Parameterization and tuning of the Bay of Biscay Atlantis model v1

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Abstract

This paper describes the parameterization and calibration of an end-to-end Atlantis model for the Bay of Biscay, characterising spatially the structure and functioning of the ecosystem. The Bay of Biscay is considered rich in terms of ecological diversity and different oceanographic events such as coastal upwelling, coastal run-off and river plumes, and seasonal currents, take place in the area. These features, in addition to the different pressures caused by human activities and management criteria, demand for concurrent modelling of all the characteristics of the Bay of Biscay ecosystem in order to improve our understanding of the system and its functioning. The modelled area is 145 970 km^2 and was divided into 36 spatial polygons, each with multiple vertical layers. The model was composed by 54 functional groups, ranging from primary producers to top predators. Our results highlighted the importance of lower trophic levels to the pelagic system and how the trophic interactions among phytoplankton and zooplankton groups impact the structure of the ecosystem. The results also demonstrate the importance of having accurate and precise data for biological processes and showed the need of further study in the age-specific data such as biomass and weight distribution per age and diet interactions between juvenile and adult fish stages. Overall, the Bay of Biscay Atlantis model has been shown to be a tool that has the potential to improve our understanding of the spatial functioning of the Bay of Biscay ecosystem that will help establishing management measures of human activities.

1. Introduction

Today, there is no ocean free from human influence (Halpern et al., 2008). Over more than a century the use of marine and coastal areas has changed from mainly fishing activities to a complexity of economic, ecological, and sociocultural activities (Ramos et al., 2015; Worm and Branch, 2012). In addition, marine ecosystems are currently being heavily impacted by climate change (Baudron et al., 2020; Perry et al., 2005).

As in other coastal systems, the Bay of Biscay (hereafter BoB), a gulf of the Atlantic Ocean located between the western coast of France and the northern coast of Spain, has been and still is subjected to multiple pressures caused by different human activities such as fishing, aquaculture, farming, industrial activities (paper milling, petroleum refining and iron and steel working), maritime transport, shipping, land-based industry, tourism, new urbanization of coastal areas, recreational uses of beaches and shores, and other pressures such as climate change and invasive species (Borja et al., 2019; Lorance et al., 2010). The BoB is considered a complex system due to the different oceanographic processes happening in the area such as coastal upwelling, coastal run-off and river plumes, seasonal currents, eddies, internal waves and tidal fronts, and variable waves and storms due to the latitudinal location (Borja et al., 2019; OSPAR, 2000). In addition, while the Spanish continental shelf is narrow and includes different submarine canyons, e.g., Cap Breton, the French continental shelf is wide. The BoB corresponds to a subtropical/boreal transition zone with a high biological diversity reflected in the ecological richness of the area (OSPAR, 2000). The area is rich in terms of phytoplankton and zooplankton taxonomic groups and species, and it contains a high microphytobenthos biodiversity (OSPAR, 2000). Likewise, the topographical complexity and the wide range of substrates in a narrow continental shelf give rise to highly diverse benthic communities (Serrano et al., 2006). A wide depth distribution of fish species can be found in the region from 0 m to more than 800 m, some of them with commercial relevance for the surrounding countries (Borja et al., 2019; ICES, 2019a). In addition, it hosts species of great interest for conservation such as cetaceans and seabirds (García-Barón et al., 2019a; García-Barón et al., 2019b). The hydrodynamic events, ecological features and the many pressures that are affecting this marine ecosystem together with the spatial management (e.g., closed areas/seasons) and management criteria (e.g., shared stocks) in the area (Borja et al., 2019; Valdés and Lavín, 2002) underline a need to make progress towards the implementation of the Ecosystem Approach

55 (EA), accounting for the spatial planning of the different activities and analysing the impacts of the variety of pressures on the ecosystem, from species to communities and ecosystem properties as a whole. EA requires an adaptive management (AM) approach that incorporates scientific methods for planning, implementing and evaluating management strategies (Schreiber et al., 2004).

Within this context, end-to-end marine ecosystem models can play an important role as they allow to

60 simulate the entire ecosystem, from oceanography to food web structure and functioning along with multiple anthropogenic pressures (Kaplan and Marshall, 2016). Atlantis is considered the best operating model currently available to assess the functioning of the entire ecosystem (Plagányi, 2007). The first Atlantis model was developed in South-eastern Australia by Fulton et al. (2007) and it was used for management strategy evaluation (MSE). The Atlantis framework is now implemented worldwide to

65 investigate different management strategies (e.g., Ainsworth et al. (2012); Fulton et al. (2014); Hansen et al. (2019a)), climate change effects (e.g., Bossier et al. (2021); Fay et al. (2017); Ortega-Cisneros et al. (2018)), oil spill (e.g., Ainsworth et al. (2018); Morzaria-Luna et al. (2018)) or agricultural practices and land-use, urbanisation, climate and freshwater extraction and additional habitat disturbance or recovery (Condie et al., 2012), and interaction effects of fishing, ocean warming and ocean acidification (Griffith

70 et al., 2012).

The BoB ecosystem structure and functioning has already been studied using a series of Ecopath with Ecosim (EwE) approaches, some representing subareas (Lassalle et al., 2011; López López, 2017; Moullec et al., 2017; Sánchez and Olaso, 2004) whereas Corrales et al. (2022) developed an EwE for the whole BoB area. These models, however, did not study the area in three dimensions. This paper presents

75 the first spatially resolved three-dimensional model development (parameterization and calibration) for the whole BoB area using the Atlantis framework. The main objective of the study was to obtain a calibrated/reasonable Atlantis model for the BoB ecosystem that helps us gain knowledge on the structure and functioning of the ecosystem in three dimensions to inform ecosystem-based fisheries management measures.

2. Materials and methods

2.1. Study area and time period

This study encompasses the BoB ecosystem, from Ribadeo (Galicia, Spain) to Raz (France), covering ICES divisions 8ab and 8c (Fig. 1). The model comprises the French continental shelf and the Cantabrian Sea, from 0 m up to 4000 m depth, covering an area of 145 970 km^2. The BoB Atlantis model was initialized on January 1st, 2000, and the initial state represents the mean ecosystem functioning from 2000 to 2003, the period where accurate and accessible data is available, especially catch data. The model was projected forward for 40 years on a 24-hour time step.

The bathymetric limits of the model were determined using ecological and fishery characteristics. Coastal waters were included as they serve as important feeding and breeding grounds for many species, and they are the primary fishing grounds for coastal artisanal fleet and recreational fishermen; the limit of 4000 m is assumed to cover the Cap Breton Canyon, where the 1000 m isobath is found only 3 km from the coast (Lavin et al., 2006).
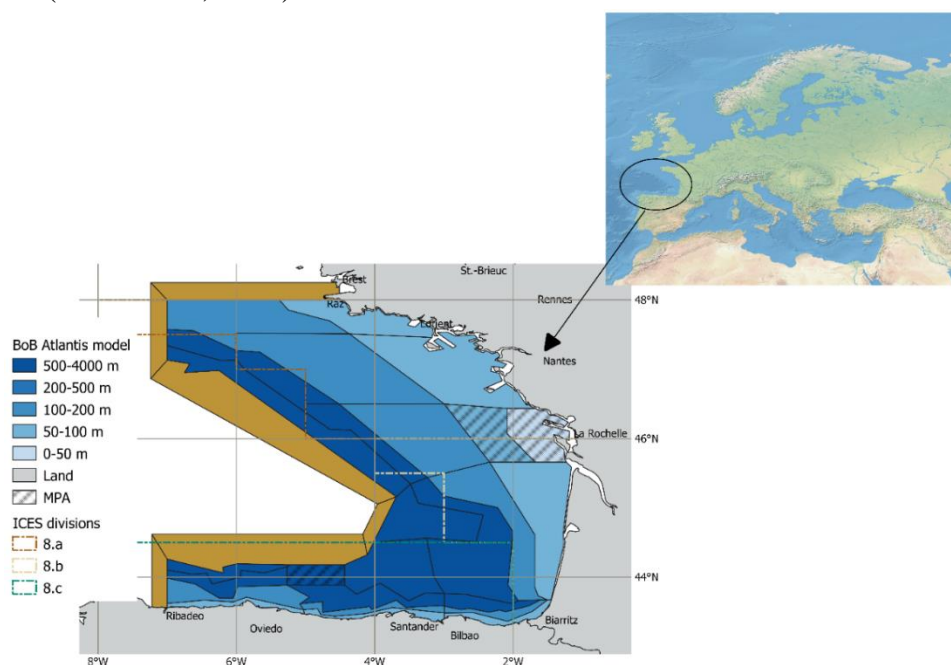
Figure 1. Overview of the BoB Atlantis model polygons (blue) and boundary polygons (yellow) covering the model domain. The depth layers are categorized using different blue colours: dark blue corresponds to the deepest layer (500-4000 m) while light blue corresponds to the shallowest layer (0-50 m). Land is coloured grey and MPAs are shaded. ICES divisions are differentiated in brown (8a), yellow (8b) and green (8c).

2.2. The Atlantis modelling framework

Atlantis is a three-dimensional, species-based and age-structured biophysical modelling framework intended for use in MSE – a simulation technique based on modelling each part of the AM cycle – so it includes all its components: biophysical system, human uses of the system, socioeconomic drivers of human uses and the three major components of an AM strategy (monitoring, assessment and management decision process) (Fulton et al., 2011). All of these components are simulated in sub-models and then integrated, making it possible to move towards an integrated and qualitative assessment of the ecosystem (Audzijonyte et al., 2019; Fulton et al., 2011).

At the core of Atlantis is the biophysical sub-model, a deterministic (differential equation) and spatially resolved three-dimensional model, which is based on a map made up of the user defined irregular polygons and depth layers (Audzijonyte et al., 2017; Fulton et al., 2011). This polygon representation facilitates tracking the flows of nutrients (usually nitrogen and silica, although others are possible) through the main biological groups in the studied ecosystem (Fulton et al., 2011; Link et al., 2010). Representation of the physical environment also occurs within the polygons that correspond to the simulated marine system´s main geographical and bioregional features coupled with an oceanographic transport model. The primary ecological processes considered are growth, consumption, production, waste production, migration, recruitment, habitat dependency and mortality. These processes are represented as either biomass pools, age-structured biomass pools or age-structured groups (Audzijonyte et al., 2017); lower trophic level invertebrate groups are generally treated as biomass pools, while a user-defined age- and stock-structured formulation is used to describe vertebrate and some high trophic level invertebrate groups (Link et al., 2010; Pethybridge et al., 2019). In biomass pools the processes are modelled through biomass turnover, whilst in age-structured groups, the state variables are numbers-at-age and weight-at-age (tracked as reserve and structural nitrogen), which can be converted to biomass by $(SN + RN)*Nums$, where SN and RN are the structural and reserve weight, and $Nums$ is the numbers in an age group (Audzijonyte et al., 2017).

2.3. The Bay of Biscay Atlantis model

2.3.1. Code version

The Atlantis source code is hosted in a subversion (SVN) repository (Audzijonyte et al., 2017). The

135 BoB Atlantis model was built using code version 6540.

2.3.2. Grid design

The spatial domain of the BoB Atlantis model was divided into 36 irregular polygons. Non-dynamic polygons (Fig. 1, marked in yellow) represented borders of the model domain (boundary polygons). These polygons are necessary to allow for exchange of water nutrients to and from dynamic model domain. All

140 dynamic polygons (Fig. 1, marked in blue) were divided into depth layers, containing up to five layers defined by the following isobaths: 0-50 m, 50-100 m, 100-200 m, 200-500 m and > 500 m, up to 4000 m depth. The number of layers is subjected to the geography of the polygon, depending on the mean depth of the polygon. Each polygon also contains a single 1 m thick sediment layer.

The spatial structure was based on: i) information on the boundaries of the ICES divisions 8ab and

145 8c (ICES); ii) bathymetry and species distribution collected from the BIOMAN surveys (pers. comm. Maria Santos); iii) MPAs gathered from the European Environment Agency (EEA); and iv) seabed substrate types map of the European sea areas obtained from the European Marine Observation and Data Network (EMODnet) (Vasquez et al., 2021).

2.3.3. Oceanographic forcing

150 Atlantis does not calculate volume fluxes (m^3 s^{-1}) itself but uses hydrodynamic data from oceanographic models to specify these fluxes across polygon faces. It needs input at daily or 12-hour resolution, which makes it challenging to use observations, as these usually have gaps in time and/or space. Temperature and salinity conditions can be calculated by the model using simple routines or calculated using data from oceanographic models (Audzijonyte et al., 2017).

155 For the BoB Atlantis model, volume fluxes between polygons for all depth layers were computed using E.U. Copernicus Marine Service Information for the Iberia-Biscay-Ireland (IBI) area (Aznar et al., 2016). The data was allocated to each Atlantis polygon boundary and interpolated to daily data using the

software R version 4.0.4 (R Core Team, 2021). For consistency with the fluxes, temperature and salinity were also forced using E.U. Copernicus Marine Service Information for the Iberia-Biscay-Ireland (IBI)

160 area (Aznar et al., 2016). The information used corresponded to the simulation of the year 2000 with a daily time step, which was repeated for the whole simulation. This way the influence of environmental factors was neutralized.

2.3.4. Functional groups design and biological components

The definition of functional groups was done considering previously developed ecosystem models

165 (López López, 2017; Moullec et al., 2017; Sánchez and Olaso, 2004). Functional groups were defined based on the commercial importance of the species, data availability and ecological features of the species such as diet composition and bathymetric distribution and in line with a recent published EwE model in the BoB (Corrales et al., 2022). In total, the BoB Atlantis model comprises 54 functional groups, including 3 groups of detritus (2 natural detritus and 1 fisheries discards), 2 groups of bacteria, 3 groups of primary

170 producers, 7 groups of pelagic invertebrates, 9 groups of benthic invertebrates, 9 groups of pelagic fishes, 13 groups of benthic fishes, 1 group of pelagic elasmobranchs, 3 groups of benthic elasmobranchs, 2 groups of marine mammals and 2 groups of seabirds (Table 1; Table S1; Fig. 2). Main commercially targeted species and/or species with an important ecological role were parameterised as separate components (marked with * in Table 1).

175 **Table 1.** Description of functional groups included in the Bay of Biscay Atlantis model. Commercially relevant functional groups and key functional groups are marked with *.

Code	Group	Code	Group
SBD	Diving and pursuit divers' seabirds	CBE	Benthic cephalopods
SBS	Surface feeding seabirds	CBP	Squids
BWH	Baleen whales	NEP	Norway lobster *
CET	Toothed cetaceans	CRP	Pelagic crab *
SHB	Demersal sharks	SHR	Zooplankton feeding shrimps
SHP	Pelagic sharks	DFB	Benthos-feeders decapods
SHD	Deep water sharks	DFD	Detritus-feeders decapods
SSK	Skates and rays	BIV	Bivalves
BFT	Bluefin tuna *	POL	Polychaetes
ALB	Albacore *	SB	Suprabenthos
OPE	Other large pelagic fishes	ECH	Echinoderms
MAC	Mackerel *	INV	Other invertebrates

HOM	Horse mackerel *	ZG	Gelatinous zooplankton
PIL	Sardine *	ZL	Macrozooplankton (> 2000 µm)
ANE	Anchovy *	ZM	Mesozooplankton (200-2000 µm)
OPL	Other planktivorous fishes	ZS	Microzooplankton (< 200 µm)
FMP	Mesopelagic fishes	PP	Benthic primary producers
ANF	Anglerfish *	PL	Large phytoplankton (> 20 µm)
BSS	Seabass *	PS	Small phytoplankton (< 20µm)
WHB	Blue whiting *	PB	Pelagic bacteria
HKE	Hake *	BB	Sediment bacteria
COD	Cods	DL	Labile detritus
MEG	Megrim *	DR	Refractory detritus
SOL	Common sole *	DC	Carrion
FFL	Flatfishes		
MUL	Mullets *		
FDL	Large demersal fishes		
FDM	Medium demersal fishes		
FDS	Small demersal fishes		
FSD	Deep sea fishes		

For each vertebrate group in Atlantis, the number of cohorts and the number of calendar years each of these represent are flexible (Audzijonyte et al., 2017). In the BoB Atlantis model, age-structured functional groups with a lifespan of 10 or more years, had 10 age-classes representing from 1 up to 9 years. Age-structured functional groups with a shorter lifespan than 10 years included a similar number of cohorts to their lifespan. Additionally, all the age-structured functional groups were split up into adult and juvenile stages, where information on fraction of mature for each age class was provided to the model. In Atlantis, when reaching maturity, the individuals are allowed to switch feeding habitats, distribution and migration routes (Audzijonyte et al., 2017). However, the sexual maturation is not assumed to occur at the same time as the ontogenetic shift in habitat and prey usage, but is expressed by the spawning ogive (Audzijonyte et al., 2017). The larval period is not explicitly modelled; in age-structured groups, after a defined larval time, nitrogen created as spawn is temporally removed from the model and returned as recruits (Audzijonyte et al., 2017). In the BoB Atlantis model, a modified Beverton-Holt spawn and species biomass dependent recruitment relationship was implemented for the recruitment of fish-species, and a constant recruitment for seabirds, marine mammals and elasmobranchs. The detailed explanation of the parameters of each of the age-structured functional groups used to initialize the BoB Atlantis model

and the final parameter values after calibration process are included in Section S1 and Section S2, respectively.

In the BoB Atlantis model, pelagic and benthic invertebrate groups were defined as biomass pools. For these groups, the biomass in tonnes was converted to milligram Nitrogen using an assumed Redfied ratio of 5.7 (Redfield, 1958) between dry weight and nitrogen weight. In Atlantis, in contrast to age-structured groups, reproduction in biomass pools is not explicitly modelled (Audzijonyte et al., 2017). The detailed explanation of the parameters of each of the biomass pool groups used to initialize the BoB Atlantis model and the final parameters values after the calibration process are included in Section S1 and Section S2, respectively.

In Atlantis, natural mortality accounts for mortality factors explicitly not modelled, such as mortality due to age or illness (Audzijonyte et al., 2017). Linear mortality terms should ideally be as low as possible, if not zero, whereas quadratic mortality terms at lower trophic levels should be low or zero, and of moderate size for the top predators (Audzijonyte et al., 2017). Due to the need of low levels of natural mortality, the mortality values found in the literature were not feasible for the model, also because they often include predation mortality. Therefore, the natural mortality parameter values used in the BoB Atlantis model were based upon tuning. Additional term of mortality connected to starvation of 0.0001 per day was used (Fulton et al., 2007; Hansen et al., 2016), but as mortality due to oxygen limitation and acidification were rather unlikely, these parameter values were not used.
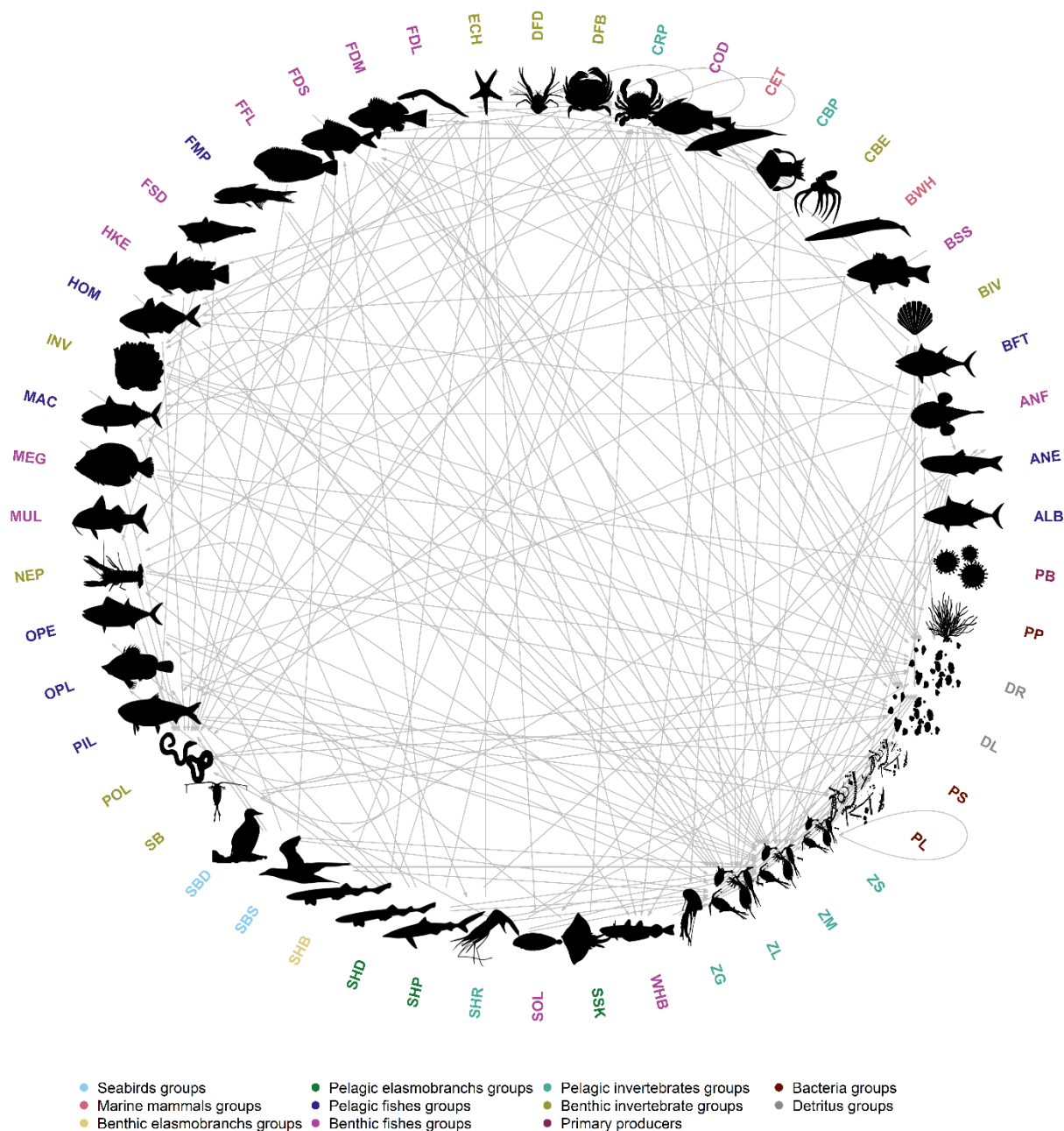
Figure 2. Schematic representation of the Bay of Biscay Atlantis model representing the period 2000-2003 (the abbreviations of the functional groups are listed in Table 1). Black figures and grey arrows represent the species included in the model and their interactions with other species. If the functional group included in the model is composed of several species (Section S1), the species with which the functional group has been parameterized is used in the figure.

2.3.5. Inputs/Observations

Biomass estimates were obtained using data from DEMERSALES and EVHOE bottom trawl surveys from the Spanish Institute of Oceanography (IEO) and the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) (ICES, 2017), PELACUS and PELGAS acoustic surveys from IEO and IFREMER (Masse et al., 2018), TRIENAL acoustic survey from IEO and AZTI (ICES, 2019b), visual surveys (Laran et al., 2017; Pettex et al., 2017), stock assessments, EwE model (Corrales et al., 2022) and other information found in the literature (Table 2; Section S1).

Table 2. Description of source of information used in the calculation of biomass estimates for functional groups included in the Bay of Biscay Atlantis model.

Group	Source
Seabirds groups	Visual survey (Pettex et al., 2017)
Marine mammals groups	Visual survey (Laran et al., 2017)
Benthic elasmobranch groups	DEMERSALES and EVHOE surveys
Pelagic elasmobranchs groups	EwE model
Pelagic fishes groups	PELACUS and PELGAS surveys
Tuna fish groups	Stock assessment (ICCAT, 2016, 2017)
Other large pelagic fishes, mesopelagic fishes	EwE model
Mackerel	TRIENAL survey
Anchovy	Stock assessment (ICES, 2019c)
Benthic fishes groups	DEMERSALES and EVHOE surveys
Pelagic and benthic invertebrate groups	DEMERSALES and EVHOE surveys
Bivalves, polychaetes, suprabenthos, echinoderms, other invertebrates, gelatinous zooplankton	Literature
Zooplankton	EwE model
Behic primary producers	Literature
Phytoplankton	Copernicus (Aznar et al., 2016)
Bacteria	ICES Report (ICES, 2012)
Detritus groups, carrion	EwE model

The simplest form of spatial distribution for vertebrates was used in the BoB Atlantis model, called "prescribed movement" (Audzijonyte et al., 2017). Using this option, the spatial distributions were predefined by interpolating the proportion of biomass in each polygon for each quarter of the year. This way, the model will distribute vertebrate biomass between the polygons the same way each year and the horizontal movement will not be mostly or entirely overwritten by the movement and distribution due to food availability. The proportion of biomass for each polygons was defined using information collected

from: i) Pettex et al. (2017) for seabirds groups; ii) Laran et al. (2017) for marine mammals groups; iii) egg distribution from the BIOMAN survey for the year 2018 for sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) (pers. comm. Maria Santos); and iv) DEMERSALES and EVHOE
235 bottom trawl survey (ICES, 2017) for the remaining functional groups except for pelagic sharks and tuna fish groups. For these groups (pelagic sharks, bluefin tuna (*Thunnus thynnus*) and albacore (*Thunnus alalunga*)) it was not possible to differentiate the horizontal distribution per life stage (juvenile/adult) or season due to poor information available, and, therefore, homogeneous horizontal distribution was assumed for both stages and seasons (Section S3, Fig. S1). Regarding the vertical distribution, only
240 anchovy daytime, nigh-time, adult and juvenile vertical distributions were found (Boyra et al., 2013).

The diet information was obtained collecting information of stomach content from IEO's database together with trophic information gathered from published and unpublished studies on stomach content analysis, giving preference to local or surrounding areas (the detailed calibrated input diet matrix can be found in Section S4, Table S7). Remarkably, the described dietary preferences of 35 species of fish from
245 the DEMERSALES trawl surveys for the 2000-2003 period were used (pers. comm. Izaskun Preciado).

2.4. Calibration process of the Bay of Biscay Atlantis model

The calibration process of the BoB Atlantis model was performed stepwise and bottom up, starting with the lower trophic level groups up to top predators, through two different stages: i) calibration of a simplified NPZD (Nutrient, Phytoplankton, Zooplankton and Detrital matter) model, meaning only the
250 nutrients, organic matter and planktonic functional groups were active; and ii) calibration of the full system model, meaning all the functional groups were active. In the calibration process of the full system model, the spatial structure of each of the functional groups was analysed. However, the validation was only done for anchovy and sardine. For these species, we compared the spatial distribution during spring derived from Atlantis and the egg distribution from the BIOMAN survey for the period 2019-2020 in
255 May.

In Atlantis, there are typically three phases of calibration: i) unfished system; ii) constant fishing; and iii) historical fishing and environmental drivers (Audzijonyte et al., 2017; Pethybridge et al., 2019). In the absence of fishing, the main goal of the calibration process was to produce stable unfished levels of

biomass through time under stable environmental conditions and reasonable individuals' weight-at-age.
260 That is, keep all groups from going extinct and obtain stable biomass and individuals' weight-at-age that
are not oscillating more than ±20-50% from their initial values. Similar to other ecosystem models with
a large number of parameters, many parameters in Atlantis (e.g., oceanographic and physical parameters
such as water fluxes, resuspension, point-source scaling, eddy strengths) do not need changing after the
model development (Pethybridge et al., 2019). Other parameters, however, are crucial in terms of model
265 sensitivity such as growth and consumption, recruitment and mortality (Audzijonyte et al., 2017;
Pethybridge et al., 2019). In this study we focused on growth and mortality parameters. The equations for
these parameters are given below, and the parameters that have been changed during the calibration
process are highlighted in bold.

Growth of primary producers (G_{pp}) is represented by the equation (Audzijonyte et al., 2017):

$$G_{pp} = B_{pp} * mum * \delta_{light} * \delta_{nutrient} * \delta_{space} * \delta_{eddy} * pHscalar \tag{1}$$

270 where B_{pp} is the biomass of the primary produces (tonnes), **mum** is the maximum growth rate (mgN per
day), and δ_{light}, $\delta_{nutrient}$, δ_{space}, δ_{eddy} and $pHscalar$ are light, nutrient, space, eddy and pH scalar limiting
factors. $pHscalar$ is 1 in the BoB Atlantis model.

Growth in biomass-pool consumers is determined by the consumed food or grazing term (Gr) and
assimilation efficiency, whereas the growth in age-structured consumers is determined by the consumed
275 food or grazing term (Gr), assimilation efficiency and optional maintenance or respiration costs (Rs). The
grazing term (Gr) is the amount of biomass of a specific prey consumed by a consumer, modelled for
biomass-pool consumers and age-structured consumer with the equation (Audzijonyte et al., 2017):

$$Gr_{prey} = \frac{B * C * B^*_{prey}}{1 + \frac{C * \sum_i (E_i * B^*_{prey,i})}{mum}} \tag{2}$$

where B is the feeding biomass of predator CX (mgN per m³), **C** is the consumption rate (m³ mgN per
day), **mum** is the maximum growth rate (mgN per day), and B^*_{prey} is the available biomass of $prey$ after
280 the overlap, habitat and size refuge was taken into account.

The mortality components includes predation, natural mortality divided into linear and quadratic mortality (density dependent mortality), and additional mortality due to starvation, temperature, pH or other factors (Audzijonyte et al., 2019). Predation is determined by the user-defined **predator-prey matrix**, which sets the availability of each prey biomass to a particular predator. For age-structured groups, four values are given for each predator-prey combination: juvenile-juvenile, juvenile-adult, adult-juvenile and adult-adult (Audzijonyte et al., 2017).

Natural mortality of primary producer is represented by (Audzijonyte et al., 2017):

$$M_{PP} = \left(\left(\frac{KLYS \cdot B_{PP}}{\delta_{nutrient} + 0.1} \right) + mL \cdot B_{pp}(mL \cdot B_{PP} + mA \cdot B_{PP}) \right) \qquad (3)$$

where $KLYS$ (day^{-1}) is the lysis rate, B_{pp} is the biomass, $\delta_{nutrient}$ is the nutrient limiting factor, $\boldsymbol{mL}$ (day^{-1}) is the linear mortality rate and mA is the optional acidification mortality.

Natural mortality of a consumer is represented by (Audzijonyte et al., 2017):

$$M_{XX} = \left((mL + mQ \cdot xx + mSt + (1 - \delta_{O2}) \cdot mO + mE) \cdot xx \right) \cdot mortsc \qquad (4)$$

where $\boldsymbol{mL}$ is linear mortality rate (day^{-1}), $\boldsymbol{mQ}$ is quadratic mortality rate (day^{-1}), xx is the biomass if consumer is biomass-pool or number if is age-structured group, mSt is starvation mortality rate (day^{-1}) for age-structured group only, δ_{O2} is the oxygen limiting factor, mO is oxygen mortality rate (day^{-1}) for biomass-pool group only, mE is the optional extra mortality for age-structured group only and $mortsc$ is the optional external mortality scalar. δ_{O2} is 1 in the BoB Atlantis model.

2.4.1. Simulations

Considering the elements that comprises the growth of planktonic groups (Eq. (1)-(2)), the NPZD calibration process was done starting by: i) nutrient limitation mechanism; ii) primary producers; and iii) zooplankton groups (Simulations 01-14, Section S5, Table S8).

At each step of the full system calibration process, one group at a time was calibrated, starting from pelagic and benthic invertebrate groups up to seabirds and marine mammals (Simulations 15-134, Section

S5, Table S8). In each simulation of each step of the full system calibration process, only one parameter was changed.

3. Results

305 3.1. Biomass trends

The main objective of the calibration of the BoB Atlantis model was to keep all groups from going extinct and obtain a stable system with all components within reasonable limits. For the BoB Atlantis model, "reasonable limits" means biomass and individuals' weight-at-age staying within ±50% from their initial values (Section S5, Fig. S2 and Fig. S3). A majority (73%) of the groups reach a balanced equilibrium after 15 years into the simulation. This period is called "spin-up" period (Pethybridge et al., 2019). Pelagic sharks, mackerels, horse mackerels, other planktivorous fishes, common sole and medium demersal fishes had upward or downward trends after this period but remained within ±50% from their initial biomass (Fig. 3). For benthic cephalopods, Norway lobster, zooplankton feeding shrimps, bivalves and echinoderms it was not possible to obtain a stable biomass, but the groups were kept from going extinct (Fig. 3). Benthic cephalopods and Norway lobster had upward trends, whilst zooplankton feeding shrimps had downward tendency. In the case of echinoderms, the biomass started with an upward trend, turning the trend downward in the last eight years.
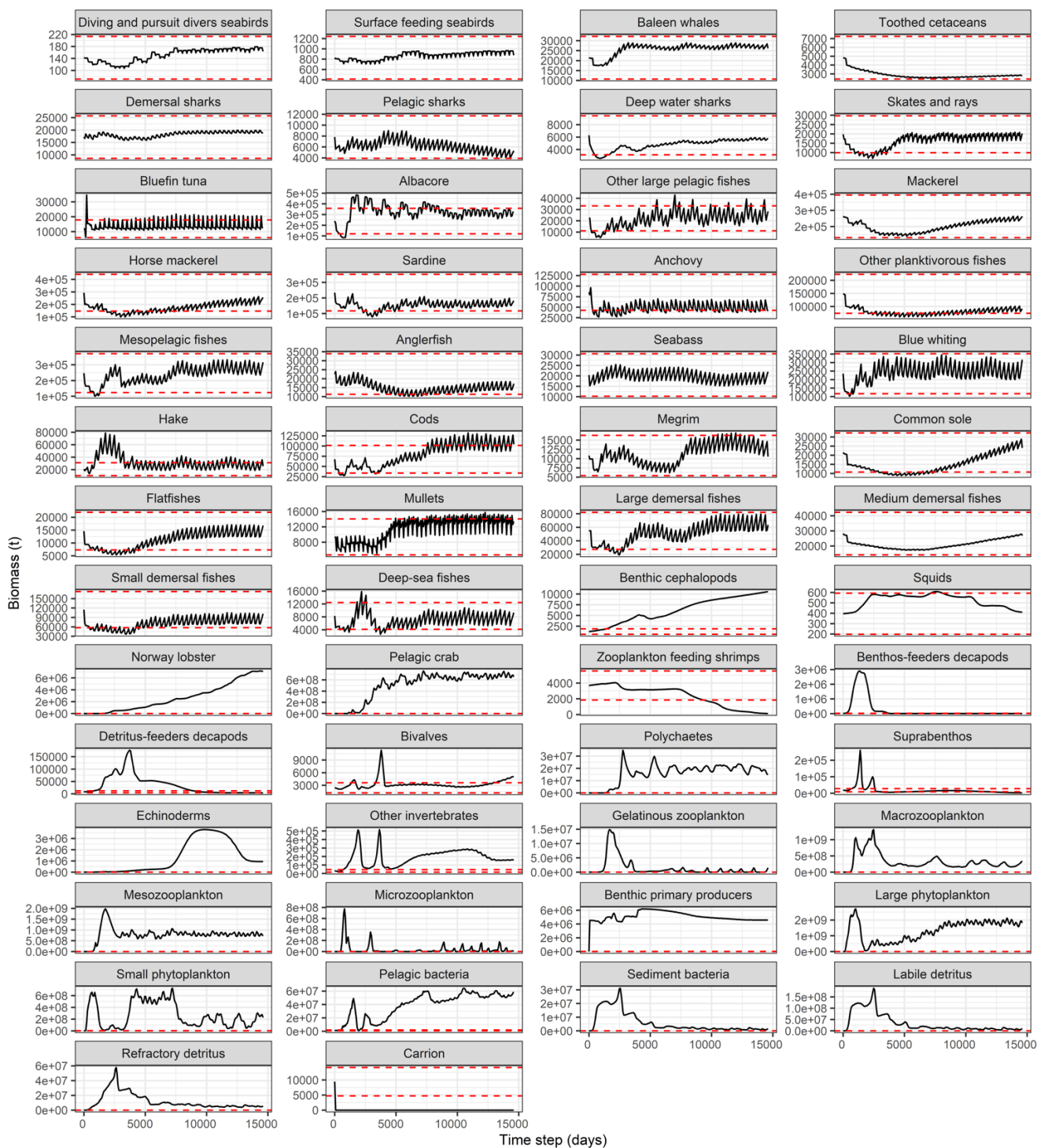
Figure 3. Time series evolution of the Bay of Biscay Atlantis model groups in the 40-year run. Dashed red line corresponds to the initial biomass value ±50% line.

3.2. Calibration process

3.2.1. NPZD calibration process

In the initial simulation, the macrozooplankton group disappeared completely from the system within the first 15 years and the small phytoplankton had an exponential behaviour instead of a seasonal behaviour (Fig. 4, (b) and (g); marked in dashed line). Considering the computational cost of running a 40-year simulation (approximately 3 hours), and the potential number of runs needed to re-parameterize the unrealistic behaviour in the lower trophic levels, the NPZD calibration process was done with a 15-year simulation (the 40-year final simulation run can be found in Fig. 3).
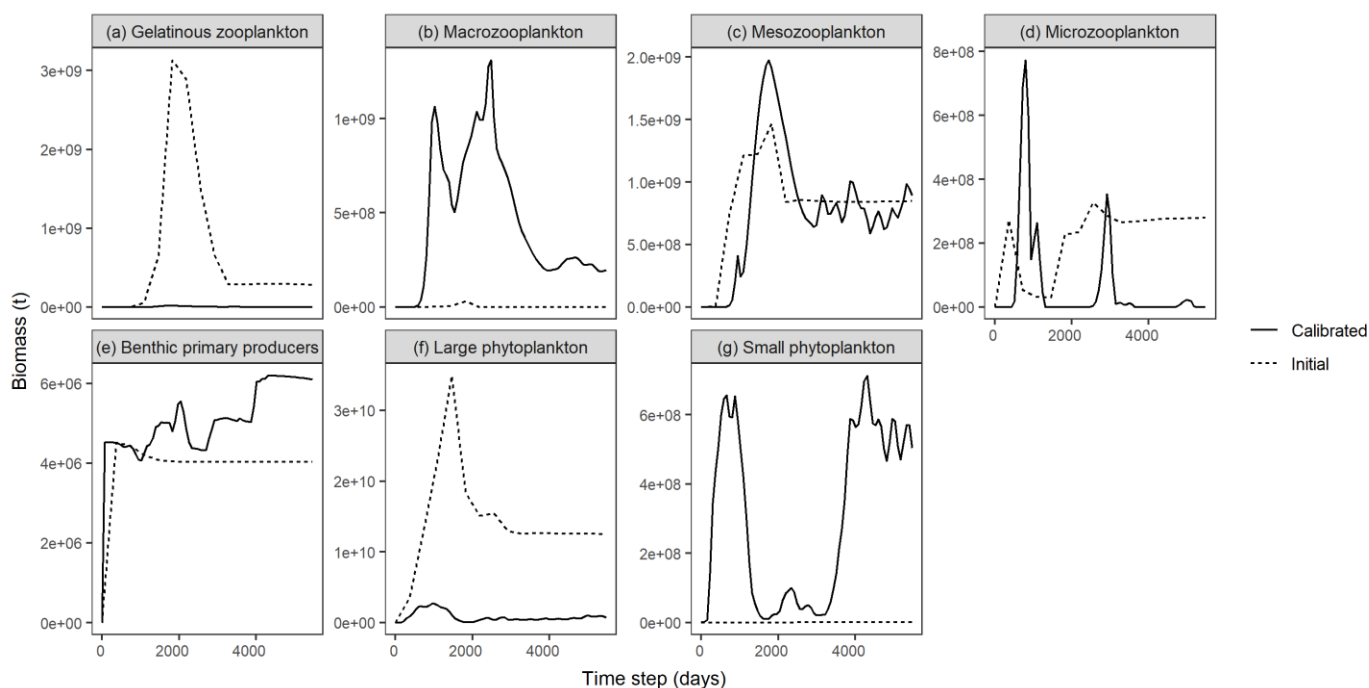
Figure 4. Time series evolution of the initial simulation (dashed line) and calibrated simulation (solid line) of the Bay of Biscay Atlantis model NPZD groups in the 15-year run.

In the initial simulations, the sinking rates of phytoplankton were not properly parameterized, thus leading to a build-up of nutrients in the upper layers (Fig. 5; marked in dashed line). In addition, the initial horizontal concentration of NO_3 and NH3 were patchy (results not shown). Therefore, NO_3 and NH_3 nutrient values were modified. The new concentration values of NH_3 and NO_3 were stablished based

on the values of the SE-Australian Atlantis model (Fulton et al., 2004) and the NoBa Atlantis model (Hansen et al., 2016).

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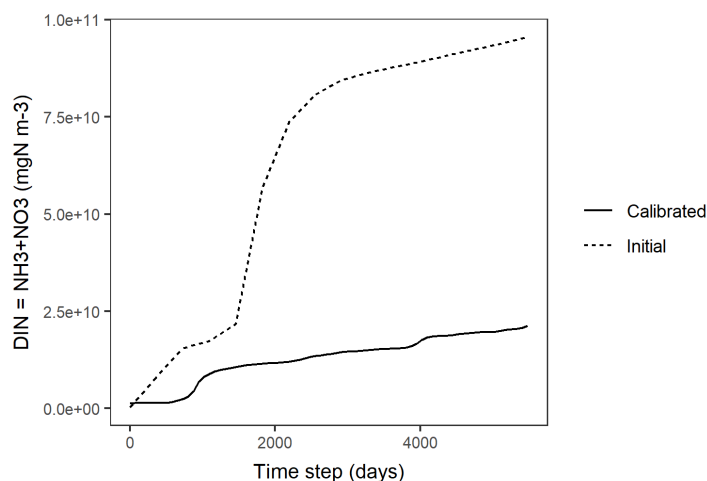
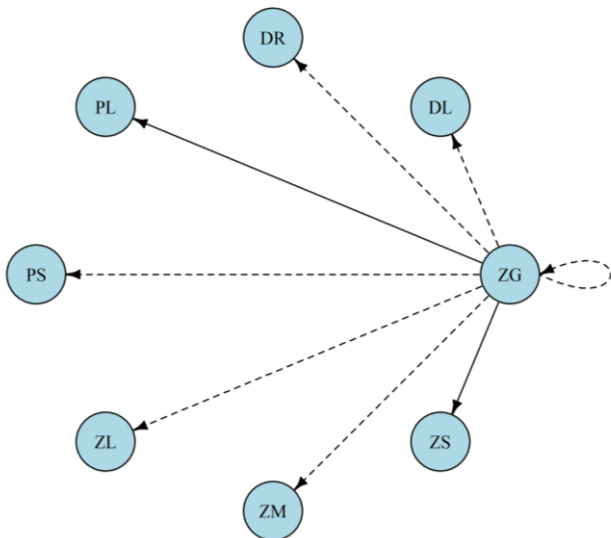
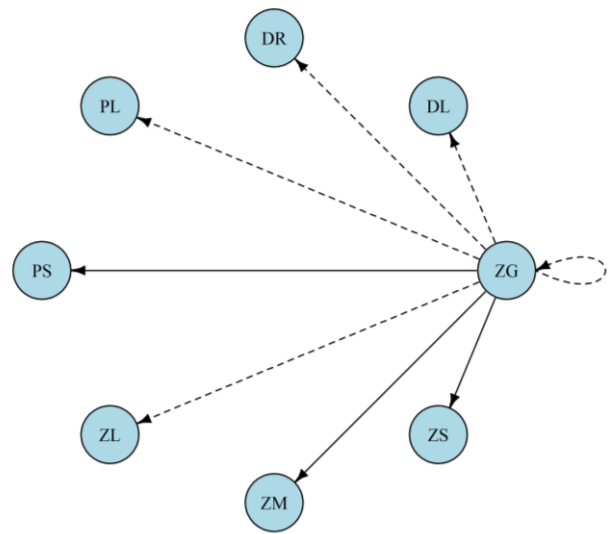
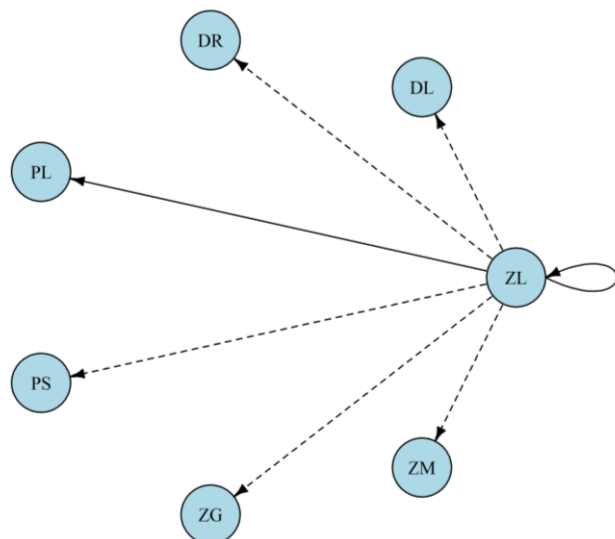


Figure 5. Time series evolution of the initial simulation (dashed line) and calibrated simulation (solid line) of the Bay of
350   Biscay Atlantis nutrients in the 15-year run.

The aim of the second step of the NPZD calibration process was first to obtain the seasonal pattern of small phytoplankton, and second, to obtain reasonable biomass limits according to Fulton et al. (2004). To accomplish both objectives, same initial small and large phytoplankton values (in mgN m^{-3}) were set
355   in all polygons and layers. Based on Hansen et al. (2016), a value of 0.1 mgN m^{-3} per polygon and layer was used. In the next step, the linear mortality rate for small phytoplankton was added and the diet link between microzooplankton and small phytoplankton decreased from 0.31 to 0.005 to avoid the mismatch between the growth and mortality rates.

Finally, the zooplankton groups were calibrated. During this process we found that the cannibalism
360   and the diet links between macrozooplankton and mesozooplankton groups were strongly related to the zooplankton biomass pattern (results not shown). These links were considerably decreased to avoid the collapse of this groups. In the case of cannibalism, a decrease of 10^6 was required for each of the zooplankton group, from 0.01 to $1 \cdot 10^{-7}$ for gelatinous zooplankton, from 0.03 to $3 \cdot 10^{-7}$ for macrozooplankton, from 0.02 to $2 \cdot 10^{-7}$ for mesozooplankton and from 0.02 to $2 \cdot 10^{-7}$ for
365   microzooplankton. The link between macrozooplankton and mesozooplankton was also decreased, from 0.6 to 0.0006. To ensure that macrozooplankton had enough food to eat, a link with microzooplankton was added to its diet. For gelatinous zooplankton the major changes were decreasing the importance of

large phytoplankton and increasing the importance of small phytoplankton and mesozooplankton in its diet (Fig. 6, (a)-(b)). Regarding macrozooplankton, the cannibalism was reduced whilst small phytoplankton diet proportion was increased (Fig. 6, (c)-(d)). Finally, for mesozooplankton and microzooplankton, the cannibalism was also decreased and the links to detritus groups were increased, resulting in refractory and labile detritus becoming the main prey for mesozooplankton and labile detritus for microzooplankton (Fig. 6, (e)-(h)).

(a) Initial network for gelatinous zooplankton

(b) Calibrated network for gelatinous zooplankton

(c) Initial network for macrozooplankton

(d) Calibrated network for macrozooplankton

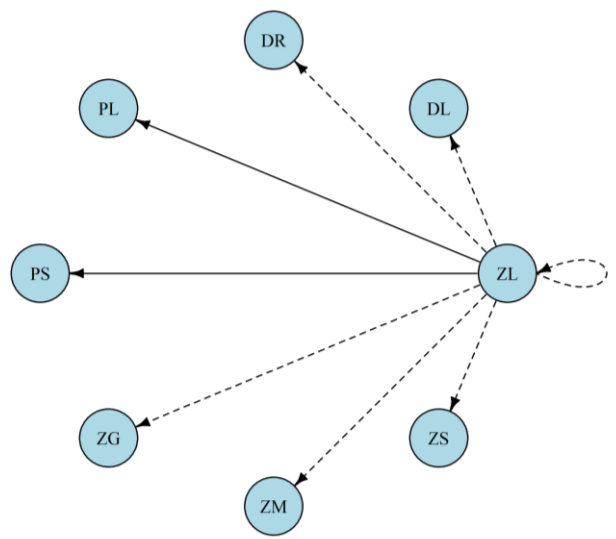
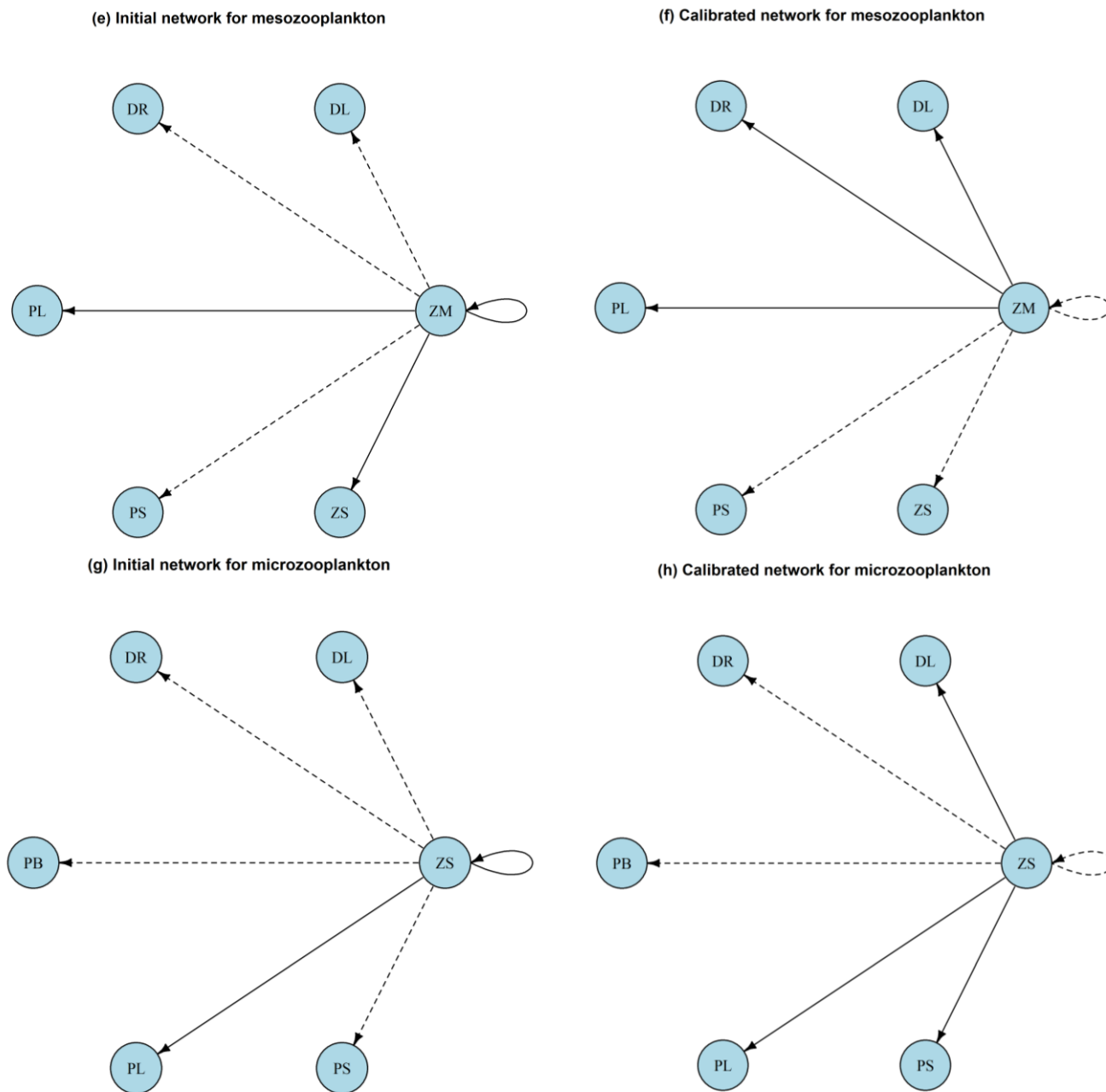



Figure 6. Trophic networks showing the mean proportion of the diet of: (a) non-calibrated and (b) calibrated simulation for gelatinous zooplankton; (c) non-calibrated and (d) calibrated simulation for macrozooplankton; (e) non-calibrated and (f) calibrated simulation for mesozooplankton; (g) non-calibrated and (h) calibrated simulation for microzooplankton; of the Bay of Biscay Atlantis model removing the spin-up period. The dashed line represents diet proportion < 0.1, whilst solid line represents diet proportion ≥ 0.1. Abbreviations: ZG: Gelatinous zooplankton; ZL: Macrozooplankton; ZM: Mesozooplankton; ZS: Microzooplankton; PL: Large phytoplankton; PS: Small phytoplankton; PB: Pelagic bacteria; DL: Labile detritus; DR: Refractory detritus.

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3.2.2. Full system calibration process

Changes in pelagic and benthic invertebrate groups' parameters had a strong impact on all the groups included in the BoB Atlantis model (results not shown). Therefore, we focused the calibration of these groups on keeping them from going extinct (Fig. 3). It is worth mentioning that the cannibalism and the trophic links between the two cephalopod groups had a high impact on the biomass trend of both groups. In the case of squids, a decrease in the cannibalism proportion (from 0.05 to $5 \cdot 10^{-7}$) and the diet proportion between squids and benthic cephalopods (from 0.011 to 0.00011) together with an increase (round up to the next number) in the remaining diet proportions were necessary to avoid the collapse of the group. For benthic cephalopods, the cannibalism proportion value and the diet proportion between benthic and squids were decreased (from 0.0567 to $5.67 \cdot 10^{-7}$ and from 0.0174 to 0.0002 respectively). For both cephalopod groups the resulting diet was similar comparing with the non-calibrated system considering which prey appear in the diet (results not shown).

As observed throughout the NPZD and the pelagic and benthic invertebrate groups calibration processes, the predator-prey links were also important in the calibration process of the fish groups (Section S5, Table S8), specially for sea bass and mackerel, pointing out an important benthic-pelagic coupling. Sea bass diet proportion values were doubled to avoid the collapse of the population, whereas the diet proportions on adult mackerel were considerably decreased (multiplying by 0.001). For both species, the obtained trophic networks were almost identical. The only difference was the decreasing importance of macrozooplankton in the diet of seabass.

Anchovy and sardine were generally distributed in accordance with observations for 2019 but not very precise for 2020 (Fig. 7). Higher abundances were obtained in the model in the South Coast of France, which corresponds to the highest concentration of eggs from BIOMAN survey in 2019. In addition, the lower biomass values of sardine were predicted in the Spanish coast, which are in line with BIOMAN survey in both years. However, the model was not able to differentiate between low and high biomass values of anchovy in the Spanish coast, mainly for 2020 in the middle area of the Spanish coast

430   where there is a high concentration area of eggs from BIOMAN survey in 2019. This result could be

expected due to the seasonal prescribed horizontal movement used for this species.
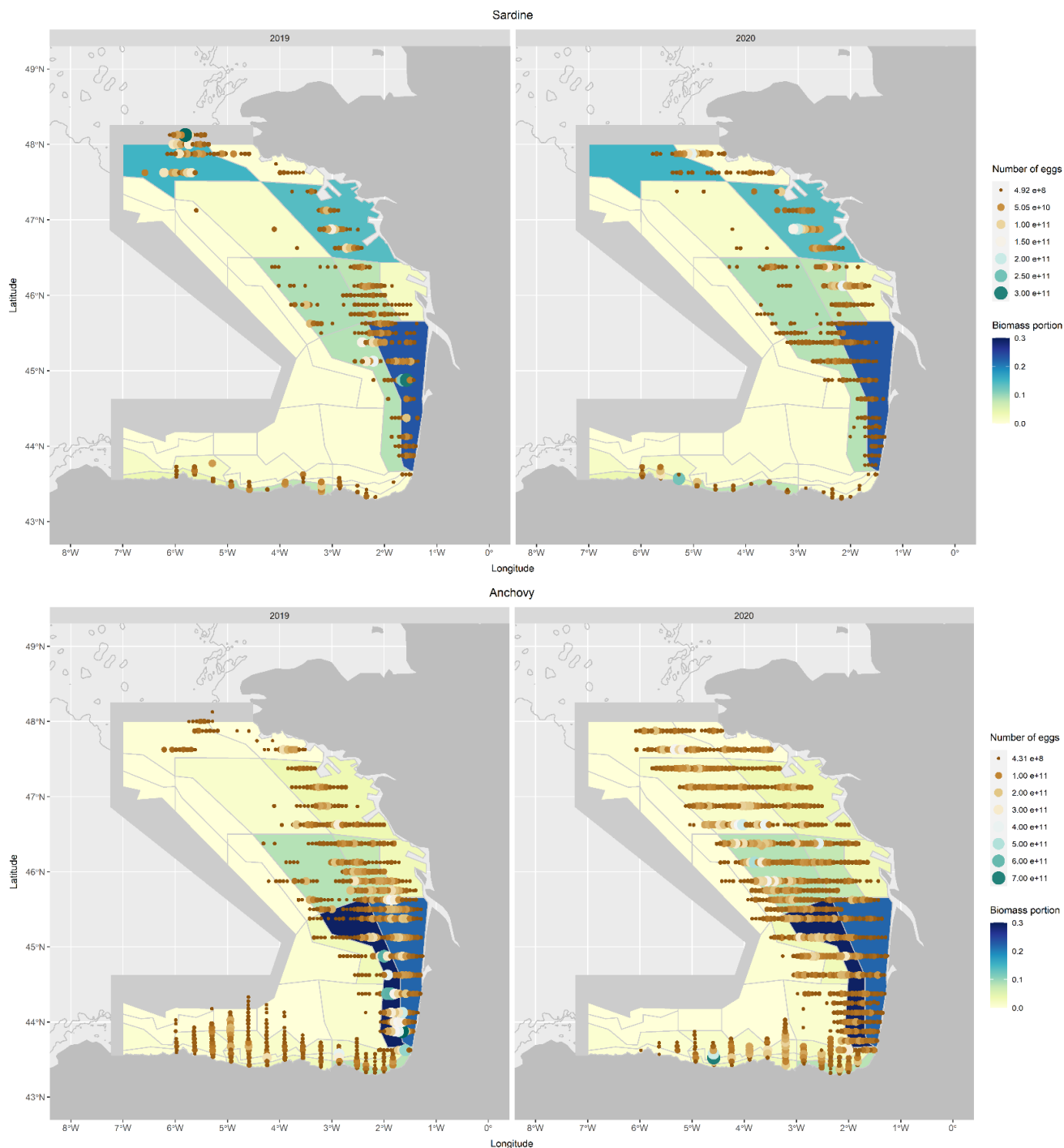
Figure 7. Spatial distribution of anchovy and sardine biomasses forecast by Atlantis in spring and the egg distribution from BIOMAN survey during Mar for 2019 and 2020.

4. Discussion

435 Contrary to other ecosystem models previously developed in the area (Corrales et al., 2022; Lassalle et al., 2011; López López, 2017; Moullec et al., 2017; Sánchez and Olaso, 2004), the present study characterized spatially the structure and functioning of the whole ecosystem in the BoB using an Atlantis model. The Atlantis implementation in the BoB fulfil the objective of simulating a stable and balanced ecosystem after the spin-up period. Hence, all functional groups survived throughout the model run with 440 proper biomass levels in case of pelagic and benthic invertebrates and primary producer functional groups. Fish, elasmobranchs, marine mammals and seabird functional groups were within ±50% of the initial values. In addition, there was a reasonable fit between the model distribution and the observed spatial distribution of anchovy and sardine in accordance with survey data. Therefore, the present study provides a helpful and robust tool for the spatial evaluation of the BoB and for any future ecosystem-445 based management of the area.

4.1. Ecosystem structural characteristics and trophic interactions

The development of the BoB Atlantis model highlighted the strong trophic interactions between benthic-pelagic groups in the system and showed the importance of bottom-up control. In addition, the calibration of the BoB Atlantis model showed: i) the influence of primary producers and pelagic and 450 benthic invertebrate functional groups on the fish species/functional groups; ii) the important role of cannibalism in the dynamic of the species; iii) the need of spatiotemporal distribution validation.

The changes on the parameters of primary producers and pelagic and benthic invertebrate functional groups during the NPZD and the full-system calibration process to obtain biomass levels within ±50% had great impact in the fish species/functional groups, in some cases collapsing the species/functional 455 groups. For zooplankton and cephalopod groups, we found that the cannibalism was the most important characteristic. As stated by Rudolf (2007), the cannibalism is an understudied subject and systematically underrepresented in ecosystem models, with the few studies available only focusing on cannibalism in higher trophic levels, ignoring that cannibalism also occurs at lower trophic levels and could play an important role in the dynamic of species. For zooplankton, seabass and mackerel functional groups where 460 diet link values were changed during the calibration process, similar trophic networks were obtained although with different proportions. These differences could be attributed to the way the diet connection

matrix had to be specified and the way the final realised diet is obtained in Atlantis models. For age-structured groups the four combinations between juvenile and adult must be specified (Audzijonyte et al., 2017). The final realised diet is influenced by the predators' gape size limitations and feeding rates,

465   spatiotemporal co-occurrences and in some cases nutritional quality and spawning status. Therefore, the spatial distribution plays an important role in the calculation of the final diet, showing a need for a spatial distribution validation. However, the spatial distribution validation was only possible for anchovy and sardine. In general, the spatial distribution obtained in the model was consistent with egg distribution from BIOMAN survey, but the model showed poor precision for the year 2020 characterizing the areas

470   where higher egg distribution was observed. This could be attributed to intrinsic features of Atlantis (the way spatial distribution is modelled within the approach), settings during model development and how environmental preferences (i.e., temperature and/or salinity) were defined. In Atlantis, there are multiple options for movement for the species. The most common is prescribed movement, while also density dependent movement is frequently used (Audzijonyte et al., 2017). If prescribed movement is used, the

475   spatial distribution will be determined by the user defined proportion of biomass in each polygon for each quarter of the year and for adult and juvenile stages. If density-dependent movement is used, the spatial distribution will be determined by the food availability in different polygons (Audzijonyte et al., 2017). For the BoB Atlantis model prescribed movement was used and the same horizontal distribution was defined for each quarter and adult/juvenile stage. Therefore, differences with survey data were

480   expected as survey data is more specific in time and adult/juvenile stage. In addition, if a species/functional groups is sensitive to temperature and/or salinity, its spatial distribution will be affected by the values of these environmental variables in a polygon, and the species/functional group could die if none of the polygon have suitable conditions (Audzijonyte et al., 2017). We therefore suggest exploring spatial distribution and following spatial validation in the studies as the biomass of a

485   species/functional group could vary and the movement of the species/functional group be affected by environmental variables.

4.2. Information gaps identified during model development

The most challenging part of building an Atlantis model is data intensity. Atlantis does not have graphical interface or default model parameters (Audzijonyte et al., 2019), the users must decide the

490   formulation to be applied and provide all the parameters, making assumptions necessary. It should be

noted that although the most updated and accurate data was used to parameterize the BoB Atlantis model,

there are still some knowledge gaps and important uncertainty exists. The knowledge gaps are mainly

related to biomass, spatial distribution, age specific estimates and predator-prey interactions. For pelagic

sharks, other large pelagic fishes, mesopelagic fishes and zooplankton functional groups biomass

495   estimates from surveys were not available and, in consequence, information from the EwE model

developed in the area (Corrales et al., 2022) was used. The EwE model covers a smaller area than BoB

Atlantis model does, 120 433 km^2 and 145 970 km^2 respectively. Therefore, a higher biomass values for

these groups should be expected in the BoB Atlantis model. Acoustic and bottom trawl scientific surveys

used to characterize the spatial distribution of the species/functional groups are carried out in different

500   seasons (spring and autumn, respectively), which could have important implications on the

parameterization and characterization of the model as abundance and spatial distribution of

species/functional groups could vary seasonally (Lloret Lloret et al., 2022; Vilas et al., 2020).

Additionally, density-dependent movement was neglected when dictating the spatial distribution of

species/functional groups. The spatial distributions were not related to total biomass trends, the

505   proportion of the biomass provided was interpolated in each polygon for each quarter of the year

(Audzijonyte et al., 2017). The surveys or the information found in the literature do not provide age-

specific biomass, spatial and length-weight data, which makes difficult the parameterization of age-

structured groups. The more refined the data used in the model, the more tailored the model will be to

the system. As such, continued data collection and its improvement is critical to increase data availability

510   and quality, and, therefore, model accuracy. As new information is being generated, the model could be

updated. But any update/change of a model with refined observations would impact the behaviour of

species/functional groups, requiring the model to be re-calibrated. Shannon et al. (2020) updated and re-

fit an existing Ecosim model based on new available data and managed to improve model fits for some

species and emphasized the importance of species-specific functional response studies. Finally, although

515   quantitative diet information on stomach content of fish species from IEO database was precise, diet

information for many organisms (especially for low trophic levels) was scarce. It should be mentioned

that most of the available stomach content diet information does not consider ontogenic changes in the

diet which, therefore, represent an important limitation to define accurately the four values required for each predator-prey combination.

4.3. Concluding remarks

In this paper we have introduced the development of the first calibrated end-to-end Atlantis model for the BoB, with the aim of characterizing spatially the structure of the whole ecosystem. The strong trophic interactions between species/functional groups (benthic-pelagic coupling) included in the BoB Atlantis model suggests that the current single species management scheme in the BoB should be improved to incorporate ecosystem characteristics, in particular from low trophic level organisms dwelling both the pelagic and benthic systems. In addition, some data limitation was identified during the calibration process which confirms the need for a sensitivity analysis (Bracis et al., 2020; Cariboni et al., 2007; Hansen et al., 2019b; Sturludottir et al., 2018).

Future work should include the introduction of fisheries into the model and the following calibration. This will allow to obtain more realistic biomass values for all species/functional groups included in the BoB Atlantis model enabling us to move towards ecosystem-based fisheries management, and spatially assess the BoB ecosystem.

As a general conclusion, the BoB Atlantis model served not only as a tool for the spatial assessment of the BoB ecosystem, but also to identify data-poor areas which need more information and research. This was particular the case for spatial distributions of the species/functional groups, diet interactions considering juvenile and adult stages and biomass and biological parameters per age.

Code availability

Atlantis ecosystem modelling software is free of charge and available for everyone. Due to CSIRO licensing requirements, new users must register to access the code. To register please send an email to atlantis@csiro.au with your name, institution and one sentence summary about the intended use of the model. This information is required to filter out fake registrations (bots), and to plan future model development and user support. For further details see https ://github.com/ Atlantis-Ecosystem-Model/ Atlantis_example_and_instructions.

Data availability

545   The datasets generated for this study are available on an official request to the corresponding author.

Author contribution

ALGZ, XC and EA prepared the data to parameterize the BoB Atlantis model; ALGZ, CH, IQ, XC and EA parameterized the model; ALGZ and CH calibrated the model; ALGZ wrote the original draft of the article; ALGZ, CH, XC, IQ, IP and EA reviewed and edited the manuscript.

550   **Declaration of competing interest**

The authors declare that they have no conflict of interest.

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