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Vertical migration effects on the dispersion and recruitment of European anchovy larvae: From spawning to nursery areas

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ABSTRACT

Recruitment of European anchovy has been traditionally thought to largely depend on the passive transport and dispersion of eggs and larvae from spawning to nursery areas. Knowledge of the factors influencing the vertical distribution of fish early stages, and consequently influencing the transport, is a crucial issue in fisheries science. The aim of this study is to assess the relevance of diel vertical migration (DVM) as a mechanism involved in the transport of European anchovy larvae toward nursery areas taking into account age/stage-dependent vertical migration (i.e., the maximum migration). We developed a simplified vertical migration sub-model for anchovy larvae included in an Individual-based (IBM) hydrodynamic coupled model. Two types of simulation experiments were conducted: (1) 'Pure' Lagrangian (passive) transport experiments and (2) biological behavior transport experiments with a realistic scheme for egg-buoyancy, larval growth, and DVM scheme. We detected high variability in the trajectory and final position of larvae with 14 mm length between the passive and biological behavior experiments. The particles were less clustered in the passive transport experiment. In the biological experiment the particles were aggregated depending on the mesoscale oceanographic structures, evidencing a transport associated to filaments and meanders. The formation of schools was facilitated by the transport in filaments and larvae transported within filaments generally avoided the nucleus of the eddies and the central part of the North Current. Moreover, our results suggest that there is interconnectivity between all the anchovy sub-populations in the NW Mediterranean and that the Gulf of Lions and the shelf waters surrounding the Ebro River Delta are the most important areas for anchovy reproduction in this region. Additionally, we detected that the pre-recruitment is higher in those years when the larvae retention is favored. We underline that bottlenecks in larval transport modeling are related to the scarcity of knowledge in developmental biology and behavior of anchovy larvae and emergent mechanistic processes.

1. Introduction

The biological processes affecting the vertical position of eggs and larvae are recognized as critical components of realistic models of fish egg-larval dispersion (Brochier et al., 2008; Huret et al., 2010; Parada et al., 2003, 2008; Ospina-Alvarez et al., 2011). The diel vertical migration (DVM) pattern is a daily behavior that has been described for various aquatic organisms from diverse phyla. The usual pattern involves displacement from shallow depths at night to greater depths during the day (Enright and Hamner, 1967; Fortier and Leggett, 1983; Haldorson et al., 1993; Stenevik et al., 2007). Migrants appear to use deep waters as a dark daytime refuge where their probability of being predated is lower than near the surface (Gauthier and Rose, 2002; Hays, 2003) and feed near the surface, with higher available food, at night (Haney, 1988; Hays, 2003). Particularly in marine environments, there has been relatively little consideration of the causes and consequences of the individual differences in migration behavior, such as those related with the nutritional condition (Hays, 2003) and there is generally poor information available on the vertical distribution of yolk-sac and feeding larvae. However, larvae migrate toward a given maximum depth at day that depends on the larval size (i.e., larger larvae migrate deeper than smaller larvae). Previous studies were based on a migration scheme that established a fixed position for the larvae in the surface at night and at a given depth during the day (Brochier et al., 2008; Nicolle et al., 2009; Parada et al., 2008, 2012).

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This scheme does not take into account any of the intermediate depths during migration and that the smaller larvae have a reduced migration capacity.

Californian anchovy (*Engraulis mordax*) larvae have been detected at 105 m depth; however, 87% of the larvae occurred above 41 m, within the upper mixed layer, which emphasizes the important role of the thermocline on the vertical positions (Ahlstrom, 1959). The vertical distribution of European anchovy (*Engraulis encrasicolus*) larvae was first studied by Palomera (1991). This study found that larvae avoid surface layers during daytime, with the larger larvae (<10 mm) carrying out photoperiod-related diel migrations, and thus remain in deeper waters during the day, as suggested by a high resolution sampling design (Olivar et al., 2001).

Recruitment of European anchovy has been traditionally thought to be largely dependent on the passive transport and dispersion of eggs and larvae from spawning to nursery areas (Borja et al., 1998; Hinckley et al., 1996; Mullon et al., 2002). Egg and larval transport is defined as the horizontal translocation of a particle in a bidimensional plane from an initial (x_1, y_1) to a final (x_2, y_2) position, that is, perpendicular and parallel to the coastline. The vertical axis (z or depth) has been ignored in order to simplify the analyses (Pineda et al., 2007). However, this dimension is critical for the transport of a biological particle (e.g., egg/early stage larvae) because the early stages of pelagic fish in the water column determine (i) the extent and direction in which they might be displaced or transported, (ii) their development rates and (iii) mortality, depending on the overlap with their predators, ambient food and physiochemical conditions; and these three factors condition impacts on (iv) pre-recruitment and recruitment success (e.g., Mullon et al., 2003; Page et al., 1989; Parada et al., 2003; Stenevik et al., 2007). Therefore, eggs and larvae might encounter different currents at various depths during their development that as a whole affect the horizontal transport. In consequence, traveling from an initial to a final position eggs and larvae are transported horizontally, but when mechanisms influencing the vertical position are considered, they may also be transported by diffusive and advective processes (Allain et al., 2001; Cowen, 2006; Epifanio and Garvine, 2001; Haug et al., 1986; Lett et al., 2007).

Spawning patterns are a fundamental issue for understanding fish-stock variability in the context of life-history strategies (Aoki and Murayama, 1993). The environmental conditions that prevail during spawning could have an important influence on the survival of eggs and larvae. In this context, populations of small pelagic fish exhibit reproductive strategies resulting from past natural selection pressure, allowing them to adapt to high habitat variability (Brochier et al., 2009). For example: at a long timescale, anchovy and sardine regime series in Pacific populations are related to global decadal climate variability of surface air temperature (Chavez et al., 2003) probably because the species distribution contracts to a central (optimal) range during population crashes (Lecomte et al., 2004); at a short timescale, anchovy presents a seasonal trend regarding the average larval size at first feeding, this is an adaptive advantage in the winter months when cold water temperatures produce slower growth rates compared with the summer when the growth is more rapid (Hunter, 1977); at a reproductive-level behavior, European anchovy spawns preferably around midnight (Somarakis et al., 2004) to minimize the risk of being predated and maximize the eggs survival.

Moreover, variability in biometric and physiological characteristics between populations and subpopulations have been recognized as ecological advantages (Grant et al., 2010; Riveiro et al., 2011; Whitehead et al., 1988).

Knowledge of the factors influencing the vertical distribution of fish early stages, and consequently influencing the transport, is a crucial issue in fisheries science (Galarza et al., 2009; Goarant et al., 2007; Pineda et al., 2007). Many of the developed analyses are sensitive to the initial conditions of eggs and early-larvae in the water column: the egg production methods, models of the egg and larval survival, transport and drift and the recently developed coupled hydrodynamic-IBMs (Goarant et al., 2007; Parada et al., 2008; Ospina-Alvarez et al., 2011; Solemdal and Sundby, 1981; Stenevik et al., 2007). Studying the reproductive strategies at adequate temporal and spatial scales is crucial for understanding adult–early stages relationships.

The commercial exploitation of small pelagic fishes in the North Western Mediterranean (NWM) has been significant since the early 1940s, but it was not until the 1960s with the improvements in fishing technology that the catches of European anchovy substantially increased (Palomera et al., 2007).

The NWM Sea is formed by the northern part of the Provençal basin, the Gulf of Lions, the Ligurian Sea, the Catalan Sea and by the Balearic Sea (Millot, 1990). It covers an area of around 200,000 km^2 and presents several submarine canyons, some of which almost reaching the coast line (Millot, 1990; Salat, 1996). It is one of the most productive regions in the Mediterranean Sea, given the relatively stable coastal circulation and the discharge of two large rivers (the Rhone, in the north, and the Ebre, in the south). The discharge of the Rhone and the Ebre rivers, the wastewater from large cities, a vertical mixing, the influence of the winds and a local upwelling, are the main inputs of nutrients in the region (Millot, 1990; Salat, 1996). The discharge of these rivers brings a big input of productive water into the Mediterranean Sea, given the contributions that the rivers themselves receive from extensive agriculture and farming in their riverbed (Cruzado et al., 2002; Millot, 1990; Lloret et al., 2004). In addition to the local and regional effects of river outflows, the effect of the currents and therefore the interactions between the Mediterranean Sea and the Atlantic Ocean, influence the whole functioning and comportment of the NWM ecosystems. A south westward current, commonly called the Northern Current (NC), dominates the region flowing along the edge of the continental shelf, associated with a shelf-slope front that separates the less saline inshore waters from the waters of the open sea. This creates a mesoscale-dominated system with relatively high activity and spatial and temporal variability, especially in the upper layer during the stratified season (Echevin et al., 2003; Millot, 1990).

The aim of this study is to assess how the relevance of DVM as a mechanism involved in the transport of larvae toward nursery areas taking into account age/stage-dependent vertical migration (i.e., the maximum migration). To accomplish our objectives we developed a simplified vertical migration model for European anchovy larvae in the NW Mediterranean. The DVM is included as a module in an Individual-based model (IBM) hydrodynamic coupled model. We discuss our results in the context of oceanographic processes affecting the transport and dispersion of early larvae from the spawning to the pre-recruitment zones.

2. Methods

In this study, we focused on the European anchovy larvae DVM effects on transport efficiency during the reproduction peak in 2007 and 2008 in the NW Mediterranean. We developed a DVM scheme that depends on age and larval stage. Processes such as spawning, egg development, hatching, larval growth and DVM were programmed into a modified version of the modeling tool ICHTHYOP (Lett et al., 2008) (Fig. 1).

2.1. Biological data collection

We integrated biological data from three different surveys: (1) for the larval growth sub-model we used information from data collected in the ARO-2000 cruise, conducted from 31 May to 12