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Simulating anchovy's full life cycle in the northern Aegean Sea (eastern Mediterranean): A coupled hydro-biogeochemical–IBM model

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ABSTRACT

A 3-D full life cycle population model for the North Aegean Sea (NAS) anchovy stock is presented. The model is two-way coupled with a hydrodynamic–biogeochemical model (POM–ERSEM). The anchovy life span is divided into seven life stages/age classes. Embryos and early larvae are passive particles, but subsequent stages exhibit active horizontal movements based on specific rules. A bioenergetics model simulates the growth in both the larval and juvenile/adult stages, while the microzooplankton and mesozooplankton fields of the biogeochemical model provide the food for fish consumption. The super-individual approach is adopted for the representation of the anchovy population. A dynamic egg production module, with an energy allocation algorithm, is embedded in the bioenergetics equation and produces eggs based on a new conceptual model for anchovy vitellogenesis. A model simulation for the period 2003–2006 with realistic initial conditions reproduced well the magnitude of population biomass and daily egg production estimated from acoustic and daily egg production method (DEPM) surveys, carried out in the NAS during June 2003–2006. Model simulated adult and egg habitats were also in good agreement with observed spatial distributions of acoustic biomass and egg abundance in June. Sensitivity simulations were performed to investigate the effect of different formulations adopted for key processes, such as reproduction and movement. The effect of the anchovy population on plankton dynamics was also investigated, by comparing simulations adopting a two-way or a one-way coupling of the fish with the biogeochemical model.

Introduction

Small pelagic fish (SPF), such as anchovy and sardine, comprise species that are plankton feeders, playing an important role in marine food webs as they are the principal means of transferring production from plankton to larger predators, including marine mammals and seabirds (Fréon et al., 2005). Fishing these species can have large impacts on other groups (vertebrate, invertebrate, primary and secondary producers) of the ecosystem (Smith et al., 2011). In addition, SPF have a short life span, high fecundities and by feeding on the plankton-based food chains, they respond rapidly to changes in ocean conditions (Alheit et al., 2009). Thereby, they are extremely variable in their abundance at both inter-annual and inter-decadal scales (Alheit et al., 2009). An effective management system for these resources would need to incorporate an understanding of the mechanisms that control the variations in abundance, distribution and productivity of the populations, as well as the ecosystem interactions and feedbacks these variations may set in motion. Furthermore, the extreme variability that characterizes the SPF recruitment implies that traditional fishery management measures, based on estimates of long term average yield from stock assessment, may not be effective in preventing episodes of serious overfishing (Fréon et al., 2005). There is an increasing need to understand how physics, biogeochemistry and biology combine to produce the observed patterns of population variability and to enhance ecosystem considerations in the management of the SPF resources by developing state-of-the-art end-to-end models (Fulton, 2010; Rose et al., 2010).

The European anchovy (*Engraulis encrasicolus*) is one of the most important SPF in the Mediterranean Sea. Three major stocks exist in the basin, supporting the largest SPF fisheries in the area. These stocks inhabit the NW Mediterranean (Catalan Sea and Gulf of Lions), the Adriatic Sea and the northern Aegean Sea (Somarakis et al., 2004). The above areas are characterized by wide continental shelves, exceptionally higher productivity, in relation to the highly oligotrophic character of other Mediterranean regions and

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favorable conditions for larval survival (Agostini and Bakun, 2002). Moreover, these suitable anchovy habitats are spatially restricted and separated from each other by deep, extremely oligotrophic basins, which would not be likely to support anchovy feeding and reproduction (Somarakis et al., 2004). For example, in our case study area, i.e. the Aegean Sea, there is a sharp contrast in productivity between its northern and southern basin and anchovy schools are practically absent from the later (Stergiou et al., 1997). Anchovies remain close to the areas of higher productivity and many density dependent controls have been identified such as on plankton consumption (Nikolioudakis et al., 2014), daily egg production (Somarakis et al., 2012) and larval mortality (Somarakis and Nikolioudakis, 2007).

End-to-end models (E2E) provide today a thriving approach in marine ecosystem dynamics. They attempt to unify the different levels of the food web from climate to lower trophic levels to fish and fisheries (Travers et al., 2007; Rose et al., 2010). Numerous biophysical modelling studies have contributed to a better understanding of fish dynamics and their ecological response to climate change and management actions (Travers et al., 2007; Lett et al., 2009; Hinrichsen et al., 2011; Ito et al., 2013). A full life cycle fish model was developed by Huse and Ellingen (2008) to represent the migration, spatial and population dynamics of capelin in the Barents Sea. The model was then used to perform simulations with present day climate and a future climate scenario. The climate warming scenario showed a shift in the adult distribution, with a parallel shift of spawning habitats and an earlier starting of spawning activity. In the North Western Pacific, a two-dimensional individual-based fish model was developed to evaluate the effect of movement on the recruitment success of Japanese sardine (Okunishi et al., 2012). For Pacific saury, Ito et al. (2013) investigated the fish growth response under global warming scenarios using an ecosystem-based bioenergetics/migration model. Simulations predicted future shifts in size distribution and abundance of saury, contributing to a more comprehensive understanding of fish responses to climate change.

The development of a full life cycle model for a small pelagic fish needs a complex, multi-step approach. It requires knowledge on a suite of processes (growth, spawning and movement strategy, planktonic prey selection), during the course of fish development (Huse and Ellingen, 2008; Wang et al., 2013). A 3-D IBM was developed for the first time in the North Aegean Sea (NAS, eastern Mediterranean, (Fig. 1)) by coupling the full life cycle of anchovy (from eggs to adults) with a 3-D hydrodynamic–biogeochemical lower trophic level model (LTL). The IBM consists of several modules: the bioenergetics approach (Mukai et al., 2007; Politikos et al., 2011) is used to simulate anchovy growth and reproduction under seasonally varying food and temperature conditions, provided by the LTL model. The anchovy population is controlled by natural and fishing mortalities, which are updated as the fish pass through successive life stages. Physical and biological cues determine fish advection/movement. Finally, an energy allocation algorithm, based on the approach of Pecquerie et al. (2009), is used to control egg production, taking into account all basic characteristics of anchovy spawning strategy in the NAS.

Once the IBM model was coupled and tuned, it was then used to simulate the anchovy population dynamics in the NAS through an interannual hindcast simulation for the period 2003–2006. The simulated somatic growth, population biomass and egg production were compared with available field data, derived mainly from acoustic and daily egg production (DEPM) surveys, carried out during early summer in the same period (2003–2006). Additional sensitivity simulations were performed to investigate the effect of different formulations adopted for key processes, such as reproduction and movement. Finally, through the two-way coupling of the fish with the LTL model, the effect of the anchovy population on plankton dynamics was also investigated.

Materials and methods

Lower trophic model (LTL)

The three-dimensional, coupled lower trophic model used in this study has been developed for the NAS ecosystem, as described in Tsiaras et al. (2012) and Tsiaras et al. (2014). It consists of a hydrodynamic model, based on POM (Princeton Ocean Model; Blumberg and Mellor, 1983) and a comprehensive biogeochemical model, based on ERSEM (European Regional Seas Ecosystem Model, Baretta et al., 1995; Petihakis et al., 2002). Both models are widely used in the scientific community and have been previously implemented in the area (Kourafalou and Tsiaras, 2007; Politikos et al., 2011; Tsiaras et al., 2010; Tsiaras et al., 2012, 2014). The biogeochemical component has been adopted from Petihakis et al. (2002), being further calibrated and validated against remote sensing and in situ data (Politikos et al., 2011; Tsiaras et al., 2014). ERSEM may be characterised as generic, following the functional group approach, where organisms are separated according to their trophic role (producers, consumers, etc.) and subdivided according to their size (Fig. 2). Organic carbon is produced and transferred within the trophic web through physiological and population processes, while variable nutrient pools of nitrogen, phosphorus and silicate are dynamically coupled with the carbon dynamics. Briefly, there are four groups of primary producers, ranging from the very small picophytoplankton (<2 μm) to the significantly larger diatoms and dinoflagellates (20–200 μm). There are also three zooplanktonic groups (heterotrophic nanoflagellates, microzooplankton, mesozooplankton) that each feed on more than one food source among phytoplankton and bacteria groups (Fig. 2). A significant advantage of this particular model is the detailed description of the microbial food web, which is particularly suitable for the simulation of the most important ecosystem characteristics within the environment of the Eastern Mediterranean. For more details on the biophysical model description, the interested reader can refer to Petihakis et al. (2002), Kourafalou and Tsiaras (2007) and Tsiaras et al. (2012, 2014). The LTL model domain is shown in Fig. 1. The horizontal resolution is 1/10° (∼10 km), while 25 sigma-levels are resolved in the vertical, with logarithmic distribution approaching the surface.

Anchovy IBM model

Life cycle stages and age classes

Anchovies are considered to have a maximum lifespan of 3.5 years (Somarakis et al., 2006), which is divided into seven life stages/age classes. The length thresholds and reference dates for the transition from one life stage/age class to the next are shown in Table 1. Specifically, the early life history (ELS) is divided into three stages according to length: (a) embryonic (egg + yolk sac larvae) (<3.5 mm, autotrophic stage), (b) early larval (<11 mm) and (c) late larval stage (11–42 mm).

The various stages of anchovy's life history were based on documented differences in feeding preferences and movement capabilities. The first two stages (<11 mm, i.e. egg, yolk sac, preflexion and early postflexion larvae) have limited swimming capabilities, un-developed vertical migration behaviour and feed on microzooplankton (Somarakis and Nikolioudakis, 2010). Late larval and juvenile stage anchovies have developed significant behavioural and swimming capabilities and are able to respond effectively to physical transport. Vertical migration behaviour has been fully developed by these stages, while a shift in feeding preferences from microzooplankton to mesozooplankton is taking place during the late larval stage (Nikolioudakis, 2011).

Although length at 50% maturity of the NAS anchovy is 105 mm (Somarakis et al., 2006), it was more convenient to adopt a reference