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Decadal-scale changes in southern California sciaenids under different levels of harvesting pressure

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Miller, E. F., Pondella II, D. J., Beck, D. S., and Herbinson, K. T. 2011. Decadal-scale changes in southern California sciaenids under different levels of harvesting pressure. – ICES Journal of Marine Science, 68: 2123–2133.

Received 18 May 2011; accepted 8 September 2011

A unique 38-year time-series of power-plant entrapment data collected across \sim 170 km of the southern California coastline was examined to describe the decadal-scale trends in common Southern California Bight sciaenid abundance in relation to oceanographic conditions. Adult catches for five of seven species declined at differing rates and severity. Declines of up to 94% were detected in historically common species such as *Genyonemus lineatus*, whereas historically less abundant species have increased dramatically, e.g. *Umbrina roncador* (2626%). Over time, the entrapped community became increasingly influenced by species with more southerly distributions, indicated by a significant decline in the average latitudinal midpoint of the community. This shift was significantly related to rising ocean temperature and took place in the early to mid-1980s. The observed species-specific abundance changes in all species except *Atractoscion nobilis* were significantly correlated with sea surface temperature, nearshore plankton volumetric biomass, *G. lineatus* or *Seriphus politus* nearshore larval density, or a combination of these. Patterns in *A. nobilis* abundance were the most isolated, likely reflecting its standing as an intensively fished species, unlike the other six species evaluated. The consistent relationship with environmental indices strongly supported the notion of a faunal shift driven by bottom-up forcing.

Keywords: bottom-up forcing, climate change, El Niño, faunal shift, power plant, sciaenids.

Introduction

Changes in the distribution, composition, and abundance of biological communities, including marine fish, have been increasingly attributed to rising ambient temperatures (McCarty, 2001; Walther et al., 2002; Genner et al., 2004). Such changes in exploited marine fish communities are further complicated by historical harvest effects, such as reduced size and age structure, which may result in greater sensitivity to environmental effects (Brander, 2007; Genner et al., 2010). The Southern California Bight represents a microcosm of many of these global challenges, e.g. harvesting and oceanographic change (Harley et al., 2006). Marine population declines are well documented from the area, with many of these declines attributed to negative responses associated with changing ocean conditions (Roemmich and McGowan, 1995; Holbrook et al., 1997), but also to commercial overfishing (Allen et al., 2007; Pondella and Allen, 2008). The highly urbanized Bight also supports an extensive recreational fishing industry with an average of 11 million fish harvested annually, typically accounting for 65% of the state-wide recreational harvest (Leet et al., 2001).

The Southern California Bight sciaenids (family Sciaenidae) represent one model group to examine decadal-scale changes under similar environmental conditions but differing harvest pressures. Their distribution is generally restricted to the nearshore environment, including select Channel Islands (Moser *et al.*, 2001;

Miller *et al.*, 2008, 2009). This coastally restricted distribution exposes them to a unique set of environmental conditions (Bograd and Lynn, 2003) not commonly encountered in the assessments of more oceanic species, such as those used by Hare and Mantua (2000), among others. Three of the seven species common to the area support commercial and recreational fisheries of varying size (white sea bass *Atractoscion nobilis*, white croaker *Genyonemus lineatus*, and queenfish *Seriphus politus*; Love *et al.*, 1984; Moore and Wild, 2001; Allen *et al.*, 2007). White sea bass, the largest of the southern California sciaenids, supported a commercial fishery that collapsed in the early 1980s before rebounding in the late 1990s (Allen *et al.*, 2007). Commercial landings of white croaker often include queenfish, and they were not separated in the records before 1972 (Moore and Wild, 2001).

Recreational fishers primarily target white sea bass from charter or private boats, whereas white croaker and queenfish are most commonly taken from man-made structures such as piers and jetties (Love, 2006). Since 1915, three species have been reserved for recreational anglers and were predominantly taken by surf-anglers (yellowfin croaker *Umbrina roncador*, spotfin croaker *Roncador stearnsii*, and California corbina *Menticirrhus undulatus*; O'Brien and Oliphant, 2001; Valle and Oliphant, 2001a, b; Love, 2006, Pondella *et al.*, 2008). Black croaker, *Cheilotrema saturnum*, has not been targeted by either commercial or recreational fisheries in California (Limbaugh, 1961; Miller *et al.*, 2008).

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Utilizing the Southern California Bight sciaenids and their variable harvesting histories, we attempted to examine variations in nearshore abundance for indications of environmental effects beyond the interannual variability induced by brief El Niño Southern Oscillation (ENSO) events (Barry et al., 1995; Lea and Rosenblatt, 2000), such as consistent increasing or decreasing abundance patterns spanning a decade or more (Barry et al., 1995). Prior conclusions on the effects of climate change on marine resources were founded on evidence ranging from the disappearance of once-common species, through the introduction of new species that were, historically, more equatorially distributed, to a simple shift in abundance between these groups wherein the historically common species declined in abundance while the less common, but more equatorially distributed, species became more common with time (Barry et al., 1995; Genner et al., 2004; Harley et al., 2006).

The seven sciaenid species common to southern California cumulatively represent a wide biogeographic range (Horn et al., 2006). In general, ichthyoplankton sampling indicates the centre of distribution for the Southern California Bight sciaenids to lie at ca. 34-35°N or in Santa Monica Bay, CA (Moser et al., 2001). White croaker and queenfish both range farther north (Horn et al., 2006), with peak larval densities in Santa Monica Bay, CA, and a secondary peak in queenfish densities near Dana Point, CA, at $\sim 33.5^{\circ}$ N (Moser *et al.*, 2001). Yellowfin and spotfin croakers are most commonly encountered in the more southern areas of the Southern California Bight, often in San Diego County and along the coastline of Baja California, Mexico (O'Brien and Oliphant, 2001; Valle and Oliphant, 2001b; Horn et al., 2006). White sea bass has the largest range of the seven species, whereas California corbina and black croaker both range from Point Conception south into Mexican waters, with little information on their preferred range (Horn et al., 2006). Miller et al. (2008), however, reported the densities of black croaker to peak in gillnets set at Palos Verdes, CA. Insufficient data on larval distribution exists to describe similarly the centre of distributions for the sciaenids other than white croaker and queenfish.

The analysis primarily uses the power-plant entrapmentmonitoring results, a unique time-series of the nearshore fish community near cooling-water intake structures. These intakes sample the community by entraining fish in the cooling-water drawn into the plant in abundances proportional to the results of more traditional sampling techniques, e.g. trawl, diver transect, done in proximity to an intake (Brooks et al., 2002; Greenwood, 2008). Greenwood (2008) found that fish caught during monitoring surveys at a power plant with an intake situated above the seafloor were significantly similar to those caught during concurrent midwater trawl sampling. Likewise, Brooks et al. (2002) found a significant relationship between power-plant survey data and diver-transect counts made next to a monitored power-plant intake. Because of these similarities with the traditional sampling techniques, power-plant monitoring data have been used to describe population trends in otherwise data-poor species or communities (Brooks et al., 2002; Genner et al., 2004; Miller et al., 2009).

The Southern California Bight power-plant entrapmentmonitoring dataseries includes data collected from an area spanning nearly 170 km of coastline from San Clemente to Ventura, CA, at least one major oceanographic regime shift, in 1977, two large ENSO events (Bograd and Lynn, 2003; McGowan *et al.*, 2003, and references therein), and one significant change in power-plant cooling-water usage in 1983/84 (EFM, unpublished data). Utilizing these data, we tested the sciaenid community's response to changing environmental conditions, e.g. ocean warming. Patterns described by Holbrook *et al.* (1997), Genner *et al.* (2004), and Perry *et al.* (2005), among others, represent a pervasive common response in marine biological systems to their changing environment. Therefore, there should be a similar faunal shift in southern California sciaenid assemblage, regardless of fishing pressure, if the environment is in fact the primary factor regulating their abundances.

Methods

Data sources

Species-specific abundance (juvenile and adult) was monitored at five coastal power plants between Ventura and San Diego, CA (Figure 1), during two survey types, cumulatively referred to as entrapment surveys. In all, 1973 surveys were completed from 1972 to 2009 (Table 1): Ormond Beach generating station (OBGS, one intake, n = 196, 1975–2009), El Segundo generating station (ESGS, two intakes, station total n = 348, 1972–2009), Redondo Beach generating station (RBGS, three intakes, station total n =394, 1972-2009), Huntington Beach generating station (HBGS, one intake, n = 270, 1972 - 2009), and San Onofre Nuclear generating station (SONGS, three intakes, station total n = 765, 1972– 2009, excluding 1975). Seawater withdrawal was curtailed or stopped and heat treatments discontinued at some intakes during the time-series: one ESGS intake in 2003, one RBGS intake in 1988, and one SONGS intake in 1993. Two new intakes at SONGS began operating in 1983 (Unit 2) and 1984 (Unit 3). The discontinued flows were proportionally minimal reductions, whereas the addition at SONGS represented the largest change in withdrawal volumes during the monitoring period.

These five power plants were unique in that the entrained fish accumulate in forebays for weeks or months until the next heat treatment (described below), with only small numbers impinged during the interim period (EFM, unpublished data and pers. obs.). Natural mortality as a consequence of predation within the forebay was not documented, but assumed to be consistent across power plants and years. The first entrapment survey type (impingement) included identification and enumeration of all the fish impinged upon steel mesh travelling screens (typical mesh size 1-cm bar) during heat treatments at each plant. Heat treatments involve recirculating a portion of the heated discharge stream through the cooling-water system to control biofouling; they took place on average at variable 7-12 week cycles. All material exposed to the cooling water within the physical structures of the plant was likewise exposed to these elevated temperatures, usually >38°C. Visual survey, or "fish chase", was the second survey type and was unique to SONGS Units 2 and 3. Abundance estimates were recorded during the operation of the unique, unit-specific fish return system during each visual survey before heat treatment (Miller et al., 2009). Data recorded during impingement and visual surveys were combined and analysed cumulatively as entrapment surveys.

All five facilities withdrew cooling water from open coastal areas with offshore intake structures along the 8-15 m isobaths. Each intake opening was ~ 4 m above the seafloor. The design and operation of the cooling-water system(s) at each facility did not select preferentially on size class or sex, but rather an individual fish's behaviour and swimming performance typically



Figure 1. Location of the five power plants used in the study as well as King Harbor, where the plankton and ichthyoplankton (1974–2006) were collected. Power plants include OBGS, ESGS, RBGS, HBGS, and SONGS.

Table 1. Biogeographic range latitudinal midpoint (MP), percentage frequency of occurrence (FO), and mean entrapment rate (Rate, count per 10^6 m^3) of sciaenids recorded at each of the five power plants depicted in Figure 1, 1972–2009.

	МР	OBGS		ESGS		RBGS		HBGS		SONGS		All plant	
Species		FO	Rate	FO	Rate	FO	Rate	FO	Rate	FO	Rate	FO	Rate
White sea bass	41	2	0.1	10	0.1	4	0.2	46	0.4	12	0.0	13	0.14
Black croaker	29	4	0.1	62	0.3	43	0.6	60	0.5	22	0.1	37	0.30
White croaker	37	35	3.4	50	75.3	63	1.6	96	70.5	43	0.8	45	31.11
California corbina	29	2	0.0	19	0.1	5	0.0	52	0.5	7	0.0	14	0.17
Spotfin croaker	29	0	0.0	0	0.0	1	0.1	5	0.2	30	0.9	12	0.87
Queenfish	35	88	45.7	84	50.9	42	8.8	98	393.7	91	12.5	80	83.68
Yellowfin croaker	29	1	0.3	9	1.3	8	0.4	9	0.3	59	9.0	27	7.05
Number of surveys		196		348		394		270		765		1 973	

A minimum value of ≥ 0.1 fish per 10⁶ m³ per survey was used for FO calculation. Data for "All plant" reference the total occurrences (FO) and the mean entrapment rate (Rate) across all plants. The mean entrapment rates exceeding the all-plant mean are shown emboldened.

determined its susceptibility to the intake flow (Helvey, 1985). The mean water volume circulated (sampled) between heat treatments varied by facility from $52.6 \times 10^6 \text{ m}^3$ ($\pm 2.8 \text{ s.e.}$) at ESGS to $338.1 \times 10^6 \text{ m}^3$ (± 78.1) at SONGS.

Midwater fish are more commonly entrapped by midwater intakes than demersal species, e.g. flatfish (Greenwood, 2008). This belief was confirmed by utilizing data from three offshore sampling programmes conducted near SONGS. Midwater fish were targeted during lampara netting from 1978 to 1986 (excluding 1983) directly offshore of SONGS using the methods described in Allen and DeMartini (1983). Nearshore gillnets were fished quarterly offshore of SONGS along the 9- and 14-m isobaths at stations within 2 km upcoast or downcoast of the facility from 1976 to 1980, excluding 1977. Each net measured 45.7 m long by 1.8 m deep and had six panels 7.6 m long of the variable mesh in sizes 22, 25, 38, 46, 53, and 76 mm bar. Nets were set \sim 1 h before sunset and retrieved 1 h after sunrise. Finally, otter trawl sampling was completed quarterly using the methods described by Love et al. (1986), although only data from stations offshore of SONGS were included in this analysis.

The mean annual sea surface temperature (SST) recorded at the Scripps Institution of Oceanography Pier (1917-2009; Shore Station Programme, 2011) and mean annual zooplankton volumetric biomass (ml) collected in King Harbor, Redondo Beach, CA, served as indicators of environmental conditions. Post-flexion white croaker and queenfish ichthyoplankton density (count per 1000 m³), also collected in King Harbor, Redondo Beach, CA (Stephens and Pondella, 2002), was used as an independent time-series to gauge potential sampling bias in the entrapment series. Each population parameter (entrapment rate and ichthyoplankton density) was tested against the temperature and zooplankton series separately, because zooplankton biomass patterns were correlated with seawater temperature (Roemmich and McGowan, 1995). For five sciaenid species, the annual estimated recreational catches (1980-1989 and 1993-2003) were compiled from the Marine Recreational Fisheries Monitoring Programme database (RecFIN, 2011) for all fishing modes inshore of 3 nautical miles off southern California. Spotfin and black croakers were not analysed because of there being insufficient RecFin data for either species. Spearman's rank

correlation was used to compare the entrapment rate and RecFin patterns.

Entrapment trends

The mean annual entrapment rate at SONGS for each species was compared with each offshore net-sampling technique by fitting a best-fit linear regression through the annual data from each series. Annual mean catch was used by species from each offshore net method. To account for gross differences in abundance linked to sampling efficiency, all data were converted to *z*-scores (Quinn and Keough, 2002) before comparison. Few data met parametric assumptions, and the gillnet series was limited to 4 years, so conclusions on similarities were based on the size of the coefficient of determination (R^2) with a minimum threshold of 0.10 designated *a priori*.

The raw total annual entrapment of all sciaenids against total annual circulated cooling-water flow, all five plants combined, was plotted, and a best-fit linear regression was used to illustrate the relationship between the two parameters. The species abundance distributions (SADs; McGill *et al.*, 2007), or percentage of total entrapment, for the first (1972–1981) and the final (2000–2009) decades recorded in the time-series were examined for differences in species proportions between the two periods. Only data from HBGS and SONGS, combined, were used in the SADs, because these were the only sites where all seven species were found during at least five surveys (Table 1).

Power-plant entrapment (impingement + fish chases) surveyspecific abundance was standardized (entrapment rate) by the total cooling-water volume (10⁶ m³) circulated through each forebay since the previous heat treatment. This removed the effect of the differing pumping rates and capacities between the plants and years at each plant, to the extent possible. The speciesspecific entrapment rates by power plant were compared using Spearman's rank correlation. Biogeographic distribution midpoints for each species (Table 1) were calculated based on the range endpoints presented in Horn et al. (2006). The annual entrapment rate-weighted mean latitudinal midpoint for each survey (sciaenids only) was calculated for ESGS, HBGS, and SONGS. Surveys from OBGS and RBGS were excluded owing to the relative rarity of several sciaenid species in surveys at these sites. Least-squares regression was used to describe the overall pattern in annual mean latitude midpoint and the relationship between the annual mean latitude midpoint and the annual mean SST. The effect of each plant's contribution position was tested using a Kruskal-Wallis test with a Dunn-Sidak multiple comparison pairwise test (Quinn and Keough, 2002) of the annual mean latitude midpoint for the entrapped community at each of the three plants used in the analysis. Entrapment rates and larval densities by species were compared against both SST and King Harbor plankton biomass using the Spearman rank correlation. All correlation and regression analyses were completed using SigmaPlot v. 11 (SYSTAT, 2008).

Results

All seven species were taken at the five power plants, although <0.1 spotfin croaker per 10^6 m³ was taken at OBGS and ESGS (Table 1). The mean fish standard lengths recorded during surveys ranged from 109 mm (± 0.09) for queenfish to 250 mm (± 0.40) for spotfin croaker. All seven species were most common at HBGS and SONGS, with the HBGS mean entrapment rates for five of the seven species above average. Spotfin and

yellowfin croakers were more common at SONGS than at any other plant. These differences resulted in variable correlations (Table 2). The rates of entrapment of white croaker were the most similar between plants, with six significant correlations, including the only significant, negative correlation (r = -0.51, p < 0.01, n = 31) between the northernmost plant (OBGS) and the southernmost (SONGS). HBGS most consistently correlated with other facilities, most commonly with RBGS and ESGS. Species-specific comparisons between entrapment rates and off-shore net sampling found similar patterns in abundance for six of the seven species (Supplementary Figure S1). Coefficients of determination ranged from 0.14 for yellowfin croaker to 0.82 for white sea bass. The most explanatory relationships were between entrapment and either the gillnet or the lampara sampling. Trawl sampling bore little resemblance to the entrapment series.

The total annual sciaenid entrapment and circulated flow were unrelated ($R^2 = 0.06$; Figure 2). Entrapment totals peaked before 1987, with nearly all annual totals since tightly clustered under 200 000 fish at $4-6 \times 10^9$ m³ of cooling water circulated. SSTs during this earlier period were cooler than the latter years (Figure 3a). Between 1972 and 1982, 13% of the daily SST, on average, was >20°C. During the 26 years since 1982, SST exceeded 20°C on 23% of days each year, on average, including 48% of 1997 days. Since 1972, the mean annual SST progressively warmed at an average rate of 0.04°C per year ($R^2 = 0.32$), from 16.9°C in 1972 to 18.2°C in 2009. Simultaneously, the mean annual plankton biomass (ml) declined by 8.7 ml year⁻¹ on average ($R^2 = 0.63$), from a peak of 456.1 ml in 1975 to a low of 80.9 ml in 1993 (Figure 3b).

Queenfish was the most commonly entrapped species followed by, in descending order, white croaker, yellowfin croaker, spotfin croaker, black croaker, California corbina, and white sea bass (Table 1). Entrapment of three of the seven common sciaenids (queenfish, California corbina, and black croaker) declined after 1986 by between 74% (black croaker) and 86% (queenfish; Figure 4). The mean annual entrapment rate of white croaker declined (94%) after 1975 relative to its pre-1976 mean annual level. Spotfin and yellowfin croakers were generally more common after 1998, except 1973, when both species were relatively abundant. Their post-1998 mean annual entrapment rates were 295% (spotfin croaker) and 2626% (yellowfin croaker) higher than the mean annual pre-1999 entrapment rates. For both species, these rates were heavily influenced by the 2006 surveys when 1722% (spotfin croaker) and 10 023% (yellowfin croaker) more individuals of each species were recorded relative to the rest of the post-1998 period. Entrapment rates of white sea bass were erratic compared with the other species, with persistently elevated levels through 1986 and abundance peaks in 1997, 2001, and 2004. Sciaenid recreational catch rates were significantly correlated with entrapment rates for white croaker (r = 0.50, p =0.02, n = 21), California corbina (r = 0.49, p = 0.03, n = 20), and queenfish (r = 0.64, p < 0.01, n = 20). White sea bass and vellowfin croaker exhibited no such correlation.

Differences in the SADs between the first and the final decade of monitoring further illustrated a faunal shift (Figure 5). During the first decade, white croaker and queenfish combined to account for an average of 66% of the cumulative entrapment at HBGS and SONGS, whereas the combination of spotfin and yellowfin croakers accounted for <0.1%. During the final decade analysed, the mean annual contribution of white croaker and queenfish combined declined to an average of 28.3%, whereas that of yellowfin

Parameter	HBGS	OBGS	RBGS	SONGS	Parameter	HBGS	OBGS	RBGS	SONGS	
-	١	White sea bass				i	Black croaker			
ESGS	0.32	0.16	0.13	0.20	ESGS	- 0.09	0.28	0.21	-0.31	
р	0.06	0.38	0.43	0.24	р	0.61	0.12	0.22	0.06	
n	36	32	37	37	n	36	32	37	37	
HBGS		-0.10	0.36	0.09	HBGS		-0.02	0.25	0.40	
р		0.61	0.04	0.62	р		0.90	0.15	0.02	
n		30	35	35	п		30	35	35	
OBGS			-0.23	0.03	OBGS			0.23	-0.30	
р			0.20	0.85	р			0.20	0.10	
n			32	31	п			32	31	
RBGS				0.14	RBGS				-0.07	
р				0.41	р				0.69	
n				36	п				36	
White croaker					California corbina					
ESGS	0.68	0.37	0.45	-0.05	ESGS	0.62	0.27	0.23	-0.13	
р	0.00	0.04	0.01	0.76	р	0.00	0.13	0.18	0.44	
HBGS		0.08	0.47	0.07	HBGS		0.27	0.16	-0.08	
р		0.66	0.00	0.70	р		0.15	0.37	0.63	
OBGS			0.57	-0.51	OBGS			0.54	-0.19	
р			0.00	0.00	р			0.00	0.29	
RBGS				-0.31	RBGS				-0.24	
р				0.07	р				0.17	
		Queenfish			Yellowfin croaker					
ESGS	0.70	0.10	0.21	0.14	ESGS	0.15	-0.26	0.28	-0.03	
р	0.00	0.57	0.21	0.42	р	0.39	0.15	0.09	0.85	
HBGS		0.08	0.37	0.19	HBGS		0.41	0.16	0.01	
р		0.66	0.03	0.27	р		0.02	0.36	0.97	
OBGS			0.08	-0.08	OBGS			-0.02	-0.02	
р			0.64	0.66	р			0.91	0.92	
RBGS				-0.03	RBGS				-0.26	
р				0.86	р				0.13	

Table 2. Inter-plant Spearman's rank correlation results for entrapment rates (count per 10^6 m^3) of white sea bass, black croaker, white croaker, California corbina, queenfish, and yellowfin croaker entrapped at the five power plants (Figure 1), 1972–2009.

Spotfin croakers are not included because they are rare away from HBGS and SONGS (Table 1). Emboldening denotes significance at the p = 0.05 level. Sample size (*n*) was the same for all species as represented in plant-by-plant comparisons. Power-plant acronyms are consistent with those used in Figure 1.



Figure 2. Total entrapped raw abundance and annual cooling-water volume circulation flow recorded across the five power plants (Figure 1), cumulatively. The numbers represent observation years, 1972–2009.

and spotfin croakers rose to 4%. These patterns were further supported by changes in the mean annual latitude midpoint (Figure 6a). A significant ($R^2 = 0.38$, p < 0.001) southern influence in the mean annual midpoint was observed with an average

shift of 0.03°N per year. This pattern was significantly correlated with the mean annual SST ($R^2 = 0.24$, p = 0.002; Figure 6b). Before 1981, the entrapped sciaenid community's mean latitudinal midpoint was >34.5°N, but after 1980, the influence of more southerly distributed species increased, with the community's midpoint centred south of 34.5°N for 21 of 29 years. The effect of power-plant location on this pattern was discounted because no significant differences were detected between the northernmost (ESGS) and southernmost (SONGS) plants used in the analysis (Q = 0.171, p > 0.05). A significant difference was detected overall (Kruskal–Wallis, H = 52.769, d.f. = 2, p < 0.001) with the difference attributable to HBGS, which differed from both ESGS and SONGS. The differences between plants are likely attributable to the more frequent occurrence of white croaker and queenfish at HBGS. This community shift was mirrored in the SST. In 1976, the mean annual SST was >17°C for the first time since 1972, and it exceeded that threshold again in 30 of the subsequent 34 years of sampling.

Larval white croaker and queenfish densities trended similarly to their respective entrapment rates (Figure 7). The mean annual larval density of white croaker peaked in 1975 at 960 fish 1000 m³ (\pm 550), then declined to virtually zero, with none taken in 1997 and 2005. Persisting after the 1994 sampling year (153 fish per 1000 m³ \pm 85), the mean annual density of white croaker never again exceeded 45 fish per 1000 m³. Queenfish



Figure 3. (a) Mean (\pm s.e.) annual SST recorded at the Scripps Institution of Oceanography Pier in La Jolla, CA, 1972–2009, and (b) mean annual zooplankton volumetric biomass collected at King Harbor, Redondo Beach, CA, 1974–2006.



Figure 4. Mean annual entrapment rate (\pm s.e.) for each of the seven common sciaenids observed during entrapment surveys at the five power plants (Figure 1), 1972–2009.

larval densities followed a similar pattern, with peak densities before 1987 and none collected in 7 of the 19 years of sampling since, never again reaching the level observed in, and before, 1987.

In terms of entrapment rate, only white sea bass of the seven species analysed did not correlate with SST, plankton biomass, or either series of larval density (Table 3). Black croaker, white croaker, California corbina, and queenfish entrapment rates each significantly correlated with SST, plankton biomass, and both series of larval density. Each of these was negatively correlated with SST (r = -0.38 to -0.54), positively correlated with plankton biomass (r = 0.55 - 0.61), and positively correlated with both series of larval density (r = 0.47 - 0.70). Of all four species, white croaker and queenfish generally had one of the higher correlation coefficients in each of the analyses. Neither yellowfin nor spotfin croakers significantly correlated with SST or mean annual plankton biomass. Both species were significantly negatively correlated with both series of larval density (r = -0.35 to -0.50; Supplementary Figure S2). The mean annual plankton biomass significantly negatively correlated with SST (r = -0.61, p <0.01, n = 33), and positively with white croaker (r = 0.71, p <0.01, n = 33) and queenfish (r = 0.82, p < 0.01, n = 33) larval density. Both series of larval density were significantly negatively correlated with SST. The larval densities were significantly correlated with each other (r = 0.81, p < 0.01, n = 33).

Discussion

Most southern California sciaenids have been in decline since 1986, with some declining much earlier (e.g. white croaker; Figure 4). Species with more southern distributions (e.g. yellowfin croaker; Horn *et al.*, 2006) increased in the 1990s after the once-common species declined. These trends were consistent with a faunal shift in response to changing environmental conditions, similar to what has been documented in other marine fish communities (Holbrook *et al.*, 1997; Genner *et al.*, 2004; Perry *et al.*, 2005; Harley *et al.*, 2006). Declines in most entrapment rates were consistent with a negative response to changing ocean conditions, e.g. ocean warming (Figure 3), that began with the 1977 regime shift and were further exacerbated by the 1982–1984 California *El Niño* (Bograd and Lynn, 2003; McGowan *et al.*, 2003). Based on the community's response, nearshore oceanographic conditions failed to return to their pre-*El Niño* state after 1984. The most

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Figure 5. Percentage of total entrapment recorded during (a) the first decade (1972 - 1981), and (b) the final decade (2000 - 2009) of this monitoring at HBGS and SONGS, cumulatively, for each of the seven sciaenids common to southern California. Each dot represents an annual value, and the line represents the mean percentage across all years in the period of analysis.



Figure 6. (a) Mean annual abundance-weighted (\pm s.e.) biogeographic range latitudinal midpoint (°N) of the sciaenids entrapped at the five power plants (Figure 1), 1972–2009, and (b) mean annual abundance-weighted biogeographic range latitudinal midpoint (°N) of the entrapped sciaenids across all five power plants and mean annual SST (°C), 1972–2009, recorded at San Clemente Pier, San Clemente, CA, near SONGS. In (b), the reference line for 34.5°N is drawn.

significant change in juvenile/adult abundances recorded during entrapment surveys was in the early to mid-1980s (Figures 2 and 4). This transition was also detected in queenfish larval density (Figure 7) and in community latitudinal midpoint (Figure 6). Perhaps most importantly, the shift in the latitudinal midpoint was before the start of SONGS Units 2 and 3, which resulted in substantially more entrapment at the southernmost location used in the analysis here. This further supports the use of this analysis and discounts the potential impact of the shift in sampling effort to the south with the onset of additional entrapment at SONGS. Rather, the timing and between-plant comparisons further suggest that the pattern described was representative of the southern California sciaenid community, and not a site-specific factor induced by sampling. The 1980 threshold was largely a reflection of the declining abundance of white croaker while the other species became temporarily more common (Figure 4).

The timing of this change in the southern California sciaenid community is similar to that reported elsewhere across faunal



Figure 7. Mean annual larval white croaker and queenfish density $(\pm s.e.)$ recorded in King Harbor sampling, 1974–2006.

Table 3. Spearman's rank correlation results for each species-specific entrapment rate (1972–2009) and the SST recorded at the Scripps Institution of Oceanography Pier (1972–2009), mean annual plankton volumetric biomass (ml) observed in King Harbor, Redondo Beach, California (KHP), and the mean annual larval density of white croaker (KH wc) and queenfish (KH qu) recorded in King Harbor.

Species/parameter	SST	КНР	KH wc	KH qu
White sea bass	0.16	0.07	0.03	0.14
р	0.35	0.72	0.89	0.43
п	38	33	33	33
Black croaker	-0.38	0.56	0.54	0.65
р	0.02	0.00	0.00	0.00
п	38	33	33	33
White croaker	-0.54	0.61	0.58	0.54
р	0.00	0.00	0.00	0.00
п	38	33	33	33
California corbina	-0.50	0.55	0.51	0.47
р	0.00	0.00	0.00	0.01
n	38	33	33	33
Spotfin croaker	0.13	-0.25	- 0.48	-0.35
р	0.43	0.17	0.00	0.04
n	38	33	33	33
Queenfish	-0.42	0.57	0.70	0.69
р	0.01	0.00	0.00	0.00
n	38	33	33	33
Yellowfin croaker	0.11	-0.33	-0.50	-0.36
р	0.51	0.07	0.00	0.04
n	38	33	33	33
SST		-0.61	- 0.57	-0.58
р		0.00	0.00	0.00
n		33	33	33
KHP			0.71	0.82
р			0.00	0.00
n			33	33

All King Harbor sampling was conducted from 1974 to 2006. Emboldened values denote significance at the p = 0.05 level.

groups, including the North Atlantic (Reid *et al.*, 1998; Beaugrand *et al.*, 2003; Alheit *et al.*, 2005; Henderson, 2007; Henderson *et al.*, 2011), Southern Ocean (Weimerskirch *et al.*, 2003), SE Pacific (Alheit and Niquen, 2004; Alheit and Bakun, 2010), Black Sea (Alheit *et al.*, 2005), Eastern Pacific (Alheit and Bakun, 2010), and elsewhere in California (Holbrook *et al.*, 1997). Unfortunately, few studies in the southern California area span a similar distance with comparable temporal resolution as the data

used herein. For example, the California Cooperative Oceanic Fisheries Investigation conducted monthly surveys, but only at a triennial frequency between 1966 and 1984, after which quarterly surveys were conducted annually (Bograd and Lynn, 2003). Whereas empirical verification of the similarity in these patterns requires an analysis outside the scope of this study, they do provide additional support for an environmental source of the majority of the observed changes in southern California sciaenids.

Conditions in the early to mid-1980s were characterized by substantial oceanographic perturbations in both the Pacific and Atlantic that were likely linked to the 1982–1984 ENSO (Alheit and Bakun, 2010; Henderson *et al.*, 2011). Alheit and Bakun (2010) hypothesized that this connection largely resulted from the cascading effects of the 1982–1984 Pacific ENSO, which altered atmospheric patterns causing an Atlantic ENSO, a pattern also observed during the similarly strong 1997/1998 ENSO. Not all communities responded identically, however, coolwater species failing to decline in all instances. Moreover, the 1997/1998 ENSO, although of similar strength, did not result in a corresponding faunal shift, but it did induce a substantial temporary influx of tourist species into the southern California area (Lea and Rosenblatt, 2000).

Altered temperature, upwelling, stratification, and other oceanographic conditions have been described in most ocean basins in response to this global perturbation (Alheit and Bakun, 2010), similar to the post-1977 conditions in the nearshore Southern California Bight described by Bograd and Lynn (2003). The strengthening of poleward coastal flow in the Southern California Bight provides a further conveyance for the increased import of tourist species from more southerly latitudes, similar to the extremes observed during the 1997/1998 ENSO (Figure 6a).

Significant negative correlations between four species with declining entrapment rates and both SST and plankton biomass (Table 3) provide additional evidence of environmental forcing on these populations. The inclusion of plankton biomass as an indicator of environmental effects assumes a cause-and-effect relationship between plankton dynamics and oceanographic conditions, and the results reported by Roemmich and McGowan (1995) support this assumption. Furthermore, the simultaneous declines in larval densities of white croaker and queenfish (Figure 6), and their significant negative correlations with SST but positive correlations with plankton biomass (Table 3), suggest a cascading effect of environmental regulation working through the system. Significant correlations between white croaker and queenfish larval densities suggest that each may be reacting to similar environmental conditions. Analysis of larval patterns was limited to white croaker and queenfish, because larvae of the other species have been taken only infrequently off southern California (McGowen, 1993; Moser et al., 2001).

Gadomski and Caddell (1996) documented poor egg hatching of white croaker at water temperatures $>20^{\circ}$ C, a threshold more commonly exceeded since 1982. This further supports the assumption that the variability in larval density of white croaker reflected warming ocean conditions after 1977 and the ENSO event beginning in 1982 (Bograd and Lynn, 2003; McGowan *et al.*, 2003). The impact of water temperature on the physiological functions of fish was not documented during this study, but it has been investigated by others (Pörtner and Knust, 2007; Pörtner *et al.*, 2008, 2010; Pörtner and Peck, 2010). Elevated dissolved oxygen and metabolic demand, among other functions, resulted from exposure to warmer water temperatures, with the most demonstrative effect during the larval period. The significant correlations between white croaker and queenfish larval densities and both rising SST and declining zooplankton densities align with these hypotheses, in addition to the effect on egg hatching rates of white croaker observed by Gadomski and Caddell (1996). Water temperature does not likely account for all the observed changes, but its consistent significant correlation with various oceanographic parameters, e.g. dissolved oxygen, nutrients, productivity (Bograd and Lynn, 2003; McGowan *et al.*, 2003), suggests that it acts as a suitable proxy and was therefore appropriate to use in this analysis.

The consistency of the patterns observed suggests that environmental forcing, rather than harvesting, was the factor most influential in driving the Southern California Bight sciaenid community, with the possible exception of white sea bass (Allen et al., 2007; Pondella and Allen, 2008). A definitive analysis of harvesting effects is hampered by the lack of an estimate of standing stock for any of the sciaenids analysed here, but reasonable conclusions can be drawn regarding the absolute harvest pressure(s) applied to each. This, of course, does not account for the relative impact of each fishery, however. These pressures were apparently greatest for white sea bass among southern California sciaenids (Allen et al., 2007), with only white croaker and queenfish, of the others, commercially harvested in southern California. Neither species, however, exhibited a similar disconnect from the environmental and productivity patterns to that seen in white sea bass. Rather, white croaker and queenfish entrapment rates were each significantly correlated with all the other parameters tested. The other sciaenids were all less intensively targeted by recreational fishers and consistently exhibited patterns consistent with environmental forcing, e.g. correlation with temperature and/or productivity parameters. Recreational anglers traditionally target white sea bass in vessel-based fisheries; white croaker were taken in a variety of ways (e.g. from beach and bank, piers, and private boats); the other species were among the ten most common species taken from beaches and banks or man-made structures such as fishing piers (Love, 2006). In southern California, vessel-based fishing accounts for 68% of all fishing pressure, but <10% of angler trips are made to beaches and banks, and the other 22% of trips target man-made structures (Love, 2006). Therefore, the recreational harvest pressure on fish supporting largely shoreline fisheries was likely less than on those targeted by vessels.

Despite the variable harvesting pressure applied to each species, the similarities in entrapment trends over time and their correlations with other independent environmental or biological parameters and the temporal similarities in the community shifts documented from other locales, including southern California, discounts harvesting pressure as the main driver of change in southern California sciaenids. Unfortunately, insufficient data exist to fully rule out the potential effect of harvesting pressure, especially given the often synergistic or cumulative effects of harvest pressure and environmental conditions (Brander, 2007; Hsieh *et al.*, 2008).

To conclude, therefore, population trends in six of the seven sciaenid species analysed here represent a community shift likely in response to changing environmental conditions consistent with a global pattern of change. Harvest pressures can largely be discounted owing to the general consistency in the relationships between the abundance indices and the environmental/productivity metrics, despite the wide-ranging continuum of fishing pressure ranging from intensive commercial pressure to limited beach and bank recreational fishing.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the paper. Additional material related to the verification of the similarities in sampling effectiveness between entrapment, lampara net, gillnet, and otter trawlnet are presented. Figures depicting the relationship between entrapment and the most similar offshore net-sampling technique are provided by species, with the associated coefficient of determination. Additional figures depicting the relationship between species-specific entrapment rates and the mean annual larval white croaker and queenfish densities are also provided.

Acknowledgements

We thank P. Tennant, K. Anthony, S. Maghy, A. Sanchez, and K. Whelan for their support of the entrapment monitoring and use of the data. R. A. Miller inspired the work. We thank Wayne Ishimoto and Kim Damico of Chevron Products Company for their continued support of the project, S. Schroeter for graciously providing the lampara net catch data, J. A. McGowan for insightful discussions that greatly improved the study, and C. Tharp, E. Parnell, and two anonymous reviewers for their comments that greatly improved the final manuscript.

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