ENVIRONMENT-DRIVEN TRENDS IN FISH LARVAL ABUNDANCE PREDICT FISHERY RECRUITMENT IN TWO TEMPERATE REEF CONGENERS: MECHANISMS AND IMPLICATIONS FOR MANAGEMENT

Erica T. Jarvis Mason[1*], Andrew R. Thompson[2], Brice X. Semmens[1]

[1]Scripps Institution of Oceanography, University of California San Diego, California, USA

[2]Southwest Fisheries Science Center, NOAA Fisheries, California, USA

*Corresponding author: etmason@ucsd.edu

ABSTRACT

Environmental and biological processes acting on fish larvae were long thought to drive fishery cohort strength, but predictive ability oftentimes fell short and larval abundance is now considered to be more useful as a proxy for spawning stock biomass. In the face of a changing ocean, studies that relate environmental covariates, larval abundance, and fishery recruitment are still worthy of continued research, especially in data-limited contexts. Here we focus on a decades-long popular recreational-only multispecies fishery whose population status and recovery potential are uncertain. We leveraged 54 years of ichthyoplankton data (1963-2016) and a powerful species distribution modeling framework to 1) reconstruct species-specific standardized indices of larval abundance, 2) test these indices as a useful indicator of adult stock status or predictor of future fishery recruitment, and 3) to evaluate spatiotemporal trends in their population dynamics relative to environmental variables. Contrary to expectation, species-specific larval abundance predicted future catch across multiple catch data sets, with recent elevated larval abundance suggesting fishery recovery is imminent. Additionally, we identified strong relationships between environmental variables and species-specific larval abundance, thereby providing additional tools for predicting future fishery recruitment and anticipating population change. Our findings paint a path forward for improving estimates of current and future fishery status under changing natural and anthropogenic influences and the incorporation of ecosystem considerations into fishery management.

1. INTRODUCTION

An ecosystem approach to fishery management (Dolan et al. 2016) includes consideration of the many biological and environmental factors that have historically, and are currently, influencing fished populations. This, of course, also requires having information and resources to adequately evaluate the status of fish populations. Unfortunately, many small-scale fisheries lack such a robust approach, partly because data and resources are lacking. Given that the economic and ecological impacts of some marine recreational fisheries have rivaled that of commercial fisheries (Cooke & Cowx 2004, Lewin et al. 2019), and that overexploitation dampens the ecosystem resilience of fish populations (Perry et al. 2010, Ziegler et al. 2023), there is a clear need for research that leads to more robust population assessments for recreational-only and small-scale commercial fisheries.

One of the most popular and economically important recreational-only marine fisheries in California, USA, and perhaps even the world, is the southern California saltwater bass (*Paralabrax* spp.) fishery, which consists of Barred Sand Bass (BSB, *P. nebulifer*), Kelp Bass (KB, *P. clathratus*), and Spotted Sand Bass (SSB, *P. maculatofasciatus*). This multi-species fishery has persisted since the early 20th century, but catches have remained at historic lows since 2013 and are thought to primarily reflect a depressed population of BSB (a species targeted during spawning aggregations; Jarvis et al. 2010, 2014, Erisman et al. 2011). Dramatic catch declines for BSB and KB began in 2005, following a period of increasing fishing mortality and population recruitment failure (Jarvis et al. 2014a). In contrast, SSB is almost entirely catch-and-release, limited to bays and estuary habitat, and presumed to have a healthier population. In 2013, regulations for the saltwater basses became more restrictive (CCR Title 14, Section 28.30), but the fishery has not recovered, casting further uncertainty into the status and recovery potential

of the BSB and KB populations. Adding to that uncertainty is the unknown impact that a warming ocean will have on these populations. Thus, research on the population dynamics of the saltwater basses may help with anticipating change and aid in the rebuilding and future management.

Differences in the geographic ranges, habitats, and reproductive strategies of the three saltwater basses suggest different sensitivities to fishing pressure and environmental conditions, and thus, differences in their resilience to climate change impacts. KB have occurred as far north as the cool temperate coast of the state of Washington, USA, while BSB and SSB have a maximum northern range extent that is approximately 1,000 km to the south, off the central California coast. The southernmost occurrence for KB is southern Baja California, Mexico, and for BSB and SSB, it is equatorward in the tropical waters of Acapulco, Mexico; SSB also have populations in the Gulf of California (Heemstra 1995). As a group, the saltwater basses have responded to decadal shifts in oceanographic conditions throughout the history of the fishery, being relatively more abundant during warmer ocean temperature regimes (Moser et al. 2001b, Hsieh et al. 2005, Jarvis et al. 2014a) and at one time, more common north of southern California (Hubbs 1948). Therefore, it is possible that northern latitudinal shifts in saltwater bass larvae abundance have taken place through time, coinciding with decadal-scale oceanographic cycles and climate-driven increases in sea surface temperature (SST, Auth et al. 2018). Yet, at finer temporal scales, the saltwater basses may show differential population responses associated with seasonal or interannual oceanographic variability (i.e., upwelling, El Niño). Thus, understanding the relative role environmental variability has had on saltwater bass populations with respect to their vulnerability to harvest (i.e., catch-and-release versus aggregation-based), should help us understand which species may be resilient to climate change impacts.

Southern California is uniquely data-rich in terms of long-term coastal oceanography data, and thus represents an ideal testbed for the development of ecosystem-assessment methods. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) is one of the world's largest and longest-standing fisheries oceanography surveys (Gallo et al. 2019), and since 1951, has conducted quarterly surveys to collect biological samples (e.g., fish larvae abundance, zooplankton biomass) and hydrographic data at discrete sampling locations throughout the Southern California Bight (SCB). Due to its long temporal coverage and high spatial resolution, the survey has enabled researchers to detect natural and anthropogenic influence on larval fish populations in southern California (Hsieh et al. 2008, Asch 2015, Thompson et al. 2017), and to assist resource managers in fishery assessments (Moser et al. 2001b, McClatchie 2014, Gallo et al. 2019). Combined with other oceanographic and fishery data streams, CalCOFI provides the unique opportunity to assess historical and recent spatiotemporal trends in saltwater bass populations. Indeed, interest in parsing the CalCOFI *Paralabrax* spp. larval time series to species funded research in the 1970s and 1980s to develop morphological and genetic tools for doing so (Butler et al. 1982, Graves et al. 1990), but successful species discrimination across larval stages was only recently made possible with the development of a robust taxonomic key (Jarvis Mason et al. 2022).

Larval abundance has long been considered a proxy for spawning stock biomass (Hilborn & Walters 1992, Cowan & Shaw 2002). Indeed, CalCOFI fish larvae have been incorporated in west coast fishery stock assessments or used for monitoring status and trends (see Gallo et al. 2019 for a description of examples). Thus, if we assume bass larval abundance is a function of the biomass of reproductive females in the population, then fishery managers are provided with an easy, reliable means of tracking the status and trends of adult bass fish stocks. On the other

hand, there is reason to believe the abundance of larvae of sufficient size to be caught in CalCOFI nets reflects future recruitment; that is, since larval fish dynamics are so highly influenced by environmental variability, the processes affecting larval growth and mortality are thought to drive future fishery year class strength (Hjort 1914, Lasker 1984, 1987, Cushing 1990, Houde 2001). However, due to continued abiotic and biotic pressures on subsequent life stages, the accuracy of recruitment prediction is generally considered to be higher the closer the index measure is to the age of fishery recruitment (e.g., the juvenile or subadult stage, Bradford 1992, Cowan & Shaw 2002). Jarvis et al. (2014) reported strong relationships between combined *Paralabrax* spp. larval abundance and species-specific fishery recruitment strength between 1997 and 2012, but it is unknown whether this relationship translates using species level larval abundance over a longer period.

Here, we unlock the CalCOFI *Paralabrax* spp. larval archive for the first time. In doing so, we intend to generate an index of southern California bass larvae abundance to improve species-specific estimates of population status and trends and to identify environmental indicators of population health and climate forcing (e.g., latitudinal shifts in abundance). We also explore species-specific relationships between larval abundance and spawning stock size to unravel whether long-held beliefs regarding larval abundance and spawning stock hold true for the saltwater basses and to discern the utility of any identified larvae-environment relationships as a tool for assessing adult status or for predicting future fishery recruitment. In the face of a changing ocean, the ability to identify potential environmental indicators of population status or future fishery recruitment (i.e., potential management action triggers) will be ever more important for guiding sustainable fishery management (especially in data-limited contexts) and may be a key determinate in the fate of this historical fishery.

2. METHODS

2.1. *CalCOFI Survey and Study Region*

We focused on *Paralabrax* spp. larvae collected in CalCOFI surveys conducted along the continental shelf off southern California and Baja California (Fig. 1a), during July cruises from 1963 to 2016 because: 1) July corresponds to peak spawning for BSB and KB, 2) *Paralabrax* spp. larvae occur nearshore (Moser et al. 2001a), and, 3) at the time of this study, the CalCOFI ichthyoplankton archive was being updated in reverse chronological order to current taxonomic standards (1963 and 2016 were the most historical and recent years available, respectively). Two changes to CalCOFI zooplankton sampling occurred during this period, 1) in 1969, the depth from which nets were obliquely towed increased from 140 m to 210 m (or from within 5 m of the seafloor in shallower waters), and 2) in 1978, the sampling gear changed from ring nets to paired bongo nets (Thompson et al. 2017). Survey coverage has varied spatially and temporally, with more consistent temporal coverage in the SCB (Fig. 1a) and additional, shallower, coastal stations added in 2004 (Gallo et al. 2019).

The study region is part of the California Current Ecosystem, in which the offshore California Current (CC) brings cool, nutrient-rich waters equatorward from north of Pt. Conception, CA (34.2°N), before branching shoreward toward the U.S.A./Mexico border (32.2°N), and then poleward along the southern California coast, forming the counterclockwise southern California Eddy within the SCB in the summer months (Fig. 1b, Hickey 1993, McClatchie 2014). The southern branch of the CC continues to flow equatorward, offshore of

Baja California. Thus, the study region generally consists of cooler temperate waters to the north and subtropical waters to the south (Fig. 1b, McClatchie 2014).

2.2. *Identification of Formalin Preserved Larvae*

Two taxonomists sorted and processed *Paralabrax* spp. larvae from archived CalCOFI cruise station vials. We assigned the larval stage of each larva according to notochord development and then assigned species using pigmentation patterns described in Jarvis Mason et al. (2022). We excluded yolk sac larvae as these could not be reliably identified, and we excluded *P. auroguttatus* (Goldspotted Sand Bass) because its population is rare north of Baja California Sur. We photographed all larvae and recorded the presence/absence of stage-specific morphological characters described in Jarvis Mason et al. (2022). For quality assurance, we selected a random, temporally stratified, subset of samples (10%) to be identified by both taxonomists. We reviewed and resolved all identifications with taxonomic disagreement. Four station vials contained hundreds of *Paralabrax* spp. larvae, and we subsampled at least 10% of the contents of these vials and then extrapolated the raw species counts based on the proportion of each species identified in the subsample, including any unidentified or yolk sac larvae. The two taxonomists regularly collaborated to resolve any outstanding, difficult-to-identify larvae.

To characterize the overall sample of visually identified *Paralabrax* spp. larvae, we summarized the raw numbers of larvae by species, larval stage, and region (southern California, Baja California) and we plotted their geographic distributions. For subsequent analyses, we standardized the *Paralabrax* spp. counts in each sample by the standard haul factor to obtain the number of larvae under ten m^2 of sea surface (Thompson et al. 2017). This standardized raw count we refer to as larval abundance. There were 26 samples from 12 cruises in which larvae

were so damaged as to not be identifiable to species or there was a discrepancy in the number of *Paralabrax* spp. larvae reported in the database versus the number observed in the sample vial (e.g., missing larvae). In this case, we estimated larval abundance (the standardized counts) at these stations based on the average proportion of each species standardized count at that station over the course of the entire study period. Beforehand, we re-sorted the original station vials and any corresponding reference collection vials to check if missing *Paralabrax* spp. larvae were not removed during the first sort.

2.3. *Standardized Index of Larval Abundance*

We used species distribution models (SDMs) to generate standardized indices of bass larval abundance in southern California. We did not include larval abundance data from Baja California because July CalCOFI survey coverage extending into Baja California Sur, was restricted to the early part of the time series (prior to 1980). We chose a geostatistical generalized mixed effects model framework that can incorporate spatial and spatiotemporal random fields (effects) to account for latent variables that may contribute to observations being correlated in space and time. The spatial random field captures latent spatial variation that is unchanging through time (e.g., seafloor depth), while the spatiotemporal random field captures latent time varying spatial patterns (e.g., dynamic biological and oceanographic processes). This type of SDM can therefore account for unbalanced sampling effort and thus, is more precise than other SDM methods at estimating abundance (Thorson et al. 2015, Brodie et al. 2020). We fit SDMs with the R package `sdmTMB`, which estimates parameters of the Gaussian random fields using the Integrated Nested Laplace Approximation (INLA) and implements maximum marginal likelihood estimation with Template Model Builder (TMB, Anderson et al. 2022).

We modeled bass larval abundance as a function of variables that may affect "catchability" but not abundance (e.g., when and where you survey, gear type). For both species, we considered year, hour, day/night by net type (to account for gear changes, Thompson et al. 2017), and distance to shore. We did not consider the increase in tow depth because southern California *Paralabrax* spp. larvae are most abundant inshore of the 36 m depth contour (Lavenberg et al. 1986). We modeled bass larval abundance Y at location s and time t using a Tweedie observation error family (positive continuous density values that also contain zeros) and a log link:

$$Y_{s,t} = \ln(\mu_{s,t}),$$

$$\mu_{s,t} = \boldsymbol{X}_{s,t}\boldsymbol{\beta} + \omega_s + \epsilon_{s,t},$$

$$\omega_s \sim \boldsymbol{MVNormal}(\mathbf{0}, \textstyle\sum_{\omega_s}),$$

$$\epsilon_{s,t} \sim \boldsymbol{MVNormal}(\mathbf{0}, \textstyle\sum_{\epsilon_{s,t}}),$$ where,

$\mu_{s,t}$ represents mean abundance at location s and time t,

$\mathbf{X}_{s,t}$ is a vector of main effects, time varying effects, or spatially varying effects corresponding to location s and time t,

$\boldsymbol{\beta}$ is a vector of corresponding effects slope parameters, and

ω_s and $\epsilon_{s,t}$, are the spatial and spatiotemporal random effects, respectively, assumed to be drawn from a multivariate normal distribution with covariance matrices.

The model uses a predictive-process stochastic partial differential equation (SPDE) triangulated spatial mesh to approximate the spatial component of the Gaussian random fields via bilinear interpolation between the mesh vertices (knots, Anderson et al. 2022). We specified a minimum cutoff of ten km between mesh knots and incorporated a physical barrier mesh to

account for the coast and islands, in which we specified a spatial range of 0.1 (i.e., fractional distance of spatial independence), which corresponds to a spatial correlation decay rate that is ten times faster over land than over water (Fig. S1, Anderson et al. 2022). The specified spatial resolution of the knots was fine enough to prevent overfitting of the model, given the number of data points.

Given data gaps for some years, we could not model year as a factor variable. We specified all main effects as a penalized smooth function (as with generalized additive models, GAMs, Wood 2017) and allowed the model to select the basis function (wiggliness), except for the hour variable, in which we specified a cyclic smooth with a 24-h basis function. We specified day/night by net type as a smoothed factor. We first identified the appropriate main effects for inclusion in the model using AIC, and then we used Restricted Maximum Likelihood (REML)-generated AIC values to identify the appropriate random effects model structure (e.g., spatial field on or off, year as independent, first-order autoregressive (ar1), or a random walk). We specified missing years for model estimation of larval abundance. We did not consider models that did not pass all model diagnostic checks (e.g., tests for convergence, positive definite Hessian matrix, large standard errors associated with model parameter estimates).

To generate an area-weighted standardized index of larval abundance, we used our model to predict abundance across a fine-scale grid covering the southern California CalCOFI survey region, with a grid cell resolution of 5 km x 5 km.

2.4. *Relationship with Fishery Catch Data*

For both species, we tested for a positive correlation between the index of larval abundance and spawning stock biomass, in which we used catch records from CDFW

Commercial Passenger Fishing Vessel (CPFV) logbooks (1975-2016) as a proxy for spawning stock biomass (see Jarvis et al. 2014a for a detailed description of catch data sets). We chose to use the catch data because they represent the only index of abundance of saltwater bass abundance that matches the geographic extent of the CalCOFI larval abundance data. Typically, catch-per-unit-effort (CPUE) is considered an appropriate catch metric to use as an index of abundance because it accounts for changes in fishing effort over time. However, in this fishery, catch and CPUE directly correspond (Jarvis et al. 2014a) and species-specific CPUE at the trip level is not available prior to 1980. CPFV catch records reflect only fish kept (harvested catch).

We considered only biologically plausible lags (i.e., catch cannot lead larvae) from zero to ten years and standardized all data to a mean of zero. We performed cross-correlation analysis using the R package `funtimes` in which a 95% confidence band provided guidance for interpreting correlations that may be influenced by the presence of autocorrelation in either or both datasets (i.e., coefficients falling within the band may be an artifact of non-stationarity, Lyubchich et al. 2023). We also explored the relationship between species-specific larvae abundance estimates and estimates of *total* catch (harvest plus catch released alive or dead) by all fishing modes combined, available from the Marine Fisheries Statistical Survey (MRFSS, 1980-2003) and the California Recreational Fisheries Survey (CRFS, 2005-2016). Estimates from the MRFSS and CRFS are not calculated based on the same sampling design; however, since we were not concerned with absolute abundance estimates, we combined the time series and standardized the single time series to a mean of zero.

We assumed a positive correlation between larvae and catch at a lag of 0 years to indicate a positive relationship between spawning stock biomass and larval abundance, where larval

abundance is a function of the biomass of reproductive age females in the water (i.e., the higher the spawning stock biomass, the higher the larval abundance).

2.5. *Spatiotemporal Trends in Larval Abundance*

To explore changes in larval abundance through time, we plotted spatiotemporal trends in larval abundance of both species using predicted annual abundances defined by a 5 km x 5 km resolution grid (exclusive of land and within the southern California CalCOFI survey area) and the parameter estimates generated from the index standardization model (Anderson et al. 2022). These trends included both fixed and random effects. We also separately plotted trends in the spatiotemporal random effects ($\epsilon_{s,t}$) to visually explore what patterns in the plots of fixed and random effects were being driven by latent spatiotemporal processes.

2.6. *Relationship with Environmental Variables*

We also used the R package `sdmTMB` to model the influence of site-specific prey availability and temperature, as well as larger-scale oceanographic indices on bass larval abundance. Not all environmental variables of interest were available as far back as 1963, so we first modeled a smaller set of variables across the entire time series (1963 and 2016, Model 1) and then incorporated additional variables over a shorter period (1984 to 2016, Model 2). In addition, data available for modeling bass larval abundance was limited to those years for which a July CalCOFI cruise took place, as `sdmTMB` does not allow for NAs.

For both species in Model 1, we included the station specific CalCOFI temperature (°C, averaged across the upper ten meters) and square root transformed zooplankton biomass measured as zooplankton displacement volume (cm^3/1000 m^3 strained). We also included the

North Pacific Gyre Oscillation index (NPGO) for the month of July and the Oceanic Niño Index (ONI) for June/July, and distance from the mainland shoreline (km). The NPGO and the ONI are larger-scale climate pattern indices related to regional nutrient fluctuations (or, mechanisms driving plankton ecosystem dynamics) and surface temperature anomalies in the east-central tropical Pacific associated with the El Niño Southern Oscillation (ENSO), respectively (Di Lorenzo et al. 2008, NOAA 2023).

For both species in Model 2, we included all variables from Model 1, and two additional variables: an upwelling index and isothermal layer depth (ILD, m). We included upwelling because we wanted a more local measure of potential nutrient availability (versus the larger-scale NPGO), and we included ILD because spawning BSB orient to the thermocline during spawning season (McKinzie et al. 2014). In the study region, the ILD roughly corresponds to the mixed layer depth (MLD), which is the depth where temperature differs by 0.5 °C from the sea surface (i.e., we assume no salinity barrier layer between the MLD and ILD). We used a mean Bakun upwelling index (m^3/sec) for June/July at latitude 33°N, where positive values indicate wind-driven offshore transport (Bakun 1973). For both species, we considered another candidate Model 2 where the Bakun index was substituted for both the Biologically Effective Upwelled Transport Index (BEUTI) and Coastal Upwelling Transport Index (CUTI) specific to the southern California region, which provide a measure of nitrate flux through the mixed layer and coastal vertical transport, respectively (Jacox et al. 2018, data from Hunsicker et al. 2022). Positive BEUTI values indicate nitrate flux into the mixed layer and positive CUTI values indicate coastal upwelling. For BSB, we also considered a candidate Model 2 that substituted upwelling in the SCB with upwelling off northern Baja California (Bakun index at latitude 30°N)

because older recruits (~ 2-y) showed a negative correlation with upwelling south of the SCB at a 2-y lag (Jarvis et al. 2004).

For each individual model, we identified the most parsimonious random effect structure using REML AIC values. We used model AIC values to identify the most parsimonious among the Model 2 candidate models for each species. When comparing fixed effects candidate models, we only considered models having the same random effects structure. We visually explored the conditional effects of important explanatory variables using the R package `visreg` (Breheny & Burchett 2019).

For all models, we standardized all non-index variables to a mean of zero. We used the R package `corrplot` (Wei & Simko 2021) to visually identify any explanatory variables that were strongly correlated (e.g., coefficients greater than 0.4), with the intention that strongly correlated explanatory variables would be further evaluated with conditional effects plots and the number of variables reduced, if necessary. As `sdmTMB` cannot handle NA values, we used the inverse distance-weighted interpolation method to fill in any missing within-cruise CalCOFI station data prior to analysis.

2.7. *Latitudinal Shifts in Larval Abundance*

To detect potential latitudinal shifts in bass larval abundance over time, we used larval abundance predictions from the standardized index of abundance models and a species distribution function (SDF) estimator within `sdmTMB` to calculate temporal trends in the center of gravity for both species (COG, Thorson et al. 2016, Anderson et al. 2022). For larvae of both species, we plotted changes in the annual COG, grouped by decade and mean July SST. We

obtained mean July SSTs off Pt. Dume, CA, which is approximately centrally located along the southern California coast (Carter et al. 2022).

3. RESULTS

We examined a total of 1,267 "*Paralabrax"* spp. larvae sorted from original station vials (143 samples), of which 1,118 larvae could be positively identified as southern California *Paralabrax* spp.; most (60.2%) were collected off Baja California (Fig. S2). Southern California larvae consisted of 64.6% KB, 31.3% BSB, and 4.1% SSB. Off Baja California, numbers were highest for BSB (76.5%), followed by KB (16.5%) and SSB (7.0%). Preflexion larvae were encountered more frequently across species and region; postflexion larvae were least common (Fig. S2). By station, KB were relatively more common offshore, while BSB and SSB were restricted to nearshore stations, with the highest numbers on average off Baja California Sur, south of Punta Eugenia (Fig. S3). SSB larvae in the CalCOFI time series were rare, particularly in southern California, indicating CalCOFI is not a representative survey for SSB larvae in this region.

There were four sub-sampled stations with high numbers of larvae that occurred off Baja California in the 1960s. Extrapolated species counts for these stations increased the overall raw larval count by an additional 1,716 larvae comprised of 93.0% BSB, 5.6% SSB, and 1.2% KB; we did not further extrapolate the counts by larval stage. The standardized raw counts of species-specific bass larval abundance in southern California indicated KB larval abundance was generally higher year-to-year than that of BSB (Fig. S4). Off Baja California, peaks in bass larval abundance occurred in the early 1960s and consisted primarily of BSB, while low abundances from 1989 onward were representative of a single Baja California CalCOFI survey line (93.4) off

the very northern part of Baja California (Fig. S4), in which line 93.4 was the only Baja California CalCOFI line surveyed in those years. Cruises in 1981 and 1984 did not extend south beyond Punta Eugenia, Baja California (Fig. 1).

3.1 *Temporal Trends in Larval Abundance*

The most parsimonious index standardization models included BSB larval abundance as a time-varying function of distance to shore (smoothed), incorporated all random effects, including an independent spatiotemporal field across years ("iid"); the resulting index for KB included larval abundance as a function of year (smoothed) with all random effects, and an independent spatiotemporal field across years (Table 1; see Table S1 for parameter estimates of the main and fixed effects). Temporal trends in the standardized index of larval abundance for both species showed similar sporadic larval pulses in 1981, 1989, 2012, and 2014 (Fig. 2). Compared to BSB, KB larval abundance estimates were less variable and less uncertain, with generally higher abundance between strong larval pulses. Larval abundance for both species was exceptionally low between the late 1990s and early 2000s. BSB larval abundance increased from lower levels in the 1960s, declined through the 1990s and early 2000s, and increased again through the mid-2010s (Fig. 2a). In contrast, KB larval abundance steadily declined between the early 1980s and early 2000s before increasing again into the 2010s to levels similarly observed before the 1980s (Fig. 2b).

3.2. *Spatiotemporal Trends in Larval Abundance*

Predicted bass larval abundance off southern California also showed geographic differences through time. BSB larval abundance was generally low throughout much of the SCB,

with the highest densities occurring nearshore and primarily along the central and southern coast (Fig. S5). In contrast, KB larval abundance was relatively higher throughout the SCB, with hotspots occurring primarily at the northwest Channel Islands (Fig. S6). KB larval abundance was particularly low throughout the SCB between 1995 and 2003. Spatiotemporal random effects plots for BSB and KB also showed different patterns through time (Fig. S7, S8), in which deviations from the fixed effects predictions varied depending on species, location, and year.

3.3. *Relationship with Fishery Catch Data*

We found no relationship at a lag of zero between bass larval abundance estimates and fishery catch data, except for a marginal relationship at a lag of zero between KB larval abundance and the harvest data set (Fig. 3). In contrast, for both species, we found moderate strong lagged relationships between larval abundance and all catch data sets. For example, the highest correlations between BSB larval abundance and total catch estimates were positive from -8 to -10 years, indicating BSB larvae can predict total catch eight to ten years into the future (Fig. 3a). We found a similar trend with the BSB harvest data set, in which the highest correlations indicated larvae led catch by seven to ten years. For KB, larval abundance led total catch estimates by two to ten years, and with the harvest data, larvae led catch by five to ten years (Fig. 3b).

3.4. *Relationship with Environmental Variables*

July CalCOFI cruises occurred triennially between the mid-1960s and mid-1990s, otherwise, July temperature and zooplankton data were available annually (Fig. 4). The larger

scale environmental variables were available annually but the BEUTI, CUTI, and ILD for southern California were only available from 1980 onward (Fig. 4). There was little multicollinearity among the 45 combinations of environmental variables and most correlations were weak (< 0.20, Fig. S9). However, there were three relatively strong correlations; one between the BEUTI and the CUTI (0.700), one between the BEUTI and the NPGO (0.550) and one between the Bakun index 33°N and the NPGO (0.470). Moderate correlations existed between the Bakun index 33°N and ILD (-0.390), ONI and NPGB (-0.350), distance from shore and temperature (-0.310), and between the Bakun index and BEUTI (0.270). The remaining correlations were weak or non-existent (Fig. S9).

In southern California, over the entire study period, 1963 to 2016, CalCOFI station-specific temperature (mean from surface to 10m) and zooplankton biomass were positive predictors of bass larval abundance for both species (Fig. 5, S10, S11). For BSB, there was also a strong negative relationship with distance to shore (higher larval abundance nearshore), and a strong positive relationship with NPGO (the higher the NPGO, the higher BSB larval abundance, Fig. 5a, S11).

Over the shorter study period, 1984 to 2016, the ILD was strongly negatively related to bass larval abundance (high bass larval abundance with shallower ILD, Fig. 6, S12, S13). Of the different upwelling indices considered (Bakun, BEUTI, CUTI), models with the Bakun index were more parsimonious (Table 2); however, none of the upwelling indices showed a relationship to bass larval abundance. Positive relationships with temperature and zooplankton abundance remained important for both species during the shorter period, while NPGO became less important for BSB (Fig. 6a, S13).

3.5. *Latitudinal Shifts in Bass Larval Abundance*

Bass larval abundance center of gravity within the SCB remained remarkably stable between the 1960s and 2010s (Fig. 7). The larval BSB center of gravity remained centrally located along the mainland coast, fluctuating off Santa Monica Bay to the north and Huntington Beach to the south (Fig. 7a). In contrast, the larval KB center of gravity was shifted to the north and offshore, closer to the northwest Channel Islands (Fig. 7b). We observed no consistent northward or southward directional movement in the center of gravity for either bass species, when grouped by decade or by mean July SST.

4. DISCUSSION

Our reconstructed larval indices of abundance span over half a century and represent the longest species-specific, fishery-independent time series for the saltwater basses in southern California, USA. Though larval abundance is generally considered to be a suitable proxy for adult spawning stock biomass, our results indicate southern California bass larvae abundance over the last several decades is a better reflection of future catch in the fishery, as both BSB and KB larval abundance had moderate to strong predictive power in forecasting fish catches. In addition, for both species, this result was consistent across different catch data sets (i.e., total harvest and estimates of total catch [harvest plus releases]), further validating the relationship. Moreover, the utility of this predictive power for fishery management is bolstered by the strong relationships we identified between bass larval abundance and environmental variables (e.g., temperature, zooplankton biomass, MLD), and thus, paints a path forward for an ecosystem approach to managing this fishery. Additionally, our analysis revealed species-specific temporal and spatiotemporal trends, as well as differences in the strength of environment-species

relationships, suggesting potential differences in their resilience and recovery potential with respect to intrinsic oceanographic variability and climate change impacts.

4.1. *Saltwater Bass Larvae Predict Future Catch*

Once considered the "recruitment problem" in fisheries, variability in fishery year-class strength is now understood to be driven by a multitude of factors affecting both pre- and post-recruitment stages, including maternal effects, and is likely to vary by species and population (Houde 2008). Thus, although the challenge of forecasting fishery recruitment remains, research that identifies even modest prediction capabilities is recognized as valuable for informing management. This recognition allows us to more freely accept that prediction may be easier for some species than others, even if we cannot identify all the mechanisms driving those relationships. The added challenge, however, is that predictive ability has been shown to break down for some species due to environment-driven spatiotemporal variability in the strength of the predictive relationships (White et al. 2019, Litzow et al. 2020), making long-term monitoring and re-evaluation an essential part of these respective research efforts. This is especially critical when environment-species relationships are identified based on shorter time series, as change may include both magnitude and direction. A strength of this study is that our results are based on several multidecadal time series. Thus, at least part of the variability in the relationships we identified between larvae and environmental covariates reflects any inherent long-term interannual and decadal variability influencing the strength of those relationships through time.

Stock-recruitment dynamics dictate a positive relationship between spawning stock biomass and the number of new recruits (eggs, larvae; Hilborn & Walters 1992), such that changes in larval abundance should on average reflect female spawner biomass. However, the

stock-recruitment relationship has very weak predictive power for most marine fish populations due to environment-mediated stochasticity (Cury et al. 2014), and there are examples where larval abundance data better reflects future fishery year-class strength (Cushing 1990, Stige et al. 2013, White et al. 2019, Schilling et al. 2022). It is important to note that these examples do not presuppose a lack of a general trend for larger spawning stocks to produce larger recruitments, as this would imply that stocks can be fished hard regardless of stock size (Hilborn & Walters 1992). The presumed relationship between spawning stock biomass and larvae in the same year relies on 1) appreciable spawning occurring every year, 2) minimal (or spatiotemporally consistent) mortality prior to larvae being surveyed, and 3) that larvae are locally sourced within the region. In the case of saltwater basses, the breakdown in this relationship may be partly driven by two above, but for BSB, also appear to include a lack of consistent, appreciable, locally sourced recruitment from year to year.

In this study, the relationship between bass larval abundance and future fishery catch may also exist because southern California represents the northern extent of the geographic range for these species, especially for BSB. For example, populations at their geographic margins tend to experience higher larval recruitment variability (Myers 1991, Neill et al. 1994, Levin et al. 1997), which is typically reflected in future fish catch (Armsworth 2002). Schilling et al. (2020) reported a recent example of this, in which they found a positive correlation between predicted Bluefish (*Pomatomus saltatrix*) larval settlement and fishery CPUE data at the southern end of its distribution. Regardless of the mechanism, the moderate to strong correlations we identified between bass larval abundance and future catch were observed across multiple catch sets and corresponded to biologically meaningful lags. Both species have similar growth rates, becoming susceptible to hook-and-line fishing gear at two to three years of age and reaching size at fishery

recruitment between five and seven years for most of the time series (e.g., after 2012, an increase in the minimum size limit (MSL) corresponded with fish ages seven to nine years old, (Love et al. 1996, Jarvis et al. 2014a, Walker et al. 2020b). While the highest correlations for both species across both catch data sets corresponded to the age of fishery recruits, the correlations across other lags are likely an artifact of the catch data being comprised of many cohorts. Thus, restricting the analysis to catch comprised of fish at fishery recruitment size or just those fish representing the modal length of the catch may result in even stronger relationships at one or two lags (Jarvis et al. 2014a, Schilling et al. 2022). We chose not to focus on specific length frequencies because length data were only available for one data set, and we wanted to have the ability to test the larva/catch relationship across all available catch data sets.

One potential caveat to using the catch data as a proxy for spawning stock biomass, in the case of BSB, is that hyperstable catches (i.e., stable, high catches) in aggregation-based fisheries can occur during a population decline, resulting in a nonlinear relationship between catch and abundance and an overestimate of abundance at low population sizes (Sadovy de Mitcheson 2016). However, given the strong correlations revealed between BSB larval abundance and future catches in two different data sets, we deduce there is a low probability that the lack of a relationship between BSB larval abundance and catch at a lag of zero resulted from hyperstability. Moreover, our findings are consistent with previous research showing positive relationships between early life history indices of abundance and future saltwater bass fishery recruitment over shorter periods (Jarvis et al. 2014a, Miller & Erisman 2014).

4.2. *Species-specific Differences in Bass Larval Abundance Trends*

Trends in the standardized indices of larval abundance for both species suggest that the populations of KB and BSB in southern California experienced similar sporadic, strong larval pulses however, our results also indicate that the KB population has more reliably persisted, having less variable and higher larval abundance between strong sporadic recruitment pulses than BSB. This pattern for KB is consistent with locally sourced larval recruitment (Selkoe et al. 2007) and higher densities (Warner 1985), and explains the marginal relationship revealed between KB larval abundance and catch at a lag of zero. In contrast, BSB larval trends may be more influenced by seeding from Baja California, Mexico (a region with relatively higher BSB larval abundance). Arafeh-Dalmau et al. (2022) demonstrated transboundary larval connectivity between the SCB and northern Baja California of several hundred kilometers (e.g., ~400 km north from Mexico to California in summer and winter and ~400 km from the SCB to northern Baja California throughout the year), and this dispersal was important to species with a longer pelagic larval duration (PLD), like that of BSB and KB (~ one lunar month, Findlay & Allen 2002).

The inferred difference in population persistence between the two saltwater basses is also consistent with previous anecdotal reports suggesting BSB has fluctuated in its contribution to the saltwater bass catch, depending on temperature-driven availability (Young 1969, Frey 1971, Feder et al. 1974). Natural log larval abundance trends also identified species-specific differences in decadal-scale availability, with BSB larvae being relatively more abundant during the 1980s and 1990s (a warm period) and KB larvae showing a dramatic, sustained decline during that same period. Nevertheless, in the last decade, larval abundance for both species showed dramatic increases. Our results suggest these trends are due to different environmental

influences on saltwater bass larvae and different sensitivities to the same environmental influence.

4.3. *Temperature, Zooplankton, and Mixed Layer Depth Predict Bass Larval Abundance*

We found strong relationships between saltwater bass larval abundance and temperature, zooplankton biomass, and MLD. In general, our model results indicated bass larval abundance was higher when temperatures are warmer, zooplankton biomass is higher, and the MLD is shallower. The relationships between larvae and temperature and zooplankton biomass are not surprising, as peak spawning for KB and BSB occurs during the warm summer months (Erisman & Allen 2005, Jarvis et al. 2014b) following the spring transition in the SCB (McClatchie 2014). Our metric for zooplankton biomass was displacement volume, which is highly influenced by the presence of pelagic tunicates (i.e., salps) and other large gelatinous organisms (Lavaniegos & Ohman 2007). Thus, we further explored the relationship between bass larval abundance and zooplankton biomass *a posteriori* by substituting species-specific zooplankton biomass (e.g., *Calanus productus*) from spring cruises, as these data were not available for July cruises. We reasoned that increased copepod biomass available to important adult bass prey species (e.g., coastal forage fishes) in the spring might translate into positive maternal conditioning of larvae in summer (Walsh 2023), but model fits to the data were not improved. Further research is necessary to understand the importance of bass larval prey and maternal effects on bass larval survival.

The MLD had the strongest relationship with bass larval abundance (e.g., shallower MLDs predict higher bass larval abundance). This relationship might be explained by “seasonal trophic amplification” in nutrient-rich regions like the CCE (Xue et al. 2022). In these regions,

phytoplankton and zooplankton become more concentrated within shallower MLDs, thereby increasing prey encounter rates and consequently, grazing rates of zooplankton, such that higher feeding efficiency in these regions is driven more by seasonal changes in the depth of the mixed layer than by the amount of food present (Xue et al. 2022). In an analysis of environmental covariates on the biological response of larval fish communities in the California Current Ecosystem, the ILD (referred to here as MLD) had the highest ability to predict ecosystem state within southern California (Hunsicker et al. 2022). Despite the saltwater basses showing relationships with the same environmental variables (e.g., MLD, temperature, zooplankton), relationships with temperature and zooplankton biomass were relatively stronger for BSB than they were for KB, suggesting BSB is more sensitive to cooler temperatures and declines in zooplankton biomass. Indeed, BSB was historically considered a southern, subtropical/tropical species with an impermanent southern California presence (Young 1963, 1969, Frey 1971, Feder et al. 1974).

If waters off southern California continue to warm, we might expect a shallowing of the MLD (due to increased stratification of warm surface waters) and thus, higher, less variable, BSB larval recruitment. However, the assumption that climate-driven increased stratification will result in MLD shoaling belies evidence to the contrary (Somavilla et al. 2017), including a recent global analysis that documented a deepening of the MLD over the last five decades at a rate of 5-10 m dec^{-1}, despite concomitant increases in stratification (Sallée et al. 2021). Thus, if this trend continues, and southern California saltwater bass abundance is truly a function of the MLD, then a deeper mixed layer might counteract surface warming benefits by decreasing the concentration of prey items. This deepening also has the potential to result in shallow, nearshore depths ("kelp-

forest depths") becoming nutrient-poor (Parnell et al. 2010), which could have impacts on KB larval settlement (White and Caselle 2008).

Additional abiotic processes (beyond those examined here) are likely to influence KB larval recruitment dynamics. For example, the timing, direction, and strength of ocean currents impacting larval dispersal influences if and where they are transported onshore to settle, particularly in the physically dynamic SCB (Warner 1985). The primary KB larval hotspot was the Northwest Channel Islands, which is influenced by the "transition zone" in the SCB where many ocean currents converge. White & Caselle (2008) reported that in southern California, the density of Giant Kelp (*Macrocystis pyrifera*) had a positive effect on KB recruitment, but the relationship was conditioned on larval supply, whereby adult densities were largely a function of whether there was a match between areas of high larval supply and areas of higher kelp stipe density. In that study, the authors explain how eddies and temperature fronts may drive a match-mismatch between KB larval supply and kelp spore supply.

We did not incorporate ocean currents in our analysis, but larval dispersal and retention is likely equally important for BSB. Whereas we found the predicted geographic distribution of KB larvae through time showed broad distribution within the SCB with hotspots at the Northwest Channel Islands, BSB larvae were almost exclusively distributed nearshore along the mainland coast, suggesting different processes acting on their distributions (White et al. 2019). Indeed, we observed differences in the two species' model's spatiotemporal fields over time that indicate different latent forcing of dynamic biotic and abiotic processes. It is therefore possible that different environmental conditions cue broad scale synchronized spawning events to take advantage of tides and currents that help retain larvae close to shore (BSB) or provide broad dispersal to increase the probability of reaching areas with Giant Kelp, including at offshore

islands (KB). Differences in spawning aggregation formation and migration may also contribute to spatiotemporal variability in these species' larval distributions, as BSB form large spawning aggregations at a few predictable locations, while KB spawning aggregations are smaller and more broadly distributed (Erisman & Allen 2006, Jarvis et al. 2010).

All else equal, warmer temperatures for summer spawners are better for higher growth and survival of their eggs and larvae (Gadomski & Caddell 1996); however, during the warm regime of the 1980s and 1990s, the SCB shifted to nutrient-poor conditions and experienced a higher frequency of storms events, both of which negatively impacted kelp forests in the region (Parnell et al. 2010). Thus, the steady decline in KB larval recruitment during that period may be indirectly associated with regional declines in kelp, despite more optimal temperatures for larval growth and survival (Jarvis et al. 2014a). This could be one driver explaining why our models revealed the influence of temperature on larval KB larval abundance was not as strong as that for BSB. In contrast to KB, BSB larval abundance was lower during the 1960s and 1970s relative to the warmer 1980s and 1990s.

Despite both species showing positive trends with temperature, we did not find evidence of a northward latitudinal shift in larval abundance through time. Although climate-driven phenological and distribution shifts have been well-documented around the world (Pinsky et al. 2020) and historical bass populations extended much farther north than southern California during the region's tropicalization of the mid-1800s (Hubbs 1948), previous research on larval distribution/phenology shifts in the CCE have shown that species responses to climate change are not omnipresent (Hsieh et al. 2009, Asch 2015, Auth et al. 2018). In addition, northward larval dispersal of nearshore species beyond the well-known geographic break at Pt. Conception

in the SCB, at least during the last sixty years, is thought to be limited more so by hydrographic features than temperature (Warner 1985).

4.4. *Implications for Management*

Despite sustained low fishery catches in the early-to-mid-2010s, we found that larval abundance for both species peaked. Given our findings that larval abundance predicts future catches, the increase in larval abundance suggests fishery recovery is imminent. Indeed, fishery-independent indices of adult BSB and KB densities show an upward trend in recent years (CDFW 2021, 2023). Theoretically, based on larvae/catch relationships reported here, the first peak in recent larval recruitment (2012) should have been evident in catches as early as 2020 (corresponding with an average fishery recruitment age of eight years for both species); however, fishery recovery may still be too early to detect. This is because fishing in 2020 was impacted by the COVID-19 pandemic as harbors were closed to recreational boaters and some commercial sportfishing vessel operations were also temporarily closed. In addition, CRFS estimates of catch and fishing effort were impacted by reductions in survey effort (April to June 2020) and modifications to sampling protocols through September 2021 (CDFG 2023).

Collectively, our results pave the way for an ecosystem approach to management of this fishery and bring us closer toward readying the fishery for climate change. Such an approach should consider (among other factors) species-specific differences in larvae-environment relationships and factors influencing differences in temporal and spatiotemporal trends in larval abundance and distributions. Perhaps one of the most important conclusions of our study is that these two basses have different population dynamics: 1) larval recruitment patterns indicate differences in the persistence of their populations in southern California (i.e., background

recruitment levels for KB are higher and less episodic, which is consistent with locally-sourced recruitment (Selkoe et al. 2007) and higher densities (Warner 1985) and has implications regarding their resilience to harvest impacts and climate change, 2) relative to KB, BSB larval recruitment is more closely tied to temperature, which is consistent with historical reports of BSB availability in southern California and has implications for resilience to harvest impacts and climate change, and 3) KB larval recruitment at offshore islands in the northern SCB is a notable hotspot, which has implications associated with habitat protection (e.g., Marine Protected Areas). In contrast, BSB larval recruitment is limited to the mainland coast and given its sporadic nature and more southerly larval distribution in the SCB, may be influenced more so by sporadic northward advection of larvae from Baja California as has been suggested for other fishery species in the region (Smith & Moser 1988, Allen & Franklin 1992, Ben-Aderet et al. 2020). This too has implications with respect to harvest impacts and climate change, as future transboundary connectivity between the SCB and Mexico is predicted to be significantly reduced (assuming decreased PLDs and lower kelp persistence), thus highlighting the importance of protecting habitats important for larval connectivity and binational conservation efforts to manage the collective resource (Arafeh-Dalmau et al. 2022).

Environment-species relationships are typically nonstationary and may not only change in magnitude, but direction (White et al. 2019). Here, we had the opportunity to test whether strong environmental relationships we identified using data spanning 54 years (1963-2016) held up using a shorter part of the time series (1984-2016). Although the influence of temperature and zooplankton biomass was important in both periods for both species, the influence of the NPGO on BSB larval abundance was weakened/lost in the shorter time series. The shorter time series began just before the well-documented 1988-89 North Pacific climate shift (Hare & Mantua

2000) after which, previously established physical and ecological relationships with the NPGO (Di Lorenzo et al. 2008) became weaker (Litzow et al. 2020). Thus, we recommend regular monitoring and re-evaluation of the relationships identified here. This recommendation points to the value of maintaining long-term monitoring data streams, like CalCOFI, particularly for other data-limited state-managed fisheries. Future research into the role that maternal effects and prey type and condition play in bass larval dynamics will likely provide additional, important ecosystem considerations for managing this culturally and economically important recreational-only fishery.

ACKNOWLEDGEMENTS

This research was supported by a grant awarded by the California Ocean Protection Council (Proposition 84 Competitive Grant Program, Project R/OPCSFAQ-09) and administered by the California Sea Grant College Program. We thank CalCOFI cruise participants, past and present, M. Human and S. Charter for help with accessing archival specimens, L. Bulkeley, R. Quaal, and V. Tang for help with sorting samples, L. Bulkeley for help with identifying the formalin preserved *Paralabrax* spp. larvae to species, W. Watson for sharing his taxonomic expertise in larval fish identification, and E. Ward for guidance with sdmTMB.

LITERATURE CITED

Allen LG, Franklin MP (1992) Abundance, distribution, and settlement of young-of-the-year white seabass *Atractoscion nobilis* in the Southern California Bight, 1988- 89. Fish Bull 90:633–641.

Anderson SC, Ward EJ, English PA, Barnett LAK (2022) SdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. bioRxiv 2022.03.24.485545:1–17.

Arafeh-Dalmau N, Munguia-Vega A, Micheli F, Vilalta-Navas A, Villasenor-Derbez JC, Précoma-de la Mora M, Shoeman DS, Medellín-Ortiz A, Cavanaugh KC, Sosa-Nishizaki O, Burnham TLU, Knight CJ, Woodson CB, Abas M, Abadía-Cardoso AL, Aburto-Oropeza O, Esgro MW, Espinosa-Andrade N, Beas-Luna R, Cardenas N, Carr MH, Dale KE, Cisneros-Soberanis F, Flores-Morales A, Fulton S, García-Rodriguez E, Giron-Nava A, Gleason MG, Green AL, Hernández-Velasco A, Ibarra-Macias B, Johnson AF, Lorda J, Malpica-Cruz L, Montaño-Moctezuma, G, Olguin-Jacobson C, Parés-Sierra A, Raimondi PT, Ramírez-Ortiz G, Ramirez-Valdez A, Reyes-Bonilla H, Saarman E, Saldaña-Ruiz LE, Smith A, Soldatini C, Suárez A, Torres-Moye G, Walther M, Watson EB, Worden S, Possingham HP (2022) Towards transboundary networks of climate-smart marine reserves in the Southern California Bight. bioRxiv doi: https://doi.org/10.1101/2022.01.04.475006

Armsworth PR (2002) Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. Ecology 83:1092–1104.

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Natl Acad Sci U S A 112:E4065–E4074.

Auth TD, Daly EA, Brodeur RD, Fisher JL (2018) Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. Glob Chang Biol 24:259–272.

Bakun A (1973) Coastal Upwelling Indices, West Coast of North America, 1946-71. NOAA Technical Report NMFS SSRF-671, National Oceanic and Atmospheric Administration, 12 pp.

Ben-Aderet N, Johnston EM, Cravey R, Sandin SA (2020) Revisiting the life history of yellowtail jack (*Seriola dorsalis*) in the Southern California Bight: New evidence for ontogenetic habitat shifts and regional differences in a changing environment. Fish Bull 118:157–170.

Bradford MJ (1992) Precision of recruitment predictions from early life stages of marine fishes. Fish Bull 90:439–453.

Breheny P, Burchett W (2019) Visualization of Regression Models Using visreg. R J 9:56–71.

Brodie SJ, Thorson JT, Carroll G, Hazen EL, Bograd S, Haltuch MA, Holsman KK, Kotwicki S,

Samhouri JF, Willis-Norton E, Selden RL (2020) Trade-offs in covariate selection for species distribution models: a methodological comparison. Ecography (Cop) 43:11–24.

Butler JL, Moser HG, Hageman GS, Nordgren LE (1982) Developmental stages of three california sea basses. 23.

Carter ML, Flick, Reinhard E. Terrill E, Beckhaus, Elena C. Martin K, Fey CL, Walker, Patricia W. Largier, John L. McGowan JA (2022) Shore Stations Program Data Archive: Current and historical coastal ocean temperature and salinity measurements from California stations. UC San Diego Library Digital Collections. https://doi.org/10.6075/J00001XZ

Cavole LM, Demko AM, Diner RE, Giddings A, Koester I, Pagniello CMLS, Paulsen ML, Ramirez-Valdez A, Schwenck SM, Yen NK, Zill ME, Franks PJS (2016) Biological impacts of the 2013–2015 warm-water anomaly in the northeast Pacific: Winners, Losers, and the Future. Oceanography 29:273–285.

CDFW (2023) Barred Sand Bass, *Paralabrax nebulifer*, Enhanced Status Report. California Department of Fish and Wildlife. https://marinespecies.wildlife.ca.gov/barred-sand-bass/

CDFW (2021) Kelp Bass, *Paralabrax clathratus*, Enhanced Status Report. California Department of Fish and Wildlife. https://marinespecies.wildlife.ca.gov/kelp-bass/true/

Cowan JH, Shaw RF (2002) Recruitment. In: *Fishery Science: The Unique Contributions of Early Life Stages*. Fuiman LA, Werner RG (eds) Wiley-Blackwell, p 336

Cury PM, Fromentin JM, Figuet S, Bonhommeau S (2014) Resolving Hjort's Dilemma: how is recruitment related to spawning stock biomass in marine fish? Oceanography 27:42–47.

Cushing DH (1990) Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293.

Dolan TE, Patrick WS, Link JS (2016) Management: a US fisheries reference point perspective. 73:1042–1050.

Erisman BE, Allen LG (2005) Color Patterns and Associated Behaviors in the Kelp Bass, *Paralabrax clathratus* (Teleostei: Serranidae). Bull South Calif Acad Sci 104:45–62.

Erisman BE, Allen LG (2006) Reproductive behaviour of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, USA J Fish Biol 68:157–184.

Erisman BE, Allen LG, Claisse JT, Pondella DJ, Miller EF, Murray JH, Walters C (2011) The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Can J Fish Aquat Sci 68:1705–1716.

Feder HM, Turner CH, Limbaugh C (1974) Observations On Fishes Associated With Kelp Beds in Southern California. Fish Bull 160.

Findlay AM, Allen LG (2002) Temporal patterns of settlement in the temperate reef fish Paralabrax clathratus. Mar Ecol Prog Ser 238:237–248.

Frey HW (ed) (1971) California's Living Marine Resources and Their Utilization. In: *California's Living Marine Resources and Their Utilization*. California Department of Fish and Game, Sacramento, USA

Gadomski DM, Caddell SM (1996) Effects of temperature on the development and survival of eggs of four coastal California fishes. Fish Bull 94:41–48.

Gallo ND, Drenkard E, Thompson AR, Weber ED, Wilson-Vandenberg D, McClatchie S, Koslow JA, Semmens BX (2019) Bridging From Monitoring to Solutions-Based Thinking: Lessons From CalCOFI for Understanding and Adapting to Marine Climate Change Impacts. Front Mar Sci 6:1–21.

Graves JE, Curtis MJ, Oeth PA, Waples RS (1990) Biochemical genetics of southern California basses of the genus Paralabrax: Specific indentification of fresh and ethanol-preserved individual eggs and early larvae. Fish Bull 88:59–66.

Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog Oceanogr 47:103–145.

Heemstra PC (1995) Serranidae. Meros, serranos, guasetas, enjambres, baquetas, indios, loros, gallinas, cabrillas, garropas. In: *Guia FAO para Identification de Especies para lo Fines de la Pesca. Pacifico Centro-Oriental. 3 Vols.* Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem V (eds) FAO, Rome, p 1565–1613

Hickey BM (1993) Physical Oceanography. In: *Ecology of the Southern California Bight: A synthesis and interpretation*. Dailey M, Reish D, Anderson J (eds) University of California Press, Berkeley and Los Angeles, California, USA, p 19–70

Hilborn R, Walters CJ (1992) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, USA.

Hjort J (1914) Fluctuations in the great fisheries of Northern Europe. Rapp rocès-Verbaux 20 :1–228.

Houde ED (2001) Fish Larvae. Encycl Ocean Sci :928–938.

Houde ED (2008) Emerging from Hjort's shadow. J Northwest Atl Fish Sci 41:53–70.

Hsieh CH, Kim HJ, Watson W, Di Lorenzo E, Sugihara G (2009) Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. Glob Chang Biol 15:2137–2152.

Hsieh CH, Reiss C, Watson W, Allen MJ, Hunter JR, Lea RN, Rosenblatt RH, Smith PE, Sugihara G (2005) A comparison of long-term trends and variability in populations of

larvae of exploited and unexploited fishes in the Southern California region: A community approach. Prog Oceanogr 67:160–185.

Hsieh CH, Reiss CS, Hewitt RP, Sugihara G (2008) Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. Can J Fish Aquat Sci 65:947–961.

Hubbs C (1948) Changes in the fish fauna of western north america correlated with changes in ocean temperature. J Mar Res VII:459–482.

Hunsicker ME, Ward EJ, Litzow MA, Anderson SC, Harvey CJ, Field JC, Gao J, Jacox MG, Melin S, Thompson AR, Warzybok P (2022) Tracking and forecasting community responses to climate perturbations in the California Current Ecosystem. PLOS Clim 1:e0000014.

Jacox MG, Edwards CA, Hazen EL, Bograd SJ (2018) Coastal Upwelling Revisited: Ekman, Bakun, and Improved Upwelling Indices for the U.S. West Coast. J Geophys Res Ocean 123:7332–7350.

Jarvis ET, Allen MJ, Smith RW (2004) Comparison of recreational fish catch trends to environment-species relationships and fishery-independent data in the Southern California Bight, 1980-2000. Calif Coop Ocean Fish Investig Reports 45:167–179.

Jarvis ET, Gliniak HL, Valle CF (2014a) Effects of fishing and the environment on the long-term sustainability of the recreational saltwater bass fishery in southern California. Calif Fish Game 100:234–259.

Jarvis ET, Linardich C, Valle CF (2010) Spawning-Related Movements of Barred Sand Bass, *Paralabrax nebulifer*, in Southern California: Interpretations from Two Decades of Historical Tag and Recapture Data. Bull South Calif Acad Sci 109:123–143.

Jarvis ET, Loke-Smith KA, Evans K, Kloppe RE, Young KA, Valle CF (2014b) Reproductive potential and spawning periodicity in barred sand bass (*Paralabrax nebulifer*) from the San Pedro Shelf, southern California. Calif Fish Game 100:289–309.

Jarvis Mason ET, Bulkeley L, Watson WW, Sawkins ACS, Craig MT, Hyde JR, Thompson AR, Semmens BX (2022) Decoding comparable morphologies: Pigmentation validated for identifying southern California *Paralabrax* larvae. J Fish Taxon 25:9–25.

Lasker R (1981) The Role of a Stable Ocean in Larval Fish Survival and Subsequent Recruitment. In: *Marine Fish Larvae Morphology, Ecology, and Relation to Fisheries*. Lasker R (ed) Washington Sea Grant Program, Seattle and London, p 80–85

Lavaniegos BE, Ohman MD (2007) Coherence of long-term variations of zooplankton in two sectors of the California Current System. Prog Oceanogr 75:42–69.

Lavenberg RJ, McGowen GE, Jahn AE, Petersen JH, Sciarrotta TC (1986) Abundance of Southern California nearshore ichthyoplankon: 1978-1984. CalCOFI Rep 27:53–64.

Lasker R (1984) The Role of a Stable Ocean in Larval Fish Survival and Subsequent Recruitment. In: *Marine Fish Larvae Morphology, Ecology, and Relation to Fisheries*. Lasker R (ed) Washington Sea Grant Program, p 80–85

Levin PS, Chiasson W, Green JM (1997) Geographic differences in recruitment and population structure of a temperate reef fish. Mar Ecol Prog Ser 161:23–35.

Lewin WC, Weltersbach MS, Ferter K, Hyder K, Mugerza E, Prellezo R, Radford Z, Zarauz L, Strehlow HV (2019) Potential Environmental Impacts of Recreational Fishing on Marine Fish Stocks and Ecosystems. Rev Fish Sci Aquac 27:287–330.

Litzow MA, Hunsicker ME, Bond NA, Burke BJ, Cunningham CJ, Gosselin JL, Norton EL, Ward EJ, Zador SG (2020) The changing physical and ecological meanings of North Pacific Ocean climate indices. Proc Natl Acad Sci U S A 117:7665–7671.

Love MS, Brooks A, Busatto D, Stephens J, Gregory PA (1996) Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the southern California Bight. Fish Bull 94:472–481.

Lyubchich V, Gel Y, Vishwakarma S (2023) Funtimes: Functions for Time Series Analysis.

McClatchie S (2014) Regional Fisheries Oceanography of the California Current System. Springer Netherlands, Dordrecht.

McKinzie MK, Jarvis ET, Lowe CG (2014) Fine-scale horizontal and vertical movement of barred sand bass, *Paralabrax nebulifer*, during spawning and non-spawning seasons. Fish Res 150:66–75.

Miller EF, Erisman B (2014) Long-term trends of southern California's kelp and barred sand bass populations: A fishery-independent assessment. Calif Coop Ocean Fish Investig Reports 55:1–9.

Moser HG, Charter RL, Smith PE, Ambrose D a, Watson W, Charter SR, Sandknop EM (2001a) Distributional atlas of fish larvae and eggs in the Southern California Bight region: 1951-1998. CalCOFI Atlas 34:1951–1998.

Moser HG, Charter RL, Watson W, Ambrose DA, Hill KT, Smith PE, Butler JL, Sandknop EM, Charter SR (2001b) The CalCOFI ichthyoplankton time series: Potential contributions to the management of rocky-shore fishes. Calif Coop Ocean Fish Investig Reports 42:112–128.

Mullon C, Fréon P, Cury P (2005) The dynamics of collapse in world fisheries. Fish Fish 6:111–120.

Myers RA (1991) Recruitment variability and range of three fish species. NAFO Sci Counc Stud 16:21–24.

Neill WH, Miller JM, Van Der Veer HW, Winemiller KO (1994) Ecophysiology of marine fish.

Netherlands J Sea Res 32:135–152.

Nielsen JM, Popp BN, Winder M (2015) Meta-analysis of amino acid stable nitrogen isotope ratios for estimating trophic position in marine organisms. Oecologia 178:631–642.

NOAA (2023) El Niño/Southern Oscillation (ENSO). National Centers for Environmental Information. https://www.ncei.noaa.gov/access/monitoring/enso/sst (accessed 9 February 2023)

Oliver ECJ (2019) Mean warming not variability drives marine heatwave trends. Clim Dyn 53:1653–1659.

Parnell PE, Miller EF, Lennert-Cody CE, Dayton PK, Carter ML, Stebbins TD (2010) The response of giant kelp (*Macrocystis pyrifera*) in southern California to low-frequency climate forcing. Limnol Oceanogr 55:2686–2702.

Perry RI, Cury P, Brander K, Jennings S, Möllmann C, Planque B (2010) Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. J Mar Syst.

Pinsky ML, Selden RL, Kitchel ZJ (2020) Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. Ann Rev Mar Sci 12:153–179.

Sadovy Y, Domeier M (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24:254–262.

Sallée JB, Pellichero V, Akhoudas C, Pauthenet E, Vignes L, Schmidtko S, Garabato AN, Sutherland P, Kuusela M (2021) Summertime increases in upper-ocean stratification and mixed-layer depth. Nature 591:592–598.

Schilling HT, Everett JD, Smith JA, Stewart J, Hughes JM, Roughan M, Kerry C, Suthers IM (2020) Multiple spawning events promote increased larval dispersal of a predatory fish in a western boundary current. Fish Oceanogr 29:309–323.

Schilling HT, Hinchliffe C, Gillson JP, Miskiewicz AG, Suthers IM (2022) Coastal winds and larval fish abundance indicate a recruitment mechanism for southeast Australian estuarine fisheries. Fish Oceanogr 31:40–55.

Selkoe KA, Vogel A, Gaines SD (2007) Effects of ephemeral circulation on recruitment and connectivity of nearshore fish populations spanning Southern and Baja California. Mar Ecol Prog Ser 351:209–220.

Shelton AO, Mangel M (2011) Fluctuations of fish populations and the magnifying effects of fishing. Proc Natl Acad Sci U S A 108:7075–7080.

Somavilla R, Gonzalez-Pola C, Fernandez-Diaz J (2017) The warmer the ocean surface, the shallower the mixed layer. How much of this is true? J Geophys Res Ocean 122:1–22.

Smith PE, Moser HG (1988) CalCOFI time series: an overview of fishes. CalCOFI Rep 29:66–

78.

Stige LC, Hunsicker ME, Bailey KM, Yaragina NA, Hunt GL (2013) Predicting fish recruitment from juvenile abundance and environmental indices. Mar Ecol Prog Ser 480:245–261.

Thompson AR, Ben-Aderet NJ, Bowlin NM, Kacev D, Swalethorp R, Watson W (2022) Putting the Pacific marine heatwave into perspective: The response of larval fish off southern California to unprecedented warming in 2014–2016 relative to the previous 65 years. Glob Chang Biol 28:1766–1785.

Thompson AR, Chen DC, Guo LW, Hyde JR, Watson W (2017) Larval abundances of rockfishes that were historically targeted by fishing increased over 16 years in association with a large marine protected area. R Soc Open Sci 4.

Thorson JT, Monnahan CC, Cope JM (2015) The potential impact of time-variation in vital rates on fisheries management targets for marine fishes. Fish Res 169:8–17.

Thorson JT, Pinsky ML, Ward EJ (2016) Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. Methods Ecol Evol 7:990–1002.

Walker HJ, Hastings PA, Hyde JR, Lea RN, Snodgrass OE, Bellquist LF (2020a) Unusual occurrences of fishes in the Southern California Current System during the warm water period of 2014–2018. Estuar Coast Shelf Sci.

Walker KM, Pentilla KM, Jarvis-Mason ET, Valle CF (2020b) Validated age and growth of Barred Sand Bass within the Southern California Bight. Calif Fish Wildl J 106:205–220.

Walsh K (2023) Diet and Maternal Investment in Larval Sebastes spp. – Implication for Growth and Survival. UC San Diego. ProQuest ID: Walsh_ucsd_0033M_22163. Merritt ID: ark:/13030/m5qs2jp5. Retrieved from https://escholarship.org/uc/item/1d20n17d.

Warner RR (1985) Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. J Mar Res 43:719–742.

Wei T, Simko V (2021) R package ‘corrplot’: Visualization of a Correlation Matrix.

White JW, Carr MH, Caselle JE, Washburn L, Brock Woodson C, Palumbi SR, Carlson PM, Warner RR, Menge BA, Barth JA, Blanchette CA, Raimondi PT, Milligan K (2019) Special issue on PISCO: Partnership for Interdisciplinary Studies of Coastal Oceans. Connectivity, dispersal, and recruitment connecting benthic communities and the coastal ocean. Oceanography 32:50.

White JW, Caselle JE (2008) Scale-dependent changes in the importance of larval supply and habitat to abundance of a reef fish. Ecology 89:1323–1333.

Wood S (2017). *Generalized Additive Models: An Introduction with R*, 2 edition. Chapman and Hall/CRC.

Xue T, Frenger I, Oschlies A, Stock CA, Koeve W, John JG, Prowe AEF (2022) Mixed Layer Depth Promotes Trophic Amplification on a Seasonal Scale. Geophys Res Lett 49:1–11.

Young P (1969) The California Partyboat Fishery 1947–1967. Calif Dep Fish Game, Fish Bull 145.

Young PH (1963) The kelp bass (*Paralabrax clathratus*) and its fishery, 1947-1958. Calif Dep Fish Game, Fish Bull 122.

Ziegler SL, Johnson JM, Brooks RO, Johnston EM, Mohay JL, Ruttenberg BI, Starr RM, Waltz GT, Wendt DE, Hamilton SL (2023) Marine protected areas, marine heatwaves, and the resilience of nearshore fish communities. Sci Rep 13:1–13.

Table 1. Results comparison* of species distribution models used to generate a standardized index of larval abundance for a) Barred Sand Bass and b) Kelp Bass in southern California, USA, 1963-2016.

a) Barred Sand Bass

Formula	Time-varying	Spatial	Spatio-temporal	Passed sanity check?	REML AIC	AIC
~ 0 + dist	**y**	**on**	**iid**	**y**	**722.17**	**715.08**
~ 0 + dist	n	on	ar1	y	728.05	--
~ 0 + dist	n	on	rw	n	--	--
~ 0 + dist	y	off	iid	y	727.32	--
~ 0 + dist	n	off	rw	n	--	--
~ 0 + dist + s(hour, bs = "cc", k = 24)	y	on	iid	n	--	--
~ 0 + dist + s(day_night, by = net_type, bs = "fs")	y	on	iid	n	--	--

b) Kelp Bass

Formula	Time-varying	Spatial	Spatio-temporal	Passed sanity check?	REML AIC	AIC
~ s(year)	**n**	**on**	**iid**	**y**	**1503.69**	**1501.45**
~ s(year)	n	on	ar1	y	1505.68	--
~ s(year)	n	on	rw	n	--	--
~ s(year)	n	off	iid	y	1506.32	--
~ s(year)	n	off	ar1	y	1507.96	--
~ s(year) + s(hour, bs = "cc", k = 24)	n	on	iid	y	--	1503.45
~ s(year) + s(day_night, by = net_type, bs = "fs")	n	on	iid	n	--	--

*****Main effects are listed in the formula. Time-varying refers to time-varying main effects, spatial and spatiotemporal refer to the random effects, sanity check refers to model checking for convergence, large standard deviation of the random effects, and other parameters. Iid = independent and identically distributed, ar1 = first-order autoregressive, rw = random walk, REML = restricted maximum likelihood, AIC = Akaiki information criteria. See methods in the main text for covariate descriptions.

Table 2. Results comparison* of species distribution models used to measure the effects of environmental influence on larval abundance for a) Barred Sand Bass and b) Kelp Bass in southern California, USA. Bold represents top model.

a) Barred Sand Bass

Formula	Time-varying	Spatial	Spatio-temporal	Passed sanity check?	REML AIC	AIC
Model 1, 1963-2016						
~ dist_km + temp.10m + npgo + zoop + oni	**n**	**off**	**off**	**y**	**--**	**--**
~ dist_km + temp.10m + npgo + zoop + oni	n	on	iid	n	--	--
~ dist_km + temp.10m + npgo + zoop + oni	n	off	iid	n	--	--
Model 2, 1984-2016						
~ dist_km + temp.10m + npgo + zoop + oni + bakun33 + south.ild	**n**	**off**	**iid**	**y**	**566.39**	**555.19**
~ dist_km + temp.10m + npgo + zoop + oni + bakun33 + south.ild	n	on	iid	y	568.39	--
~ dist_km + temp.10m + npgo + zoop + oni + bakun30 + south.ild	n	off	iid	y	565.36	552.95
~ dist_km + temp.10m + npgo + zoop + oni + bakun30 + south.ild	n	on	iid	n	--	--
~ dist_km + temp.10m + npgo + zoop + oni + south.beuti + south.cuti + south.ild	n	off	iid	y	--	556.63

b) Kelp Bass

Formula	Time-varying	Spatial	Spatio-temporal	Passed sanity check?	REML AIC	AIC
Model 1, 1963-2016						
~ dist_km + temp.10m + npgo + zoop + oni	**n**	**on**	**iid**	**y**	**1343.04**	**--**
~ dist_km + temp.10m + npgo + zoop + oni	n	off	iid	y	1344.79	--
Model 2, 1984-2016						
~ dist_km + temp.10m + npgo + zoop + oni + bakun33 + south.ild	**n**	**on**	**iid**	**y**	**995.56**	**--**
~ dist_km + temp.10m + npgo + zoop + oni + bakun33 + south.ild	n	off	iid	y	996.17	--
~ dist_km + temp.10m + npgo + zoop + oni + south.beuti + south.cuti + south.ild	n	on	iid	n	--	--

***Main effects are listed in the formula. Time-varying refers to time-varying main effects, spatial and spatiotemporal refer to the random effects, sanity check refers to model checking for convergence, large standard deviation of the random effects, and other parameters. See methods in the main text for covariate descriptions.

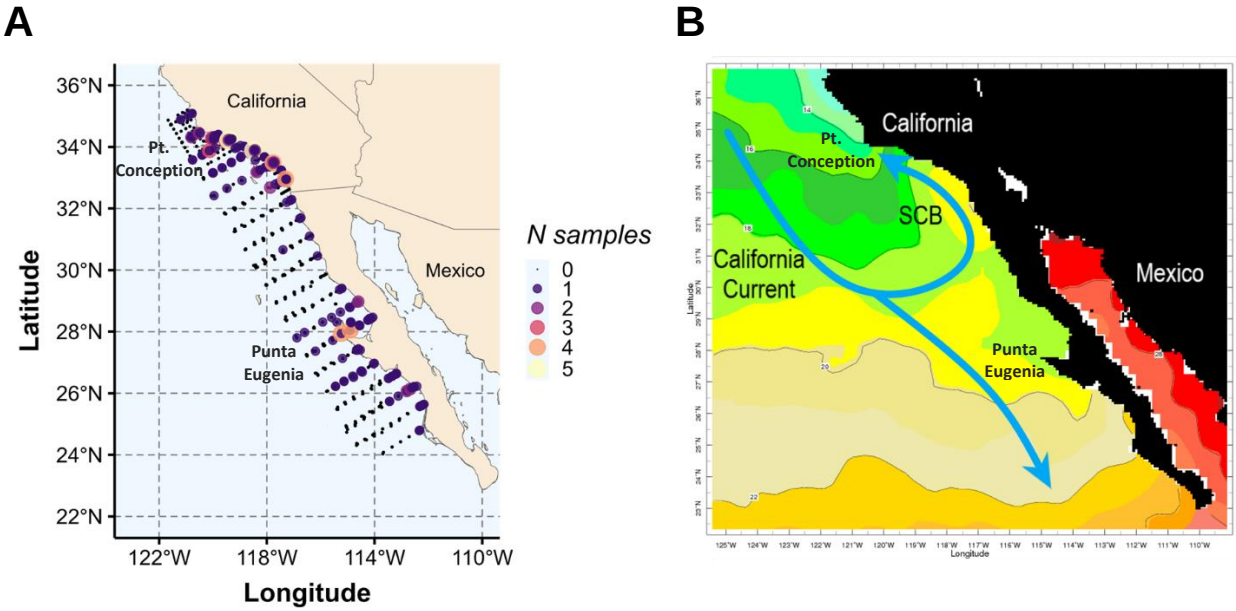


Figure 1. Maps of a) CalCOFI station locations surveyed during July cruises and numbers of samples per station from 1963 to 2016 from which formalin preserved *Paralabrax* spp. larvae were identified to species, and b) representative sea surface temperature contours off southern California, USA and Baja California, Mexico in the month of July (NOAA NCDC OISST version2p1 AVHRR monthly sea surface temperature data). Blue arrows depict the directional flow of the California Current. CalCOFI = California Cooperative Oceanic Fisheries Investigations, SCB = Southern California Bight. Shaded temperature contours range from 14 °C in the north to 26 °C off the southern tip of Baja California and up to >28 °C into the Gulf of California, Mexico.

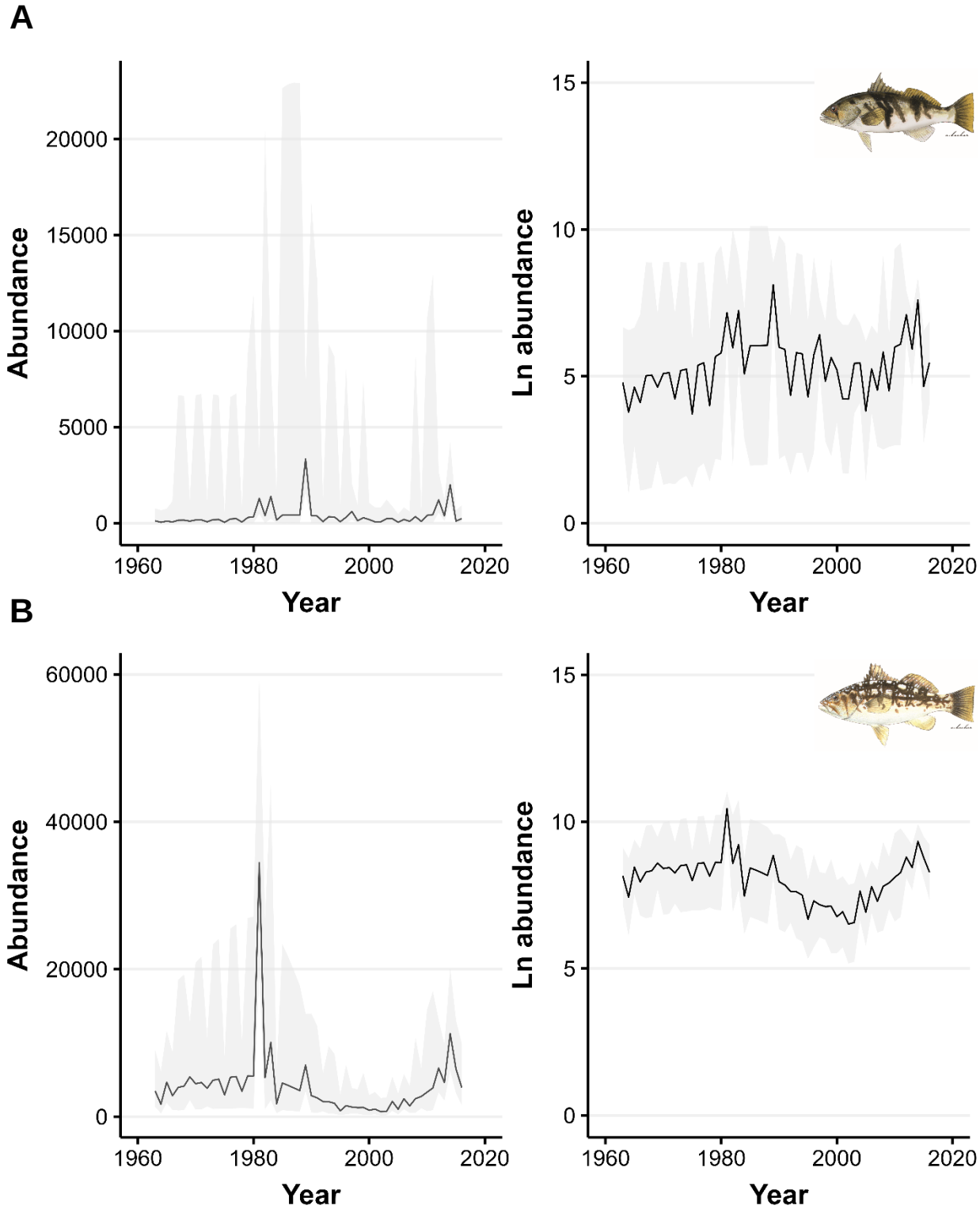


Figure 2. Standardized indices of larval abundance on the link scale (left panels) and natural log scale (right panels) for a) Barred Sand Bass and b) Kelp Bass in southern California, USA, 1963-2016. Shaded ribbons denote 95% confidence intervals.

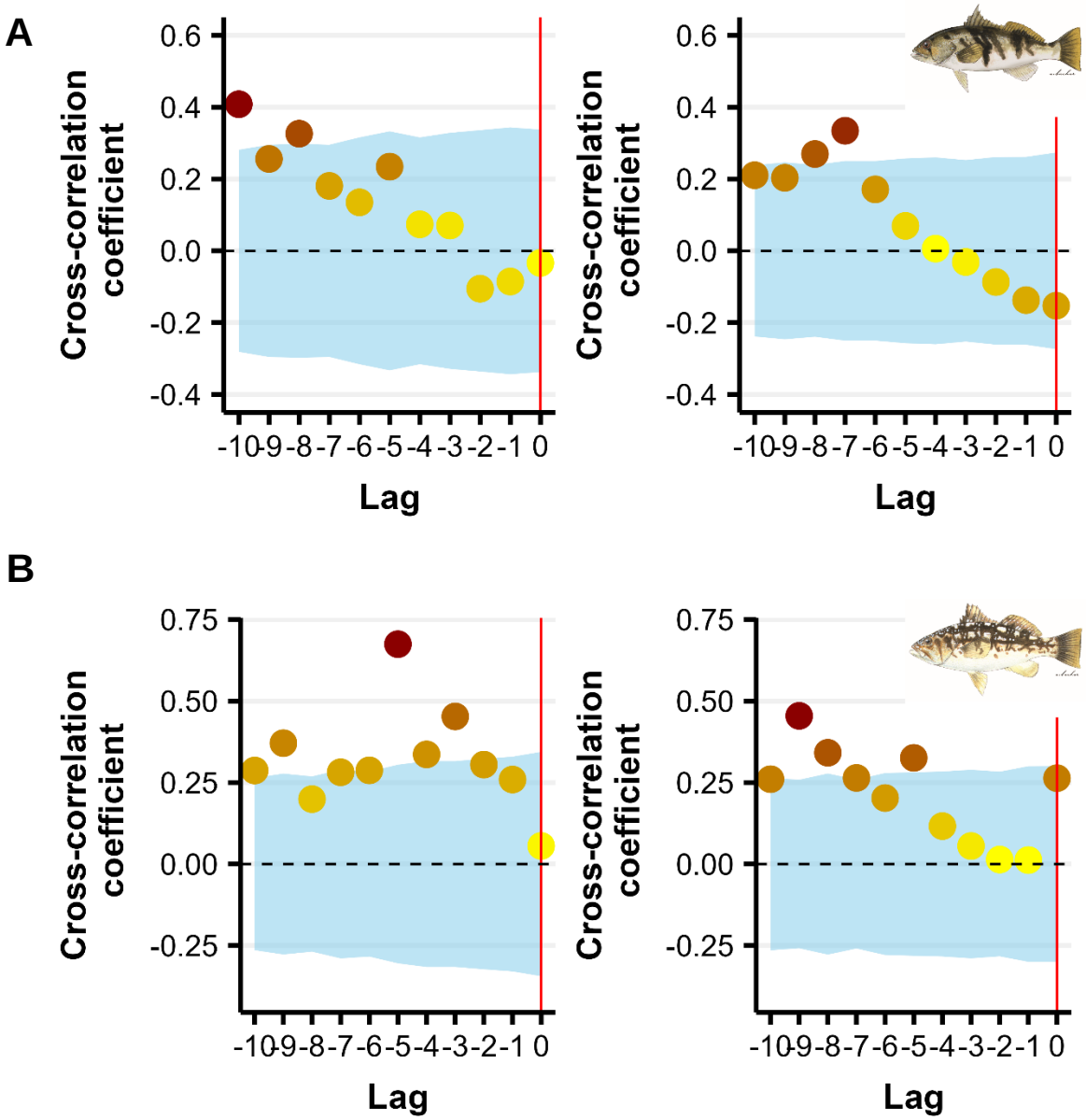


Figure 3. Cross-correlation coefficients between larval abundance and total catch estimates (left panels) and total numbers harvested (right panels) across yearly lags for a) Barred Sand Bass and b) Kelp Bass in southern California, USA. Negative lags represent larvae leading catch. Shaded ribbon denotes the 95% confidence band where coefficients falling within may be an artifact of nonstationarity in one or both time series. Gradation in shading of points depicts the strength of relationship, ranging from lighter (zero or weak) to darker (moderate to strong).

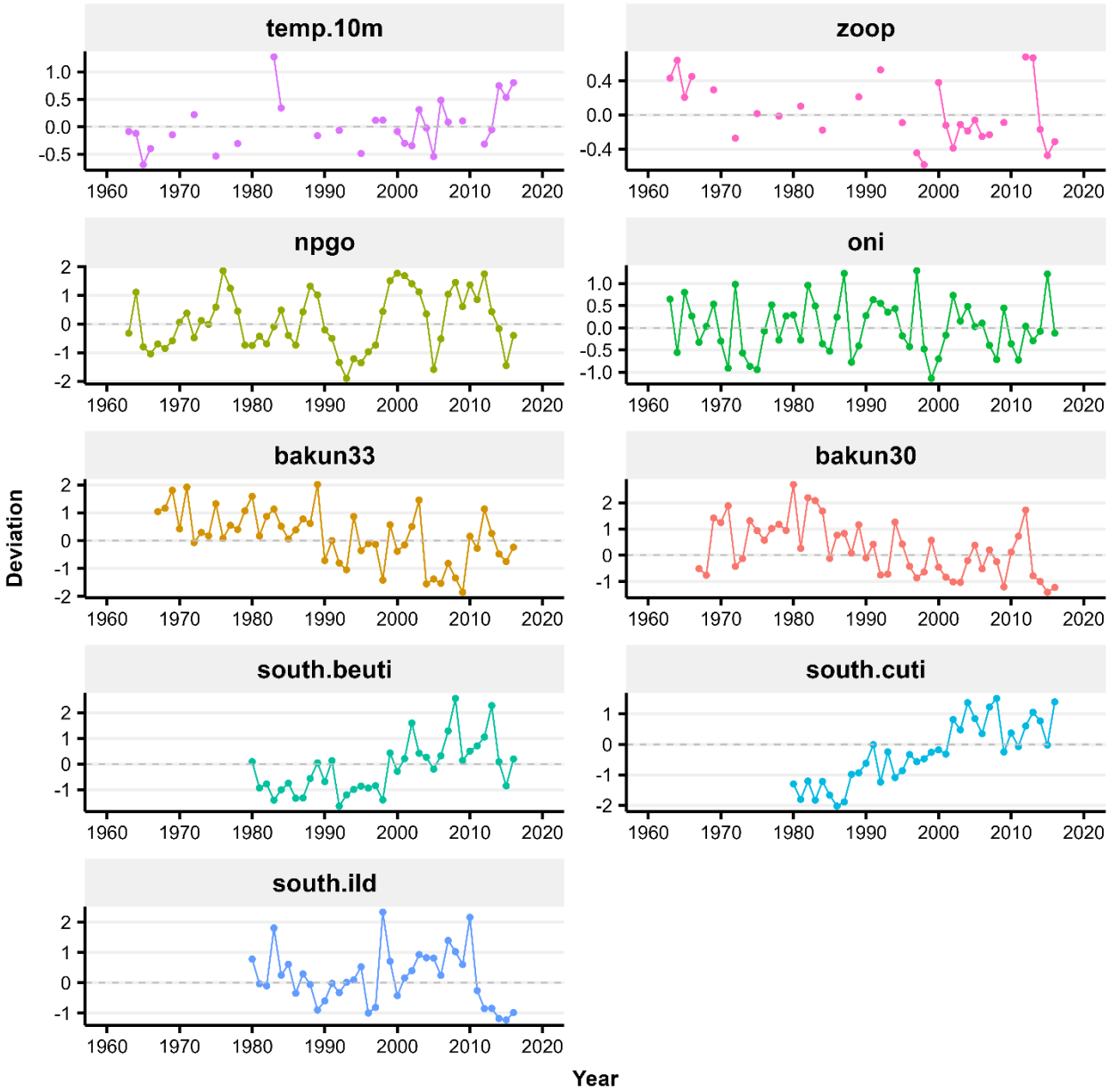


Figure 4. Temporal trends in regional and local environmental variables selected for modeling southern California, USA, *Paralabrax* spp. larval abundance. Temp.10m = CalCOFI ocean temperature averaged from the sea surface down to 10 m depth, zoop = CalCOFI zooplankton biomass, npgo = North Pacific Gyre Oscillation index for July, oni = Ocean Niño Index for June/July, bakun33 = Bakun upwelling index at 33°N, bakun33 = Bakun upwelling index at 30°N, south.beuti = Biologically Enhanced Upwelling Index, south.cuti = Coastal Upwelling Transport Index, south.ild = isothermal layer depth. CalCOFI = California Cooperative Oceanic Fisheries Investigations.

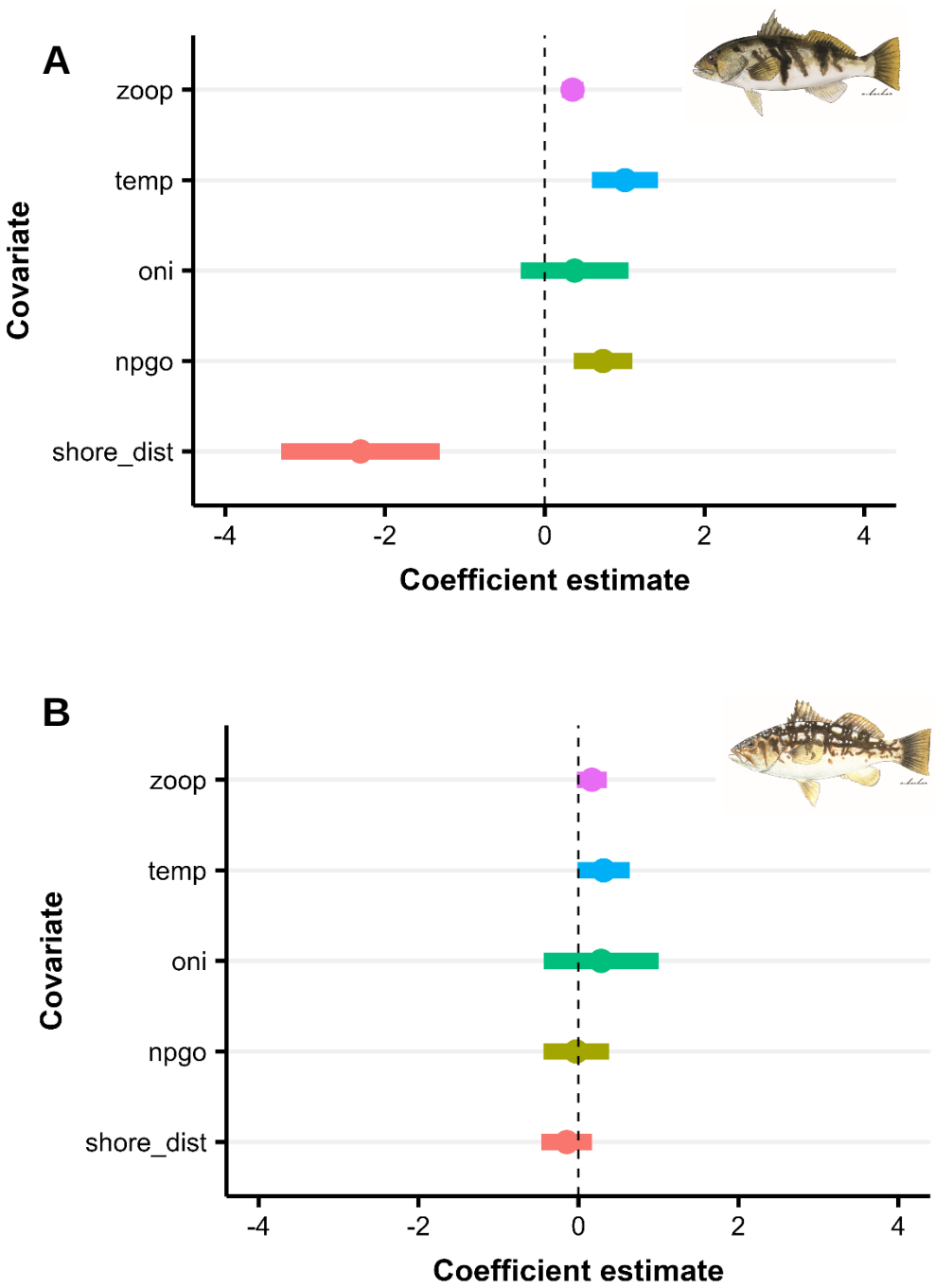
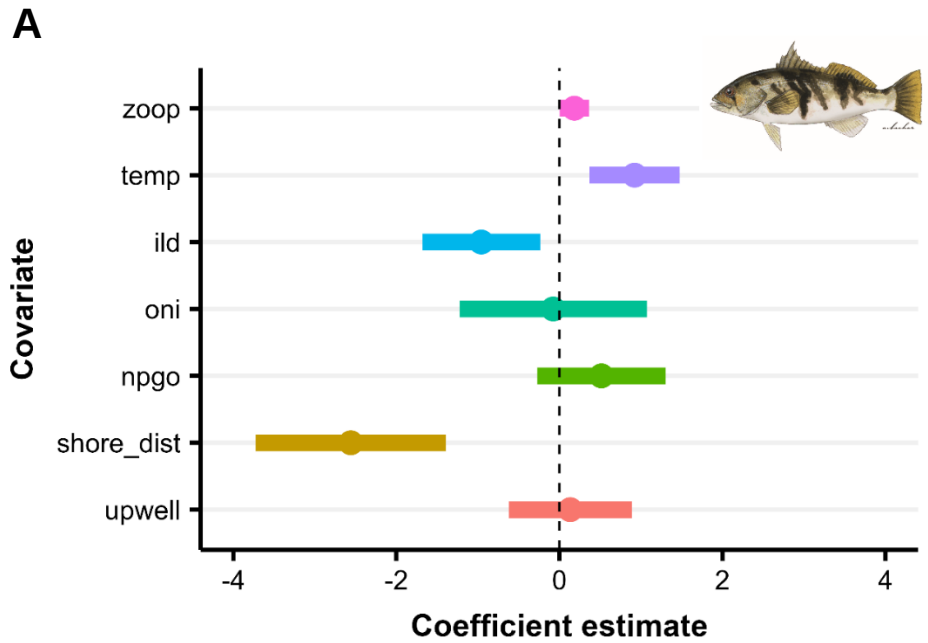


Figure 5. Model 1 coefficient estimates of the generalized linear mixed effects model depicting the relationships between bass larval abundance and environmental covariates from 1963 to 2016 for a) Barred Sand Bass and b) Kelp Bass in southern California, USA. zoop = CalCOFI zooplankton biomass, temp = CalCOFI ocean temperature averaged over upper 10 m, oni = Ocean Niño Index for June/July, npgo = North Pacific Gyre Oscillation index for July, and shore_dist = distance from survey station to mainland coast. Model coefficients greater than (less than) one reflect positive (negative) relationships. Lines depict 95% confidence intervals. CalCOFI = California Cooperative Oceanic Fisheries Investigations.



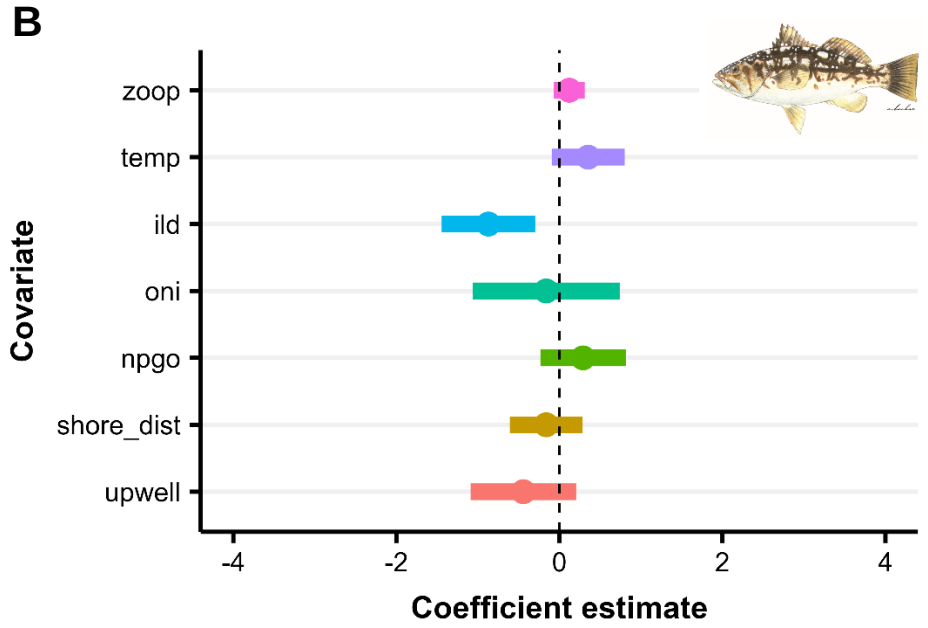


Figure 6. Model 2 coefficient estimates of the generalized linear mixed effects model depicting the relationships between bass larval abundance and environmental covariates from 1984 to 2016 for a) Barred Sand Bass and b) Kelp Bass in southern California, USA. zoop = CalCOFI zooplankton biomass, temp = CalCOFI ocean temperature averaged over upper 10 m, south.ild = isothermal layer depth, oni = Ocean Niño Index for June/July, npgo = North Pacific Gyre Oscillation index for July, shore_dist = distance from survey station to mainland coast, bakun33 = Bakun upwelling index at 33°N. Model coefficients greater than (less than) one reflect positive (negative) relationships. Lines depict 95% confidence intervals. CalCOFI = California Cooperative Oceanic Fisheries Investigations**.**

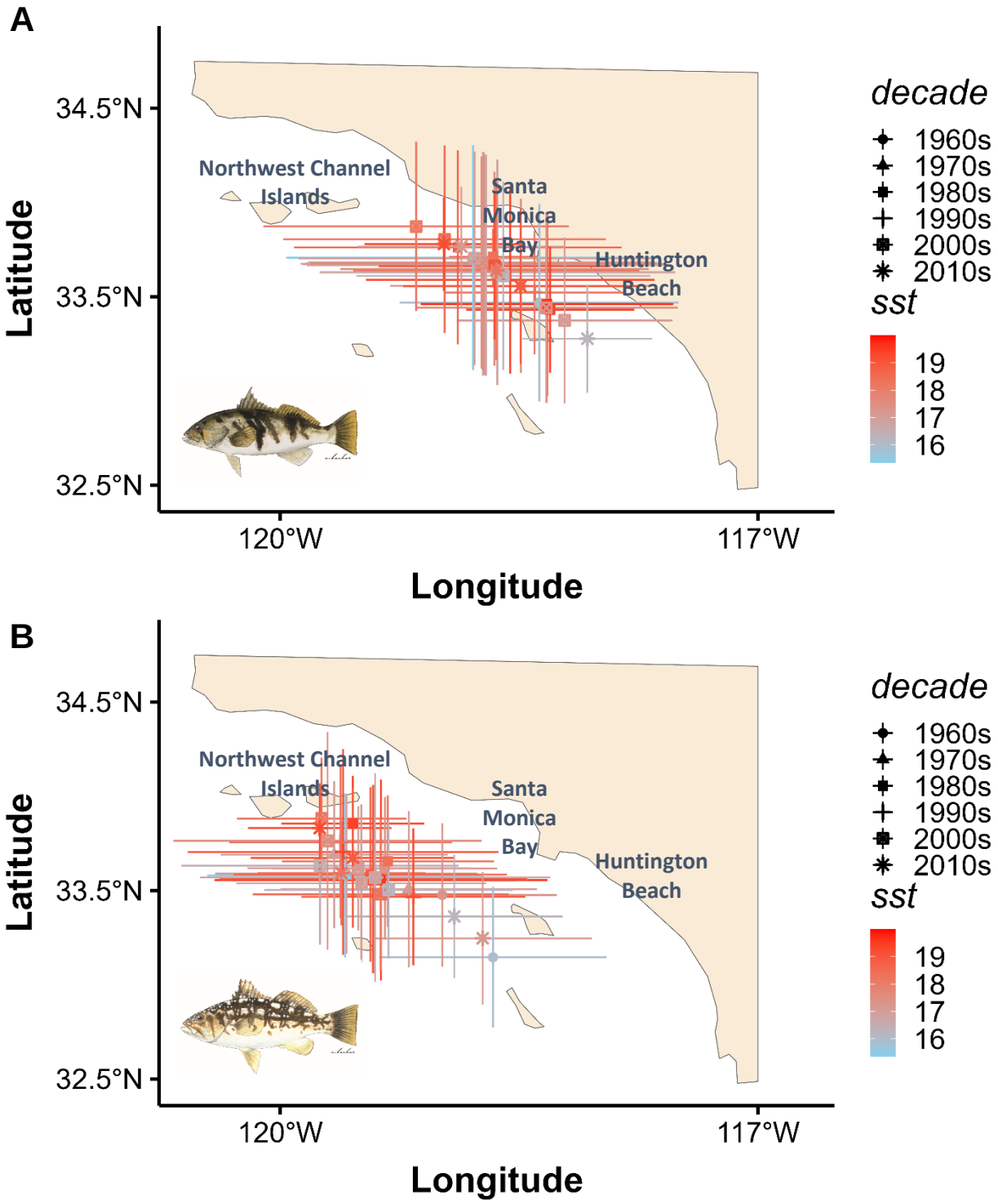


Figure 7. Decadal trends in the mean center of gravity for larval distributions of a) Barred Sand Bass and b) Kelp Bass in southern California, USA, 1963 to 2016, by decade (symbols) and annual mean sea surface temperature (colored dots/lines). Lines depict latitudinal and longitudinal 95% confidence intervals.