Title

Reconstructing the population dynamics of southern California Paralabrax spp. in the face of a changing ocean

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Reconstructing the population dynamics of southern California *Paralabrax* spp. in the face of a changing ocean

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Marine Biology

by

Erica Teresa Mason

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2023

The Dissertation of Erica Teresa Mason is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2023

DEDICATION

In memory of my dear friend and mentor, Jim Allen. In so many ways, the following pages were influenced by what I learned from you.

And to my son, Zane. This is for you, my love.

EPIGRAPH

"What's good for the fish is what's good for the people."

- Norm Harry, Paiute Tribe

TABLE OF CONTENTS

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

.

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

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Jarvis Mason, E.T., L. Bulkeley, W.W. Watson, Sawkins Salazar, A.C., M.T. Craig, J.R. Hyde, A.R. Thompson, B.X. Semmens. 2022. Decoding comparable morphologies: pigmentation validated for identifying southern California *Paralabrax* larvae. *FishTaxa* 25:9-25.

Mason, E.T., A.N. Kellum, J.A. Chiu, G.T. Waltz, S. Murray, D.E. Wendt, R.M. Starr, and B.X. Semmens. 2020. Long-term participation in collaborative fisheries research improves angler opinions on marine protected areas. *Peer J* 8:e10146 DOI 10.7717/peerj.10146.

Walker, K.M., K.M. Penttila, **E. Jarvis-Mason**, C.F. Valle. 2020. Validated age and growth of Barred Sand Bass within the southern California Bight. *California Fish and Game* 104(4):205-215.

Jarvis, E.T., H.L. Gliniak, and C.F. Valle. 2014. Effects of fishing and the environment on the long-term sustainability of the recreational saltwater bass fishery in southern California. *California Fish and Game* 100(2):234-259.

Jarvis, E.T., K.A. Loke-Smith, K. Evans, R.E. Kloppe, K.A. Young, and C.F. Valle. 2014. Reproductive potential and spawning periodicity in barred sand bass (*Paralabrax nebulifer*) from the San Pedro Shelf, southern California. *California Fish and Game* 100(2):289-309.

McKinzie, M., **E.T. Jarvis**, and C.G. Lowe. 2014. Fine-scale horizontal and vertical movement of barred sand bass, *Paralabrax nebulifer*, during spawning and non-spawning seasons. *Fisheries Research* 150:66-75.

Lyons, K., **E.T. Jarvis**, S. Jorgensen, K. Weng, J. O'Sullivan, C. Winkler, and C.G. Lowe. 2013. The degree and result of gillnet fishery interactions with juvenile white sharks in southern California assessed by fishery-independent and -dependent methods. *Fisheries Research* 147:370-380.

Lowe, C.G., M.E. Blasius, **E.T. Jarvis**, T.J. Mason, G.D. Goodmanlowe, and J.B. O'Sullivan. 2012. Historic fishery interactions with white sharks in the southern California Bight. pp. 169-198 in: Domeier, M.L. (ed.), *Global perspectives on the biology and life history of the white shark*. Taylor and Francis Group, LLC., Florida.

Jarvis, E.T., C. Linardich, and C.F. Valle. 2010. Spawning-related movements of barred sand bass, *Paralabrax nebulifer,* in southern California: Interpretations from two decades of historical tag and recapture data. *Southern California Academy of Sciences Bulletin* 109:123-143.

Jarvis, E.T., H.L. Gliniak, O. Horning, and C. Linardich. 2009. The occurrence of juvenile Mexican lookdown, *Selene brevoortii* (Gill 1863), in Seal Beach, California. *California Fish and Game* 95:188-192.

Lowe, C.G., K.M. Anthony, **E.T. Jarvis**, L.F. Bellquist, and M.S. Love. 2009. Site fidelity of characteristic fish species at offshore petroleum platforms in the Santa Barbara Channel. *Marine and Coastal Fisheries* 1:71-89.

Jarvis, E.T. and C.G. Lowe. 2008. The effects of barotrauma on the catch-and-release survival of southern California nearshore and shelf rockfishes (Scorpaenidae, *Sebastes* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 65:1286–1296.

Jarvis, E., K. Schiff, L. Sabin, and M.J. Allen. 2007. Chlorinated hydrocarbons in pelagic forage fishes and squid of the southern California Bight. *Environmental Toxicology and Chemistry* 26:2290-2298.

Jarvis, E.T., M.J. Allen, and R.W. Smith. 2004. southern California recreational fish catches compared to environment-species relationships and fishery-independent data, 1980-2000. *CalCOFI Reports* 45:167-179.

FIELDS OF STUDY

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Professor Brice X. Semmens

ABSTRACT OF THE DISSERTATION

Reconstructing the population dynamics of southern California *Paralabrax* spp. in the face of a changing ocean

by

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Doctor of Philosophy in Marine Biology

University of California San Diego, 2023

Brice X. Semmens, Chair

Fishery managers are tasked with preparing our fisheries for climate change, but doing so requires data to assess population status and environmental drivers, and data is typically limited. Many small-scale fisheries, like recreational-only fisheries, have a paucity of information and resources to perform robust assessments, which results in data-limited management measures that can inadvertently increase the vulnerability of the resource to detrimental harvest and climate change impacts. Here I focus on the popular and overexploited southern California recreational saltwater bass fishery, which despite its economic and cultural significance to the state, lacks long-term species-specific data and formal population assessments. By leveraging a variety of disparate data sets, taxonomy methods, and advanced quantitative methods, I reconstruct the population dynamics of the two focal species, Barred Sand Bass (*Paralabrax nebulifer*) and Kelp Bass (*P. clathratus*), over most of the last century and across rapidly changing ocean conditions. I begin with Barred Sand Bass and build a bespoke Bayesian capture-mark-reencounter model to estimate demographic rates over three historical periods spanning 54 years. Using these rates, I generate, for the first time, estimates of abundance, and along with other data sources (juvenile recruitment, adult densities, harvest, and sea surface temperature) and historical accounts in the literature, I demonstrate how the environment and harvest have contributed to long-term fluctuations in productivity. I then develop a robust method to construct and validate a taxonomic key for distinguishing southern California *Paralabrax* spp. larvae and use this key to unlock a larval abundance data set with high spatial and temporal resolution. Using these larval data within a geostatistical modeling framework, I generate species-specific standardized indices of larval abundance, quantify the influence of environmental covariates on their long-term spatiotemporal patterns, and explore the predictive power of the larval time series to anticipate future catches. Based on these modeling efforts, I contribute improved fishery management tools for monitoring status and trends and demonstrate species-specific population dynamics, highlighting the species' different susceptibilities to harvest and climate change impacts. Taken together, these studies pave the way toward an ecosystem and climate-ready approach to fisheries management for this important group of fishes.

CHAPTER 1

Recruitment limitation increases susceptibility to fishing-induced collapse in a spawning aggregation fishery

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Brice X. Semmens

Abstract

Aggregation-based fisheries are notorious for booms and busts driven by aggregation discovery and subsequent fishing-induced collapse. However, sporadic recruitment in some since-protected populations has delayed recovery, suggesting recruitment-limitation may be a key driver of their population dynamics and fishery recovery potential. To glean insight into this dynamic, we focused on an overexploited temperate aggregate spawner (Barred Sand Bass, *Paralabrax nebulifer*) and leveraged a long-term mark-recapture data set spanning different oceanographic and harvest histories in a bespoke Bayesian capture-mark-reencounter modeling framework. We coupled this demographic analysis with long-term trends in sea surface temperature, harvest, adult and juvenile densities, and historical accounts in the literature. Our results indicate a history of multidecadal windows of fishing opportunity and fishing-induced collapse. The appearance of these windows in time appears largely driven by sporadic, warm water pulses, in which larvae may not be locally sourced. At present, traditional aggregations remain absent following a period of fishery collapse despite evidence of incipient population recovery. The lack of an associated fishery recovery suggests that harvest on spawning aggregations may have reduced densities enough to impact the behaviors driving aggregation dynamics. Aggregate spawner populations that are dependent on sporadic strong recruitment, especially those at their geographic margins, are thus highly susceptible to sudden and potentially extended periods of collapse, making them ill-suited to high CPUE fishing that occurs on spawning grounds. If the goal is to balance the protection of spawning aggregations with long-term fishery sustainability, then limiting aggregation-based fishing during spawning season may be the best insurance policy against collapse and recovery failure.

1.1 **Introduction**

Fishes that form large spawning aggregations (i.e., aggregate spawners) are commonly exploited by artisanal, recreational, and commercial fisheries worldwide. However, relative to fishes that do not aggregate to spawn, they are highly vulnerable to overfishing due to the spatiotemporal predictability of their aggregations and other life-history characteristics typical of aggregate spawners (e.g., slow growth, depensatory dynamics, Sadovy de Mitcheson 2016). Transient aggregate spawners migrate tens to hundreds of kilometers to form large aggregations for weeks to months (Domeier & Colin 1997). This behavior makes them especially vulnerable to harvest impacts, compared to resident spawners that form smaller aggregations over brief periods, either seasonally or year-round (i.e., group spawners). Indeed, overfishing has contributed to the collapse of many fisheries based on transient spawning aggregations (Chollett et al. 2020), and recovery has taken decades (Sadovy & Eklund 1999, Aguilar-Perera 2006, Waterhouse et al. 2020) or failed to occur altogether (Perälä et al. 2022).

In the last century, aggregation-based fisheries have been characterized as “boom and bust,” in which a population is discovered and then quickly decimated. However, some fish populations are largely driven by sporadic recruitment events (Vert-Pre et al. 2013, Stock et al. 2021). These populations may have experienced recruitment-limitation prior to discovery of the fishery, and aggregation-based fishing on spawning grounds would have acted to further limit recruitment potential during periods of unfavorable conditions, accelerating the imminent “bust” trajectory and delaying recovery.

Barred Sand Bass (Family Serranidae, *Paralabrax nebulifer;* hereafter, BSB) is a transient aggregate spawner (Jarvis et al. 2010, Teesdale et al. 2015) that once comprised a highly popular aggregation-based recreational fishery in southern California, USA. The species is managed within a multispecies complex (i.e., saltwater basses) that includes two other congeners, Kelp Bass, *P. clathratus*, and Spotted Sand Bass, *P. maculatofasciatus*. Historically, BSB formed massive spawning aggregations at several locations along the coast, in which the spawning grounds became well-known BSB fishing “hot spots” (Love et al. 1996a). During the 1980s and 1990s, BSB fishing was a focal summer pastime, but a sharp decline in catch-per-unit-effort (CPUE) in the mid-2000s called into question the sustainability of the fishery (Jarvis et al. 2010, Erisman et al. 2011) and prompted the implementation of tighter fishing regulations in 2013 (Jarvis et al. 2014). In the decade since, BSB recreational landings and CPUE have fallen to all-time lows (CDFW 2020), and the spawning aggregations have seemingly disappeared, with no signs of fishery recovery (Bellquist et al. 2017).

The delay or lack of recovery in overfished aggregate spawner populations despite measures to enhance populations, may be the result of one or more factors including long-lived, slow-growing life history characteristics, sporadic recruitment (Semmens et al. 2007, Stock et al. 2021), and Allee effects (Allee 1931, 1938, Stephens et al. 1999), such as changes in fish reproductive behavior at low densities (e.g., loss of social transmission of spawning ground locations; Warner 1988, 1990, Bolden 2000, Semmens et al. 2008). Depensation may also be a factor (e.g., if a population is fished to a point at which densities are so low that it is unable to replenish itself), but it can be difficult to detect unless stock sizes are reduced to <1% of unfished spawning biomass (Liermann and Hilborn 2001, Hilborn et al. 2014). Although there is evidence that recovery is possible when fishing mortality is majorly curtailed (Hilborn et al. 2014, Chollett et al. 2020, Waterhouse et al. 2020), such recoveries are subject to environmental drivers, with many fished populations showing recruitment fluctuations driven by oceanography (i.e., transport, temperature regimes) rather than (or in addition to) spawning stock biomass (Vert-Pre et al. 2013). Such variability in recruitment mediates both the resilience of the stock to overfishing, and the determinism of stock recovery following management (Kuparinen et al. 2014).

Though the effect of fishing on the decline of the BSB fishery was well documented in the last decade (Erisman et al. 2011, Jarvis et al. 2014, Miller & Erisman 2014, Bellquist et al. 2017), the contribution of changing ocean conditions to this decline and lack of recovery remains less understood. Temporal trends in fishery-independent data suggest BSB larval and juvenile recruitment in southern California has fluctuated in response to environmental conditions (Stephens et al. 1986, 1994, Jarvis et al. 2014), responding favorably to warm-water conditions (Moser et al. 2001, Hsieh et al. 2005, Jarvis et al. 2014). BSB are commonly distributed from Bahia Magdalena in southern Baja California, Mexico to central California, USA (Heemstra 1995, Love & Passerelli 2020), but they are rare north of Pt. Conception (the northern most point of southern California). Historically, their distribution and availability in California was considered tightly coupled to warm water conditions (Hubbs 1948, Young 1969, Frey 1971, Feder et al. 1974). If BSB recruitment in southern California is more closely tied to environmental conditions than spawning stock biomass, it is likely that climate change will drive changes in recruitment frequency/intensity, in addition to a shift in the geographic range of the population (Hubbs 1948, Pinsky et al. 2020, Walker et al. 2020a). While predicting future stock status may be challenging, examining the historical population dynamics of the species in southern California, in relation to both harvest and the environment, will likely provide context for the anticipated changes a warming ocean will bring.

Population variability in BSB may be at least partially driven by changes in the cumulative effects of environmental drivers and fishing pressure on mortality. In fished populations, total mortality is the sum of mortality due to fishing and natural causes (i.e., predation, disease). Fishing mortality can be derived from a formal stock assessment (data-rich fisheries), catch-curve analysis (data-poor fisheries), or mark-recapture models, with the latter being the recommended method because it provides direct estimates of total mortality (Pine et al. 2003). Mark recapture models can also estimate the discrete form of fishing mortality (i.e., annual exploitation or harvest rate), which represents the fraction of the population removed due to fishing. Hence, along with estimates of total harvest in the fishery, one can derive the population size from which harvest was drawn.

Here, we take advantage of a long-term mark-recapture data set spanning different oceanographic regimes and harvest histories and develop a Bayesian capture-mark-reencounter (CMR) framework to glean insight into the long-term population dynamics of BSB. Specifically, we estimate demographic rates (e.g., growth, survival, exploitation) and population size during these regimes and compare them to long-term trends in sea surface temperature (SST), fishery-independent surveys of adult densities, and harvest. Additionally, we model young-of-the-year densities (juvenile recruitment) as a function of SST, adult densities, and harvest and look for signs of population recovery in adult and juvenile densities in the last decade. Finally, we attempt to reconcile our findings with historical accounts of BSB distribution and availability in the literature. In doing so, we seek to resolve long-standing uncertainty in the role of time-variant, sporadic recruitment in the dynamics of this economically and culturally important aggregation-based fishery.

1.2 Methods

Tagging Studies

We analyzed BSB tagging data collected by the California Department of Fish and Wildlife (CDFW, formerly the California Department of Fish Game) between 1962 and 1970 (1960s) and between 1989 and 1999 (1990s), as well as tagging data collected by researchers at Scripps Institution of Oceanography (SIO), UC San Diego, between October 2012 and February 2015 (2010s). In all three periods, BSB were captured by hook-and-line (a small subset in the 1990s were trawl-caught), measured to the nearest mm TL, tagged with external T-bar tags printed with a unique identification number, “Reward”, and phone number, and subsequently released (see Jarvis et al. 2010 for a detailed description of the CDFW tagging studies). Tagging rewards across study periods included low value non-monetary and monetary incentives (e.g., hats, $5 cash, gas cards).

During the 1960s and 1990s, tagging effort was focused primarily during peak spawning (June-August) and was distributed throughout the southern California coast, including spawning and non-spawning grounds (Fig. 1.1, Jarvis et al. 2010). In the 2010s, tagging occurred year-round at spawning and non-spawning grounds primarily off San Diego, CA, USA (Fig. 1.1). Some tagging occurred inside a marine protected area (MPA), in which take is prohibited year-round. We filtered the 2010s data to exclude fish tagged in the MPA, as it is likely these fish had a lower probability of capture by anglers restricted to fishing outside of the MPA.

Tagging Data

In the 1960s and 1990s, the disposition of reencountered fish (i.e., kept or released) was not always provided. Unless otherwise reported, we assumed all sublegal fish recaptured by anglers were released and all legal-size fish were retained (but see *Growth Estimation* below). During the 1960s, 1990s, and through February 2013, the minimum size limit (MSL) was 305 mm (12 inches TL), corresponding to a fishery recruitment age of five to six years; afterward the MSL increased to 356 mm (14 inches TL, Jarvis et al. 2014), corresponding to fishery recruitment at age seven to eight years. Records with unknown tagging lengths were removed from the analysis. See Supplement S1 (Appendix) for additional details on data formatting.

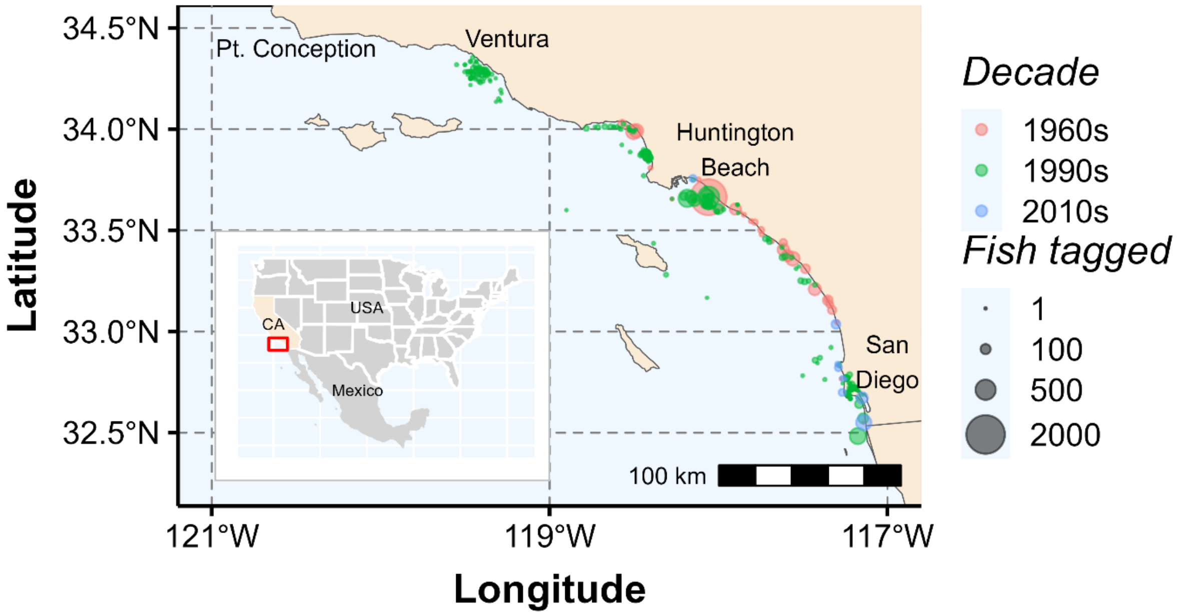

Figure 1.1. Map of Barred Sand Bass tagging locations in southern California (CA), USA, by decade.

Data processing and filtering of the tag and recapture data resulted in capture histories for 6,473 tagged BSB across the three tagging periods (1960s, 1990s, and 2010s), which represented nearly 25 years of data spanning five decades (Fig. 1.1, Table 1.1). Both the number of tagged fish and proportion of recaptures was highest in the 1960s and lowest in the 2010s, and the average size of fish tagged increased over time (Table 1.1).

Table 1.1. Summary tag and recapture statistics by tagging period (1960s: 1962-1970, 1990s: 1989-1999, 2010s: 2012-2015) for Barred Sand Bass tagged and released in southern California, USA

	1960s	1990s	2010s
No. of years	9	11	2.3
Tagged fish[a]	3,335	2,696	442
Total length (mm)			
range	218 - 551	178 - 647	171 - 544
mean (± SD)	303 ± 34	339 ± 62	386 ± 60
% mature[b]	89%	94%	97%
% legal size[c]	38%	69%	75%
Recaptured fish	255	130	12
Recapture rate	8%	5%	3%
Total length (mm)[d]			
no. reported lengths	243	65	1
range	260 - 577	305 - 508	375 - 375
mean (± SD)	330 ± 36	348 ± 35	375
% mature[b]	98%	100%	100%
% legal size[c]	84%	100%	100%

[a] Fish tagged in the last year during the 1960s and 1990s were not included in the analysis. For the 1960s and 1990s, we include only fish tagged in June-August, and for the 2010s, we include fish

[b] Based on size at 100% maturity (≥ 270 mm).

[c] Legal size during the 1960s and 1990s was ≥ 305 mm; legal size increased to ≥ 356 mm in March 2013.

[d] Lengths not reported for all recaptured fish.

Capture-mark-reencounter (CMR) Model

Demographic Rates

We used a Bayesian multistate framework (Kéry & Schaub 2012) to estimate the following four probabilities:

ϕ_t (true survival) = the probability a fish alive at occasion t is alive at occasion $t + 1$,

p_t (recapture probability) = the probability a fish at risk of capture at occasion t is recaptured by a biologist at occasion t,

κ_t (recovery probability or harvest rate/fishing mortality) = the probability a fish is caught and kept by an angler from occasion t to $t + 1$ and the tag reported (caught and kept and reported at any time from occasion t through the interval between t and $t + 1$), and

R_t (resighting probability or catch-and-release (CAR) rate) = the probability a fish at risk of capture at occasion *t* is caught and released (i.e., resighted) by an angler in occasion *t* and the tag reported.

Our bespoke approach differs from traditional CMR models (Barker 1997, Riecke et al. 2021) in two ways. First, we assumed no permanent emigration and thus, excluded the fidelity parameters (*F* and *F'*). This assumption was based on the CMR area being sufficiently large to include the geographic area for tagging and variability in BSB mean home range size and migration distance to spawning grounds (Mason & Lowe 2010, Jarvis et al. 2010). Second, we excluded the few CAR encounters in the interval between survey occasions (1960s: $n = 47$, 1990s: $n = 22$, 2010s: $n = 2$). The Barker model estimates the probability of CAR at *t*, $t + 1$ (the non-survey interval), given the fish survives to occasion $t + 1$ (*R*) or dies after being resighted (*R'*). The latter parameter is a notorious nuisance parameter and is difficult to estimate. Including it in our model would add undue complexity given the limited number of CARs outside of peak spawning. Thus, we estimated our angler resighting parameter only during the summer survey occasions (R_t).

As there was no expectation that survival or fishing mortality was the same across decades, and because no recaptures occurred between decadal tagging periods, we fit separate models for each tagging period. We used beta distributions with flat priors for all four parameters (Table S1). We used simulated data during model development to validate our ability to estimate true parameter values. For each model, we generated three Markov Chain Monte Carlo (MCMC) chains of 20,000 iterations, discarding the first 5,000 and saving every fifth iteration. We used a marginalized likelihood function to increase MCMC convergence speed (Yackulic et al. 2020), and we reported mean and Bayesian 95% credible intervals for each estimated and derived parameter (see *Harvest Rates* and *Population Size* below for derived quantities). We analyzed all CMR models in JAGS (Plummer 2003) with the R package `jagsUI` (Kellner 2021).

Given that most tagging in the 1960s and 1990s occurred during the Summer, we based our models on annual survey occasions, in which there was a single (Summer) tagging occasion per year (i.e., fish tagged outside of June-August were excluded from analysis). For the 2010s model, we modeled monthly survey occasions because tagging occurred year-round on a more consistent basis. As a result, we included a fixed effect of season (Summer, non-Summer) on survival, harvest, and CAR rates in the 2010s. We adjusted monthly harvest rates in the 2010s to annual harvest rates. Data filtering resulted in zero biologist recaptures and angler CARs in the 1990s and so the biologist recaptures (p) and CAR (R) parameters were fixed to zero in the 1990s model (Table S1).

Tag Retention

To account for tag loss, we first separately modeled the probability of retaining a tag with data from a Kelp Bass double-tagging study that occurred off San Diego, CA, USA, from 2012 to 2016 (see Bellquist 2015 for a detailed description of methods). Given that similar tagging methods were used by trained biologists in each of the three BSB tagging studies, and that Kelp Bass is a local congener of BSB with similar growth rates and overlapping habitat use (Lowe et al. 2003, Mason & Lowe 2010, Logan & Lowe 2018), we assumed tag retention rates to be similar between the two species and across tagging periods. We used a Bayesian hidden state framework in JAGS (Su & Yajima 2021, Plummer et al. 2022) to model tag retention as a function of time at liberty (see Supplement S2 in the Appendix).

Of the 673 Kelp Bass double-tagged in the tag retention experiment (Bellquist 2015), a total of 129 fish were recaptured within 3.7 years (31 with a single tag intact and 98 with both tags intact). The cumulative probability of a fish in the double tagging study retaining at least one tag was ~ 87% in the first year and fell to less than 10% after eight years (Fig. S1a). The probability (non-cumulative) of a fish retaining a tag, as a function of time at liberty, decreased from ~75% after two years at liberty to ~50% after five years (Fig. S1b).

The model estimated time-dependent probabilities of retaining a tag (*tr*, Fig. S1) were incorporated into the CMR model framework for the 1960s and 1990s (see *State-transition and observation matrices* below). We defined the time-dependent tag retention priors with a beta distribution in which the shape parameters of each prior beta distribution in the CMR model were based on the mean and variance of the time-dependent tag retention posterior distributions derived from the tag retention model (Table S1). Given the short duration of the 2010s study (27 months), we simply incorporated a prior for the discrete annual tag retention rate, exp($-\beta$), termed r (Table S1).

Growth Estimation

Our bespoke approach also accounts for potential harvest of sub-legal-size fish and CAR of legal-size fish. To do so, we incorporated growth in our model, such that at each time step (occasion), the size of each fish, if not supplied by the data, was estimated and the fish assigned a size class (sublegal or legal), whereby the probability of harvest (κ) and the probability of CAR (R) were estimated for both sublegal- and legal-size fish. To estimate BSB growth, we used the von Bertalanffy growth function (VBGF; Love et al. 1996b, Walker et al. 2020b). However, given that the parameters of the traditional VBGF are highly correlated (e.g., k, L_∞; Ogle 2016), we instead used the Francis parameterization of the VBGF to estimate three growth parameters (L1, L2, and L3) in the CMR models. To generate priors for the Francis growth parameters in the CMR model, we separately modeled BSB growth using BSB age and growth data collected in southern California from 2011 to 2016 (Walker et al. 2020b) and the Francis parameterization of the VBGF in the R package `FSA` (see Supplement S3 in the Appendix, Ogle et al. 2022).

The 736 BSB collected in the age and growth study (Walker et al. 2020b) ranged in age from young-of-the-year to 25 years, while total lengths ranged from 114 – 600 mm. The mean growth parameter estimates and 95% confidence intervals used to define priors in the CMR models were $L1_3$ = 236 mm, CI: 229- 242 mm (mean size at age 3 y); $L2_{9.5}$ = 403 mm (mean size at age 9.5 y), CI: 400-406 mm; $L3_{16}$ = 495 mm, CI: 487-502 mm (mean size at age 16 y, see Table S1 for priors). BSB males reach maturity between 2 and 5 years, and females between 2 and 5 years (Love et al. 1996b).

Given that fish growth in our model was informed by growth increments between recapture and tagging (or previous recapture events), which are independent of the size structure of the population, our model estimates of growth are robust to any fishing-influenced truncation in the length frequency distribution over time. Moreover, since we used the Francis parameterization of the VBGF to estimate growth, our estimates are directly comparable to estimates obtained by traditional age and growth studies using otolith increments (Francis 1988) and are more directly attributable to growth rate than if just sizes at age were sampled (Enberg et al. 2012).

State-transition and observation matrices

Using a multi-state approach (Kéry & Schaub 2012), we defined the state transition matrix (S) to calculate the state transition probability for the three possible latent states in occasion *t+1* (columns), given the latent state in occasion *t* (rows): (1) alive with tag, (2) recently dead (recovered), and (3) dead,

$$s_{i,t} = \begin{bmatrix} \varphi_{c_{i,t}} * tr_{t-f_i+1} & \kappa_{c_{i,t}} * tr_{t-f_i+1} & (1 - \varphi_{c_{i,t}}) - \kappa_{c_{i,t}}) \, * \, tr_{t-f_i+1} \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{bmatrix}, \text{ where,}$$

$c_{i,t}$ refers to the size class of individual *i* (legal, sublegal) at occasion t,

tr_{t-fi+1} is the tag retention probability at occasion $t + 1$, specific to the length of time the fish was at liberty, where f_i refers to the occasion of tagging. Note that for the 2010s model, instead of the time-varying *tr* parameter, we used a constant annual probability of tag retention (*r*, Table S1) that was converted to a monthly rate ($r.mo. = r^{1/12}$). In addition, the survival and harvest rate parameters were also indexed on season (spawning, nonspawning) at occasion *t* (e.g., $\varphi_{c_{(i,t),t}}$).

We defined the observation matrix (O) to calculate the probability of observing each of the five following possibilities in occasion *t* (columns), given the latent state in occasion t (rows): (1) recapture by a biologist and resighting by an angler, (2) recapture by a biologist, (3) resighting by an angler, (4) caught, kept, and reported by an angler, and (5), not seen or reported, where,

$$o_{i,t} = \begin{bmatrix} p_t \, * \, R_{c_{i,t}} & p_t \, * \, (1 - R_{c_{i,t}}) & (1 - p_t) * R_{c_{i,t}} & 0 & (1 - p_t) \, * \, (1 - R_{c_{i,t}}) \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}.$$

Note that for the 2010s model, the class and season indices were dealt with in the same manner as the state matrix above.

Capture-history and Length Matrices

We constructed capture histories for each tagged fish and excluded fish tagged in the last survey occasion from the analysis. For a description of how we assigned recoveries to the correction survey occasion, see Supplement S1 (Appendix).

We constructed a length matrix consisting of lengths recorded at the occasion of release and those reported for angler resightings and angler recoveries. Given that our 1960s and 1990s CMR models estimated growth in annual increments, lengths of fish reported during the interval between survey occasions were assigned NAs. The length matrices for each period were supplied as data for the growth estimation portion of the CMR models.

Deriving Population Size

Harvest Rates Conditioned on Tag Reporting

The CMR model estimates of exploitation (i.e., harvest rate, κ) are dependent on tags of all resighted and recovered BSB being reported. When tag reporting is less than 100%, harvest estimates will be biased lower than the true harvest rate (Sackett & Catalano 2017). Given that tag reporting rates were unknown in this study and that reporting rates are known to vary widely across fisheries (Denson et al. 2002) we derived conditional size-specific harvest rates according to three hypothetical tag reporting rates of 25%, 50%, and 75%. In this prior sensitivity analysis, for each tag reporting rate, we assigned a corresponding beta distribution in the CMR model that we used *a posteriori* to derive posterior estimates of the conditional harvest rate under each tag reporting scenario. Thus, for each decade and size class, the conditional harvest rate represents the model-estimated mean harvest rate divided by the tag reporting rate.

Population Size Conditioned on Tag Reporting

To calculate population estimates for each decade, we applied the mean conditional size-specific harvest rates to the annual size-specific harvest from each tagging period, where the annual legal size BSB harvest divided by the conditional harvest rate of legal size BSB equals the population of legal size BSB (see Supplement S4 in the Appendix on estimating size-specific harvest; the relative proportions of annual size-specific harvest are reported in Table S2). In the 1960s CMR, there was only a single year of size-specific catches for which to apply the size-specific conditional harvest rates, which yielded a single estimate of population size under each tag reporting scenario. In contrast, we were able to apply size-specific conditional harvest rates to multiple years of harvest in the 1990s and 2010s to yield annual estimates of population size under each tag reporting scenario.

To explore decadal trends in population size (and size-specific conditional harvest rates), we used the R packages `tidybayes` and `ggdist` (Kay 2022a,b) to generate posterior distribution plots for each decade and tag reporting rate; these distributions represented the combined annual Bayesian posterior distributions.

Comparison to SST, Adult Densities, and Harvest

We obtained daily SST measurements (degrees Celsius) collected at the northern end of Santa Monica Bay, off Point Dume, CA, USA, from 1954 to (Carter et al. 2022). Santa Monica Bay, which is centrally located along the southern California coast, is a traditional BSB aggregation spawning ground. We chose Point Dume because it is the nearest Shore Station (Carter et al. 2022) to the location of diver surveys of adult and juvenile BSB in King Harbor, Redondo Beach, CA, USA (see below). From these, we derived a mean summer (June-August) SST for each year.

We obtained diver survey densities of adult (≥ 220 mm) and juvenile (< 150 mm, young-of-the-year) BSB from 1974 to 2022 in King Harbor, CA, USA, collected by the Vantuna Research Group (VRG), Occidental College (unpublished data; see Stephens et al. 1986 for a detailed description of methods). King Harbor is located within Santa Monica Bay.

We plotted temporal trends in SST, adult densities, and harvest to compare their decadal means occurring during each tagging period and their overall patterns throughout the time series. Here, we were focused on trends and not absolute values (e.g., was used the trend in SST in Santa Monica Bay as a proxy for the SST trend experienced in the southern California region). To identify potential lagged relationships between SST and adult density and between SST and harvest, we calculated cross-correlation coefficients from lags zero to ten years using the R package `funtimes` (Lyubchich et al. 2023). Positive correlations occurring at a lag of zero suggest influence of SST on the adult population, whereas positive correlations occurring at lags greater than three years (i.e., SST predicts future adult densities or harvest) suggest influence of SST on the early life history stages.

Relationship Between Juvenile Recruitment and SST

To explore potential relationships between juvenile (young-of-the-year) recruitment and SST, we also considered the Ocean Niño Index (ONI), as El Niño was shown to have a positive effect on BSB larval abundances off Baja California (Avendaño-Ibarra et al. 2009). We obtained the ONI data as monthly index values (NOAA 2023a), which we averaged to obtain mean annual indices. We standardized the annual summer SSTs and annual recruitment densities to a mean of zero and tested for lagged correlations between SST and recruitment and between ONI and recruitment from lags zero to three years using the R package `funtimes` (Lyubchich et al. 2023). We further explored the influence of SST and ONI on juvenile recruitment with a generalized additive model (GAM) using the R package `mgcv` (Wood 2017). To account for possible confounding effects of spawning biomass and harvest impacts on juvenile recruitment, we incorporated adult densities and CPFV harvest in our model, but we excluded the period after the fishery collapse (after 2005), in which BSB CPFV harvest was consistently less than the historic minimum (88 thousand BSB in 1978). We specified a Tweedie observation error family (positive continuous density values that also contain zeros) and a log link, allowing the model to estimate the shape of the Tweedie distribution parameter. We specified all main effects as a penalized smooth function with a basis function (i.e., 'wiggliness') of three. We tested three temperature models, 1) one with SST only (lag of zero), and 2) one with SST and ONI (both with lag of zero), and 3) one with SST (lag of zero) and ONI (lag of one). We performed model checks for convergence and basis function misspecification. We selected the most parsimonious model based on the lowest Akaiki information criterion (AIC) value and we report model fit as the percent deviance explained. We visually explored the conditional effects of important explanatory variables using the R package `visreg` (Breheny & Burchett 2019).

Historical accounts

Given limited species-specific harvest records and fishery-independent data prior to the mid-1970s, we gathered historical points of reference for BSB availability from the literature (see Supplement S5 in the Appendix for search terms). We compiled a table of BSB accounts spanning the mid-1800s through the late 1970s that referred to the relative contribution of BSB to commercial or recreational harvest, or that made any mention of BSB distribution, availability, or spawning in southern California. We then created a graphical timeline for contextualizing these accounts with respect to changes in BSB fishing regulations, the oceanographic climate, and trends in Rockbass CPFV harvest (the longest harvest time series). For the graphical timeline, we plotted monthly indices of the Pacific Decadal Oscillation (PDO, a measure of SST anomalies, NOAA 2023b) along with a 12-month running mean. We noted decadal-scale periods of predominately cool or warm temperature regimes (Minobe 1997, Mantua et al. 1997) associated with assemblage shifts in California's fishes as described in Hubbs (1948), McCall (1996), and Overland et al. (2008). We also noted major El Niño events resulting in either seasonal warm water intrusions of subtropical and tropical fauna or decadal-scale northern range expansions of temperate/subtropical/tropical fauna in California (Hubbs 1948, Radovich 1961, Lea & Rosenblatt 2000, McClatchie 2014, Walker et al. 2020a).

Data Availability

Data and code pertaining to the CMR model are available online in a GitHub repository: https://github.com/ETJarvisMason/bsb-CMR. We performed all analyses in R 4.0.3 (R-Core-Team 2020).

1.3 Results

Decadal Trends in Demographic Rates

Mean annual BSB survival (ϕ) differed by size class (legal vs sublegal) and was higher for sublegal fish than legal-size fish, except in the 2010s (Fig. 1.2). By decade, mean annual survival was highest in the 1960s and lowest in the 1990s. Mean annual survival of legal-size BSB in the 2010s was higher than in the 1990s, but survival of sublegal fish in the 2010s was lower than in both the 1990s and the 1960s (Fig. 1.2). Overall, the estimated annual survival rates are substantially lower than would be expected based on the size distribution of fish tagged in the study (e.g., the sizes of the biggest fish tagged correspond to BSB aged 10+ years old). Biologist recapture rates (p) of tagged BSB were low ($\leq 1\%$) across all tagging periods. The mean annual probability of a sublegal BSB CAR (R) during the 1960s was 4%; in the 2010s during the summer spawning season, it was ~3%, while outside of the spawning season, the probability was essentially zero. The probability of legal-size CAR was also near zero in the 1960s and the 2010s, regardless of season.

There were too few recapture lengths from which to model growth in the 2010s; however, given that (Walker et al. 2020b) collected BSB for age and growth during the same period (2011-2015), we included Francis VBGF growth parameter estimates from those data for comparison with the 1960s and 1990s CMR growth estimates. The CMR decadal growth estimates indicated BSB grew faster and reached a smaller size over time (Fig. 1.3).

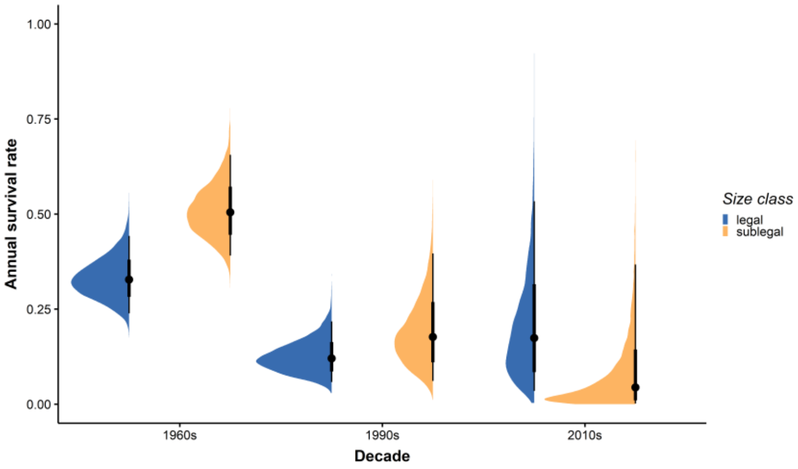

Figure 1.2. Bayesian capture-mark-reencounter model posterior distributions and mean annual survival and 50 and 95% credible intervals (dots plus thick and thin lines) for legal- and sublegal-size Barred Sand Bass across tagging periods. Annual survival rate is the proportion surviving in a year.

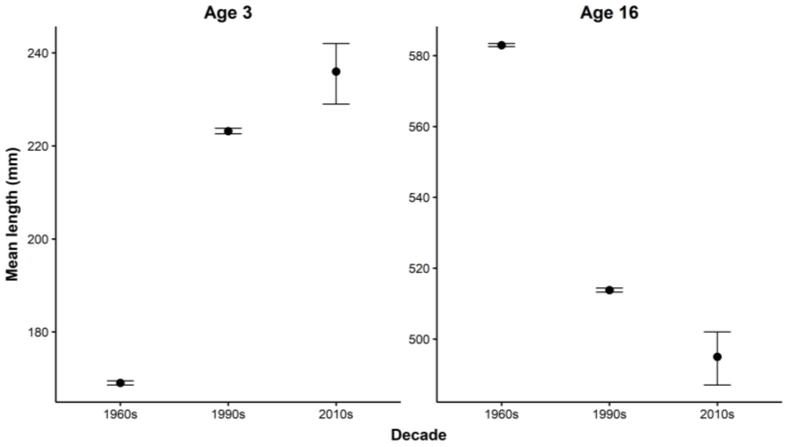

Figure 1.3. Estimates of Barred Sand Bass mean lengths at ages 3 and 16 across tagging periods. The 1960s and 1990s estimates represent mean Bayesian posteriors and 95% credible intervals estimated in the respective capture-mark-reencounter model, while the 2010s estimates represent mean and 95% confidence intervals derived from Barred Sand Bass age and growth data collected from 2011 to 2016 and fit to the Francis parameterization of the von Bertalanffy growth function (there were too few recapture lengths in the 2010s data to estimate growth).

Decadal Trends in Exploitation and Population Size

Harvest rates estimated by our CMR model were conservative as they assumed a 100% tag reporting rate; however, we observed an overall decrease in legal-size harvest rates over time, with the 1960s harvest rate more than ~2x and ~5x higher than the 1990s and 2010s harvest rates, respectively (Fig. S2). Harvest rates of sublegal-size BSB were low across decades but increased slightly in the 2010s (Fig. S2). Conditional harvest rates showed a similar pattern. Harvest rates under a 25% reporting rate were highest but the most uncertain (Fig. 1.4a).

The conditional decadal estimates of mean annual BSB population sizes (i.e., estimates across three hypothetical tag reporting scenarios) generally showed an increase between the 1960s and 1990s, in which the population approximately doubled (Fig. 1.4b). By the 2010s, the mean annual population had declined by nearly an order of magnitude to ~1/3 the size it had been in the 1960s, though there was greater uncertainty in the 2010s estimate (Fig. 1.4b). A posteriori, both the maximum and minimum conditional mean population estimate across decades occurred under a 25% tag reporting rate (maximum: ~ 19 million BSB in 1993, minimum: ~ 549,000 in 2014).

Comparison to SST, Adult Densities, and Harvest

Overall, trends in our population estimates corresponded to trends in SST and fishery-independent and -dependent data during the same time periods (Fig. 1.5). Adult densities were not available prior to 1974, but the lower adult densities in the 1970s followed on from our relatively smaller population estimate in the 1960s (compared to the 1990s, Fig. 1.5b). Likewise, relative to the 1990s, BSB harvest by all fishing modes combined and by CPFVs alone was lower in the 1960s and lowest in the 2010s (Fig. 1.5c).

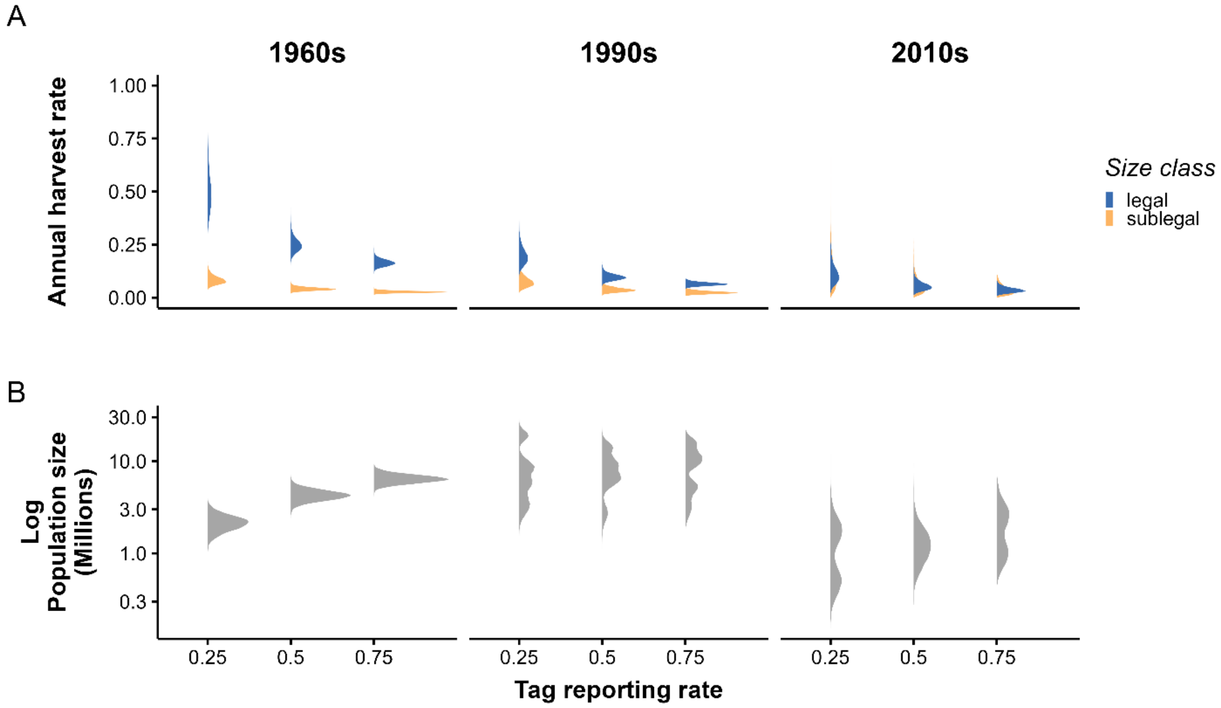

Figure 1.4. Bayesian capture-mark-reencounter model posterior distributions of Barred Sand Bass a) size-specific annual harvest rates and b) log population size, conditioned on 25%, 50%, and 75% tag reporting rates. Log population size in each decade represents the sum of legal and sublegal-size bass across multiple years, except for the 1960s, in which only one year of harvest was available for estimating population sizes. Annual harvest rate is the proportion of fish dying due to fishing.

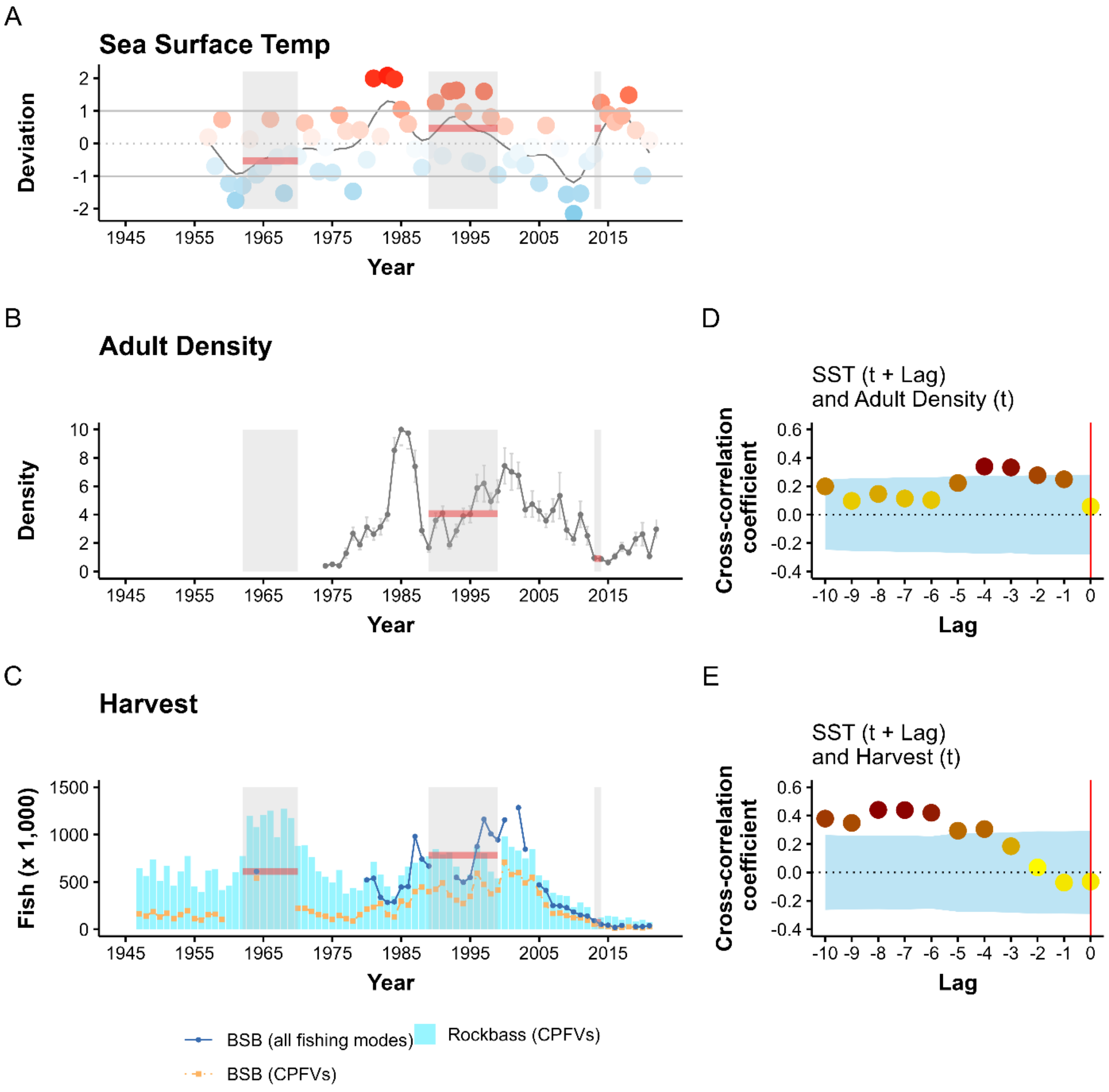

Figure 1.5. Temporal trends in a) average monthly summer sea surface temperatures on the central coast of southern California, USA, 1956-2021, b) mean annual adult densities (fish/transect) of Barred Sand Bass as measured on diver surveys on the central coast of southern California, 1974-2022, c) total Barred Sand Bass harvest in southern California across all recreational fishing modes (solid line with closed circles; 1964 and 1980-2021), and cross-correlation coefficients for d) SST and lagged adult densities, and e) SST and lagged Commercial Passenger Fishing Vessel (CPFV) harvest of Barred Sand Bass. CPFV harvest of Barred Sand Bass (dashed dotted line with closed squares) and Rockbass (bars) is included for comparison. Rockbass CPFV harvest records represent the combined harvest of Barred Sand Bass and Kelp Bass. BSB CPFV harvest for the years 1947-1959 and 1970-1973 represent Rockbass harvest multiplied by a factor of 0.25 to reflect estimates of BSB percent composition during those periods (note that for the period 1970-1973, 0.25 is likely conservative). Horizontal lines depict means for SST, adult densities, and total harvest during each tagging period (shaded rectangular regions).

Trends in BSB harvest were reflected in the large fluctuations in Rockbass (= Kelp Bass and Barred Sand Bass) CPFV harvest (Fig. 1.5c). The first fluctuation in Rockbass harvest consisted of a substantial increase in the 1960s followed by a decline in the 1970s, and the second was an increase into the 1980s and 1990s followed by a precipitous decline in the 2000s. During the second fluctuation in Rockbass harvest, BSB temporal trends followed an "M" pattern, like that of the SST trend, though lagged slightly (Fig. 1.5). For example, all trends increased from low levels prior to 1980 to the first peak in the "M" around 1985. This was followed by a dip and subsequent increase to the second peak in the "M" around the early 2000s. Following the "M" pattern, the trends diverged, with SST and adult densities increasing, while harvest remained low after 2015 (Fig. 1.5).

We found that adult densities lagged SST by three to four years, corresponding to the age at which BSB become mature (Fig. 1.5d), and we found that harvest lagged SST by four to ten years, corresponding to the ages at which BSB have recruited into the fishery (Fig. 1.5e). Though the adult densities represent data from an individual location in southern California, the biologically meaningful lagged relationships between adult densities and SST, and between harvest and SST, suggests the adult density data are representative of Bight-wide trends.

Relationship Between Juvenile Recruitment and SST

During the 1990s tagging period, the mean SST was above average (Fig. 1.6a), the ONI was mostly neutral except for the major El Niño event in 1997 (Fig. 1.6b), and recruitment was generally below average (Fig. 1.6c). Between 1974 and 2012, there were three peaks in recruitment (one spanning the years 1977-79, one in 1984, and one in 1998; however, from 2013 to 2021, BSB recruitment remained at elevated levels (Fig. 1.6c). Juvenile recruit density showed the highest correlation with SST at a lag of zero (Fig. 1.6d) and the highest correlation with the ONI at a lag of one (Fig. 1.6e). After accounting for adult densities and harvest, there was a strong relationship between recruitment and SST, and the model fit was improved after incorporating the ONI at a lag of one year, with 36.3% of the deviance explained (Table 1.2). The conditional plot showed a stronger effect of SST on juvenile recruitment with increasing values of ONI, representative of La Niña, Neutral, and El Niño conditions (Fig. 1.6f).

Historical Accounts

Sources for the BSB historical accounts included scientific journal publications (n = 16), a fishing guide, a publication on the status of California's marine resources, and several government documents (n = 4) available online and by request, including CDFW administrative reports (n =3), and a CDFW monthly report (Fig. 1.7). When considered collectively, the historical accounts corresponded with the results of our quantitative analysis, in which periods of reportedly higher and lower BSB population abundance were generally associated with decadal-scale fluctuations in ocean temperature. Most notable were four periods, 1) the mid-19th century, in which the southern California fish fauna was described as tropical and the distribution of BSB was documented as far north as Monterey in central California (Fig. 1.7a; Girard 1858, Hubbs 1948), 2) the subsequent cool and warm periods (Fig. 1.7b-e), in which BSB appear to have been abundant, but not nearly as abundant as KB (Fig. 1.6d; Clark 1933, Collyer 1947), 3) the second cool period (Fig. 1.7f-h), in which BSB was referred to by CDFW field biologists as "scarce", "a more southern species", and comprising "a very small portion of the catch" (Young 1963, Young 1969, Feder et al. 1974), and 4) a short window in the 1960s (during the second cool period) when observations made by CDFW field biologists conducting diver and fishing surveys

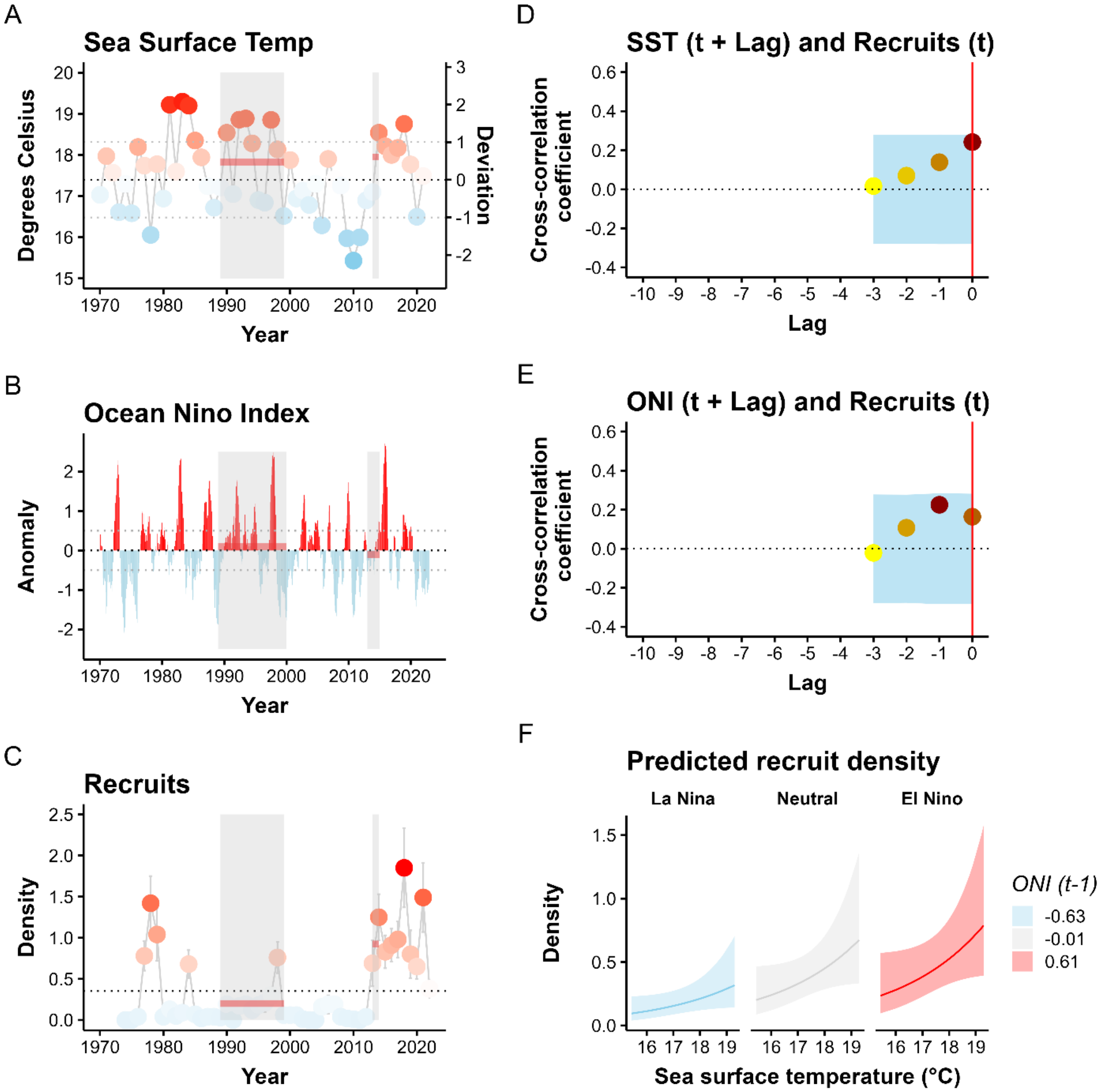

Figure 1.6. Temporal trends in a) summer sea surface temperatures on the central coast of southern California, USA, 1970-2021, b) mean annual Ocean Niño Index anomalies c) mean annual densities of Barred Sand Bass recruits as measured on diver surveys on the central coast of southern California, 1974-2022, c) cross-correlations of lagged SST and recruits, d) cross-correlations of lagged ONI and recruits, and d) conditional plot of SST and juvenile recruits across different values of the ONI. Horizontal red lines depict means during each tagging period (shaded gray regions).

Table 1.2. Results of the generalized additive model of juvenile (young-of-the-year) Barred Sand Bass densities as a function of smoothed temperature (SST and ONI), adult densities, and harvest in southern California, USA.

Model	Formula	Passed checks?	Deviance Explained	AIC	Tweedie	Intercept Coeff.	*p*-values				
							Intercept	sst	ad	lands	oni
3	~ s(sst) + s(ad) + s(lands) + s(oni.1)	y	36.3%	-13.4	1.55	-2.1813	**2.24E-13**	**0.0023**	0.9105	0.1474	**0.0141**
2	~ s(sst) + s(ad) + s(lands) + s(oni)	y	27.5%	-11.4	1.58	-2.1183	**6.24E-13**	**0.0018**	0.8841	0.3493	0.0501
1	~ s(sst) + s(ad) + s(lands)	y	23.5%	-9.32	1.58	-2.0699	**1.26E-12**	**0.0019**	0.6116	0.2041	--

sst = sea surface temperature, modeled with a lag of zero, from the Shore Stations Program (Carter et al. 2022)
ad = adult densities, these and juvenile densities from Vantuna Research Group, Occidental College
lands = recreational landings, from California Department of Fish and Wildlife Commercial Passenger Fishing Vessel logbook records (harvested fish)
oni = Oceanic Niño Index, zero lag, from https://www.ncei.noaa.gov/access/monitoring/enso/sst
oni.1 = Oceanic Niño Index, one year lag
Tweedie = estimated shape parameter for Tweedie distribution
Coeff. = model coefficient

indicated a dramatic increase in the numbers of BSB in southern California (Fig. 1.7g). This observed increase in BSB availability was also reflected in the substantial increase in Rockbass harvest at the time (Fig. 1.7) and came on the heels of one of the most significant El Niño events documented in southern California (the 1957/58 El Niño; Fig. 1.7g). By the end of the second cool regime in the late 1970s, Rockbass harvest had declined and returned to being dominated by Kelp Bass (Fig. 1.6c, 1.7i; Wine 1978, 1979a,b). BSB CPFV CPUE was 5-10x lower than it would be a decade later, in the late 1980s (Fig. 1.7i; Love et al. 1996a). The tightening and relaxation of Rockbass regulations appear to have corresponded with decadal-scale, temperature-driven availability (i.e., relaxation of the bag limit occurred in the early 1970s following the increase in Rockbass taken in the fishery in the earl-to-mid 1960s (Fig. 1.6c, 1.7), while tightening of regulations occurred in the early 1950s and mid-1970s following the declines in Rockbass taken in the fishery. For a more detailed narrative of BSB historical accounts, see Supplement S6 (Appendix).

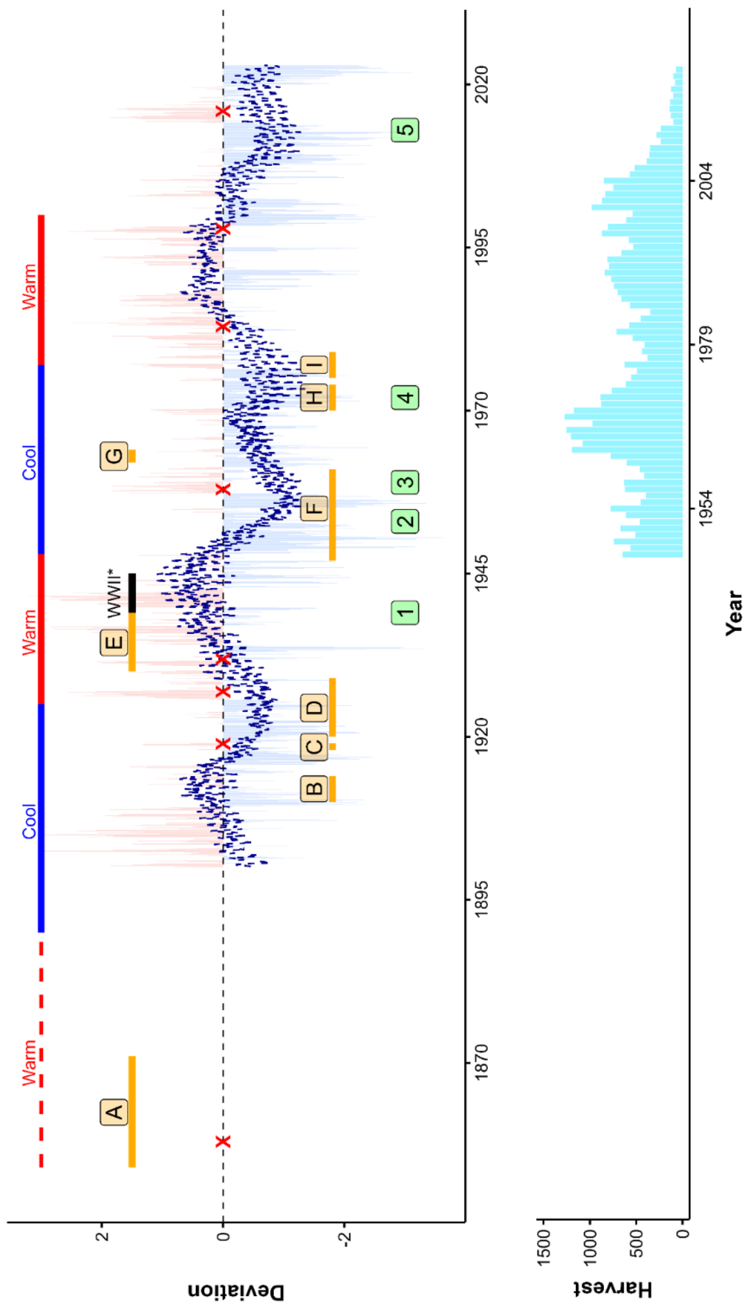

Figure 1.7. Graphical timeline (left) and trends in Rockbass CPFV harvest (thousands of fish, right) for contextualizing historical accounts of Barred Sand Bass harvest, distribution, and availability in California, USA, from the mid-nineteenth century to the 2020s (lookup table next page). Rockbass catch includes Kelp Bass. The trend line represents a 12-month running average of the Pacific Decadal Oscillation, a measure of SST anomalies); periods designated as cool and warm are based on Minobe (1997) and Mantua et al. (1997). **X** = El Niño resulting in either seasonal warm water intrusions of subtropical and tropical fauna or decadal-scale northern range expansions of temperate/subtropical fauna in California. *No Commercial Passenger Fishing Vessel fishing permitted for five years during World War II.

Key	Period	Species account	Source
A	1854-1869	The taxonomic species description for BSB is based on two specimens collected off Monterey, CA in 1854. A subsequent publication describes the Monterey fish fauna during this period as “made up to a considerable degree of fishes now characteristic of the relatively warm waters south of Point Conception”, and “five or six kinds that do not now occur so far north or are so rare as not to be collectable by any such dribbling survey as that of the 1850's. These southern types are the sand bass, *Paralabrax nebulifer*…”. The southern California fish fauna during this period is described as tropical.	Girard 1888, Hubbs 1948
B	early 1910s	An iconic fishing guide of the time makes no mention of BSB, but highlights a cohabiting congener, Kelp Bass, as a "nuisance".	Holder 1912
C	late 1910s	BSB is noted as being "rather abundant on the coast of southern California“.	Starks 1919
D	1920s	BSB is reported to be a minor component of “Rockbass” commercial harvest, comprising an estimated 25% of the total landings of Kelp Bass and BSB. Commercial harvest of Rockbass was reported to be the result of incidental catches in other fisheries targeting rockfish and California Sheephead. By weight, the annual commercial Rockbass harvest was roughly one-third of that reported in the recreational Rockbass CPFV fishery.	Clark 1933; Collyer 1949
E	1930s	The first accounting of the CPFV logbook records reports that Rockbass harvest is comprised of “mostly” Kelp Bass, with “some” BSB.	Croker 1940
	1934	In documenting fished species of Mission Bay in San Diego, CA, the authors state, "This fish is very common everywhere at all seasons and is taken by anglers in the channels of all parts of the bay. Specimens up to five pounds are to be caught. A desirable species."	Fry & Croker 1934
1,2,3	1939- 1959	1) Bag limit implemented to include all three *Paralabrax* species : 15 fish in aggregate (1939), 2) bag limit changes twice; 15 fish in aggregate (1949), 15 fish in aggregate, with not more than 10 of any one species (1951), and 3) the sale or purchase is prohibited (1953) and a minimum size limit is implemented and progressively increased from 10.5 inches in 1957 to 12 inches in 1959.	Jarvis et al. 2014a
F	1947-1958	With respect to CPFV harvest, BSB is noted to comprise "a very small portion of the catch“. BSB is referred to as “scarce” from the late-1940s to the early 1960s, but especially during the 1950s when ocean temperatures were cooler; “There is good reason to believe an extended cold-water phase in southern California would drive sand bass south, out of range of all but a few partyboats“ Partyboats = CPFVs	Young 1963; Young 1969
	1958-1961	Scientific divers make underwater observations of BSB associated with artificial reef habitats in the northern part of the Southern California Bight (SCB) but not in numbers comparable to Kelp Bass.	Carlisle et al. 1963
G	1962	In discussing the rationale for implementing a BSB tagging study "…where did the tremendous population of adult sand bass that's in our waters this summer come from, will it move away when winter comes, will it be fished out?…“	CDFG 1962
	1960-1965	Underwater observations of BSB spawning aggregations are documented by CDFW biologists. BSB are commonly encountered on diver surveys of artificial reefs, especially in Santa Monica Bay; 12–14-inch fish most common.	Turner et al. 1969
	1960s	BSB is referred to as "A more southern species frequenting our coast in and subsequent to periods of warmer waters. Because of this it is caught less commonly than kelp bass, but the two often are caught together close to bottom". "Recently, 1960 to 1970, barred sand bass have formed an important part of the sport catch."	Feder et al. 1974
	1964	BSB comprises 50% of the combined Kelp Bass and BSB catch made by private boaters.	Pinkas et al. 1965
H	early 1970s	On the population status and management of BSB, the author foreshadows a future absence of BSB in southern California, “One cloud on the horizon—barred sand bass have not always been present in large numbers in southern California.” Estimates the stock size of Kelp Bass and BSB combined at 4.2 million legal-size fish. “Sub-legal-size fish are estimated to be 5 to 10 times as numerous.”	Frey (editor) 1971
4	1972-1975	Bag limit is increased and then decreased again: 20 fish in aggregate, with not more than 10 of any one species (1972), 10 fish in aggregate, with not more than 10 of any one species (1975).	Jarvis et al. 2014a
I	mid-to-late 1970s	The relative proportion of BSB in the total Kelp Bass & BSB private boat catch falls from 58% to 39% between 1975-77 and 1978-79; San Diego County (southern SCB) dominates the BSB catch in 1975-77. BSB CPUE in the late 1970s is 5-10x lower than in the late 1980s. Low CPUE in the 1970s is attributed to low abundance.	Wine 1978, 1979a,b; Love et al. 1996a
5	2013	The bag limit is reduced to 5 fish, with not more than 5 of any one species; the MSL is increased from 12 inches to 14 inches.	Jarvis et al. 2014a

Figure 1.7 (continued). Look up table for the graphical timeline (previous page), representing historical accounts of Barred Sand Bass harvest, distribution, and availability (letters), and fishing regulation changes (numbers) in California, USA, from the mid-nineteenth century to the 2020s.

1.4 Discussion

We have taken advantage of a multidecadal tag and recapture dataset to generate the first estimates of historical and contemporary BSB demographic rates and population size spanning different oceanographic regimes and harvest histories. Our estimates, combined with a variety of long-term data streams and historical accounts, indicate the BSB fishery in southern California, USA, between 1962 and 2014 can be characterized by two windows of fishing opportunity; these windows appear largely driven by decadal-scale, sporadic, warm-water recruitment events followed by efficient harvest on spawning aggregations. The last window resulted in a prolonged period of fishery collapse, in which we estimate the population declined by nearly an order of magnitude. Despite signs of incipient population recovery, we see no evidence if this in the fishery. We discuss our results with respect to environmentally driven recruitment variability, aggregation-based fishery dynamics, and the potential for fishery recovery.

Sporadic, warm-water recruitment pulses

At least since 1974, the BSB population in southern California has had extended periods of minimal juvenile (young-of-the-year) recruitment that showed a strong relationship with SST, especially following El Niño events (Fig. 1.5c,d, Table 1.2). Moreover, this influence of SST on the early life history stage was detected in future adult densities and harvest, implicating temperature as a driver of future fishery recruitment. Our results are consistent with other studies; Miller & Erisman (2014) found that young-of-the-year BSB abundance from 1979 to 2010 was highly episodic, having a moderate positive relationship with SST and strong positive relationship with future CPUE in the fishery. In addition, Jarvis et al. (2014) found that

Paralabrax spp. larval abundance and SST between 1996 and 2012 were positively correlated with future fishery recruitment strength.

Correspondence between trends in larvae or juvenile abundance and future harvest/CPUE is characteristic of a population driven by recruitment limitation, in which varying recruitment levels are good predictors of subsequent population size (Armsworth 2002). This is noteworthy because periodic fluctuations in harvest/CPUE are generally presumed to be atypical of aggregation-based fisheries. Aggregate spawners are vulnerable to hyperstability, in which stable catch rates mask population declines when aggregation densities are maintained (Sadovy & Domeier 2005, Erisman et al. 2011). For example, among overexploited fisheries, "plateau-shaped" harvest trajectories are common in hyperstable fisheries ("i.e., a sudden fall after a relatively long and stable persistence of high-level catches"); however, BSB showed a more "erratic" harvest trajectory ("i.e., a fall after several ups and downs", Mullon et al. 2005). Although we focus here on harvest rather than CPUE, harvest trends in this fishery correspond with CPUE trends through time (Jarvis et al. 2014, CDFW 2020). Effort shifts associated with the availability of more desirable species can contribute to interannual fluctuations in recreational harvest (Dotson and Charter 2003, Blincow and Semmens 2022); nevertheless, we identified a relationship between SST and harvest at biologically meaningful lags.

Given the sporadic nature of BSB juvenile recruitment and positive correlation with ONI, it is possible that the southern California population is dependent on El Niño-driven larval transport (Lilly et al. 2022). Anomalously warm events, like El Niño, could facilitate poleward advection of BSB larvae into southern California (McClatchie et al. 2018, Cimino et al. 2021, Lilly et al. 2022). Indeed, genetic connectivity exists between BSB populations in the two regions (Paterson et al. 2015) and recruitment dependence on Baja California fish populations has been suggested for other fishes in southern California (Smith & Moser 1988, Allen & Franklin 1992, Ben-Aderet et al. 2020). In contrast to BSB, the Kelp Bass population in southern California, which has more reliably persisted, was found to be locally sourced (Selkoe et al. 2007). The southern California BSB population is at the northern extent of its core population range, and recruitment is typically more variable for marine populations at their geographic margins (Myers 1991, Neill et al. 1994, Levin et al. 1997).

Relative to the BSB spawning season in southern California, the spawning season off Baja California is more protracted (May through Feb), with a Summer and Fall peak in larval abundance and higher abundance during El Niño events (Avendaño-Ibarra et al. 2009). Thus, following an El Niño year, a portion of young-of-the-year recruits in southern California may represent northward advected Baja California larvae from the previous summer or fall, which would correspond to the one-year lag we observed between the ONI and juvenile densities.

Shifting Baselines

Historical ecology is a valuable tool that can increase our understanding of the factors influencing fluctuations in populations and consequently improve our ability to evaluate a population's potential for decline and recovery (Scarborough et al. 2022). In this study, when considered collectively, the historical accounts of BSB that we gathered also served to validate the results of our quantitative analysis; that is, periods of reportedly higher and lower BSB population abundance were associated with decadal-scale fluctuations in ocean temperature.

One notable finding was that observations of increased BSB availability in the 1960s were reflected in the substantial increase in Rockbass CPFV harvest during that period (Fig. 1.5c). Prior to this study, the increase in Rockbass harvest in the 1960s could not be attributed to

Kelp Bass or BSB based on CPFV logbook records alone due to inconsistencies in species-specific reporting prior to 1975. However, additional catch survey data gathered from that period (Pinkas et al.1968) indicate the contribution of BSB to Rockbass harvest doubled relative to previous estimates (Fig. 1.5c, 1.7g). The dramatic increase in BSB availability occurred five years after the strong 1957-58 El Niño, a period corresponding to the age when BSB recruit into the fishery (at the time, age five to six) and one that further supports our findings relating sporadic juvenile recruitment pulses to warm water events.

Given the high fishing mortality in the 1960s and apparent recruitment limitation in the southern California BSB population, it is not surprising that harvest quickly returned to low levels by the mid-1970s. The decrease in availability was correctly foreshadowed by resource managers (Frey 1971) and yet, they did not express concern, as they had come to expect lower BSB abundance during cooler conditions. Thus, a “healthy” BSB population is likely to look different to different people, depending on the lifetime of perspective (Bellquist et al. 2017). This is an important point because we found that the exceptional increased availability of BSB during the warm regime of the 1980s and 1990s was not the norm for much of the last century, and thus, expectations for the level of recovery and more importantly, future allowable take, will likely need to be tempered. Usually, the opposite is true, where shifting baselines or institutional amnesia result in diminished expectations of what the size of a healthy aggregate spawner population should be, inadvertently resulting in less conservative, less effective, management measures (Fulton 2023).

Impacts to Aggregation Dynamics?

Juvenile recruitment has remained well above average since 2013, despite the low population size estimated for the 2010s. Between 2012 and 2020, southern California experienced several marine heatwaves (MHW, 2014-15, 2019, 2020, 2021), including a strong El Niño (2015-16). The effects of this dramatic alteration of the Southern California Bight ecosystem were profound (Leising 2015, Cavole et al. 2016, Walker et al. 2020a) and, in some cases, atypical of expectation based on previously established environment-species relationships (McClatchie et al. 2018, Thompson et al. 2019, 2022). This anomalous warm water is likely to have had a positive effect on any locally sourced BSB larvae and may have also resulted in externally sourced BSB larvae from Baja California. Although MHWs lack the strong northward horizontal transport characteristic of El Niño (Amaya et al. 2020), they can result in an "abrupt diminishing of upwelling" off Baja California (Jiménez-Quiroz et al. 2019), thereby eliminating any barrier to northward larval transport that is typically present during the summer months. For example, an adult Goldspotted Sand Bass (*P. auroguttatus*, a species rare north of Baja California Sur), was first documented in southern California, off Santa Barbara, in 2018 (Love et al. 2019).

High juvenile recruitment levels hint at population recovery, but they have not yet been reflected in the fishery. Under the current MSL, BSB are expected to recruit to the fishery at approximately eight years of age; thus, the earliest indication of fishery recovery should have been evident in 2020. Following sustained recent juvenile recruitment, adult densities increased to more than double the levels prior to 2015; however, BSB harvest has remained exceptionally low. One explanation for the lack of fishery recruitment despite high juvenile recruitment and higher adult densities, could be simply that it is still too early to detect in the harvest data, as boat access to ocean fishing was halted during the pandemic. Another reason could be a change in the behavioral drivers associated with BSB aggregation dynamics. In healthy transient aggregate spawner populations, the permanence of spawning aggregation locations is maintained by social transmission over many generations (e.g., older adults know where to go from experience and younger adults learn by following older adults, Warner 1988). When harvest removes enough of the older adults or densities are low enough, social transmission is interrupted. This may result in many smaller localized aggregations or the establishment of new aggregation sites at locations unknown to anglers (Warner 1988, Waterhouse et al. 2020). An acoustic telemetry study off San Diego, CA between 2012 and 2016 showed evidence of adult BSB spawning season migrations to a previously undocumented aggregation site, however, the larger traditional spawning grounds never manifested aggregations (Bellquist 2015).

Trends in Demographic Rates

Between the 1960s and 1990s, technological advances in locating aggregations afforded greater precision in targeting spawning sites (Allen & Hovey 2001), and so we expected a higher exploitation rate in the 1990s. However, it was generally the case that annual exploitation was highest in the 1960s and lower in the 1990s. This could be in part due to a higher number of licensed anglers in the 1960s than in the 1990s (~3x more, Bellquist 2015). In addition, the harvest period means were similar and our CMR model results indicate the BSB population size in the 1990s was bigger relative to the 1960s. Thus, even though targeting spawning aggregations may have become easier by the 1990s, the sizable increase in BSB population size would have resulted in a smaller fraction of BSB being removed due to fishing, despite increased harvest efficiency.

Our population estimates suggest that the prolonged fishery collapse following the window of BSB fishing opportunity in the 1980s and 1990s, represented an almost 100-fold decline in the population. The first window of fishing opportunity in the 1960s did not result in a similar delayed fishery recovery. One difference between the two periods is that temperatures following the second collapse remained cooler longer and there was no major El Niño event for nearly a decade. Additionally, if the exploitation rate in the in the late 1990s/early 2000s was higher than that of the 1960s, that may have also contributed to delayed recovery.

When there is not 100% cooperation in reporting taggd fish, exploitation rates will be biased low (Sackett & Catalano 2017). We do not know what the tag reporting rates were across the three tagging periods; however, the 1990s conditional estimates of exploitation under the 50 and 75% reporting rates are most similar to the annual 1990s exploitation rates reported by Jarvis et al. (2014) using catch curves (~11%). We assume that tag reporting in the 1960s was at least as high as 50-75%, due to enhanced outreach and cooperation with the fishing community at that time (Young 1963). Tag reporting incentives were similar across all three tagging periods.

Based on the size structure of the tagged populations in each of the three tagging decades, we are certain our model estimates of survival are biased low, which could be due to 1) decreased tag reporting over time (due to e.g., faded ink, excessive biogenic growth on tags; Waterhouse & Hoenig 2012) or 2) invalid assumptions regarding fidelity of tagged BSB to the southern California tagging area (e.g., we assumed no permanent emigration; Barker 1997). The latter is much less likely since BSB home ranges are small and the average migration distance to spawning grounds in southern California is ~ 15 km (Jarvis et al. 2010, Mason & Lowe 2010). Despite this bias, the trend in our survival estimates (highest in the 1960s, lowest in the 1990s) suggests that conditions in the 1990s were less favorable to adult BSB survival even though exploitation was lower. The slight increase in survival of legal-size BSB in the 2010s coincided with the implementation of tighter fishing regulations in 2013, while survival of sublegal-size BSB in the 2010s was lowest of the three tagging periods. This lower survival rate may have also contributed to a lack of fishery recovery, though the mechanism is unclear.

Our model estimates of BSB growth in the 1960s are the first published historical estimates prior to the 1990s (Love et al. 1996b). We detected directional changes in the mean-size-at age through time, in which the magnitude of change was greater between the 1960s and 1990s than between the 1990s and 2010s; BSB grew slightly faster by age 3 and grew slower by age 16. Fish growth rates can show high phenotypic plasticity resulting from the environment (e.g., temperature, food availability), density-dependent processes, and fishing. However, when larger, older fish are predominantly harvested, changes to growth and maturity can result from fishing-induced evolution (Enberg et al. 2012). Just prior to the fishery collapse in the mid-2000s, BSB catches switched from being dominated by young adult fishery recruits to older, larger fish (Jarvis et al. 2014). BSB size and age at maturity have not been re-evaluated since the 1990s (Love et al. 1996b).

Recovery and Management Preparedness

Although naturally driven periods of extended warm water conditions in southern California have historically occurred, periods of anomalously warm conditions in southern California are predicted to increase with climate change (Oliver 2019), and secular ocean warming may more permanently shift the center of the BSB geographic distribution northward into southern California (Pinsky et al. 2020). The record of an adult Goldspotted Sand Bass in southern California, four years after the 2014 MHW, is evidence of this potential (Love et al.

2019). Nevertheless, current regulations may not be adequate to prevent quick collapse of a new emerging cohort and thus, management preparedness is prudent.

Environmental recruitment variability decreases resilience to fishing and increases recovery uncertainty (Kuparinen et al. 2014) and should thus be a concern when managing aggregate spawner fisheries. It is clear from the data that high CPUE in a recruitment-limited, aggregation-based fishery is not sustainable and may force the fishery to exist in perpetual boom-and-bust. Moreover, sporadic recruitment is likely to delay recovery (Stock et al. 2021), especially during a suboptimal temperature regime. Such a model of fishing opportunity is unwise for recreational fisheries that are known to have considerable social and economic benefits (Griffiths et al. 2017, Lovell et al. 2020) and are intended to be sustainable for future generations. The tighter fishing regulations in 2013 were intended to reduce fishing mortality of all three saltwater basses in southern California, but BSB does not appear to have benefited yet. Instead, recovery and insurance against a future collapse may be contingent on management measures that consider environmental recruitment variability and ensure BSB reproductive resilience (Lowerre-Barbieri et al. 2015, 2017). Time closures during spawning would go the farthest in ensuring BSB reproductive resilience and help to balance the protection of spawning aggregations with sustainability of the fishery (Erisman et al. 2020). Nassau Grouper (*Epinephelus striatus*), another aggregate spawning serranid that exhibits sporadic pulse recruitment (Stock et al. 2021, 2023), showed evidence of recovery 15 years following conservation measures, including seasonal closures (Waterhouse et al. 2020).

Given that seeding from Baja California may have importance to the southern California BSB population, we recommend monitoring Baja California fishery landings and assessments (DOF 2021), in addition to southern California juvenile and adult densities and environmental data (e.g., SST, ONI). Standing stock estimates from standardized hydroacoustic surveys at principal spawning aggregation locations (Allen et al. 2020), within-season mark recapture, and ROV surveys could also potentially provide valuable management insight. Finally, more research is necessary to better understand the role of the environment on BSB early life history.

Lessons Learned

Our quantitative and qualitative analysis spans 168 years and provides an example of a transient aggregate spawner population whose contemporary decadal availability appears largely a function of sporadic, warm water recruitment pulses followed by efficient harvest on spawning aggregations. The positive relationship between SST, lagged ONI, and sporadic juvenile recruitment provides context for why we observed differences in the duration of windows of fishing opportunity, as well as fishery recovery. For aggregate spawner populations with oceanographic-driven sporadic recruitment, we deduce that juvenile recruitment is likely to be a good indicator of future fishery recruitment. Although this understanding may aid in anticipating boom and bust periods, intense spawning aggregation fishing combined with recruitment limitation can nevertheless result in rapid and dramatic catch declines, even with long-standing harvest limits in place (e.g., minimum size limit, bag limit). In other words, recruitment limitation in transient aggregate spawner populations (especially those occurring at the extremes of their geographic range) makes them particularly vulnerable to sudden and prolonged fishery collapse and good candidates for spawning season restrictions. Our results demonstrate the importance of historical context and long-term monitoring in resolving the role of sporadic recruitment and aggregation-based fishing in driving the population dynamics of an iconic aggregate spawner.

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Literature Cited

Aguilar-Perera A (2006) Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast. Mar Ecol Prog Ser 327:289–296.

Allee W (1931) Animal Aggregations, a Study in General Sociology. University of Chicago Press, Chicago, USA.

Allee W (1938) The Social Life of Animals, First Edition. WW Norton Inc., New York, USA.

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.

Allen LG, Hovey TE (2001) Barred sand bass. In: *California's living marine resources: a status report.* Leet WS, Dewees CM, Klingbeil R, Larson EJ (eds) Department of Fish and Game, Sacramento, USA, p 224–225

Allen LG, Won C, Bolser DG, Erisman BE (2020) Feasibility of hydroacoustic surveys of spawning aggregations for monitoring Barred Sand Bass populations off southern California. Calif Fish Game 106:139–155.

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

Avendaño-Ibarra R, Hernández-Rivas ME, de Silva-Dávila R (2009) Reproductive Strategies of Sea Basses based on Larval Abundance in Magdalena Bay, Mexico, 1982–1986. North Am J Fish Manag 29:205–215.

Barker RJ (1997) Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics 53:666–677.

Bellquist LF, Semmens BX, Stohs S, Siddall A (2017) Impacts of recently implemented recreational fisheries regulations on the Commercial Passenger Fishing Vessel fishery for *Paralabrax* sp. In California. Mar Policy 86:134–143.

Bellquist LF (2015) A historical perspective of California recreational fisheries using a new database of 'trophy' fish records (1966-2013), combined with fisheries analyses of three species in the genus Paralabrax. PhD dissertation, University of California, San Diego, CA

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.

Blincow KM, Semmens BX (2022) The effect of sea surface temperature on the structure and connectivity of species landings interaction networks in a multispecies recreational fishery. 1119:1109–1119.

Bolden SK (2000) Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bajamas. Fish Bull 96:642–644.

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

CDFG [California Department of Fish and Game] (1962) Report for the month of August, 1962. Dept. of Fish and Game Records, Regional Reports, F3498:582-614.

Carlisle J, Turner C, Ebert E (1963) Artificial Habitat in the Marine Environment. Fish Bull 124.

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

Chollett I, Priest M, Fulton S, Heyman WD (2020) Should we protect extirpated fish spawning aggregation sites? Biol Conserv 241:108395.

Cimino MA, Jacox MG, Bograd SJ, Brodie S, Carroll G, Hazen EL, Lavaniegos BE, Morales MM, Satterthwaite E, Rykaczewski RR (2021) Anomalous poleward advection facilitates episodic range expansions of pelagic red crabs in the eastern North Pacific. Limnol Oceanogr 66:3176–3189.

Clark FN (1933) Rock bass (*Paralabrax*) in the California commercial fishery. Calif Fish Game 19:25–35.

Collyer R (1949) The Commercial Fish Catch of California for the Year 1947: With an Historical Review 1916-1947. Fish Bull:268.

Croker RS (1940) Three Years of Fisheries Statistics on Marine Sport Fishing in California. Trans Am Fish Soc 69:111–118.

Denson MR, Jenkins WE, Woodward AG, Smith TIJ (2002) Tag-reporting levels for red drum (*Sciaenops ocellatus*) caught by anglers in South Carolina and Georgia estuaries. Fish Bull 100:35–41.

DOF Official Gazette of the Federation (2021) Fisheries Management Plan of Verdillo *(Paralabrax nebulifer* Girard 1854) in la Baja California Peninsula, published on February 12, 2021. Ministry of Agriculture and Rural Development, Mexico City, Mexico.

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. Bull Mar Sci 60:698–726.

Dotson RC, Charter RL (2003) Trends in the southern California sport fishery. CalCOFI Reports 44:94–106.

Enberg K, Jørgensen C, Dunlop ES, Varpe Ø, Boukal DS, Baulier L, Eliassen S, Heino M (2012) Fishing-induced evolution of growth concepts mechanisms and the empirical evidence. Mar Ecol 33:1–25.

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.

Erisman BE, Grüss A, Mascareñas-Osorio I, Lícon-González H, Johnson AF, López-Sagástegui C (2020) Balancing conservation and utilization in spawning aggregation fisheries : a trade-off analysis of an overexploited marine fish. ICES J Mar Sci 77:148–161.

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

Francis RICC (1988) Are growth parameters estimated from tagging and age-length data comparable? Can J Fish Aquat Sci 45:936–942.

Frey HW (ed) (1971) Kelp and sand bass In: *California's Living Marine Resources and Their Utilization*. California Department of Fish and Game, Sacramento, USA, p 93-94

Fulton S (2023) Institutional amnesia pushes fish spawning aggregations towards extirpation. People Nat 5:489–495.

Fry D, Croker RS (1934) A preliminary survey of Mission Bay State Park. Calif Fish Game 20:1–13.

Girard C (1858) Fishes. In: *General report upon the zoology of the several Pacific railroad routes. Explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean.* 10(4):1-400.

Griffiths SP, Bryant J, Raymond HF, Newcombe PA (2017) Quantifying subjective human dimensions of recreational fishing: does good health come to those who bait? Fish Fish 18:171–184.

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

Hilborn R, Hively DJ, Jensen OP, Branch TA (2014) The dynamics of fish populations at low abundance and prospects for rebuilding and recovery. 71:2141–2151.

Holder CF (1912) The fishes of the Pacific coast, a handbook for sportsmen and tourists. Dodge Publishing Company, New York, USA.

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.

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

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.

Kay M (2022a) ggdist: Visualizations of Distributions and Uncertainty. R package version 3.2.0

Kay M (2022b) Tidybayes: Tidy Data and Geoms for Bayesian Models. R package version 3.0.2

Kellner K (2021) JagsUI: a wrapper around “rjags” to streamline “JAGS” analyses. R package version 1.4.2

Kéry M, Schaub M (2012) Chapter 9 – Estimation of Survival and Movement from Capture–Recapture Data Using Multistate Models. In: *Bayesian Population Analysis using WinBUGS*. Kéry M, Schaub M (eds) Academic Press, p 263–313

Kuparinen A, Keith DM, Hutchings JA (2014) Increased environmentally driven recruitment variability decreases resilience to fishing and increases uncertainty of recovery. ICES J Mar Sci 71:1507–1514.

Lea RN, Rosenblatt RH (2000) Observations on fishes associated with the 1997-98 El Niño off California. CalCOFI Reports 41:117–129.

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.

Liermann M, Hilborn R (2001) Depensation: evidence, models and implications. Fish Fish 2:33–58.

Lilly LE, Cornuelle BD, Ohman MD (2022) Using a Lagrangian particle tracking model to evaluate impacts of El Niño-related advection on euphausiids in the southern California Current System. Deep Res Part I Oceanogr Res Pap 187.

Logan RK, Lowe CG (2018) Residency and inter-reef connectivity of three gamefishes between natural reefs and a large mitigation artificial reef. Mar Ecol Prog Ser 593:111–126.

Di Lorenzo E, Schneider N, Cobb KM, Franks PJS, Chhak K, Miller AJ, McWilliams JC, Bograd SJ, Arango H, Curchitser E, Powell TM, Rivière P (2008) North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophys Res Lett 35:2–7.

Love MS, Brooks A, Ally JRR (1996a) An analysis of commercial passenger fishing vessel fisheries for kelp bass and barred sand bass in the Southern California Bight. Calif Fish Game 82:105-121.

Love MS, Brooks A, Busatto D, Stephens J, Gregory PA (1996b) 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.

Love MS, McCrea M, Johnston D, Butterfield A (2019) First Authenticated Record of the Goldspotted Sand Bass, *Paralabrax auroguttatus* from California Waters. Bull South Calif Acad Sci.

Love MS, Passerelli JK (2020) Miller and Lea's Guide to the Coastal Marine Fishes of California, 2nd ed. University of California Agriculture and Natural Resources.

Lovell SJ, Hilger J, Rollins E, Olsen NA, Steinback S (2020) The Economic Contribution of Marine Angler Expenditures on Fishing Trips in the United States, 2017. NOAA Technical Memorandum NMFS-F/SPO-201.

Lowe CG, Topping DT, Cartamil DP, Papastamatiou YP (2003) Movement patterns, home range, and habitat utilization of adult kelp bass. Mar Ecol Prog Ser 256:205–216.

Lowerre-Barbieri S, Crabtree L, Switzer T, Burnsed SW, Guenther C (2015) Assessing reproductive resilience: An example with South Atlantic red snapper *Lutjanus campechanus*. Mar Ecol Prog Ser 526:125–141.

Lowerre-Barbieri S, DeCelles G, Pepin P, Catalán IA, Muhling B, Erisman BE, Cadrin SX, Ospina-Alvarez A, Stachura MM, Tringali MD, Burnsed SW, Paris CB (2017) Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish Fish 18:285–312.

Lyubchich V, Gel Y, Vishwakarma S (2023) Package Funtimes: Functions for Time Series Analysis version 9.1

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. Bull Am Meteorol Soc 78:1069–1079.

Mason TJ, Lowe CG (2010) Home range, habitat use, and site fidelity of barred sand bass within a southern California marine protected area. Fish Res 106:93–101.

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

McClatchie S, Gao J, Drenkard EJ, Thompson AR, Watson W, Ciannelli L, Bograd SJ, Thorson JT (2018) Interannual and Secular Variability of Larvae of Mesopelagic and Forage Fishes in the Southern California Current System. J Geophys Res Ocean 123:6277–6295.

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

Minobe S (1997) A 50–70 year climatic oscillation over the North Pacific and North America. Geophys Res Lett 24:683–686.

MacCall AD (1996) Patterns of low-frequency variability in fish populations of the California Current. CalCOFI Reports 37:100–110.

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

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.

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

NOAA (2023b) Pacific Decadal Oscillation. National Centers for Environmental Information https://www.ncei.noaa.gov/access/monitoring/pdo/ (accessed 9 Jan 2023)

Ogle DH (2016) Introductory Fisheries Analyses with R. CRC Press.

Ogle DH, Doll J, Wheeler P (2022) Package ' FSA ' version 0.9.3

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

Overland J, Rodionov S, Minobe S, Bond N (2008) North Pacific regime shifts: Definitions, issues and recent transitions. Prog Oceanogr 77:92–102.

Paterson CN, Chabot CL, Robertson JM, Erisman B, Cota-Nieto JJ, Allen LG (2015) The genetic diversity and population structure of barred sand bass, *Paralabrax nebulifer*: A historically important fisheries species off southern and Baja California. CalCOFI Reports 56:1–13.

Perälä T, Hutchings JA, Kuparinen A (2022) Allee effects and the Allee-effect zone in northwest Atlantic cod. Biol Lett 18:3–8.

Pine WE, Pollock KH, Hightower JE, Kwak TJ, Rice JA (2003) A Review of Tagging Methods for Estimating Fish Population Size and Components of Mortality. Fish Res 28:10–23.

Pinkas MS, Oliphant CW, Haugen L (1968) Southern California marine sport-fishing survey: private boats, 1964; shoreline, 1965-66. Calif Dep Fish Game, Fish Bull 143

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.

Plummer M (2003) JAGS: A program for analysis of Bayesian models using Gibbs sampling. Proc 3rd Int Work Distrib Stat Comput Vienna, Austria.

Plummer M, Stukalov A, Denwood M (2022) Package ‘ rjags ’ version 4-13.

Pondella DJ, Allen LG (2008) The decline and recovery of four predatory fishes from the Southern California Bight. Mar Biol 154:307–313.

R-Core-Team (2020) R: A language and environment for statistical computing.

Radovich J (1961) Relationships of Some Marine Organisms of the Northeast Pacific to Water Temperatures Particularly During 1957 Through 1959. Calif Dep Fish Game, Fish Bull 112

Riecke T V., Gibson D, Leach AG, Lindberg MS, Schaub M, Sedinger JS (2021) Bayesian mark–recapture–resight–recovery models: increasing user flexibility in the BUGS language. Ecosphere 12:1–10.

Roedel PM (1953) Common Ocean Fishes of the California Coast. Calif Dep Fish Game, Fish Bull:91

Sackett DK, Catalano M (2017) Spatial heterogeneity, variable rewards, tag loss, and tagging mortality affect the performance of mark–recapture designs to estimate exploitation: An example using red snapper in the northern Gulf of Mexico. North Am J Fish Manag 37:558–573.

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

Sadovy Y, Eklund a. M (1999) Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichenstein, 1822). Fao Fish Synopsis:68.

Sadovy de Mitcheson Y (2016) Mainstreaming Fish Spawning Aggregations into Fishery Management Calls for a Precautionary Approach. Bioscience 66:295–306.

Scarborough C, Welch S, Wilson J, Gleason MG, Saccomanno VR, Halpern BS (2022) The historical ecology of coastal California. Ocean Coast Manag 230:1–16.

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.

Semmens B, Bush P, Heppell S, Johnson B, McCoy C, Pattengill-Semmens C, Waylen L (2008) Charting a Course for Nassau Grouper Recovery in the Caribbean: What We've Learned and What We Still Need to Know. In: *Proceedings of the 60th Gulf and Caribbean Fisheries Institute, November 5 – 9, 2007, Punta Cana, Dominican Republic.* Gulf and Caribbean Fisheries Institute, Marathon, FL, USA, p 607–609.

Smith PE, Moser HG (1988) CalCOFI time series: an overview of fishes. CalCOFI Rep 29:66–78.

Stephens JS, Jr., Jordan GA, Morris PA, Singer MM, McGowen GE (1986) Can we relate larval fish abundance to recruitment or population stability? A preliminary analysis of recruitment to a temperate rocky reef. CalCOFI Rep 27:65–83.

Stephens JS, Morris PA, Pondella DJ, Koonce TA, Jordan GA (1994) Overview of the Dynamics of an Urban Artificial. Bull Mar Sci 55:1224–1239.

Stephens PA, Sutherland WJ, Freckleton RP (1999) What Is the Allee Effect? Oikos 87:185–190.

Starks EC (1919) The basses and bass-like fishes of California. Families Serranidae, Haemulidae, Kyphosidae. Calif Fish Game 5:56–68.

Stock BC, Heppell SA, Waterhouse L, Dove IC, Pattengill-Semmens C V., McCoy CM, Bush PG, Ebanks-Petrie G, Semmens BX (2021) Pulse recruitment and recovery of Cayman Islands Nassau Grouper (*Epinephelus striatus*) spawning aggregations revealed by in situ length-frequency data. ICES J Mar Sci 78:277–292.

Su Y-S, Yajima M (2021) Package 'R2jags' version 0.5-7

Teesdale GN, Wolfe BW, Lowe CG (2015) Patterns of home ranging, site fidelity, and seasonal spawning migration of barred sand bass caught within the Palos Verdes Shelf Superfund Site. Mar Ecol Prog Ser 539:255–269.

Turner CH, Ebert EE, Given RR (1969) Man-Made Reef Ecology. Calif Dep Fish Game, Fish Bull 146

Vert-Pre KA, Amoroso RO, Jensen OP, Hilborn R (2013) Frequency and intensity of productivity regime shifts in marine fish stocks. Proc Natl Acad Sci U S A 110:1779–1784.

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.

Warner RR (1990) Male versus female influences on mating-site determination in a coral reef fish. Anim Behav 39:540–548.

Warner RR (1988) Traditionality of mating-site preferences in a coral reef fish. Nature 335:719–721.

Waterhouse L, Heppell SA, Pattengill-Semmens CV., McCoy C, Bush P, Johnson BC, Semmens BX (2020) Recovery of critically endangered Nassau grouper (Epinephelus striatus) in the Cayman Islands following targeted conservation actions. Proc Natl Acad Sci U S A 117:1587–1595.

Waterhouse L, Hoenig JM (2012) Tagging models for estimating survival rates when tag visibility changes over time: Partial-year tabulation of recaptures. North Am J Fish Manag 32:147–158.

Wine V (1978) Southern California Independent Sport Fishing Survey Annual Report No. 2. Mar Resour Adm Rep No 78-2:84.

Wine V (1979a) Southern California Independent Sport Fishing Survey Annual Report No. 3. Mar Resour Adm Rep No 79-3:105.

Wine V (1979b) Southern California Marine Sport Fishing: Private-Boat Catch and Effort, 1975-1976. Mar Resour Adm Rep No 79-11:64.

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

Yackulic CB, Dodrill M, Dzul M, Sanderlin JS, Reid JA (2020) A need for speed in Bayesian population models: a practical guide to marginalizing and recovering discrete latent states. Ecol Appl 30:1–19.

Young P (1969) The California Partyboat Fishery 1947–1967. Calif Dep Fish Game, Fish Bull 45

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

CHAPTER 1 APPENDIX

Supplemental Material

S1. *Data Formatting and Processing*

Recaptures

We assumed a reencountered fish was recaptured by a biologist if the recapture occurred on the same date and at the same location as a survey occasion *and* the recapture length was not missing. We estimated missing dates based on time at liberty (in years) calculated from the difference in age between tag and recapture events using published von Bertalanffy age and growth parameters from the 1990s (Love et al. 1996a). If a tagging date was missing and there was also a missing recapture length, the tagging date was deduced based on sampling dates at the tag location and the sequence of tag identification numbers at that location.

We identified outliers in the reported lengths of recaptured Barred Sand Bass (BSB) by first calculating growth increments of recaptured fish and standardizing them by time at liberty in years (mm yr^{-1}). We then examined the distributions of growth increments over fish lengths in 50 mm TL bins from 250 – 600 mm. We flagged negative growth and increments greater than 150 cm in a year as outliers (n = 84) and replaced the corresponding reported recapture lengths with NA.

Assignment of Recovery Occasions

In the 1960s and 1990s data, if a fish was tagged the year prior and caught and kept the following year, but before the next survey occasion (e.g., Jan-May), then the fish did not survive the interval from *t* to *t*+1, and we recorded the recovery observation as occurring in that same year

(t+1). However, if a fish was tagged the year prior and caught and kept the following year during or after the following survey occasion (i.e., Jun-Dec), then the fish survived the interval from t to t+1 and we recorded the recovery observation as occurring in the subsequent year, t+2. Thus, we pushed recovery occasions out by one occasion unless the fish was recovered before June. In the 2010s data, we pushed all recovery occasions out by one occasion since the non-survey interval was sufficiently short (less than one month).

S2. *Tag Retention Model*

We used a Bayesian hidden state framework in JAGS (Su & Yajima 2021, Plummer et al. 2022) and Kelp Bass double-tagging data (Bellquist 2015) to model BSB tag retention as a function of time at liberty:

$$Q_i = \alpha * \exp\text{-}(\beta * t^{\gamma}), \text{ where,}$$

Q_i is the fish-specific probability of retaining a tag after recapture interval t,

α is the probability of retaining a tag immediately after release,

β is the continuous rate of long-term (chronic) tag loss (note that $\exp(-\beta)$ is the discrete rate of retention in a single time step),

t is the time at liberty, and

γ is a quadratic term.

The model provided an estimate of tag retention and uncertainty by incorporating the probability of a fish retaining both tags and just one tag, where,

$p_1 = (1 – Q_i) * Q_i + Q_i * (1 – Q_i)$ is the probability of retaining the first tag and losing the second tag or losing the first tag and retaining the second tag, and

$p_2 = Q_i * Q_i$ is the probability of retaining both tags.

The likelihood of the data was then drawn from a binomial distribution of one trial with probability equal to p_2. We first derived posterior estimates of the cumulative tag retention (Q_t) over time from one to ten years at liberty (the maximum number of survey occasions) and then solved for the mean time-dependent probabilities of retaining a tag with the following equation:

$$tr_t = 1 - (Q_{t-1} - Q_t)/Q_{t-1},$$ where,

tr_t is the probability of a retaining a tag after recapture interval t,

Q_{t-1} is the cumulative probability of retaining a tag at time $t-1$, and

Q_t is the cumulative probability of retaining a tag at time t.

S3. Growth Model

We used the Francis parameterization of the Von Bertalanffy Growth Function (VFGF) in the R package `FSA` (Ogle et al. 2022) and Barred Sand Bass age and growth data from Walker et al. (2020) to estimate BSB growth parameters,

$$E[L|t] = L1 + (L3 - L1)\,\frac{1 - r^{2\frac{t-t_1}{t_3-t_1}}}{1 - r^2}$$, where,

$E[L|t]$ represents the estimated length at age,

$L1$, $L2$, and $L3$ are the mean lengths at ages t_1, t_2, and t_3,

t_1 and t_3 are not estimated but are assigned to correspond to “young” and “old” ages, respectively,

$t_2 = t_1+t_3 / 2$, and

$r = L3 - L2 / L2 - L1$.

We used the length parameter estimates generated from the Francis parameterization of the VBGF to define the priors in our CMR models (Table S1). For the 1960s and 1990s, we used length parameter estimates based on $t_1 = 3$ years and $t_3 = 16$ years. In the 2010s model, we modeled monthly growth, and thus, length priors were based on the age of fish in months: t_1 = 24 months and t_3 = 192 months (Table S1). We chose a smaller age at t_1 for the 2010s model because the minimum size tagged was smaller than in the 1960s and 1990s.

S4. *Size-specific Estimates of Annual Harvest*

Harvest includes fish caught and kept by Commercial Passenger Fishing Vessels (CPFVs), private boaters, and shore anglers. We obtained harvest in numbers from California Department of Fish and Wildlife (CDFW) CPFV logbooks between 1947 and 2021. Harvest for BSB prior to 1975 was likely underreported because although catches of "sand bass" could be recorded in catch logs, Kelp Bass was the only *Paralabrax* species that was pre-printed on the logs for entering catch, and captains were not required to distinguish the bass species in their records (Croker 1940, Young 1969). Historically, CDFW biologists estimated BSB comprised a small portion of the bass catch through the 1950s (~25%; Clark 1933, Roedel 1953, Young 1969), but this increased to ~50% by at least the mid-1960s (Pinkas et al. 1968) and returned to 25% by at least the mid-1970s. We applied these percentages to the overall numbers of harvested bass (historically referred to as "Rockbass") reported in the logbooks to calculate estimated annual BSB CPFV catches prior to 1975.

Estimates of private boat and shore-based harvest from the 1960s were only available from 1964-65 (private boat) and 1965 (shore-based; Pinkas et al. 1968). Thus, for the 1960s we have a single estimate of BSB harvest, in which the CPFV estimate from 1964 and the estimated private boat and shoreline catch were combined. For the other two decades, given that the CPFV logbook data is the longest running record of recreational bass harvest, we chose to account for other methods of BSB take by adjusting the annual BSB CPFV harvest. To do so, we added numbers equivalent to the proportion of private and shore-based BSB harvest in each year, according to the relative proportion of harvest by fishing modes available from southern California recreational survey estimates, which are based on angler-intercept and telephone surveys (1980-2003: Marine Fisheries Statistical Survey [MRFSS], 2005-2017: California Recreational Fisheries Survey [CRFS]; Table S2). Thus, the adjusted BSB harvest, which represents the total estimated harvest of BSB, was then comparable across years.

For each year of available harvest, we estimated the proportion of sublegal and legal-size fish harvested. For 1964, we multiplied BSB harvest by the proportion of sublegal and legal-size harvested BSB measured in recreational angler-intercept surveys by CDFW biologists in the year 1975 (Wine 1978), as this was the earliest year for which length data in the recreational harvest was available (Table S2). For the 1990s and 2010s, the annual harvest was split into sublegal and legal size by multiplying the total annual harvest by the relative annual proportions of both size classes obtained from recreational angler surveys (Table S2). We applied these size-specific estimates of annual harvest (sublegal and legal) to CMR model estimates of exploitation to derive size-specific estimates of population size during each tagging period (see *Harvest Rates* and *Population Size* below).

S5. Search Terms for Historical Literature Review

We conducted our historical literature review on the Web of Science search engine, as well as with Google Scholar. Search terms included "Barred Sand Bass," "Sand Bass," "Sandbass," "*Paralabrax nebulifer*," "rockbass," and "rock bass."

S6. *Detailed Narrative of Historical BSB Accounts*

Between the 1850s and 1970s there were two extended warm periods in southern California, USA: the first warm period was from 1854 to 1870 and the second was from about 1925 to 1947; however, relative to the first warm period and the warm period in the 1980s and 1990s, the second warm period was only moderately warm (Fig. 1.7; Hubbs 1948, McClatchie 2014). BSB was first taxonomically described in 1854 during the first warm period, when its distribution was documented as far north as Monterey, CA (Fig. 1.7a; Girard 1858, Hubbs 1948). In the early 20th century, accounts of BSB in the literature shifted from no mention to being noted as a minor species in California's early commercial fishery (Fig. 1.7b,c,d). During the moderately warm period (1925-1947), CDFW biologists estimated the commercial Rockbass harvest consisted of 25% BSB and 75% Kelp Bass. Most commercial Rockbass were incidentally taken when fishing for other species (i.e., rockfish, California Sheephead); by weight, recreational Rockbass harvest was three times higher than commercial Rockbass harvest.

Between 1920 and 1939, CPFV fishing became more affordable and by 1936, a catch logbook was required to be submitted (Fig. 1.7e). Shortly after, in 1939, a bag limit for the three saltwater basses of 15 fish in aggregate was implemented. The early description of the combined CPFV bass harvest was "mostly" Kelp Bass, with "some" BSB (Croker 1940). During the warmest part of the moderately warm period in the mid-1940s, there was a five-year reprieve from CPFV fishing due to World War II, and thus, no catch records exist (Young 1969). Following the war, the oceanographic climate shifted to a cold regime, during which BSB were reportedly "scarce" and comprised a "very small portion of the catch" (Fig. 1.7f; Young 1963, Young 1969). In the 1950s, a series of sportfishing regulations were implemented for the basses due to concerns over the Kelp Bass resource and declining catches (Fig. 1.7; Jarvis et al. 2014).

In 1962, CDFW field biologists noted “tremendous” numbers of BSB in southern California waters and initiated the BSB tagging study from which our model results are drawn (Fig. 1.7g; CDFG 1962). This apparent dramatic increase in BSB availability was also referenced in Young (1969), Frey (1971), and Feder et al. (1974), and was reflected in the substantial increase in Rockbass harvest during the 1960s (Fig. 1.5c). The 1962 increase in availability came on the heels of one of the most significant El Niño events documented in southern California (the 1957/58 El Niño; Fig. 1.7g). However, compared to the average SST in the 1990s, the 1960s were still relatively cool (Fig. 1.5a). It was also during the 1960s that underwater observations of BSB spawning aggregations were first documented (Fig. 1.7g). During this time, CDFW field biologists referred to BSB as “a more southern species frequenting our coast in and subsequent to periods of warmer waters,” and “Recently, 1960 to 1970, barred sand bass have formed an important part of the sport catch." (Fig. 1.7g, Feder et al. 1974).

Following the increase in Rockbass harvest during the 1960s, the Rockbass bag limit was increased in 1972 from 15 fish in combination with not more than ten of any one species, to 20 fish in combination with not more than ten of any one species (Fig. 1.7). Nevertheless, a year earlier, when reporting on the status of the BSB population, CDFW resource managers foreshadowed a decrease in BSB availability in southern California, “One cloud on the horizon—barred sand bass have not always been present in large numbers in southern California.” (Fig. 1.7h; Frey 1971). Shortly thereafter, harvest declined dramatically and the Rockbass bag limit was reduced by half to ten fish in combination. By the mid-to-late 1970s, Rockbass harvest returned to being dominated by Kelp Bass, and BSB CPFV CPUE was calculated to be 5-10x lower than was later observed in the 1980s during the subsequent warm regime (Fig. 1.7i, Love et al. 1996b).

Supplemental Tables

Table S1. Prior parameter distributions used in the Bayesian capture-mark-reencounter models in this study. yal = years at liberty.

Model	Parameter	θ	Distribution
1960s and 1990s	true survival	ϕ	beta(1,1)
	recapture probability	p	beta(1,1)*
	recovery probability	κ	beta(1,1)
	resighting probability	R	beta(1,1)*
	mean length at age 3 y	$L1$	normal(236,10)
	mean length at age 9.5 y	$L2$	normal(403,10)
	mean length at age 16 y	$L3$	normal(495,10)
	probability tag retained after 1 yal	tr_1	beta(1120,162)
	probability tag retained after 2 yal	tr_2	beta(72,23)
	probability tag retained after 3 yal	tr_3	beta(11,7)
	probability tag retained after 4 yal	tr_4	beta(6,6)
	probability tag retained after 1 yal	tr_5	beta(5,6)
	probability tag retained after 2 yal	tr_6	beta(4,6)
	probability tag retained after 1 yal	tr_7	beta(4,6)
	probability tag retained after 2 yal	tr_8	beta(3,6)
	probability tag retained after 1 yal	tr_9	beta(3,6)
	probability tag retained after 2 yal	tr_{10}	beta(3,6)
	probability tag retained after 1 yal	tr_{11}	beta(3,6)
2010s	true survival	ϕ	beta(1,1)
	recapture probability	p	beta(1,1)
	recovery probability	κ	beta(1,1)
	resighting probability	R	beta(1,1)
	mean length at age 24 mos	$L1$	normal(191,100)
	mean length at age 108 mos	$L2$	normal(391,100)
	mean length at age192 mos	$L3$	normal(487,100)
	annual tag retention rate	r	beta(140,27)

*This parameter fixed at zero in the 1990s mark-resight-recovery model.

Table S2. Compilation of Barred Sand Bass (BSB) harvest statistics used in calculating the estimated mean annual numbers of legal- and sublegal-size fish harvested in the fishery during each tagging period. Prop. = proportion, CPFV = Commercial Passenger Fishing Vessel.

		Angler-intercept/Phone Survey Estimates[a]						
Decade	Year	Prop. Legal Size	Total observed (measured)	Shore-based	Party/Charter Boats	Private/Rental Boats	Total BSB Harvest (all fishing modes)	CPFV BSB Harvest
1960s[b]	1964	0.85[c]	5,562[c]	7,318[b]	no estimate	64,513[b]	610,831	539,000[d]
				Prop. of Total				
1990s[e]	1989	0.98	1,636	--	0.59	0.40	1,295,773	787,074
	1993	0.97	2,086	0.00	0.56	0.43	731,182	309,000
	1994	0.97	1,393	0.03	0.54	0.43	703,763	270,000
	1995	0.97	--	0.02	0.64	0.34	801,512	349,000
	1996	0.97	1,948	0.01	0.68	0.32	743,805	591,000
	1997	0.98	1,062	0.02	0.41	0.57	462,973	476,000
	1998	0.98	1,460	0.01	0.37	0.62	417,633	376,000
	1999	0.98	3,925	0.00	0.44	0.56	488,743	414,000
2010s[f]	2013	0.91	1,031	0.05	0.62	0.34	64,796	56,000
	2014	0.89	1,264	0.02	0.76	0.22	69,474	39,000

[a] Harvest estimates are provided for shore-based fishing (man-made structures, beach and bank) and boat-based fishing from CPFVs (Commercial Passenger Fishing Vessels; party/charter) and privately-owned/rental boats. Estimates are derived from a combination of angler intercept surveys and phone surveys of effort.

[b] Harvest estimates from Pinkas et al. (1968). The shore-based estimates are for the 1964/1965 season (July - June). The private boat estimates are for the year 1964 (January - December). Total harvest includes the estimate for CPFV

[c] Data source is for the year 1975, Wines (1978).

[d] Harvest estimates are for the year 1964 (January - December). Total bass harvested by CPFVs in 1964 was 1,078,000 fish; we applied a factor of 0.5 to this number to estimate BSB harvest; BSB comprised ~50% of the private boat harvest during this year (Pinkas et al. 1968).

[e] Survey proportions and harvest estimates obtained from the National Oceanic and Atmospheric Administration, Marine Recreational Fisheries Statistics Survey, 1980–2003.

[f] Survey proportions and harvest estimates obtained from the California Recreational Fisheries Survey, 2004–2021.

Supplemental Figures

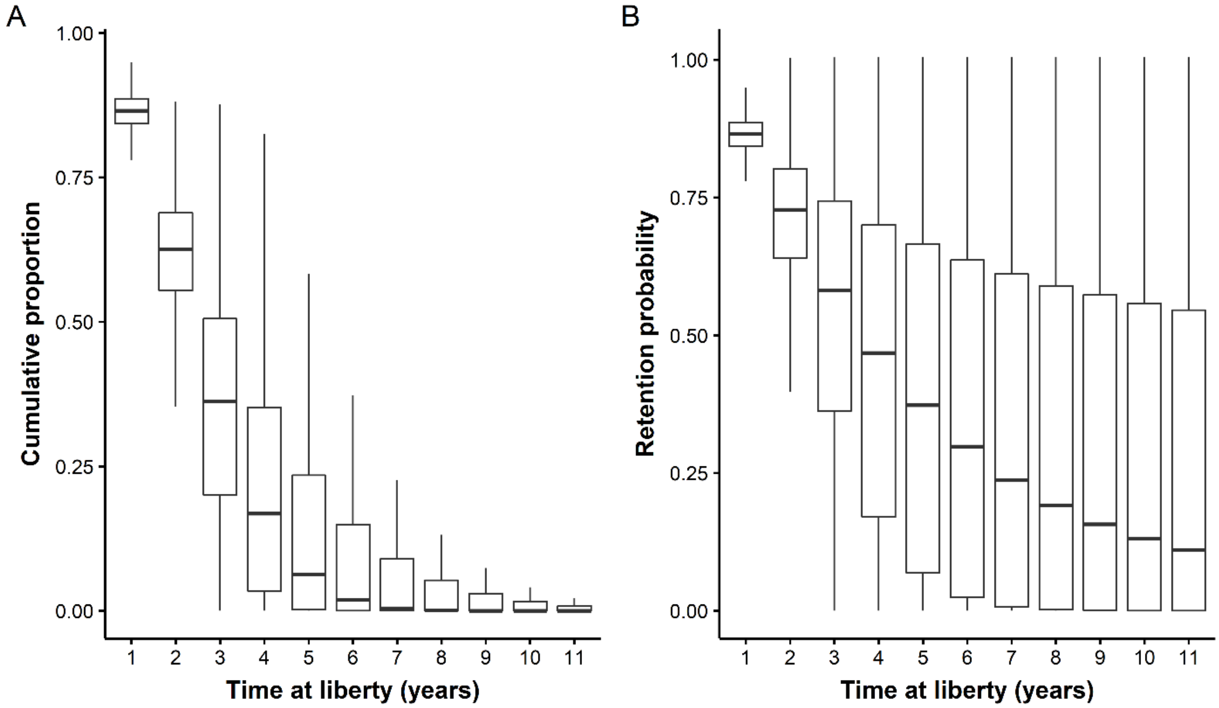

Figure S1. Box plots of Bayesian posterior estimates (mean and 95% Credible Intervals) of the a) cumulative proportion of double-tagged Kelp Bass retaining at least one tag over time, and b) the associated time-dependent tag retention probabilities applied as tag retention priors in the Barred Sand Bass capture-mark-reencounter models.

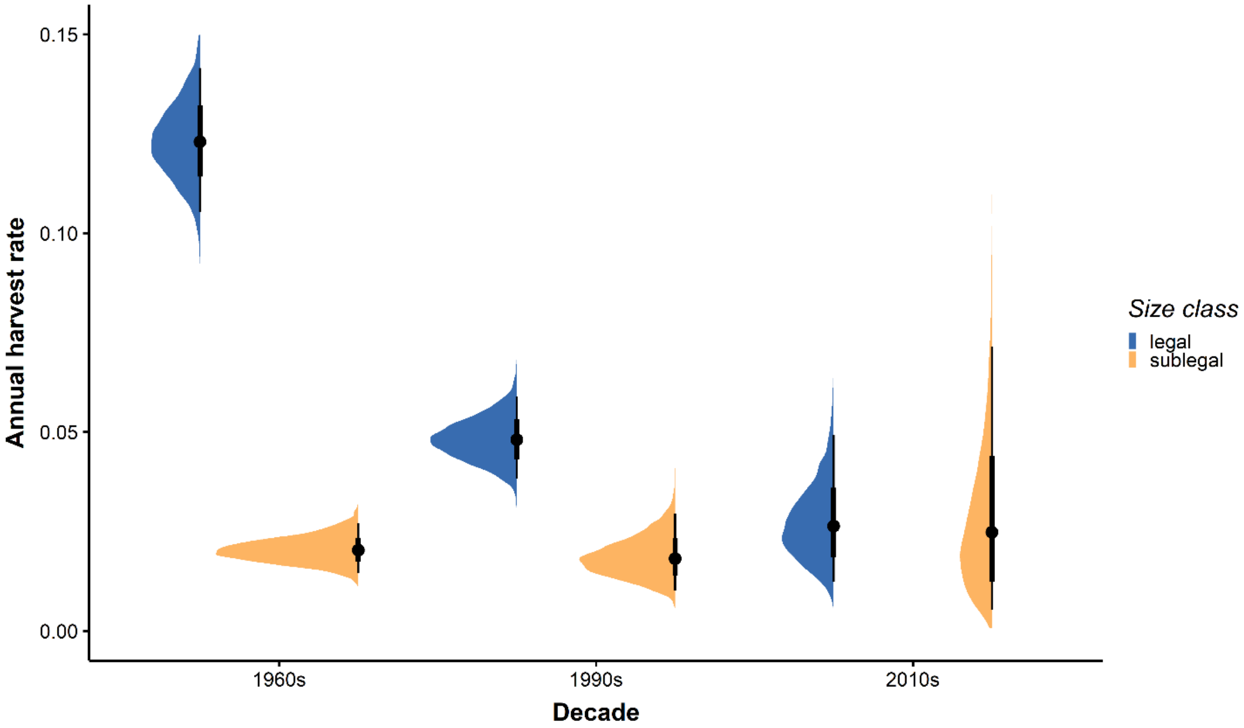

Figure S2. Bayesian capture-mark-reencounter model posterior distributions and mean and 95% credible intervals (dots plus thick and thin lines) of annual harvest rates for legal- and sublegal-size Barred Sand Bass across tagging periods. The estimates are conservative, as they assume a 100% tag reporting rate.

Literature Cited

Bellquist LF (2015) A historical perspective of California recreational fisheries using a new database of ‘trophy’ fish records (1966-2013), combined with fisheries analyses of three species in the genus Paralabrax. PhD dissertation, University of California, San Diego, CA

CDFG [California Department of Fish and Game] (1962) Report for the month of August, 1962. Dept. of Fish and Game Records, Regional Reports, F3498:582-614.

Carlisle J, Turner C, Ebert E (1963) Artificial Habitat in the Marine Environment. Calif Dep Fish Game, Fish Bull 124.

Clark FN (1933) Rock bass (*Paralabrax*) in the California commercial fishery. Calif Fish Game 19:25–35.

Collyer R (1949) The Commercial Fish Catch of California for the Year 1947: With an Historical Review 1916-1947. Fish Bull:268

Croker RS (1940) Three Years of Fisheries Statistics on Marine Sport Fishing in California. Trans Am Fish Soc 69:111–118.

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

Frey HW (ed) (1971) Kelp and sand bass In: *California’s Living Marine Resources and Their Utilization*. California Department of Fish and Game, Sacramento, USA, p 93-94.

Fry D, Croker RS (1934) A preliminary survey of Mission Bay State Park. Calif Fish Game 20:1–13.

Girard C (1858) Fishes. In: *General report upon the zoology of the several Pacific railroad routes. Explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean.* 10(4):1-400.

Holder CF (1912) The fishes of the Pacific coast, a handbook for sportsmen and tourists. Dodge Publishing Company, New York, USA.

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

Jarvis ET, Gliniak HL, Valle CF (2014) 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.

Love MS, Brooks A, Busatto D, Stephens J, Gregory PA (1996a) 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.

Love MS, Brooks A, Ally JRR (1996b) An analysis of commercial passenger fishing vessel fisheries for kelp bass and barred sand bass in the southern California Bight. Calif Fish Game 82:105-121.

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

Ogle DH, Doll J, Wheeler P (2022) Package ‘ FSA ’ version 0.9.3

Pinkas MS, Oliphant CW, Haugen L (1968) southern California marine sport-fishing survey: private boats, 1964; shoreline, 1965-66. Calif Dep Fish Game, Fish Bull 143

Plummer M, Stukalov A, Denwood M (2022) Package ‘ rjags ’ version 4-13.

Starks EC (1919) The basses and bass-like fishes of California. Families Serranidae, Haemulidae, Kyphosidae. Calif Fish Game 5:56–68.

Su Y-S, Yajima M (2021) Package ‘R2jags’ version 0.5-7

Turner CH, Ebert EE, Given RR (1969) Man-Made Reef Ecology. Calif Dep Fish Game, Fish Bull 146

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

Wine V (1978) southern California Independent Sport Fishing Survey Annual Report No. 2. Mar Resour Adm Rep No 78-2:84.

Wine V (1979a) southern California Independent Sport Fishing Survey Annual Report No. 3. Mar Resour Adm Rep No 79-3:105.

Wine V (1979b) southern California Marine Sport Fishing: Private-Boat Catch and Effort, 1975-1976. Mar Resour Adm Rep No 79-11:64.

Young P (1969) The California Partyboat Fishery 1947–1967. Calif Dep Fish Game, Fish Bull 45

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

CHAPTER 2

Decoding comparable morphologies: pigmentation validated for identifying southern California *Paralabrax* larvae

Synopsis

Here we present a taxonomic key for identifying southern California *Paralabrax* spp. preflexion, flexion, and postflexion larval developmental stages. Using a combination of methods including classical taxonomy, machine learning, and molecular validation, we successfully identify useful pigmentation patterns to delineate the three southern California *Paralabrax* species within each development stage. We further demonstrate a high probability of accurate and precise species delineation using the key. The key enables us to leverage existing and nearshore ichthyoplankton survey collections to assess long-term species-specific trends in southern California *Paralabrax* spp. larvae for the first time and is the foundation for Chapter 4.

This chapter is presented as a paper. “Decoding comparable morphologies: pigmentation validated for identifying southern California *Paralabrax* larvae,” was published in *FishTaxa* in 2022.

Note the following correction to the last sentence on page 74 of this dissertation (page 17 of the publication) in the Results section entitled, “Key to the larvae of…”. The sentence should read, “Larvae that display these characters are not necessarily *Paralabrax*, but larvae that *do not* are not *Paralabrax*.”

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Decoding comparable morphologies: Pigmentation validated for identifying southern California *Paralabrax* larvae

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Abstract

The distribution and trends in larval fish abundance are often used to assess the status and trends of marine fish populations. However, for closely related species whose larvae are morphologically similar and whose genetic identities may be degraded by formalin preservation, unraveling species-specific larval abundances from long-term monitoring efforts presents a challenge. We used statistical methods and the molecular identities of 107 ethanol-preserved specimens to construct and test a taxonomic key based on pigmentation patterns observed in three species of *Paralabrax* (family Serranidae) from southern California. Previously, larvae of these species were not thought to be reliably distinguishable based on morphology or pigmentation. However, when using pigmentation characters paired with molecular identities, a Random Forest Classifier provided a tool for structuring and refining a taxonomic key to distinguish species. Following calibration and key refinement, the probabilities of achieving accurate and precise species classifications using our taxonomic key were ≥96%, indicating that ventral and pectoral fin pigmentation patterns can discriminate *Paralabrax* larvae. Importantly, we can now leverage existing and future ichthyoplankton survey collections to assess species-specific trends in larval abundance without requiring expensive and lab-intensive genetic analyses used with formalin-fixed specimens.

Keywords: Larvae, Pigmentation, Key, Random forest, Molecular validation.

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Introduction

Sea basses in the genus *Paralabrax* are targets of a popular recreational fishery in southern California (Jarvis et al. 2014a; Bellquist et al. 2017) and comprise important artisanal fisheries in Baja California, Mexico (Erisman et al. 2017; Cota-Nieto et al. 2018). Catches of two of the three species in southern California, *P. clathratus* (Kelp Bass) and *P. nebulifer* (Barred Sand Bass) have remained depressed since the mid-2000s, calling into question their population status and recovery potential (Erisman et al. 2010; Jarvis et al. 2014a). The third species, *P. maculatofasciatus* (Spotted Sand Bass), is primarily catch-and-release. Unfortunately, the long-term population dynamics of all three species are unknown due to a lack of species-specific fishery-dependent and -independent data. A potential source of fishery-independent time series data comes from the California Cooperative Oceanic Fisheries Investigations (CalCOFI), which has systematically sampled fish larvae, including *Paralabrax*, since 1951 (McClatchie 2014). Larval abundance can be used as a proxy of adult fish spawning stock biomass (Ralston and McFarlane 2010; He et al. 2015), but to date, *Paralabrax* larvae have not been able to be reliably identified to the species level. Here, we develop a novel technique to identify *Paralabrax* larvae and unlock a powerful data set to assist with managing these important species.

Paralabrax larvae (Family Serranidae) in southern California reside in shallow coastal waters and embayments during the summer and have a planktonic life duration of approximately one month (Findlay and Allen 2002; Allen and Block 2012). At settlement, *P. clathratus, P. maculatofasciatus,* and *P. nebulifer* are readily distinguished from one another by the presence and numbers of horizontal or vertical bars on the body and the relative height of the third dorsal fin spine (Butler et al. 1982; Love and Passerelli 2020). In contrast, their larval stages are morphologically similar, having overlapping meristics and morphometrics (Butler et al.

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1982; Watson 1998). Butler et al. (1982) documented the developmental larval stages of these three species for a small sample of larvae reared from eggs collected in the wild and identified a few distinguishing characters primarily relating to dorsal and ventral pigmentation patterns. However, diagnostic characters were not found for *P. nebulifer* and *P. maculatofasciatus* during notochord flexion, and the authors noted that pigmentation varied within larval stages. Owing to their similar morphologies and variability in pigmentation, larvae were not reliably identified to species and are only identified to genus in the CalCOFI database.

With additional *Paralabrax* larvae and genetic barcoding for validation, the potential exists to discern the extent of intraspecific pigment variation within each developmental stage and thus develop a reliable key for identifying *Paralabrax* larvae to species. A robust key would provide higher confidence in classifying *Paralabrax* larvae based on morphology. In addition, the key would provide a cost-effective means of identifying *Paralabrax* larvae in formalin-preserved ichthyoplankton collections and on-going ichthyoplankton monitoring surveys off southern California and Baja California, Mexico, including CalCOFI and Investigaciónes Méxicanas de la Corriente de California (IMECOCAL; Moser et al. 2001; Gaxiola-Castrol and Najera-Martinez 2002; Gallo et al. 2019). Herein, we use classical and modern taxonomic methods to construct, refine, and test a taxonomic key for distinguishing preflexion, flexion, and postflexion larval stages of *Paralabrax* spp. in southern California.

Materials and Methods

Taxon sorting: Since 1951, CalCOFI has collected and archived quarterly plankton samples from fixed stations offshore of California, USA, and Baja California, Mexico (Fig. 1; see McClatchie (2014) for an overview of the CalCOFI program). From 1951-1977, samples were collected using obliquely towed ring nets (Thompson et al. 2017). In 1978, ring nets were replaced with paired bongo nets (0.71 m diameter, 505 μm-mesh sizes) towed obliquely from a maximum depth of 210 m in deep waters and 5 m above the bottom in shallow water (McClatchie 2014). The starboard net contents are fixed and preserved in 5% neutrally buffered formalin while, since 1997, the contents of the port net have been preserved in 95% tris-buffered ethanol. Notably, ethanol preserves, while formalin degrades, DNA.

We sorted *Paralabrax* larvae from ethanol-preserved CalCOFI plankton samples collected in years with high larval counts in the starboard net (1998, 2004, 2006, 2012, 2013, and 2014). We selected samples inshore of CalCOFI station 60 (over the continental shelf; Fig. 1) because *Paralabrax* larvae occur relatively close to shore (Watson and Davis 1989). We also limited sorting to July cruises because *Paralabrax* spp. in southern California spawn almost exclusively in summer (Erisman and Allen 2005; Allen and Block 2012; Jarvis et al. 2014b; McKinzie et al. 2014). All ethanol-preserved larvae analyzed in this study are archived in the SWFSC larval fish collection; a select few were moved to the reference collection.

DNA extraction, PCR amplification, and sequencing: We developed and tested genus-specific primers to amplify a 282 base pair region of the mitochondrial (mt) cytochrome C oxidase subunit I (COI) gene for use in discriminating *Paralabrax* spp. This includes *P. auroguttatus* (Goldspotted Sand Bass), a southern species whose larvae may periodically enter the CalCOFI survey region during warm water periods. We removed the right eyeball or a small piece of muscle tissue from each larva and DNA was extracted using chelex 100 (Biorad laboratories) boiling protocol (Hyde et al. 2005) or the Qiagen DNeasy Blood & Tissue 96 extraction kit (Qiagen, Inc., Valencia, CA) following manufacturer's protocol.

We used polymerase chain reaction (PCR) to amplify the primer-specific region of the mt COI gene in 10 μl reactions containing 67 mM Tris-HCl pH 8.8, 16.6 mM $[NH_4]^2SO_4$, 10 mM β- mercaptoethanol, 2 mM $MgCl_2$, 800 μM dNTPs, 0.5mg/ml Bovine Serum Albumin (BSA), 0.25μM of each primer (ParaF1 5' CCT TCT TAT

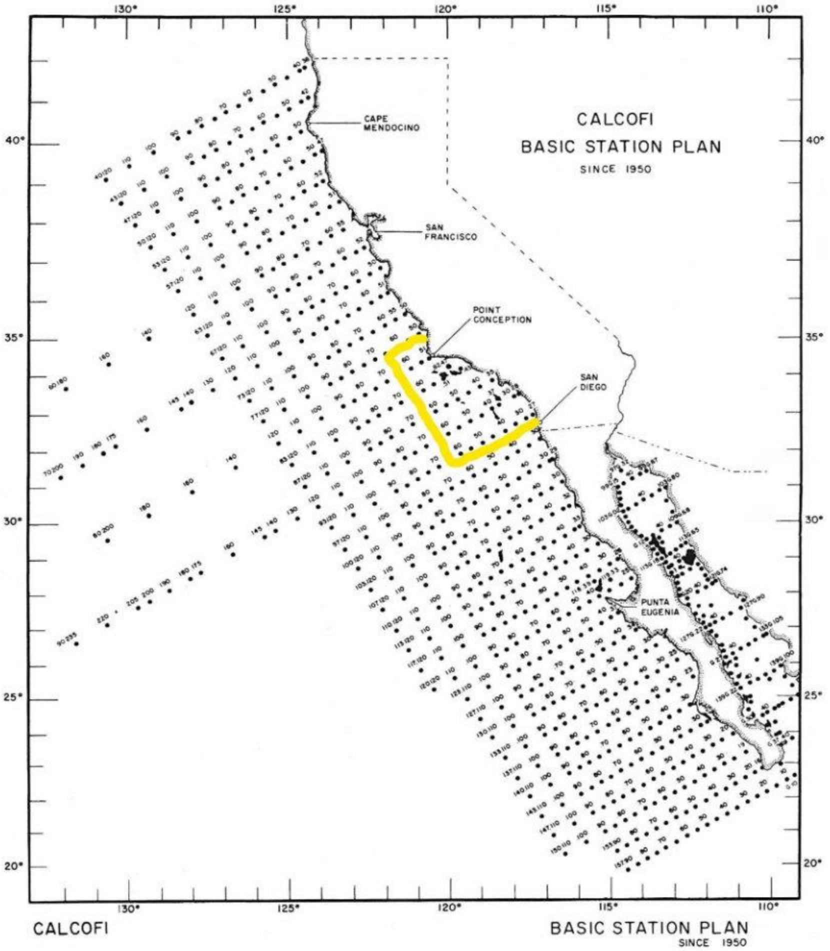

Figure 1. California Cooperative Fisheries Investigations (CalCOFI) hydrographic and planktonic sampling stations (since 1950 and 1951, respectively) off the coasts of California, USA, and Baja California, Mexico. Stations inside yellow lines indicate the region selected for sorting *Paralabrax* larvae from archived CalCOFI zooplankton samples, to construct and test a taxonomic key.

TCG AGC CGA GC-3'; ParaF2 5' GCA GGT ACA GGC TGA ACAG-3'), 0.25 units of *Taq* (*Thermus aquaticus*) DNA polymerase, and 1 μL of DNeasy extracted DNA or Chelex supernatant containing DNA template. Thermal cycling consisted of an initial denaturation at 94°C for 2 min followed by 35 cycles of 94°C for 30 s, 55°C for 1 min, and 72°C for 1 min, followed by a final extension at 72°C for 3 min. For each set of PCRs, we included a no-template negative control. We visualized PCR products on a 2% agarose gel stained with ethidium bromide. We used ExoSap-IT (Affymetrix) to remove excess primers and unincorporated dNTPs, following manufacturer's protocol. Cycle sequence reactions were performed in one direction using BigDye v3.1 (Life Technologies) and the forward PCR primer 5' following manufacturer's protocol. We precipitated the sequence reactions using ethanol and sodium acetate and resuspended in HiDi formamide prior to being run on an ABI3730 Genetic Analyzer (Life Technologies). We used Sequencher v4.9 (GeneCodes) to edit the sequences, which were then compared to reference sequences in GenBank® (http://www.ncbi.nlm.nih.gov/genbank/; accession numbers: MK029994.1, *P. clathratus*; MT311637.1, *P. nebulifer*; MG837969.1, *P. maculatofasciatus*).

Taxonomic key development and validation: We identified salient morphological characters described in Butler et al. (1982) across preflexion, flexion, and postflexion stages. These included the size, number, and location of dorsal and ventral melanophores and the presence or absence of other pigmentation (e.g., on the crown, pectoral fins, and mediolateral trunk). Yolk sac larvae were deemed visually indistinguishable and not included for analysis. We assigned the larval stage based on notochord development (Miller and Kendall 2019). For each larva, two taxonomists recorded larval stage and stage-specific morphological characters. Taxonomists were blind to the molecular identity of each larva and there was no attempt to assign species at this first step.

For every larva (*i*), we used the known molecular identity and data recorded in the morphological characters table to model each of *j* possible species classifications (stage-specific) using multinomial logistic regression in a Bayesian framework (McElreath 2019) with the R package r2jags, a wrapper for rjags (R-Core-Team 2020; Plummer 2021; Su and Yajima 2021):

$$logit(p[i,j] \;=\; \beta[1,j] \;+\beta[2,j] \;*k[1,i] \;+\beta[3,j] \;*k[2,i]\ldots\beta[n,j]*k[n,i].$$

We treated a larva's species classification as drawn from a multinomial probability distribution, where each classification is a linear function of *k* stage-specific morphological traits. We used normally distributed priors for the slope parameter and the beta parameters associated with each stage-specific morphological character. We used data recorded by the two taxonomists in separate models to examine posterior probability distributions for each larva's multinomial classification and to answer the following questions. For each larval stage, do the characters clearly distinguish a single species classification with high probability for most larvae? For each larval stage, do the characters accurately predict the true species for most larvae? Is there variability in model performance across larval stage and between taxonomists? Thus, this was an exploratory step used early on to determine which character traits required recalibration by taxonomists and thus which traits required clarification of the descriptions in the characters table; ultimately, the taxonomic key.

We used a machine learning algorithm, Random Forest Classifier (RFC, Cutler et al. 2007), in the R package, randomForest (Liaw and Wiener 2002a, b; R-Core-Team 2020), to identify the most important characters for accurate stage-specific species prediction ("variable importance"). We used a small subset of the data collected in the first step to train each stage-specific model. To test the models, the RFC generated a species classification for each new larva in the remaining testing data set, in which many random subsets of morphological traits were used to create a forest of decision trees that each resulted in a species classification. The ultimate species classification was based on the majority vote (classification) in the random forest and variable importance was provided as the mean decrease in accuracy across all trees in the forest when a specific variable (i.e., pigmentation character) was excluded.

As additional molecular identities became available, the taxonomists recalibrated and we refined the key where necessary. The RFC variable importance feature was useful for identifying which character(s) to include at the beginning of each stage-specific key. We evaluated the performance of the key before and after the final key refinement by calculating the probability of accurate and precise identifications with a binomial model using Bayesian methods and the R package r2jags (R-Core-Team 2020; Plummer 2021; Su and Yajima 2021). We also constructed multi-class, pre and post error "confusion" matrices to characterize additional measures of classification performance (overall and by species) using the R package caret (Kuhn 2022). These performance measures included sensitivity, specificity, precision, and balanced accuracy (see Jiao and Du (2016) for a review of performance measures).

Results

Molecular identities: We obtained DNA sequences for 119 *Paralabrax* larvae, of which preflexion larvae were dominant (64.7%), followed by flexion (21.8%) and postflexion larvae (10.1%); 3.4% could not be staged. By species, *P. clathratus* and *P. nebulifer* were the most common (47.9% and 46.2%, respectively). There were few *P. maculatofasciatus* (5.9%) and no *P. auroguttatus* (Table 1). Of the *P. maculatofasciatus* with molecular identities, six were preflexion and one was flexion (Table 1).

Important pigmentation characters: Dorsal and ventral pigmentation varied within and among species. However, the RFC identified aspects of ventral pigmentation as being the most important character in preflexion stages for species delineation (e.g., the presence and location of a large ventral pigment patch and the presence or absence of a series of closely spaced, uniform melanophores; Fig. 2a). Thus, we structured the preflexion key to begin with ventral pigmentation followed by other pigmentation. We found that preflexion *P. clathratus* and *P. maculatofasciatus* typically had few ventral melanophores (Fig. 3a, b), however they had a large ventral pigment patch midway between the anus and the end of the notochord (Fig. 3d). In *P. clathratus*, this patch is on the eighth or ninth post-anal myomere, while in *P. maculatofasciatus*, it is on the sixth or seventh post-anal myomere (Fig. 3a, b). In each case, the postanal dorsal melanophore, if present, was located directly above the postanal ventral patch. It was common for the postanal dorsal melanophore in preflexion *P. clathratus* and the middle dorsal melanophore in preflexion *P. maculatofasciatus* to be more prominent relative to the other dorsal melanophores (i.e., darker or larger). In contrast, preflexion *P. nebulifer* typically had a series of numerous small uniform melanophores along the ventral margin (~10-20), with usually more than one melanophore per myomere; it was also common for one of the ventral melanophores to be prominent relative to the other ventral pigment (Fig. 3c, e). Preflexion *P. clathratus* and *P. maculatofasciatus* occasionally had a series of small uniform melanophores along the ventral margin (in addition to the large ventral patch), but these were typically not as closely spaced as in *P. nebulifer*.

The RFC identified pectoral wfin pigmentation as the most important flexion stage character for species classification (Fig. 2b). Flexion *P. clathratus* commonly had pectoral fin pigment, but this pigmentation did not occur with any of the flexion *P. nebulifer*. While there was only one flexion *P. maculatofasciatus* for comparison, it had pectoral fin pigment but no crown, mediolateral trunk, or dorsal pigment. The large ventral pigment patch was typically present throughout the flexion stage in *P. clathratus* and may be retained to early flexion in *P. maculatofasciatus* (Fig. 4a, b). We found that ventral melanophores of flexion *P. nebulifer* were typically closer together and may become dense (Fig. 4c). In many flexion larvae of this species, the pigment along the ventral midline of each myomere appears to eventually coalesce into linear segments or a single continuous line of pigment.

Table 1. Numbers of ethanol-preserved *Paralabrax* larvae, identified by molecular methods for use in developing and testing a taxonomic key, by larval stage and species. Twelve of these specimens were in poor condition and could not be morphologically identified.

Species	Preflexion	Flexion	Postflexion	Not Staged	Total
P. clathratus	41	13	2	1	55
P. maculatofasciatus	6	1	0	0	7
P. nebulifer	30	13	9	3	57
Total	77	27	11	4	119

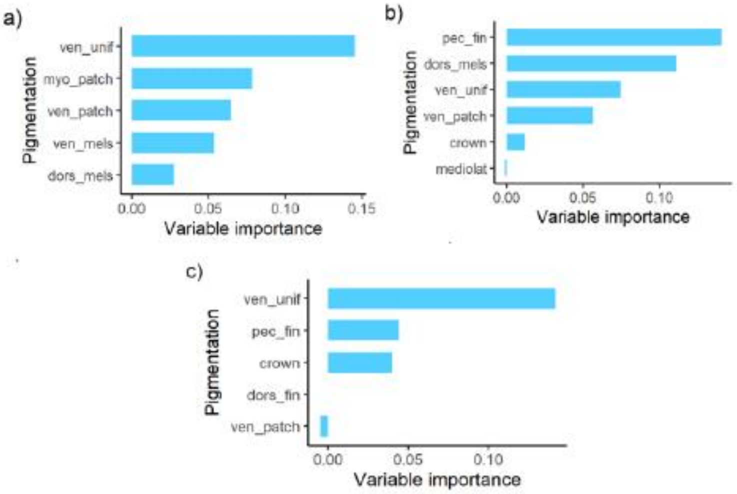

Figure 2. Random forest variable importance plots depicting the relative importance of pigmentation characters in contributing to accurate species delineation in *Paralabrax* spp. larvae for (a) preflexion, (b) flexion, and (c) postflexion developmental stages. Descriptions of pigmentation abbreviations include the following: crown = crown pigment, dors_fin = dorsal fin pigment, dors_mels = number and location (anterior, mid, posterior) of dorsal melanophores, mediolat = presence/absence of mediolateral pigment on trunk and/ozzr horizontal septum pigment, myo_patch = location of large postanal ventral pigment patch (myomere number), pec_fin = presence/absence of pectoral fin pigment on one or both pectoral fins, ven_mels = number of postanal ventral melanophores; ven_patch = presence/absence of large postanal ventral pigment patch, ven_unif = presence/absence of a postanal series of uniform ventral melanophores.

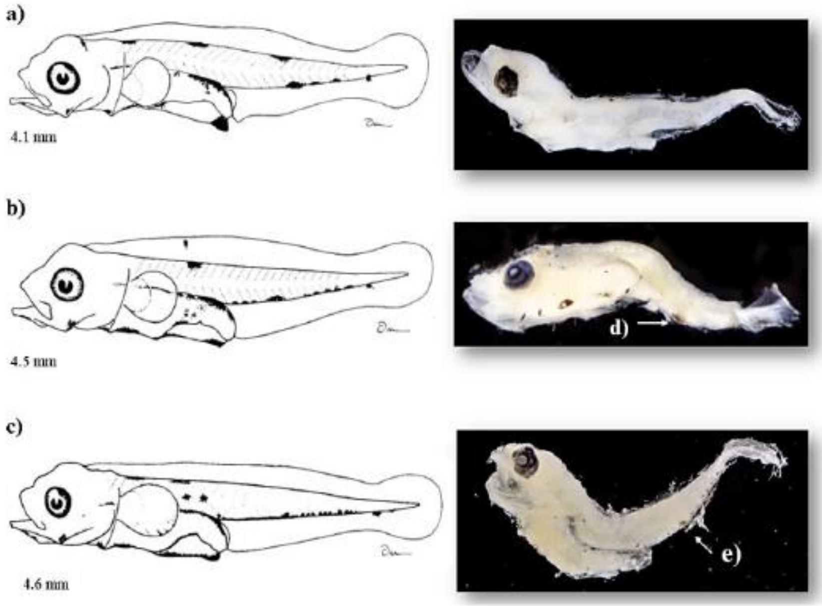

Figure 3. Illustrative and photographic comparison of preflexion stage larvae of (a) *Paralabrax clathratus*, (b) *P. maculatofasciatus*, (c) *P. nebulifer* (Butler et. al., 1982), and the (d) large postanal ventral midline melanophore versus (e) prominent postanal ventral midline melanophore typical of preflexion of both *P. clathratus* and *P. maculatofasciatus* and *P. nebulifer*, respectively. Representative photographs were taken of ethanol-preserved larvae used in constructing and validating the taxonomic key.

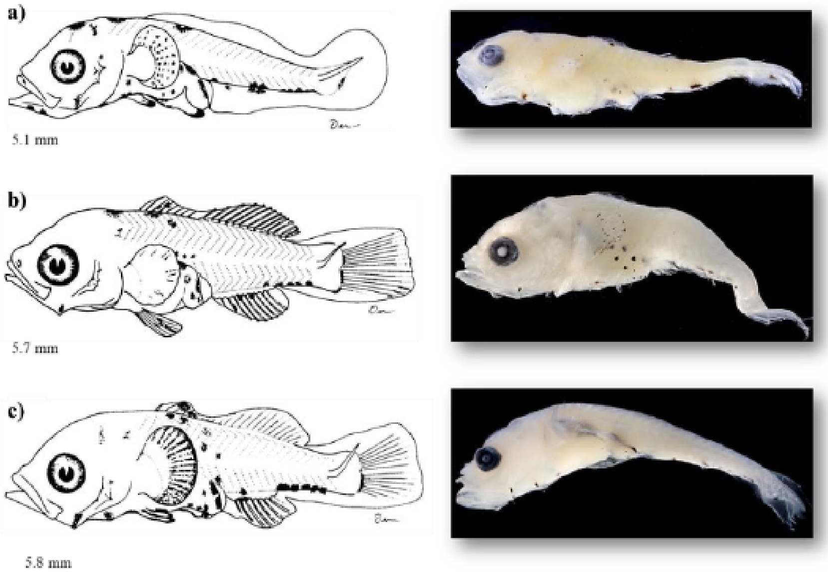

Figure 4. Illustrative and photographic comparison of flexion stage larvae of (a) *Paralabrax clathratus*, (b) *P. maculatofasciatus*, and (c) *P. nebulifer* (Butler et. al., 1982). Representative photographs were taken of ethanol-preserved larvae used in constructing and validating the taxonomic key.

The most important postflexion stage character identified by the RFC was ventral pigment (Fig. 2c). However, this result was based on only 13 larvae that were mostly early postflexion stage (Fig. 5a-c). In contrast, our observations indicated that postflexion *Paralabrax* larvae are more easily distinguished by the dorsal, trunk, and head pigmentation characters, as described in Butler et al. (1982). For example, we observed a series of dorsal saddles in one *P. clathratus* larva, in contrast to the single dorsal saddle observed in one *P. nebulifer* larva (Fig. 5d, f). We also observed snout pigment in one *P. nebulifer* larva (Fig. 5f). Early postflexion *P. clathratus* typically retained the large postanal ventral patch and had a combination of the pectoral, crown, and dorsal fin pigment; while early postflexion *P. nebulifer* typically had a continuous, uniform series of ventral pigment and only occasionally had pigmentation on the crown and/or dorsal or pectoral fins. There were no *P. maculatofasciatus* postflexion larvae for comparison.

Some dorsal pigmentation patterns were more common in one species than in the others, and thus we placed this character later in the preflexion and flexion keys to provide additional species confirmation. With respect to the retention of all three dorsal pigment patches in preflexion *P. clathratus* and *P. maculatofasciatius*, Butler et al. (1982) reported a specific total length and snout:anus length cutoff to distinguish the two species. However, in our preflexion key, we chose not to use a specific length as a dichotomous pathway for this character, as larvae growth can vary temporally and spatially. Instead, we used "early" and "mid-to-late" preflexion to denote likely retention in both species and retention in only *P. clathratus*, respectively.

Comparisons to *P. auroguttatus*: As no *P. auroguttatus* were genetically identified in this study, we chose to exclude this species from the key. However, we found that ventral pigmentation patterns important for distinguishing southern California *Paralabrax* larvae appear distinct from the ventral pigmentation pattern of preflexion and flexion stage *P. auroguttatus* larvae described in Avendaño-Ibarra (2004). For example, in both preflexion and flexion *P. auroguttatus*, there is typically a prominent ventral patch located on the second

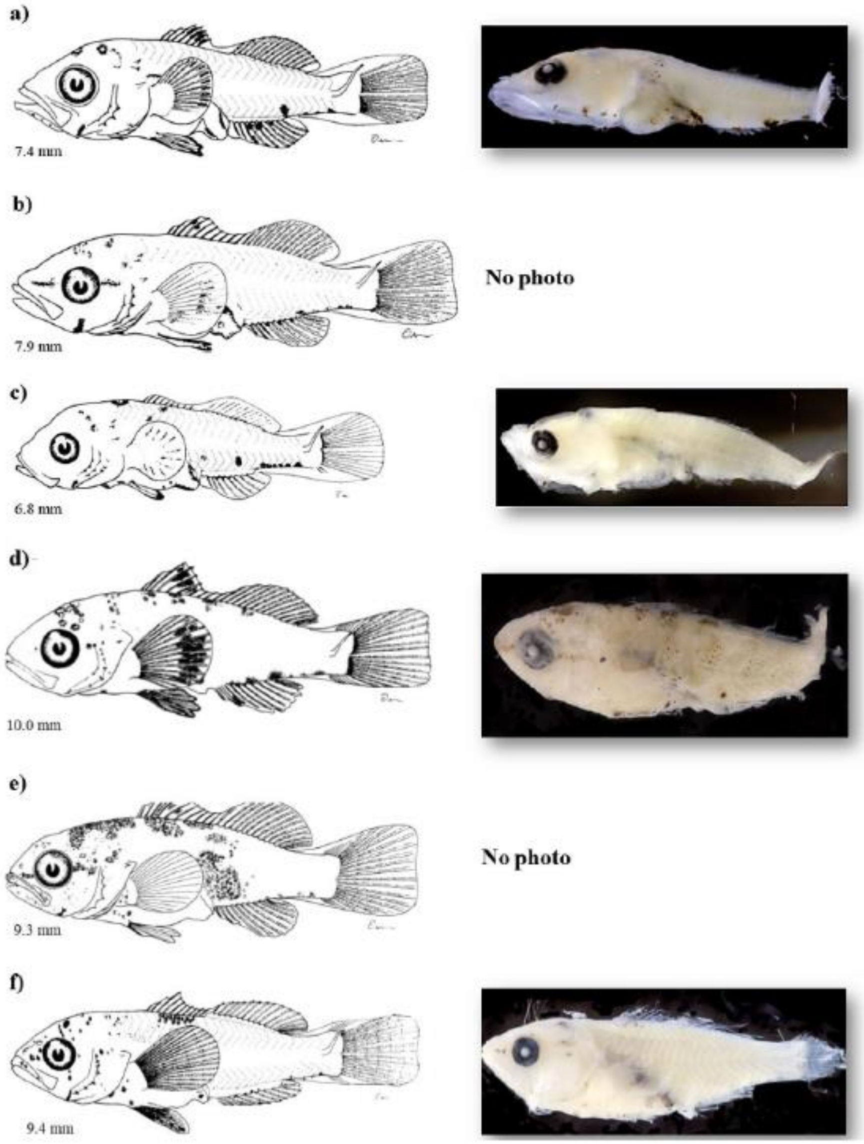

Figure 5. Illustrative and photographic comparison of early postflexion stage larvae of (a) *Paralabrax clathratus*, (b) *P. maculatofasciatus*, and (c) *P. nebulifer* (Butler et. al., 1982), and larger postflexion stage larvae of (d) *P. clathratus*, (e) *P. maculatofasciatus*, and (f) *P. nebulifer* (Butler et al. 1982). Representative photographs were taken of ethanol-preserved larvae used in constructing and validating the taxonomic key.

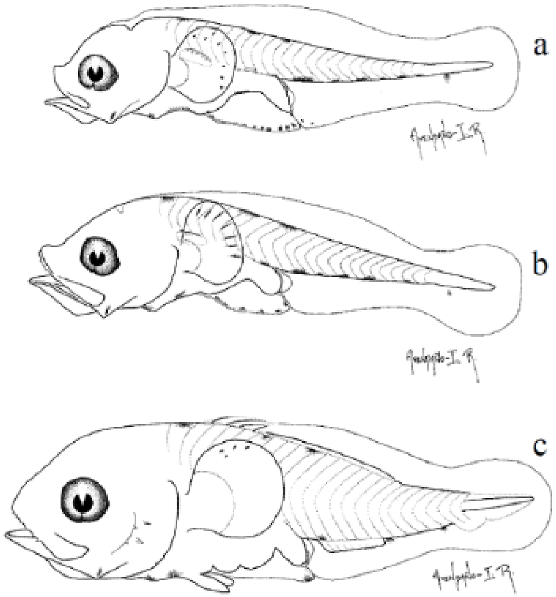

Figure 6. Illustrative comparison of larvae of *Paralabrax auroguttatus* representing (a) early preflexion (length 2.0 mm), (b) preflexion (3.0 mm), and (c) flexion (4.3 mm) developmental stages (Avendaño-Ibarra 2004).

postanal myomere, and the posterior dorsal melanophore, if present, is located directly above, such that the middle and posterior dorsal melanophores are closer together than in *P. clathratus* and *P. maculatofasciatus* (Fig. 6). In addition, preflexion *P. auroguttatus* typically have pectoral fin pigmentation, and we observed this to be less common in preflexion *P. maculatofasciatus* and *P. clathratus*.

Taxonomic key validation: Overall, 12 *Paralabrax* larvae with molecular identifications could not be visually identified to species level due to their poor condition. Thus, data on 107 larvae were used for validation. In the initial stage of key development, differences in the performance of the logistic regression model between taxonomists indicated that calibration was required in assigning larval stages and ventral pigmentation characters. For example, there was taxonomist bias in what constituted a large ventral pigment patch, which required the character description to be clarified within the key to limit subjectivity.

Post-calibration and key refinement, key performance increased overall (Fig. 7) and by species (Table 2). Overall, the final key achieved 97% accuracy and 96% precision (Fig. 7). By species, balanced accuracy was high for all three species (≥96%, Table 2). Precision was lowest for *P. maculatofasciatus* (70%), resulting from three false positives, in which three *P. clathratus* larvae were misclassified as *P. maculatofasciatus* (Table 2).

Key to the larvae of southern California species of *Paralabrax*

Larval *Paralabrax* are typical serranines, having 24-25 myomeres (usually 24), a moderate body shape (body depth typically ~ 15-30% body length) with preanal length about half of body length, an initially straight gut that coils during flexion stage, relatively few, small spines on the head, and pectoral girdle beginning late in preflexion stage (e.g., Watson 1996). Larvae that display these characters are not necessarily *Paralabrax*, but larvae that do are not *Paralabrax*.

Preflexion stage I
Flexion stage II
Postflexion stage III

I. Preflexion stage

1a. Ventral postanal midline melanophores arranged in a continuous, nearly uniform series[1], containing
    A. A single prominent postanal ventral melanophore[2] large/patch-like relative to other ventral midline pigment 2
    B. A single prominent postanal ventral melanophore[2] not large/patch-like relative to other ventral midline pigment or not present 3
1b. Ventral postanal melanophores not arranged in a continuous, uniform series 2
2a. Prominent, postanal ventral melanophore located on 6th or 7th postanal myomere .... *P. maculatofasciatus*[3]
2b. Prominent, postanal ventral melanophore located on 8th or 9th postanal myomere .... *P. clathratus*[4]
2c. Prominent, postanal ventral melanophore location on postanal myomere(s) not discernable (postanal myomeres not countable) 4
3a. Ventral postanal melanophores numerous (>10, as many as 20)
    A. Pectoral fin and/or crown pigment 2
    B. No pectoral fin pigment and no crown pigment .... *P. nebulife*[5]
3b. Ventral postanal melanophores few (<=10) 2
4a. One dorsal melanophore located mid dorsal .... *P. maculatofasciatus*
4b. Two dorsal melanophores located anterior/mid .... *P. maculatofasciatus*
4c. Two dorsal melanophores located mid/posterior .... *P. clathratus*
4d. Three dorsal melanophores located anterior/mid/posterior
    A. Horizontal septum melanophore(s) present .... *P. maculatofasciatus*
    B. No horizontal septum melanophore(s)
        a. Early preflexion .... *P. clathratus*[6] or *P. maculatofasciatus*[7]
        b. Mid-to-late preflexion .... *P. clathratus*

II. Flexion stage

1a. Pectoral fin pigment present on one or both fins 2
1b. No pectoral fin pigment 5
2a. Mediolateral trunk pigment present (not including lateral gut pigment) and/or horizontal septum pigment present .... *P. maculatofasciatus*
2b. No mediolateral trunk pigment or horizontal septum pigment 3

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[1] The postanal ventral melanophore series may originate at the first postanal myomere or near mid-tail and extends to the notochord tip.

[2] When present, the large postanal ventral patch is typically apparent from both the ventral and lateral views and may have a stellate or dendritic appearance. The large patch is also typically darker and generally more than 5-10x the size of other ventral midline pigment, whereas a prominent ventral melanophore is typically only 2-3x larger in size than other ventral midline pigment.

[3] Typically, has either one dorsal melanophore located mid dorsal or two located anterior/mid is also possible); the middle dorsal melanophore is typically more prominent relative to other dorsal melanophores and relative to the middle dorsal pigment of the other two species; all three dorsal melanophores may be large and dendritic in some larvae; may also have horizontal septum melanophores; may also have crown and pectoral fin pigmentation at this stage.

[4] Typically, has either 2 or 3 dorsal melanophores located mid/posterior or anterior/mid/posterior, however, other patterns are possible (e.g., anterior/mid in late pre-flexion; a single posterior melanophore); the posterior dorsal melanophore is commonly prominent relative to other dorsal melanophores and relative to the posterior dorsal pigment of the other two species; lacks horizontal septum melanophores at this stage; may also have pectoral fin pigmentation at this stage.

[5] Typically, has either one or two dorsal melanophores located anterior (or mid dorsal) or anterior/mid; the anterior dorsal melanophore is commonly prominent relative to the other dorsal melanophores and relative to the anterior dorsal pigment of the other two species; early preflexion stage retains three dorsal melanophores; may also have horizontal septum melanophores.

3a. Crown pigment present .... *P. clathratus*
3b. No crown pigment 4
4a. Three dorsal melanophores located anterior/mid/posterior .... *P. clathratus*
4b. Two dorsal melanophores located anterior/mid (mid is typically prominent) .... *P. maculatofasciatus*
4c. Two dorsal melanophores located mid/posterior (posterior is typically prominent) .... *P. clathratus*
4d. One dorsal melanophore located mid dorsal.................... *P. clathratus*[6] *or P.maculatofasciatus*[7] (latter case is more common)
4e. One dorsal melanophore located posterior dorsal.................... *P. clathratus*
4f. No dorsal melanophores.................... *P. maculatofasciatus*
5a. Mediolateral trunk pigment present (not including lateral gut pigment) and/or horizontal septum pigment present.................... 6
5b. No mediolateral trunk pigment or horizontal septum pigment .... *P. maculatofasciatus*[8] *or P. nebulifer*[9]
6a. Crown pigment present.................... *P. nebulifer*
6b. No crown pigment .... *P. maculatofasciatus*[7] *or P. nebulifer*[8]

III. Postflexion stage

1a. Prominent postanal ventral melanophore large/patch-like; may be visible both ventrally and laterally .... *P. clathratus*
1b. Prominent postanal ventral melanophore not large/patch-like or not present 2
2a. Dorsolateral pigmentation below the base of the first dorsal fin 4
2b. No dorsolateral pigmentation 3
3a. Pectoral fin pigment, and
   A. Pigment forms horizontal stripe from snout through eye to operculum.................... *P. maculatofasciatus*
   B. No pigmentation on snout.................... *P. clathratus*
3b. Lacking pectoral fin pigmentation or not discernable 5
4a. Pigment on trunk of body, and
   A. Discrete dorsal saddles extend to trunk as vertical bars .... *P. clathratus*[10]
   B. Dorsolateral pigment lacks saddle pattern.................... *P. maculatofasciatus*
4b. No trunk pigment, and
   A. Discrete dorsal saddles beginning to form vertical bars.................... *P. clathratus*[11]
   B. A single broad dorsal saddle under dorsal fin or just forming.................... *P. nebulifer*[12]
5a. Snout pigment appears to form horizontal stripe through eye to operculum .... *P. maculatofasciatus*
5b. Lacking pigment on snout .... *P. nebulifer*[13]

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[6] Typically, retains large ventral patch throughout stage.
[7] May retain large ventral patch in early flexion. Ventral midline pigment may coalesce into linear segments.
[8] May retain large ventral patch in early flexion. Ventral midline pigment may coalesce into linear segments.
[9] Ventral midline pigment may coalesce into linear segments, becoming dense.
[10] Also typically with crown pigmentation; if discernable, first dorsal fin pigment heavy. Late postflexion typically with horizontal stripe from snout through eye to operculum.
[11] Typically with crown pigmentation; if discernable, first dorsal fin pigment heavy.
[12] Late postflexion stage typically has occipital pigment as well as snout pigment, which may extend horizontally through the eye to the operculum. May also have both crown and pectoral fin pigment in late postflexion.
[13] Early to mid postflexion stage may have crown pigment, but pectoral fin pigment found only in late postflexion.

Table 2. Confusion matrices of the numbers of larvae a) pre and b) post taxonomic key refinement, and c) associated classification performance metrics (in proportions) by species. PCLA = *P. clathratus*, PMAC = *P. maculatofasciatus*, PNEB = *P. nebulifer*, NA = not *Paralabrax* spp. For each species, sensitivity is the true positive rate (proportion correct in column), specificity is the true negative rate (proportion correct of all true non-positives), precision is the positive rate of the taxonomic key (proportion correct in row), and balanced accuracy is the mean of sensitivity and specificity.

a)

		True ID			
		PCLA	PMAC	PNEB	NA
Key ID	PCLA	44	1	1	0
	PMAC	0	2	0	0
	PNEB	6	3	47	0
	NA	2	1	0	9

b)

		True ID			
		PCLA	PMAC	PNEB	NA
Key ID	PCLA	48	0	0	0
	PMAC	3	7	0	0
	PNEB	1	0	48	0
	NA	0	0	0	9

c)

	PCLA		PMAC		PNEB	
	Pre	Post	Pre	Post	Pre	Post
Sensitivity	0.85	0.92	0.29	1.00	0.98	1.00
Specificity	0.97	1.00	1.00	0.97	0.87	0.99
Precision	0.96	1.00	1.00	0.70	0.84	0.98
Balanced Accuracy	0.91	0.96	0.64	0.99	0.92	0.99

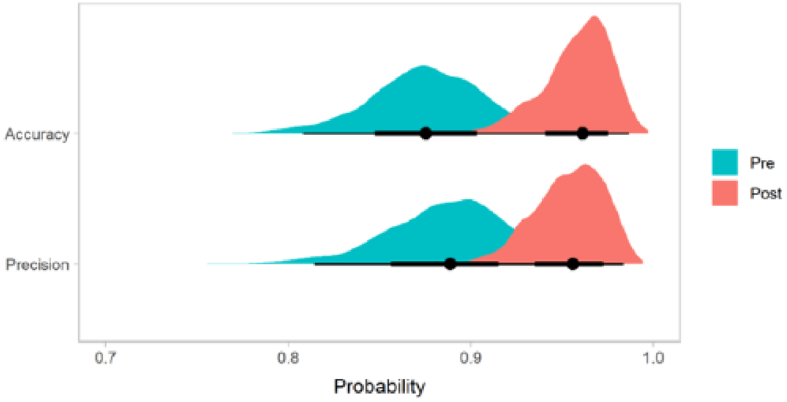

Figure 7. Probability density plots of accurate and precise species classification using the taxonomic key to identify *Paralabrax* larvae, pre and post key refinement. Point estimates and intervals depict Bayesian posterior medians and 66% and 95% credible intervals

Discussion

Using previous knowledge of pigmentation patterns in larval *Paralabrax* from southern California, coupled with machine learning and validation with DNA barcoding, we successfully constructed a robust taxonomic key for use with preflexion, flexion, and postflexion developmental stages. Until now, decades of formalin-preserved *Paralabrax* larvae collected in oceanographic monitoring surveys off California and Baja California could not be visually identified to species level with reasonable certainty due to similarities in their morphology (Moser et al. 2001). In addition, pigmentation patterns observed in a small number of laboratory-reared *Paralabrax* larvae had never been validated on a larger sample size using molecular techniques. The ability to differentiate *Paralabrax* larvae in southern California using morphology alone, with a high degree of confidence, allows access to past, present, and future trends in larval abundance, a proxy commonly used in assessing adult fish spawning stock biomass.

Each larval stage key provides several pathways to distinguish larvae of the three *Paralabrax* species in southern California. One instance in both the preflexion and flexion keys leads to either *P. clathratus* or *P. maculatofasciatus* and two instances in the flexion key lead to either *P. nebulifer* or *P. maculatofasciatus*. In these cases, the location of collection may facilitate accurate identification. For example, adult *P. maculatofasciatus* spawn near the entrances of bays and estuaries (Allen et al. 1995), but the CalCOFI survey in southern California is limited to coastal and offshore waters. If *P. maculatofasciatus* larvae are typically retained within bays and estuaries, this would explain why very few were identified in the CalCOFI plankton samples analyzed in this study. In addition, further south off Baja California, Mexico, the larval abundances of *P. maculatofasciatus* and *P. nebulifer* are higher relative to *P. clathratus* (Avendaño-Ibarra 2004; Avendaño-Ibarra et al. 2004). Thus, depending on the habitat and geographic location of collection, it is likely that when arriving at one of these "either or" key endpoints, one could deduce the true species more often than not.

Pigmentation patterns are useful for distinguishing bass larvae (across preservatives): Pigmentation patterns in fish larvae are largely transient and can vary within and among species. This may result from the ontogenetic migration of melanophores (e.g., dorsal trunk pigment onto dorsal fin) and/or melanophore expansion and contraction. However, we found pigmentation patterns useful for distinguishing among *Paralabrax* larvae from preflexion to postflexion stages. Reliance on pigmentation in the absence of morphometric or meristic characters has also been useful for identifying species of rockfish (subgenus *Pteropodus*) and engraulid larvae (Wang and Tzeng 1997; Taylor and Watson 2004).

Preservation methods can also affect pigmentation in fish larvae (Schnell et al. 2016), suggesting that this morphological feature is less reliable for identifying preserved specimens. In this study, the utility of the pigmentation patterns observed by Butler et al. (1982) in fresh, formalin-preserved *Paralabrax* larvae was tested with ethanol-preserved larvae. Despite our test specimens being preserved in ethanol, most pigmentation patterns were retained, and morphological identities determined using our key were achieved with high accuracy and precision. We have subsequently used our key on decades-old formalin-preserved *Paralabrax* larvae and found that specimens maintained for 50+ years still had reliable pigmentation patterns for classification (data not shown). We also found that melanophores visually identified in older formalin-preserved samples were typically lighter and smaller than those observed in ethanol-preserved, or younger, formalin-preserved samples, indicating that a careful eye is needed when using our key on specimens preserved in formalin for many decades.

Ventral and pectoral fin pigment most important: Prior to this study, we hypothesized that dorsal pigmentation in *Paralabrax* spp. would be the most useful character for delineating species. For example, the presence of three dorsal pigment patches was thought to be a typical pattern in early *P. clathratus* development, while *P. maculatofasciatus* and *P. nebulifer* were thought to have one and two dorsal melanophore(s), respectively (Butler et al. 1982; Watson, 1998). While we also observed these dorsal pigment patterns, there was sufficient interspecific variation such that this character alone was unreliable for species assignment. Contrary to our initial hypothesis, we found ventral pigmentation patterns were more important for accurately classifying preflexion larvae and pectoral fin pigment more important for accurate classification of flexion larvae. Thus, when identifying *Paralabrax* larvae, dorsal pigmentation in preflexion and flexion larvae is best used for final confirmation or corroboration of a species identity once the other pigmentation is already visually established.

Our key also has value for use with *Paralabrax* larvae collected off Baja California, Mexico, and the Gulf of

California. Ventral pigment characters that are important for distinguishing southern California *Paralabrax* larvae also appear distinct from *P. auroguttatus* at the preflexion and flexion stages. Larvae of *P. auroguttatus* can co-occur with the other three *Paralabrax* species along the Pacific Baja California coast but are more common in the Gulf of California (Avendaño-Ibarra et al. 2004, 2014). Larvae of *P. maculatofasciatus,* and *P. nebulifer* have also been documented in the Gulf of California (Avendaño-Ibarra et al. 2014); however, given their adult distributions (Heemstra 1995; Love and Passerelli 2020), larvae of *P. nebulifer* probably occur there relatively less frequently. With a possible northern latitudinal geographic range shift or range expansion of *P. auroguttatus* into southern California waters associated with ocean warming, the ability to distinguish *P. auroguttatus* from southern California *Paralabrax* larvae is likely to become more relevant in the not-too-distant future.

In general, the stage-specific distinguishing features described in Butler et al. (1982) were consistent with our observations; however, we note four major differences here. First, we observed numerous (>10) postanal, midventral melanophores in a few specimens of preflexion stage *P. clathratus* and *P. maculatofasciatus*, whereas Butler et al. (1982) reported 4-8 (mean = 6.2) and 6-11 (mean = 8.0) for each species, respectively. Second, Butler et al. (1982) noted that preflexion *P. clathratus* could be distinguished from the other two species by a lack of horizontal septum pigment, suggesting that this character was common in preflexion *P. nebulifer* and *P. maculatofasciatus*. In this study, horizontal septum pigment was rarely observed in preflexion larvae of the latter two species. However, we did occasionally observe some form of lateral pigment in flexion stage larvae. Thus, it may be that horizontal septum pigment in preflexion larvae is more easily lost during ethanol fixation and preservation. Nevertheless, we chose to include it in the preflexion key because when it is present, it is useful. Third, we found that preserved preflexion *P. clathratus* typically did not have a discernable prominent triangular ventral fin fold pigment patch as described in Butler et al. (1982). Given that net capture of larvae can damage the delicate fin fold, this character is likely more useful with fresh or freshly preserved *Paralabrax* larvae (Butler et al. 1982). Finally, on occasion, we observed pectoral fin pigment in preflexion *P. clathratus* and *P. maculatofasciatus* and in flexion stage *P. maculatofasciatus*, whereas Butler et al. (1982) only noted the formation of pectoral fin pigment in *P. clathratus* during flexion.

A multipronged approach is instrumental for robust key development: We have built upon the classical taxonomic approach for developing a morphological key by incorporating statistical methods and molecular identification as validation. Statistical methods provided an unbiased tool to aid in structuring and refining the key, and the molecular identifications allowed us to test the accuracy and precision of the key. We found multinomial logistic regression a useful exploratory tool for identifying taxonomist-specific subjectivity in assigning larval stages and morphological features. After recalibration, the key was improved to better define the character traits. The RFC was important for identifying which character(s) to include at the beginning of the key because it uncovered the most important characters contributing to high classification accuracy. This multipronged approach provided a reliable, accurate, and cost-effective means to visually identify southern California *Paralabrax* larvae based on pigmentation patterns alone.

The efficacy of the technique we developed, could be applied to other species whose identity thus far has been difficult to discern based on morphology. For example, rockfishes, *Sebastes* spp., were the fourth most common taxon sampled in CalCOFI surveys between 1951-1998 (Moser et al. 2001), but only a handful of rockfish larvae can currently be identified to species based on morphology (e.g., *Sebastes jordani*, *S. paucispinis*, and *S. levis*). Molecular identification of ethanol-preserved larvae from 2005 (Thompson et al. 2016) and 1998-2013 (Thompson et al. 2017) identified 39 species. Given that pigmentation patterns are consistent among species within at least some rockfish subgenera (Taylor and Watson 2004; Watson and Robertson 2004; Watson et al. 2016), this technique may help to identify species-specific characteristics for larval rockfishes.

For many years, *Paralabrax* larvae from southern California were deemed too morphologically similar for species identification. However, we have validated pigmentation patterns as reliable for identifying southern California *Paralabrax* larvae across preservation types. We can now leverage existing and future ichthyoplankton survey collections to evaluate trends in larval abundance of *Paralabrax* spp. from southern California. We have also shown that although pigmentation patterns in fish larvae can commonly show intra- and interspecific variability (Watson 1998; Gray et al. 2006), when they are considered collectively within a strategically arranged taxonomic key, they can be useful for discriminating closely related, morphologically similar species. When constructing a taxonomic key for use with other morphologically similar larvae, we recommend using machine-learning tools along with molecular validation to increase the accuracy and precision of the key's performance.

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Literature cited

Allen L.G., Block H.E. 2012. Planktonic larval duration, settlement, and growth rates of the young-of-the-year of two sand basses (*Paralabrax nebulifer* and *P. maculatofasciatus*: Fam. Serranidae) from Southern California. Southern California Academy of Sciences Bulletin 111: 15-21.

Avendaño-Ibarra R. 2004. Cambios en la abundancia larval del genero *Paralabrax* (Pisces: Serranidae) en Bahía Magdalena, durante 1982-1986. M.Sc. thesis, Departamento de Plancton y Ecología Marina, Instituto Politécnico Nacional Centro Interdisciplinario de Ciencias Marinas. 112 p.

Avendaño-Ibarra R., Aceves-Medina G., Godínez-Domínguez E., De Silva-Dávila R., Jiménez-Rosenberg S.P.A., Urias-Leyva H., Robinson C.J. 2014. Fish larvae from the Gulf of California to Colima, Mexico: An update. Check List 10: 106-121.

Avendaño-Ibarra R., Funes-Rodríguez R., Hinojosa-Medina A., González-Armas R., Aceves-Medina G. 2004. Seasonal abundance of fish larvae in a subtropical lagoon in the west coast of the Baja California Peninsula. Estuarine, Coastal and Shelf Science 61: 125-135.

Butler J.L., Moser H.G., Hageman G.S., Nordgren L.E. 1982. Developmental stages of three California sea basses. California Cooperative Fisheries Investigations Reports 23: 252-268.

Cota-Nieto J.J., Erisman B., Aburto-Oropeza O., Moreno-Báez M., Hinojosa-Arango G., Johnson A.F. 2018. Participatory management in a small-scale coastal fishery-Punta Abreojos, Pacific coast of Baja California Sur, Mexico. Regional Studies in Marine Science 18: 68-79.

Cutler D.R., Edwards T.C., Beard K.H., Cutler A., Hess K.T., Gibson J., Lawler J.J. 2007. Random forests for classification in ecology. Ecology 88: 2783-2792.

Erisman B.E., Allen L.G. 2005. Color Patterns and Associated Behaviors in the Kelp Bass, *Paralabrax clathratus* (Teleostei: Serranidae). Bulletin, Southern California Academy of Sciences 104: 45-62.

Erisman B.E., Allen L.G., Claisse J.T., Pondella II D.J., Miller E.F., Murray J.H., Walters C. 2011. The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Canadian Journal of Fisheries and Aquatic Sciences 68: 1705-1716.

Erisman B.E., Cota-Nieto J.J., Moreno-Báez M., Aburto-Oropeza O. 2017. Vulnerability of spawning aggregations of a coastal marine fish to a small-scale fishery. Marine Biology 164:1–18.

Findlay A.M., Allen L.G. 2002. Temporal patterns of settlement in the temperate reef fish *Paralabrax clathratus*. Marine Ecology Progress Series 238: 237-248.

Gallo N.D., Drenkard E., Thompson A.R., Weber E.D., Wilson-Vandenberg D., Mcclatchie S., Koslow, J.A., Semmens B.X. 2019. Bridging from monitoring to solutions-based thinking: lessons from CalCOFI for understanding and adapting to marine climate change impacts. Frontiers in Marine Science 6: 1-21.

Gaxiola-Castrol G., Najera-Martinez S. 2002. The Mexican oceanographic North Pacific program: IMECOCAL. In: H.P. Batchelder, G.A. McFarlane, B.A. Megrey, D.L. Mackas, W.T. Peterson (Eds.). PICES Scientific Report No. 20. PICES-GLOBEC international program on climate change and carrying capacity. North Pacific Marine Science Organization (PICES). Sidney, B.C., Canada. pp. 14-16.

Gray A.K., Kendall A.W., Wing B.L., Carls M.G., Heifetz J., Li Z., Gharrett A.J. 2006. Identification and first documentation of larval rockfishes in southeast Alaskan waters was possible using mitochondrial markers but not pigmentation patterns. Transactions of the American Fisheries Society 135: 1-11.

Heemstra P.C. 1995. Serranidae. Meros, serranos, guasetas, enjambres, baquetas, indios, loros, gallinas, cabrillas, garropas. In: W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter, V. Niem (Eds.). Guia FAO para identification de especies para lo fines de la pesca. Pacifico Centro-Oriental. Volume II. FAO, Rome, Italy. pp: 1565-1613.

Hyde J.R., Lynn E., Humphreys R., Musyl M., West A.P., Vetter R. 2005. Shipboard identification of fish eggs and larvae by multiplex PCR, and description of fertilized eggs of blue marlin, shortbill spearfish, and wahoo. Marine Ecology Progress Series 286: 269-277.

Jarvis E.T., Gliniak H.L., Valle C.F. 2014a. Effects of fishing and the environment on the long-term sustainability of the recreational saltwater bass fishery in southern California. California Fish and Game 100: 234-259.

Jarvis E.T., Loke-Smith K.A., Evans K., Kloppe R.E., Young K.A., Valle C.F. 2014b. Reproductive potential and spawning periodicity in barred sand bass (*Paralabrax nebulifer*) from the San Pedro Shelf, southern California. California Fish and Game 100: 289-309.

Jiao Y., Du P. 2016. Performance measures in evaluating machine learning based bioinformatics predictors for classifications. Quantitative Biology 4: 320-330.

Kuhn M. 2022. Package "caret": Classification and Regression Training. R package version 6.0-91. Available from: https://CRAN.R-project.org/package=caret.

Liaw A., Wiener M. 2002a. Classification and regression by randomforest. R News 2: 18-22.

Liaw A., Wiener M. 2022b. Package "randomforest." Available from: https://cran.r-project.org/web/packages /randomforest/index.html.

Love M.S., Passerelli J.K. 2020. Miller and Lea's guide to the coastal marine fishes of California, 2nd edition. University of California Agriculture and Natural Resources 202. 419 p.

McClatchie S. 2014. Regional fisheries oceanography of the California current system. The CalCOFI program. Springer. 235 p.

McElreath, R. 2019. Statistical Rethinking 2nd Edition. CRC Press. 601 p.

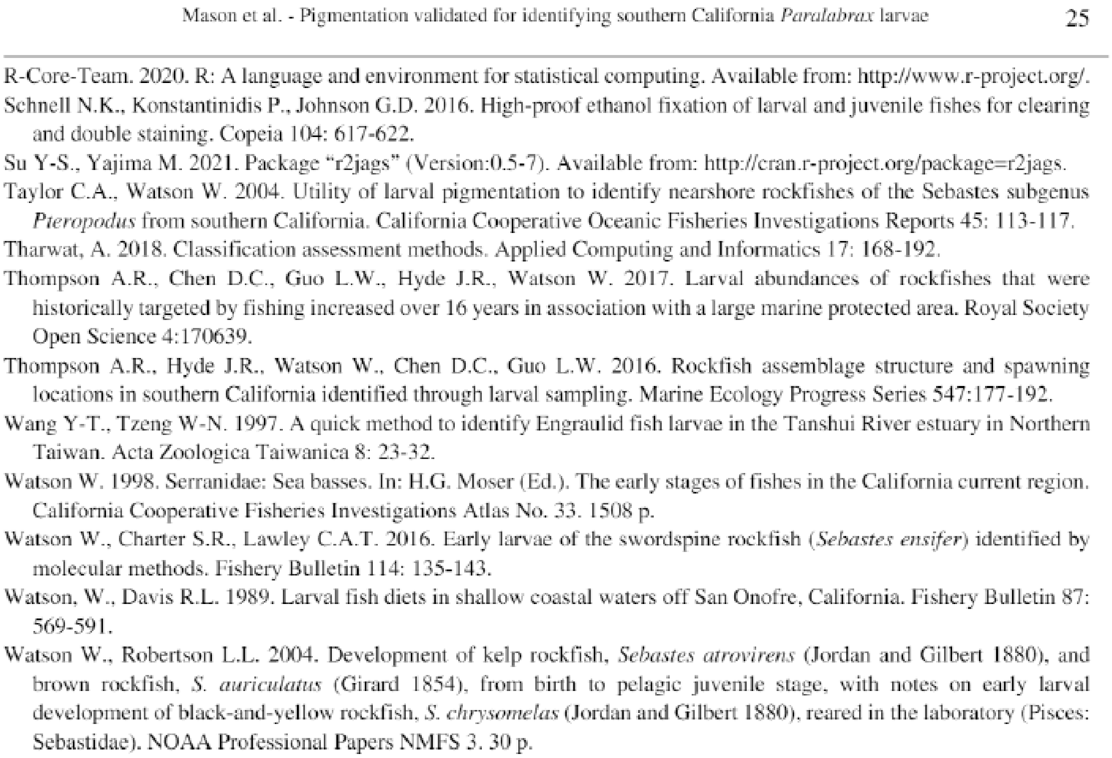
McKinzie M.K., Jarvis E.T., Lowe C.G. 2014. Fine-scale horizontal and vertical movement of barred sand bass, *Paralabrax nebulifer*, during spawning and non-spawning seasons. Fisheries Research 150: 66-75.

Miller B., Kendall A.W. 2009. Early life history of marine fishes. Berkeley: University of California Press. 376 p.

Miller E.F., Erisman B. 2014. Long-term trends of southern California's kelp and barred sand bass populations: A fishery-independent assessment. California Cooperative Oceanic Fisheries Investigations Reports 55: 1-9.

Moser H.G., Charter R.L., Watson W., Ambrose D.A., Hill K.T., Smith P.E., Butler J.L., Sandknop E.M., Charter S.R. 2001. The CalCOFI ichthyoplankton time series: Potential contributions to the management of rocky-shore fishes. California Cooperative Oceanic Fisheries Investigations Reports 42: 112-128.

Plummer M. 2021. Package 'rjags'. Available from: https://cran.r-project.org/web/packages/rjags/index.html.



R-Core-Team. 2020. R: A language and environment for statistical computing. Available from: http://www.r-project.org/.

Schnell N.K., Konstantinidis P., Johnson G.D. 2016. High-proof ethanol fixation of larval and juvenile fishes for clearing and double staining. Copeia 104: 617-622.

Su Y-S., Yajima M. 2021. Package "r2jags" (Version:0.5-7). Available from: http://cran.r-project.org/package=r2jags.

Taylor C.A., Watson W. 2004. Utility of larval pigmentation to identify nearshore rockfishes of the Sebastes subgenus *Pteropodus* from southern California. California Cooperative Oceanic Fisheries Investigations Reports 45: 113-117.

Tharwat, A. 2018. Classification assessment methods. Applied Computing and Informatics 17: 168-192.

Thompson A.R., Chen D.C., Guo L.W., Hyde J.R., 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. Royal Society Open Science 4:170639.

Thompson A.R., Hyde J.R., Watson W., Chen D.C., Guo L.W. 2016. Rockfish assemblage structure and spawning locations in southern California identified through larval sampling. Marine Ecology Progress Series 547:177-192.

Wang Y-T., Tzeng W-N. 1997. A quick method to identify Engraulid fish larvae in the Tanshui River estuary in Northern Taiwan. Acta Zoologica Taiwanica 8: 23-32.

Watson W. 1998. Serranidae: Sea basses. In: H.G. Moser (Ed.). The early stages of fishes in the California current region. California Cooperative Fisheries Investigations Atlas No. 33. 1508 p.

Watson W., Charter S.R., Lawley C.A.T. 2016. Early larvae of the swordspine rockfish (*Sebastes ensifer*) identified by molecular methods. Fishery Bulletin 114: 135-143.

Watson, W., Davis R.L. 1989. Larval fish diets in shallow coastal waters off San Onofre, California. Fishery Bulletin 87: 569-591.

Watson W., Robertson L.L. 2004. Development of kelp rockfish, *Sebastes atrovirens* (Jordan and Gilbert 1880), and brown rockfish, *S. auriculatus* (Girard 1854), from birth to pelagic juvenile stage, with notes on early larval development of black-and-yellow rockfish, *S. chrysomelas* (Jordan and Gilbert 1880), reared in the laboratory (Pisces: Sebastidae). NOAA Professional Papers NMFS 3. 30 p.

Chapter 2, in full, is a reprint of the material as it appears in **Jarvis Mason, E.T.,** Bulkeley, L., Watson, W.W., Sawkins Salazar, A.C., Craig, M.T., Hyde, J.R., Thompson, A.R., Semmens, B.X. 2022. Decoding comparable morphologies: pigmentation validated for identifying southern California *Paralabrax* larvae. *FishTaxa* 25, 9-25. The dissertation author was the primary investigator and author of this material.

CHAPTER 3

A robust template for increasing taxonomic quality assurance in an era of declining taxonomic capacity

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Abstract

Sound conservation efforts heavily rely on accurate taxonomic identification of organisms. Yet, in an era of limited taxonomic capacity, confidence in taxonomic expertise has waned. Here, we present a robust template for identifying taxonomic calibration needs and improving taxonomic quality assurance. Our method includes six steps for use in a variety of applications, including constructing taxonomic keys or field guides, taxonomic training, and conducting standardized periodic quality control and quality assurance measures. This method includes a novel combination of classical taxonomy and modern statistical methods (i.e., Bayesian inference, machine learning) that are useful in identifying important taxonomic characters and taxonomic bias, where and when taxonomic calibration is required, and measuring performance in classifications over time. The template is easy to implement, has wide application, and will be useful for maintaining high taxonomic standards in long-term monitoring efforts and taxonomic key development, even in cases where taxonomic capacity is limited.

3.1 Introduction

Whether a policy maker's aim is to track biodiversity gains and losses or to monitor changes in species' distributions and abundance, their sound conservation efforts heavily rely on accurate taxonomic identification and classification of organisms. Yet, concerns regarding the ongoing decline in taxonomic capacity are prevalent in the literature (Hopkins & Freckleton 2002, McQuatters-Gollop et al. 2017, Saunders 2020); thus, tangible solutions are necessary to counter the associated perceived decline in taxonomic quality assurance (Bik 2017). Technological advances (e.g., molecular, machine learning) have increased our ability to accurately identify and classify organisms (Gold et al. 2021, Goode et al. 2021). However, classical taxonomy and systematics remain essential to these efforts and in some cases, may be the primary tool available, even when taxonomic capacity is limited.

Undoubtedly, the global pandemic of 2020 contributed to already limited taxonomic capacity, affecting researchers worldwide. Motivated by our own limited taxonomic capacity at the height of the pandemic, we developed a multipronged approach to construct a robust taxonomic key critical for completing a multi-species spatiotemporal analysis (Jarvis Mason et al. 2022). At its core, the successful development of a robust species-specific time-series is accurate species identification. As such, Jarvis Mason et al.'s (2022) key was developed based on a need to identify formalin preserved larvae of the serranid fish genus *Paralabrax* and thus, because the identifications could not ultimately be verified through molecular identification (formalin degrades DNA), there was a strong need to demonstrate a high degree of certainty in accurately discriminating among three southern California, USA, *Paralabrax* congeners. This is because prior to development of our key, southern California *Paralabrax* larvae proved to be a problematic group for species discrimination due to similarities in morphology, despite research intended to remedy the problem (Butler et al. 1982, Graves et al. 1990). Just as the pandemic began, we had two taxonomists, one microscope, a preliminary taxonomic key, a limited number of ethanol preserved molecular identifications, and no access to laboratory facilities for further genetic testing. We chose to tackle our problem with a multipronged approach, in which we combined classical visual taxonomy, statistical methods, and molecular identifications of ethanol preserved larvae for validation. After multiple key refinements and periodic taxonomist calibration, we successfully constructed a key in which we demonstrated >96% accuracy and precision in species identifications (across different larval stages) using the key (Jarvis Mason et al. 2022).

Here, we provide a detailed roadmap of our approach to robust taxonomic key development (Fig. 3.1). Whereas Jarvis Mason et al. 2022 provide the key and a brief overview of the approach used to develop the key, here we place emphasis on the process of 1) testing the utility of a select group of character traits for key development, 2) identifying potential taxonomist bias and where to focus taxonomic calibration efforts, 3) testing for accuracy and precision across species and taxonomists, and 4) the post-key development quality assurance process for larval identifications. Finally, we discuss the many ways (beyond key development) one or more steps in our template can be implemented into taxonomic research or biological monitoring programs depending on the user's specific application and needs. All steps can be implemented with ease, in programs with full or limited taxonomic resources, and for the added benefit of incorporating high taxonomic standards into existing and future monitoring programs.

3.2 Methodological approach

Early on, we developed a simple, preliminary key that included a few of the salient, stage-specific morphological characters described for *Paralabrax* in Butler et al. (1982). Using two consecutive batches of molecularly identified specimens, we tested the preliminary key's utility on specimens in Batch 1 with five taxonomists ranging in skill from novice to expert and on specimens in Batch 2 with three of the novice taxonomists used with Batch 1. The results from this exercise revealed several important considerations for next steps. First, accuracy and precision in identifications decreased dramatically between the first and second batches while variability among taxonomists increased (Fig. 3.2). We identified several factors contributing to

1

Develop training data set with known ids

Record morphological characters for each specimen (taxonomists are blind to known ids).

Taxonomic ids are NOT assigned.

2

Use predictive model to test traits

Test the utility of the suite of morphological characters at distinguishing species.

Identify species/traits requiring taxonomic calibration.

3

Use machine learning to identify important traits

Identify the most important morphological characters for accurate species prediction.

4

Develop/refine taxonomic key and recalibrate

Emphasize important traits toward the beginning of the key.

Identify descriptions of traits that require more clarity.

5

Test key for accuracy and precision

Randomize known ids and using refined key, assign taxonomic ids.

Check accuracy and precision across species/taxonomists.

6

Perform periodic QA/QC checks

Calculate percent agreement. Flag discrepancies and reidentify respective specimens.

Figure 3.1. Multipronged approached for robust taxonomic key development.

these results, including the potential for pigment loss caused by preservation, greater intraspecific pigment variability than was anticipated, inadequate training of novice taxonomists in notochord flexion for accurate larval staging, and a lack of strict utilization of the morphological key with the second batch of specimens. Furthermore, it was also deemed possible that taxonomist calibration was necessary for certain characters (e.g., external hindbrain pigment mistaken for dorsal/dorsolateral mid-brain pigment). Thus, we decided that moving forward would require taxonomists to record characters for every larva examined.

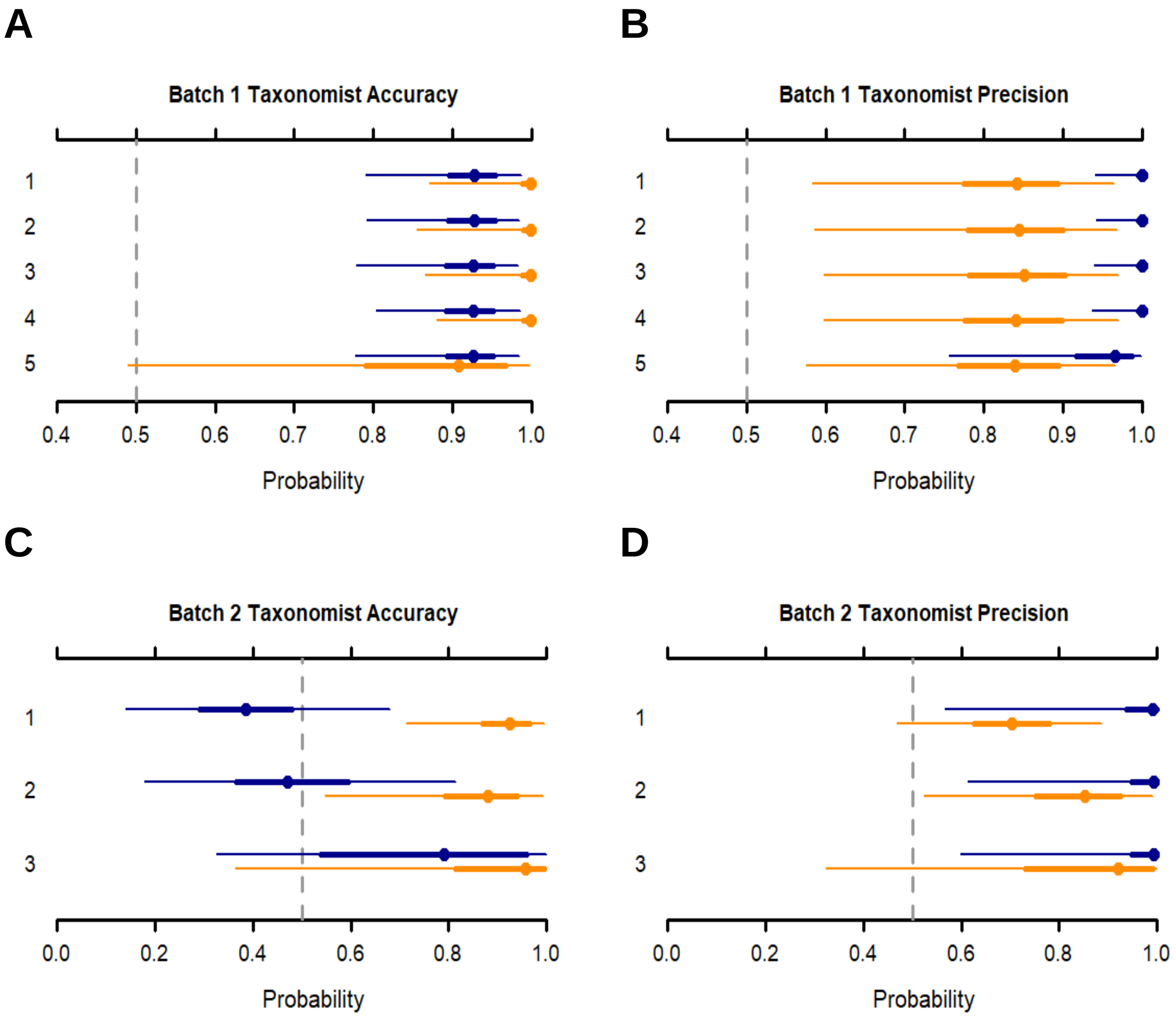

Figure 3.2. Preliminary tests of taxonomic accuracy and precision by taxonomist and species (purple = Barred Sand Bass, orange = Kelp Bass) using two training data sets, a) Batch 1 accuracy, b) Batch 1 precision, c) Batch 2 accuracy, and d) Batch 2 precision. Probability estimates depict Bayesian posterior median and 50% (thick line) and 90% (thin line) credible intervals. In panels A and B, taxonomist was treated as a random effect, and in panels C and D taxonomist was treated as a fixed effect.

For our case study, we developed a multipronged approach to taxonomic key development and post key development implementation that included six primary steps (Fig. 3.1):

1. **Develop training data set with known ids:** Obtain specimens for a group of species with known, verified, identities and identify any presumed or existing character traits that will be considered for species delineation. Create data set with character trait descriptions/counts/measurements for each specimen.
2. **Use predictive model to test traits:** Implement multiclass logistic regression classification methods to test the utility of the selected suite of characters to accurately predict the true species identity with high probability; identify areas in need of improved resolution. Select the suite of character traits that together will provide reliable identification.
3. **Use machine learning to identify important characters:** Implement machine learning methods to identify the most important morphological characters for distinguishing species. Establish the hierarchy of characters from most to least useful within the best suite of characters. Identify species/traits requiring taxonomic calibration.
4. **Develop and refine key:** Using the predictive model results and hierarchy of characters, establish the species distinctions (if any) made possible by each character. Emphasize characters having the broadest application across species at the beginning of the key. Identify descriptions of traits that require more clarity; recalibrate.

5. **Test key for accuracy and precision:** Randomize specimens with known identifications and using the refined key, assign species. Check accuracy and precision across species/taxonomists to ensure reliability of key.
6. **Perform periodic quality control checks:** Calculate percent agreement among taxonomists on a random subset of specimens. Flag discrepancies and reidentify respective specimens. Recalibrate, as necessary, to correct for drift in performance.

Data and code for analyses reported here are available online in a GitHub repository: https://github.com/ ETJarvisMason/tax_QA. We performed all analyses in R 4.2.2 (R-Core-Team 2022).

Template for Robust Taxonomic Key Development

Step 1 – Training Specimens and Data Set

Other Applications: Taxonomic Training of Morphologically Similar Species, Identification of Taxonomist Accuracy and Precision and Calibration Needs

In step 1 of our process (Fig. 3.1), we developed a training data set using molecular identifications of a subset of ethanol preserved *Paralabrax* larvae and some of the characters in the preliminary key as well as other candidate characters (for genetic methods, see Jarvis Mason et al. 2022). For other applications in the use of this template, collection vouchers or reference collection specimens may replace molecularly identified training specimens (e.g., previously validated by a taxonomist specialist, molecular identification, or reared offspring of known identification). Character traits for key consideration may be both qualitative and quantitative (i.e., descriptive, morphometric, and meristic characters).

During the pandemic we were limited to just two taxonomists. For each specimen, the two taxonomists digitally recorded larval stage and stage-specific characters in a morphological character traits table on a laptop sitting adjacent to the microscope (Table 3.1). Taxonomists were blind to the molecular identities of each larva and there was no attempt to assign species at this first step. Taxonomists also took several photographs of each larva (e.g., left and right sides, close-up images of pigmented areas), which were saved on the computer for future reference. Depending on the user's application, character traits tables can be designed for the field or laboratory setting.

Table 3.1. Simplified example of a morphological character traits table used for evaluating character traits across different larval fish developmental stages for taxonomic species discrimination among three species of southern California, USA, *Paralabrax*. Header letters correspond to descriptions of specific character traits. Depending on the character trait, responses recorded across characters (columns) for each specimen (rows) may be binomial (presence=1/absence=0), numeric (counts), categorical (A = anterior dorsal, M = mid dorsal, P = posterior dorsal), categorical ordinal (1 = lacks continuous uniform ventral melanophores, 2 = few (<= 10) ventral melanophores, 3 = many (>10) ventral melanophores), or continuous (5.2 mm).

	Preflexion Characters				Flexion Characters					Postflexion Characters				
Larva	A	B	C	D	E	F	G	H	I	J	K	L	M	N
1	1	0	2	A										
2					0	0	1	0	0					
3					1	0	0	1	0					
4	1	0	2	A										
5										1	2	1	0	0
6					0	0	1	0	0					
7	0	1	0	AMP										

Step 2 – Use Predictive Model to Test Utility of Selected Traits

Other Applications: Taxonomic Training of Morphologically Similar Species, Identification of Taxonomist Calibration Needs, Selection of Characters

In step 2 (Fig. 3.1) we used the known molecular identities and data recorded in the morphological characters table in a multinomial logistic regression Bayesian framework to model the probability of each of three species classifications for every larva (Jarvis Mason et al. 2022):

$$logit(p_{i,j}) = \beta_{1,j} + \beta_{2,j} * k_{1,i} + \beta_{3,j} * k_{2,i} \ldots \beta_{n,j} * k_{n,i}, \text{ where,}$$

$p_{i,j}$ = the probability of specimen *i* being one of *j* classifications, where each classification is drawn from a multinomial probability distribution, and

$\beta_{1,j}$ = the intercept, and all other β parameters correspond to character trait *k* for specimen *i*, up to the n^{th} *k* character trait.

We set the first set of covariates for the first classification category to zero to represent the reference category. Thus, the model parameter estimates for the remaining β parameters are relative to the reference classification (i.e., if the reference classification is species A, then parameter estimates for the character traits for species B will represent the degree to which a particular trait is useful for distinguishing species B from A). We used normally distributed priors for each β parameter.

While the specific model framework we chose to use at this step (e.g., JAGS in R with R package `r2jags`) allows for maximum flexibility in model specification (e.g., specifying distributional forms of priors, the ability to incorporate random effects; Plummer 2022, Su and Yajima 2021), other users may prefer to use alternative R packages that offer specific functions for implementing Bayesian multinomial logistic regression (e.g., R packages `UPG`, `rethinking`, McElreath 2019, Zens et al. 2020). With respect to characters that are categorical, if a character trait has the same response recorded across all observed specimens, that character is not useful in the model and should be removed. The number of specimens to include for testing a suite of characters is going to depend on the number of potential species being considered and the number of characters that are most influential in accurate species delineation. It is desirable to have as many specimens as possible representing a variety of sizes across developmental stages. Thus, establishing whether to increase the sample size of the training data set will be specific to the user and the species group.

In step 2, we were primarily concerned with exploring the utility of the suite of stage-specific characters to correctly identify each larva. Due to variability in taxonomist skill and interspecific variability in character traits, we used the data recorded by each taxonomist in a separate model for each larval stage. In this framework, the model output includes the Bayesian posterior probability distributions and 95% credible intervals for each larva's multinomial classification (i.e., species probability), which we plotted to determine whether the characters clearly distinguished a single species classification with high probability for most larvae (i.e., is there clear separation in the species probability distributions for most larva?). We also compared plots for each model to see if there was consistency in results between the two taxonomists (Fig. 3.3). Within these plots we incorporated the true species identities (based on molecular identifications) to quickly visualize whether the suite of characters accurately predicted the true species for most larvae (Fig. 3.3).

If a user's model output results in moderate to strong overlap among species probability distributions, we recommend identifying other candidate characters and starting over. We also recommend exploring caterpillar plots of the model's coefficient estimates to

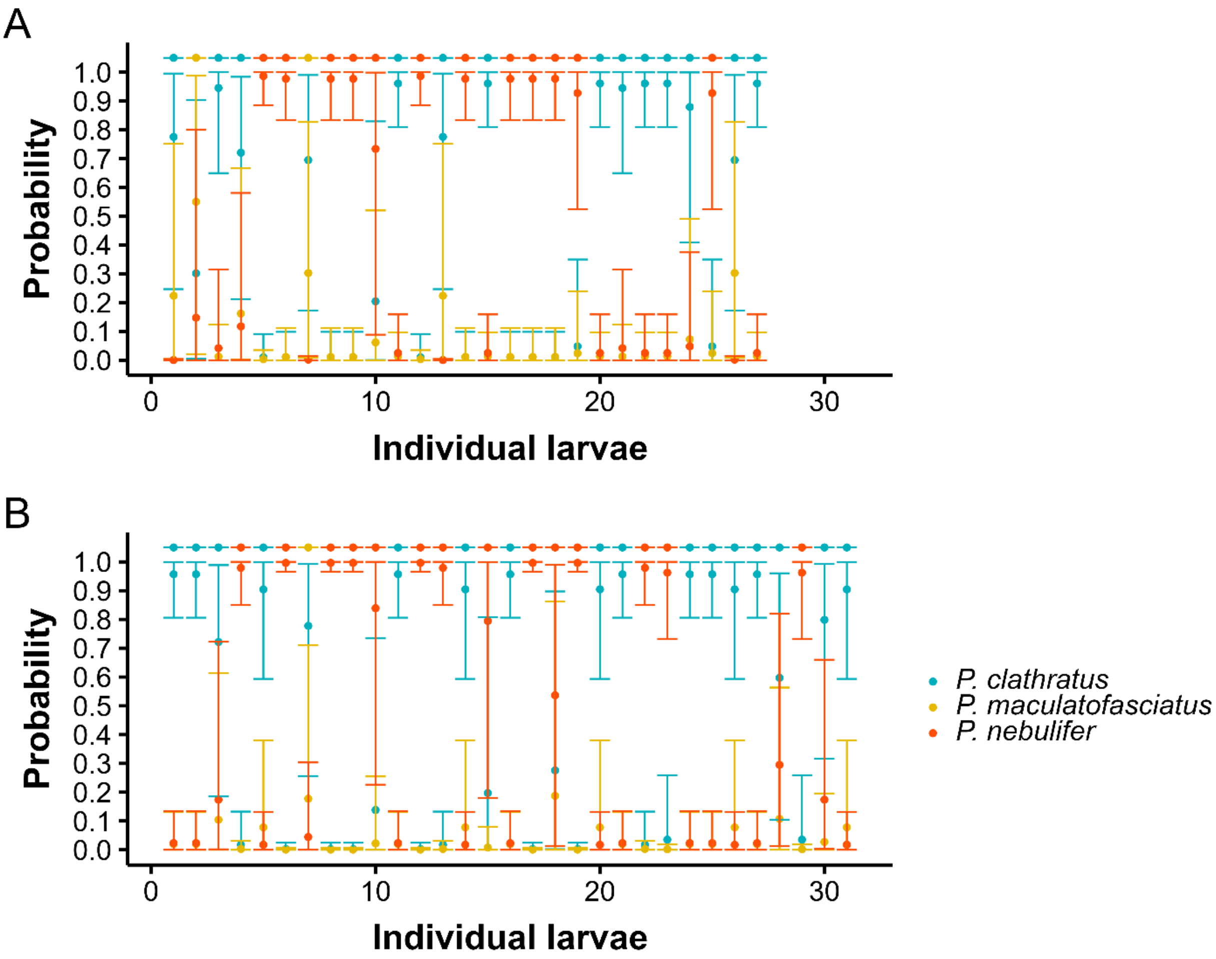

Figure 3.3. The probability that an individual preflexion larvae is each of three species of *Paralabrax* based on a suite of morphological character traits independently recorded by two taxonomists (panels A and B). The true identities of each larva (as determined by molecular identification) are shown at the top of each panel. Each probability depicts Bayesian posterior medians and 95% Credible Intervals. Individual larvae numbers do not correspond to the same larva in each panel. Differences in the number of individual larvae between panels reflect differences in taxonomist assignment of larval development stage.

identify which characters warrant retaining for further consideration in key development and to identify any taxonomic calibration needs (Fig. 3.4). Any clear overlap of model coefficients with zero indicate characters that may not be suitable for further consideration, whereas coefficients with no overlap or only moderate overlap of zero (i.e., zero not contained with the Bayesian 50% credible interval) should be retained (Fig. 3.4). It is

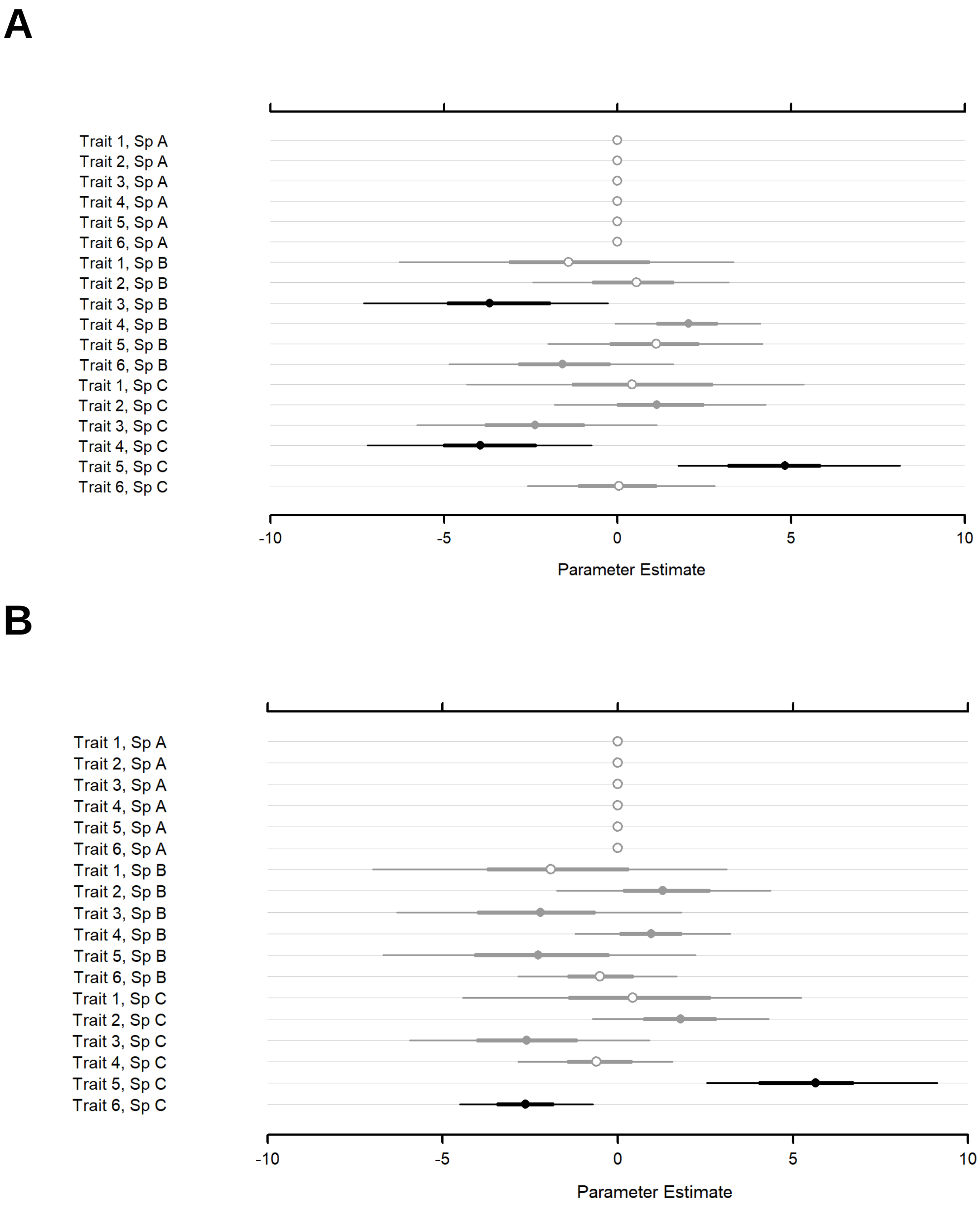

Figure 3.4. Caterpillar plots of multinomial logistic regression model parameter estimates (Bayesian posterior medians and credible intervals) by taxonomic character trait and species (A, B, C) for data recorded on the same specimens by two different taxonomists (panels A and B). Credible lines depict 50% (thick) and 90% (thin) intervals. Open gray circles indicate both 50% and 90% credible intervals overlap with zero, while closed gray circles indicate only 90% credible intervals overlap with zero. Species A is the reference species and thus parameter estimates are NULL. Parameter estimates are shown relative to species A (i.e., in panel A, Trait 5 has strong ability to differentiate species B from species A).

important to note that some characters having no predictive power may still be useful characters for species confirmation after all other character traits have been considered. For example, it can be helpful to include ancillary characters along with the primary key character(s) in the final couplet for a species for confirmation of species identity (Jarvis Mason et al. 2022).

Discrepancies between model results among taxonomists suggest a need for additional taxonomist training and calibration or the need to clarify or improve qualitative character descriptions that define the characters used in the characters table. Careful review of the model's posterior probability distributions and model coefficients is thus helpful in identifying which species/characters are influencing taxonomist bias. Once the user is satisfied with the suite of characters for constructing a preliminary key, then they are ready for step 3.

Some taxonomy programs may have species groups that are only problematic for newly trained taxonomists. In this case, rather than using the model to help identify the utility of characters for species discrimination, taxonomy groups can use known, well-established key characters among a sample of voucher specimens to build a model that can be useful solely for the purpose of exposing differences among taxonomist skill and the specific morphological traits that are causing confusion. This would be helpful for informing taxonomist calibration as well as future trainings.

Step 3 – Identify the Most Important Characters for Species Delineation

Other Applications: Confirmation or Rejection of Presumed Key Characters, Identification of Taxonomist Calibration Needs

In step 3 (Fig. 3.1) we used a Random Forest Classifier (RFC) in the R package `randomForest` (Liaw & Weiner 2002, 2022) to home in on which specific characters were most successful in accurate species assignment across larval stages, as well as the general hierarchy of the characters. The model output of interest was ‘Variable Importance’ (see Jarvis Mason et al. 2022), in which we plotted variable importance plots by larval stage and taxonomist to visually compare character trait performance (Fig. 3.5). The higher values indicate higher variable performance, while negative values or positive values near zero indicate no predictive power. In our case, we found inconsistencies in variable importance for preflexion stage larvae between taxonomists (Fig. 3.5). If variability among taxonomists exists, we recommend users identify which character(s) are contributing to the bias by having taxonomists examine the specimens together, discussing any potential sources of subjectivity using photographs as aids, and proceed with further taxonomist training and calibration.

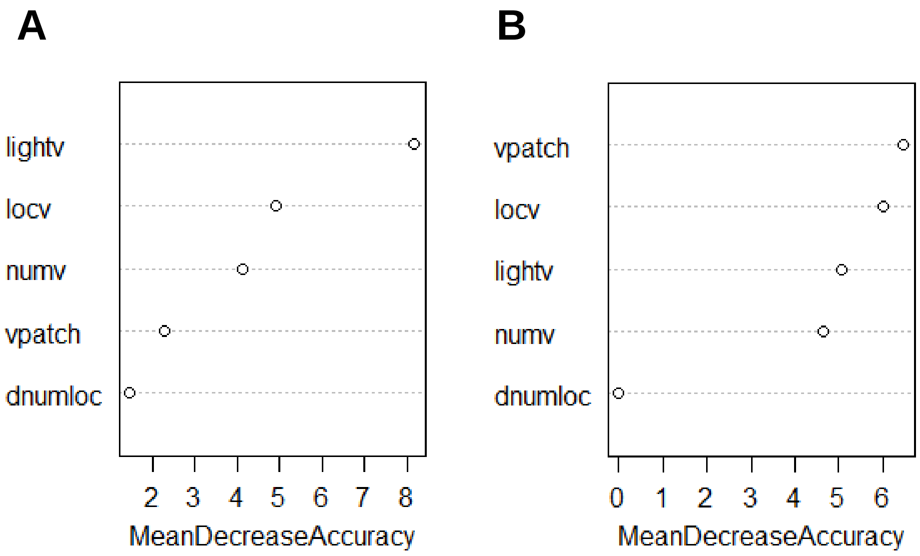

Figure 3.5. Random forest variable importance plots depicting the relative importance of pigmentation characters in contributing to accurate species delineation of *Paralabrax* spp. preflexion larvae based on data collected by two taxonomists on the same specimens (panels A and B). The higher the value, the higher the importance of the character. Descriptions of pigmentation abbreviations are as follows: lightv = presence/absence of a postanal series of uniform ventral melanophores, locv = location of large postanal ventral pigment patch (myomere number), vpatch = presence/absence of large postanal ventral pigment patch, numv = number of postanal ventral melanophores, dnumloc = number and location (anterior, mid, posterior) of dorsal melanophores.

Contrary to expectation, certain characters we initially presumed to be important for discriminating species were ultimately not as important as other characters (e.g., dorsal pigmentation, Jarvis Mason et al. 2022). Thus, in addition to identifying important traits for key development and identifying potential taxonomist bias, step 3 is also a valuable tool for confirming or refuting unvalidated, long-standing beliefs regarding the importance of specific morphological characters in delineating morphologically similar species and which characters are useful for taxonomist training.

Step 4 – Develop and Refine Key

Other Applications: Periodic Quality Assurance Checks During Key Development, Identifying Calibration Needs, Identifying Confusing Language

In step 4 (Fig. 3.1) we used information gained in steps 2 and 3 to determine how best to organize our stage-specific taxonomic key. We were also able to identify the more subjective character traits and rephrased character descriptions with more clarity. When developing a dichotomous key, characters having the broadest application across species should be placed at the beginning of the key. In our case, it turned out that emphasizing the most important character (identified in step 3) at the beginning of the stage-specific keys resulted in earlier delineation of one species from the other two (Jarvis Mason 2022).

Step 5 – Test Key for Accuracy and Precision

Other Applications: Taxonomic Training, Evaluating Taxonomist Performance

We randomized the ethanol preserved samples with known identities and using the refined key, two taxonomists assigned larval stage, digitally recorded data in the morphological characters table, and at this step, also identified each larva to species. Here, genetically identified samples can be substituted with other voucher specimens. We used Bayesian methods to separately model accuracy and precision of taxonomist identifications for each species in a binomial model, treating taxonomist as a fixed effect of classification accuracy and precision (when there are five or more taxonomists, then the model can be reformulated to include a random effect of taxonomist, see code available at https://github.com/ ETJarvisMason/tax_QA):

$$Y_{i,j} \sim dbinom(\theta_{i,j}, n_{i,j}), \text{ where,}$$

$\theta_{i,j}$, in the case of accuracy, is the taxonomist-specific proportion of *n known individuals* of species *j* that are true positives, and in the case of precision, $\theta_{i,j}$ is the taxonomist-specific proportion of *n classifications* of species *j* that are true positives.

We treated θ as drawn from a binomial distribution with uninformative shape parameters ($\alpha = 1$, $\beta = 1$). Our goal was that identifications made using the key would result in at least 90% accuracy and precision for each species. Different users may have various levels of expectation regarding key performance. As such, steps 4 and 5 may require several iterations.

Step 6 – Perform Periodic QA/QC checks

Other applications: Taxonomic Training, Quality Control of Identifications

In step 6 (Fig. 3.1), post key development, we selected a separate small subset of formalin preserved specimens (10%) to be identified by both taxonomists. We then calculated percent taxonomic agreement in specimen identifications, in which we were aiming for greater than 90% agreement. If necessary, taxonomists recalibrated, and where there were differences in identification, those larvae were revisited and reidentified.

Absent two taxonomists for calculating percent agreement, monitoring groups can have a taxonomist periodically complete the morphological traits table and assign species for a small subset of specimens. Using the model in step 2, one can use the new data to predict the species identifications for comparison with the taxonomist's final identification. Percent agreement can be calculated and if it falls below a predetermined data quality objective (DQO, e.g., < 90% agreement), specimens resulting in discrepancies can be flagged and reviewed. Some users tasked with bioassessment monitoring within the same survey region may consider using this step to compare percent agreement with model predictions on difficult taxonomic groups across agencies or laboratories.

DQOs may vary by organization. It is important that accuracy, precision, and percent agreement goals represent the DQO specified in the organization's quality assurance/quality control (QA/QC) protocol (McDermott et al. 2011). Beyond satisfying reporting requirements, periodic evaluation of taxonomist or interagency performance aids in decreasing taxonomist errors over time.

3.3 Discussion

In the year 2020, the world's health and economy were devastated by a global pandemic, resulting in, among other catastrophes, severe limits to scientific research capacity, including taxonomic capacity. Researchers worldwide inevitably developed innovative solutions to deal with limited resources for conducting newly funded research and maintaining long-term monitoring efforts (Robertis et al. 2021). In that same vein, we adapted our taxonomic approach to incorporate a multitude of taxonomic tools to increase taxonomic assurance, and when considered together, can be tailored to fit many specific taxonomic needs or concerns, despite limits to taxonomic capacity.

Uses, Applications, and Benefits

In the field of taxonomy there are two broad categories: research taxonomy and production taxonomy (Stribling et al. 2003). Research taxonomy refers to scientific inquiry intended to document and describe new species, geographic range expansions, salient morphological/anatomical characters of specific groups of species, and phylogenetic relationships. Focus is generally on a single species or group of species, with emphasis on high taxonomic resolution (Stribling et al. 2003). In contrast, production taxonomy refers to small and large-scale business efforts to collect, inventory, and report biological data for long-term community assessments and may or may not include research taxonomy or require high taxonomic resolution. One sector of production taxonomy that is increasing includes participatory science (i.e., citizen science), in which volunteers from the public assist scientists in identifying organisms (Ashley et al. 2022). Our template has utility across all sectors.

Though the primary use of our template was for taxonomic key development to increase the reliability of our identifications of formalin preserved specimens, our method can be applied to a multitude of specific needs across many applications in taxonomy. These methods provide quality control measures to increase quality assurance. Here, quality control refers to measures taken to reduce identification errors, while quality assurance refers to confidence in the accuracy and quality of the data reported. Applications of our quality controls measure include, but are not limited to, resolving long-standing identification issues for “difficult” species groups, identification of formalin preserved specimens for which genetic analysis is unfruitful, resolving taxonomic bias due to taxonomist subjectivity in interpretation of dichotomous keys and character descriptions, updating and reevaluating outdated or problematic dichotomous keys or voucher specimens, periodic calibration checks for maintaining quality assurance, and auditing. Whereas quality control can also include evaluating performance in the enumeration of organisms, our method focuses on increasing intrinsic taxonomic data quality of classifications (i.e., accuracy, objectivity, consistency, and credibility; Vaddepalli et al. 2023).

End-users of taxonomic data require high quality data for resource management and environmental policy decisions such as those related to habitat protection, fishing and hunting regulations, designation listings of endangered species, and mediating climate change impacts to biodiversity. Indeed, in the face of climate change, ensuring high quality taxonomic data is ever more important, as species range expansions and latitudinal shifts in geographic distributions are likely to result in increased encounters with unfamiliar species (Pinsky et al. 2020). This will impact bioassessment monitoring groups, including citizen science programs, and opportunistic species occurrence data collected by the public through online applications (Sharma et al. 2018, Ball-Damero et al. 2019). Our method offers quality control measures that may help to reduce confusion and increase taxonomist precision. Finally, just as taxonomy data producers have a responsibility to provide high quality taxonomic data, end-users have a responsibility to understand the uncertainty in the quality of data produced. Our method serves both efforts and helps to establish the importance of reporting how taxonomic identifications are made and at what level of confidence so that hopefully, the practice becomes a norm (Bianchi & Goncalves 2021).

Potential sources of error introduced into taxonomic data may include variability in taxonomist skill, reliance on ephemeral morphological characters (i.e., coloration), potential transfer of misguided or outdated knowledge among generations of taxonomists, taxonomist bias (i.e., consistent misinterpretation of dichotomous keys or morphological features), improper handling, storage, and preservation of specimens, and poor lighting or optical equipment (Stribling et al. 2003). Due to the many ways that taxonomic data quality can be compromised, the industry standard is to identify specific DQOs and to implement regular QA/QC measures to ensure those DQOs are being met (Stribling 2003). This often comes in the form of specifying protocols for data collection, identifying appropriate training materials (e.g., manuals, photographs, videos, keys, guides), special procedures for dealing with problematic species, and independent taxonomic verification by specialists (Stribling et al. 2003, 2008). Our template aids this process by providing an easy, objective approach that reduces errors and ultimately, the time required for independent taxonomic verification by a taxonomic expert.

Practicality and Value

DNA barcoding is often used as an alternative to morphological identification (Ko et al. 2013), as a tool to augment existing methods (Hammer et al. 2020) and has been shown to increase the sensitivity of bioassessments to detect slight changes in ecosystems (Stein et al. 2014). However, for bioassessments borne out of production taxonomy, relying on barcoding for all identifications or for providing periodic genetic taxonomic verification or validation, may not be possible for rare or endangered species or may not be logistically or economically feasible (Radinger et al. 2019). Like artificial intelligence and machine learning algorithms that can be used to classify or identify problem organisms (e.g., Borba et al. 2021), our method incorporates objective training of a model. However, instead of relying on the model or a decision tree to predict based on new data, we use the model training process to inform identifications with the human eye, as well as to inform calibration and performance. In either case, aside from automatic computer-based identification methods using images of specimens (Ärje et al. 2020), data on morphological or anatomical characters must be recorded. The value this eventually holds is worth the initial effort and investment in time to potentially resolve the issue, as not only is accuracy and precision improved, but so too is the overall taxonomic resolution of the data the program reports or analyses. Furthermore, we provide access to the data and code, which can be implemented by novice users and modified as needed by more advanced users. Once the training set is developed, the template requires no (to little) extra effort beyond what is typically expected in long-term biological monitoring programs.

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Literature Cited

Ärje J, Melvad C, Jeppesen MR, Madsen SA, Raitoharju J, Rasmussen MS, Iosifidis A, Tirronen V, Gabbouj M, Meissner K, Høye TT (2020) Automatic image-based identification and biomass estimation of invertebrates. Methods Ecol Evol 11:922–931.

Ashley EA, Pattengill-Semmens C V, Orr JW, Nichols JD, Gaydos JK (2022) Documenting fishes in an inland sea with citizen scientist diver surveys: using taxonomic expertise to inform the observation potential of fish species. Environ Monit Assess 194:227.

Ball-Damerow JE, Brenskelle L, Barve N, Soltis PS, Sierwald P, Rüdiger B, LaFrance R, Ariño AH, Gurainick RP (2019) Research applications of primary biodiversity databases in the digital age. PLoS One 14:1–26.

Bianchi FM, Gonçalves LT (2021) Getting science priorities straight: how to increase the reliability of specimen identification? Biol Lett 17:20200874.

Bik HM (2017) Let's rise up to unite taxonomy and technology. PLoS Biol 15:4–7.

Borba VH, Martin C, Roberto J, Silva M, Xavier SCC, Mello FL De, Iñiguez AM (2021) Machine learning approach to support taxonomic species discrimination based on helminth collections data. Parasit Vectors:1–15.

Butler, JL, Moser HG, Hageman GS, Nordgren LE (1982) Developmental stages of three California sea basses. *CalCOFI Reports*, 23:252-268.

Gold Z, Sprague J, Kushner DJ, Marin EZ, Barber PH (2021) EDNA metabarcoding as a biomonitoring tool for marine protected areas. PLoS One 16:1–19.

Goode K, Weber MJ, Matthews A, Pierce CL (2021) Evaluation of a Random Forest Model to Identify Invasive Carp Eggs Based on Morphometric Features. North Am J Fish Manag:1–15.

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

Hammer MP, Taillebois L, King AJ, Crook DA, Wedd D, Adams M, Bertozzi T, Unmack PJ, Hoese DF (2021) Unravelling the taxonomy and identification of a problematic group of benthic fishes from tropical rivers (Gobiidae: *Glossogobius*). J Fish Biol 99:87–100.

Hopkins GW, Freckleton RP (2002) Declines in the numbers of amateur and professional taxonomists: Implications for conservation. Anim Conserv 5:245–249.

Jarvis Mason ET, Bulkeley L, Watson WW, Sawkins Salazar AC, 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.

Ko HL, Wang YT, Chiu TS, Lee MA, Leu MY, Chang KZ, Chen WY, Shao KT (2013) Evaluating the Accuracy of Morphological Identification of Larval Fishes by Applying DNA Barcoding. PLoS One 8:3–9.

Liaw A, Wiener M (2002) Classification and regression by randomforest. R News 2:18–22.

Liaw A, Wiener M (2022) Package "randomforest." Available from: https://cran.r-project.org/web/packages/randomforest/index.html.

McDermott H, Paull T, Strachan S (2011) CABIN laboratory methods: processing, taxonomy, and quality control of benthic macroinvertebrate samples. Environment Canada, Ontario, Ottowa, Canada, p 36

McElreath R (2019) Statistical Rethinking: A Bayesian Course with Examples in R and STAN, 2nd ed. CRC Press.

McQuatters-Gollop A, Johns DG, Bresnan E, Skinner J, Rombouts I, Stern R, Aubert A, Johansen M, Bedford J, Knights A (2017) From microscope to management: The critical value of plankton taxonomy to marine policy and biodiversity conservation. Mar Policy 83:1–10.

Moulton II, SR, Carter JL, Grotheer SA, Cuffney TF, Short TM (2000) Methods of analysis by the U.S. Geological Survey National Water Quality Laboratory — processing, taxonomy, and quality control of benthic macroinvertebrate samples. Open-File Report 00-212. Denver, Colorado, USA

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.

Plummer M, Stukalov A, Denwood M (2022) Package ' rjags '.

Radinger J, Magurran AE, Benejam L, Britton JR, Carlson SM, Diego J, Hernández A, Almodóvar A, Delgado CF, Nicola GG, Oliva FJ, Mar P, Emili T, Berthou G (2019) Effective monitoring of freshwater fish. Fish Fish 20:729–747.

Robertis A De, Levine M, Lauffenburger N, Honkalehto T, Ianelli J, Monnahan CC, Towler R, Jones D, Stienessen S, Mckelvey D (2021) Uncrewed surface vehicle (USV) survey of walleye pollock, *Gadus chalcogrammus*, in response to the cancellation of ship-based surveys. ICES J Mar Sci 0:1–12.

Saunders TE (2020) Taxonomy at a crossroads: Communicating value, building capability, and seizing opportunities for the future. Megataxa 1:63–66.

Sharma N, Colucci-Gray L, Siddharthan A, Comont R, van der Wal, R (2019) Designing online species identification tools for biological recording: the impact on data quality and citizen science learning. PeerJ 6:e5965.

Stein ED, White BP, Mazor RD, Jackson JK, Battle JM, Miller PE, Pilgrim EM, Sweeney BW (2014) Does DNA barcoding improve performance of traditional stream bioassessment metrics? Freshw Sci 33:302–311.

Stribling JB, Moulton II SR, Lester G (2003) Determining the quality of taxonomic data. J North Am Benthol Soc 22:621–631.

Stribling JB, Pavlik KL, Holdsworth SM, Leppo EW (2008) Data quality, performance, and uncertainty in taxonomic identification for biological assessments. 27:906–919.

Su Y-S, Yajima M (2021) Package ‘R2jags’ (Version:0.5-7).

Vaddepalli K, Palacin V, Porras J, Happonen A (2023) Taxonomy of Data Quality Metrics in Digital Citizen Science. In: *Intelligent Sustainable Systems*. Nagar AK, Singh Jat D, Mishra DK, Joshi A (eds) Springer Nature Singapore, Singapore, p 391–410

Zens G, Frühwirth-Schnatter S, Wagner H (2021) Efficient Bayesian Modeling of Binary and Categorical Data in R: The UPG Package.

CHAPTER 4

Environmentally driven trends in fish larval abundance predict fishery recruitment in two temperate reef congeners: mechanisms and implications for management

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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 relating environmental covariates and 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 and 2) to evaluate spatiotemporal trends in their population dynamics relative to environmental variables. Importantly, we tested bass larval abundance as a useful indicator of adult stock status and predictor of future fishery recruitment. Contrary to expectation, species-specific larval abundance predicted future catch across multiple catch data sets. Strong relationships between environmental variables and larval abundance demonstrate additional considerations in predicting future fishery recruitment and population status. 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.

4.1 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 likely result in 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 and at one time, more common north of southern California (Hubbs 1948, Moser et al. 2001b, Hsieh et al. 2005, Jarvis et al. 2014a). Thus, it is possible that northern latitudinal shifts in saltwater bass larvae abundance have taken place through time, coinciding with decadal 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 survey (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 defined 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. 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 has only recently been 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, Cushing 1990, Lasker 1987, 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 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 (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.

4.2 Methods

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, during July cruises from 1963 to 2016 (Fig. 4.1a) because: 1) July corresponds to peak spawning for *P. nebulifer* and *P. clathratus*, 2) *Paralabrax* spp. larvae occur nearshore (Moser et al. 2001a), and, 3) the CalCOFI ichthyoplankton archive is currently 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: 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 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. 4.1a) 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./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. 4.1b, McClatchie 2014, Hickey 1993). 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. 4.1b, McClatchie 2014).

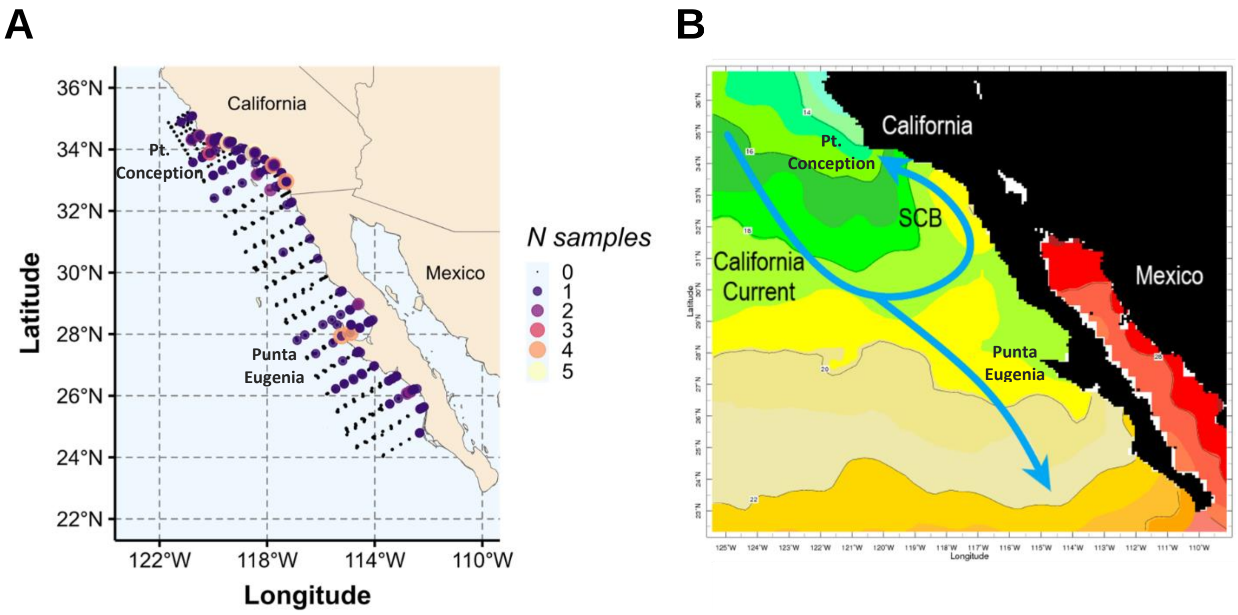

Figure 4.1. Maps of a) CalCOFI station locations surveyed during July cruises and numbers of samples per station from 1963 to 2016 from which formalin preserved *Paralabrax* spp. larvae were identified to species, and b) representative sea surface temperature contours off southern California, USA and 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 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.

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 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. When 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 (i.e., missing larvae), we estimated the missing count based on the average proportion of each species 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. 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 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 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.

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:

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

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

$$\omega_s \sim \boldsymbol{MVNormal}(\boldsymbol{0}, \Sigma_{\omega_s}),$$

$$\epsilon_{s,t} \sim \boldsymbol{MVNormal}(\boldsymbol{0}, \Sigma_{\epsilon_{s,t}}), \text{ where,}$$

$\mu_{s,t}$ 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 (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.

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). 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, we were able to substitute catch for CPUE because for this fishery the two directly correspond (Jarvis et al. 2014a) and because species-specific CPUE at the trip level was not available prior to 1980. CPFV catch records reflect only fish kept (harvested catch). Hyperstable catches, stable catches despite population declines, are known to occur in aggregation-based fisheries (e.g., BSB), and as such, CPUE/catch may overestimate abundance and result in a non-linear relationship. Nevertheless, 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.

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).

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.

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 (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. 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.

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).

4.3 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.

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).

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 4.1; 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. 4.2). 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. 4.2a). 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. 4.2b).

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 vary depending on species, location, and year.

Relationship with Fishery Catch Data

We found no relationship at a lag of zero between species-specific bass larval abundance estimates and fishery catch data, with either catch data set (Fig. 4.3). However, for both species, we found larval abundance led fishery catch data from between two and ten years, depending on the species and catch data set. 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. 4.3a). We found a similar trend with the harvest catch 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 catch data, larvae led catch by five to ten years (Fig. 4.3b). The biggest difference between KB and BSB is that KB also showed a positive correlation at a lag of zero (though not as strong as the other lags) and BSB did not (Fig. 4.3).

Table 4.1. 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.

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. 4.4). The larger

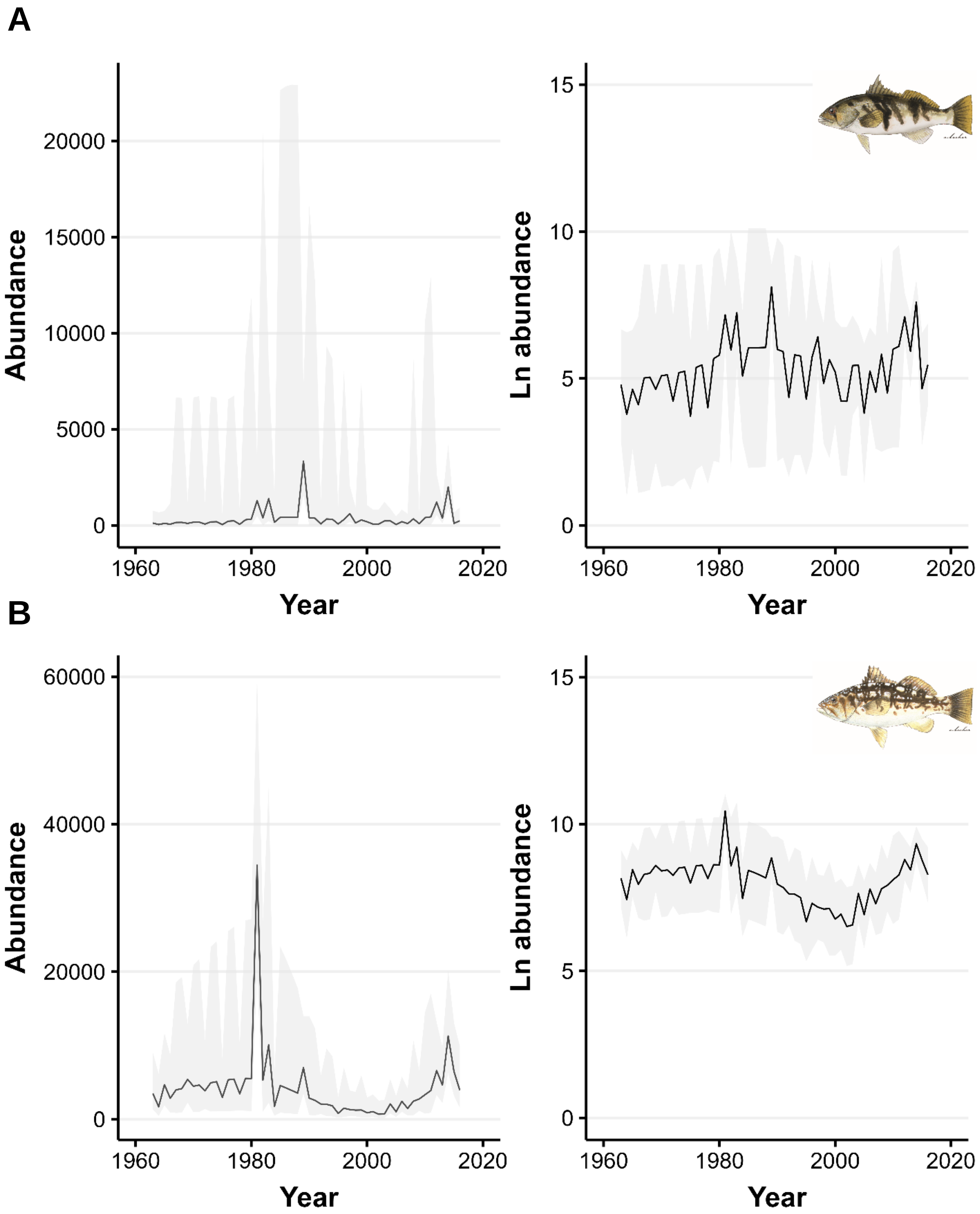

Figure 4.2. Standardized indices of larval abundance on the link scale (left panels) and natural log scale (right panels) for a) Barred Sand Bass and b) Kelp Bass in southern California, USA, 1963-2016. Shaded ribbons denote 95% confidence intervals.

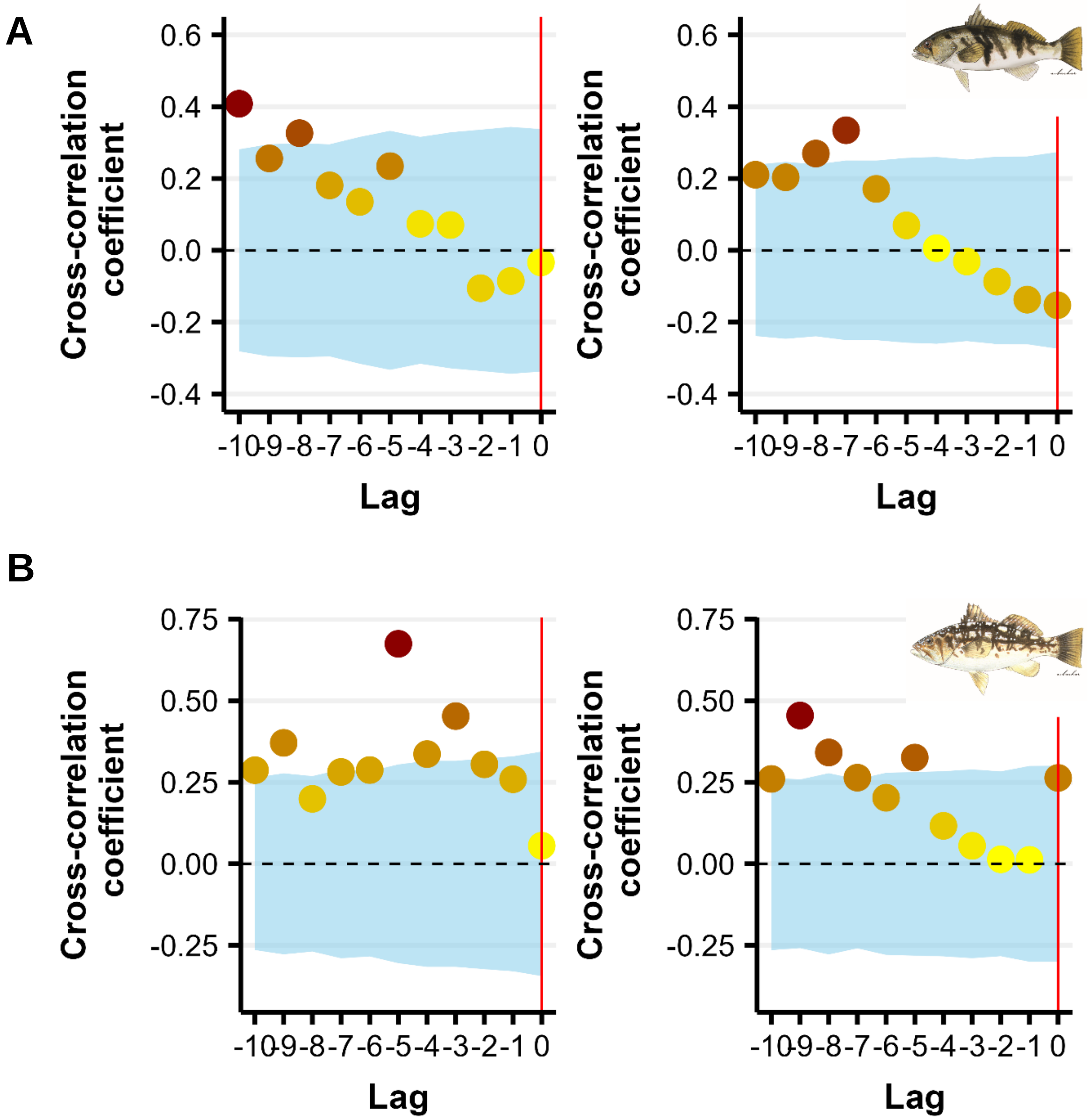

Figure 4.3. Cross-correlation coefficients between lagged larval abundance and total catch estimates (left panels) and total numbers harvested (right panels) for a) Barred Sand Bass and b) Kelp Bass in southern California, USA. Negative lags represent larvae leading catch. Shaded ribbon denotes the 95% 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).

scale environmental variables were available annually but the BEUTI, CUTI, and ILD for southern California were only available from 1980 onward (Fig. 4.4). There was little collinearity among the 45 combinations of environmental variables (most correlations were

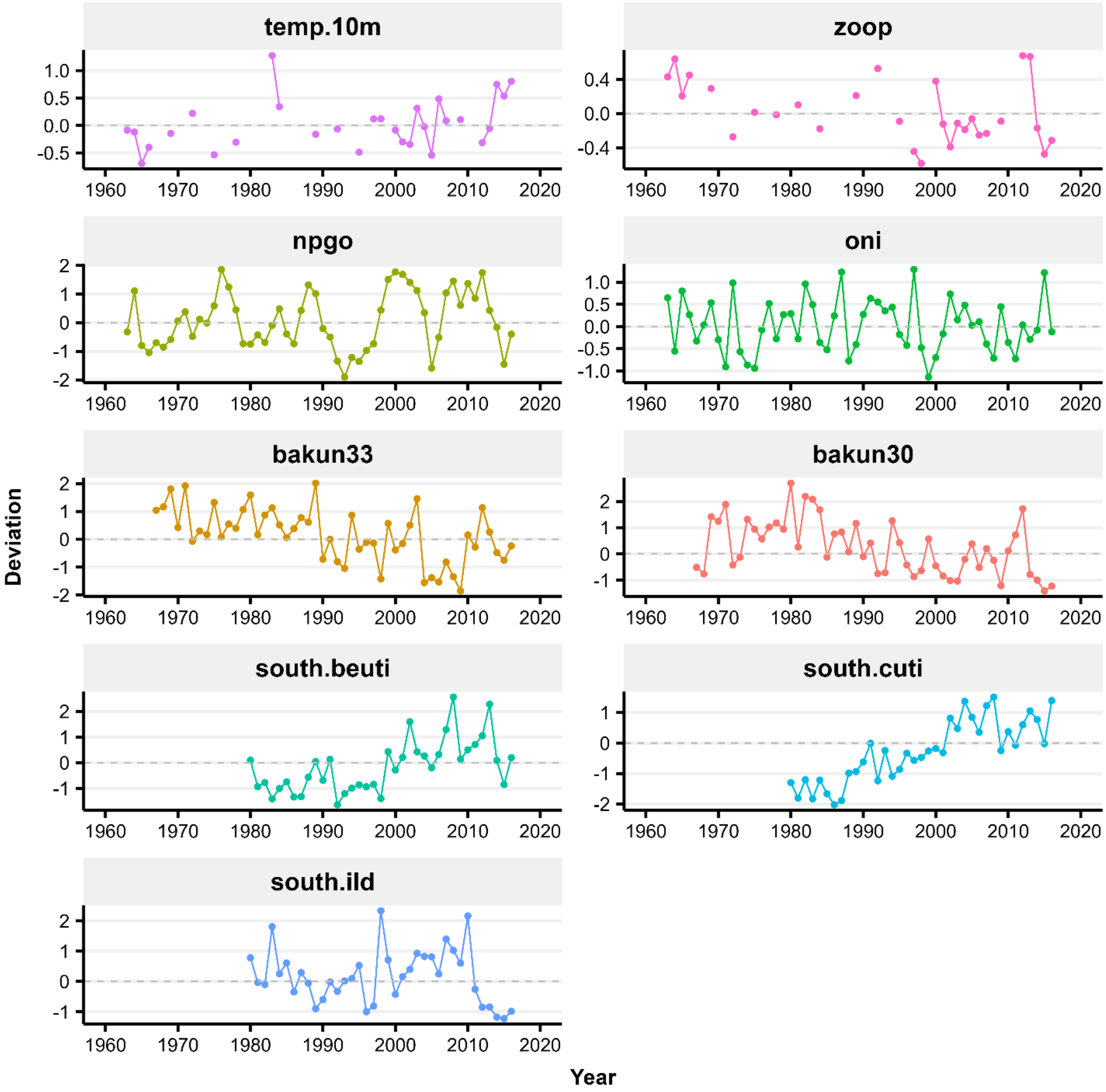

Figure 4.4. Temporal trends in standardized environmental variables selected for modeling southern California, USA, *Paralabrax* spp. larval abundance. Temp.10m = CalCOFI temperature averaged from the sea surface down to 10 m depth, zoop = CalCOFI zooplankton biomass, npgo = North Pacific Gyre Oscillation 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 Fisheries Investigations

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. 4.5, 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. 4.5a, 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. 4.6, S12, S13). Of the different upwelling indices considered (Bakun, BEUTI, CUTI), models with the Bakun index were more parsimonious (Table 4.2); 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. 4.6a, S13).

Latitudinal Shifts in Bass Larval Abundance

Bass larval abundance center of gravity within the SCB remained remarkably consistent

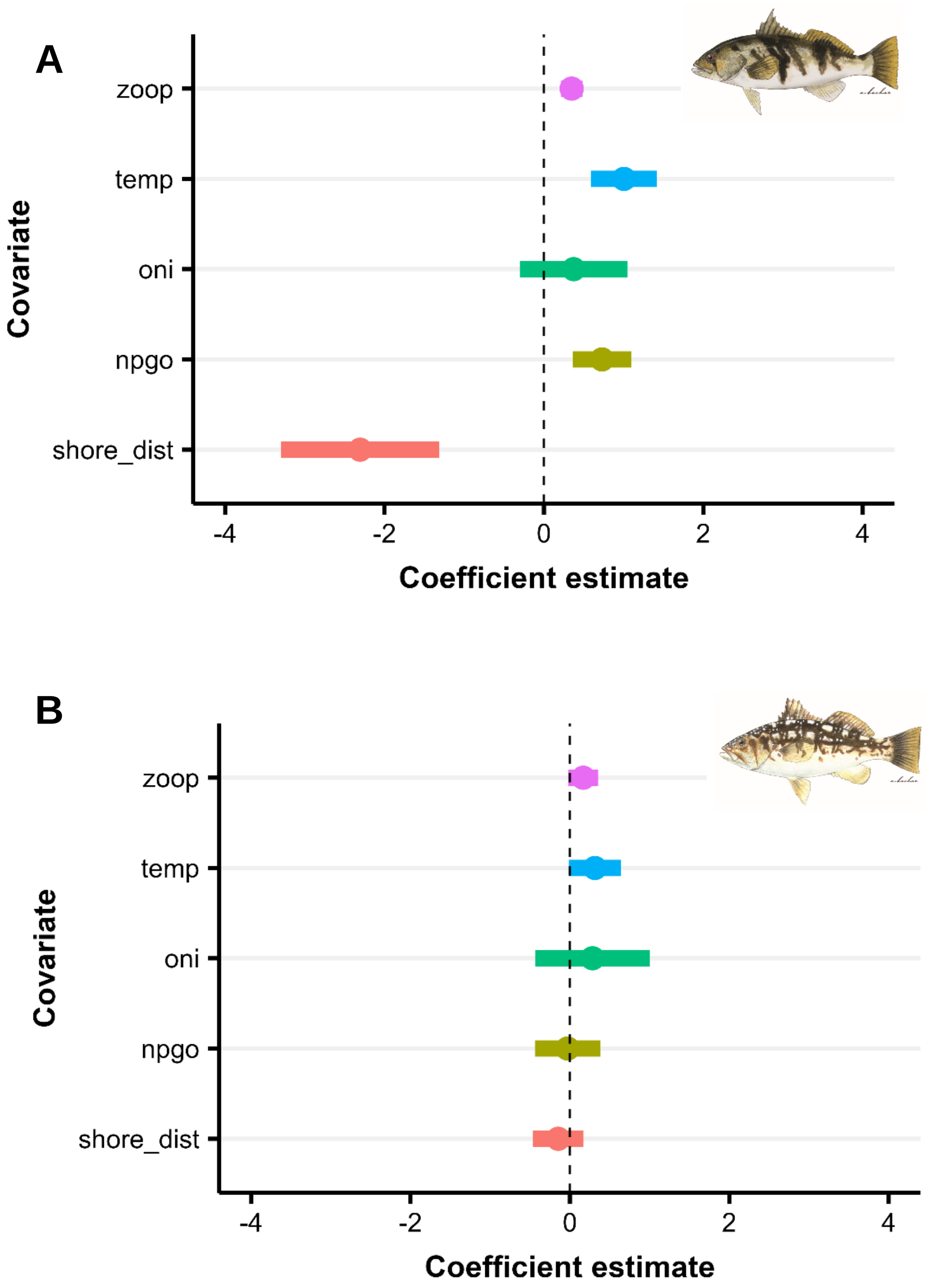

Figure 4.5. Model 1 coefficient estimates of the generalized linear mixed effects model depicting the relationships between bass larval abundance and environmental covariates from 1963 to 2016 for a) Barred Sand Bass and b) Kelp Bass in southern California, USA zoop = CalCOFI zooplankton biomass, temp = CalCOFI 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 to mainland coast. Coefficients greater than (less than) one indicate positive (negative) relationships. Lines depict 95% confidence intervals.

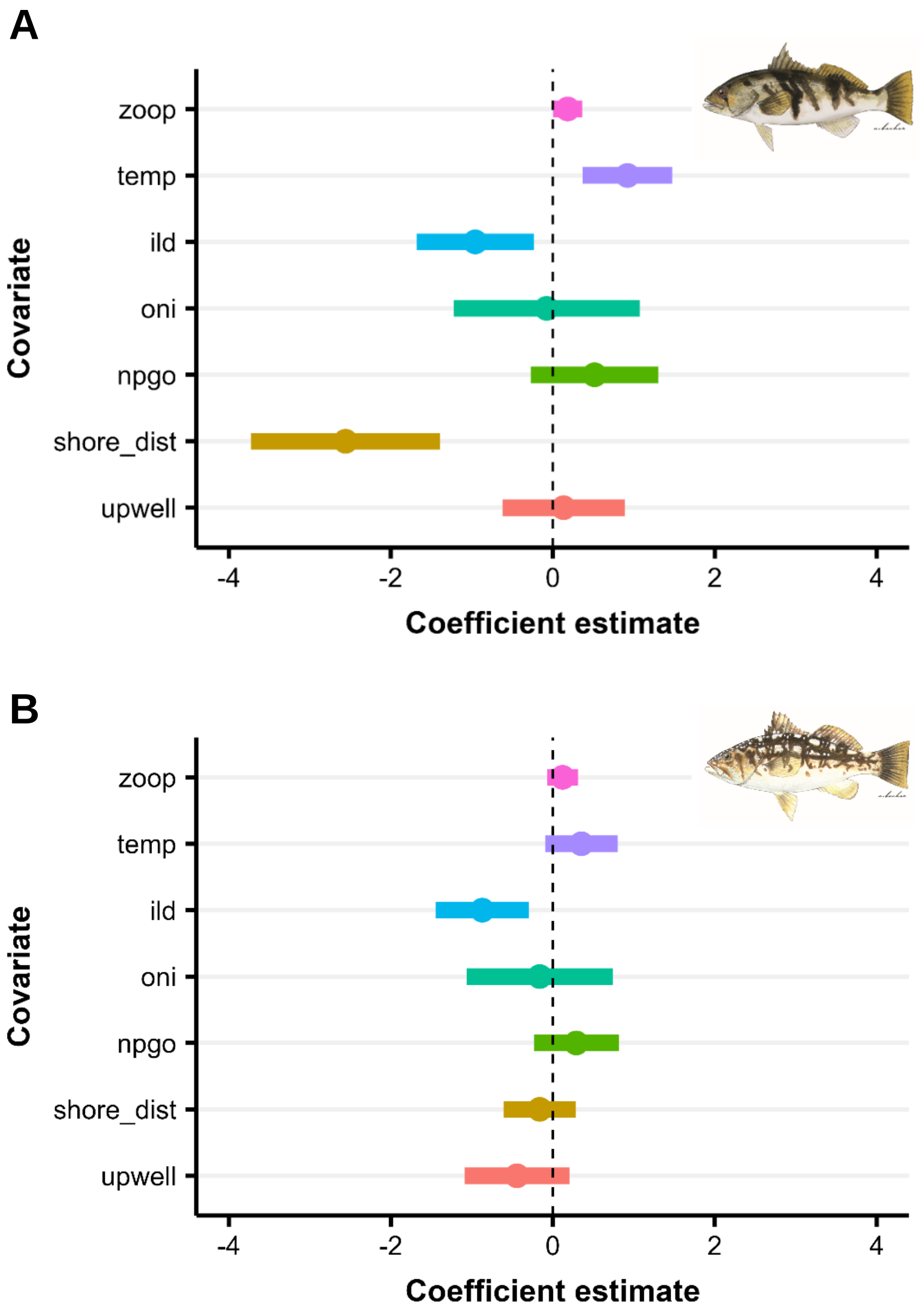

Figure 4.6. Model 2 coefficient estimates of the generalized linear mixed effects model depicting the relationships between bass larval abundance and environmental covariates from 1984 to 2016 for a) Barred Sand Bass and b) Kelp Bass in southern California, USA zoop = CalCOFI zooplankton biomass, temp = CalCOFI 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 to mainland coast, bakun33 = Bakun upwelling index at 33°N. Coefficients greater than (less than) one indicate positive (negative) relationships. Lines depict 95% confidence intervals. Coefficients greater than (less than) one indicate positive (negative) relationships. Lines depict 95% confidence intervals.

Table 4.2. 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. Iid = independent and identically distributed, ar1 = first-order autoregressive, rw = random walk, REML = restricted maximum likelihood, AIC = Akaiki information criteria.

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.

4.4 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.

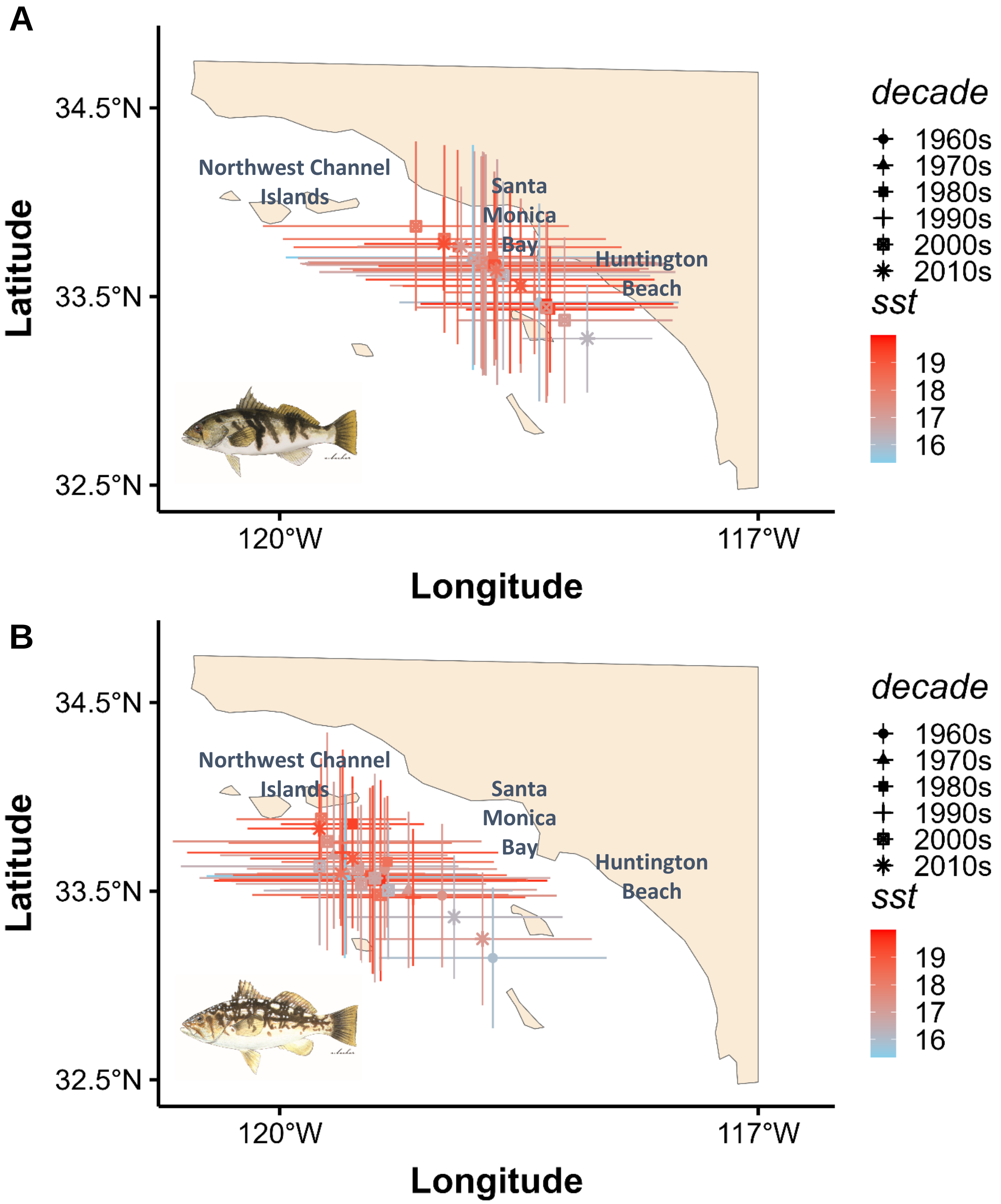

Figure 4.7. Decadal trends in the mean center of gravity for larval distributions of a) Barred Sand Bass and b) Kelp Bass in southern California, USA, 1963 to 2016, by decade (symbols) and annual mean sea surface temperature (colored dots/lines). Lines depict latitudinal and longitudinal 95% confidence intervals.

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 not just the magnitude but the direction as well. 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 adult 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 the saltwater basses, the breakdown in this relationship may be partly driven by two above, but for BSB, also includes 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 these data were only available for one catch data set, and we wanted to have a more direct comparison of the larva/catch relationship across different catch data sets. Nonetheless, 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).

Trends in the standardized indices of larval abundance for both species suggest that the populations of KB and BSB in southern California experience 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). In contrast, BSB larval trends may be more influenced by seeding from Baja California, Mexico (a region with relatively higher BSB larval abundance, see Chapter 1). 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 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 (Jarvis et al. 2014a, see also Chapter 1). Natural log larval abundance trends also identified species-specific differences in decadal-scale availability, with BSB larvae being relatively less abundant during the 1960s and 1970s (a cool period) and KB larvae showing a dramatic, sustained decline between the 1980s and early 2000s. 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.

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 is 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, see also Chapter 1). 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 is the Northwest Channel Islands, which is influenced by the "transition zone" in the SCB where many ocean currents converge. In southern California, the density of Giant Kelp (*Macrocystis pyrifera*) has a positive effect on KB recruitment, but this relationship is conditioned on larval supply, whereby adult densities are largely a function of whether there is a match between areas of high larval supply and areas of higher kelp stipe density (White & Caselle 2008). 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 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 (this study), suggesting different processes acting on their distributions (White et al. 2019). Indeed, we observed differences in their 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 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).

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 (see Population Status and Dynamics, The Species, 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 a fishery recruitment age of eight years); 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 the bass 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 (i.e., the BSB population in southern California relies on sporadic, warm-water larval recruitment pulses), 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 (see Chapter 1). 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 relationships identified using data spanning 54 years (1963-2016) held up using a shorter 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 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.

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Chapter 4, in full, is in preparation for submission for publication and is printed here with the permission of all co-authors, including Andrew R. Thompson and Brice X. Semmens. The dissertation author was the primary investigator and author of this material.

Literature Cited

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.

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.

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.

CHAPTER 4 APPENDIX

Supplemental Tables

Table S1. Parameter estimates* from the species distribution models of environmental influence on a) Barred Sand Bass and b) Kelp Bass larval abundance in southern California, USA.

a) Barred Sand Bass

	term	estimate	std.error	conf.low	conf.high
Model 1 (1963-2016)	phi	12.4	--	10.0	15.4
	tweedie_p	1.4	--	1.3	1.4
	(Intercept)	-2.440	0.396	-3.210	-1.660
	dist_km	-2.300	0.512	-3.310	-1.300
	temp.10m	1.010	0.217	0.583	1.430
	npgo	0.731	0.192	0.355	1.110
	zoop	0.350	0.071	0.211	0.489
	oni	0.371	0.352	-0.319	1.060
Model 2 (1984-2016)	range	135.0	--	52.1	351.0
	phi	6.43	--	4.90	8.44
	sigma_E	16.20	--	6.76	38.70
	(Intercept)	-3.280	0.597	-4.450	-2.110
	dist_km	-2.560	0.593	-3.720	-1.400
	temp.10m	0.923	0.281	0.373	1.470
	npgo	0.516	0.402	-0.272	1.300
	zoop	0.184	0.091	0.004	0.364
	oni	-0.075	0.586	-1.220	1.070
	bakun33	0.135	0.382	-0.613	0.883
	south.ild	-0.958	0.368	-1.680	-0.236

a) Kelp Bass

	term	estimate	std.error	conf.low	conf.high
Model 1 (1963-2016)	range	208	--	114	380
	phi	8.38	--	7.14	9.84
	sigma_O	9.35	--	2.83	30.90
	sigma_E	19.70	--	11.90	32.40
	tweedie_p	1.22	--	1.17	1.28
	(Intercept)	-0.249	0.444	-1.120	0.622
	dist_km	-0.145	0.221	-0.578	0.288
	temp.10m	0.425	0.199	0.034	0.815
	npgo	-0.017	0.214	-0.436	0.403
	zoop	0.171	0.096	-0.017	0.359
	oni	0.296	0.373	-0.435	1.030
Model 2 (1984-2016)	range	197	--	94.1	411
	phi	8.11	--	6.94	9.48
	sigma_O	8.50	--	2.11	34.20
	sigma_E	18.20	--	8.98	36.90
	tweedie_p	1.17	--	1.12	1.23
	(Intercept)	-0.400	0.446	-1.360	0.386
	dist_km	-0.100	0.228	-0.608	0.286
	temp.10m	0.300	0.229	-0.095	0.802
	npgo	0.200	0.267	-0.234	0.814
	zoop	0.100	0.097	-0.068	0.311
	oni	-0.100	0.460	-1.060	0.740
	bakun33	-0.400	0.330	-1.090	0.204
	south.ild	-0.800	0.293	-1.440	-0.297

*range = the distance where two points become independent, phi = observation error, sigma_O = standard deviation (SD) of spatial effect, sigma_E = SD of spatiotemporal process, tweedie_p = tweedie parameter between 1 and 2.

Supplemental Figures

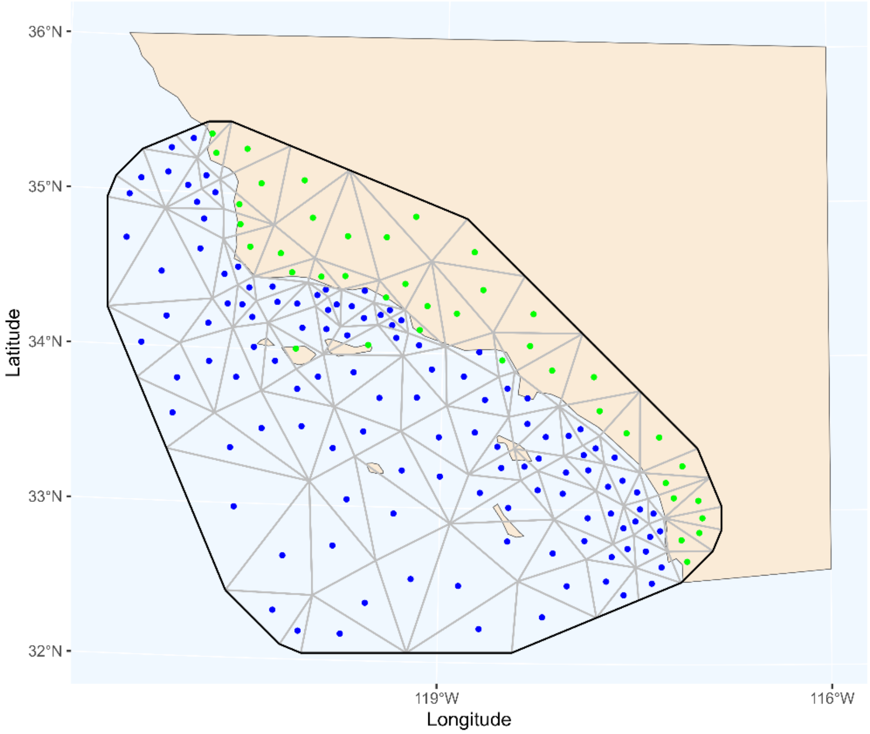

Figure S1. Geostatistical mesh (triangles with blue dots) and barrier mesh (triangles with green dots) generated with the R package `sdmTMB` and based on Kelp Bass larvae data collected in July CalCOFI cruises off southern California, USA, 1963-2016.

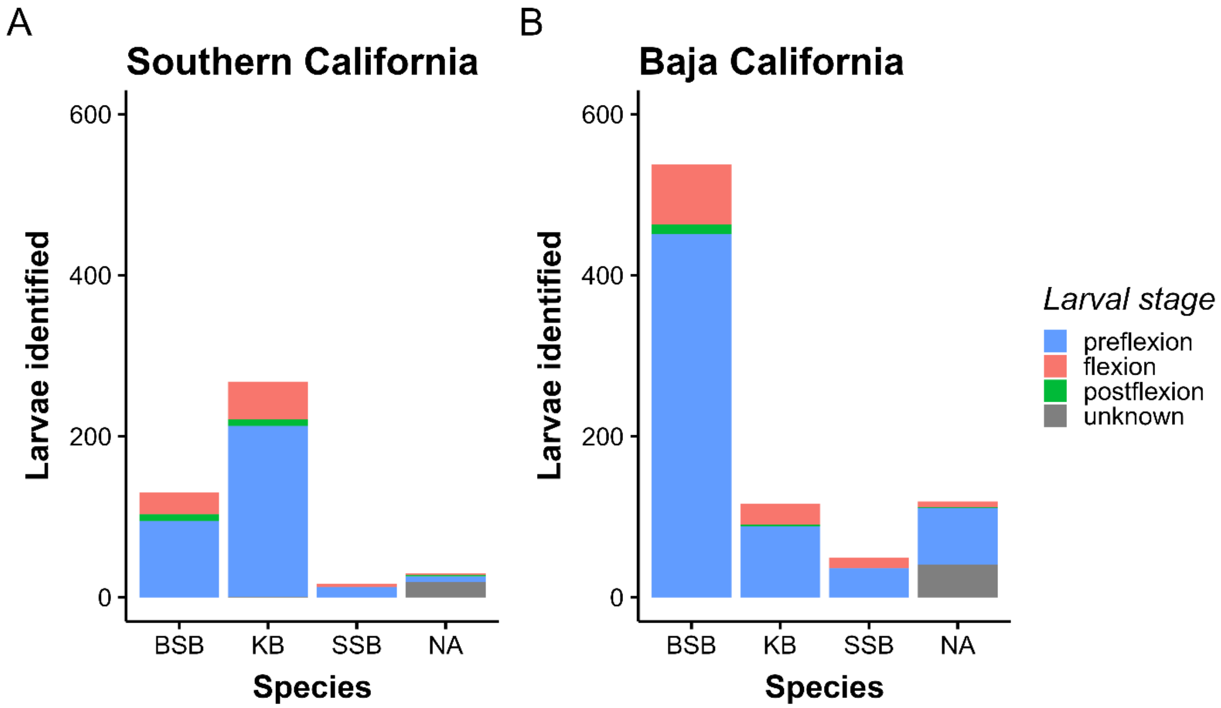

Figure S2. Numbers of identified formalin preserved *Paralabrax* spp. larvae, by species and larval stage, originally collected in July CalCOFI cruises off a) southern California, USA, and b) Baja California, Mexico, from 1963 to 2016.

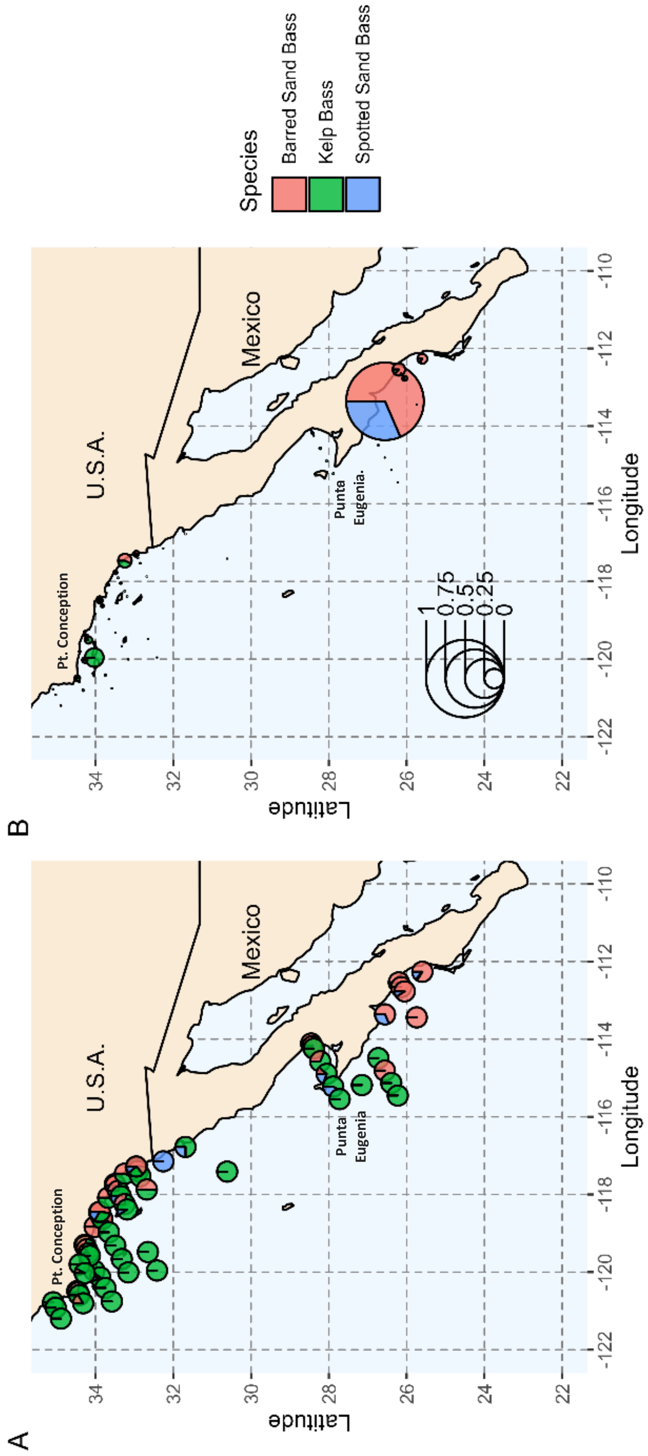

Figure S3. Maps of a) the relative proportion of formalin preserved *Paralabrax* spp. larvae identified by species and station from July CalCOFI cruises, and b) the same as (a) above, standardized by the mean maximum number of larvae per species per station (= 12.4 larvae) over the entire survey period from 1963 to 2016.

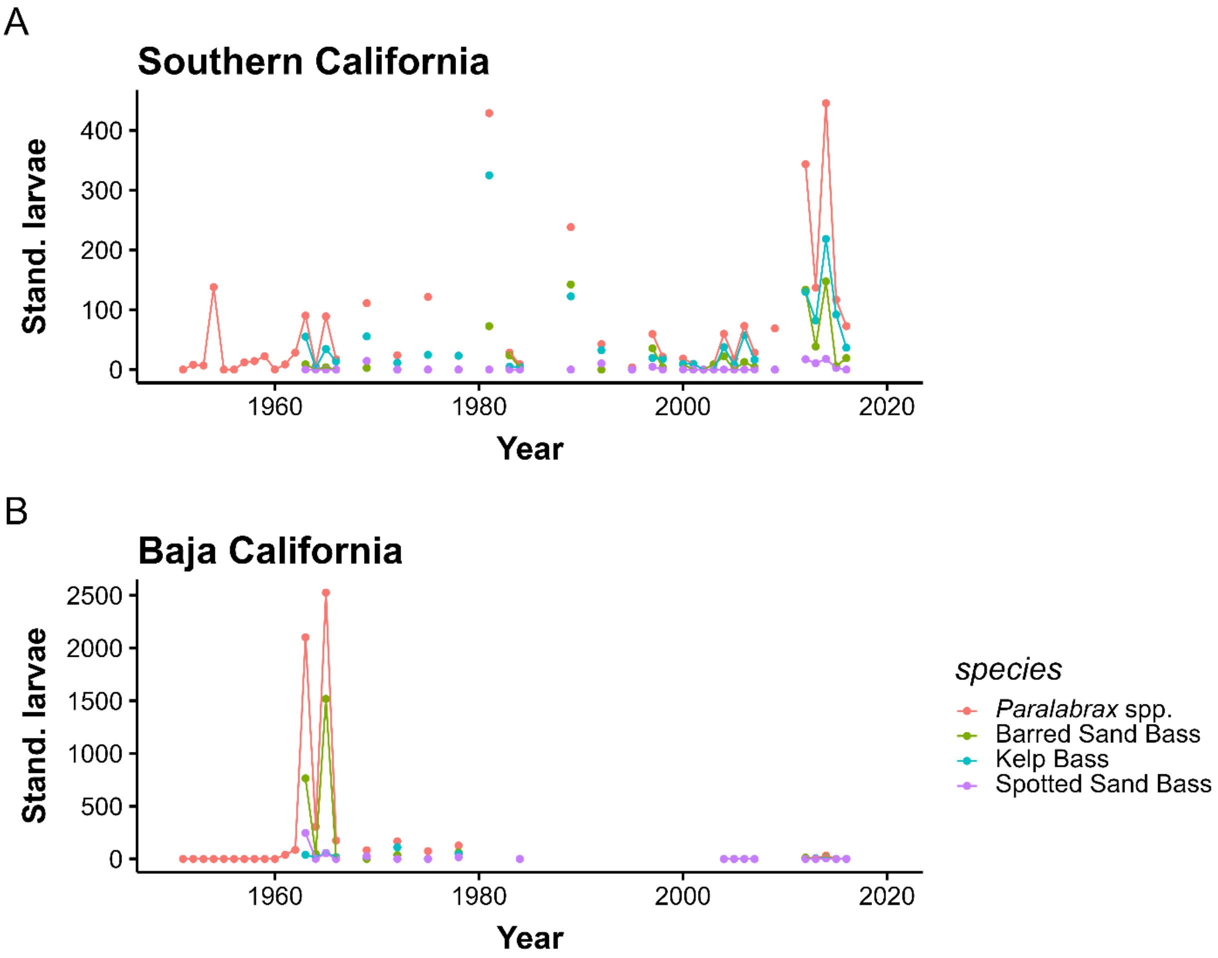

Figure S4. Temporal trends in the standardized raw larval counts (larvae under ten m^2 of sea surface) for *Paralabrax* spp. larvae combined and by species (Barred Sand Bass, Kelp Bass, and Barred Sand Bass) collected in July CalCOFI cruises in a) southern California, USA, and b) Baja California, Mexico, 1950-2016. Note that *Paralabrax* spp. larvae counts in some years may include *P. auroguttatus* (Goldspotted Sand Bass), especially off Baja California.

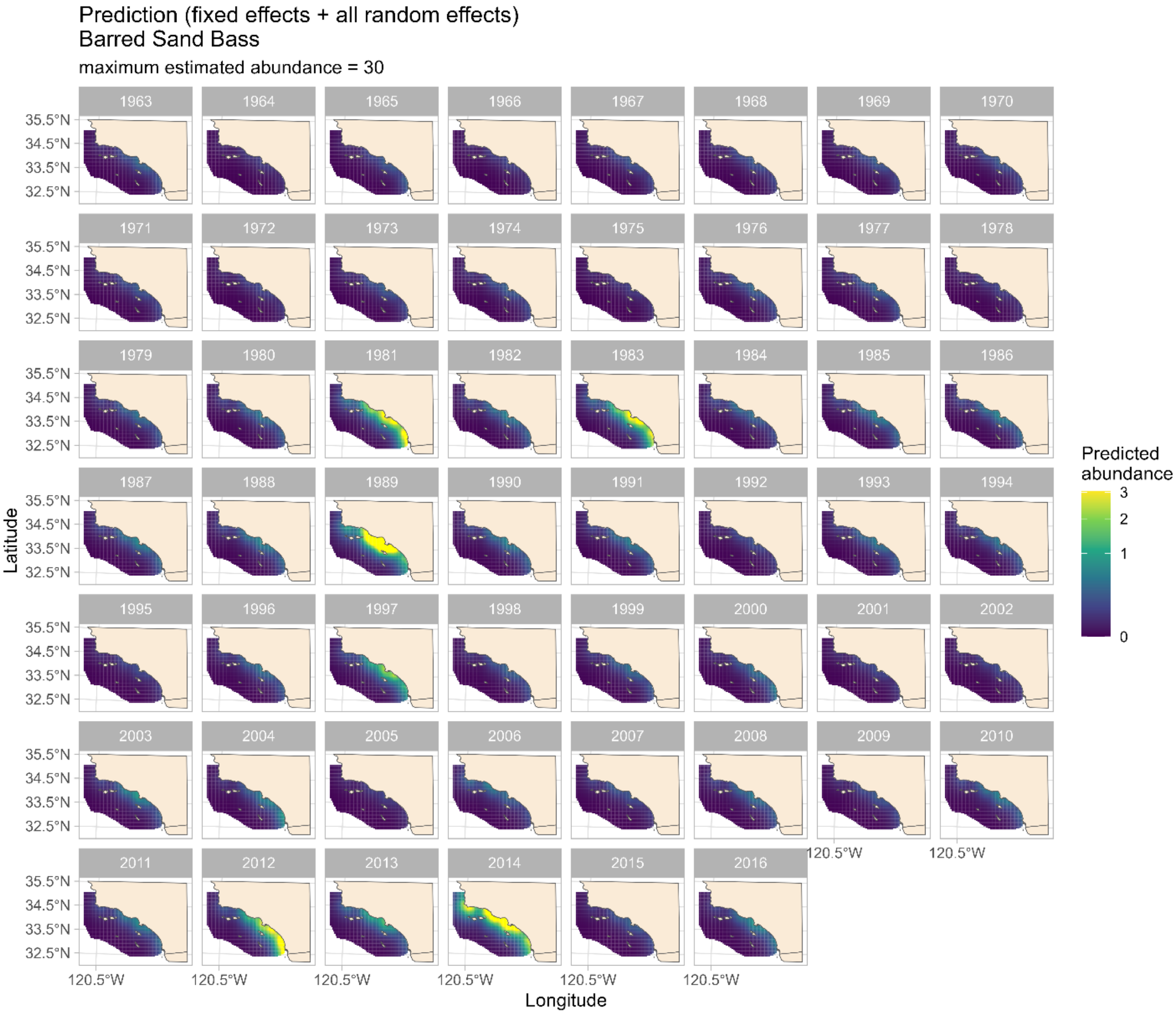

Figure S5. Predicted Barred Sand Bass larval abundance in southern California, USA, by year, 1963-2016. Scale bar denotes abundance on the natural log scale. The legend color ramp ranging from light to dark denotes higher and lower abundance, respectively.

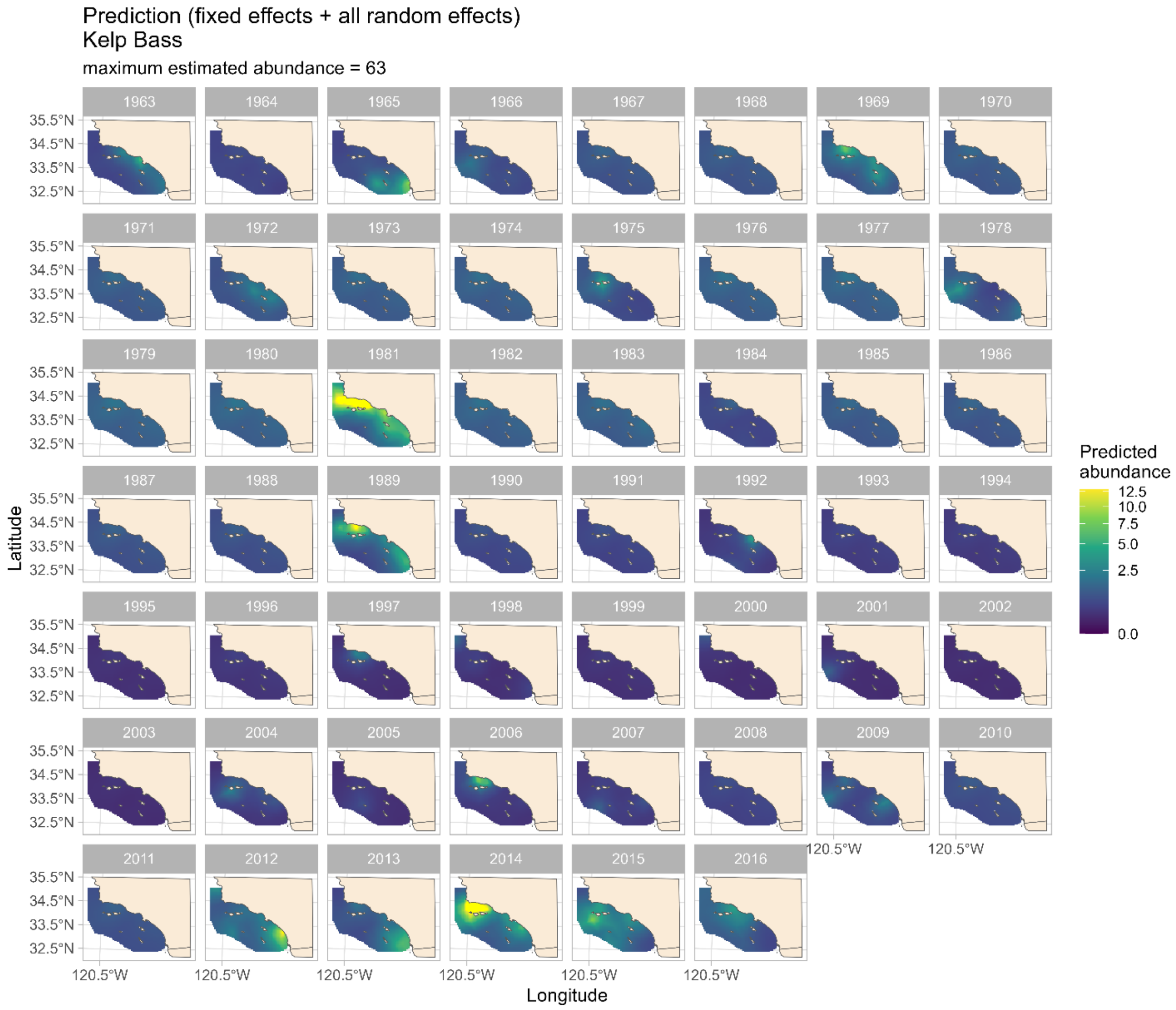

Figure S6. Predicted Kelp Bass larval abundance in southern California, USA, by year, 1963-2016. Scale bar denotes abundance on the natural log scale. The legend color ramp ranging from light to dark denotes higher and lower abundance, respectively.

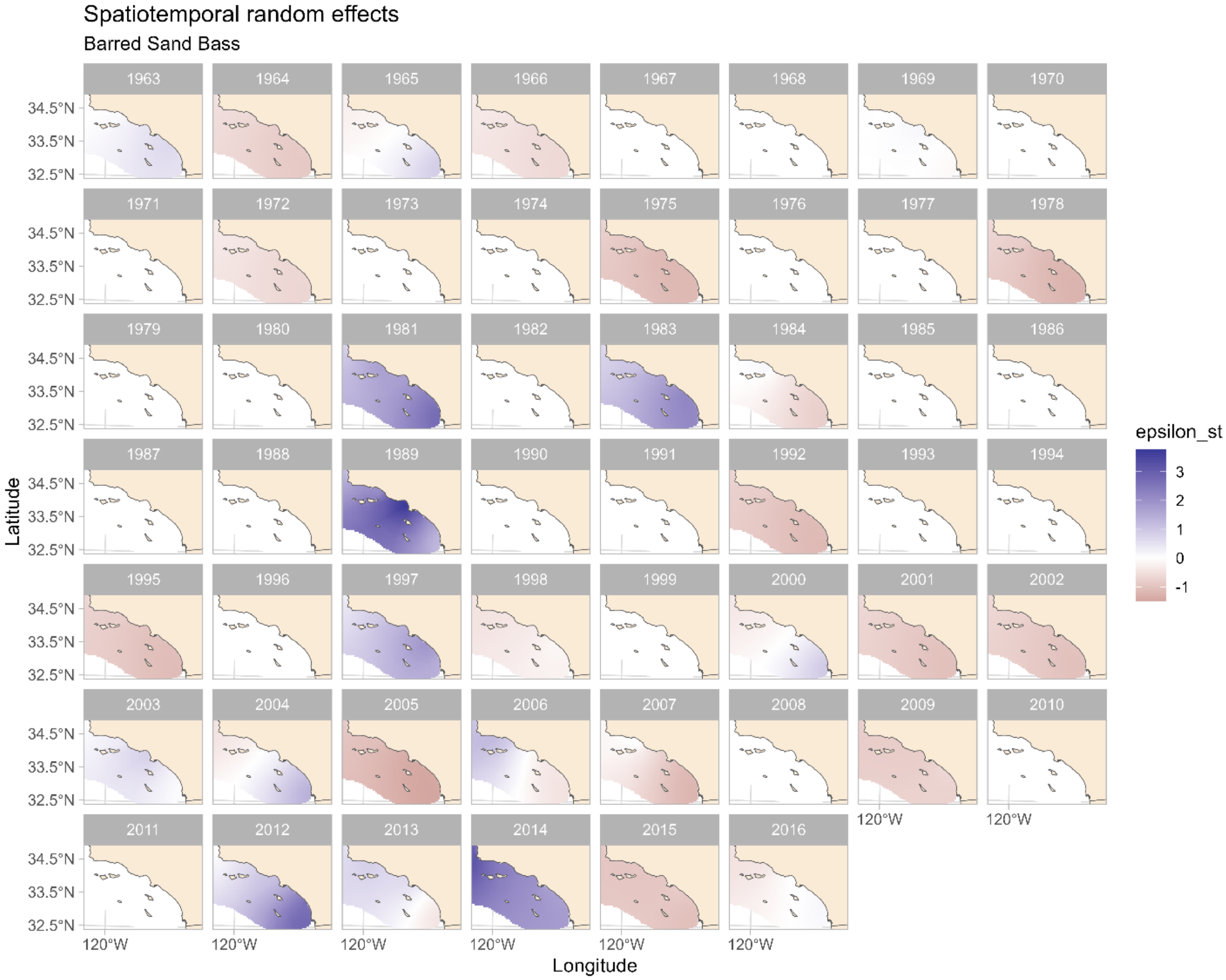

Figure S7. Deviations from the fixed effect predictions and spatial random effect deviations derived from the standardized index of abundance model for Barred Sand Bass in southern California, USA, 1963-2016. Deviations represent the spatiotemporal influence of latent variables on Barred Sand Bass larval abundance (i.e., biotic, and abiotic factors that are changing through time and that are not accounted for in the model).

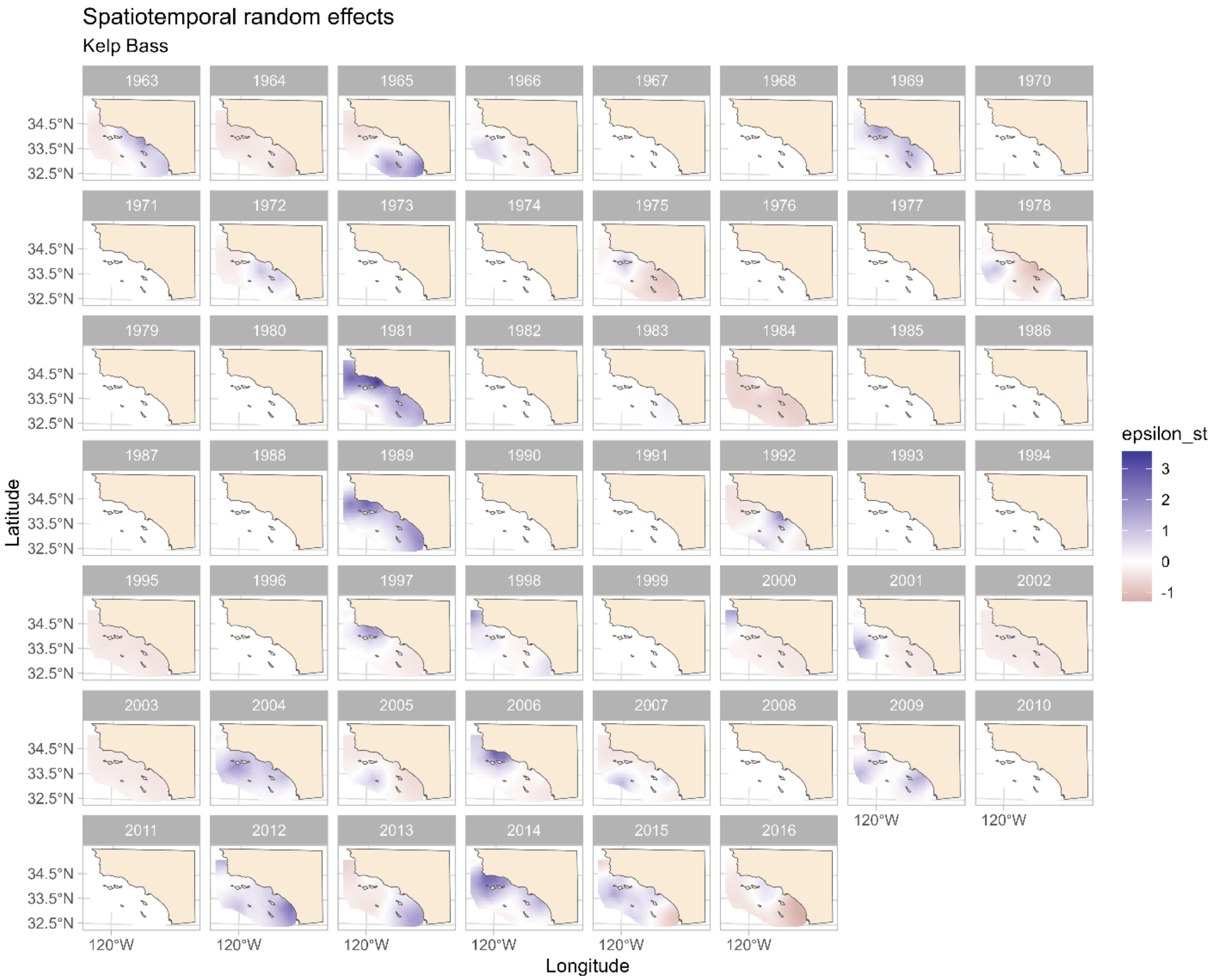

Figure S8. Deviations from the fixed effect predictions and spatial random effect deviations derived from the standardized index of abundance model for Kelp Bass in southern California, USA, 1963-2016. Deviations represent the spatiotemporal influence of latent variables on Kelp Bass larval abundance (i.e., biotic, and abiotic factors that are changing through time and that are not accounted for in the model).

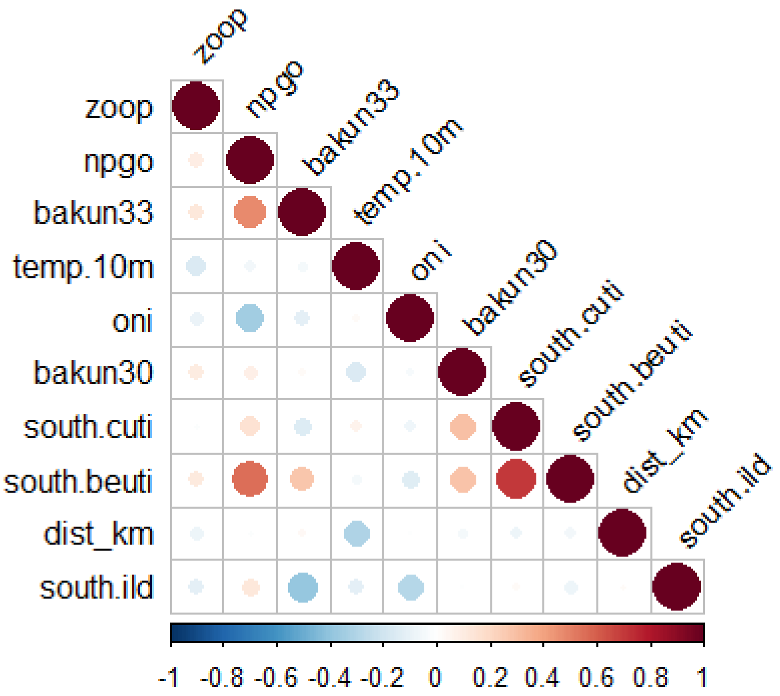

Figure S9. Correlation matrix of environmental variables selected for modeling species-specific *Paralabrax* spp. larval abundance in southern California, USA. dist_km = distance to mainland coast, south.ild = isothermal layer depth, zoop = CalCOFI zooplankton biomass, npgo = North Pacific Gyre Oscillation index for July, bakun33 = Bakun upwelling index at 33°N, temp.10m = CalCOFI temperature averaged over the upper 10 m, oni = Ocean Niño Index for June/July, bakun33 = Bakun upwelling index at 30°N, south.beuti = Biologically Enhanced Upwelling Index, south.cuti = Coastal Upwelling Transport Index.

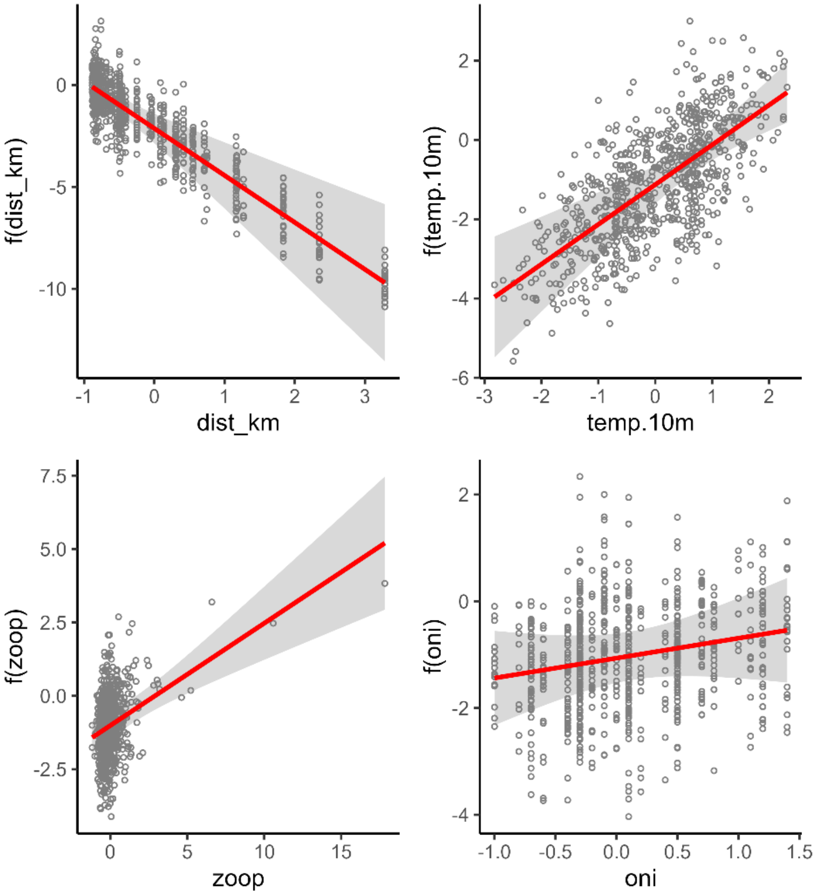

Figure S10. Model 1 conditional effects plots representing the predicted effects of select environmental covariates on Barred Sand Bass larval abundance in southern California, USA, 1963-2016. Shaded ribbon depicts the 95% confidence band, and the points depict partial residuals. Individual covariate effects are conditioned on the other covariates being fixed at their median values. dist_km = distance to mainland coast, zoop = CalCOFI zooplankton biomass, temp = CalCOFI temperature averaged over the upper 10 m, oni = Ocean Niño Index for June/July, npgo = North Pacific Gyre Oscillation index for July.

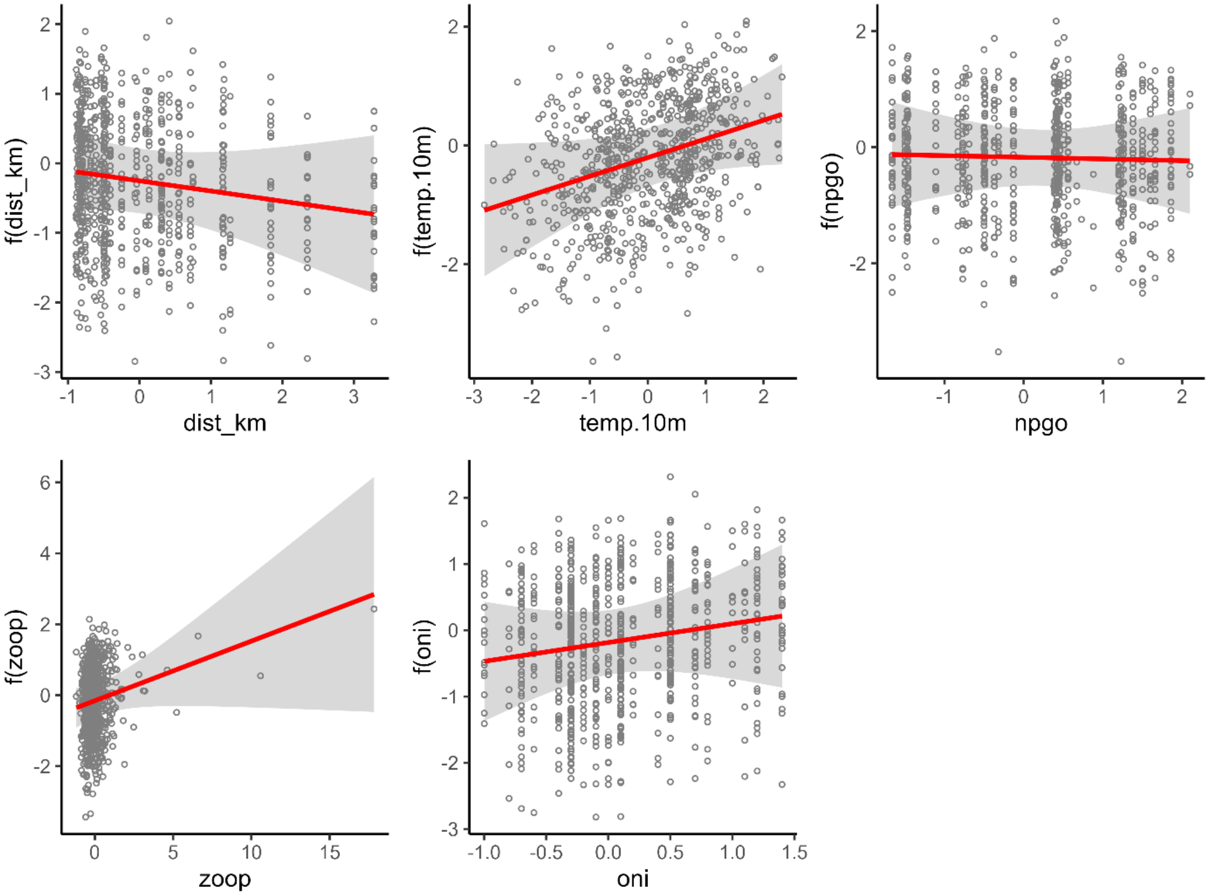

Figure S11. Model 1 conditional plots representing the predicted effects of environmental covariates on Kelp Bass larval abundance in southern California, USA, 1963-2016. Shaded ribbon depicts the 95% confidence band, and the points depict partial residuals. Individual covariate effects are conditioned on the other covariates being fixed at their median values. dist_km = distance to mainland coast, zoop = CalCOFI zooplankton biomass, temp = CalCOFI temperature averaged over the upper 10 m, oni = Ocean Niño Index for June/July, npgo = North Pacific Gyre Oscillation index for July.

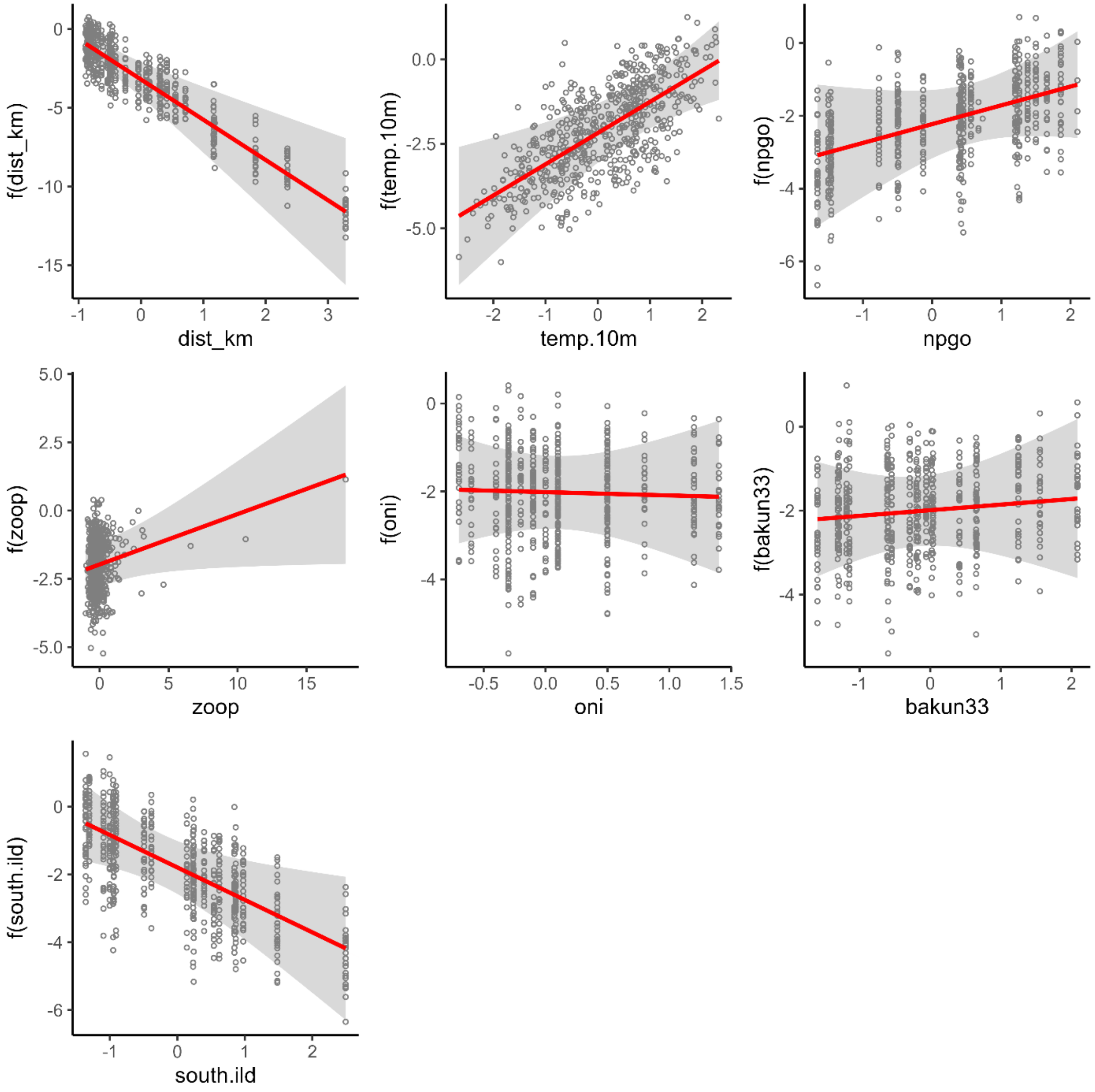

Figure S12. Model 2 conditional plots representing the predicted effects of environmental covariates on Barred Sand Bass larval abundance in southern California, USA, 1984-2016. Shaded ribbon depicts the 95% confidence band, and the points depict partial residuals. Individual covariate effects are conditioned on the other covariates being fixed at their median values. dist_km = distance to mainland coast, zoop = CalCOFI zooplankton biomass, south.ild = isothermal layer depth, temp.10m = CalCOFI temperature averaged over the upper 10 m, oni = Ocean Niño Index for June/July, npgo = North Pacific Gyre Oscillation index for July, and bakun33 = Bakun upwelling index at 33°N.

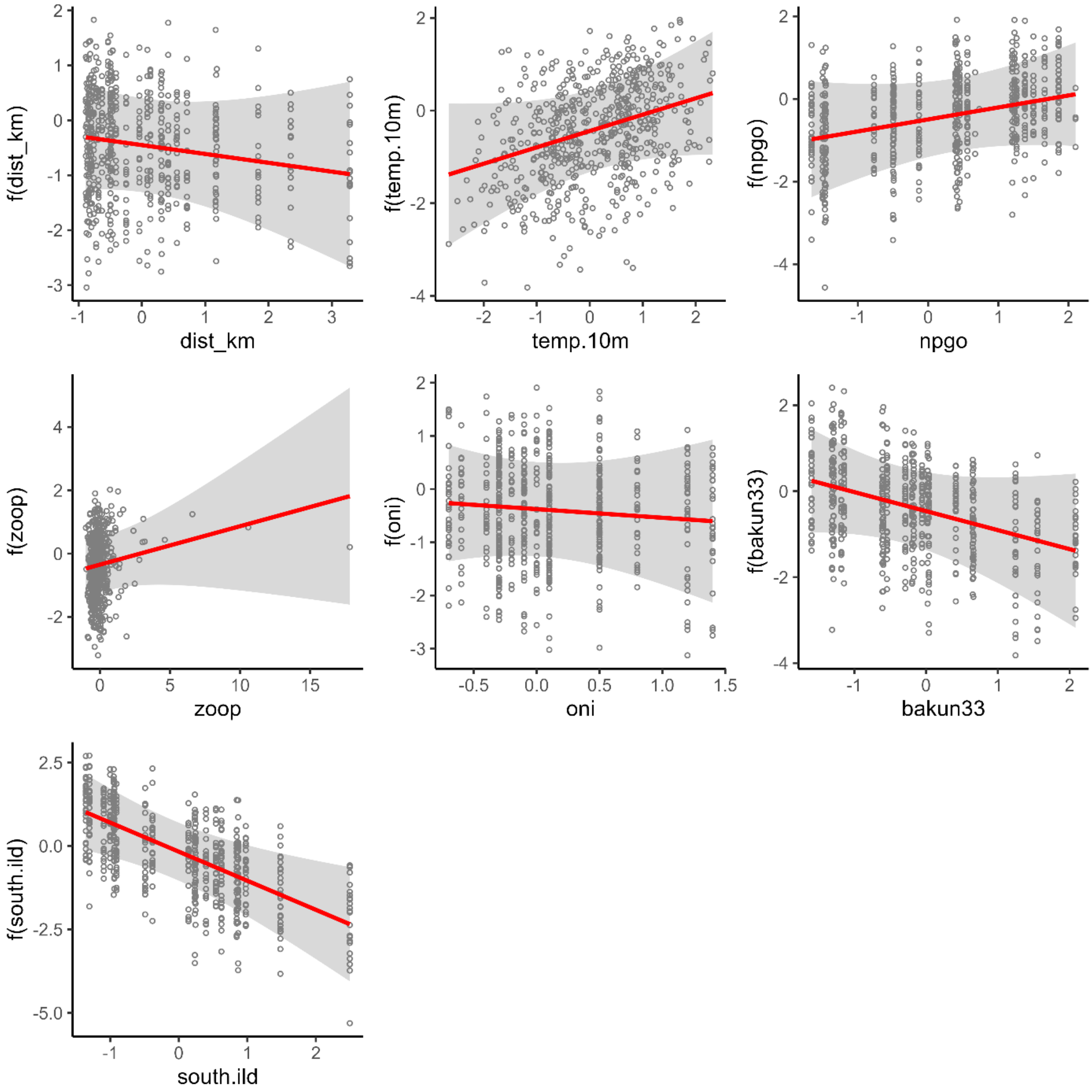

Figure S13. Model 2 conditional plots representing the predicted effects of environmental covariates on Barred Sand Bass larval abundance in southern California, USA, 1984-2016. Shaded ribbon depicts the 95% confidence band, and the points depict partial residuals. Individual covariate effects are conditioned on the other covariates being fixed at their median values. dist_km = distance to mainland coast, zoop = CalCOFI zooplankton biomass, south.ild = isothermal layer depth, temp.10m = CalCOFI temperature averaged over the upper 10 m, oni = Ocean Niño Index for June/July, npgo = North Pacific Gyre Oscillation index for July, and bakun33 = Bakun upwelling index at 33°N.