	1.8 (3.6)
Sebastes spp.	29	14.5[d] (4.5)	29	0.1 (1.0)
Merluccius productus	232	60.9[e] (15.3)	232	2.1 (2.0)
Trachurus symmetricus	7	64.7[e] (39.3)	7	12.5 (17.6)
Myctophidae	16	50.1[e] (15.8)	16	1.9 (1.4)
Fishes (other)	942	49.7[f,g] (34.9)	942	2.5[f,g] (7.3)
Engraulis mordax bait	29	100.0[d] (22.8)	29	13.6 (7.0)
Sardinops sagax bait	39	145.5[d] (16.2)	39	33.0 (12.9)
Scomber japonicus bait	8	227.7[e] (36.1)	8	60.9 (21.5)

[a]Wet weight. [b]Tip of rostrum to end of telson (mm). [c]Beak lower rostral length (mm). [d]Standard length (mm). [e]Total length (mm). [f]Taxonomic mean. [g]'Other' category measurements include unknown and identified (above) fishes

Table 3. *Thunnus alalunga.* Energy density (*ED*, mean ± SD) values (kJ g⁻¹) of prey common to 4 studies of juvenile albacore diet in the California Current System

Prey category	*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

varies geometrically: $C_B = C \times ED^{-1}$. Thus, the sensitivity of the model depends on the magnitude of ED_n. Due to the high proportion of fish in albacore diet, the 4 studies cluster along the flat portion of the curve relating consumption rates to prey *ED* (Fig. 2).

In general, over a period of 55 yr and 3 regions of the CCS, albacore primarily consumed anchovy, saury, and cephalopods, based on percent energetic contribution (*E*). Table 4 describes the spatial and temporal patterns evident in juvenile albacore diet, to the extent that data were available.

In the northern region, anchovy were the largest single-species component of diet; however, anchovy were far more predominant (68% versus 30%) in 1968–1969 than in 2005–2006. In the late 1960s, cephalopods were the second most important prey group (14%). All other taxa each comprised less than 10% of the diet, with saury (8%), myctophids (5%), and crustaceans (4%) being notable. In 2005–2006, the sum of all crustaceans comprised the largest component of the diet (31.5%); the group Crustaceans was primarily undifferentiated decapods or euphausiids. Juvenile hake appeared in albacore diet for the first time on record in 2005–2006 and were the second most important (21%) single-species prey group in the northern region, followed by cephalopods (5%) and juvenile sardine (4%).

The central region contained data from all 4 diet studies and showed, overall, a predominance of saury and cephalopods in the diet, with important exceptions. Anchovy were the most important (38%) prey in 1949–1950, while hake were the most important (38%) during 2005–2006. In these 2 studies, saury and cephalopods were, respectively, the second and third most important prey groups, whereas they were the first and second most important groups during the intervening studies (1954–1957 and 1968–1969). Cephalopods dominated diet in the central region in 1968–1969 (63%), the highest contribution of cephalopods in any interval. Crustaceans were a less important component of diet here, comprising only 1 to 10% of *E*.

Diet in the southern region, generally speaking, was dominated by the same prey: saury was the most important group in 1949–1950 (61%) and 1968–1969 (59%), while cephalopods were either the second or third most important group in all 3 studies available. In the earliest study, crustaceans comprised the second most important group (11%). Anchovy were important in 1968–1969 (17%) and 2005–2006 (67%) but were not significant in 1949–1950. Notably, sardine was the second most important component of diet (15%) in this region during the 2005–2006 study, and hake were not present.
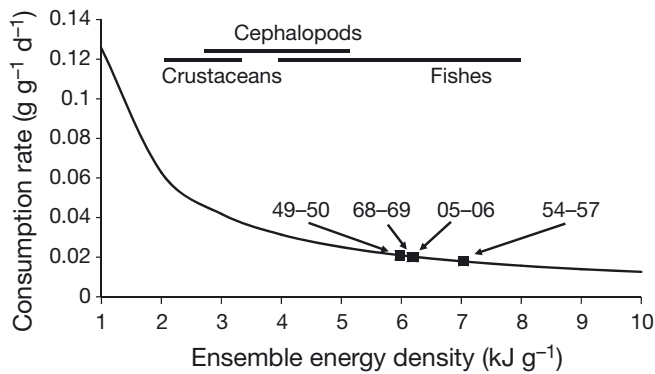
Fig. 2. *Thunnus alalunga*. Influence of prey energy density (*ED*) on steady-state daily consumption rates of juvenile albacore. Rates were calculated according to Essington (2003) for age-3 albacore (mean weight 5.9 kg). The ensemble energy density (a weighted mean, ED_n) calculated for the 4 diet studies is marked. The range of *ED* values for prey species is shown for reference

ED_n estimated for the 4 studies was comparable, ranging from 6.0 to 7.0 kJ g^{-1} with low variability (Table 5). A juvenile albacore feeding in the CCS consumed between 18.0 to 21.0 g of prey per kg of body mass per day (C_B). Using an age-3 albacore (5.9 kg, 65 cm) as an example, this estimate of C_B translates into a steady-state energetic intake of between 106.2 and 123.9 g per albacore per day.

The mean annual *Q:B* was consistent between studies and ranged from 6.7 to 8.0 yr^{-1} (Fig. 3). The greatest variability occurred early in the time series when 3 diet studies were close in time. The studies in the late 1960s and 2005–2006 had similar ED_n values and the *Q:B* line is relatively flat through this period. Given the wide temporal spacing between these studies, it is impossible to know whether changes in diet (and hence changes in *Q:B*) were gradual or sudden; the weighting function used here assumed the former.

DISCUSSION

Spatial and temporal patterns

This study presents observational evidence that only 2 or 3 species of fish were important prey items for juvenile albacore in the CCS. Based on 4 diet studies, juvenile albacore obtain greater than 60% of their total energetic intake from 2 species of coastal pelagic fish: Northern anchovy *Engraulis mordax* and Pacific saury *Cololabis saira*. These results have been consistent over 50 yr and are corroborated by other studies of juvenile albacore (not analyzed here due to scope) which found saury and anchovy were dominant prey off Vancouver Island during 1941–1947 (Hart et al.

Table 4. *Thunnus alalunga*. Energetic contribution (*E*, %) of prey to diet of juvenile albacore in the California Current. Studies are: McHugh (1952), Iversen (1962), Pinkas et al. (1971), and Glaser (this study). Columns are years data were collected. Prey categories represent taxa in common to the 4 studies, in general distinguishing any species category accounting for ≥1% of *E*

Prey category	1949–1950	1954–1957	1968–1969	2005–2006
Northern				
Amphipods	–	–	0.0	0.7
Pleuroncodes planipes	–	–	0.0	0.0
Euphausiids	–	–	0.0	14.1
Crustaceans (unid.)	–	–	3.9	17.4
Cephalopods	–	–	14.3	4.7
Cololabis saira	–	–	8.1	0.7
Engraulis mordax	–	–	67.8	29.8
Sardinops sagax	–	–	0.0	4.3
Sebastes spp.	–	–	0.1	4.3
Merluccius productus	–	–	0.0	20.9
Trachurus symmetricus	–	–	0.0	0.0
Myctophidae	–	–	5.4	0.5
Paralepididae	–	–	0.1	0.0
Vinciguerria lucetia	–	–	0.0	0.0
Fishes (other)	–	–	0.3	2.5
Central				
Amphipods	0.9	0.1	0.3	1.2
Pleuroncodes planipes	0.0	0.0	0.0	0.0
Euphausiids	6.5	0.4	2.6	0.4
Crustaceans (unid.)	3.4	0.0	0.1	0.3
Cephalopods	11.6	10.3	63.3	18.9
Cololabis saira	22.3	85.1	17.2	30.5
Engraulis mordax	37.6	0.0	2.1	1.5
Sardinops sagax	0.0	0.0	0.0	0.5
Sebastes spp.	1.5	0.0	1.1	2.8
Merluccius productus	0.0	0.0	0.0	37.6
Trachurus symmetricus	0.0	0.0	0.0	0.0
Myctophidae	1.2	1.1	8.6	0.6
Paralepididae	0.0	0.0	0.4	0.0
Vinciguerria lucetia	0.0	0.0	0.0	0.0
Fishes (other)	15.0	3.0	4.3	5.7
Southern				
Amphipods	1.4	–	0.0	0.5
Pleuroncodes planipes	5.8	–	0.3	0.0
Euphausiids	3.5	–	0.1	0.1
Crustaceans (unid.)	0.4	–	0.0	3.5
Cephalopods	9.0	–	18.5	11.4
Cololabis saira	61.4	–	59.1	0.4
Engraulis mordax	2.8	–	17.1	67.4
Sardinops sagax	0.0	–	0.0	15.3
Sebastes spp.	0.9	–	0.4	0.0
Merluccius productus	1.8	–	0.0	0.0
Trachurus symmetricus	0.0	–	0.1	0.0
Myctophidae	0.7	–	0.6	0.0
Paralepididae	0.0	–	0.1	0.0
Vinciguerria lucetia	3.3	–	0.0	0.0
Fishes (other)	8.9	–	3.8	1.5

1948), saury were the dominant prey off Oregon during 1970 (Pearcy 1973), and juvenile anchovy were the dominant prey off Southern California during 1983 (Bernard et al. 1985). Finally, cephalopods were an

Table 5. *Thunnus alalunga.* Estimates of diet-derived bioenergetic parameters (mean ± SD**)** for juvenile albacore from 4 diet studies. Values were calculated from aggregated study data (not separated into regions). The ensemble*ED* is the weighted mean energy density value. Consumption rate and daily demand (prey biomass consumed at steady-state) were calculated using a bioenergetics model (Essington 2003) for an age-3 albacore of mean weight (5.9 kg)

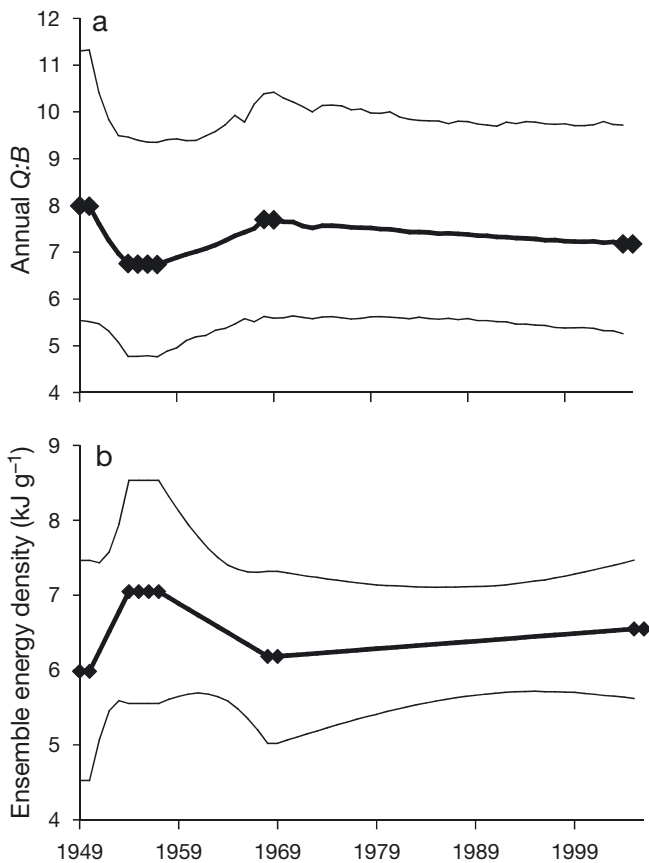| Data collection	Ensemble ED (kJ g^{-1})	Consumption (g g^{-1} d^{-1})	Demand (g albacore^{-1} d^{-1})	Source
1949–1950	6.0 ± 0.9	0.021 ± 0.005	124.5 ± 28.8	McHugh (1952)
1954–1957	7.0 ± 0.9	0.018 ± 0.004	105.7 ± 20.9	Iversen (1962)
1968–1969	6.2 ± 0.7	0.020 ± 0.004	120.4 ± 26.0	Pinkas et al. (1971)
2005–2006	6.2 ± 0.9	0.020 ± 0.004	119.6 ± 24.7	This study

Fig. 3. *Thunnus alalunga.* Consumption metrics for juvenile albacore in the California Current System calculated from a bioenergetics model (Essington 2003). (◆) years when data from a diet study parameterized the model; years between studies were extrapolated. The 90% confidence intervals (thin line) were obtained from a Monte Carlo simulation. (a) Annual consumption to biomass ratio (*Q:B*). (b) Ensemble energy density (ED_n) of prey suite

important component of albacore diet in all 3 regions investigated.

There have been important spatial and temporal exceptions to these general patterns. Saury occurred in much lower proportions in juvenile albacore diet in the northern region (note that Pearcy 1973 found significant amounts of saury in diet in this region, but data were collected over only 6 d and from a limited spatial area). Crustaceans were significant only in the northern region in one study (2005–2006). Anchovy were always important in the northern region, but were only found in large quantities in the central region during 1954–1957 when they were not found in the southern region. For all other studies, including one sampling trip in 1983 (Bernard et al. 1985), anchovy were important in the southern region. Hake were an important component in the northern and central regions during 2005–2006, but were not documented in notable quantities in other studies. Finally, sardine were important in the southern region (and occurred in the northern region) during 2005–2006, but not elsewhere.

It has long been hypothesized (Laurs & Lynn 1991), and more recently demonstrated (Barr 2009), that the juvenile albacore population in the CCS is made up of northern and southern subpopulations, split around 40° N, with differing migration routes and possibly growth rates. In diet, saury were less abundant north of 44° N, and hake were absent south of 33° N. Otherwise, there are no strong regional patterns to diet that could differentially affect these subpopulations.

Juvenile albacore prey almost exclusively on YOY fishes, with the exception of predation on adult saury. Data collected in 2005–2006 quantify these results, while the discussions of prey sizes in historical studies corroborate them. Comments by Hart et al. (1948), Iversen (1962), and Pinkas et al. (1971) suggested fish prey were of juvenile sizes. Measurements of individual volume (McHugh 1952) and length (Bernard et al. 1985) demonstrated that fact. Finally, albacore also consumed juvenile (but not adult) Japanese anchovy *Engraulis japonicus* in the Western Pacific Ocean (Watanabe et al. 2004).

Prey preferences: anchovy over sardine

The CCS contains many species of forage fish: anchovy, saury, hake, sardine, jack mackerel *Trachurus symmetricus*, and Pacific mackerel *Scomber japonicus*. Jack mackerel and Pacific mackerel have never been found in significant quantities as prey of albacore, and sardine were only important in the southern region during 2005–2006. These results belie the conventional wisdom that albacore are true generalists (Pinkas et al. 1971, Watanabe et al. 2004, Consoli et al.

2008) and suggest that albacore have diet preferences. Without concurrently quantifying relative abundance of prey, in particular of YOY fishes, I cannot demonstrate that juvenile albacore are selectively consuming anchovy, saury, and sometimes hake over sardine and mackerel. Nevertheless, observational evidence suggests that juvenile albacore are not consuming prey in proportion to their relative abundance at the scale of the California Current ecosystem.

Continuous long-term biomass time series for YOY fishes are available for hake and Pacific mackerel (1966 to present and 1929 to present, respectively). Sardine time series contain a gap from 1964 to 1981, anchovy data span 1963 to 1994 and are limited to the southern subpopulation, and jack mackerel and saury are not assessed (Fig. 4). Consequently, the 2 primary prey species are too data-poor to make conclusive statements about preference or selectivity. However, Fig. 4 does support some conjecture. When time series coincide, YOY Pacific mackerel were considerably less abundant than sardine, anchovy, or hake, and they did not appear in albacore diet. During 1968–1969 (Pinkas et al. 1971), abundance of YOY anchovy and hake were comparable; sardine were not assessed but were

assumed to have been far less abundant (Jacobson & MacCall 1995). By the 2005–2006 study, anchovy assessments were no longer carried out. Sardine recruitment has been high over the past 2 decades, and YOY sardine were more abundant than YOY hake and likely were more abundant than anchovy during 2005 and 2006 (Hill et al. 2007). Thus, one might expect sardine to be more common in diet recently if relative abundance in the CCS were the dominant predictor of diet habits.

These 4 diet studies failed to find sardine in significant quantities, with the important exception of the southern region during 2005–2006. Thus, while it is assumed that sardine were higher in abundance than anchovy in the CCS during this period (Hill et al. 2007), the diet of albacore did not reflect a major shift in prey species from anchovy to sardine. However, the finding of significant predation on sardine in the southern CCS indicates that, during periods of higher sardine abundance, albacore can and do consume them. Sardine recruitment during 2005 and 2006 was higher than during the 1950s and 1960s (when past diet studies were conducted), but recruitment was lower on average than over the past decade (Hill et al. 2007, Fig. 4). Had diet data been col-
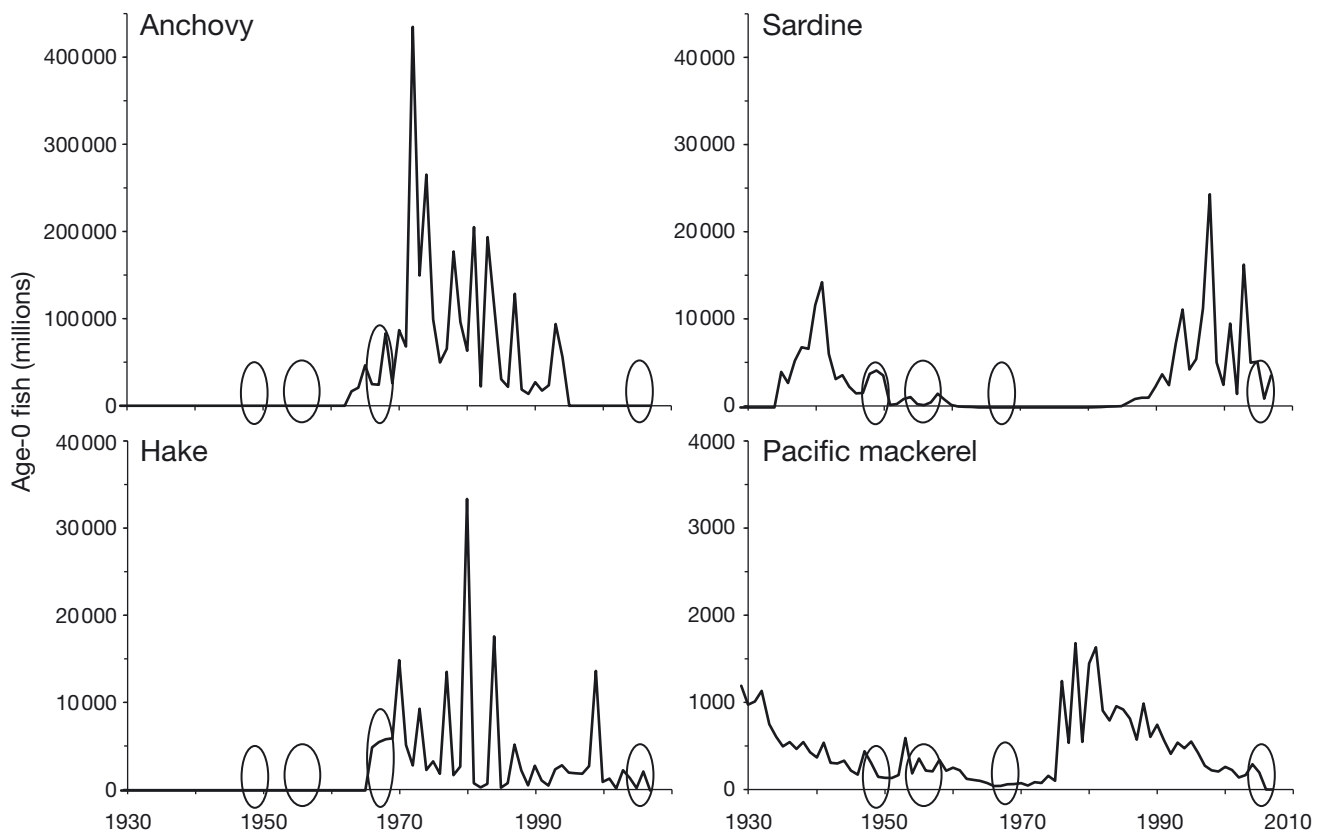

Fig. 4. Time series of abundance for age-0 (recruitment) anchovy (Jacobson et al. 1995), sardine (Jacobson & MacCall 1995, Hill et al. 2007), hake (Helser et al. 2006), and Pacific mackerel (Hill & Crone 2005). Diet study years are circled. Note the different y-axes. For anchovy, biomass was converted to numbers based on a mean weight of age-0 anchovy of 10 g (Methot 1989)

lected during years of high sardine recruitment (e.g. 1998 or 2003), predation on juvenile sardine may have rivaled or exceeded predation on anchovy.

Several important caveats to these conjectures must be made. First, the population estimates from which Fig. 4 was constructed are age-based stock assessments associated with high uncertainty in mortality rates and thus in recruitment biomass (see assessment reports cited). Second, the time series describe populations or subpopulations that do not fully overlap each other or span the CCS. Anchovy data are for the central substock residing south of 35° N (Jacobson et al. 1995a), and anchovy biomass estimates for the northern substock do not exist. Furthermore, with a possible northward shift in hake spawning grounds (Phillips et al. 2007), the hake population is unlikely to overlap the southern anchovy population. Finally, adult sardine and mackerel tend to occupy waters further offshore than hake or anchovy (Agostini et al. 2006, Checkley et al. 2000). Consequently, inferences must be made carefully; data simply are not available to conclude whether active preferences in albacore diet exist.

Thermal preferences drive predation

Optimal foraging theory provides several hypotheses for why albacore may consume anchovy, saury, and (recently) hake instead of sardine (MacArthur & Pianka 1966, 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 difference in swimming speed of sardine and anchovy (van der Lingen 1995). Second, sardine could be of inferior energetic quality (Emlen 1966); however, sardine is considerably higher in *ED* than hake, slightly higher than anchovy, and only slightly lower than saury (Table 3). Third, albacore may not co-exist with sardine at mesoscales or during feeding events.

Adult sardine live further offshore than anchovy, saury, or juvenile hake, and the species have distinct spawning regions (Checkley et al. 2000). Sardine spawn in warmer (13° to 25°C) offshore waters (Lluch-Belda et al. 1991) 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 [respectively, 11.5 to 16.5°C (Lluch-Belda et al. 1991) and 13 to 18°C (Kurita 2006)]. Newly spawned hake are found in nearshore waters during spring and summer (Saunders & McFarlane 1997). The optimal thermal range for albacore is 16 to 19°C, and optimal foraging models predict albacore will hunt in waters just above the threshold at which thermal stress accu-

mulates (Kirby et al. 2000). Under conditions of uniform prey, albacore hunt in cold, nearshore waters to the exclusion of warmer, offshore waters (Kirby et al. 2000). Under conditions of variable prey abundance and energy densities, albacore are predicted to occupy warmer offshore waters when satiated, but the majority of daylight hours would be spent foraging in colder nearshore waters. This study empirically supports the model predictions of Kirby et al. (2000): juvenile albacore prefer hunting in the habitat of YOY anchovy, saury, and hake to that of sardine, even during periods of high sardine abundance.

It is possible that data collection did not adequately sample sardine habitat, especially given that sardine live further offshore than anchovy, and fishing vessels have economic incentives to stay as close to shore as possible. However, sampling locations did occur within the spatial extent of sardine spawning habitat described by egg distributions (Checkley et al. 2000) in the southern CCS, and egg, larval, and adult distributions in the northern CCS (Emmett et al. 2005).

These results raise an interesting question regarding sardine and anchovy population dynamics. Over the past century, the populations of these 2 coastal pelagic species have fluctuated asynchronously (Soutar & Isaacs 1974, Schwartzlose et al. 1999). 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 2 species be considered competitors?

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, Agostini et al. 2006, Phillips et al. 2007). Hake have the highest degree of spatial patchiness in egg and larval distribution of any fish in the CCS (Lo et al. 1997) and the geographic center of hake spawning can move annually (Horne & Smith 1997, Phillips et al. 2007). Abundance is also highly patchy in time, being 3 to 10 times greater in outstanding years of recruitment than in an average year (Horne & Smith 1997). None of the major spikes in hake recruitment co-occurred with the 3 historical diet studies. The absence of hake prey in those studies could be due to a temporal mis-match in hake spawning and albacore predation, or a temporal or spatial mis-match in hake presence and stomach sampling. Furthermore, the finding of hake in diet in the central and northern regions during 2005–2006 is corroborated by high relative values of hake catch per unit effort (CPUE) during 2003 to 2006 compared to the previous 4 decades (although, strikingly, CPUE was lowest during 2005–2006) (Phillips et al. 2007).

Reconceptualizing albacore foraging

This study reconceptualizes historical diet studies by translating numeric gut content data into the currency of energetics. 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 a biologically meaningful quantity. In this light, 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 1 of 4 studies found *E* greater than 3%. Likewise, cephalopods were 30% of energetic intake during the 1968–1969 study, but elsewhere they contributed less than 12%. If only species richness of diet is considered, the 10 species of cephalopods consumed make diet appear more diverse. While the importance of weak predator–prey interactions should not be ignored (McCann et al. 1998), research efforts could focus on a more narrow range of prey.

This refined view of juvenile albacore diet habits suggests that their classification as generalist predators should be qualified. Undoubtedly juvenile 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 the entire CCS as an aggregated food web, as many ecosystem models do (e.g. Field et al. 2006), albacore do not consume some species (namely, sardine) in proportion to abundance in the environment. However, when smaller spatial scales are considered, albacore consume prey they encounter, possibly in proportion to the rate of encounter.

Importance of energy density and diet stability

Accounting for variability in prey *ED* is important for accurate modeling of predator consumption rates (Stewart & Binkowski 1986). *ED* values can differ significantly within a species, depending primarily on reproductive status (Kitts 2004) and size (Ciannelli et al. 2002). However, other studies have shown weak or no relationships between size and *ED* (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 for interpreting variability in *ED* comes from studies that focus on juvenile fishes (Arrhenius & Hansson 1996, Ciannelli et al. 2002, Tirelli et al. 2006). Among juvenile fishes, *ED* increases linearly with growth, but the intraspecies variability at any given time is low. Thus, when focusing on a subpopulation of predators in a given region and season, interspecies variability in prey *ED* is more important than intraspecies variability due to size or spawning status.

The choice of ED_n used in a bioenergetics model can have a significant impact on calculated consumption rates for certain types of predators (Fig. 2). There is a geometrically decreasing relationship between the biomass a predator must consume to maintain stable energetic intake and the ED_n of prey. The steepest portion of the curve in Fig. 2 demonstrates the importance of calculating ED_n using weighted means. For example, if albacore diet were 75% *Pleuroncodes planipes* (a pelagic decapod) and 25% *Engraulis mordax*, ED_n would be 3.9 kJ g^{-1} and an age-3 albacore would need to consume 190.5 g d^{-1}, or 3.2% of its body weight, to maintain stable energetic intake or growth. However, if diet were 25% *P. planipes* and 75% *E. mordax*, ED_n would be 5.8 kJ g^{-1} and that same albacore would need to consume only 128.8 g d^{-1}, or 2.2% of body weight. Furthermore, the arithmetic (non-weighted) mean of the individual *ED* values is 4.8 kJ g^{-1}, inaccurately quantifying consumption of 154.8 g d^{-1}. When scaled to the population level, as in 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 3 main prey items of albacore vary in *ED*, the range of values lies on the asymptotic portion of the curve in Fig. 2 and energetic tradeoffs between prey items may be of small consequence to daily biomass consumption. Hypothetically, a 25% difference in daily demand could impact growth rates. However, given the proportional composition of species in albacore diet, the ED_n values are strikingly similar. This suggests that albacore maintain a stable base of prey—from an energetics standpoint. Finally, it should be noted that fish are unlikely to adjust biomass consumption while holding growth constant, or to change growth rate while holding consumption rates constant. More likely, there is plasticity in both rates and the overall impact would be a less pronounced adjustment to both.

This is not to neglect the possibility of detrimental shifts in prey quality in the future, nor to discount the importance of variable ED_n in other types of predators. Changes in relative ED 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. 1998, Kitts 2004). If the suite of prey available to juvenile albacore in the CCS were to change significantly, particularly if anchovy or saury were replaced by lower energy prey, juvenile albacore would either switch prey, increase rates of biomass consumption, or face declining growth rates. In general, the type of predator is a critical consideration when assessing variable prey ED. For predators that consume primarily crustaceans or other lowED prey (the steep portion of the curve in Fig. 2), interspecies variability can lead to dramatic differences in daily rates. However, for piscivores or predators that consume high ED prey (the flat portion of the curve in Fig. 2), the interspecies differences may contribute much less to overall variability in growth rates or population dynamics.

The low variability in ED_n translates into equally stable $Q:B$. The value for $Q:B$ calculated here (mean 7.3) is lower than the 13.4 calculated by Essington (2003), but his model used a mean ED value of 5.0 and applied to the full North Pacific population of albacore (adults significantly increase the ratio). 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. As ecosystem models begin to incorporate measurements of uncertainty, field-verified data such as these are increasingly needed (Christensen & Walters 2004).

Results from the past 50 yr should offer some reassurance that diet, biomass consumption and ED_n values for juvenile albacore are stable, even during periods of widespread change in the CCS (e.g. Hare & Mantua 2000, McGowan et al. 2003). Lavaniegos & Ohman (2007) showed that carbon biomass of zooplankton in the CCS has remained stable throughout the oceanic changes evident during 1976 to 1977. Despite changes in species composition of zooplankton since the mid-1950s (Ohman & Venrick 2003), the total biomass of zooplankton has remained stable. Although zooplankton are not a major source of energy to albacore, stable carbon biomass estimates at these lower trophic levels suggest that the overall food web has redundancies.

This study supports recent calls (Link 2007) to expand data collection for species that are not currently assessed. Heavy fishing pressure has been linked to serial depletion of top predators: when one commercial species is fished to low abundances, fisheries have economic incentives to switch target species and changes

to the food web result (Pauly et al. 2002, Link 2007). Newly fished species are rarely as well studied as historically profitable fisheries, an alarming aspect of serial depletion (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, make it impossible to know whether the recent increase in hake in albacore diet is a result of fewer anchovy or saury in the environment. In the CCS, human catches of anchovy and saury are low and zero, respectively, suggesting juvenile 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 continue in order to sustain world protein demand (Pauly et al. 2002). Collection of more thorough data on saury and resumption of stock assessments of anchovy may be prudent undertakings now, before these stocks face new 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.

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