## Food for Thought

# Sixty-five years of northern anchovy population studies in the southern California Current: a review and suggestion for sensible management

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The central stock of northern anchovy (CSNA; *Engraulis mordax*), the most abundant small pelagic fish in the southern California Current, is key to ecosystem functions. We review drivers of its population dynamics in relation to management. Springtime upwelling intensity lagged by 2 years co-varied positively with CSNA biomass, as did the abundance of Pacific sardine (*Sardinops sagax*; weakly negative). CSNA population dynamics indicate the need for a multi-species stock assessment, but given serious challenges with modelling population collapse and recovery dynamics, and its moderate fisheries, we suggest that sensible management could be a simple 2-tier harvest control rule designed to emphasize the key trophic role of CSNA in the ecosystem while maintaining moderate socio-economic services. We recommend a monitoring fishery of no more than 5 KMT year$^{-1}$ split between central and southern California when the stock falls below the long-term median abundance estimate of 380 KMT across the California portion of its range, and a catch limit of 25 KMT year$^{-1}$ when the stock is above this reference point. This rule would be precautionary, serving to maintain the most important small pelagic forage in the ecosystem, various fisheries interests, and information streams when the population is in a collapsed state.

**Keywords:** CalCOFI, *Engraulis mordax*, fishery management, forage fish, low-frequency cycle, population biology, review, trophic relationships, upwelling ecosystems

## Introduction

Despite decades of highly detailed observational and experimental research coupled with numerical modelling, the population ecology of most small pelagic fish remains enigmatic, with population fluctuations difficult to understand and nearly impossible to predict (but see Zwolinski and Demer, 2012 with response from MacCall *et al.*, 2012; van der Sleen *et al.*, 2018). Anchovies are a key component of this mysterious group of fish and are vitally important to trophic relationships and fisheries globally. Distributed primarily in subtropical to temperate regions and often associated with boundary-current upwellings (Checkley *et al.*, 2017), anchovies are believed to have evolved in estuarine environments (Bakun, 2014). Of >140 anchovy species, few (<10) are the targets of modern-day commercial fisheries, but these fisheries can be substantial (e.g. Barange *et al.*, 1999). Indeed, the largest single-species fishery in the world targets Peruvian anchoveta (*Engraulis ringens*; Freon *et al.*, 2008) with 3–6 million metric tonnes landed each year (FAO, 2019

The northern anchovy (*Engraulis mordax*) is one of the least abundant oceanic anchovy species in the world (Checkley *et al.*, 2017), distributed in the northeast Pacific from Haida Gwaii (Queen Charlotte Islands), Canada, to Cape San Lucas, Mexico (Miller and Lea, 1972; Hart, 1973), with three defined subpopulations (Vrooman *et al.*, 1981; Figure 1). The northern
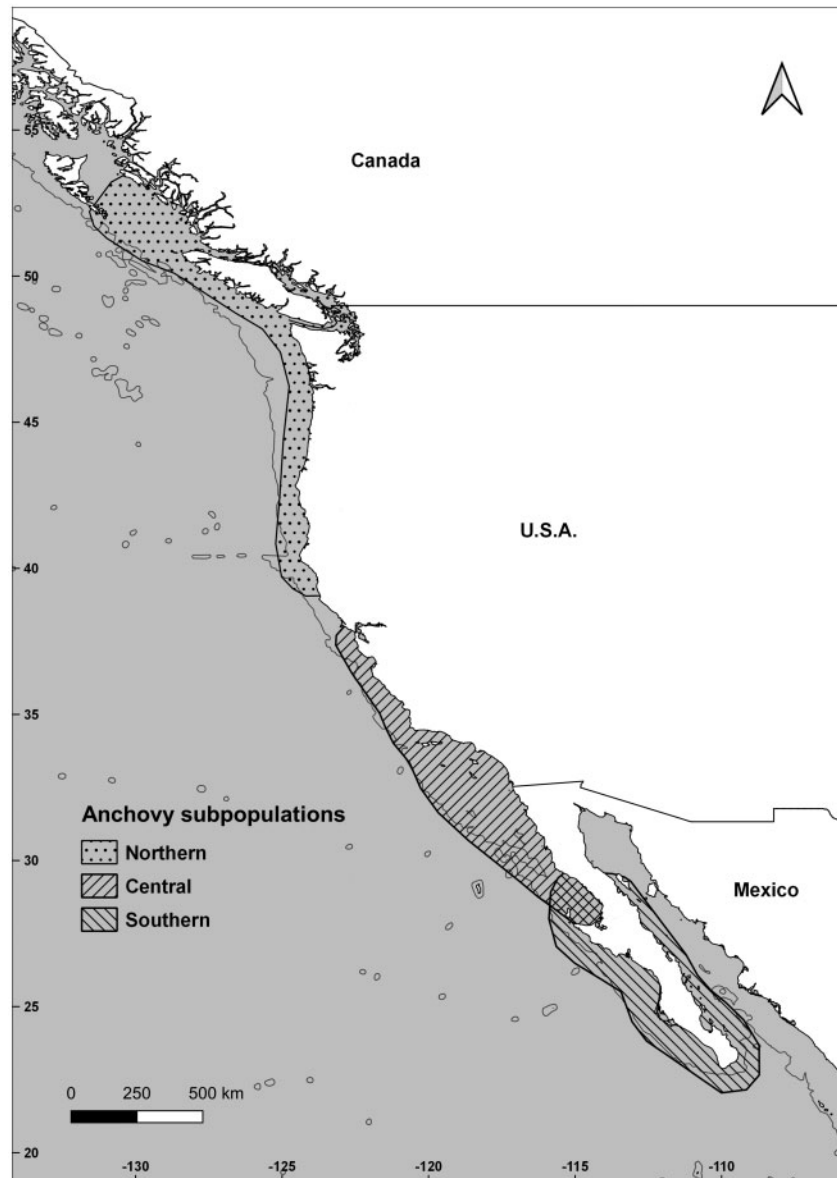
**Figure 1.** Map of western North American coastline with delineations of the northern anchovy stocks (redrawn from Smith and Lasker, 1978).

subpopulation is found from Haida Gwaii to northern California, the central subpopulation extends from San Francisco Bay to central Baja California in the southern California Current Ecosystem (CCE), and the southern subpopulation is found from central to southern Baja California and into the Gulf of California. The central subpopulation, hereafter central stock of northern anchovy (CSNA), is the most abundant of these and is extremely well studied (e.g. Smith, 1972; Parrish *et al.*, 1985; Peterman and Bradford, 1987; Lindegren *et al.*, 2013; MacCall *et al.*, 2016; Rykaczewski, 2019). CSNA is extremely important to trophic interactions in the CCE, with at least 64 species of upper trophic level predators known to rely on CSNA for sustenance (Szoboszlai *et al.*, 2015; Koehn *et al.*, 2016). Fisheries mortality of CSNA, while sizeable at times in the late 1970s and early 1980s (Methot, 1989; Jacobson *et al.*, 1994), has been generally low thereafter (e.g. CalCOFI, 2010). By comparison, major changes in potential intra-guild interactions brought about through the

demise of sardines in the 1940s (Radovich, 1982) and changes in other coastal pelagic species (e.g. Pacific mackerel, *Scomber japonicus*; MacCall *et al.*, 1985) may have been substantial.

Owing to its recent small fishery, CSNA was placed in the "monitored only" as opposed to "actively managed" management category by the Pacific Fishery Management Council (PFMC) in 1998 (PFMC, 1998). As a result, the last comprehensive stock assessment for CSNA was completed in 1994 (Jacobson *et al.*, 1994, 1995). A default harvest control rule was considered for CSNA and resulted in a static allowable biological catch of 25 KMT year$^{-1}$. However, this number was to be used as a "rough index to (CSNA) population productivity" and was not intended to be used as a management or fisheries goal (PFMC, 1998: Supplementary Appendix SB, p. 104). In the present study, our overarching goals are twofold: (i) to update and re-conceptualize key drivers of population variability across an apparent population cycle and (ii) to provide a roadmap for sensible management

of this key species given its population attributes, role in energy flow in the ecosystem, and management challenges. To meet these goals, we review what is known of CSNA life-history characteristics, examine biomass fluctuations relative to environmental and biotic conditions, and present a scenario option for future ecosystem-oriented fisheries management. New analyses include investigating non-mutually exclusive hypotheses concerning co-variance of CSNA biomass with (i) variability in the Pacific Decadal Oscillation (PDO; Chavez *et al.*, 2003), (ii) coastal up-welling (Checkley *et al.*, 2017), (iii) current flows (MacCall, 2009), (iv) intra-guild interactions with sardine and other small pelagics (MacCall, 1996, 2009), and (v) potential fisheries impacts (Lindegren *et al.*, 2013). Our review and brief analysis of environmental covariates and suggestions for sensible management is timely as CSNA has been the subject of a recent fisheries-related lawsuit (Oceana, Inc., v. Ross) and ongoing management controversies (McClatchie *et al.*, 2018). As of now, management of this important forage fish in the CCE remains unresolved.

## Are CSNA data deficient?

The most extensive data on CSNA come from the exceptional long-term study of the California Cooperative Oceanic Fisheries Investigations (CalCOFI), a collaboration between State of California (California Department of Fish and Wildlife and the University of California at San Diego/Scripps Institution of Oceanography) and federal agencies [National Oceanic and Atmospheric Administration (NOAA)-National Marine Fisheries Service (NMFS)] (Radovich, 1982). More recently, surveys for sardine and CSNA have been conducted using acoustic-trawl methodology (Zwolinski *et al.*, 2014, 2017). The CalCOFI programme began in the early 1950s in response to the collapse of the California sardine fishery (*Sardinops sagax*; Bograd *et al.*, 2003) and now provides one of the first empirical assessments of population parameters for a small pelagic fish species over an entire putative ∼60-year population cycle (Baumgartner *et al.*, 1992; MacCall, 2009; McClatchie *et al.*, 2017). The CalCOFI programme provides seasonally resolved data on productivity in the form of egg and larvae standing stocks in the core of the CSNA range. Information on juvenile (age 0) and adult (age 1+) abundance is also available from southern to central California from 2004 to present (1990 to present for central California), based on the annual Rockfish Recruitment and Ecosystem Assessment Survey conducted by NOAA-NMFS (Ralston *et al.*, 2015; Thompson *et al.*, 2018; Santora *et al.*, 2020). This survey is separate from CalCOFI but covers much of the mostly nearshore epi-pelagic habitat of CSNA throughout its range in California. Owing to these comprehensive datasets as well as substantial information on the consumption of CSNA by predators and the availability of various fisheries statistics and well-designed models (e.g. Methot, 1989), we think that CSNA is not data deficient but actually is rather data rich. While it is true that some data are missing, for example egg and larval abundances of the portion of the CSNA stock living off Pacific Baja California and age/size compositions of landings before 2014, we think that the existing datasets can be analysed to provide annual abundance estimates that are reasonable for the management of its small fishery (MacCall *et al.*, 2016; Thayer *et al.*, 2017; Dorval *et al.*, 2018; Farallon Institute, unpublished data, https://bit.ly/30MA1zs).

# Review of life-history attributes
## Geographic structure

Major CSNA spawning centres along the California coast are the Southern California Bight (Ensenada to Point Conception) a coastal area somewhat protected by the offshore Channel Islands and in the lee of the Point Conception headland that generates a large neritic upwelling gyre (Fiedler *et al.*, 1986), and Monterey Bay to San Francisco on the central California coast. Relative to other small pelagic fish, anchovy are poor swimmers (Bakun, 2014), but while not considered migratory, CSNA expands well offshore from these centres of spawning and along the coast when abundance is high. This dynamic is described by MacCall's basin model (MacCall, 1990), although the model appears to describe the anchovy distribution better when sardines are absent. Shifts in spawning sites and range correspond to El Niño-Southern Oscillation (ENSO) events and other forms of changing ocean conditions (Fiedler *et al.*, 1986; Reiss *et al.*, 2008; Weber and McClatchie, 2010), with northward redistribution of CSNA during years of warmer water. Range expansion and contraction of CSNA is the key component of its population dynamics, whereby small-scale/local ecological conditions (e.g. low predation, high prey availability) may result in disproportionate population growth, swelling the population along and off the coast. Subsequently, this can lead to different pressures, such as offshore predators and/or less favourable environmental conditions operating on the larger, but geographically more diffuse population.

## Spawning and development

Described by Bakun (2001) as "reproductive machines", a mature CSNA female is capable of producing up to ∼14 000 eggs per year (Parrish *et al.*, 1986). CSNA can spawn throughout the year, though most spawning takes place in February and March, immediately prior to the period of peak alongshore Ekman transport off southern California (Parrish *et al.*, 1986). There has been no significant unidirectional trend in the mean spawning date of CSNA, but variability between years and decades is apparent (Asch, 2015). CSNA may spawn every 6–8 d (Smith, 1972; Lasker, 1988; MacCall, 2009), and spawning may be aligned with peak plankton production, thereby providing food resources to developing larvae (based upon Contreras-Reyes *et al.*, 2016, regarding Chilean anchoveta). Highly variable reproductive effort of CSNA can result in explosive population growth (see below) and is seen as an evolutionary mechanism designed to take advantage of rarely occurring sequential years of favourable ecological conditions (Bakun, 2014). CSNA eggs hatch within 7 d of spawning (Smith, 1985), after which larvae have ∼4 d to find food before starving (Lasker, 1975). CSNA are in the larval stage until they reach ∼35 mm in length (∼90 d) and then are of late juvenile and pre-recruit stages until they reach ∼100–110 mm (varies by region); during this time, they typically reside within 50 m of the surface (Ahlstrom, 1959).

Larval mortality is high, up to 95% (Peterman and Bradford, 1987), but is also highly variable and can be low. Prey availability early in the larval stage is hypothesized to determine annual reproductive success (Lasker, 1975). Age at maturity and recruitment is currently considered to be 1 year, though earlier estimates were 2 years (Smith, 1985). Interestingly, the maximum age of CSNA appears to have dropped from 8 to 4 years (Mais, 1981; MacCall, 2009), indicating that CSNA may have undergone

a major life-history change since the environmental shift event in 1977 (see McGowan *et al.*, 2003 for information about this shift).

Age-4 anchovy are ten times more productive than age-1 anchovy (Parrish *et al.*, 1986), suggesting that sharp shifts in age structure and possibly body condition may affect the reproductive success of CSNA. Body condition indices of CSNA are not available over the duration of study, but some more recent data are available from seabird-based sampling. In this case, body condition (Fulton's *K*) varies on multi-year scales, with the periods 1992–1997 and 2010–2015 being significantly lower than the middle of the time series, 1999–2004 (Farallon Institute, unpublished data, see Supplementary Figure SM1).

## Foraging and food habits

Like other anchovies, CSNA have large gill-rakers that allow them to feed in turbid estuarine and nearshore waters and consume relatively large planktivorous prey at all developmental stages (Bakun, 2014). Anchovy diet ontogenetically shifts from fish eggs, including their own species (Berner, 1959; Chiappa-Carrara and Gallardo-Cabello, 1993), dinoflagellates, diatoms, and copepod nauplii (Lasker, 1975; Scura and Jerde, 1977; Smith, 1985; Morote *et al.*, 2010), to increasingly larger micro-crustacean zooplankton (Hunter, 1981), including euphausiids, by the adult stage (Lasker, 1981). There appears to be a general preference for upwelling-related diatoms in the younger age classes (Skrivanek and Hendy, 2015). Composition of the plankton community impacts foraging success of anchovy, owing to within-group dietary preferences, such as an inability to consume spiny, filamentous diatoms (Scura and Jerde, 1977). Unarmoured dinoflagellates such as *Gymnodinium splendens* are a good food source (and may be a requirement for first-feeding larvae), whereas the armoured red-tide dinoflagellate *Gonyaulax polyedra* is also readily eaten, but this species is poisonous to anchovy and causes mortality (Scura and Jerde, 1977; Lasker, 1988). Gelatinous zooplankton can dominate anchovy diet in warm years despite their low energy content (Brodeur *et al.*, 2019). Notably, the food size range of first-feeding anchovy larvae overlaps with the ranges of first-feeding sardine, jack mackerel (*Trachurus symmetricus*), and other larvae, suggesting potential exploitative competition for food at the larval stage (Arthur, 1977; Hunter, 1981), but this hypothesis has yet to be tested.

## CSNA abundance, 1951–2015

CSNA is characterized by highly variable population dynamics (Lasker, 1988; MacCall *et al.*, 2016), with biomass varying by two orders of magnitude between its collapsed state (defined herein as <100 KMT; e.g. in the early 1950s and early 2010s) to short-term peaks in the biomass of up to ~2 million MT in some years (e.g. 1964–1966, 1986, and 2005–2006; Figure 2, based on MacCall *et al.*, 2016; Thayer *et al.*, 2017). The MacCall *et al.* biomass time series is based on CalCOFI egg and larval surveys, scaled up to the entire range of CSNA, including Mexico, using daily egg production methodology (see MacCall *et al.*, 2016 for details of assumptions and data sources; see Davison *et al.*, 2017 for considerations of data quality). Thayer *et al.* (2017) updated the time series and provide a correction to the original daily egg production method used by MacCall *et al.*, which altered biomass estimates slightly. There are gaps in the MacCall/Thayer *et al.* time series (which we abbreviate to M/T) from the mid-1960s to mid-1980s, but other biomass estimates based on stock assessments are available for

comparison (Methot, 1989; Jacobson *et al.*, 1995; Figure 3). Biomass estimates for years of overlap are correlated (Methot-M/T: Spearman rho = 0.63, $p = 0.001$; Jacobson-M/T rho = 0.31, $p = 0.162$). However, it is clear that neither of the stock assessment estimates picked up the peaks in biomass reported by MacCall *et al.* (2016). This difference is probably related to the estimation approaches used by Methot and Jacobson *et al.*. In particular, Jacobson *et al.* minimized recruitment deviations to constrain the solution and obtain a constant average recruitment for modelling purposes (Jacobson *et al.*, 1994). For that analysis, low recruitments were nudged higher and higher recruitments nudged lower to obtain a smooth anchovy stock–recruitment relationship. Jacobson *et al.* also eliminated the lower abundance years prior to 1963, probably to facilitate the use of a constant average recruitment (Jacobson *et al.*, 1995; Figure 3).

Excluding the spike in abundance in 1975, biomass averaged ~525 KMT from 1967 to 1985 and ~275 KMT from 1987 to 2004, peaked at ~2 million MT in 2005–2006, and then declined to <100 KMT between 2009 and 2015. The CSNA population thus grew from a collapsed state in the early 1950s, demonstrated two periods of relative stability at different levels from 1967 to 2004 (notably coinciding with the absence and then presence of sardines), and then showed a short-term spike in abundance in 2005–2006 before collapsing again and remaining low from 2009 to 2015. When we include only one period of collapse, 2009–2015 (i.e. excluding data from 1951 to 1956 because we do not know when this collapse began), the long-term median biomass for the full population cycle of 1957–2015 is 380.9 KMT. Post-2015 changes in abundance using the MacCall *et al.* (2016) method, as well as other techniques (acoustic-trawl surveys), are discussed later in this article in relation to potential management scenarios. Briefly, recent estimates of biomass indicate that the population has rebounded substantially after 2015; however, estimates are based on different techniques that may not be strictly comparable to the MacCall *et al.* (2016) method. A thorough comparison of these methods and the resulting estimates is beyond the scope of this article, but we provide preliminary comparisons in the Supplementary Material (JAT and WJS, unpublished data).

## Drivers of CSNA population dynamics
### Pacific Decadal Oscillation

Chavez *et al.* (2003) hypothesized that low-frequency environmental shifts, on a roughly 50-year cycle as shown by the alternating positive and negative phases of the PDO, predict small pelagic fish population fluctuations in the Pacific Ocean. Mechanistically, in the eastern Northeast Pacific, negative phases of the PDO are thought to be positively correlated with the magnitude of upwelling, resulting in cooler ocean temperatures and greater primary productivity in the form of large diatoms, which may facilitate high anchovy productivity and recruitment through bottom-up trophic mechanisms (Rykaczewski, 2019). Upwelling is also thought to influence egg production by affecting growth, and hence size, and fecundity of spawners or larval growth, and hence larval survival. Recently, Jacox *et al.* (2014) reported that upwelling and PDO are negatively correlated in the northern and central CCE, but they did not address this relationship for the southern CCE, which is the focal spawning habitat for CSNA. Upwelling north of Point Conception influences primary productivity to the south, at least in the outer shelf region (M. Jacox, pers. comm.).
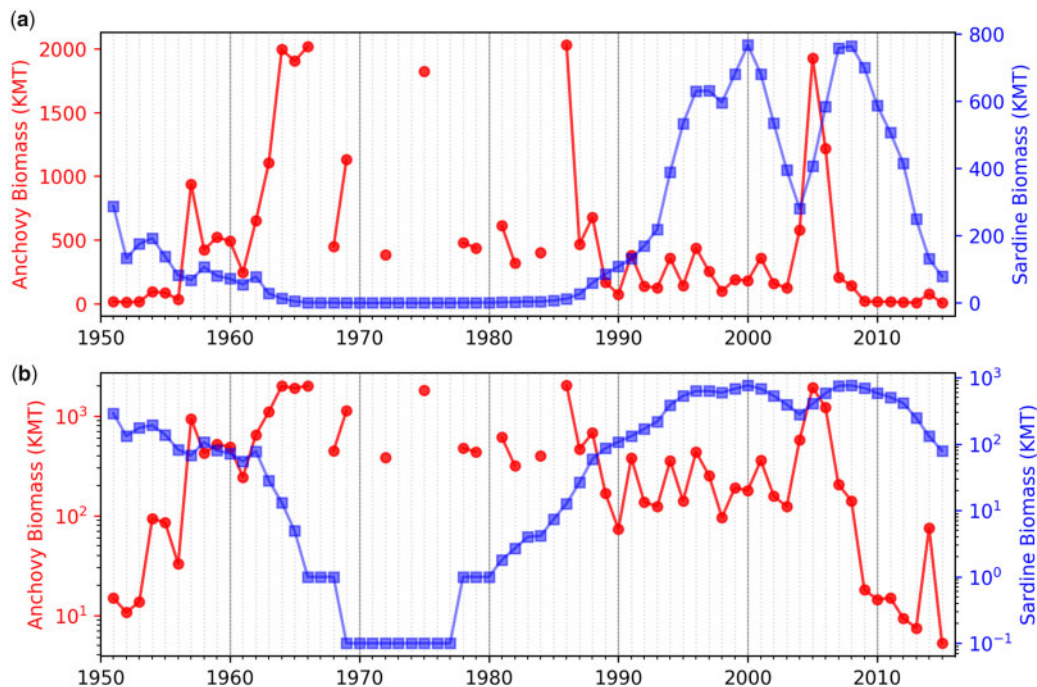
**Figure 2.** Biomass of CSNA and Pacific sardine 1951–2015 on (a) linear and (b) logarithmic scales. CSNA data are from MacCall *et al.* (2016) and were updated by Thayer *et al.* (2017). Sardine data are from Hill *et al.* (2017), with early data standardized by ADM (unpublished data).
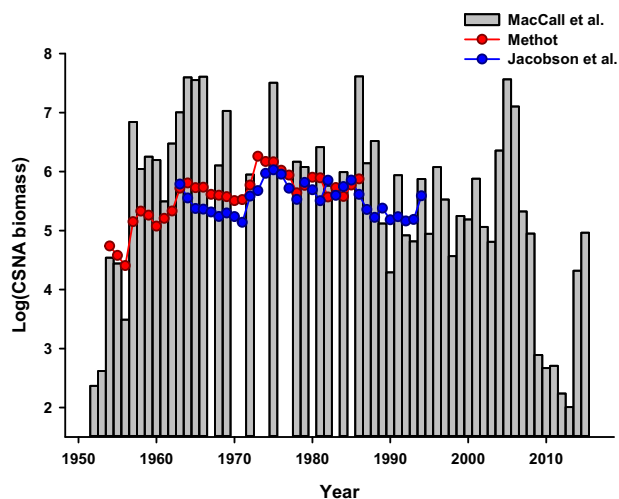


**Figure 3.** Biomass of CSNA based on the abundance estimate of MacCall *et al.* (2016) (bars) and stock assessments using stock synthesis by Methot (1989) (red points) and Jacobson *et al.* (1995) (blue points).

Positive PDO phases, however, are warmer and therefore conducive to smaller phytoplankton and a stable ocean environment favourable for the production and recruitment of sardine. Chavez *et al.* applied this idea to anchovy–sardine pairs residing off Peru, Japan, and California, but environmental covariates of population fluctuations were not examined quantitatively.

   With respect to CSNA, we found no consistent relationship with PDO, Multivariate ENSO Index (MEI; https://www.esrl.noaa.gov/psd/enso/, downloaded Sept. 2018), or local temperature over one cycle of high-to-low biomass, 1957–2015 (Table 1).

From a purely descriptive standpoint, during the period 1957–1963 (Figure 4), the winter PDO was in a cold phase, which corresponded to a general pattern of anchovy population growth at that time. From the mid-1960s to mid-1980s, while the anchovy population was relatively stable at a moderately high level, the winter PDO was variable with numerous shifts between positive and negative values (Figure 4). From the late 1980s to late 1990s, the anchovy population was stable at a lower level and the PDO was positive (warm). However, the PDO changed to a general cold phase from the late 1990s through mid-2010s, but that time the anchovy population declined to a collapsed state. Thus, while the early part of the CSNA biomass time series may appear to support the PDO hypothesis and undoubtedly contributed to Chavez *et al.*'s interpretations, overall there does not appear to be a relationship at either low-frequency or interannual time scales with the PDO.

### Upwelling

In reviewing the potential effects of climate change on sardines and anchovies worldwide, Checkley *et al.* (2017) provided the hypothesis that anchovy population fluctuations are primarily related to upwelling, based on the fact that anchovies generally occur throughout the world in upwelling-based ecosystems. The pattern of spring upwelling at 33°N in the northeast Pacific fits with anchovy biomass estimates reasonably well, with increased upwelling in the 1950s and generally decreased upwelling from the mid-1960s through early 1990s (Table 1 and Figures 4 and 5). However, upwelling does not correspond with the spike in biomass in the mid-2000s nor the collapse in biomass after 2008 (Figure 5). Nonetheless, springtime upwelling was the only physical environmental variable significantly related to CSNA biomass over the period 1957–2015 (Table 1).

**Table 1.** Regression results testing the effect of the previous years' CSNA biomass, sardine biomass, and environmental drivers on CSNA biomass in the current year.

| Models | N | F | $p > F$ | $R^2$ | AIC | Term | Coefficient | t | $p > \lvert t \rvert$ |
|---|---|---|---|---|---|---|---|---|---|
| biomass ~biomass_lag1 | **42** | **43.62** | **<0.0001** | **0.522** | **121.548** | **biomass_lag1** | **0.714** | **6.600** | **<0.001** |
| biomass ~biomass_lag1 and log(sardine biomass)_lag1 | 42 | 25.11 | <0.0001 | 0.563 | 119.764 | biomass_lag1 | 0.612 | 5.220 | <0.001 |
| | | | | | | log(sardine biomass)_lag1 | −0.412 | −1.920 | 0.063 |
| biomass ~biomass_lag1 and log(sardine biomass)_lag2 | 42 | 22.75 | <0.0001 | 0.538 | 122.046 | biomass_lag1 | 0.648 | 5.360 | <0.001 |
| | | | | | | log(sardine biomass)_lag2 | −0.104 | −1.190 | 0.241 |
| biomass ~biomass_lag1 and PDO_lag1 | 42 | 21.46 | <0.0001 | 0.524 | 123.345 | biomass_lag1 | 0.726 | 6.450 | <0.001 |
| | | | | | | PDO_lag1 | −0.073 | −0.430 | 0.666 |
| biomass ~biomass_lag1 and PDO_lag2 | 42 | 24.67 | <0.0001 | 0.559 | 120.182 | biomass_lag1 | 0.759 | 7.020 | <0.001 |
| | | | | | | PDO_lag2 | −0.283 | −1.800 | 0.079 |
| biomass ~biomass_lag1 and MEI_lag1 | 42 | 21.84 | <0.0001 | 0.528 | 122.960 | biomass_lag1 | 0.708 | 6.500 | <0.001 |
| | | | | | | MEI_lag1 | −0.149 | −0.740 | 0.463 |
| biomass ~biomass_lag1 and MEI_lag2 | 42 | 23.89 | <0.0001 | 0.551 | 120.929 | biomass_lag1 | 0.710 | 6.690 | <0.001 |
| | | | | | | MEI_lag2 | −0.289 | −1.580 | 0.121 |
| biomass ~biomass_lag1 and SST_lag1 | 42 | 22.01 | <0.0001 | 0.530 | 122.784 | biomass_lag1 | 0.714 | 6.580 | <0.001 |
| | | | | | | SST_lag1 | −0.196 | −0.850 | 0.403 |
| biomass ~biomass_lag1 and SST_lag2 | 42 | 22.37 | <0.0001 | 0.534 | 122.420 | biomass_lag1 | 0.704 | 6.480 | <0.001 |
| | | | | | | SST_lag2 | −0.230 | −1.030 | 0.309 |
| biomass ~biomass_lag1 and BUI_lag1 | 42 | 22.12 | <0.0001 | 0.531 | 122.679 | biomass_lag1 | 0.713 | 6.570 | <0.001 |
| | | | | | | BUI_lag1 | 0.003 | 0.900 | 0.372 |
| biomass ~biomass_lag1 and BUI_lag2 | **42** | **27.1** | **<0.0001** | **0.582** | **117.928** | **biomass_lag1** | **0.698** | **6.800** | **<0.001** |
| | | | | | | **BUI_lag2** | **0.007** | **2.360** | **0.023** |
| biomass ~biomass_lag1 and sealevel_lag1 | 42 | 24.77 | <0.0001 | 0.560 | 120.082 | biomass_lag1 | 0.613 | 5.160 | <0.001 |
| | | | | | | sealevel_lag1 | −8.577 | −1.830 | 0.075 |
| biomass ~biomass_lag1 and sealevel_lag2 | 42 | 26.47 | <0.0001 | 0.576 | 118.504 | **biomass_lag1** | **0.598** | **5.180** | **<0.001** |
| | | | | | | **sealevel_lag2** | **−10.985** | **−2.230** | **0.032** |

Sardine biomass and environmental drivers were lagged 1 and 2 years, respectively. CSNA and sardine biomass were log-transformed. Bold results indicate significance ($p \leq 0.05$) of the covariate.
SST, sea surface temperature; BUI, Bakun Upwelling Index; AIC, Akaike information criterion.

Mechanistically, sustained, moderate ($>5\,\text{m s}^{-1}$; García-Reyes *et al.*, 2014) alongshore winds that drive coastal upwelling are thought to increase the abundance of zooplankton prey for anchovy (e.g. copepods; Rykaczewski and Checkley, 2008), thereby lowering larval mortality (Lasker, 1988). High winds (e.g. daily average $>10\,\text{m s}^{-1}$) may cause excessive turbulent mixing that disrupts a well-stratified water column and dissipates prey while increasing Ekman transport, which may carry anchovy eggs and larvae into suboptimal offshore areas (Peterman and Bradford, 1987; Lasker, 1988), lowering recruitment and biomass (Yáñez *et al.*, 2008). Thus, upwelling may have a dome-shaped relationship with CSNA productivity and larval mortality (Cury *et al.*, 1995). Indeed, Peterman and Bradford (1987) showed that monthly periods of calm winds linearly decreased the instantaneous daily mortality rate of CSNA larvae by affecting prey availability, partially supporting the dome hypothesis. However, we did not find any non-linear effects of upwelling on CSNA biomass (Table 1).

## Current flow

MacCall (2009) suggested that meridional current flow, rather than upwelling *per se*, may benefit the CSNA population through the advection of key prey or water masses from the northern CCE and perhaps Gulf of Alaska. MacCall also suggested that high alongshore flows maintain the cooler temperatures that CSNA prefers for spawning and growth. There are no current flow indices in the CCE over the 65-year study period, aside from sea level measurements (Chelton and Davis, 1982), which are difficult to interpret as they may be a proxy for upwelling or flow rates. We found that sea level correlates with CSNA biomass (Table 1) but only after the year 2000. Sea level increased throughout the study period and was generally below the mean from 1950 to 1990 before increasing steadily thereafter. The rapid increase in sea level after 2000 corresponds with the collapse in biomass after 2008 (Figure 4). Recently, the Ocean Surface Current Analyses Real-time (Dohan, 2017) product provides surface currents averaged over the top 30 m of the upper ocean. Mixed layer velocities are calculated from satellite-sensed sea surface height gradients, ocean vector winds, and sea surface temperature fields using geostrophy, Ekman transport, and thermal wind dynamics (Dohan, 2017). As the availability and time period of these data grow in the near future, it is important to analyse how large-scale flows may affect CSNA biomass.

## Intra-guild interactions

CSNA share their trophic level with a number of potential competitors and predators of their eggs and larvae including age-0 juvenile
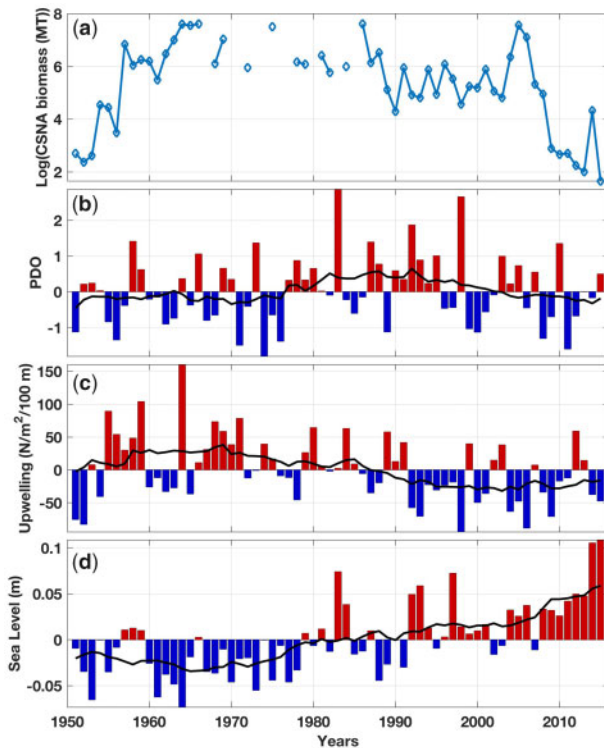
**Figure 4.** For 1950–2015 (a) biomass of CSNA (KMT, log scale) in relation to (b) January–March PDO, (c) April–June upwelling index anomalies (N m$^{-2}$ 100 m$^{-1}$) at 33°N, and (d) April–June sea level anomalies (m) at Los Angeles. The black line on the lower panels indicates a 12-month moving average.

groundfish, cephalopods, and other small pelagic fish, notably jack mackerel, Pacific/chub mackerel, and Pacific sardine. Abundances of anchovy and sardine purportedly alternate (e.g. Schwartzlose *et al.*, 1999), but this hypothesis is equivocal (e.g. McClatchie *et al.*, 2017). Nonetheless, it seems reasonable to hypothesize that anchovy covaries in relation to the abundance of other members of their guild (e.g. MacCall, 1996), though the mechanisms of interaction may be varied and unintuitive. The more neritic CSNA often inhabits different areas than sardines and mackerels, as those species are found in more pelagic habitats. While some have hypothesized that competition and/or predation are important drivers of the population dynamics of both anchovies and sardines (see review in Radovich, 1982), MacCall (2009) and others (e.g. Sugihara *et al.*, 2012) have dismissed hypotheses of competitive exclusion and predation (see also MacCall, 1983). However, it is possible that the dominance of one species limits the habitat use of the other through interference competition (MacCall, 2009). Owing to the effects of high fishing mortality and over-exploitation of the California sardine stock (Radovich, 1982; Zwolinski and Demer, 2013), and the fact that there are no data on anchovies before 1951 when sardines were abundant, it is difficult to evaluate the relationship between sardine and CSNA abundance. Indeed, following the collapse of the stock in the 1940s, the sardine population remained in a collapsed state from the mid-1960s to early 1990s (Figure 2). Sardine increased in the mid-1990s to a peak of ~800 KMT in 2000, before a short-term decrease in the early 2000s that was followed by a longer-term decrease in the 2010s. From these patterns of sardine population fluctuations, we find weak support
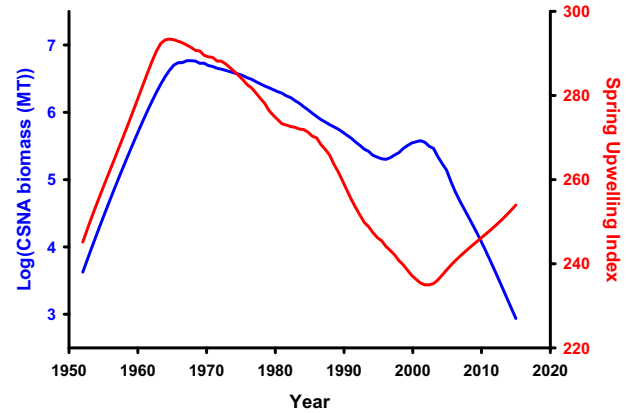


**Figure 5.** CSNA biomass, 1952–2015 (log MT; blue) and April–June upwelling index lagged by 1 year (1951–2014; red) smoothed with a Loess function (sampling proportion = 0.4).

for a correlation between sardine and CSNA over the time period of interest (1957–2015; Table 1). In particular, following the sardine recovery in the mid-1990s, the anchovy population was stable, albeit at relatively low levels, throughout the 1990s when the sardine population grew substantially. The decline in sardine in the early 2000s and corresponding spike in anchovy biomass in 2004–2006, however, is suggestive of an interaction between these species, or, more likely in our view, opposing responses of each species to the environmental variation in the early 2000s, years of strong upwelling and cold temperatures. In the late 2000s and early 2010s, both species were in decline, suggesting that there was no interaction over the past decade and that ocean conditions from the mid-2000s to mid-2010s affected both species negatively.

Sardine and both mackerel species are potential consumers of anchovy eggs and larvae (Szeinfeld, 1991; Bertrand *et al.*, 2004), with the predation rate likely related to the spatial habitat overlap between species. Cannibalism is also a likely cause of egg/larval mortality (Hunter and Leong, 1981). There was a precipitous decline in CSNA egg and larval survivorship during the 2000s (Fissel *et al.*, 2011; MacCall *et al.*, 2016; Thayer *et al.*, 2017), the cause of which is not presently known, but filter-feeding cannibalism by adults is a likely possibility (MacCall, 1990). Cannibalism intensity would be proportional to the density of adults, with adult densities increasing nearshore under conditions of severe population decline. If true, severe population decline could result in a positive feedback mechanism wherein low CSNA numbers could be maintained by cannibalism. We do not know if this has occurred in this population, but there is potential for this mechanism given recent population fluctuations and redistribution towards more neritic habitats. Alternatively, the 2014–2016 North Pacific marine heat wave (Di Lorenzo and Mantua, 2016) could have pushed the population closer to shore. Compression of the nearshore upwelling habitat has been implicated in how the marine heat wave affected the coastal ecosystem (Gentemann *et al.*, 2017; Jones *et al.*, 2018; Santora *et al.*, 2020), but this would only apply to the years 2014–2016, and the CSNA collapse began in 2009.

## Natural mortality
CSNA is a critically important food resource in the CCE (Szoboszlai *et al.*, 2015; Koehn *et al.*, 2016); adults and juveniles are prey for at least 64 species of predators including large
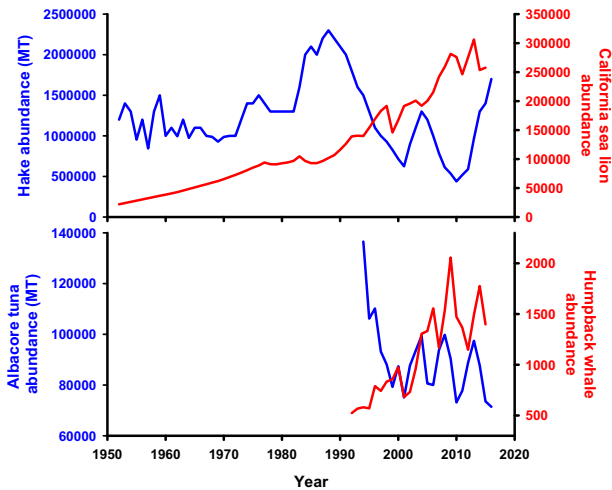
**Figure 6.** Population size of key top predators of CSNA, 1950–2016. Top: Pacific hake [Berger *et al.* 2017 (modified: total biomass divided by three to obtain biomass of age-5+ fish likely to consume CSNA)] and California sea lion [Carretta *et al.*, 2017; Laake *et al.*, 2018 (modified: 1960, 1962–1967, 1979–1980, and 2012 filled by trend analysis from surrounding years; 1958–1959, 1961, 1968–1974 imputed twice based on an average difference between Carretta *et al.* and Laake *et al.* from 1975 to 1981)]. Bottom: albacore tuna [International Scientific Committee for Tuna and Tuna-like species in the North Pacific Ocean, 2017 (modified: sum of both sexes ages 2–4 based on numbers and weight at age from the base model of the 2017 stock assessment, assuming that 40% of that biomass is in the eastern North Pacific and 56% of the eastern North Pacific biomass is found from San Francisco, United States, to Ensenada, Mexico; S. Teo, pers. comm. to SD)] and humpback whales (after Calambokidis *et al.*, 2017; Table 2). Fish are shown in blue, and marine mammals are shown in red.

predatory fishes and cephalopods, as well as numerous marine birds and mammals. The extensive use of age-0 and age-1+ anchovies as forage for top predators indicates that natural mortality (predation) could affect CSNA population dynamics, especially during periods of population collapse (Bakun, 2006). CSNA predators have different metabolic rates, population trends, sizes, and patterns of spatial residence, all of which affect consumption and thus CSNA natural mortality rates. Indeed, perhaps a dozen large and abundant predators cause most of the CSNA mortality (Szoboszlai *et al.*, 2015; Koehn *et al.*, 2017). For this contribution, we have considered the abundance of four of these species, including two major pelagic fish predators, Pacific hake (*Merluccius productus*) and albacore tuna (*Thunnus alalunga*), and two marine mammals, California sea lion (*Zalophus californianus*) and humpback whales (*Megaptera novaeangliae*). Other species of interest that are not highlighted here include long-beaked common dolphin (*Delphinus capensis*), a resident species along the southern California coast, Chinook salmon (*Oncorhynchus tshawytscha*), and common murre (*Uria aalge*), an abundant seabird. The latter two predators mainly overlap with CSNA in the northern part of its range. Hake and albacore spatially overlap with CSNA for only part of the year (fall/winter for hake and summer for albacore), but during periods of high abundance and offshore range expansion, CSNA may overlap with these predators more often. California sea lions and humpback whales are coastal predators that reside in CSNA habitat roughly

year-round. The adult and juvenile predation component of natural mortality has been hypothesized to have a large effect on CSNA and has changed through time (MacCall, 1974; MacCall *et al.*, 1985; Methot, 1989). Overall, there is no clear pattern of changes in predator populations relative to that of the CSNA (Figure 6). There is a strong negative correlation (rho = −0.65) between the abundance of California sea lions and CSNA lagged by 1 year, but this relationship is likely spurious due to the trend of increasing sea lion abundance and the severe decline in CSNA in the 2000s. It may be that different predators exert effects at different times under differing environmental conditions.

## Fisheries

Landings in California were negligible before 1952 (Jacobson *et al.*, 1995; Schwartzlose *et al.*, 1999) and then were quite modest in comparison to biomass prior to 2009 when the severe decline occurred. Peak landings of 340 KMT were taken in 1981, falling to ~5 KMT year$^{-1}$ in the mid-1990s and remaining mostly <20 KMT year$^{-1}$ since then. Average landings across the time series were ~60 KMT year$^{-1}$ vs. ~500 KMT average estimated biomass, or a 12% long-term exploitation rate, but most annual landings were <5% of biomass. From 2009 to 2015, although small numerically, landings were proportionally large (>~20% of biomass) due to the collapse and low population size. Despite the low fisheries take of CSNA, fishing has reduced average lifespan, net lifetime fecundity, and mean spawning age, probably resulting in more variability in population dynamics (Lindegren *et al.*, 2013).

## Taking stock

Work in the 1950s on the basic biology of CSNA (McHugh, 1951; Berner, 1959) laid the foundation for the boom in anchovy population dynamics studies in the 1960s and 1970s, dominated by the triumvirate of Lasker (1981, 1988), MacCall (1974, 1983), and Parrish *et al.* (1985, 1986). Many early studies explored linear relationships between one or a few environmental factors and core biological parameters of the species. These include wind vs. larval survival (Peterman and Bradford, 1987), temperature vs. fecundity (Methot, 1989), dependence on certain food types (Scura and Jerde, 1977; Fiedler *et al.*, 1986; Lasker, 1988), and relationships with predators (Lasker, 1981; Mais, 1981; Crawford, 1987; Methot, 1989). Population dynamics models that include physical and biological environmental effects (e.g. Methot, 1989; Jacobson *et al.*, 1994) and concepts of non-linear relationships with environmental variables (Cury *et al.*, 1995) appeared in the mid–late 1980s and 1990s. In part, non-linearity was seen as a solution to conflicting linear relationships [e.g. the effect of stability on anchovy abundance in Lasker (1988) and McGowan *et al.* (2003)] that may have appeared when only part of the full variable range of conditions was sampled. Previously, there have been various proposals to partition anchovy abundance into discrete states, presumably stemming from intuitive attempts to simplify the situation for modelling, or based on the fact that few, if any, variables explain CSNA biomass or measurements of standing stock over more than a few years. Examples of discrete states include collapse, breakout, and boom (Bakun, 2006; McClatchie *et al.*, 2017; van der Sleen *et al.*, 2018), which may be one of the critical aspects of management of the stock in the future.

Overall, despite our conviction that CSNA is not data deficient, and aside from upwelling intensity, there are precious few

factors that are clearly related to CSNA biomass and which could be used for a population dynamics model and in management. In essence, we examined no physical or biological variable that related to CSNA biomass across the entire time series from an initial recovery to subsequent collapse. These include potential competitor and key predator abundances, and well-known climate indices such as the PDO and MEI. We found, as have others, that CSNA biomass is related to one or a few of these variables for a period of years or decades, but in all cases correlations broke down, were weak, or changed over time. Such nonstationarity (i.e. changing relationships through time) in external drivers of population dynamics may indicate that only internal population drivers are appropriate for population modelling. Indeed, the most promising predictor, serial autocorrelation of biomass from one year to the next explained 55% of the year-to-year variation in logged CSNA biomass; the population also had the potential to vary by orders of magnitude between adjacent years. The clear volatility of CSNA population dynamics probably reflects a number of complementary (favourable) or antagonistic (unfavourable) forcing factors, whose relationships to anchovy production or recruitment are more complex than simple linear relationships. It is therefore clear from our review and evaluation of the data that traditional fisheries models of CSNA population dynamics may not be possible to parameterize, especially during periods of collapse and recovery when the population is most volatile. We agree that some promising factors have yet to be tested, such as flow rate of the California Current, the influence of eddies, or combinations of variables such as upwelling/stratification or predation/fishery removals as a whole, but indices for these variables are still under development. More complex population dynamics models that account for multiple species and changes in biophysical relations (Litzow et al., 2018; van der Sleen et al., 2018) and that relate to the internal dynamics of the population (Ciannelli et al., 2012; Botsford et al., 2014; van der Sleen et al., 2018) are probably needed, but we are currently far from making this kind of complex model a reality, let alone using it for management. Indeed, given the small fishery for CSNA, developing new models and conducting a thorough stock assessment remain a low priority for agencies currently charged with modelling the population.

## Sensible approach to management

Viewing CSNA population dynamics from a multi-species standpoint, as well as taking into account the critical importance of CSNA in ecosystem functions, affords us a perspective on a possible sensible ecosystem-based fishery management strategy. Even for coastal pelagic species with smoother population changes, management is fraught with challenges including fundamental controversies over non-linear population dynamics and the role of these species in ecosystems (Smith et al., 2011). CSNA provides clear examples of these management issues: their population is highly volatile, they are expensive and difficult to measure accurately, and they are driven by poorly understood internal population and external factors, all while being vitally important to the feeding ecology of California Current predators and energy transfer from lower to upper trophic levels. While the fishery for CSNA is small, it is an important part of California wetfish and sport fishing industries (D. Pleshner Steele, pers. comm.). The fishing industry therefore seeks, beyond all else, sustainability in landings and economic benefits, even if the fisheries landings are smaller than desired. On the opposing side, conservationists seek

to minimize catches to protect biomass to maintain health of the ecosystem and its upper trophic level species. Recreational fishing interests have long argued for the protections of CSNA as a forage reserve (Radovich, 1982). If one desires salmon, rockfish, and other charismatic marine fauna represented by seabirds and marine mammals, one needs an abundant and productive CSNA population. The conservation position also acknowledges that CSNA is difficult to measure and predict but takes the position that—because they are so critical to trophic interactions—ecosystem-based fisheries management needs to be extremely precautionary.

In the Alaskan North Pacific, the North PFMC enacted a moratorium on federally managed forage fish fisheries in 2000 (Witherell et al., 2000), a policy that has effectively protected many of the small pelagic fish there from exploitation (the exception being Pacific herring, which has large fisheries in various regions of Alaska) and may have facilitated healthy upper trophic level populations including large piscivorous fish, seabirds, and marine mammals of commercial, ecological, and economic values. Given how important CSNA is to the southern and central CCE, enacting a prohibition on fishing them is not an unreasonable suggestion, but we do not support this option as it may enable a policy of neglect in which no data on the population would be collected. In the CCE, the PFMC enacted a ban on krill fisheries development due to the significance of krill in trophic interactions, a motion that was supported by the recreational and commercial fishing industries as well as the marine conservation community, but as a result, data on krill are now often lacking.

Since the population collapse of 2009–2015, there has been a substantial increase in CSNA biomass, with the rapid recovery in the late 2010s reminiscent of the rapid population growth in the late 1950s. Biomass in 2016 was estimated to be ~150 KMT and over 1 million MT in 2017 and 2018 (Farallon Institute, unpublished data, https://bit.ly/30MA1zs; see Supplementary Material). Such impressively rapid changes in biomass suggest that a sensible management strategy needs not be based on precise abundance estimates. If CSNA is measured in orders of magnitude, this should be sufficient to achieve two fundamental management objectives: (i) protect ecosystem functions through maintaining CSNA trophic interactions and (ii) maintain sustainability of a small fishery with moderate socio-economic services in perpetuity, if industry is willing to accept generally low catches overall. It is important to mention here that the industry may have been fortunate when PFMC management shifted to "monitored" status in the 1990s. If the fishery had remained on an assessment-based quota policy, the collapse of 2009–2015 would have resulted in a legal classification of CSNA as "overfished", which would have required implementation of a rebuilding plan and closed any commercial fishing. In this case, the quota would have been zero, or at least very low, instead of the current long-term quota of 25 KMT year$^{-1}$.

The first management strategy to consider is therefore a conventional one, whereby one assumes that a long-term population dynamics model adequately describes the population fluctuations—even if one really cannot be developed or is low priority as discussed above. This was the original approach in the 1970s, which indicated that the probability of CSNA falling below 300 KMT was very small (PFMC, 1978, 1983). Based on this model, 300 KMT was set as a cut-off term in the harvest control rule, a threshold below which fishing would be prohibited except for live bait. However, it is clear that the model failed to capture both

rapid increases and collapses that characterize this population. While it was acknowledged that the model did not account for the very low biomasses of the early 1950s, this was attributed to a number of factors, including lack of faith in the early CalCOFI methodology and the fact that sardines were still present in the system (ADM, pers. obs.). In fact, the original model worked well until about 1990, when CSNA biomass declined and remained below 300 KMT for the better part of 20 years (Figure 2), but something else then changed as well. The reappearance of sardines is one explanation, but environmental shifts also provide an explanation. The year 1990 has been identified as a tipping point in ecosystem dynamics (Sydeman *et al.*, 2013; see also Cloern *et al.*, 2010). Importantly, the North Pacific Gyre Oscillation mode is thought to have become more dominant and the PDO mode less dominant since 1990 (Di Lorenzo *et al.*, 2008; Sydeman *et al.*, 2013; Newman *et al.*, 2016). Correspondingly, there were also shifts in ENSO dynamics from the eastern (canonical) mode to central Pacific (Modoki) mode (Di Lorenzo *et al.*, 2010). Such atmospheric-oceanographic events appear to temporally align with the recent decreased influence of upwelling on CSNA population dynamics (Figure 5). Management also shifted at the time with the PFMC abandoning CSNA stock assessments and annual quota-making, so a model of the new conditions affecting the post-1990 CSNA population was never developed. Of course, the later brief expansion to high abundance, followed by rapid collapse, most certainly would not have been anticipated by any model, so a conventional long-term population dynamics model would not have prevented an overfishing designation (note that actual overfishing had nothing at all to do with the recent severe decline in CSNA; see MacCall *et al.*, 2016 for details). Therefore, it is clear that a long-term static population model for CSNA is not a preferred alternative, but a more dynamic model has not yet been developed.

Consequently, we advocate for a very simple adaptive approach. First, we specify that abundance can be monitored unilaterally in US waters, such that successful management of the US portion is therefore possible independently of what happens in Mexico. We consider two states of anchovy productivity, one below and one above the median anchovy spawning biomass value observed over the range of its recent population estimates (380 KMT). The basic rule would be if abundance is >380 KMT based on the methodologies outlined in MacCall *et al.* (2016; see Supplementary Material for comparisons with other population estimation techniques), then the maximum allowable harvest would be ~25 KMT year$^{-1}$, based on recent (NOAA, 2019) and previous estimates of an optimal yield (PFMC, 1983). If the spawning biomass estimate is below the median abundance (i.e. 0–380 KMT), then the quota would be decreased to 5 KMT year$^{-1}$ with half coming from central California and half from southern California; at this time, fishing would be considered "experimental" to maintain monitoring and data streams concerning this ecologically critical species. This is a similar approach to the use of a cut-off term for the management of sardine, in which fishing is curtailed when sardine biomass is estimated to be <150 KMT, but some experimental fishing is allowed to track cohort productivity and potential population recovery (PFMC, 1998). We need the same kind of information stream for CSNA. Our higher cut-off term for the forage reserve of CSNA (380 KMT) is based on the fact that CSNA is more abundant than sardine and is more important for ecosystem functions because they are smaller and therefore more available as prey for smaller

predators such as juvenile predatory fish (e.g. albacore, salmon), seabirds, and many piscivorous marine mammals. In the future, one may also wish to include a "sardine trigger" based on estimated sardine biomass for re-evaluation, but at present, the sardine fishery is below cut-off and is closed, and if history predicts the future, it may remain that way for decades. This means that the current CSNA population, even in a recently partially recovered state, is even more important for ecosystem functions, as there are fewer alternative forage fish species in abundance in the ecosystem, including other clupeids like herring (Sydeman *et al.*, 2018).

In essence, McInnis (1983) had it right. He wrote:

> One characteristic of the anchovy resource which influences management policy is that the abundance of spawners fluctuates widely over short periods. The fluctuation occurred even before a significant fishery existed. Management which relies on fixed regulatory measures such as fixed quotas would not satisfy the needs of the fishery or the resource from year to year. The resource can fluctuate to such an extent that the word "average" has little practical meaning for efficient management. If the average yield were harvested annually, the resource could be greatly over-fished in some years . . . .

In our view, high levels of anchovy abundance sufficient to support both a fishery and predator populations can be defined as occurring when the population exceeds the long-term median biomass of 380 KMT. We note that predator populations in the southern and central CCE are much larger now than they were in the past (e.g. Figure 6), when a forage/population reserve cut-off of 300 KMT for the fishery was originally proposed (PFMC, 1983). In addition, according to the recent global meta-analysis on seabirds by Cury *et al.* (2011), a forage reserve of one-third of the maximum biomass is required to maintain the annual productivity of predators (seabirds being the model predator in this case). Importantly, the benchmark set by Cury *et al.* is not based on estimates of the amount of prey consumed, but rather estimates of the amount of prey needed in the ecosystem for predators to find and handle enough prey to maintain productivity above the threshold where it starts to decline, assuming a Type II numerical response curve. As the maximum biomass of CSNA is ~2 million MT, Cury *et al.*'s benchmark would place the cut-off at ~666 KMT, which we think is too large for this highly variable CSNA population. Robinson *et al.* (2015) estimated that a forage reserve of one-fifth (20%) of the maximum observed biomass would be needed to maintain the annual survivorship of predators (penguins in this case), which would place the cut-off at ~400 KMT. This cut-off is closer to the median biomass threshold we have recommended above.

Finally, we note that in the past, CSNA management included a spatial component, utilizing inshore no-take marine protected areas (MPAs) for the protection of juveniles, anchovy refugia, and foraging opportunities for central-place foraging predators (PFMC, 1983, 2000). These spatial components were advocated for by the State of California in relation to recreational fishing and endangered species interests and are also sensible. We know where these refugia are based and could also limit or prohibit fishing in these areas to facilitate population recovery and trophic interactions. Key refugia appear to be in the Gulf of the Farallones, Monterey Bay, and the inner portion of the Santa

Barbara Basin. These regions should be targeted as forage reserve MPAs, but are also regions where experimental fisheries may desire to operate when the population is in its collapsed state.

## Concluding remarks

The CSNA is one of the best-studied anchovy stocks in the world, with decades of academic and governmental efforts aimed at understanding its population dynamics. The remarkable CalCOFI programme was designed to understand the ecology of anchovy and sardine populations in the California Current, including physical and biological drivers. This programme has now reached a milestone of longevity of over six decades, enabling a retrospective examination of the resulting literature and available data. In this contribution, we have reviewed many of the pertinent literature and re-evaluated some of the key variables proposed to determine CSNA population dynamics. Upwelling intensity lagged to the years of anchovy spawning and larval production is the most enticing environmental variable examined, but even the correlation with upwelling appeared to break down over time. Observations suggest that the covariance of upwelling intensity and CSNA biomass weakened in the mid–late 1990s, which could be related to climate change (Rykaczewski et al., 2015). At that time, some short-term periods of alignment between sardines, anchovy predator populations, and CSNA biomass are evident, but these periods were also characterized by substantial environmental changes, such as the delayed/interrupted upwelling of 2005–2006 (e.g. Schwing et al., 2006) or the recent unprecedented North Pacific marine heat wave of 2014–2016 (e.g. Gentemann et al., 2017). Given this complexity, population dynamics modelling of CSNA is unlikely to reproduce abundance fluctuations in a robust manner, indicating that management may be best served by a simple static two-state harvest control rule in which modest fisheries are allowed when abundance exceeds the long-term median of abundance and is reduced to experimental fishing when the population is within or apparently moving towards a collapsed state.

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

## References

Ahlstrom, E. H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fisheries Bulletin, 60: 107–146.

Arthur, D. 1977. Distribution, size, and abundance of microcopepods in the California Current system and their possible influence on survival of marine teleost larvae. Fisheries Bulletin, 75: 601–611.

Asch, R. G. 2015. Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proceedings of the National Academy of Sciences of the United States of America, 112: E4065–E4074.

Bakun, A. 2001. "School-mix feedback": a different way to think about low frequency variability in large mobile fish populations. Progress in Oceanography, 49: 485–511.

Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: navigating the "predator pit" topographies. Progress in Oceanography, 68: 271–288.

Bakun, A. 2014. Active opportunistic species as potential diagnostic markers for comparative tracking of complex marine ecosystem responses to global trends. ICES Journal of Marine Science, 71: 2281–2292.

Barange, M., Hampton, I., and Roel, B. A. 1999. Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys. South African Journal of Marine Science, 21: 367–391.

Baumgartner, T. R., Soutar, A., and Ferreira-Bartrina, V. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. California Cooperative Fisheries Investigations Reports, 33: 24–40.

Berger, A. M., Grandin, C. J., Taylor, I. G., Edwards, A. M., and Cox, S. 2017. Status of the Pacific hake (whiting) stock in U.S. and Canadian waters in 2017. Prepared by the Joint Technical Committee of the U.S. and Canada Hake/Whiting Agreement, National Marine Fisheries Service and Fisheries and Oceans Canada. 202 pp.

Berner, L. Jr 1959. The food of the larvae of the northern anchovy *Engraulis mordax*. International Tropical Tuna Commission Bulletin, 4: 1–22.

Bertrand, A., Segura, M., Gutierrez, M., and Vasquez, L. 2004. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish and Fisheries, 5: 296–316.

Bograd, S. J., Checkley, D. A. Jr, and Wooster, W. S. 2003. CalCOFI: a half century of physical, chemical and biological research in the California Current System. Deep-Sea Research Part II, 50: 2349–2353.

Botsford, L. W., Holland, M. D., Field, J. C., and Hastings, A. 2014. Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. ICES Journal of Marine Science, 71: 2158–2170.

Brodeur, R. D., Hunsicker, M. E., Hann, A., and Miller, T. W. 2019. Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: a shift to gelatinous food sources. Marine Ecology Progress Series, 617–618: 149–163.

Calambokidis, J., Barlow, J., Flynn, K., Dobson, E., and Steiger, G. H. 2017. Update on abundance, trends, and migrations of humpback whales along the U.S. West Coast. SC/A17/NP/13 Report to the International Whaling Commission. 18 pp.

California Cooperative Oceanic Fisheries Investigations (CalCOFI). 2010. California Cooperative Oceanic Fisheries Investigations Reports, 51: 219 pp.

Carretta, J. V., Forney, K. A., Oleson, E. M., Weller, D. W., Lang, A. R., Baker, J., Muto, M. M. et al. 2017. U.S. Pacific marine mammal stock assessments: 2016. NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFSC-577. 414 pp.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E., and Niquen, M. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science, 300: 217–221.

Checkley, D. M., Asch, R. G., and Rykaczewski, R. R. 2017. Climate, anchovy, and sardine. Annual Review of Marine Science, 9: 8.1–8.25.

Chelton, D. B., and Davis, R. E. 1982. Monthly mean sea-level variability along the West Coast of North America. Journal of Physical Oceanography, 12: 757–784.

Chiappa-Carrara, X., and Gallardo-Cabello, M. 1993. Feeding behavior and dietary composition of the northern anchovy, *Engraulis mordax* Girard (Pisces: Engraulidae), off Baja California, Mexico. Ciencias Marinas, 19: 285–305.

Ciannelli, L., Bartolino, V., and Chan, K. S. 2012. Nonadditive and nonstationary properties in the spatial distribution of a large marine fish population. Proceeding Royal Society London B, 279: 3635–3642.

Cloern, J. E., Hieb, K. A., Jacobson, T., Sanso, B., Di Lorenzo, E., Stacey, M. T., Largier, J. L. *et al.* 2010. Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific. Geophysical Research Letters, 37: L21602.

Contreras-Reyes, J. E., Canales, T. M., and Rojas, P. M. 2016. Influence of climate variability on anchovy reproductive timing off northern Chile. Journal of Marine Systems, 164: 67–75.

Crawford, R. J. M. 1987. Food and population variability in five regions supporting large stocks of anchovy, sardine, and horse mackerel. South African Journal of Marine Science, 5: 735–757.

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., Mills, J. A. *et al.* 2011. Global seabird response to forage fish depletion—one-third for the birds. Science, 334: 1703–1706.

Cury, P., Roy, C., Mendelssohn, R., Bakun, A., Husby, D. M., and Parrish, R. H. 1995. Moderate is better: exploring nonlinear climatic effects on the Californian northern anchovy *Engraulis mordax*. *In* Climate Change and Northern Fish Populations, pp. 417–424. Ed. by R. J. Beamish. Canadian Special Publication of Fisheries and Aquatic Sciences.

Davison, P. C., Sydeman, W. J., and Thayer, J. A. 2017. Are there temporal or spatial gaps in recent estimates of anchovy off California? California Cooperative Oceanic Fisheries Investigations Reports, 58: 56–68.

Di Lorenzo, E., Cobb, K. M., Furtado, J. C., Schneider, N., Anderson, B. T., Bracco, A., Alexander, M. A. *et al.* 2010. Central Pacific El Niño and decadal climate change in the North Pacific Ocean. Nature Geoscience, 3: 762–765.

Di Lorenzo, E., and Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nature Climate Change, 6: 1042–1048.

Di Lorenzo, E., Schneider, N., Cobb, K. M., Franks, P. J. S., Chhak, K., Miller, A. J., McWilliams, J. C. *et al.* 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters, 35: L08607.

Dohan, K. 2017. Ocean surface currents from satellite data. Earth and Space Science, 122: 2647–2651.

Dorval, E., Macewicz, B. J., Griffith, D. A., and Gu, Y. 2018. Spawning biomass of the central stock of northern anchovy (*Engraulis mordax*) estimated from the daily egg production method off California in 2017. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-607.

Food and Agriculture Organization of the United Nations (FAO). 2019. *FAO Yearbook*. Fishery and Aquaculture Statistics 2017. Food and Agriculture Organization of the United Nations, Rome. 108 pp.

Fiedler, P. C., Methot, R. D., and Hewitt, R. P. 1986. Effects of California El Niño 1982-1984 on the northern anchovy. Journal of Marine Research, 44: 317–338.

Fissel, B. E., Lo, N. C. H., and Herrick, S. F. Jr 2011. Daily egg production, spawning biomass and recruitment for the central subpopulation of northern anchovy 1981-2009. California

Cooperative Oceanic Fisheries Investigations Reports, 52: 116–129.

Freon, P., Bouchon, M., Mullon, C., Garcia, C., and Niquen, M. 2008. Interdecadal variability of anchoveta abundance and overcapacity of the fishery in Peru. Progress in Oceanography, 79: 401–412.

García-Reyes, M., Largier, J. L., and Sydeman, W. J. 2014. Synoptic-scale upwelling indices and predictions of phyto- and zooplankton populations. Progress in Oceanography, 120: 177–188.

Gentemann, C. L., Fewings, M. R., and García-Reyes, M. 2017. Satellite sea surface temperatures along the West Coast of the United States during the 2014-2016 northeast Pacific marine heat wave. Geophysical Research Letters, 44: 312–319.

Hart, J. L. 1973. Pacific Fishes of Canada. Fisheries Research Board of Canada, Ottawa, Canada. p. 740.

Hill, K. T., Crone, P. R., and Zwolinski, J. P. 2017. Assessment of the Pacific sardine resource in 2017 for U.S. management in 2017-18. Pacific Fishery Management Council, April 2017 Briefing Book, Agenda Item G.5.a. Portland, OR. 146 pp.

Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. *In* Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries, pp. 34–77. Ed. by R. Lasker. Washington Sea Grant Program, Seattle, WA.

Hunter, J. R., and Leong, R. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fishery Bulletin, 79: 215–230.

International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean. 2017. Annex 12: Stock assessment of albacore tuna in the North Pacific Ocean in 2017. Report of the Albacore Working Group. 103 pp.

Jacobson, L., Lo, N., and Barnes, J. 1994. A biomass-based assessment model for northern anchovy, *Engraulis mordax*. Fishery Bulletin, 92: 711–724.

Jacobson, L. D., Lo, N. C. H., Herrick, S. F. Jr, and Bishop, T. N. 1995. Spawning biomass of the Northern Anchovy in 1995 and status of the coastal pelagic fishery during 1994. 52 pp.

Jacox, M. G., Moore, A. M., Edwards, C. A., and Fiechter, J. 2014. Spatially resolved upwelling in the California Current System and its connections to climate variability. Geophysical Research Letters, 41: 3189–3196.

Jones, T., Parrish, J. K., Peterson, W. T., Bjorkstedt, E. P., Bond, N. A., Ballance, L. T., Bowes, V. *et al.* 2018. Massive mortality of a planktivorous seabird in response to a marine heatwave. Geophysical Research Letters, 45: 3193–3202.

Koehn, L. E., Essington, T. E., Marshall, K. N., Kaplan, I. C., Sydeman, W. J., Szoboszlai, A. I., and Thayer, J. A. 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current Ecosystem. Ecological Modeling, 335: 87–100.

Koehn, L. E., Essington, T. E., Marshall, K. N., Sydeman, W. J., Szoboszlai, A. I., and Thayer, J. A. 2017. Trade-offs between forage fish fisheries and their predators in the California Current. ICES Journal of Marine Science, 74: 2448–2458.

Laake, J. L., Lowry, M. S., DeLong, R. L., Melin, S. R., and Carretta, J. V. 2018. Population growth and status of California sea lions. The Journal of Wildlife Management, 82: 583–595.

Lasker, R. 1975. Field criteria for survival of anchovy larvae—relation between inshore chlorophyll maximum layers and successful 1st feeding. Fishery Bulletin, 73: 453–462.

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy *Engraulis mordax* in the California Current USA contrasting years 1975–1978. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer, 178: 375–388.

Lasker, R. 1988. Studies on the northern anchovy; biology, recruitment and fishery oceanography. Edited by the Japanese Society of Fisheries Oceanography. 23–42 pp.

Lindegren, M., Checkley, D. M. Jr, Rouyer, T., MacCall, A. D., and Stenseth, N. C. 2013. Climate, fishing, and fluctuations of sardine and anchovy in the California Current. Proceedings of the National Academy of Sciences of the United States of America, 110: 13672–13677.

Litzow, M., Ciannelli, L., Puerta, P., Wettstein, J., Rykaczewski, R. R., and Opiekun, M. 2018. Nonstationary climate-salmon relationship in the Gulf of Alaska. Proceedings of the Royal Society of London B, 285: 20181855.

MacCall, A. D. 1974. The mortality rate of *Engraulis mordax* in southern California. California Cooperative Fisheries Investigations Reports, 17: 131–135.

MacCall, A. D. 1983. Variability of pelagic fish stocks off California. FAO Fisheries Report, 291: 101–112.

MacCall, A. D. 1990. Dynamic Geography of Marine Fish Populations. University of Washington Press, Seattle, WA. 153 pp.

MacCall, A. D. 1996. Patterns of low frequency variability in fish populations of the California Current. California Cooperative Fisheries Investigations Reports, 37: 100–110.

MacCall, A. D. 2009. Mechanisms of low frequency fluctuations in sardine and anchovy populations. *In* Climate Change and Small Pelagic Fish, pp. 285–299. Ed. by D. M. Checkley, J. Alheit, Y. Oozeki, and C. Roy. Cambridge University Press, Cambridge.

MacCall, A. D., Hill, K. T., Crone, P., and Emmett, R. 2012. Weak evidence for sardine collapse. Proceedings of the National Academy of Sciences of the United States of America, 109: E1131.

MacCall, A. D., Klingbeil, R. A., and Methot, R. D. 1985. Recent increased abundance and potential productivity of Pacific mackerel (*Scomber japonicus*). California Cooperative Fisheries Investigations Reports, 26: 119–129.

MacCall, A. D., Sydeman, W. J., Davison, P. C., and Thayer, J. A. 2016. Recent collapse of northern anchovy biomass off California. Fisheries Research, 175: 87–94.

Mais, K. F. 1981. Age-composition changes in the anchovy, *Engraulis mordax*, central population. California Cooperative Oceanic Fisheries Investigations Reports, 22: 82–87.

McClatchie, S., Hendy, I., Thompson, A., and Watson, W. 2017. Collapse and recovery of forage fish populations prior to commercial exploitation. Geophysical Research Letters, 44: 1877–1885.

McClatchie, S., Vetter, R. D., and Hendy, I. L. 2018. Forage fish, small pelagic fisheries and recovering predators: managing expectations. Animal Conservation, 21: 445–447.

McGowan, J. A., Bograd, S. J., Lynn, R. J., and Miller, A. J. 2003. The biological response to the 1977 regime shift in the California Current. Deep-Sea Research Part II, 50: 2567–2582.

McHugh, J. L. 1951. Meristic variations and populations of northern anchovy (*Engraulis mordax*). Scripps Institution of Oceanography, La Jolla, CA.

McInnis, R. 1983. Anchovy management by quota. *In* Papers Presented at the Expert Consultation on the Regulation of Fishing Effort (Fishing Mortality). Rome, 17-26 January 1983. A Preparatory Meeting for the FAO World Conference on Fisheries Management and Development, FAO Fisheries Report, 289: 421–430.

Methot, R. D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. American Fisheries Society Symposium, 6: 66–82.

Miller, D. J., and Lea, R. N. 1972. Guide to the Coastal Marine Fishes of California. Fish Bulletin, 157. California Department of Fish and Game. 235 pp.

Morote, E., Olivar, M. P., Villate, F., and Uriarte, I. 2010. A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the northwest Mediterranean: influence of prey availability and ontogeny. ICES Journal of Marine Science, 67: 897–908.

National Oceanic and Atmospheric Administration (NOAA). 2019. Fisheries off West Coast states; coastal pelagic species fisheries; multi-year harvest specifications for the central subpopulation of northern anchovy. Federal Register, 84: 13585–13861. Document number 84 FR 13858.

Newman, M., Alexander, M. A., Ault, T. R., Cobb, K. M., Deser, C., Di Lorenzo, E., Mantua, N. J. *et al.* 2016. The Pacific Decadal Oscillation, revisited. Journal of Climate, 29: 4399–4427.

Oceana, Inc. v. Ross, 275 F. Supp. 3d 270 (D.D.C. 2017). No. 1: 15-cv-01220-ESH, United States District Court, District of Columbia.

Pacific Fishery Management Council (PFMC). 1978. Northern Anchovy Fishery Final Environmental Impact Statement and Fishery Management Plan.

Pacific Fishery Management Council (PFMC). 1983. Northern Anchovy Fishery Management Plan Amendment 5.

Pacific Fishery Management Council (PFMC). 1998. Amendment 8 (To the Northern Anchovy Fishery Management Plan) incorporating a name change to: The Coastal Pelagic Species Fishery Management Plan.

Pacific Fishery Management Council (PFMC). 2000. Northern Anchovy Fishery Management Plan Amendment 6.

Parrish, R. H., Mallicoate, D. L., and Klingbeil, R. A. 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fishery Bulletin, 84: 503–517.

Parrish, R. H., Mallicoate, D. L., and Mais, K. F. 1985. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. Fishery Bulletin, 83: 483–496.

Peterman, R. M., and Bradford, M. J. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science, 235: 354–356.

Radovich, J. 1982. The collapse of the California sardine fishery: what have we learned? California Cooperative Oceanic Fisheries Investigations Reports, 23: 56–78.

Ralston, S., Field, J. C., and Sakuma, K. M. 2015. Long-term variation in a central California pelagic forage assemblage. Journal of Marine Systems, 146: 26–37.

Reiss, C. S., Checkley, D. M., and Bograd, S. J. 2008. Remotely sensed spawning habitat of Pacific sardine (*Sardinops sagax*) and Northern anchovy (*Engraulis mordax*) within the California Current. Fisheries Oceanography, 17: 126–136.

Robinson, W. M. L., Butterworth, D. S., and Plaganyi, E. E. 2015. Quantifying the projected impact of the South African sardine fishery on the Robben Island penguin colony. ICES Journal of Marine Science, 72: 1822–1833.

Rykaczewski, R. R. 2019. Changes in mesozooplankton size structure along a trophic gradient in the California Current Ecosystem and implications for small pelagic fish. Marine Ecology Progress Series, 617–618: 165–182.

Rykaczewski, R. R., and Checkley, D. M. Jr 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceedings of the National Academy of Sciences of the United States of America, 105: 1965–1970.

Rykaczewski, R. R., Dunne, J. P., Sydeman, W. J., Garcia-Reyes, M., Black, B. A., and Bograd, S. J. 2015. Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21$^{st}$ century. Geophysical Research Letters, 42: 6424–6431.

Santora, J. A., Mantua, N. J., Schroeder, I. D., Field, J. C., Hazen, E. L., Bograd, S. J., Sydeman, W. J. *et al.* 2020. Marine heatwave causes habitat compression impacting forage species, crab fishery timing and whale entanglements. Nature Communications, 11: 536.

Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher, W. J. *et al.* 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science, 21: 289–347.

Schwing, F. B., Bond, N. A., Bograd, S. J., Mitchell, T., Alexander, M. A., and Mantua, N. 2006. Delayed coastal upwelling along the US West Coast in 2005: a historical perspective. Geophysical Research Letters, 33: L22S01.

Scura, E., and Jerde, C. 1977. Various species of phytoplankton as food for larval northern anchovy, *Engraulis mordax*, and relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. Fishery Bulletin, 75: 577–583.

Skrivanek, A., and Hendy, I. 2015. A 500-year climate catch: pelagic fish scales and paleoproductivity in the Santa Barbara Basin from the medieval climate anomaly to the little ice age (AD 1000-1500). Quaternary International, 387: 36–45.

Smith, P. E. 1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fishery Bulletin, 70: 849–874.

Smith, P. E. 1985. Year-class strength and survival of O-group clupeoids. Canadian Journal of Fisheries and Aquatic Sciences, 42: s69–s82.

Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H. *et al.* 2011. Impacts of fishing low-trophic level species on marine ecosystems. Science, 333: 1147–1150.

Smith, P. E., and Lasker, R. 1978. Position of larval fish in an ecosystem. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer, 173: 77–84.

Sugihara, G., May, R., Ye, H., Hsieh, C., Deyle, E., Fogarty, M., and Munch, S. 2012. Detecting causality in complex ecosystems. Science, 338: 496–500.

Sydeman, W. J., Garcia-Reyes, M., Szoboszlai, A. I., Thompson, S. A., and Thayer, J. A. 2018. Forecasting herring biomass using environmental and population parameters. Fisheries Research, 205: 141–148.

Sydeman, W. J., Santora, J. A., Thompson, S. A., Marinovic, B., and Di Lorenzo, E. 2013. Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. Global Change Biology, 19: 1662–1675.

Szeinfeld, E. V. 1991. Cannibalism and intraguild predation in clupeoids. Marine Ecology Progress Series, 79: 17–26.

Szoboszlai, A. I., Thayer, J. A., Wood, S. A., Sydeman, W. J., and Koehn, L. E. 2015. Forage species in predator diets: synthesis of data from the California Current. Ecological Informatics, 29: 45–56.

Thayer, J. A., MacCall, A. D., Davison, P. C., and Sydeman, W. J. 2017. California anchovy population remains low, 2012-2016. California Cooperative Oceanic Fisheries Investigations Reports, 58: 69–76.

Thompson, A. R., Schroeder, I. D., Bograd, S. J., Hazen, E. L., Jacox, M. G., Leising, A., Wells, B. K. *et al.* 2018. State of the California Current 2017–2018: still not quite normal in the north and getting interesting in the south. California Cooperative Oceanic Fisheries Investigations Reports, 59: 1–66.

van der Sleen, P., Rykaczewski, R. R., Turley, B. D., Sydeman, W. J., García-Reyes, M., Bograd, S. J., van der Lingen, C. D. *et al.* 2018. Non-stationary responses in anchovy (*Engraulis encrasicolus*) recruitment to coastal upwelling in the Southern Benguela. Marine Ecology Progress Series, 596: 155–164.

Vrooman, A. M., Paloma, P. A., and Zweifel, J. R. 1981. Electrophoretic, morphometric, and meristic studies of subpopulations of northern anchovy, *Engraulis mordax*. California Fish and Game, 67: 39–51.

Weber, E. D., and McClatchie, S. 2010. Predictive models of northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* spawning habitat in the California Current. Marine Ecology Progress Series, 406: 251–263.

Witherell, D., Pautzke, C., and Fluharty, D. 2000. An ecosystem-based approach for Alaska groundfish fisheries. ICES Journal of Marine Science, 57: 771–777.

Yáñez, E., Hormazabal, S., Silva, C., Montecinos, A., Barbieri, M. A., Valdenegro, A., Ordenes, A. *et al.* 2008. Coupling between the environment and the pelagic resources exploited off northern Chile: ecosystem indicators and a conceptual model. Latin American Journal of Aquatic Research, 36: 159–181.

Zwolinski, J. P., and Demer, D. A. 2012. A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. Proceedings of the National Academy of Sciences, 109: 4175–4180.

Zwolinski, J. P., Demer, D. A., Cutter, G. R., Stierhoff, K., and Macewicz, B. J. 2014. Building on fisheries acoustics for marine ecosystem surveys. Oceanography, 27: 68–79.

Zwolinski, J. P., Demer, D. A., Macewicz, B. J., Cutter G. R. Jr, Mau, S., Murfin, D., Palance, D. *et al.* 2017. Distribution, biomass and demography of the central-stock northern anchovy during summer 2016, estimated from acoustic-trawl sampling. NOAA Technical Report. NOAA-TM-NMFS-SWFSC-572. 18 pp.

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