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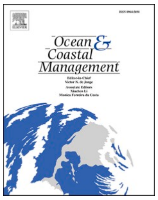

Exploring the influence of upwelling on the total allowed catch and harvests of a benthic gastropod managed under a territorial user rights for fisheries regime along the Chilean coast.

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ABSTRACT

While there is a broad understanding of upwelling impacts on the functioning of marine ecosystems, empirical data that link this process to commercial species landings have not received the attention they deserve. The aim of this study was to explore the role of coastal upwelling in determining total allowable catch (TAC) and harvests of benthic fisheries, managed through a policy which assigns Territorial User Rights to Fishers (TURFs) along the Chilean coast. We used official historical TAC (217 TURFs) and harvest data (224 TURFs) for one of the most important benthic gastropod resources ("Loco", *Concholepas concholepas*) of the TURF system. TAC and harvest data ranged from 2001 to 2018 and were used to explore relations with an index of seasonal coastal upwelling, derived from a spatiotemporal decomposition, of sea surface temperature along the same study areas and period. Using Bayesian generalized linear multilevel models (TURFs as group-level effect), we showed a positive and significant effect of the upwelling over TAC and harvest of Loco. Model results explained 47% of TAC and 34% of harvests. The effects of upwelling were comparatively stronger to the effects of the area (hectares) and the number of fisher members of the TURF. In addition, models estimates showed negative inter-annual trends during the study period, for TAC and harvests, and that these differed as function of upwelling variability. Understanding the role of upwelling gives objective criteria to begin addressing the differential role that social and environmental aspects play in overall TURF performance, allowing to begin hypothesizing over socially driven deviances from predicted patterns.

1. Introduction

Major coastal upwelling zones occur along the edges of the eastern boundary currents of the Pacific and Atlantic Oceans (California, Humboldt, Iberian/Canary, and Benguela current). These regions are the most productive ecosystems of the world and support extensive commercial fisheries (Brochier et al., 2011; Chavez and Messié, 2009; Garrido et al., 2017; Santos et al., 2018; Teixeira et al., 2016). There is a broad literature aimed at understanding of the impacts of coastal upwelling process, ranging from a molecular level (i.e. biosynthetic capability) to population (e.g. higher growth rate, colonization rate, reproductive timing) and community impacts (e.g. higher predation rate, competition rate, facilitation rate) (Aldana et al., 2017; Fuentes et al., 2017; Menge et al., 2003; Menge and Menge, 2013; Palumbi, 2003; Pulgar et al., 2011; Zuloaga et al., 2018). These studies indicate the importance of nutrient availability as a bottom-up process, in determining the "pace of life" in coastal system (Menge et al., 2003).

The Humboldt Current System (HCS) which extends from ∼42° S up to about the equator, is one of the most productive marine ecosystems on earth (Montecino and Lange, 2009). Upwelling occurs when equator ward winds transport surface waters off-shore, replacing them by cold and nutrient-rich sub-surface layers (Sobarzo et al., 2007). The input of

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nutrients into the euphotic zone in conjunction with seasonality in light availability (mostly austral spring-summer seasons), promotes an increase in primary productivity (Hernández et al., 2012; Montero et al., 2007; Vergara et al., 2017). This enhanced productivity, triggers important changes at higher trophic levels (Thiel et al., 2007).

Recent studies have evidenced that upwelling-favoring winds (including in the HCS) have intensified in last decades (Bakun et al., 2015; García-Reyes et al., 2015; Rykaczewski et al., 2015; Wang et al., 2015). However, great uncertainty exists on the potentially counteracting effects of intensifying winds and increasing thermal stratification (Bakun et al., 2015; García-Reyes et al., 2015). As a consequence, many authors have highlighted the need for research on the influences of present and predicted future upwelling process over marine species, ecosystems (García-Reyes et al., 2015; Wang et al., 2015) and the fisheries that depend on them (Perez-Matus et al., 2017).

The harvesting of marine species by humans can have dramatic effects on the structure and functioning of marine communities (Botsford et al., 1997; Dayton et al., 1977; Estes et al., 2011; Hockey and Bosman, 1986; Siegfried et al., 1985). As such, the management of fisheries is a global priority which has increasingly been shifting towards collaborative co-management arrangements. In small-scale fisheries these arrangements include the granting of Territorial User Rights for Fisheries (TURFs) under the premise that they can create incentives for fisher communities to achieve sustainability (Gelcich et al., 2017). TURFs ensure fishers the right to limit or control access to fishery resources within a limited sea territory; to determine the amount and kind of use of resources; to benefit from the use of resources and to have access to future returns from the conservation of those resources (Gallardo et al., 2011).

Chile implemented a national scale TURF system under the Fisheries and Aquaculture law Number 18.992, of 1991. TURFs in Chile are termed Management and Exploitation Areas for Benthic Resource (MEABRs) and are aimed to manage benthic resources (Castilla and Fernandez, 1998; Gelcich et al., 2010, 2008; Manríquez and Castilla, 2001). Under the MEABR regime, the Chilean Undersecretary of Fisheries assigns a total allowable catch (TACs) to artisanal fisher associations for each TURF based on stock assessments performed jointly by fishers and biological consultants. Studies which have assessed biological impacts of the system find that key commercially important benthic species show increases in abundance and size in MEABRs respect to open-access areas (Castilla and Fernandez, 1998; Gelcich et al., 2008, 2019; Molina et al., 2014).

While Chile has more than 450 functioning MEABRs (Gelcich et al., 2017) there has been little focus on the role that upwelling might have over TACs setting and the harvest of important benthic resources in these areas (Pérez-Matus et al., 2017). A long-standing hypothesis of the positive effects of habitat productivity on harvest of bentic species, within MEABRs, was proposed 23 years ago (Stotz, 1997). In this study we tested the hypothesis by determining the role of upwelling variability over TURF performance. We specifically use TACs and harvests of the economically important benthic gastropod *Concholepas concholepas* (known as "Loco") (Castilla, 1999), to elucidate the underlying importance of coastal upwelling, as a bottom-up process, under areas managed through MEABR regimes. We used the historical data of TACs and harvests of Loco (from 2001 to 2018) in each MEABR provided by the Undersecretary of Fisheries for the Chilean coast. This information was then associated to an upwelling index derived from remotely sensed sea surface temperature measured during the same period of time. Thereby, allowing us to explore how the spatiotemporal variation of TACs setting and harvest of Loco in MEABRs is influenced by upwelling-driven nutrient availability along the HCS.

2. Methods

2.1. Total allowable catch and harvest of loco in MEABRs along the Chilean coast

We analyzed official data of TACs (the Chilean Undersecretary of Fisheries assignation for each resource in MEABRs) (from 2001 through 2018) and harvests (the declared landings by fishers in each MEABR) of Loco (from 2001 through 2016) in MEABRs between latitudes 18 and 41°S in the coast of Chile (SERNAPESCA, December 2016 and December 2018). The data included (for both TAC and harvest); weight of Loco (tons), the date (month and year), MEABR ID to which the TAC or harvest belongs and the number of fisher association members who manage the MEABR (mean $\pm$ SD $=$ 56 $\pm$ 42 fishers). The Undersecretary of fisheries provided a file (kmz) with the geographical areas (i.e. polygon) of all MEABRs (http://subpesca.cl). With this information we calculated the area (hectare) of the MEABRs (mean $\pm$ SD $=$ 162 $\pm$ 239 ha). MEABRs with five or more officially assigned TACs or harvests were included in the analysis. TACs data included 217 MEABRs and 10,079 records and harvest data included 224 MEABRs and 10,052 records.

2.2. Index of seasonal coastal upwelling along the Chilean coast

A widely used upwelling index in ecology is the Bakun index (Bakun, 1973). The Bakun index has been useful in tracking the variability of upwelling and linking bottom-up effects with ecological patterns (Black et al., 2011; Menge and Menge, 2013; Navarrete et al., 2005, 2002). However, it has a coarse spatial resolution and does not account for smaller-scale factors (e.g. topography, bathymetry) and inner-shelf hydrodynamics (Aravena et al., 2014; McPhee-Shaw et al., 2007; Pickett and Schwing, 2006). Identifying upwelling centers from thermal image variations, has been a long-standing method applied in ecology (Broitman et al., 2001; Navarrete et al., 2005; Nielsen and Navarrete, 2004; Wieters, 2005). However, to our knowledge, at the HCS there is no available upwelling index that integrates the upwelling processes from macro to local scales (but see, Tapia et al., 2009).

In this study we determine the seasonal costal upwelling amplitude associated to MEABRs along the Chilean coast using remotely sensed sea surface temperature (SST, °C). Monthly satellite rasters of surface temperature were obtained for the study area (-72.6855 °W, -34.8706 °S, -70.9717 °W, -28.894°S) using moderate-resolution imaging spectroradiometer (MODIS-aqua-4km) from July 2002 to December 2016. These were downloaded from the Giovanni free-online data system (http://giovanni.gsfc.nasa.gov). In order to create an index for seasonal coastal upwelling along the Chilean coast, a spatiotemporal decomposition of the SST was performed. Specifically, we used the Decompose and the GetTsStatisticsRaster functions available in the greenbrown package (Forkel et al., 2015, 2013) for R (R Core Team, 2017). This function decomposes time series using a simple 5 step-wise approach; (1) The mean of the series is calculated, (2) a trend over the full length of the time series is estimated, (3) the mean and the trend components from previous steps are subtracted from the annual values to derive the trend-removed and mean-centered annual anomalies, (4) The mean, the trend component and the annual anomalies from previous steps are subtracted from the original time series to estimate the mean seasonal cycle (and its range). In the last step (5), short term anomalies are computed by subtracting all components from step 1 to 4 to the original time series. Accordingly, this function allows to separate the time series of each grid cell (4 km^2) into: (a) overall trend, (b) inter-annual variability, (c) seasonal amplitude (range) and (d) short-term variability (Forkel et al., 2013).

Using this approach, we obtained a raster of the seasonal amplitude of SST (henceforth, SAM-SST) for the entire Chilean coast. From this raster we extracted the mean of the SAM-SST for each MEABR (mean value within MEABRs delimitations). The SAM-SST is based on seasonal variations of temperature, so areas with no upwelling impact will have very contrasting temperature in cold-seasons (autumn-winter) in comparison to warm seasons (spring-summer, i.e. high values of SAM-SST), while areas with strong upwelling will have similar values of temperature (i.e. low) throughout the year, due to the cold, nutrient rich waters upwelled during spring-summer (i.e. low values of SAM-SST, see, Tapia et al., 2014).

2.3. Data analysis

We used Bayesian generalized linear multilevel models implemented with the Stan computation engine (Stan Development Team, 2017) with NUTS sampling (Carpenter et al., 2017) via the brms package (Bürkner, 2017; 2018) for R. Both response variables (TAC and harvest, in tons) presented right skewness and therefore were modeled using the lognormal distribution. For each response variable (TAC and harvest) we started with a null model (M0_{TAC} and M0_{HAR}, for TAC and harvest, respectively) with the MEABR ID as a random effect (random intercepts). From these null models we generated four alternative nested models for both TAC and harvest; M1_{TAC} and M1_{HAR} with the inclusion of the area of the MEABRs (log hectare) and the number of members of the MEABRs (log of the number of fishers), as fixed variables. M2_{TAC} and M2_{HAR} with the inclusion of SAM-SST (continuum variable) as fixed variable. M3_{TAC} and M3_{HAR} with the inclusion of the year (factor) as fixed variable, and M4_{TAC} and M4_{HAR} with the inclusion of an interaction between SAM-SST and the year. Prior to running the models, correlations between covariates were examined. These analyzes showed a low correlation between covariates (range of Spearman r = 0.16–0.24). To choose the most informative model(s) we used the leave-one-out cross-validation (LOO) available in the loo package of R. This approach, estimates prediction accuracy from a fitted Bayesian model (using the log-likelihood) and has shown various advantages over simpler estimates of predictive error such as AIC and DIC (Vehtari et al., 2017). For all models we used weakly informative prior for the coefficients of covariates (i.e. normal distribution with a mean of zero and a standard deviation of 10) and for the random effect (half Student-t distribution with 3 degrees of freedom with a mean of zero and a standard deviation of 10). For all models, we ran six chains of 6000 iterations with a warm-up period of 3000 iterations and a thinning rate of 10 iterations (i.e. total post-warm-up samples per model = 18,000). Convergence and mixing of chains were inspected visually using trace and density plots available in the brms package. In addition we ensured that each estimate had more than 400 effective samples and the Gelman-Rubin statistic (Rhat) values were below 1.05 (Gelman and Hill, 2006).

3. Results

Spatiotemporal decomposition of SST exhibit a clear pattern of seasonal coastal upwelling along the Chilean coast, with a marked increase in SAM-SST (i.e. decrease of seasonal upwelling intensity) in a south-north direction. Between ~40° S (south of Valdivia) to 31–32° S a macro-zone is observed with the lowest SAM-SST, showing a high influence of costal upwelling within South-central Chile, with its cores near Concepcion and Constitucion and with an offshore extension of >200 km (Fig. 1). Moving north of 30° S SAM-SST increase up to ~23° S (near Iquique) where a second meso-zone of seasonal coastal upwelling is observed (i.e decrease of SAM-SST; Fig. 1). At a local-scale (i.e. MEABRs), SAM-SST showed the same bimodal pattern observed at a macro-scale (Fig. 2a).

Based on the leave-one-out cross-validation (LOO), the best Bayesian multilevel model for TAC (i.e. M4_{TAC}, Bayesian $R^2 = 47\%$) and harvest of Loco (i.e. M4_{HAR}, Bayesian $R^2 = 34\%$) had MEABR ID as random effect and the following fixed effects: the area of the MEABR (ha), the number of members of the MEABR (fishers) and an interaction between SAM-SST and the year (Table 1). To test the hypothesis of our work we inspected estimates from these models ($\text{M4}_{\text{TAC}}/\text{M4}_{\text{HAR}}$) and for comparison purposes we also inspected results from models M3_{TAC} and M3_{HAR} (i.e. models without the interaction between the year and SAM-SST). All models showed a significant negative (95% credible interval does not include zero) effect of SAM-SST over TACs and harvests of Loco (Tables 2 and 3), meaning that for MEABRs with higher seasonal variation of sea surface temperature (less influence of upwelling) less tons of TACs and harvests were expected along the coast of Chile (Fig. 3).

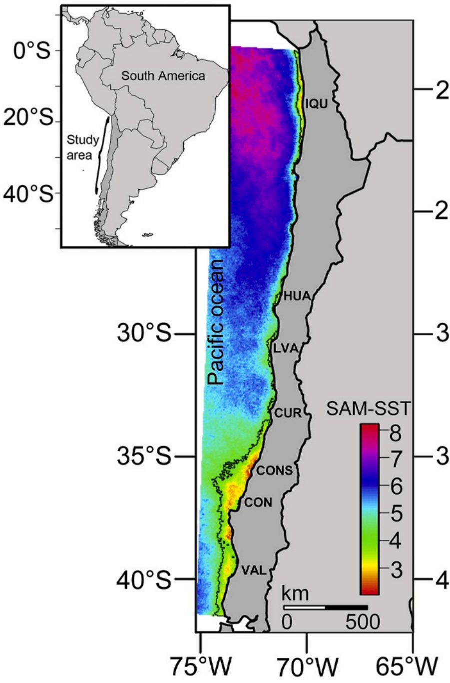

Fig. 1. Spatial pattern of seasonal amplitude of sea surface temperature (SAM-SST, °C) along the Chilean coast. Results derived from the spatiotemporal decomposition of moderate-resolution imaging spectroradiometer. Note that areas with strong upwelling will have low values of SAM-SST, due to similar water temperature (cold) during autumn-winter (low light availability) and spring-summer seasons (cold-nutrient rich upwelled waters). The black contour depicts areas most impacted by coastal upwelling (95 percentile of lowest SAM-SST). The main near-upwelling localities (only as geographic referential) are shown: VAL=Valdivia, CON= Concepcion, CONS=Constitucion, CUR=Curaumilla point, LVA = Lengua de vaca, HUA=Huasco, IQU=Iquique. The embedded map shows the location of the study area in western South America.

We also found a significant positive effect of the area and the number of fisher members, over TAC and harvest of Loco (Fig. 3), but these effects were all of lower magnitude (in absolute value) in comparison to the effect of SAM-SST (Tables 2 and 3). Considering MEABRs as random effect, coefficients from models $\text{M4}_{\text{TAC}}/\text{M4}_{\text{HAR}}$, showed a significant variation along the coast of Chile (group-Level effects; Tables 2 and 3), and exhibited a bimodal distribution with the highest positive values at the southern-end and at the northern-end of the study area, where the main upwelling areas occurs (Fig. 2b and c). Overall, TACs and harvest of Loco showed a negative trend during the study period, however expected effects from models $\text{M4}_{\text{TAC}}/\text{M4}_{\text{HAR}}$ evidenced that these trends differed as a function of SAM-SST (i.e. interaction between SAM-SST and the year), with consistently higher TACs and harvest of Loco at lower values of SAM-SST (greater influence of upwelling; Fig. 4a and b). At an average value of SAM-SST, the average MEABR TAC and harvest during the study period was 2.8 and 2.7 tons, respectively (Fig. 4c and d). In comparison, at one standard deviation above the average SAM-SST (less influence of upwelling), the average TAC and harvest during the study period was 1.8 and 1.7. While at one standard deviation below the average SAM-SST (greater influence of upwelling), the average TAC and harvest during the study period was 4.4 and 4.1 tons (Fig. 4c and d).

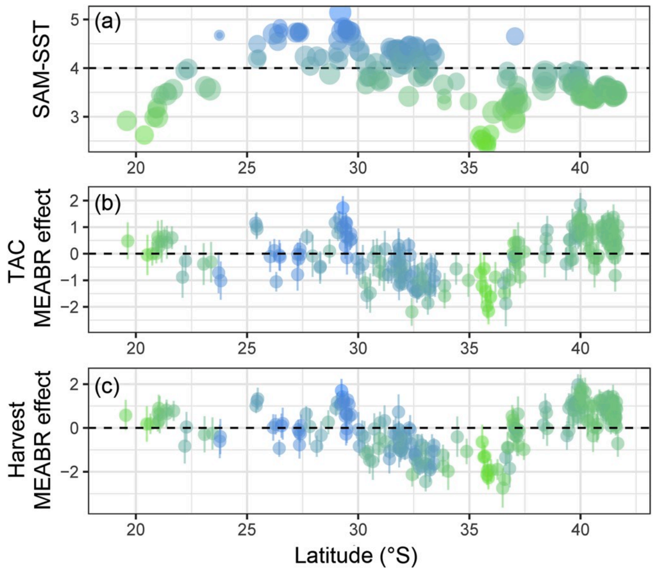

Fig. 2. (a) Latitudinal pattern of MEABRs upwelling conditions along the Chilean coast. The mean seasonal amplitude of sea surface temperature (SAM-SST) of each MEABR (average SAM-SST within MEABR spatial delimitation) is shown. Each point in the scatter-plot corresponds to a MEABR and its size is proportional to their area (ha). (b) Posterior means and 95% credible intervals of MEABRs parameters (random intercepts) as estimated for TACs of Loco by model $M4_{TAC}$. (c) Posterior means and 95% credible intervals of MEABR parameters (random intercepts) as estimated for harvests of Loco by model $M4_{HAR}$. The color of the points (MEABRs) in plots (b) and (c) correspond to their upwelling condition (i.e. SAM-SST shown in plot a). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Models for TACs (Total allowable catch) and harvest of Loco (*C. Concholepas*) in response to; SAM-SST (seasonal amplitude of SST), the area of the MEABR, the number of fisher members (NM) of the MEABR and the year as fixed variables and MEABR ID as random effect. Models are sorted by increasing LOO values. LOO: leave-one-out cross-validation; ΔLOO: LOO differences between *ith* model and the best model.

Response variable	Model	Random	Fixed	LOO	ΔLOO
TAC (kg)	**$M4_{TAC}$**	**MEABR**	**SAM-SST + Area + NM + Year * SAM-SST**	**34,166**	**-**
	$M3_{TAC}$	MEABR	SAM-SST + Area + NM + Year + SAM-SST	34,261	95
	$M2_{TAC}$	MEABR	SAM-SST + Area + NM	35,040	874
	$M1_{TAC}$	MEABR	Area + NM	35,043	877.1
	$M0_{TAC}$	MEABR	–	35,044	878.2
Harvest (kg)	**$M4_{HAR}$**	**MEABR**	**SAM-SST + Area + NM + Year * SAM-SST**	**29,335**	**-**
	$M3_{HAR}$	MEABR	SAM-SST + Area + NM + Year + SAM-SST	29,454	118.3
	$M2_{HAR}$	MEABR	SAM-SST + Area + NM	30,188	852.5
	$M1_{HAR}$	MEABR	Area + NM	30,190	854.3
	$M0_{HAR}$	MEABR	–	30,192	856.4

Table 2

Coefficients, their standard errors, and 95% credible intervals (CI) estimated by models $M3_{TAC}$ and $M4_{TAC}$ for TACs of Loco (tons) during the study period. The SAM-SST coefficient of $M4_{TAC}$ shows its average effect for all years. All parameters are significant (95% credible interval does not include zero).

$M3_{TAC}$ Group-Level Effects:	Est. coef.	Est. SE	l-95% CI	U-95% CI	Rhat
sd (MEABR)	**0.91**	**0.05**	**0.82**	**1**	1.0
$M3_{TAC}$ Population-Level Effects:					
Intercept	**1.51**	**0.65**	**0.25**	**2.78**	1.0
SAM-SST	**−0.81**	**0.12**	**−1.04**	**−0.58**	1.0
Log (Area)	**0.23**	**0.07**	**0.09**	**0.37**	1.0
log (Number of members)	**0.44**	**0.11**	**0.23**	**0.65**	1.0
Model $M4_{TAC}$					
$M4_{TAC}$ Group-Level Effects:	Est. coef.	Est. SE	l-95% CI	U-95% CI	Rhat
sd (MEABR)	**0.90**	**0.05**	**0.81**	**1.00**	1.0
$M4_{TAC}$ Population-Level Effects:					
Intercept	**1.49**	**0.88**	**−0.23**	**3.21**	1.0
SAM-SST	**−0.80**	**0.19**	**−1.18**	**−0.44**	1.0
Log (Area)	**0.22**	**0.07**	**0.08**	**0.35**	1.0
log (Number of members)	**0.45**	**0.10**	**0.25**	**0.66**	1.0

Table 3

Coefficients, their standard errors, and 95% credible intervals (CI) estimated by models $M3_{HAR}$ and $M4_{HAR}$ for harvests of Loco (tons) during the study period. The SAM-SST coefficient of $M4_{HAR}$ shows its average effect for all years. All parameters are significant (95% credible interval does not include zero).

$M3_{HAR}$ Group-Level Effects:	Est. coef.	Est. SE	l-95% CI	U-95% CI	Rhat
sd (MEABR)	**1.07**	**0.05**	**0.97**	**1.18**	1.0
$M3_{HAR}$ Population-Level Effects:					
Intercept	**1.01**	**0.75**	**−0.45**	**2.47**	1.0
SAM-SST	**−0.77**	**0.14**	**−1.05**	**−0.51**	1.0
Log (Area)	**0.24**	**0.08**	**0.08**	**0.41**	1.0
Log (Number of members)	**0.48**	**0.12**	**0.24**	**0.72**	1.0
Model $M4_{HAR}$					
$M4_{HAR}$ Group-Level Effects:	Est. coef.	Est. SE	l-95% CI	U-95% CI	Rhat
sd (MEABR)	**1.06**	**0.05**	**0.97**	**1.18**	1.0
$M4_{HAR}$ Population-Level Effects:					
Intercept	**0.43**	**0.97**	**−1.49**	**2.33**	1.0
SAM-SST	**−0.63**	**0.20**	**−1.03**	**−0.24**	1.0
Log (Area)	**0.24**	**0.08**	**0.07**	**0.40**	1.0
Log (Number of members)	**0.48**	**0.12**	**0.24**	**0.72**	1.0

4. Discussion

In this study, we aimed to elucidate the underlying importance of upwelling, as a bottom-up process, over TURF performance along the Chilean coast. While variability between MEABRs was evident, our study indicated that MEABRs located in high productive upwelling zones had significantly higher TACs and harvests compared with those located in non-upwelling zones. Based on a spatiotemporal decomposition (14 years) of remotely sensed SST our results showed a clear spatial pattern of seasonal coastal upwelling along the Chilean coast with two macro-zones (from south to north; 40-32°S and 22-18°S), together with intermediate points of upwelling (~30°S). This upwelling distribution is in accordance with previous studies that identified upwelling centers from thermal variations (Aravena et al., 2014; Navarrete et al., 2005; Nielsen and Navarrete, 2004; Pinochet et al., 2019; Tapia et al., 2009; Wieters, 2005). As such, our results contribute to the a growing amount of evidence supporting the hypothesis that at 30–32°S there is a spatial transition in ecological process associated to consistent changes in the recruitment, abundances and composition of intertidal communities (Broitman et al., 2001; Camus, 2001; Lara et al., 2019; Navarrete et al., 2005; Tapia et al., 2014; Wieters et al., 2009).

While MEABRs presented high variation along the Chilean coast (MEABRs as random effect), the underlying influence of coastal upwelling on Loco's TACs and harvests was consistent during the study period. In fact, models explained 47% and 34% of TACs and harvests of Loco, respectively. Results showed that there is a 95% of probability of finding a positive effect of coastal upwelling (or negative effect of SAM-

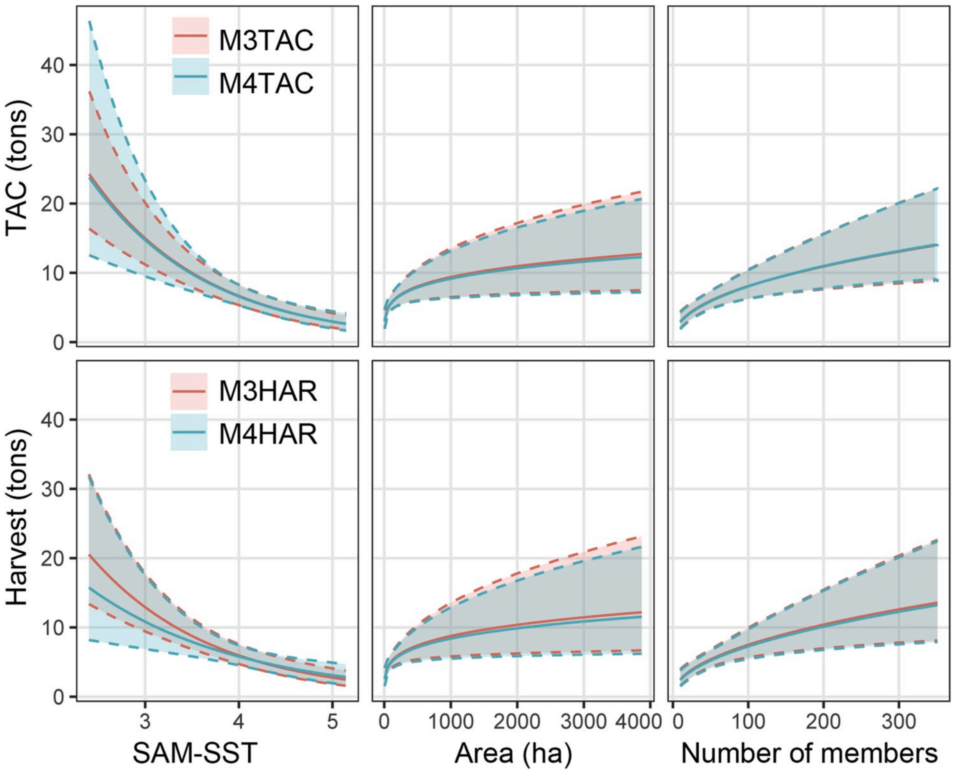

Fig. 3. Expected effect of SAM-SST, the area of the MEABRS and the number of members (fishers) over TACs (estimated by models $M3_{TAC}$ and $M4_{TAC}$) and harvests of Loco (estimated by models $M3_{HAR}$ and $M4_{HAR}$). Posterior means and 95% credible intervals of each variable with all other numerical covariates being set to their mean and categorical covariates being set to their reference categories (i.e. conditional effects) are shown.

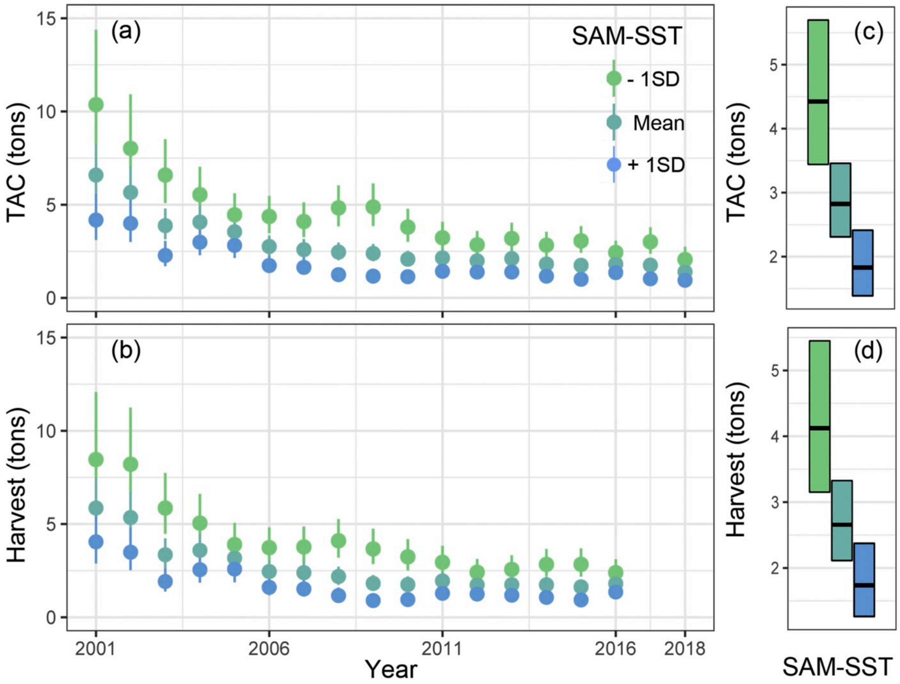

Fig. 4. Expected effect of the interaction between SAM-SST and the year, over (a) TACs (estimated by model $M4_{TAC}$) and (d) harvests of Loco (estimated by model $M4_{HAR}$). For each year, posterior means and 95% credible intervals for the average SAM-SST of all MEABRs, the average SAM-SST plus one standard deviation and the average SAM-SST minus one standard deviation are shown. The mean and 95% credible intervals for the entire study period and for the same levels of SAM-SST described above are shown for TACs (tons) and harvest (tons). All other numerical covariates were set to their mean (i.e. conditional effects of the interaction).

SST) over TACs and harvests of Loco, and that these effects were of greater magnitude in comparison to the effects of the MEABR area (ha) and the number of members (fishers). In addition, we showed a negative temporal trend in TAC and harvest of Loco, however these trends were different by upwelling conditions, with consistently lower TACs and harvests in non-upwelling located MEABRs.

These patterns likely arise in response to ecological processes occurring at different spatiotemporal scales, from auto-ecological to macro-ecological processes. Loco's diet is based mainly on suspension feeders (e.g. barnacles and mussels). This short food chain provides highly efficient energy acquisition from primary producers in upwelled waters (Stotz, 1997; Stotz et al., 2003). Results complement the findings of other studies that have described the impact of upwelling on intertidal fishes, algae and key-hole limpets which show upwelling is directly associated to growth rates, biosynthetic activity (RNA:DNA ratio), earlier reproductive tissue development, and gene expression (Aldana et al., 2017; Fuentes et al., 2017; Pulgar et al., 2013, 2012; 2011; Zuloaga et al., 2018).

The impacts of environmental drivers, such as upwelling, on resources performance has not been a criterion in the design and analysis of the MEABRs system, and could play a critical role when thinking of this policy as a network in which some areas can be sources and others sinks, for example in terms of larvae production. In this line, and considering the documented impact of upwelling on the performance of animals and on MEABRs described in this work, the MEABRs located in high productivity zones may represent critical nodes to sustain connectivity and the functioning of the marine network within HCS. Therefore guiding the design of specific support programs, such as enforcement investments. Our study represents an important contribution in relating environmental drivers with MEABRs performance in Chile, attempting to better inform the policy from an overall network perspective along the coast (Gelcich et al., 2019). Estimations along the coast of central Chile show that MEABRs show a 20-fold increase in Loco's larvae releases in comparison to open access areas (Blanco et al., 2017). If these differences are due mainly to the density and the size of the females (Manríquez and Castilla, 2001), we can hypothesize that TURFs within upwelling centers acts as sources of larvae to TURFs with lower productivity (and open access areas). In this sense Pérez-Matus et al. (2017), in Central Chile revealed significant impact of upwelling on subtidal kelp forest. Their results, suggest that human management over benthic resources through TURFs, can provide different benefits for some key species under the influence of upwelling, in contrast to TURFs in downstream areas. In line to our broader scale result, all these findings reveal the need to both develop in depth case studies aimed at understanding the interplay between, human harvesting, management and oceanographic conditions on the role of MEABRs as an overarching network aimed at the sustainability of subtidal habitats.

Our results show a negative temporal trend in TACs and in Loco's harvests. The trends differed between upwelling and non-upwelling conditions, calling further attention to the role of habitat productivity in ensuring the resilience of these fisheries, an issue that has not been previously considered in TURFs management (Gelcich et al., 2019). TAC decline could be driven by many interactive causes which include variability in recruitment and stock abundance, differential growth rates and/or natural mortality. On the other hand TAC tendency could also be confounded by socio-cultural aspects such as poaching, underreporting of official landings in areas where TACs and harvests are comparably lower (Oyanedel et al., 2018), lack of interest in pursuing TURF management associated to development of other fisheries, local unemployment, poverty (Leal et al., 2010) or increasing age of fishers (Tam et al., 2018). It is critical to explore how these drivers of change might be interplaying in different ways with MEABRs productivity in future studies.

Deviations from the main trends (for both TACs and harvests of Loco) between upwelling conditions along the Chilean coast (see Fig. 2), and the unexplained variability of our models (more than half the variability), is also probably related to differences in management and the social structures of stakeholder groups which are engaged in the co-management process (Cinner et al., 2012; Crona et al., 2017; Marín et al., 2012). Social structures play a particularly important role over the level of enforcement of TURFs, which in turn has proven to be the key for TURF outcomes to be achieved (Gelcich et al., 2012; Pérez-Matus et al., 2017). A recent systematic review, showed increases in biomass, abundance, size and CPUE (catch per unit of effort) of target species in well-enforced TURFs (Gelcich et al., 2019). Important changes in harvest traits could also be related to illegal fishing and the underreporting of catches (Oyanedel et al., 2018). The relationship between; illegal fishing, underreporting of catches and how TURF enforcement may change, as function of incentives generated by increased productivity in upwelling conditions, represent an interesting venue that needs more research.

In conclusion, this study has addressed the relationship between an important benthic fisheries resource and major oceanographic process. Our results showed that the performance of MEABRs (TAC and harvest) are related to seasonal coastal upwelling along the Chilean coast, highlighting the underlying influence of a bottom-up process. The ecological significance of determining coastal zones with high and low impact of seasonal coastal upwelling, provides important information to design structured inquiries into the role that social dimensions play in overall performance. Interestingly, it sets the scene to identify "bright" or "dark" spots (i.e. as deviations from expectations, see Cinner et al., 2016) in TURF management which would allow to address the complexities of rights based management implementation. We truly believe that incorporating ocean dynamics and productivity in addition to social determinants as part of a marine governance program could enlighten the way fisheries are governed.

5. Data access

All data contained in this work are available from National Service of Fishing (SERNAPESCA) and from the Giovanni online data (http://giovanni.gsfc.nasa.gov) system.

6. Conflict of interest

We declare that no conflict of interest exist.

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References

Aldana, M., García-Huidobro, M.R., Pulgar, V.M., Pulgar, J., 2017. Upwelling promotes earlier onset & increased rate of Gonadal development of four coastal herbivores. Bull. Mar. Sci. 93, 671–688. https://doi.org/10.5343/bms.2016.1063.

Aravena, G., Broitman, B., Stenseth, N.C., 2014. Twelve years of change in coastal upwelling along the central-northern coast of Chile: spatially heterogeneous responses to climatic variability. PloS One 9. https://doi.org/10.1371/journal.pone.0090276.

Bakun, A., 1973. Coastal Upwelling Indices, West Coast of North America, 1946-71. NOAA Technical Report NMFS SSRF-671.

Bakun, A., Black, B.A., Bograd, S.J., Miller, A.J., Rykaczewski, R.R., Sydeman, W.J., 2015. Anticipated effects of climate change on coastal upwelling ecosystems. Curr. Clim. Chang. Rep. 1, 85–93. https://doi.org/10.1007/s40641-015-0008-4.

Black, B.A., Schroeder, I.D., Sydeman, W.J., Bograd, S.J., Wells, B.K., Schwing, F.B., 2011. Winter and summer upwelling modes and their biological importance in the California Current Ecosystem. Global Change Biol. 17, 2536–2545. https://doi.org/10.1111/j.1365-2486.2011.02422.x.

Blanco, M., Ospina-Álvarez, A., González, C., Fernández, M., 2017. Egg production patterns of two invertebrate species in rocky subtidal areas under different fishing regimes along the coast of central Chile. PloS One 12, 1–18. https://doi.org/10.1371/journal.pone.0176758.

Botsford, L.W., Castilla, J.C., Peterson, C.H., 1997. The management of fisheries and marine ecosystems. Science 84 277, 509–515. https://doi.org/10.1126/science.277.5325.509.

Brochier, T., Lett, C., Fréon, P., 2011. Investigating the "northern Humboldt paradox" from model comparisons of small pelagic fish reproductive strategies in eastern boundary upwelling ecosystems. Fish Fish. 12, 94–109. https://doi.org/10.1111/j.1467-2979.2010.00385.x.

Broitman, B., Navarrete, S., Smith, F., Gaines, S., 2001. Geographic variation of southeastern pacific intertidal communities. Mar. Ecol. Prog. Ser. 224, 21–34. https://doi.org/10.3354/meps224021.

Bürkner, P.C., 2018. Advanced Bayesian multilevel modeling with the R package brms. RSA J. 10, 395–411. https://doi.org/10.32614/RJ-2018-017.

Bürkner, P.C., 2017. brms: an R package for Bayesian multilevel models using Stan. J. Stat. Software 80, 1–28. https://doi.org/10.18637/jss.v080.i01.

Camus, P.A., 2001. Marine biogeography of continental Chile. Rev. Chil. Hist. Nat. 74, 587–617.

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., Riddell, A., 2017. Stan: a probabilistic programming language. J. Stat. Software 76, 1–32.

Castilla, J.C., 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends Ecol. Evol. 14 (7), 280–283. https://doi.org/10.1016/S0169-5347(99)01602-X.

Castilla, J.C., Fernandez, M., 1998. Small-scale benthic fisheries in Chile: On co-management and sustainable use of benthic invertebrates. Ecological Applications 8 (sp1), S124–S132. https://doi.org/10.1890/1051-0761(1998)8[S124:SBFICO]2.0.CO;2.

Chavez, F.P., Messié, M., 2009. A comparison of eastern boundary upwelling ecosystems. Prog. Oceanogr. 83, 80–96. https://doi.org/10.1016/j.pocean.2009.07.032.

Cinner, J.E., Huchery, C., MacNeil, M.A., Graham, N.A.J., McClanahan, T.R., Maina, J., Maire, E., Kittinger, J.N., Hicks, C.C., Mora, C., Allison, E.H., D'Agata, S., Hoey, A., Feary, D.A., Crowder, L., Williams, I.D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G., Stuart-Smith, R.D., Sandin, S.A., Green, A.L., Hardt, M.J., Beger, M., Friedlander, A., Campbell, S.J., Holmes, K.E., Wilson, S.K., Brokovich, E., Brooks, A. J., Cruz-Motta, J.J., Booth, D.J., Chabanet, P., Gough, C., Tupper, M., Ferse, S.C.A., Sumaila, U.R., Mouillot, D., 2016. Bright spots among the world's coral reefs. Nature 535, 416–419. https://doi.org/10.1038/nature18607.

Cinner, J.E., McClanahan, T.R., MacNeil, M.A., Graham, N.A.J., Daw, T.M., Mukminin, A., Feary, D.A., Rabearisoa, A.L., Wamukota, A., Jiddawi, N., Campbell, S.J., Baird, A.H., Januchowski-Hartley, F.A., Hamed, S., Lahari, R., Morove, T., Kuange, J., 2012. Comanagement of coral reef social-ecological systems. Proc. Natl. Acad. Sci. Unit. States Am. 109, 5219–5222. https://doi.org/10.1073/pnas.1121215109.

Crona, B., Gelcich, S., Bodin, Ö., 2017. The importance of interplay between leadership and social capital in shaping outcomes of rights-based fisheries governance. World Dev. 91, 70–83. https://doi.org/10.1016/j.worlddev.2016.10.006.

Dayton, P.K., Rosenthal, R.J., Mahen, L.C., Antezana, T., 1977. Population structure and foraging biology of the predaceous chilean asteroid Meyenaster gelatinosus and the escape biology of its prey. Mar. Biol. 39, 361–370. https://doi.org/10.1007/BF00391939.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. Science 333, 301–306. https://doi.org/10.1126/science.1205106.

Forkel, M., Carvalhais, N., Verbesselt, J., Mahecha, M.D., Neigh, C.S.R., Reichstein, M., 2013. Trend Change detection in NDVI time series: effects of inter-annual variability and methodology. Rem. Sens. 5, 2113–2144. https://doi.org/10.3390/rs5052113.

Forkel, M., Migliavacca, M., Thonicke, K., Reichstein, M., Schaphoff, S., Weber, U., Carvalhais, N., 2015. Codominant water control on global interannual variability and trends in land surface phenology and greenness. Global Change Biol. 21, 3414–3435. https://doi.org/10.1111/gcb.12950.

Fuentes, E.N., Zuloaga, R., Almarza, O., Mendez, K., Valdés, J.A., Molina, A., Pulgar, J., 2017. Upwelling-derived oceanographic conditions impact growth performance and growth-related gene expression in intertidal fish. Comp. Biochem. Physiol. B Biochem. Mol. Biol. 214, 12–18. https://doi.org/10.1016/j.cbpb.2017.09.001.

Gallardo, G.L., Stotz, W., Aburto, J., Mondaca, C., Vera, K., 2011. Emerging commons within artisanal fisheries. The Chilean territorial use rights in fisheries (TURFs) within a broader coastal landscape. Int. J. Commons 5, 459–484. https://doi.org/10.18352/ijc.281.

García-Reyes, M., Sydeman, W.J., Schoeman, D.S., Rykaczewski, R.R., Black, B.A., Smit, A.J., Bograd, S.J., 2015. Under pressure: climate change, upwelling, and eastern boundary upwelling ecosystems. Front. Mar. Sci. 2, 1–10. https://doi.org/10.3389/fmars.2015.00109.

Garrido, S., Silva, A., Marques, V., Figueiredo, I., Bryère, P., Mangin, A., Santos, A.M.P., 2017. Temperature and food-mediated variability of European Atlantic sardine recruitment. Prog. Oceanogr. 159, 267–275. https://doi.org/10.1016/j.pocean.2017.10.006.

Gelcich, S., Cinner, J., Donlan, C.J., Tapia-Lewin, S., Godoy, N., Castilla, J.C., 2017. Fishers' perceptions on the Chilean coastal TURF system after two decades: problems, benefits, and emerging needs. Bull. Mar. Sci. 93, 53–67. https://doi.org/10.5343/bms.2015.1082.

Gelcich, S., Fernández, M., Godoy, N., Canepa, A., Prado, L., Castilla, J.C., 2012. Territorial user rights for fisheries as ancillary instruments for marine coastal conservation in Chile. Conserv. Biol. 26, 1005–1015. https://doi.org/10.1111/j.1523-1739.2012.01928.x.

Gelcich, S., Godoy, N., Prado, L., Castilla, J.C., 2008. Add-on conservation benefits of marine territorial user rights fishery policies in central Chile. Ecol. Appl. 18, 273–281. https://doi.org/10.1890/06-1896.1.

Gelcich, S., Hughes, T.P., Olsson, P., Folke, C., Defeo, O., Fernandez, M., Foale, S., Gunderson, L.H., Rodriguez-Sickert, C., Scheffer, M., Steneck, R.S., Castilla, J.C., 2010. Navigating transformations in governance of Chilean marine coastal resources. Proc. Natl. Acad. Sci. Unit. States Am. 107, 16794–16799. https://doi.org/10.1073/pnas.1012021107.

Gelcich, S., Martínez-Harms, M.J., Tapia-Lewin, S., Vasquez-Lavin, F., Ruano-Chamorro, C., 2019. Comanagement of small-scale fisheries and ecosystem services. Conserv. Lett. e12637 https://doi.org/10.1111/conl.12637.

Gelman, A., Hill, J., 2006. Data Analysis Using Regression and Multilevel/hierarchical Models. Cambridge university press, New York.

Hernández, K., Yannicelli, B., Montecinos, A., Ramos, M., González, H.E., Daneri, G., 2012. Temporal variability of incidental solar radiation and modulating factors in a coastal upwelling area (36°S). Prog. Oceanogr. 92–95, 18–32. https://doi.org/10.1016/j.pocean.2011.07.011.

Hockey, P.A.R., Bosman, A.L., 1986. Man as an intertidal predator in transkei: disturbance, community convergence and management of a natural food resource. Oikos 46, 3–14. https://doi.org/10.2307/3565373.

Lara, C., Saldías, G.S., Cazelles, B., Rivadeneira, M.M., Haye, P.A., Broitman, B.R., 2019. Coastal biophysical processes and the biogeography of rocky intertidal species along the south-eastern Pacific. J. Biogeogr. 46, 420–431. https://doi.org/10.1111/jbi.13492.

Leal, C.P., Quiñones, R.A., Chávez, C., 2010. What factors affect the decision making process when setting TACs?: the case of Chilean fisheries. Mar. Pol. 34, 1183–1195. https://doi.org/10.1016/j.marpol.2010.04.002.

Manríquez, P.H., Castilla, J.C., 2001. Significance of marine protected areas in central Chile as seeding grounds for the gastropod Concholepas concholepas. Mar. Ecol. Prog. Ser. 215, 201–211. https://doi.org/10.3354/meps215201.

Marín, A., Gelcich, S., Castilla, J.C., Berkes, F., 2012. Exploring social capital in Chile's coastal benthic comanagement. Ecol. Soc. 17, 13. https://doi.org/10.5751/ES-04562-170113.

McPhee-Shaw, E.E., Siegel, D.A., Washburn, L., Brzezinski, M.A., Jones, J.L., Leydecker, A., Melack, J., 2007. Mechanisms for nutrient delivery to the inner shelf: observations from the santa barbara channel. Limnol. Oceanogr. 52, 1748–1766. https://doi.org/10.4319/lo.2007.52.5.1748.

Menge, B.A., Lubchenco, J., Bracken, M.E.S., Chan, F., Foley, M.M., Freidenburg, T.L., Gaines, S.D., Hudson, G., Krenz, C., Leslie, H., Menge, D.N.L., Russell, R., Webster, M.S., 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proc. Natl. Acad. Sci. Unit. States Am. 100, 12229–12234. https://doi.org/10.1073/pnas.1534875100.

Menge, B.A., Menge, D.N.L., 2013. Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. Ecol. Monogr. 83, 283–310. https://doi.org/10.1890/12-1706.1.

Molina, P., Ojeda, F.P., Aldana, M., Pulgar, V.M., Roberto García-Huidobro, M., Pulgar, J., 2014. Spatial and temporal variability in subtidal macroinvertebrates diversity patterns in a management and exploitation area for benthic resources (MEABRs). Ocean Coast Manag. 93, 121–128. https://doi.org/10.1016/j.ocecoaman.2014.03.005.

Montecino, V., Lange, C.B., 2009. The Humboldt Current System: ecosystem components and processes, fisheries, and sediment studies. Prog. Oceanogr. 83, 65–79. https://doi.org/10.1016/j.pocean.2009.07.041.

Montero, P., Daneri, G., Cuevas, L.A., González, H.E., Jacob, B., Lizárraga, L., Menschel, E., 2007. Productivity cycles in the coastal upwelling area off Concepción: the importance of diatoms and bacterioplankton in the organic carbon flux. Prog. Oceanogr. 75, 518–530. https://doi.org/10.1016/j.pocean.2007.08.013.

Navarrete, S.A., Broitman, B., Wieters, E.A., Finke, G.R., Venegas, R.M., Sotomayor, A., 2002. Recruitment of intertidal invertebrates in the southeast pacific: interannual variability and the 1997-1998 el niño. Limnol. Oceanogr. 47, 791–802. https://doi.org/10.4319/lo.2002.47.3.0791.

Navarrete, S.A., Wieters, E.A., Broitman, B.R., Castilla, J.C., 2005. Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. Proc. Natl. Acad. Sci. U.S.A. 102, 18046–18051. https://doi.org/10.1073/pnas.0509119102.

Nielsen, K.J., Navarrete, S.A., 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecol. Lett. 7, 31–41. https://doi.org/10.1046/j.1461-0248.2003.00542.x.

Oyanedel, R., Keim, A., Castilla, J.C., Gelcich, S., 2018. Illegal fishing and territorial user rights in Chile. Conserv. Biol. 32, 619–627. https://doi.org/10.1111/cobi.13048.

Palumbi, S.R., 2003. Ecological subsidies alter the structure of marine communities. Proc. Natl. Acad. Sci. Unit. States Am. 100, 11927–11928. https://doi.org/10.1073/pnas.2335832100.

Pérez-Matus, A., Carrasco, S.A., Gelcich, S., Fernandez, M., Wieters, E.A., 2017. Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in Central Chile. Ecosphere 8. https://doi.org/10.1002/ecs2.1808.

Pickett, M.H., Schwing, F.B., 2006. Evaluating upwelling estimates off the west coasts of North and South America. Fish. Oceanogr. 15, 256–269. https://doi.org/10.1111/j.1365-2419.2005.00400.x.

Pinochet, A., Garcés-Vargas, J., Lara, C., Olguín, F., 2019. Seasonal variability of upwelling off central-southern Chile. Rem. Sens. 11, 1737. https://doi.org/10.3390/rs11151737.

Pulgar, J., Alvarez, M., Delgadillo, A., Herrera, I., Benitez, S., Morales, J.P., Molina, P., Aldana, M., Pulgar, V.M., 2012. Impact of wave exposure on seasonal morphological and reproductive responses of the intertidal limpet Fissurella crassa (Mollusca: archaegastropoda). J. Mar. Biol. Assoc. U. K. 92, 1595–1601. https://doi.org/10.1017/S0025315412000173.

Pulgar, J., Alvarez, M., Morales, J., Garcia-Huidobro, M., Aldana, M., Ojeda, F.P., Pulgar, V.M., 2011. Impact of oceanic upwelling on morphometric and molecular indices of an intertidal fish scartichthys viridis (Blenniidae). Mar. Freshw. Behav. Physiol. 44, 33–42. https://doi.org/10.1080/10236244.2010.533512.

Pulgar, J., Poblete, E., Alvarez, M., Morales, J.P., Aranda, B., Aldana, M., Pulgar, V.M., 2013. Can upwelling signals be detected in intertidal fishes of different trophic levels? J. Fish. Biol. 83, 1407–1415. https://doi.org/10.1111/jfb.12220.

R Core Team, 2017. R Core Team (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rykaczewski, R.R., Dunne, J.P., Sydeman, W.J., García-Reyes, M., Black, B.A., Bograd, S. J., 2015. Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. Geophys. Res. Lett. 42, 6424–6431. https://doi.org/10.1002/2015GL064694.

Santos, A.M.P., Nieblas, A.E., Verley, P., Teles-Machado, A., Bonhommeau, S., Lett, C., Garrido, S., Peliz, A., 2018. Sardine (Sardina pilchardus) larval dispersal in the Iberian upwelling system, using coupled biophysical techniques. Prog. Oceanogr. 162, 83–97. https://doi.org/10.1016/j.pocean.2018.02.011.

Siegfried, W.R., Hockey, P.A.R., Crowe, A.A., 1985. Exploitation and conservation of Brown mussel stocks by coastal people of transkei. Environ. Conserv. 12, 303–307. https://doi.org/10.1017/S037689290003441X.

Sobarzo, M., Bravo, L., Donoso, D., Garcés-Vargas, J., Schneider, W., 2007. Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. Prog. Oceanogr. 75, 363–382. https://doi.org/10.1016/j.pocean.2007.08.022.

Stan Development Team, 2017. Stan Modeling Language User's Guide and Reference Manual.

Stotz, W., 1997. The management areas in the fishery law: first experiences and evaluation of utility as a management tool for Concholepas concholepas. Estud. Oceanol. 16, 67–86.

Stotz, W.B., Gonzalez, S.A., Caillaux, L., Aburto, J., 2003. Quantitative evaluation of the diet and feeding behavior of the carnivorous gastropod, Concholepas concholepas (Bruguiere, 1789) (muricidae) in subtidal habitats in the southeastern pacific upwelling system. J. Shellfish Res. 22, 147–164.

Tam, J., Chan, K.M.A., Satterfield, T., Singh, G.G., Gelcich, S., 2018. Gone fishing? Intergenerational cultural shifts can undermine common property co-managed fisheries. Mar. Pol. 90, 1–5. https://doi.org/10.1016/j.marpol.2018.01.025.

Tapia, F.J., Largier, J.L., Castillo, M., Wieters, E.A., Navarrete, S.A., 2014. Latitudinal discontinuity in thermal conditions along the nearshore of central-northern Chile. PloS One 9. https://doi.org/10.1371/journal.pone.0110841.

Tapia, F.J., Navarrete, S.A., Castillo, M., Menge, B.A., Castilla, J.C., Largier, J., Wieters, E.A., Broitman, B.L., Barth, J.A., 2009. Thermal indices of upwelling effects on inner-shelf habitats. Prog. Oceanogr. 83, 278–287. https://doi.org/10.1016/j.pocean.2009.07.035.

Teixeira, C.M., Gamito, R., Leitão, F., Murta, A.G., Cabral, H.N., Erzini, K., Costa, M.J., 2016. Environmental influence on commercial fishery landings of small pelagic fish in Portugal. Reg. Environ. Change 16, 709–716. https://doi.org/10.1007/s10113-015-0786-1.

Thiel, M., Macaya, E.C., Acuña, E., Arntz, W.E., Bastias, H., Brokordt, K., Camus, P.A., Castilla, J.C., Castro, L.R., Cortés, M., Dumont, C.P., Escribano, R., Fernandez, M., Gajardo, J.A., Gaymer, C.F., Gomez, I., González, A.E., González, H.E., Haye, P.A., Illanes, J.-E., Iriarte, J.L., Lancellotti, D.A., Luna-Jorquera, G., Luxoro, C., Manriquez, P.H., Marín, V., Muñoz, P., Navarrete, S.A., Perez, E., Poulin, E., Sellanes, J., Sepúlveda, H.H., Stotz, W., Tala, F., Thomas, A., Vargas, C.A., Vasquez, J.A., Vega, J.M.A., 2007. The Humboldt Current System of northern and central Chile - oceanographic processes, ecological interactions and socioeconomic feedback. Oceanogr. Mar. Biol. Annu. Rev. 45, 195–344. https://doi.org/10.1091/mbc.E04-05-0427.

Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. 27, 1413–1432. https://doi.org/10.1007/s11222-016-9696-4.

Vergara, O.A., Echevín, V., Hito, H., Quiñones, R.A., 2017. Controlling factors of the seasonal variability of productivity in the southern Humboldt Current System (30-40 ° S): a biophysical modeling approach Continental Shelf Research Controlling factors of the seasonal variability of productivity in the southe. Continent. Shelf Res. 148, 89–103. https://doi.org/10.1016/j.csr.2017.08.013.

Wang, D., Gouhier, T.C., Menge, B.A., Ganguly, A.R., 2015. Intensification and spatial homogenization of coastal upwelling under climate change. Nature 518, 390–394. https://doi.org/10.1038/nature14235.

Wieters, E.A., 2005. Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. Mar. Ecol. Prog. Ser. 301, 43–54. https://doi.org/10.3354/meps301043.

Wieters, E.A., Broitman, B.R., Branch, G.M., 2009. Benthic community structure and spatiotemporal thermal regimes in two upwelling ecosystems: comparisons between South Africa and Chile. Limnol. Oceanogr. 54, 1060–1072. https://doi.org/10.4319/lo.2009.54.4.1060.

Zuloaga, R., Almarza, O., Valdés, J.A., Molina, A., Pulgar, J., 2018. Oceanographic upwelling conditions influence signaling pathways involved in muscle growth of intertidal fish. Comp. Biochem. Physiol. B Biochem. Mol. Biol. 218, 37–43. https://doi.org/10.1016/j.cbpb.2018.02.001.