

# Climate, fishing, and fluctuations of sardine and anchovy in the California Current

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Since the days of Elton, population cycles have challenged ecologists and resource managers. Although the underlying mechanisms remain debated, theory holds that both density-dependent and density-independent processes shape the dynamics. One striking example is the large-scale fluctuations of sardine and anchovy observed across the major upwelling areas of the world. Despite a long history of research, the causes of these fluctuations remain unresolved and heavily debated, with significant implications for fisheries management. We here model the underlying causes of these fluctuations, using the California Current Ecosystem as a case study, and show that the dynamics, accurately reproduced since A.D. 1661 onward, are explained by interacting density-dependent processes (i.e., through species-specific life-history traits) and climate forcing. Furthermore, we demonstrate how fishing modifies the dynamics and show that the sardine collapse of the 1950s was largely unavoidable given poor recruitment conditions. Our approach provides unique insight into the origin of sardine–anchovy fluctuations and a knowledge base for sustainable fisheries management in the California Current Ecosystem and beyond.

species replacement | population modeling | climate change | ecosystem-based management

Marine fish typically show multidecadal fluctuations in abundance, mainly attributed to overexploitation (1), climate (2), or a combination of both (3). Furthermore, such low-frequency variability may arise from density-dependent processes (i.e., cohort-resonance) potentially masking external or anthropogenic effects (4), whereas fishing-induced demographic changes increase short-term variability (5–7). To understand these fluctuations, it is essential to disentangle anthropogenic forcing from internal processes, as well as understanding the way they interact (7). One of the most striking examples of population fluctuations is the alternating regimes of sardine and anchovy observed across the major upwelling areas of the world (8, 9). Although ocean–atmosphere forcing is considered the main underlying driver (8–11), no generally accepted theory regarding sardine–anchovy fluctuations presently exists (12). Nevertheless, insight accumulated over a long history of research highlights that the key to understanding population cycles in general, and the sardine–anchovy puzzle in particular, lies not in identifying a single factor but a combination of interacting factors (12–14).

In the California Current Ecosystem (CCE), the Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) exhibit pronounced fluctuations, spanning several orders of magnitude in terms of biomass (15, 16). These fluctuations, occurring with a dominant periodicity of ~60 y (15, 16), have been linked to changes in the strength and position of the Aleutian Low, as reflected by the Pacific Decadal Oscillation (PDO) index (17, 18), and correlated with patterns of flow, upwelling, and physical/biotic conditions (10, 12, 19). Furthermore, fishing has been suggested to affect the dynamics [e.g., the rate of collapse of the Pacific sardine in the early 1950s (20)], whereas interspecific competition is considered unsubstantiated (12), owing to the lack of negative correlation between sardine and anchovy

in sediment records (15, 16), no significant causal association between sardine and anchovy landings (11), and marginal niche overlap in terms of habitat and prey preferences (19, 21). Without accounting for potential synergies of external and anthropogenic factors or how internal processes modify the response to climate and fishing, our understanding of sardine–anchovy fluctuations, as well as prospects for sustainable management in the face of climate change (22), are limited. To address these issues, we here investigate the underlying causes of the sardine–anchovy fluctuations in the CCE using a model setup (Fig. 1A and *SI Appendix*) consisting of age-structured population models (23, 24) based on numbers (sardine) or biomass (anchovy), environmentally sensitive stock-recruitment (S-R) models (25–27), and a climate module capable of simulating the natural (red-shifted) variability of the marine environment (28, 29).

## Results and Discussion

According to previous knowledge of recruitment dynamics (25–27), the fitted S-R models demonstrate a high degree of explained variance (77.2% and 70.9% for sardine and anchovy, respectively) (*SI Appendix*, Tables S3 and S4). In addition, a cross-validation routine (*SI Appendix*) shows high  $R^2$  values when fitted to a random subset of the data and accuracy in predicting the remaining data (*SI Appendix*, Fig. S1). Furthermore, model residuals were normally distributed and temporally uncorrelated (*SI Appendix*, Fig. S2). The functional relationships between recruitment (R) and spawning stock biomass (SSB) were represented by dome-shaped curves (*SI Appendix*, Fig. S3 A and B), illustrating density-dependent regulation due to resource competition at high stock levels (25–27). The climate effect showed a positive (curvilinear) and negative (linear) relationship (*SI Appendix*, Fig. S3 C and D), reflecting opposite responses of sardine and anchovy recruitment to sea surface temperature (SST) (8–11). In the case of sardine recruitment, the slight nonlinear relationship may represent a dome-shaped response (30), but with a downward slope at much higher temperatures than observed in the SST time-series used during model fitting. Although temperature influences key physiological processes (e.g., growth and maturation), the opposite response to SST is likely mediated by changes in thermal stratification, mixing, upwelling, or associated alterations in habitat availability and zooplankton composition (12, 19, 21). The final models recreate the long-term and interannual variability in recruitment, with the observed estimates well within the confidence intervals (*SI Appendix*, Fig. S3 E and F). As illustrated by a

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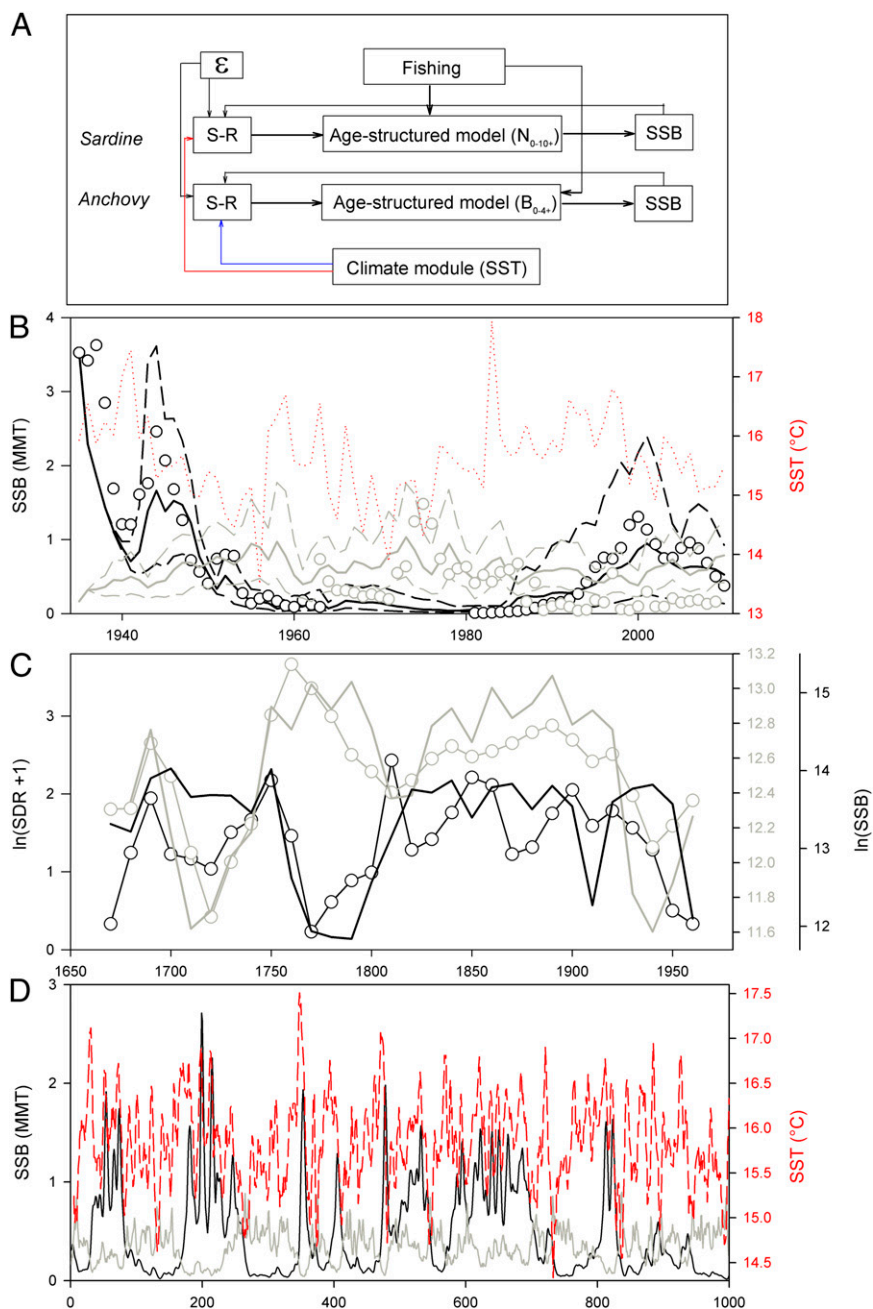
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**Fig. 1.** Model setup, validation, and simulation. (A) A schematic description of model setup, consisting of cohort models using numbers (N) or biomass (B), S-R models with resampled noise ( $\epsilon$ ), and a climate module simulating SST. (B) Model validation by hindcasting sardine (black) and anchovy (gray) SSB from 1935 onward, as well as from 1661 onward (C), compared with SDRs (circles). Correlations between estimated SSB and observed SDR:  $r = 0.52$ ,  $P = 0.004$  (sardine) and  $r = 0.85$ ,  $P < 0.001$  (anchovy). Solid and dashed lines indicate simulations with 95% confidence intervals and circles observations. (D) A single run forced by simulated SST (red; 5-y running mean).

number of validation exercises (*SI Appendix*), our model setup was able to accurately hindcast the population dynamics throughout the 20th century (Fig. 1B), including the collapse and subsequent recovery of the sardine (during the 1950s and 1980s), as well as periods covered by stock assessments (*SI Appendix*, Fig. S4). More strikingly, the model was able to recreate the sardine–anchovy fluctuations over the past  $\sim 350$  y (Fig. 1C), as inferred from fish scale deposition rates (SDRs) (15, 16), when forced by a paleo-climatic reconstruction of the PDO from A.D. 1661 onward (31) (*SI Appendix*). Furthermore, a frequency analysis comparing the Fourier spectra of simulations with observed time scales of

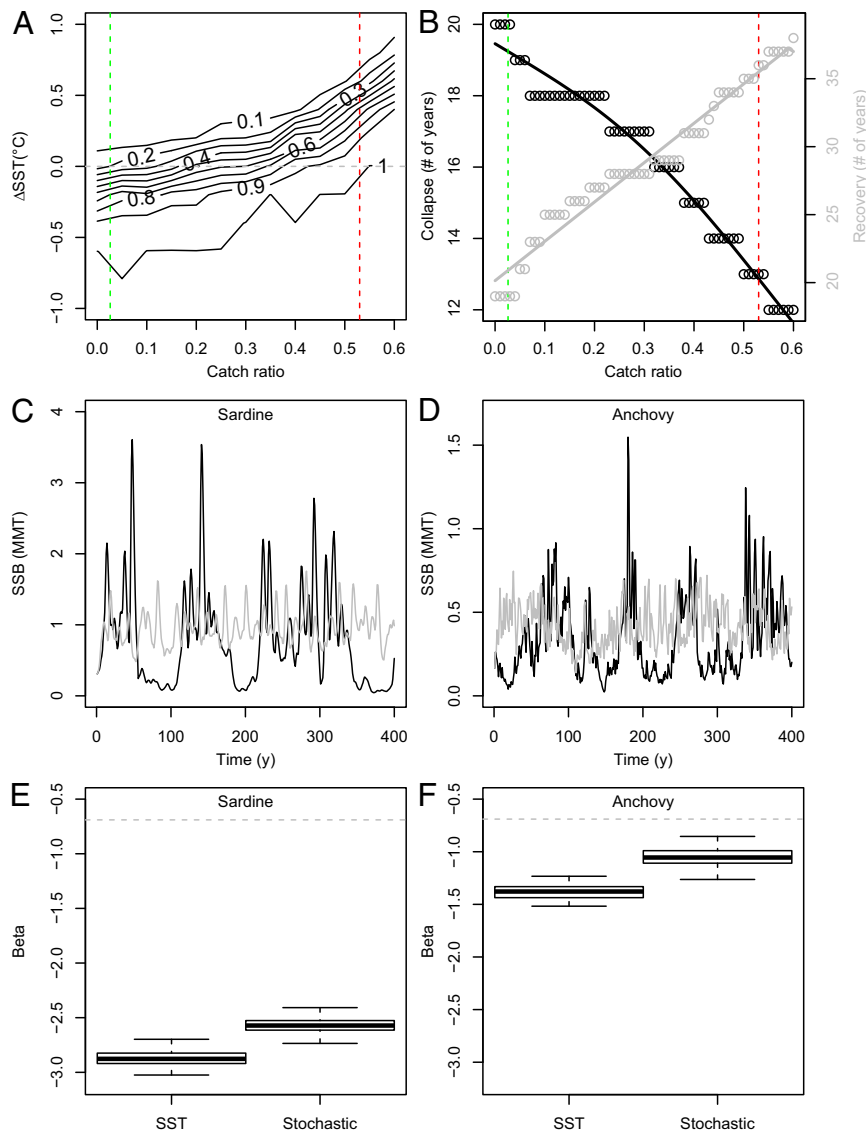
variability from SDRs (15) confirms the occurrence of 50- to 100-y cycles for both species, with dominant periodicities of  $\sim 60$  and  $\sim 80$  y for anchovy and sardine, respectively (*SI Appendix*, Fig. S5).

To examine the relative importance and potential synergy of external and internal processes on population regulation and provide insight into the ongoing debate of climate vs. fishing effects, particularly regarding the Pacific sardine (32, 33), the validated model was used to explore whether, given the present knowledge on climate forcing and density-dependent regulation, the sardine stock could in hindsight have been managed to avoid the drastic collapse in the early 1950s. We performed multiple

stochastic simulations and estimated the probability of collapse as the percentage of simulations in which SSB falls below 0.09 million metric tons (MMT) for each combination of SST (i.e.,  $\pm 1^\circ\text{C}$  of observed SST) and exploitation (i.e., annual catch ratios ranging from 0 to 60% of SSB). This threshold was based on the probability density function of sardine SSB after multiple long-term simulations without fishing (e.g., Fig. 1D) and defined as the peak of the lower mode of the bimodal distribution (SI Appendix, Fig. S6). Hence, the threshold represents the predominant minimum SSB in the absence of fishing below which the stock is considered as collapsed. The simulations were initialized at the mean SSB before the collapse (1942–1947), run for 20 y, and replicated 1,000 times for each combination of climate and fishing. Our results show that the stock collapse was largely unavoidable regardless of exploitation level, but especially given extreme catch ratios (e.g., 54% occurred before the collapse), resulting in a  $\sim 100\%$  risk of decline below the biomass limit (Fig.

24). Although lower catch ratios would not eliminate the probability of collapse (i.e.,  $\sim 20\%$  risk at zero catch), reducing exploitation would markedly affect the rate of decline (20) (i.e., delay the stock collapse and accelerate its subsequent recovery; Fig. 2B).

Note that if competition is erroneously introduced into the model [i.e., by allowing growth and juvenile mortality to depend on the SSB of the competing species (SI Appendix)], the previously proposed reduction fishery on anchovy (34) would have proved a misguided management strategy (12), not promoting sardine recovery but causing a marked decline of anchovy as well (SI Appendix, Fig. S7). Such a decline would potentially have impaired the main pathway of energy flow to higher trophic levels (e.g., tunas, marine mammals, and birds) and induced drastic changes in the structure and functioning of this wasp-waist ecosystem (35). Hence, the success of ecosystem-based management strategies (36) hinges on a thorough understanding of the complex interactions of multiple external and internal



**Fig. 2.** Climate, fishing, and density-dependent effects. (A) Probability of sardine collapse and (B) the mean number of years until collapse and subsequent recovery above 0.09 MMT for each combination of SST ( $\pm 1^\circ\text{C}$  change relative to observed SST; Fig. 1B) and catch ratios. Dashed lines show the observed SST (gray), maximum catch ratios (red) before the collapse, and mean catch ratios in the 1980s (green). Single runs of SSB and boxplots of  $\beta$  (after 1,000 runs) for sardine (C and E) and anchovy (D and F) when forced by SST (black) or by Gaussian noise alone (gray). Gray dashed lines indicate  $\beta$  of the input SST time series.

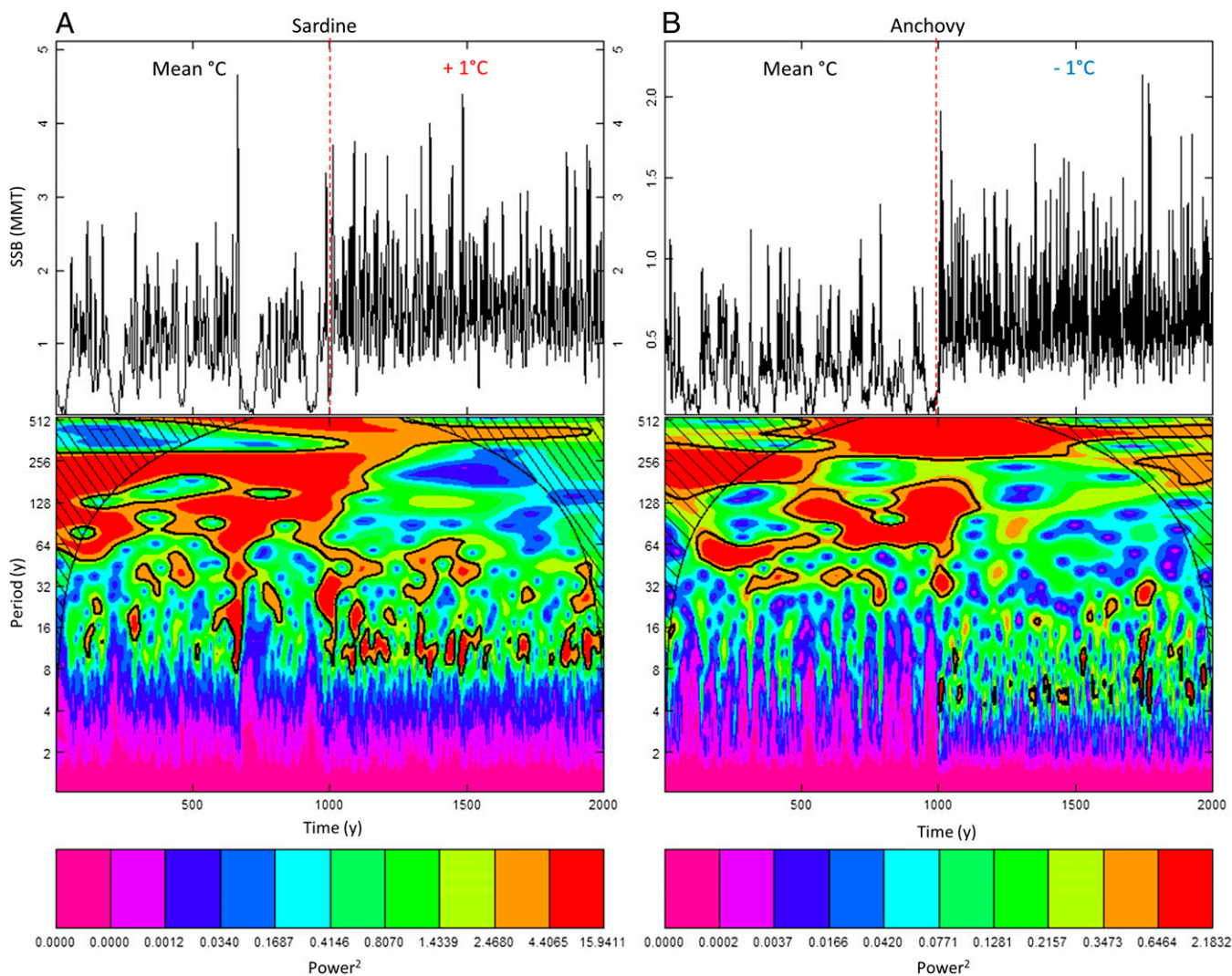


processes impacting ecosystems at large, and population dynamics in particular.

We further disentangled density-dependent and density-independent effects regulating the sardine–anchovy dynamics by performing multiple simulations forced either by climate (SST) or Gaussian noise alone (resampled from the residuals of the S-R models) and without fishing. As a measure of population variability we estimated the spectral exponent ( $\beta$ ), the slope of the power spectrum of SSB in log coordinates (7, 27), for each species and run. Our results show pronounced low-frequency variability, whether forced by red-shifted (climate) or white noise, caused by cohort-resonance of the recruitment signal (Fig. 2 C and D). The longer fluctuations of sardine (increasingly negative  $\beta$ ) compared with anchovy (Fig. 2 E and F) are due to differences in life-history traits (e.g., slower growth, later maturation, lower natural mortality; *SI Appendix*), as well as the degree of density-dependence in the S-R relationship (*SI Appendix*, Fig. S3 A and B). To visualize the effect of density-dependence, we simulated long-term population dynamics under mean and favorable SST regimes for recruitment (i.e., +1 °C for sardine and –1 °C for anchovy; Fig. 3). These simulations illustrate that during mean SST lower-frequency climate-induced variability

dominates, whereas during favorable SST conditions (and high SSB) shorter periods of ~10 and ~5 y are induced through density-dependent feedbacks, corresponding to the life span of sardine and anchovy, respectively. Note that shorter-term variability is superimposed on the longer-term cycles, not only in our simulations (e.g., Fig. 1D) but in the observed population dynamics throughout the 20th century (e.g., the high sardine SSBs during the 1930s and 2000s; Fig. 1B). This highlights how the interplay and shifting importance of different sources of variability across time scales [i.e., stochastic recruitment processes (interannual), cohort-resonance (mainly decadal), and red-shifted climate forcing (multidecadal)] combine to create the sardine–anchovy fluctuations.

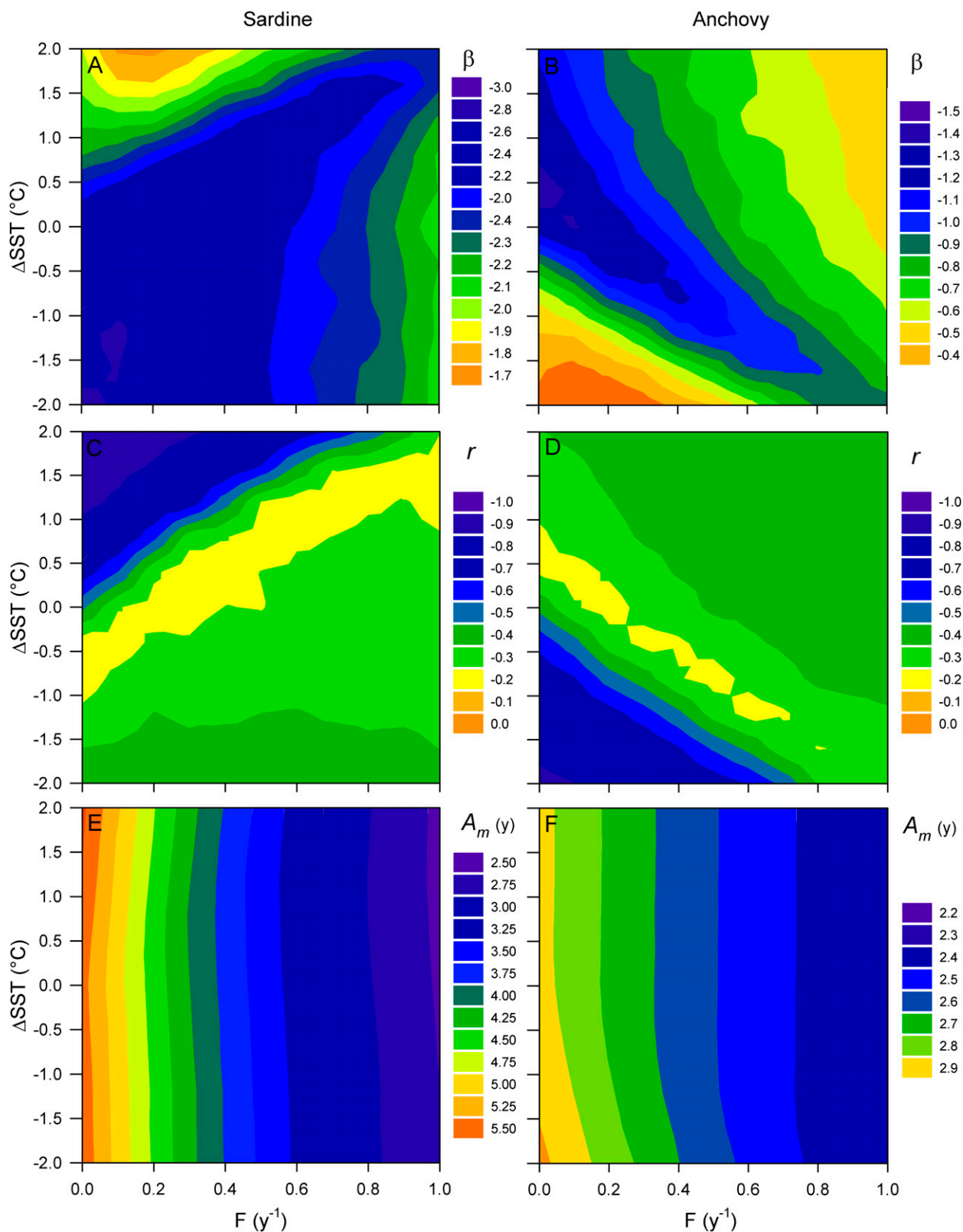
Finally, we illustrate potential management implications by investigating how synergistic effects of climate and fishing influence population variability (5–7). We estimated the mean value of  $\beta$  (from SSB) for each combination of SST (i.e.,  $\pm 2$  °C of mean SST, reflecting the range of SST) and exploitation [i.e., annual fishing mortalities (F) ranging from 0 to 1] after 1,000 stochastic runs. As a proxy for the strength of density-dependence and the degree of demographic truncation, we derived the mean correlation coefficient between SSB and productivity [i.e.,  $\ln$



**Fig. 3.** Long-term population dynamics in response to temperature changes. A wavelet plot of simulated sardine (A) and anchovy (B) dynamics forced by mean and favorable SST regimes (i.e., an increase and decrease by 1 °C for sardine and anchovy, respectively, during the last 1,000 y). Black contour lines indicate areas of significance, as well as the cone of influence (dashed) within which edge effects are present and estimated periodicities uncertain.

(R/SSB)] and the (weighted) mean age-of-spawner, respectively. We show that both climate and fishing alter the variability of

sardine and anchovy dynamics (Fig. 4 A and B), but through different internal processes. Climate primarily induce long-term



**Fig. 4.** Causes of variability. (A and B) The population variability ( $\beta$ ), (C and D) correlation ( $r$ ) between SSB and  $\ln(R/\text{SSB})$ , and (E and F) weighted mean age-of-spawner ( $A_m$ ) for sardine (Left) and anchovy (Right) in response to climate (i.e., increase and decrease in mean SST by  $2^{\circ}\text{C}$ ) and exploitation [fishing mortality ( $F$ ) from 0 to 1].

variability (e.g., Fig. 2 C and D) but may induce short-term fluctuations through increasing density-dependent feedbacks at high stock size, illustrated by increasingly negative correlation between SSB and productivity during favorable SST regimes for sardine (warm) and anchovy (cold) (Fig. 4 C and D). Fishing-induced demographic changes, illustrated by decreasing mean age-of-spawner (Fig. 4 E and F), may not only reduce the harvestable stock but induce high-frequency (stochastic) variability, generally considered as undesirable from both a management and conservation viewpoint (7, 37).

We have shown how climate variability and density-dependent processes, mediated through species-specific life-history traits, interact and give rise to the sardine–anchovy fluctuations in the CCE, and how fishing may modify the range and rate of population change. Hence, our approach provides unique insight into the synergy and underlying factors of the sardine–anchovy puzzle and a knowledge base for sustainable management of these important marine resources. We suggest that our approach, accurately reproducing the dynamics in the CCE over the past ~350 y, combined with complementary modeling (11) and meta-analytical techniques (12), could provide an appropriate framework to further unravel the origin of the apparent synchrony and teleconnections among sardine and anchovy populations worldwide (38).

## Materials and Methods

To investigate and simulate the population dynamics of Pacific sardine and northern anchovy, we developed and applied a model setup (Fig. 1A and

*SI Appendix*) consisting of (i) age-structured cohort models (23, 24) based on numbers-at-age (sardine) or biomass-at-age (anchovy); (ii) environmentally sensitive S-R models (25–27); and (iii) a  $1/f^{\beta}$  climate module (28, 29) capable of generating surrogate climate time series accurately resembling the natural (red-shifted) variability of the observed SST time series used during S-R model fitting. The population dynamic simulations were performed by estimating R (i.e., based on the S-R models) given by the values of SST and SSB. In addition, a stochastic element was included by adding Gaussian noise ( $\epsilon$ ; resampled randomly from the residuals of the S-R models) to account for unexplained sources of recruitment variability. After having accounted for intrinsic processes (i.e., growth, maturation, and natural mortality), as well as external factors (i.e., fishing mortality) in the age-structured cohort models, the forward simulation loop is reiterated by estimating R in the following year. We performed a number of validation exercises by hindcasting the population dynamics of sardine and anchovy over multiple time scales (*SI Appendix*). To assess the uncertainty of the simulations, 1,000 replications were run with Gaussian noise (i.e., resampled randomly from the residuals of the S-R models) added at each time step. Mean values and the 95% confidence interval of the hindcasted dynamics were computed. All statistical analyses were conducted using R software version 2.12.1 ([www.r-project.org](http://www.r-project.org)).

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