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

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ABSTRACT: Spawning aggregation-based fisheries are notorious for booms and busts driven by aggregation discovery and subsequent fishing-induced collapse. However, environment-driven 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 custom 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 point to a history of multidecadal windows of fishing opportunity and fishing-induced collapse largely driven by sporadic, warm-water recruitment events, in which recruits may be externally sourced and local recruitment is negatively influenced by harvest. Following the last collapse, recruitment remained elevated due to novel, anomalously warm conditions. Despite signs of incipient population recovery, spawning aggregations remain absent, indicating that other potential factors (e.g. continued fishing during spawning season, Allee effects) have delayed fishery recovery to date. Recruitment-limited aggregate spawner populations, especially those at their geographic margins, are highly susceptible to sudden and potentially extended periods of collapse, making them ill-suited to high catch-per-unit-effort fishing that occurs on spawning grounds. If the goal is to balance protecting spawning aggregations with long-term fishery sustainability, then limiting aggregation-based fishing during the spawning season is likely the best insurance policy against collapse and recovery failure.

KEY WORDS: Sporadic recruitment · Transient aggregate spawner · Fishery collapse · Bayesian mark–recapture · *Paralabrax nebulifer*

1. INTRODUCTION

Fishes that form large spawning aggregations, i.e. aggregate spawners, are commonly exploited by artisanal, recreational, and commercial fisheries worldwide. However, 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).

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This is especially true for transient aggregate spawners that migrate long distances to form exceptionally large spawning aggregations for weeks to months (Domeier & Colin 1997, Heyman et al. 2019). 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).

The delay or lack of recovery in overfished aggregate spawner populations despite measures to enhance populations is contrary to compensatory population dynamics, in which traditional fisheries management is rooted (i.e. that per capita population growth rate increases at low stock sizes). One explanation includes the Allee effect (Allee 1931, 1938, Stephens et al. 1999), also referred to as depensation in fisheries science, in which a population's per capita growth rate declines upon reaching a low level, i.e. the 'Allee-effect threshold' (Hutchings 2015). In an extreme case, a population could potentially be fished to a point at which densities are so low that it is unable to replenish itself, i.e. reaches yet another threshold, 'the Allee threshold' (Hutchings 2015), but this can be difficult to detect unless stock sizes are very small (Liermann & Hilborn 2001, Hilborn et al. 2014, Perälä & Kuparinen 2017). It is also possible that residual Allee effects could delay fishery recovery even after a population begins to rebound. For example, in aggregation-based fisheries, low densities of adults could potentially disrupt the behavioral dynamics of spawning aggregation formation, resulting in the loss of generational transfer of historical spawning ground locations (Warner 1988, 1990, Bolden 2000, Semmens et al. 2008).

Yet another factor that could delay recovery in aggregation-based fisheries is recruitment limitation, or environment-driven sporadic recruitment (Semmens et al. 2008, Stock et al. 2021). 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 (e.g. transport and temperature regimes) rather than, or in addition to, spawning stock biomass (Vert-pre et al. 2013, Szuwalski et al. 2015). 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). For example, a population 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.

One prominent case of delayed recovery in a transient aggregate spawner fishery is that of barred sand bass *Paralabrax nebulifer* (Family Serranidae) in southern California, USA. Barred sand bass (BSB) were once the target of a highly popular aggregation-based recreational-only fishery during the summer spawning season (Love et al. 1996a, Erisman et al. 2011, Jarvis et al. 2014). Historically, BSB would migrate on average 10s of km to form massive spawning aggregations at several locations along the coast (Jarvis et al. 2010, Teesdale et al. 2015), 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 (e.g. an increased minimum size limit and decreased daily bag limit, 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). Adding to the uncertainty of recovery is a lack of population estimates and knowledge of the oceanographic drivers influencing BSB population dynamics. Given the lack of formal stock-recruit data for this fishery, which greatly limits detection of an Allee effect, it seems reasonable to determine whether environment-driven recruitment-limitation can be ruled out as a driver of population dynamics and delayed recovery in this fishery.

Although the effect of fishing on the decline of the BSB fishery is well documented (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 poorly 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), generally favoring warmer oceanographic climates (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

Santa Cruz, CA, USA (Heemstra 1995, Love & Passerelli 2020), but they are rare north of Pt. Conception. Historically, their distribution and availability in California were considered tightly coupled to warm water conditions (Young 1969). 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 and intensity, in addition to a shift in the geographic range of the population (Auth et al. 2018, Pinsky et al. 2020). 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 may 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 may be derived from a formal stock assessment (data-rich fisheries), catch-curve analysis (data-poor fisheries), and/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. 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 long-term mark–recapture data spanning different oceanographic regimes and harvest histories and develop a custom 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 (YOY) juvenile recruit densities as a function of SST, adult densities, and harvest, and look for signs of population recovery 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 environment-driven sporadic recruitment in the dynamics of this economically and culturally important spawning aggregation-based fishery.

2. MATERIALS AND METHODS

2.1. Tagging studies

We analyzed BSB tagging data collected by the California Department of Fish and Wildlife (CDFW, formerly the California Department of Fish and 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 3 periods, BSB were captured by hook-and-line (26% in the 1990s were trawl-caught), measured to the nearest mm total length (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 description of the CDFW tagging studies). Tagging rewards across study periods included low-value non-monetary and monetary incentives (e.g. hats, US$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 locations (Jarvis et al. 2010; Fig. 1). In the 2010s, tagging occurred year-round at spawning and non-spawning locations primarily off San Diego, CA (Fig. 1). Some tagging in the 2010s 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. Similarly, we excluded a group of fish tagged at a single location on the Mexico coast in the 1990s (Jarvis et al. 2010). Both excluded sites are not shown in Fig. 1.

Further data processing and filtering of the tag and recapture data (Text S1 in the Supplement at www.int-res.com/articles/suppl/m738p203_supp.pdf) resulted in capture histories for 6473 tagged BSB across the 3 tagging periods (1960s, 1990s, and 2010s), which represented nearly 25 yr of data spanning 5 decades (Fig. 1, Table 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).

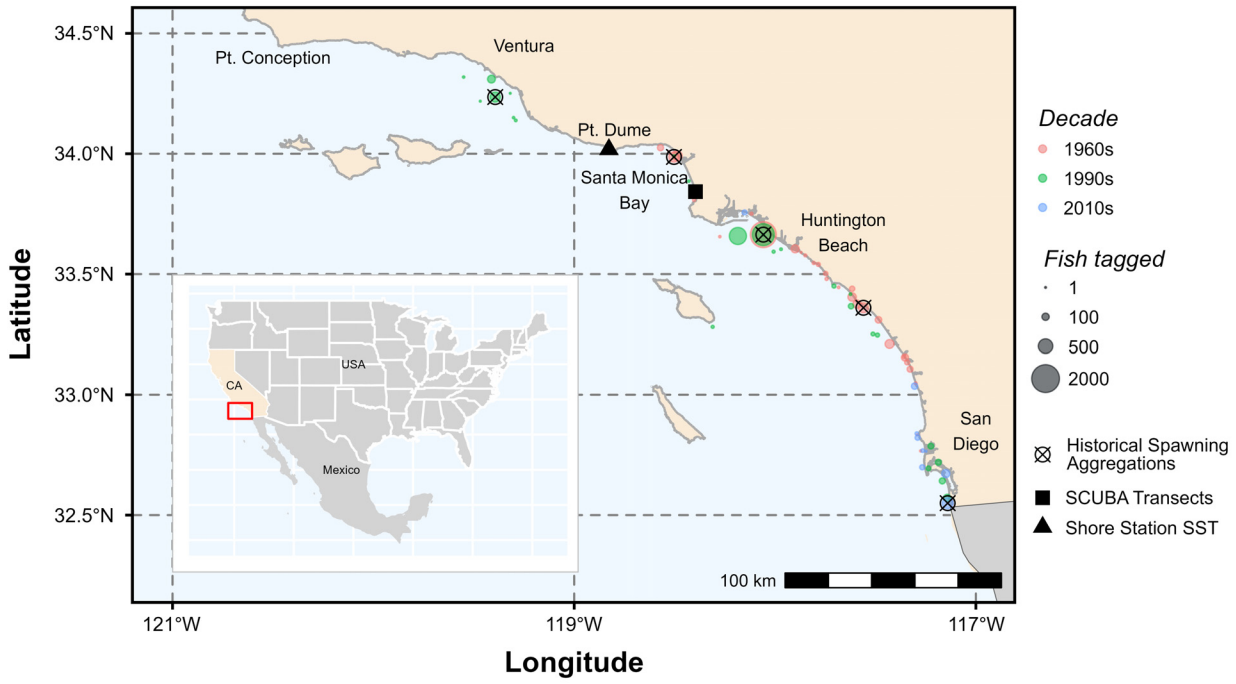

Fig. 1. Barred sand bass *Paralabrax nebulifer* tagging locations (circles) in southern California (CA), USA, by decade and numbers of fish tagged, the location of SCUBA transects where juvenile (young-of-the-year) recruit and adult density data were collected, the location of Shore Station sea surface temperature (SST) data collection, and locations of historical spawning aggregations

2.2. CMR model

2.2.1. Parameters (demographic rates)

We used a multistate Bayesian approach (Kéry & Schaub 2012) to estimate the following 4 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) = 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 (=resighted by an angler) at occasion t and the tag reported.

Our approach differs from traditional CMR models (Barker 1997, Riecke et al. 2021) in 2 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 (±SD) home range size (10 003 ± 3819 m^2, Mason & Lowe 2010) and migration distance to spawning grounds (17 ± 15 km, Jarvis et al. 2010). Second, we excluded any CAR encounters in the interval between survey occasions (1960s: n = 47 [18.4%]; 1990s: n = 22 [16.9%]; 2010s: n = 2 [16.7%]). The Barker (1997) model estimates the probability of CAR during the non-survey interval, given the fish survives to occasion $t + 1$ (R) or dies after being resighted (R'). The latter parameter is a nuisance parameter and is difficult to estimate. Including it in our model would add undue complexity given that most CARs occurred during 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 tagging studies, we fit separate models for each tagging period. We used beta distributions with flat priors for all 4 parameters (Table S1). We simulated data during model development to validate our ability to estimate true parameter values. For each model, we generated 3 Markov chain Monte Carlo (MCMC) chains of 20 000 iterations, discarding the first 5000 and saving every 5th iteration, and used a Gelman-Rubin metric value close to 1

Table 1. Summary tag and recapture statistics by tagging period (1960s: 1962–1970, 1990s: 1989–1999, 2010s: 2012–2015) for barred sand bass *Paralabrax nebulifer* tagged and released in southern California, USA. Recapture length outliers are not included in the reported range, mean, and proportions. Fish tagged in the last year during the 1960s and 1990s were not included in the analysis. For the 1960s and 1990s, we included only fish tagged in June–August, and for the 2010s, we included fish tagged monthly from October 2012 through January 2015. Percent mature is based on size at 100% maturity (≥270 mm total length). Legal size during the 1960s and 1990s was ≥305 mm total length; legal size increased to ≥356 mm total length in March 2013. Lengths were not always reported with recapture information

	1960s	1990s	2010s
No. of years	9	11	2.3
Tagged fish	3335	2696	442
Total length (mm)			
Range	218–551	178–647	171–544
Mean ± SD	303 ± 34	339 ± 62	386 ± 60
% mature	89	94	97
% legal size	38	69	75
Recaptured fish[a]	255 (243)	130 (65)	12 (1)[b]
Recapture rate (%)	8	5	3
Total length (mm)			
Range	260–577	305–508	375–375
Mean ± SD	330 ± 36	348 ± 35	375
% mature	98	100	100
% legal size	84	100	100

[a](no. of recaptures with reported lengths)
[b]Due to the low sample size, we used growth estimates from K. Walker et al. (2020) to compare with the capture–mark–reencounter model growth estimates from the 1960s and 1990s

(<1.01) to check for model convergence on each parameter. We used a marginalized likelihood function to increase MCMC convergence speed (Yackulic et al. 2020), and we report posteriors and mean probabilities plus 66% highest density intervals (= the 66% most likely values in the credible interval) for each estimated and derived parameter (see Sections 2.3.1 and 2.3.2 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 opted for these models to be based 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. In contrast, for the 2010s model, we modeled monthly survey occasions because tagging occurred year-round. As a result, we included a fixed effect of season (Summer, non-Summer) on survival, harvest, and CAR rates in the 2010s and then adjusted the monthly harvest rates to annual harvest rates. Data processing and filtering (Text S1) 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).

2.2.2. Tag retention

To account for tag loss, we first separately modeled the probability of retaining a tag with data from a double-tagging study for kelp bass *Paralabrax clathratus* that occurred off San Diego from 2012 to 2016 (see Bellquist 2015 for a description of methods). We assumed tag retention rates to be similar between this species and BSB and across tagging periods, given that similar tagging methods were used by trained biologists in each of the 3 BSB tagging studies and that kelp bass is a local congener of BSB with a similar growth rate and overlapping habitat use (Love et al. 1996b, Lowe et al. 2003, Mason & Lowe 2010, Logan & Lowe 2018). We used a Bayesian hidden state framework in JAGS (Su & Yajima 2021, Plummer et al. 2022) to model tag retention over time at liberty, as a function of age of tag (Text S2).

Of the 673 kelp bass double-tagged in the tag retention experiment (Bellquist 2015), a total of 129 fish were recaptured within 3.7 yr (31 with a single tag intact and 98 with both tags intact). The cumulative probability of (or proportion of fish) retaining at least 1 tag in the double tagging study was ~86% in the first year and fell to ~9% after 7 yr (Fig. S1A). Initial tag retention was estimated at ~96%, and the discrete annual rate of tag retention was estimated at ~90%. The calculated probability (non-cumulative) of a fish retaining a tag, as a function of age of tag, decreased from ~86% in the first year to ~34% after 7 yr (Fig. S1B).

The model-estimated time-dependent probabilities of retaining a tag (tr, Fig. S1B) were incorporated as priors into the 1960s and 1990s CMR models for estimating the state of fish at every occasion (see Section 2.2.4). 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 mo), and that not all fish were tagged at the beginning of the study, we incorporated into the 2010s CMR model a prior for the discrete annual tag retention rate, $\exp(-\beta)$, termed r (Table S1).

2.2.3. Growth estimation

BSB is a small-bodied, slow-growing serranid, with the growth asymptote for the mean size-at-age around 600 mm and the oldest aged individual being 25 yr (K. Walker et al. 2020). During the 1960s, 1990s, and through February 2013, the minimum size limit (MSL) in the fishery was 305 mm (12 inches) total length (TL), corresponding to a fishery recruitment age of approximately 5 to 6 yr; afterward, the MSL increased to 356 mm (14 inches) TL (Jarvis et al. 2014), corresponding to fishery recruitment at approximately 8 yr. BSB males reach maturity between 2 and 4 yr and females between 2 and 5 yr (Love et al. 1996b). Thus, over time, the MSL allowed for at least 1 yr of spawning before entering the fishery.

Our model accounts for potential harvest of sublegal-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); 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 3 growth parameters ($L1$, $L2$, and $L3$) in the CMR models. These parameters correspond to mean lengths at specific ages (Text S3). 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 (K. Walker et al. 2020) and the Francis parameterization of the VBGF in the R package 'FSA' (Ogle et al. 2022; Text S3).

The 736 BSB collected in the age and growth study (K. Walker et al. 2020) ranged in age from young-of-the-year (YOY, age 0 to nearly age 1) to 25 yr, while TL ranged from 114 to 600 mm. The mean growth parameter estimates and 95% confidence intervals used to define growth priors in the CMR models were $L1_3$ = 236 mm, CI: 229–242 mm (mean size at age 3 yr); $L2_{9.5}$ = 403 mm (mean size at age 9.5 yr), CI: 400–406 mm; $L3_{16}$ = 495 mm, CI: 487–502 mm (mean size at age 16 yr; see Table S1 for priors).

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).

2.2.4. State-transition and observation matrices

Using a multistate Bayesian approach (Kéry & Schaub 2012), we defined the state transition matrix (**S**) to calculate the state transition probability for the 3 possible latent states in occasion $t + 1$ (columns), given the latent state in occasion t (rows): (1) alive with tag, (2) dead, and (3) unavailable for capture, i.e. dead by natural causes or lost tag:

$$\mathbf{S}_{i,t} = \begin{bmatrix} \varphi_{c_{i,t}} \times tr_{t-f_i+1} & \kappa_{c_{i,t}} \times tr_{t-f_i+1} & \left(1-\varphi_{c_{i,t}}-\kappa_{c_{i,t}}\right)\times tr_{t-f_i+1}+\left(1-tr_{t-f_i+1}\right) \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{bmatrix} \quad (1)$$

where $c_{i,t}$ refers to the size class of individual i (legal, sublegal) at occasion t, and tr_{t-f_i+1} is the tag retention probability at occasion $t + 1$, specific to the length of time the fish was at liberty (age of tag), 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 discrete 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 (Summer, non-Summer) at occasion t (e.g. $\varphi_{c_{i,t}}$).

We defined the observation matrix (**O**) to calculate the probability of observing each of 5 of the following possibilities at occasion $t + 1$ (columns), given the latent state at 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:

$$\mathbf{O}_{i,t} = \begin{bmatrix} p_t \times R_{c_{i,t}} & p_t \times \left(1-R_{c_{i,t}}\right) & \left(1-p_t\right)\times R_{c_{i,t}} & 0 & \left(1-p_t\right)\times\left(1-R_{c_{i,t}}\right) \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \quad (2)$$

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

2.2.5. 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 corresponding survey occasions, see Text S1.

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 at each survey occasion, lengths of fish reported during the interval between survey occasions were coded 'NA' (not available), as growth estimated from these lengths would not represent a full year of growth. The length matrices for each period were supplied as data for the growth estimation portion of the CMR models.

2.3. Deriving population size

2.3.1. 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 3 hypothetical tag reporting probabilities of approximately 25, 50, and 75%. In this prior sensitivity analysis, for each tag reporting scenario, we assigned a corresponding beta distribution in the CMR model that we used *a posteriori*, in which we divided the posterior estimates of harvest rate by the prior distribution of the respective tag reporting scenario. The assigned tag reporting priors included uncertainty of approximately ±10% around the mean probabilities (Fig. S2).

2.3.2. 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 Text S4 on estimating size-specific harvest; the relative proportions of annual size-specific harvest are reported in Table S2). In the 1960s CMR model, there was only a single year of size-specific catches for which to apply the size-specific conditional harvest rates, which yielded a single annual estimate of population size for the 1960s under each tag reporting scenario. In contrast, we were able to apply size-specific conditional harvest rates to the mean harvest across multiple years in the 1990s and 2010s to yield a mean annual estimate of population size under each tag reporting scenario. To explore decadal trends in population size and size-specific conditional harvest rates, we generated posterior distribution plots for each decade and tag reporting rate using the R packages 'tidybayes' and 'ggdist' (Kay 2022a,b).

2.4. Comparison to SST, juvenile and adult densities, and harvest

We obtained diver survey densities of adult (⩾220 mm) and juvenile (<150 mm, YOY) BSB from 1974 to 2022 in King Harbor, Redondo Beach, CA (Fig. 1), collected by the Vantuna Research Group (VRG), Occidental College (unpublished data; see Stephens et al. 1986 for a description of methods). Following an approximate pelagic larval duration of 1 lunar month (Allen & Block 2012), recruits settle into inshore nursery areas like bays and harbors (Love et al. 1996b). Once settled, recruits remain in these areas for about a year before moving deeper into the open ocean nearshore; adults primarily associate with ecotone habitat (here, the interface between hard and soft bottom) during the non-spawning season and sand flats during the summer spawning season (Mason & Lowe 2010, McKinzie et al. 2014).

We obtained daily SST measurements (°C) collected from 1954 to 2022 at the northern end of Santa Monica Bay, off Point Dume, CA (Carter et al. 2022; Fig. 1). From these, we derived a mean summer (June—August) SST for each year. Of the coastal locations with available long-term SST data in southern California (Carter et al. 2022), Pt. Dume is nearest to the location of the SCUBA transect data (diver surveys) analyzed in this study (Fig. 1). In addition, although absolute SSTs differ along the southern California coast, long-term trends in SST are similar coastwide, i.e. SST trends in Santa Monica Bay follow SST trends along the southern California coast (Carter et al. 2022).

We plotted temporal trends in SST, adult densities, and harvest to compare their decadal means occur-

ring during each tagging period and their overall patterns throughout the time series. We used several harvest data sources (e.g. commercial passenger fishing vessel (CPFV) logbook data, harvest estimates across all fishing modes, technical reports) spanning different periods to reconstruct historic BSB CPFV harvest (Text S4). We chose to use harvest data rather than CPUE because the available time series for harvest was longer and because in this fishery, harvest trends closely correspond with CPUE trends through time (Jarvis et al. 2014, CDFW 2020).

To identify potential lagged relationships between SST and adult density and between SST and harvest, we calculated Pearson cross-correlation coefficients from lags 0 to 10 yr using the R package 'funtimes' (Lyubchich et al. 2023). Notably, the adult density data represent BSB at least 2–3 yr of age, which is approximately 2–3 yr younger than fishery recruitment age over most of the time series. Positive correlations occurring at a lag of 0 yr suggest influence of SST on the adult population, whereas positive correlations occurring at lags greater than 2–3 yr, i.e. when SST predicts future adult densities or harvest, suggest influence of SST on the early life history stages. Lastly, we tested for correlations between adult densities and BSB CPFV harvest. The R package 'funtimes' uses a bootstrap approach to account for potential autocorrelation among time series at each lag; of primary interest are correlations occurring near or outside the reported 95% confidence region.

2.5. Relationship between YOY juvenile recruitment and SST

To explore potential relationships between YOY juvenile recruitment and temperature, we also considered the Oceanic Niño Index (ONI), as El Niño was shown to have a positive effect on BSB larval abundances off Baja California, Mexico (Avendaño-Ibarra et al. 2009). We obtained the ONI data as monthly index values (NOAA 2023a), which we plotted for comparison with temporal trends in mean annual SST and YOY juvenile recruitment. We then calculated mean annual indices for the ONI and tested for lagged correlations between YOY juvenile recruitment and SST and the ONI from lags 0 to 3 yr using the R package 'funtimes' (Lyubchich et al. 2023). Again, YOY juvenile recruits represent BSB age 0 to nearly age 1. Using the lags identified from the cross-correlation analysis, we further explored the influence of SST and ONI on YOY juvenile recruitment with a generalized additive model (GAM) using the R package 'mgcv' (Wood 2017). We tested several candidate YOY juvenile recruitment models, a temperature-only model with SST (lag of 0) and ONI (lag of 1), and 5 additional models intended to account for possible confounding effects of spawning biomass and harvest impacts, including one without the ONI term. For these, we first separately incorporated BSB CPFV harvest as a proxy for the impact of removals on recruitment and then incorporated adult densities as a proxy for spawning stock biomass. For both covariates, we tested lags of 0 and 1 yr given the potential that some YOY juvenile recruits may be closer in age to 1 yr.

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 and allowed the model to automatically select the basis dimension, i.e. k parameter, or 'wiggliness' of each covariate. We performed model checks for convergence, basis function misspecification, and concurvity, i.e. nonlinear form of collinearity (Wood 2017). For all GAMs, we allowed the model to perform automatic term selection (select = TRUE) and smoothness (method = REML). We selected the most parsimonious model based on both the lowest Akaike's information criterion (AIC) value and model fit, which we report as the percent deviance explained. We visually explored the conditional effects of important explanatory variables using the R package 'visreg' (Breheny & Burchett 2017).

2.6. 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 Text S5 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, which represents harvest of kelp bass and BSB combined and the longest continuous harvest time series that includes BSB (Text S4). For the graphical

timeline, we plotted monthly indices of the Pacific Decadal Oscillation (PDO, a measure of SST anomalies; Di Lorenzo et al. 2008, NOAA 2023b) along with a 12 mo running mean. We chose to use the PDO due to the lack of alternative temperature data sources available during the historical period. We noted decadal-scale periods of predominately cool or warm temperature regimes (Mantua et al. 1997, Minobe 1997) associated with assemblage shifts in California's fishes as described by Hubbs (1948), MacCall (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, H. Walker et al. 2020).

3. RESULTS

3.1. 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. 2). By decade, mean annual survival was highest in the 1960s and lowest in the 1990s. Mean annual survival of legal-size BSB was higher in the 2010s than in the 1990s, but survival of sublegal fish was in the 2010s lower than in both the 1960s and the 1990s (Fig. 2). Biologist recapture rates (p) of tagged BSB were low (⩽1%) across all tagging periods. Angler CAR rates could only be estimated for the 1960s and 2010s and were generally low (0–4%) compared to harvest rates (see Section 3.2), but were nevertheless slightly conservative, as they assume 100% tag reporting.

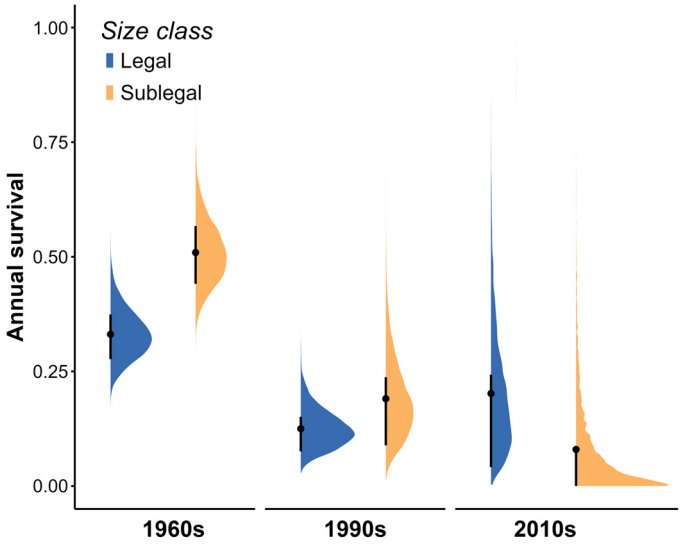

Fig. 2. Bayesian capture–mark–reencounter model posterior distributions and mean annual survival plus 66% highest density intervals (dots plus lines) for legal- and sublegal-size barred sand bass *Paralabrax nebulifer* across tagging periods in southern California, USA. Annual survival rate is the proportion surviving in a year

The CMR decadal growth parameter estimates combined with the 2010s VBGF parameter estimates indicated BSB grew faster to reach a given size-at-age by year 3 but reached a smaller overall size at age 16; at the intermediate age (9.5 yr), BSB in the 1990s reached a larger overall size (Fig. 3).

3.2. Decadal trends in harvest rates and population size

Like the CAR rates, harvest rates estimated by our CMR model were also conservative because they are conditional on angler reporting rates. Without adjusting for tag reporting, we observed an overall decrease in legal-size harvest rates over time, with the 1960s harvest rate more than ~2× and ~5× higher than the 1990s and 2010s harvest rates, respectively (Fig. S3). Harvest rates of sublegal-size BSB were low across decades but increased slightly in the 2010s (Fig. S3). After adjusting for different tag reporting rates, with uncertainty, conditional harvest rates showed a similar pattern, regardless of tag reporting rate combination across decades. Harvest rates under a 25% reporting rate were highest but the most uncertain (Fig. 4A).

The conditional estimates of mean BSB population size increased with increased tag reporting rates (Fig. 4B). Given the higher uncertainty in conditional harvest rates under the lowest probability tag reporting scenario (Fig. 4A), we focused our comparison of mean decadal population estimates under the 50 and 75% tag reporting scenarios. Regardless of tag reporting combination across decades, the population increased by at least 50% to as much as double between the 1960s and 1990s (Fig. 4B). By the 2010s, the mean population size had declined nearly 10-fold to ~1 to 3 million BSB under the 50 and 75% tag reporting scenarios. This was roughly 1/3 the size it had been in the 1960s, though there was greater uncertainty in the 2010s estimate (Fig. 4B). The maximum and minimum conditional mean population estimate across decades were ~16 million BSB in the 1990s under a 75% tag reporting rate and ~1.4 million BSB in the 2010s under a 50% tag reporting rate (Fig. 4B).

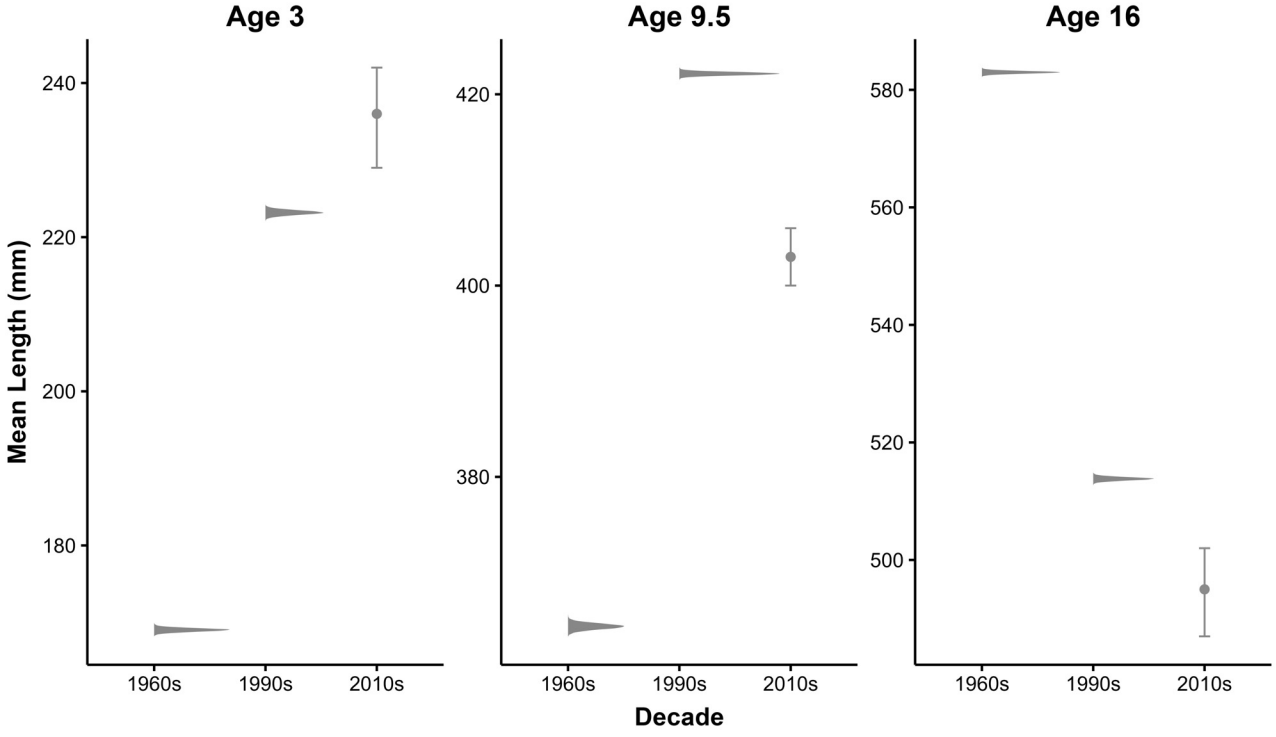

Fig. 3. Growth parameter estimates of barred sand bass *Paralabrax nebulifer* mean size-at-ages 3, 9.5, and 16 yr across tagging periods in southern California, USA. The 1960s and 1990s growth parameter estimates represent capture–mark–reencounter model Bayesian posteriors for the Francis parameters, $L1_3$, $L2_{9.5}$, and $L3_{16}$, of the von Bertalanffy growth function, while the 2010s estimates represent mean and 95% confidence intervals derived from age and growth data collected from 2011 to 2016 (K. Walker et al. 2020) and fit to the Francis parameterization of the von Bertalanffy growth function (there were too few recapture lengths in the 2010s data to accurately estimate growth in the 2010s capture–mark–reencounter model). Mean lengths represent total length

3.3. Comparison to SST, adult densities, and harvest

Trends in our population estimates corresponded to trends in SST and fishery-independent and -dependent data during the same time periods (Fig. 5). Adult densities were not available prior to 1974, but the lower adult densities in the 1970s were consistent with our smaller population estimate in the 1960s (relative to the 1990s); the population estimates and adult densities were also lowest in the 2010s (Fig. 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. 5C). Trends in BSB harvest were reflected in the large fluctuations in rockbass (=kelp bass and BSB) CPFV harvest, corresponding to 2 windows of increased fishing opportunity for BSB (Fig. 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. Overall, trends in adult densities and harvest appeared to lag SST trends; however, after the fishery collapse during the last tagging period, trends diverged, with adult densities trending upward following the increase in SST (albeit still at low levels), while BSB harvest remained low after 2015 (Fig. 5).

Cross-correlation analysis revealed adult densities lagged SST by 3 to 4 yr (Fig. 5D), and harvest lagged SST by 4 to 10 yr (Fig. 5E). The highest correlations between SST and harvest were strong and occurred at lags of 6, 7, and 8 yr, corresponding to the approximate age of fishery recruits, while the highest correlations between SST and adult densities corresponded to the approximate age of maturity (Fig. 5D,E). BSB CPFV harvest lagged adult densities by 0–5 yr, with the highest correlations ($r > 0.6$) occurring at 1, 2, and 3 yr lags (Fig. 5F).

3.4. Relationship between YOY juvenile recruitment and SST

During the 1990s tagging period, when the population size was estimated to be the highest, YOY

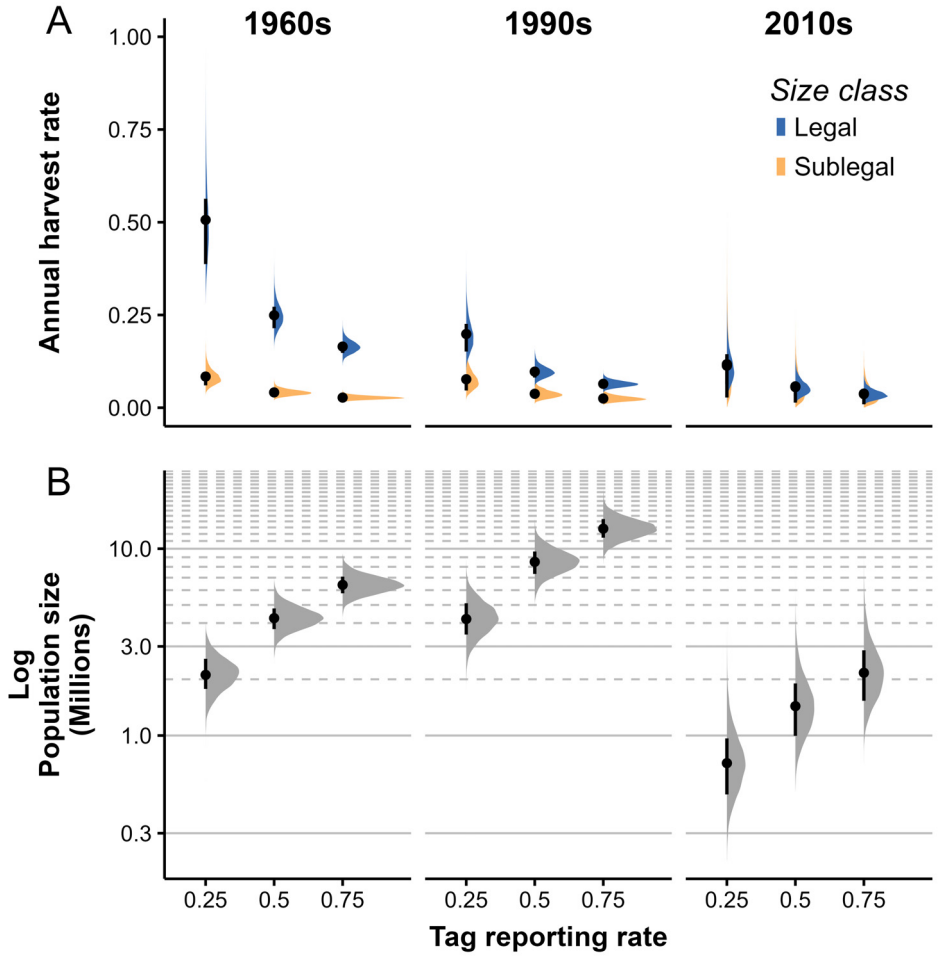

Fig. 4. Bayesian capture–mark–reencounter model posterior distributions and means plus 66% high density intervals (dots plus lines) of barred sand bass *Paralabrax nebulifer* (A) estimated size-specific annual harvest rates and (B) derived log population size conditioned on tag reporting scenario in southern California, USA, with mean probabilities of reporting a tag = 25, 50, and 75%. Annual harvest rate is the proportion of fish dying each year due to fishing

juvenile recruitment was generally below average, while the mean SST was above average, and the ONI was mostly neutral except for the major El Niño event in 1997 (Fig. 6). Between 1974 and 2012, YOY juvenile recruitment was sporadic, with only 3 of the 40 yr showing strong peaks (one spanning the years 1977–1979, one in 1984, and one in 1998); however, during the fishery collapse, from 2013 to 2021, YOY juvenile recruitment remained at elevated levels, coincident with elevated SSTs (Fig. 6C). Cross-correlation analysis revealed YOY juvenile recruit density showed the highest correlation with SST at a lag of 0 (Fig. 6D) and the highest correlation with the ONI at a lag of 1 (Fig. 6E). These correlations were only marginal and weak; however, the temperature-only GAM revealed a strong positive relationship between YOY juvenile recruitment and ONI (1 yr lag) and a marginally important relationship between YOY juvenile recruitment and SST (0 yr lag), with 19.5% of the deviance explained (Table 2). The conditional effects plot for the temperature-only model showed a positive nonlinear effect of SST on YOY juvenile recruitment across increasing values of ONI, representative of La Niña, neutral, and El Niño conditions (Fig. 6F). Given that harvest showed marginally high concurvity with adult densities (0.58), we compared models with and without the adult density term. Accounting for harvest greatly improved model fit (59.9% deviance explained), with the most parsimonious models incorporating harvest at a zero lag (Table 2). Adult densities at a zero lag did not improve model fit and only slightly improved model fit when lagged by 1 yr; relative to SST, ONI, and harvest, adult densities

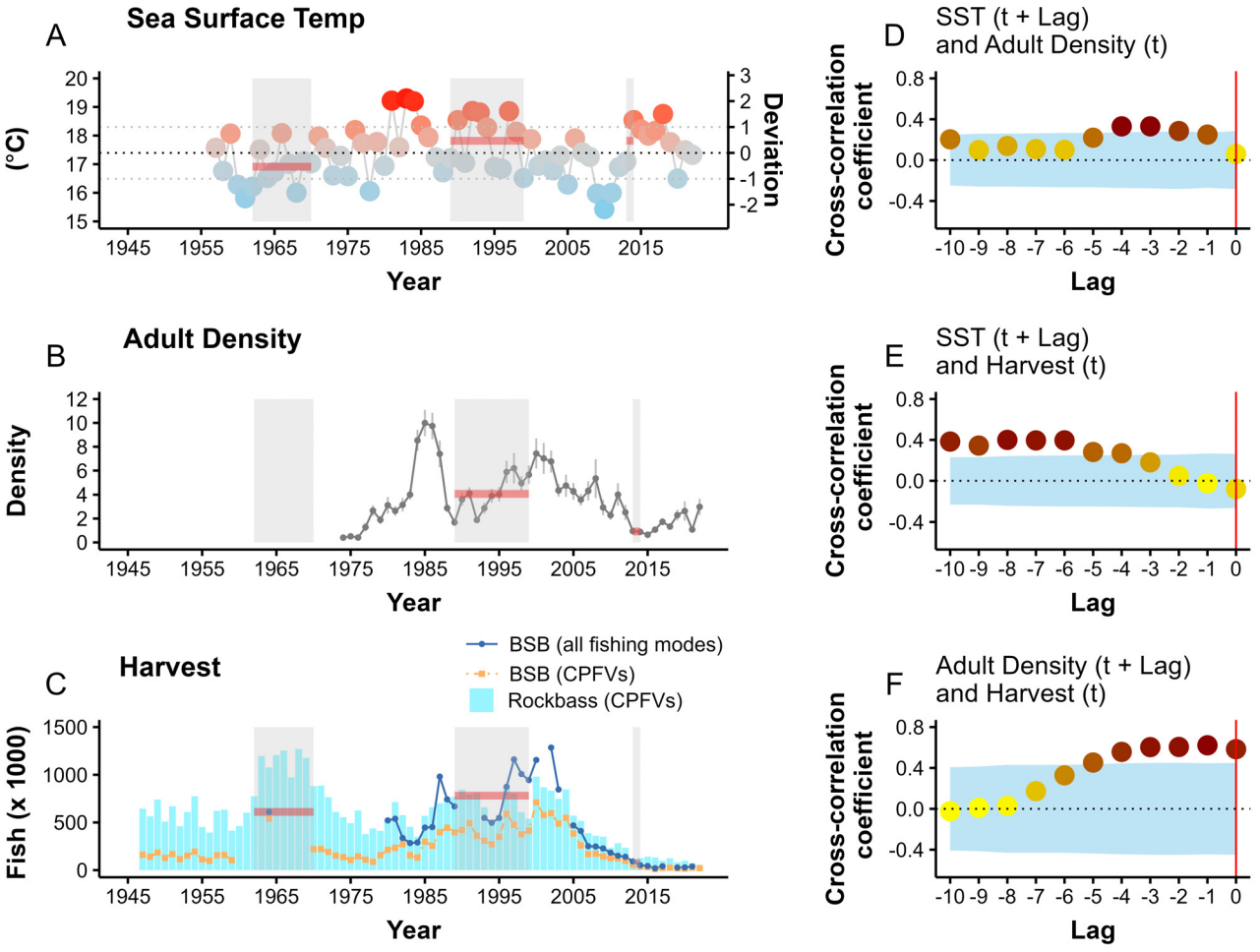

Fig. 5. Temporal trends in (A) mean annual summer sea surface temperatures (SST) at Pt. Dume, California, USA, 1956–2022, (B) mean (±SE) annual adult densities (fish/transect) of barred sand bass *Paralabrax nebulifer* (BSB) as measured on diver surveys in King Harbor, California, USA, 1974–2022, (C) total southern California BSB harvest across all recreational fishing modes 1964 and 1980–2021), commercial passenger fishing vessel (CPFV) harvest of BSB (1947–2022), CPFV harvest of rockbass (=kelp bass *P. clathratus* and BSB), and Pearson cross-correlation coefficients and shaded blue 95% bootstrap confidence regions for (D) SST and adult densities, (E) SST and CPFV harvest of BSB, and (F) adult densities and CPFV harvest of BSB. Horizontal red lines in A, B, and C depict means during each BSB tagging period (shaded rectangles)

were not a driver of YOY juvenile recruit densities (Table 2).

The reduced GAM, having only SST (0 yr lag), ONI (1 yr lag), and BSB CPFV harvest (0 yr lag) as predictors of YOY juvenile recruit density showed a strong positive relationship between YOY juvenile recruitment and both SST and ONI (Fig. 7A,B). With respect to harvest, there was a strong negative relationship between YOY juvenile recruitment and harvest (Fig. 7C). After accounting for harvest, the conditional effect of SST on YOY juvenile recruitment across increasing values of ONI was similar to the temperature-only model, but predicted increases in YOY juvenile recruit densities were less pronounced (Fig. 7D).

3.5. Historical accounts

Sources for 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. S4). 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 generally corresponded to decadal-scale fluctuations in ocean temperature. Most notable were 3 periods: (1) the mid-19th century, in which the southern Cali-

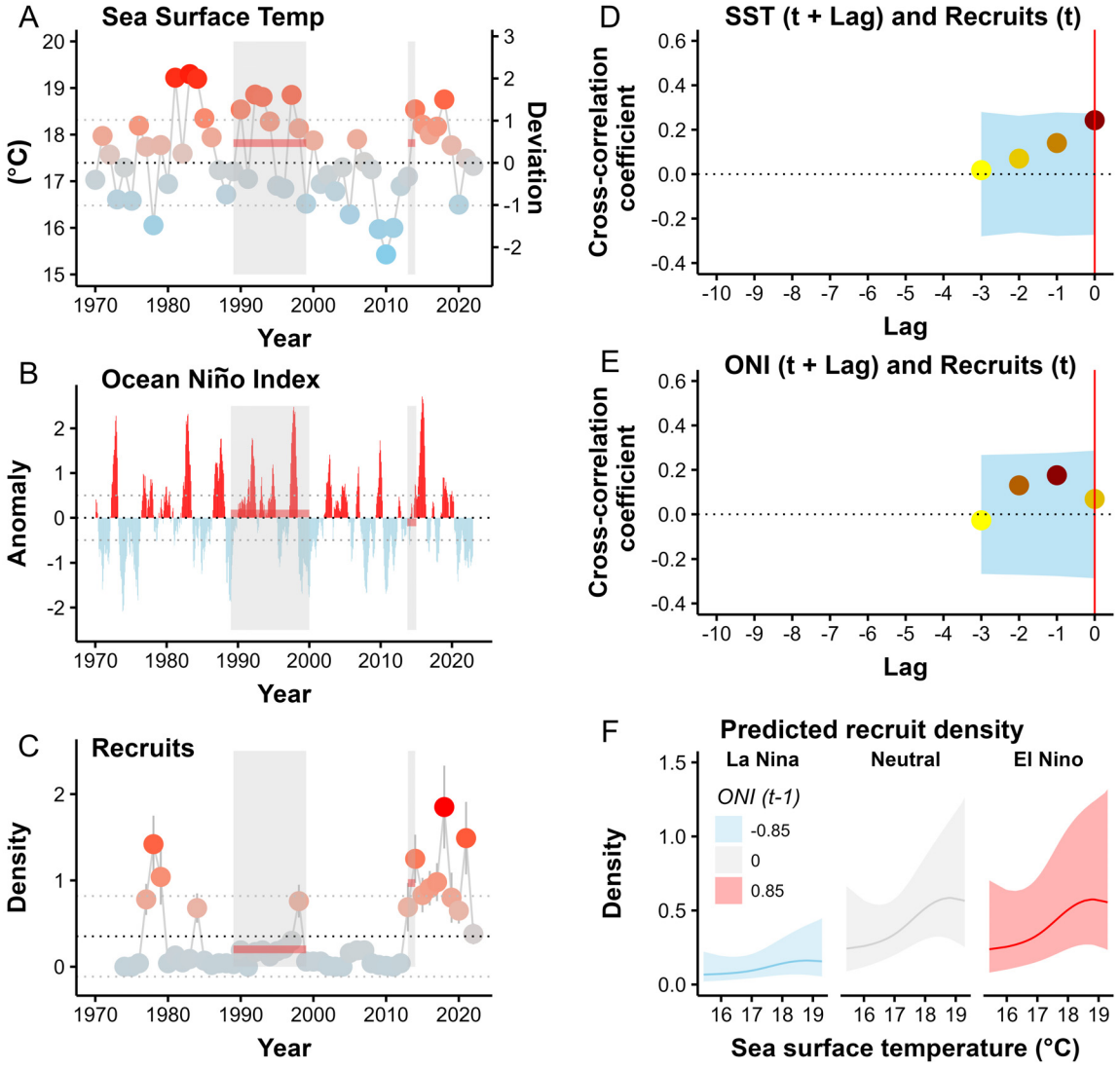

Fig. 6. Temporal trends in (A) mean annual summer sea surface temperatures (SST) at Pt. Dume, California, USA, 1970–2022, (B) monthly Oceanic Niño Index (ONI) anomalies, 1970–2022 (dotted lines represent threshold values corresponding to El Niño (≥ 0.5) and La Niña conditions (≤ −0.5), respectively), and (C) mean annual densities of barred sand bass *Paralabrax nebulifer* juvenile (young-of-the-year) recruits as measured on diver surveys in King Harbor, California, USA, 1974–2022, with Pearson cross-correlation coefficients and shaded blue 95% bootstrap confidence regions for (D) SST (°C) and recruits and (E) ONI and recruits, and (F) the effect of SST on juvenile recruit density across different values of the ONI (lagged by 1 yr). Horizontal red lines in A, B, and C depict means during each tagging period (shaded rectangles)

fornia fish fauna was described as tropical and BSB was first described from a specimen as far north as Monterey in central California (Girard 1858, Hubbs 1948), (2) the cool regime of the 1950s and 1960s (1947–1976; Mantua et al. 1997, Minobe 1997), 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' relative to kelp bass (Young 1963, 1969, Feder et al. 1974), and (3) a short window in the 1960s when observations made by CDFW field biologists conducting field surveys indicated a dramatic increase in the numbers of BSB in southern California (CDFG 1962, Turner et al. 1969). This observed increase in BSB availability was also reflected in the substantial increase in rockbass harvest at the time (Fig. 5C) and occurred 5 to 6 yr following one of the most significant El Niño events documented in southern California (the 1957/58 El Niño, Radovich 1961). The period of higher rockbass harvest was short-lived, and by the end of the cool regime in the mid-to-late 1970s, rockbass harvest had dramatically declined and returned to being dominated

Table 2. Results of the generalized additive models of juvenile (young-of-the-year) barred sand bass *Paralabrax nebulifer* recruit densities as a smoothed function of sea surface temperature (SST) (from the Shore Stations Program; Carter et al. 2022), Oceanic Niño Index (oni) (from NOAA 2023a), adult densities (ad), and harvest (lands) in southern California, USA, from 1974 to 2022. Tweedie: estimated shape parameter for Tweedie distribution; coeff.: model coefficient. Covariates denoted with '.l' were lagged by 1 yr. Adult and juvenile recruit densities are from Vantuna Research Group, Occidental College. Recreational landings are from California Department of Fish and Wildlife Commercial Passenger Fishing Vessel logbook records (=harvested fish). AIC: Akaike's information criterion. Significant values ($p < 0.05$) are highlighted in **bold**

Model Formula	Deviance explained (%)	AIC	Tweedie	Intercept coeff.	p			
					sst	ad	lands	oni.l
~ s(sst) + s(oni.1) + s(lands) + s(ad.l)	60.8	4.2	1.514	−1.514	**0.020**	0.614	**7.51×10^{-7}**	**0.003**
~ s(sst) + s(oni.1) + s(lands) + s(ad)	59.9	8.4	1.506	−1.589	**0.019**	0.852	**2.00×10^{-16}**	**0.002**
~ s(sst) + s(oni.1) + s(lands)	59.9	8.4	1.506	−1.589	**0.019**	–	**2.00×10^{-16}**	**0.002**
~ s(sst) + s(oni.1) + s(lands.l)	52.8	11.8	1.531	−1.534	**0.018**	–	**2.00×10^{-16}**	**0.003**
~ s(sst) + s(lands)	44.4	19.1	1.558	−1.454	**0.031**	–	**1.75×10^{-6}**	–
~ s(sst) + s(oni.l)	19.5	39.9	1.665	−1.239	0.056	–	–	**0.012**

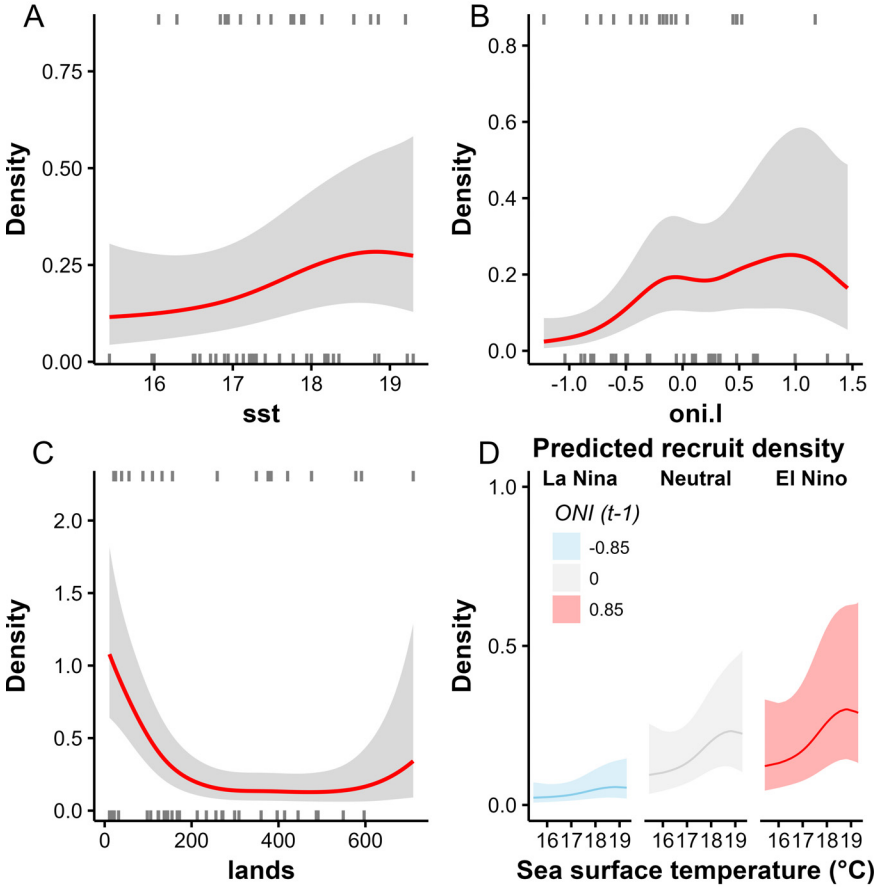

Fig. 7. Conditional effects plots for the generalized additive model of barred sand bass *Paralabrax nebulifer* juvenile (young-of-the-year) recruit density in southern California, 1974–2022 as a function of (A) mean annual summer sea surface temperatures (sst, °C), (B) monthly Oceanic Niño Index (ONI) anomalies (oni.l, lagged by 1 yr) and (C) commercial passenger fishing vessel harvest (lands), and (D) the effect of SST on juvenile recruit density across different values of the ONI after accounting for harvest. Shaded ribbon depicts the 95% confidence band. Effects of individual covariates (shown in A, B, and C) and multiple covariates (D) on juvenile recruit density are conditioned on the other covariates being fixed at their median values. Upper and lower vertical bars in A, B, and C depict positive and negative residuals, respectively

by kelp bass (Fig. 5C; Wine 1978, 1979a,b). Love et al. (1996a) reported BSB CPFV CPUE at this time was 5–10× lower than it was a decade later, during the subsequent warm regime. For a detailed narrative of BSB historical accounts, including the graphical timeline (Fig. S4), see Text S6.

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 historical accounts in the literature and a variety of long-term data streams representing different life history stages, indicate the BSB fishery in southern California between 1962 and 2014 can be characterized by 2 windows of fishing opportunity that were largely driven by 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 approximately one order of magnitude. Despite this dramatically reduced population size and evidence of recruitment limitation in

the 40 yr prior, YOY juvenile recruitment remained elevated in the decade since and was associated with novel, anomalously warm water conditions. Thus, we can confirm that recruitment limitation was not a factor contributing to delayed recovery to date. Based on these findings, we postulate that sporadic strong YOY juvenile recruitment events in southern California may not have been entirely locally sourced and that as a result of the recent elevated recruitment, there is high potential for fishery recovery when these recruits enter the fishery. Nevertheless, despite signs of incipient population recovery, the spawning aggregations remain absent, suggesting that other potential factors (e.g. continued fishing on spawning aggregations, Allee effects) have impacted fishery recovery to date.

4.1. Sporadic, warm-water recruitment pulses

At least since 1974, the BSB population in southern California has had extended periods of minimal YOY juvenile recruitment with intermittent peaks showing a positive relationship with SST, especially following El Niño events (Fig. 7D). We also found that harvest negatively influenced YOY juvenile recruit densities, effectively dampening the positive temperature effects. Nevertheless, the influence of SST on this early life history stage was also detected in relationships between SST and future adult densities and harvest, implicating SST as a predictor of fishery recruitment. For example, cross-correlation analysis revealed adult densities lagged SST by 3 to 4 yr, corresponding to the age at which BSB become mature (Fig. 5D), and the highest correlations between SST and harvest occurred at 6, 7, and 8 yr lags (Fig. 5E), corresponding to the approximate age of fishery recruits. Though the adult densities are from a single location in southern California, the strong correlation between adult densities and the landings data (bight-wide data) suggest these data are representative of bight-wide trends in adult densities. Moreover, our results relating temperature and BSB trends are consistent with other studies; Miller & Erisman (2014) found that YOY 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. A more recent analysis, spanning 1963 to 2016, revealed BSB larval abundance in southern California has been sporadic, influenced in part by SST, and predictive of future catches (Jarvis Mason preprint doi:10.1101/2023.10.11.561723).

Correspondence between early life history stage recruitment and fluctuations in 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 atypical of aggregation-based fishery catch dynamics. Aggregate spawners typically show hyperstable catches, in which population declines are masked by stable harvest/CPUE as 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', Mullon et al. 2005, p. 111); however, BSB showed a more 'erratic' harvest trajectory ('i.e. a fall after several ups and downs', Mullon et al. 2005, p. 111). Although effort shifts can contribute to interannual fluctuations in recreational harvest (Dotson & Charter 2003, Blincow & Semmens 2022), our results indicate the periodic 'ups' in BSB harvest are primarily attributable to sporadic, warm water recruitment pulses.

YOY juvenile recruitment remained well above average after 2013, despite the low population size estimated for the 2010s when the fishery collapsed. Between 2012 and 2020, southern California experienced several marine heatwaves (MHWs: 2014–2015 ['the Blob'], 2019, 2020, 2021), including a strong El Niño (2015–2016). The effects of this dramatic alteration of the Southern California Bight ecosystem were profound (Leising et al. 2015, Cavole et al. 2016, H. Walker et al. 2020) 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, Mexico. 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.

Given that strong YOY juvenile recruitment pulses in southern California were only sporadic, and that local recruit densities are negatively influenced by harvest and positively influenced by SST and the ONI, it is possible that the southern California pop-

ulation is dependent on sporadic El Niño-driven larval transport from Baja California (Lilly et al. 2022). Anomalous poleward advection of larvae into southern California is commonly (but not always) associated with El Niño events (McClatchie et al. 2018, Cimino et al. 2021, Lilly et al. 2022). Indeed, a high degree of genetic connectivity exists between BSB populations in the 2 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 February), 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 YOY juvenile recruits in southern California may represent northward advected Baja California larvae from the previous summer or fall, which would correspond to the 1 yr lag we observed between the ONI and YOY juvenile recruit densities. Nevertheless, the degree to which BSB larval recruitment is seeded from Baja California warrants further research.

4.2. Impacts on aggregation dynamics?

Following sustained high YOY juvenile recruitment associated with anomalously warm conditions since the mid-2010s, adult densities more than doubled (albeit still at lower levels); however, BSB harvest remained exceptionally low. Under the current MSL, BSB are expected to recruit to the fishery at an average age of 8 yr; thus, the earliest indication of fishery recovery should have been evident in recent years. One explanation for the lack of fishery recruitment despite high YOY juvenile recruitment and higher adult densities could simply be that it is still too early to detect in the harvest data, as boat access to ocean fishing was halted during the COVID-19 pandemic and some commercial sportfishing vessel operations were also temporarily closed. We also cannot rule out the possibility of a potential residual Allee effect associated with the population decline and fishery collapse in the mid-2010s. For example, 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, 1990). If 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, 1990, Waterhouse et al. 2020). An acoustic telemetry study off San Diego 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).

4.3. 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. Contrary to expectation, conditional harvest rates were generally higher in the 1960s and lower in the 1990s, regardless of tag reporting rate. This may be in part due to a higher number of licensed anglers in the 1960s than in the 1990s (~3× more, Bellquist 2015). However, the mean annual harvest of sublegal- and legal-sized fish in both decades was similar during the 2 periods (Table S2), 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.

Harvest rates were most uncertain under the 25% tag reporting scenario. Although tag reporting rates were unknown for each tagging period, we assume they ranged from moderate (~50%) to high (~75%). Of the 3 conditional harvest rates for the 1990s, the harvest rate under a mean 50% probability of reporting a tag was most similar to the BSB exploitation rates reported for the 1990s using catch curves (~11%, Jarvis et al. 2014). We presume that tag reporting in the 1960s was at least as high or higher due to enhanced outreach and cooperation with the fishing community

at that time (Collyer & Young 1953, Young 1963). It is possible that cooperation to report tags was not as high in the 2010s, given the increased take restrictions in 2013.

Overall, the estimated annual survival rates were substantially lower than would be expected based on the size distribution of fish tagged in the study (e.g. the size distribution of fish tagged included large BSB corresponding in age to 10+ yr old, suggesting a much higher survival rate). This could be due to (1) decreased tag reporting over time (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 3 tagging periods. This lower survival rate may have also contributed to a lack of fishery recovery, though the exact mechanism(s) driving the lower survival rate (e.g. potential non-compliance with the new MSL, environmental conditions, predation) are not known.

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 (Fig. 3). 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). BSB size and age at maturity have not been re-evaluated since the 1990s (Love et al. 1996b), but we know that just prior to the beginning of 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). This trend also points to a lack of consistent, appreciable local recruitment during this period.

4.4. 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 (Fig. 5D,E).

One notable finding was that the substantial increase in rockbass (=kelp bass and BSB) CPFV harvest we observed in the 1960s was reflected in historic observations of increased BSB availability during that period (CDFG 1962, Turner et al. 1969; Fig. S4G). 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 (Text S4). However, in addition to the historic accounts of increased availability, additional catch survey data we gathered from that period indicated that the relative contribution of BSB to rockbass harvest doubled compared to historical estimates (Pinkas et al.1968). The dramatic increase in BSB availability occurred 5 to 6 yr after the exceptionally strong 1957–1958 El Niño (Fig. S4), a period corresponding to the approximate age when BSB recruited into the fishery (5–6 yr) and one that further supports our findings relating sporadic YOY juvenile recruitment pulses to warm water events. Importantly, this timing, along with trends in adult densities, does not support El Niño-driven adult migration as a plausible explanation for the observed population fluctuations. Finally, being able to link the substantial increase in rockbass harvest in the 1960s to increased BSB availability was critical in discovering this fishery experienced more than one boom and bust period.

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. We found that 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 (Young 1963, 1969, Feder et al. 1974). Thus, a 'healthy' BSB population is likely to look different to different people, depending on the lifetime of perspective (Bellquist et al. 2017). Perhaps with the exception of

the 'tropical' southern California conditions in the late 1800s, when BSB was first described from a specimen collected much farther north than its typical distribution (Girard 1858, Hubbs 1948), we found that the sustained increased availability of BSB in southern California during the warm regime of the 1980s and 1990s was not the norm over the historical period analyzed. Shifting baselines and 'institutional amnesia' can 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).

4.5. Management implications

Given the relationship we identified between recruitment and warm water pulses, we might anticipate that the predicted increase in MHWs (Oliver 2019) and secular ocean warming would benefit the BSB population in the future with perhaps more appreciable local recruitment and a shift in the center of the BSB geographic distribution northward into southern California (Pinsky et al. 2020). Although recent trends in YOY juvenile recruitment suggest fishery recovery is imminent, current regulations may not be adequate to prevent the quick collapse of a new emerging cohort and thus, management preparedness is prudent. Nassau grouper *Epinephelus striatus*, which also exhibits sporadic pulse recruitment (Stock et al. 2021, 2023), showed evidence of recovery 15 yr following conservation measures that included seasonal closures (Waterhouse et al. 2020). Similarly, a seasonal closure for BSB could potentially serve to enhance local recruitment, especially during favorable oceanographic conditions (Fig. 7C,D), and limit the potential for subsequent collapse and delayed recovery.

Our population estimates suggest that the prolonged fishery collapse following the second window of BSB fishing opportunity in the last century resulted from an approximate 10-fold decline in the population (Fig. 4). The first window of fishing opportunity in the 1960s did not result in a similar prolonged collapse. One difference between the 2 periods is that temperatures during the catch declines that preceded the second collapse remained cooler longer. Perhaps more importantly, there was no major El Niño event for nearly a decade (Fig. 5; Fig. S4), and northward advection of Baja California source waters was weak from 1999 through the early 2000s (Cimino et al. 2021). There is also no evidence to suggest that illegal fishing or underreporting of catch increased over that time period. Additionally, the reduced population size during the second fishery collapse may have surpassed an 'Allee-effect threshold', i.e. a level that prolonged collapse or delayed/impeded recovery (Hutchings 2015, Sadovy de Mitcheson 2016). If true, then a potential conservative 'Allee-effect threshold' for BSB, based on our CMR decadal population estimates of adult BSB, could be somewhere around 3 million fish. Moreover, we found that YOY juvenile recruitment was more influenced by warm water pulses and harvest than by adult densities, suggesting recruitment is less tied to spawning stock biomass than might otherwise be assumed. This breakdown, or lack of a spawner–recruit relationship is not uncommon (Lowerre-Barbieri et al. 2015, 2017, Heyman et al. 2019), and should be explored further if a formal stock assessment is considered for BSB.

Our results demonstrate that even with long-standing harvest limits in place (e.g. MSL, bag limit), spawning aggregation-based fishing in recruitment-limited populations may force the fishery to exist in perpetual boom-and-bust. 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. Thus, if the goal is to maintain reliable recreational fishing opportunities for a recruitment-limited transient aggregate spawner, limiting high CPUE fishing opportunities, i.e. limiting fishing during the spawning season, may be the best insurance against sudden, prolonged collapse and would balance the protection of spawning aggregations with long-term fishery sustainability (Erisman et al. 2020). 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.

Data availability. Data and code pertaining to the CMR models (simulation, growth, tag retention, CMR models by decade) are available online in a GitHub repository: https://github.com/ETJarvisMason/bsb-CMR. Data and code pertaining to the GAMs (predicting YOY juvenile recruit density) are available online in a separate GitHub repository: https://github.com/ETJarvisMason/bsb-GAM. We performed all analyses in R 4.0.3 (R Core Team 2020).

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