



Modelling the cumulative spatial–temporal effects of environmental drivers and fishing in a NW Mediterranean marine ecosystem



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ABSTRACT

To realistically predict spatial–temporal dynamics of species in marine ecosystems it is essential to consider environmental conditions in conjunction with human activities and food web dynamics. In this study, we used *Ecospace*, the spatial–temporal dynamic module of *Ecopath with Ecosim* (*EwE*) food web model, to drive a spatially explicit marine food web model representing the Southern Catalan Sea (NW Mediterranean) with various environmental drivers and with fishing. We then evaluated the individual and joint effects of environmental conditions and fishing in various compartments of the food web. First we used a previously developed *EwE* model fitted to time series of data from 1978 to 2010 as a baseline configuration. The model included 40 functional groups and four fishing fleets. We first ran the original *Ecospace* spatial–temporal dynamic model using the original habitat configuration, in addition to fishing, and we predicted species distributions and abundances. Afterwards, we ran the new habitat foraging capacity model using the most important environmental drivers linked with the Ebro River delta dynamics (salinity, temperature, and primary production), in addition to depth, substrate and fishing, and we compared results with those from the original implementation of *Ecospace*. Three commercial species, European hake (*Merluccius merluccius*), anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), were used to analyse results. Species distributions more closely matched the empirical information available from the study area when using the new habitat capacity model. Results suggested that the historical impacts of fishing and environmental conditions on the biomass and distributions of hake, anchovy and sardine were not additive, but mainly cumulative with a synergistic or antagonistic effect. Fishing had the highest impact on spatial modelling results while the spatial distribution of primary producers and depth followed in importance. This study contributes to the development of more reliable predictions of regional change in marine ecosystems of the Mediterranean Sea.

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1. Introduction

Biodiversity, natural resources, and ecosystem services change in response to human stressors, such as climate change and fishing activities that often have cumulative effects (Crain et al., 2008; Darling and Côté, 2008; Halpern et al., 2008). The need to consider changes in the environment as well as human activities when analysing and managing marine ecosystems highlights the necessity to perform integrated analyses (Link, 2011). Since the productivity of marine resources depends on the ecological state of

communities and ecosystems, and on external drivers, the dynamics of target species in conjunction with the dynamics of non-target organisms, trophic relationships and energy flows, environmental drivers and human impacts have to be considered to manage marine resources properly (Christensen et al., 2011).

In the last decade, the scientific community has made substantial progress in the identification and quantification of multiple human threats that impact marine diversity, habitats and ecosystems (Jackson et al., 2001; Lotze et al., 2006; Halpern et al., 2008). Currently, there is an increasing knowledge on the quantification of these multiple drivers, also in the Mediterranean Sea (Coll et al., 2012; Micheli et al., 2013). However, the way these drivers may interact and combine to impact patterns of marine ecosystems is not well known (Crain et al., 2008; Darling and Côté, 2008).

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Multiple drivers may interact and their effects may cause impacts that accumulate in an additive way (thus the sum of their individual impacts is equal to the total impact) or may act synergistically or antagonistically (when the sum of individual impacts are greater or lower than the separated effects, respectively) at different ecological levels (Mackinson et al., 2009; Ainsworth et al., 2011). Despite their importance, a comprehensive understanding of these impacts and their interactions is mostly lacking. Therefore, there is a growing need to develop and use novel methodologies of data integration, assimilation and modelling human impacts at different scales, taking into account spatial–temporal dynamics (Coll et al., 2013a).

Species distribution models and ecosystem models are two methodologies that are developed to study the spatial and temporal dynamics of marine resources and ecosystems (Guisan and Zimmermann, 2000; Fulton, 2010). The main aim of statistical modelling is to use the information about where a species occurs and the relationship with associated environmental conditions to predict how likely the species is to occur in non-sampled locations. Different techniques to apply species distribution models (SDM) exist and have been widely applied to the marine environment (e.g., Kaschner et al., 2001; Jones et al., 2012), including the Mediterranean Sea (e.g., Morfin et al., 2012; Pennino et al., 2013; Saraux et al., 2014). Despite their popularity, it is known that environmental drivers alone may not be sufficient to account for species distributions (Navarro et al., 2015). Other ecological processes, including trophic interactions (such as competition, predation, and facilitation), behavioural parameters, and population dynamics may affect the spatial arrangement of a species, in addition to human activities.

These processes can be considered in process-based oriented modelling, like in food web models such as *Ecopath with Ecosim* (*EwE*) approach (Christensen and Walters, 2004). *EwE* is a freely available software and approach that allows building food web models by describing the ecosystem by means of energy flows between functional groups, each representing a species, a subgroup of a species (e.g., juveniles and adults) or a group of species that have functional and ecological similarities. The functional groups can be set to represent consumers and primary producers, as well as non-living groups (e.g., detritus).

EwE consists of three main linked routines that have been developed over the last three decades: *Ecopath*, *Ecosim* and *Ecospace*. *Ecopath* is the mass-balance routine that allows building of spatially and time-averaged models of the trophic web (Polovina, 1984; Christensen and Pauly, 1992), and which serves to parameterize the dynamic modules of *EwE*; *Ecosim* is the time dynamic routine (Walters et al., 1997, 2000); and *Ecospace* is the spatial–temporal dynamic module that allows representing temporal and spatial 2D dynamics of trophic web components (Walters et al., 1999, 2010). Critical overviews of *EwE* approach and descriptions of the recent developments are available in the literature (Christensen and Walters, 2004; Steenbeek et al., 2014, 2016; Ainsworth and Walters, 2015; Coll et al., 2015a; Heymans et al., 2016).

Ecospace has been widely applied to quantify the spatial impact of fisheries on marine species (Christensen et al., 2003, 2014a, 2015), to analyse the impact of management scenarios such as the establishment of marine protected areas, and to assess the correlation of spatial distributions of marine species and fishing effort (Walters, 2000; Martell et al., 2005; Fouzai et al., 2012). *Ecospace* can also be used to develop spatial optimization routines (Christensen et al., 2009) and to assess the impact of climate change on marine ecosystems by linking *Ecospace* with low trophic level models (Fulton, 2011) or by driving *Ecospace* directly with external spatial–temporal data (Steenbeek et al., 2013, 2016).

Despite their capabilities, available tools offered limited capacity to model cumulative impacts of stressors and

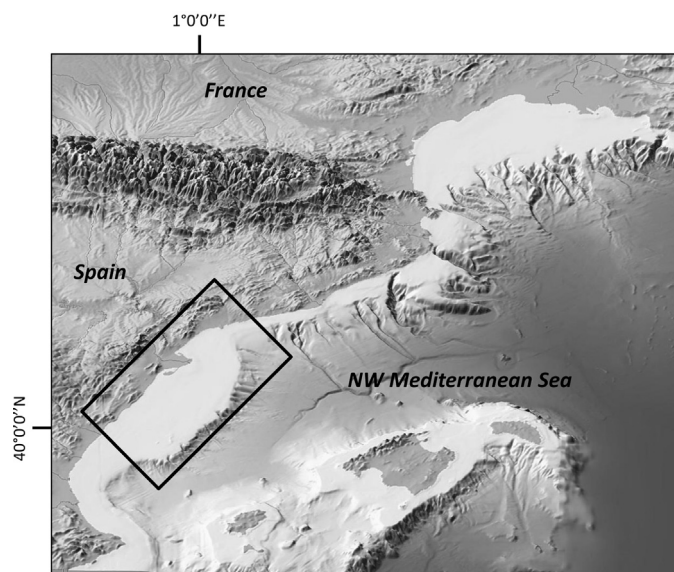


Fig. 1. Study area located within the Balearic Sea, NW Mediterranean Sea.

produce integrated assessments that take both food web dynamics and spatial–temporal environmental and human variability into account (Steenbeek et al., 2013). To overcome some limitations, the habitat foraging capacity model was recently added to *Ecospace* (Christensen et al., 2014b). This new development offers the ability to spatially drive foraging capacity of species from the cumulative effects of multiple physical, oceanographic, and environmental conditions (such as depth, bottom type, temperature, salinity, oxygen concentrations and primary production). The habitat foraging capacity model runs in *Ecospace* in conjunction with the food web and fisheries dynamics. This development, in combination with the spatial–temporal framework module (Steenbeek et al., 2013), bridged the gap between envelope environmental models and classic food web models (Christensen et al., 2014b, 2015).

In this study we applied the new habitat foraging capacity model (Christensen et al., 2014b) to study the distribution of three commercially important fish species (European hake *Merluccius merluccius*, sardine *Sardina pilchardus* and anchovy *Engraulis encrasicolus*) of the Southern Catalan Sea (NW Mediterranean Sea, Fig. 1) and evaluate the combined effects of environmental drivers (primary production, salinity, temperature, depth and substrate), in addition to fishing, and food web structure in their dynamics.

The NW Mediterranean Sea is one of the most important fishing grounds of the Mediterranean Sea, particularly the region surrounding the Ebro Delta area (Coll et al., 2012). Important environmental parameters drive the dynamics of commercial species in the area, such as small pelagic fish and important demersal species (Lloret et al., 2004; Palomera et al., 2005, 2007; Martín et al., 2008; Ospina-Alvarez et al., 2015). Previous studies looking at the temporal dynamics of marine resources identified that both environmental factors, human activities and the structure of the food web were key elements to predict ecosystem dynamics (Coll et al., 2006, 2008; Mackinson et al., 2009).

2. Materials and methods

2.1. Study area

Our study area was located on the Catalan Sea (within the Balearic Sea, NW Mediterranean Sea, Fig. 1). The NW Mediterranean Sea is an area of relatively high productivity due to a combined

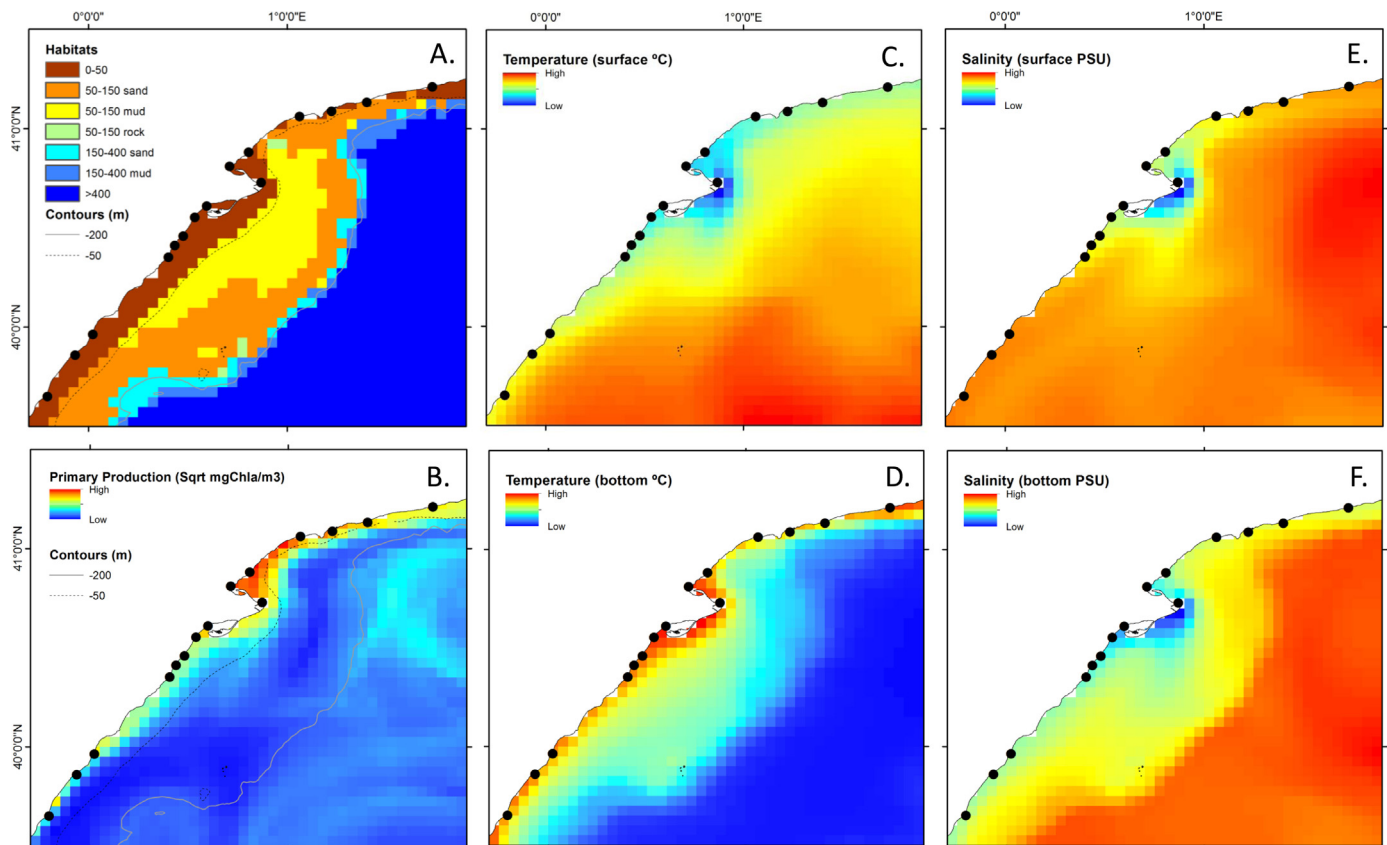


Fig. 2. Spatial distributions of (a) habitats, (b) primary production, (c) surface temperature, (d) bottom temperature, (e) surface salinity and (f) bottom salinity data used to drive the Southern Catalan Sea *Ecospace* model.

effect of the Northern current and the runoff of the Ebro and Rhone Rivers (Estrada, 1996; Bosc et al., 2004). In the northern area, the continental shelf is narrower, with the Northern current flowing south-westwards along the continental slope, towards the wider continental shelf surrounding the Ebro Delta River. The area is an important fishing ground for small pelagic fish (Palomera et al., 2007) and demersal mesopredators (Leonart and Maynou, 2003). It is also important for marine predatory species at risk, such as marine mammals and seabirds (Coll et al., 2015b).

2.2. The food web EwE model

The ecological modelling approach *Ecopath with Ecosim*, *EwE* (Christensen and Walters, 2004; Christensen et al., 2008) was used to model the study area. A description and the main equations of the model are summarized in Appendix A.

In this study, we used an available ecosystem model developed with *Ecopath* representing the South Catalan Sea in 1978 that had been previously fitted to time series of data from 1978 to 2010 using the temporal dynamic model *Ecosim* (Coll et al., 2008, 2013b). The model was expressed in terms of biomass as $t\ km^2$, and production and catch as $t\ km^2\ year^{-1}$. The model included 40 functional groups and four fishing fleets (bottom trawling, purse seine, long lining and tuna fishing), covering an area of 5000 km^2 with depths from 50 to 400 m (Coll et al., 2006). The functional groups included primary and secondary producers, from phytoplankton to large predatory species. One commercial species, European hake (*M. merluccius*), was represented in two age classes, juvenile hake (<2 years old or <25 cm) and adult hake (≥ 2 years old or ≥ 25 cm) (Coll et al., 2006).

To fit the model to data a series of fishing effort and fishing mortality time series, in addition to time series of a primary production anomaly, were used to drive the dynamics of the food web. Biomass and catch time series of commercial groups were used to compare observed versus predicted results (Coll et al., 2008, 2013b).

2.2.1. The Ecospace original model

The *Ecospace* spatial-temporal original model (hereafter *Ecospace* original, or EO) had been previously developed in the study area to analyse the dynamics of commercial species (Vargiu, 2008; Vargiu et al., 2009). In the original *Ecospace* model (Fig. 2a), the definition of a base map of habitat information was used by integrating depth strata and bottom type (Díaz et al., 1990).

Species preferences were assigned to these habitat types based on the biology and ecology of the species included in each functional group of the ecosystem model, such as their depth distributions and their preferred sediment type (Table S1) (Riedl, 1983; Whitehead et al., 1986; Quignard and Tomasini, 2000; FAO, 2009; Jereb and Roper, 2010; Coll et al., 2012; Froese and Pauly, 2013; Palomares and Pauly, 2013).

In addition, the model required (i) the dispersal rate of each functional group in 'preferred' habitats, (ii) the relative dispersal rate in 'non-preferred' habitats, and (iii) the relative feeding rate in non-preferred habitat by functional group (Table S2) (Vargiu, 2008; Vargiu et al., 2009), in addition to fishing information (Table S3) and the spatial distribution of primary production (Fig. 2b). These parameters and the development of the modelling application were done following the procedure of Fouzai et al. (2012) applied to the North-Central Adriatic Sea.

2.2.2. The habitat foraging capacity model

The *Ecospace* original model (EO) was limited in the way habitat was represented as a fixed parameter, providing limited support to represent changes in the quality and extent of habitats (Christensen et al., 2014b). The EO assumed homogenous conditions within each spatial cell, and local, but possibly relevant variations within cells, could not be represented. A way forward was to define a continuous relative habitat capacity for each functional group in each cell (Christensen et al., 2014b). In the new habitat foraging capacity model (Christensen et al., 2014b) (hereafter capacity model, or CM), the proportion of a cell that a species (or functional group) can use is a continuous value from 0 to 1, and allows inclusion of as many environmental drivers as needed to define the foraging capacity of a cell for a species.

In this study, we used the new CM to evaluate the combined effects of environmental conditions and fishing, in the ecosystem dynamics of the Southern Catalan Sea. We included surface and bottom salinity and temperature as main environmental drivers (Fig. 2c–f) linked to the distribution of adult and juvenile European hake, sardine and anchovy, in addition to primary production and depth (Figs. 1 and 2b). The substrate types information (such as mud, sand, rock and coarse mixed sediments) (Fig. 2a) was applied to define hake habitat capacity, too.

Key environmental drivers (salinity and temperature), as well as primary production (deduced from phytoplankton biomass through Chlorophyll-a calculation), originated from a regional application of the ROMS model (www.myroms.org, Shchepetkin

and McWilliams, 2005) coupled to a biogeochemical nitrogen-based plankton model (Fennel et al., 2006). This coupled model implementation was tested in the Western Mediterranean (Alboran Sea) in previous work (Macias et al., 2011).

The ROMS implementation used here was adapted to the study area (Catalan Sea) with a grid of 2 km × 2 km resolution and a vertical resolution of 40 levels. Both boundary and atmospheric forcing conditions were climatologies. The boundary conditions were obtained from the NEMO model, which is available from <http://www.nemo-ocean.eu>, and the simulations used in this work were reported in Adani et al. (2011). NEMO output was interpolated to the ROMS grid and imposed to a sponge layer of 10 horizontal grid points with a nudging relaxation time of 30 days. For the biological variables, boundary conditions were set-up as in Fennel et al. (2006). The meteorological forcing climatology was calculated from the European Center of Medium Weather Forecast (hereafter ECMWF) data, derived from ERA-40 reanalysis for air temperature, short wave radiation, long wave radiation, precipitation, cloud cover and salt flux. For pressure at the surface, we used the ECMWF Era-Interim reanalysis. QuickScat blind data was used for wind forcing (both zonal and meridional). We ran the model using both boundary conditions and atmospheric forcing climatologies to obtain a stable initial state during eight years. After this spin-up period, we used the ninth year as the year of study with the same climatological conditions used for the spin-up period and results were used as averaged climatology conditions from 1978 to 2010.

Table 1
Ecological modelling simulations developed in the study. The table highlights environmental drivers and fishing included in the simulations.

Simulations	Ecosim fitting		Ecospace Original - EO			Ecospace Habitat Capacity - CM			
	PP anomaly	F	PP spatial	F	H	PP spatial	F	H	FR
1 <i>Baseline_Ecosim</i>	X	X							
2 <i>Spatial_EO</i>			X	X	X				
3 <i>Spatial_CM</i>						X	X	X	X
4 <i>Spatial_CM-NF</i>						X		X	X
5 <i>Spatial_CM-NPP</i>							X	X	X
6 <i>Spatial_CM_ND</i>						X	X	X	T, S
7 <i>Spatial_CM_NT</i>						X	X	X	D, S
8 <i>Spatial_CM_NS</i>						X	X	X	D, T

PP: primary production; F: fishing; H: habitat; FR: foraging response for hake, anchovy and sardine; D: depth, T: temperature; S: Salinity.

The spatial pattern of primary production was used to drive the dynamics of the phytoplankton group, as in the EO model. The environmental envelopes needed to parameterized the functional responses in the CM (Christensen et al., 2014b) linking the environmental drivers with hake, anchovy and sardine were obtained from the literature (Riedl, 1983; Whitehead et al., 1986; Quignard and Tomasini, 2000; Palomera et al., 2007; FAO, 2009; Jereb and Roper, 2010; Coll et al., 2012; Froese and Pauly, 2013; Giannoulaki et al., 2013; Kaschner et al., 2013; Palomares and Pauly, 2013) (Fig. S1). For the rest of the functional groups, we used the habitat foraging settings and the original configuration of habitats as in EO was maintained (Table S1).

2.3. Food web simulations and analyses

Using the original *Ecosim* run and both EO and CM spatial *Ecospace* configurations, a series of simulations were run and compared (Table 1):

- (1) **Baseline_Ecosim**: Results from the original *Ecosim* model fitted to time series from 1978 to 2010 (Coll et al., 2008, 2009) were used as a baseline (these results do not include spatial information). This simulation included the time series of a primary production anomaly resulting from the fitting.
- (2) **Spatial_EO**: The *Ecospace* original model (EO) was used to run a first spatial-temporal scenario to predict species distributions

and abundances from 1978 to 2010. The original configurations of habitats and fishing (Tables S1 and S3 and Fig. 2a) from 1978 to 2010 were included as main drivers of the model, as well as the spatial pattern of primary production to drive phytoplankton spatial dynamics (Fig. 2b).

- (3) **Spatial_CM**: We used the *Ecospace* CM (Christensen et al., 2014b) to run a third scenario from 1978 to 2010 adding the environmental layers of salinity, temperature and depth (Fig. 2c–f), in addition to substrate type for hake (Fig. 2a), to drive the foraging capacity of hake, sardine and anchovy functional groups in the model. Fishing and primary production were also included as in simulation 2.
- (4) **Spatial_CM-NF**: A fourth scenario removing fishing from 1978 to 2010, but using the environmental layers of simulation 3, was run to exclude the effect of fishing.
- (5) **Spatial_CM-NPP**: A fifth scenario removing the layer of primary production (Fig. 2b) from simulation 3 was run from 1978 to 2010 to exclude the effect of primary production spatial dynamics.

We then assessed the individual influence of changes associated with environmental drivers by running CM simulations with one environmental parameter at a time:

- (6) **Spatial_CM-ND**: The depth layer was removed as a driver from the HC model to hake, anchovy and sardine from simulation 3.

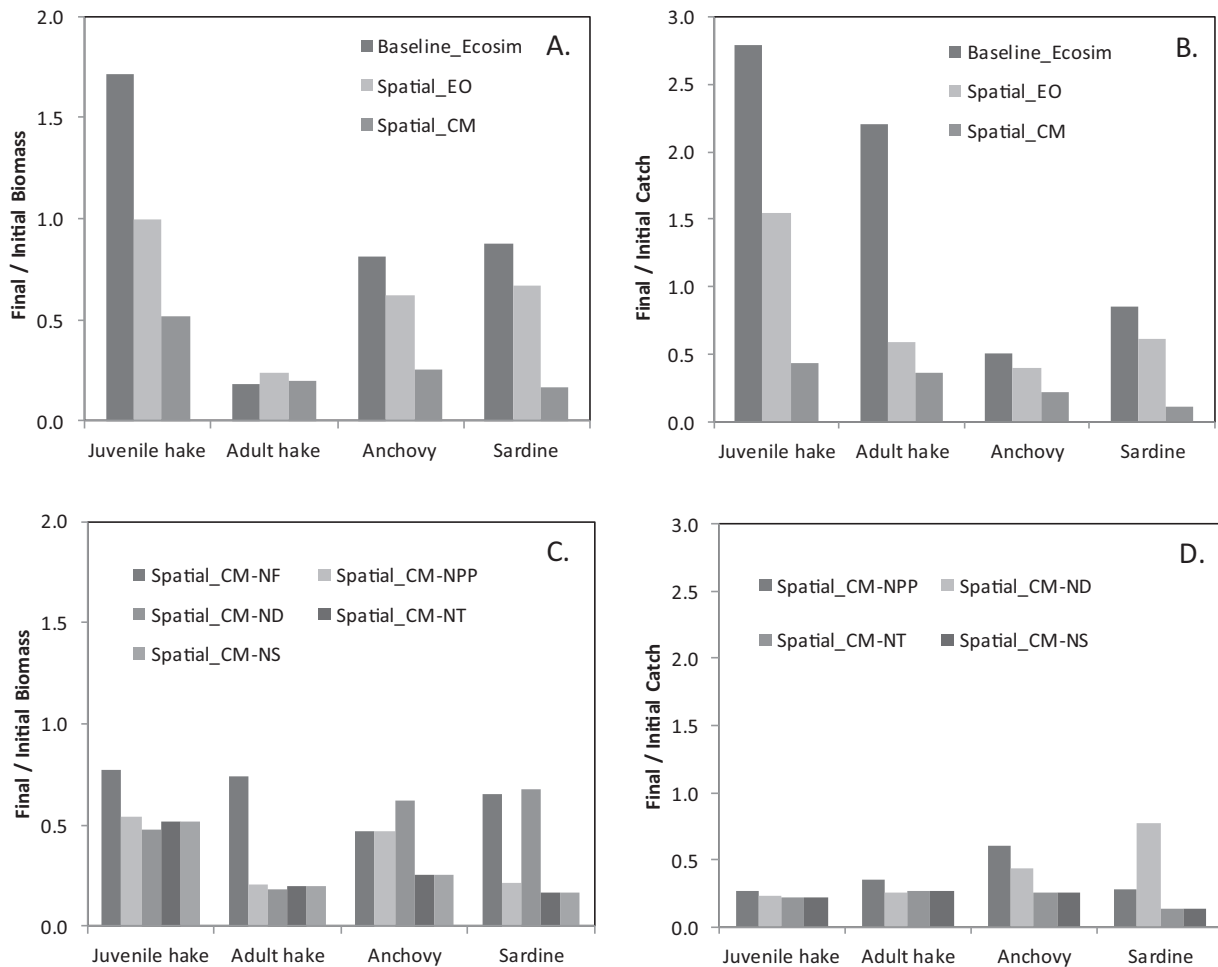


Fig. 3. Biomass and catch (final/initial ratios) using an average of the final five years (2006–2010) with the initial five years (1978–1982) of results from the simulations) of juvenile and adult hake, anchovy and sardine resulting from the different modelling simulations (Table 1), (a, b) *Baseline_Ecosim*, *Spatial_EO* and *Spatial_CM* configurations, and (c, d) *Spatial_CM-NF*, *Spatial_CM-NPP*, *Spatial_CM-ND*, *Spatial_CM-NT*, and *Spatial_CM-NS*. A value >1 (over the black horizontal line) shows a positive increase of the ratio.

- (7) **Spatial_CM-NT**: The temperature layer was removed as a driver from the HC model to hake, anchovy and sardine from simulation 3.
- (8) **Spatial_CM-NS**: The salinity layer was removed as a driver from the HC model to anchovy and sardine from simulation 3.

Comparing simulations 2 and 3 we assessed the role of the different configuration of *Ecospace* (EO versus CM) in our results. Comparing simulations 3 and 4 allowed us to assess the role of fishing, while comparing simulations 3 and 5 we assessed the role of spatial information on primary production. Comparing simulation 3 with 6, 7 or 8 we assessed the role of individual environmental drivers.

We ran all the simulations from 1978 to 2010 and we compared results of species distributions and abundances. Results were compared as non-spatial (*Ecosim*) and spatially explicit (*Ecospace*) time series for biomass for hake, anchovy and sardine. Spatial results from 1978 analysed corresponded to the end of the first year, thus the temporal (*Ecosim*) or spatial-temporal (*Ecospace*) models had been running for a full year.

Ecological indicators using biomass and catch data were also computed. Specifically, ratios of final versus initial total biomass and catch, and biomass and catch of fish, invertebrates, demersal groups, pelagic groups and predators were analysed, in addition with time series of predicted biomasses.

3. Results

3.1. Comparison of *Ecospace* original with the capacity model

As a general trend, the overall biomasses and catches results from the implementation of the spatial dimension showed relevant decreases compared to the baseline *Ecosim*. Moreover the biomass and catch results for the *Ecospace* original model (*Spatial_EO*) were more optimistic than the ones resulting from the new habitat capacity model (*Spatial_CM*). Under *Spatial_EO*, the biomass of adult hake, anchovy and sardine showed a decrease of 77%, 38% and 33%, respectively, from 1978 to 2010 (Fig. 3a and Table 2). Under the *Spatial_CM*, these three commercial species showed a decrease of 80%, 75% and 83%, respectively (Fig. 3a). On the contrary, the biomass of juvenile hake showed a substantial increase (72%) under the *Baseline_Ecosim*, showed hardly any decline (1%) under *Spatial_EO* and showed a decline of 48% under *Spatial_CM*.

In general, catches under the *Baseline_Ecosim* were higher than under the *Spatial_EO* scenario, and those were higher than the ones predicted under the *Spatial_CM* scenario (Fig. 3b). Thus, the decreases of catch over time were most pronounced under the latest scenario. The catch of both juvenile and adult hake had increased under the *Baseline_Ecosim* scenario (by 178% and 121%, respectively), but declined under the other two scenarios, with the exception of juvenile hake under the *Spatial_EO* (Fig. 3b).

The spatial distribution of adult and juvenile hake, anchovy and sardine was substantially different under the *Spatial_CM* scenario compared to the original spatial configuration (*Spatial_EO*) (Fig. 4 and Fig. S2, showing results for 1978 under *Spatial_EO* configuration). Under the *Spatial_CM* scenario, adult and juvenile hake distributions showed higher concentration of biomass in specific areas of the continental shelf and slope (Fig. 4a and b shows results of *Spatial_CM* in 1978, Fig. 5a and b represents results of *Spatial_CM* over *Spatial_EO*). For adult hake, the distributions showed higher concentrations in the deeper part of the shelf through the whole area, while juvenile hake was concentrated in the northern part of the shelf and upper slope. The distribution of anchovy was also higher under the *Spatial_CM* scenario in the continental platform (Figs. 4c and 5c), while sardine's distribution was higher in the

Table 2

Biomass changes (%) of juvenile hake, adult hake, anchovy and sardine comparing an average of the final five years (2006–2010) with the initial five years (1978–1982) of results from the simulations described in Table 1. Results of the new habitat foraging capacity model simulation (*Spatial_CM*) are highlighted in grey for comparison purposes.

	Biomass change (% Bf/Bi)			
	Juvenile hake	Adult hake	Anchovy	Sardine
<i>Baseline_Ecosim</i>	72	-82	-19	-13
<i>Spatial_EO</i>	-1	-77	-38	-33
<i>Spatial_CM</i>	-48	-80	-75	-83
<i>Spatial_CM-NF</i>	-23	-26	-53	-35
<i>Spatial_CM-NPP</i>	-46	-79	-53	-79
<i>Spatial_CM-ND</i>	-52	-82	-38	-33
<i>Spatial_CM-NT</i>	-49	-80	-75	-83
<i>Spatial_CM-NS</i>	-48	-80	-75	-84

coastal area and some part of the continental shelf if compared with the distribution from the original configuration (*Spatial_EO*) (Figs. 4d and 5d).

3.2. Spatial-temporal dynamics of marine species

The *Baseline_Ecosim* temporal simulation showed a temporal biomass decline of adult hake (Fig. 6b, 82% comparing the first and last five years of the simulation), anchovy (Fig. 6c, 19%) and sardine (Fig. 6d, 13%) (Table 2). Juvenile hake showed an increase (72%) (Fig. 6a). However, at the end of the spatial-temporal simulations, the biomass of the three commercial species had declined under both *Spatial_EO* and *Spatial_CM* scenarios in comparison with the *Baseline_Ecosim*, thus results were substantially different when moving towards a spatial-temporal modelling approach (Fig. 6 and Table 2).

In the case of adult hake biomass, both under the *Spatial_EO* and *Spatial_CM* configurations, the total biomass of the species declined with time (77% and 80%, respectively), but less than under the baseline scenario (Figs. 3a and 6b). The juvenile hake biomass dynamics under the *Spatial_EO* configuration showed an increase of biomass during the 1990s and after a decline, while under the *Spatial_CM* configuration juvenile hake showed a decline with time of 48% (Figs. 3a and 6a). Anchovy biomass declined more strongly (by 75%) under *Spatial_CM* configuration with time (Figs. 3a and 6c), while sardine showed a decline in both *Spatial_EO* and *Spatial_CM* configuration but the latter was stronger as well, with a decline of 83% (Figs. 3a and 6d).

At the end of the simulations (in year 2010), the distribution of adult hake, anchovy and sardine had changed substantially (Fig. 7)

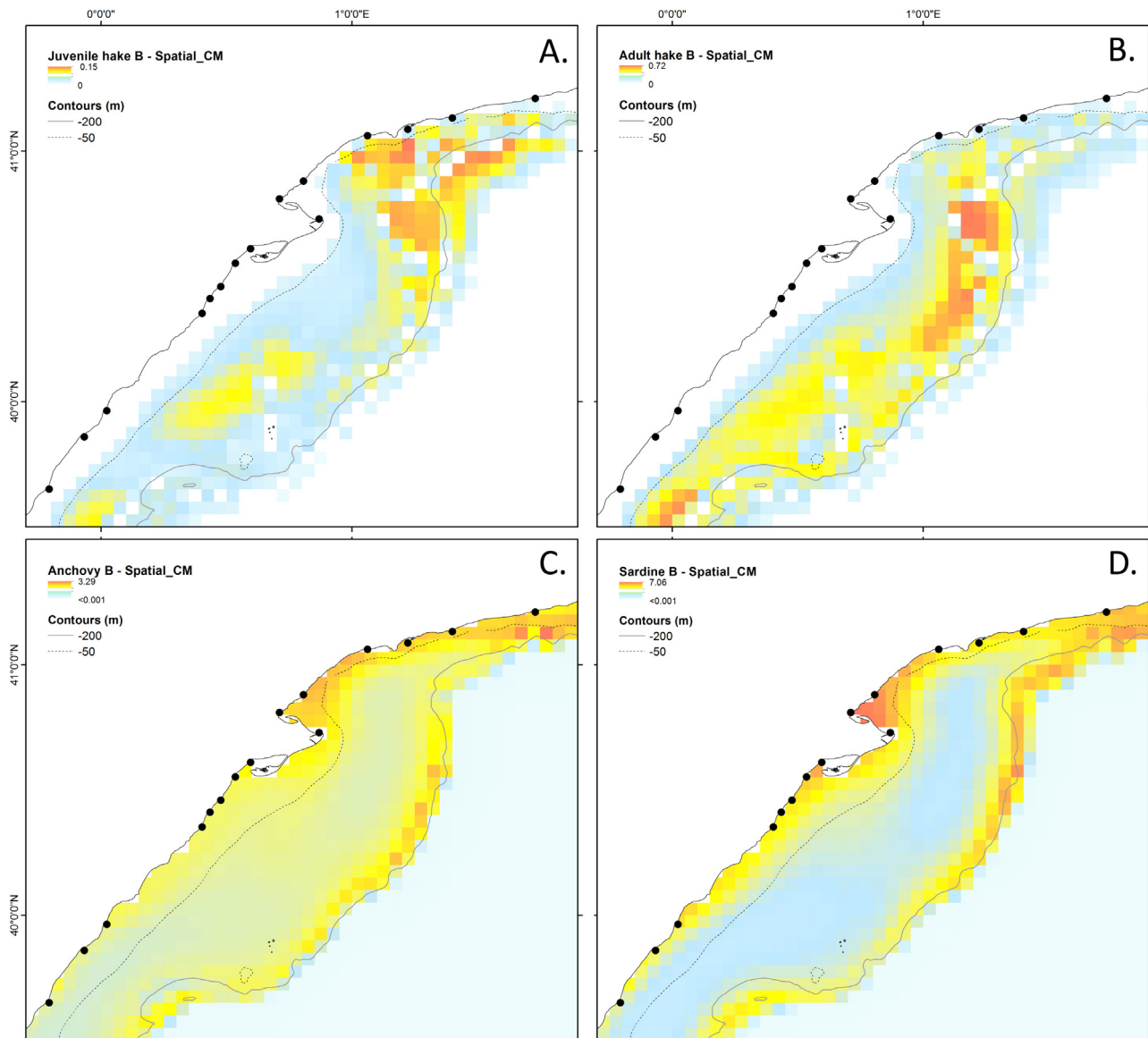


Fig. 4. Biomass distributions (t) of (a) juvenile hake, (b) adult hake, (c) anchovy, and (d) sardine in 1978 under the *Spatial_CM* configuration.

if compared with that from 1978 (Fig. 4). Adult hake biomass was still concentrated in areas of the continental shelf but those concentrations were lower than 30 years ago (Fig. 7b). Anchovy and sardine concentrations had diminished though the area and were highest at the end of the continental shelf (Fig. 7c and d). On the contrary, juvenile hake had maintained its main distribution (Fig. 7a), showing concentrations in various areas. These distributions were substantially different from the distributions of the habitat capacity obtained from the model that shows potential suitable habitat for the studied species before the food web dynamics and fishing impacts have taken place (Fig. S3).

3.3. Ecosystem changes over time

Ecological indicators based on biomass results showed overall higher values for *Spatial_CM* scenario, followed by the *Spatial_EO* scenario, and were the lowest under *Baseline_Ecosim* (Fig. 8a). Under the *Baseline_Ecosim* simulation, total biomass had increased by 50%, the biomass of demersal invertebrates had increased by 40% and the biomass of demersal organisms had increased by 127%, while

fish biomass and predators' biomass had declined by 1% and 19%, respectively (Table 3).

When going spatial (*Spatial_EO* and *Spatial_CM* simulations), results showed higher increases (of 10 times) on the demersal (mostly non-commercial) invertebrates and demersal organisms compared to the baseline (Table 3). This was translated in higher total biomass under *Spatial_EO* and *Spatial_CM* scenarios. Biomass of fish, pelagic organisms and predators also showed increases under the spatial scenarios.

Ecological indicators based on catch results from the *Baseline_Ecosim* scenario were quite different from the other two spatial ones as well (Fig. 8b), reflecting the changes in biomasses.

3.4. Individual and joint effects of drivers

When removing fishing as a driver of the ecosystem model (*Spatial_CM-NF*), results showed clear differences compared with the *Spatial_CM* configuration, with higher biomasses of juvenile and adult hake, of anchovy and of sardine (Fig. 3a and c and Table 2). Under this scenario, the biomass of juvenile and adult

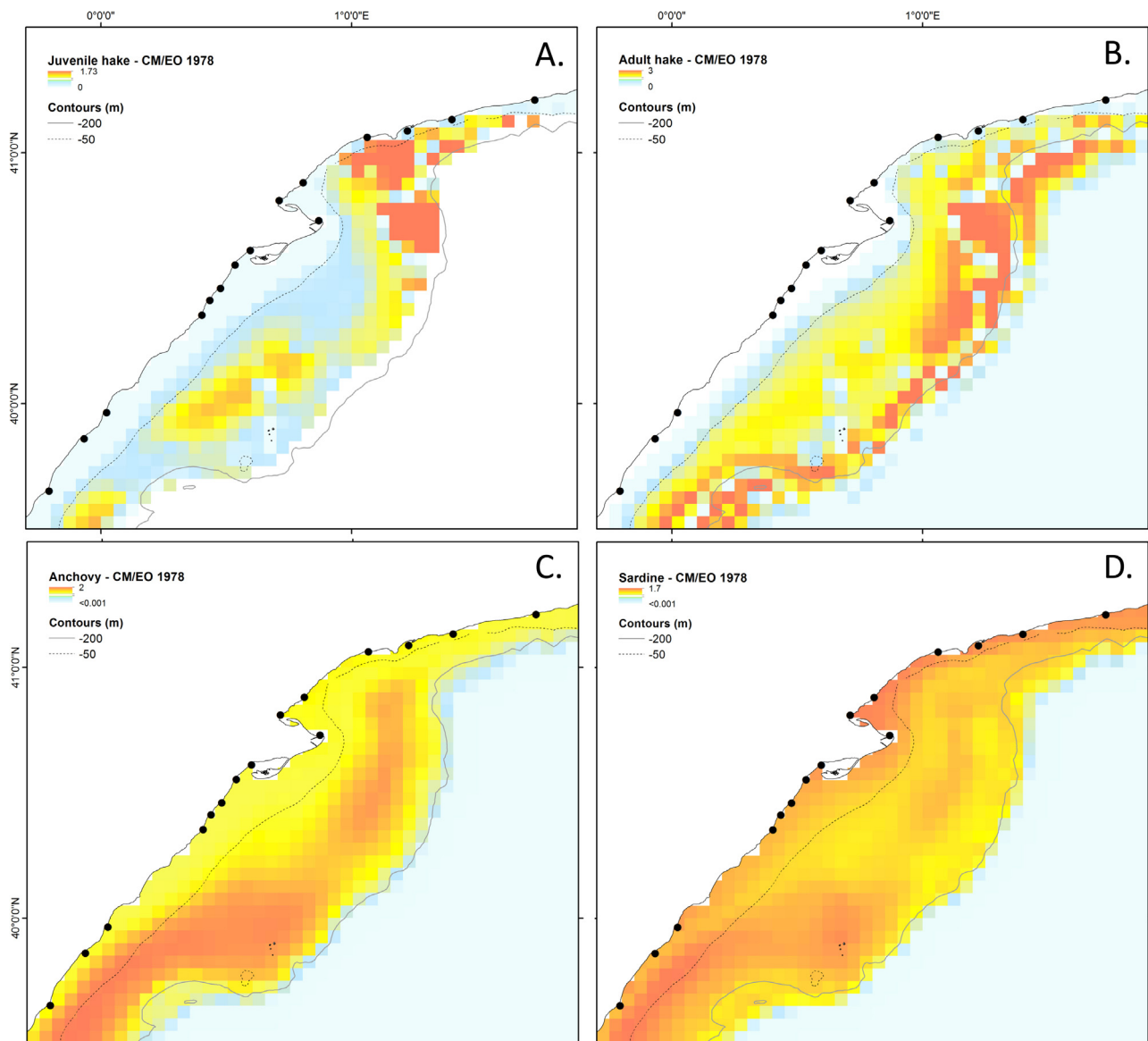


Fig. 5. Comparison of biomass distributions of (a) juvenile hake, (b) adult hake, (c) anchovy, and (d) sardine in 1978 between the *Spatial_CM* and the *Spatial_EO* configuration (*Spatial_CM*/*Spatial_EO* results).

hake, anchovy and sardine showed lower declines with time (23%, 26%, 53% and 35%, respectively) (Table 2). All the ecological indicators showed lowest values when fishing was removed due to lower levels of biomass of non-commercial invertebrate species being predicted under the non-fishing scenario (Fig. 8c and Table 3).

When removing the spatial distribution of primary producers from the model (*Spatial_CM-NPP*), the biomass of the four groups declined slightly less than under the *Spatial_CM* scenario (Fig. 3c and Table 2), with declines between 46% and 79%. This scenario had a lower impact on ecological indicators (Fig. 8c). Predicted catch, especially that of hake, was lower than under *Spatial_CM* scenario (Fig. 3d).

Removing the depth (*Spatial_CM-ND*) as a driver of the spatial distributions of hake, anchovy and sardine did not have strong results on the biomass and catch of hake (Fig. 3c and d), if compared with results from *Spatial_CM* (Table 2). However, the impact on anchovy and sardine was larger. Both anchovy and sardine showed higher biomass predictions when depth was removed, thus their historical decline was predicted to be smaller (by 38% and 33%, respectively). The impact of removing depth on the ecological

indicators was important both in terms of biomass and also catch (Fig. 8c and d) due to an impact on non-commercial invertebrates, mainly from the demersal compartment.

Removing temperature and salinity from the simulations (*Spatial_CM-NT* and *Spatial_CM-NS*, respectively) showed the lowest impacts on results, which were similar to the *Spatial_CM* configuration, both in terms of biomass (Figs. 3c and 8c and Table 2) and catch (Figs. 3d and 8d). When removing temperature as a driver, the decline of juvenile and adult hake was 49% and 80%, respectively, and that of anchovy and sardine was 75% and 83%. When removing salinity similar results were observed (Table 2). Similar results were observed for the ecological indicators both considering biomass and catch (Fig. 8c and d and Table 3).

These results suggested that the impacts of fishing and environmental drivers on the biomass and distributions dynamics of hake, anchovy and sardine were not additive, but mainly cumulative with a synergistic or antagonistic effect (Table 2 and Figs. 3c and d and 8c and d), thus the sum of individual contribution did not result in the overall contribution when factors were included in the simulations together. In general, fishing had the

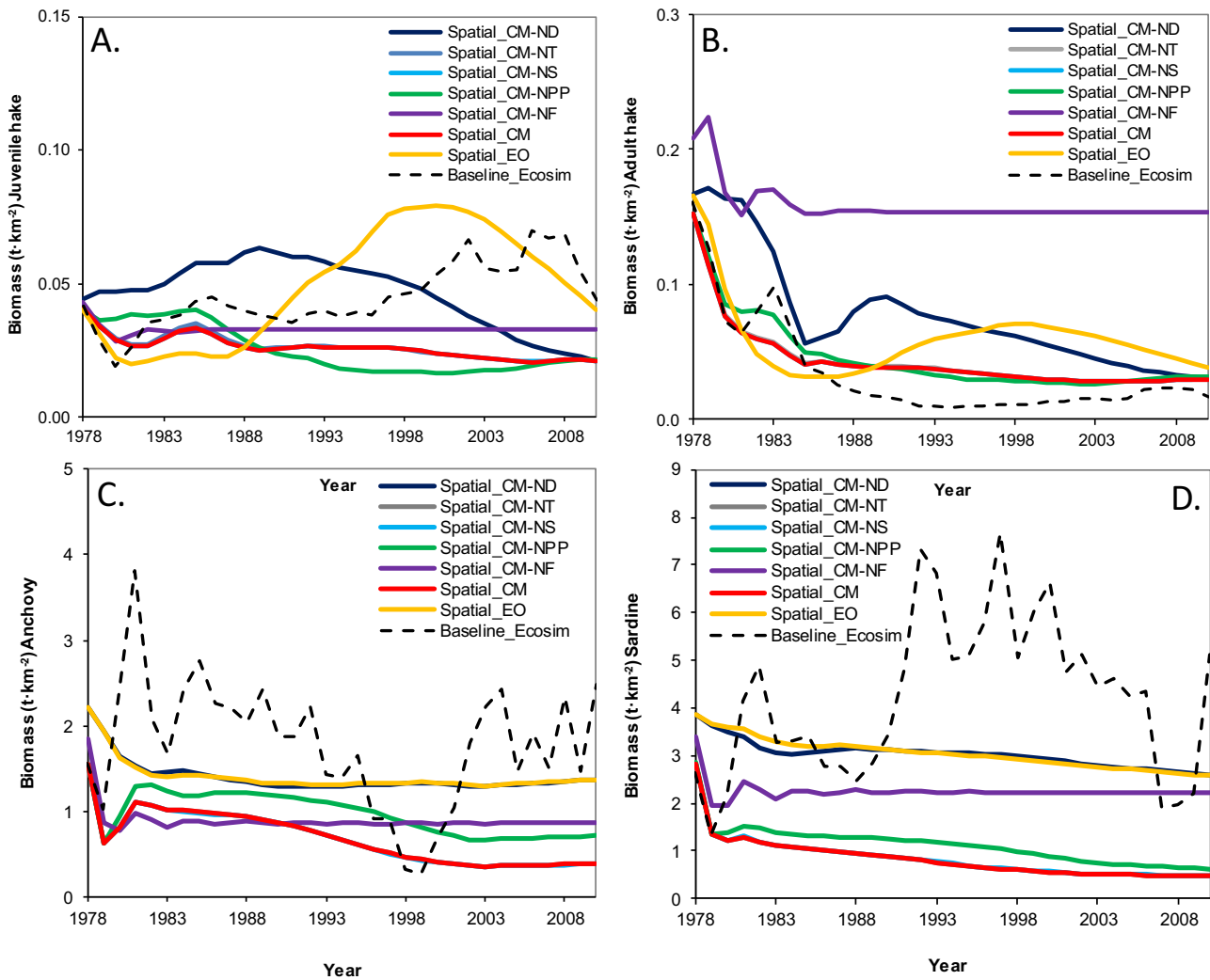


Fig. 6. Biomass time series ($t\ km^{-2}$) of (a) juvenile hake, (b) adult hake, (c) anchovy, and (d) sardine from 1978 to 2010 from the different modelling simulations (Table 1).

highest impact on results when excluded from the simulations, and the spatial and temporal distributions of biomass of the four groups changed substantially (Table 2). The spatial distribution of primary producers followed in importance, especially for the dynamics of anchovy and sardine, and the depth factor was very relevant for these two small pelagic fish as well. Temperature and salinity had more modest impacts as factors conditioning the spatial and temporal distribution of hake, anchovy and sardine in the study area.

At the ecosystem level, ecological indicators also showed cumulative effects (Fig. 8c and d).

4. Discussion

4.1. Comparison of Ecospace original with the capacity model

This study is one of the first applications of the new habitat capacity model in *Ecospace* (Christensen et al., 2014b) and illustrates its capabilities. It shows that the spatial-temporal modelling at the local level is possible if environmental, ecological and human activities are included with enough spatial detail, a challenge that it is present in most of the modelling initiatives to date (Barange et al., 2010).

Species distributions and abundances resulting from the new habitat capacity model were substantially different from the ones obtained using the original *Ecospace* configuration. These results

highlight the importance of including spatially explicit time series for environmental drivers to realistically predict species distributions and abundances, in addition to human activities and food web dynamics. Studying the factors that affect the spatial distribution of marine biodiversity is a central issue to ecology, and this knowledge is essential to evaluate biodiversity patterns, to predict the impact of environmental change and anthropogenic activities, and to design useful management programmes (Navarro et al., 2015).

Future additions to the analysis presented here should include the use of spatial-temporal varying environmental functions instead of climatologies applying the spatial-temporal data framework (Steenbeek et al., 2013). To do this the ROMS model can be run in two different modes: first starting from the climatological run as a basic state, and implementing a meteorological forcing reanalysis for the simulated year, quantifying the differences from the current simulations. Secondly, using future climate change scenarios and meteorological forcing variables to simulate future scenarios in the CM. In addition, changes in other oceanographic conditions potentially affecting marine species and ecosystems of the Mediterranean Sea due to climate change should be taken into account when spatial information is available about these, such as the decrease in rainfall and wind, and the acidification of seawater (Calvo et al., 2012).

Further steps should also include formal validations of the spatial-temporal modelling results in line with the validation of

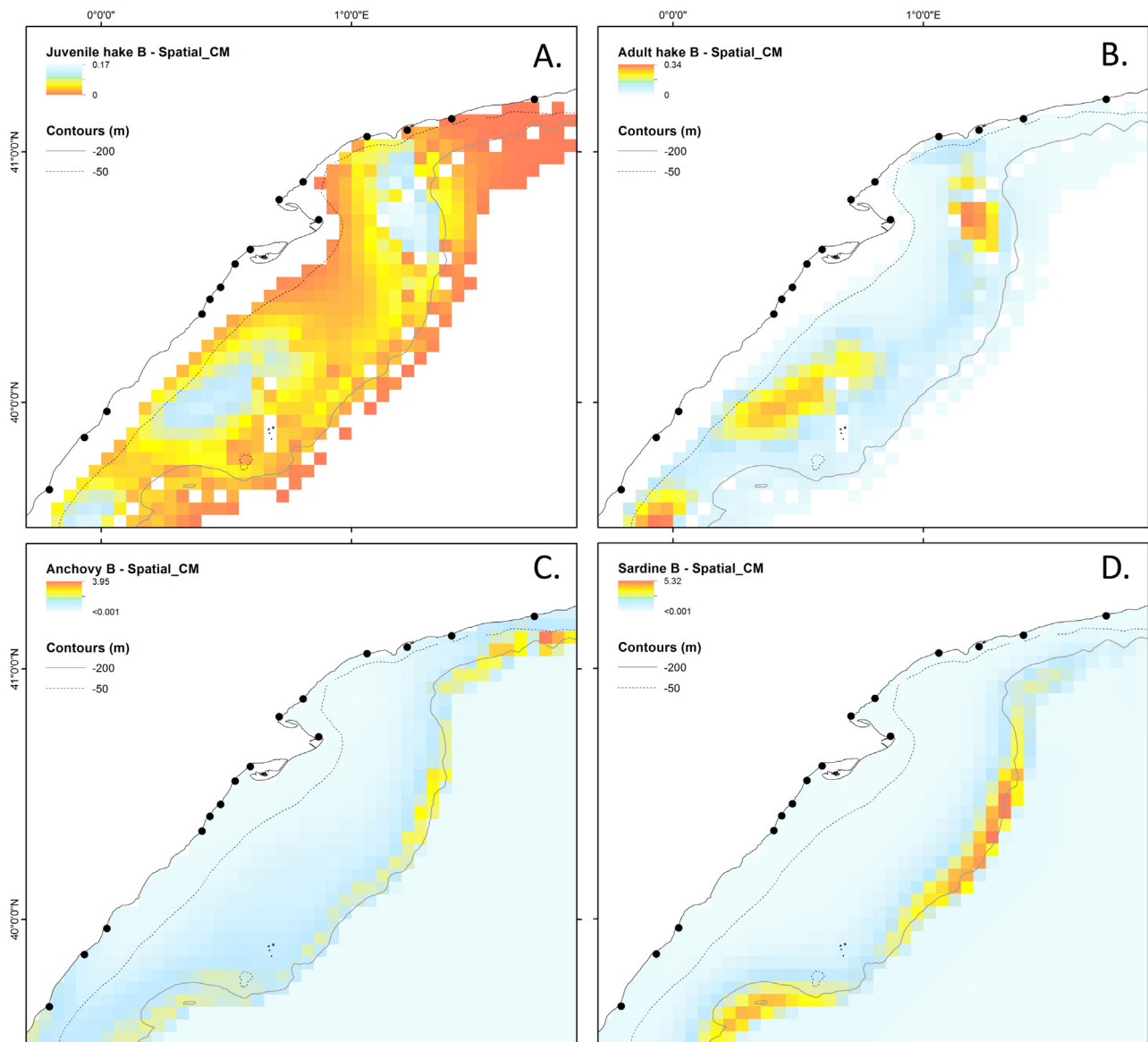


Fig. 7. Biomass distributions (t) of (a) juvenile hake, (b) adult hake, (c) anchovy, and (d) sardine in 2010 under the *Spatial_CM* configuration.

temporal results already available by fitting Ecosim models to time series of data (Mackinson et al., 2009). So far, the lack of empirical data at a suitable spatial–temporal resolution challenges this advance. However, these developments would further increase the realism of the approach (Coll et al., 2015a).

4.2. Spatial–temporal dynamics of marine species and the ecosystem

The existing information of the distribution patterns for the three species considered in this study is scarce and is mainly derived from studies of distributions of eggs and larvae, or the recruitment areas of hake, anchovy and sardine.

However, in general, results obtained with the habitat capacity model more closely match the empirical information available from the study area. For example, in the case of hake, Olivar et al. (2003) showed that in the northern part of our study area, eggs and larvae were distributed coinciding with the principal fishing grounds of the spawning population, the shelf edge (Recasens et al., 1998). In addition, Maynou et al. (2003) found that hake nursery areas were mainly located in the central part of the continental shelf between

68 and 168 m depth. These results are in agreement with predicted distributions from the spatial–temporal CM model.

Ichthyoplankton and acoustic surveys performed in the past for sardine and anchovy provide the main information for the distribution of both species, with more exhaustive information available in the case of anchovy (Palomera et al., 2007). The spawning area distribution for anchovy shows maximum densities in the edge of the continental shelf (Palomera, 1992; Olivar et al., 2001). Abad et al. (1998b) reported that spatial distributions of adult anchovies are similar to that of the spawning areas throughout the year. On the contrary, recruitment areas located in the coastal zone and mainly into the bays in the northern part of the area. Nevertheless, Ospina-Alvarez et al. (2015) highlighted with the development of connectivity modelling studies that the spawning and potential nursery areas for anchovy can vary strongly among years.

Regarding sardine, during the spawning period, this species is distributed mainly in the coastal area and the central part of the continental shelf (Olivar et al., 2001), while the main recruitment area of this species in the Northwestern Mediterranean Sea is the continental shelf around the Ebro river delta (Abad et al., 1998a).

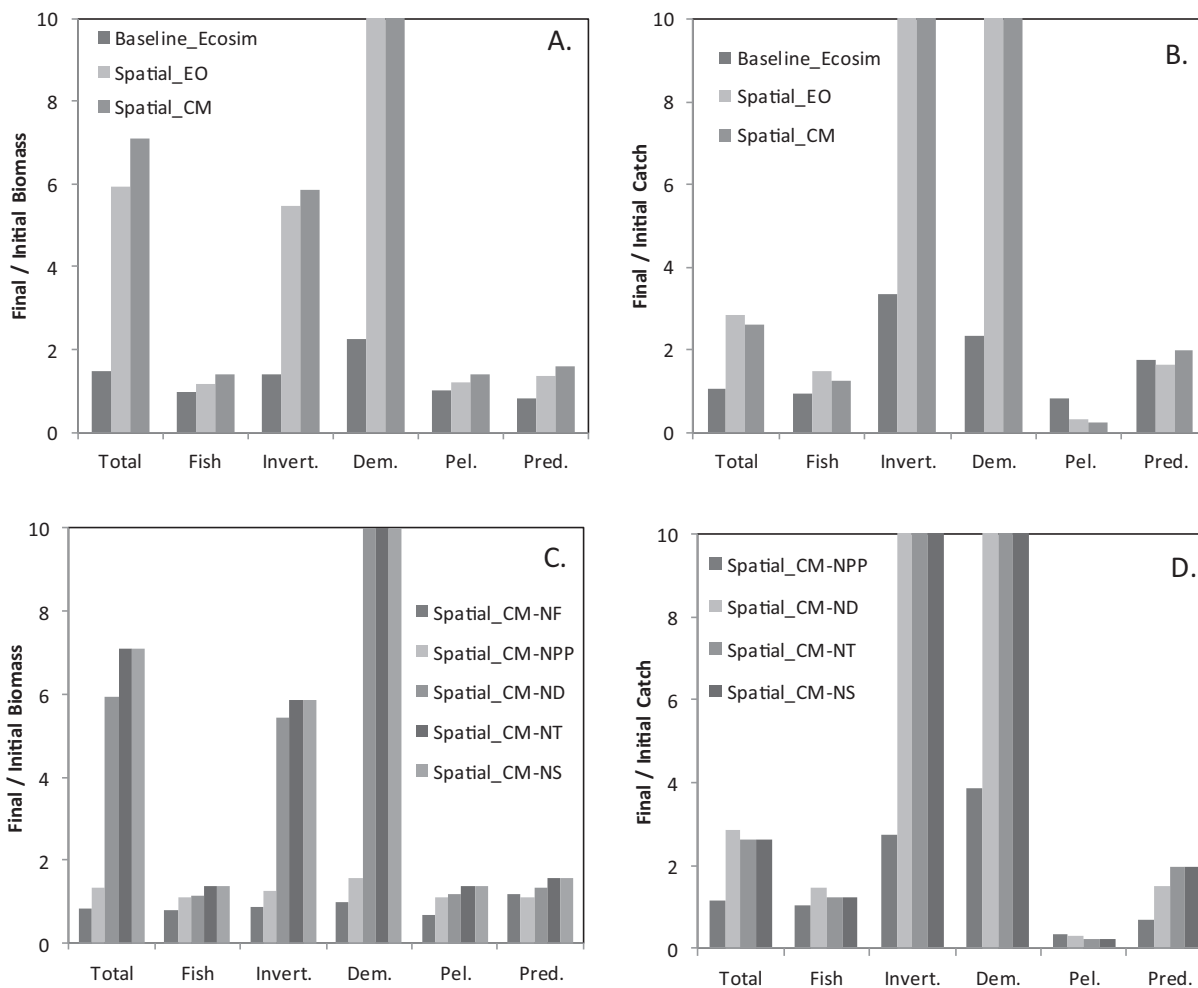


Fig. 8. Ecological indicators based on biomass and catch values (final/initial ratios using an average of the final five years (2006–2010) with the initial five years (1978–1982) of results from the simulations) resulting from the different modelling simulations (Table 1). (a, b) *Baseline_Ecosim*, *Spatial_EO* and *Spatial_CM* configurations, and (c, d) *Spatial_CM-NF*, *Spatial_CM-NPP*, *Spatial_CM-ND*, *Spatial_CM-NT*, and *Spatial_CM-NS*. A value >1 (over the black horizontal line) shows a positive increase of the ratio.

Table 3

Ecological indicators change (%) comparing an average of the final five years (2006–2010) with the initial five years (1978–1982) of the simulations described in Table 1. Indicators included are total biomass (Total), biomass of fish (Fish), biomass of invertebrates (Invert.), biomass of demersal species (Dem.), biomass of pelagic species (Pel.), and biomass of predators (Pred.). Results of the new habitat foraging capacity model simulation (*Spatial_CM*) are highlighted in grey for comparison purposes.

	% change from initial biomass (%Bf/Bi)					
	Total	Fish	Invert.	Dem.	Pel.	Pred.
<i>Baseline_Ecosim</i>	50	-1	40	127	-0.2	-19
<i>Spatial_EO</i>	495	16	446	1051	20	35
<i>Spatial_CM</i>	608	39	486	1146	39	58
<i>Spatial_CM-NF</i>	-15	-20	-11	1	-30	19
<i>Spatial_CM-NPP</i>	36	12	27	58	13	10
<i>Spatial_CM-ND</i>	493	16	445	1048	20	34
<i>Spatial_CM-NT</i>	608	39	486	1146	39	58
<i>Spatial_CM-NS</i>	609	39	486	1147	39	58

This study also confirmed as well the temporal changes that several species of the area have gone through, showing a general decline in species biomass for the three commercial species analysed. This is evident if we compare the spatial habitat capacity of the study area for the three species included in this analysis (Fig. S3) with the predictions of biomass after accounting for environmental drivers, human activities and the food web interactions. The decrease of abundance in the area is mainly due to an increase of fishing effort (Coll et al., 2014), as shown in other modelling exercises, and confirmed with stock assessments and fisheries independent data (Leonart and Maynou, 2003; Coll et al., 2008, 2013b, 2014; Colloca et al., 2013). This is also the case for sardine and anchovy, which are in clear decline in the ecosystem (Palomera et al., 2007) and in the northern areas such as the Gulf of Lions (Van Beveren et al., 2016).

The overall increase of ecosystem degradation in the study area was also highlighted with this new approach, as previously described using ecological indicators (Libralato et al., 2008; Coll et al., 2010). An interesting result is the increase of non-commercial invertebrate species, mainly demersal, over time. This is due to the increase of fishing effort in the area, followed by the decrease of commercial species and the decrease of predation mortality and competition. Therefore, non-commercial species such as demersal invertebrates have increased their abundance in the system mainly due to a trophic cascade. This is in line with field observations from

the area (de Juan et al., 2007, 2011) and results from other modelling exercises (Coll et al., 2008, 2013b, 2014), providing evidence for the notable ecosystem impacts of fishing.

4.3. Individual and joint effects of drivers

The study confirmed that both fishing and environmental drivers, in addition to food web interactions, are necessary to predict marine species distributions (Mackinson et al., 2009). The most important factor driving the species spatial–temporal dynamics of the three species studied here is fishing, because these are commercial species that have been – and still are – fully exploited or overexploited in the study area (Palomera et al., 2007; Colloca et al., 2013; Coll et al., 2014). These results are also in line with parallel studies using other modelling approaches (Travers-Trolet et al., 2014).

However, the distribution of primary production and depth follow in importance as important drivers, in line with other studies from the literature (Lloret et al., 2004, 2006; Palomera et al., 2007; Mackinson et al., 2009). In case of demersal fish species, this result is also in line with the analysis of the relative role of the environment, human activities and spatial factors in the spatial distribution of marine biodiversity in the Western Mediterranean Sea (Navarro et al., 2015).

It is interesting to highlight that salinity and temperature, although important, were less relevant to describe the spatial patterns of the species. Navarro et al. (2015) found similar results regarding temperature and target demersal fish species in the same study area. These results can be explained because the study area includes most of the range of suitable values that describe the environmental envelopes define by salinity and temperature for our study species (Fig. S1). However, these results can also be due to the fact that we used annual averaged climatologies for the environmental parameters included in the analysis, omitting potentially important seasonal patterns. In the case of anchovy, previous studies have shown the importance of seasonal changes of river runoff, linked with changes in salinity, in the abundance of this species (Lloret et al., 2004). The dynamics of sardine has been observed to be linked with lower temperature conditions during the reproduction season in winter (Palomera et al., 2007).

In addition, our study shows that the effects of environmental conditions and fishing tend to accumulate in a synergistic or antagonistic way, where the sum of individual contribution does not result in the overall contribution when factors are included in the simulations together. Specifically, fishing and the distribution of primary producers contributed negatively to the decline of biomass, and depth contributed positively. This is in line with laboratory and meta-analysis studies that highlight a high prevalence of cumulative effects (Crain et al., 2008). Similarly, Navarro et al. (2015) showed how the joint effects of the interaction of environmental drivers, human activities and the spatial component of species distribution were very important to describe the biodiversity patterns of demersal species in the study area and how individual factors can only provide a partial explanation of the spatial patterns.

As a general conclusion, this study underpins the need to develop comprehensive spatial–temporal analyses that include both environmental factors and human activities together, in addition to food web effects, and that are able to evaluate their cumulative effects. In this study we used available environmental local data and knowledge about which factors drive species dynamics. When developing these analyses, however, it is advisable to explore the auto-correlation in space and time of the explanatory variables to better explore the complex possible interactions of the functions that define the habitat foraging capacity model. As explained in Christensen et al. (2014a,b), the habitat foraging

capacity is determined by the multiplying effects of each environmental function per each functional group. If the functions are correlated in time and/or space there is a risk of overfitting the data and of misunderstanding the main variables that are having a greater effect of the ecosystem. One way to solve this issue is to use species distribution modelling results to inform the best combination of environmental parameters to use in Ecospace.

Overall, this study sets the baseline to further develop spatial–temporal analyses and move forward the evaluation of future scenarios of global change in the Western Mediterranean Sea, including the impact of climate variability and change.

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Appendix A. Ecopath with Ecosim (EwE) approach

The basic routine *Ecopath* describes the balance between production of the functional group and all consumptions. The model is built on a system of linear equations to describe the average flows of mass and energy between the species groups during a period of time, normally a year. The flow to and from each functional group is described by the following equation:

$$B_i \cdot \left(\frac{P}{B}\right)_i = \sum B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} + Y_i + E_i + BA_i + B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i) \quad (1)$$

where B_i is the biomass of group i , P/B_i is the production per unit of biomass, Y_i is the total fishery catch rate, E_i is the net migration rate (emigration–immigration), BA_i is the biomass accumulation rate, EE_i is the ‘ecotrophic efficiency’, or the proportion of the production that is utilized in the system, B_j is the biomass of consumers or predators j , $(Q/B)_j$ is the consumption per unit of biomass of j , and DC_{ji} is the fraction of i in the diet of j .

Ecopath requires a series of inputs for each functional group i , mostly biomass (B_i), diet (DC_{ij}), consumption and production per unit of biomass (Q/B_i and P/B_i), and fishing yields and other exports (Y_i and E_i). Among B , P/B , Q/B , EE , one parameter can be estimated by the model and the others are mandatory inputs (Christensen and Walters, 2004).

Ecosim is used to simulate ecosystem effects of fishing mortality changes and environmental forcing over time (Christensen and Walters, 2004; Christensen et al., 2008). The process uses a system of time-dependent differential equations from the baseline mass-balance model (Eq. (1)), where the biomass growth rate is expressed as:

$$\frac{dB_i}{dt} = g_i \cdot \sum Q_{ji} - \sum Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i \quad (2)$$

where dB_i/dt represents the growth rate of group i during the time interval dt in terms of its biomass B_i , g_i is the net growth efficiency (production/consumption ratio, P/Q), M_i is the non-predation ($(P/B)_i \cdot B_i(1 - EE_i)$) natural mortality rate, F_i is fishing mortality rate, e_i is emigration rate, I_i is immigration rate and $e_i \cdot B_i - I_i$ is the net migration rate. The two summations estimate consumption rates, the first expressing the total consumption by group i , and the second the predation by all predators on the same group i .

The consumption rates, Q_{ji} , are calculated based on the ‘foraging arena’ concept, where B_i s are divided into vulnerable and

invulnerable components (Ahrens et al., 2012). *Ecosim* simulations are especially sensitive to the 'vulnerability' settings, which incorporates density-dependency and expresses how far a group is from its carrying capacity (Christensen and Walters, 2004; Christensen et al., 2008).

The set of *Ecosim* equations are used in the spatial routine *Ecospace* that models the biomass dynamics in a two-dimensional space (Walters et al., 1999). In the original *Ecospace*, the spatial extent of the ecosystem is represented by a grid of cells, where each of one can be defined as land or water and, and in the last case, a habitat type can be assigned to the cell in the original configuration of the approach (Christensen et al., 2014b). A series of habitats can be then defined and then the species can be assigned to a preferred habitat. The fishing fleets can be depicted as operating in a specific region and cells could be defined as MPA (no taking zones, e.g., Walters et al., 2000). Moreover, on the spatial grid relative variations of the primary productivity and of the fishing costs (e.g., far from the fishing port the costs will be higher) can be incorporated, while the model can take into account changes in the average dispersal rates of the organisms and other behavioural parameters (Christensen et al., 2005).

In the original *Ecospace*, habitat structures with associated impact on biomass distributions and trophic interactions had been represented by a binary habitat use pattern, with each spatial cell being either entirely suitable – or entirely unsuitable – for species/functional groups. Therefore, the original version of *Ecospace* assumed homogenous conditions within each spatial cell, and local, but possibly relevant variations within cells, could not be represented. To overcome these limitations of the original configuration of *Ecospace*, the habitat foraging capacity model was added (Christensen et al., 2014b). This model offers the ability to spatially drive foraging capacity of species from the cumulative effects of multiple physical, oceanographic, and environmental drivers.

The habitat foraging capacity model runs in *Ecospace* in conjunction to the food web and fisheries dynamics. The model defines a continuous relative habitat capacity for each functional group in each cell (Christensen et al., 2014b), and the proportion of a cell that a species (or functional group) can use is a continuous value from 0 to 1, allowing for the inclusion of as many environmental factors as needed to define the foraging capacity of a cell for a species.

This development, in combination with the recently added spatial-temporal framework module (Steenbeek et al., 2013), bridges the gap between envelope environmental models and classic ecosystem food web models (Christensen et al., 2014b, 2015).

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.03.020>.

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