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ARTICLE

Patterns of Life History and Habitat Use of an Important Recreational Fishery Species, Spotfin Croaker, and Their Potential Fishery Implications

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Abstract

Spotfin croakers *Roncador stearnsii*, a prized recreational catch, were collected throughout the Southern California Bight, primarily as bycatch from a long-term, scientific gill-net collection effort. The maximum otolith-based age in the present study was 24 years—14 years greater than in a previous scale-based aging study. Multiple models were used to estimate mean length at age, including models that utilize larvae as well as juveniles and adults, and the model selection results suggest sexual dimorphism in growth patterns. The juvenile and adult catch per unit effort reflected a clear pattern of habitat selectivity, with fish strongly preferring soft-bottom habitats. Catches in rocky-reef areas were limited but tended to increase with water temperature. The data also suggest that spotfin croakers segregate themselves sexually during the spawning season, when recreational fishing from jetties will target males and fish caught in bays and estuaries are more likely to be spawning females. These results provide further evidence for the importance of protection and restoration efforts for estuaries and bays along this well-developed coastline. The growth of larvae captured in plankton tows in July and September 2004 was substantially faster than that of larvae sampled in May, which coincided with warmer sea surface temperatures, highlighting a potentially important relationship relating temperature (and therefore geography) and settlement success.

While reducing fisheries bycatch is often a major goal of ecosystem-based management efforts (Hall and Mainprize 2004; Pikitch et al. 2004), species that are incidentally caught can provide novel and economically viable opportunities to

gather life history and habitat use information for species that are not otherwise easily collected in large quantities. These often include recreationally fished species that are not also caught commercially. Recreational fisheries can have appreciable

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impacts on the density and size structure of marine fish populations (Schroeder and Love 2002; Coleman et al. 2004; Tetreault and Ambrose 2007), but in many cases their impacts on the ecosystem are not well studied (Lewin et al. 2006; McPhee et al. 2002). As ecosystem approaches to fisheries management are developed, amassing life history information for a large suite of species will be important so that broader concerns can be considered in the design and impact assessment of management strategies (King and McFarlane 2003; Pikitch et al. 2004; Lynch 2006).

Incidental catch from a large-scale scientific gill-net sampling effort targeting juvenile white seabass *Atractoscion nobilis* (Pondella and Allen 2000) provided such an opportunity. White seabass is a valuable commercial and recreational species that has been the focus of a large fishery replenishment effort in the Southern California Bight (SCB). The Nearshore Gill Net Sampling Program for white seabass (ages 1–4) conducted by the California Department of Fish and Game's (CDFG) Ocean Resources Enhancement and Hatchery Program (OREHP) has provided an extensive amount of information on the target species (Allen et al. 2007; Williams et al. 2007; Pondella and Allen 2008). Given the low selectivity of multiple-size-mesh scientific gill-nets, many other species were also caught (Dotson et al. 2009), providing samples to investigate their life history characteristics (Bottinelli and Allen 2007; Froeschke et al. 2007; Miller et al. 2008, 2009; Pondella and Allen 2000, 2008; Pondella et al. 2008). Additionally, various other collections involving nonselective methods, including entrainment, impingement, and entrapment studies conducted at several SCB coastal power plants, either in accordance with U.S. Clean Water Act (CWA) section 316(b) or as a part of heat treatments, have provided a wealth of information on the adult, juvenile, and larval stages of many nearshore species (Herbinson et al. 1999; Miller 2007; Pondella et al. 2008; Miller et al. 2009).

Spotfin croakers *Roncador stearnsii* (family Sciaenidae) have long been prized by recreational anglers in Southern California for their "fighting spirit and delicate taste" and are typically caught in the surf zone from the beach and from man-made structures, such as piers and jetties (Skogsberg 1939). After being deemed overexploited by commercial fishers just after the turn of the 20th century, spotfin croakers, yellowfin croakers *Umbrina roncador* and California corbinas *Menticirrhus undulatus*, were designated solely for recreational take and made illegal to buy or sell by 1915 (Skogsberg 1939; Carlisle et al. 1960; Joseph 1962). The accessibility of this species and relaxed licensing and reporting requirements for pier fishing in California make accurately quantifying the recreational catch difficult. According to data summarized by RecFIN (Recreational Fisheries Information Network, Pacific States Marine Fisheries Commission; <http://www.recfin.org>), the recreational catch of spotfin croakers declined slightly during the 1980s and remained relatively low in the 1990s. Unfortunately, recent estimates (post 2003) have been calculated using a different technique, making comparisons with previous time periods inappropriate due

to calibration uncertainties (Pacific RecFIN Statistical Subcommittee 2007).

Habitat use and life history information for this important recreational species has been limited and based on outdated aging techniques that are not as reliable as current methods. Spotfin croakers are typically described as being soft-bottom, nearshore dwellers that aggregate in bays and depressions just beyond the surf zone and near sand–rock interfaces (Nelson 2006). Spotfin croakers have generally been described as ranging from Point Conception to Mazatlan, including the Gulf of California, but are rarely captured north of Los Angeles (Joseph 1962; Miller and Lea 1972; Feder et al. 1974; Baxter 1980; Eschmeyer and Herald 1983; Love 1991;). Limited tagging studies conducted by the CDFG showed movement from bay to bay, with fish tagged in Los Angeles Harbor being recaptured as far as Oceanside, nearly 100 km to the south (Baxter 1980; Valle and Oliphant 2001). The age and growth of this species were investigated nearly five decades ago; however, larval fish were not studied nor were many fish over the age of 5 (Joseph 1962). A likely explanation for the lack of older fish was that the ages for that study were based on scales, which have been shown to underestimate age, while otolith-based ages tend to be more accurate and precise, particularly with older individuals (Lowerre-Barbieri et al. 1994; Secor et al. 1995).

The aim of this study was to examine fine-scale life history patterns for this important recreational fishery species. The extensive OREHP gill-net catch data were used to look for patterns associated with geography, habitat type, and water temperature. A subset of the gill-net data, where the sex of individuals was determined, was then used to examine fine-scale, sex-specific patterns of habitat use. Finally, age and growth were examined for both larvae and postsettlement juveniles and adults.

METHODS

Fish collections and age estimation.—From 1995 to 2008, scientific gill-nets were typically set four times per year (during April, June, August, and October). Nets were set at 19 stations throughout the SCB, 13 in nearshore coastal waters and 6 in embayments (Figure 1). On a typical sampling occasion, six nets were deployed on the bottom near sunset and left overnight, then retrieved within a few hours after sunrise. Nets were 45.7 m long and 2.4 m deep and included six 7.6-m panels, two panels for each of three square mesh sizes: 25.4, 38.2, and 50.8 mm. In embayments, nets were set at a minimum depth of 2.5 m. At coastal sites, nets were set perpendicular to the shore or to the kelp *Macrocystis pyrifera* forest edge in water depths of 5–14 m. Surface temperatures were taken at each net at the time of sampling. When temperatures were unavailable for a sampling event (5.0% of the events), we used data from the nearest Southern California Coastal Ocean Observing System (SCCOOS) station (<http://www.sccoos.org>). The treatment of bycatch species varied over the 13-year sampling effort. Typically, only the total length (TL; mm) of juvenile and adult spotfin croakers captured

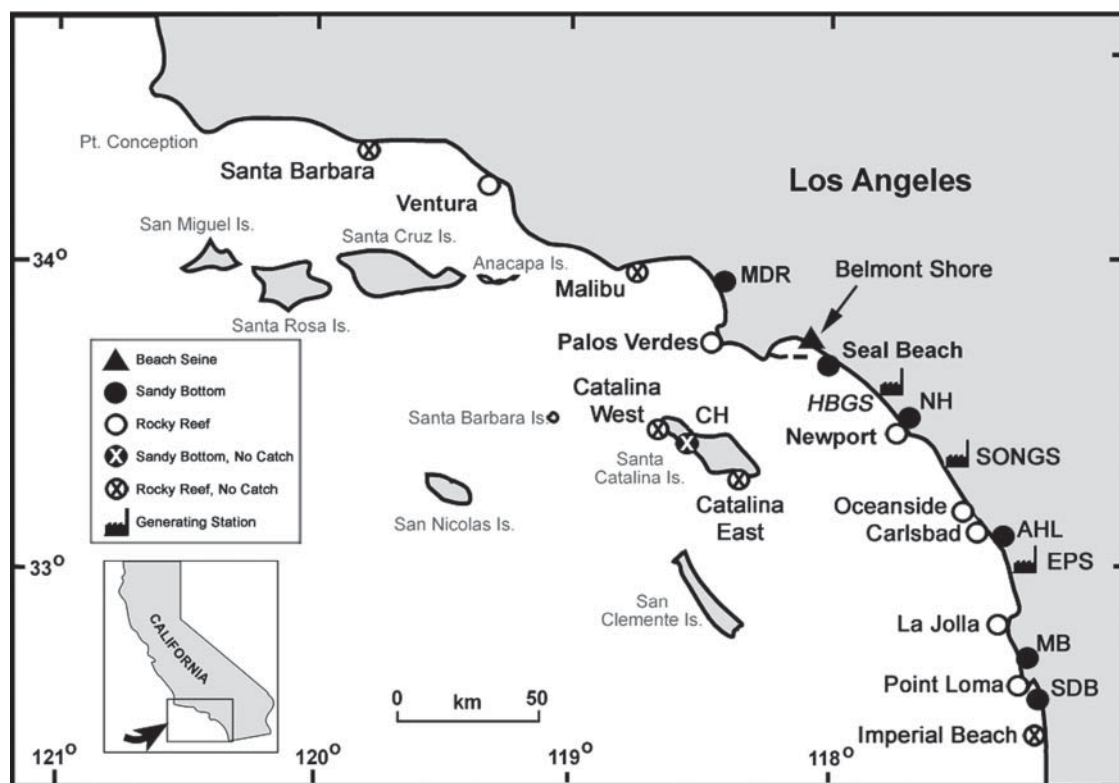


FIGURE 1. Locations of Ocean Resources Enhancement and Hatchery Program gill-net stations, coastal generating stations, and the CDFG beach seine site where sampling took place. Gill-net embayment sites are as follows: MDR = Marina del Rey, CH = Catalina Harbor, HBGS = Huntington Beach Generating Station, NH = Newport Harbor, SONGS = San Onofre Nuclear Generating Station, AHL = Agua Hedionda Lagoon, EPS = Encina Power Station, MB = Mission Bay, and SDB = San Diego Bay.

were measured. However, for some periods (details provided in Results), fish were weighed to the nearest gram, TL and standard length (SL) were measured to the nearest millimeter, sex was determined by macroscopic examination of the gonads, and sagittal otoliths were extracted. Extracted sagittae were cleaned and stored dry.

Additionally, juvenile and adult spotfin croakers collected in the SCB by other methods were used for the present study. Fish were collected during monthly CDFG beach-seine surveys at Belmont Shore (Figure 1) from 1995 to 1997 (Valle and Oliphant 2001) using a 30-m \times 3-m net with 1.9-cm mesh and a 1.8-m \times 1.8-m \times 1.8-m bag in the center. Samples were also collected during heat treatments in 1994 at San Onofre Nuclear Generating Station and in 2005 at Encina Power Station (Figure 1). These fish were measured and sexed and had their sagittae extracted and stored as described above.

Single sagittae from juvenile and adult spotfin croakers were mounted on a wood block using cyanoacrylate (SuperGlue) and sectioned on the transverse axis through the focus using a Buehler-Isomet low-speed saw with a 0.75-mm acetate spacer (Allen et al. 1995). 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 (Williams et al. 2007). The

polished otolith sections were submerged in 70% ethanol and viewed at 10 \times magnification under a dissecting microscope using reflected light (Allen et al. 1995). The reflected light produced series of light opaque and dark translucent bands. The age of each fish was estimated by counting complete pairs of opaque and translucent bands (i.e., increments), which were assumed to be annuli. Each otolith was read to agreement two to three times by two readers without knowledge of any prior reading. Edge analysis was performed to support the assumption of annually produced increments by determining whether the outer edge of each sectioned sagitta was opaque or translucent to reflected light (Francis et al. 1992; Allen et al. 1995; Andrews et al. 2005).

The larval spotfin croakers used for age estimation were collected for CWA 316(b) studies during oblique plankton tows near the Huntington Beach generating station's cooling water intake (Figure 1) on three occasions in 2004: 4 May, 7 July, and 1 September. Larval fish were fixed in a 10% solution of formalin and then stored in 70% ethanol, a practice that has been shown not to affect otolith size, growth rate estimation, or age determination in larval fish (Butler 1992; Kristoffersen and Salvanes 1998; Miller et al. 2011). Each larva was placed on a glass slide, kept moist with a 70% solution of ethanol, viewed through a dissecting scope under cross-polarized light

at 10–16 × magnification, and photographed through the ocular lens using a digital camera. The cross-polarized light made the sagitta stand out relative to the other soft tissue. Sagittae were removed from the larvae with high-gauge hypodermic needles. A sagitta from each individual was submerged in immersion oil (Findlay and Allen 2002), viewed with a compound microscope, and digitally photographed using transmitted light at 100–400× magnification. The transmitted light produced dark opaque and light translucent areas that were assumed to be bipartite daily growth increments, as is the case for many fish found in the SCB (Campana 1984; Cordes and Allen 1997; Love et al. 2007). Larval length and sagittal diameter were measured from the digital photographs to the nearest 1.5 μm. Black-and-white, color, bas-relief, and embossed versions of each otolith image were produced, and growth rings were counted on each image. Agreement was often reached with all four images, and counts were accepted when at least three images agreed. In the few cases where only two of four images agreed, an additional count was conducted by naked eye through the ocular, after which all otoliths had three counts that agreed.

Data analysis and modeling.—All statistical analyses were conducted using R (R Development Core Team 2011). Hypotheses were investigated via model selection using the second-order bias-corrected Akaike's information criterion (AIC_c) unless otherwise noted. For each analysis, sets of various model parameterizations were constructed and ranked according to AIC_c . Akaike weights (w_i) were calculated to assess the relative likelihood of each model in a set and were interpreted as the weight of evidence in favor of the hypothesis represented by the model (Akaike 1973; Burnham and Anderson 2002). When estimable, 95% likelihood profile confidence intervals were produced for parameter estimates (Bolker 2008).

Gill-net CPUE analysis.—Geographic patterns in catch per unit effort (CPUE; mean number of fish caught per standardized sampling event) from OREHP gill-net collections across the SCB were examined for evidence of the influence of geography (in the form of latitude), habitat use, and surface temperature. The model set contained models of mean CPUE as a single mean, as a linear function of latitude with a log-link (*latitude*), and as a linear function of surface temperature at the time of collection with a log-link (*temp*). The log-link function ensures that CPUE is nonnegative (Zuur et al. 2009). Additionally, we included models that estimated habitat specific parameters (*habitat*) for the three models mentioned previously, for a total of six models in the set. Sites were either designated as “soft,” which included a sand bottom site offshore from Seal Beach and all embayments with soft bottoms (Marina del Rey, Catalina Harbor, Newport Harbor, Agua Hedionda, Mission Bay, and San Diego Bay), or as “hard,” where nets were set proximate to rocky reefs (Ventura, Malibu, Palos Verdes, Newport, Carlsbad, Oceanside, La Jolla, Point Loma, and Imperial Beach) (Figure 1). Models were fitted by minimizing the negative log-likelihood assuming that CPUE follows a negative binomial error distribution. The “ecological” parameterization of the negative binomial was

used following Bolker (2008), which is defined by a mean μ and an overdispersion parameter d that measures the amount of heterogeneity in the data (i.e., as d decreases the overdispersion increases). When d is large, the variance approaches the mean and the negative binomial converges on a Poisson distribution (Zuur et al. 2009). Additionally, site- and year-specific mean CPUEs with 95% likelihood profile confidence intervals were estimated. Finally, for a subset of the gill-net catches for which spotfin croakers were measured and sexed, the size distributions and sex ratios of males and females caught at soft-bottom sites inside and outside of embayments were examined.

Larval age and growth.—Larval growth rates (m) were estimated by assuming a linear relationship between larval SL and age in days. To look for evidence of differences in larval growth rates among the three collection dates, we compared a linear model fitted to all data (with a single slope parameter, m_{all}) with a model that estimated a separate slope parameter for each collection date (m_{may} , m_{jul} , m_{sep}). A single y-intercept, which approximates length at age 0 d, was estimated for each model. Parameter estimates were obtained by minimizing the negative log-likelihood assuming that the relationship between length and age is normally distributed, with a separate standard deviation (σ) for each slope parameter estimated. Examination of model residuals confirmed that these assumptions were appropriate.

Juvenile and adult age and growth.—Juvenile and adult growth rates were estimated using multiple growth models, each assuming growth rates change with respect to age in a different manner (Katsanevakis and Maravelias 2008; Lin and Tzeng 2009). The von Bertalanffy growth function (VBGF) assumes that growth decreases linearly with length:

$$L_t = l_{\infty} [1 - e^{-k(t-t_0)}];$$

- L_t = the mean length at time t ;
- l_{∞} = the mean asymptotic maximum length;
- k = the rate at which TL reaches l_{∞} (per year);
- t_0 = the theoretical age at which the fish would have a length of 0 assuming that the larval fish followed the post-settlement growth pattern.

This assumption is crude at best, and t_0 is essentially an arbitrary constant (Beverton and Holt 1993).

The Gompertz growth function (GOMP) assumes that growth decreases exponentially with length:

$$L_t = l_{\infty} e^{[1 - e^{-k_2(t-t_1)}]};$$

- L_t = the mean length at time t ;
- l_{∞} = the mean asymptotic maximum length;
- k_2 = the rate of exponential decrease in the growth rate with age (per year);
- t_1 = a constant similar to t_0 in the VBGF.

The parameterization used here is described in more detail in Katsanevakis and Maravelias (2008). While GOMP is a sigmoidal function, when it is fitted to length at age data, typically only the part of the model after the inflection point is fitted to the data; therefore, it may not offer evidence that the growth rate increases early in life before subsequently decreasing.

Finally, the power function (POWER) does not become asymptotic and has the form

$$L_t = a_0 + a_1 t^b;$$

- L_t = the mean length at time t ;
 a_0 = the y -intercept or, in biological terms, the mean length at age 0 (i.e., the mean length of all fish with less than one increment);
 a_1 and b = parameters that describe the shape of the curve but that have no biological interpretation.

To investigate whether growth was sexually dimorphic, the candidate model set contained each function fitted to all data and all combinations of each function with parameters estimated for each sex separately, for a total of 12 models. Parameter estimates for all models were obtained by minimizing the negative log likelihood, assuming that length at age t is normally distributed with mean L_t and standard deviation σ (Claisse et al. 2009). Examination of model residuals confirmed that these assumptions were appropriate. The SL range of age-0 fish (i.e., fish with less than one increment) in the sample was 137–188 mm, clearly biased toward the larger sizes in the age-class due to the method of sampling. Since this would lead to an overestimate of the mean size of age-0 fish in the models, age-0 fish were excluded from the analyses.

The VBGF parameter k is also sometimes used to estimate other important characteristics about fish populations (Pauly 1980; Charnov 2008). However, excluding small fish, which are often hard to collect, can affect the estimation of k (Craig 1999; Kritzer et al. 2001; Berumen 2005). Therefore, in an attempt to estimate VBGF parameters that also reflect the growth at the youngest ages, we fitted sex-specific VBGF functions to a sample that included the larval fish. Sex, unidentifiable for larval fish, was assigned randomly using a 1:1 sex ratio. The ages of larval fish were scaled so that the mean size at $t = 0$ was consistent with the model being fitted to annual increments (Claisse et al. 2009). For comparison purposes, we also fitted the sex-specific VBGF functions to the original sample (i.e., fish \geq age-1) with t_0 fixed at -0.5 , which is similar to fixing the length at age 0 and has become a common practice in the coral reef fish literature (Kritzer et al. 2001; Berumen 2005; Trip et al. 2008).

RESULTS

Gill-Net CPUE Patterns

A total of 16,756 spotfin croakers were captured during OREHP gill-net sampling. While all sites were sampled each

year, spotfin croakers were captured at only 13 of the 19 sites (Figure 1; Table 1). No spotfin croakers were captured at the Santa Barbara site or any of the island sites. Since Santa Barbara is at the far northern edge of their published range and spotfin croakers are relatively rare at Santa Catalina Island (Miller and Lea 1972; Love 1991), the Santa Barbara and Santa Catalina Island collection sites were excluded from the subsequent analysis. There were 643 sampling occasions, typically occurring every 2 months from April through October (April: 136 events; June: 174 events; August: 160 events; and October: 173 events; see Table 2 for annual event counts). Catch per unit effort (CPUE) was standardized to six nets per sampling event. During most sampling occasions six nets (mean = 5.9 ± 0.6) were set; however, there were rare occasions when as few as three or as many as eight nets were set.

Model selection revealed that both habitat and temperature influenced mean CPUE. Models that included habitat-specific parameters were all ranked well above models in which habitat-specific parameters were not included (Table 3). Mean CPUE was around 35 times greater when nets were set over soft bottoms than over hard bottoms (Table 1). The highest ranked model in the set (Table 3), which received all of the support ($w_i = 1$), modeled the effects of surface water temperature on mean CPUE separately for soft- and hard-bottom sites. While water temperatures were significantly warmer for nets set over soft bottoms than over hard bottoms (t -test assuming equal variances: $t = -9.40$; $df = 641$; $P < 0.001$; Table 1), the range of temperatures between the two habitat types still overlapped considerably (Figure 2). While there was actually no relationship between temperature and catch at soft-bottom sites (slope = 0.013; 95% confidence interval [CI] = -0.094 to $+0.12$), there was a positive relationship between CPUE and temperature when nets were set above a hard bottom (slope = 0.74; 95% CI = 0.43–1.04; Figure 2). Additionally, visual examination of the data reveals that almost no fish were caught in the hard-bottom habitats when surface temperatures were below 17°C. We also examined post hoc the influence of the single large catch in the hard habitat (CPUE = 203 at 19.1°C; Figure 2) on the relationship to temperature in that habitat by refitting the model with this data point removed. While it did affect the shape of the line with respect to the remaining data (dotted line, Figure 2), CPUE still exhibited a positive linear relationship to temperature on the log-link scale (slope = 0.62; 95% CI = 0.40–0.88).

Estimates of the overdispersion parameter d from the negative binomial error distribution were low for all models in the set (range, 0.24–0.06), reflective of the high proportion of 0 catches at most sites combined with relatively few large catches. While this is visually evident as well, it provides further support for the selection of a negative binomial error distribution over a Poisson error distribution. There were clear site-specific differences in mean CPUE (Table 1), ranging from lows at Malibu (0) and Imperial Beach (0) to highs at Agua Hedionda (147.0) and Newport Bay (138.7). The six sites with the highest mean CPUEs

TABLE 1. Sampling, covariate, and results summary for OREHP gill-net catch per unit effort (CPUE) analysis. Factors are as follows: n = the number of sampling events; mean CPUE = the maximum likelihood estimate of fish caught per sampling event assuming a negative binomial error distribution; LCI, UCI = the lower and upper 95% likelihood profile confidence limits; max catch = the maximum number of fish caught during a single sampling event; and temperature = the sea surface temperature at the sampling site during collection.

Location and habitat	n	Latitude	Habitat	Mean CPUE	LCI	UCI	Max catch	Temperature			
								Mean	SD	Min	Max
Ventura	43	34.29	Hard	0.0	NA	NA	1	16.6	1.8	12.7	20.6
Malibu	45	34.03	Hard	0.0	0.0	0.0	0	18.8	2.1	14.2	22.0
Marina del Rey	40	33.98	Soft	1.4	0.6	3.8	21	20.4	2.3	14.4	24.6
Palos Verdes	43	33.80	Hard	0.2	0.1	0.7	3	18.0	2.0	14.1	23.0
Seal Beach	43	33.73	Soft	28.9	15.0	67.1	206	20.2	2.7	14.8	26.6
Newport Bay	42	33.61	Soft	138.7	102.0	208.1	564	20.2	2.2	15.8	24.5
Newport	43	33.56	Hard	1.5	0.8	3.4	18	18.3	2.3	12.8	22.3
Oceanside	41	33.21	Hard	2.5	0.7	28.4	38	18.8	2.3	14.0	24.2
Agua Hedionda	42	33.14	Soft	147.0	114.3	195.7	349	19.6	2.5	14.9	24.8
Carlsbad	42	33.13	Hard	12.1	6.1	29.3	203	19.3	2.2	14.4	24.9
La Jolla	44	32.85	Hard	0.8	0.4	2.5	11	18.5	2.0	14.0	23.7
Mission Bay	46	32.78	Soft	51.1	30.7	96.0	270	19.1	2.4	14.1	23.7
Point Loma	44	32.66	Hard	0.1	NA	NA	1	18.3	2.3	14.3	23.7
San Diego Bay	43	32.66	Soft	23.3	14.2	41.9	126	20.5	2.1	15.5	24.3
Imperial Beach	42	32.58	Hard	0.0	0.0	0.0	0	17.3	1.8	13.5	20.8
Hard habitat	387			1.9	1.2	3.1	203	18.2	2.2	12.7	24.9
Soft habitat	256			65.7	51.8	85.4	564	20.0	2.4	14.1	26.6
Total	643			31.6	24.7	41.4	564	18.9	2.5	12.7	26.6

were soft-bottom sites. There was also high variability in CPUE within most sites; the minimum CPUE was 0 at all sites, while the maximum CPUE ranged from 0 to 564 (Table 1). The annual differences in mean CPUE across all sites were relatively small, with large 95% CIs that overlapped substantially and tended to be asymmetrical with larger upper intervals (Table 2).

Sexual Differences in Soft-Bottom Habitat Use

Though sex information was only collected for a few sampling periods, sexual differences were found in the patterns of habitat use between different types of soft-bottom sites. At Seal Beach, a relatively unprotected soft-bottom site located adjacent to a jetty and approximately 500 m offshore, 92% of the spotfin croakers caught during gill-net sampling in 2001–2003 were male (significantly different from a 1:1 sex ratio: $n = 460$, $\chi^2 = 323.9$, $P < 0.001$). At Agua Hedionda (1997 and 1998) and Newport Bay (1997), two protected bay and estuary sites, a higher percentage of females were caught, 60% and 79% respectively (both significantly different from a 1:1 sex ratio; Agua Hedionda: $n = 453$, $\chi^2 = 19.1$, $P < 0.001$; Newport Bay: $n = 200$, $\chi^2 = 78.6$, $P < 0.001$). The sex-specific size distributions from these habitat types suggest that across our recorded size

range females are present in embayments during the spring–summer sampling period while some males remain segregated in offshore soft-bottom habitats (Figure 3).

TABLE 2. Annual sampling and results summary for the OREHP catch per unit effort (CPUE) analysis. See Table 1 for additional information.

Year	n	Mean CPUE	LCI	UCI
1996	39	10.1	3.3	61.8
1997	60	11.3	4.9	36.7
1998	60	38.1	16.6	126.1
1999	58	47.0	21.1	175.4
2000	60	27.3	13.1	77.3
2001	60	17.3	7.7	52.4
2002	60	18.1	8.7	48.8
2003	60	16.9	7.6	50.2
2004	59	21.2	11.0	49.3
2005	42	39.1	16.0	143.6
2006	23	41.3	11.7	405.3
2007	40	40.2	17.2	136.9
2008	22	40.0	12.9	281.9

TABLE 3. Model selection results. For each of the three analyses, models were ranked according to the difference in the Akaike information criterion corrected for small sample size (ΔAIC_c) and Akaike weight (w_i); N_p = the number of estimated parameters in each model. The first analysis related gillnet catch per unit effort (CPUE) to habitat type, latitude of the collection site, and sea surface temperature at the time of collection. The second analysis examined the influence of collection month on larval growth rates (m). The third analysis examined juvenile and adult age and growth using parameterizations of the von Bertalanffy growth function (VBGF), the Gompertz growth function (GOMP), and the power function (POWER) in all possible combinations with all of the data or those for each sex separately (assumed annual ages fitted to ages ≥ 1).

Model		AIC_c	ΔAIC_c	w_i	N_p	
Gill-net CPUE						
Habitat temperature (<i>habitat, temp</i>)		2,933.3	0.0	1.00	6	
Habitat (<i>habitat</i>)		2,954.3	21.0	0.00	4	
Habitat, latitude (<i>habitat, latitude</i>)		2,958.6	25.3	0.00	6	
Temperature (<i>temp</i>)		3,186.6	253.3	0.00	3	
Single mean (<i>single mean</i>)		3,197.1	263.8	0.00	2	
Latitude (<i>latitude</i>)		3,197.4	264.1	0.00	3	
Larval growth						
$m_{\text{may}}, m_{\text{jul}}, m_{\text{sep}}$		160.2	0.0	1.00	7	
m_{all}		230.4	70.2	0.00	3	
Juvenile and adult age and growth						
All data	Females					
	POWER	POWER	8,357.7	0.0	0.79	8
	VBGF	POWER	8,360.5	2.8	0.19	8
	GOMP	POWER	8,365.1	7.4	0.02	8
	POWER	VBGF	8,371.2	13.5	0.00	8
	VBGF	VBGF	8,374.0	16.3	0.00	8
	POWER	GOMP	8,376.0	18.3	0.00	8
	GOMP	VBGF	8,378.5	20.8	0.00	8
	VBGF	GOMP	8,378.8	21.1	0.00	8
	GOMP	GOMP	8,383.4	25.7	0.00	8
	POWER		8,483.0	125.3	0.00	4
	VBGF		8,505.7	148.0	0.00	4
GOMP		8,516.4	158.7	0.00	4	

Larval Growth

One hundred spotfin croaker larvae were captured and aged assuming daily deposition of increments. The ages of the larvae ranged from 15 to 26 d, 4–15 d, and 3–28 d for the May, July, and September collections, respectively. A post hoc examination of daily sea surface temperatures from Newport Beach (near the Huntington Beach generating station; data obtained from SCCOOS, <http://www.sccoos.org>) revealed that sea surface temperatures, averaged over the lifespan of the oldest fish in each sample, were much lower in May (mean \pm SE = 15.1 \pm 0.2°C) than in July (18.3 \pm 0.2°C) and September (19.0 \pm 0.1°C) (Figure 4). Collection date had a clear influence on larval growth rate, with the model that estimated collection-specific growth rates receiving all of the support ($w_i = 1$; Table 3). For the 19 larval fish collected on 4 May 2004, the mean daily growth rate (95% likelihood profile confidence interval) was 0.17 mm/d (0.15–0.19). This was 32% lower than the rate of 0.25 mm/d (0.19–0.30) for the 23 individuals collected on 7 July 2004 and 0.25 mm/d (0.22–0.27) for the 58 individuals

collected on 1 September 2004 (Figure 5). There was also a strong significant linear relationship between otolith diameter (μm) and TL (mm) ($TL = 1.4 + 0.035 \cdot \text{otolith diameter}$; $r^2 = 0.92$; $P < 0.001$).

Juvenile and Adult Length at Age Relationship

A total of 916 spotfin croakers were measured, weighted, and sexed and had one of their sagittae sectioned and aged. The sample included 399 females and 462 males captured in gill nets from 1997 to 2004 from all sites where spotfin croakers were caught, with the exception of Ventura and Point Loma. Additionally, it included fish that were caught during beach-seine collections at Belmont Shore from 1995 to 1997 (27 females), and 5 larger fish (3 females and 2 males) from heat treatments at Encina Power Station and 2 larger females from heat treatments at San Onofre Nuclear Generating Station. The vast majority of individuals that we examined were identifiable as males or females through macroscopic examination of the gonads, even at a young age. However, a reliable estimate of size- or age-

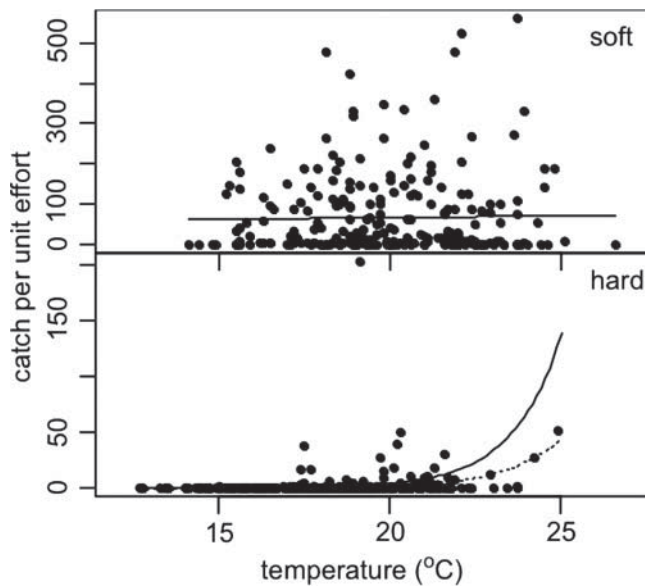


FIGURE 2. Relationships implied by the highest-ranked model (Table 3) between gill-net catch per unit effort of spotfin croakers and sea surface temperature at the time of collection, by habitat type (soft bottom or rocky reef). The solid curves represent the original models back-transformed from the log-link scale, the dotted curve the back-transformed model fitted to the data without the largest catch outlier.

at-maturity could not be obtained, as no histological examination was performed to confirm the development of mature gonads. The relationship between SL (mm) and TL (mm) was $SL = 0.82 \cdot TL - 3.62$ ($r^2 = 0.99$; $P < 0.001$). The relationship between SL and weight (g) was $weight = 0.000060 \cdot SL^{2.84}$ ($r^2 = 0.94$; $P < 0.001$).

Otolith edge analysis revealed that otoliths with opaque edges occurred most frequently among fish collected in June (69.6%; $n = 250$) and August (75.1%; $n = 387$), with a substantially lower incidence by October (12.9%; $n = 240$). Otoliths from fish collected during November and February all had translucent edges, but the sample sizes from those months were extremely low. This is consistent with the assumption that increments form once a year during the summer, as has been noted for many species found in the SCB (Allen et al. 1995; Andrews et al. 2005), including other croakers from the SCB (e.g., black croaker *Cheilotrema saturnum* [Miller et al. 2008]; yellowfin croaker [Pondella et al. 2008]) and other sciaenids found elsewhere (e.g., red drum *Sciaenops ocellatus* [Ross et al. 1995]; black drum *Pogonias cromis* [Jones and Wells 1998]; brown meagre *Sciaena umbra* [La Mesa et al. 2008]). Spotfin croakers are long-lived, with a potential lifespan of at least 24 years assuming that otolith increments are formed once each year. Age-0 fish (fish with <1 increment) were excluded from the analyses as sampling was clearly biased toward the larger sizes in that age-class, leaving 431 females and 464 males in the remaining sample.

Model selection clearly supported models that assumed sexually dimorphic differences in growth pattern (Table 3). Mean

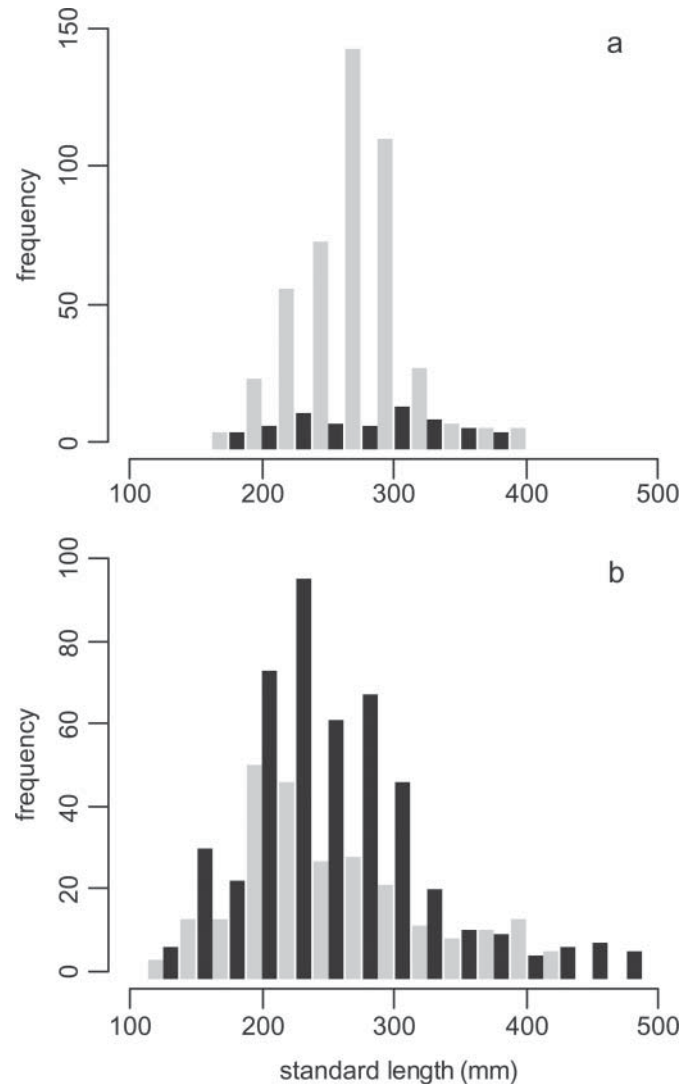


FIGURE 3. Size structures of female (black bars) and male (gray bars) spotfin croakers collected in soft-bottom habitat at (a) an offshore site (Seal Beach [2001–2003]) and (b) two embayment sites (Agua Hedionda [1997–1998], and Newport Harbor [1997]).

growth rates appeared to be similar through age 3, after which the models suggest that females grew faster on average (Figure 6a). The sex-specific POWER model received the most support ($w_i = 0.79$; Table 3), suggesting that growth rates do not approach an asymptote over this age range. According to the sex-specific POWER model, older females (>6 years) were 30–52 mm larger than males on average. However, at least until the oldest ages, the differences between the mean size at age predicted by the sex-specific POWER functions and the sex-specific VBGF functions were relatively small for both males and females (Figure 6a). Mean length at age (and thus growth rate) was also more variable in females than males (i.e., σ was larger for females than for males in all models; Table 4). Param-

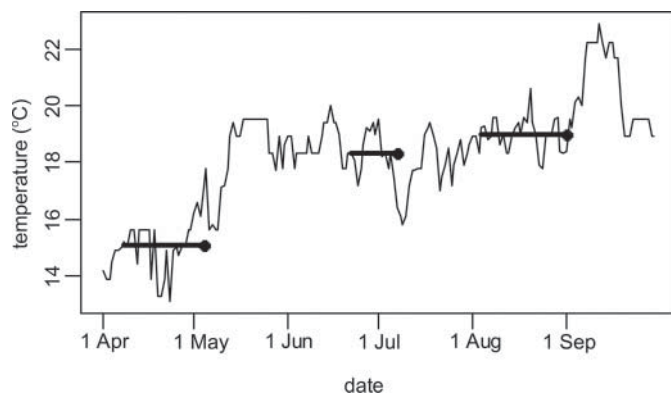


FIGURE 4. Daily sea surface temperatures from Newport Beach near the Huntington Beach Generating Station in 2004 (Southern California Coastal Ocean Observing System data). The three larval collections are indicated by the black circles and plotted at the mean temperatures over the periods (dark lines) during which the oldest individuals in each collection were alive.

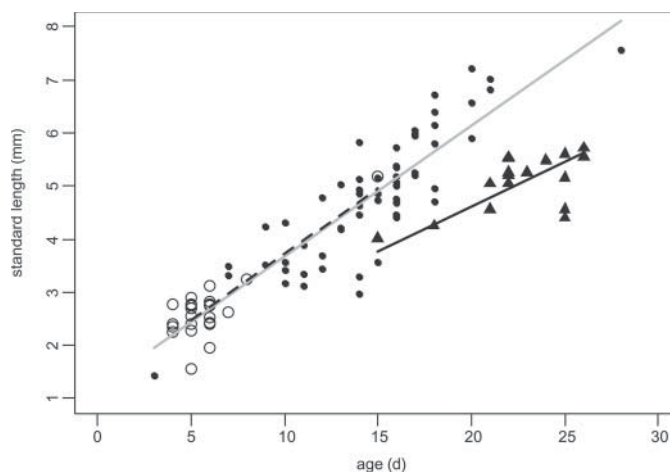


FIGURE 5. Larval fish length at age data for May (triangles and black line), July (open circles and dashed line), and September 2004 (closed circles and gray line). The slopes of the three lines indicate the mean growth rates for the different months.

eter estimates were also reported for models that did not assume sexual dimorphism for use in future comparative studies.

When sex-specific VBGFs were fitted to a sample that included the larval fish, the parameter estimates for both males and females drastically underestimated mean size at the older (>10 years) ages (Figure 6b). The values of l_{∞} were substantially smaller (~ 100 mm), while the k values were around 3–7 times larger than those from the VBGFs fitted to the sample without larval fish. Fitting sex-specific VBGFs with t_0 fixed at -0.5 yielded results that were nearly identical to those that included the larval fish and thus were omitted.

DISCUSSION

Habitat Use Patterns

Assuming that the CPUE of spotfin croakers in the present study correlates with local abundance (Harley et al. 2001), there was clear evidence of habitat selectivity for this species, with fish strongly preferring soft-bottom habitats. This is consistent with previous general descriptions of their habitat use (Valle and Oliphant 2001; Nelson 2006). While the previous life history study of this species only sampled in soft-bottom habitats (Joseph 1962), the present study documents that spotfin croakers

TABLE 4. Parameter estimates (95% likelihood profile confidence intervals in parentheses) for three functions estimating the mean length at age for spotfin croakers: the power function (POWER) fitted to data for fish 1 year and older, the von Bertalanffy growth function (VBGF) fitted to data for fish 1 year and older, and the von Bertalanffy growth function fitted to data for larval fish as well as those 1 year and older.

Parameter	Males	Females	Both sexes
POWER (\geq age 1)			
a_0	158 (121–186)	21 (–135 to +84)	70 (8–115)
a_1	77 (54–111)	196 (135–320)	153 (110–198)
b	0.43 (0.34–0.53)	0.29 (0.17–0.37)	0.31 (0.24–0.38)
σ (mm)	22 (20–23)	31 (29–33)	28 (26–29)
VBGF (\geq age 1)			
l_{∞} (mm)	467 (444–502)	468 (445–498)	460 (443–480)
k (per year)	0.10 (0.08–0.12)	0.17 (0.14–0.20)	0.13 (0.12–0.15)
t_0	–6.3 (–7.6 to –5.4)	–2.8 (–3.4 to –2.3)	–4.1 (–4.6 to –3.6)
σ (mm)	22 (21–23)	31 (29–33)	28 (27–29)
VBGF with larval fish			
l_{∞} (mm)	325 (318–332)	381 (377–394)	341 (335–348)
k (per year)	0.68 (0.62–0.76)	0.47 (0.42–0.51)	0.59 (0.55–0.63)
t_0	–0.51 (–0.56 to –0.47)	–0.58 (–0.65 to –0.52)	–0.53 (–0.58 to –0.50)
σ (mm)	31 (29–33)	35 (33–37)	34 (33–36)

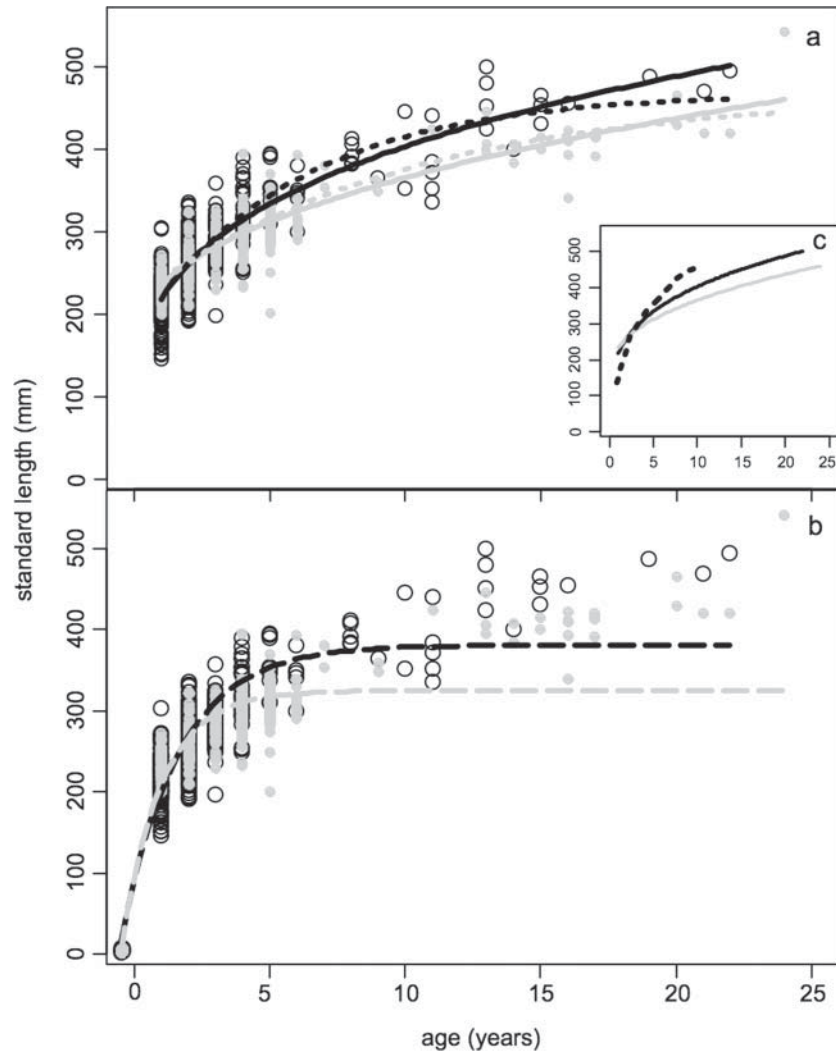


FIGURE 6. Relationships between length and age for female (open circles and black lines) and male spotfin croakers (solid circles and gray lines). Panel (a) shows sex-specific power (solid lines) and von Bertalanffy growth functions (dotted lines) fitted to data for individuals age-1 and older. Panel (b) shows sex-specific von Bertalanffy growth functions (dashed lines) fitted to data for larval fish as well as individuals age-1 and older. Panel (c) shows the difference in the relationships between length and age from the present study (based on otolith aging data from a fitted power function [females, black solid line; males, gray solid line]) and Joseph (1962) (based on ages estimated from scales [both sexes combined, dashed line]).

are also present in rocky-reef habitats, albeit less frequently and at lower densities. Soft-bottom sites tended to have warmer water temperatures during sampling than hard-bottom sites, probably due to shallower depths in the embayments. These differences could reflect an overall preference for warmer waters, as this species is at the northern end of its geographic range. Additionally, benthic invertebrates (common prey items for spotfin croakers) have been shown to occur at higher densities in embayments (Mikel et al. 2007, Appendix F). Spotfin croakers were caught in hard-bottom habitats almost exclusively when temperatures were above 17°C, possibly to traverse between embayments or other soft-bottom habitats during the summer months when temperatures are warmer. While it is possible that temperature could be positively correlated with activity levels and thus

catchability, there was no relationship between temperature and CPUE within soft-bottom habitats. Spotfin croakers in the SCB are near their historical northern limit, so there is an expectation that CPUE will generally decrease at higher latitudes. This, however, is not the case in the SCB. Given the lack of support for geography in the model it is clear that, at the relatively small spatial scale of this study, local environmental features have a greater influence on the distribution of abundance than does latitude.

Spotfin croakers also appear to segregate themselves sexually within different soft-bottom habitats during the spring and summer months. The gill-net catch at a nonembayment sandy-bottom site located adjacent to a jetty and approximately 500 m offshore was comprised almost entirely of males over a period of 3 consecutive years, suggesting that fishing from large jetties

targets males. Conversely, more females were caught at two protected bay and estuary sites during the spring–summer sampling period that corresponds to the spotfin croaker spawning season (Skogsberg 1939).

Larval Growth

The growth of the larval spotfin croakers sampled as a part of CWA 316(b) studies in July and September 2004 was substantially faster than that of those sampled in May of that year. Given that the samples contained larvae with a wide range of ages, including many more than a week old, and that the larval duration of spotfin croakers is about 25 d (Moser 1996; Watson 1982), it is possible that larvae were retained locally for most of their lifespan, and it is important to consider the effect of sea surface temperature near the collection site over that lifespan. Daily sea surface temperatures, averaged over the lifespan of the oldest fish in each sample, were much lower in May than in July and September (Figure 4). Positive correlations between sea surface temperature and growth have been shown in other larval and adult fish (Schmidt-Nielsen 1984; Brander 1995; Lehodey and Grandperrin 1996; Anderson and Dalley 2000; Gillooly et al. 2002; Brown et al. 2004; Mollmann et al. 2005; Williams et al. 2007). This important relationship is also highlighted in several studies relating larval growth rates to settlement success (Houde 1987, 1997; Bergenius et al. 2002) and settlement success to latitude (Houde 1989). As stated previously, spotfin croakers in the SCB are near their historical northern limit. It should be noted however, that the growth rate estimate for the July sample is dominated by a single older individual, leaving no replication for the trend established by the other two samples. Other factors, such as food resources, could play roles in the growth difference, but the magnitude of the difference (>30%) is substantial enough that it could result in differences in post-settlement survival (Gagliano et al. 2007; Hamilton et al. 2008) and warrants further investigation.

Juvenile and adult age and growth.—The maximum age determined from the otolith samples in the present study was 24 years. This represents a longer lifespan than for some sciaenids that reach a similar maximum size, such as the brown meagre (19 years; La Mesa et al. 2008) and yellowfin croaker (Pondella et al. 2008), but substantially less than that of the red drum (Ross et al. 1995) and the black drum (Jones and Wells 1998), which reach a maximum age of over 50 years and a maximum length well above 1 m. Our results also demonstrate a maximum age for this species that is 14 years greater than that obtained by a previous study which based ages on annuli from scales (Joseph 1962). After age 4, it would appear that the use of spotfin croaker scales drastically underestimates age (Figure 5c). This finding is consistent with results of previous studies of other species that found otoliths to be more accurate than scales in the estimation of age (Lowerre-Barbieri et al. 1994; Secor et al. 1995). Joseph (1962) noted that resolving annuli in scales appeared to become more difficult after age 3, possibly reflecting changes in growth

related to spawning activity. The underestimation of age then leads to an overestimate of growth rate (Figure 6c).

The model selection results suggest sexual dimorphism in the growth patterns and adult sizes of spotfin croakers. Joseph (1962) was unable to make this distinction as a result of his aging methods. The annual increments in sagittae used in this study were easier to distinguish beyond age 3, and this is where most of the difference between the two studies lies. Additionally, sex was not identified in most of the samples used in the Joseph (1962) study, as scales were removed for aging before fish were tagged and released. In this study, mean lengths at age were similar for the sexes through ages 3, and the sexual size dimorphism was due to faster female growth after age 3. Similar sexual differences in growth patterns have been observed in other sciaenids (La Mesa et al. 2008; Miller et al. 2008, 2009; Pondella et al. 2008). This could be reflective of habitat use differences if males tend to reside further offshore and bays and estuaries are preferential habitat in terms of growth; however, the ecological determinants of sexual size dimorphism are often hard to establish (Shine 1989).

Model selection support for the POWER models over the VBGF suggests a nonasymptotic pattern of growth in this species. Despite the differences in model selection results, estimates of mean length at age were quite similar for the VBGF and the POWER models, at least until the oldest ages for females. The model selection process is sensitive to the quality of data available in addition to the actual pattern of growth (Katsanevakis and Maravelias 2008), and it is important to be pragmatic when interpreting the implications of the models selected (Araya and Cubillos 2006). The effects of this were amplified when VBGFs were fitted to data that also included the larval fish. Their inclusion at the left end of the VBGF curves outweighed the influence of the older individuals on the right side of the curves, leading to underestimation of mean size at the older ages for both females and males. Further, since the VBGF parameter k reflects the time it takes for mean size to approach its asymptote, values of k are also overestimated for both sexes in this model. Additionally, including the larval fish had the same effect as constraining the model to a certain length at age 0. Therefore, caution should be taken when constraining the lower end of the curve so that the final fit is considered across the entire age range and l_{∞} is not underestimated and k is not overestimated (Cailliet et al. 2006).

Management Applications

Logistically, it is difficult to adequately sample the younger and older ages for most fish species, particularly in studies such as ours in which the samples were incidentally caught even when scientific gill-nets were used to minimize size selectivity. The fit of the growth curves then tends to depend more on medium-sized and middle-aged individuals. This should be considered when researchers and managers are using growth model parameters (typically VBGF parameters) for purposes other than simply estimating mean size at age (e.g., Pauly 1980;

Charnov 2008). In the present study, the sex-specific POWER models provided the best description of mean length at age for the spotfin croakers in our sample, suggesting a nonasymptotic pattern of growth in this species. However, the estimates of mean length at age were quite similar in the VBGF and the POWER models across the ages in our sample, so that using the more standard VBGF may be justifiable in future applications. However, we would advise against using the estimates of the VBGF parameter k reported here to approximate other aspects of spotfin croaker biology. The values derived from the sample that included the larval fish were clearly overestimated, and those derived from the sample without larval fish probably do not accurately reflect the growth at the youngest ages. If estimates of other demographic parameters are going to be based on their relationship to VBGF parameters, the sample size, the size–age distribution in the sample, and how the model was fitted to the data (e.g., constrained versus unconstrained) should all be considered, as each can influence the estimation of VBGF parameters (Craig 1999; Kritzer et al. 2001; Araya and Cubillos 2006; Katsanevakis and Maravelias 2008).

Recreational fishing should be considered in ecosystem-based resource management strategies because it can have clear impacts on fish populations, resulting in overfishing of valuable species (Coleman et al. 2004; Erisman et al. 2011). As these approaches to fishery management are developed for species such as the spotfin croaker, it is also important to recognize the potential influence of local environmental factors, such as temperature and habitat characteristics, on larval dispersal, growth, and postsettlement survival. Our results show that small variations in the timing of spawning activities in this species can impact the growth of larvae, potentially affecting postsettlement mortality. Additionally, adult habitat selection analyses provide further evidence for the importance of protection and restoration efforts for estuaries and bays along this well-developed coastline (Zedler 1991; Lafferty 2005; Pondella 2009). Spawning by other sciaenids has been observed in estuaries (Ross et al. 1995; Reyier et al. 2011), and direct mortality and sublethal effects from recreational fisheries have been shown to impact adult populations (Coleman et al. 2004; Reyier et al. 2011). Our results provide evidence that bays and estuaries are important spawning habitats for spotfin croakers and that recreational fishing in these habitats would result in a greater take of females. More fine-scale studies of habitat use and spatially explicit fishing patterns are needed for this (and similar) species within the SCB to better understand the habitat use patterns related to spawning and the potential impacts of recreational fishing on these processes.

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