



Do albacore exert top-down pressure on northern anchovy? Estimating anchovy mortality as a result of predation by juvenile north pacific albacore in the California current system

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ABSTRACT

Quantifying the mortality of marine fishes is important for understanding spawner–recruit relationships, predicting year-class strength, and improving fishery stock assessment models. There is increasing evidence that pelagic predators can exert a top-down influence on prey, especially during critical early life-history stages. The objective of this study was to quantify predation by North Pacific albacore on Northern anchovy in the California current system (CCS). I estimated the abundance of juvenile albacore in the CCS from 1966–2005 using stock assessment models and spatially explicit catch-per-unit-effort time series. Anchovy abundance (1966–93), both recruitment and total biomass, was obtained from a stock assessment model. Annual rates of anchovy consumption by albacore were calculated using diet studies of albacore in the CCS, an age-structured bioenergetics model, and regional estimates of albacore abundance. The range of estimates was large: albacore may remove from less than 1% to over 17% of anchovy pre-recruitment biomass annually. Relationships between predation and recruitment biomass were consistent with expectations from top-down effects, but further study is required. This is the first attempt to quantify a specific source of mortality on anchovy recruits and to demonstrate potential top-down effects of predation on anchovy.

Key words: albacore, anchovy, California current system, predation, recruitment mortality, top-down regulation

INTRODUCTION

The seminal observation by Hjort (1914) that mortality in early life stages of marine fishes significantly impacts the future abundance 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 and Roughgarden, 1999), affect the mortality rates of larval and juvenile fishes. Understanding sources and variability of early mortality is critical for 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 although 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 and Holt, 1957; Quinn and Deriso, 1999).

The balance between top-down and bottom-up regulation of populations, and whether one force dominates the other, determines the organization of communities (Hunter and Price, 1992; Roughgarden *et al.*, 1994; Cury *et al.*, 2000; Menge, 2000; Shurin *et al.*, 2002; Munch *et al.*, 2005). Top-down effects of predation can alter the diversity of ecosystems (Paine, 1974), realized niches (Connell, 1961), and the relative 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 drivers, 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

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(Hunter and Price, 1992; Roughgarden *et al.*, 1994; Munch *et al.*, 2005).

Most of our understanding of population regulation in marine communities has been generated by studies in intertidal zones because the 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 incredibly difficult. As a result, pelagic ecology has moved towards ecosystem-level models that trace flows of mass and energy as a means of quantifying species interactions (e.g., McCann *et al.*, 1998; Cury *et al.*, 2000; Christensen and Walters, 2004). These models are important tools for investigating ecosystem responses to fishing pressure and natural mortality, changes in species diversity and abundance, and changes in productivity through scenario-based simulations. However, the large numbers of parameters and high degrees of taxonomic aggregation in these models can make species-level interactions more opaque, and isolating one predator–prey relationship in such models can be suspect (Cox *et al.*, 2002).

Given limitations imposed by 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 modeling 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 a significant 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 to verify the hypotheses generated by complex, highly parameterized ecosystem models.

Here, I investigate the relationship between North Pacific albacore (*Thunnus alalunga*) 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 summer and fall months as they migrate through the CCS. North Pacific albacore live throughout the North Pacific and do not

mix with populations of albacore in other ocean basins. Although the albacore population is managed as one stock, there is evidence that subpopulations exist with varying growth rates (Laurs, 1983), migration patterns (Otsu and Uchida, 1959; Laurs and Lynn, 1991; Kimura *et al.*, 1997), and feeding habits (Pinkas *et al.*, 1971; Glaser, 2010). Adult albacore (aged 5 yr and older) spawn in the tropical and subtropical central North Pacific (Otsu and Uchida, 1959) and are distributed throughout the central gyre, where they are harvested by distant-water longline fisheries (Stocker, 2005). Juvenile albacore (aged 1–4 yr) migrate into CCS waters in late spring, at which point they are harvested by commercial troll and recreational pole fisheries of the Eastern Pacific. In late fall, members of this juvenile subpopulation migrate either to the western North Pacific, in which they might be harvested by pole and line, gillnet, and longline fisheries of Japan, Korea, and Taiwan, or south into coastal waters of central Baja Mexico (Otsu and Uchida, 1962; Ichinokawa *et al.*, 2008). 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 a dominant prey item of juvenile albacore during the past 40 yr (Pinkas *et al.*, 1971; Bernard *et al.*, 1985; Glaser, 2010). 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 in the CCS: 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 southern Baja; and a stock confined to the Gulf of California (Schwartzlose *et al.*, 1999). Their populations undergo large swings in abundance that can cause range expansions or contractions. Over the past century, anchovy have fluctuated asynchronously with another pelagic forage species, Pacific sardine (*Sardinops sagax*) (Soutar and 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 ocean circulation (Schwartzlose *et al.*, 1999), and food availability (Schwartzlose *et al.*, 1999; Rykaczewski and Checkley, 2008). 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 population dynamics.

The objective of this study is to quantify the impact of predation by albacore on Northern anchovy in the CCS. First, I estimate the abundance of juvenile North Pacific albacore in three regions of the CCS during 1966–2005. Next, I quantify the annual consumption of anchovy by juvenile albacore in the CCS, and estimate the contribution of predation to total mortality on the central stock of Northern anchovy in the southern CCS. Finally, I test the hypothesis that albacore exert top-down pressure on anchovy.

METHODS

Data

Catch (number of fish) and effort (number of boat-days) were collected from voluntarily submitted log-books from the U.S. commercial troll fishery based in the CCS. Data were provided by the Southwest Fisheries Science Center aggregated to $1^\circ \times 1^\circ \times$ month cells and cover the period 1966–2005 for a total of 10 209 cells with non-zero effort. Annual commercial catch data for all North Pacific albacore fisheries also were obtained from the SWFSC. Population abundance estimates for North Pacific albacore were taken from an age-based stock assessment model (virtual population analysis, model scenario D1) produced by the International Scientific Committee Albacore Working Group (ISC 2006). Anchovy abundance estimates were available only for the central stock of Northern anchovy during 1963–94 (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 anchovy recruitment biomass (age 0), spawning stock biomass, and total stock biomass. Albacore diet data were obtained from 371 stomachs collected in the CCS during June–October 2005 and 2006 (Glaser, 2010), and from 900 stomachs collected in the CCS during 1968 and 1969 as reported in Pinkas *et al.* (1971).

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 assumption behind

the low estimate is self-evident: if an albacore was caught in the CCS, it was residing in the CCS at that time.

The second data set, Pacific-wide, age-structured estimates from a stock assessment model (ISC 2006), represents a high estimate of albacore abundance (hereafter high estimate). The high estimate relies on the key assumption that patterns of temporal variability in the subpopulation of albacore in the CCS can be described by the variability in Pacific-wide stock assessment estimates of all albacore in the North Pacific aged 2–4 yr. This assumption is based on the following line of reasoning. First, 99% of albacore landed in the CCS are juveniles (Fig. 1). Secondly, the migration patterns of juveniles, described above, show juvenile albacore in the CCS during 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). Thirdly, the U.S. troll and Japanese pole and line fisheries account for 80–90% of all juvenile albacore landings in the North Pacific (Fig. 1). Fourthly, although the units of effort are different in the two fisheries, their standardized catch-per-unit-effort (CPUE) time series, indices of relative abundance, are strongly correlated ($P < 0.005$; Fig. 2). This coherence suggests the albacore landed by both fisheries have similar dynamics and the patterns in CPUE likely reflect changes to the full subpopulation of juveniles.

Consequently, I assumed that the patterns of variability in the CCS subpopulation are the same as Pacific-wide patterns of variability in juveniles and combined abundances of albacore aged 2, 3 and 4 yr estimated by the ISC stock assessment model. This high estimate therefore assumes all juveniles aged 2, 3 and 4 yr are present in the CCS. This assumption is unlikely: tagging studies demonstrate an annual net migration of albacore from east to west and a significant subpopulation residing in the Kuroshio Current that never enters the CCS (Ichinokawa *et al.*, 2008). This estimate therefore represents an extreme upper bound on abundance.

To refine this abundance envelope, I scaled both estimates by a constant percentage. The mean fishing mortality rate imposed on North Pacific albacore is $F = 0.75$ (ISC 2006), equal to 53% of the population annually. The low estimate (based on catch) was therefore scaled up by 1.89. There are no reliable estimates for the percentage of the juvenile population living in the western versus eastern North Pacific. The ratio of landings by the Japanese pole and line fishery

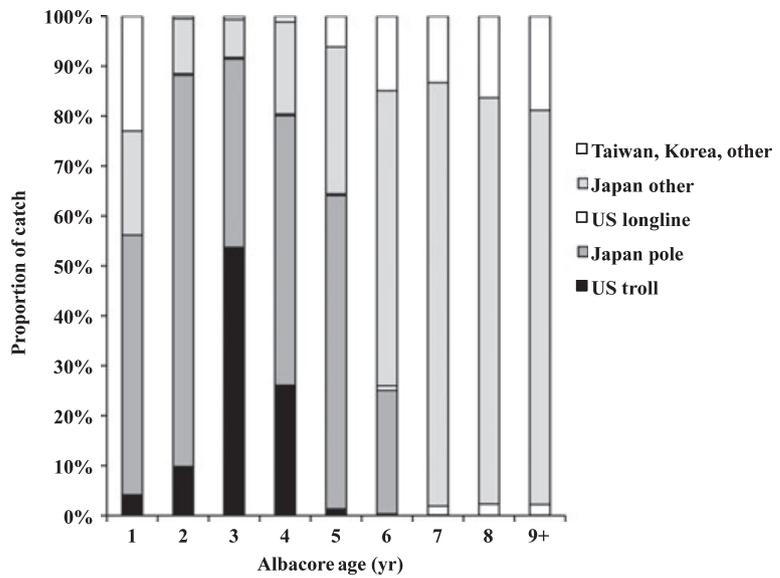


Figure 1. Age composition of landings in major fisheries for albacore in the North Pacific Ocean. The Japanese pole fishery and U.S. troll fishery harvest the majority of juvenile (≤ 4 yr of age) albacore that are landed. Data are aggregated from 1966–2005 for all fisheries that report data to the ISC.

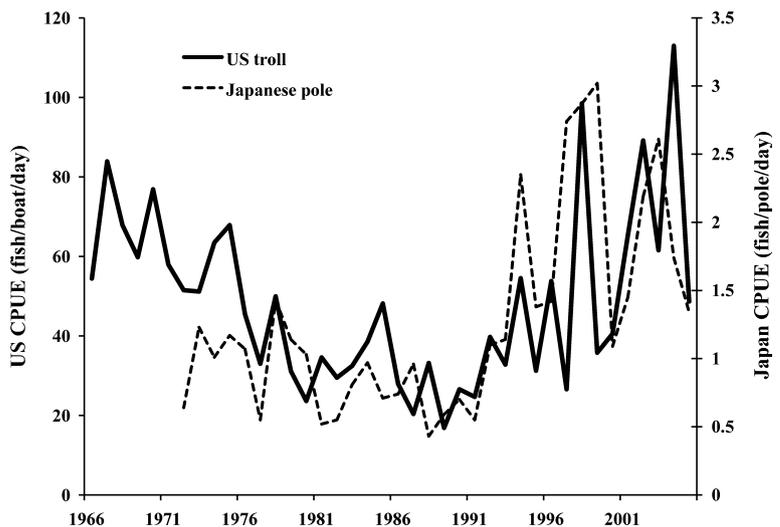


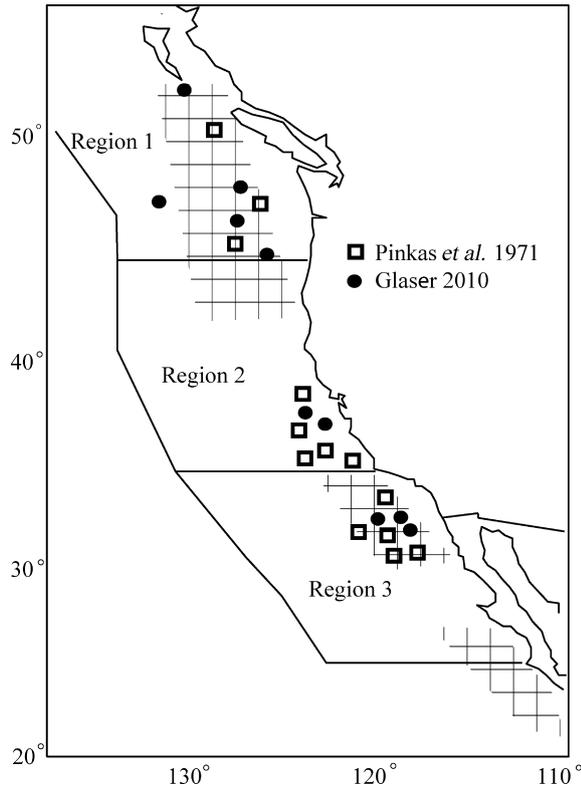
Figure 2. Indices of relative abundance of albacore caught by two major fisheries. Units are not directly comparable, but time series are correlated through time (Pearson sample correlation coefficient, $r = 0.486$, $P < 0.005$).

(Western Pacific) to the that of the U.S. troll fishery (Eastern Pacific) for age classes 2–4 is 3 : 2. If units of effort for the two fisheries were the same, the ratio of CPUE for the two fisheries could be used directly. In lieu of this, and based on the best information of migration routes for juveniles in the North Pacific (Ichinokawa *et al.*, 2008), the high estimate was scaled down by 40%, representing the fraction of all juveniles landed in the CCS.

Both albacore and anchovy are not evenly distributed throughout the CCS and, importantly, predation on anchovy by albacore varies spatially (Glaser, 2010). I further divided the juvenile albacore subpopulation into three regions of the CCS: Region 1 (44°–50°N latitude), Region 2 (34°–43°59'N) and Region 3 (25°–33°59'N) (Fig. 3). Each region extends 10° from

the North American coastline, approximating the mean boundaries of the CCS (Hickey, 1998). The definition of these regions reflected an attempt to balance the limitations of the three relevant data sets: (i) the collection sites of stomach samples from Pinkas *et al.* (1971) and Glaser (2010), (ii) the boundaries of the CCS anchovy stocks, and (iii) the distribution of 1° × 1° albacore CPUE cells. The boundaries of Region 3 were fairly straightforward. Pinkas *et al.* (1971) defined the region south of Point Conception as one region of albacore diet, it is a known biogeographic region (the Southern California Bight) and the vast majority of the central anchovy stock resides between Point Conception in southern California and Point Descanso in northern Baja (Jacobson *et al.*, 1994; Schwartzlose *et al.*, 1999). The choice of latitudinal

Figure 3. Regions used to partition albacore abundance in the California current system. Symbols denote areas of sampling for diet habits of albacore. Cross-hatching denotes approximate distribution of the northern, central and southern stocks of anchovy.



boundary between Regions 1 and 2 balanced the occurrence of stomach sampling, the distribution of the northern anchovy stock (which is less well known than that of the central stock), and availability of CPUE data.

The relative abundance of albacore in these three regions was calculated by comparing standardized regional CPUE time series. In the creation of all three regions, it was desirable to assign CPUE cells as evenly as possible so regression tree standardization could draw from approximately equal sample sizes. The standardized indices were treated as proportions and multiplied by the total abundance of albacore in the CCS to calculate regional abundances.

Standardizing CPUE time series

Catch (number of albacore) and effort (number of boat-days) in each $1^\circ \times 1^\circ \times$ month cell were used to calculate a standardized regional time series of 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 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 and 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. Secondly, 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 used less frequently than GLMs but has been shown to be more parsimonious, results in significantly fewer parameters, and accounts for non-linear relationships between variables (Watters and 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 (mean catch per effort in each group) associated with a given combination of predictor variables.

Random forest (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, 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.

In all, 500 randomizations were run for each region and the mean square errors for the final trees were 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 CPUE index was treated as 100% of estimated annual abundance, and other monthly estimates were scaled proportionally.

Estimating albacore consumption of anchovy

A bioenergetics model (Essington, 2003; Glaser, 2010) was used to calculate albacore consumption rates of anchovy on a daily basis. Consumption rate is a function of albacore age and the energy density of available prey. Albacore daily consumption was estimated using an ensemble prey energy density of 6.2 kJ g^{-1} , the weighted mean value calculated from albacore diet in studies done in 1968–69 (Pinkas *et al.*, 1971) and 2005–06 (Glaser, 2010). Consumption rate was further refined by the age-structure of the sub-population in the CCS. 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:

$$B_a = \sum_{r=1}^3 \sum_{m=1}^{12} B_{A,r,m} \times C \times \% \text{diet}_r \times \text{days}_m \quad (1)$$

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

The percentage of diet comprised of anchovy varied between two studies that flanked the albacore abundance time series and between the three regions (Pinkas *et al.*, 1971; Glaser, 2010). The percentage of anchovy in diet in a given year was linearly weighted based on the proximity in time to the two diet studies. Diet data were collected in 1968, 1969, 2005 and 2006. From 1968/1969 to 2005/2006, anchovy biomass in albacore diet varied from 74.2 to 23% in Region 1, from 3.8 to 1% in Region 2, and from 28.5 to 67% in Region 3.

In the natural environment (i.e., not during baited fishing events), albacore consume recently spawned anchovy (Bernard *et al.*, 1985; this study). Monthly variability in the length of anchovy consumed was

analyzed using measurements from albacore gut contents collected in 2005 and 2006 ($N = 421$ anchovy). 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 1963–94 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 estimated as a parameter in the model. Jacobson *et al.* (1995) estimated the central stock of Northern anchovy only, which coincides with Region 3 in this study (Fig. 3). Using estimates of albacore abundance and consumption in Region 3, I calculated the proportion of anchovy recruitment biomass consumed annually. I estimated the contribution of predation to anchovy mortality according to

$$M_t = (Z \times B_{c,t}) / B_t \times (1 - e^{-Z}) \quad (2)$$

where M_t is the instantaneous mortality at time t imposed by albacore, Z is total mortality (here assumed to be 0.8 per yr after Jacobson *et al.*, 1994), $B_{c,t}$ is the biomass of anchovy consumed by albacore at time t , and B_t is the biomass of anchovy in the environment. Because predation is exclusively on newly spawned anchovy, 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 predation and anchovy recruitment, and between predation and total anchovy biomass, in Region 3. Analysis was performed on normalized (mean = 0, SD 1.0) first differences ($x_t - x_{t-1}$) to remove serial autocorrelation. Thus, the analysis tests for correlation between year-to-year changes. Borrowing generalizations gleaned from experiments in intertidal zones, I expected an inverse relationship between predation and anchovy recruitment in the following year. I therefore tested both contemporary values, and predation values lagged 1 yr. To test for possible effects in the adult population, I lagged predation by 2 and 3 yr. If predation on recruitment biomass has a pronounced impact on the full anchovy population, I expected to see an effect on the adult population further in the future as cohorts age.

RESULTS

Two estimates of albacore population size in the CCS 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) (Fig. 4). The 1970s and 1990s were periods of high catch, whereas the 1980s had much lower catches. The high estimate, derived from stock assessment models of age groups 2–4, 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 most numerous in Region 1 and least numerous in Region 3 (Fig. 5). The standardized indices of abundance for the three regions demonstrated the same patterns as the stock assessment 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 estimates of

Pacific-wide abundance. The CPUE for the Region 3 was fairly stable through time, whereas Region 1 had pronounced changes beginning in the early 1970s and around 2001. The regression tree model produced acceptable fits to data (Region 1 $R^2 = 0.37$, Region 2 $R^2 = 0.37$, Region 3 $R^2 = 0.43$).

Standardized regional CPUE indices were translated into estimates of abundance in the three regions (Fig. 6). Based on the low estimate, in any given year Region 3 contained between 487 and 8022 mt of albacore, Region 2 between 595 and 10 120 mt, and Region 1 between 909 and 14 677 mt. Based on the high estimate, Region 3 contained between 24 435 and 86 662 mt, Region 2 between 31 169 and 106 118 mt, and Region 1 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 (Fig. 7). In Region 3,

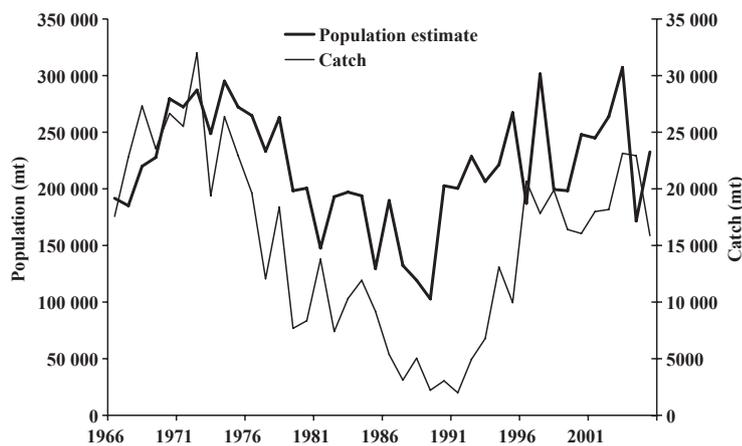


Figure 4. Estimates of albacore biomass in the CCS. The low estimate is the total catch by the U.S. and Canada troll fisheries operating in the Eastern Pacific Ocean which land albacore aged 2–4 (see Fig. 1). The high estimate is the biomass of all albacore aged 2–4 estimated from a Pacific-wide stock assessment model (ISC 2006).

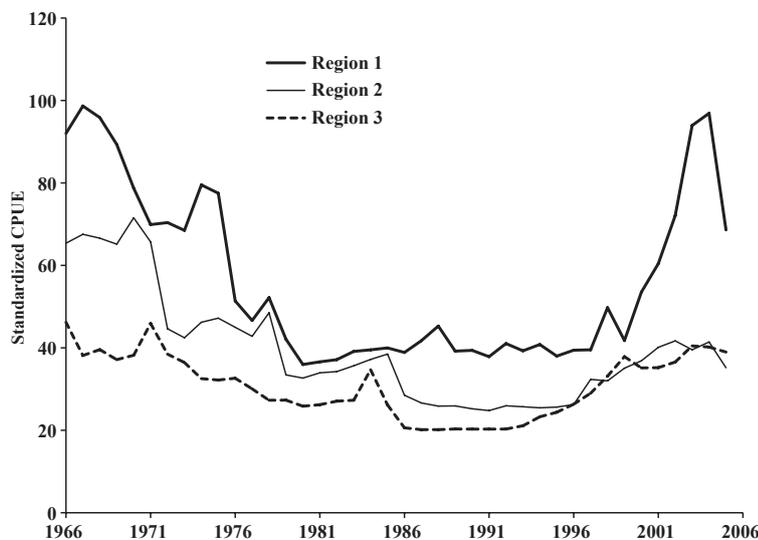


Figure 5. Standardized indices of relative abundance of albacore in the CCS in three regions.

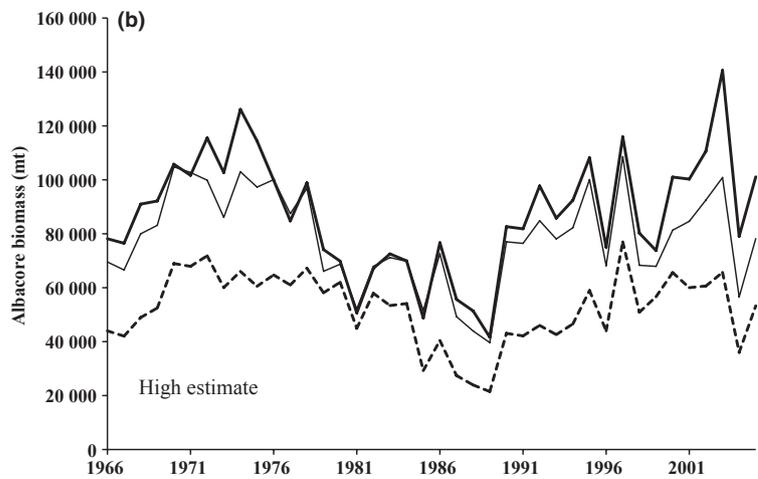
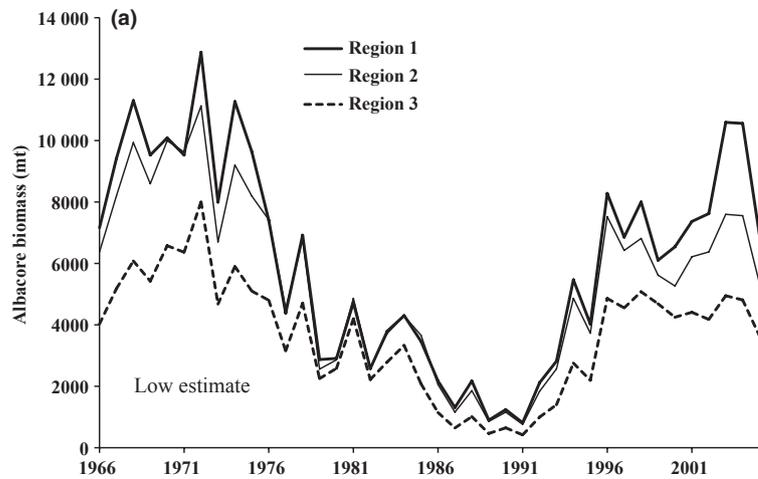


Figure 6. Estimates of albacore biomass in three regions of the CCS. (a) Low estimate is based on landings data alone. (b) High estimate is based on a stock assessment model.

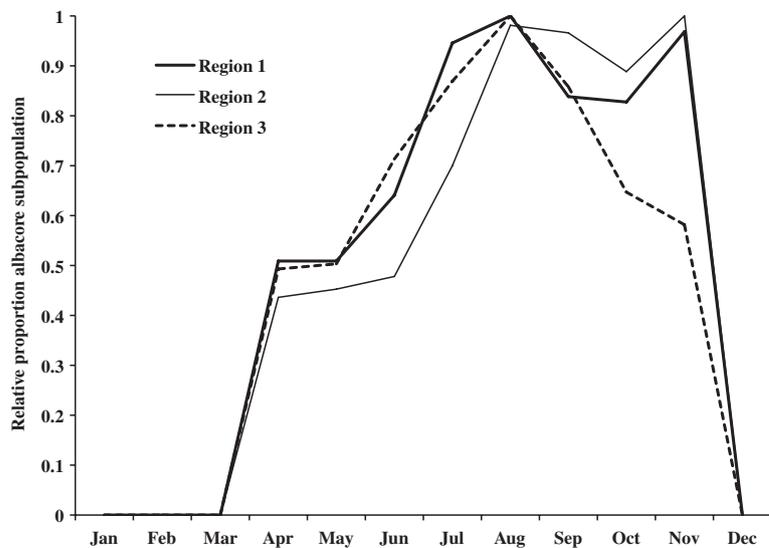


Figure 7. Seasonal distribution of albacore in the CCS from standardized CPUE data.

albacore catch rates rapidly dropped off beginning in September, whereas catch rates in Regions 2 and 3 remained high until November. During December through March, albacore catch rates in the CCS were zero.

The scaled low and high estimates are more realistic estimates of albacore abundance and therefore anchovy

consumption in the CCS. Annual consumption of anchovy in the three regions of the CCS ranged from 128 mt (Region 2, scaled low estimate) to 126 787 mt (Region 1, scaled high estimate) (Table 1). Altogether, albacore likely removed between 4516 mt and 162 195 mt of anchovy annually from the CCS ecosystem (Fig. 8). Human catch of anchovy (FAO

Year	Low estimate			High estimate		
	Region 1	Region 2	Region 3	Region 1	Region 2	Region 3
1966	19 907	858	3909	217 238	9361	42 654
1967	26 178	1104	5022	212 590	8963	40 785
1968	31 419	1337	5896	252 924	10 767	47 462
1969	26 481	1157	5261	256 145	11 190	50 889
1970	27 504	1317	6617	288 394	13 812	69 387
1971	25 468	1241	6636	271 796	13 247	70 818
1972	33 727	1407	8637	302 675	12 630	77 511
1973	20 519	828	5216	263 535	10 640	66 995
1974	28 328	1112	6799	316 967	12 444	76 077
1975	23 703	967	6058	281 467	11 478	71 937
1976	17 828	857	5880	240 357	11 556	79 274
1977	10 310	509	3976	199 461	9854	76 922
1978	15 917	744	6100	227 475	10 631	87 176
1979	6451	274	3001	166 596	7070	77 503
1980	6377	298	3537	153 202	7157	84 977
1981	10 117	495	5901	108 354	5297	63 205
1982	5376	257	3204	140 195	6715	83 563
1983	7718	357	4131	147 529	6832	78 973
1984	8521	400	5044	138 524	6503	82 009
1985	6668	332	3222	93 999	4677	45 418
1986	4067	180	1818	143 671	6376	64 210
1987	2381	98	1047	101 354	4188	44 559
1988	3841	153	1681	90 811	3612	39 745
1989	1539	68	787	71 363	3145	36 487
1990	2062	89	1122	137 226	5921	74 694
1991	1308	56	742	131 551	5659	74 604
1992	3288	131	1799	151 935	6041	83 150
1993	4231	175	2580	128 764	5338	78 523
1994	7914	321	5179	133 810	5420	87 557
1995	5618	235	4207	150 856	6312	112 963
1996	11 105	453	9487	100 587	4104	85 934
1997	8829	369	9052	149 312	6232	153 096
1998	9880	372	10 282	99 055	3727	103 092
1999	7208	293	9659	87 143	3537	116 773
2000	7379	259	8912	113 954	4004	137 636
2001	7917	288	9410	107 762	3927	128 084
2002	7787	278	9069	113 015	4031	131 614
2003	10 253	312	10 919	136 108	4145	144 942
2004	9659	289	10 793	72 313	2164	80 808
2005	5944	189	8287	87 116	2771	121 453

Table 1. Annual consumption of anchovy (mt) by albacore in three regions of the CCS.

'Low estimate' assumes albacore biomass equal to landings; 'high estimate' assumes albacore biomass from stock assessments. The scaled estimates in Fig. 8 can be recovered by multiplying the low estimate by 1.89 and the high estimate by 0.4.

Figure 8. Annual consumption of anchovy by juvenile albacore in the CCS, and human landings.

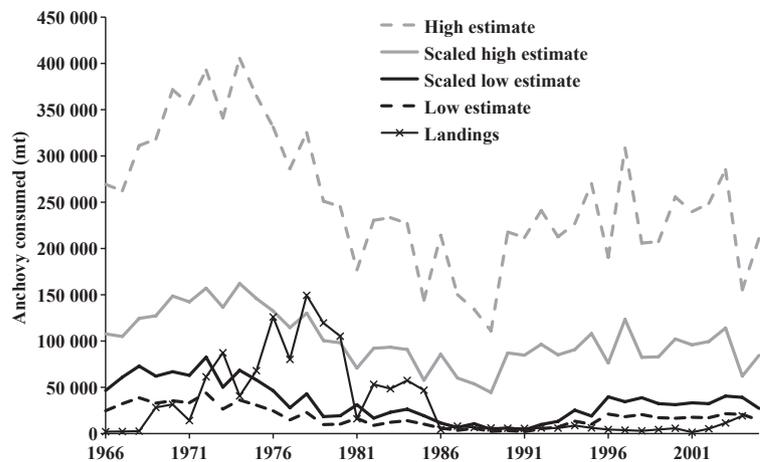
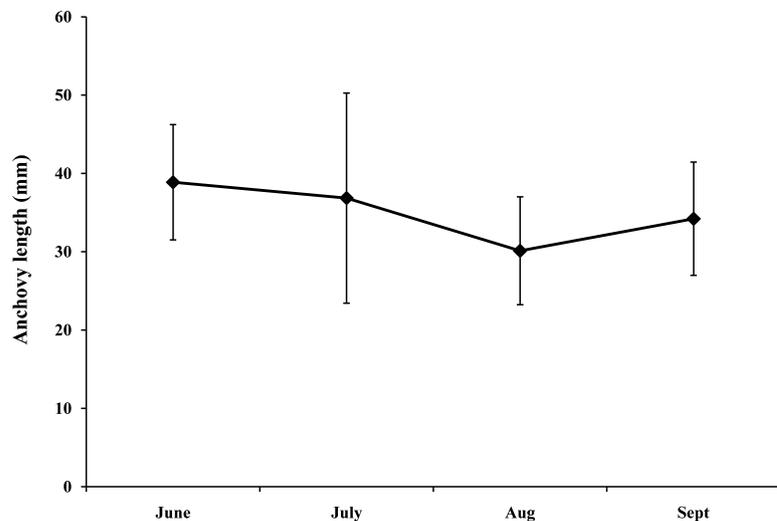


Figure 9. Size of anchovy found in albacore stomachs by month, collected in 2005 and 2006. One-tailed ANOVA $F = 11.998$, $df = 3$, $P < 0.001$. Bars are one standard deviation.



landings data) since 1966 has ranged from 1450 mt (1998) to 149 000 mt (1975). From the mid-1960s to the mid-1980s, human predation on anchovy was approximately equal that of albacore. However, since 1983, human landings have been far less and lie below all estimates of albacore predation (Fig. 8).

Albacore consistently preyed on young anchovy, even as the season progressed (Fig. 9). Mean size of anchovy prey ranged from 24 to 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) (Fig. 10). Recruitment biomass peaked in 1972 at 4 348 000 mt and had a low of 88 000 mt in 1989. Based on this

model, albacore annually consumed between 0.1 and 17% of central stock anchovy recruitment biomass (Fig. 11, scaled estimates). These levels of consumption translate into instantaneous rates of mortality of 0.003–0.02 per yr for the scaled low estimate of albacore consumption, and 0.01–0.25 per yr for the scaled high estimate (Fig. 11). Assuming a total mortality rate (not including fishing) for anchovy of 0.8 per yr (Methot, 1989), albacore predation can account for <1% and up to 33% of juvenile natural mortality.

Correlation analysis revealed possible significant relationships between changes in anchovy biomass consumed by albacore and changes in the recruitment biomass of the central stock of the anchovy (Table 2, Fig. 12). However, findings were inconsistent between the high and low estimates of consumption. Statistically significant relationships were found only when analyzing the low estimate of albacore predation. First,

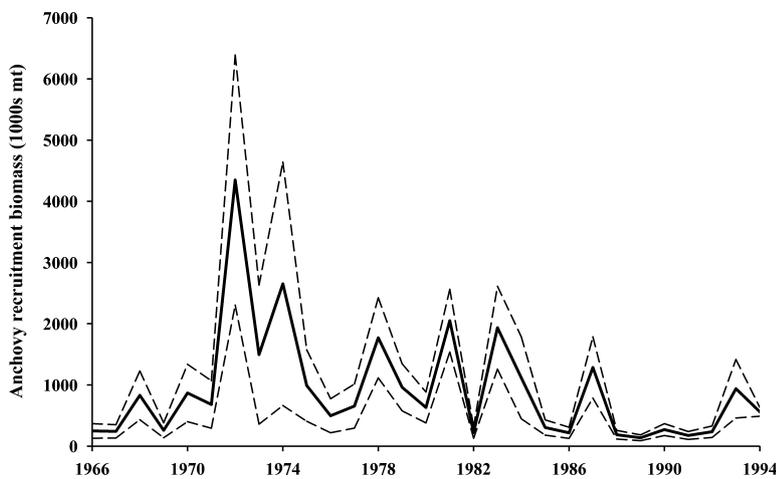


Figure 10. Calculated biomass of anchovy recruitment (young of year fish) for the Northern anchovy central stock in the CCS. Dashed lines are \pm the CV. Data from Jacobson *et al.* (1995).

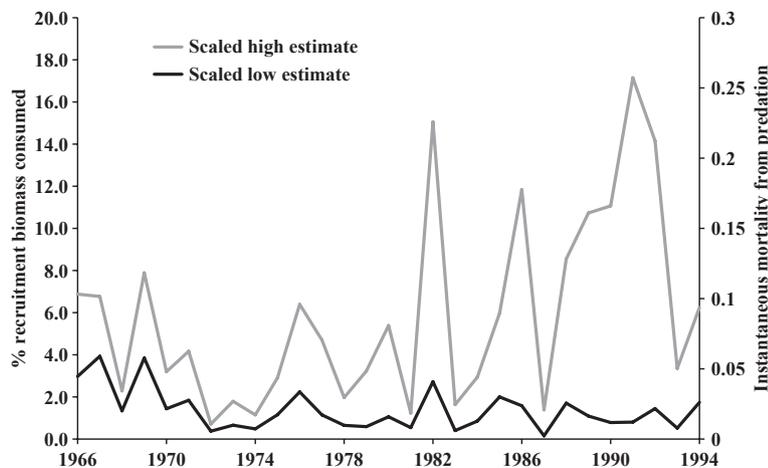


Figure 11. Proportion of recruitment biomass in the anchovy central stock consumed by juvenile albacore and instantaneous mortality on anchovy recruits imposed by albacore predation.

Table 2. Pearson sample correlation coefficients (r) between anchovy recruitment biomass and albacore predation in Region 3 of the CCS. Predation at time t -lag, recruitment at time t .

Predation	Anchovy	Lag	r	P -value
Low estimate	Recruitment	0	0.647	0.0002
		1	-0.484	0.011
	Total population	2	-0.255	0.209
High estimate	Recruitment	3	0.161	0.443
		0	0.063	0.751
	Total population	1	0.173	0.388
		2	0.220	0.209
		3	0.007	0.974

there was a positive relationship between changes in recruitment abundance and changes in predation in the same year ($P = 0.0002$). Secondly, there was a negative relationship between changes in predation in

year t and changes in recruitment abundance in year $t + 1$ ($P = 0.011$). Relationships were not significant using the high estimate of predation or for any estimates of the adult anchovy population.

DISCUSSION

Estimates of changes in predation and changes in anchovy recruitment biomass are consistent with the hypothesis that albacore exert top-down pressure on anchovy when the low estimate of predation is considered. The failure to find consistency between the high and low estimates of predation warrants a conservative conclusion. The high estimate of predation was derived from the high estimate of albacore abundance, based on Pacific-wide estimates of the juvenile population from a stock assessment model. The low estimate of predation was derived from the low estimate of albacore abundance, based on CCS-specific landings data. The correlation analysis was performed

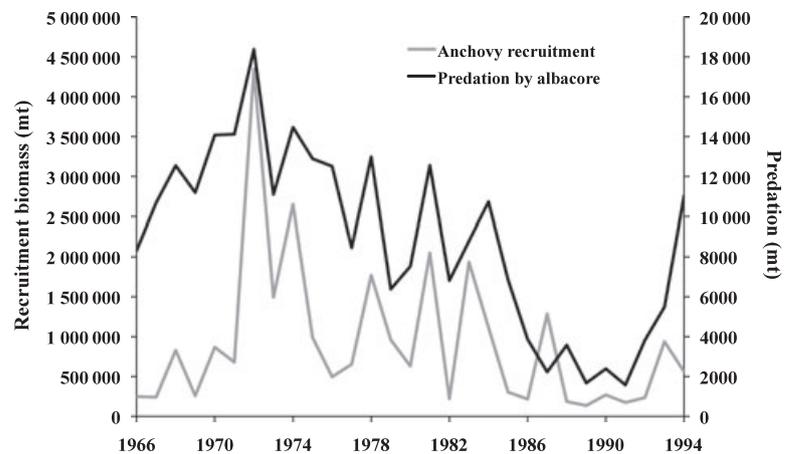


Figure 12. Temporal correlation between predation (scaled low estimate) and anchovy recruitment in the central stock. Significant relationships were found for contemporaneous estimates ($P = 0.002$) and at recruitment lagging predation 1 yr ($P = 0.011$).

on first-difference data. Therefore, the relationships are between year-to-year changes in predation and abundance, or the interannual dynamics of the data. The relationships are not between the actual levels of predation (high or low) and anchovy biomass. The low estimate may be a more accurate reflection of year-to-year changes in the albacore population in the CCS. For one, the data are collected locally. For another, gear and effort do not change dramatically over a 1-yr time frame in this fishery. Finally, the landings data are assumed to have low observation error, whereas the high estimate likely contains greater error (discussed below). However, the failure to find consistent results between the two estimates of predation and the effect on anchovy recruitment leaves the question unresolved.

The full context of the data is important for the interpretation of the correlation analysis. The anchovy stock assessment model (Jacobson *et al.*, 1995) estimates recruitment biomass on July 1 of a given fishing season and assumes anchovy recruit to the fishery at 0.5 yr of age. The anchovy consumed by albacore in the CCS are pre-recruits. At a mean length of 30–39 mm, these anchovy are between 40 and 80 days old and thus the age-class estimated for recruitment by Jacobson *et al.* (1995) does not include these anchovy. Therefore, anchovy consumed in year t during July–October will be represented in the stock assessment model in year $t + 1$ as recruits. The statistically significant negative relationship between predation in year t and anchovy recruitment in year $t + 1$ suggests that periods of increase in albacore abundance and predation 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 are one

mechanism by which stability is conferred on such models (May, 1973). The finding that the relationship breaks down beyond a 1-yr time lag in the adult population is consistent with predictions from models that demonstrate that the effects of top-down pressure will be most visible in early life-history stages and will impact recruitment for short time periods, whereas bottom-up forcing is best observed in adult populations and over longer periods of observation (Jacobson *et al.*, 2001; Munch *et al.*, 2005).

To date, observational studies of pelagic ecosystems rely on correlations between time series to make conclusions about top-down and bottom-up effects (Cury *et al.*, 2000). 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 and Essington, 2008), and agree with hypotheses of anchovy specialists (Smith, 1985; Methot, 1989; Jacobson *et al.*, 1995). However, several factors that are omitted from this simple correlation could alternately explain the patterns observed. Environmental factors could confound these findings, and they are elaborated below. The decline in anchovy recruitment biomass during the 1980s coincided with an increase in sardine recruitment; if there is direct competition between the species, observed patterns could be unrelated to predation pressure (e.g., Chavez *et al.*, 2003). Indeed, there is no evidence that sardine is a significant prey item of albacore (Glaser, 2010). Finally, the high level of observational noise inherent in population estimates such as these is cause for cautious conclusions in any type of linear correlation analysis. The findings here should encourage more direct methods of testing for top-down effects in systems that preclude experimental manipulation.

The positive relationship between contemporaneous predation (low estimate) and anchovy recruitment biomass in Region 3 suggests two possibilities. First, environmental drivers that favor anchovy recruitment could act as an aggregating mechanism for albacore schools. There is strong evidence that albacore are distributed along environmental temperature and productivity gradients in the CCS (Laurs *et al.*, 1984; Polovina *et al.*, 2001). Furthermore, optimal foraging models predict that albacore hunting preferences, based on physiological concerns, will coincide with the water temperatures preferred by anchovy (Lluch-Belda *et al.*, 1991; Kirby *et al.*, 2000). The relationship likely reflects a local attraction for albacore coupled with a bottom-up effect of environmental drivers on anchovy recruitment. Secondly, albacore could simply be attracted to areas of high forage biomass (MacArthur and Pianka, 1966; Bakun, 2001; Polovina *et al.*, 2001), regardless of physical environmental concerns.

The lack of relationship between predation and the total anchovy population is consistent with effects of predation being limited to recruits. 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 age groups 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 would be required. However, Munch *et al.* (2005) demonstrate that, with such lengthy lags, the effects of earlier top-down factors will be swamped by bottom-up forces acting on the adult population. The observations documented here are consistent with their model predictions.

High mortality rates in newly spawned 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 anchovy recruits sufficient for such an impact. The low and high estimates of albacore consumption provide bounds to the possible levels of consumption, while the scaled estimates are more realistic. I find albacore may account for 1–30% of total mortality (assuming $Z = 0.8$ per yr; Methot, 1989). Predation mortality by albacore is directed at 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 report catch and effort data accurately. 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 Glaser (2010) 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 stratify the albacore subpopulation. If more diet studies were available during the time of anchovy assessments, it would 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 changed 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). Bias analysis revealed the presence of 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 predation and recruitment biomass, and between predation and total anchovy biomass, would be strongly confounded. Finally, the estimates for recruitment are a function of sea surface temperature

(SST), a variable strongly associated with anchovy egg production (Methot, 1989). Although 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, used to divide albacore distribution into months and regions, 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 fish 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 and Deriso, 1999; Maunder and 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 catchabilities). 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 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 and within the range of R^2 values for most CPUE standardization models (as reported by Watters and 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, is justified and, in fact, more reliable. The model developed here could be criticized for omitting SST, a variable shown to have a strong influence on albacore movement patterns (Laurs *et al.*, 1984; Zainuddin *et al.*, 2006). However, Watters and Deriso (2000) demonstrated that when space and time variables were included in a regression tree standardization, environmental variables were frequently superfluous. The resolution of space and time variables used here ($1^\circ \times 1^\circ \times$ month) matches that of most commonly available environ-

mental variables (such as COADs SST or wind data), and thus any interaction between space and time variables accounts for effects that may come from environmental drivers.

This study is the first to quantify mortality imposed on juvenile Northern anchovy in the CCS 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 may be related to recruitment biomass, findings which are consistent with expectations of top-down regulation. This is neither conclusive nor the 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, there is no active management plan for either species that restricts catch or effort by fisheries. During periods of high catch (1970–80), human predation on adult anchovy was similar to predation by albacore on anchovy pre-recruits. 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 population dynamics, 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; Navarrete *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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