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Life History, Ecology, and Long-term Demographics of Queenfish

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Abstract.—Queenfish *Seriphus politus* were collected at coastal power plants from San Clemente to Ventura, California. Power functions best described relations between otolith length, width, or weight and either standard length (SL) or total body weight. The length–weight relationship was described by the following equation: $\text{weight} = 10^{-5} \times \text{SL}^{3.09}$. Individuals were aged to 12 years by using sagittal otolith sections. Females grew at a significantly faster rate than males. Both sexes reached 50% maturity by 100 mm SL, or shortly after age 1. The total annual instantaneous mortality coefficient was estimated at 0.42. Catalina Harbor (on the windward side of Santa Catalina Island) and Ventura were the most populous sites based on gill-net catch per unit effort from 1995 to 2006. Juvenile and adult queenfish populations have declined since 1980 in a significant relationship with nearshore plankton biomass. Larval queenfish densities recorded in King Harbor (Redondo Beach) have declined since 1987. Long-term recruitment estimates indicated peak recruitment prior to 1976, with three subsequent downward baseline shifts.

The croakers (Sciaenidae) constitute a substantial portion of the local ichthyofauna throughout their range, with over 270 identified species worldwide (Nelson 2006), and many species support commercial fisheries, recreational fisheries, or both (Sasaki 2001). Within southern California, queenfish *Seriphus politus* were frequently landed by shore anglers from 1995 to 2000 (Love 2006) and targeted by commercial fisherman, often commingled with white croakers *Genyonemus lineatus* in landings (Moore and Wild 2001). This frequency of occurrence in fishery landings (commercial and recreational) is consistent with their relatively high abundance in fishery-independent nearshore adult and larval fish surveys throughout southern California (Allen and DeMartini 1983; Barnett et al. 1984; DeMartini and Allen 1984; Love et al. 1984; Walker et al. 1987; McGowen 1993; Pondella and Allen 2000). Queenfish adults and larvae are coastally dependent, predominantly occurring in the nearshore waters; densities were generally greater prior to 1980 (Lavenberg et al. 1986; McGowen 1993; Moser et al. 2001). Despite their prevalence throughout the nearshore Southern California Bight, little life

history information on queenfish is available. Much of the available data are limited to reproduction (summer spawning), feeding (planktivorous), and diel migration patterns (Hobson and Chess 1976; DeMartini and Fountain 1981; DeMartini and Allen 1984; DeMartini et al. 1985). No information on growth, longevity, mortality, distribution, recruitment, or long-term abundance trends has been published. Without an understanding of these parameters, any future management policies, either single species or ecosystem based, would be severely limited as they pertain to queenfish. Therefore, this research was intended to document queenfish age and growth, annual mortality, spatial and temporal distributions, and recruitment trends.

Methods

Age at length and otolith morphometrics.—From May 2006 to March 2007, 821 individuals were collected for age-at-length and morphometric analyses during surveys at the following three California power plants: Scattergood Generating Station (SGS) in El Segundo; Huntington Beach Generating Station (HBGS) in Huntington Beach; and San Onofre Nuclear Generating Station (SONGS) near San Clemente (Figure 1). All individuals were measured to the nearest millimeter standard length (SL), weighed to the nearest gram, and sexed macroscopically, and their sagittal otoliths were removed. All three facilities withdraw cooling water through offshore, velocity-

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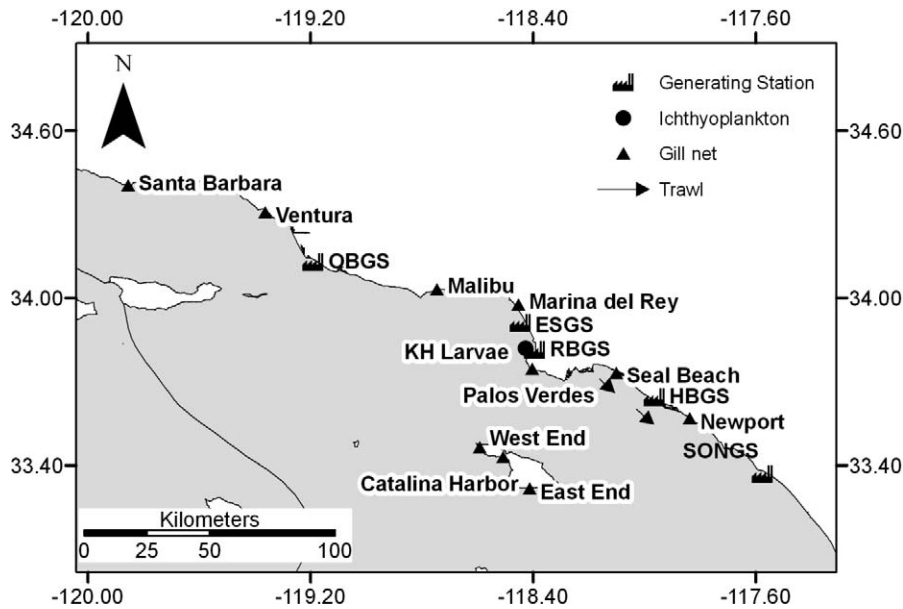


FIGURE 1.—Locations of all gill-net, trawl, and larval sampling stations and power plant sampling sites from which queenfish were collected in southern California (QBGS = Ormond Beach Generating Station; ESGS = El Segundo Generating Station; RBGS = Redondo Beach Generating Station; KH Larvae = King Harbor larval sampling site; HBGS = Huntington Beach Generating Station; SONGS = San Onofre Nuclear Generating Station).

capped intakes. Intakes for HBGS and SGS are located approximately 500 m offshore at a depth of 5 and 6 m, respectively, along relatively continuous stretches of sandy-bottom habitat. The SONGS withdraws seawater through three intake structures located adjacent to low- and mid-relief rocky reef habitat inshore and adjacent to a bed of giant kelp *Macrocystis pyrifera* (San Onofre kelp bed). Two SONGS intakes are located approximately 960 m offshore at a depth of 9 m, while the third is located 900 m offshore at a depth of 8 m. A χ^2 test was used to confirm that the size distribution of impinged queenfish samples was consistent with that of individuals taken during nearby otter trawl surveys. Annual otter trawl surveys conducted offshore of the San Gabriel River mouth in Seal Beach and the HBGS from 2001 to 2006 were used for size comparison (Figure 1). Both data sets were $\log_e(x + 1)$ transformed prior to analysis.

A subset of otoliths was measured (length $n = 226$; width $n = 228$) and weighed ($n = 226$; Table 1). One

otolith from each pair was sectioned as per the procedures of Allen et al. (1995). Sections submerged in a 70% solution of ethanol were read under reflected light with a stereoscope by a single reader. A minimum of two readings per section were made, with a minimum of 1 month separating each reading. If no agreement between the two readings occurred, then a third and final reading was made. Agreement was reached on the otoliths of all but one individual. Annular formation was confirmed by using otolith edge analysis. Data were fitted to the von Bertalanffy growth model by using the von Bertalanffy Iterative Approach software program (FAO 2005):

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

where L_t = length at time t , L_{∞} = the theoretical maximum length, k = a constant expressing the rate of approach to L_{∞} , and t_0 = the theoretical age at which $L_t = 0$.

Von Bertalanffy models were constructed for all

TABLE 1.—Equations describing the relationship between otolith weight, length, or width and total body weight (TBW) or standard length (SL) of queenfish captured along the coast of southern California.

Dependent variable	Otolith weight (g) ($n = 226$)	Otolith length (mm) ($n = 226$)	Otolith width (mm) ($n = 228$)
TBW (g)	$TBW = 2,688(\text{otolith weight})^{1.4854}$	$TBW = 0.0263(\text{otolith length})^{3.7049}$	$TBW = 0.0115(\text{otolith width})^{5.5869}$
SL (mm)	$SL = 503.59(\text{otolith weight})^{0.4669}$	$SL = 13.511(\text{otolith length})^{1.1605}$	$SL = 10.406(\text{otolith width})^{1.7511}$

individuals combined and for each sex; immature or sex-undetermined individuals were excluded from the sex-specific analysis. The difference between sex-specific growth rates was tested by analysis of residual sum of squares (ARSS) derived by nonlinear regression (Haddon 2001). The instantaneous total annual mortality coefficient (Z) was estimated by catch-curve analysis of age-at-length samples (Ricker 1975; Haddon 2001). Per Haddon (2001), the \log_e transformed abundance of ages 1 to 12 was plotted with Z equal to the slope of the best-fit linear regression through the points. Age and length at 50% maturity for males and females were derived per King (2007) based on summer (June to September) samples.

Spatial and temporal distribution.—Multiple fishery-independent data sets were analyzed, including nearshore scientific gill-net surveys, power plant entrapment monitoring, nearshore otter trawl surveys, and long-term ichthyoplankton monitoring. Nearshore scientific gill-net surveys were completed as described by Allen et al. (2007), Miller et al. (2008), and Pondella et al. (2008). The mean length of gill-net-sampled queenfish was calculated for the study period to test for size bias. Spatial and temporal gill-net catch data were standardized per sampling period as mean abundance per gill net or temporal catch per unit effort (CPUE) across all stations occupied within the sampling period. Fishes and other organic and inorganic material are entrained as power plants withdraw cooling water from source water bodies. Entrapment monitoring included two survey types based on the facility surveyed. Impingement, which consisted of surveying all the fish impinged upon steel mesh traveling screens (typically 1 cm^2), was monitored during heat treatments at HBGS, SONGS, El Segundo Generating Station (ESGS), Redondo Beach Generating Station (RBGS), and Ormond Beach Generating Station (OBGS; Figure 1). A heat treatment is a facility process of entraining the heated discharge stream to control biofouling within the cooling water system. Heat treatments at each of the five facilities occurred at variable 7–12-week cycles. See Miller (2007) for a more complete description of the heat treatment process. Visual estimates of fishes returned to the ocean by the SONGS fish return system were also included. The SONGS fish return system is unique in that the fish do not contact the traveling screens as they are raised in a water-tight steel tray, deposited into a dedicated water conduit, and discharged 400 m offshore at a depth of 6 m. Prior to deposition into the return conduit, the contents (species and estimated abundance) were recorded. These estimates were periodically verified as a condition of regulatory

compliance. Impingement surveys were also conducted at SONGS.

Similarities between the trend in mean monthly sea surface temperature (SST) recorded at Newport Beach Pier, Newport Beach (SCCOOS 2009), and temporal gill-net CPUE by sampling month were tested by using linear regression. Spatial distribution was evaluated through the station-specific mean CPUE (spatial CPUE) across all years. Tests for differences in spatial-specific abundances were completed with a one-way analysis of variance (ANOVA) with a Bonferroni multiple comparison test. Data met the model assumptions after $\log_e(x + 1)$ transformation.

Long-term abundance recorded during entrapment monitoring at HBGS, SONGS, ESGS, and RBGS from 1972 to 2007 and at OBGS from 1979 to 2007 was used for temporal analysis (Figure 1). All annual entrapment data were standardized to annual cooling water flow and the number of surveys by using the following equation: entrapment index (EI) = annual abundance/[annual cooling water flow (10^9 m^3) \times annual number of surveys]. A generalized additive model (GAM) was used to compare annual EI with the mean August SST (1972–2007) recorded at the Newport Beach Pier and the mean annual plankton biomass (1974–2006) measured at King Harbor, Redondo Beach (described below; Figure 1). Both the EI and plankton biomass data sets were nonnormally distributed. The plankton biomass data were normalized by \log_e transformation, while the EI was normalized by the following transformation: $(\log_e[\text{EI}])^{0.25}$. The EI for 2001 was an outlier; therefore, the 2001 data for all three parameters (EI, SST, and plankton biomass) were removed from the model.

Seasonal trends in queenfish coastal abundance were examined by using entrapment monitoring results. Cooling water flow volumes at SONGS (Units 2 and 3) varied less than 10% annually, on average, from 1984 to 2007, while volumes at the other stations declined with time. Therefore, the mean monthly entrapment was calculated from surveys at SONGS (Units 2 and 3) (1984–2007) without standardization and was compared with mean monthly SST recorded at the Newport Beach Pier (1984–2007; Table 1) by using linear regression. Both parameters met the model assumptions.

Total annual summer otter trawl catch was recorded during near-annual surveys at three sites offshore of HBGS (1976–2001, 2004, and 2007): at the facility's discharge point and 1 km upcoast and downcoast of the discharge point along the 6-m isobath (Figure 1). All sampling was completed with a 7.62-m otter trawl (38.1-mm square-mesh body; 12.7-mm square-mesh cod end) fished for 10 min. Annual sampling occurred

in August except during the 1986 survey (July 28). The mean catch per trawl (and SE) was calculated for each year. A generalized linear model (GLM) was used to examine possible relationships between the mean annual August SST and the mean annual catch per trawl after fourth-root transformation as $(x + 1)^{0.25}$, which normalized the distribution and removed all zeroes from the analysis.

Monthly plankton surveys were conducted in King Harbor (Figure 1) from 1974 to 2006 by using a vertically stratified design targeting surface, midwater, and epibenthic strata via the techniques described by Stephens and Pondella (2002). Ichthyoplankton densities (number/1,000 m³) and plankton biomass (milliliters) were calculated from these surveys. These collections occurred adjacent to the cooling water intake at RBGS. Linear regression was used to compare the trends in the mean annual plankton metric and the total annual cooling water withdrawal at RBGS (1979–2006) after $\log_e(x + 1)$ transformation of all three parameters. A cross-correlation was used to test the temporal relationship between larval densities and the EI.

Recruitment trends.—Historic recruitment patterns were estimated by mortality-adjusted hindcasting of age-class abundance of the age and growth samples and individuals measured during heat treatment surveys (1979–2007) at SONGS, HBGS, RBGS, and ESGS. Lengths were unavailable for OBGS from 1990 to 2000; therefore, the facility was excluded from the analysis. Each measured, impinged individual was assigned to an age-class based on the von Bertalanffy parameters derived in this study. Mortality-adjusted annual recruitment was estimated by the modified Ricker (1975) equation described by Allen et al. (1995):

$$N_t = N_0(1/S)^t,$$

where N_0 = the number of fish in a year-class at $t = 0$, N_t = the estimated number of recruits at t years in the past corrected for mortality, and S = the annual estimated survivorship.

Impingement-based recruitment estimates required adjustment to account for variation in the percent measured at each facility. On any given survey, a random subsample of up to 200 individuals was measured (nearest mm) from the total impinged abundance. Total abundance was estimated based on the biomass of the measured subsample over the total species-specific biomass. Additional adjustments were made to account for variation in the annual number of surveys conducted and total annual cooling water flow at each facility. For each survey year, a recruitment index (RI) was derived through the equation:

$$\sum_{i=1}^n = (N_0/PM)/(HT \times CF)_i,$$

where PM = the total annual proportion measured during heat treatments, HT = the number of heat treatments in each year, and CF = the total annual volume (10⁹ m³) of cooling water circulated.

The annual abundance of young-of-the-year (age-0) individuals shorter than 100 mm SL was recorded during impingement surveys at SONGS and HBGS (1979–2007). An age-0 index was derived by standardizing in the same fashion as described for the RI. Comparisons were made between the RI and the age-0 index by using linear regression. Model assumptions were met by square-root transformation of the RI and \log_{10} transformation of the age-0 index. Spearman's rank correlation was used to compare the RI, age-0 index, and the larval index without transformation. By using a GAM, both the RI and the age-0 index were compared against the coastal upwelling index (CUI; NOAA 2009) and the mean annual August SST recorded at Newport Beach Pier (SCCOOS 2009). Neither index was normally distributed. The RI required \log_e and fourth-root transformations to meet normality, while fourth-root transformation normalized the age-0 index. All statistical tests were performed by using the Statistical Package for the Social Sciences version 12 (SPSS, Inc., Chicago, Illinois) at the 0.05 significance level. Data transformations and standardizations were performed in Microsoft Excel. Normality was determined by the Shapiro–Wilk test at a significance level of 0.05.

Results

Morphometrics, Age at Length, and Mortality

Otolith length, weight, and width were best described by power functions, indicating an allometric relationship between otolith growth and somatic growth (Table 1). The length–weight relationship was best described by the power function, $\text{weight} = 10^{-5} \times \text{SL}^{3.09}$ ($R^2 = 0.98$). No significant differences were detected between the age-at-length and offshore size distributions. Both sexes reached 50% maturity by age 1, or approximately 100 mm SL. Juvenile and adult queenfish were collected during 8 months from May 2006 to March 2007, providing a seasonal distribution for otolith edge analysis. Annulus formation was indicated by a gradual shift from translucent edges to opaque edges from January to June. The proportion of otoliths with translucent edges again increased from summer to fall, and the same proportion of translucent edges was observed in January and November.

Von Bertalanffy parameters for the total sample ($n = 820$) were 181.1 for L_∞ , 0.3 for k , and -1.4 for t_0 .

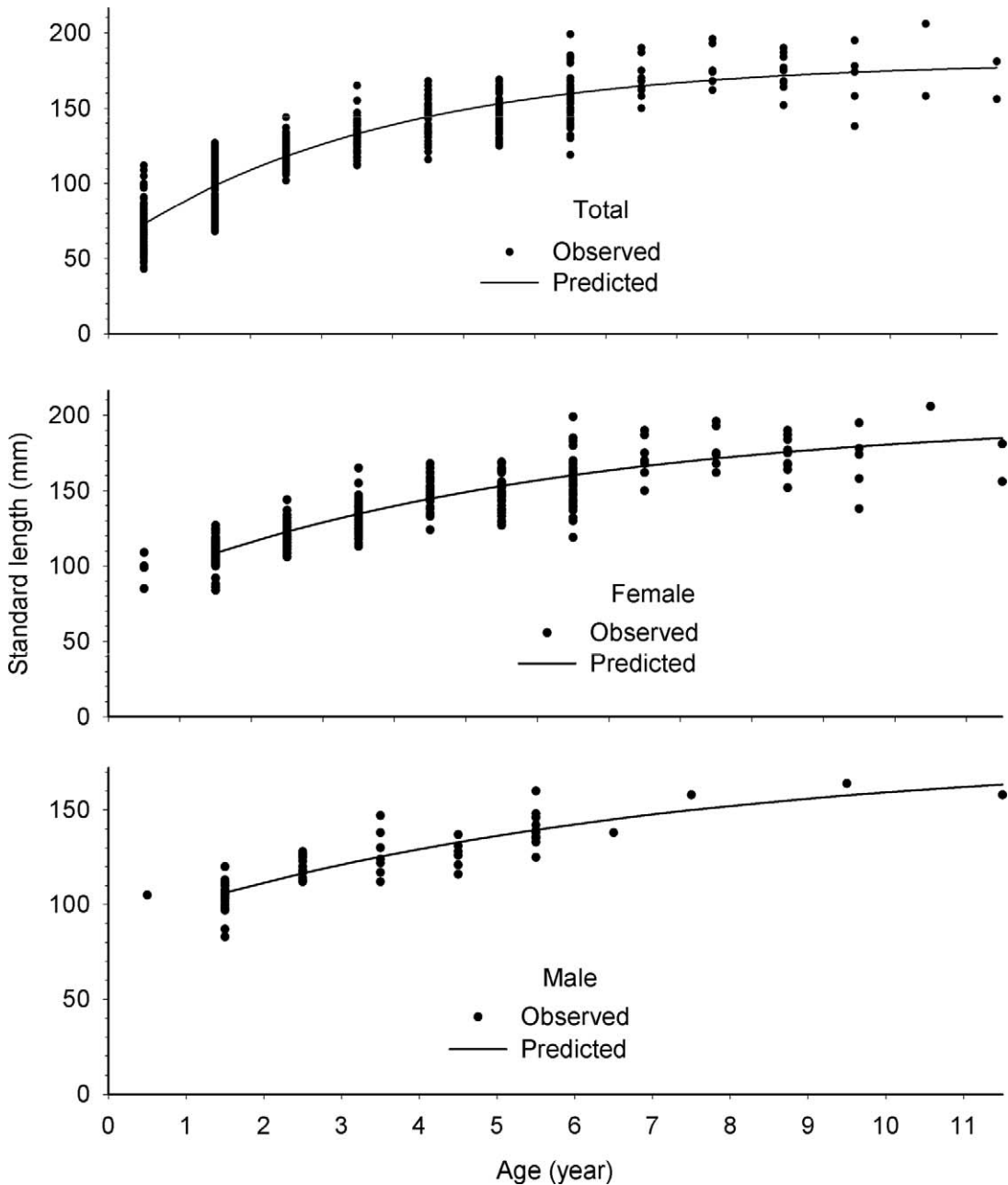


FIGURE 2.—Observed age at length and von Bertalanffy model-predicted age at length (standard length [mm]) for queenfish in the total sample ($n = 820$), females only ($n = 376$), and males only ($n = 90$).

Observed ages for the total sample ranged from less than 1 year to 12 years (Figure 2). The von Bertalanffy parameters describing females ($n = 376$) were 198.9 for L_{∞} , 0.2 for k , and -3.1 for t_0 ; parameters describing males ($n = 90$) were 179.9 for L_{∞} , 0.2 for k , and -4.5 for t_0 . The remaining 354 individuals were juvenile or

sex undetermined. Female queenfish attained a larger predicted size than males and grew at a significantly faster rate than males (ARSS: $F = 16.92$; $df = 1, 463$; $P < 0.0001$; Figure 2). Both sexes reached 50% maturity shortly after attaining age 1, or 100 mm SL. The Z was estimated at 0.42 ($R^2 = 0.94$).

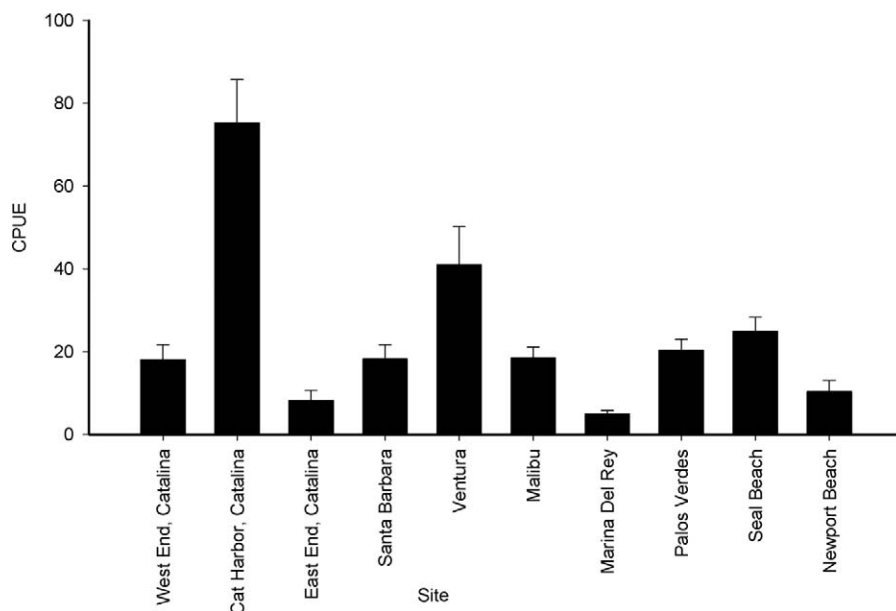


FIGURE 3.—Mean (+SE) queenfish catch per unit effort (CPUE) by gill-net sampling station in southern California, 1995–2006 (Cat Harbor = Catalina Harbor).

Spatial and Temporal Distribution

Fewer than 9% of the queenfish taken during gill-net sampling were smaller than 162 mm SL, while 88% were between 163 and 212 mm SL. Queenfish spatial CPUE distribution differed significantly by station (ANOVA: $F = 14.71$; $df = 9, 103$; $P < 0.0001$; Figure 3). Overall, Catalina Harbor had the highest CPUE, with approximately 75 individuals/net set on average. Along the mainland, CPUE was highest at Ventura on average, with approximately 45 individuals/net set. Bonferroni multiple comparison test results indicated that the CPUE at Catalina Harbor was significantly higher than those at all other stations except Ventura. Marina del Rey contributed the lowest CPUE on average. Mainland sites at Santa Barbara, Malibu, Palos Verdes, and Seal Beach, as well as the west end of Santa Catalina Island, had similar mean CPUE values.

Temporal CPUE increased to a peak midway through the time series (1999–2003), with similar levels at the start and end of the timeline (Figure 4). Peaking in June 2000 and April 2002, temporal CPUE was not significantly correlated with SST. The CPUE at Santa Catalina Island was highest during the middle years of the time series, while the CPUEs at coastal sites (e.g., Ventura) were, on average, higher during the later years (Figure 5). The Catalina Harbor CPUE was highest in 2000 and 2002, while the Ventura CPUE peaked from 2002 to 2004.

The queenfish EI increased between 1972 and its peak in 1980 before generally declining through 2008 (Figure 6A). The seasonal EI at SONGS increased through the summer months in a significant relationship with mean monthly SST ($R^2 = 0.51$, $P = 0.009$; Figure 6B), peaking in August on average. Mean annual August SST was not, however, significantly related to the interannual EI variation. Mean annual plankton biomass in King Harbor, which also declined over this time, significantly explained 48% of the observed EI variance (GAM: $R^2 = 0.48$, $df = 29$, $P < 0.001$; Figure 6A).

Trawl catches were generally cyclical, reaching peaks in 1983 (370 fish/rawl) and 1993 (327 fish/rawl; Figure 7). Each peak was followed by substantial declines lasting at least 10 years. Recent catches have remained low, with no individuals taken in 2004 or 2007, the two most recent surveys analyzed. Observed trends in the trawl catch were not significantly explained by SST (GLM: $R^2 = 0.10$, $df = 26$, $P = 0.11$).

Annual mean larval queenfish density in King Harbor peaked in 1975 and has declined since then in a positive correlation with cooling water withdrawals at RBGS ($R^2 = 0.47$, $df = 27$, $P < 0.001$; Figure 8A). Annual mean plankton biomass also declined commensurate with cooling water flow at RBGS ($R^2 = 0.18$, $df = 26$, $P = 0.03$). After 1988, mean larval

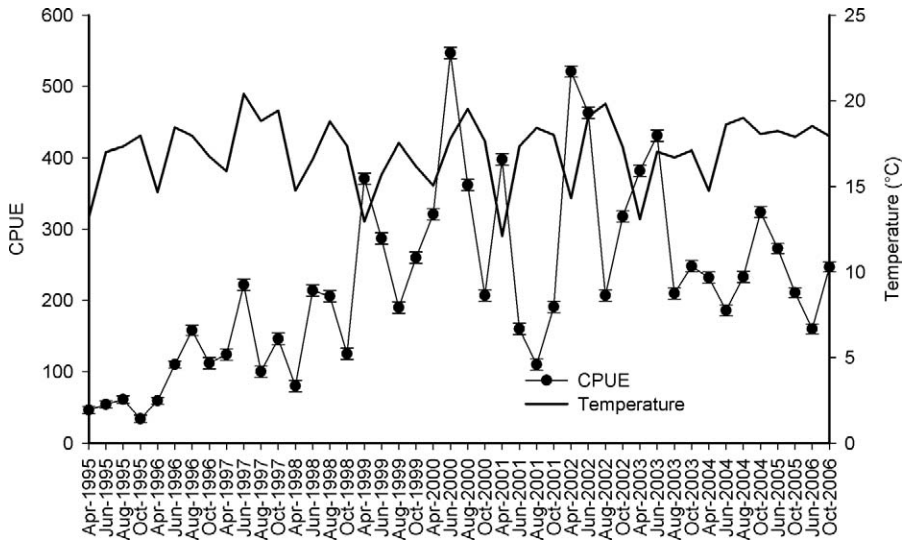


FIGURE 4.—Mean (\pm SE) queenfish catch per unit effort (CPUE) in gill nets and mean sea surface temperature ($^{\circ}$ C) by survey month at all stations sampled from Newport Beach to Santa Barbara, California, including three sites at Santa Catalina Island, 1995–2006.

density remained below 20 fish/1,000 m^3 . From 1990 to 2006, densities exceeded 5 fish/1,000 m^3 in only 2 out of 17 years. Queenfish larvae were essentially absent from samples collected in 6 of those 17 years. The annual age-0 index peaked in 1985 before markedly declining, with high interannual variation

from 1987 to 2006 (Figure 8B). Annual patterns in mean annual larval densities recorded in King Harbor were significantly correlated with the age-0 index ($r = 0.41$, $df = 27$, $P = 0.03$). Cross-correlation analysis identified up to a 7-year lag between the larval time series and the EI ($r = 0.56$ – 0.71).

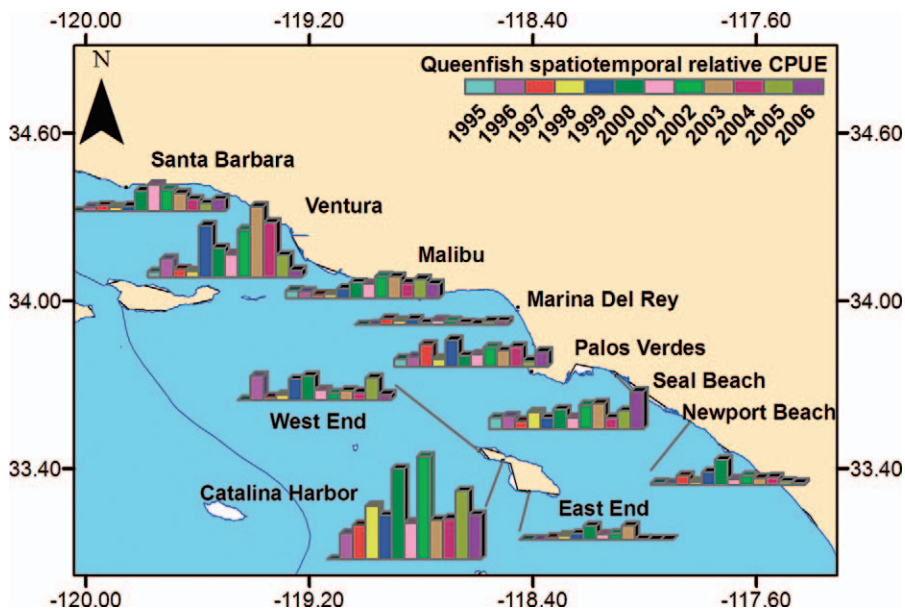


FIGURE 5.—Relative spatiotemporal queenfish catch per unit effort (CPUE) recorded at 10 gill-net sampling sites in southern California, 1995–2006.

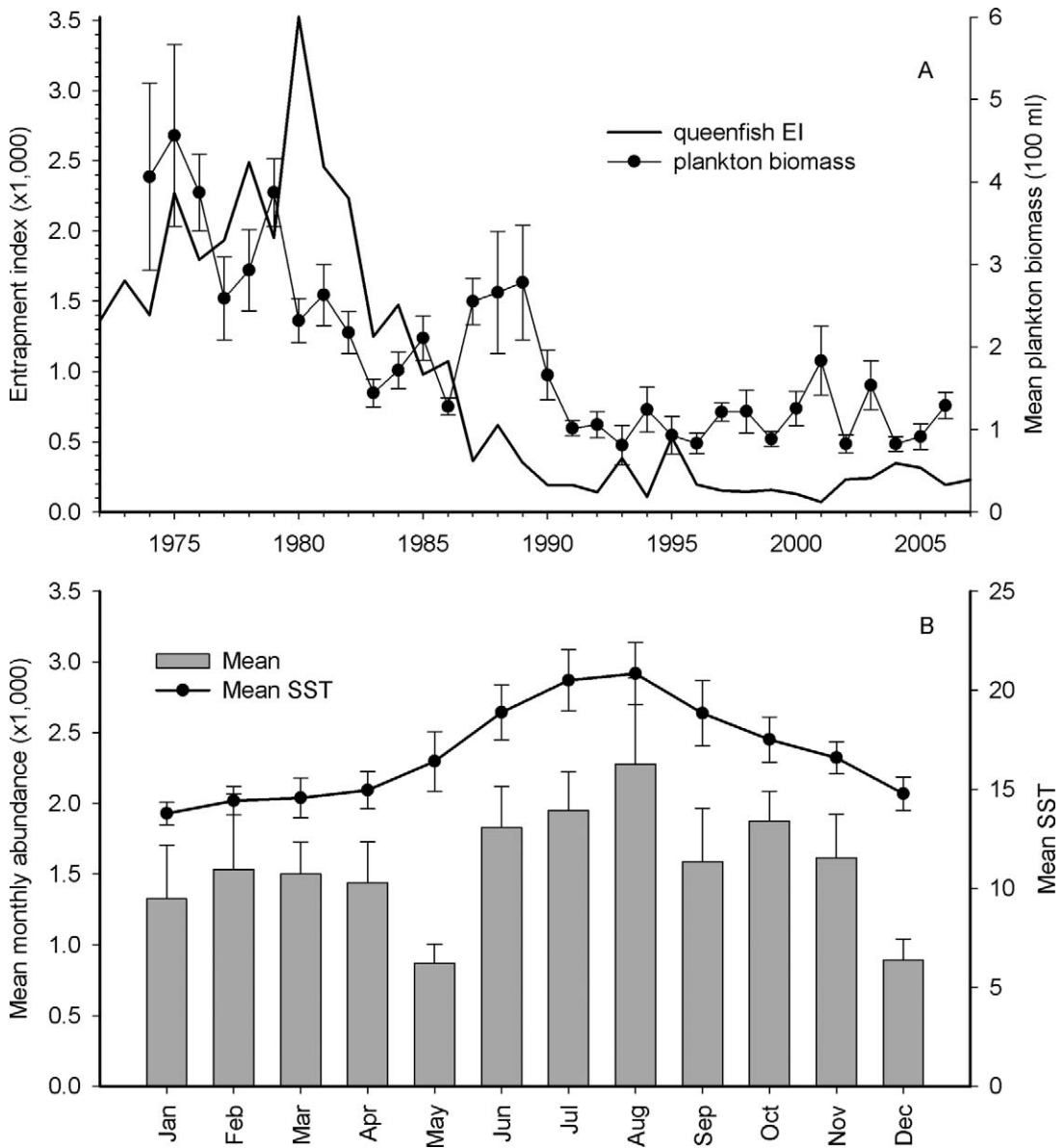


FIGURE 6.—(A) Mean (\pm SE) plankton biomass measured in King Harbor and queenfish standardized entrapment abundance (entrapment index) at Ormond Beach Generating Station (OBGS), El Segundo Generating Station, Redondo Beach Generating Station, Huntington Beach Generating Station, and San Onofre Nuclear Generating Station (SONGS), California (OBGS sampling period [1979–2007] was shorter than that used for the remaining sites [1972–2007]); and (B) mean (\pm SE) monthly entrapment abundance of queenfish at SONGS (1984–2007) and mean (\pm SE) monthly sea surface temperature (SST, $^{\circ}$ C) recorded at Newport Beach Pier (1984–2007).

Recruitment Trends

The queenfish RI was variable but generally higher prior to 1975 (Figure 8). At least three extended stable periods were observed; the stable period characterized by the highest RI values was between 1975 and 1982, and the RI progressively declined thereafter. Linear

regression of the transformed age-0 index and RI described a significant relationship ($R^2 = 0.36$, $df = 27$, $P < 0.001$). The RI was significantly correlated with trends in the age-0 index ($r = 0.58$, $df = 27$, $P < 0.001$) and the mean annual larval densities in King Harbor ($r = 0.83$, $df = 32$, $P < 0.001$). Trends in larval density

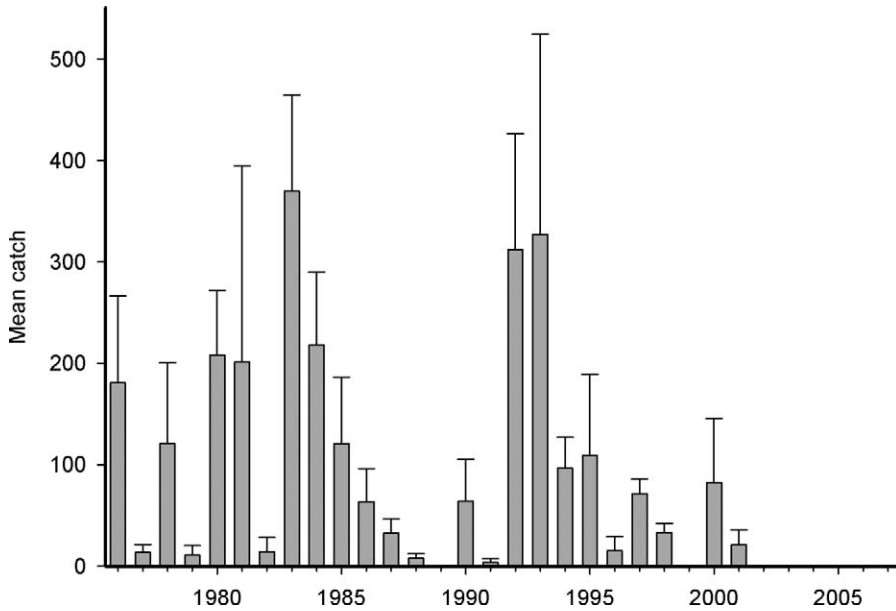


FIGURE 7.—Mean (\pm SE) queenfish catch per minute trawled as recorded in otter trawl surveys offshore of Huntington Beach Generating Station, California, in 1976–2001, 2004, and 2006–2007.

were significantly correlated with the age-0 index ($r = 0.41$, $df = 27$, $P = 0.03$). Thirty-five percent of the variance in the age-0 index was explained by the combined factors of SST and CUI ($R^2 = 0.35$, $df = 25$, $P = 0.005$). Neither factor (SST or CUI) was significantly related to the RI.

Discussion

Queenfish growth dynamics were consistent with other common southern California sciaenids, as well as trends identified for the family in general. Their maximum age (12 years) was similar to the maximum age reported for their close congener, the white croaker (Love et al. 1984), with an overall growth trajectory similar to other California sciaenid otolith-based growth estimates (Miller et al. 2008; Pondella et al. 2008). The determination of annulus formation in queenfish agreed with previous otolith research describing sciaenids, such as weakfish *Cynoscion regalis* and spotted seatrout *Cynoscion nebulosus* (Lowerre-Barbieri et al. 1994; Ihde and Chittenden 2003).

The mainland spatial gill-net CPUE was consistent with historic bightwide ichthyoplankton densities (Lavenberg et al. 1986; McGowen 1993; Moser et al. 2001). Sampling at Catalina Harbor, however, recorded the highest CPUE despite the relative absence or low density of larval queenfish outside the coastal margin (Lavenberg et al. 1986; Moser et al. 2001). The

Catalina Harbor CPUE was also elevated largely during periods when the mainland sites' CPUEs were reduced (Figure 6). This may relate to variations in recruitment based on localized oceanographic conditions. Limited nocturnal migration to deeper water has been reported for coastal queenfish populations (Allen and DeMartini 1983); however, there is no information on possible long-distance migration, especially across a deepwater channel like the San Pedro Channel.

Seasonally, queenfish were more abundant during the summer months when seawater temperatures were elevated (Figure 6B), corresponding with their reported reproductive season (Goldberg 1976; DeMartini and Fountain 1981). Similar patterns were observed in two other common southern California sciaenids, the black croaker *Cheilotrema saturnum* and yellowfin croaker *Umbrina roncadore* (Miller et al. 2008; Pondella et al. 2008). Queenfish larval densities near SONGS further support this notion: annual abundance peaks were recorded between late spring and fall (Walker et al. 1987). The timing of the appearance of larvae, reproductively active periods, and recorded abundance trends suggests that queenfish may be forming spawning aggregations during the summer months.

Multiple factors in the spatiotemporal distribution of queenfish, specifically the observed trends in all time series, suggest that populations were regulated by environmental sources. For example, the mid-series inflection point observed in the gill-net CPUE series

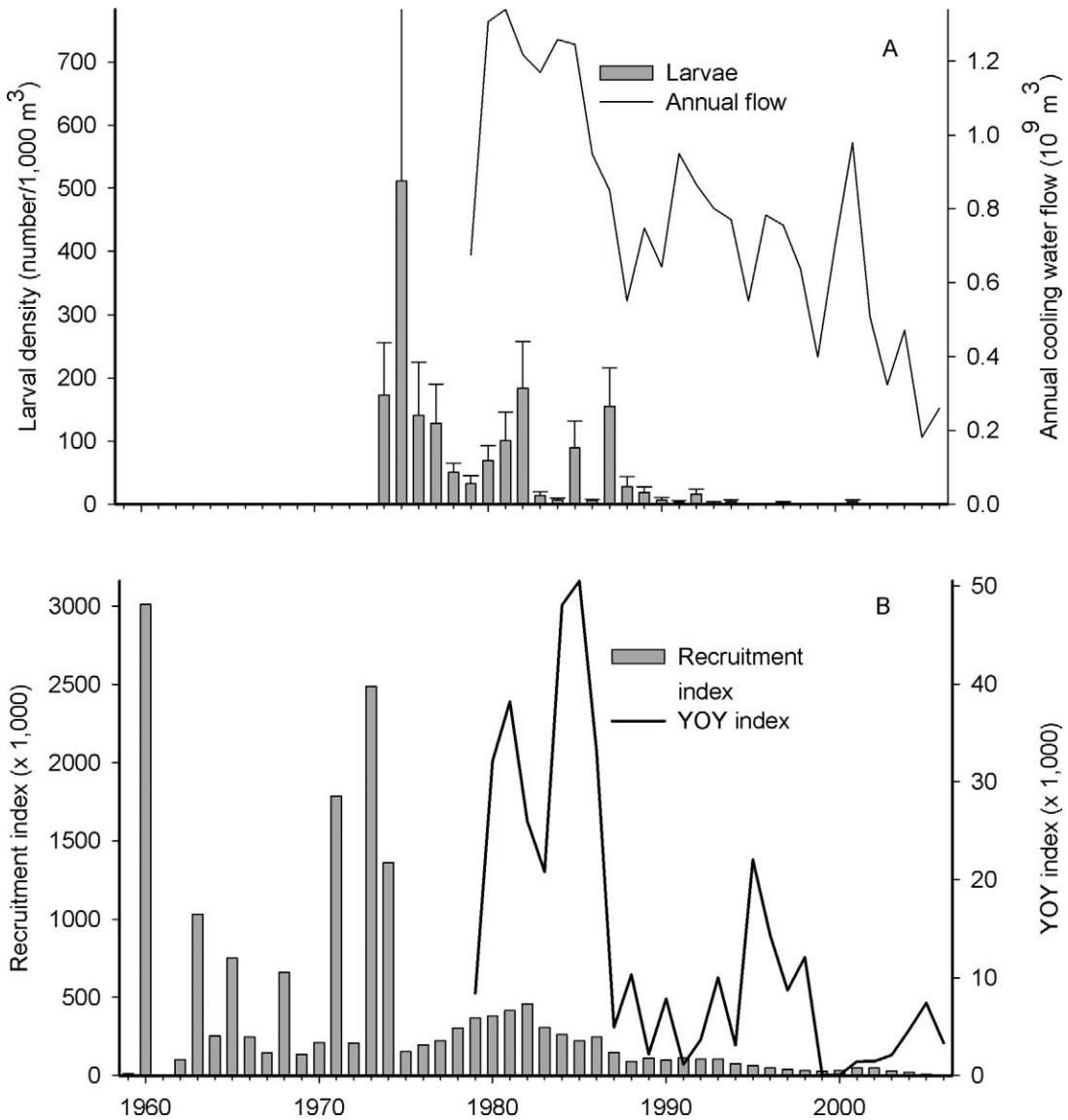


FIGURE 8.—(A) Mean (+SE) queenfish larval density (number/1,000 m³) recorded in King Harbor, Redondo Beach, California, and total annual cooling water flow (10⁹ m³) at Redondo Beach Generating Station (RBGS); and (B) queenfish recruitment index (1959–2006) and young-of-the-year (YOY; age-0) index (1979–2006) measured during impingement surveys at El Segundo Generating Station, RBGS, Huntington Beach Generating Station, and San Onofre Nuclear Generating Station.

occurred well after the last major fishing regulation change (i.e., the 1994 ban on nearshore commercial gill nets; Allen et al. 2007) but in the continued presence of most other anthropogenic factors, such as wastewater discharge, recreational fishing, and power plant cooling. Given the size distribution of queenfish taken during the gill-net survey (>162 mm, or >3 years old), the CPUE declines beginning in 2002 reflect population changes in 1998 or 1999, possibly poor recruit-

ment during either the 1997–1998 El Niño–Southern Oscillation (ENSO) or the 1999 La Niña. This suggests that the measured CPUE variability was an expression of recruitment dynamics, such as larval productivity or survival (Houde 1987; Cowan and Shaw 2002). Significant relationships were found among the spatially disparate larval densities, RI, and age-0 index. While the RI represents estimates based on length-derived age-class assignments and an assumption of

stable Z , the confluence with direct measures of subjuvenile individuals suggests that the RI may accurately reflect recruitment dynamics. Both the RI and age-0 index indicated that 1998 was a relatively robust year-class, while the 1999 and 2000 year-classes were relatively poor (Figure 8B). The CUIs in the southern California area (33°N) were among the lowest on record during the 1998 ENSO but reached near-historic levels during the 1999 La Niña; both of these phenomena corresponded with anomalously warm (1998) or cool (1999) SSTs (Schwing et al. 2000). This indicates that queenfish recruitment favored the warmer waters associated with the 1998 ENSO, whereas the cool period in 1999 severely impacted recruitment. These patterns were borne out in the significant relationships between the age-0 index and both SST and CUI.

The extensive record provided by the EI indicates that adult populations have declined along much of the Southern California Bight over the last 3 decades (Figures 5, 7, and 8). While the EI records a continued increase after the 1977 regime shift (McGowan et al. 2003), the trend rapidly declined after 1980. Cross-correlation analysis, however, identified an extensive time lag between larval densities and the EI, suggesting that the timing observed in the EI trend may reflect a population response to the 1977 regime shift. The short life span and high Z of queenfish further indicate that this is a plausible time period for a prior recruitment failure to be manifested in the adult populations, such as the depletion of the early 1970s strong year-classes (Figure 8B). After the rapid decline of the 1980s, queenfish populations appear to have stabilized to a state of punctuated equilibrium since at least 1990.

Declines in the EI were significantly related to the decline in King Harbor plankton biomass, which generally mirrored the larger patterns described for the California Current System by Roemmich and McGowan (1995), persisting through 2006, although plankton biomass markedly increased in 1999 (Goericke et al. 2007). These declines in macrozooplankton throughout the area presumably increased the natural mortality of the planktivorous queenfish (Hobson and Chess 1976) due to reduced feeding opportunities. The relationship between the two trends is consistent with that predicted by McGowan et al. (1996) and may be indicative of the overall effects of climate change.

Consistent declines across all analyzed time series generally agreed with overall productivity trends in the North Pacific (Roemmich and McGowan 1995; McGowan et al. 2003). While the King Harbor plankton (including ichthyoplankton) were collected near a power plant cooling water intake structure, the significant positive relationship between the relevant

data sets discounts the possibility that the plant's withdrawals reasonably contributed to the observed declines. Rather, the decline in King Harbor larval queenfish densities was consistent with the bightwide trend observed since 1977 (Moser et al. 2001). These regional declines are further suggestive of a more regional, bottom-up forcing and general declines in coastal productivity along the West Coast of North America since the 1977 regime shift (McGowan et al. 2003; Ware and Thomson 2005).

Potential changes in top-down regulation, such as increases in predation by white seabass *Atractoscion nobilis* or giant sea bass *Stereolepis gigas* as queenfish populations increase (Allen et al. 2007; Pondella and Allen 2008), cannot be completely disregarded based on examination of the gill-net CPUE or EI. The reported overall decline in fish populations, however, is not generally consistent with the notion of top-down regulation of a lower-trophic, planktivorous species (Brooks et al. 2002; Jackson 2008). Queenfish are reportedly preyed upon by numerous piscivorous fish species, most of which are mid-level piscivores, such as kelp bass *Paralabrax clathratus* and California halibut *Paralichthys californicus*, which are common nearshore-resident predators (Feder et al. 1974; DeMartini et al. 1985). Allen and Hovey (2001) and Dotson and Charter (2003) reported that kelp bass populations (or a complex consisting of kelp bass and barred sand bass *Paralabrax nebulifer*) were declining at the end of the 1990s. California halibut populations maintained generally stable populations between 1970 and 2000 based on both recreational and commercial fishery statistics (Kramer et al. 2001).

Conclusions

Overall, queenfish vital rates, as determined herein, were consistent with those of other sciaenids common to the Southern California Bight. Queenfish populations have declined with time, and these declines have been coincident with previously reported declines in zooplankton biomass throughout the western North Pacific. Declines in zooplankton may have doubly impacted the planktivorous queenfish through reduced predation opportunities for both larvae and adults. Oceanographic variability and its cascading effects may have markedly impacted southern California's queenfish populations.

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