The masked influence of remote ENSO-related drivers on the trophic dynamics of Independencia Bay, Peru: Insights for management from time-series analysis and food-web modelling

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A B S T R A C T

Independencia Bay is a very productive ecosystem in central-south Peru and a hotspot for the artisanal diving fishery and the aquaculture of scallop *Argopecten purpuratus*. Warm waters from strong Canonical El Niño (EN) events can have negative and positive effects along the coast, such as mass mortalities of scallops in the north and their extraordinary increase in landings and effort in the central-south. Other variations of EN are more localised and mainly affect the north of Peru, though they may indirectly affect Independencia Bay, such as through the migration of pelagic fish as their habitat expands, or the migration of scallop divers as their main resource collapses. In the context of ecosystem-based management, it is relevant to investigate how these combined effects are shaping the structure and dynamics of this ecosystem, to inform the decision-making process and allow for management strategies to be tested and improved. In this study, we used time series correlation analysis and a food-web model to study the role of environmental and fisheries-related drivers on Independencia Bay during a relatively stable period (2007–2020). We also investigated the influence on the ecosystem of changes originating in Sechura Bay (mainly through effects associated with the 2017 Coastal EN), aiming to elucidate probable masked effects of EN and provide insights for integrated ecosystem-based management in the region. We suggest that during our study period, there was a migration of effort to Independencia mainly following the mass mortalities of scallops in Sechura, apparently related to overstocking of seeds, in addition to the reported migration triggered by the 2017 EN, despite it being comparatively shortlived. In any case, the fishing effort in Independencia Bay increased considerably between 2012 and 2016 and it was the main driver of change in the ecosystem during this period, along with trophic interactions and a forced bottom-up control (primary production anomaly), as seen in the model's fitting procedure results. We suggest that the system's variations in production might be related to a combination of local drivers and teleconnection effects, such as the migration of effort from Sechura Bay and the Pacific Decadal Oscillation's general influence on the Eastern Pacific. The decline in the biomass of many groups in recent years, calls for a better integrated management that addresses local and remote environmental drivers, ecological changes, and perhaps most importantly, social aspects such as migration. We call for a local fisheries management option for Independencia Bay that is not independent of what happens in other regions of the coast.

1. Introduction

Climatic and fisheries-related drivers can transform the structure and functioning of marine ecosystems through the years, steering them over different temporal and spatial resolutions (Alms and Wolff, 2019; Defeo et al., 2014; Salvatteci et al., 2022; Serpetti et al., 2017). Depending on the nature and extent of these drivers, their effect can be felt from a local to a regional scale, with direct or indirect impacts on the ecosystems. For example, primary production might be locally forced by the wind or by water input from a river, or an increase in fishing effort could be driven by external forces such as international market prices. Some of these effects may come from remote environmental drivers that operate at

larger temporal and spatial scales, like El Niño Southern Oscillation (ENSO) in the Pacific Ocean, which can affect ecosystems around the world through teleconnection effects (Espinoza-Morriberón et al., 2019; Gutiérrez et al., 2016; Takahashi et al., 2011; Schwing et al., 2010). Along the Peruvian coast, warm El Niño (EN) events can positively affect some fisheries and collapse others (Arntz et al., 1991, 2006; Estrella Arellano and Swartzman, 2010; Ñiquen and Bouchon, 2004; Taylor, 2008), also triggering the migration of fishers between social-ecological systems (Badjeck et al., 2009; Kluger et al., 2018). In the context of ecosystem-based management, it is relevant to investigate how these combined multi-scale effects are moulding the trophic structure and resource-use dynamics of certain ecosystems, to inform the decision-making process and allow for future strategies to be designed and tested. In this study, we focus on Independencia Bay, a very productive ecosystem off south-central Peru that has been the subject of coastal-marine research and management for decades (Arntz et al., 1991; Del Solar et al., 2022; Riascos et al., 2016; Takahashi and Dewitte, 2016; Tarazona et al., 1988, 2007; Taylor et al., 2008a, b)

Located within the highly productive eastern boundary Northern Humboldt Current Upwelling System (NHCUS), Independencia Bay has long been a hotspot for artisanal fisheries (mainly divers using surface-supplied air, also known as a hookah diving system) and the aquaculture of scallop *Argopecten purpuratus*, being particularly susceptible to strong EN events (Mendo et al., 2016; Tarazona et al., 1988; Wolff, 1987). While these interannual EN events are not yet fully understood, as explained by Ken Takahashi, lead researcher at the Peruvian Geophysical Institute (IGP), during a 2023 talk[1] on the impacts of EN, there are different general characterisations based on their location, geographic extension and persistence along the equatorial Pacific. For example, the so-called *EN Modoki* shows high-temperature anomalies in the Central Pacific but a weaker signal towards the East. In contrast, there is a recently defined different type of EN that exhibits strong temperature anomalies but mainly in the northern part of the coastal Eastern Pacific. The 1925 strong event was reported as an EN, but it is now evident that it had the characteristics and impact of what we currently identify as a *Coastal EN*, coined after the very strong warming event of 2017 (Dewitte and Takahashi, 2019; Takahashi and Martínez, 2019). Notably, this type of event is often considered a marine heathwave but it is locally known (and will be called in this paper) as *Coastal EN*. This highly localised warming event lasted roughly two months and mainly impacted the north coast of Peru, not showing evidence of its immediate impact on Independencia Bay, as seen in measurements of remote-sensed sea surface temperature (SST; Del Solar et al., 2022). While writing this paper, a Coastal EN event was confirmed between March and May 2023, with similar effects along the coast, expected to last until early 2024.

However, the strongest effects of ENSO in the Peruvian upwelling system are produced by larger warm EN events, often referred to as "classical" or "canonical", which present high-temperature anomalies all along the Pacific and typically have a global impact. The last two extraordinary[2] of such events occurred during the summer periods of '1983–84 and '1997–98, having acute effects along the Peruvian coast (Takahashi and Dewitte, 2016) down to the Pisco Region and Independencia Bay in the central-south coastal area (and even beyond to the coast of northern Chile). The main direct impacts of such strong EN events are the increase in temperature, the reduction of primary production and the mixing and reoxygenation of the water column. As most

trophic interactions in Independencia Bay are bottom-up driven, the effects of EN cascade along the food web, shifting the trophic dynamics therein (Arntz et al., 2006; Takahashi and Dewitte, 2016; Tarazona et al., 1988; Taylor et al., 2008a, b). This type of EN has a generally negative effect on many cold-adapted benthic invertebrates, such as the mussel *Aulacomya ater* and the predatory Rock crab *Romaleon setosum* (previously known as *Cancer polyodon* or *C. setosus*[3]). In contrast, EN conditions favour warm-tolerant species, such as the purple snail *Thais chocolata*, the octopus *mimus* and, in particular, the scallop *Argopecten purpuratus*, which increases its biomass more than fifty-fold (Mendo et al., 2016; Mendo and Wolff, 2003; Taylor et al., 2008a, b). The flourishing of scallops in Independencia causes a big surge in the diving effort, also sustained by the migration of fishers who flee from the destructive effects of EN on the infrastructure and livelihoods of local villages along northern Peru. In particular, there is mass mortality of scallops in Sechura Bay, nullifying the aquaculture activities therein (Arntz et al., 1991; Badjeck et al., 2009; Kluger et al., 2018; Mendo et al., 2016).

Nevertheless, the effects of the Canonical EN on Independencia Bay are temporary and the ecosystem generally returns to its previous configuration after a couple of years, fuelled in part by the reoxygenation that took place during EN (Arntz et al., 2006; Taylor et al., 2008a, b). Only the Canonical EN has had a direct impact on Independencia Bay, but the similarly devastating effects of the 2017 Coastal EN on the scallop aquaculture of Sechura Bay once again triggered the migration of fishers, shifting the diving effort to central-south Peru. However, unlike during the Canonical EN, the local resources at Independencia Bay did not seem to increase in productivity during this period, leading to the potential overfishing of certain species, particularly those targeted by the diving fishery. To our knowledge, the impacts of this increase in effort have not been yet studied outside of the strong EN conditions observed in the past (Arntz et al., 2006; Taylor et al., 2008a, b).

In this study, we aimed to advance our understanding of Independencia Bay's trophic dynamics during an environmentally stable period 2007–2020 (i.e., without strong Canonical events), while investigating the role of fisheries along documented trends and patterns. We suggest that the varying nature of the different EN impacts can be confounded with other factors (e.g., socio-economic trends) to create highly uncertain patterns of change within these coastal social-ecological systems (SES). The objectives of the present paper were to (i) identify the main drivers of change in the ecosystem dynamics of the bay, using trophic modelling and historical time series of fisheries and environmental data, and (ii) understand the direct and indirect effects of the 2014–2018 EN period, including the Coastal EN of 2017, on the resource productivity and fishery of Independencia Bay. Furthermore, we aim to provide insights for users and managers regarding the potential teleconnection effects coming from Sechura Bay in northern Peru, pushing towards a more integrated approach to management.

To study the role of environmental and fishing drivers on the trophic and resource-use dynamics of Independencia Bay, we used a pre-constructed mass-balanced Ecopath with Ecosim (EwE; Christensen and Pauly, 1992; Christensen and Walters, 2004; Heymans et al., 2016) trophic model of this system, as described in Del Solar et al. (2022). It was built for the LN-year 2007, including data from 2006 through 2008. We then subjected this reference model to time series data of biomass, fisheries (i.e., landings and effort per species and gear for the whole bay) and remote-sensed environmental parameters and proxies (i.e., SST, Chl-a, wind and regional multi-variate indices), for the period 2007–2020. Such a model would allow us to explore to which degree the biomass, production and consumption trends estimated are driven mostly by environmental and fisheries variables, by the trophic interactions operating within, or by a combination of all. In parallel, we correlated these time series with the primary production (PP) anomaly

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[1] Online talk as part of the Peruvian-related forum "How prepared are we to face the Yaku cyclone, El Niño phenomenom and climate change?" Streamed and stored on the platform YouTube, at https://www.youtube.com/watch?v=QFqkxGA2ulM&t=16s. (Takahashi, 2023)

[2] Generally, EN and LN periods are measured by the magnitude of SST anomalies over a period of a few months at the EN1+2 Region. The thresholds range from (−1.8 °C) cold-strong to warm-extraordinary (3 °C) events (http://enfen.gob.pe).

[3] https://www.marinespecies.org/.

produced by the EwE model. By including and excluding different drivers from the fitting process, we could fine-tune the model that best described the trophic-related changes in Independencia Bay between 2007 and 2020, and the drivers behind them. We included information from Sechura Bay to assess if variations in SST and fishing effort were associated with any changes occurring in Independencia Bay.

2. Methods

2.1. Study area

Independencia Bay lies between 14°10′ and 14°11′ South, adjacent to one of the four main upwelling plumes along the Peruvian coast. It has a water-surface area of around 150 km² and is partially enclosed by La Vieja Island (Fig. 1). The 30 m isobath lies very close to the shore, fringing at about 1 km. Between this point and the bay's mouth (~7 km from the beach), the depth varies and reaches down to ~90 m. Although the oxygen minimum layer off Peru is relatively shallow (~30 m of depth, Arntz et al., 1991; Bertrand et al., 2010; Chavez et al., 2008), anoxia events are not a recurrent issue in Independencia, in contrast to other Peruvian bays like Paracas or Sechura, partly due to its comparatively steeper bathymetry and higher water circulation (Arntz et al., 1991; Quispe et al., 2010; Aguirre-Velarde et al., 2016; Cueto-Vega et al., 2021). The water in this bay is typically cold and nutrient-rich, maintaining relatively stable conditions since 2006, as observed in the monthly-averaged SST and chlorophyll concentrations obtained from remote sensing (updated from Del Solar et al., 2022). The mean SST value over this period was 16.99 °C (SD = 2.1), showing a slight decreasing trend, especially in recent years. In contrast, Chl-a values (which are a proxy for primary production) have followed a generally positive trend since 2000.

This ecosystem is highly productive and efficient in transferring primary production through the food web, supporting similar catches per unit of area and relatively higher gross efficiencies (catch per net primary production) compared to larger highly productive systems such as Sechura Bay, in northern Peru (Del Solar et al., 2022; Taylor et al., 2008a, b). Situated at the coast of the northern boundary of the Atacama desert, with no river to transport particulate organic matter and pollutants into the system, and being protected by the Paracas National Reserve, Independencia Bay is a relatively undisturbed ecosystem. Thanks to these characteristics, this bay has long been a hotspot for artisanal fisheries (mainly divers using surface-supplied air, also known as a hookah diving system) and aquaculture of scallop *Argopecten purpuratus* (Arntz et al., 1991; Guevara et al.,; Mendo et al., 2016), but net-fishery for fish is also occurring. On the north side of the bay, there is a small shallow inlet named Laguna Grande (large lagoon), which is the main landing site in the bay, the other one being Rancherio (Fig. 1). This inlet is commonly known by local actors as being a nursing ground for different species of fish. Though it is illegal to fish inside Laguna Grande, several purse seiners are regularly spotted doing their activities there. Most of the landings are then taken to San Andrés, which is the main landing and commerce site in Pisco (Fig. 1). Based on landings data provided by the Peruvian Marine Research Institute (IMARPE), the main resources extracted from the bay over the past two decades have been: scallop *A. purpuratus*, mussel *Aulacomya ater*, clams *Gari solida* and *Ensis macha*, rock crab *Romaleon setosum*, grunt *Isacia conceptionis* and mackerel *Trachurus murphyi*.

2.2. Fisheries and environmental time-series and correlations

The multi-gear and multi-specific fisheries dynamic was assessed using monthly time series of landings and effort provided by IMARPE[4] in

the context of the bilateral German-Peruvian research project Humboldt Tipping[5]: per trip, species, landing site, fishing ground and gear. The effort was calculated as number of trips times the hold capacity, which was measured in tonnes. This dataset was processed to obtain total monthly values per species caught and gear used, from 1996 to 2020, and then plotted to analyse the trends in landings and effort per fleet and functional group, as defined in the EwE model described below (Del Solar et al., 2022). Although the model was built for the LN year 2007, those prior ten years of information serve as a context for the dynamics seen from 2007 onwards, given our current good understanding of the bay's general response during a strong EN cycle, such as that of 83–84′ or 97–98' (Arntz et al., 2006; Tarazona et al., 1988; Taylor et al., 2008a, b).

The environmental variables and indices used were obtained from publicly available remote sensing data at different scales (Table 1): Regional (PDO, ICEN), National (ITCP) and Local (SST and PP - using Chl-a as a proxy). The Regional and National indices obtained are values of SST anomalies (using very long-term climatologies) calculated for specific areas along the Pacific Ocean and Peruvian coast (Table 1). For SST and Chl-a values at the Local level, we downloaded data for the whole Peruvian Exclusive Economic Zone (EEZ) and filtered the data to our areas of interest (Independencia and Sechura), to obtain average monthly values for each bay (Table 1).

We performed a correlation analysis between all of the time series, including the primary production (PP) anomaly obtained from the Independencia Bay EwE model (see details below), to assess the influence of these time series at different scales on the dynamics of our study site. The correlation between environmental variables allowed us to see the link between the oscillations at different scales and the cascading effects down to the local bay level. The correlation within the fisheries' time series (i.e., effort and landings) by species (or functional group) and fleet (gear), with their total values, helped us assess which groups or fleets were driving the changes in total effort and landings, in association with the PP anomaly obtained from the model. These correlations include the fishing effort of Sechura Bay and Independencia Bay, to assess how much the fishers from Sechura might be migrating their effort towards Independencia, particularly during the EN period of 2014–2017. We tested for lagged correlations using the astsa package (function lag2.plot, Stoffer and Poison, 2024) of the R software (R Core Team, 2023), which allows the comparisons of two variables at a time.

2.3. Ecopath with ecosim: time-series fitting procedure, PP anomaly curves and hypotheses testing

Trophic modelling approaches such as Ecopath with Ecosim (EwE) have proven suitable for describing and assessing ecosystem changes and their drivers, being useful for designing and testing fisheries management strategies (Christensen and Pauly, 1992; Christensen and Walters, 2004; Coll and Steenbeek, 2017; Heymans et al., 2016). The EwE modelling approach uses a software suite that comprises three main components: Ecopath, Ecosim and Ecospace. They work hierarchically to allow a mass-balanced snapshot model to be fitted to temporal and spatial data and simulate its past and future states (Christensen and Pauly, 1992; Christensen and Walters, 2004; Heymans et al., 2016). In this study, we used Ecosim to simulate changes in biomass and catch of the different groups and fleets of an Independencia Bay Ecopath model (Del Solar et al., 2022),[6] fitted to the time-series data provided by IMARPE for the period 2007–2020. To drive the model, we used fishing effort and remote-sensed environmental parameters and proxies (i.e., SST, Chl-a and Wind), updated from (Del Solar et al., 2022). Details on the Ecopath model construction can be found in the mentioned paper.

Based on the initial parameters of the Ecopath master equations (Christensen and Walters, 2004), Ecosim works by running a series of
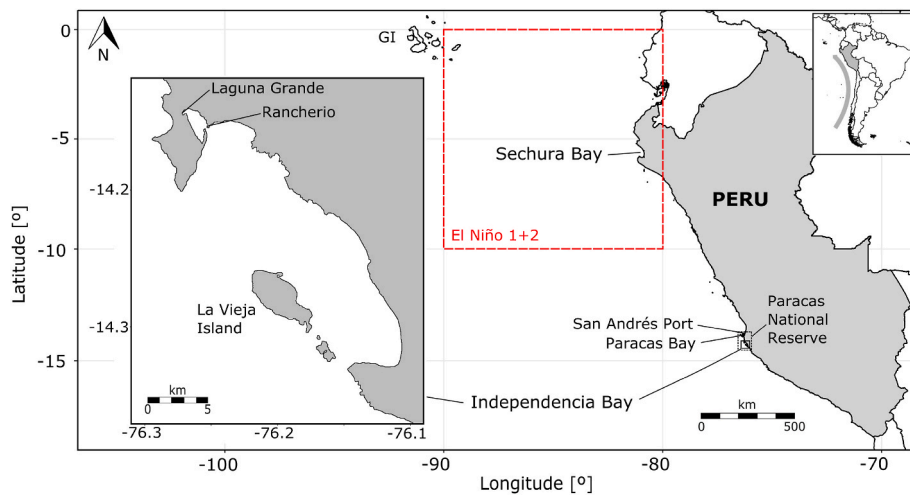

Fig. 1. Map of study site Independencia Bay, located in Peru, western coast of South America. As a reference, the study region known as El Niño 1 + 2 and the Paracas National Reserve are shown. The grey curved arrow in the box at the upper right corner represents the Humboldt Current. GI: Galapagos Islands.

Table 1
Envrionmental time series used in the correlation analysis.

Parameter	Spatial scale	Description	Temporal scale	Data resolution	Source
Pacific Decadal Oscillation (PDO)	North Eastern Pacific Ocean	SST anomalies 30 years climatology	1900–2023	Monthly	Public available: https://psl.noaa.gov/gcos_wgsp/Timeseries/
Coastal Ninyo Index (ICEN, EN1+2)	Tropical Eastern Pacific Ocean	SST anomalies 30 years climatology	1900–2023	Monthly	Public available: https://psl.noaa.gov/gcos_wgsp/Timeseries/
Thermal Coastal Peruvian Index (ITCP)	Coastal Upwelling System (05°S-19°S)	SST anomalies 30 years climatology	1900–2023	Monthly	Quispe-Ccalluari et al., 2016 Public available: https://www.imarpe.gob.pe/
Sea Surface Temperature	Independencia Bay Sechura Bay	OSTIA satellite system	2006–2023	Daily (4 × 4km2)	Stark et al., 2007 Public available: https://data.marine.copernicus.eu/products/
Chlorophyll a	Independencia Bay Sechura Bay	MODIS-AQUA satellite system	1997–2023	Daily (4 × 4km2)	Provided by IMARPE

coupled differential equations that express the biomass dynamics over time:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_k Q_{ik} + I_i - (M_i + F_i + e_i).B_i$$

where the biomass variation of group i through time (dB_i/dt) equals its net growth efficiency (g_i) times its total consumption of all prey (Q_{ji}), equivalent to its production P_i, plus an immigration rate I_i, minus all mortalities and exports, i.e., predation mortality Q_{ik}, natural mortality rate M_i, fishing mortality rate F_i, and emigration rate e_i.

The calculation of the consumption rates Q_{ji} is based on the "foraging arena" concept, which describes the predator-prey interactions as a tradeoff between feeding opportunity and predation risk (Christensen and Walters, 2004; Ahrens et al., 2012). In Ecosim, the exchange rate between these 'vulnerable' and 'un-vulnerable' states of the different functional groups is known as the vulnerability v_{ji}, which can be set between one and infinity and determines if the control of each predator-prey interaction is bottom-up ($v = 1$), top-down ($v > 2$) or intermediate ($v = 2$). These values indicate how far away from its carrying capacity the predator is in relation to each prey, or how much an increase in predator biomass would affect the predation mortality of its prey. The default v is 2, which indicates neither a top-down nor bottom-up control, but a mixed control setting. The consumption equation (Eq. 2) of group i over prey j (Q_{ji}) also includes variables such as

the rate of effective search (a_{ij}), predator and prey relative feeding time (T), user-defined mediation (M_{ji}) and seasonal or long-term (S_{ji}) forcing effects, and effects of handling time (D_i; Ahrens et al., 2012; Christensen et al., 2008; Christensen and Walters, 2004; Guénette et al., 2008; Walters et al., 1997).

$$Q_{ji} = \frac{a_{ij}.v_{ji}.B_j.P_i.T_j.T_i.S_{ji}.M_{ji}/D_i}{v_{ji} + v_{ji}.T_j.M_{ji} + a_{ij}.M_{ji}.P_i.S_{ji}.T_i/D_i}$$

To adjust the model predictions to time series reference data, the EwE fitting procedure 'forces' the time dynamics of the model as bottom-up and top-down controls, through primary production (PP) and fishing mortality (or effort), respectively, using the sums of squares differences (SS) to measure how well the model fits the data (Mackinson et al., 2009). Depending on user selection, the fitting procedure tweaks the PP anomaly curve and the vulnerabilities (v) in the search for the best combination that reduces SS differences between model simulations and reference data as much as possible. The PP anomaly search routine detects relevant variations in the productivity of the system and associates them with a potential bottom-up effect to explain fluctuations in biomass and catches during the study period. The anomaly curve thus represents an unknown function that can play a bottom-up control on the ecosystem (Mackinson et al., 2009). Furthermore, the effects of bottom-up and top-down controls (e.g., PP and fishing) depend on how the various model ecosystem components interact (Scott et al., 2016). To

better understand the relationship between the model's PP anomaly with other local and remote factors, we correlated the anomaly curves of our best models with the environmental and fisheries-related time series (see section 2.2). Given that the PP anomaly curve is an output of the model, which was fitted using fishing effort time series as input, we want to explore through their correlation how much the increase in effort of the different fleets might be triggering the changes in PP anomaly estimated, or if the effort is merely a consequence of the increased productivity and subsequent abundance.

The stepwise fitting routine incorporated in EwE (Scott et al., 2016) allowed us to perform sequential fitting procedures, each time automatically changing the number of parameters to be used in the search for different vulnerabilities and PP anomaly curves. Different runs of the stepwise procedure were performed to identify the main variables driving the trophic and resource-use dynamics of Independencia Bay, changing the time series of biomass and catches, and including (or not) the environmental forcing. For all runs, we used the vulnerability (v) search by predator, and not predator-prey, meaning that the model estimated a single vulnerability value for each predator across its prey portfolio, instead of focusing on those individual interactions to which the model is more sensitive. The main initial states of the different runs were: (i) no forced biomasses or catches and no environmental drivers; (ii) no forced biomasses or catches and forced environmental drivers, i. e., SST forced on consumers (positively on scallops, predatory snails and large pelagics; negatively on cangrid crabs, mussels and clams), Chl-a or Wind forced on the search rate of all consumers; (iii) forced biomass of phytoplankton, scallops, mussels and crabs (individually and together) with and without environmental forcing; and (iv) forced catches of scallops, clams, mussels and crabs (individually and together) with and without environmental forcing. Depending on these initial parameters, the stepwise fitting procedure performs sequential runs that fall under one of eight main hypotheses (Table 2), as defined by Mackinson et al. (2009) and suggested by Heymans et al. (2016).

A list of the best models was filtered based primarily on their lower SS and AICc values, but also visually by assessing the fit of all groups and in particular those of highest interest for the fishery (i.e., rock crabs, mussels, clams, scallops and pelagic fish).

3. Results

3.1. Landings and effort per species and gear

Fig. 2 shows a summarised plot that portrays the total yearly landings and effort (number of trips times the size of the fishing hold) per main taxonomical group, i.e., fish, invertebrates and macroalgae, from 1996 to 2020. As expected, there is a clear dominance of invertebrates throughout the series. In particular, there is a huge surge between 1998 and 1999, caused by the overwhelming increase in the scallop population during the extraordinary EN 97–98. If we exclude scallops from the landings dataset, we obtain a clear pattern of two peaks in the total landings since 1996 (Fig. 2B). The first peak develops circa the end of the EN 97–98 cycle, reaching its high point between 2002 and 2004, after which the landings decrease steadily until 2012, down to pre-EN levels (Fig. 2). The main groups targeted during this period were mussels, clams, rock crabs and littoral and large pelagic fish. This suggests that part of the excess diving effort that increased over EN switched to target other species once scallops returned to their previous low biomass levels. Mussel landings dominated until 2002–2004 and then decreased by half, trading places with clams, which doubled their landings the next year. This high point of clams did not last too long and plummeted fast, allowing the mussel landings and effort to slightly recover in 2007, just to decrease again and follow the trend of all the other resources (Fig. 2B).

The second peak of landings and effort occurred between 2012 and 2018, reaching the highest point around 2016. This increase was led by the same resources as before but showing different proportions. In particular, large pelagics, clams and crabs showed the largest overall increase in their landings during this period, while mussels stayed on their general decreasing path observed after EN 97–98 (Fig. 2B). There is also a considerable increase in small pelagics in 2014, which coincides with the peak of clam landings during this later period. In terms of gears, the highest increase of effort was from hookah divers targeting both fish and invertebrates (excluding crabs, clams, scallops and mussels). However, although most species showed a substantial increase in landings between 2012 and 2016, the largest growth came from purse seiners (targeting pelagic and littoral fish), which almost doubled their production during that period. Between 2017 and 2020, the landings decreased considerably to about half of their peak total amount (Fig. 2B). The total effort also decreased similarly but lasted a bit longer before plummeting in 2020, perhaps caused by the COVID-19 pandemic.

The trend of total CPUE, calculated as total landings over total effort, shows a general decline after the 97–98 EN event throughout the rest of the study period, with peaks around 2007 and 2015 (Fig. 2C). When split between nets[7] and diving fisheries, it is clear that these bumps are generated mainly by the CPUE of the net fisheries (purse seiners, predominantly). During the period 2012–2018, there is a strong increase in the diving fishery effort, which is as high as the peak seen during EN 97–98, though the diving CPUE keeps decreasing. In contrast, a slight change in the landings of the net fisheries generates a huge increase in CPUE, even with relatively constant levels of effort. More detailed plots from 2007 onwards of landings and effort of invertebrate and fish groups can be found in the supplementary material.

3.2. Time series fitting

All models generated by all runs of the EwE's stepwise fitting procedure were contrasted by plotting their computed SS differences between simulated and observed values against their corrected Aikake values (AICc). This allowed us to visually assess those models (hypotheses) that show a greater reduction in SS while not increasing AICc considerably. Overall, the best fitting models were those that included fishing effort as a driver and incorporated the trophic interaction (vulnerability) and primary production anomaly searches in the fitting process (i.e., hypothesis test 8 of Table 2). Furthermore, including forced biomasses and catches and environmental drivers did not improve the fit, but rather worsened it. The final model used 37 parameters (32 vulnerabilities and 5 splines for the anomaly curve) and had a SS reduction of 98.74%. Furthermore, Table 2 shows that using only 'Fishery and trophic interactions' (hypothesis test 6) also reduces the SS substantially, but with fewer parameters and a considerably higher AICc value compared to that of hypothesis 8. This suggests that the fishing effort and the trophic interactions alone can explain most of the variation in the biomass and catches occurring during the study period, but that there is also a relevant underlying natural productivity oscillation driving the system (captured in the PP anomaly curve).

The stepwise fitting procedure was repeated using different initial states, i.e., with forced (or not) biomasses, catches and environmental drivers, as described in the main text. This table shows the results of the best runs, which are from the state (i), i.e., with no forcings of any kind.

A list of the best models was filtered based primarily on their lower SS and AICc values, though a few other model runs had lower SS than these chosen ones, but higher AICc values. They also showed unrealistic vulnerabilities and PP anomaly curves that suggest that these models were overfitted (Christensen et al., 2008), so we dismissed them from the calculation of the average PP anomaly curve that was used for the correlation analysis. All the PP anomaly curves generated by these best models showed a similar trend, with relatively stable conditions throughout the study period, but showing a noticeable rise in the productivity of the system between 2013 and 2016, with its highest peak

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[7] These 'net fisheries' group also includes 'hook and line'.

Table 2
Test hypotheses and results from the best models.

|	Test hypotheses	Num of Parameters	SS Start	SS End	% SS reduction	AICc
1	Baseline	–	19294.3			
2	Baseline and trophic Interactions (vulnerabilities)	32		896.6	95.35	319.9
3	Baseline and environment (PP anomaly)	5		9263.0	51.99	1619.0
4	Baseline, trophic interaction and environment	37		821.5	95.74	280.4
5	Fishery (Effort)	–	30760.0			
6	Fishery and trophic interactions	32		407.5	98.68	−138.3
7	Fishery and environment	5		14559.0	52.67	1882
8	Fishery, trophic interaction and environment	37		388.5	98.74	−166.9
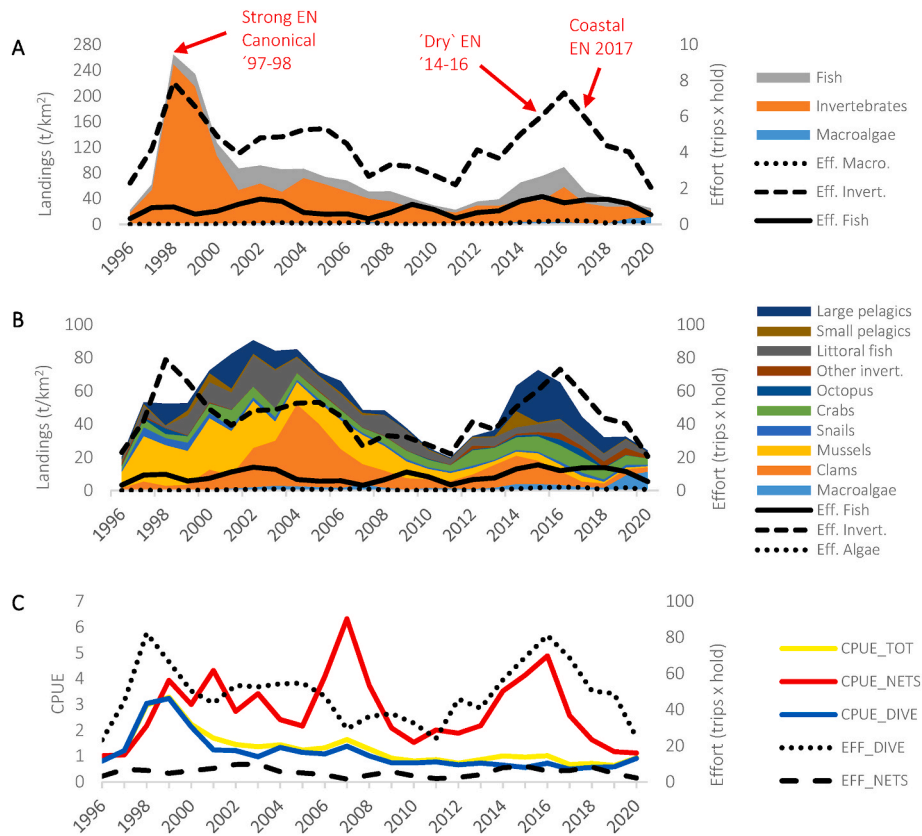
Fig. 2. Total landings and effort per (A) taxonomical group, (B) without scallops and (C) as CPUE per gear type, calculated as landings (t/km^2) over effort (number of trips times hold size in tonnes), times 1000. In panel (C), 'CPUE_NETS' include all net-type gear, i.e., drift, bottom and purse seines.

around 2015, as seen in the average curve, which differs slightly from the final model's anomaly curve (Fig. 3). Overall, the best model shows a considerably better fit of catches, compared to the biomass simulations.
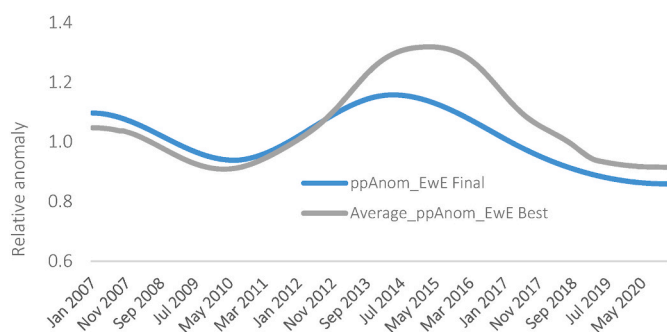

Fig. 3. Primary production anomaly curves of the final model used and of the average of the best models.

Almost all catch simulations fit the reference data trends, with the noticeable exception of octopus, bonitos and mackerels. For biomass, almost all fits show an overall decrease during the study period (2007–2020), with a small peak showing for most groups around 2013–2015 (Fig. 4). This trend is also shown for the phytoplankton simulation, contrary to the reference values calculated from Chl-a remote sensing, which show a rising trend, reflected in the calculated values of phytoplankton biomass.

Regarding the biomass simulated for our main groups of focus (i.e., scallops, clams, mussels, snails, crabs, octopus, littoral fish and mackerels), the trends do not necessarily follow the observed values but still show a general decline for most of them (Fig. 4A). The most notable exception would be the scallop trend, which stays constant throughout the study period, not showing the obvious increase in biomass shown in the reference data provided by IMARPE in 2015 and 2016. The biomass simulations for Ribbed mussels, Semele clams, Rock crabs and Frog shells seem to capture the decreasing trend relatively well, particularly from 2013 onwards. Razor clams also show a peak in biomass around 2013 and the following decrease towards 2020, but they show the
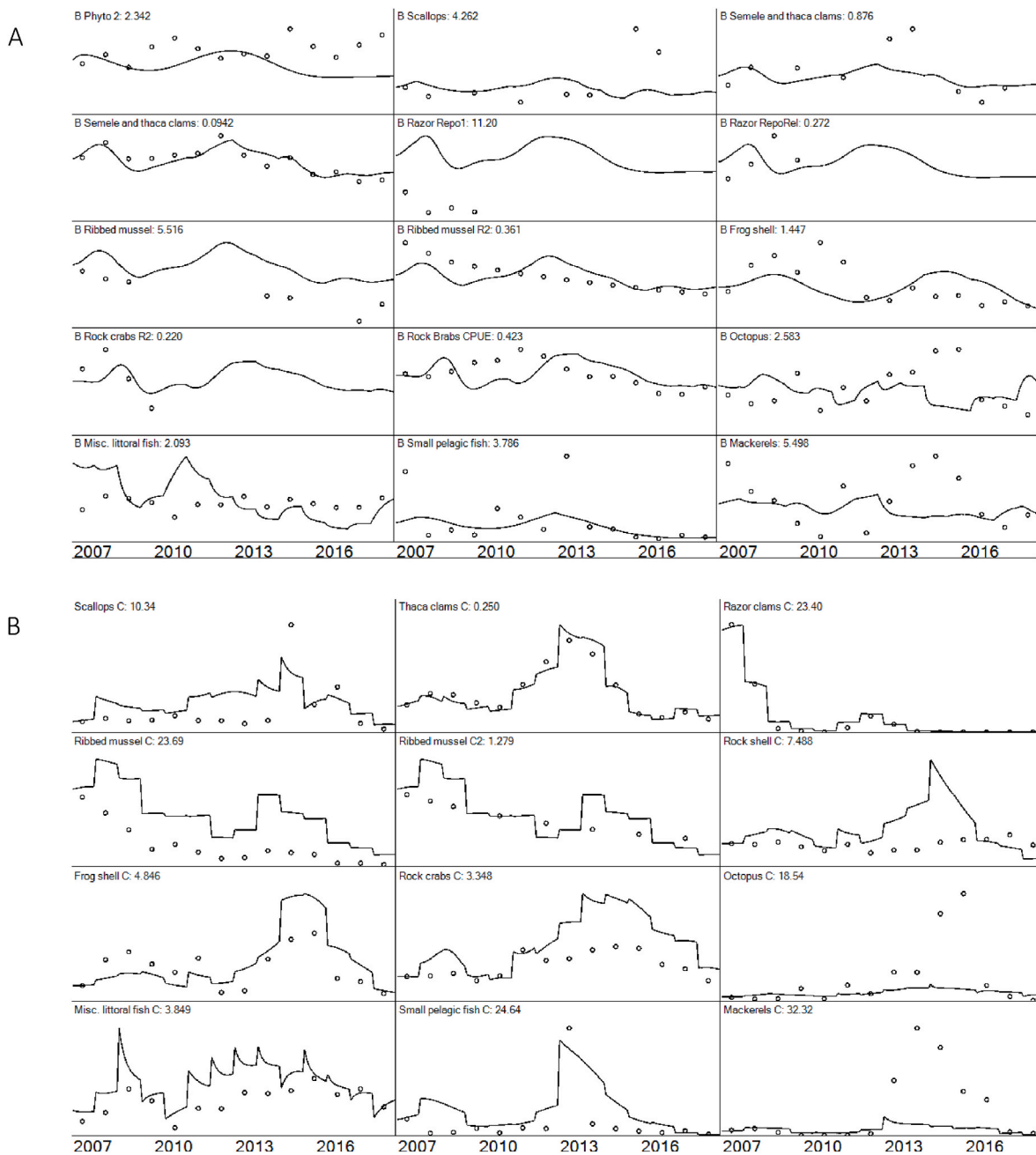
Fig. 4. Biomass (A) and Catch (B) simulations from the final EwE model of phytoplankton and the main resources. The value next to each group represents the contribution of each to the total Sums of Squares.

highest discrepancy with the reference data, which shows a steep decrease in biomass starting in 2007 (Fig. 4A). When looking at the catches, all of these focus groups have a very close fit with the reference values, in terms of their overall trends, which again show a peak between 2013 and 2016, approximately. However, the model tends to overestimate the catches, particularly of Scallops, Ribbed mussels, Rock shells and Rock crabs, during this period (Fig. 4B).

3.3. Correlations: fisheries, environment and primary production anomaly (Ewe)

To better understand which specific fisheries were driving the total effort and landings in Independencia Bay, we ran correlation analyses between the eleven defined fleets for the period 1996–2020. As expected, the highest correlation values were between diving and total effort (0.99***, spearman test; Fig. 5). When correlated by individual fleets, Purse seines and Mussel diving showed the highest correlation to total landings (~0.60***), whereas, to total effort, it was more balanced between most fleets (from 0.30*** to 0.50***), except for mussels and razor clams (0.14* and −0.03, respectively). This suggests that the mussel fishery is relevant to the total landing pattern, but has a different trend in effort than most fisheries, as shown in Fig. S1. When correlating the fisheries trends for the 2007–2020 timeframe (Ecosim model period), we see similar correlation values as before. It is notable, however, that the diving fishery targeting Rock crabs seems to have acquired more relevane during this period, as seen in their correlation with total values, particularly in terms of effort. Regarding the environmental drivers, we used the following variables and indices for the final correlation analysis: PDO, ICEN, ITCP and SST and Chl-a from inside Independencia Bay (Fig. 5). There was a stronger correlation of PDO
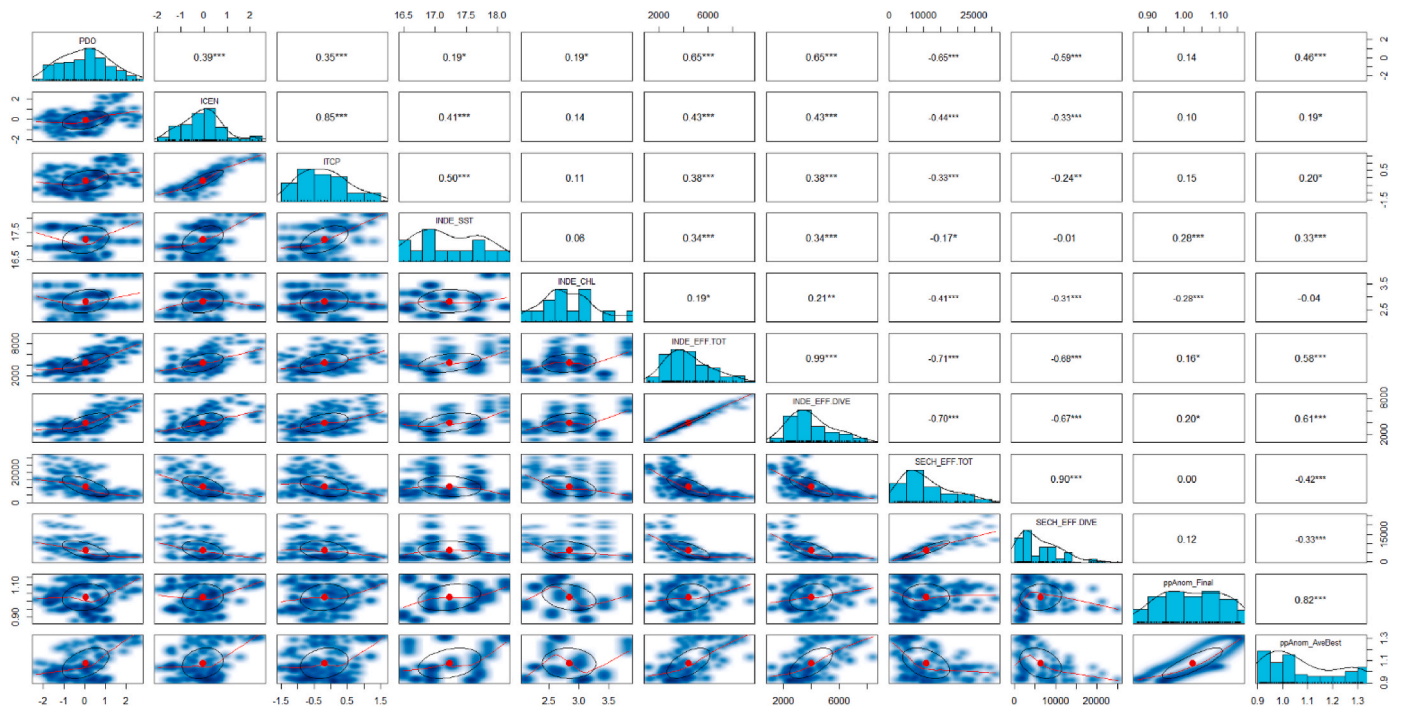
Fig. 5. Correlation of environmental and fisheries-related drivers from Independencia and Sechura, and PP anomaly curve (from the final model and from the average of the best models). INDE = Independencia Bay, SECH = Sechura Bay.

with the fishing effort of Independencia Bay (0.65***), than with these other variables and indices. The total effort in Sechura Bay is also highly correlated with PDO, though inversely (−0.65***). Correlations with monthly and yearly time lags did not show a significant difference between the correlation values at time-lag 0, suggesting that any correlation between these SST-based environmental indices can be assumed to be "instantaneous", for our purposes. There same goes for lag comparisons that include fishing effort.

The correlations of the environmental variables and indices with the PP anomaly obtained from the EwE models (Fig. 5) show that the broadest indices tested (i.e., PDO, ICEN and ITCP) were not strongly correlated with the anomaly curve, which was, instead, more correlated with SST and Chl-a measurements from inside the bay (0.28*** and −0.28***), suggesting more local effects. When using the average PP anomaly curve calculated from the best-ranked models, there was a stronger correlation with PDO (0.46***). The estimated PP anomaly curve has a slight correlation with the dive-fishing effort trend of Independencia Bay (0.20*) while not showing any relation with Sechura Bay. When using the average PP anomaly curve, there is a strong positive correlation with total effort in Independencia, while having a negative one with Sechura (0.58*** and −0.42***), suggesting a connection between the systems. Within the diving fishery of Independencia Bay, the PP anomaly curve is very strongly correlated with the fishing effort of Semele clams, Razor clams and Ribbed mussels, even higher than with the average PP anomaly curve.

Since 2007, PDO has shown mostly negative anomalies, except for the warm phase between 2014 and 2018 (Fig. 6). All the other temperature-related indices show a similar pattern that coincides with the PDO phases, though with varying spans and amplitudes (Fig. 6). In particular, the more coastal of the Regional indices (i.e., ICEN and ITCP), which are highly correlated to each other (0.85***, Fig. 5), show two distinct peaks within this warm period: between 2015 and 2016, and early 2017. Even when both bays' SST oscillate similarly through the seasons and years, the 2017 event was relatively short but strong enough to trigger a spike in the SST of Sechura Bay. (Fig. 6; Del Solar et al., 2022). Despite this, and although the SST trend signal from the Regional indices was also captured in Independencia Bay, there was no

spike during the summer of 2017, particularly compared to Sechura (Fig. 6).

4. Discussion

In this study, we used a food-web model of Independencia Bay (Del Solar et al., 2022) and time series data to study the role of environmental and fisheries-related drivers on its trophic structure and resource-use dynamics during a relatively stable period, i.e., without the impact of strong EN conditions (2007–2020). We also investigated the influence on the ecosystem of changes originating in Sechura Bay (mainly through effects associated with Coastal EN), aiming to elucidate probable masked effects of EN and provide insights for integrated ecosystem-based management in the region.

4.1. Drivers of change: trophic modelling time series analysis

4.1.1. Bottom-up vs. top-down effects

Our best models were those that included fishing effort as a driver and incorporated the search for vulnerabilities (trophic interactions) and primary production (PP) anomalies in the fitting procedure. The inclusion of SST as a forcing function on the search rate of consumers did not improve the fitting. Given that the environmental conditions were relatively stable during our study period (2007–2020), this suggests that the system is not too sensitive to non-trophic interactions (environmental drivers) during normal conditions, as opposed to the SST-mediated scallop boom occurring during strong EN (Taylor et al., 2008a, b; Wolff, 1987). The PP anomaly search routine can detect relevant variations in the productivity of the system and associates them with a potential bottom-up effect to explain fluctuations in biomass and catches during the study period. Having the PP anomaly curve as part of the best model fit does not necessarily mean that there is an environmental bottom-up control of the system. As the anomaly search routine accounts for discrepancies between biomass and catches, the shape of the curve might also be influenced by strong peaks and troughs in the fishing effort, which are not always related to increases in the system's productivity. As mentioned above, the biggest reduction of SS in our
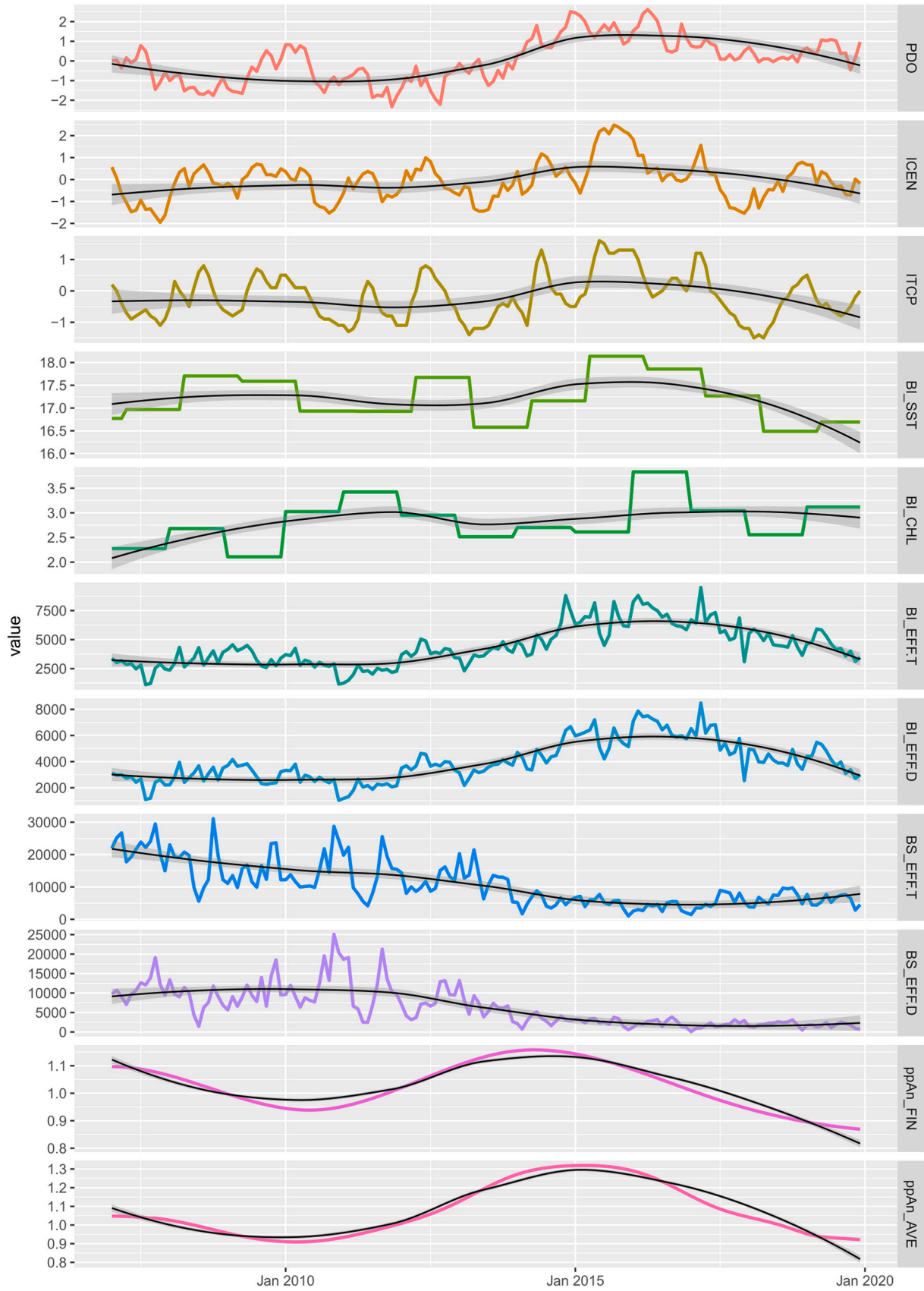
Fig. 6. Comparison of time series of environmental and fisheries-related drivers from Independencia and Sechura, and PP anomaly curve (from the final model and from the average of the best models). BI = Independencia Bay, BS = Sechura Bay. All the time series have a LOESS smoother.

model was obtained when including fisheries, trophic interactions and PP anomaly in the fitting procedure (−98.7%, Table 2). Using only the trophic interactions and the fisheries was close but not enough, and including just fisheries and the PP anomaly gave a reduction of SS of only 52.7%, pointing to the importance of the trophic interactions in regulating the dynamics within the system.

Given that there is a limited number of parameters to be used before risking overfitting the model, it can be argued that searching for vulnerabilities by predator allows for a broader assessment of how trophic interactions are driven in the system, compared to a predator-prey search that might be more useful when specific (predatory) interactions strongly affect the model. We tried both options and found our best fits when searching by predator, which may be related to the fact that Independencia Bay is a highly productive bottom-up driven system, where changes are largely controlled by primary production and its efficient transfer through the food web (Del Solar et al., 2022; Tarazona et al., 1988; Taylor et al., 2008a, b). This suggests that most of the groups might be following the general trends of the primary production biomass and that no individual interactions might be heavily impacting the system more than others (Christensen, 1996; Christensen and Walters, 2004).

Vulnerability (v) values, and thus trophic control, can be impacted by fisheries and the environment. On the one hand, the environmental envelope can influence the diversity, biomass and catches of the different species over a specific timeframe, and specifically impact their rates of production and consumption in the short term. For example, during strong canonical EN, scallops proliferated rapidly through non-trophic metabolic effects (directly affected by SST) and were no longer limited by phytoplankton, enhanced by the reduction of predation by crabs (Taylor et al., 2008a, b; Wolff, 1987). On the other hand, fishing down the food web can increase the vulnerability (v) of some consumers by further removing higher trophic levels from their carrying capacity in comparison with lower trophic levels (Christensen, 1996; Rehren et al., 2022). In our model, almost all of the trophic interactions in Independencia Bay were bottom-up driven ($v = 1$), indicating that most consumers, from filter-feeding invertebrates to carnivorous fish, were close to their carrying capacity during this period (Christensen et al., 2008). Out of 32 groups, the notable exceptions were the non-fished invertebrates 'Other clams', 'Misc. filter-feeders' and 'Other grazers', and the target groups 'Green sea urchins' and 'Frog shells', all of which appear to be very far away from their carrying capacities ($v > 1000$). This contradicts the notion that non-fished species would be at or close to their natural carrying capacity. Nevertheless, the simulated biomass curves of these groups seem to peak right after a general decline of some of their main direct competitors, indicating that the higher vulnerability of these groups (particularly the non-fished resources) could allow them to greatly increase their biomass when the pressure from other groups is released, which also coincides with a decline in the biomass of their main predator, the cangrid crabs. In the case of the grazers, the high vulnerability can be also explained by the large amount of macroalgae available in the system (EE of macroalgae groups is between 0.15 and 0.7).

The Rock crabs are the main predators of most invertebrates in this system, and so they probably are able to target different prey depending on their abundance. However, even when their consumption rate remains relatively constant during the study period, we see a decline in their biomass that generally follows their prey trends (consistent with $v = 1$) and also coincides with an increase in 'Crabs diving' effort and landings that peak around 2015. Furthermore, Rock crabs have a relatively high trophic impact (Del Solar et al., 2022), meaning that they can influence the dynamics of other species and their related fisheries, especially after strong fluctuation periods such as EN, where Rock crabs are temporarily depleted but recuperate quickly thereafter. Their preys, which are mostly sessile invertebrates with high exposure and sensitivity to the environment, and thus have a high vulnerability to climate change (Ramos et al., 2022), can be particularly susceptible to a combination of

long-term climatic, trophic and fisheries effects (Defeo et al., 2014; Ramos et al., 2022). Furthermore, spat and juveniles of bivalves, particularly mussels, can be preyed upon by rock crabs and littoral fish when food is scarce (Capelle et al., 2016; Cranford et al., 2012; Kamermans et al., 2009), putting more pressure on the system.

4.1.2. Environmental and fisheries-related (teleconnection) effects

The PP anomaly curve used in the final model shows relatively stable conditions during the study period (2007 and 2020), with a slight overall decline throughout and a noticeable rise in productivity between 2012 and 2017, peaking circa 2015. The shape of this anomaly curve can also be seen in the EwE-simulated biomass of phytoplankton, which is then propagated and perceived through the food web simulations (Fig. 4A). However, this pattern is not significantly correlated with the reference biomass values of phytoplankton, derived from remote sensing of Chl-a, suggesting that even when almost all predator-prey interactions were estimated as bottom-up controlled ($v = 1$), the ecosystem is not necessarily driven by fluctuations in the biomass of phytoplankton (e.g., even variations in species composition of phytoplankton, which we unfortunately did not have). This can also be perceived when we force this biomass into the model, as it worsens the overall fit, also pointing to the fact that there are rather other factors, such as fisheries, driving the system (outside the EN window). Furthermore, we suspect that the large biomass of macroalgae in the system could be influencing the PP anomaly curve, though most of it (Rhodymenia) has a relatively low transfer rate up the system (EE = 0.15).

The regional indices of SST anomalies, such as PDO, ICEN and ITCP, not only report on the status and development of extreme EN events but also indicate general warm or cold periods over a longer span. These indices decrease their correlation value/power towards smaller spatial scales, i.e., from PDO to local SST at Independencia, being the strongest between ICEN and ITCP (0.85***), and the weakest between PDO and Independencia-SST (0.19*). This suggests that even when the large scale (PDO) and the local (Independencia-SST) indices are very weakly correlated, there seems to be a cascading effect measured along the intermediate indices (ICEN and ITCP). In terms of effort, the strongest correlation is with PDO, decreasing towards the more local SST indices. This further suggests teleconnection effects between the large scale regional variations and local productivity, outside the window of a strong Canonical EN event.

These periods can be associated with an oscillation in productivity, due to changing patterns in vital rates with varying SST anomalies. Of course, this breaks up during strong EN events, where the steep temperature rise disproportionately affects the resources and trophic interactions therein (Mendo et al., 2016; Taylor et al., 2008a, b; Wolff, 1987). In the case of Sechura Bay, the oscillations and peaks of SST are highly correlated with most EN-related indices, which is anytime the phenomenon reaches the coast. In general, it is difficult to fairly compare these correlation results with each other, given that some indices work on longer time spans and larger scales, and exhibit a smoother pattern (e.g., PDO), compared with the smaller and more variable region of EN1+2 (ICEN), for example, which shows a slightly more erratic pattern. So, we still need to visually assess and compare the time series to understand why certain patterns correlate better than others in this study (Fig. 6). When visually comparing the PP anomaly curve of the Independencia EwE model with these SST indices, it seems that they have the same pattern of oscillation, but it is clear that the PP anomaly rises and peaks before the indices. So, either they are not really influencing the anomaly curve estimated by the model's best fit, or there is some relation that might be masked by other effects. There is a noticeable difference between the anomaly curve of the final model vs. the average curve (Fig. 3), particularly in the location and breadth of their peaks, suggesting that most models were pushing the bottom-up control to account for the surge in effort and landings around 2015. So, the average anomaly curve suggests that there is a more pronounced

and prolonged increase in productivity in the system, whereas the model fitted to time series data suggests that this productivity declines faster.

However, the PP anomaly of the system cannot be explained by the environmental variations alone, given that the model improved when the fishing effort was included as a driver. Furthermore, the high correlation between the PP anomaly and the effort of clams, and to a lesser extent mussels and scallops, suggests that the observed increase in the productivity (fitted by the model as a bottom-up control) is related to an increase in effort and landings of the clams, which were the first to start rising around 2011, after a constant decline since before 2007. It is strange that the mussels are also correlated when they do not show the same hump as other resources, though this might be because of their overall decreasing trajectory, which matches that of the PP anomaly. Almost all groups show a steep increase in effort after 2011, led by Semele clams and Rock crabs and with the notable exception of Ribbed mussels, which seem important in terms of total landings, but have an overall decreasing effort and CPUE trends (Fig. S1). It is noteworthy that the increase in effort and landings of Rock crabs is the third largest, after Semele clams and Scallops, and has a broader span than most groups (including fish), showing its importance in the fisheries (and the already discussed relevance to the trophic interactions) of Independencia Bay.

The rise and fall in the effort of 'Semele clams' happens faster than all other groups, which appear to peak between 2016 and 2017, probably driven by the effort migration from Sechura Bay (see Supplementary Material). In this sense, there have been reports of Scallops mass mortalities in Sechura in 2012–2013, 2015–2016 and 2017–2018 that could be associated with small increases in effort at Independencia, though they might have been short enough not to trigger a full-on fishers migration, compared to the EN 97–98, which was stronger and lasted longer. Particularly, there is a strong spike in the effort and landings of Scallops in 2016, but this is not fully captured in the model for this species.

We speculate that the model is calculating its PP anomaly curve putting a lot of weight on the fisheries drivers. Even when there is a spike in effort and landings around 2016–2017, it is perhaps for too brief a period to create a big enough difference to be captured in the anomaly curve, compared to the changes occurring in effort and landings since 2011, mainly with the clams and cangrid crabs. The CPUE data also shows that this increase in effort is not accompanied by a proportional increase in the landings, suggesting that relative biomass is generally decreasing throughout the food web, something that is also shown in the final EwE model (Fig. 4A). This suggests that the increase in local effort at the beginning (2011) could have been in part responsible for the increase in productivity anomaly perceived by the model, but then could not be sustained due to the effects of trophic interactions and given that the environmental conditions were not really favourable to withstand such pressures. The only groups that showed a notable increase in CPUE were small and large pelagic fish (Fig. S2), suggesting that their increment in landings was related to an increment in their production in the system, as opposed to the invertebrates. This suggests that these fishes were more abundant during this period in southern nearshore regions, perhaps driven by warming waters coming in from the north, which would corner anchovetas near the coast and allow for their predators to follow and roam more freely in a larger area of warm water. Furthermore, a migration of effort targeting these large pelagics (Purse seine) is also possible. According to the model, the variations in landings over time tend to be driven by the amount caught by the Purse seiners and the divers that target Ribbed mussels, even with a relatively constant variation in effort throughout most fleets.

4.2. On the effects of the 2017 Coastal EN on Independencia Bay

We explored the direct and indirect effects of the 2014–2018 warm period (in particular of the infamous Coastal EN of 2017) on the primary productivity and fisheries of Independencia Bay, through the lens of time series trophic modelling. The main effects of strong Canonical

events are fairly understood, but there is still high uncertainty regarding this and other versions of EN. Even when clear broad EN categories exist, i.e., Canonical, Coastal and Modoki, (Takahashi et al., 2011; Takahashi and Martínez, 2019), it is still difficult to accurately define the development and effects of the different EN periods. The main decadal oscillations have been very well represented in hindcast, but there is still some nuance regarding the consequences of EN events at interannual scales, particularly when the effects and responses vary (and are connected) between the many social-ecological systems (SES) along the Peruvian coast. In line with our original hypothesis, this suggests that different EN events may impact the system in diverse ways, which are additionally confounded by other factors and result in unclear patterns of change, the disentanglement of which may be complex and cumbersome. When looking at the Canonical EN events of 83–84′ and 97–98′, it is clear how teleconnection effects from the Central-East Pacific had direct impacts and subsequent effects on Independencia Bay: remote large-scale and long-term variability led to local changes in SST, which in turn led to high scallop production, which led to the increase of the local diving fishing effort. However, during the 2015–2016 EN, all the Global and National indicators were checked, but the effects along the coast were far from the devasting ones typically associated with this type of Canonical EN, and it was labelled as a dry event even when minor rains caused some problems in northern Peru in 2016. However, the next year, the so-called Coastal EN abruptly happened and its effects were very local but very strong, temporally impacting different areas along the north-central coast of Peru with thunderstorms, particularly in the north (e.g., Sechura Bay).

Almost all types of EN negatively affect the production of scallops in Sechura Bay (as well as other effects from physical damage in the surrounding towns), except those like the dry EN event of 2014–2016. The reported mass mortalities during the previous decade (thrice between 2012 and 2018) were apparently not associated with increased rain and river input into the bay, but with hypoxia and anoxia events related to other factors such as natural events or the overstocking of scallops (Aguirre-Velarde et al., 2016; Aguirre-Velarde, personal communication, October 4, 2019; Cueto-Vega et al., 2021). Nevertheless, these mass mortalities apparently led to migration towards the South as early as 2012 (shown as a decrease in total effort; Fig. 6), which is likely to explain the increase in effort in Independencia Bay (Figs. 2 and 6), though some unknown factors may be occurring locally at Independencia to explain such a big rise in the effort and landings (mainly of clams and crabs).

4.3. Outlook and management considerations

When studying enclosed nearshore ecosystems, such as bays and capes, changes in trophic dynamics and fishing effort could be most likely attributed, or reduced to, local drivers, even when teleconnection effects are evident, while the impacts of remote factors on local fisheries-related drivers are perhaps less obvious. We suggest that there are different impacts from EN in Independencia Bay that are not necessarily associated with the strong Canonical events, mostly from remote drivers such as effort migration from Sechura Bay. Over the last decades, this migration has typically been triggered by scallop mass-mortality due to Canonical EN (associated with increased scallop biomass in southern Peru). However, during our study period, migration from North to South may have occurred as early as 2012, as observed in the fishing effort trends. The spatial extension and time span of the different EN events may be crucial to trigger or not these migrations, particularly when these may be confounded by other local factors. So, given the high variability associated with EN (Gutiérrez et al., 2016; Takahashi et al., 2011; Takahashi and Martínez, 2019), and considering that most migration processes not only depend on climatic factors but on socio-economic and political considerations, this situation poses various challenges towards understanding and possibly predicting how a particular social-ecological system is shaped over time, in relation to

other systems to which it might be connected. We suggest that during our study period there was a migration of effort to Independencia Bay mainly due to mass mortalities of scallops in Sechura (probably related to overstocking of seeds), in addition to the reported migration of 2017 (Kluger et al., 2018), though we question if the Coastal EN was long enough to trigger such a strong migration. In any case, fishing effort in Independencia Bay increased considerably during 2012 and 2016 and it was the main driver of change in the ecosystem during this period, as seen in the fitting procedure results. We suggest that this increase might be related to a combination of local drivers (e.g., fishers recuperating from the 2007 earthquake[8]) and teleconnection effects, such as the migration of effort from Sechura and PDO's general influence on the Eastern Pacific. Further studies could tackle this statement in more detail by deepening the knowledge of the different elements (i.e., masked drivers or masking factors) individually and in synergy with each other (e.g., monitoring of individual fishers' migration along the coast and investigating potential hidden teleconnection effects of indices such as PDO on the environment at the bay's resolution).

In the context of climate change and a general increase in fishing effort, some trophic dynamics within Independencia Bay may already be shifting. This means that even when the system has shown signs of maturity and resilience, and has bounced back from previous strong EN (Del Solar et al., 2022; Taylor et al., 2008a, b), an accumulation of effects may be already changing the ecosystem's capacity to respond to future events. For example, during the Canonical EN, there has been an overall improvement in ecosystem efficiency due to a reduction in primary production and higher utilisation of phytoplankton and detrital matter by scallops (Taylor et al., 2008a, b; Wolff, 1987). However, this fishery dependence on one species might be pushing the system into a less resilient, more vulnerable state (Ramos et al., 2022), particularly when there are varying confounding effects from the different types of EN and the different types of social-ecological responses.

We call for a local fisheries management option for Independencia Bay that is not independent of what happens in other regions of the coast. It has been reported and it almost seems obvious that there is immigration into Independencia from Sechura, but this needs to be properly quantified and categorised in order to pursue appropriate management strategies and measures locally but considering the whole coastline. We showed that there was an effort increase in Independencia during the study period, but with a corresponding decline in the biomass of many groups, which calls for a better integrated management that addresses local and remote environmental drivers, ecological changes, and perhaps most importantly, social aspects such as migration.

There are currently two fishing bans that refer to Independencia Bay's resources: mussels and bonitos. Furthermore, in 2021 the Fisheries Management Regulation for Benthic Resources was launched, which broadly aims to provide with Territorial Use Rights to formal fisher associations that provide a yearly harvest plan. In this study we suggest that the fisheries regulation includes aspects of effort migration or nomade fishing into its management strategy, particularly when these migrations are not necessarily accompanied by an increase in productivity. Fisheries management should take into account the effects of teleconnections among areas along the coastline, as these can cascade through the different SES. Monitoring programs for fisheries and fish stocks should accordingly be coordinated across sites to facilitate such management endeavour. As pointed out in Del Solar et al. (2023), the connectivity between marine systems in Peru is often not addressed in management plans that end up fragmented, mainly due to a lack of cohesion and transversality between the responsible institutions, particularly in the case of Marine Protected Areas, such as the one where Independencia Bay resides (Fig. 1).

Trophic modelling approaches such as Ecopath with Ecosim (EwE)

have proven suitable for describing and assessing ecosystem changes and their respective drivers over time. These kinds of models are becoming increasingly relevant and useful tools in the decision-making process of ecosystem-based fisheries management (EBFM), though their operationalisation is still difficult to design and apply (Kolding et al., 2015; Link, 2022[9]). However, they can still provide insights during their development of how different systems behave and respond, and how different management options might look like. By knowing the reported effects of strong Canonical ENs in Independencia Bay (mainly from EN '83–84 and '97–98) and using what we have learned from the Coastal EN thus far, we could simulate and compare potential future effects of different types of EN in the system. Our next steps are to explore the future combined effects of fisheries and environmental drivers by simulating different types of EN and varying their intensity and frequency, which could lead to tipping points situations, particularly in the context of increasing pressures from local and foreign markets.

CRediT authorship contribution statement

Alonso Del Solar: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Giovanni Romagnoni:** Conceptualization, Supervision, Validation, Writing – original draft, Writing – review & editing. **Matthias Wolff:** Conceptualization, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2024.107047.

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[8] In July 2007, an earthquake of 7.8° hit the Pisco Region, mainly impacting infrastructure and homes, and potentially stalling the fishing effort.

[9] This topic was developed by Jason Link during an Ecopath with Ecosim online lecture in January 2021, as part of the "Fish 501: Ecosystem modelling" course of the University of British Columbia. Streamed and stored on the platform YouTube, at https://www.youtube.com/watch?v=kOJLnY5eRE0.

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