

El Niño periods increase growth of juvenile white seabass (*Atractoscion nobilis*) in the Southern California Bight

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Abstract Studies of the impact of El Niño periods on marine species have usually focused on negative, highly visible effects, e.g., decreasing growth rates or increasing mortality due to a decline in primary productivity in typically nutrient rich upwelling zones; but positive effects related to elevated water temperature are also known. This study examined how the growth rate of juvenile white seabass, *Atractoscion nobilis*, responded to changes in ocean temperature in an El Niño period (1997–1998) in the northern portion of the Southern California Bight, USA. Growth rates of juvenile white seabass during their first 4 years of life were estimated as the slopes of linear relationships between body mass and age (from otoliths) of 800 fish collected at 11 stations throughout the bight. Growth rates differed significantly among cohorts hatched in 1996–2001. Specifically, white seabass that hatched in 1996 and 1997 grew significantly faster than those that hatched in 1998,

1999, and 2001. These differences in growth rates of cohorts appeared to be driven by variation in sea-surface temperature (SST). Growth rates averaged over the first three or 4 years of life were significantly positively correlated to average daily SST during the first 1–4 years of life. Increased growth of juvenile white seabass during the warm El Niño period likely provided a number of benefits to this warm-temperate species. This study demonstrated that some species will benefit from these warm-water periods despite reduced system-wide primary production.

Introduction

Factors that affect growth rates of fishes can have important impacts on population dynamics, for example, via effects of size on mortality, age at first maturity, and fecundity. Slower than usual growth can increase mortality by prolonging the period that young fish are susceptible to predation, as susceptibility is typically size-dependent (Pfister 1997; Sogard 1997; Carr and Syms 2006). Similarly, factors that slow growth can reduce reproductive output because fecundity is usually strongly size-dependent (Weatherly 1972). Elevated sea-surface temperatures (SST) raise the metabolism of fishes, which can in turn increase growth rates if sufficient food is available (Schmidt-Nielsen 1984; Gillooly et al. 2002; Brown et al. 2004) and temperatures do not rise above species-specific thermal windows (Pörtner 2002; Pörtner and Knust 2007).

Significant positive correlations between growth and SST have been detected in a variety of marine fishes (Brander 1995; Lehodey and Granperrin 1996; Anderson and Dalley 2000; Möllmann et al. 2005), but studies of strong El Niño periods have generally documented highly visible, negative effects of temporary warm-water conditions

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on populations of temperate fishes and their food sources. Areas of the eastern Pacific Ocean affected by El Niño conditions have shown a marked decline in fish abundance at all trophic levels (Guillén et al. 1971; Bakun and Parrish 1982), as well as reductions in growth rates and reproductive success (Barber and Chavez 1983; Chavez et al. 2002). Low nutrient levels in warmer surface waters cause a decline in primary productivity, which apparently results in a shortage of food throughout the food web. This lack of food can have major consequences. For example, a mass die off of the orangemouth corvina, *Cynoscion xanthalmus*, off northern Perú was attributed to starvation during El Niño conditions (Valdevia et al. 1983). Studying the impacts of El Niño conditions may give us insight into the expected effects of longer-term global warming trends.

During El Niño periods in southern California, USA, nutrient and primary productivity levels decline (Chavez et al. 2002). Coupled with strong storms, which uproot giant kelp (*Macrocystis pyrifera*) holdfasts (Dayton et al. 1998), there is usually a significant decline in the abundance of giant kelp (Grove et al. 2002), a major habitat for fish and invertebrates (Dayton et al. 1998; Stephens Jr et al. 2006). The 1997–98 El Niño was a particularly strong period (Chavez et al. 2002) that caused major physical, chemical, and biological changes along the southern California coast. From May 1997 to March 1998, SST was 2–4°C higher than average. During the La Niña period of May 1998 through August 2000, SST was 0–3°C below normal (Fig. 1). These significant temperature variations provided an excellent opportunity to test the effects of temperature on growth.

We studied the effects of SST during 1996–2004 on growth rates of the white seabass, *Atractoscion nobilis*. This species is the largest croaker (family Sciaenidae) in

California waters, reaching lengths of 1.5 m and weights of 40 kg (Miller and Lea 1972; Eschmeyer et al. 1983). Maximum longevity is about 25 years (J. Williams et al., unpublished data); and maturity is reached after about 4 years (Clark 1930; Thomas 1968). Spawning in southern California occurs from March to September with a peak in June (Donohoe 1997). The range of the white seabass typically extends from Bahía Magdalena, Mexico to Point Conception California, though in warmer years individuals have been caught as far north as Juneau, Alaska (Miller and Lea 1972; Vojkovich and Reed 1983; Eschmeyer et al. 1983). This species normally occupies water ranging in temperature from 13 to 21°C (M. Steele, personal observations). Adults are often found in kelp beds or over rocky reefs up to 120 m depth, while juveniles settle in bays and among algal debris along sandy beaches (Allen and Franklin 1988; 1992; Eschmeyer et al. 1983). It is an important commercial and recreational species (Vojkovich and Reed 1983). The commercial catch of white seabass began decreasing in the early 1900s (Skogsberg 1939; Methot 1983; Collins 1981), and the sport catch began to decline from a peak catch of 64,000 individuals in 1949 to only 284 in 1978, but has since returned to levels above 11,000 fish captured per year (Thomas 1968; Vojkovich and Reed 1983; Vojkovich and Crooke 2001). The decline in landings has generally been attributed to over-fishing (Thomas 1968; Vojkovich and Reed 1983; Sherman and Alexander 1986). Despite being an economically important species and concerns over the apparent population decline, no studies on the life history of white seabass >1 year old have been conducted since Thomas (1968). The current study tested the hypothesis that growth rates of juvenile (<5 year old) white seabass in the Southern California Bight were affected by elevated SST (or correlated changes) caused by El Niño conditions.

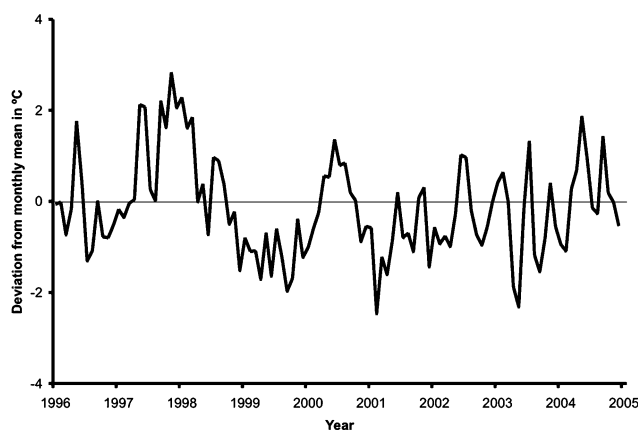


Fig. 1 Monthly SST anomalies from 1996–2004 compared to average monthly sea-surface temperatures from 1955–2004. Data are mean values of temperatures off Newport Beach, CA and Santa Barbara, CA. Data were obtained from Southern California Ocean Observing System (<http://www.scoos.org/>)

Materials and methods

Field collection

Juvenile white seabass were captured within the northern portion of the Southern California Bight in April, June, August, and October from 1995 to 2004. A total of ten stations, eight in nearshore coastal waters, and two in embayments, were sampled each year. The stations were located off the coast of Santa Barbara, Ventura, Malibu, Marina del Rey, Palos Verdes, Seal Beach, Newport Beach, Santa Catalina East, Santa Catalina West, and Catalina Harbor (Fig. 2). In the summers of 2000 and 2001 an 11th station was sampled at Santa Cruz Island.

Scientific gill nets were used to sample the juvenile white seabass as in Pondella and Allen (2000). Nets were 45.7 m in length and 2.4 m in depth and included six 7.6-m

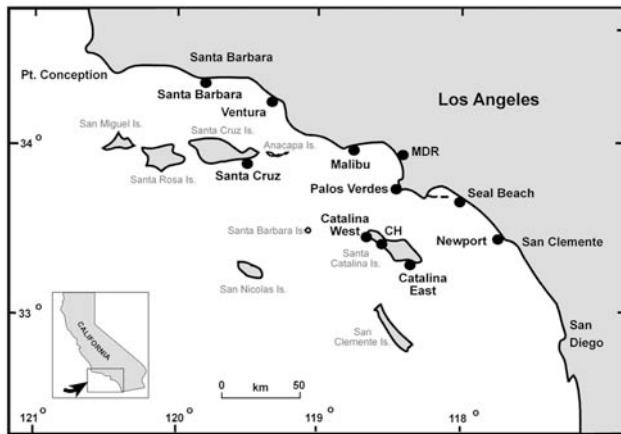


Fig. 2 Study area showing ten stations sampled from 1997–2004 and a supplementary station at Santa Cruz Island that was sampled only in 2000 and 2001. *MDR* Marina del Rey, *CH* Catalina Harbor

panels with two panels for each of the three square mesh sizes: 25.4, 38.2, and 50.8 mm. These small mesh sizes targeted juveniles and few adults were captured. At all coastal sites, eight gill nets were set in the same locations for each sampling effort and included both sand/rock and reef/kelp habitats. Nets were set perpendicular to shore or to the kelp forest edge in water depths of 5–14 m. In embayments, six gill nets were set in a minimum depth of 2.5 m. Each net was deployed near sunset and left overnight until retrieval within a few hours after sunrise.

Each of the 6,777 white seabass captured was measured to the nearest millimeter (SL and TL), weighed (± 10 g), and its sagittal otoliths were removed, cleaned, and stored in coin envelopes. For this study, 100 fish were randomly selected from each sampling year from 1997 to 2004 for a total of 800. Samples from 1995 and 1996 were either not available or did not include adequate numbers for the present study. Fish with missing or broken otoliths were excluded, as were fish lacking measurements of body mass. Although hatchery produced white seabass were present in the study area (and identified by a coded wire tag), we studied only wild individuals.

Otolith preparation

The sagittal otolith in the best condition (i.e., unbroken) for each fish was used for measurement and aging. The length and width of each otolith was recorded (± 0.01 mm) using digital calipers and each otolith was weighed (± 0.0001 g) on an analytical balance. Otoliths were then mounted individually on wood blocks using cyanoacrylate glue and sectioned through the focus using a Buehler-Isomet low speed saw with two 0.3-mm diamond wafering blades separated with an acetate spacer to create a 0.75-mm transverse

section. Sections were removed from the wood block and stored dry in 1.5-ml microcentrifuge tubes. Both sides of each section were sanded wet using 400-grit waterproof sandpaper until the section was approximately 0.5 mm thick. The section was then briefly polished using 600-grit waterproof sandpaper. Polished otolith sections were submerged in mineral oil on a depression slide and viewed at $40\times$ magnification under an Olympus BH-2 compound microscope using transmitted light. The transmitted light produced dark opaque areas and light translucent areas (Fig. 3).

Aging and validation

The age of each fish was estimated by counting each complete pair of opaque and translucent bands (annuli), which were most easily viewed on secondary primordia. Edge analysis was performed on each otolith by determining whether the outer edge of each section was opaque or translucent to the transmitted light. The edge analysis was used to validate the age estimates by testing for annual formation of opaque growth zones. To account for the growth of the white seabass during the sampling season, the month of capture was added to the year class. For example, a year class II fish captured in August would be considered to be age 2.58 (assuming a 1 January hatch date).

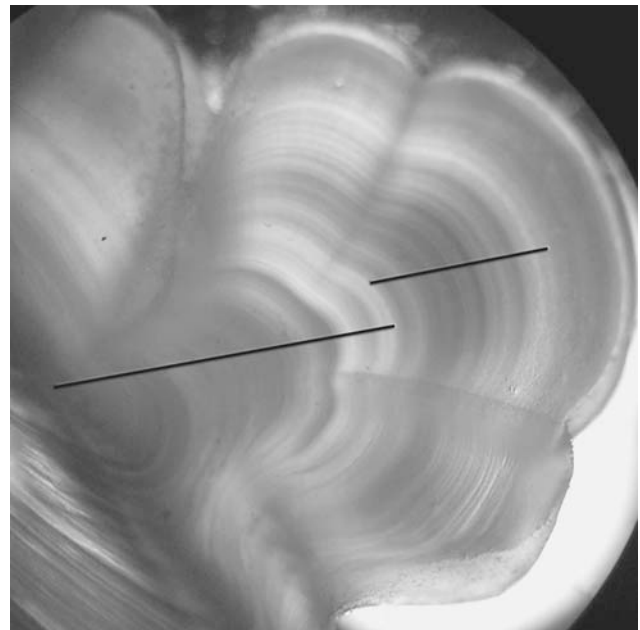


Fig. 3 Cross-section of an otolith of a white seabass estimated to be 2.42 years old, viewed under a compound microscope at $40\times$ magnification. Full bipartite annuli (pairs of dark, opaque, and light, translucent bands) are labeled with *black lines*. This fish was captured in June 1997 at the Malibu station

Each otolith was read two to three times to agreement. Second and third readings were done “blind” (i.e., without knowledge of the prior reading) at least 1 month after the initial reading. The first reading was performed on a compound microscope at 40 \times magnification, whereas the second reading was done from digital photographs taken through the ocular of the microscope using an Olympus Stylus 500 digital camera. In cases of disagreement, the otolith was viewed a third time under the compound microscope where agreement was reached for all samples.

Statistical analyses

The growth rate of each cohort was estimated as the slope of a linear relationship between mass and age using ordinary least squares linear regression. Six statistical outliers (as identified by Systat 11) were excluded from these and other analyses. These outliers most likely resulted from incorrect measurements or recording errors. Fewer than 2% of the white seabass were determined to be 5 years older, and therefore only fish younger than five were used in the analyses. Additionally, fish that had hatched before 1996 or after 2001 were excluded from analysis because less than 3 years of their growth history was available. In total, 625 samples that were determined to have hatch years between 1996 and 2001 and were younger than 5 years were used for the analyses of mass at age.

Analysis of covariance (ANCOVA) was used to determine whether growth rates (slopes) differed among different cohorts (hatch years). Pairwise differences in growth rates between cohorts were tested by a separate ANCOVA for each pair of cohorts, which included only those two cohorts and age in the model. To account for experimentwise error rate in multiple comparisons, significance levels were adjusted to $\alpha = 0.003$ using the Bonferroni method (Sokal and Rohlf 2001). The data met the assumptions of normality and homogeneity of variances.

To determine whether water temperature affected growth rates of the six cohorts, we evaluated whether the growth rate (slope of the relationship between mass and age) of each cohort was related to the water temperature experienced by it. The average temperature from the end of one sampling season to the end of the next was estimated as the mean of average daily temperatures taken from Newport Bay and Santa Barbara, California (Fig. 1) from November through October of each year. In addition to single-year means, mean temperatures for 2, 3, and 4-year spans were tested for correlation with growth rates for all hatch years over 1, 2, 3, and 4 years of growth to test whether growth of juvenile white seabass was correlated with SST and for how long the significant growth and temperature relationship existed.

Results

Annuli (bipartite bands) appeared to be formed once a year. Otolith edge analysis showed that otoliths with opaque edges occurred most frequently in August with the lowest incidence occurring in April (Supplementary Figure 1). Further supporting the interpretation that annuli represented accurately recorded age, otolith width was significantly linearly related to age ($r^2 = 0.70$, $P < 0.01$), as was otolith length ($r^2 = 0.78$, $P < 0.01$), and otolith mass ($r^2 = 0.79$, $P < 0.01$) (Fig. 4).

Growth rates for each cohort (hatch year) ranged between 310.9 g year⁻¹ (hatch year 1998) and 526.7 g year⁻¹ (hatch year 1996), with statistically significant linear regressions for every cohort (r^2 range = 0.62–0.86, $P < 0.01$; Fig. 5). Growth rates differed significantly among cohorts (ANCOVA; $P < 0.001$; Table 1), with white seabass that hatched in 1996 having a significantly higher growth rate than white seabass that hatched in 1998 ($P < 0.001$), 2000 ($P < 0.001$), and 2001 ($P < 0.001$) (Table 2). Growth rates also differed significantly between 1997 and 1998 ($P < 0.001$), 1997 and 2001 ($P = 0.003$), 1998 and 1999 ($P = 0.001$), and 1998 and 2000 ($P = 0.001$). Though the difference in the slope coefficients from 1996 and 1999 was wider than the difference between 1996 and 2000, it was not statistically significant. This is likely due to poor precision of the slope estimate for the 1999 cohort due to low sample size (45) relative to other cohorts (e.g., $n = 141$ for the 2000 cohort).

Water temperature appeared to have a positive effect on growth rates of juvenile white seabass. Growth rate over the first 3 years of life was significantly positively correlated with mean SST during the first year of life ($r = 0.73$, $P = 0.05$), the first 2 years of life ($r = 0.76$, $P = 0.04$), and

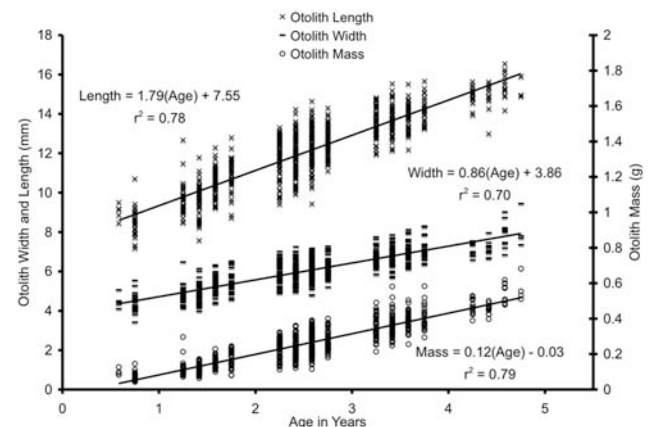


Fig. 4 Relationships between otolith width (mm), length (mm), and mass (g), and age of juvenile white seabass

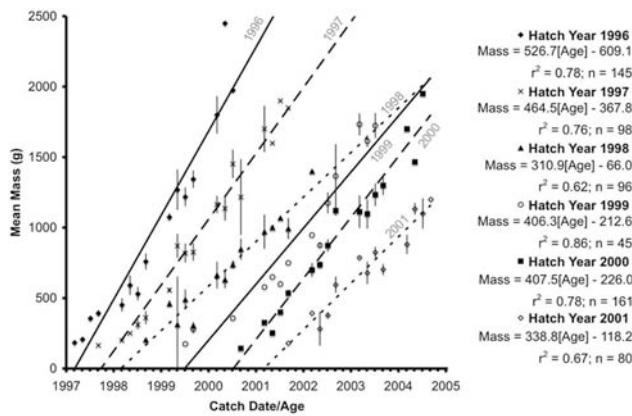


Fig. 5 Mass (g) at age for six cohorts (hatch year) of juvenile white seabass. For clarity, each point is the mean mass of all fish captured in a month (\pm SE), but regression equations were fit using the mass and age of each individual

Table 1 Results of analysis of covariance testing for effects of age and cohort (hatch year) on body mass of juvenile white seabass

Source	SS	dF	MS	F-ratio	P-value
Age	7.10×10^7	1	7.10×10^7	1,549.9	<0.001
Hatch year	2.2×10^6	5	4.3×10^5	9.567	<0.001
Hatch year \times age	2.4×10^6	5	4.8×10^5	10.475	<0.001
Error	2.8×10^7	606	45,834		

The interaction term tests whether growth rates (slope of the relationship between mass and age) differed among cohorts hatching in different years

Table 2 P-values of multiple pairwise comparisons of growth rates among cohorts for the hatch years 1996–2001

Hatch year	1996	1997	1998	1999	2000
1997	0.085	–	–	–	–
1998	<0.001*	<0.001*	–	–	–
1999	0.004	0.255	0.001*	–	–
2000	<0.001*	0.059	0.001*	0.967	–
2001	<0.001*	0.003*	0.461	0.070	0.043

* Significant differences at $\alpha = 0.003$ (Bonferroni correction)

the first 3 years of life ($r = 0.74$, $P = 0.04$) (Fig. 6). Growth rate over the first 4 years of life was significantly correlated with mean SST during the first year of life ($r = 0.82$, $P = 0.04$), the first 2 years of life ($r = 0.85$, $P = 0.03$), the first 3 years of life, and the first 4 years of life ($r = 0.96$, $P < 0.01$). Temperatures experienced during the first full year or first 2 years of life, however, did not correlate with growth over the first full year or first 2 years.

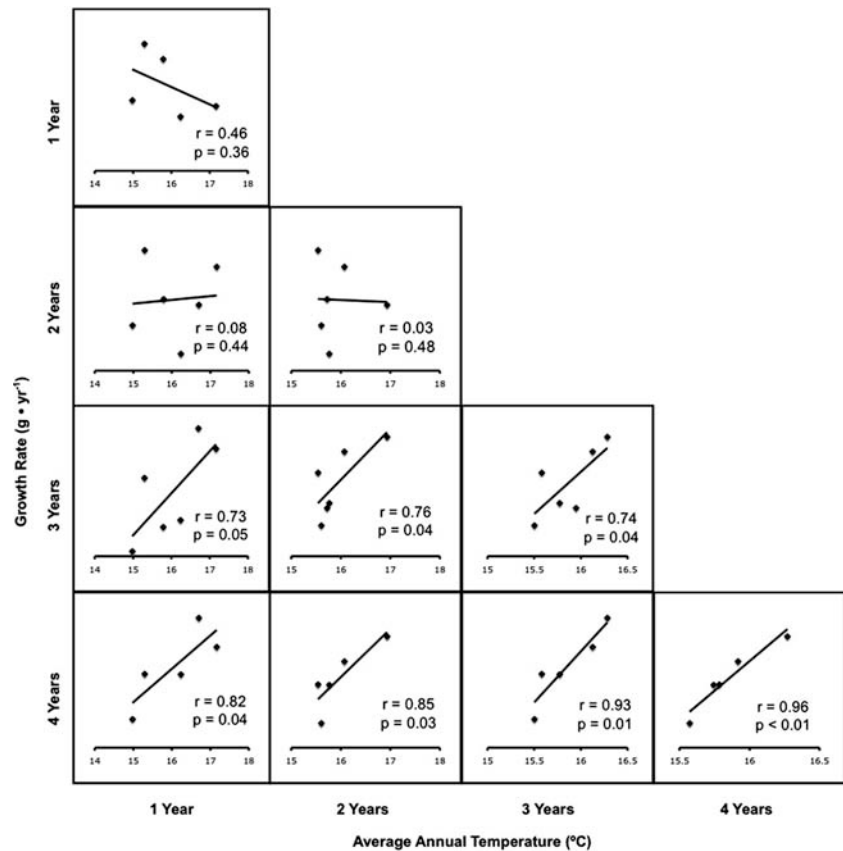
Discussion

Cohorts of juvenile white seabass that hatched between 1996 and 2001 grew at significantly different rates, and these differences appeared to be related to water temperature, with faster growth during warm periods. Although this pattern was statistically detectable over 3–4 years of growth history, it was not evident over the first 1–2 years of life. This lack of correlation between growth and water temperature early in life is most likely a methodological problem attributable to the small number of samples and wide range of sizes and ages (due to a 6-month long spawning period) during this brief portion of the lifespan. For example, because we could only age fish to the nearest year, an individual that hatched in April would be assigned the same age as one that hatched in September, and if both were caught in August of the following year they would be assigned the same age (1.7), even though one had much more time to grow. The relative magnitude of such errors declines with age.

Our finding of increased growth of white seabass with elevated water temperature is similar to findings of studies on Atlantic cod (Brander 1995; Anderson and Dalley 2000; Pörtner et al. 2001; Swain et al. 2003; Drinkwater 2005; Rätz and Lloret 2005) and alfoncino (*Beryx splendens*) (Lehodey and Granperrin 1996), but contrasts with the findings of studies on Pacific mackerel (Watanabe and Yatsu 2004). Variable effects of elevated water temperatures on growth of fishes are to be expected because of the interplay between effects of water temperature on rates of tissue synthesis and metabolism, and the association between water temperature and nutrient concentrations. Over the range of temperatures normally encountered during natural warm-water periods, increasing water temperatures will likely increase the rate at which new tissues can be synthesized, but increased growth will only be realized if food is sufficiently abundant to outweigh increased metabolic costs incurred at warmer temperatures (Brett et al. 1969) and species-specific thermal maxima are not exceeded (Pörtner 2002; Takasuka and Aoki 2006; Pörtner and Knust 2007). If food is a limited resource and its abundance does not increase with climbing water temperatures, growth rates will decline.

Warmer water tends to have lower concentrations of nutrients and oxygen, and lower primary production (Barber and Chavez 1983; Chavez et al. 2002). This reduced primary productivity can negatively affect food webs from the bottom up (Ware and Thomson 2005). Off the coast of Perú and in the Galápagos Islands, the warm water in 1973 and 1983 caused near local extinction of Peruvian anchovy (*Engraulis ringens*) and jack mackerel (*Trachurus symmetricus*), whereas Pacific sardine (*Sardinops sagax*), a species with an affinity for warm water,

Fig. 6 Growth rate versus mean annual water temperature for growth over 1–4 years of life and water temperature averaged over 1–4 years of life. Each point represents the growth rate (slope of the relationship between mass and age) of a cohort (hatch year) of juvenile white seabass. Note: temperature scales differ between columns of graphs



migrated toward higher latitudes (Barber and Chavez 1983). A similar situation occurred along the California coast with Pacific mackerel (Sinclair et al. 1985), jack mackerel, Pacific sardine, and northern anchovy (*E. mordax*) during the 1997–1998 El Niño period (Chavez et al. 2002).

This investigation is the first to show temperature-dependent growth rates for a nearshore fish species in the eastern Pacific. Positive temperature-dependent growth rates in juvenile white seabass suggest that during years when local ocean temperatures were elevated, metabolic rate was elevated and food was sufficiently abundant to meet the elevated metabolic demands. This finding comes as somewhat of a surprise because a sharp decrease was detected in the population sizes of rocky reef fishes (Holbrook et al. 1997) and market squid (*Loligo opalescens*) (Reiss et al. 2004) in the Southern California Bight during warm-water periods. Given the general decline in fish abundance in the Bight during warm-water periods, it seems likely that prey of the piscivorous white seabass declined in abundance during the warm-water periods when white seabass grew rapidly. The finding of increased growth rates during these warm periods implies that juvenile white seabass were not food limited and most likely preyed upon increased numbers of Pacific mackerel and Pacific sardine as alternative prey items.

Increased growth of juvenile white seabass during warm-water periods could also be explained by declines in population densities during these periods, reducing competition for food. This possibility seems unlikely because the catch of juvenile white seabass in our gill net sampling program increased during to the 1997–1998 El Niño (Allen et al., unpublished data), implying that if anything, competition for food should have been more severe. The mechanisms underlying this population increase are unknown, but may include enhanced northward transport of larvae spawned off Baja California, enhanced local reproductive success, or improved larval and juvenile survival during warm-water periods. For example, juvenile survival may have been enhanced for large, fast-growing juveniles by reduced risk of predation (Margulies 1989; Sogard 1997) or access to a wider range of food sources. In general, white seabass of all ages are more abundant in southern California during El Niño periods (Dayton et al. 1998). While previous work on the effects of El Niño on marine communities has focused primarily on the negative effects of these periods, this study highlights the point that the impacts of these and similar climate changes are complex and likely species and area specific.

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