

Environmental variability and fishing effects on the Pacific sardine fisheries in the Gulf of California

Alfredo Giron-Nava, Exequiel Ezcurra, Antoine Brias, Enriqueta Velarde, Ethan Deyle, Andrés M. Cisneros-Montemayor, Stephan B. Munch, George Sugihara, and Octavio Aburto-Oropeza

Abstract: Small pelagic fish support some of the largest fisheries globally, yet there is an ongoing debate about the magnitude of the impacts of environmental processes and fishing activities on target species. We use a nonparametric, nonlinear approach to quantify these effects on the Pacific sardine (*Sardinops sagax*) in the Gulf of California. We show that the effect of fishing pressure and environmental variability are comparable. Furthermore, when predicting total catches, the best models account for both drivers. By using empirical dynamic programming with average environmental conditions, we calculated optimal policies to ensure long-term sustainable fisheries. The first policy, the equilibrium maximum sustainable yield, suggests that the fishery could sustain an annual catch of $\sim 2.16 \times 10^5$ tonnes. The second policy with dynamic optimal effort, reveals that the effort from 2 to 4 years ago impacts the current maximum sustainable effort. Consecutive years of high effort require a reduction to let the stock recover. Our work highlights a new framework that embraces the complex processes that drive fisheries population dynamics yet produces simple and robust advice to ensure long-term sustainable fisheries.

Résumé : Si les petits poissons pélagiques soutiennent certaines des plus importantes pêches du monde, un débat se poursuit quant à la magnitude des impacts de processus environnementaux et des activités de pêche sur des espèces visées. Nous utilisons une approche non linéaire et non paramétrique pour quantifier ces effets sur la sardine du Pacifique (*Sardinops sagax*) dans le golfe de Californie. Nous démontrons que la pression de pêche et la variabilité environnementale ont des effets comparables. En outre, pour ce qui est de prédire les prises totales, les meilleurs modèles tiennent compte de ces deux facteurs. En combinant la programmation dynamique empirique aux conditions environnementales moyennes, nous établissons les politiques optimales pour assurer la durabilité à long terme de la pêche. La première politique, concernant le rendement équilibré maximal, indique que la pêche pourrait soutenir des prises annuelles de $\sim 2,16 \times 10^5$ tonnes. La deuxième politique, qui intègre l'effort optimal dynamique, révèle que l'effort durant les deux à quatre années précédentes a une incidence sur l'effort équilibré maximal actuel. Des années consécutives d'effort élevé requièrent une réduction pour permettre au stock de se rétablir. Nos travaux mettent en lumière un nouveau cadre qui tient compte des processus complexes qui modulent la dynamique des populations de ressources halieutiques, tout en produisant des avis simples et robustes pour assurer la pérennité de ces ressources. [Traduit par la Rédaction]

Introduction

Small pelagic fish, such as sardines and anchovies, support the largest fisheries in the world, contributing up to 37% of global landings by weight (Essington et al. 2015), and are generally recognized as forage fish providing a vital source of food and trophic links within marine ecosystems (Pikitch et al. 2012). However, these stocks are subject to large fluctuations, with total landings

often varying by two orders of magnitude over just a couple of years (Lluch-belda et al. 1986; Shelton and Mangel 2011; Velarde et al. 2013). Such high variability is often attributed to known linkages among life histories (Winemiller and Rose 1992), stochastic processes, and environmental drivers, such as temperature, wind patterns, and primary productivity (Baumgartner et al. 1992; Lluch-Cota et al. 2007; Shelton and Mangel 2011). As such, there has been a strong push to incorporate environmental

Received 7 January 2020. Accepted 7 December 2020.

A. Giron-Nava. Scripps Institution of Oceanography, University of California San Diego, 9500 Gilman Dr., La Jolla, CA 92093, USA; National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, 735 State St. #300, Santa Barbara, CA 93101, USA; Future Earth, School of Global Environmental Sustainability, Colorado State University, Fort Collins, CO 80523, USA.

E. Ezcurra. The University of California Institute for Mexico and the United States (UC MEXUS), Center of Conservation Biology (CCB), Department of Botany and Plant Sciences, University of California Riverside, 900 University Avenue, Riverside, CA 92521, USA.

A. Brias and S.B. Munch. Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, CA, 95060, USA; Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA 95064, USA.

E. Velarde. Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Hidalgo 617, Col. Río Jamapa, Boca del Río, Veracruz, 94290, Mexico.

E. Deyle. Scripps Institution of Oceanography, University of California San Diego, 9500 Gilman Dr., La Jolla, CA 92093, USA; Boston University, One Silber Way, Boston, MA 02215, USA.

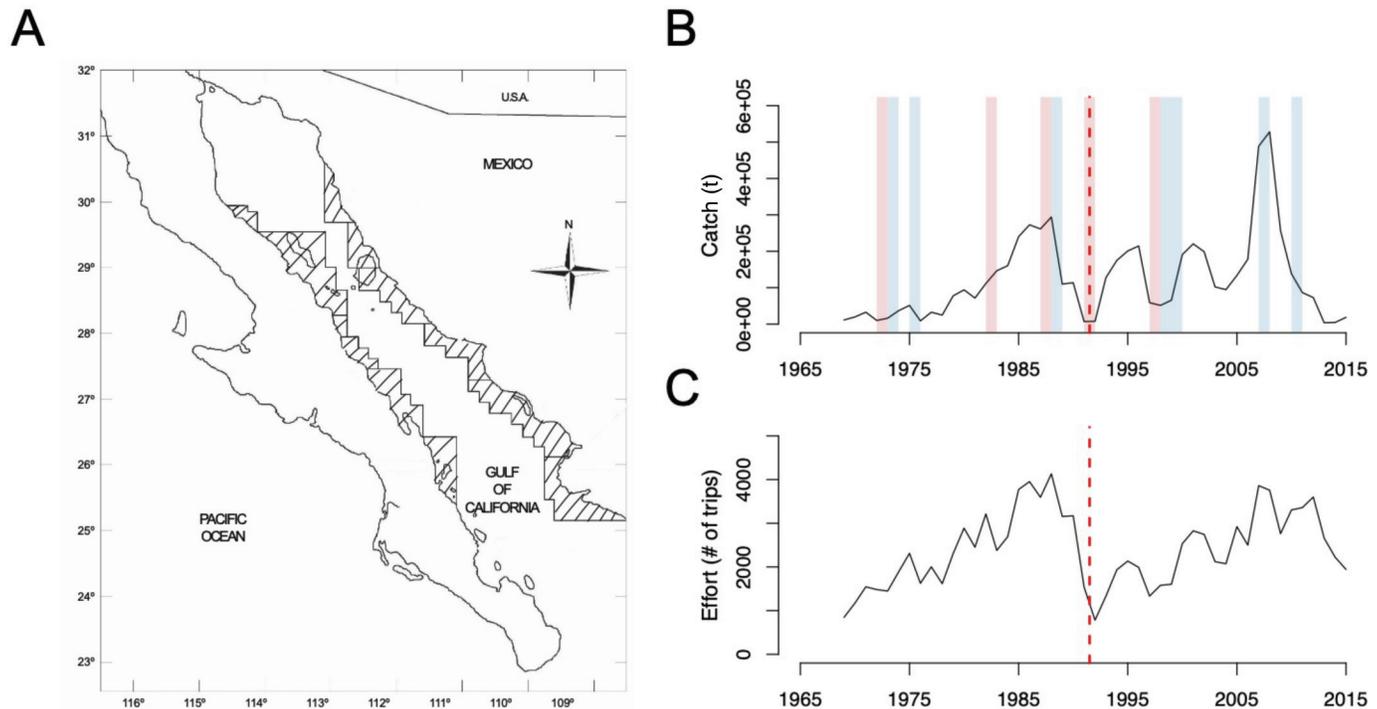
A.M. Cisneros-Montemayor. Institute for the Oceans and Fisheries, The University of British Columbia, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada.

G. Sugihara and O. Aburto-Oropeza. Scripps Institution of Oceanography, University of California San Diego, 9500 Gilman Dr., La Jolla, CA 92093, USA.

Corresponding author: Alfredo Giron-Nava (email: giron@nceas.ucsb.edu).

Copyright remains with the author(s) or their institution(s). This work is licensed under a [Creative Commons Attribution 4.0 International License](https://creativecommons.org/licenses/by/4.0/) (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

Fig. 1. (A) Map of Pacific sardine fishing zones in the Gulf of California (adapted from Lanz et al. 2008); (B) total catch in tonnes; and (C) total effort in number of trips. The shaded areas in panel B represent strong El Niño (red) and La Niña (blue) events, which are defined as five consecutive overlapping 3-month periods at or above a 1.5 °C anomaly. The red dotted lines indicate the first fishery collapse in 1991–1992. [Colour online.]



indices in models to predict recruitment and set harvest quotas (Punt et al. 2014; Szuwalski and Hilborn 2015). Additionally, there is also a strong case for the influence of fishing pressure on driving forage fish population dynamics and amplifying potential collapses triggered by poor environmental conditions (Essington et al. 2015). The debate between the impacts of environmental variability and fishing on fish population dynamics is a long-standing one, particularly for small-pelagic fisheries (Pikitch 2015).

Pacific sardine (*Sardinops sagax*) fishery in the Gulf of California, Mexico

The Gulf of California, Mexico, is one of the most productive and biodiverse marine ecoregions in the world (Lluch-Cota et al. 2007), contributing ~50% of Mexico's total fisheries landings. Small pelagic fish captured in the Gulf of California alone contribute up to 21% of the total national reported catch by weight, with Pacific sardine historically being the dominant species caught (Velarde et al. 2015a). This purse seine fishery developed in the late 1960s in the very productive waters around the city of Guaymas (Fig. 1A), which remains the largest port for sardine fisheries in Mexico (Cisneros-Mata et al. 1995). In 1991, the fishery experienced its first collapse, going from total annual landings of almost 300 000 tonnes (t) to less than 10 000 t in a period of 2 years (Cisneros-Mata et al. 1995; Velarde et al. 2013) (Fig. 1B). Since then, the fishery has undergone three more collapses with a periodicity between 3 and 8 years, showing a boom and bust dynamic behavior. Fisheries managers in the region have assumed that boom and bust cycles are primarily driven by large-scale environmental variability (Lluch-belda et al. 1986; Nevárez-Martínez et al. 2001; Velarde et al. 2004; Arreguín-Sánchez et al. 2017), particularly the Pacific Decadal Oscillation (PDO) and El Niño Southern Oscillation (ENSO) (Lluch-belda et al. 1986; Nevárez-Martínez et al. 2001; Velarde et al. 2004). As such, fishing is often assumed to have a small effect on observed population and catch dynamics. Taking a precautionary approach, it has been recommended

that to deal with the unpredictable environmental conditions and minimize the impacts of fishing, it is preferable to set a constant harvest rate (HR = 0.25–0.29) relative to the total available biomass (De Anda-Montañez et al. 2010). Still, the official regulations for this fishery are not species-specific, as the Pacific sardine is grouped with other small pelagics in the region. For this whole group, Mexican regulations establish a maximum effort of 4000–6000 trips per year, with a maximum catch of 700 000 t·year⁻¹ (CONAPESCA 2012). Unfortunately, the lack of specificity on these regulations have resulted in a lack of enforcement of a quota limit for the fleet, which historically has fished until the end of the season or until the fishery is not profitable anymore (Velarde et al. 2013). Given these dynamics, it has been reasonable to assume that the total catch per season is representative of the total abundance (Velarde et al. 2004).

Contributing to the ongoing debate on how environmental variability and fishing drive forage fish population dynamics in small-pelagic fisheries, here we use the case study of the Pacific sardine to ask the following questions: How does the effect of fishing activities compare with that of environmental variability on the population dynamics for this fishery? Also, how can we use this information to make better predictions that inform management?

To characterize and quantify the causal influence of environmental variability and fishing pressure on the population dynamics of the Pacific sardine in the Gulf of California, we use a nonparametric time series approach for detecting causation in ecological systems known as Convergent Cross Mapping (CCM; Sugihara et al. 2012), which is part of the Empirical Dynamic Modelling (EDM) framework (Sugihara 1994; Sugihara et al. 2012). Armed with this information, we then construct a model to test whether incorporating explicit estimates of fishing effects improves the predictability of fisheries yields. Finally, we build a dynamic model to estimate a harvest policy that optimizes the long-term sustainability of the fishery.

Materials and methods

Our analysis is divided into three components: (i) a multivariate linear analysis to test lagged and unlagged correlations between environmental variables and Pacific sardine catch and catch per unit effort (CPUE) as a benchmark for predictability; (ii) a nonparametric analysis using CCM and multivariate EDM to test for the causal influence of environmental variables and fishing effort on total catch and CPUE as an index of abundance; and (iii) a dynamic model to estimate a harvest policy that optimizes the long-term sustainability of the fishery.

We collected fisheries-dependent data on total catch, effort, and CPUE from the fishing fleet that operates in the Gulf of California (Fig. 1). Note that our metric of effort is the number of fishing trips per year. This metric has many limitations (e.g., does not consider the number of days per trip, searching time, or technology improvements over time); however, this currently represents the best available dataset for effort. The data span from 1969 to 2015 and were obtained from published material (Cisneros-Mata et al. 1995; Lanz et al. 2008; Velarde et al. 2015a) and updated with data extracted from the annual reports of the Centro Regional de Investigación Pesquera in Guaymas.

We also collected the annual average for environmental indices spanning the time range from 1951 to 2015. The collected variables were the El Niño Southern Oscillation Index (SOI) (NOAA 2020a), the Pacific Decadal Oscillation (PDO) index (NOAA 2020b), and an upwelling index derived from wind measurements at the mouth of the Gulf of California (21°N, 107°W), which was the closest monitoring station that had data for the whole time span (NOAA 2020c). The upwelling index was specific for the spring season, often associated with the spawning period for Pacific sardine (Alvarez et al. 2017).

Setting a predictability benchmark with a multivariate linear analysis

To create a baseline linear model (a model that assumes the explanatory variables act independently of each other), we evaluated the linear correlation and the lagged linear correlation (up to 10 lags) between the total catch and the explanatory variables (effort, SOI, PDO, and upwelling index; refer to online Supplementary Fig. S1¹). For each explanatory variable, we selected the lag with the highest predictability and used this to construct a multivariate model.

To test the predictability of this and the nonlinear dynamic models in a comparable way, we employ leave-one-out (LOO) cross-validation for all of them. Thus, for each prediction we exclude the observed single time point to be predicted and build the multivariate model with the rest of the time points. This is then repeated to generate an out-of-sample prediction for each time point. Finally, we performed a linear regression between the predicted and observed values. We report the predictability of each model in terms of the Pearson correlation coefficient (ρ).

Using nonlinear dynamics to improve predictability

We used EDM to construct a model in a way that does not assume the variables are independent of each other, but that have the potential to interact in a manner that the observations themselves dictate. EDM is a set of time series analysis methods based on the notion that a time series is the product of a nonlinear dynamic system. Thus, a time series can be thought of as a way of recording observations on the “attractor” of such a system, where the attractor is a geometric shape that arises from the underlying governing rules or dynamic equations that describe how the variables change and interact through time (see <https://youtube/fevurdpiRYg>). If the active coordinate variables are known, such attractors are easily constructed from time

series data and can be used to predict future states of the system by following the trajectories of points nearby to the point of interest in the n -dimensional space (Dixon et al. 1999; Deyle et al. 2016).

Typically, however, it is difficult to measure or even to know all the variables that interact in an ecosystem: the variables that would be required to reconstruct the original attractor. However, Takens’ theorem states that insofar as variables interact, their time series must share information about each other, and this allows one to recover information about the whole system from only one time series (Takens 1981). Assuming that the collected time series is x_t , one can reconstruct a “shadow” version of the original attractor by using lagged time series (e.g., x_{t-1} , x_{t-2}) as proxies for other unknown time series of the same system. The principles and mechanics of EDM and Takens’ theorem are further explained in a series of short animations (<http://tinyurl.com/EDM-intro>).

Within the EDM framework, a technique called CCM is used to test whether variables have a causal effect on each other: whether changes in one variable produce changes in another, possibly uncorrelated variable. CCM uses Takens’ theorem to predict values of a causal driver from the shadow attractor produced from the driven variable (Sugihara et al. 2012). Causal effect is established if one can predict the driver variable from the driven variable. For example, if the shadow attractor constructed from, for example, sardine time series can be used to postdict what the sea surface temperature (SST) was, then SST was a causal driver. Thus, CCM is able to identify directional influence. This has been demonstrated for Pacific sardine and northern anchovy (*Engraulis mordax*) in the California Current System, both being causally driven by SST, but not driving the dynamics of each other, nor driving temperature (Sugihara et al. 2012; Deyle et al. 2016). In this study, we used CCM to identify whether any of the explanatory variables (effort, SOI, PDO, or upwelling) had a causal influence on the time series of total catch, its derivative, or CPUE.

Once the relevant causal variables have been identified through CCM, it is possible to build a multivariate nonparametric model. For example, if we were to predict total catch and knew that upwelling had a strong causal influence on it, instead of reconstructing an attractor by using three time lags of total catch, we would use two and substitute the third one for the upwelling time series. Here, we first reconstruct the attractor for total catch and CPUE with an $E = 3$ (E is the embedding dimension, which represents the number of time series — number of variables, or coordinates — used to reconstruct an attractor). Then, we use different combinations of total catch, CPUE, and the explanatory time series with lags between 0 and 4 to reconstruct new attractors and predict total catch 2 years into the future.

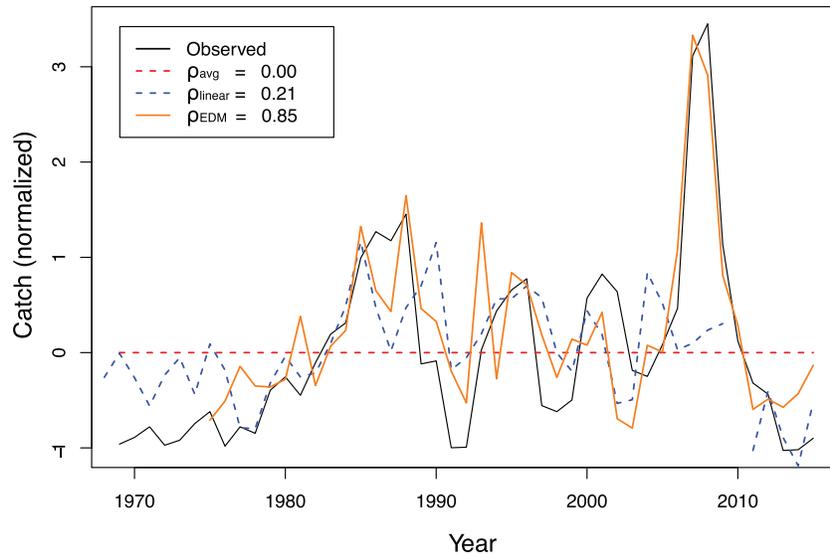
Proposing new harvest policies through empirical dynamic programming (EDP)

Next we seek to obtain harvest guidelines using empirical dynamics. Our goal is to determine the harvest policy that maximizes the long-term cumulative catch, $J = \sum_{t=1}^{\infty} \gamma^t C_t$, where C_t is the catch in year t . The term $\gamma < 1$, typically referred to as the discount rate, is merely a numerical device to ensure that the sum converges. Note that if C is constant (i.e., $C_t = C^*$ as in a traditional steady state, maximum sustainable yield (MSY) policy), then J simplifies to $C^*/(1 - \gamma)$.

A “harvest policy” consists of a rule for determining the next effort, typically as a function of the current state. However, since we are using lags to reconstruct the system dynamics with EDM, the “current” state may include several past values as well. Although modern practice typically evaluates one or more candidate policies through “management strategy evaluation” (Punt et al. 2016), the policies considered are often somewhat ad hoc.

¹Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2020-0010>.

Fig. 2. Total catch observations (black solid line) and predictions with three different models: (i) assuming the average catch is the prediction (red dashed line), (ii) using the best multivariate linear model with lags of environmental upwelling and El Niño Southern Oscillation (ENSO; blue dashed line), and (iii) using the best multivariate Empirical Dynamic Model (EDM; orange solid line). The presented predictability (ρ) was derived from leave-one-out (LOO) cross-validations. [Colour online.]



An orthodox — though still relevant — benchmark is the “optimal” policy, found using dynamic programming (Mangel and Dowling 2016) or optimal control theory (Clarke 1986).

Our algorithm uses approximate dynamic programming (Powell 2007) to determine the optimal harvest policy given an empirical dynamic model of catch and effort. This “empirical dynamic programming” (EDP; Brias and Munch 2021) approach generalizes the algorithm proposed by Boettiger et al. (2015), which did not make use of EDM and was strictly limited to one-dimensional (1D) dynamics. EDP overcomes this 1D limitation and can handle multiple species and multiple objectives in a scalable way. Details of the algorithm and extensive simulation testing are provided in Brias and Munch (in review). Here, we focus on the application of EDP to sardines.

To reconstruct the state dynamics, we modeled catch as a function of previous catch (C) and effort (F) every other year (given the 2 years reproduction age for Pacific sardine):

$$C_t = G_{GP}(C_{t-2}, C_{t-4}, C_{t-6}, F_t, F_{t-2}, F_{t-4}, F_{t-6})$$

The G_{GP} function was estimated from the observed time series using Gaussian process EDM (Munch et al. 2017) with a squared-exponential kernel and an Automatic Relevance Determination prior. This condition ensures the algorithm’s stability. To ensure stability of the EDP algorithm, we conditioned the GP to drop the catch to 0 whenever the previous effort is over the maximum encountered in the data (supposing here that an infinite effort will lead to biomass extinction). To find the optimal policy, we applied a temporal difference learning algorithm based on the estimated G_{GP} (Powell 2007). This, essentially, determines effort as a function of the current state (i.e., $F_t = H(C_{t-2}, C_{t-4}, C_{t-6}, F_{t-2}, F_{t-4}, F_{t-6})$) such that the cumulative catch J is maximized when the dynamics evolve according to the estimated G_{GP} . To complement this dynamic control policy, we also estimated the optimal steady-state policy, (i.e., the F that maximizes C subject to the dynamical constraint $C = G_{GP}(C, C, C, F, F, F, F)$). Note that this is precisely analogous to finding MSY, albeit with a nonparametric production model.

To evaluate the expected performance of the EDP policy, we run the following simulations: (i) apply the near-optimal policy given by the EDP algorithm (suggesting a different fishing effort per year), (ii) apply a “reactive policy” to simulate current

conditions (fishers increasing total effort when catch is low and reduce effort when total catch goes below the historical minimum), and (iii) constant effort (using the value that gives the maximum sustainable catch computed by the EDP over 100 years). For each policy, this consists of three steps:

1. Use the focal policy to determine effort
2. Predict the catch using the GP
3. Update the state and repeat

We start all the simulations from a system that has just collapsed (we use the values of catches and efforts of 1993 as initial conditions) and report the average results for 100 runs. Note that since this approach marginalizes over environmental variation (i.e., any environmental dependence of catch is treated as noise), the resulting policies are for the average environment. Optimal control for explicitly time-varying environmental conditions are more challenging to estimate and are in development.

Results

The status quo: multivariate linear regression

We found a significant correlation between each of the explanatory variables and total catch, although for most of them, it was only after taking into account time lags (Supplementary Fig. S1¹). We found that fishing effort was correlated with total catch at 0, 1, and marginally at 2 time steps. The SOI was only negatively correlated at 4 time steps, while the PDO was positively correlated at 2, 3, and 4 time steps. Finally, the upwelling index was positively correlated from 4 through 10 time steps. Given the very high correlation between catch and effort at no time lag, we only used the largest possible and still significant time lag (2) for subsequent analyses in an attempt to decouple the immediate effects of fishing harder to catch more. For the rest of the variables, we used the smallest significant lag. Thus, the selected time lags were 2, 4, 2, and 4 for effort, SOI, PDO, and upwelling, respectively. By using these time lags, the best multiple linear regression model selected upwelling and the SOI as the two variables that together could explain the most observed variability in total catch. The achieved R^2 was equal to 0.28, while the LOO cross-validation predictability was equal to 0.21 (Fig. 2).

Fig. 3. Convergent cross-mapping (CCM) among the three analyzed fishery variables (catch, Δ catch, and catch per unit effort (CPUE)) against the four explanatory variables (fishing effort, Southern Oscillation Index (SOI), Pacific Decadal Oscillation (PDO), and upwelling index). The red lines indicate a causal influence from the explanatory variable to the fishery. The black lines indicate a causal influence from the fishery variables to the explanatory variables. Only significant ($\alpha = 0.05$) results are shown. [Colour online.]

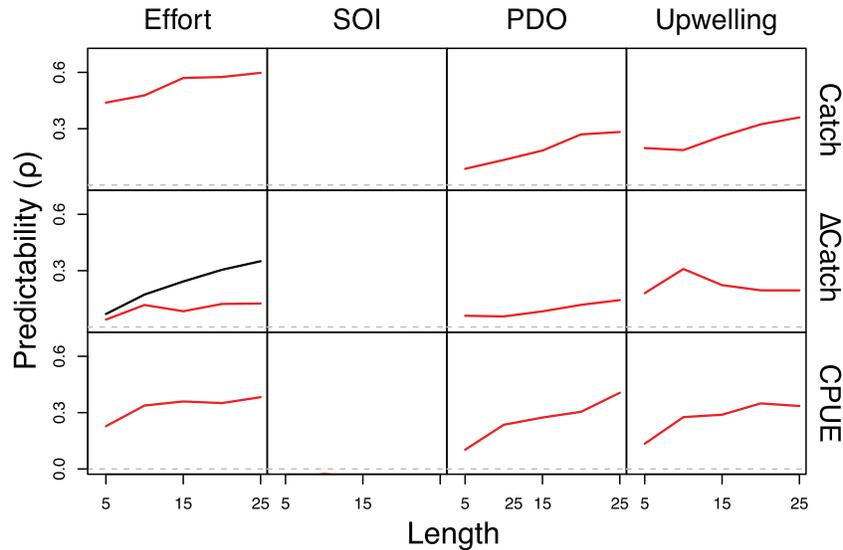


Table 1. Top five nonlinear empirical models to predict total catch 2 years into the future.

Model	Var1	Var2	Var3	ρ
C2P1E4	Catch lag 2	PDO lag 1	Effort lag 4	0.85
U1U4E4	Upw lag 1	Upw lag 4	Effort lag 4	0.83
E2U4E4	Effort lag 2	Upw lag 4	Effort lag 4	0.83
C2U4U1	Catch lag 2	Upw lag 4	Upw lag 1	0.82
S1U4U1	SOI lag 1	Upw lag 4	Upw lag 1	0.81
Univariate	Catch lag 0	Catch lag 1	Catch lag 2	0.51

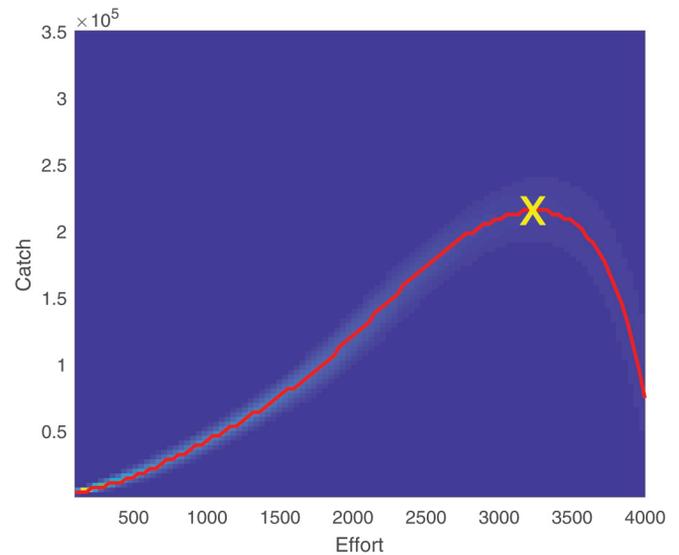
Note: For each model, the indicated explanatory variables substitute one time series of lagged total catch to build a new manifold. All models were done with an $E = 3$, as this was the identified embedding dimension to predict total catch. Models are sorted from more explanatory to less explanatory power. The univariate model refers to using only the total catch time series and lags of it to build the attractor.

Improved predictability through EDM

We performed a CCM analysis to detect whether the explanatory variables (effort and environmental variability) had a causal influence on catch, Δ catch, and CPUE (Fig. 3). We found a strong effect of effort on total catch and CPUE, as well as a strong effect of Δ catch in current effort. This means that the comparison between this year’s and last year’s catch influences effort, as fishers will try to make as much or more profit as last year, also known as displaying a “reactive” behavior (maximize today’s rent without considering the future). The SOI showed no causal effect on any of the fishery variables. The PDO and the upwelling index showed a weak causal influence on Δ catch and a stronger influence on total catch and CPUE, comparable to the effect of fishing effort.

By using the identified variables that are causally coupled to total catch, we built a univariate model (using the catch time series and lags of it) and multivariate nonlinear predictive models to predict total catch 2 years into the future. We found that the univariate model achieved a predictability equal to 0.51, with mean absolute error equal to 0.69 (Table 1). However, when incorporating the explanatory variables at different time lags, the best five models ranged in predictability between 0.81 and 0.85. The best model ($\rho = 0.85$, mean absolute error = 0.45) used total catch

Fig. 4. Probability that catch is at equilibrium conditional on effort held constant, according to the Gaussian process used for the Empirical Dynamics Programming. The red line is the most likely steady state for a given level of effort. The maximum sustainable effort and catch are indicated by the yellow cross. [Colour online.]

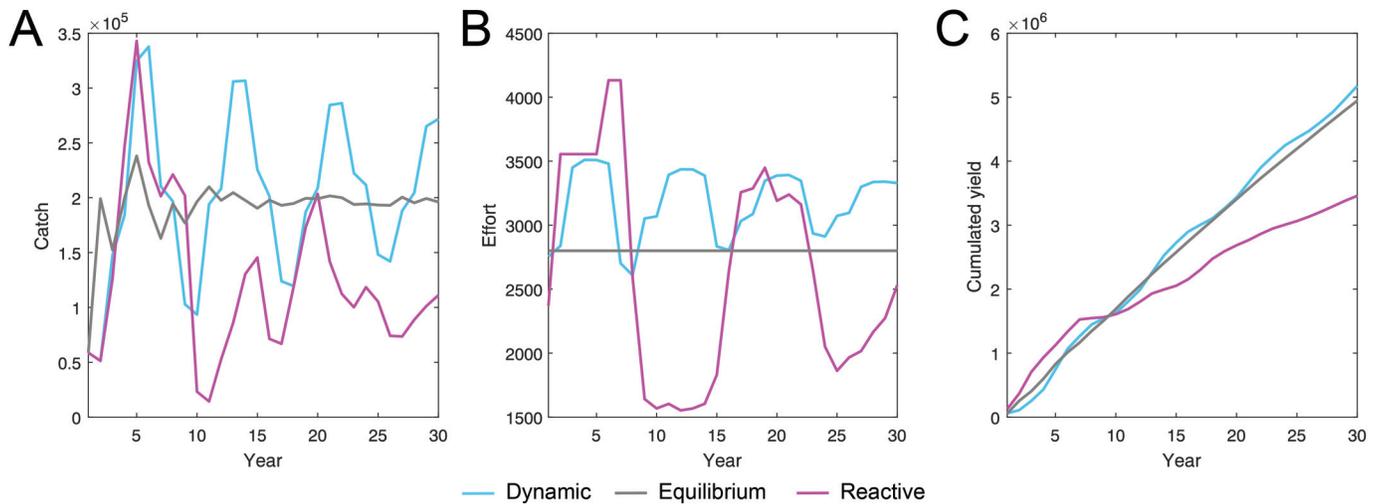


with a lag of 2 years, the PDO with a lag of 1 year, and effort with a lag of 4 years. The rest of the top five models used also the SOI and upwelling index (Table 1). In particular, the fifth best model did not use effort or catch data, highlighting the relevance of environmental variability, but which could be improved with fishery-dependent data.

Harvest policies through EDP

The GP was fit using 3 lags of catch and 4 lags of effort, assuming average environmental conditions, resulting in in-sample predictability of $\rho = 0.83$ and out of sample predictability

Fig. 5. Simulation of (A) total annual catch, (B) effort, and (C) cumulative yield over time starting from the 1993 situation (average of 100 runs). The blue policy is given by the Empirical Dynamics Programming (EDP) algorithm. (C) Cumulative yield over time is given by $\sum_{t=1}^T \gamma^t C_t$, from year 1 to the current year T . The grey policy (horizontal line in panel B) maintains the effort giving the maximum CPUE ($E_t = 2700$). The magenta policy is the reactive policy (fishers increasing total effort when catch is low, decreasing to the minimum encountered in the data if the annual yield is negative). [Colour online.]



(starting from year 25) of $\rho = 0.78$. The reactive behavior scenario showed a maximum catch equal to 3.5×10^5 t in year 5 of the simulation; however, as catch decreased and effort increased, the fishery collapsed after year 10. In contrast, both the equilibrium maximum sustainable effort and the EDP policy resulted in a similar long-term sustainable catch (Fig. 4, Fig. 5C). The average catch for the equilibrium maximum sustainable effort was approximately equal to 2.16×10^5 t·year⁻¹, while the EDP policy resulted in an oscillating behavior with maximum total annual catch equal to 3.42×10^5 t·year⁻¹ and a minimum equal to 0.71×10^5 t·year⁻¹ (Fig. 5A).

Discussion

This manuscript contributes to resolving a long-standing question in the fisheries management of small pelagics: How do the effects of fishing effort compare with those of environmental variability in driving the population dynamics? And how can including this information into predictive models help to inform fisheries management?

Identifying and quantifying causal relationships

As in previous reports, our findings show that environmental variability has a detectable effect on the Pacific sardine's population dynamics in the Gulf of California (Cisneros-Mata et al. 1995; Nevárez-Martínez et al. 2001; Petatán-Ramírez et al. 2019). In previous work, however, most of the temporal variability in the population has been primarily associated with long-term environmental phenomena that change SST and primary productivity distributions (Petatán-Ramírez et al. 2019), such as El Niño (Nevárez-Martínez et al. 2001; Velarde et al. 2004). Even though it is possible to appreciate some degree of correlation between the fishery collapses and El Niño events in 1987–1988, 1991–1992, and 1997–1998 (Fig. 1B), it is also clear that for the following two collapses, that was not the case. Instead, it has been suggested that in the last decade, the Gulf of California SST anomalies have decoupled from El Niño events, with as many as five warm decoupled anomalies that occurred between 2007 and 2016 (Velarde et al. 2015b). Unfortunately, the mechanisms by which El Niño affects the oceanographic local conditions in the Gulf of California are still poorly understood (Herrera-Cervantes et al. 2007). Recent research suggests that while the southern Gulf might be generally forced by the

Eastern Tropical Pacific and possibly by El Niño, the region closer to Guaymas, and thus to the sardine's spawning grounds, is forced primarily by tidal mixing in the Midriff Islands region (Lluch-Cota et al. 2007; Herrera-Cervantes et al. 2007). Although there is some evidence for the effects of El Niño on SST (Frawley et al. 2019), a demonstration of its effects on primary productivity in the Central Gulf of California has proven more difficult (Santamaria-del-Angel et al. 1994; Kahru et al. 2004; Lluch-Cota et al. 2007).

Our results also show that the effect of fisheries on the sardine stock is comparable to that of environmental variability. Through CCM, we identified that fishing activities have a causal influence in total catch, Δ catch, and CPUE (Fig. 3). We also found that Δ catch influences the amount of effort in the current season. This supports the idea that fishers in the region follow a behavior that prioritizes the value of the fishery today and does not consider future scenarios. More broadly and contributing to the ongoing debate on how environmental variability and fishing behavior drive the population dynamics of fisheries species around the world, our results using CCM are a step forward in identifying and quantifying causal relationships within these variables.

Improving predictability

Based on the premise of unpredictability and a conservative approach (Martínez-Aguilar et al. 2009), current management strategies for the Pacific sardine fishery have set a constant harvest quota, which implicitly estimates that the prediction each year should be equal to the mean total catch. Such an assumption, unfortunately, leads to no real predictability (Fig. 2). Some authors have suggested that there is a linear correlation between environmental variability and total landings (Nevárez-Martínez et al. 2001). To test this hypothesis, we used the most optimized version of a multivariate linear model and estimated its predictability, which was $\rho = 0.21$ (Fig. 2). Even though this prediction has some power, thus indicating the importance of environmental variability, it is still far from reliable to establish a dynamic management scheme (Martínez-Aguilar et al. 2009). Using EDM, we demonstrated that incorporating fishing effort and environmental variability into a dynamic model can yield predictions of total catch with $\rho = 0.85$ (Table 1; Fig. 2).

Furthermore, when analyzing the residuals for all the models (Supplementary Fig. S2¹), we observe that EDM was the only

approach able to capture the boom and boost dynamics before they happened (2 years ahead) within 1 standard deviation throughout the whole time period. This was possible due to the ability of EDM to capture the complex dynamics of the system, and as such, the signal of the boom and boost cycles was present in the fishery and environmental indices a couple of years before they happened. Our approach demonstrates that not only it is necessary to identify and use the proper explanatory variables, but also to use a modelling scheme that does not rely on predefined assumptions (e.g., functional approximations), expectations of stability or equilibrium, or simply autoregressive schemes (Ward and Staunton-Smith 2002; Ives et al. 2003; Giron-Nava et al. 2020) to make predictions about future states of the system. We propose that the use of EDM in a fisheries context could help navigate complex management scenarios where predicting future states is of crucial importance given changing environmental conditions. This echoes the results of a recent global meta-analysis demonstrating that EDM outperformed linear autoregressive models in predicting recruitment for 185 fish stocks (Munch et al. 2018), showing the advantages of an equation-free approach when working in highly dynamic and complex systems.

Towards dynamic management

Assuming that catch and effort data are the only data available for most fisheries, we calculated optimal policies to ensure a long-term sustainable fishery using only these two variables. The first policy, the equilibrium maximum sustainable yield, suggests that if managed effectively, the fishery could sustain a catch of $\sim 2.16 \times 10^5$ t·year⁻¹ (under average environmental conditions). The second policy, the EDP policy with dynamic optimal effort, reveals that the effort from 2 and 4 years in the past can impact the current effort required to keep the system's sustainability. Consecutive years of high fishing effort require a reduction in the current catch to let the stock recover (Supplementary Fig. S6¹). Even though this policy is adjusted every year, in the long run, the total catch after 100 years is almost equal to that from the equilibrium maximum effort (Fig. 5C). Our simulations also show that when the catches are low, policies that prioritize current over long-term value (e.g., reactive behavior) should be avoided to allow for the system's recovery (Fig. 5A). If the current value prioritization behavior is exaggerated, as in the simulations, it highlights that current practices can generate higher catches than the optimal policies in the short term but lead the ecosystem to a rapid collapse and the observed boom and boost dynamic behavior. In terms of developing a real-world policy, it might be more feasible to consider the equilibrium maximum sustainable yield, as it is simpler and in the long term yields nearly the same catch as the more complex and adaptive dynamic policy.

In this work, the GP model and resulting EDP policy are functions only of catch, effort, and their time lags. As such, this treats environment-dependent variation in catch as noise and effectively averages over environmental conditions throughout the time period. This presents obvious limitations in that it cannot account for extremely low or high primary productivity scenarios and the potential impacts on fish populations. However, as we demonstrated with CCM and the nonlinear multivariate model, fishing effort has a strong causal influence on the population dynamics. Therefore, by taking a precautionary approach during low productivity scenarios (and 2 subsequent years), managers might be able to prevent a fishery-driven collapse. Incorporating explicit estimates of environmental variability and extreme scenarios into the EDP framework is a work currently in progress. If successfully implemented, dynamic policies that consider external drivers, such as environmental variability, might be able to generate cumulative larger catches than the equilibrium policy over the long term. However, the success of this approach will depend critically on the accuracy of available environmental forecasts.

When thinking about the trade-offs among sustainability, human livelihoods, and the inherent complexities of fisheries management, we must recognize that a fisheries policy should be as robust and simple as possible. By using the Pacific sardine fishery in the Gulf of California as an example of a highly variable and difficult to manage small-pelagic fishery, we have shown that estimating an equilibrium sustainable effort could represent an upper limit for both the effort and catch. However, for these policies to be effective, they should be sensitive to other external drivers, such as market pressures, extreme environmental events, and the importance of these resources as key components of the ecosystem to link primary productivity to upper trophic levels. Our work thus offers an insight into a new framework for fisheries management based on embracing the complex processes that drive population dynamics yet producing relatively simple and robust policies. In particular, this work was able to move forward the discussion of the comparative effects of environmental variability and fishing effort on the population dynamics of small-pelagic fisheries (in this case the Pacific sardine in the Gulf of California), demonstrating that both have an effect, with fishing effort being dominant when predicting the fishery up to 2 years ahead. This finding was only possible due to the application of new analytical tools that embrace the complexity of the system and use it to detect causal relationships between the observed variables (Sugihara et al. 2012), thus making of this paper primarily a methodological contribution to fisheries science. The next question is how to use this information to refine the models that account for these coupled effects and to inform policies that ensure the long-term sustainable exploitation of these resources that sustain both important fisheries and are a central part of the ecosystem.

Acknowledgements

This work was supported by the Walton Family Foundation, the Sugihara Family Trust, the Deutsche Bank–Jameson Complexity Studies Fund, the McQuown Fund, and the McQuown Chair in Natural Sciences, University of California, San Diego. AGN was funded by Consejo Nacional de Ciencia y Tecnología (CONACYT; CVU 579904) and Fulbright Garcia-Robles (LASPAA ID 20140963) doctoral program fellowships. ACM was supported by the Nippon foundation Nereus Program. AB was supported with a grant from the Lenfest Oceans Program to SBM. GS and ED were supported by DoD-Strategic Environmental Research and Development Program 15 RC-2509, NSF DEB-1655203, NSF ABI-1667584, DOI USDI-NPS, and P20AC00527. Thanks to Anastasia Quintana and Chris Free for comments on an early version of this manuscript. The authors declare no conflicts of interest.

References

- Alvarez, C., Andracka, S., Anhalzer, G., and Morgan, S. 2017. Small pelagics fishery in Sonora, Gulf of California. SCS Global Services, Emeryville, Calif.
- Arreguín-Sánchez, F., del Monte-Luna, P., Zetina-Rejón, M.J., and Albañez-Lucero, M.O. 2017. The Gulf of California large marine ecosystem: Fisheries and other natural resources. *Environ. Dev.* 22: 71–77. doi:10.1016/j.envdev.2017.03.002.
- 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. *CalCOFI Rep.* 33(January): 24–40. doi:10.1016/S0001-4575(97)00105-X.
- Boettiger, C., Mangel, M., and Munch, S. 2015. Avoiding tipping points in fisheries management through Gaussian process dynamic programming. *Proc. R. Soc. B.* 282(1801): 8–11. doi:10.1098/rspb.2014.1631. PMID:25567644.
- Brias, A., and Munch, S.B. 2021. Ecosystem based multi-species management using Empirical Dynamic Programming. *Ecol. Modell.* 441: 109423. doi:10.1016/j.ecolmodel.2020.109423.
- Cisneros-Mata, M.A., Nevárez-Martínez, M.O., and Hammann, M.G. 1995. The rise and fall of the Pacific sardine, *Sardinops sagax caeruleus* Girard, in the Gulf of California, Mexico. *Calif. Coop. Ocean. Fish. Investig. Rep.* 36(August 2016): 136–143. Available from http://www.calcofi.org/publications/calcofiereports/v36/Vol_36_Cisneros_etal.pdf.
- Clarke, F. 1986. Perturbed optimal control problems. *IEEE Trans. Automat. Contr.* 31(6): 535–542. doi:10.1109/TAC.1986.1104318.

- CONAPESCA. 2012. Carta Nacional Pesquera 2012. In Diario Oficial. Instituto Nacional de Pesca. Available from <https://www.gob.mx/inapesca/documentos/carta-nacional-pesquera-2012>.
- De Anda-Montañez, J.A., Ramos-Rodríguez, A., and Martínez-Aguilar, S. 2010. Effects of environmental variability on recruitment and bioeconomic modelling in the Pacific sardine (*Sardinops sagax caerulea*) fishery from Magdalena Bay, Baja California Sur, Mexico. *Sci. Mar.* **74**(March): 25–35. doi:10.3989/scimar.2010.74n1025.
- Deyle, E.R., May, R.M., Munch, S.B., and Sugihara, G. 2016. Tracking and forecasting ecosystem interactions in real time. *Proc. R. Soc. B Biol. Sci.* **283**(1822): 20152258. doi:10.1098/rspb.2015.2258. PMID:26763700.
- Dixon, P., Milicich, M., and Sugihara, G. 1999. Episodic fluctuations in larval supply. *Science*, **283**: 1528–1530. doi:10.1126/science.283.5407.1528. PMID:10066174.
- Essington, T.E., Moriarty, P.E., Froehlich, H.E., Hodgson, E.E., Koehn, L.E., Oken, K.L., et al. 2015. Fishing amplifies forage fish population collapses. *Proc. Natl. Acad. Sci.* **112**(21): 6648–6652. doi:10.1073/pnas.1422020112. PMID:25848018.
- Frawley, T.H., Briscoe, D.K., Daniel, P.C., Britten, G.L., Crowder, L.B., Robinson, C.J., and Gilly, W.F. 2019. Impacts of a shift to a warm-water regime in the Gulf of California on jumbo squid (*Dosidicus gigas*). *ICES J. Mar. Sci.* doi:10.1093/icesjms/fsz133.
- Giron-Nava, A., Munch, S.B., Johnson, A.F., Deyle, E., James, C.C., Saberski, E., et al. 2020. Circularity in fisheries data weakens real world prediction. *Sci. Rep.* **10**(1): 6977. doi:10.1038/s41598-020-63773-3. PMID:32332835.
- Herrera-Cervantes, H., Lluch-Cota, D.B., Lluch-Cota, S.E., and Gutiérrez-de-Velasco, S.G. 2007. The ENSO signature in sea-surface temperature in the Gulf of California. *J. Mar. Res.* **65**(5): 589–605. doi:10.1357/002224007783649529.
- Ives, A.R., Dennis, B., Cottingham, K.L., and Carpenter, S.R. 2003. Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.* **73**(2): 301–330. doi:10.1890/0012-9615(2003)073[0301:ECSAEI]2.0.CO;2.
- Kahru, M., Marinone, S.G., Lluch-Cota, S.E., Parés-Sierra, A., and Greg Mitchell, B. 2004. Ocean-color variability in the Gulf of California: scales from days to ENSO. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **51**(1–3): 139–146. doi:10.1016/j.dsr2.2003.04.001.
- Lanz, E., Nevárez-Martínez, M.O., López-Martínez, J., and Dworak, J.A. 2008. Spatial distribution and species composition of small pelagic fishes in the Gulf of California. *Rev. Biol. Trop.* **56**(2): 575–590. doi:10.15517/rbt.v56i2.5609. PMID:19256429.
- Lluch-Belda, D., Magallon, F.J., and Schwartzlose, R. 1986. Large fluctuations in the sardine fishery in the Gulf of California: Possible Causes. *Cal-COFI Reports XXVII*: 136–140.
- Lluch-Cota, S.E., Aragón-Noriega, E.A., Arreguín-Sánchez, F., Auriolos-Gamboa, D., Jesús Bautista-Romero, J., Brusca, R.C., et al. 2007. The Gulf of California: Review of ecosystem status and sustainability challenges. *Prog. Oceanogr.* **73**(1): 1–26. doi:10.1016/j.poccean.2007.01.013.
- Mangel, M., and Dowling, N.A. 2016. Reference points for optimal yield: a framework for assessing economic, conservation, and sociocultural tradeoffs in ecosystem-based fishery management. *Coast. Manag.* **44**(5): 517–528. doi:10.1080/08920753.2016.1208884.
- Martínez-Aguilar, S., de Anda-Montañez, J.A., Arreguín-Sánchez, F., and Cisneros-Mata, M.A. 2009. Constant harvest rate for the Pacific sardine (*Sardinops caeruleus*) fishery in the Gulf of California based on catchability-at-length estimations. *Fish. Res.* **99**(2): 74–82. doi:10.1016/j.fishres.2009.05.002.
- Munch, S.B., Poynor, V., and Arriaza, J.L. 2017. Circumventing structural uncertainty: a Bayesian perspective on nonlinear forecasting for ecology. *Ecol. Complex.* **32**: 134–143. doi:10.1016/j.ecocom.2016.08.006.
- Munch, S.B., Giron-Nava, A., and Sugihara, G. 2018. Nonlinear dynamics and noise in fisheries recruitment: a global meta-analysis. *Fish. Fish.* **19**: 964–973. doi:10.1111/faf.12304.
- Nevárez-Martínez, M.O., Lluch-Belda, D., Cisneros-Mata, M.A., Pablo Santos-Molina, J., De los, A., Martínez-Zavala, M., and Lluch-Cota, S.E. 2001. Distribution and abundance of the Pacific sardine (*Sardinops sagax*) in the Gulf of California and their relation with the environment. *Prog. Oceanogr.* **49**(1–4): 565–580. doi:10.1016/S0079-6611(01)00041-6.
- NOAA. 2020a. Southern Oscillation Index (SOI). Available from <https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/>.
- NOAA. 2020b. Pacific Decadal Oscillation (PDO). Available from <https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/ca-pdo.cfm>.
- NOAA. 2020c. North Pacific Upwelling Indices. Available from <https://www.pfel.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html>.
- Petataín-Ramírez, D., Ojeda-Ruiz, M.A., Sánchez-Velasco, L., Rivas, D., Reyes-Bonilla, H., Cruz-Piñón, G., et al. 2019. Potential changes in the distribution of suitable habitat for Pacific sardine (*Sardinops sagax*) under climate change scenarios. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **169–170**: 104632. doi:10.1016/j.dsr2.2019.07.020.
- Pikitch, E.K. 2015. Stop-loss order for forage fish fisheries. *Proc. Natl. Acad. Sci.* **112**(21): 6529–6530. doi:10.1073/pnas.1505403112.
- Pikitch, E., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Essington, T., et al. 2012. Little fish, big impact: managing a crucial link in ocean food webs. In *Lenfest Ocean Peofem*. Washington, D.C. Available from <https://publications.csiro.au/rpr/pub?list=BRO&pid=csiro:EP124359&sb=RECENT&n=10&rpp=10&page=292&tr=4231&dr=all&dc4.browseYear=2012>.
- Powell, W.B. 2007. Approximate dynamic programming. Solving the cruises of dimensionality. New York.
- Punt, A.E., A'mar, T., Bond, N.A., Butterworth, D.S., de Moor, C.L., De Oliveira, J.A.A., et al. 2014. Fisheries management under climate and environmental uncertainty: control rules and performance simulation. *ICES J. Mar. Sci.* **71**(8): 2208–2220. doi:10.1093/icesjms/fst057.
- Punt, A.E., Butterworth, D.S., de Moor, C.L., De Oliveira, J.A.A., and Haddon, M. 2016. Management strategy evaluation: best practices. *Fish. Fish.* **17**(2): 303–334. doi:10.1111/faf.12104.
- Santamaria-del-Angel, E., Alvarez-Borrego, S., and Müller-Karger, F. 1994. The 1982–1984 El Niño in the Gulf of California as seen in coastal zone color scanner imagery. *J. Geophys. Res.* **99**(C4): 7423–7431. doi:10.1029/93JC02147.
- Shelton, A.O., and Mangel, M. 2011. Fluctuations of fish populations and the magnifying effects of fishing. *Proc. Natl. Acad. Sci.* **108**(17): 7075–7080. doi:10.1073/pnas.1100334108. PMID:21482785.
- Sugihara, G. 1994. Nonlinear forecasting for the classification of natural time series. doi:10.1098/rsta.1994.0106.
- Sugihara, G., May, R., Ye, H., Hsieh, C., Deyle, E., Fogarty, M., and Munch, S. 2012. Detecting causality in complex ecosystems. *Science*, **338**(6106): 496–500. doi:10.1126/science.1227079. PMID:22997134.
- Szuwalski, C.S., and Hilborn, R. 2015. Environment drives forage fish productivity. *Proc. Natl. Acad. Sci. U S A.* **112**(26): E3314–E3315. doi:10.1073/pnas.1507990112. PMID:26048908.
- Takens, F. 1981. Detecting strange attractors in turbulence. In *Symposium on dynamical systems and turbulence*. Edited by D.A. Rand and L.S. Young. Berlin. pp. 366–381.
- Velarde, E., Ezcurra, E., Cisneros-Mata, M.A., and Lavín, M.F. 2004. Seabird ecology, El Niño anomalies, and prediction of sardine fisheries in the Gulf of California. *Ecol. Appl.* **14**(2): 607–615. doi:10.1890/02-5320.
- Velarde, E., Ezcurra, E., and Anderson, D.W. 2013. Seabird diets provide early warning of sardine fishery declines in the Gulf of California. *Sci. Rep.* **3**: 1332. doi:10.1038/srep01332. PMID:23434761.
- Velarde, E., Ezcurra, E., and Anderson, D.W. 2015a. Seabird diet predicts following-season commercial catch of Gulf of California Pacific Sardine and Northern Anchovy. *J. Mar. Syst.* **146**: 82–88. doi:10.1016/j.jmarsys.2014.08.014.
- Velarde, E., Ezcurra, E., Horn, M.H., and Patton, R.T. 2015b. Warm oceanographic anomalies and fishing pressure drive seabird nesting north. *Sci. Adv.* **1**(5): e1400210. doi:10.1126/sciadv.1400210. PMID:26601193.
- Ward, T., and Staunton-Smith, J. 2002. Comparison of the spawning patterns and fisheries biology of the sardine, *Sardinops sagax*, in temperate South Australia and sub-tropical southern Queensland. *Fish. Res.* **56**: 37–49. doi:10.1016/S0165-7836(01)00314-9.
- Winemiller, K.O., and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* **49**(10): 2196–2218. doi:10.1139/f92-242.