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Modeling the early life history of jack mackerel in the southeastern Pacific: an approach to population connectivity

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Abstract

Currently, there are numerous transport simulation studies that have demonstrated the importance of hydrodynamics for advection, transport and finally the recruitment of early stages of marine pelagic species. Furthermore, recent studies have shown that the predictability of the models is improved by including realistic information about the locations and synchronization of spawning in setup and initial configuration of the transport models. In this paper, information regarding the location and seasonality of jack mackerel spawning was included in a scheme of biophysical modeling with the aim of studying the connectivity between spawning and nursery areas and its effect on the dynamics of recruitment. The results demonstrated that i) hydrodynamic model used in the scheme of biophysical modeling performed well in reproducing the interannual variability of oceanographic conditions of the study area; ii) there is connectivity between the main spawning area located in the oceanic area off central-southern Chile and the nursery grounds in the coastal area of northern Chile and southern Peru; iii) early stages of jack mackerel can be transported from Peru to the north, reaching the nursery ground and eventually contributing to recruitment, iv) spawning occurring in the coastal area of northern Chile is highly retained within the breeding area and could contribute to the dynamics of recruitment of jack mackerel. In addition, the results suggested that the transport paths for early stages are closely linked to the pattern of surface circulation and that mesoscale processes can affect retention or advection locally. This model allowed to satisfactorily simulate the early life history of horse mackerel; however, longer-term studies are necessary to demonstrate the predictability of the dynamics of recruitment.

1. Introduction

Stock structure hypothesis can be tested considering different methods including genetics, life history patterns, otolith microelements and parasites, and more recently, considering mark-recapture experiments and modeling life history to explain connectivity (Cadrin *et al*. 2014). Based on the use of physics of the ocean and early stage distribution of fish, biophysical models can be used to understand connectivity between different spawning areas to nursery grounds and their relationship with recruitment success (Calò *et al*. 2013).Thus, connectivity in marine populations results from the dispersal of eggs and larvae, and from the movement (daily, seasonal and ontogenetic) of juveniles and adults. Along the fish ontogeny, large-scale cues related to sensory and locomotors abilities, play an important role that should be considered in addition to larval transport (Staaterman *et al*. 2013).

Recent attempts are also made to address how biophysical modeling can help fisheries management, reducing spatio-temporal uncertainties of ecological processes and assisting management efforts in rebuilding fish stocks (Hinrichsen *et al*. 2013). The spatial structure of the oceanic spawning of jack mackerel off Chile has been well described by Cubillos *et al*. (2008), and the first experience of a biophysical model of connectivity regarding Jack mackerel was published by Vásquez *et al*. (2013), demonstrating that early stages of jack mackerel from the Southeastern Pacific can be transported from the spawning grounds centered at more than 600 nm from the coast at 36°S to coastal areas off Chile.

Within the SPRFMO, it is recognized that climate variability (El Niño – La Niña events) and Regime shift have an influence in the distribution of Jack Mackerel and also may be affecting recruitment success and stock productivity (SPRFMO 2014). Thus, stock assessment of jack mackerel considers two different stock-recruitment functions according to levels of recruitment. There also exist different stock structure hypotheses under discussion of SPRFMO and plausible management strategies are evaluated under different scenarios of population and stock structure.

With the purpose to understand the connectivity between different spawning areas and the nursery ground off coastal areas and their contribution to recruitment success, we developed a biophysical model. Connectivity was evaluated considering different source areas under extreme conditions like El Niño/La Niña events and results are discussed to understand population structure of jack mackerel in the Southeastern Pacific.

2. Materials and methods

2.1. The model

An Individual based model (IBM) of jack mackerel early life stages was coupled to a 3D hydrodynamic model with a customized version of the free modeling tool Ichthyop 3.2. (http://www.ichthyop.org/; Lett *et al*., 2008). In the following subsections, the implementation of the IBM is explained following the ODD (Overview, Design concepts, Details) protocol (Grimm *et al*., 2006, 2010). Considering that the main model is described in these terms (Lett *et al*., 2008), the specifications are based on customized version.

2.1.1. Purpose

The conceptual approach of this work is summarized in Figure 1. The purpose of the IBM simulations were to test hypotheses related to connectivity between spawning and nursery areas for jack mackerel in the southeastern Pacific through the modeling of the transport of eggs and larvae to the juvenile stage. The key life stage examined here was the early juvenile stage which consists of individuals who have reached 2 months of age and performing at least diel migration (Santander & Flores, 1983). This study follows the pattern-oriented approach recommended for obtaining ecological knowledge from IBM applications (e.g. Mullon *et al*., 2003; Catalán *et al*., 2013). Thus, the aim of this paper is not to predict but to evaluate the most likely destination for jack mackerel spawning from an inter-annual perspective, based on all available information about adult reproduction and behavioral aspects of the early stages. The approach is based on i) describing the spatial and temporal patterns of jack mackerel spawning for Peru, northern and southern Chile, ii) simulating the transport process for early stages of mackerel through a biophysical model, iii) analyzing the results in terms of population connectivity and reproductive success of each area evaluated, iv), and clarifying the conceptual model for jack mackerel early life history dynamics in the southeastern Pacific. The simulations were performed for two contrasting years in terms of oceanographic regime (1997-1998, 2010-2011) considering observed and estimated information to describe the reproductive season and using an interannual run for the physical model.

2.1.2. Entities, state variables and scales

The model consists of virtual jack mackerel and their marine physical environment. At each time step, the individuals are described by the following state variables: age (days since spawning), location (longitude, latitude and depth in the water column), length (standard, length in mm) and status (alive or dead). The environment variables with which virtual jack mackerel interact are the three-dimensional fields of current velocities (m s^{-1}), temperature (°C), and salinity.

The virtual environment is provided by an interannual Regional Ocean Modeling System (ROMS_AGRIF v3.0, www.romsagrif.org) with 10-km resolution and 32 sigma-levels, and configured for the southeastern Pacific in the domain 67ºW, 132ºW, 10ºN, 47ºS and 610 x 587 grid points. Atmospheric forcing data were provided by the PSD (Physical Sciences Division, NOAA/OAR/ESRL) using NCEP-DOE reanalysis 2 product to obtain the interannual atmospheric conditions. The western, northern and southern open boundary and initial conditions were taken from the Estimating the Circulation and Climate of the Ocean (ECCO) global data assimilation product (Wunsch & Heimbach, 2007). The bathymetry used was ETOPO2 with resolution 4-km. These boundary conditions were interpolated to the ROMS grid and imposed on a sponge layer of 10 horizontal grid points. A spin-up period of 1 year was assumed using both boundary conditions and atmospheric forcing data. After the model was stable, the initial state is used to begin the simulation for the 1994-2014 period. In this study, simulations for 1997-1998 and 2010-2011 August to January were performed. The model used for daily runs is validated by comparing simulated variables to satellite data using variability analysis based on Empirical Orthogonal Functions (EOF) in time and space, which is a common and straightforward tool to compare simulated variables and satellite data sets in the model performance assessments.

The ROMS fields were interpolated temporally and spatially in the IBM to determine the values of the environmental variables at any individual location. The time step for drifting simulation was 30 min and the outputs were recorded every 6 hours for later analysis. Each individual was simulated for up to 180 days to evaluate ways drift. However, an individual was considered "successful" when reaching 2 months old which is reasonable for a mainly planktonic nature of individuals.

2.1.3. Process overview and scheduling

Virtual eggs were released within the specified period in the virtual environment according to the observed spawning conditions defined by the data availability. For three different areas located in Peru, northern Chile and southern Chile, the spawning season duration and the spawning location were established using the information from eggs and larvae abundance collected during annual surveys (see below for details) and from reproductive indicators of adult females. From the spatial distribution of eggs and larvae registered in the surveys, the initial scaled-down abundance and distribution of the 20,000 particles were established in order to conduct the experiments. The virtual eggs were released in the first 50 m of the water column in accordance with the records of vertical stratified sampling performed in southern Chile. During the spawning season, releases of particles were performed every 7 days corresponding to the estimated spawning frequency for jack mackerel.

2.1.4. Design concepts

Stochasticity. To establish the appropriate number of particles in the transport experiments, repeated trials were performed in which the amount of particles at release was increased (1000, 5000, 10,000, 15,000, 20,000, 25,000 and 30,000), the ensemble average and the standard deviation were defined and the point at which these statistics stabilized was determined. The amount of 20,000 particles was established as representative of the desired ensemble average. Thus, we assumed that no repetition of the runs was necessary and that only one simulation was necessary for each set of parameter and for each day.

Observations. The model output is primarily presented as charts of the distribution and abundance of individuals that reached 2 months of age and which were confined in the nursery area, located between 15° and 30°S and between the coast and 200 nautical miles. The number of recruits in a particular geographic area is a function of the number of accumulated particles, which is summed for comparison between areas.

2.1.5. Initialization

To evaluate the reproductive success in a geographic context, three release areas were established based on the historic records of jack mackerel spawning coastal area off Peru, coastal area off northern Chile, oceanic area off central-southern Chile. For the first, the release zone was based on the distribution of larvae (no information related to the distribution of eggs) reported by Ayón & Correa (2013), assuming that the larvae presence is an indicator of reproductive activity (Figure 2). Because of the scarcity of information, two periods were established with average spatial distribution patterns: 1990-1999 and 2000-2010 which were considered representative of spawning area for 1997 and 2010 experiments, respectively. For northern Chile, egg distribution recorded by surveys and reported by Braun & Valenzuela (2008) were used to establish average conditions for two periods: 1993-1999 and 2000-2006, which were considered representative of spawning area for 1997 and 2010 experiments, respectively (Figure 3). Finally, for oceanic southern Chile, where the main spawning area is located, egg distribution recorded for surveys performed to carry out the spawning biomass estimation by the daily egg production method (see Núñez *et al*., 2008 for details; Figure 4). Spawning synchronization was defined by the annual cycle of gonadosomatic index, which came from observations of biological samples in the case of Chile and from those reported by Perea *et al*. (2013) for Peru. The vertical distribution of spawning was defined by stratified sampling of eggs made in the oceanic area south central Chile and summarized in Arcos *et al*. (2005) and Sepúlveda *et al*. (2006). Finally, in each simulation, 20,000 particles representing recently spawned eggs were released at midnight every 7 days which correspond to the jack mackerel spawning frequency.

2.1.6. Diel vertical migration

Linked to individual growth, the diel vertical migration sub-model defines changes in the vertical position of individuals overt time. The individuals performed DVM from surface to an increasing depth that depends on their age, from 12 days old (age of flexion; Vasquez *et al*., 2013) until the end of the simulation, with a maximum depth of 60 m.

2.1.7. Mortality

Mortality is temperature dependent considering that eggs die if they are exposed to temperatures below 12°C and over 24°C. In the absence of empirical experiments to evaluate mortality, this criterion was defined by the limits of temperature where spawning has been observed historically (see Cubillos *et al*., 2008 as an example). Further sources of mortality are not included.

3. Results

3.1. Hydrodynamic model validation

To explore the performance of the model on the inter-annual timescale, a comparison between Pathfinder satellite and ROMS sea surface temperature was performed. The spatial and temporal modes of variability of the SST were calculated based on EOFs, and then compared to the Pathfinder dataset from 1994 to 2012. The first two modes of variability for the principal components of SST explained a large percentage of the variance (48% and 66% for observed and model data respectively). In the model these modes appear as distinct while in the observations the second mode is not independent of higher modes. Nevertheless, the first PC of SST (Figure 5) is consistent with observations in their spatial patterns and share strong and significant correlation with the observed PC temporal evolution. The first mode of variability of the temporal PC for SST showed a high correlation level between the modeled and observed data (R2= 0.93; Figure 3c, d). The spatial expression of satellite and model data showed a high coherence, reproducing the main oceanographic features through the entire analyzed domain (Figure 3a, b). However, it revealed some differences in the coastal region, which could be related to upwelling dynamics.

3.2. Simulated juvenile recruitment success

Peru spawning zone: for the 1997 peak spawning season slightly high proportion (30%) of individuals was transported southward reaching the criteria for recruitment success. A portion of these individuals had a pattern of dispersion near the coast, while another was transported offshore and then entered the area of recruitment, which was mainly recorded for the period from August to September (Figure 6). The monthly contribution to recruitment was analyzed for the entire spawning season in relation to the magnitude of the release per month. The monthly contribution to the recruitment of juvenile jack mackerel, in relation to the release date was highly variable, ranging from 50.3% in November to 19.24% in January. Spatial contribution to recruitment was mainly centered between 16° and 19°S, yielding over 60% of successful individuals (Figure 9 left panel).

Northern Chile spawning zone: for the 1997 peak spawning season, a high percentage of individuals (41%) was retained within the nursery area to achieve the criteria of recruitment (live up to 2 months old). A fraction of these individuals was advected offshore and then returned and entered the breeding area to provide recruitment, which was mainly observed for spawning occurred between August and October (Figure 7). The monthly contribution to recruitment was analyzed for the entire spawning season in relation to the magnitude of the release per month. The monthly contribution to the recruitment of juvenile jack mackerel, in relation to the release date was highly variable, ranging from 43.8% in October to 6.7% in January. Spatial contribution to recruitment was mainly centered between 16° and 19°S, yielding over 60% of successful individuals (Figure 9, middle panel).

Southern Chile spawning zone: this corresponds to the main mackerel spawning area in terms of abundance and it is located approximately 1,000 kilometers away from the nursery ground. However at this distance, modeling established connectivity between jack mackerel spawning stock and recruits by transport eggs and larvae. For the 1997 peak spawning season, 3.5% of the released individuals successfully reached the nursery ground. Individuals recruited successfully followed two main routes of transportation, the first through the ocean sector which connected on more than 120 days time (which could exceed the planktonic stage and is arguably) directly to the northern boundary of the nursery ground (reaching even Peru) from spawning occurred mainly in the months of August, September and October; and the second with individuals who reached the nursery area through southern limit in about 70 days (Figure 8). The monthly contribution to recruitment was analyzed for the entire spawning season in relation to the magnitude of the release per month. The monthly contribution to the recruitment of juvenile mackerel, in relation to the release date was highly variable, ranging from 4.5% in August to 0.5% in January. Spatial contribution to recruitment was mainly centered between 26° and 30°S, yielding over 80% of successful individuals (Figure 9, left panel).

4. Concluding remarks

i) ROMS hydrodynamic model used in the scheme of biophysical modeling performed well in reproducing the interannual variability of oceanographic conditions of the study area.

ii) There is connectivity between the main spawning area located in the oceanic area off central-southern Chile and the nursery grounds in the coastal area of northern Chile and southern Peru;

iii) Early stages of jack mackerel can be transported from Peru to the north, reaching the nursery ground and eventually contributing to recruitment;

iv) Spawning occurring in the coastal area of northern Chile is highly retained within the area of breeding and could contribute to the dynamics of jack mackerel recruitment.

v) The results suggested that the transport paths for early stages are closely linked to the pattern of surface circulation and that mesoscale processes can affect retention or advection locally.

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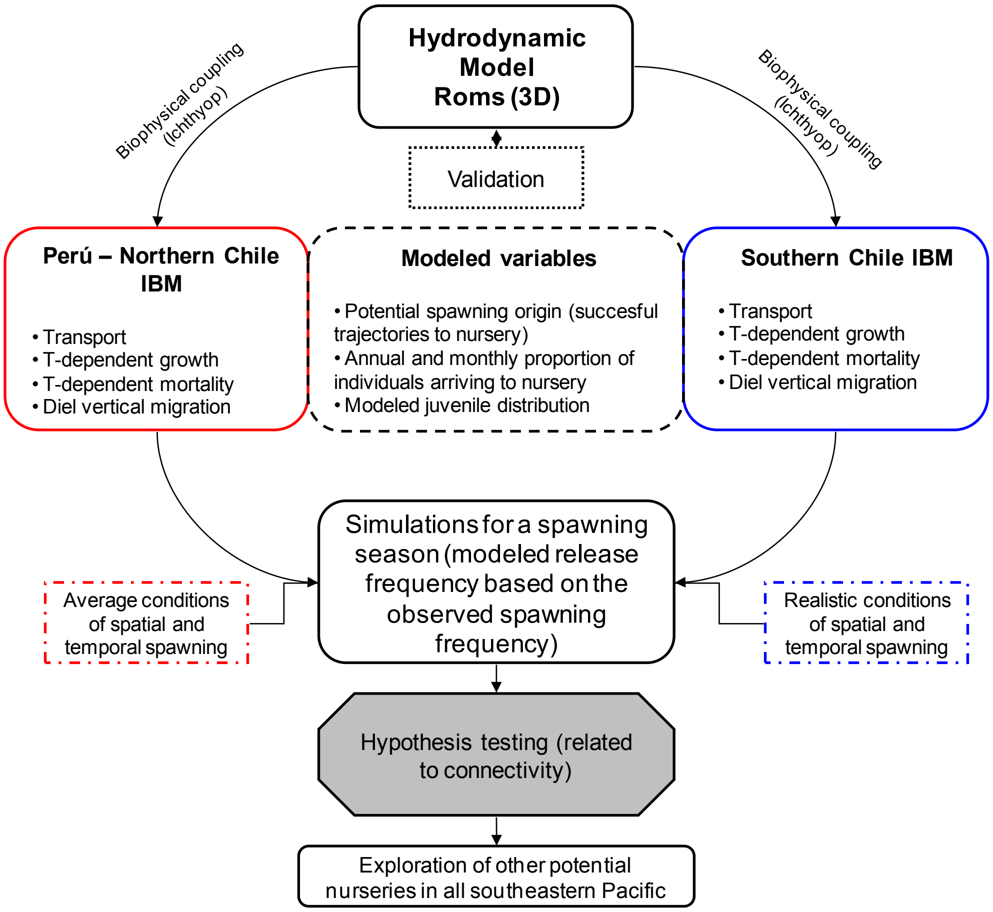

Figure 1. Conceptual diagram of the study. Modeled variables correspond to the outputs of biophysical model and challenge the dynamics of jack mackerel early life stage dynamics in the southeastern Pacific.

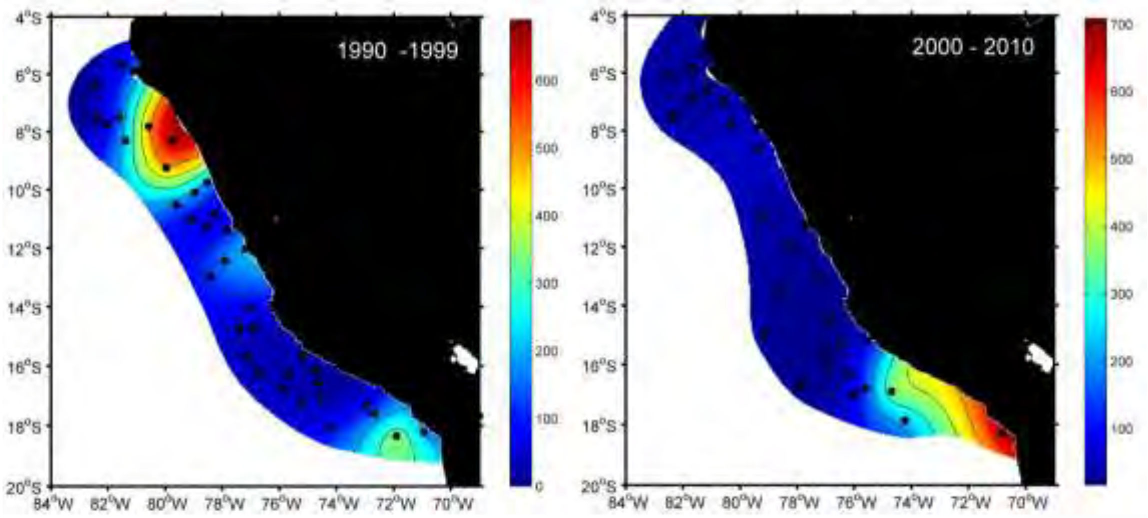

Figure 2. Observed distribution of jack mackerel larvae off coastal Peru on which the initialization of the biophysical model is based.

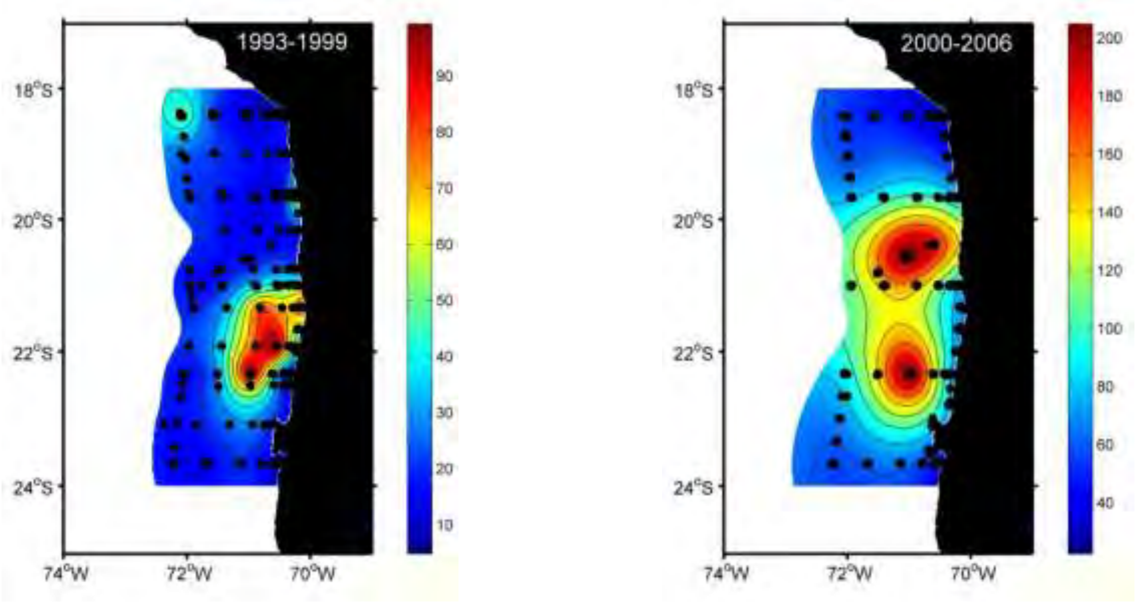

Figure 3. Observed distribution of jack mackerel larvae eggs off coastal Chile on which the initialization of the biophysical model is based.

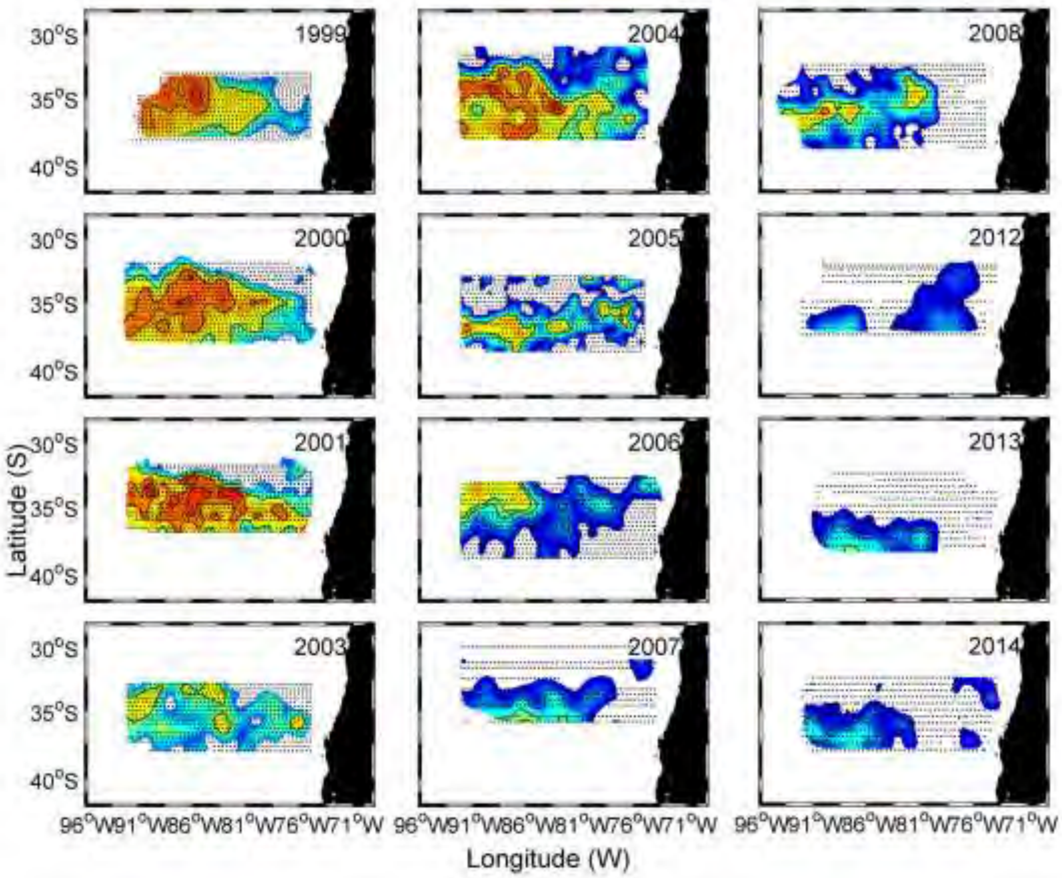

Figure 4. Observed distribution of jack mackerel larvae in the oceanic zone off central Chile on which the initialization of the biophysical model is based.

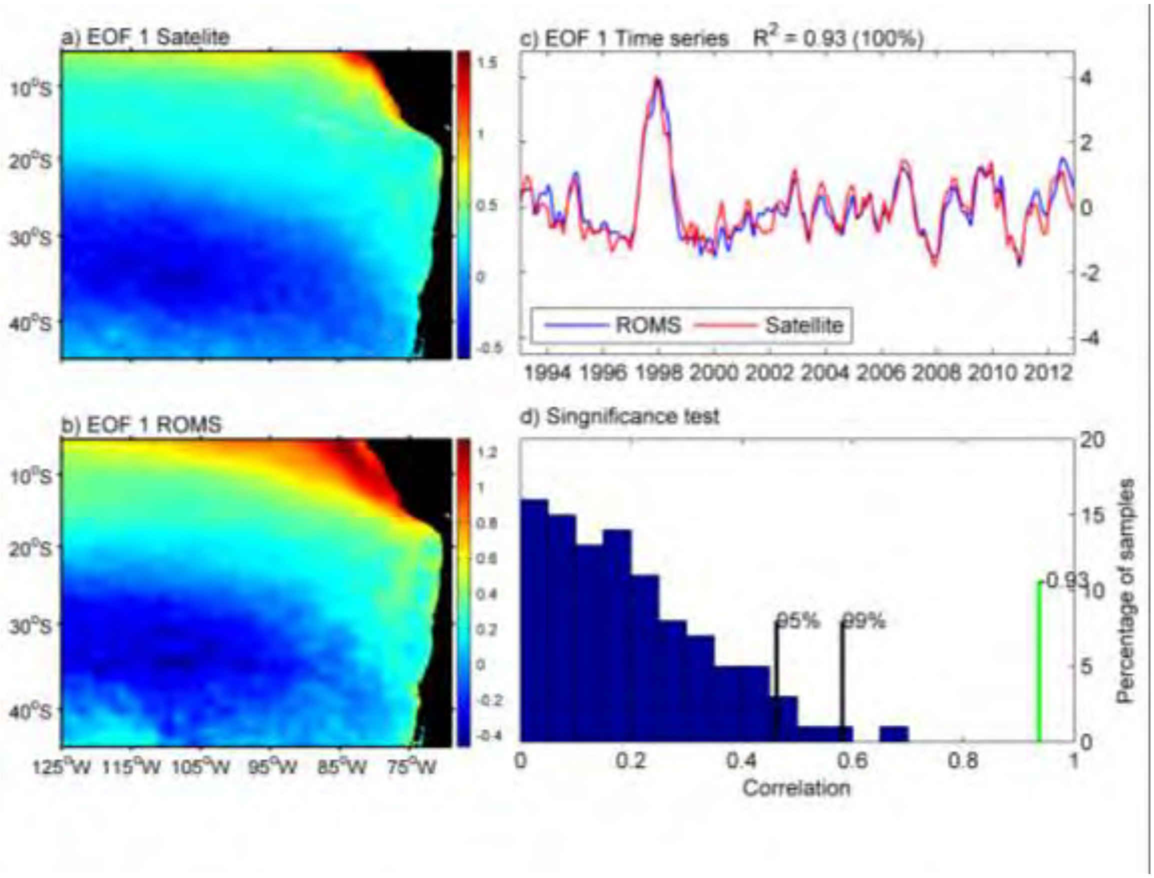

Figure 5. Summary of the validation of the hydrodynamic model. EOF's first mode of variability for Sea Surface Temperature. Spatial domain for a) Pathfinder satellite data and b) ROMS model. c) 1994 – 2012 time series for Pathfinder satellite and ROMS model data. Significance of correlation between time series based on the probability density function of the cross-correlation coefficients.

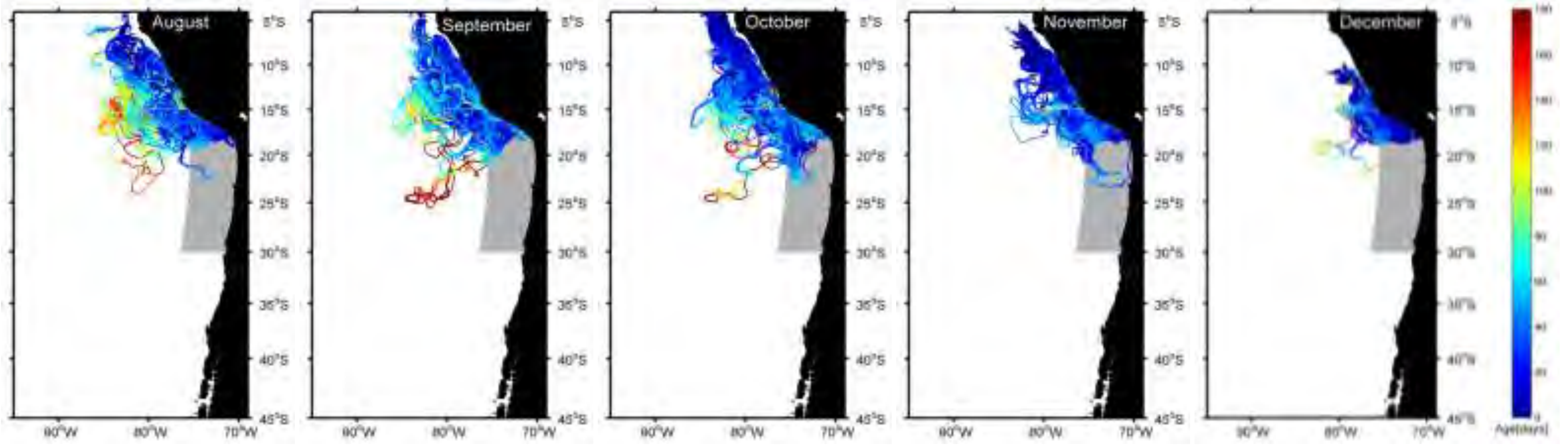

Figure 6. Tracking of the recruited individuals released by months in the 1997 spawning season for Peru's spawning zone. The color bar represents the age of the individuals. The nursery area is identified with a grey polygon.

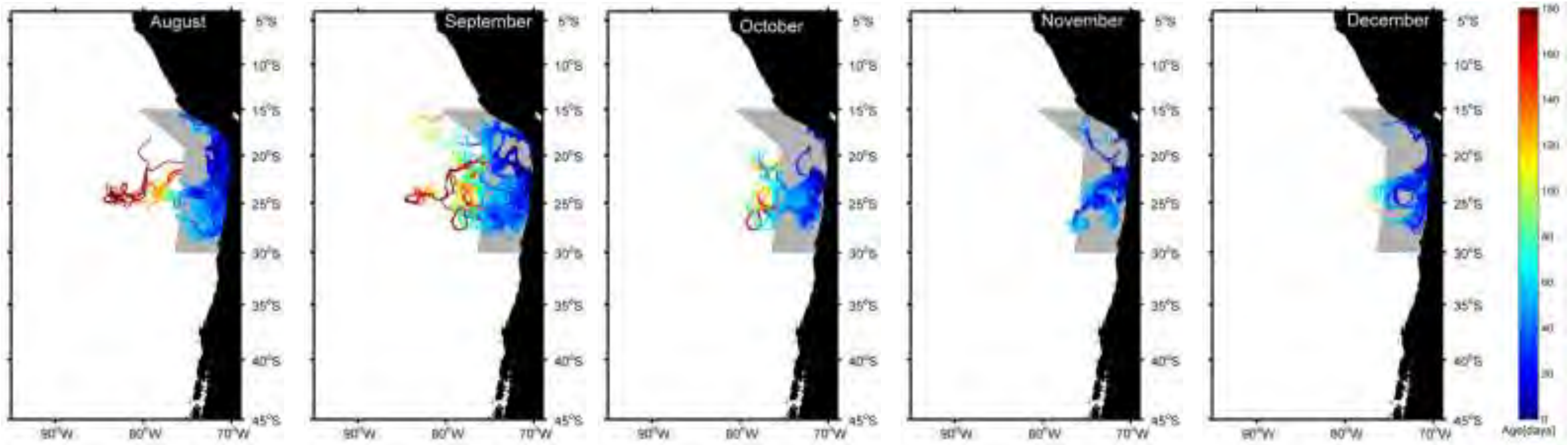

Figure 6. Tracking of the recruited individuals released by months in the 1997 spawning season for northern Chile's spawning zone. The color bar represents the age of the individuals. The nursery area is identified with a grey polygon.

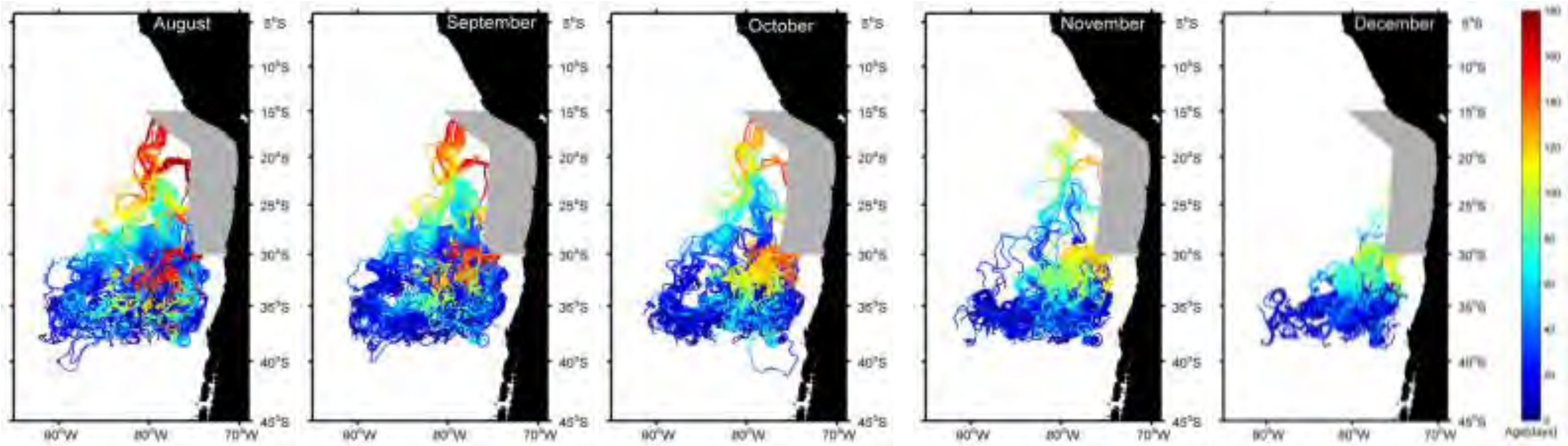

Figure 8. Tracking of the recruited individuals released by months in the 1997 spawning season for southern Chile's spawning zone. The color bar represents the age of the individuals. The nursery area is identified with a grey polygon.

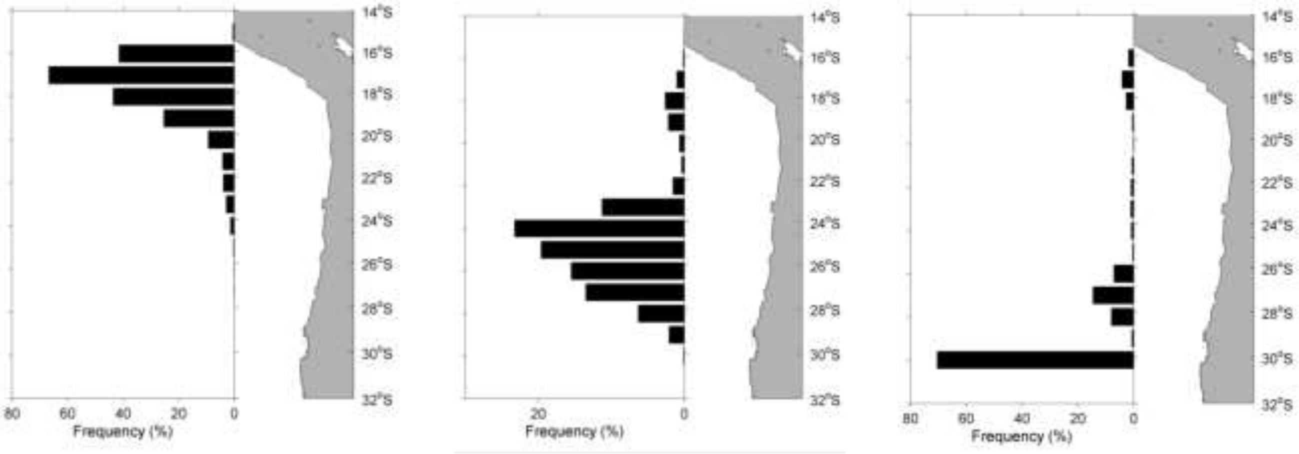

Figure 9. Latitudinal contribution to the recruitment of juvenile in the nursery ground. Spawning areas off Peru (left panel), northern Chile (middle panel) and south-central Chile (right panel).