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Enrichment, concentration and retention processes in relation to anchovy (*Engraulis ringens*) eggs and larvae distributions in the northern Humboldt upwelling ecosystem ☆

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Abstract

A Lagrangian model is used to simulate and quantify in the northern Humboldt upwelling ecosystem the processes of enrichment, concentration and retention, identified by Bakun [Bakun, A., 1996. Patterns in the ocean. Ocean processes and marine population dynamics. University of California Sea Grant, California, USA, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico, 323 pp.] as being important for the survival and recruitment of early life stages of pelagic fish. The method relies on tracking the positions of particles within water velocity fields generated by a three-dimensional hydrodynamic model. Simple criteria for considering particles as participating to enrichment, concentration or retention are used to derive indices of the three processes. We analyse the spatial distribution of and seasonal variability in these indices. The results are discussed in relation to anchovy (*Engraulis ringens*) eggs and larvae distributions off Peru, and to a comparable study conducted in the southern Benguela upwelling ecosystem.

Keywords: Lagrangian model; Ocean triad; Enrichment; Concentration; Retention; Pelagic fish; Recruitment; Ichthyoplankton; Peru; Hydrodynamic model; Mesoscale

1. Introduction

An increasing number of studies stress the influence that mesoscale hydrodynamic structures have on the dynamics of fish early life stages in eastern boundary current upwelling systems. For example, Logerwell and Smith (2001) found an association between offshore sardine survival and the presence of mesoscale eddies in the California Current upwelling system. Rodríguez et al. (1999, 2001, 2004) showed that retention and dispersion due to mesoscale features influenced the horizontal distribution of fish eggs and larvae in the northern Canary Current upwelling system. Castro and Hernández (2000) and Rodríguez-Graña and Castro (2003) argued that mesoscale filaments and plumes influence the composition of the ichthyoplankton community in the southern Humboldt Current upwelling system. Hutchings et al.

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(2002) mentioned the impacts of mesoscale activity on fish reproductive patterns in the Benguela Current upwelling system.

Nowadays hydrodynamic models produce realistic water circulation simulations at the regional scale. These simulations are increasingly used in connection with individual-based models of fish early life stages dynamics (Werner et al., 2001). Such "coupled" models have been used to study how water circulation affects transport of fish eggs and larvae (Quinlan et al., 1999; Allain et al., 2003; Huggett et al., 2003; Skogen et al., 2003; Ådlandsvik et al., 2004; Thorpe et al., 2004), their retention (Stenevik et al., 2003; Santos et al., 2004) or both (Voss et al., 1999; Hannah et al., 2000; Hinrichsen et al., 2001a,b, 2003, 2005; Miller et al., in press). The effects of water temperature on growth and mortality of ichthyoplankton (Miller et al., 1998; Bartsch and Coombs, 2001; Brickman et al., 2001; Pedersen et al., 2001; Mullon et al., 2003) and of water density on their vertical displacement (Hinckley et al., 1996; Hinckley, 1999; Parada et al., 2003) have also been considered in these models.

The success of recent coupled models attests that they are good tools for studying how biological and physical processes, and their interactions, affect the dynamics of fish early life stages. These works are, however, difficult to compare as they concern different species in various locations, and rely on different hydrodynamic models operating at various spatial and temporal scales. Considering coupled models within a generic framework would help this comparison. A step in this direction was achieved with the method proposed by Lett et al. (in press), which couples a hydrodynamic model and a Lagrangian particle-tracking model within the framework of Bakun's fundamental triad processes (Bakun, 1996). Bakun proposed an integrated theory of how the physical environment may influence the recruitment of marine populations having pelagic early life stages, based on three fundamental processes, enrichment, concentration and retention. Enrichment and concentration processes lead to areas where there is enough food that is sufficiently aggregated for larvae to feed, and retention processes enable them to stay in these favourable areas.

A first application was designed to study the spatial and seasonal variability of enrichment and retention in the southern Benguela upwelling system, and discussed regarding the reproductive strategies of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) off South Africa (Lett et al., in press). Here we use the same methodology to study Bakun's fundamental triad processes in the northern Humboldt upwelling system in relation to anchovy (*Engraulis ringens*) eggs and larvae distributions off Peru, and we compare the results of the two studies.

2. Methods

2.1. Anchovy eggs and larvae distributions

Between 1964 and 2003, 132 surveys were carried out by the Instituto del Mar del Perú (IMARPE) to assess anchovy (and other species) abundance. Ichthyoplankton samples were taken with Hensen nets of 0.33 m^2 mouth area and 300 µm mesh size, by vertical hauls between 0 and 50 m. The samples were fixed in 2% formaldehyde buffered with borax. Einarsson and Rojas de Mendiola (1963) was used for the taxonomy determination. Eggs and larvae were removed from the samples for counting. When their abundance was too high (more than 500 approx.), they were counted in only half or quarter of the entire sample and subsequently raised accordingly. This extensive dataset is under analysis at IMARPE and a comprehensive description of it will be presented in more detail in a forthcoming paper.

2.2. The hydrodynamic model

The ocean model is the Regional Oceanic Modeling System (ROMS). The reader is referred to Shchepetkin and McWilliams (2005) for a complete description of the model. ROMS solves the Primitive Equations in an Earth-centered rotating environment, based on the Boussinesq approximation and hydrostatic vertical momentum balance. ROMS is discretized in coastline- and terrain-following curvilinear coordinates. The model grid, forcing, initial and boundary conditions are built using the ROMSTOOLS package (Penven, 2003). To encompass the whole Peru Upwelling System, the grid extends from 20°S to 3°N and from 90°W to 70°W at a resolution of 1/9° (i.e., 10 km). The grid contains 192 by 256 points and 32 vertical levels.

As a first approach, we concentrate on the mean circulation and the seasonal cycle, leaving aside the interannual variability. The model is forced by COADS ocean surface monthly climatology for the heat and fresh water fluxes, and by a monthly climatology derived from QuikSCAT satellite scatterometer data for the wind stress. The three lateral open boundaries are forced using a climatology derived from the OCCAM global ocean model (Saunders et al., 1999). The model solution reaches a statistical equilibrium after a spinup of about 2 years. A complete description of the model configuration, analysis and validation is given by Penven et al. (2005). The average behaviour of the model and its variability has been checked against observed data and the close comparison between model output and observations provides confidence in the reliability of the model output to