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A coupled movement and bioenergetics model to explore the spawning migration of anchovy in the Bay of Biscay

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ABSTRACT

Adult anchovies in the Bay of Biscay perform north to south migration from late winter to early summer for spawning. However, what triggers and drives the geographic shift of the population remains unclear and poorly understood. An individual-based fish model has been implemented to explore the potential mechanisms that control anchovy's movement routes toward its spawning habitats. To achieve this goal, two fish movement behaviors – gradient detection through restricted area search and kinesis – simulated fish response to its dynamic environment. A bioenergetics model was used to represent individual growth and reproduction along the fish trajectory. The environmental forcing (food, temperature) of the model was provided by a coupled physical–biogeochemical model. We followed a hypothesis-testing strategy to actualize a series of simulations using different cues and computational assumptions. The gradient detection behavior was found as the most suitable mechanism to recreate the observed shift of anchovy distribution under the combined effect of sea-surface temperature and zooplankton. In addition, our results suggested that southward movement occurred more actively from early April to middle May following favorably the spatio-temporal evolution of zooplankton and temperature. In terms of fish bioenergetics, individuals who ended up in the southern part of the bay presented better condition based on energy content, proposing the resulting energy gain as an ecological explanation for this migration. The kinesis approach resulted in a moderate performance, producing distribution pattern with the highest spread. Finally, model performance was not significantly affected by changes on the starting date, initial fish distribution and number of particles used in the simulations, whereas it was drastically influenced by the adopted cues.

1. Introduction

Small pelagic fish undergo migrations between distinct habitats to support their feeding and reproduction requirements. These migrations represent an efficient strategy for the maximization of fitness at individual and population scale and are highly driven by seasonal environmental variations (Checkley et al., 2009; Giannoulaki et al., 2014). Moreover, geographic shifts of fish distributions to their spawning grounds are indispensable to ensure the survival of offsprings and consequently, recruitment success (Fréon et al., 2010; Ward et al., 2003). Identifying the conditions that define the temporal coincidence between fish physiological needs and these displacements to suitable areas is crucial for understanding fish migration dynamics (Chen et al., 2010; Lo et al., 2010) and investigate their response to future climate changes (Okunishi et al., 2012a).

Adult anchovies in the Bay of Biscay (BoB) exhibit seasonal movements and their distribution patterns have been documented in ICES (2010, Chap. 8). Spawning primarily occurs over spring to summer in highly productive areas such as river plumes, shelf break fronts, and oceanic eddies mostly found in the southeast corner of the bay where large anchovy aggregations are observed (Motos et al., 1996; Koutsikopoulos and Le Cann, 1996). After spawning, dispersal to the north, especially for larger fish, has been confirmed by the analysis of fishing activity (Uriarte et al., 1996) and reanalysis of anchovy presence data derived from PELGAS surveys (Petitgas et al., 2011). However, the exact mechanisms, as well as what triggers the starting and ending period of these geographic shifts remain uncertain and poorly understood (Petitgas et al., 2013). As anchovy fishery in the BoB interacts strongly with anchovy distribution (ICES, 2014; Uriarte et al., 1996), and given that management strategy evaluation is strongly sensitive to fish

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seasonal distribution (Lehuta et al., 2013), understanding migration ecology is key in proposing adequate spatio-temporal management strategies.

Simulating fish movement through spatially explicit individual-based models (IBMs) has been proven an efficient approach for exploring the link between fish migration dynamics and their living conditions. Indeed, IBMs have been successfully used to identify spawning migration routes (Barbaro et al., 2009; Okunishi et al., 2009), predict recruitment (Okunishi et al., 2012b; Xu et al., 2013), study the influence of physical environment on fish biomass inter-annual variability (Politikos et al., 2014; Rose et al., 2015) and investigate the impacts of climate change on fish growth and distribution patterns (Huse and Ellingsen, 2008; Ito et al., 2013).

The ultimate goal of the paper is to identify the key environmental drivers that control BoB anchovy's southward movement for spawning. To this end, we developed a horizontal two-dimensional IBM model through which we tested a series of hypotheses. Under different rules of swimming, we simulated fish movement following conceptually two behavioral approaches, i.e. the gradient area search (Politikos et al., 2014; Tu et al., 2012) and kinesis (Okunishi et al., 2009; Rose et al., 2015). The bioenergetic model developed in Huret et al. (submitted for publication) was used to depict individual growth and reproduction along anchovy's trajectory and define behavioral cues based on fish physiological needs. Sea water temperature and zooplankton fields were extracted from a three dimensional lower trophic model and then used as environmental forcing to trigger anchovy's response to its dynamic spatial environment. The IBM model was implemented for adult stage. Its skill was examined by comparing model results with distribution maps derived from seasonally acquired survey data. A reference run and ten additional experiments were performed to compare the simulated fish spatial patterns under several behavioral and computational assumptions. In Section 4, we analyze the implications of simulation outputs and document the model limitations.

2. Materials and methods

2.1. Anchovy bioenergetics

The configuration of the bioenergetic model developed in Huret et al. (submitted for publication) was used to simulate anchovy's growth and spawning activity. It is based on the Dynamic Energy Budget (DEB) theory (Kooijman, 2010) which tracks the energy fluxes within the fish organism through the physiological processes of assimilation, maintenance, maturation, growth and reproduction. For the analysis of our results, we used the model products which describe fish length, fish wet weight, fish energy and the energy allocated to reproduction (Huret et al., submitted for publication). The main inputs of the bioenergetic model are: food density and temperature, which were provided by the forcing environment described in Section 2.2.

2.2. Forcing environment

ECO-MARS3D (Lazure and Dumas, 2008) is a coupled physical–biogeochemical model which describes the general patterns of hydrodynamics and lower trophic dynamics at the seasonal and multi-decadal scale in the BoB (Huret et al., 2013). The current configuration has a numerical grid of 4 km × 4 km resolution in the horizontal and 30 sigma layers in the vertical and it provides the living conditions of anchovy. Hence, three day climatology of temperature fields during 1982–2007 and a weekly climatology of two zooplankton groups (micro- and meso-zooplankton) averaged over 2001–2005 were extracted and used as the forcing inputs for the IBM model. Zooplankton and temperature fields define the fish consumption rates and metabolic requirements in the DEB model, as well as the movement decision rules (see Section 2.3).

2.3. Movement

Individual fish behavior is controlled by a diversity of external (environmental cues, density dependent processes, interspecific relations) and internal factors (physiology, sociability, age) (Planque et al., 2011). Furthermore, bigger fish, conversely to early life stages, can also actively direct their own locomotion and shift their geographical distributions in order to reach optimum habitat conditions (Lett et al., 2009). These complexities and uncertainties on how individuals discern and react to their environment have led in the development of different approaches for representing behavioral movement within numerical models, like restricted area search, kinesis, event-based and run and tumble (Watkins and Rose, 2013). In terms of mathematical structure, these approaches are considered as biased correlated random walk, where the change in fish direction may depend on various cues such as currents, prey availability, temperature, salinity and fish condition (Humston et al., 2004; Okunishi et al., 2009; Xu et al., 2013). In this section, we identify the potential cues for our case study and describe the adopted movement algorithms.

2.3.1. Potential cues

In autumn, adult anchovy is distributed in northern BoB for feeding while in spring the major spawning grounds are located in the south (ICES, 2010). The shift of the population from north to south is supposedly driven by the search of optimum oceanographic conditions and high productivity areas in an effort to cover the physiological needs of a multiple batch spawner and the survival of offsprings (Petitgas et al., 2013). However, the exact drivers and timing are uncertain. Thus, possible cues were considered based on existing hypothesis.

Anchovy spawning to the southern part of the bay seems to be triggered by the warming of surface water (Koutsikopoulos and Le Cann, 1996) following the progression of the associated stratification, which starts in April in the south and extends progressively to the north (Motos et al., 1996). Meanwhile, planktonic spring production increases reaching its highest biomass values during late spring and summer (Poulet et al., 1996). Based on the aforementioned information and following our hypothesis testing strategy, zooplankton and sea surface temperature were tested as potential cues to induce north to south movement of anchovy.

Ultimately, searching for areas which maximize fish physiological response has also been proposed to be very effective at reproducing observed distributions. For instance, the growth rate was considered as the key driver of fish behavior in order to simulate the migration and growth patterns of sardine in the western North Pacific (Okunishi et al., 2012a,b) and investigate the influence of physical and plankton variability on Peruvian anchovy recruitment (Xu et al., 2013). In our study, the component of the DEB model which calculates the remaining energy that goes for somatic growth after covering maintenance costs (Huret et al., submitted for publication) represented the index of optimum habitat search, as it integrates concurrently the effects of food, temperature and physiological requirements.

2.3.2. Movement algorithms

The movement algorithms were built using the Lagrangian approach which permits the individual fish tracking in the continuous space of a grid (Okunishi et al., 2012b; Watkins and Rose, 2013).