# Drivers of trophodynamics of the open-ocean and deep-sea environments of the Azores, NE Atlantic

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A B S T R A C T

Marine ecosystems associated with mid-oceanic elevations harbour unique pelagic and benthic biodiversity and sustain food webs critical for Nature's contributions to people (NCP). The United Nations Sustainable Development Goals and the Convention on the Law of the Sea recognize the need to implement ecosystem-based management approaches to conserve the structure and functioning of oceanic and deep-sea ecosystems within sustainable reference points. However, uncertainties regarding the interactions between multiple drivers of change, and their impacts on the state of these ecosystems and the NCP, present significant challenges to effective management. Trophic models offer a holistic approach to identify the main drivers affecting the dynamics of marine ecosystems. Here, we used a food web model of the open-ocean and deep-sea environments of the Azores for identifying the drivers that best explain historical biomass trends of demersal fish of high commercial value. Our hindcast simulations suggested that historical trends can be explained by the combined effects of deep-sea fisheries exploitation and variability in environmental conditions, likely dominated by primary productivity anomalies. In particular, deficits in primary production and high levels of fishing exploitation might have contributed to the pronounced decline in biomass observed between 2008 and 2012. These findings reinforce that failure to consider environmental factors in ecosystem-based management may result in shortfalls at achieving biodiversity conservation and sustainability objectives, particularly in the context of climate change.

## 1. Introduction

Marine ecosystems associated with mid-oceanic elevations, such as ridges, seamounts, and island shelves, harbour unique pelagic and benthic biodiversity (Dunn et al., 2018; Priede et al., 2022; Morato et al., 2010) and sustain complex food webs that are fundamental to Nature's Contributions to People (NCP, Díaz et al., 2018; Thurber et al., 2014; La Bianca et al., 2023). NCP encompass the myriad ways in which the biodiversity of organisms, ecosystems, and their associated ecological and evolutionary processes enhance human quality of life (Díaz et al., 2018). These contributions include food provision from fisheries and climate regulation, both of which are vital for food security and overall human well-being (Thurber et al., 2014). To ensure that future generations continue to benefit from NCP, international management goals such as those encompassed in the United Nations Sustainable Development Goals (SDG) and the Convention on the Law of the Sea (UNCLOS) recognize the need to implement ecosystem-based management

approaches that successfully conserve the *status* (i.e., structure and functioning) of oceanic and deep-sea ecosystems within sustainable reference points (UN 2015, UNGA 5th session of the Intergovernmental conference, 4th March 2023; Gjerde and Vierros, 2021). Effective management requires robust scientific knowledge on how these ecosystems function and how multiple drivers of ecosystem status interact and affect the productivity, biodiversity and trophodynamics of the system (Danovaro et al., 2017; Dunn et al., 2018; Levin et al., 2020).

The drivers of ecosystem status, their interactions, and their effects on the productivity, biodiversity and trophodynamics of oceanic and deep-sea ecosystems remain poorly understood (Ortuño Crespo and Dunn, 2017; Levin et al., 2019; Danovaro et al., 2020). Knowledge gaps are primarily due to the lack of rich long-term datasets that track the evolution of the state of these remote systems and their potential drivers of change (Henson et al. 2016) and the logistical challenges of empirically quantifying the effects of multiple drivers across different trophic levels (Boyd et al., 2018). However, evidence for regime shifts in large

pelagic ecosystems (e.g., Beaugrand et al., 2008, 2015; Möllmann and Diekmann, 2012; Lynam et al., 2017), combined with evidence of the sensitivity of deep-sea benthic communities to fishing-induced impacts (e.g., Clark et al., 2016) and the role of oceanographic conditions in promoting seamount productivity (e.g. Morato et al., 2016), support the contention that the trophodynamics of oceanic deep-sea systems are likely driven by the interaction of fisheries exploitation with environmental factors.

This leads to the key question of how multiple drivers, acting in concert, ultimately force structural and functional changes in the system. Unsustainable fishing practices have led to a decline in the abundance and size of pelagic and benthic species living in seamounts and their surrounding waters and long-term loss of biodiversity (Worm et al., 2005; Baum and Worm 2009; Norse et al., 2012; Clark et al., 2016). As the loss of biodiversity undermines the stability of marine food webs (Rooney and McCann 2012; Cardinale et al., 2012; Loreau and De Mazancourt 2013) and, therefore, the ability of the system to maintain its function and structure in the face of disturbance, fishing pressure may expose oceanic ecosystems to greater vulnerability to significant system restructuring (Folke et al., 2004; Worm et al., 2006). In this case, environmental factors might play a crucial role in pushing the system into states of difficult recovery (Beaugrand, 2009; Möllmann and Diekmann, 2012; Möllmann et al., 2015), characterised by ecosystems with a different structure and functioning (Scheffer and Carpenter 2003), and therefore, with an altered capacity for providing the myriad of NCP (Ullah et al., 2018; Bartley et al., 2019; Nagelkerken et al., 2020). Consequently, the quantification of the role of anthropogenic and environmental drivers on the overall dynamics of oceanic ecosystems becomes a paramount task if the goal is to develop ecosystem-based management strategies that successfully ensure the future stability and functioning of these complex systems.

Trophic modelling tools offer a holistic approach to quantitatively assess the effects of multiples drivers on ecosystem status. These tools address complex ecological processes and dynamics resulting from the interplay between food web interactions, human activities, environmental conditions and management actions (reviews in Geary et al., 2020, Steenbeek et al., 2021). Thereby, they offer robust capabilities for representing the complex dynamics of marine ecosystems (Fulton et al., 2003; Lewis et al., 2021; Mueter et al., 2021) and integrating anthropogenic and environmental drivers into a single framework. Through retrospective analysis, trophic modelling tools allow for the quantitative assessment of the role of different drivers at explaining historical ecosystem trends (e.g., Mackinson et al., 2009; Bentley et al., 2020; Tsagarakis et al., 2022). These attributes have conferred trophic models with the capacity to derive ecological information relevant to the operationalization of ecosystem-based management approaches around the world (Chagaris et al. 2020; Bentley et al. 2021; Craig and Link 2023).

Situated along the mid-Atlantic Ridge, the broader region of the Azores (Portugal) presents a compelling case study for trophic modelling of open-ocean and deep-sea environments. Extensive scientific research in the region has contributed to the development of a trophic modelling framework that significantly advanced our understanding on the functioning of seamount ecosystems and the sustainability of deep-sea fisheries (Pitcher et al., 2010; Morato et al., 2009, 2016). If model uncertainties and limitations are appropriately addressed (Heymans et al., 2011), these models can be crucial to provide insights on the drivers of trophodynamics and associated effects. Deep-sea fisheries exploitation emerges as a plausible driver, with mounting evidence suggesting significant pressure on local fish stocks (Diogo et al., 2015; Santos et al., 2023; Medeiros-Leal et al., 2023) and impact on benthic vulnerable marine ecosystems (Sampaio et al., 2012; Pham et al., 2014). Nevertheless, the broader impacts of deep-sea fisheries activities on the trophodynamics remain poorly understood. Conversely, the marine environment of the region is highly dynamic, as expected for mid-ocean regions. Environmental conditions are influenced by complex large-scale water circulation flows, which interact with regional irregular topography and local winds and alter surface temperatures, primary production and subsequent food supply at the deep-sea floor (Bashmachnikov et al., 2004; Amorim et al., 2017; Caldeira and Reis, 2017). Thus, the dynamic climatology and oceanography likely impacts the productivity of higher trophic levels (Sala et al., 2016; Caldeira and Reis, 2017), leading to the hypothesis that environmental factors play an important role as drivers of trophodynamics.

Here, we modelled temporal trophodynamics of the Azores deep-sea and open-ocean environments over the past two decades i) to quantify the contribution of anthropogenic (i.e., fisheries) and environmental driversat explaining the historical inter-annual variability of demersal fish stock's biomass and ii) to build scenarios on the oceanographic variables that potentially act as environmental drivers of trophodynamics. This retrospective analysis aims to gather the most robust ecosystem information available on the historical drivers of trophodynamics and their impact on the deep-sea ecosystem of the Azores, thereby supporting ecosystem-based management.

## 2. Methodology

### 2.1. Study area

The study area encompasses the Azores subarea of the Portuguese Exclusive Economic Zone (hereafter Azores EEZ), located in the Northeast Atlantic Ocean between 33 and 43° N and 20-35° W (Fig. 1). The Azores EEZ covers an area of about 1 000 000 km$^2$ with an average depth of approximately 3000 m (Peran et al., 2016). As a volcanic archipelago of recent origin, the submarine topography is highly irregular, containing numerous submarine geomorphological features (Morato et al., 2008; Peran et al., 2016). These include seamounts-like features and ridges which harbour diverse deep-water cold-water coral habitats (Morato et al., 2021; Taranto et al., 2023), sponge grounds (Tempera et al., 2012), hydrothermal vents (Boschen-Rose and Colaco (2021)) and serve as habitat for demersal fish species of high commercial value (Menezes et al., 2006; Parra et al., 2017).

The complex oceanography of the area is demarked by large-scale ocean circulation processes driven by the eastward-flowing Gulf Stream. The Gulf Stream produces a complex system of currents characterized by numerous unstable eddies and meanders (Alves and Colin de Verdière (1999); Bashmachnikov et al., 2009). The dominant current in the north of the archipelago corresponds to the North Atlantic Current, that supports the Atlantic Meridional Overturning Circulation. Conversely, in the south of the archipelago, the Azores Current dominates the oceanographic features and constitutes the northeast boundary of the North Atlantic subtropical gyre (Sala et al., 2016; Caldeira and Reis, 2017; Frazão et al., 2022). The thermal front associated with the Azores Current (Azores Front) divides different biogeochemical regimes (Fründt and Waniek, 2012; Frazão et al., 2022) — the cold and more productive temperate waters of the eastern North Atlantic in the north and the warm and oligotrophic waters in the south.

Fishing plays a vital role in the economy of the Azores, with the deep-water bottom longline and handline fleet being the most significant fishery in terms of landed value and the second-largest in weight (Carvalho et al., 2011). Overall, it represents 30 % of the total reconstructed catches (Pham et al., 2013; Fauconnet et al., 2019) for the period between 1997 and 2018 (Fig. 2). The fishery operates predominantly at a local small-scale (Carvalho et al., 2011) and targets fishing grounds down to 1200 m deep, which account for about 2 % of the total EEZ area (Peran et al., 2016). Fleet dynamics are mainly driven by the blackspot seabream (*Pagellus bogaraveo*), wreckfish (*Polyprion americanus*) and alfonsinos (*Beryx decadactylus* and *Beryx splendens*), which are the main targeted species (Menezes et al., 2006; Santos et al., 2019; Pinho et al., 2020). However, this demersal fishery is typically a mixed species fisheries and fishing effort is also directed to other commercially important species such as the blackbelly rosefish (*Helicolenus*
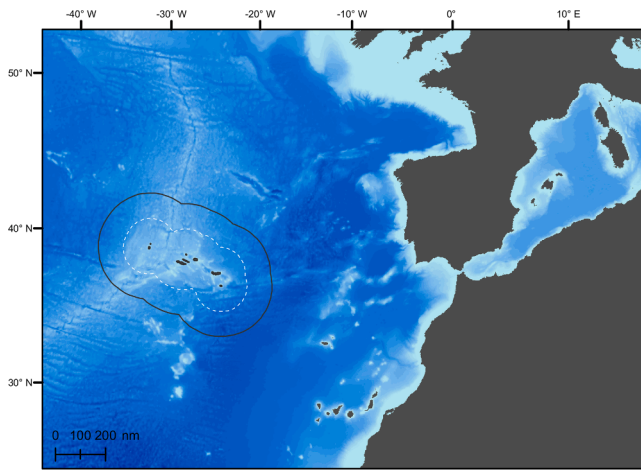
**Fig. 1.** Map of the archipelago of the Azores, in the Northeast Atlantic. The black solid line demarks model domain – the Exclusive Economic Zone (EEZ), i. e., the 200 nautical miles limit around the Azores archipelago. The dashed white line shows the 100 nautical miles where access is limited to Portuguese fishing vessels only (Reg. EU N. 1380/2013).

*dactylopterus)*, European conger (*Conger conger*) and forkbeard (*Phycis phycis*). Available knowledge on the biological and exploitation status of most demersal and benthopelagic fish stocks is limited due to uncertainties in estimates of growth, mortality, maturity and biomass that prevent the application of robust stock assessment models for most species (Santos et al., 2020). Some of these fish stocks inhabiting deeper waters were sporadically harvested by the experimental drifting deepwater longline, which predominately targets the black scabbardfish (*Aphanopus carbo*) (Machete et al., 2011). The drifting deep-water longline fishery has never become established and represents 0.6 % of the total reconstructed catches (Pham et al., 2013, Fauconnet et al., 2019) for the period between 1997 and 2018. Between 2001 and 2002, an exploratory bottom trawl fishery for the orange roughy (*Hoplostethus atlanticus*) was conducted in some seamounts of the archipelago (Melo et al., 2002). However, the perceived negative impacts of bottom trawling and the high vulnerability of orange roughy to exploitation led

to a ban on this gear in most parts of the EEZ, first by local authorities and then at European level. In the pelagic realm, the pole and line tuna & livebait fishery (including the live-bait) is the most significant in terms of landed weight (Carvalho et al., 2011), followed by the small-size pelagic fisheries targeting mostly blue jack mackerel (*Trachurus picturatus*) and chub mackerel (*Scomber colias*) (Fig. 2). They represent 35 % and 13 % the total reconstructed catches (Pham et al., 2013; Fauconnet et al., 2019) for the period between 1997 and 2018, respectively. Pelagic longlines from Azores, Portugal mainland and foreign countries also operate in region and target swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*). They represent 3.7 %, 5.1 % and 5.0 % of total reconstructed catches, respectively. The foreign fleets, started operating in 2004, upon the European Council Regulation (EC) No 1954/2003 of 4 November 2003 on the management of the fishing effort in Portuguese waters. Other fisheries operating in the region correspond to the harvesting for commercial coastal invertebrates (e.g., *Octopus vulgaris*), the recreational fishing and the artisanal squid fishery targeting *Loligo forbesii* (Morato, 2012; Pham et al., 2013).

### 2.2. Modelling approach to hindcast trophodynamics

We modelled the trophodynamics of the Azores open-ocean and deep-sea ecosystem with Ecosim, the temporal module of the Ecopath with Ecosim modelling suite (see Christensen and Walters, 2004). Ecosim is a dynamic modelling platform (Walters et al., 2000) that uses Ecopath structure as initial conditions for temporal simulations of ecosystems' biomass dynamics. The Ecopath model underlying the Ecosim model of the Azores characterised the food web structure of the deep-sea and open-ocean environments for the reference year 1997 (Morato et al., 2016). The model was designed to address ecological and fisheries questions related to the deep-sea benthic realm of the Azores EEZ, but included trophic links to other compartments of the ecosystem. Thus, the model is composed of 45 functional groups, including detritus, primary producers, benthic invertebrates, fish groups, and megafauna represented by marine mammals, sea turtles and a seabird group. Some demersal and benthopelagic fish are represented as individual species compartments due to their commercial interest and/or to allow species-specific management simulations with the EwE model (Morato et al., 2016). These correspond to: *Helicolenus dactylopterus, Conger*
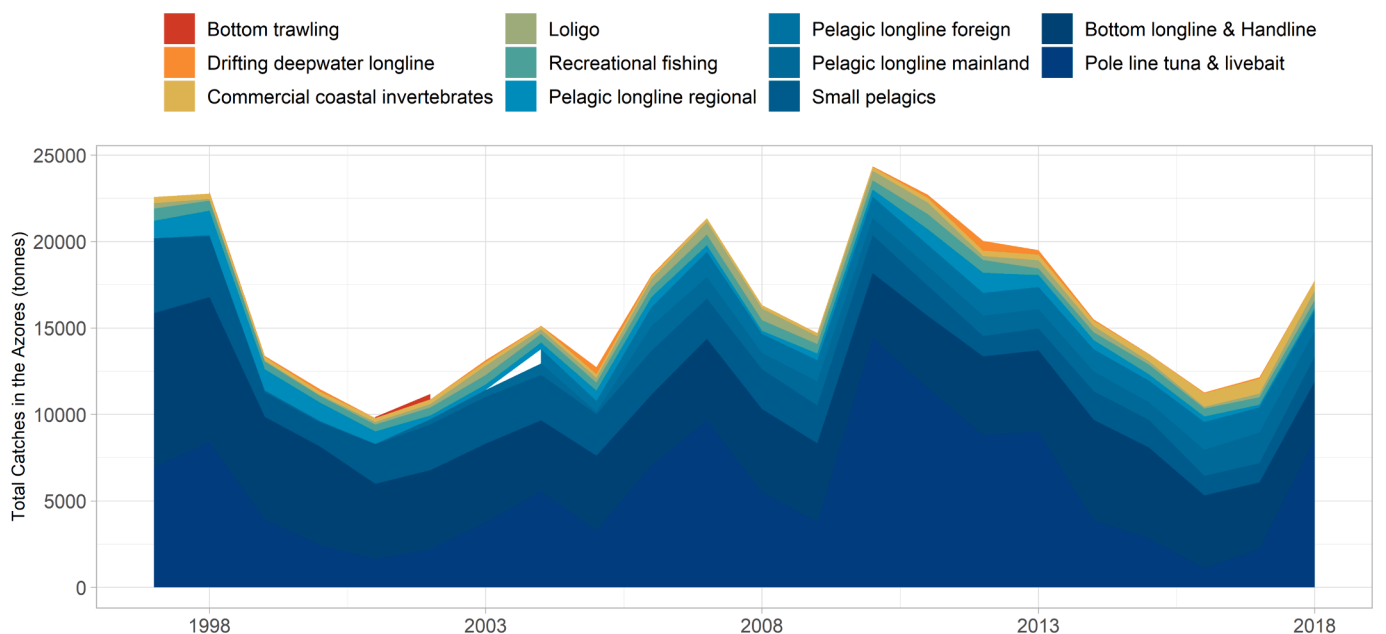


**Fig. 2.** Total reconstructed catches (in tonnes) of each fleet (official landings and estimates of illegal, unreported, and unregulated catch and discards as described in Pham et al., (2013) and Fauconnet et al., (2019)) operating in the Azores for the period 1997–2018.

*conger, Pontinus kuhlii, Raja clavata, Phycis phycis, Pagrus pagrus, Beryx splendens, Beryx decadactylus, Pagellus bogaraveo, Mora moro* and *Lepidopus caudatus*. Fishing exploitation of modelled functional groups and species is represented by 11 fishing fleets that operate in the region, as described in Section 2.1. The model spatial domain is confined to the limits of the Azores EEZ (total of 954,563 km$^2$, Fig. 1).

Ecosim simulates the temporal evolution of the biomass of food web compartments by implementing a classical system of differential equations derived from the Ecopath's system of algebraic equations. Using the biomass of food web compartments as state variables, the system of differential equations (see Christensen and Walters, 2004) describe the interactions between predators and prey, while considering the combined effects of fishing, predation and natural mortality, production changes and eventual net migrations. Predator consumption rates are modelled based on principles of foraging arena theory (Ahrens et al., 2012). Accordingly, the availability of a prey group's biomass to each predator group transits between vulnerable and refuge states (Ahrens et al., 2012). This concept is implemented using the vulnerability parameter, which determines the maximum increase in mortality rate that a predator can exert on a prey group. The default vulnerability value (v = 2) implies a mixed mechanism of trophic control, whereas higher values of this parameter mean that predator consumption controls prey biomass (top-down control), and lower values mean prey biomass controls predator biomass (bottom-up control).

### 2.3. Fitting historical trophodynamics to time-series

We forced the Azores Ecosim model with time-series of fishing effort from the reference year 1997 to 2018 (Fig. 3). Different data sources were used to construct these time-series. The fishing effort of the focal fishery – the bottom longline and handline fleet – was estimated by multiplying the sum of landing events by the average number of hooks per fishing segment (longliners & handliners). The number of hooks

were provided by the European Commission's Data Collection Framework (DCF). Effort for the other fleets, i.e., the pole and line tuna, pelagic longline regional, small pelagics, drifting deep-water longline, commercial coastal invertebrates and squid fisheries, were estimated as the number of landings events, provided by the DCF. The effort of recreational fishing activities was estimated using an index derived from local human population, extracted from local statistics (https://srea.azores.gov.pt/). Effort estimations of bottom trawling were proportional to fishery catches. The fishing effort of pelagic longlines from Portugal mainland and foreigner countries was estimated using Vessel Monitoring System (VMS) data and landings from Pham et al. (2013) when VMS data was unavailable. This was the available information for the purpose of this study and was considered a realistic representation of fishing effort in the Azores.

We adopted a fitting to time-series procedure (Mackinson et al., 2009) to identify the suite of drivers that best explain historical trophodynamics of the Azores and thus maximise the models' statistical fit. We used time-series of relative biomass and of absolute catches spanning from 1997 and 2018 as reference datasets of the fitting procedure. The reference time-series of relative biomass (Figure S2) were obtained based on a standardized relative abundance index derived from the bottom longline scientific surveys in the Azores region (Menezes et al., 2006; Pinho et al., 2020). The abundance index was calculated for the monospecific functional groups *Pontinus kuhlii, Raja clavata, Phycis phycis, Pagrus pagrus, Pagellus bogaraveo, Helicolenus dactylopterus, Conger conger,* and *Mora moro*. In addition, abundance indexes were estimated for the large-size demersal, large-size shallow-water, medium-size shallow-water fish groups, and benthic sharks and rays, using data of the representative species *Polyprion americanus, Serranus atricauda, Pagellus acarne*, and *Galeorhinus galeus*, respectively. The surveys occurred during spring season, covered the shelves and slopes of the nine islands, major banks and seamounts of the Azores region and followed a randomly stratified design by area and depth strata (Menezes



**Fig. 3.** Annual time-series of fishing effort used to drive the trophodynamics of the Azores Ecosim model. The black dashed line represents 1 as the reference value for 1997. Estimates are multipliers of fishing mortality estimated with Ecopath for the reference year (simulated fishing mortalities reported inFigure S1). Fleets with minimal catch values registered in 1997 (Morato et al., 2016) highlighted in grey.

et al., 2006; Pinho et al., 2020). The data collected during the survey serve as the basis for scientific advice in the Azores EEZ for stocks currently being assessed by the International Council for the Exploration of the Sea (Santos et al. 2020). Since no surveys were conducted in 1998, 2006, 2009, 2014, and 2015, we estimated the missing values by averaging the data from the two closest preceding and two closest following available years. For the years 2014 and 2015, we calculated the average using the three nearest years: 2012, 2013, and 2016 for 2014, and 2013, 2016, and 2017 for 2015. The time-series of the relative abundance index were obtained calculating a 3-year moving average (% of total abundance) and are relative to the reference year 1997. The reference time-series of absolute catches of harvested model groups (Figure S3), derived from a reconstruction of total catches in the Azores. The dataset comprises official landings and estimates of illegal, unreported, and unregulated catch (IUU) and discards within the EEZ (Pham et al., 2013; Morato et al., 2016; Fauconnet et al., 2019). Catch estimates were expressed in tonnes of wet weight per square kilometre of modelled area.

The fitting-to-time-series procedure included two different steps: i) the inclusion of primary production (PP) anomalies to simulate the effect of environmental drivers on trophodynamics, and ii) the calibration of predator–prey vulnerabilities to simulate the effect of mediation of trophic interactions (TI) in the system (Ahrens et al., 2012). Primary production anomalies were used as multipliers of the production-to-biomass (PB) ratios of primary producers to influence the total energy amount reaching higher trophic levels via bottom-up effects (Heymans et al., 2016). We considered two different PP anomalies in this study. First, the PP anomaly corresponded to an annual time-series of registered net primary production (NPP) in the Azores EEZ from 1998 and 2018 (Amorim et al., 2017). A second type of PP anomaly was estimated with the model, using a nonlinear fitting to time-series procedure that calculates multipliers of PB ratios of primary producers that maximize model's goodness-of-fit (see Scott et al., 2016; Heymans et al., 2016). We performed optimisation searches for the best anomalies, with and without the influence of NPP. These model-estimated anomalies (Mackinson et al., 2009) aimed to represent the myriad of environmental factors that might impact ecosystem dynamics but remain largely unknown for the modelled area (Morato et al., 2009). These include large-scale indices of climate variability and physical processes that impact primary production and produce effects on higher trophic levels (e.g., mesoscale eddy interactions, or seamount-induced upwelling). In the second step, we estimated the vulnerability parameters using a nonlinear fitting to time-series procedure (Scott et al., 2016, Heymans et al., 2016) to find the optimal vulnerability multipliers, which were homogenously applied across all predator–prey interactions of predator functional groups (i.e., *search by predator*).

We conducted a series of model calibration iterations simulating the individual and combined effects of drivers of trophodynamics (Table 1) to identify the configuration that maximizes the goodness-of-fit of the model. Statistical fit was measured in the form of sum of squared (SS) deviation between predicted and observed log biomasses and catches and second-order Akaike Information Criterion (AICc). We performed five different model calibrations (Table 1) by simulating the effects of fishing alone (Phase I), the combined effects of fishing and environmental factors without mediation of trophic interactions (TI) (Phase II), and the effects of fishing and environmental factors with mediation of trophic interactions (Phase III) (Table 1). For each phase, one or more trials were conducted. Trial 1 assumed fishing effort as the only driver of trophodynamics, constant primary producer production-to-biomass ratio and default vulnerability exchange rates (v-2) were applied (Phase I). Trials 2–4, assumed fishing effort and PP anomalies as drivers of trophodynamics and default vulnerability exchange rates (v = 2) (Phase II). The registered time-series of net primary production failed in explaining the reference time-series, as manifested in model's statistical fit. Therefore, trial 5 assumed fishing effort and model estimated anomaly with no influence of NPP as drivers of trophodynamics, and fitted predator–prey vulnerabilities (Phase III). The sequence of

calibration iterations resulted from preliminary diagnosis trials checking whether the fitting-to-time-series procedure should be conducted with no influence of fishing as a driver of trophodynamics and whether vulnerabilities should be calibrated prior to the input of PP anomalies (Mackinson 2014).

Preliminary calibration iterations were performed with no weights attributed to the reference time-series. Predictions showed large deviations from observed trends (i.e., underestimations and overestimations, see Figure S4 and S5), highlighting limitations in the time-series of fishing effort or the model itself at explaining both biomass and catch historical patterns. To overcome this limitation, calibration iterations were further performed with low weights attributed to the reference time-series of catch (details on Supplementary Material). Consequently, the evaluation of model performance prioritized the agreement of model predictions with the time-series of relative biomass, which were the main focus of the study. Despite the small contribution of catch time-series to model evaluation, we included them in the fitting procedure because the statistical fit of some components (e.g., *Pagellus bogaraveo, Pontinus kuhlii,* large and medium-sized shallow water groups) deteriorates when the model is fitted without time-series of absolute catches. The calibrations considered all species and functional groups targeted by fishing activities, except Algae and Shrimps (catch time-series), *Lepidopus caudatus* (biomass and catch time-series) and both *Beryx* spp. (biomass time-series). These were excluded to avoid noise in the calibration process, generated from: i) high contribution to the total SS but minimal contribution to fishing catches (Algae and Shrimps), ii) atypical peaks in biomass and catch time-series, not representative of the perceived dynamics of the species in the EEZ (*Lepidopus caudatus)* (Pinho et al., 2020), and iii) inadequate estimates of biomass, due to the possible effect of external factors influencing species dynamics outside of the Azores EEZ (*Beryx* spp.) (Santos et al., 2019).

To avoid model overfitting, we ensured the number of estimated parameters was inferior to available degrees of freedom. A maximum of 21 vulnerabilities could thus be estimated, considering we had 44 time-series available (biomass and catch) and were interested at estimating one value per year for the model estimated primary production anomalies (22 parameters). Finally, we assessed the impact of Ecopath input parameter uncertainty on temporal predictions of the final model, using a Monte Carlo approach (Steenbeek et al., 2018). The algorithm generated random variation from normal distribution around Ecopath parameters, using confidence intervals assigned on Ecopath data through a pedigree routine which is based on the origin of input data (Table S1). We ran 1000 iterations per simulation and used the 5th and 95th percentile of the distribution estimates to plot model results.

### 2.4. Environmental drivers of trophodynamics

We measured the similarity between a set of environmental variables acting at the scale of the North Atlantic Basin and the Azores EEZ between 1998 and 2018 with the primary production anomaly estimated over model's fitting-to-time-series procedure. Similarity was measured using the dynamic time wrapping (DTW) algorithm implemented in the R package "dtw" (Giorgino 2009). This algorithm identified optimum non-linear temporal alignments and distortions between registered and model predicted variables. To determine the optimal alignment, the algorithm estimated the cumulative distance between each pair of related data points and calculated the shortest path using a cumulative distance matrix (Berndt and Clifford, 1994; Aghabozorgi et al., 2015). The path which generated the smallest distance represented the optimal alignment between variables and was plotted for visual inspection.

The basin-scale variables used for comparison with the primary production anomaly corresponded to indices of climate variability, which have reportedly driven changes in marine ecosystems in the Atlantic – the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) (eg., Edwards et al., 2013; Paiva et al.,

**Table 1**

Statistical fits of the calibration trials of the Azores Ecosim model. Each trial assumed alternative calibration configurations for simulating the effect of drivers of trophodynamics (fishing, environment and trophic interactions) in the model. NPP is the net primary production and FF the forcing function estimated with the model to represent production anomaly; SS is sum of squared deviation; n is number of available degrees of freedom; k is number of estimated parameters (maximum of 43 accounting with 22 values of estimated productivity and 21 vulnerabilities). AICc is second-order Akaike Information Criterion. GOF is goodness-of-fit measured as % of AICc reduction in relation to respective calibration trial assuming individual effects of drivers.

| PHASE I — INDIVIDUAL EFFECTS OF DRIVERS OF TROPHODYNAMICS | | | | | | |
|---|---|---|---|---|---|---|
| **TRIAL** | **STEPS** | **SS** | **n** | **k** | **AIC** | **AICc** | **GOF** |
| 1 | Fishing | 40.90 | 967 | 0 | −3058.69 | −3058.69 | 0 |

| PHASE II — COMBINED EFFECTS OF DRIVERS OF TROPHODYNAMICS | | | | | | |
|---|---|---|---|---|---|---|
| **TRIAL** | **STEPS** | **SS** | **n** | **k** | **AIC** | **AICc** | **GOF** |
| 2 | Fishing + Environment (NPP) | 35.40 | 967 | 0 | −3198.34 | −3198.34 | 4.6 |
| 3 | Fishing + Environment (FF) | 25.64 | 967 | 22 | −3466.25 | −3465.27 | 13.3 |
| 4 | Fishing + Environment (FF & NPP) | 25.66 | 967 | 22 | −3465.67 | −3464.69 | 13.3 |

| PHASE III — COMBINED EFFECTS OF DRIVERS MEDIATED BY TROPHIC INTERACTIONS | | | | | | |
|---|---|---|---|---|---|---|
| **TRIAL** | **STEPS** | **SS** | **n** | **k** | **AIC** | **AICc** | **GOF** |
| 5 | Fishing + Environment (FF) + TI | 19.49 | 967 | 43 | −3689.23 | −3685.31 | 20.5 |

2013; Nye et al., 2014). Annual estimates of these variables were obtained from the NOAA Earth System Research Laboratory (ESRL) website (https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/). We also compiled regional-scale oceanographic variables, corresponding to net primary production (NPP), sea surface temperature (SST), chlorophyll-a concentration (Chl-a), particulate organic carbon (POC) and particulate inorganic carbon (PIC). The annual NPP estimates from 1998 to 2018 were obtained from the SEAWIFS sensor and are based on the standard algorithm of the Vertically Generalised Production Model (VGPM; Behrenfeld and Falkowski, 1997). A global grid with a size of $1/12°$ ($\approx 9$ km) was used in both latitude and longitude. Annual SST estimates from 1998 to 2018 were obtained from monthly data products from the National Oceanographic Data Centre's AVHRR Pathfinder sensor (version 5.0 and 5.1 SST) with a horizontal resolution of approximately 4 km. For the period between 1998 and 2002, the annual average values of sea surface Chl-a concentration, POC and PIC were estimated from the monthly data products of NASA Ocean Color obtained from the SEA-WIFS sensor and compiled for the Azores EEZ with a horizontal resolution of about 9 km (NASA /OEL/OBPG, 2003). For the period between 2003 and 2018, the annual average values of these variables were estimated from the monthly data products of NASA Ocean Colour obtained from the MODIS sensor and compiled for the Azores EEZ with a horizontal resolution of about 4 km (NASA/OEL/OBPG, 2014) (Amorim et al., 2017). Additionally, we integrated the satellite-derived estimates of surface Chl-a over the actual euphotic depth (i.e., depth-integrated Chl-a) (Morel and Berthon 1989, Morel and Maritorena 2001, Lee et al., 2007). Satellite-derived estimates of surface NPP, SST, Chl-a, PIC and POC were averaged across the modelled area to obtain annual estimates for each variable. Estimates of basin and regional scale variables were normalized to obtain z-scores, making them comparable to the model-estimated anomaly (Fig. 4). Pearson correlation coefficients were calculated between values of all the environmental variables to test for possible covariation (Dalgaard, 2008).

## 3. Results

### 3.1. Fitting to time-series

Simulations assuming only fishing as a driver of food web dynamics (Phase I, trial 1) produced an AICc value of −3058.69 and SS value of 40.90 (Table 1). The sequential inclusion of environmental drivers in the simulations improved the goodness-of-fit. In fact, the simulations forced with fishing and registered net primary production (Phase II, trial 2) produced an AICc value of −3198.34 and SS value of 35.40, corresponding to an improvement of 4.6 % in goodness-of-fit, whereas model

estimated anomalies promoted improvements of 13.3 % (Table 1). The estimated production anomaly that produced the best statistical fit of the model (Phase II, trial 3) exhibited high temporal variability, with maximal values being predicted in 2003 and minimal values in 2008, 2010 and 2012 (Fig. 5). The calibration of the predator–prey vulnerabilities with the highest sensitivity (Phase III, trial 5) further improved the goodness-of-fit of the model by 20.5 %, in relation to the trial 1 (Table 1). The iterative search for the optimal number of vulnerabilities (Table S2) was obtained with 21 "predator" vulnerabilities, resulting in a final AICc of −3685.31 and SS deviation of 19.49 (Table II). The calibration revealed a prevalence of the top-down mechanisms of trophic control, since the most sensitive interactions obtained vulnerabilities values > 2 (Table S3). This mechanism predominantly described the trophic interactions of the benthic energetic pathway, such as *Phycis phycis, Conger conger* and the groups large sized shallow water fish and benthic sharks and rays on their preys. Conversely, food availability was predicted to regulate the dynamics of pelagic (e.g., tunas) and bentho-pelagic predators (e.g., *Pagellus bogaraveo, Pagrus pagrus)* via bottom-up processes (vulnerabilities < 2).

### 3.2. Hindcasting trends

The differences in statistical fit obtained in the simulation of trophodynamics with individual and combined effects of fishing and environmental drivers (Table 1) is demonstrated by the ability of the model to replicate the inter-annual reference patterns of relative biomass (Fig. 6). The time series indicate the existence of common patterns in inter-annual variability among modelled benthic fish species and functional groups. The most widespread pattern in the time series of biomass is characterised by a bell-shape curve in biomass estimates that peaks between 2004 and 2008 and then declines through 2012, followed by an increasing trend in biomass values through the end of the time series. This pattern was observed for most food web components, but there are exceptions. For example, the medium-size shallow-water fish and benthic sharks and rays showed a general downward trend in biomass over time, with smaller peaks recorded around 2004. The time series of *Helicolenus dactylopterus* indicate a general downward trend in biomass after 2000, but this trend reversed after 2012. The bell-shape pattern was less pronounced in the time series of *Conger conger*, as the peak in recorded biomass appeared to occur at the end of the model period (Fig. 6). Model simulations assuming fishing as the sole driver of biomass variability (trial 1) failed to reproduce the observed dynamics over time, although the low SS for some species (e.g. *Pagellus bogaraveo, Conger conger*) suggests that model predictions are close to the average reference values. Conversely, the observed patterns were largely

**Fig. 4.** Time series of z-scores for recorded environmental variables acting in the North Atlantic basin and at the regional scale of the Azores. The black dashed line represents a 5-year moving average of variable estimates.
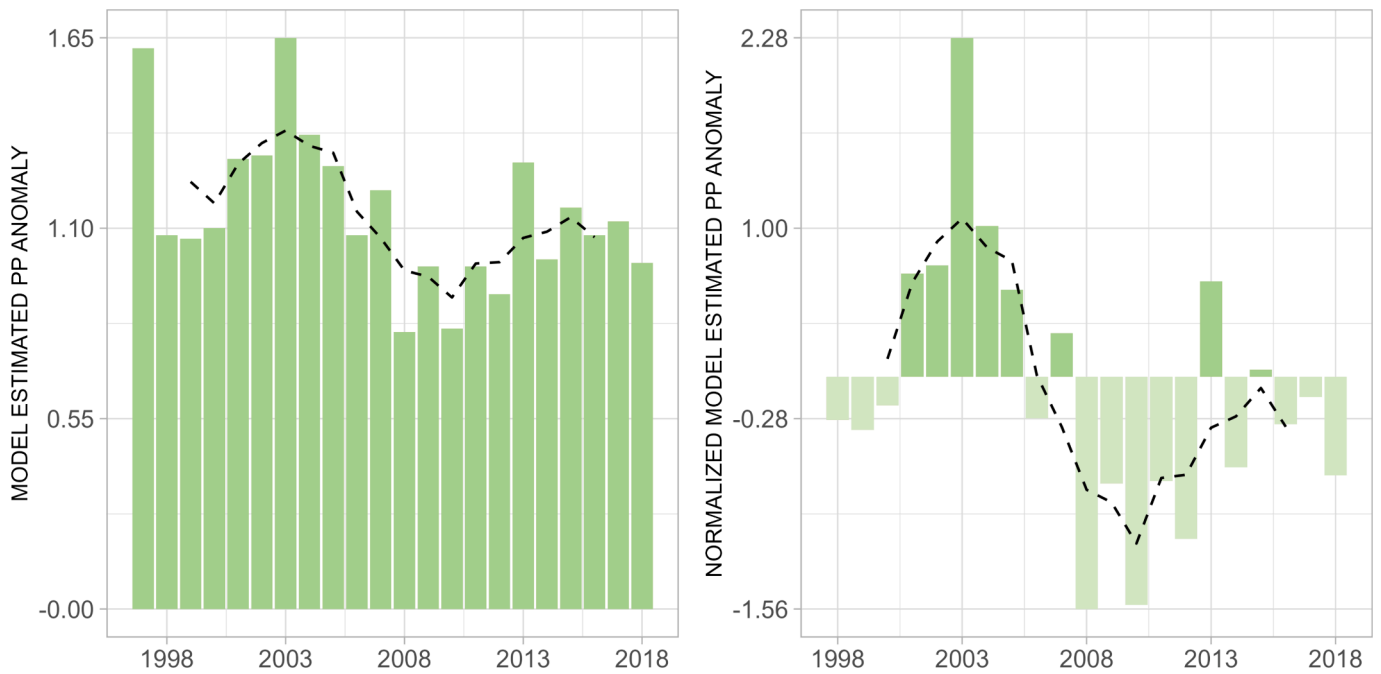


**Fig. 5.** Primary production anomaly estimated with the Azores Ecosim model over the fitting to-time-series procedure. Values are relative to Ecopath initial values (left panel) and normalised (right panel). The black dashed line represents a 5-year moving average of variable estimates.

reproduced by the model when fishing-induced trophodynamics were used in combination with the model-estimated production anomaly and trophic interaction effects. Despite some deviations from the observed estimates, especially in the last years of the simulation, the model satisfactorily reproduced the dynamics of *Raja clavata, Pagellus bogaraveo, Pagrus pagrus*, large-size demersal and shallow-water fish, benthic sharks and rays. However, the model exhibited poor capabilities to replicate the dynamics of *Conger conger*, especially after 2005 (Fig. 6).

### 3.3. Similarity between estimated production anomaly and environmental variables

We found significant positive correlations between NPP, surface Chl-a, depth-integrated Chl-a and POC ($r > 0.96$, $p < 0.01$; Table S4) and between PIC and SST ($r = 0.68$, $p < 0.01$; Table S4). Therefore, we measured the similarity between the production anomaly estimated with the best fit model and the environmental condition indices NAO, AMO, NPP and SST (Fig. 7 and Figure S5). The anomaly reached the
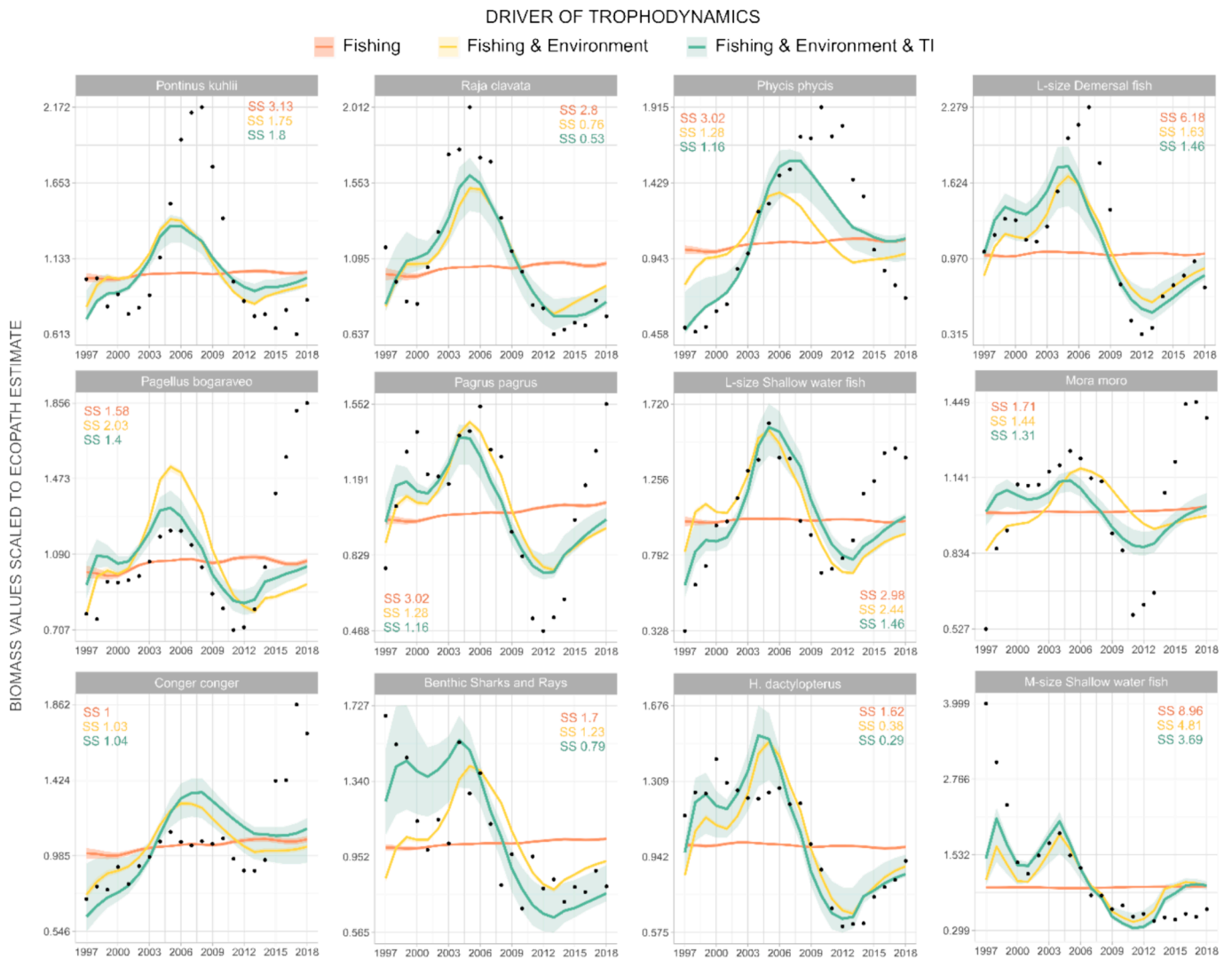
**Fig. 6.** Observed (black dots) and predicted temporal trends in biomass (solid lines) from the Ecosim model of the Azores (y-axis), when trophodynamics are forced with fishing effort (red line), fishing effort and environmental factors (yellow line), fishing effort, environmental factors and trophic interactions (green line). The sums of squares deviation (SS) associated to each simulation is reported. Shading represents the 5th and 95th percentiles of simulation as estimated by the Monte Carlo routine. TI refers to trophic interaction, S to small-size, M to medium-size and L to large-size.
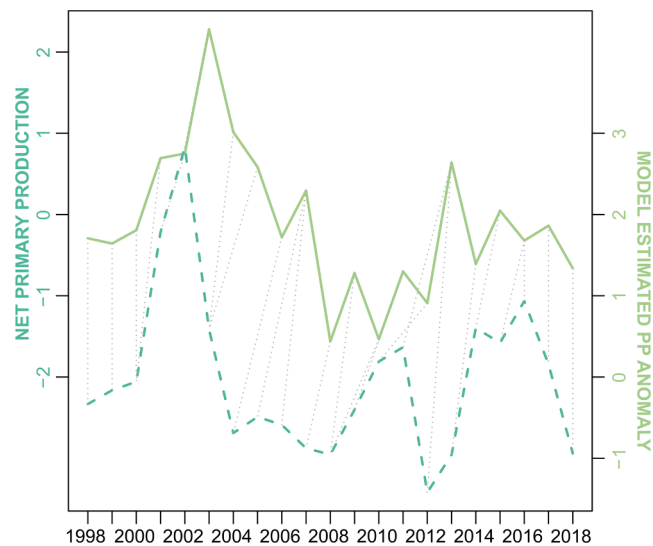


**Fig. 7.** Optimal alignment between model estimated PP anomaly and NPP recorded from satellite data. Alignment was identified with the dynamic time wrapping algorithm over the period between 1998 and 2018.

highest degrees of similarity with NPP (87.78 %), followed by AMO (81.54 %), SST (80.71 %) and NAO (75.92 %) (Table S5). Visual inspection of the alignment between variables, suggests that model estimated patterns of primary productivity tend to match registered values of net primary production with time lag of one year, but time lag of two years could also be noted (Fig. 7). The agreement was primarily characterised by maximal peaks of the forcing function corresponding with maximal peaks of registered net primary production. For example, the algorithm suggests that predicted increasing trajectories between 2000 and 2004, match those registered between 1999 and 2003. Further in the time-series, the algorithm matched the predicted positive peaks of 2013 and 2015 with the positive peaks registered in 2011 and 2014, respectively. Nonetheless, the time wrapping algorithm used to detect alignment of the two time-series also attributed a correspondence of maximal peaks of the forcing function (e.g., 2009 and 2011) with minimal peaks of registered NPP (2008) in certain years of the simulation.

## 4. Discussion

### 4.1. Significance of fishing pressure as a driver of trophodynamics

Since ecosystem-scale experiments are rarely practicable, fitting to

time-series procedures, such as those adopted within the Ecopath with Ecosim (EwE) modeling approach, have helped identify, from a range of alternative hypotheses, the drivers that best explain historical trends in marine ecosystems around the world (Mackinson et al., 2009; Colléter et al., 2015; Stock et al., 2023). In this study, we initiated the procedure assuming that fishing effort could explain the historical patterns of interannual variability in the biomass of commercially important fish species and functional groups in the Azores. However, model predictions suggests that fishing as a single driver of trophodynamics does not explain the observed trends. There are several possible justifications. Firstly, it is possible that the spatial patterns of upper ocean temperature render the Azores trophodynamics to be more strongly regulated by bottom-up than top-down drivers (Boyce et al., 2015), implying that the ecosystem may be less sensitive to the top-down forcing of fisheries exploitation (Petrie et al. 2009). However, if such patterns apply in the Azores, it could be expected that the majority of estimated predator vulnerability multipliers were $< 1$, suggesting dominant bottom-up trophic control (Bentley et al., 2020). Yet, the predictions of our model actually suggest a majority of top-down control via predation, namely for trophic interactions involved in the benthic energetic pathway, implying that stronger fishing effects could be expected. This lead us to speculate that the impacts of fishing are possibly being dampened in the system as an effect of structural properties of the food web (i.e., robustness, persistence or trophic interaction strength) (O'Gorman and Emmerson, 2009; Andersen and Pedersen, 2010; Gilarranz et al., 2016). Notably, further studies are needed to quantify the specific dependencies of predation rates on the densities of prey components in the ecosystem, the effects of fishing across trophic levels and to identify the stabilising properties of the system.

Our simulations also indicated that energy flows between fisheries and the rest of the food web are generally low compared to the energy flows within the living food web itself. This may help explain why the effects of fishing alone are difficult to detect within a whole food web approach. The local fishing practices in the Azores, characterized by small-scale operations using hook-and-line gear (Carvalho et al., 2011), likely contribute to the low energy flows from fisheries and may have mitigated the broader ecological impacts of fishing. These methods are highly selective and generally cause less damage to the seafloor and marine habitats compared to more disruptive practices such as bottom trawling, potentially minimizing ecosystem-wide effects (Pham et al., 2014). However, these arguments should not be interpreted as a claim that fishing practices in the Azores are inherently sustainable. Such conclusions cannot be generalized, particularly when considering that in regions with a long history of intensive predator fish exploitation, fishing has emerged as a dominant driver of trophodynamics (Frank et al., 2005; Mackinson et al., 2009).

Finally, we acknowledge that technical limitations associated with the model and time-series data are the factors that might best explain the results. These issues can stem from the lack of spatial representation of trophodynamics (Brito et al., 2023), the mass-balanced estimates used as initial conditions for dynamic modelling, and limitations in the accuracy of fisheries data. Although we used the best available data to construct the Ecopath model (including diet and growth parameters), the reference exploitation status of the system remains uncertain due to the lack of absolute biomass estimates for most ecosystem components (Morato et al., 2016). The main discrepancies observed between model predictions and time-series data, including opposite trends, likely result from limitations in the input fishing effort data. Although the metrics used to measure the effort of each fishing fleet are based on the best available knowledge of fishing operations in the Azores, they remain incomplete due to poorly quantifiable changes in fishing operations over time, such as changes in daily fishing time and catchability. Consequently, these metrics may not accurately reflect real changes in fishing mortality, further compounded by uncertainties in reference biomass estimates. These uncertainties hinder the models' ability to fully represent fishing's impact on fish stock biomass variability and

underscore the need to adopt an ensemble of models to separately explain historical patterns of biomass and catches in the Azores. Inputting species-specific fishing mortality estimates or better estimates of species biomass would likely help the model explain the observed patterns. It is also important to note that the time series of relative biomass used to evaluate model predictions have limitations due to sample design and survey methods (Pinho et al., 2020). Survey data might need adjustment for minor sampling differences that can affect catchability, such as water currents, soak time, gear saturation, and competition for hooks (Kuriyama et al., 2019; Pinho et al., 2020). To improve estimate accuracy, it may be beneficial to pre-process the data to obtain standardized time series (e.g., Panzeri et al., 2021). Developing reference time series for other components of the food web, especially those at lower trophic levels, is a challenging but necessary step for a more integrative understanding of oceanic and deep-sea trophodynamics in the Azores. Additionally, future model developments should incorporate life history traits to account for variations in trophic interactions and fishing pressure throughout the life histories of species (Pinho et al., 2014).

### 4.2. Significance of environmental drivers and trophic interactions at shaping trophodynamics

The weak signal in model predictions under fishing-forcing led us to investigate whether other factors, in combination with fishing pressure, might help explain historical trends. In line with other food web and ecosystem dynamics studies (e.g., Möllmann et al., 2011; Dragon et al., 2015; Serpetti et al., 2017), we quantified the role of environmental factors impacting the basis of the ecosystem and trophic interactions at explaining the trends. In initial modelling trials, we tested whether recorded values of net primary production improved the goodness-of-fit. Although the fit of the model improved, the biomass trends for most species and functional groups could not be satisfactorily captured by the model predictions. This result highlights that, beyond net primary production (NPP), multiple factors might influence the dynamics of the food web via bottom-up processes (Morato et al., 2009), helping to explain the observed patterns. Thus, we decided to adopt the standard method of identifying a production anomaly that maximizes the goodness-of-fit, and compare estimated patterns with recorded environmental variables acting at basin and regional scales. The analysis revealed a notable alignment between the anomaly and recorded values of NPP but the correspondence showed a temporal delay of one to two years, with maximal peaks of the anomaly matching those of NPP recorded from satellite measurements. The temporal delay between these variables is expected because primary production dynamics are transmitted to higher trophic levels through recruitment, growth (Durant et al., 2005; Trathan et al., 2007), and trophic interactions (Layer et al., 2010; Olesen et al., 2010), resulting in time-lagged responses. This temporal delay also partially explains why calibration trials using registered NPP time-series produced worse statistical fits compared to trials using the model-estimated anomaly under environmental forcing. These results further highlight the importance of variables affecting food supply in sustaining the energetic demands of the fauna in the Mid-Atlantic Ridge (Priede et al., 2013, 2022). The transfer of basal energy between phytoplankton and benthopelagic and pelagic predators (e.g., *Pagellus bogaraveo*, tunas) likely involves zooplankton, small-pelagic, and mesopelagic fish, as highlighted in the analysis of sensitive predator–prey interactions and documented in Morato et al. (2009) and Colaço et al. (2013). This opens a future line of model development to better understand how climate-induced changes in primary production affect higher trophic levels and the overall structure of the Azores deep-sea ecosystem (Frederiksen et al., 2006; Maureaud et al., 2017).

We further acknowledge that although primary productivity anomalies may be a predominant driver, other environmental factors may also impact trophodynamics and be reflected in the shape of the forcing function. The potential influence of multiple processes exerting bottom-

up effects in the Azores ecosystem explains the poor statistical fits obtained during preliminary calibration runs forced with lagged versions of net primary production (NPP) (not shown), as well as the maximal and minimal matches between model-estimated production anomalies and recorded NPP values in certain years. The similarity scores between the model-estimated anomalies of primary production and the SST, NAO, and AMO indices suggest that these variables may also play a role in trophodynamic processes. Several studies have identified links between these indices and the variability and pathway of oceanographic phenomena oceanographic phenomena, such as the Gulf Stream and the Azores Front, which are critical to productivity patterns in the region (Fründt and Waniek, 2012; Seidov et al., 2017; Nigam et al., 2018; Frazão et al., 2022). However, the influence of these phenomena on the temporal and spatial dynamics of higher trophic levels, particularly demersal fish, remains poorly understood. Further investigations are warranted to examine potential nonlinearities within the system and determine whether information from these indices is encoded in the shape of the estimated forcing function (Sugihara et al., 2012). It is also important to note that mesoscale eddy systems and physical processes associated with seamount-induced upwelling influence biological production (Bashmachnikov et al., 2009; Lavelle and Mohn, 2010; Godø et al., 2012), introducing further uncertainty regarding the role of these factors on trophodynamics. When modelling deep-sea oceanic ecosystems, such as that of the Azores, it is essential to acknowledge the uncertainties inherent in attempting to capture a variety of processes potentially influencing trophodynamics using a single and simple forcing function.

### 4.3. Effects of drivers in the ecosystem

Thus, our results show that the trophodynamics of the open-ocean and deep-sea ecosystems of the Azores are more likely explained by the interaction of fishing and environmental drivers over time rather than individual effects of fishing. The temporal oscillation pattern of model's estimated production anomaly simulating environmental forcing, in combination with variations in fishing pressure of the deep-sea bottom longline & handline fleet, helped to explain the reference patterns of exploited biomass of the Azores. For example, the estimated anomaly suggests enhanced primary productivity between 1999 and 2002, a period marked by reduced fishing effort levels and thus with an apparent dominance of bottom-up control. These two factors (higher food supply and lower fishing pressure) resulted in more energy reaching higher trophic levels and increased fish stock biomass through 2003–2007, for most modelled species and functional groups. After this period, fishing effort tended to increase, reaching new highs in 2007 and 2008. This factor, combined with a decline in estimated productivity, led to a reduction in predicted biomass for most modelled stocks, reaching minimum values around 2012, in concordance with the reference time-series. Upon 2012, the fishing effort tended to increase again, but an increase in primary productivity of the system seems to have helped the recovery of some fish stocks. Our results are in line with local studies documenting that historical fishing pressure levels have promoted significant effects on benthic fish stocks, namely between 2008 and 2012 (e.g., Santos et al., 2019, 2023; ICES 2019), and preliminary correlation analysis suggest the influence of climate variability on the dynamics of a benthic species (Pinho et al., 2011). Thus, our results suggest that the modelled oceanic populations, from low to high trophic levels, are sensitive to patterns of primary production. This consideration implies that it is necessary to account for variability in environmental conditions and fishing pressure in order to successfully reproduce historical food web trends in the Azores (Mackinson et al., 2009; Christensen et al., 2015).

The important role that the apparent combined effect of fishing and environmental drivers exerts on trophodynamics poses important implications for biodiversity conservation and sustainable fisheries management in the Azores, especially in the face of climate change.

Projections of climate change impacts on the ocean indicate that most deep-sea ecosystems will be affected by changes in various oceanographic properties, including decays in net primary production (Sweetman et al., 2017). If deficits in primary production and high levels of fishing exploitation negatively impact the ecosystem, as our results suggest, failing to consider future climate-induced changes in primary production could lead to management plans that fall short of achieving biodiversity and sustainability targets (Levin and Le Bris 2015). Therefore, new approaches are needed to incorporate ecosystem information into current management advice in order to take into account the impact of climate change on ecosystem state and production of fish stocks. For instance, stock assessment approaches, that still provide invaluable information for tactical short-term management, might not be sufficient to capture long term trajectories. Therefore, trophic models as the one developed in this study are essential tools that complement single species stock assessment for strategic regional science-based management plans as they provide the ecosystem information needed to examine policy decisions in an ecosystem-level context in the long term. Nevertheless, operational uses of such model results might require ensemble approaches capable of overcoming the limitations of individual models (Lotze et al., 2019; Tittensor et al., 2018) and the generally poor accuracy of ecosystem models (e.g., Planque 2016; Celić et al., 2018). Further development of such aspects might substantially improve the ability to predict and further ensure the long-term provisioning of the NCP that the oceanic food web of the Azores supports.

#### CRediT authorship contribution statement

**Joana Brito:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Ambre Soszynski:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Johanna J. Heymans:** Conceptualization. **Simone Libralato:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Eva Giacomello:** Writing – review & editing, Data curation. **Laurence Fauconnet:** Data curation. **Gui M. Menezes:** Writing – review & editing, Data curation. **Telmo Morato:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

#### 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

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2024.103357.

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