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## UNIVERSITY OF CALIFORNIA SAN DIEGO

Uncovering the complex dynamics of socio-environmental fisheries management

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy
in

Oceanography

by<br>Jose Alfredo Giron Nava

Committee in charge:
Professor Octavio Aburto, Chair
Professor George Sugihara, Co-Chair
Professor Richard Carson
Professor Peter Franks
Professor Stuart Sandin

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|  | Co-chair |
| :--- | :---: |
|  | Chair |

University of California San Diego
2019

## DEDICATION

A mis padres por siempre decirme que la palabra "no puedo" no existe (aunque sean dos palabras).

## EPIGRAPH

"Education is a human right with immense power to transform. On its foundation rest the cornerstones of freedom, democracy and sustainable human development."

- Kofi Annan $-7^{\text {th }}$ Secretary General of the United Nations


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I firmly believe that the great problems that humanity face must be tackled by many people working together for a greater purpose. This dissertation is the result of many collaborations, meetings and conversations with people that have shaped my way of thinking and have helped me to become a better scientist.

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Chapter 1, in full, is a reprint of the material as it appears in Fish and Fisheries 2018. Giron-Nava, A., Johnson, A.F., Cisneros-Montemayor, A.M., Aburto-Oropeza, O. The dissertation author was the primary investigator and author of this material.

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## VITA

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# ABSTRACT OF THE DISSERTATION 

Uncovering the complex dynamics of socio-environmental fisheries management
by

Jose Alfredo Giron Nava

Doctor of Philosophy in Oceanography

University of California San Diego, 2019

Professor Octavio Aburto Oropeza, Chair
Professor George Sugihara, Co-Chair

Fisheries are complex systems affected by environmental variability, species interactions, and human behavior. As such, this dissertation aims to study them as social-ecological systems. First, by questioning current modeling approaches, and then, by proposing the use of new methods that account for their inherent complexities. Chapter 1 asks whether aiming for Maximum Sustainable Yield, a standard objective for sustainable exploitation, could also
generate economic stability for fishing communities in the Gulf of California, Mexico. We found that sustainable practices could increase total revenues by more than $70 \%$, however, this would not be enough for $80 \%$ of fishers in the region to live above local poverty levels. As such, I frame the possibility to move away from traditional, equation-based, fisheries management towards dynamic and adaptive frameworks. Chapter 2 explores the use of Empirical Dynamics Modeling (EDM), a nonlinear and nonparametric method, to study marine ecosystems. By using a long-term planktonic time series from the North Sea, we found that longer time series help to detect nonlinear and state-dependent processes, also improving time series' predictability. Chapter 3 uses a global database of stock assessments to find that traditional stock-recruitment models are somewhat successful at predicting data derived from assessment methods that introduce assumed stock-recruitment relationships. However, they are poor at predicting data that does not make such assumptions. We demonstrate that EDM is a better framework to predict future recruitment overall. Chapter 4 uses EDM to find that environmental processes and fishing pressure have both a detectable and comparable effect on the Pacific sardine's population dynamics in the Gulf of California, traditionally thought to be affected only by long-term climatic variability. We develop an EDM-based model using fishing and environmental effects to predict catch two years ahead. This dissertation questions the use of equation-based models for fisheries management. Instead, it proposes the use of EDM as a way not only to improve realworld predictability, but also to consider both ecological and social processes with a unified quantitative approach.

## CHAPTER 1:

Managing at Maximum Sustainable Yield does not ensure economic wellbeing for artisanal fishers

ALFREDO GIRON-NAVA, ANDREW F. JOHNSON, ANDRES CISNEROS-MONTEMAYOR, OCTAVIO ABURTO-OROPEZA

# Managing at Maximum Sustainable Yield does not ensure economic well-being for artisanal fishers 

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#### Abstract

Maximum Sustainable Yield (MSY) is a common target for fisheries aiming to achieve long-term ecological sustainability. Although achieving MSY may ensure the longterm sustainability of fish populations, we ask whether it will provide economic security for fishers. Here we use 16 years of daily landing records to estimate potential catches and revenues per capita if fisheries were exploited at MSY in 11 subregions across Mexico. We then compare fishers' estimated revenues per capita against national poverty limits at the household level. Our results show that even if MSY is reached in artisanal fisheries, the overcapacity of fleets and the dissipation of rents threatens the economic well-being of fishers and their families, pushing revenues per capita below poverty levels. Our work demonstrates the importance of resolving the trade-offs between achieving economic, social and environmental objectives when managing for the long-term sustainable use of natural resources.


## KEYWORDS

coastal communities, economic diversification, fisheries management, Malthusian overfishing, poverty, sustainable fishing

## 1 | INTRODUCTION

The common-pool, open-access nature of many natural resource extractions leads to overcapacity and increased competition between stakeholders. The subsequent overexploitation of such natural resources is often referred to as "the tragedy of the commons," and it frequently operates in many marine fisheries (Ostrom, Burger, Field Norgaard, \& Policansky, 1999). This mechanism of marine ecosystem deterioration, also known as Malthusian overfishing, places human population growth at the centre of the problem, stating that we may have "too many fishers chasing too few fish [and revenues]" (Pauly, 1990). However, recent studies suggest that this vision is incomplete, noting that other drivers may be equally or more important in determining overfishing patterns. These include technological advances, demand and distribution trends, marginalization and equity issues, and problems in governance (Finkbeiner et al., 2017; Steneck,

2009; Toth \& Szigeti, 2016). Notwithstanding extensive evidence of overexploitation in numerous fisheries globally and declines in total global landings (Costello et al., 2012; Pauly \& Zeller, 2016; Worm et al., 2009), many political leaders and fisheries authorities have continued to promote investments in fishing fleet capacity, with the expectation of increasing the contributions of fishing to national economies (Bell, Watson, \& Ye, 2016; Notimex, 2017; Pais, 2017). Technological advancements have also driven the expansion of fisheries farther offshore and into deeper waters (Swartz, Sala, Tracey, Watson, \& Pauly, 2010; Watson \& Morato, 2013). Despite such efforts to increase fisheries catches and revenues through the continuous increase of global fishing effort, global landings still show a steady decline over the last 20 years (Pauly \& Zeller, 2016). This situation not only compromises fisheries themselves, but also the economic well-being of people highly dependent on them (Ding, Chen, Chen, \& Tian, 2017) as revenues per capita for fishers continues to

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decrease, pushing them below poverty levels in many regions of the world (Béné, 2003).

Almost 20 million people around the world depend on fisheries as their primary source of income, and another 36 million partially depend on them (Béné et al., 2016; FAO, 2016). Approximately 80\% of those wholly dependent on fisheries earn incomes below official, country-specific poverty levels, particularly in artisanal fisheries (Béné et al., 2016; FAO, 2016). These fisheries employ 96\% of fishers and make up to $32 \%$ of global catches (Jacquet \& Pauly, 2008), highlighting their importance as a means of livelihood for coastal communities (Béné, 2003). In some places, strong local leadership and a long fishery tradition have played a central role in promoting the success of artisanal fisheries management programs (Gutiérrez, Hilborn, \& Defeo, 2011; Sutton \& Rudd, 2014), such as in the community of Punta Abreojos in Baja California Sur, Mexico (Cota-Nieto et al., 2018), or the Hawaiian Archipelago (Schemmel \& Friedlander, 2017). In many other locations, however, current management and governance of artisanal fisheries tend to be weak, leading to the overexploitation of marine resources and the degradations of coastal ecosystems (Costello et al., 2012; Freire \& García-Allut, 2000; Sala, Aburto-oropeza, Reza, Paredes, \& López-Lemus, 2004).

In order to promote the sustainable use of marine resources, one of the common target reference points is to achieve Maximum Sustainable Yield (MSY) (Quinn, 2003). Even though MSY is exclusively a biological reference point and maximizing economic (or social) objectives requires potentially quite different management strategies and targets (e.g. Maximum Economic Yield-MEY, Ecosystem Based Management-EBM, etc.), it remains the primary management objective promoted by many countries and by the FAO (2016). Within that context, the primary objective of this study was to evaluate whether attaining environmental sustainability through MSY can also bring sustainable economic benefits for fishers. To do so, we ask three questions: (a) How does the economic value of fishery resources influence the distribution of fishers? (b) What would the economic revenues be for fishers in a region that is managed at MSY and how would it compare to current revenues? And (c) can fisheries exploited at MSY ensure the economic well-being of fishers?

To answer these research questions, we make the following assumptions: (a) MSY can be estimated and fully implemented for all marine resources targeted by artisanal fishers, (b) stocks recover fully so that MSY is achieved, (c) the current number of fishers and units of effort remain constant, and (d) value from yield is equally distributed among all fishers. We use 16 years of daily fishery landings records (>3.5 million individual records) from 28 Local Fisheries Offices (LFOs) in the Gulf of California (GoC), Mexico, a globally recognized biodiversity hotspot with complex fisheries and socio-political structures (Leslie et al., 2015; Lluch-Cota et al., 2007). Landings from the GoC account for more than $50 \%$ of Mexico's national fisheries production in total volume and support more than 56,000 People [directly employed] in the Fishing Sector (PFS) (Azuz-Adeath \& Cortés-Ruiz, 2016). Artisanal fisheries in the GoC represent only $35 \%$ of the total landings by volume, but as much as $68 \%$ of the total revenues. We employ a catch-only fisheries stock assessment method (Froese,

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Demirel, Coro, Kleisner, \& Winker, 2017) to estimate the stock status for 121 resources that represent $95 \%$ of the total revenues from artisanal fisheries in the region. We then calculate the expected catch and revenues per capita for fishers that would be generated at MSY and compare them to national poverty levels. Given the wide variety of coastal communities in the Gulf of California and their high dependence in artisanal fisheries, our case study serves to raise awareness of a problem that will continue to worsen as the global number of fishers increases and total landings decrease or plateau at best (Pauly \& Zeller, 2016).

## 2 | METHODS

## 2.1 | Fisheries landings records

We obtained the national fisheries landings records from 2001 to 2016 for the 27 Local Fisheries Offices (LFO) in the Gulf of California (Figure 1). These data are available for interactive consultation at https://doi.org/10.13022/m3mw2p (Ramírez-Valdez, Johnson, Giron-Nava, \& Aburto-Oropeza, 2014). These records include more than 3.5 million individual reports of the total weight and average price of the resources caught by fishers (Erisman et al., 2011). Accounting for Illegal Unregulated and Unreported (IUU) fisheries is a common problem in official national fisheries records. In Mexico, this mis- and/or lack of reporting can add up to $50 \%$ of the total landing values (Cisneros-Montemayor, Cisneros-Mata, Harper, \& Pauly, 2013). Using published correction factors per species (CisnerosMontemayor et al., 2013), we calculated time series of corrected total landings. Given the vast diversity of socio-ecological structures


FIGURE 1 (a) Map of Local Fisheries Offices (LFOs) grouped per subregion. See Supporting information Table S1 for details on the offices that are included for each subregion. (b) People directly employed in the Fisheries Sector (PFS) per subregion obtained from the Mexican National Census (INEGI), (c) number of artisanal boats per subregion from Johnson et al. (2017), and (d) ratio between PFS and total population. Subregions are sorted in the bar charts from lowest to highest number of people directly employed in the Fisheries Sector (PFS) [Colour figure can be viewed at wileyonlinelibrary.com]
in the Gulf of California, and the differences between geographic areas, the LFOs were grouped into 11 subregions of at least 120 km of coastline each, which has been identified as the minimum distance that separates potentially distinct stocks for habitat-specific organisms in sandy beaches, rocky shores, estuaries and rocky reefs in the Gulf of California (Anadón, del Mar Mancha-Cisneros, Best, \& Gerber, 2013). The subregions selected using the distance criteria were reassessed based on peer-review literature and expert knowledge to ensure that they reflected the different socio-ecological characteristics of the regions identified (Erisman et al., 2011; Leslie et al., 2015) (Figure 1a). See Supporting information Table S1 for details on the offices that are included for each subregion.

We calculated the total ex-vessel revenues (money received by fishermen upon landing catch) by multiplying the total catch in tonnes by the average ex-vessel price per tonne. Species were clustered in fishing resources, which were a group of species registered under a unique name in the official records (e.g. shrimp contains blue shrimp (Litopenaeus stylirostris, Penaeidae), estuarine shrimp (Litapenaeus spp., Penaeidae) and others). In order to reduce unnecessary noise from resources that contribute very little to the total revenues per subregion, we selected the resources that accounted for $>95 \%$ of each subregion total fisheries revenues (Supporting information Table S2). Each resource in each subregion is referred to as a Fisheries Spatial Unit (FSU).

We also obtained time series from the FAO for the resources presented in Supporting information Table S2 from 1950 to 2015.

These data were used to estimate the prior for the initial standing stock biomass in 2001 as described below in Estimating fisheries reference points from catch-only data.

## 2.2 | Demographic and fishing vessels data

We obtained data on the total coastal population and the number of people related to fisheries economic activities for all the municipalities in Mexico, referred to as People [directly employed] in the Fisheries Sector (PFS) (Figure 1b). Data were obtained from the Mexican National Institute of Statistics and Geography (INEGI-Instituto Nacional de Estadística y Geografía) per municipality and were used to create Thiessen (Voronoi) Polygons using the software ArcGIS 10.2 to select which municipalities corresponded to each of the defined fisheries subregions. Spatially explicit estimates of the number of artisanal boats were obtained from Johnson et al. (2017) as a metric of fishing effort (Figure 1c). We also estimated the importance of fisheries for each subregion as the ratio PFS:Total population (Figure 1d).

## 2.3 | Estimating fisheries reference points from catch-only data

Given that catch data are the only available source of information about these artisanal fisheries, and that there are no fishery independent stock assessments throughout the whole region, we

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used the catch-only algorithm for total annual landings time se ries developed by Froese et al. (2017) to estimate fisheries reference points for each FSU (e.g. standing biomass, exploitation rate, intrinsic rate of population growth, carrying capacity and Maximum Sustainable Yield). All the code was implemented in R version 3.2.3 (all of the code is provided in Supporting information S1). This method estimates reference points from catch data and a qualitative estimate of resilience per FSU as reported in Fishbase (Froese \& Pauly, 2011). For each FSU, the catch-only algorithm assigns prior distributions of the possible values of the intrinsic rate of population growth $(r)$ and the standing biomass as a proportion of biomass at carrying capacity $\left(B / B_{k}\right)$. The $B / B_{k}$ priors are then used to estimate carrying capacity $(k)$ priors. Using a Monte Carlo approach, we tested each combination of $r$ and $k$ values from the prior distributions (referred as $r$-k pairs) to find "viable" pairs, defined as those which could simulate standing biomass time series restricted by the two following conditions: (s) never predicting a negative biomass value after subtracting the reported catch, and (b) always constraining pairs by the prior condition ranges defined for the standing biomass at the beginning, mid-point and end of the time series. Each viable $r$ - $k$ pair was stored and used to estimate the reported $r$ and $k$ values for each FSU.

In order to avoid misleading results derived from decadal trends that might not be captured in our time series (2001-2016), we used FAO historical records for the Mexican Pacific from 1950 to 2015 to estimate initial standing biomass prior distributions. For resources that started being fished on or after 2001 according to the FAO's records, the $B / B_{k}$ values at the beginning, middle and end of the time series were selected by following the standard method proposed by Froese et al. (2017). For resources that started being fished before 2001, we determined the prior of the initial $B / B_{k}$ by comparing the maximum landings before and after 2001. In cases where the historical maximum landing was significantly greater ( $t$ test, $p<0.05$ ) than the average landings between 2000 and 2002, we set the initial status of the population as depleted $\left(B / B_{k}=[0.2-\right.$ $0.5])$. We assigned all the prior distribution values by following the rules further explained in the Supporting information S1.

In the case of fish resources, the prior distributions of $r$ were selected following Froese et al. (2017) based on qualitative estimates of resilience reported in FishBase (Froese \& Pauly, 2011) as follows: very low (0.015-0.1), low (0.05-0.5), medium (0.2-0.8) and high (0.6-1.5). For invertebrates, we searched the peer-review literature extensively to obtain estimates of the resilience or the $r$ value ranges. Prior distributions of $k$ values were selected based on the catch time series of each FSU. The minimum value of the $k$ distribution was set as the maximum catch ever reported in the time series, and the maximum value was selected based on the coefficient $B / B_{k}$

The reported $r$ value for each stock was estimated as the 75 th percentile of the distribution of $r$ values, with $95 \%$ confidence intervals. The reported $k$ value was obtained from the linear regression between $\log (k)$ and $\log (r)$, for all $r$-k pairs where $r$ was larger than the 50th percentile. The regression is shown in Equation 1. The 95\% confidence intervals of k were estimated from the residuals of the
linear regression for the lower and upper confidence intervals of $r$. See Methods in Froese et al. (2017) for more details.

$$
\begin{equation*}
\mathrm{MSY}=\frac{r k}{4} \rightarrow \log (k)=\log (4 \mathrm{MSY})+(-1) \log (r) \tag{1}
\end{equation*}
$$

The MSY was estimated as in Equation 2 for each FSU. Along with the MSY, we estimated time series of stock's biomass, fishing mortality (Equation 3), biomass at MSY (Equation 4) and fishing mortality at MSY (Equation 5). We also calculated the coefficients $B / B_{M S Y}$ and $F / F_{M S Y}$. In order to explore recent patterns in standing stock biomass and fishing mortality relative to MSY, we calculated the trends of $B / B_{M S Y}$ and $F / F_{M S Y}$ as the average rate of change in the last 5 years of the time series (2012-2016) (Supporting information Figure S1B and C).
$\mathrm{MSY}=0.25 r k$
$\mathrm{~F}=$ catch/Biomass
$\mathrm{B}_{\mathrm{MSY}}=k / 2$
$\mathrm{~F}_{\mathrm{MSY}}=r / 2$

Given that Froese et al. (2017) originally developed their method to be used along with long time series ( $50+$ years), we explored the effect of time series length on population parameter estimations. To do so, we used 24 simulated stocks and compared the performance of the models when using the last 15, 30 and 50 years of data for each of them. We found no significant differences for the estimated parameters when using different time series lengths. The results are presented in Supporting information S2.

## 2.4 | Estimating rents at MSY

The rent was estimated as the total revenues from fishing minus the total costs from fishing. In the case of MSY, total rent increases come from both an increase in total revenues given the increase of total catch, as well as a reduction in operation costs through reduced effort. Through a review of the peer-review literature, we estimated that the current marginal rent of artisanal fisheries in the GoC is $12 \%$ (Aburto-Oropeza et al., 2016; Cisneros-Mata, 2016). We also estimated that $60 \%$ of the total revenues are used to pay fishers' salaries (as explained below). The additional 28\% of the total revenues are used towards miscellaneous variable costs such as gear, bait, food, fuel, maintenance and repairs (CisnerosMata, 2016). We assumed that these variable costs are reduced proportionally with effort. We also assumed that even at MSY, fishers would still receive $60 \%$ of the total revenues in salaries, with the extra revenue (after accounting for lower overall costs) representing rent accruing to the owner of the vessel (who may not be a fisher). Once we estimated the effort that would be necessary to achieve MSY, we calculated revenues, costs and rents
We estimated the monthly Revenues Per Capita (RPC) (per fisher) for each subregion under two scenarios, the current monthly average landings in the last 5 years (2012-2016) and the landings that would occur if all the fisheries were exploited at MSY. To do so, we estimated the total revenues $\left(R_{T}\right)$ per subregion based on Equation 6, in which $n$ represents the number of species per subregion that account for $95 \%$ of the total revenues within a subregion.

$$
\begin{equation*}
R_{T}=\sum_{i=1}^{n}\left(\text { catch }_{i} \times \text { ex vessel price }{ }_{i}\right) \tag{6}
\end{equation*}
$$



By taking the estimates from Johnson et al. (2017) of the number of boats in the GoC, we calculated the total revenues per boat per subregion (Equation 7).

$$
\begin{equation*}
R_{\text {boat }}=R_{T} / \text { boats } \tag{7}
\end{equation*}
$$

On average, fishing boats in the Gulf of California operate with 2.7 fishers per trip (Cisneros-Mata, 2016), and fishers divide 60\% of the total revenues among them as salaries; therefore, $60 \%$ of the total revenues were divided among the fishers to calculate the Revenues Per Capita (RPC).

$$
\begin{equation*}
\mathrm{RPC}=0.6 R_{\text {boat }} /(2.7) \tag{8}
\end{equation*}
$$

In order to compare the RPC to the minimum amount of money that a fisher needs to support a family under the minimum-livelihood requirements, we defined an Economic Well-being Limit (EWL). The EWL was calculated based on the price of a basket of goods, health, personal care, house maintenance, education, clothing, communications, public transportation and recreation. According to the Mexican National Council for the Evaluation of Social Development Policy (CONEVAL), a family in Mexico needs US\$95 and \$150 per month per family member to live above the rural EWL and the urban EWL respectively (CONEVAL, 2016). On average, a family in Mexico has 3.7 members, as reported by INEGI (INEGI, 2016). Thus, the average monthly household rural EWL is approximately $\$ 351$, while the urban EWL is $\$ 555$. We compared the RPC for the current catch (2012-2016) and the catch at MSY to the EWLs (Figure 3).

## 3 | RESULTS

## 3.1 | Resource selection and importance

There were between five and fifteen FSUs per subregion representing $95 \%$ of the total revenues in the Gulf of California (Supporting information Table S2). We found that the most valuable resource represents a higher percentage of the total revenues (Figure 2) in subregions with higher PFS $\left(R^{2}=0.70, F_{1,9}=20.8, P<0.01\right)$.

FIGURE 2 Percentage of revenues generated by each of the resources that comprise $95 \%$ of the total revenues per subregion (FSU). Black bars represent the FSU per subregion that generates the highest percentage of total revenues. The subsequent grey bars represent the remaining FSU for that subregion. Subregions are sorted from lowest to highest number of people directly employed in the Fisheries Sector (PFS)

The most valuable FSU is henceforth referred to as the top FSU. We also found a positive correlation between the price per kg of the top FSU per subregion and the number of PFS ( $R^{2}=0.67$, $F_{1,7}=14.52, P<0.01$ ), suggesting that places with more valuable resources attract more people into the fishery. For example, in Mazatlan (MZ), the subregion with the most PFS, shrimp was the top FSU with an average price of $\$ 4,886$ per tonne and represented $73 \%$ of the total revenues. In contrast, in Bahia de los Angeles (BA), a subregion with five times fewer PFS than MZ, octopus (Octopus sp., Octopodidae) was the top FSU with a lower average price of $\$ 1,985$ per tonne and contributed only $36 \%$ of the total revenues. The subregions of Puerto Peñasco (PP) and Santa Clara (SC) were outliers in the relationship between PFS and price per kg of the top FSU (Cook's distance $\geq 0.15$ ), with higher values per kg than expected. This was possibly due to their geographic isolation from other subregions and proximity to the United States shrimp markets. We did not find a relationship between the economic value of the resources and the relative importance of fisheries across subregions, measured as the ratio of PFS:total population (Figure 1d).

### 3.2 The degree of exploitation of SSF in the GoC and potential revenues

Of the 121 FSUs analysed, $69 \%$ were overfished $\left(B / B_{M S Y}<1\right)$ and still being fished at unsustainable levels ( $F / F_{M S Y}>1$ ), $13 \%$ were overfished but recovering by being fished at sustainable levels $\left(F / F_{M S Y}<1\right)$, $11 \%$ were not overfished $\left(B / B_{M S Y}>1\right)$ but fished at unsustainable levels, and $7 \%$ were not overfished and were being fished sustainably (Supporting information Figure S1A). Overall, $82 \%$ of FSUs were overfished and $80 \%$ were subject to unsustainable fishing pressure. The overall trend between 2012 and 2016


FIGURE 3 Comparison between average current Revenues Per Capita (RPC) between 2001 and 2016, potential RPC expected at MSY, and the Economic Well-being Limits (EWL) for rural and urban areas per subregion. Error bars in the current RPC were calculated as one standard error of the average RPC. Error bars in the RPC at MSY were calculated from the r and $\mathrm{k} 95^{\text {th }}$ confidence intervals of all the species per subregion. Subregions are ordered from lowest to highest number of people directly employed in the Fisheries Sector (PFS) [Colour figure can be viewed at wileyonlinelibrary.com]
shows that the biomass of 61\% of the FSUs declined (Supporting information Figure S1B) and $65 \%$ increased their fishing mortality (Supporting information Figure S1C).

The mean annual revenues reported for the 121 analysed FSUs over the last 5 years (2012-2016) was $\$ 108 \mathrm{~m} \pm 5 \mathrm{~m}$, and $\$ 141 \mathrm{~m} \pm 7 \mathrm{~m}$ ( $31 \%$ higher) after accounting for unreported catch. In contrast, we estimate that total profits from these FSUs would be $\$ 240 \mathrm{~m} \pm 14 \mathrm{~m}$ ( $70 \%$ increase) if they were all fished at their respective MSY.

## 3.3 | Income analysis

As of 2016, the average monthly net revenue (i.e. revenue minus fishing costs) per capita (RPC) per subregion was $\$ 190,46 \%$ below the $\$ 351$ necessary for the rural Economic Well-being Limit (EWL), and $65 \%$ below the $\$ 555$ for the urban EWL (Figure 3). Subregions can be categorized into three groups: (a) those which under current conditions are below the rural EWL and remain below even if fished at MSY ( $n=7,79.6 \%$ PFS); (b) those which under current conditions are below the rural EWL and go above if fished at MSY ( $n=2,10.5 \%$ PFS); and (c) those which under current conditions are above the rural EWL and remain above at MSY ( $n=2,9.9 \%$ PFS). Under current conditions, nine of the 11 subregions, which account for $90 \%$ of the PFS, reported monthly RPC lower than the rural EWL. All the subregions reported RPC lower than the urban EWL. Under the MSY scenario, only four subregions ( $20 \%$ of PFS) would be able to make RPC above the rural EWL, and no subregion would report RPC higher than the urban EWL.

## 4 | DISCUSSION

In this study, we demonstrate that subregions with a few, high-value resources made a disproportionate part of their total revenues from them and were exploited by more fishers than subregions with many low value species (Figure 2). Even though this result is to be expected based on economic theory (higher rents are to be distributed
among more people at equilibrium), to our knowledge this is the first empirical and spatially explicit demonstration of this argument for artisanal fisheries. Focusing on high value and abundant species may be more economically viable (Anderson et al., 2017); however, it increases the economic vulnerability of fishing communities to external shocks, such as market and climate variability. For example, the subregions in the Upper Gulf of California that rely heavily on shrimp fisheries were drastically affected when shrimp fisheries were banned in May 2015 in the region and had to receive economic compensations in order to compensate for the economic shock of a forced fishery closure (Aburto-Oropeza et al., 2016). Recent studies demonstrate that diversification in the number of target species fished can reduce such risks, which is already an important strategy in tropical and subtropical multispecies fisheries (Anderson et al., 2017; Pellowe \& Leslie, 2017; Sievanen, 2014).

We also explored whether achieving MSY in artisanal fisheries can ensure the economic well-being of fishers. Our results show that stocks in the GoC managed at MSY could increase the total annual revenues by approximately $70 \%$, which is above global estimates that calculated an increase of $51 \%$ after accounting for unreported catch (Costello et al., 2016). However, when we compare this increase in revenues against national poverty levels, managing at MSY will not ensure the economic well-being for $80 \%$ of fishers. It is noteworthy that the subregions capable of reaching the EWL through management at MSY all have significantly lower numbers of fishers than those that would not reach the EWL even at MSY. This highlights the role that overcapacity likely plays in driving RPC below the EWL (Figure 3), as even regions with highly valuable resources are unable to support fishers above the EWL when the numbers of fishers are high as well.

Our estimates of fishers' income correspond well with previous work and official estimates by Mexican authorities. In 2007, the Mexican Secretariat for Employment and Social Provision estimated that fishers received a monthly average income of \$196 (2016 USD), number that was closely corroborated (\$186 (2016 USD)) by researchers who performed interviews in the Gulf of California
between 2006 and 2008 (Mancini et al., 2011). Even though we expect some seasonality in the availability of some resources and therefore in the revenues (i.e. regions where shrimp is the top FSU get revenues above average from September to November and below average from January through May), calculating such fine resolution temporal patterns is beyond the scope of this manuscript. Such pursuit, however, would be helpful when considering temporal management strategies in future works. Still, we think that the monthly average revenue over the year is a valid reference point, as poverty lines themselves are calculated in this way (CONEVAL, 2016) and other economic sectors might experience similar variability (e.g. agriculture, construction, etc.).

The lack of economic capacity of fisheries to support fishers above poverty levels in some cases has resulted in the need to diversify fishing techniques, fishing areas and even occupations (Sievanen, 2014). Some alternative occupations commonly used to supplement fisheries income in the Gulf of California include tourist providers, carpenters, painters and maintenance workers; however, in recent years, such occupations have been increasingly difficult to find as secondary jobs (Sievanen, 2014). Another way to supplement household income is through economic contributions of other family members. Our estimates of RPC therefore may underestimate total household income. In order to account for this factor, we considered that in $2016,62 \% \pm 1.1 \%$ of the average household income in northwestern Mexico was contributed by the heads of family and the rest by other family members (INEGI, 2016). However, even when accounting for potential additional income within fisher-households from other family members, the average household income at MSY for the whole region goes from $\$ 190$ USD to just $\$ 306$ USD, and only five ( $23.6 \%$ PFS) subregions would achieve a household income above the rural EWL and four ( $20.0 \%$ PFS) above the urban EWL.

It is commonly accepted that the use of catch-only methods for estimating stock biomass ( $B / \mathrm{B}_{\mathrm{MSY}}$ ) and fishing mortality ( $F / F_{\mathrm{MSY}}$ ) should be considered cautiously, as they do not account for size structure, stock-recruitment relationships or changes in effort. Nevertheless, these methods have been widely tested and show consistent results with statistics from well-assessed fisheries, even when using broad taxonomic groups of marine resources as in data from the Food and Agricultural Organization (FAO) (Costello et al., 2012; Free, Jensen, Wiedenmann, \& Deroba, 2017; Froese et al., 2017). Catch-only methods are most commonly used with at least 30 years of time series data (Froese et al., 2017). Our analysis, however, used 16, which means that some decadal trends in stock biomass could have been missed. We addressed this issue in two ways. First, we tested whether the estimation of population parameters varied significantly with time series length and we did not find any significant differences (Supporting information S2). Second, we incorporated historical landing records reported to the FAO since 1950 (Methods) to estimate priors for the initial stock biomass $\left(B / B_{k}\right)$. We decided to use data from FAO as it has been demonstrated to be consistent with the official catch data used in this study (ArreguínSánchez \& Arcos-Huitrón, 2011). In addition, fishery-independent assessments by local fisheries experts and the Mexican National

Fisheries Institute (INAPESCA) estimate that between 83\% and 90\% of fisheries in the GoC are either fully or overexploited (ArreguínSánchez \& Arcos-Huitrón, 2011; DOF, 2012), also consistent with the $82 \%$ calculated in this study. Global analyses have reported that small and unassessed fisheries are the ones most likely to be in the worst condition, with an average $B / B_{\text {MSY }}$ of 0.60 (Costello et al., 2012). This result corresponds well with the average $B / B_{\text {MSY }}$ value for the FSUs analysed in this study of 0.63.

Unfortunately, the reductions in fishing capacity required to alleviate the negative impacts of overfishing often result in a loss of fishing access for fishers who may be entirely dependent on marine resources for their livelihood. In developing countries where fishers have fewer economic alternatives, implementing such solutions might be difficult, as governments would need to provide sufficient opportunities for people to opt out of fisheries permanently, if they would accept such alternatives at all (Béné et al., 2016; Weeratunge et al., 2014). Furthermore, while it is intuitive that recovered and sustainable fisheries increase catches and revenues, it is still debated who should enjoy from such benefits (Clark, Munro, \& Sumaila, 2005; Jensen, 2002). In particular, as fishing effort and mortality decrease in an overfished system and lead to more abundant fish stocks, fishers need to spend less time and effort to catch the same amount fish. This results in a reduction of operating costs and thus in higher net profits. Part of these profits from better management and exclusive access could be collected in the form of taxes or licensing fees to benefit the general public, given that fish are a public resource (Clark et al., 2005; Jensen, 2002). On the other hand, exclusive benefits to individual fishers or fishing cooperatives, which are a key incentive of compliance with access-based management, would need to be allocated in a transparent and inclusive process to facilitate implementation and avoid future conflicts (Birkenbach, Kaczan, \& Smith, 2017; Costello, Gaines, \& Lynham, 2008).

Given that specific pressures on the oceans, including overfishing and overcapacity, are regulated within wider socioecological systems (Finkbeiner et al., 2017), it is vital that the interdependencies between social and ecological processes be explicitly addressed by policymakers even when discussing benefits of reduced capacity and economic diversification. There is emerging recognition for the potential of the oceans as a platform for multiple innovative industries and wealth creation, as recently promoted within the Blue Economy framework, that are especially relevant in coastal areas that currently often rely almost exclusively on fisheries for income and livelihoods (Keen, Schwarz, \& Wini-Simeon, 2016; World Bank and United Nations Department of Economic and Social Affairs, 2017). At community scales, for example, ecotourism can contribute to or sometimes entirely transform fishing communities (e.g. Cabo Pulmo National Park in Mexico, or the transformation of manta ray fisheries to ecotourism in Western Australia and other parts of the world) (AburtoOropeza et al., 2011; Venables, Mcgregor, Brain, \& Van Keulen, 2016). Similarly, offshore wind and tidal energy projects can be used to address challenges of last-mile electrification and water desalination in remote coastal areas (Snyder \& Kaiser, 2009; Vega,

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2002), and payments for ecosystem services (e.g. mangrove restoration) may add additional incentives for ecosystem protection (Aburto-Oropeza et al., 2008; World Bank and United Nations Department of Economic and Social Affairs, 2017). Here we have demonstrated that fisheries alone will not be able to provide sufficient economic benefits to maintain fishers above local poverty levels, even if sustainably exploited and if fishing effort is kept constant. Although it might seem natural that the data in our study-uncertainty notwithstanding-could be used to estimate the number of fishers that need to be redirected into other economic sectors, the aim of our study was not to provide such a narrow solution to the problems faced by fisheries. We rather suggest that addressing fleet overcapacity is a key component of the process to achieve sustainable and economically viable fisheries, but also recognize that as part of a complex socio-ecological system, it should not be considered in isolation.

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## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

## AUTHORS' CONTRIBUTIONS

AGN designed the study, analysed the data and wrote the manuscript. AFJ and OAO designed the study and wrote the manuscript. ACM analysed the data and wrote the manuscript.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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## Chapter 1 Appendix

Managing at Maximum Sustainable Yield does not ensure economic well-being for artisanal fishers.

Supplementary Information

## By

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Table S1. List of Local Fisheries Offices per subregion

| ID | Subregion | Subregion name | Office | Longitude | Latitude |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | LP | La Paz | Cabo San Lucas | -109.916 | 22.8897 |
|  |  |  | La Paz | -110.311 | 24.1422 |
| 2 | LO | Loreto | Loreto | -111.343 | 26.0128 |
| 3 | SR | Santa Rosalia | Santa Rosalia | -112.267 | 27.3389 |
| 4 | BA | Bahia de los Angeles | Bahia de los Angeles | -113.564 | 28.9497 |
| 5 | UG | Upper Gulf of California | Golfo de Santa Clara | -114.5 | 31.6867 |
|  |  |  | San Felipe | -114.835 | 31.0275 |
| 6 | PP | Puerto Peñasco | Puerto Libertad | -112.683 | 29.9042 |
|  |  |  | Puerto Peñasco | -113.537 | 31.3167 |
| 7 | GY | Guaymas | Bahia Kino | -111.941 | 28.8228 |
|  |  |  | Guaymas | -110.899 | 27.9183 |
|  |  |  | Hermosillo | -111.526 | 28.6397 |
| 8 | HU | Huatabampo | Estacion Don | -109.024 | 26.4236 |
|  |  |  | Huatabampo | -109.642 | 26.8275 |
|  |  |  | Los Mochis | -108.997 | 25.7936 |
|  |  |  | Topolobampo | -109.056 | 25.6297 |
| 9 | GS | Guasave | Guasave | -108.47 | 25.5733 |
|  |  |  | La Reforma | -108.056 | 25.0811 |
|  |  |  | Navolato | -107.703 | 24.7656 |
| 10 | MZ | Mazatlan | Escuinapa | -105.778 | 22.8333 |
|  |  |  | Mazatlan | -106.41 | 23.2414 |
|  |  |  | Rosa Morada | -105.204 | 22.1222 |
|  |  |  | Tecuala | -105.457 | 22.3972 |
|  |  |  | Tuxpan | -105.299 | 21.9436 |
| 11 | BB | Bahia de Banderas | Cruz de Huanacaxtle | -105.382 | 20.7492 |
|  |  |  | Peñita de Jaltemba | -105.249 | 21.0386 |
|  |  |  | Puerto Vallarta | -105.227 | 20.6136 |
|  |  |  | San Blas | -105.178 | 21.7503 |
|  |  |  | Santiago Ixcuintla | -105.207 | 21.8114 |
|  |  |  | Tepic | -104.894 | 21.5164 |

Table S2. List of Important Resources (species that correspond to $95 \%$ of the total ex-vessel revenues per subregion).

| Subregion | Subregion name | Resource | \% of total revenues | Weight <br> (tonnes) | Price per tonne (USD) |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | La Paz | Red snapper | 28.09 | 32916 | 1903 |
|  |  | Lobster | 19.90 | 188458 | 10894 |
|  |  | Sharks | 11.42 | 25730 | 1487 |
|  |  | Snapper | 5.99 | 24172 | 1397 |
|  |  | Groupers | 5.83 | 29274 | 1692 |
|  |  | Sea bass | 4.43 | 33811 | 1954 |
|  |  | Jacks | 4.43 | 13599 | 786 |
|  |  | Ocean whitefish | 3.56 | 13316 | 770 |
|  |  | Clams | 3.50 | 6286 | 363 |
|  |  | Small sharks | 2.34 | 14127 | 817 |
|  |  | Flatfish | 1.88 | 25466 | 1472 |
|  |  | Octopus | 1.48 | 34976 | 2022 |
|  |  | Squid | 1.24 | 2920 | 169 |
|  |  | Rays | 1.21 | 12176 | 704 |
| 2 | Loreto | Red snapper | 44.13 | 45857 | 2651 |
|  |  | Snapper | 14.16 | 29697 | 1717 |
|  |  | Groupers | 10.49 | 36016 | 2082 |
|  |  | Jacks | 7.89 | 12937 | 748 |
|  |  | Sharks | 5.11 | 10070 | 582 |
|  |  | Ocean whitefish | 4.58 | 11378 | 658 |
|  |  | Catfish | 4.42 | 42573 | 2461 |
|  |  | Small sharks | 2.08 | 11983 | 693 |
|  |  | Rays | 1.52 | 9161 | 530 |
|  |  | Sea bass | 1.24 | 49365 | 2853 |
| 3 | Santa Rosalia | Squid | 40.20 | 4303 | 249 |
|  |  | Groupers | 13.27 | 20154 | 1165 |
|  |  | Jacks | 7.85 | 13539 | 783 |
|  |  | Flatfish | 7.12 | 29973 | 1733 |
|  |  | Lobster | 5.09 | 329168 | 19027 |
|  |  | Octopus | 4.91 | 34466 | 1992 |
|  |  | Sharks | 2.96 | 13426 | 776 |
|  |  | Snapper | 2.24 | 27932 | 1615 |
|  |  | Blue crab | 2.20 | 24220 | 1400 |
|  |  | Gulf weakfish | 2.09 | 17128 | 990 |
|  |  | Red snapper | 1.73 | 35143 | 2031 |
|  |  | Rays | 1.56 | 11475 | 663 |
|  |  | Small sharks | 1.38 | 13932 | 805 |


|  |  | Mullets | 1.29 | 9463 | 547 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Clams | 1.15 | 10072 | 582 |
| 4 | Bahia de los Angeles | Octopus | 35.70 | 34335 | 1985 |
|  |  | Squid | 14.52 | 6663 | 385 |
|  |  | Jacks | 11.15 | 14512 | 839 |
|  |  | Flatfish | 7.46 | 23218 | 1342 |
|  |  | Sharks | 7.18 | 18482 | 1068 |
|  |  | Groupers | 6.55 | 15002 | 867 |
|  |  | Catfish | 4.26 | 38325 | 2215 |
|  |  | Small sharks | 3.24 | 15945 | 922 |
|  |  | Rays | 3.00 | 14180 | 820 |
|  |  | Clams | 2.21 | 58327 | 3371 |
| 5 | Upper Gulf of California | Shrimp | 43.38 | 181339 | 10482 |
|  |  | Gulf croaker | 18.63 | 12509 | 723 |
|  |  | Mackerels | 14.32 | 14672 | 848 |
|  |  | Gulf weakfish | 11.14 | 37972 | 2195 |
|  |  | Clams | 8.50 | 18904 | 1093 |
| 6 | Puerto <br> Peñasco | Shrimp | 40.86 | 113248 | 6546 |
|  |  | Clams | 13.55 | 33761 | 1951 |
|  |  | Flatfish | 9.75 | 16837 | 973 |
|  |  | Blue crab | 9.16 | 13903 | 804 |
|  |  | Gulf croaker | 7.97 | 7819 | 452 |
|  |  | Rays | 4.71 | 10941 | 632 |
|  |  | Sharks | 3.85 | 11692 | 676 |
|  |  | Catfish | 2.73 | 32540 | 1881 |
|  |  | Snails | 2.48 | 8849 | 511 |
| 7 | Guaymas | Shrimp | 47.19 | 92128 | 5325 |
|  |  | Blue crab | 12.11 | 15737 | 910 |
|  |  | Squid | 7.76 | 4739 | 274 |
|  |  | Mackerels | 4.97 | 12691 | 734 |
|  |  | Snails | 4.07 | 18892 | 1092 |
|  |  | Flatfish | 3.73 | 24968 | 1443 |
|  |  | Octopus | 3.50 | 44905 | 2596 |
|  |  | Clams | 2.41 | 25943 | 1500 |
|  |  | Jacks | 1.92 | 18939 | 1095 |
|  |  | Snapper | 1.80 | 36781 | 2126 |
|  |  | Gulf weakfish | 1.72 | 16953 | 980 |
|  |  | Groupers | 1.50 | 30539 | 1765 |
|  |  | Catfish | 1.35 | 38766 | 2241 |
|  |  | Lobster | 1.14 | 105631 | 6106 |
| 8 | Huatabampo | Shrimp | 68.12 | 84044 | 4858 |
|  |  | Blue crab | 13.15 | 13375 | 773 |


|  |  | Red snapper | 3.36 | 35581 | 2057 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Flatfish | 3.08 | 20720 | 1198 |
|  |  | Sharks | 1.49 | 17098 | 988 |
|  |  | Mackerels | 1.31 | 13289 | 768 |
|  |  | Squid | 1.20 | 6477 | 374 |
|  |  | Gulf croaker | 1.14 | 7972 | 461 |
|  |  | Snails | 1.04 | 17674 | 1022 |
|  |  | Mullets | 0.96 | 6314 | 365 |
|  |  | Catfish | 0.86 | 26205 | 1515 |
| 9 | Navolato | Shrimp | 47.58 | 84046 | 4858 |
|  |  | Blue crab | 23.09 | 16241 | 939 |
|  |  | Gulf weakfish | 2.97 | 40693 | 2352 |
|  |  | Small sharks | 2.95 | 23378 | 1351 |
|  |  | Snapper | 2.76 | 51282 | 2964 |
|  |  | Sharks | 2.56 | 21313 | 1232 |
|  |  | Rays | 2.51 | 24829 | 1435 |
|  |  | Mullets | 2.26 | 10381 | 600 |
|  |  | Mojarra | 2.14 | 13993 | 809 |
|  |  | Catfish | 2.06 | 32660 | 1888 |
|  |  | Red snapper | 2.01 | 51710 | 2989 |
|  |  | Mackerels | 1.89 | 16234 | 938 |
| 10 | Mazatlan | Shrimp | 72.73 | 84532 | 4886 |
|  |  | Sharks | 4.70 | 9055 | 523 |
|  |  | Snooks | 3.61 | 40361 | 2333 |
|  |  | Mojarra | 3.39 | 11322 | 654 |
|  |  | Snapper | 3.19 | 41312 | 2388 |
|  |  | Squid | 2.03 | 5514 | 319 |
|  |  | Gulf weakfish | 2.01 | 22858 | 1321 |
|  |  | Catfish | 1.53 | 10980 | 635 |
| 11 | Bahia de Banderas | Mojarra | 39.94 | 15082 | 872 |
|  |  | Red snapper | 11.99 | 47114 | 2723 |
|  |  | Snapper | 8.60 | 42344 | 2448 |
|  |  | Oyster | 6.08 | 15278 | 883 |
|  |  | Shrimp | 5.21 | 46489 | 2687 |
|  |  | Mackerels | 4.78 | 20411 | 1180 |
|  |  | Snooks | 4.64 | 43327 | 2504 |
|  |  | Gulf weakfish | 4.22 | 25979 | 1502 |
|  |  | Sharks | 3.09 | 11777 | 681 |
|  |  | Catfish | 2.90 | 9415 | 544 |
|  |  | Small sharks | 2.11 | 21144 | 1222 |
|  |  | Gulf croaker | 1.12 | 13131 | 759 |
|  |  | Octopus | 1.00 | 52042 | 3008 |

Table S3. Comparison of $B / B m s y$ and $r$ values from this study with previous estimates for the Gulf of California.

| Resource | Mean B/Bmsy | $\begin{gathered} \text { SD } \\ \text { B/Bmsy } \end{gathered}$ | Mean <br> $r$ | B/Bmsy <br> Literature | Reference B/Bmsy | r <br> Literature | Reference <br> r | \% Diff. B/Bmsy | \% Diff. <br> r |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Clams | 0.36 | 0.14 | 0.52 | 0.55 | Cisneros- <br> Mata, 2016 | 0.525 | Cisneros- <br> Mata, 2016 | 9\% | 1\% |
| Catfish | 0.78 | 0.09 | 0.41 | Near msy | Arreguin, 2011 |  |  |  |  |
| Gulf croaker | 0.54 | 0.04 | 0.56 | Near msy | Arreguin, 2011 |  |  |  |  |
| Groupers | 0.47 | 0.09 | 0.28 | Overexploited | Arreguin, 2011 |  |  |  |  |
| Squid | 0.14 | 0.08 | 0.93 |  |  | 1.2 | Cisneros- <br> Mata, 2016 |  | 23\% |
| Shrimp | 0.62 | 0.11 | 0.54 | 0.7 | Cisneros- <br> Mata, 2016 | 0.6 | Cisneros- <br> Mata, 2016 | 0\% | 10\% |
| Snails | 1.02 | 0.45 | 0.57 | 0.9 | Cisneros- <br> Mata, 2016 | 0.5 | Cisneros- <br> Mata, 2016 | 0\% | 13\% |
| Small sharks | 0.47 | 0.11 | 0.06 | 0.4 | Cisneros- <br> Mata, 2016 |  | Cisneros- <br> Mata, 2016 | 0\% |  |
| Gulf weakfish | 0.52 | 0.07 | 0.54 | 0.9 | Cisneros- <br> Mata, 2016 | 0.6 | Cisneros- <br> Mata, 2016 | 34\% | 9\% |
| Red snapper | 0.87 | 0.13 | 0.56 | 0.8 | Cisneros- <br> Mata, 2016 | 0.5 | Cisneros- <br> Mata, 2016 | 0\% | 12\% |
| Blue crab | 0.82 | 0.07 | 0.57 | 0.8 | Cisneros- <br> Mata, 2016 | 0.5 | Cisneros- <br> Mata, 2016 | 0\% | 13\% |
| Jacks | 0.64 | 0.21 | 0.48 | Developing | Arreguin, 2011 |  |  |  |  |
| Lobster | 0.87 | 0.10 | 0.56 | 0.9 | Cisneros- <br> Mata, 2016 | 0.5 | Cisneros- <br> Mata, 2016 | 0\% | 11\% |


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|  |  | $\stackrel{\infty}{0}$ |  |  |  |  | $\stackrel{m}{0}$ |  | $\stackrel{\sim}{0}$ | $0$ | $\stackrel{\square}{\circ}$ |
| $\stackrel{\sim}{\sim}$ | $\begin{aligned} & \stackrel{\rightharpoonup}{t} \\ & 0 \end{aligned}$ | O. | $\stackrel{\infty}{\sim}$ | $\begin{aligned} & 6 \\ & 0 \\ & 0 \end{aligned}$ | $\stackrel{-1}{0}$ | $\stackrel{\infty}{\sim}$ | تِ | O. | $\begin{gathered} \mathrm{n} \\ 0 \\ 0 \end{gathered}$ | $\begin{aligned} & \text { ợ } \\ & 0 \end{aligned}$ | $\bigcirc$ |
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## Supplementary material 1.

Conditions to define biomass priors $\left(B / B_{k}\right)$. All methods are based on Froese et al. 2017 and adapted to incorporate historical records from FAO.

## 1) Infer $B_{\text {start }} / B_{k}$ priors from FAO historical landing reports

i. No records before 1995. $B / B_{k}=0.6-0.9$
ii. Historical max (1950-1999) < mean of 2000-2002. $\mathrm{B}_{\text {start }} / \mathrm{B}_{\mathrm{k}}=[0.5,0.8]$
iii. Historical $\max (1950-1999)=$ mean of 2000-2002. $\mathrm{B}_{\text {start }} / \mathrm{B}_{k}=[0.4,0.6]$
iv. Historical $\max (1950-1999)>$ mean of 2000-2002. $\mathrm{B}_{\text {start }} / \mathrm{B}_{\mathrm{k}}=[0.2,0.5]$

## 2) Infer $B_{\text {int }} / B_{k}$ priors from resource's time series

i. Calculate contrast between catch at intermediate and starting years.

$$
C_{\text {int }}=\frac{\left(\text { catch }_{\text {int }}-\text { catch }_{\text {start }}\right)}{\text { catch }_{\text {start }}}
$$

ii. If $C_{\text {int }}<0 . \mathrm{B}_{\text {int }} / \mathrm{B}_{\mathrm{k}}=\mathrm{B}_{\text {start }} / \mathrm{B}_{\mathrm{k}}-0.1$
iii. If $C_{\text {int }}=0$. $\mathrm{B}_{\text {int }} / \mathrm{B}_{\mathrm{k}}=\mathrm{B}_{\text {start }} / \mathrm{B}_{\mathrm{k}}$
iv. If $C_{\text {int }}>0 . \mathrm{B}_{\text {int }} / \mathrm{B}_{\mathrm{k}}=\mathrm{B}_{\text {start }} / \mathrm{B}_{\mathrm{k}}+0.1$
3) Infer $B_{\text {final }} / B_{k}$ priors from resource's time series
i. Calculate contrast between maximum catch and final catch

$$
C_{\text {final }}=\frac{\text { catch }_{\text {final }}}{\text { catch }_{\max }}
$$

ii. If $C_{\text {final }}=1 . \mathrm{B}_{\text {final }} / \mathrm{B}_{\mathrm{k}}=\mathrm{B}_{\text {start }} / \mathrm{B}_{\mathrm{k}}+0.1$
iii. If $C_{\text {final }}<0.5$. $\mathrm{B}_{\text {final }} / \mathrm{B}_{\mathrm{k}}=[0.01,0.4]$
iv. If $C_{\text {final }}<0.35$. $\mathrm{B}_{\text {final }} / \mathrm{B}_{\mathrm{k}}=[0.01,0.3]$
v. If $C_{\text {final }}<0.15$. $\mathrm{B}_{\text {final }} / \mathrm{B}_{\mathrm{k}}=[0.01,0.2]$
vi. If $C_{\text {final }}<0.05$. $\mathrm{B}_{\text {final }} / \mathrm{B}_{\mathrm{k}}=[0.01,0.1]$
vii. If $C_{\text {final }}>0.5 \& C_{\text {final }}<1$. $\mathrm{B}_{\text {final }} / \mathrm{B}_{\mathrm{k}}=\mathrm{B}_{\text {start }} / \mathrm{B}_{\mathrm{k}}$

* All differences are calculated with a margin of 20 \%


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Figure S1. Current state of fisheries and trends between 2012-2016 for 121 SFUs in the Gulf of California. A) Kobe plot (B/Bmsy vs. F/Fmsy) of SFU that represent 95\% of the total revenues per subregion. Numbers in parentheses represent the number of SFUs in each graphic quadrant. B) Distribution of the linear trend in B/Bmsy between 2012-2016 for each SFU. B.slope was calculated as the average rate of change of B/Bmsy. C) Distribution of the trend in F/Fmsy between 2012 and 2016 for each SFU. F.slope was calculated as the average rate of change of $\mathrm{F} / \mathrm{Fmsy}$.

## Supplementary material 2.

We performed an analysis to evaluate whether the estimation of population parameters $r$ (intrinsic rate of population growth) and k (carrying capacity) through the use of the catch-only method proposed by Froese et al. (2017) varies with time series length. To do so, we simulated catches of 24 stocks for a period of 50 years each. We tested a wide range of combinations between fisheries catches trends (low/medium/high catches in the beginning/middle/end of the time period), and the resilience, $r$ and $k$ for each stock (See Table S4 for specifications of each stock). We then generated 3 time series for each stock ( 15,30 and 50 years length, 72 time series in total). To simulate an analogous situation to our dataset, in which we just have access to the last 16 years, the time series for 15 and 30 years were subsampled from the end of their respective time series.

For each of the 72 time series, we estimated the population parameters as explained in Froese et al. (2017) and following the rules to assign biomass priors ( $B / B_{k}$ ) as explained in Supplementary material 1. We then estimated the ratios $r_{\text {estimated }} / r_{\text {true }}$ and $k_{\text {estimated }} / k_{\text {true }}$ and ran a one-way ANOVA between time series grouped by time series length to test whether the ratios of estimated parameters by true parameters were significantly different. The results are presented in Figure S2. We found no significant differences between population parameter estimates for different time series lengths. All estimates include the true estimate in their confidence intervals.


Figure S2. Comparison of the ratios between estimated population parameters ( $r$ and $K$ ) and true simulated population parameters (true $r$ and true K ) for different time series lengths.

Chapter 1, in full, is a reprint of the material as it appears in Fish and Fisheries 2018.
Giron-Nava, A., Johnson, A.F., Cisneros-Montemayor, A.M., Aburto-Oropeza, O. The dissertation author was the primary investigator and author of this material.

## CHAPTER 2:

## Quantitative argument for long-term ecological monitoring

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## NOTE

# Quantitative argument for long-term ecological monitoring 

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#### Abstract

Although it seems obvious that with more data, the predictive capacity of ecological models should improve, a way to demonstrate this fundamental result has not been so obvious. In particular, when the standard models themselves are inadequate (von Bertalanffy, extended Ricker etc.) no additional data will improve performance. By using time series from the Sir Alister Hardy Foundation for Ocean Science Continuous Plankton Recorder, we demonstrate that longterm observations reveal both the prevalence of nonlinear processes in species abundances and an improvement in out-of-sample predictability as the number of observations increase. The empirical results presented here quantitatively demonstrate the importance of long-term temporal data collection programs for improving ecosystem models and forecasts, and to better support environmental management actions.


KEY WORDS: Long-term monitoring • Predictability • Nonlinearity • Time series • Population dynamics • Ecological data


#### Abstract

INTRODUCTION Although there is a strong consensus for the benefits of long-term ecological monitoring and the creation of long-term datasets, there are significant fiscal and political challenges facing the continuation of these efforts. Given typical funding horizons and the inherent costs associated with long-term research programs (Callahan 1984, Magurran et al. 2010), it is no surprise that the majority of ecological research occurs within short time frames (Magnuson 1990). Ecosystem dynamics, however, may not be decipherable from observations on short timescales. Indeed, there is a growing view that nonlinear and nonstationary dynamics are common and may require


[^0]longer time series for study (Sugihara \& May 1990, Hsieh et al. 2005, Sugihara et al. 2012, Glaser et al. 2014). While most ecological models can be fit to short time series, they may subsequently fail when used to make predictions into the future or to explain changes that occur over the long term (Pilkey \& Pilkey-Jarvis 2007, Evans et al. 2012). The challenge of models to predict well has led some to suggest that scientific efforts, and particularly those in fisheries science, should be shifted away from forecasting as an attainable goal (Schindler \& Hilborn 2015). This view contradicts our natural expectation that ecosystems behave in nonrandom ways and that with more data (i.e. longer time series), models should generally improve. Although we commonly acknowledge out-
of-sample prediction to be the ultimate test for understanding, many current parametric ecosystem models fail to pass this test (Magurran et al. 2010). A possible reason is that these models are not well suited for describing nonlinear and nonstationary dynamics. Insofar as nonlinearity is to be expected in ecosystems, it is almost guaranteed that improperly formulated models will fail to achieve successful predictions, no matter how much additional data are provided.
If one were to use a minimal nonparametric nonlinear framework to model ecosystems, to what extent would short-term datasets limit predictive capabilities? In other words, what is the value of long-term ecosystem monitoring for gaining a predictive understanding of ecosystem processes? We investigate this question using a unique dataset and nonparametric analytical approach. The data are from the continuous plankton recorder (CPR) program at the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). The analytical approach is minimal in that it allows the data to inform ecological dynamics with no assumptions about underlying equations - so-called empirical dynamic models (EDMs) (Sugihara et al. 2012, DeAngelis \& Yurek 2015). Our objectives are straightforward and 2-fold: (1) to explore the relationship between time series length and the ability to detect nonlinearity, and (2) to examine the ability to predict future population abundances a month ahead as data availability/length increases.

## MATERIALS AND METHODS

## Dataset and data completeness

We use time series from the SAHFOS program, the longest and most spatially extensive planktonic ecosystem dataset currently available for the Atlantic Ocean. Our data, recorded by the CPR (Hays et al. 2005), comprise monthly average abundances of phytoplankton and zooplankton taxa in the southern North Sea ( $55^{\circ}$ to $58^{\circ} \mathrm{N}, 3^{\circ}$ to $11^{\circ} \mathrm{W}$ ) from 1958 to 2013, with sampling methods described in depth in Richardson et al. (2006). Data are available from the SAHFOS repository at http://doi.sahfos.ac.uk/ doi-library/data-for-zooplankton-and-phytoplankton-from-the-1)-southern-north-sea-and-2)-the-irish-sea. $\operatorname{aspx})$. Because of the practical limitations of identifying taxa and making counts, the time series within the SAHFOS repository count organisms at a variety of taxonomic levels (but typically either species or genus). We used the data as they are provided; thus, the time series refer to taxa rather than species.

We use 2 distinct measures to quantify the amount of data in each time series: time series length and data availability. Time series length refers to the number of data points in a time series, whereas data availability is defined as the number of nonzero values within a time series. We use the term data availability because we recognize that zeros could represent an absence of an organism or a lack of detection, and we are unable to distinguish between the two. Our analyses that examine the effect of time series length use subsampled segments from the time series with the fewest nonzero values or greatest data availability 'Effect of time-series length'.

## Effect of data availability

We investigate the degree of nonlinearity and predictability using 2 methods of time series analysis: simplex projection (Sugihara \& May 1990) and Smaps (Sugihara 1994). Simplex projection is used to assess the one-step-ahead predictive skill for each time series and is measured by the Pearson correlation coefficient ( $\rho$ ) between predictions and observations. Following Glaser et al. (2014), to minimize overfitting, we use leave-one-out cross validation, where the point being forecast is excluded from the data used to construct the forecast. Different values for the embedding dimension $(E)$ were tested (ranging from $E=1$ to $E=10$ ), and the optimal embedding dimension was selected as that which produced the highest $\rho$. We note that the optimal $E$ is a property of the data (how noisy and how long the time series are) as well as the underlying system (how complex it is in terms of numbers of variables) and indicates the number of lags that best resolves one-step-ahead forecasts. While $E$ can be informative about the complexity of the system or the number of drivers (Liu et al. 2012, Glaser et al. 2014), we caution against overinterpretation.
S-maps are used to test for nonlinear state dependence (Sugihara 1994). This involves demonstrating curvature in the attractor and is quantified by the improvement in $\rho(\Delta \rho)$ obtained with a nonlinear versus a linear model. Statistical significance for $\Delta \rho$ was determined using a randomization test. For each time series, we generated 100 surrogate time series and calculated a $\Delta \rho$ for each surrogate using the previously determined $E$. This creates a null distribution that can be compared to the original (nonshuffled) $\Delta \rho$. Nonlinearity is indicated when the $\Delta \rho$ statistic for the original time series is greater than the 0.95 quantile of the null distribution.

## Effect of time-series length

To examine the effect of time series length as a property independent of taxonomic identity, we focused on the 23 time series with the greatest data availability ( $\geq 461$ nonzero data points) and which were identified as significantly nonlinear. For each time series, we investigated the effect of varying the data length on predictability using randomly selected contiguous segments of length: 25, 50, 100, 200, 400. The subsampling was repeated 25 times at each length for each species (so that 575 [23 $\times 25$ ] subsamples were used to compute forecast performance at each length). Predictions were made using a form of leave-one-out cross validation where the predicted point is excluded to minimize overfitting. We then tested for nonlinear state dependence using S-maps as described in the previous subsection.

## Significance of nonlinearity as a function of data completeness

To test whether data availability or time series length are significant predictors of nonlinearity, we treated data availability and time series length by binning them into discrete categories (Fig. 1) and recorded the detection of nonlinearity as a binary response. Then, we fit a logistic regression using the R glm function (binomial family).


Fig. 1. Effect of data availability and time series length on nonlinearity detection. (a) Proportion of taxa identified as significantly nonlinear as a function of data availability (number of nonzero values). Numbers above each bar represent the number of taxa in that bin. (b) Proportion of taxa identified as significantly nonlinear as a function of time series length. Each bar corresponds to 575 subsamples of a specified length created by generating 25 subsamples from each of the 23 time series with the greatest data availability

## RESULTS AND DISCUSSION

The S-map analysis shows that nonlinear dynamics are more readily identified as data availability increases (Fig. 1a; p < 0.01; logistic regression, $\mathrm{df}=207$ ). For the 90 taxa with the lowest data availability ( $\leq 37$ nonzero data points out of 672), only $11 \%$ (10 taxa) showed significant nonlinear dynamics. In contrast, of the 90 taxa with 38 to 460 nonzero values, $57 \%$ ( 51 taxa) showed significant nonlinear dynamics. Finally, among the 28 taxa with the highest data availability ( $\geq 461$ nonzero values), $82 \%$ ( 23 taxa) showed significant nonlinear dynamics. In other words, the time series that are most complete also show stronger evidence for nonlinear dynamics. To test whether this effect could be driven by the specific taxa that happen to appear most often in the data, we also analyzed subsampled time series (artificially shortened from the 23 nonlinear taxa with the most data availability), finding a similar pattern (Fig. 1b; p $<0.01$; logistic regression, $\mathrm{df}=23$ ). It has been recognized that aggregating taxon levels can obscure nonlinear dynamics detection (Liu et al. 2014); however, we have shown that nonlinearity detection increases with time series length regardless of the taxonomic resolution. The subsampling procedure here obviates any taxon-specific effect related to aggregation that could reduce nonlinearity in more aggregated (linearly summed) groupings (Sugihara et. al. 1999).

A similar advantage with increased data holds for prediction; in general, greater data availability also corresponds to higher forecast skill (Fig. 2a). Using the same subsamples as in the previous paragraph, Fig. 2b shows that predictability also increases with time series length. Thus, we expect that as more data are collected, populations will be more readily identified as nonlinear and that the longer time series will enable better predictions. However, we note that even at the longest time series lengths ( $\geq 600$ nonzero values in Fig. 2a or 400 time points in Fig. 2b), the level of forecast skill can vary substantially. These differences in predictability could partially reflect differences in the natural response times (e.g. generation times), leading to differences in the density of points on the attractor (Table 1), with shorter generation times producing denser attractors;


Fig. 2. Effect of data availability and time series length on predictability ( $\rho$ ) for (a) each time series (circles) and (b) different lengths of subsampled time series. Each boxplot corresponds to 575 subsamples as in Fig. 1b. Bold lines: median; boxes: interquartile range; whiskers: minimum and maximum values

Documenting that ecosystems are capable of exhibiting predictability and that their dynamics are nonlinear is of considerable interest to agencies involved in data collection and to resource managers who must use those data. The reasonable expectation is that predictive models will improve with more data. However, if a model is a poor description of a system, no amount of additional data will improve predictability (MacNally 2000, DeAngelis \& Yurek 2015). For example, fishery stock prediction has been a difficult challenge despite continual model refinements and new data inputs (Ward et al. 2014, Schindler \& Hilborn 2015, Ye et al. 2015). The limitations of current ecosystem models to predict out of
however, they could also reflect exogenous effects, such as environmental drivers, that are not captured in the abundance time series and may therefore need to be included explicitly in forecast models (see Dixon et al. 1999, Deyle et al. 2013, and Harford et al. 2017 for examples).

Finally, we note that in addition to leave-one-out cross validation, for the 23 taxa with the highest data availability, nearly identical out-of-sample prediction results are obtained with 2 -fold cross validation. Here each half of the data series is used to predict the other half, and the predictions for the entire series are combined to calculate performance (Fig. 3). This demonstrates the robustness of the cross validation results and shows that the dynamics are stationary or essentially the same in both halves (Sugihara \& May 1990).

Table 1. Taxa whose time series have more than 600 nonzero values and the Pearson correlation coefficient ( $\rho$ ) from nonlinear prediction (from Fig. 2a)

| Taxon | $\rho$ |
| :--- | :---: |
| Oithona sp. | 0.71 |
| Total copepods | 0.70 |
| Para-pseudocalanus sp. | 0.67 |
| Acartia sp. | 0.58 |
| Chaetognaths | 0.54 |
| Chlorophyll index | 0.53 |
| Calanus I-IV | 0.48 |
| Calanus finmarchicus | 0.44 |
| Fish larvae | 0.34 |
| Calanus helgolandicus | 0.34 |
| Temora longicornis | 0.31 |
| Total hyperiids | 0.29 |

sample may arise in part from observational error in the data. However, we believe that a more significant problem is the mismatch between the traditional assumptions of equilibrium and linearity (DeAngelis \& Waterhouse 1987) and the increasing observations that many ecological systems are not in equilibrium but are demonstrably nonlinear (Fromentin \& Powers


Fig. 3. Comparison of the predictive skill ( $\rho$ ) for the 23 species with the highest data availability under 2 different cross validation schemes: (1) 2 -fold cross validation, where each half of the data series is used to predict the other half, and the predictions for the entire series are combined to calculate performance; and (2) leave-one-out cross validation. The 2 schemes produce results that do not differ significantly from each other ( $p<0.05$, paired $t$-test), showing that the dynamics are stationary in both halves of the data. Boxplots show the distribution of predictability values. Bold lines: median; boxes: interquartile range; whiskers: minimum and maximum values

2005, Hsieh et al. 2005, Glaser et al. 2014). Although short time series can be challenging to the identification of nonlinear dynamics and construction of empirical models, there have been several recent advances on this front (Hsieh et al. 2008, Glaser et al. 2011, Clark et al. 2015, Ye \& Sugihara 2016).
Data-driven approaches where causal variables and functional relationships are determined empirically may offer a viable alternative to inductive equa-tion-based approaches. For example, Sugihara et al. (2012) introduce an EDM method for using time series to identify the causal drivers of ecosystem dynamics, and several others (Dixon et al. 1999, Deyle et al. 2013, Harford et al. 2017) provide examples of incorporating these environmental effects into EDMs to forecast future ecosystem states - including apparently random events such as red tides (McGowan et al. 2017). These approaches do not rely a priori on hypothesized equations but instead infer relationships deductively as they appear in the data. With continued monitoring and longer time series, the ability of such techniques to describe nonlinear behavior will improve our understanding of ecological mechanisms, where unraveling the interdependence between environmental factors and endogenous population dynamics is certain to be critical for managing ecosystems in the context of climate change (Pershing et al. 2015). Thus, as predictive data-driven approaches continue to gain traction, investments in long-term data collection will surely yield long-term payoffs.

## CONCLUSIONS

The CPR at SAHFOS is a premiere example of how continuous long-term projects help to create new perspectives in ecology. By providing robust, longterm datasets, this program captures variability in species abundance that occurs on temporal scales ranging from interannual cycles to multidecadal shifts (Barton et al. 2003). Furthermore, SAHFOS, in collaboration with partners from around the globe, is now involved in conducting plankton counts in nearly every major ocean basin on earth. In addition to providing a long-term description of population dynamics, these spatially broad environmental monitoring programs can provide regional insights into global problems. Beyond the common sense value of collecting these data, our analyses provide a quantitative justification for continued support of these programs. These data are critical for predictability and understanding, which are particularly important
given increasing threats to global ecosystems, such as human exploitation pressures and climate change (Halpern et al. 2008).

Data archive. The data supporting the results of this study are available at http://192.171.193.159/doi-library/data-for-zooplankton-and-phytoplankton-from-the-1)-southern-north-sea-and-2)-the-irish-sea.aspx.

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## CHAPTER 3:

## Data circularity masks fisheries recruitment predictability

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#### Abstract

It is now common practice in fisheries to use data derived from total yields and model outputs to estimate stock biomass and recruitment. This low-cost alternative, however, generates data that is not useful when trying to understand the mechanisms that drive recruitment, nor to take accurate management decisions for species that are highly recruitment-driven. Using a global database of stock assessments, we find that traditional Stock-Recruitment Models (SRM), such as the Ricker and Beverton-Holt models, are somewhat successful at predicting data derived from assessment methods that introduce an assumed stock-recruitment relationship, such as in Biomass Dynamic Models. However, they are generally poor at predicting data that does not make such explicit assumptions or were purely observational. We also use Empirical Dynamics Modelling (EDM), an equation-free technique, and compare its performance to predict recruitment against the SRM. We find that EDM predicts all types of data better than the SRM models. This work aims to contextualize the need for continued observational datasets, especially when managing for short-lived species for which enhancing recruitment predictability can lead to better management strategies.


## Introduction

Faced with budget reductions for fisheries science and management worldwide, fisheries programs have experienced pressure to systematically replace observational data programs with less expensive indirect data estimations, so called synthesized data ${ }^{1,2}$. Synthesized data can be generated when sparse observations of standing stock biomass are filled in with model-based estimates to construct continuous time series ${ }^{3}$; or when there are only observations about fisheries landings and relative indices of abundance from which estimates of stock biomass and
recruitment can be derived ${ }^{4}$. These model-based estimates are heavily influenced by assumptions and preconceptions about how fish populations grow and respond to external stimuli 5. Nonetheless, such time series of stock biomass are commonly used as the input of other models and meta-analyses ${ }^{6-8}$.

A problem arises when synthesized data that were processed with explicit assumptions about the Stock-Recruitment (SR) relationship are then used to make predictions of future recruitment or stock biomass ${ }^{3,9}$. For instance, traditional Stock-Recruitment Models (SRM) can often be made to fit well to model-generated data, however, fitting is not prediction, and therefore it is not surprising that the accuracy of such predictions is often very low when tested in future years ${ }^{10,11}$. This issue has led some to conclude that it is impossible to predict recruitment ${ }^{11,12}$, often neglecting that the use of circular data and heavily parametrized models might mask such relationship.

Recent studies have taken on the problem of improving recruitment predictability and determining whether it is causally coupled to stock biomass ${ }^{12-14}$. By using a nonlinear and nonparametric framework, they have demonstrated that such relationship exists, and that recruitment is generally predictable, especially for short-lived species, such as small-pelagics ${ }^{13,15}$. Still, the issue of data circularity has been explored to a lesser extent ${ }^{3,8}$, and there is still a gap in the understanding of how using circular approaches might limit recruitment predictability.

In this study, we use 130 fish stocks from the Ransom Myers database, a global database of stock sizes and recruitment estimates to ask the following questions: (1) How well do three SRM (density independent, Ricker, and Beverton-Holt) predict the number of recruits across three different data collection and processing approaches (Biomass Dynamic Models - BDM,

Sequential Population Analysis - SPA, and Direct Observations - DO)? And (2) can S-maps, an equation-free approach from the Empirical Dynamics Modelling (EDM) framework ${ }^{16}$, provide better predictions than SRM?

The three data collection and processing approaches that we explore vary in the degree to which they incorporate assumptions about the population dynamics of fish stocks when estimating stock biomass and recruitment. While DO sampling programs collect data every year on both stock biomass and recruitment, BDM and SPA use a time series of catch (assuming perfect observations) and relative indices of abundance to estimate stock and recruitment through mathematical approximations. While doing so, select assumptions about the population dynamics are introduced ${ }^{4}$. For example, BDM require information/assumptions about growth, natural mortality, and the use of an explicit parametrized SR relationship, such as Beverton-Holt or Ricker ${ }^{4}$. On the other hand, SPA do not impose a functional form to the SR relationship, but by tracking the numbers of individuals harvested from a given year class, and an assumed known natural mortality, back calculates the total number of fish-per-age, including the number of recruits ${ }^{4}$. Based on this information, we ordered our data sets from least to most circular: DO, SPA, BDM. We were not able to recover data on the specific functional form that was introduced for each stock in the BDMs. Given this, we did not test each stock against its specific SR relationship, but rather we assumed that any kind of introduced function in the BDM would improve the predicting capacity of the SRM that were tested.

## Materials and Methods

## Ransom Myers Stock Recruitment database

We compared the predictions of the numbers of recruits through time from stock assessments using Stock-Recruitment Models (SRM) ${ }^{5}$ and an Empirical Dynamics Modelling (EDM) technique known as S-maps ${ }^{16-18}$. To do this, we used the Ransom Myers database ${ }^{19}$, a global repository of stock sizes and recruitment estimates for over 600 marine and freshwater fish populations ( $>100$ species). All populations from this database with at least 25 years of both stock size and recruitment data were included in our analysis, representing 130 populations from 36 species, spanning 8 Orders. We classified each time series according to the method through which they were generated: Biomass Dynamic Models $-\operatorname{BDM}(N=53)$, Sequential Population Analysis - SPA $(\mathrm{N}=71)$, and Direct Observations - DO $(\mathrm{N}=6)$. Table 3.1 presents a summary of the method used in each stock assessment and the length of each time series.

## Predictability - Standard Recruitment Models (SRM)

We evaluated the performance of three SRMs to predict the SR relationship in the 133 populations that were analyzed: density independence (Linear), Ricker, and Beverton-Holt ${ }^{5}$. These models assume that the number of recruits is a function of the current stock size. All models can be written in the general form $R_{t}=\alpha S_{t} g\left(S_{t}\right)$, where $R$ is recruitment, $S$ is stock size, $\alpha$ is the maximum rate of reproduction, and $g\left(S_{t}\right)$ is a function that accounts for densitydependent processes ${ }^{19}$. In the case of the density independent model, the function $g\left(S_{t}\right)=1$ and the model is a straight line that intercepts the origin $(0,0)$ with slope $\alpha$. The Ricker and BevertonHolt models introduce the term $\beta$, which is proportional to the product of fecundity and densitydependent mortality (see e.g. ${ }^{4}$ ). The three models are presented below.
(1) $R_{t}=\alpha S_{t} \quad-\quad$ Density independent
(2) $R_{t}=\alpha S_{t} e^{-\beta S_{t}}-\quad$ Ricker
(3) $R_{t}=\alpha S_{t}\left(\frac{1}{1+\beta S_{t}}\right) \quad-\quad$ Beverton-Holt

The Ricker and Beverton-Holt models were fitted on a $\log$ scale, re-written so that $y_{t}=$ $\ln \left[R_{t} / S_{t}\right]^{4}$. All models were fit using the function 'fminsearch' in Matlab R2015b.

To calculate the predictability achieved by each model, we performed a bootstrap leave-one-out cross validation. Given that the minimum length of any time series in our dataset was 25 years, the bootstrap was run 25 times for each time series with each SFM. To do this we excluded single, randomly selected points from each time series and then used 24 more randomly selected points to predict the initially excluded point. All predictions were made in the original recruitment scale. We then calculated the predictability $(\rho)$ as the Pearson correlation coefficient between the 25 observations and their respective predicted values.

## Predictability - Empirical Dynamics Modelling (EDM)

EDM is based on the idea that a time series is an observation of a state-dependent dynamic system (see introductory video https://youtu.be/fevurdpiRYg). Thus, if one were able to identify all the relevant variables (i.e. all " n " of them) and trace out the evolution of the system in this n-dimensional space, the trajectory would produce a geometric shape a.k.a. an "attractor." These attractors can be used to predict future states by following the trajectories at similar locations on the attractor ${ }^{17,20}$. However, in practice, it is difficult to collect or even to know what all the relevant variables in a system are; thus, it is not possible to reconstruct the original attractor. EDM acknowledges this fact and so relies on Takens' theorem, which states that a
single time series contains information about the whole system from which it was measured ${ }^{21}$. Assuming that the collected time series is $x_{t}$, one can reconstruct a "shadow" version of the original attractor by using lagged time series (eg. $x_{t-1}, x_{t-2}$ ) as proxies for other unknown time series of the same system. The principles and mechanics of EDM and Takens' theorem are further explained in ${ }^{22,23}$ and in a series of short animations (http://tinyurl.com/EDM-intro).

Although it is possible to construct an attractor from a single time series, predictability can often be improved by using two or more time series of variables measured from the same system ${ }^{17,24}$, such as fish stock biomass $\left(S_{t}\right)$ and number of recruits $\left(R_{t}\right)$. Therefore, we reconstruct the attractors for each population using combinations of the original time series $\left(R_{t}\right.$, $\left.S_{t}\right)$ and two time lags for each of them $\left(R_{t-1}, R_{t-2}, S_{t-1}, S_{t-2}\right)$, totaling up to 6 time series that can be combined in 63 different ways (ranging from using 1 to 6 time series at a time). In this study, we use two EDM techniques known as simplex projection ${ }^{16}$ and S-maps ${ }^{16}$ to predict numbers of recruits. Simplex projection uses the reconstructed attractor to find the nearest neighbors of a data point and follow their trajectories to calculate an average trajectory and make a prediction ${ }^{25}$. S-maps then use a tuning parameter $\theta$ to evaluate the improvement of predictability as nearest neighbors are assigned more weight in the prediction, so that $\theta=0$ equally weights all the points on the attractor, and $\theta>0$ gives more weight to nearby points. All our results report the predictability $(\rho)$ achieved from S-maps optimizing $\theta$.

## Predictability - Standard Recruitment Models (SRM)

In the same way as with the SRM, we perform a leave-one-out cross validation where each prediction involves excluding the single time point that we are trying to predict from the data that is used to build the forecast model. We then calculate $\rho$ as the Pearson correlation
coefficient between the observations and their respective predicted values for each of the 137 fish stocks. All analyses were performed using the $r E D M$ (v.2018) package in R version 3.2.3. In order to test whether a particular model's predictions were significantly different when using BDM, SPA and DO, we performed unpaired t -tests.

## Results

SRM reported the highest recruitment predictability ( $\rho$ ) when using data derived from BDM, with an average Pearson correlation coefficient of $0.39 \pm 0.04$ (s.e.), $0.40 \pm 0.04$ and 0.46 $\pm 0.04$ for the density independent, Ricker and Beverton-Holt models respectively (Figure 3.1). In contrast, the SRM performed poorly with both the SPA and the observational data sets. In the case of the SPA data, the average $\rho$ values were equal to $0.19 \pm 0.03,0.21 \pm 0.03$ and $0.22 \pm 0.03$ respectively for the same models. This represents an average decrease of $49 \%$ in the predicting capacity of SRM when using SPA as compared to BDM. Finally, in the case of DO, the average $\rho$ values were equal to $0.23 \pm 0.09,0.25 \pm 0.10$ and $0.22 \pm 0.11$ respectively (Figure 3.1). This represents an overall decrease of $43 \%$ when compared to BDM. We note that the reduction in predictability was significant $(\mathrm{P}<0.05)$ for each of the SRM when comparing BDM to SPA and DO.

EDM outperformed the three SRM in making predictions on the number of recruits regardless of the type of data used. EDM estimated Pearson correlation $\rho$ values equal to $0.59 \pm$ $0.02,0.61 \pm 0.02$ and $0.64 \pm 0.07$ for BDM, SPA and DO datasets respectively (Figure 3.1). We found no significant differences in the predictability of EDM between the different kinds of datasets $(\mathrm{P}>0.05)$.

## Discussions

Unfortunately, there is an overall lack of direct observation datasets, and even the global repository used in this study only contained 6 of them that were long enough to be analyzed. This echoes the importance of continued investments in long-term observational data collection programs without interruption ${ }^{1,2,15}$. The alternative, however, is the used of synthesized datasets. While these are useful for stock assessments when the priority is to set harvest quotas, it is questionable whether they are useful to analyze the population dynamics of target species ${ }^{3,8}$.

In this study, we demonstrate that BDM, which introduce an explicit SR relationship, are best predicted by SRM. This is to be expected, as it has been demonstrated that the estimates of fishing mortality and recruitment are highly dependent on the assumed SR relationship ${ }^{4,8}$. In contrast, SPA and direct observations had 43-49\% lower predictability when using SRM. In the case of direct observations, it is logical for such result to be the case, as no pre-conceptions were introduced into the data. However, in the case of the SPA, even though the data are treated with other assumptions, such as a constant natural mortality rates, there is never an explicit SR relationship introduced. As such, no SR dynamics are forced into the time series. The lack of predictability when using SRM in both, SPA and direct observations, shows that the assumed functional forms of SRM do not accurately describe the relationship between stock size and recruitment.

There is increasing consensus about the fact that using synthesized data to perform recruitment meta analyses might introduce too many assumptions through each individual stock assessment ${ }^{3,8}$. This has led many people to look for alternative routes to predict recruitment, primarily through environmental indices and ever-more parametrized models ${ }^{12}$. This approach,
though useful when there is a clear signal due to the susceptibility of some species' recruitment to poor environmental conditions, is far from solving the more general problem of recruitment predictability ${ }^{26,27}$. Recent work has taken on this challenge from a different perspective, using EDM as a nonlinear and non-parametric approach to test whether stock size and recruitment are causally coupled, and thus how can recruitment be predicted from stock status or catch per unit effort time series ${ }^{13,14,27}$. The results are promising, as stock size and recruitment have been consistently demonstrated to be causally coupled and predictable ${ }^{13,14}$.

In this work, we also demonstrate that EDM is better at predicting recruitment across different types of datasets and when compared to SRM ${ }^{13,14}$. EDM derives the dynamic mechanisms and causes directly from the data and thus can easily accommodate the dynamics introduced to the BDM data. However, we caution about the interpretation of the predictions derived from these datasets, as they might only reflect the expected recruitment from such models. More importantly, EDM also performs well with the DO data, and thus predicts recruitment in the real population (Figure 3.1).

EDM methods have previously been used to help improve recruitment predictability for a variety of stocks. Examples include: tuna in the North Pacific ${ }^{28}$, sockeye salmon in the Fraser River system in British Columbia ${ }^{27}$, red snapper in the Gulf of Mexico ${ }^{29}$, and menhaden in the Gulf of Mexico and the Atlantic U.S. coast ${ }^{29}$. The challenge remains to identify more precisely the species for which improved recruitment predictability would make a significant improvement to their management and on how to integrate these benchmark predictions from EDM methods more broadly into enacted management schemes that are sustainably adaptive to non-stationary harvest targets.

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## Tables

Table 3.1. List of stocks from the RAM Legacy database with 25 or more years of data. The table shows the scientific name of the species, original collection method (DO - Direct Observations, SPA - Sequential Population Analysis, BDM - Biomass Dynamics Model, length of the time series in number of years, and the predictability $(\rho)$ achieved by each of the 3 SRM and EDM.

| ID | Species | Method | Length <br> $(\mathbf{y r})$ | Linear | Ricker | Beverton <br> Holt | EDM |
| ---: | :--- | :--- | ---: | ---: | ---: | ---: | ---: |
| 1 | Alosa pseudoharengus | DO | 45 | 0.41 | 0.35 | 0.08 | 0.87 |
| 3 | Alosa pseudoharengus | DO | 35 | 0.5 | 0.67 | 0.67 | 0.79 |
| 11 | Engraulis encrasicolus | SPA | 27 | 0.81 | 0.79 | 0.82 | 0.78 |
| 13 | Salmo salar | DO | 37 | -0.43 | -0.05 | -0.21 | 0.68 |
| 14 | Salmo salar | DO | 38 | 0.38 | 0.25 | 0.35 | 0.51 |
| 24 | Thunnus obesus | SPA | 35 | 0.22 | 0.23 | -0.33 | 0.74 |
| 25 | Thunnus obesus | SPA | 26 | -0.56 | -0.35 | 0.01 | 0.47 |
| 26 | Thunnus obesus | SPA | 25 | 0.13 | 0.1 | -0.4 | 0.74 |
| 34 | Oncorhynchus <br> tshawytscha | BDM | 26 | -0.09 | -0.15 | -0.21 | 0.89 |
| 40 | Oncorhynchus keta | BDM | 38 | -0.5 | -0.04 | -0.44 | 0.31 |
| 41 | Oncorhynchus keta | BDM | 30 | 0.25 | 0.27 | 0.34 | 0.75 |
| 43 | Oncorhynchus keta | BDM | 28 | 0.45 | 0.43 | 0.48 | 0.45 |
| 44 | Oncorhynchus keta | BDM | 30 | -0.33 | -0.12 | 0.06 | 0.39 |
| 45 | Oncorhynchus keta | BDM | 25 | -0.38 | 0.12 | 0.1 | 0.73 |
| 46 | Oncorhynchus keta | BDM | 25 | -0.07 | 0.02 | 0.18 | 0.46 |
| 47 | Scomber japonicus | SPA | 36 | 0.49 | 0.35 | 0.41 | 0.4 |
| 48 | Gadus morhua | SPA | 35 | 0.7 | 0.53 | 0.6 | 0.62 |
| 49 | Gadus morhua | SPA | 28 | 0.75 | 0.7 | 0.73 | 0.89 |
| 50 | Gadus morhua | SPA | 27 | 0.29 | 0.19 | 0.39 | 0.77 |
| 53 | Gadus morhua | SPA | 31 | -0.04 | 0.16 | 0.2 | 0.75 |
| 54 | Gadus morhua | SPA | 41 | -0.27 | -0.42 | 0.08 | 0.59 |
| 55 | Gadus morhua | SPA | 33 | -0.21 | -0.32 | 0.15 | 0.83 |
| 56 | Gadus morhua | SPA | 45 | 0.11 | 0.17 | -0.19 | 0.42 |
| 62 | Gadus morhua | SPA | 33 | -0.38 | -0.23 | -0.31 | 0.54 |

Table 3.1. List of stocks from the RAM Legacy database with 25 or more years of data. Cont.

| ID | Species | Method | Length (yr) | Linear | Ricker | Beverton Holt | EDM |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 63 | Gadus morhua | DO | 35 | 0.47 | 0.48 | 0.58 | 0.65 |
| 64 | Gadus morhua | SPA | 68 | -0.1 | 0.07 | -0.08 | 0.41 |
| 65 | Gadus morhua | SPA | 27 | -0.62 | -0.15 | -0.28 | 0.54 |
| 67 | Gadus morhua | SPA | 43 | 0.24 | 0.37 | 0.33 | 0.59 |
| 68 | Gadus morhua | SPA | 45 | -0.04 | 0.26 | 0.09 | 0.66 |
| 69 | Gadus morhua | SPA | 59 | -0.28 | -0.01 | -0.1 | 0.47 |
| 70 | Gadus morhua | SPA | 30 | 0.16 | 0.25 | 0.26 | 0.43 |
| 73 | Gadus morhua | SPA | 27 | 0.12 | 0.05 | -0.65 | 0.41 |
| 77 | Promoxis annularis and nigromaculatus | DO | 28 | -0.22 | -0.22 | -0.55 | 0.52 |
| 82 | Coilia dussumieri | SPA | 26 | 0.84 | 0.78 | 0.68 | 0.61 |
| 84 | Melanogrammus aeglefinus | SPA | 38 | 0.56 | 0.47 | 0.7 | 0.67 |
| 86 | Melanogrammus aeglefinus | SPA | 26 | -0.83 | -0.6 | -0.05 | 0.76 |
| 87 | Melanogrammus aeglefinus | SPA | 68 | 0.37 | 0.33 | 0.53 | 0.76 |
| 88 | Melanogrammus aeglefinus | SPA | 33 | 0.04 | 0.26 | -0.06 | 0.64 |
| 89 | Melanogrammus aeglefinus | SPA | 28 | -0.35 | -0.27 | -0.03 | 0.33 |
| 90 | Melanogrammus aeglefinus | SPA | 44 | 0.1 | 0.26 | 0.28 | 0.51 |
| 91 | Melanogrammus aeglefinus | SPA | 32 | -0.12 | -0.4 | -0.21 | 0.88 |
| 92 | Melanogrammus aeglefinus | SPA | 66 | -0.32 | -0.4 | -0.4 | 0.58 |
| 94 | Melanogrammus aeglefinus | SPA | 29 | -0.39 | -0.34 | -0.58 | 0.65 |
| 108 | Clupea harengus | SPA | 38 | -0.13 | 0.32 | -0.06 | 0.58 |
| 110 | Clupea harengus | SPA | 65 | 0.66 | 0.51 | 0.44 | 0.75 |
| 116 | Clupea harengus | DO | 48 | 0.15 | 0.24 | 0.22 | 0.45 |
| 122 | Clupea harengus | SPA | 49 | 0.29 | 0.37 | 0.29 | 0.58 |
| 124 | Clupea harengus | SPA | 44 | 0.14 | 0.22 | 0.18 | 0.66 |
| 125 | Clupea harengus | SPA | 41 | 0.24 | 0.53 | 0.44 | 0.56 |
| 126 | Clupea harengus | SPA | 38 | -0.32 | 0.16 | -0.05 | 0.48 |

Table 3.1. List of stocks from the RAM Legacy database with 25 or more years of data. Cont.

| ID | Species | Method | Length (yr) | Linear | Ricker | Beverton Holt | EDM |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 127 | Clupea harengus | SPA | 38 | -0.3 | -0.29 | -0.07 | 0.25 |
| 128 | Clupea harengus | SPA | 38 | 0.05 | -0.1 | 0.31 | 0.6 |
| 129 | Clupea harengus | SPA | 38 | -0.45 | -0.13 | -0.32 | 0.74 |
| 135 | Clupea harengus | SPA | 38 | -0.04 | 0.07 | 0.24 | 0.64 |
| 136 | Clupea harengus | SPA | 38 | -0.35 | -0.34 | -0.46 | 0.61 |
| 140 | Penaeus orientalis | SPA | 26 | -0.03 | 0.11 | 0.11 | 0.16 |
| 142 | Salvelinus namaycush | SPA | 40 | 0.78 | 0.8 | 0.76 | 0.91 |
| 143 | Scomber scombrus | DO | 36 | 0.54 | 0.64 | 0.61 | 0.46 |
| 144 | Trachurus mediterraneus | SPA | 45 | -0.16 | -0.16 | -0.04 | 0.67 |
| 148 | Brevoortia tyrannus | SPA | 40 | 0.05 | 0.37 | 0.2 | 0.71 |
| 149 | Brevoortia patronus | SPA | 26 | 0.36 | 0.38 | 0.4 | 0.67 |
| 153 | Sebastes alutus | SPA | 30 | -0.62 | -0.53 | 0.03 | 0.56 |
| 154 | Sebastes alutus | SPA | 31 | 0.23 | 0.07 | 0.4 | 0.66 |
| 155 | Sebastes alutus | SPA | 26 | -0.81 | -0.62 | -0.03 | 0.79 |
| 156 | Sebastes alutus | SPA | 29 | 0.43 | 0.46 | 0.52 | 0.42 |
| 158 | Esox lucius | SPA | 35 | 0.15 | 0.22 | 0.16 | 0.33 |
| 159 | Esox lucius | SPA | 35 | -0.09 | 0.01 | -0.03 | 0.43 |
| 160 | Oncorhynchus gorbuscha | BDM | 25 | 0.6 | 0.63 | 0.63 | 0.51 |
| 189 | Oncorhynchus gorbuscha | BDM | 25 | 0.79 | 0.8 | 0.81 | 0.72 |
| 193 | Oncorhynchus gorbuscha | BDM | 27 | 0.1 | -0.18 | 0.33 | 0.38 |
| 194 | Oncorhynchus gorbuscha | BDM | 25 | 0.15 | 0.15 | 0 | 0.28 |
| 197 | Oncorhynchus gorbuscha | BDM | 42 | 0.1 | 0.26 | 0.25 | 0.65 |
| 200 | Oncorhynchus gorbuscha | BDM | 34 | 0.48 | 0.54 | 0.6 | 0.57 |
| 202 | Oncorhynchus gorbuscha | BDM | 27 | 0.52 | 0.55 | 0.6 | 0.72 |
| 203 | Oncorhynchus gorbuscha | BDM | 27 | 0.25 | 0.24 | 0.33 | 0.67 |
| 207 | Oncorhynchus gorbuscha | BDM | 27 | -0.66 | -0.11 | -0.05 | 0.3 |

Table 3.1. List of stocks from the RAM Legacy database with 25 or more years of data. Cont.

| ID | Species | Method | Length <br> (yr) | Linear | Ricker | Beverton <br> Holt | EDM |
| :---: | :--- | :--- | ---: | ---: | ---: | ---: | ---: |
| 208 | Oncorhynchus <br> gorbuscha | BDM | 34 | 0.05 | -0.01 | 0.31 | 0.57 |
| 211 | Oncorhynchus <br> gorbuscha | BDM | 27 | 0.04 | 0.07 | 0.47 | 0.55 |
| 212 | Oncorhynchus <br> gorbuscha | BDM | 27 | 0.48 | 0.51 | 0.56 | 0.85 |
| 217 | Pleuronectes platessa | SPA | 28 | -0.17 | -0.39 | -0.22 | 0.62 |
| 219 | Pleuronectes platessa | SPA | 35 | 0.03 | 0.08 | -0.37 | 0.48 |
| 221 | Pollachius virens | SPA | 32 | -0.26 | -0.12 | -0.07 | 0.52 |
| 222 | Pollachius virens | SPA | 32 | 0.2 | 0.2 | -0.38 | 0.55 |
| 223 | Pollachius virens | SPA | 32 | 0.12 | 0.14 | 0.35 | 0.5 |
| 224 | Pollachius virens | SPA | 33 | 0.21 | 0.27 | 0.55 | 0.55 |
| 225 | Pollachius virens | SPA | 30 | -0.01 | 0.27 | 0.24 | 0.73 |
| 233 | Anoplopoma fimbria | SPA | 25 | 0.01 | 0.07 | 0.19 | 0.54 |
| 236 | Sardinops sagax | SPA | 31 | 0.05 | 0.13 | 0.13 | 0.8 |
| 239 | Sardinops sagax | SPA | 31 | 0.7 | 0.73 | 0.71 | 0.78 |
| 245 | Thunnus maccoyii | SPA | 45 | 0.75 | 0.77 | 0.77 | 0.91 |
| 249 | Merluccius bilinearis | SPA | 33 | 0.83 | 0.82 | 0.85 | 0.95 |
| 250 | Merluccius bilinearis | SPA | 33 | 0.53 | 0.59 | 0.57 | 0.92 |
| 251 | Oncorhynchus nerka | BDM | 39 | 0.86 | 0.86 | 0.88 | 0.77 |
| 252 | Oncorhynchus nerka | BDM | 43 | 0.59 | 0.68 | 0.66 | 0.82 |
| 253 | Oncorhynchus nerka | BDM | 39 | 0.35 | 0.35 | 0.42 | 0.57 |
| 254 | Oncorhynchus nerka | BDM | 43 | 0.43 | 0.63 | 0.55 | 0.55 |
| 255 | Oncorhynchus nerka | BDM | 38 | 0.27 | 0.28 | 0.25 | 0.61 |
| 256 | Oncorhynchus nerka | BDM | 33 | 0.39 | -0.28 | 0.46 | 0.56 |
| 257 | Oncorhynchus nerka | BDM | 45 | 0.75 | 0.8 | 0.8 | 0.66 |
| 258 | Oncorhynchus nerka | BDM | 38 | -0.34 | 0.14 | -0.19 | 0.75 |
| 259 | Oncorhynchus nerka | BDM | 39 | 0.63 | 0.68 | 0.72 | 0.54 |
| 260 | Oncorhynchus nerka | BDM | 43 | 0.69 | 0.76 | 0.7 | 0.61 |
| 262 | Oncorhynchus nerka | BDM | 32 | 0.55 | 0.53 | 0.69 | 0.35 |
|  |  |  |  |  |  |  |  |

Table 3.1. List of stocks from the RAM Legacy database with 25 or more years of data. Cont.

| ID | Species | Method | Length <br> (yr) | Linear | Ricker | Beverton <br> Holt | EDM |
| ---: | :--- | :--- | ---: | ---: | ---: | ---: | ---: |
| 264 | Oncorhynchus nerka | BDM | 39 | 0.61 | 0.6 | 0.62 | 0.76 |
| 267 | Oncorhynchus nerka | BDM | 39 | 0.77 | 0.74 | 0.9 | 0.97 |
| 268 | Oncorhynchus nerka | BDM | 43 | 0.94 | 0.91 | 0.91 | 0.85 |
| 270 | Oncorhynchus nerka | BDM | 39 | -0.01 | 0.21 | -0.05 | 0.63 |
| 271 | Oncorhynchus nerka | BDM | 62 | 0.35 | 0.38 | 0.28 | 0.45 |
| 274 | Oncorhynchus nerka | BDM | 38 | 0.67 | 0.67 | 0.69 | 0.66 |
| 275 | Oncorhynchus nerka | BDM | 38 | 0.69 | 0.8 | 0.76 | 0.56 |
| 276 | Oncorhynchus nerka | BDM | 42 | 0.81 | 0.85 | 0.78 | 0.51 |
| 277 | Oncorhynchus nerka | BDM | 32 | 0.65 | 0.49 | 0.67 | 0.54 |
| 279 | Oncorhynchus nerka | BDM | 38 | 0.7 | 0.58 | 0.74 | 0.74 |
| 280 | Oncorhynchus nerka | DO | 32 | 0.17 | 0.23 | 0.28 | 0.63 |
| 283 | Oncorhynchus nerka | BDM | 42 | -0.07 | -0.03 | 0.01 | 0.55 |
| 284 | Oncorhynchus nerka | BDM | 39 | 0.23 | 0.31 | 0.24 | 0.66 |
| 285 | Oncorhynchus nerka | BDM | 45 | 0.37 | 0.4 | 0.43 | 0.26 |
| 287 | Oncorhynchus nerka | BDM | 39 | 0.63 | 0.58 | 0.53 | 0.62 |
| 288 | Oncorhynchus nerka | BDM | 43 | 0.33 | 0.66 | 0.42 | 0.61 |
| 289 | Oncorhynchus nerka | BDM | 39 | 0.72 | 0.71 | 0.83 | 0.6 |
| 290 | Oncorhynchus nerka | BDM | 43 | 0.78 | 0.8 | 0.83 | 0.46 |
| 293 | Oncorhynchus nerka | BDM | 33 | -0.12 | 0.12 | 0.14 | 0.41 |
| 294 | Oncorhynchus nerka | BDM | 30 | 0.19 | -0.12 | 0.28 | 0.64 |
| 296 | Oncorhynchus nerka | BDM | 38 | 0.59 | 0.63 | 0.59 | 0.52 |
| 298 | Oncorhynchus nerka | BDM | 39 | 0.78 | 0.04 | 0.82 | 0.67 |
| 299 | Oncorhynchus nerka | BDM | 43 | 0.43 | 0.5 | 0.44 | 0.66 |
| 301 | Oncorhynchus nerka | BDM | 40 | -0.08 | 0.18 | 0.05 | 0.5 |
| 305 | Solea vulgaris | SPA | 36 | -0.27 | -0.19 | -0.29 | 0.59 |
| 305 | Solea vulgaris | SPA | 36 | -0.27 | -0.19 | -0.29 | 0.59 |
| 311 | Sprattus sprattus | SPA | 43 | 0.55 | 0.55 | 0.54 | 0.64 |
| 323 | Merlangius merlangus | SPA | 27 | -0.34 | -0.3 | -0.18 | 0.49 |
| 324 | Merlangius merlangus | SPA | 74 | -0.37 | -0.35 | -0.29 | 0.28 |
| 326 | Merlangius merlangus | SPA | 27 | -0.69 | -0.04 | -0.05 | 0.73 |
| 331 | Thunnus albacares | SPA | 25 | 0.28 | 0.05 | 0.39 | 0.7 |

## Figures



Figure 3.1. Comparison of predictability of the Spawner-Recruit relationships using three standard recruitment models (Linear, Ricker and Beverton-Holt) and S-maps across datasets obtained with three approaches: Biomass Dynamic Models - BDM, Sequential Population Analysis - SPA, and Direct Observations - DO. The y-axis represents the average predictability as measured by the correlation coefficient between 25 observed data points and their corresponding modeled predictions. The error bars represent the standard error.

## CHAPTER 4:

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

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#### Abstract

The high variability of small pelagic fisheries is regularly attributed by fisheries managers to environmental processes, such as El Niño Southern Oscillation and the Pacific Decadal Oscillation, often neglecting the role that fisheries play themselves. Here, we use a nonparametric, nonlinear modeling approach (Empirical Dynamics Modeling) to test whether we can identify the separate effects of fishing pressure and environmental variability on the dynamics exhibited by the Pacific sardine fishery in the Gulf of California, Mexico. Our results show that the effect of fishing pressure is not only detectable but comparable to that of environmental variability. Even further, when trying to predict total catches two years into the future, the best models are those that account for both fishing effort and environmental indices together. Even though there have been reports on the mechanisms that explain the increased variability of exploited populations, our work is the first to use this knowledge to predict yields from multiple years in advance. We think that our models can be adapted to develop harvesting strategies based on predictions of high and low fisheries productivity, giving a chance to the fleet to reduce the fishing effort in time to prevent the associated economic and social loses.


## Introduction

Small pelagic fish, such as sardines and anchovies, support the largest fisheries in the world, contributing with up to $37 \%$ of global landings by weight ${ }^{1,2}$. However, these fisheries are subject to large fluctuations, with total landings often varying by two orders of magnitude over just a couple of years ${ }^{2-4}$. This high variability is often attributed to stochastic processes and environmental drivers, such as temperature, wind patterns and primary productivity ${ }^{4-6}$; often neglecting the impacts of fishing activities on the population dynamics of the target resources ${ }^{7}$.

As a result, fisheries management for these species is not always effective, as it often relies exclusively on highly uncertain climate models ${ }^{8}$.

Recent work has proposed that fishing activities might affect forage fish population dynamics and increase their variability by two main mechanisms. (1) Given that fishing is sizeselective, it truncates the age structure, making the population less capable of recovering from extreme environmental events ${ }^{9}$. And (2), higher mortality rates generate nonlinear instabilities that change the intrinsic population dynamics ${ }^{1,9}$. Still, these two effects are rarely incorporated into the models used to manage small-pelagics' fisheries ${ }^{10}$. Here, we use a case study of the Pacific sardine (Sardinops sagax) in the Gulf of California, Mexico (Fig. 4.1), to ask the following questions. How does the effect of fishing activities compare to that of environmental variability on the species' population dynamics and how can we use this information to make better predictions that inform management?

The Gulf of California, Mexico, is one of the most productive and biodiverse marine ecoregions in the world ${ }^{5}$, contributing approximately $50 \%$ of Mexico's total fisheries landings. Small pelagic fish captured in the Gulf of California alone contribute up to $21 \%$ of the total national reports by weight, with the Pacific sardine being the dominant species caught during many years ${ }^{11}$. This fishery developed in the late 1960s in the very productive waters around the city of Guaymas, which to date is still the largest port for sardine fisheries in Mexico ${ }^{12}$. In 1991, the fishery experienced its first collapse, going from total annual landings of almost 300,000 tonnes to less than 10,000 tonnes in a period of two years ${ }^{2,12}$ (Fig. 4.2a). After this first collapse, the fishery has undergone three more collapses with a periodicity of between 3-8 years, and which clearly show a boom and bust dynamic behavior (Fig. 4.2a).

Even though there is evidence suggesting that fisheries can have an impact in the population dynamics of Pacific sardine in the Gulf of California ${ }^{2,11}$, as in other regions of the world, fisheries managers in the region have assumed that the boom and bust cycles are primarily driven by large-scale environmental variability ${ }^{3,13,14}$. In particular, by the Pacific Decadal Oscillation (PDO) and El Niño Southern Oscillation (ENSO) ${ }^{3,13,14}$. As such, fishing is often assumed to have no effect on the observed dynamics and it has been recommended that to deal with the unpredictable environmental conditions, it is preferable to set a constant harvest rate $(H R=0.25-0.29)$ relative to the total available biomass ${ }^{10,15}$. In this work we use a nonparametric approach known as Empirical Dynamics Modelling (EDM) ${ }^{16,17}$ 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 then construct a model to test whether or not incorporating explicit estimates of fishing effects improves the predictability of fisheries yields.

## Materials and methods

Our analysis is divided into three components: (1) a multivariate linear analysis to test for the direct and lagged correlations between environmental variables and Pacific sardine's catch/abundance time series, (2) a non-parametric analysis by using Empirical Dynamics Modelling (EDM) to test for the causal influence of environmental variables and fishing effort on catch/abundance time series, and (3) a simple Markovian model calibrated with literature-based population parameters to test the relationships found in the previous analyses.

## Data collection

We collected fisheries dependent data from the Sonoran small pelagic fishing fleet based at the ports of Guaymas and Yavaros, Sonora, Mexico (Fig. 4.1). The data span from 1969 to 2015, and include total catch, effort in number of trips and catch per unit effort (CPUE). Most data were obtained from published material ${ }^{11,12}$ and updated with data extracted from the annual reports of the Centro Regional de Investigacion Pesquera (CRIP) in Guaymas. We present the time series for each of these three variables in Fig. 4.2.

We also collected published fisheries independent data to estimate total abundance of Pacific sardines in the region. These data are based on the proportion of Pacific sardine in the diet of Elegant Terns (Thalasseus elegans) in the Midriff Island Region (Fig. 4.1) from 1985 to $2013{ }^{11}$. Given the shorter time span of this time series, we tested whether the CPUE could be a valid proxy for abundance as estimated by the birds' stomach contents. We found a significant linear relationship between these variables (Fig. 4.S4a, $\mathrm{R}^{2}=0.34, \mathrm{P}<0.01$ ). As previous works suggest, we also tested for an exponential relationship that can account for hyperstability effects, however, the achieved correlation was much lower when compared to the linear model $\left(\mathrm{R}^{2}=\right.$ $0.14, \mathrm{P}<0.01)$. We also found a strong linear relationship between the derivatives of CPUE and the proportion of sardines in the diet of birds (Fig. 4.S4b, $\mathrm{R}^{2}=0.33, \mathrm{P}<0.01$ ). For all posterior analyses, we considered CPUE as a valid proxy for Pacific sardine's abundance.

Finally, we collected the annual average for different environmental indices spanning the time range from 1951 to 2015. The collected variables were the El Niño Southern Oscillation Index (SOI) ${ }^{18}$, the Pacific Decadal Oscillation (PDO) index ${ }^{19}$ and an upwelling index derived from wind measurements at the mouth of the Gulf of California $\left(21^{\circ} \mathrm{N}, 107^{\circ} \mathrm{W}\right)$, which was the closest monitoring station that had data for the whole time span ${ }^{20}$. The upwelling index was
specific for the spring season, often associated to the spawning period for Pacific sardine ${ }^{21}$. Fig. 4.2a shows in red and blue the strong El Niño and la Niña events respectively.

For all subsequent analyses, we consider total catch, $\Delta$ catch and CPUE as the dependent variables; while effort, ENSO, PDO and the upwelling index were considered as the explanatory variables. All variables were normalized by subtracting the mean and dividing by their standard deviation prior to every analysis.

## Multivariate linear analysis

We evaluated the linear correlation and the lagged linear correlation between the total catch and the explanatory variables as presented in the correlograms in Fig. 4.S1. We selected the lag with the highest predictability for each explanatory variable to construct a multivariate model. The optimal lags for each variable were used in posterior analyses that considered the response time of each variable to make predictions.

In order to test the predictability of the multivariate model, we ran a leave-one-out cross validation. To do it, we excluded one single time point at a time and built the multivariate model with the rest of the time points. Then, we predicted the excluded total catch value. Finally, we performed a linear regression between the predicted and observed values. We report the Pearson correlation coefficient $(\rho)$ as the predictability of this model.

## Empirical Dynamics Modelling (EDM)

EDM is a set of methods based on the idea that a time series is an observation of a statedependent dynamic system. For example, if it was possible to identify all the variables that
interact in one system, one could plot each of them in an axis of an n-variables dimensional space. Then, by connecting the dots in a sequential order, they would reveal trajectories that form a geometric shape or "attractor." Such attractors 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 22,23.

In reality, however, it is difficult to measure or even to know all the variables that interact in an ecosystem. Thus, it is impossible to reconstruct the original attractor. However, Takens' theorem states that it is possible to recover information about a whole system by using only one time series, given that this one was influenced by every other variable in the system and thus recorded information about all of them ${ }^{24}$. Assuming that the collected time series is $x_{t}$, one can reconstruct a "shadow" version of the original attractor by using lagged time series (eg. $x_{t-1}$, $\left.x_{t-2}\right)$ 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).

## Simplex projection

Simplex projection is an EDM technique that evaluates the one-step-ahead predictive skill for each individual time series. It does it by constructing a shadow manifold of the system by using an individual time series with E dimensions and $\mathrm{E}-1$ time lags. We tested the predictability achieved by using E values spanning from 1 to 10 . As with the multivariate model, predictability was measured by performing a leave-one-out cross validation. The results are presented in Fig. 4.S2. For posterior EDM analyses, we use the E value that achieved the highest predictability from simplex projection for each variable.

## Convergent Cross-Mapping (CCM)

CCM is a technique based on the concept that if two time series come from the same dynamic system, their shadow manifolds will share topological properties, and if so, they could be identified to be causally coupled ${ }^{17}$. For example, if the variables $x$ and $y$ share a common attractor, one would expect that nearby points in the attractor reconstructed by just using $x$, would map to points that would be nearby in the attractor reconstructed by just using $y$, and vice versa. Additionally, CCM is able to identify directional influence, as has been demonstrated for Pacific sardine and Northern anchovy in the California Current System, both being causally driven by Sea Surface Temperature, but not influencing each other, nor temperature ${ }^{17,23}$. In this study, we used CCM to identify if any of the explanatory variables (effort, SOI, PDO or upwelling) had a causal influence on the observed time series of total catch, its derivative, or CPUE. When testing whether variable $x$ is causally driven by $y$, we use the embedding dimension (E) for $x$ that was obtained in the simplex analysis and as reported in Fig. 4.S2. We report the predictability achieved by performing a leave-one-out cross-validation and report the Pearson correlation coefficient ( $\rho$ ) between predictions and observations. In Fig. 4.S3 we only present the significant relationships.

## Multivariate predictive EDM and scenario exploration

The predictability of a simplex projection can be improved by substituting some of the lagged time series in an attractor for the proper explanatory variable ${ }^{22,23,25}$. For example, if we were to predict total catch and we knew that upwelling had a strong causal influence on it, instead of reconstructing a manifold 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 reconstructed the
attractor for total catch and CPUE with an $\mathrm{E}=3$. Then, we used 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 and CPUE 2-years into the future. In Table 4.1 and Table 4.2, we present the five models with the highest predictability along with the univariate model predictability. The univariate model, highlighted in grey, represents the attractor that was solely reconstructed with catch or CPUE. For the rest of the models, they were constructed by substituting a lagged time series by the indicated variable with the corresponding time lag. We report the predictability and mean absolute error (m.a.e.) of the correlation between observed and predicted values by performing a leave-one-out cross validation. Given that all the models use three variables to make predictions, we considered them to be on an even ground, allowing the use of predictability as a valid metric to select for the best models.

Additionally, we evaluated the effect that increasing effort and upwelling (the two variables that were identified to have the strongest influence in the CCM analysis) would have in the dynamic behavior of total catch in subsequent years. To do so, we increased effort and upwelling at each time step by $5 \%$ of their standard deviation ${ }^{25}$. Then, we predicted what the total catch value would be two years ahead in the case of effort, and four years ahead in the case of upwelling, as these were demonstrated to be the time lags for which each variable had the strongest signal. This approach allows us not only to quantify the magnitude of the effect that increasing a variable would have, but also to know the direction. Additionally, it allows us to evaluate how different starting conditions (e.g. a certain level of initial effort) will evolve with the same perturbation. Fig. 4.3 presents the results by using the initial value for the explanatory variable in the x -axis and the coefficient ( $\Delta$ catch) / ( $\Delta$ variable) in the y -axis. We also calculated
the percentage that these changes would represent when compared to their original values as ( $\Delta$ catch\%) / ( $\Delta$ variable\%) (Fig. 4.S5).

## Markovian model

In order to test the findings from the EDM analysis that effort and environmental variability could both have an influence in future catch, we performed a simple Markovian simulation. Given that the population size was drawn to very low levels during the first collapse, we assumed that the population experienced no density dependent processes and grew in an exponential fashion. We performed an extensive literature review to obtain a stable size structure, mortality and fecundity rates for the Pacific sardine ${ }^{10,12,13,26}$. These parameters are reported in Table 4.S1. Then, we ran a Markovian simulation for 30-time steps by applying different fishing rates (F), fishing behavior, and environmental variability parameters. The fishing behavior parameter reproduced a myopic behavior, which refers to fishers expecting to catch a similar amount to what they caught last year, as has been reported for other fisheries around the world ${ }^{27,28}$. Therefore, after a good year, they would expect a good catch. If this was not the case, they would increase fishing effort by trying to compensate for the initial loses. In our model, they elevate the effort by $50 \%$. We named this parameter Adjust. On the other hand, we simulated periodic environmental variability by incorporating a sinusoidal function with approximately the SOI periodicity. This function was then multiplied by the natural mortality for each age-class. We named the parameter that turns on or off these dynamics as Env. We ran five simulations as shown in Fig. 4.4 and described below:
i. Low fishing mortality $(\mathrm{F}=0.2)$, No Adjust, No Env
ii. Low fishing mortality $(\mathrm{F}=0.2)$, No Adjust, Yes Env
iii. Medium fishing mortality $(\mathrm{F}=0.4)$, No Adjust, No Env
iv. Medium fishing mortality ( $\mathrm{F}=0.4$ ), Yes Adjust, No Env
v. Medium fishing mortality $(\mathrm{F}=0.4)$, Yes Adjust, Yes Env

All the results were normalized to the maximum catch value for each scenario to compare the dynamic behavior of the four models in the same scale from 0 to 1 . Scenario five was run several times by changing the period (3 to 7 years) and phase $\left(-180^{\circ}\right.$ to $\left.180^{\circ}\right)$ of the sinusoidal function that controlled environmental variability and hence natural mortality to test for the robustness of our results (Fig. 4.S6). The scenario five in Fig. 4.4 reports the results from the simulation with period $=7$ years and phase $=0^{\circ}$.

## Results

## 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. We found that fishing effort was correlated with total catch at $0-1$ - and marginally at 2 -time steps. The SOI was only significantly and 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 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 $\mathrm{R}^{2}$ was equal to 0.28 , while the leave-one-out cross validation predictability was equal to 0.21 .

## EDM predictability and scenario exploration

We obtained the embedding dimension values (E) for each variable through simplex projection (Fig. 4.S2). The values for catch, $\Delta$ catch and CPUE were 3, 6 and 4 respectively. For the explanatory variables, the values for effort, SOI, PDO and upwelling were $6,6,6$, and 3 respectively. These values were subsequently used in each analysis where the selected variable was being predicted from another time series.

We performed a CCM analysis to detect whether the explanatory variables had a causal influence on catch, $\Delta$ catch and CPUE (Fig. 4.S3). We found a strong effect of effort on total catch and CPUE, as well as a strong effect of $\Delta$ catch in current effort. This means that the comparison between this year and last year's catch influences effort, as fishers will try to make as much or more profit as last year. The SOI showed no causal effect on any of the fishery variables. The PDO and the upwelling index showed a weak causal influence on $\Delta$ catch and a stronger influence on total catch and CPUE, comparable to the effect of fishing effort.

We used an $\mathrm{E}=3$ (derived from Fig. 4.S2) to build a predictive model for total catch and CPUE two years into the future. We found that the univariate model achieved a predictability equal to 0.51 , with m.a.e. equal to 0.69 (Table 4.1) for total catch and equal to 0.41 for CPUE
(Table 4.2). However, when incorporating the explanatory variables at different time lags, the
best five models ranged in predictability between 0.81 to 0.85 for total catch and 0.77 to 0.80 for CPUE. In the case of total catch, the best model $(\rho=0.85$, m.a.e. $=0.45)$ used total catch with a lag of 2 years, the PDO with a lag of 1 year, and effort with a lag of 4 years. The next two best models used only effort and upwelling time lags (Table 4.1). In the case of CPUE, the best model $(\rho=0.80$, m.a.e. $=0.45)$ used SOI with lag 1 , upwelling with lag 4 and effort with lag 4. The next two best models used primarily upwelling lags (Table 4.2).

Given that effort and upwelling showed to be the most important variables to improve predictability, thus being the ones with the strongest causal influence, we performed scenario explorations to discern their effects on total catch. The scenario explorations showed that when the starting effort condition is low, increasing effort would result in higher yields 2 years into the future (Fig. 4.3a). However, as the starting effort increases, increasing effort would eventually reduce total catch, probably due to the overexploitation of the resource. On the other hand, when the starting upwelling condition is low, increasing upwelling will result in higher yields 4 years into the future (Fig. 4.3b). However, as the starting upwelling condition increases, the effect of increased upwelling will remain positive, although reaching an asymptote for the highest values. When we analyzed the changes as a percentage of the starting value, we found similar trends, with changes in catch between $-5 \%$ and $5 \%$ for increasing effort and between $0 \%$ and $2.5 \%$ for increasing upwelling (Fig. 4.S5).

## Markovian model

The Markovian model showed that for the scenario when fishing effort was low $(\mathrm{F}=0.2)$ and with the parameters Adjust and Env off, the total catch experienced an indefinite exponential growth (Fig. 4.4). On the other hand, when fishing effort was kept low, Adjust off, but Env on,
the total catch experienced cycles but still with an increasing trend. When the fishing pressure was increased $(\mathrm{F}=0.4)$, and the parameters Adjust and Env were off, the total catch showed irregularities in the exponential growth. Approximately every 6-8 years the total catch reached a semi-stable point, after which it increased in an almost exponential fashion. When keeping fishing pressure up $(\mathrm{F}=0.4)$, and turning on the Adjust parameter, the total catch started experiencing boom and bust cycles with a periodicity of approximately 5-6 years. These cycles also got more extreme with each iteration, with maximums increasing at a faster rate than minimums. Finally, when both, Adjust and Env were turned on, the total catch experienced more pronounced boom and bust cycles and higher variability, even leading to total catch decreases after a couple of cycles.

## Discussions

As in previous reports, our findings show that environmental variability, especially upwelling, has a detectable effect on the Pacific sardine's population dynamics in the Gulf of California ${ }^{12,13}$. In previous work, however, this variability has been primarily associated to longterm environmental phenomena, such as El Niño ${ }^{13,14}$. 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. 4.2a), 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 Sea Surface Temperature (SST) anomalies have decoupled from El Niño events, with as many as five warm decoupled anomalies that occurred between 2007-2016 ${ }^{29}$. The mechanisms by which El Niño affects the oceanographic local conditions in the Gulf of California are poorly understood to date ${ }^{30}$. 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 ${ }^{5,30}$. Even further, researchers in the region have not been able to find conclusive evidence regarding El Niño controlling primary productivity patterns ${ }^{5,31,32}$, thus using a metric of winddriven upwelling is a closer proxy to estimating primary production and food availability.

The Markovian model also supports the hypothesis that environmental variability can induce a cyclical dynamic behavior in the population of Pacific sardine in the Gulf of California (Fig. 4.4), even at low fishing pressure levels. However, it can also be appreciated that elevated fishing effort by itself can induce boom and bust cycles, becoming more evident when fishers have a myopic behavior ${ }^{27,28}$. Additionally, when fishing effort, myopic expectations and environmental variability act in synchrony, the boom and bust cycles become much more pronounced, show up earlier, and lead to a permanent collapse.

These results were also verified by our empirical analyses, which showed that fisheries not only have a detectable effect on the sardine's population, but even comparable to that of environmental variability. Through our EDM analyses, we identified that fishing activities have a causal influence in total catch, $\Delta$ catch and CPUE (Fig. 4.S3), something that had not been systematically demonstrated for this fishery. We also found that $\Delta$ catch influences the amount of effort in the current season. This supports the idea that fishers in the region follow a myopic behavior (our Adjust parameter in the Markovian model).

Through an empirical simulation, we were able to show the isolated effects that increasing fishing effort would have in total catch 2 years into the future, or that increasing upwelling would have 4 years into the future. Our results show an expected behavior in which increasing fishing effort when effort is originally low, yields more catch. However, increasing
effort when effort is already high, provokes a fishery collapse and thus the total catch decreases in the future (Fig. 4.3a). Conversely, increasing upwelling always results in increased total catch (Fig. 4.3b).

The more policy-relevant question, however, is whether or not incorporating fishing effort in our analyses could lead to better predictability of the fishery. This could be useful in order to enforce fishing regulations that take fisheries' effects into consideration, rather than assuming that stochastic environmental variability is the only driver ${ }^{10,33}$. Based on the premise of unpredictability, current management strategies have set a constant harvest quota, which implicitly estimates that the prediction each year should be equal to the mean total catch. Such assumption, unfortunately, leads to no real predictability (Fig. 4.S7). In contrast, some authors have suggested that there is a linear correlation between environmental variability and total landings ${ }^{13}$. 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. 4.S7). Even though this prediction is better, it is still not enough to rely on it when designing a management scheme. Through our empirical dynamic framework, we demonstrated that incorporating fishing effort and environmental variability into a dynamic model can yield to predictions of total catch with $\rho$ $=0.85$ (Table 4.1, Fig. 4.S7). We also demonstrated that CPUE could be predicted with $\rho=0.80$ (Table 4.2). Thus, not only it is necessary to identify and use the proper explanatory variables, such as catch and effort, but also to use a modelling scheme that does not rely on predefined assumptions (e.g. functional forms) to make predictions about future states of the system.

In summary, our results can be used to predict total catch and CPUE up to two years ahead, giving the fleet the opportunity to adapt by either, reducing the fleet's size, or targeting other species ${ }^{21}$, thus reducing their economic risk. Additionally, these strategies will not only
lead to the recovery of the Pacific sardine population in periods of lower abundance but can also trickle down to other parts of the marine ecosystem that heavily rely on these resources ${ }^{14,34,35}$.

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Figures


Figure 4.1. Map of the Gulf of California showing the geographical location of Guaymas and Yavaros, where the Pacific sardine fishing fleet is based. The map also highlights the Midriff Island Region, where the bird crop content samples were taken from.


Figure 4.2. Pacific sardine fisheries time series in the Gulf of California from the Sonora's fleet. (A) Total catch in tonnes. The shaded areas represent strong El Niño (red) and La Niña (blue) events, which are defined as five consecutive overlapping 3-month periods at or above $1.5^{\circ} \mathrm{C}$ anomaly. (B) Catch per unit effort (CPUE) in tonnes per trip (dashed blue line) and effort in total number of trips (solid black line). The red dotted lines indicate the first fishery collapse in 1991/1992. Data were obtained from published sources and updated with data extracted from the annual reports of the Centro Regional de Investigacion Pesquera (CRIP) in Guaymas.


Figure 4.3. Scenario exploration for the effects of increased (A) effort and (B) upwelling in total catch. The x -axis represents the starting values for effort and upwelling in a normalized scale. The y-axis represents the effect that increasing a normalized unit of effort/upwelling would have on catch in future years (two years for effort and four years for upwelling).


Figure 4.4. Simulations of total annual catch as a result of the simple Markovian model with varying fishing effort (F), fishers' myopic behavior (Adjust), and cyclical environmental variability that affects natural mortality (Env). It is observed that when effort is high and fishers behave in a myopic way, the total catch fluctuates with a period of approximately five years. The other two scenarios did not present oscillations. The results are scaled to the maximum value for each time series.

## Tables

Table 4.1. Top 5 nonlinear empirical models to predict total catch two years into the future. The univariate model refers to using only the total catch time series and lags of it to build the attractor. 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 $\mathrm{E}=3$ as this was the identified embedding dimension to predict total catch. Models are sorted from more explanatory to less explanatory power.

| Model | Var1 | Var2 | Var3 | $\boldsymbol{\rho}$ | m.a.e. |
| :--- | :--- | :--- | :--- | :---: | :---: |
| C2P1E4 | Catch lag 2 | PDO lag 1 | Effort lag 4 | 0.85 | 0.45 |
| U1U4E4 | Upw lag 1 | Upw lag 4 | Effort lag 4 | 0.83 | 0.46 |
| E2U4E4 | Effort lag 2 | Upw lag 4 | Effort lag 4 | 0.83 | 0.49 |
| C2U4U1 | Catch lag 2 | Upw lag 4 | Upw lag 1 | 0.82 | 0.48 |
| S1U4U1 | SOI lag 1 | Upw lag 4 | Upw lag 1 | 0.81 | 0.45 |
| Univariate | Catch lag 0 | Catch lag 1 | Catch lag 2 | 0.51 | 0.69 |

Table 4.2. Top 5 nonlinear empirical models to predict Catch Per Unit Effort (CPUE) two years into the future. The univariate model refers to using only the CPUE time series and lags of it to build the attractor. For each model, the indicated explanatory variables substitute one time series of lagged CPUE to build a new manifold. All models were done with an $E=3$ as this was the identified embedding dimension to predict CPUE. Models are sorted from more explanatory to less explanatory power.

| Model | Var1 | Var2 | Var3 | $\boldsymbol{\rho}$ | m.a.e. |
| :--- | :--- | :--- | :--- | :---: | :---: |
| S1U4E4 | SOI lag 1 | Upw lag 4 | Effort lag 4 | 0.80 | 0.45 |
| CP2U4U1 | CPUE lag 2 | Upw lag 4 | Upw lag 1 | 0.79 | 0.47 |
| S1U4P1 | SOI lag 1 | Upw lag 4 | PDO lag 1 | 0.78 | 0.50 |
| CP2P1E4 | CPUE lag 2 | PDO lag 1 | Effort lag 4 | 0.77 | 0.50 |
| CP2S1E4 | CPUE lag 2 | SOI lag 1 | Effort lag 4 | 0.77 | 0.52 |
| Univariate | CPUE lag 0 | CPUE lag 1 | CPUE lag 2 | 0.41 | 0.70 |

## Chapter 4 Appendix

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

## Supplementary Information

## By

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[^1]

Figure 4.S1. Correlograms between explanatory variables and total catch. The dashed lines indicate the significance thresholds.


Figure 4.S2. Nonlinearity tests for each of the time series that were used in this study. The first and third rows show the embedding dimension against predictability ( $\rho$ ), the dots indicate the value of the maximum predictability. The second and fourth rows show the parameter theta against predictability. Time series for which increasing the value of theta increases the predictability, are classified as nonlinear.


Figure 4.S3. Convergent cross-mapping (CCM) between the three analyzed fishery variables (catch, $\Delta$ catch and CPUE) against the four explanatory variables (fishing effort, SOI, 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.


Figure 4.S4. Correlation between Pacific abundance indices estimated from the fleet as Catch per Unit Effort (CPUE) and from the percentage of sardine present in the elegant terns' (Thalasseus elegans) stomach content. (A) Direct correlation between the elegant terns' diet percentage and CPUE. (B) Correlation between the annual difference between the elegant terns' diet percentage and CPUE. The annual differences in abundance are considered to be proxies for recruitment.


Figure 4.S5. Scenario exploration for the effects of increased (A) effort and (B) upwelling in total catch. The x -axis represents the starting values for effort and upwelling in a normalized scale. The $y$-axis represents the percentage change from the original value of catch that increasing a percentage unit of effort/upwelling would have in future years (two years for effort and four years for upwelling). In (A), two points were identified as outliers and excluded from the plot (Cook's distance > 0.4). However, even if included, the relationship follows the same trend.


Figure 4.S6. Simulations of relative total catch from the Markovian model ran with fishing effort $\mathrm{F}=0.3$, fishers' myopic behavior (Adjust: ON) and with environmental variability (Env: ON). The environmental variability was incorporated by using a sinusoidal function that multiplies by the natural mortality rates. In order to test for the robustness of our findings to different environmental conditions, we varied the sinusoidal function's period ( 3 to 7 years) and phase ($180^{\circ}$ to $180^{\circ}$ ). The results represent the simulated total catch scaled from 0 to 1 . The blue lines represent the average value for a particular period and across all the tried phases. The grey areas represent the bootstrapped $95 \%$ confidence intervals for the phases. It can be observed that the overall pattern is the same across different periods and phases. Total catch presents a cyclical behavior with increasing differences between the minimum and maximum values on each cycle.


Figure 4.S7. Total catch observations (black line) and predictions with three different models: (1) assuming the average catch is the prediction (red line), (2) using the best multivariate linear model with lags of environmental upwelling and ENSO (blue line), and (3) using the best multivariate EDM model (orange line). The presented predictability ( $\rho$ ) estimates the correlation between observed and predicted values.

Table 4.S1. Leslie matrix describing the fecundity and survival rates for the simple Markovian model used to simulate fishing effects in the Pacific sardine population.

| age- | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| classes |  |  |  |  |  |  |  |  |  |
| 0 | 0 | 0 | 0 | 0 | 100 | 100 | 200 | 350 | 350 |
| 1 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 |
| 6 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 |

## Conclusions

ALFREDO GIRON-NAVA

Throughout the course of this dissertation, the main and most important thing that I have learned is that studying fisheries is not only about fish. Studying fisheries needs to consider the people that fish for a living, for recreation, or even for subsistence. As such, there is no simple or one-size-fits-all solution to manage a fishery. Every case will be as dependent on the health of the ecosystem, as on the cultural set of values and interactions between fishers.

## Traditional fisheries models make too many assumptions

More than 50 years ago, brilliant fisheries scientists came up with models that could apparently estimate the sustainable rates of exploitation that a fishery could be subject to ${ }^{1}$. Today, we know that such models offer a great point of entry, but are by no means enough to correctly manage a fishery ${ }^{2}$. This is in part because these models often assume that exploited populations are stationary and at equilibrium, neglecting the effects of environmental variability and changing fishing behaviors. Recent years have seen a surge of arguments against traditional fisheries management tools, such as the concept of Maximum Sustainable Yield, which assumes that there is a constant rate of exploitation that can provide the maximum harvest for an indefinite amount of time ${ }^{1,3}$. The truth is, however, that the concept of MSY is still broadly used by fisheries managers due to its simplicity and familiarity. As such, Chapter 1 focuses on understanding whether achieving MSY (assuming it could be perfectly achieved) could also provide enough economic benefits to maintain fishers in the Gulf of California above local poverty levels. Unfortunately, we found that this is not the case, and that fishers very often have to rely on alternative sources of income to fulfill their basic necessities ${ }^{3}$. Therefore, I have aimed my research at trying new methods that could offer a viable solution to study fisheries and propose adaptive management schemes.

Throughout this dissertation, I decided to use Empirical Dynamics Modeling (EDM), a nonlinear and equation-free approach that uses empirical data to make predictions about a system. These techniques have been used to predict variables across different disciplines and problems, such as epidemics ${ }^{4}$, red tides ${ }^{5}$, solar flares ${ }^{6}$, and also fisheries ${ }^{7,8}$. Throughout my dissertation I focused on understanding the conditions under which these methods were the most effective. In Chapter 2, I demonstrated that these methods can be broadly applied to marine ecosystems, as long as there are long-term datasets available ${ }^{9}$. I also focused on adapting these methods to study old and unsolved problems in fisheries sciences, such as the prediction of the number of recruits from estimates of the numbers of adults ${ }^{10}$. Based on previous work that I had done with collaborators, we found that despite traditional fisheries knowledge, recruitment is indeed predictable from the number of adults. However, this predictability is dependent on lifehistory traits, being short-lived species the most suitable to use with an EDM approach ${ }^{11}$. In Chapter 3, I went further into understanding how different data sources could affect the usefulness of traditional fisheries models and demonstrated that EDM is always a useful alternative regardless of the data source.

## Lessons learned from a case study

After realizing that EDM could be a viable approach to understand short-lived species population dynamics, I wondered whether it could also be used to propose management strategies that account for both, environmental variability and fishing impacts. As such, I decided to study the Pacific sardine fishery in the Gulf of California, Mexico, which has traditionally been managed from a perspective in which fishing effort is not considered to have any detectable effect. Additionally, local authorities consider that the population is primarily driven by
stochastic environmental processes, making future yields hard to predict ${ }^{12}$. This has led fisheries scientist to suggest a constant fishing rate as a conservative measure to manage a highly variable fishery. In Chapter 4, I found that fishing effort has not only a detectable effect on this fishery, but that this effect is comparable to that of upwelling, the environmental variable with the strongest influence. This led me to calibrate a predictive model that is best improved when considering both effects simultaneously, and which will help me to produce a harvest policy that accounts for both effects.

## Future directions

This dissertation contributes to a large body of literature that encompasses EcosystemsBased Management and Social Ecological Systems. However, through the use of EDM, it opens up the possibility to use a quantitative framework that accounts for social and ecological processes with the common currencies of predictability and causality.

In this work, I was able to demonstrate that the methods that I have used could be especially useful for short-lived species, such as sardines, anchovies, herrings, among other small-pelagics. Still, there are a lot of research opportunities ahead to expand their use for other species, and even to combine them with other modern methods to develop a new toolkit for fisheries management that reflects all the knowledge that we have acquired since concepts like the Maximum Sustainable Yield were first proposed.

In the near future I will keep working towards expanding this toolkit and getting closer to managers. I am optimistic that we can work together with managers and local communities to find suitable targets that make use of the best tools for each particular case and that respond to ecological and social needs.

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