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Long-term population trend of northern anchovy (*Engraulis mordax*) in the California Current system

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Abstract

Ecosystem function and variability of eastern boundary upwelling systems is linked to the population dynamics of coastal pelagic fish. Developing population dynamics models of coastal pelagic species over many decades has unique challenges, and can benefit from the integration of multiple disparate sources of fisheries and resource survey information. Northern anchovy (*Engraulis mordax*) are vital trophic links in the food web of the California Current Ecosystem. Previous studies of this anchovy population had relatively narrow temporal ranges or focused on a single data source (e.g. larval abundance data). Here, we combine data sets that have informed previous studies, into one integrated statistical catch-at-age population dynamics model to estimate extended biomass and recruitment trends, providing a comprehensive account of anchovy dynamics from 1965–2021. Our results are consistent with previous biomass estimates but show an earlier peak in the 1970s that coincided with the peak of the US reduction fishery. Our results can facilitate an in-depth analysis of the environmental drivers influencing successful anchovy recruitment, serve to parameterize and evaluate performance of ecological models that mechanistically link the environment and food web to anchovy population dynamics and distribution, and provide the basis for a management strategy evaluation of this anchovy stock.

Keywords: coastal pelagic species; forage fish; population biology; anchovies; biomass; recruitment

Introduction

Anchovies (genus *Engraulis*), along with sardine (genera *Sardina*, *Sardinops*, and *Sardinella*) and other coastal pelagic species, are critical to the trophodynamics of coastal upwelling ecosystems worldwide (Schwartzlose et al. 1999, Checkley et al. 2017), where they transfer energy from plankton to larger predators, while also supporting many of the world's largest fisheries by volume (Schaefer 1970, Pikitch et al. 2014, McClatchie et al. 2016). For example, the Peruvian anchoveta (*Engraulis ringens*) supports the world's largest single-species fishery, with estimated yearly catches ranging from 4.9 to 7 million mt between 2018 and 2020; catches were far higher during the 1960s and early 1970s when the fishery accounted for 22% of global marine fish catches (Glantz 1979, FAO 2022). In common with many coastal pelagic species that fluctuate between natural cycles of boom-and-bust periods (Baumgartner et al. 1992, McClatchie et al. 2017, Salvatteci et al. 2018), the dynamics that govern population changes in

anchovy biomass remain poorly understood despite their ecological and economic importance (MacCall 2011, Sydeman et al. 2020). This is due in part to the difficulty in monitoring fishes that display both rapid fishery-independent changes in population biomass and whose distributions vary substantially in response to environment conditions (Robinson 2004, Tugores et al. 2010, Checkley et al. 2017, McClatchie et al. 2017).

The northern anchovy (*E. mordax*) supports >60 species of larger predators in coastal waters off the North American west coast (Szoboszlai et al. 2015, Koehn et al. 2016), and has been extensively studied (Sydeman et al. 2020 and references therein), notwithstanding it being one of the world's least abundant oceanic anchovy species (Checkley et al. 2017). *Engraulis mordax* are small short-lived fish which generally do not grow >16 cm in length or reach ages above 4 years (Schwartzlose et al. 1999), and suffer high mortality rates (Peterman and Bradford 1987). Northern anchovy schools are

capable of consuming a large fraction of standing zooplankton biomass (Koslow 1981), and feeding preferences shift from fish eggs, diatoms, and copepod nauplii at young ages to larger zooplankton including euphausiids during adult stages (Sydeman et al. 2020) with specific diets changing with prey availability (Koslow 1981, Hill et al. 2015). *Engraulis mordax* are highly productive coastal schooling fish, with individual females able to produce up to 14 000 eggs (Parrish et al. 1986, Baumgartner et al. 1992). However, mean spawning is highly variable across years and decades which results in boom-and-bust periods characteristic of coastal pelagic species (Baumgartner et al. 1992, Asch 2015).

Engraulis mordax is thought to occur in three subpopulations: a northern subpopulation from approximately Haida Gwaii, Canada, to northern California, USA, a central subpopulation from San Francisco Bay into central Baja California, Mexico, and a southern subpopulation from central Baja California into the Gulf of California (Sydeman et al. 2020). The central subpopulation, also known as the central stock of northern anchovy (hereafter 'anchovy'), is the most abundant of the three subpopulations and supported moderate-sized US and Mexican commercial fisheries in the California Current Ecosystem from the 1910s to the early 1990s.

Sustained monitoring of oceans and fisheries are vital for understanding ecosystem shifts and distinguishing between natural and anthropogenic driven changes in fish populations (Santora et al. 2021a, Gallo et al. 2022). There have been multiple efforts to monitor the stock size and variability of anchovy over the past 60 years. The first notable effort started in 1951 with the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program (Bograd et al. 2003, MacCall 2011, McClatchie 2014). While CalCOFI's main objective was initially to monitor sardine abundance and investigate oceanographic drivers of sardine productivity, it evolved into an ecosystem monitoring program with seasonal collections and enumeration of all identifiable species of ichthyoplankton, as well as zooplankton and physical oceanographic conditions. CalCOFI data have been used to develop time-series of relative spawning stock biomass (SSB) from 1951–2021 (MacCall et al. 2016, Thayer et al. 2017), as well as recruitment from 1981–2009 (Fissel et al. 2011). However, these estimates assume constant daily specific fecundity and do not integrate measures of adult abundance or age-composition data from sources other than CalCOFI, unlike the historical daily egg production method (DEPM) abundance estimates of northern anchovy (Bindman 1986). Several integrated stock assessments have been implemented for anchovy since the 1980s to quantify temporal changes in biomass and recruitment. However, the temporal range of these models was limited to a few decades, as they were intended to produce recent or near-future biomass estimates for management.

Integrated stock assessments fit a population dynamics model to data to estimate population parameters and the associated stock biomass trajectory that best reproduce available observations from landings and survey data (Maunder and Punt 2013). Methot (1986 and 1989) produced the first integrated statistical catch-at-age assessment for anchovy, using fishery catch data and biomass estimates from fishery-independent sonar surveys and the DEPM from 1954–1986. Jacobsen et al. (1994) used similar data, along with data from aerial spotter surveys in a biomass dynamics model that produced estimates for 1963–1991. A recent stock assessment of

anchovy was conducted in 2021, which estimated biomass and recruitment from 2015–2021 (Kuriyama et al. 2022). Collectively, these assessments show periods of high biomass prior to the fishery collapsing around 1990, followed by an extended period of low biomass up to 2015, after which anchovy biomass increased rapidly. However, there is little agreement between population models where they overlap temporally (Sydeman et al. 2020), and no population model covers multiple cycles of boom-and-bust that appear to have a periodicity of ~60–100 years (Baumgartner et al. 1992; McClatchie et al. 2017). The lack of robust estimates of recruitment and biomass spanning multiple population cycles and a range of ocean-climate conditions has hindered understanding of environmental drivers of anchovy dynamics (McClatchie et al. 2017, Sydeman et al. 2020).

The ability to manage or predict the future of a stock is limited without a robust understanding of the drivers of recruitment, particularly for short-lived, high turnover species (Basson 1999). A population model that produced biomass and recruitment estimates across a more extensive time period, which includes multiple boom-and-bust cycles, will provide a foundational baseline for improved understanding and management. In particular, the results could be used to relate estimates of recruitment with the biomass of spawners, environmental drivers, and to assess their interaction (Szuwalski et al. 2015, Pepin 2016). Such a population model would also provide a conditioned operating model (*sensu* Punt et al. 2016) that could form the basis for a management strategy evaluation (MSE) to contrast performances of management strategies under future recruitment scenarios (e.g. Haltuch et al. 2019, Kaplan et al. 2021).

Within the California Current Ecosystem, there are several data sources for anchovy that span multiple boom-and-bust cycles. These data include those used in previous assessments of anchovy (e.g. Methot 1986, Methot 1989, Jacobsen et al. 1994, Kuriyama et al. 2022), as well as newer, and never used before, data. In addition, progress in computing and software development has greatly advanced the ability to integrate disparate fisheries data sources into population analyses since the first assessments of the anchovy were conducted (Quinn 2003, Maunder and Piner 2015). We synthesized available data to produce the most temporally comprehensive integrated assessment for anchovy, and aimed to provide: (1) comprehensive estimates of historical abundance and recruitment; and, (2) a model framework with associated documentation that can facilitate future studies on the role of the environment in anchovy population dynamics or future MSE. We also discuss the challenges faced when combining disparate observation time-series into a population model, and propose the best options. We then describe our new estimates in light of recent ecosystem changes in the California Current ecosystem and suggest possible ways to best use population model outputs to relate anchovy recruitment with environmental drivers.

Methods

We used the statistical age-structured population modelling framework Stock Synthesis 3 (v3.30.21.00; Methot and Wetzel 2013) to estimate historical biomass and recruitment for anchovy. Stock Synthesis has been widely used in stock assessment modelling to estimate temporal changes in the biomass and recruitment of fish stocks in response to the effects of fishing (Methot and Wetzel 2013, Dichmont et al.

2016). This modelling framework consists of a population dynamics model of the stock of interest, here the central stock of northern anchovy ('anchovy'), as well as observation models that enable use of various types of information for a fish population (e.g. empirical measures of numbers-at-age, size-at-age and standardized measures of abundance) from fishery-dependent and -independent sources within an integrated analysis for parameter estimation (Maunder and Punt 2013). Uncertainty associated with each data source is propagated into the uncertainty of parameter estimates (e.g. natural mortality, equilibrium recruitment) and the derived quantities such as biomass and recruitment time-series using either frequentist or Bayesian methods. Here, uncertainty was quantified using the inverse Hessian method in maximum likelihood estimation (Methot and Wetzel 2013) rather than Bayesian inference to avoid prohibitively long run times.

Available data

Four types of data were available for use in the assessment (Table 1): fishery-independent abundance indices, fishery catches, age compositions (fishery-dependent and -independent), and empirical weight-at-age (fishery-dependent and -independent). Although additional length data are available from fisheries and surveys, the rapid growth of early ages, combined with high variability in growth rates over time and space, precludes effective utilization of length data in this analysis. Empirical weight-at-age observations are therefore used to transform numbers-at-age into biomass-at-age (Methot and Wetzel 2013). Data were summarized by season (S1: June–December, S2: January to May, see section; *Model Structure*) since the model has two seasons each year.

There are various fishery-independent relative indices of abundance for anchovy, not all of which were deemed suitable for use in the assessment. We initially had access to, and assessed the appropriateness of 12 indices of anchovy biomass or recruitment that covered 1951 to 2021 (Table 1). The decision to include individual indices was based on the outcomes of model diagnostics (See section 'Data and Model Selection') and expert opinion.

An index of anchovy biomass developed from coastal pelagic surveys that used an Acoustic-Trawl (AT) method conducted in the boreal summers of 2015 to 2021 (and spring 2016 and 2020) by the National Oceanic and Atmospheric Administration (NOAA) Southwest Fisheries Science Center (SWFSC) was available (Fig. 1b). The AT indices and associated coefficients of variation (CV) were derived from data collected using multi-frequency echosounders in combination with night-time surface trawls (see Renfree et al. (2023)). Surface trawls were used for species identification, numeration and measurement of target species, which allowed for species-apportioned biomass densities to be obtained from acoustic echograms (Demer et al. 2012, Zwolinski et al. 2012). This survey was considered the best recent survey estimate of anchovy biomass as it surveyed virtually the entire spatial distribution of the anchovy (some very nearshore habitat is difficult to survey with research vessels or other survey platforms). Biological samples collected during the surface trawls from the AT survey were used to derive survey (and population) weight-at-age (kg) and age-compositions from 2015–2021. Survey-specific age-length keys were constructed to convert abundance-at-length to abundance-at-age, which provided

age-composition data. Input sample sizes for these data were the number of positive trawl clusters from each survey cruise.

A relative biomass index of anchovy derived from acoustic sonar surveys conducted by the California Department of Fish and Game (now California Department of Fish and Wildlife CDFW; Mais 1974, Fig. 1b) was available from 1969–1985. Biological samples collected during these surveys provided weights-at-age (kg) for 1975–1983 and age compositions for 1967–1985 (Methot 1986). Age-composition data from the CDFW survey were taken from Methot (1989), using data sampled during the first quarter of each calendar year. Age-composition percentages for fish aged 3, 4 and 5+ in Methot (1989) were summed and input as age 3+, and the effective sample size for the CDFW survey age-composition was set to the number of aged fish divided by the typical number of fish collected per sampled load (25 fish per sample). Weights-at-age for all fishery-independent data sets, were based on data from the CDFW sonar survey from 1975–1983, and the AT surveys from 2015–2021, with weights-at-age for year-seasons without data assigned the mean values of the combined CDFW and AT surveys. AT survey weights-at-age values were calculated by converting the abundance-at-length to biomass-at-length and hence to weight-at-age. Age determination for AT data were based on the techniques described by Schwartzkopf et al. (2021), which used a June 1 birthdate based on the results of otolith edge and marginal increment analyses. Age determination for CDFW data were based on techniques described by Collins and Spratt (1969), in which June 1 was also the assumed birthdate.

The Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) provided additional potential indices of abundance from 1990–2022 (Ralston et al. 2015, Santora et al. 2021a, b). The RREAS program occurred in May and June, and sampled epipelagic forage species using pelagic midwater trawls fished during the night off the coast of central California (36°30′N–38°20′N) from 1990–2022, and from Cape Mendocino to San Diego (32°42′N–41°30′N) from 2004–2022, with the gear and methods comparable to the historical CDFW acoustic sonar surveys. While the RREAS was developed to support age-0 recruitment indices for rockfish stock assessments (Field et al. 2021), the survey also sampled a range of coastal pelagic species including anchovy, and sampled anchovy lengths from 2004–2022. Anchovy in the RREAS were size differentiated into adult fish (age 1+) >90 mm, and young-of-the-year (YOY, age 0 fish) <90 mm, and the biomass of adult and YOY catch was estimated using published length-weight relationships based on catches in numbers. Relative abundance indices for age 0 and age 1 + biomass for the RREAS were developed using a delta-generalized linear model (GLM) model (Santora et al. 2021a) implemented using the 'rstanarm' package (Goodrich et al. 2022) in R 4.3.1 (R Core Team 2023). Year effects from delta-GLMs were taken as the index of relative biomass, with modelled covariates including station, latitude and depth effects.

A spawning stock biomass index based on the daily egg production method (DEPM) was available from 1980–1985 from surveys conducted by the NOAA SWFSC during January to March from Monterey Bay, USA, to northern Baja, Mexico (Fig. 1a; Bindman 1986). A relative egg and larvae-derived SSB index (RELSSB) from 1951–2021 initially developed by MacCall et al. (2016) and updated and extended

Table 1. Type, name, source, population component, temporal availability, and spatial region of data considered.

| Data type	Source Name	Source	Description	Temporal coverage	Spatial coverage
Catch	Fishery	Commercial fishery port locations of Monterey Bay, Santa Barbara, San Pedro and Ensenada.	Total biomass (mt) of port landings.	June–December and January–May fishing seasons from 1950-2020.	Fishery off central and southern California, USA, and northern Baja California, Mexico.
Age composition	Fishery	Commercial fishery port locations of Monterey Bay, Santa Barbara, San Pedro and Ensenada.	Proportion of age 0, 1, 2, and 3+ fish.	June–December and January–May fishing seasons from 1967–1989, and from 2014–2020.	Fishery off central and southern California, USA, and northern Baja California, Mexico.
	AT	NOAA Southwest Fisheries Science Center Coastal Pelagic Survey	Proportion of age 0, 1, 2, and 3+ fish from subsampled trawl component of the survey.	Summer surveys from 2014–2019, and spring surveys in 2016 and 2020.	Entire coast from northern Vancouver Island, Canada to the USA–Mexico border.
	CDFW	California Department of Fish and Game sonar survey	Proportion of age 0, 1, 2, and 3+ fish from subsampled trawl component of the survey.	Spring or summer survey samples in US region from 1966–1985.	Point Conception, California (34.5°N) to the USA–Mexico border.
Index	AT	NOAA SWFSC Acoustic-Trawl survey	Biomass (mt) derived from acoustic surveys in combination with trawls.	Summer surveys from 2014–2019, and spring surveys in 2016 and 2020.	Portions of or entire coast from northern Vancouver Island, Canada to the northern border of Baja California Sur, Mexico.
	CDFW	California Department of Fish and Game (now the California Department of Fish and Wildlife) sonar survey	Biomass (mt) derived from acoustic surveys in combination with trawls (Mais 1974).	Spring surveys from 1968–1984.	Point Conception, California (34.5°N) to Punta Baja, Baja Califonia, Mexico (29.5°N).
	RELSSB	California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton surveys.	Relative Spawning Stock Biomass estimate derived from egg and larval counts (Thayer et al. 2017).	1951–2021 from January and April CalCOFI surveys.	Core sampling grid between Pt. Conception and the USA–Mexico border.
	DEPM	NOAA Southwest Fisheries Science Center (SWFSC) daily egg production method (DEPM) survey.	Spawning Stock Biomass derived using the daily egg production method (Bindman 1986).	1980-1985 from surveys conducted during January to March.	Monterey Bay, USA, to northern Baja, Mexico
	RREAS	Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) adult and young-of-the-year biomass index.	Relative Spawning Stock Biomass derived from the abundance of anchovy >90mm (for adults), and relative recruitment (age-0 fish) from abundance of anchovy <90 mm standard length (for young-of-the-year).	1983-2003 survey operated off of Central California (between 36°N and 38°N) during May and June, since 2004 the survey has covered most of the California coastline. Following model selection, the adult data were not retained in the model.	central California (36°30′N–38°20′N) since 1990, and from Mendocino to San Diego (32°42′N–41°30′N) since 2004
	CSL	California Sea Lion	Relative biomass derived from back-calculated anchovy weight from otoliths collected from scat samples (Curtis et al. 2022).	Samples collected during summer from 1981–2022. Following model selection, CSL data were not retained in the model.	Data were collected from rookeries on San Clemente and San Nicolas Islands through the SWFSC.
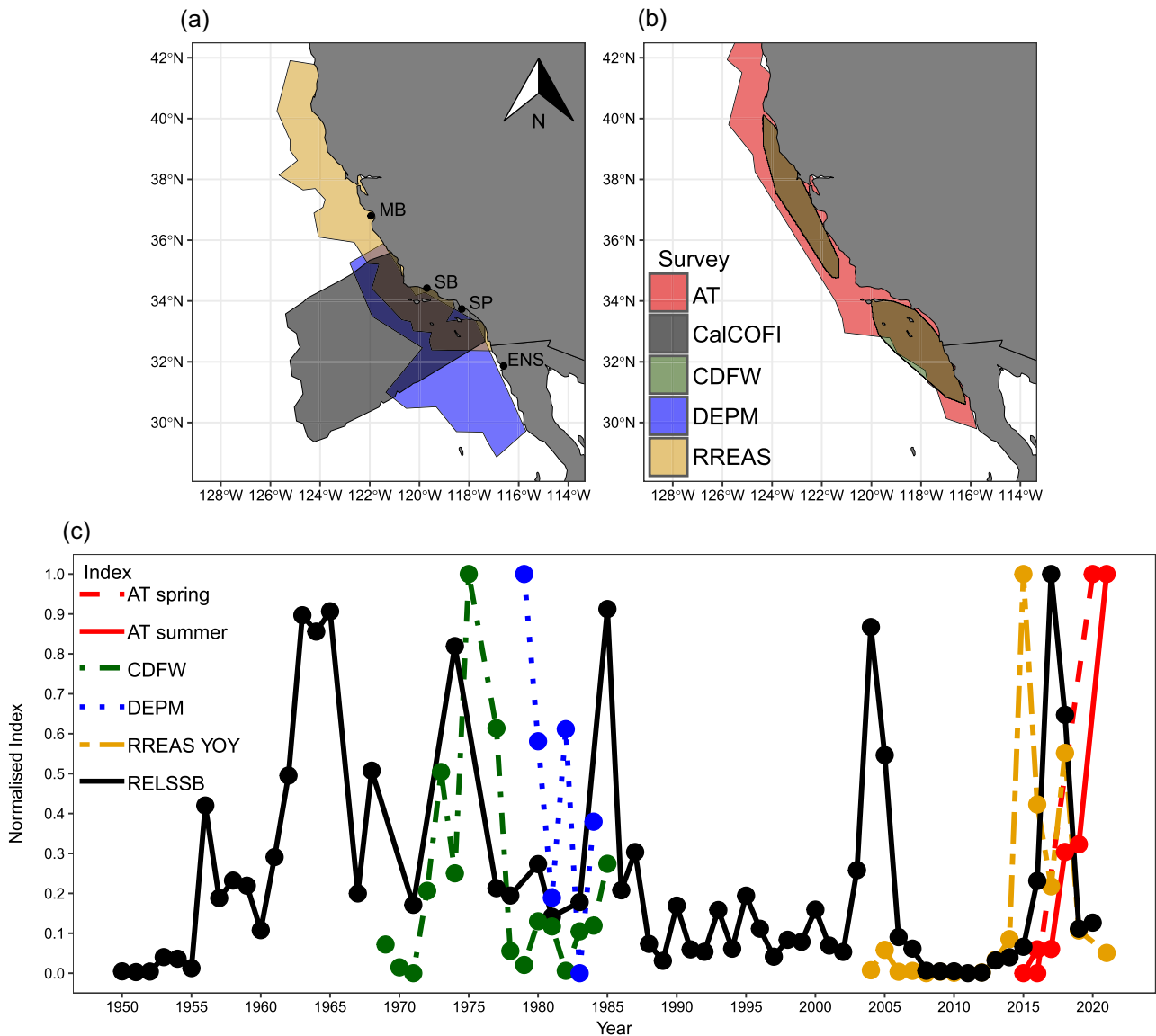
Figure 1. (a) Sampling area of anchovy surveys that collected early life stages (egg, larvae, and young of year), MB, SB, SP, and ENS show the locations of the ports of Monterey Bay, Santa Barbara, San Pedro, and Ensenada, respectively. (b) Sampling area of anchovy surveys that collected adult fish. (c) Normalized index by year for each biomass index.

by Thayer et al. (2017) was also available. The RELSSB index is based on geo-spatially weighted and summed egg and larval densities within the 'core' CalCOFI survey region (http://www.calcofi.org; lines 76.7–93.3) and then constrained by the scale of the 1980–1985 DEPM SSB estimates (Bindman 1986). MacCall et al. (2016) and Thayer et al. (2017) provide a full description of the RELSSB index.

Three non-traditional data sources were also considered:

- An index of relative abundance from 1963–1990 from aerial fish spotters based on a delta-GLM that accounted for sea surface temperature and mixed layer depth (Lo et al. 1992).
- An index of relative abundance based on the proportion of anchovy in the diet of common murre (*Uria aalge*) for 1990–2020, which has been shown to correlate strongly with catch-per-unit-effort (CPUE) of adult anchovy in the RREAS in the same region (Santora et al. 2021a)

- Indices of relative adult, and juvenile anchovy abundance from delta-GLMMs applied to California sea lion (*Zalophus californianus*) diet data that controlled for sampling location collected from rookeries on San Clemente and San Nicolas Islands through the SWFSC (CSL, Table 1). The feeding range of these rookeries is mostly in the Southern California Bight (Briscoe et al. 2018). Anchovy were enumerated using otoliths present in scat, and size was back-calculated using a linear regression of otolith diameter on standard length of sample individuals. Adults and juveniles were separated as > or < than 90 mm based on back-calculated lengths.

Fishery catches (mt) were available from 1962–2021 (Fig. 2) from the major anchovy fishing regions off central California (Monterey Bay) and southern California (Los Angeles to Santa Barbara), USA, and from northern Baja California (Ensenada), Mexico (PacFIN 2023,
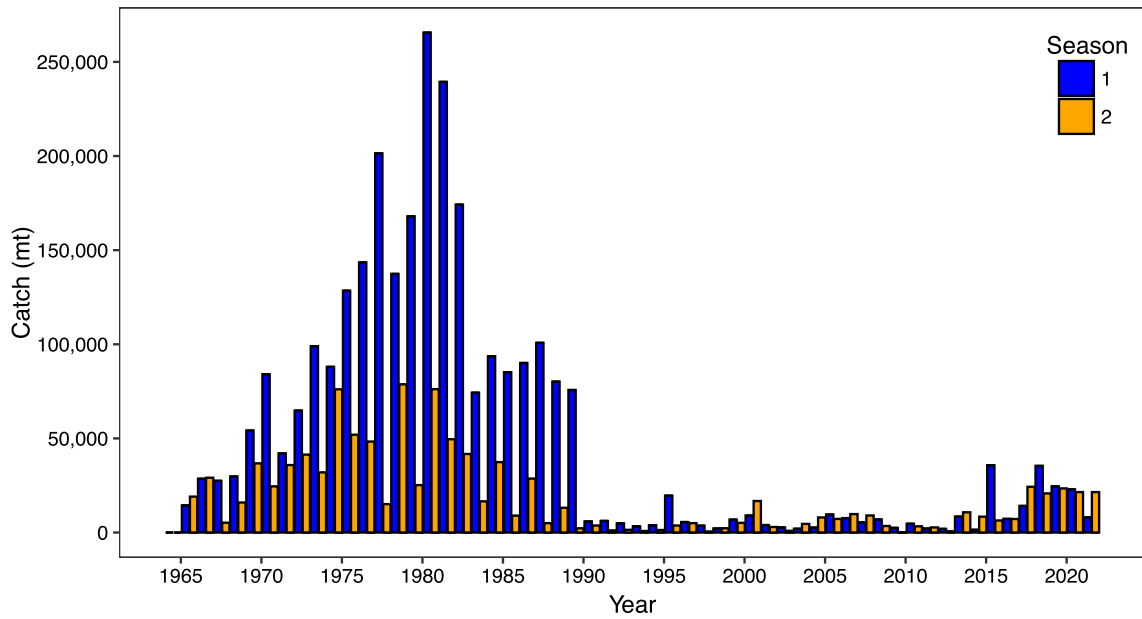
Figure 2. Catch (mt) of northern anchovy by season for combined port landings from central and southern California, USA, and Ensenada, Mexico.

CONAPESCA 2020). Biological samples for the fishery were available 1967–1989 and 2015–2021, and used to derive fishery age-compositions and mean weight-at-age estimates. Supplementary Appendix A outlines how the catch time-series and the weight-at-age matrices were constructed.

Model structure

The temporal range of the model covers 1965–2021. The model started in 1965 rather than at the start of the RELSSB index in 1951 for increased model stability based on the time period that catch and age-composition was available (Table 1). Peak spawning activity is in February (Parrish et al. 1986, Sydeman et al. 2020), so this analysis assumes that anchovy have a June 1 birthdate to clearly delineate cohorts based on otolith increment analysis (Schwartzkopf et al. 2021). Thus, the population model is based on a biological year (hereafter referred to as 'model year') that starts in June and ends in May of the following calendar year. The time steps are based on the seasonality of the fishery, where the first time-step spans June to December (S1) and the second spans January to May (S2) of the following calendar year (see Table S1). Catch data from Mexico and California were pooled into a single fishing fleet separated into two seasons (S1: June–December, and S2: January–May) (Fig. 2). The observed catches were assumed to be unbiased and relatively precise (standard error of the log(catch [mt]) of 0.05).

The population model considers only a single sex, as previous research has demonstrated no sexual dimorphism related to growth (Kuriyama et al. 2022), and assumes a sex ratio of 50:50. This assumption is used in other assessments and is supported by gonad identification of survey samples which vary around 50:50 among cruises (Bindman 1986, Parrish et al. 1986, Kuriyama et al. 2022). The model covers ages 0–3 + and assumes 73% of age-0, 93% of age-1, 99% of age-2 and 100% of age-3+ are mature based on age-at-maturity estimates determined through histological analysis and logistic

Table 2. Pre-specified and estimated parameters, and asymptotic standard deviation (SD).

	Parameter	Value	SD
Pre-specified	h	0.6	–
	σ_R	1	–
	$\text{Ln}(Q)$ AT	0	–
	$\text{Ln}(Q)$ DEPM	0	–
Estimated	M	0.68	0.08
	$\text{Ln}(R_0)$	17.36	0.24

h is steepness, σ_R is variability in recruitment about the stock-recruitment relationship, M is the instantaneous rate of natural mortality (yr^{-1}), R_0 is the equilibrium recruitment parameter (number of recruits), Q is catchability, and extra SD is an additional estimated variance parameter.

regression (Schwartzkopf et al. 2021, Kuriyama et al. 2022). The oldest age group used was 3+, due to the high mortality rates of coastal pelagic species and the rarity of fish older than age 3 in the population.

We estimated natural mortality (M) as a time- and age-invariant constant (Table 2). The spawner-recruitment relationship (i.e. the link between SSB and expected total number of age-0 fish) is modelled using a Beverton-Holt function (see Methot and Wetzel 2013 Appendix A), parameterized as;

$$R_t \sim \frac{4hR_0 SSB_y}{SSB_0(1-h) + SSB_y(5h-1)} e^{-0.5b_y\sigma_R^2 + \tilde{R}_y} \quad \tilde{R}_y \sim N\left(0; \sigma_R^2\right)$$

(1)

where the steepness parameter (h) is set to 0.6, and the average recruitment variability in log space (σ_R) set to 1. R_0 is the unfished equilibrium recruitment, SSB_0 is the unfished equilibrium spawning stock biomass. SSB_y is the spawning stock biomass at the start of the spawning season, and R_t is the recruitment at the start of S1. $\tilde{R}_y$ is the recruitment deviation. Bias-adjustments (b_y) are calculated on a yearly basis following Methot and Taylor (2011).

Likelihood profiling of h indicated that h was most likely to be around 0.45 with lower and upper confidence intervals

of 0.35 and 0.6 (Fig. S1). We considered an *h* of 0.45 to be unlikely for coastal pelagic species, for which recruitment is largely dependent on the environment, rather than SSB (Cury et al. 2014, Demer and Zwolinski 2014, Brosset et al. 2020). It is generally recommended that best practice is to estimate *h* with a prior (Punt 2023), however implementing this for coastal pelagic species is challenging. The anchovy population had an initial extended period of high biomass then an extended period of very low biomass followed by a rapid increase post 2015. This biomass trend is generally due to an increase then decrease in fishing mortality (referred to as a two-way trip), and should facilitate estimates of the population productivity (i.e. *h*). However, simulation studies have demonstrated that a two-way trip is insufficient for reliable estimates of *h* (Lee et al. 2012). Attempting to estimate productivity over a period of high contrast in abundance which is not thought to result from fishing may incorrectly demonstrate that recruitment is strongly linked to SSB, when in reality there could be two separate regimes where high or low recruitment over each period is driven by changes in the environment (Jacobson and MacCall 1995, Cury et al. 2014). There is also potential for reverse causality, in which SSB is high because of high recruitment (Szuwalski et al. 2019). We also note that the practice of using priors for values of *h* have focused on rockfish (Dorn 2002, Thorson et al. 2019), while no such studies exist for coastal pelagic species. As such, we elected to set *h* at 0.6 as this value was within the the confidence intervals suggested by the data, while somewhat reducing the influence of SSB on recruitment estimates. Biomass estimates of models with fixed *h* = 0.45 and *h* = 1 are all within the confidence intervals of the base model estimates (Fig. S2).

The logarithm of unfished equilibrium recruitment was estimated as a time-invariant parameter [$\log(R_0)$]. In preliminary analyses, the total likelihood of model variants with different parameter combinations of age-variant *M* (i.e. using constant or age-based Lorenzen; Lorenzen 2022) with and without a prior based on Hamel and Cope (2022), *h* fixed at 0.6 or 1, and σ_R fixed at 0.75, 1.0, and 1.25 were compared. Alternative model structures did not improve fits to abundance indices and increased the total likelihood compared to the base model (constant *M*, *h* = 0.6, σ_R=1), so we retained the base value for *M* and stock-recruitment parametrizations (Table S1).

Catchability (*Q*) for each survey was estimated as time-invariant except for the AT and DEPM surveys for which *Q* was set to 1 because we deemed the AT and DEPM survey estimates to be the most reliable survey approximation of 'true' biomass of anchovy based on the completeness of the survey areas and expert opinion. Setting the value of *Q* also helped to set the scale for the biomass time-series. For all but the acoustic/sonar surveys, we also estimated an additive constant to be added to the input CV (Methot et al. 2020). This had the effect of upweighting the acoustic/sonar surveys indices, which had the most comprehensive sampling coverage, over other indices of abundance. In a sensitivity analysis, we assess the impact on quantities of management interest (biomass and recruitment) of estimating an additional variance parameter for all surveys (i.e. no downweighing of other surveys relative to acoustic/sonar surveys). Strong deviations from the base case results would indicate some conflict among abundance indices.

Age-based selectivity for the fishing fleets and surveys was estimated as time-variant for some ages (see below), implemented using time blocks, to better account for interannual variability in availability of specific ages to the fishery and the AT and CDFW surveys. Age-specific selectivities were estimated as free parameters (Methot and Wetzel 2013). Availability of young anchovy (Age 1 and below) to the fishery and surveys seems to change with sea surface temperature (Methot 1989). Therefore, as in Methot (1989), the temporal breakpoints between blocks for the period up to 1989 relate to a 4-yr weighted Scripps Institute of Oceanography pier sea surface temperature index (Table S4). The index was calculated by weighting the January to February sea surface temperature ($°C_t$) for year (*t*) measured at the pier in La Jolla, California, provided in Methot (1989) by the pier temperature of the previous three years using:

$$°C_{w,t} = 0.4°C_t + 0.3°C_{t-1} + 0.2°C_{t-2} + 0.1°C_{t-3}.$$ Concurrent years (*t*) with the same weighted temperature ($°C_w$) to the nearest degree Celsius were assigned to the same block although a single block from 1990 to 2015 was used owing to the absence of age-composition data, followed by yearly blocks for each year post 2015. Age-composition data were not available from the fishery from 1990–2015 as anchovy were not caught by the US fishery (except by a small live-bait fishery). Survey age-composition data were also unavailable for 1990–2015 because, following the collapse of the anchovy population around 1990, data collection for forage fish carried out by the SWFSC, which prior to 2005 relied on the DEPM method and from 2005 on the AT survey, was not focused on anchovy. Age-composition data were not collected for the stock until its resurgence in 2015. Age-selectivity was modelled as time-varying for all ages for the fishery fleets and the CDFW survey. We allowed flexibility in the estimation of age-selectivity for the CDFW sonar to reflect how selectivity was handled by Methot (1989), who estimated the availability at age-1 and the age that fish were fully selected during cold and warm water periods. Age selectivity for the AT surveys was modelled with time-varying age-0 selectivity and time-invariant full selectivity for fish age-1+ as there is no evidence that fish with fully developed swim bladders (i.e. greater than age 0) are missed by the AT acoustic equipment and field sampling is extensive (Demer and Zwolinski 2014, Kuriyama et al. 2022). These selectivity assumptions mean that the estimate of *M* relies heavily on the AT survey age-composition and the biomass indices. This decision was made based on assessment of data quality and lack of cohort structure apparent in the CDFW age-composition data.

Data and model selection

First the appropriateness of each index of abundance was evaluated. Decisions were based on methods used to collect the data, and which aspect of the anchovy population dynamics the data capture (e.g. total biomass, SSB). Each index should be proportional to abundance, and hence representative of the entire distribution of the stock (Hilborn and Walters 1992, Maunder et al. 2020). Moreover, the index should be precise and a measure of observation uncertainty needs to be available. As this is an age-structured stock model information on what population component is represented by the index should also be provided (e.g. age-compositions).

We excluded the aerial spotter index from the assessment because the mismatch between the aerial survey data and associated biological sampling made it difficult to reliably assess which population component (i.e. adults, YOY, or both) was represented by this index (Kuriyama et al. 2022). The index

of relative abundance derived from the murre diet data was also excluded as it was not deemed representative of the entire stock owing to its small spatial coverage. Similarly, RREAS data before 2004 were not included as the area surveyed by the RREAS had a smaller spatial footprint prior to 2004.

All other data sets were considered in the model selection process, and model selection decisions were based on best practice guidelines suggested in Carvalho et al. (2021). We assessed variants of the model with different data configurations using the following model diagnostics: (1) model convergence, checking parameters were not on their bounds, size of the final gradient, invertible (positive definite) Hessian matrix, and jittering initial parameter values to verify a global minimum using the 'jitter' function in the package 'r4ss' (Carvalho et al. 2021) in R 4.3.1 (R Core Team 2023), (2) distribution of residuals to assess fits to indices (Carvalho et al. 2017) using the 'SSplotRunstest' and 'SSplotJABBAres' functions in the package 'ss3diags' (Winker et al. 2023), (3) likelihood profiles to evaluate information quality in the data and identify data conflicts (Lee et al. 2014, Wang et al. 2014) using the 'profile' function in the package 'r4ss' (Taylor et al. 2021), and (4) a retrospective analysis with the 'retro' function in 'r4ss', using mean rho (ρ_M) (Mohn 1999) for the most recent four years calculated with the 'SSplotRetro' function, and calculating the mean absolute scaled error (MASE) for the index residuals with 'SSmase', in 'ss3diags', to check the consistency of model estimates with new data (Hurtado-Ferro et al. 2015, Carvalho et al. 2017). No diagnostics were applied if a model failed the convergence diagnostics. For the base case model, we also assessed the influence of age-composition data by observing differences between an age-structured production model with recruitment (ASPM-r) and the base population model (Maunder and Piner 2015, Thorson et al. 2019).

The initial model started with the RELSSB as it covers the longest time period of any of the available indices, with catch and associated biological data from the fishery. We then added the index that was deemed most reliable given its extensive spatial coverage, the AT index and its biological data, followed by the CDFW survey data, since it provided the only historical biological data, the DEPM, which, as an absolute abundance index, provided information on scaling for the early period, and the RREAS YOY index, which was deemed a better index of recruitment than the sea lion YOY index due to its broader spatial coverage and more accurate determination of fish length. The RREAS adult index was then added, followed by the adult and YOY sea lion indices. Diagnostics were checked after the inclusion of each dataset. We also assessed if the fit to any other index degraded, and the impact on quantities of management interest such as age 1+ biomass and recruitment time series.

Following selection of the base model, estimated log recruitment deviations were extracted and autocorrelation with 1-year lagged estimates were determined for years 1965–2021, 1965–1989, 1990–2014, 2015–2021, 1965–2014, and 1990–2015, using the 'acf' function and significance was tested using a Box-Pierce test with the 'Box.test' function from 'stats' package in R 4.3.1 (R Core Team 2023). Estimates of recruitment and SSB were also extracted and $\log(R_0)$ values for the years 1965–1989, 1990–2014, 2015–2021 were estimated using nonlinear least squares with the 'nls' function from 'stats' package. Here we fit a Beverton-Holt curve (Eq. 1). All parameters were kept constant and the same as the Stock Synthesis model output except for the estimated R_0.

Results

Model selection

The final base case model after model selection contained the fishery catch, and biological data from the fishery and California Department of Fish and Wildlife (CDFW) and NOAA Southwest Fisheries Science Center Acoustic-Trawl (AT) surveys. Indices of abundance were the AT survey, CDFW sonar, daily egg production method (DEPM) and relative egg and larvae-derived SSB index (RELSSB). The Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) young-of-the-year (YOY) index was included as an index of recruitment (abundance of age-0 fish). The base model was deemed to be robust using convergence metrics and estimates appeared to be at a global minimum based on the results of jittering analysis, with acceptable output from the diagnostic tests. See Supplementary Appendix B for a step-by-step guide through the diagnostic results and model selection decisions taken to arrive at the final model.

Diagnostics for selected population model

Likelihood profiles showed general consistency on the estimate of M and for the value of R_0. Note, that these profiles are conditioned on the base model, which assumes a fixed value of steepness of 0.6 (Fig. S1). For M, the surveys showed tension where the CDFW survey data supported a high value and the AT survey data supported lower values. The age-composition and survey data were in general agreement based on the likelihood profiles, while the likelihood profile of $\log(R_0)$ for the penalty on the recruitment deviations was greater than other data sources (Fig. S1A). Among surveys, there was minor tension between the CDFW sonar and AT summer surveys indices, where the gradient of the $\log(R_0)$ and M likelihood profiles was smaller for the AT summer survey (Fig. S1B). M estimates increased with $\log(R_0)$, and decreased with increasing h up to $h = 0.6$, and which the estimate remained stable. Comparison of the SSB and recruitment time series of the population model with output from the APSM-r showed that the peaks and troughs in the recruitment and SSB time series occurred at the same time, indicating information from age-composition data was in agreement with information from the biomass indices (Fig. S3). Of 150 model runs with starting values jittered by 10% 149 runs converged, and the SSB time series estimates were within the 95% confidence intervals of the global minimum objective function run for these 149 jittered runs (Fig. S4).

Model fit and parameter estimates

The selected configuration of the population model converged with a final gradient near 0 (<1e-4), and a positive definite Hessian matrix. The full Stock Synthesis model files are available at https://github.com/charliehinchliffe/northernanchovytimeseries. The estimate of M was 0.68 yr^{-1} (± 0.08 standard deviation), and the $\log(R_0)$ value was 17.36 (± 0.24 SD). Log-transformed predicted survey index values were within the uncertainty bounds of the empirical values of each survey for the majority of years (Fig. 3). The log transformed predicted survey index was less than the empirical measure for the DEPM in 1982 (Fig. 3c), and greater than the AT summer survey in 2015 (Fig. 3b) and the RELSSB in 2020 (Fig. 3f). The fits to the age-composition data were generally good for most years (Figs. S7–S12), although the fishery
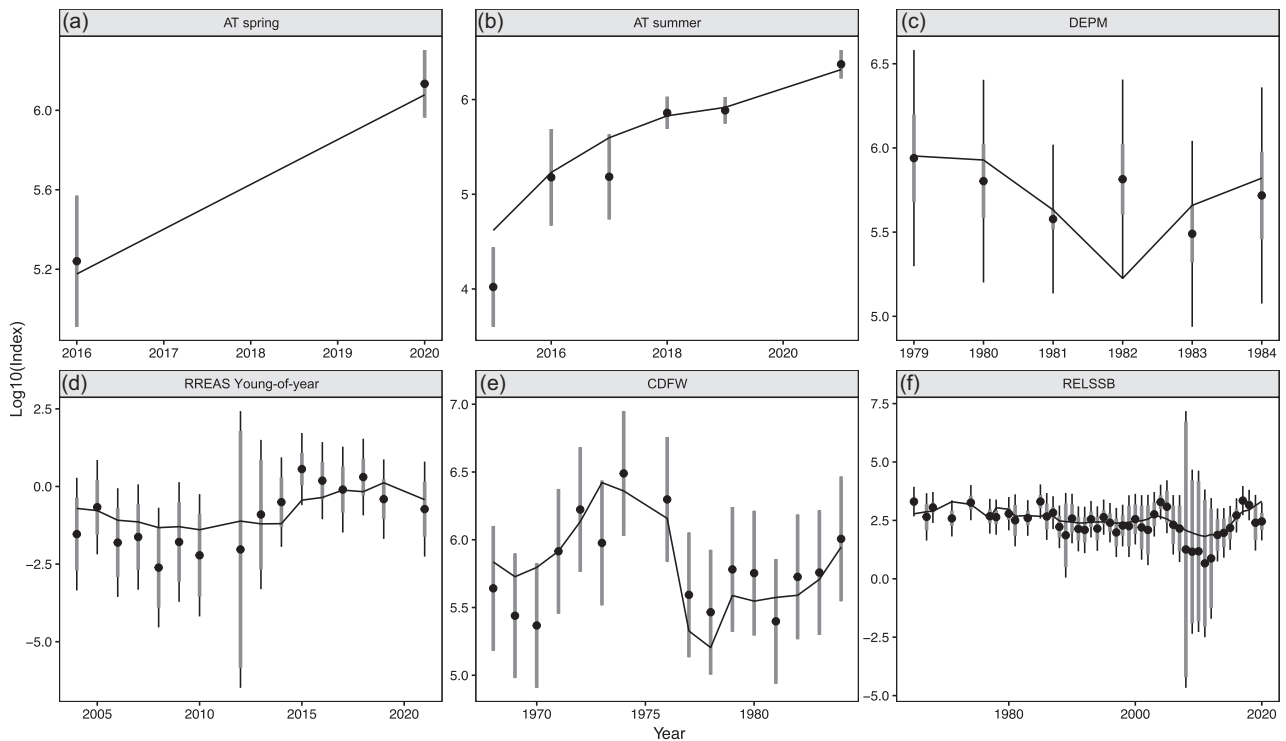
Figure 3. Log transformed biomass indices (black points), 95% uncertainty interval around index values based on the model assumption of lognormal error (grey bars), and extra uncertainty estimated by the model (thin black bars) for (a) the spring AT index, (b) the summer AT index, (c) the DEPM index, (d) the RREAS young-of-year recruitment index, (e) the CDFW index, and (f) the RELSSB index. Black trend lines show fits estimated by the selected model configuration.

proportion-at-age data were fit better than the CDFW and AT proportion-at-age data.

Biomass

Model-based estimates of biomass generally match previous estimates of high anchovy biomass during the 1960s to early 1970s, and low abundances in the late 1980s to mid-2000s (see Table S2 for season-based estimates of age 1+ and spawning stock biomass). Age 1+ biomass increased from 0.4 M mt in June 1967 to 2.2 M mt in June 1973 (Fig. 4a), and spawning stock biomass (SSB) showed a comparable increase (Fig. 4b). Following these peaks, estimated age 1+ biomass and SSB both declined to <0.4 M mt by 1978, and then increased again to almost a million mt in 1979. Subsequent comparable pulses in biomass occurred during the mid-1980s, before anchovy settled into a state of very low abundance throughout the 1990s. As landings were low, age composition data were not available, and fisheries survey data that cover the entire range of the population were very sparse from approximately 1990 through about 2004. Consequently, estimates of both SSB and recruitment are more uncertain during this period. Subsequent to a small pulse in mid-2000s anchovy biomass remained at very low levels for next decade. Model estimates suggest age 1+ biomass reached a historic minimum of 0.03 M mt in June 2015. However, it should also be recognized that the ability of most of the surveys to detect and accurately estimate the abundance at very low biomass levels is fairly limited.

There was a rapid recovery of anchovy after 2015 where the population size increased to levels comparable with the early 1970s. The biomass of anchovy demonstrated a steady increase in successive years from a historic minimum up to an age 1+ biomass of 2.1 M mt in June 2021. The estimated SSB of anchovy followed a similar trend, peaking at 1.9 M mt in 2020.

Recruitment

The population model biomass time-series for anchovy was driven by multiple periods of high recruitment throughout the late 1960s to the late 1980s, followed by an extended period of very low recruitment (Fig. 5a). Recruitment was at its historical maximum in June 1969 (191 billion individuals ± 62 billion SD). Large year classes were also evident in 1977 and 1982, with 120 billion individuals (± 24 billion SD) and 115 billion individuals (± 35 billion SD), respectively. During the 1990s, there were no year classes with more than 16 billion individuals, which was followed by a brief pulse of recruitment during the early 2000s, peaking at 34 billion individuals (± 33 billion SD) in 2002. Subsequent to this pulse, no year class had more than 5 billion individuals up to 2014. From 2014, year class strength increased successively from 23 billion individuals (± 6 billion SD) to 229 billion individuals (± 61 billion SD) in 2019.

The estimated log recruitment deviations were mostly positive until 1988 and after 2014, with mostly negative values in the years between these periods (Fig. 5b). The uncertainty in the recruitment deviation estimates is much larger for years between 1990 and 2014, which ranged in asymptotic SD from 0.35 to 0.98. In years previous to 1990, SD ranged from 0.12 to 0.69 and from 2015 to 2019 SD ranged from 0.24 to 0.43. In 2020 and 2021 the SD of the log recruitment deviation estimates was 0.87 and 0.99. Autocorre-
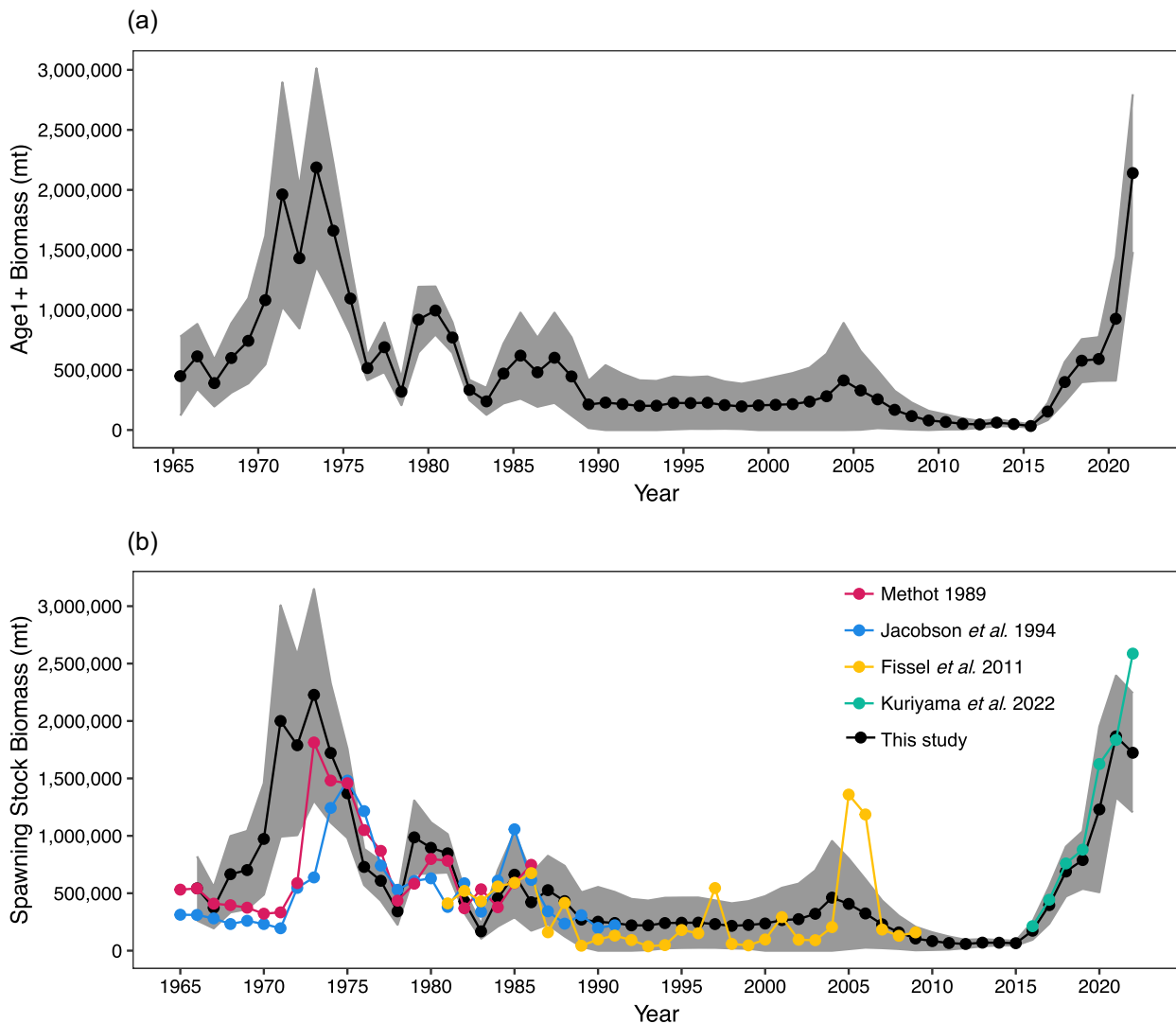
Figure 4. Estimated (a) age 1+ biomass from 1965–2021, and (b) spawning stock biomass of anchovy from 1966–2022. Coloured points and lines show spawning stock biomass from previous anchovy population models. Black points indicate model estimates and grey ribbons indicate asymptotic 95% confidence intervals.

lation (ρ) with a 1-year lag for the estimated log recruitment deviations was 0.51 ($\chi^2 = 14.52$, $P < 0.0001$) from 1965–2021, and the variability in these estimates was $\pm$ 0.94 SD. For the early period of high biomass prior to 1990 ρ was 0.14 ($\chi^2 = 0.51$, $P = 0.48$) and variability was $\pm$ 0.96 SD, from 1990–2014 when biomass was low ρ was 0.52 ($\chi^2 = 6.912$, $P = 0.009$) and variability was $\pm$ 0.61 SD, and for period from 2015 to 2021 when biomass increased rapidly ρ was only 0.01 ($\chi^2 = 0.001$, $P = 0.972$) and variability was $\pm$ 0.79 SD. For all years after 1989, or all years prior 2015, ρ is 0.69 ($\chi^2 = 15.15$, $P < 0.0001$) and 0.49 ($\chi^2 = 12.05$, $P = 0.0005$), respectively. Estimating the log equilibrium recruitment values external to Stock Synthesis for the three subperiods (Fig. 6) demonstrated that $\log(R_0)$ was larger in 1965–1989 and 2015–2021 (18.11 and 18.29, respectively) than 1990–2014 (16.96).

Discussion

We integrated multiple time series of anchovy biomass and biological metrics over seven decades to develop biomass and

recruitment estimates that resolve different phases of the population's boom-and-bust nature. The time-series of biomass estimates was similar to the historical understanding of the stock (Methot 1989, Jacobson et al. 1994, Fissel et al. 2011, Thayer et al. 2017, Swalethorp et al. 2023, Thompson et al. 2024), apart from an earlier increase in biomass in our model in the years preceding the historic peak in 1973 (Fig. 4). Notably, the highest estimate of SSB from our population model occurred in 1973, coinciding with when the reduction fishery was at its largest (Opsomer and Conrad 1994). Methot (1989) estimated SSB to also reach a maximum in 1973, although this was 20% less than our estimate. Estimates in the preceding years were much lower than found in our study, resulting in a relative difference of 80% and 70% in 1971 and 1972, respectively. Peak SSB of anchovy estimated by Jacobson et al. (1994) occurred later in 1975, and SSB was low in preceding years, similar to Methot (1989). Differences between population model output produced in this study compared to previous studies likely depend on differences in model structure and how the data were used for parameter estimation.
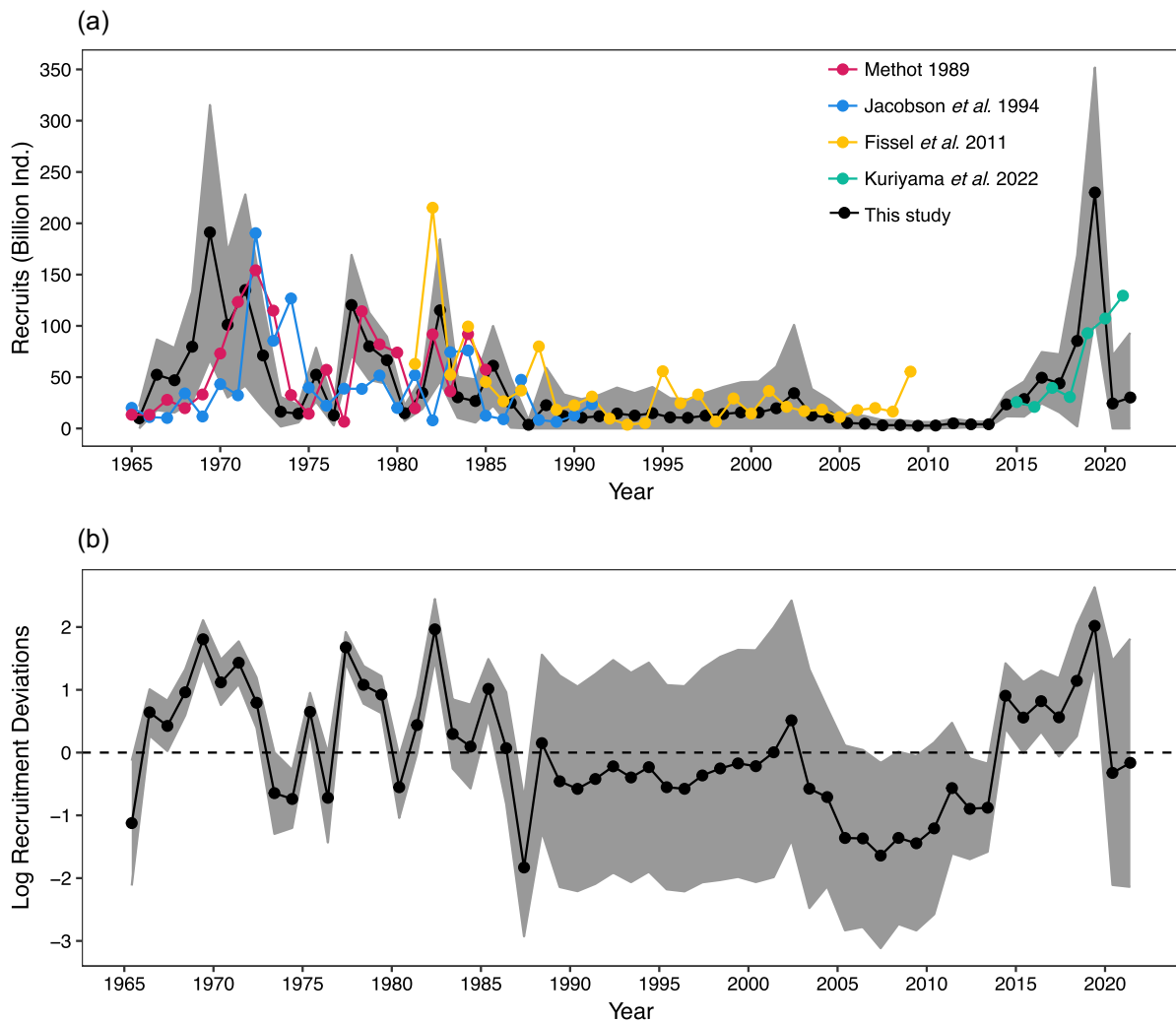
Figure 5. (a) Estimated recruitment (billions of individuals) from 1965–2021. Coloured points and lines show recruitment estimates from previous anchovy population models. Note Fissel et al. (2011) and Jacobsen et al. (1994) provided biomass of recruits (mt) so values were scaled around the geometric mean of Methot (1989), as weight at age 0 was not provided and they used the data from Methot (1989) in their growth calculation. (b) Log transformed recruitment deviation estimates from 1967–2021. Black points indicate model estimates and grey ribbons indicate asymptotic 95% confidence intervals.

The flexibility of the population modelling frameworks have increased dramatically since Methot (1989), and as such, our options for fitting-age composition data were more sophisticated (Methot and Wetzel 2013). Age-selectivity of the fishery and CDFW survey was specified as a dome-shaped function in the earliest assessment (Methot 1989), with parameter offsets for cold and warm sea states. In contrast, we estimated age-selectivity at each age class for each season in discrete time-varying blocks, which allows for flexibility in the selectivity of fish between ages 1 and 3. Selectivity for age 1–2 fish for the CDFW survey, and age 1 fish for the fishery, was low during 1967–69 and 1970–76 (Fig. S5), allowing for more age 1 and age 2 fish to be estimated in the population and resulting in an increase in the estimates of SSB. The increase in biomass during the years prior to 1973 also coincided with an increase in the RELSSB index produced by Thayer et al. (2017) which was not available to Methot (1989) or Jacobson et al. (1994).

The estimate of the rate of natural mortality (M), 0.68 yr^{-1}, is generally high and similar to estimates for other anchovy species (e.g. Iversen et al. 1993, Jacobson et al. 2001, Uriarte et

al. 2016). MacCall (1974) estimated that M for anchovy varied by year between approximately 0.62 and 0.79 yr^{-1} with a mean of 0.68 yr^{-1}. In their biomass dynamics model, Jacobson et al. (1994) assumed M to be 0.8 yr^{-1} based on what may be expected for coastal pelagic species that rarely live longer than 4 years (Hoenig 1983), while Methot (1989) assumed natural mortality varied as a function of Pacific chub mackerel (*Scomber japonicus*) biomass owing to predation and hence a range of 0.6–0.8 yr^{-1}. The most recent assessment of anchovy, albeit based on 7 years of data (Kuriyama et al. 2022) estimated M as low as 0.41 yr^{-1} ($\pm$ 0.13 SD), which was also conditional on a fixed h of 0.6. Collectively, these results suggest a decrease in M of anchovy over time, which is counter to what may be expected if the biomass and population recovery of anchovy predators is considered. For example, since the Marine Mammal Protection Act was enacted in 1972, California sea lions recovered from exploitation and increased markedly (DeLong et al. 2017, Laake et al. 2018). Humpback whales (*Megaptera novaeangliae*) have since increased (Calambokidis et al. 2017), as well common murre and Brandt's cormorants off central California (Ainley et al.
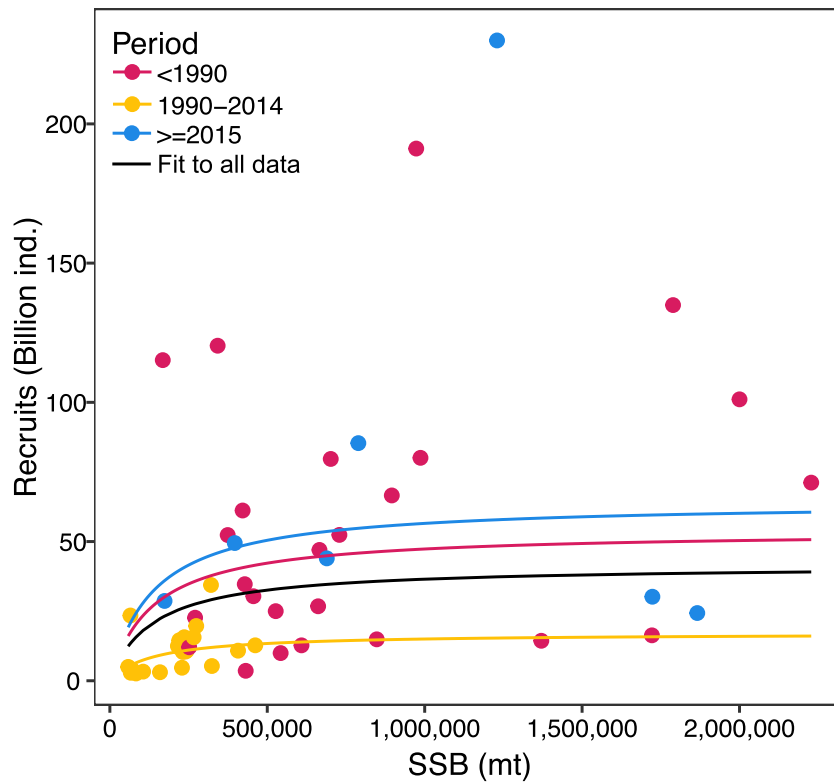
Figure 6. Recruits and spawning stock biomass (SSB) estimates (points), and estimated Beverton-Holt stock-recruit curve (black line). Point colours demonstrate the period which the estimates occurred in, and coloured lines show the Beverton-Holt stock-recruit curve externally refit to each period.

2018, Warzybok et al. 2018). However, efforts to relate northern anchovy abundance to changes in predator population size found spurious relationships, noting different predators likely exert pressure on anchovy under differing environmental conditions at different times. For example, the MacCall (1974) *M* estimates came at a time when anchovy biomass was low but rapidly increasing, just as the biomass of a key predator, Pacific bonito (*Sarda chiliensis*), had peaked and was rapidly declining (MacCall 1996). Alternatively, the decline of Pacific chub mackerel biomass in recent years (Kuriyama et al. 2023) may have reduced predation pressure on anchovy. However, interactive effects of predation or competition among forage fish remain unclear (Siple et al. 2020) and additional research is required to elucidate causes for fluctuations in *M* for anchovy.

Future considerations

The base model presented here appears to adequately capture the dynamics of anchovy to facilitate an in-depth analysis of the environmental drivers influencing successful recruitment. Other aspects of the stock may be explored using different model structures. For example, time-varying *M* may be warranted given the varied output from previous assessments as well as the conflicts in the *M* likelihood profile between the current AT biomass index and the earlier CDFW biomass index (Fig. S2B). Profiles of the CDFW biomass index suggest *M* to be greater than 0.8 yr^{-1}. There are several options that future anchovy population models may explore. Time-varying *M* may be directly linked to changes in the abundance of predator populations (Dorn and Barnes 2022), which is similar to the initial integrated assessment of anchovy by Methot

(1989), or to changes in the overlap between their respective distribution (Spencer et al. 2016). However, given there is no straightforward evidence of a predator species whose abundance directly influences anchovy abundance (Sydeman et al. 2020), the degree to which *M* should scale as a function of predator abundance is unknown (i.e. what should the baseline rate of *M* be set at) (Dorn and Barnes 2022) and complexity of spatial interactions between anchovy and multiple predators, and their alternative prey, remains poorly understood. Further empirical research is warranted before this approach is relied upon. Another approach is to estimate time-varying intrinsic *M* directly and applying annual deviations forced by some covariate such as biomass estimates of a known predator (Dorn and Barnes 2022).

Alternatively, an investigation of shifting recruitment regimes could be conducted given the relationship between R_0 and *M* (Fig. S6A). Refitting the stock-recruit curve highlighted the possibility that periods of high and low biomass reflect changes in environmentally-driven productivity common in forage fishes (Fig. 6). Comparing the autocorrelation of the estimated log recruitment deviations from 1965–2021 with the subperiods of 1965–1989, 1990–2014, and 2015–2021 supported this. Significant autocorrelation in recruitment increases the prospect of observing a strong stock-recruit relationship in stocks with entirely recruitment-driven dynamics (Szuwalski et al. 2019). The periods of high biomass had weak autocorrelation, compared to the strong autocorrelation of the longer periods tested. The duration of 1990–2014 also had a strong autocorrelation although this may result from the reliance on abundance indices during this period owing to a lack of age-composition data. Allowing the stock–recruit re-

lationship to vary through time would reduce autocorrelation of the recruitment deviations, and emphasize environment-driven changes in productivity that may mask stock–recruit relationships assessed with time-invariant methods (Szuwalski et al. 2019). This could be implemented through the use of blocks, where a regime shift parameter is estimated for each block as an offset of R_0 (Methot and Wetzel 2013, Methot et al. 2020). However, determining the temporal break points of the blocks can also require arbitrary decisions or choice of thresholds. A different way that a recruitment regime shift could be implemented would be by using an auto-correlated time-series of values for R_0. For anchovy, it may be expected that shifts in R_0 occurred during the transition between the booming and collapsed state around 1990, and the return of the stock in 2015. A benefit of this approach is that results will propagate into forecasts using the recent mean recruitment, which may be desirable for implementation of the population model in an MSE framework.

Despite many decades of extensive investigations, the physical and biological mechanisms controlling anchovy population dynamics remain unclear (Schwartzlose et al. 1999, MacCall 2011, Sydeman et al. 2020). Given the relatively low exploitation rates, particularly since 1990, the primary driver of adult population size is recruitment variability. Reliable estimates of recruitment were previously unavailable at decadal time scales, as such, most analyses seeking to relate environmental variables to anchovy populations use SSB as the dependent variable. For example, 2-year lagged sea-level and an Upwelling Index combined with anchovy SSB of the previous year were significantly correlated with anchovy biomass (Sydeman et al. 2020). However, that approach explained only marginally more variation in biomass than just the previous year's biomass estimate, and as indirect and large-scale correlations with an unknown mechanistic basis, use of correlations would come with high uncertainty under novel ecosystem conditions and climate change. The ability to resolve a mechanistic environmental driver could be hindered from the use of biomass alone, rather than recruitment itself, where the effects of the environment are dispersed across several age classes. Additionally, as Checkley et al. (2017) recognize, multiple mechanisms for these fluctuations could exist, further complicating efforts to explicitly link population dynamics to environmental drivers. Nevertheless, analysing indices of recruitment such as that produced by our long-term model may prove to be better suited than biomass to explain same-year responses of anchovy to variable physical and biological ocean conditions.

Although previous analyses that used sea surface temperature or the Pacific Decadal Oscillation index did not find a conclusive link with anchovy abundance indices (Sydeman et al. 2020), some recent research provides promising leads for explaining mechanisms leading to abundance fluctuations. For example, stable isotope analyses on larvae collected between 1960 and 2005 indicated that larval diets shifted to lower trophic levels when the population sizes were high (Swalethorp et al. 2023). Swalethorp et al. (2023) attributed a shortened food chain to increased larval survival that produced more adult biomass. In addition, anchovy abundance was positively related to the extent of cold, productive waters, specifically, when thermal habitat was compressed shoreward (Santora et al. 2021b, Schroeder et al. 2022). This habitat compression mechanism involves processes including the retention, and concentration of nutrients, and is determined

by the intensity and duration of upwelling and relaxation events, which influence the extent of cool and productive thermal habitat (Bakun 1990; Santora et al. 2017). Habitat compression (reduction of cool thermal habitat) was particularly strong and persistent during the 2014–16 marine heatwave, associated with the increased recruitment during those years that led to the anchovy population boom that started during 2017 and 18 (Santora et al. 2021b; Kuriyama et al. 2022). Therefore, it is possible the compressed habitat conditions facilitate concentration of anchovy food thus providing optimal foraging opportunity (Lasker 1978). The recruitment indices developed in our study will allow further exploration between larval diet, ocean condition, and year class strength.

The model could be valuable for use in a variety of long-term ecological analyses. For instance, biomass-at-age from our model can serve to parameterize and evaluate ecological models that incorporate drivers of anchovy population dynamics and distribution, that are mechanistically linked to the environment and food-web. This output has been used to support configuration of a model of intermediate complexity for northern anchovy, used in an ensemble configuration to quantify uncertainty from environmental drivers and predation (S. Koenigstein, pers. comm.). In addition, the extended time-series of SSB could be used to improve species distribution models for anchovy because annual biomass is an important predictor of whether anchovy occur within environmentally favourable habitat, with both stock biomass and ocean conditions determining availability of anchovy for key predators in space and time (Muhling et al. 2020). Previous work has shown that spatiotemporal availability of anchovy is a strong determinant of diet composition and reproductive success for several top predators in the central California Current (Fennie et al. 2023). The availability of anchovy biomass estimates over multiple decades will allow examination of these relationships across a much broader range of ocean conditions, and predator/prey population sizes. Recent improvements in regional climate models and ecosystem models are now supporting development of future projections of both species distributions and trophic relationships (Brodie et al. 2022). Multidecadal hindcasts of species biomass, such as those developed in this study, could characterize spatiotemporal relationships between ocean conditions, prey, and predators across longer historical timescales, potentially leading to more robust future projections.

Integrating our research outputs into food-web models of the California Current would (i) help align biological data like predators' diet or species distribution with anchovy productivity levels, (ii) contribute to more robust parameterization and calibration of these models, and (iii) bring more realism when hindcasting the past dynamics of the ecosystem. Given the key role of forage fish in the whole socio-ecosystem, and well-known and dramatic changes in their relative importance through time, this information is crucial to anticipate and forecast the potential effects of climate change in the California Current over the next decades (Smith et al. 2023).

Conclusion

We synthesized available data to produce an extended historical time-series of anchovy biomass and recruitment covering two periods of high biomass, and an intermediate period where the stock was collapsed. The model output fits with

our general understanding of fluctuations in SSB and summary biomass over the past 56 years, except that our results suggest an earlier peak in SSB during the early 1970s, which coincides with the peak of the US reduction fishery. This difference was likely driven by the inclusion of age-composition data and the use of a more flexible age-selectivity curve. Comparison of these results provides preliminary evidence that M of anchovy may have decreased since the population boom in the 1970s, which offers an interesting direction for future research to evaluate. More significantly, our results provide a continuous and internally consistent time-series of abundance and recruitment integrating the most informative sources of data, providing a robust foundation for future investigations of oceanographic and ecological mechanisms related to drivers of productivity and abundance for this critically important population.

We suggest that future studies of anchovy could utilize the population model of this paper in two important ways. First, an analysis could be conducted to relate environmental drivers to estimates of recruitment in addition to biomass estimates. Any analysis in this vein would be remiss not to incorporate the uncertainty in model estimates we provide if statistically rigorous output is desired. Second, our model framework provides a solid basis for improving anchovy management through an MSE. We suggest that further exploration of time-varying M or R_0 within the Stock Synthesis framework is a fruitful research avenue for MSE's predicting future states of anchovy under alternative harvest control rules.

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Author contributions

All authors contributed to the conception of ideas and design of the analysis. C.H. implemented the analysis and wrote the draft manuscript. All authors contributed to writing.

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflict of interest: The authors declare no conflict of interest.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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