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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.

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

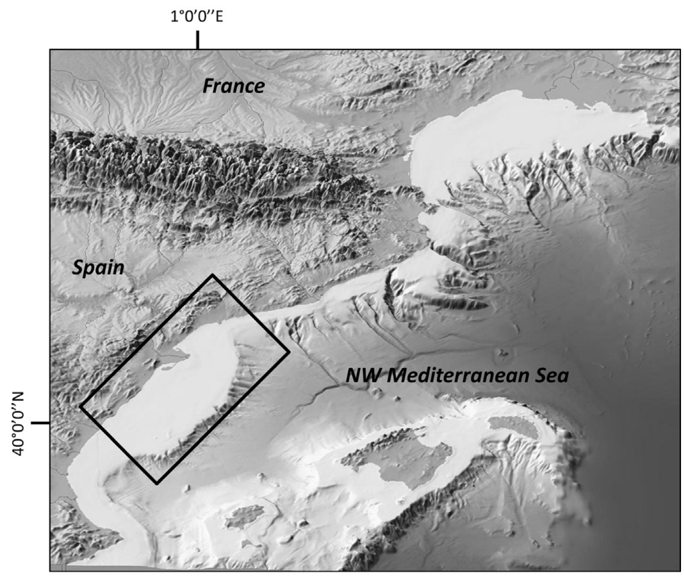

Fig. 1. Study area located within the Balearic Sea, NW Mediterranean Sea.

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