

Biophysical modelling to assess population connectivity and inter-annual variability in the recruitment patterns of jack mackerel in the southeastern Pacific

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Abstract

The jack mackerel (*Trachurus murphyi*) population has historically supported one of the most important fisheries in the southeastern Pacific Ocean, however, catches, biomass and recruitment levels have decreased steadily over the last decade to a minimum in 2008. In this context, there is increasing interest in studying jack mackerel recruitment dynamics and population structure under a scenario of small population size. At present, numerous transport simulation studies have demonstrated the importance of hydrodynamics for advection, transport and finally the recruitment of early stages of marine pelagic species. Furthermore, the dispersion of early stages is one of the key factors for population connectivity, which is especially important for species with broad geographic distribution. In order to study the patterns of connectivity between different areas of spawning and the nursery ground and its effect on the recruitment dynamics, an individual-based model (IBM) was coupled to a validated hydrodynamic model to simulate annual patterns in the early life history of jack mackerel for the period 1994-2013.

The IBM configuration included realistic initial conditions related to the location and synchrony of spawning in three spawning grounds: coastal area off Peru, coastal area off northern Chile and oceanic area off central Chile. Moreover, the transport process included

a scheme for eggs buoyancy and vertical migration for larvae. Results showed that: i) as product of oceanographic dynamics off the coast of Peru, the dispersion is highly dependent on the location of spawning area: if the jack mackerel spawning area is located off northern Peru, then predominates high advection towards offshore; on the other hand if the spawning area is located in the south-central area of Peru, there exist a greater retention, dispersion towards the south and connectivity to the nursery ground situated in the coastal area off northern Chile and southern Peru; ii) the spawning area located in northern Chile shows high levels of retention (>80%) and low interannual variability; iii) the surface circulation pattern associated with the subtropical gyre supports connectivity between the main spawning area located in the oceanic area off south-central Chile and the nursery ground. Furthermore, we propose that our simulations are coherent with the existing recruitment estimation and therefore open new possibilities for fisheries management. Finally, the proposed modelling scheme reasonably simulates the early life history of jack mackerel and can also be considered to understanding relative stock structure hypotheses. The high dispersion range and spatial overlap of modelled recruitments support the hypothesis of a single population, which is consistent with the genetic evidence of jack mackerel in the southeastern Pacific.

1. Introduction

Different approaches have been used to study and testing stock structure hypotheses for the Chilean Jack Mackerel of the southeastern Pacific. Genetic studies based in microsatellites have not revealed differences between different zones along the distribution of this transboundary species (Cardenas *et al.*, 2009). There also exist, different approaches that for instance consider alternative methods including: life history patterns, otolith microelements and parasites, and more recently, considering mark-recapture experiments and modeling life history to explain connectivity in pelagic species (Cadrin *et al.* 2013) and fidelity of spawners (Lowerre-Barbieri *et al.* 2013). Considering models based on the physics of the ocean and early stages distribution of fish, coupled 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 with sensory and locomotors abilities, play an important role that should be consider 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) and reproductive resilience (Lowerre-Barbieri *et al.* 2016).

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 in Jack mackerel was published by Vásquez *et al.* (2013), suggesting 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.

Inside SPRFMO, it is recognized that climate variability (El Niño – La Niña events) and Regime shift have an influence in distribution of Jack Mackerel and also may be affecting recruitment success and stock productivity (SPRFMO, 2013). Thus, stock assessment of

jack mackerel considers two different stock-recruitment functions according with levels of recruitment. There also exist different stock structure hypothesis under discussion of SPRFMO and plausible management strategies are evaluated under different scenarios of population and stock structure.

With the purpose to understand connectivity between different spawning areas and the nursery ground off coastal areas and their contribution to recruitment success, we develop a biophysical model. In a first study, Vásquez *et al.* (2015) evaluate connectivity considering different source areas under two extreme conditions like El Niño/La Niña events and results were discussed to understand population structure of jack mackerel in the Southeastern Pacific. This study is extending the analysis for a long period between 1994 and 2013.

2. Materials and methods

2.1. The model and conceptual approach

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). Considering that the main model is described in these terms (Lett *et al.*, 2008), the specifications are based on customized version.

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 examines here was the aerly juvenile stage which are 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 obtain 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 reproductive 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) clarifying the conceptual model for jack mackerel early life history dynamics in the southeastern Pacific. The model runs were performed for annual spawnings between 1992 and 2013, considering observed and estimated information to describe the reproductive season and using an inter-annual run for the physical model.

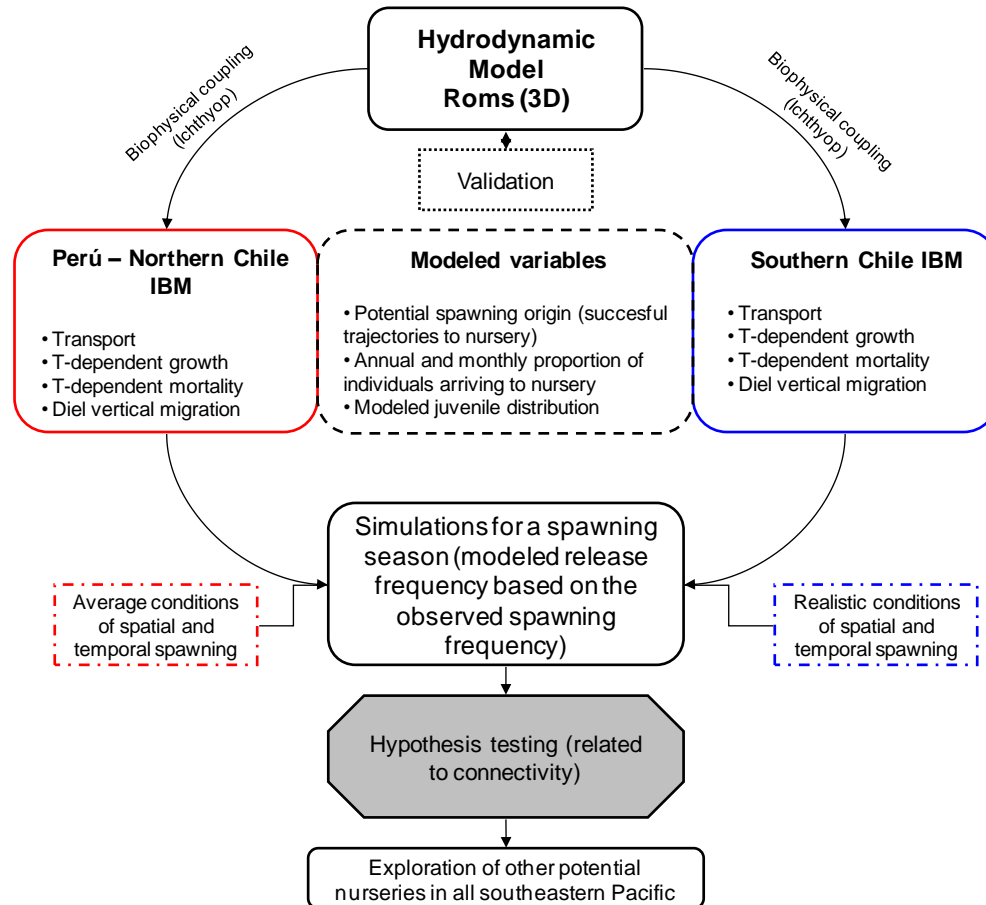


Figure 1. Conceptual diagram of the study. Modelled variables correspond to the outputs of biophysical model and challenge the dynamics of jack mackerel early life stage dynamics in the southeastern Pacific.

2.2. Entities, state variables and scales

The model consists in 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 ($^{\circ}\text{C}$) 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 67°W , 132°W , 10°N , 47°S and 610×587 grid points. Atmospheric forcing data were provided by the PSD (Physical Sciences Division, NOAA/OAR/ESRL) using NCEP-DOE reanalysis 2 data (from 1979 to 2013) to obtain the interannual atmospheric condition. The western, northern and southern oceanic boundary conditions were taken from the Estimating the Circulation and Climate of the Ocean (ECCO) global data assimilation product (Wunsch & Heimbach, 2007). 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. 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. After the model was stable and validated, the initial state is used to begin the simulation for 1994-2013 period. In this study simulations for all the reproductive seasons from 1994 to 2013 were performed from August (t) to January ($t+1$).

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 drift patterns, however an individual was considered "successful" to have 4 months old which is reasonable for a mainly planktonic nature of individuals.

2.3. 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 situated 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 perform the experiments. The virtual eggs were released in the first 50 m of the water column in accord to the recorded in vertical stratified sampling performed in southern Chile. During the spawning season, releases particles were performed every 7 days corresponding to the estimated spawning frequency for jack mackerel.

2.4. 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 were increased (1.000, 5.000, 10.000, 15.000, 20.000, 25.000 and 30.000), defined the ensemble average and the standard deviation and determined the point at which these statistics stabilized. 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 reached 2 months of age and which were confined in the area

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.

2.5. 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 1994-1998 and 2000-2013 experiments, respectively. For northern Chile, eggs 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 situated, eggs 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 Sepulveda *et al.* (2006). Finally, in each simulation, 20,000 particles represented recently spawned eggs were released at midnight every 7 days which correspond to the jack mackerel spawning frequency.

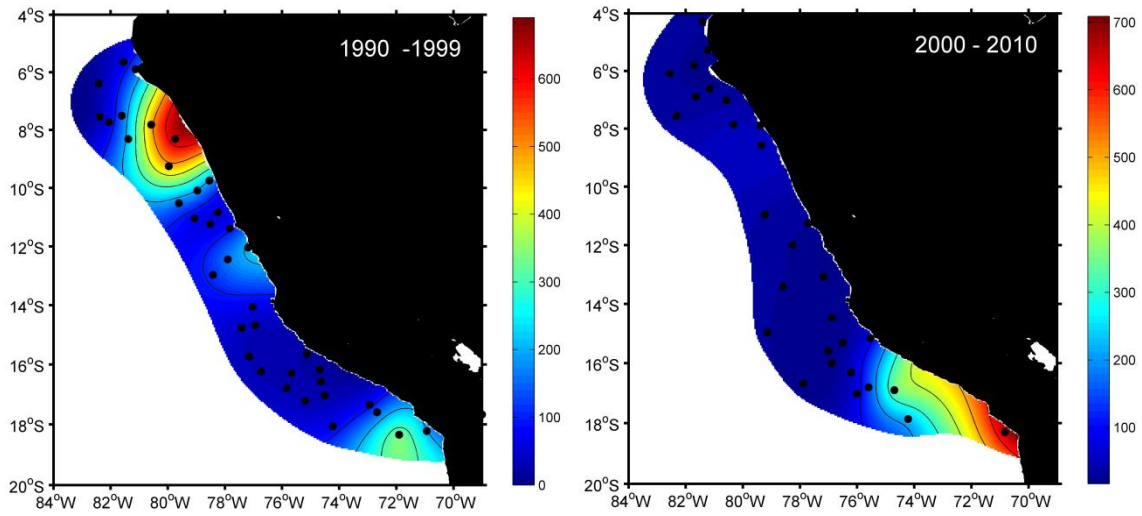


Figure 2. Observed distribution of jack mackerel larvae off Peru in which the initialization of the biophysical model is based.

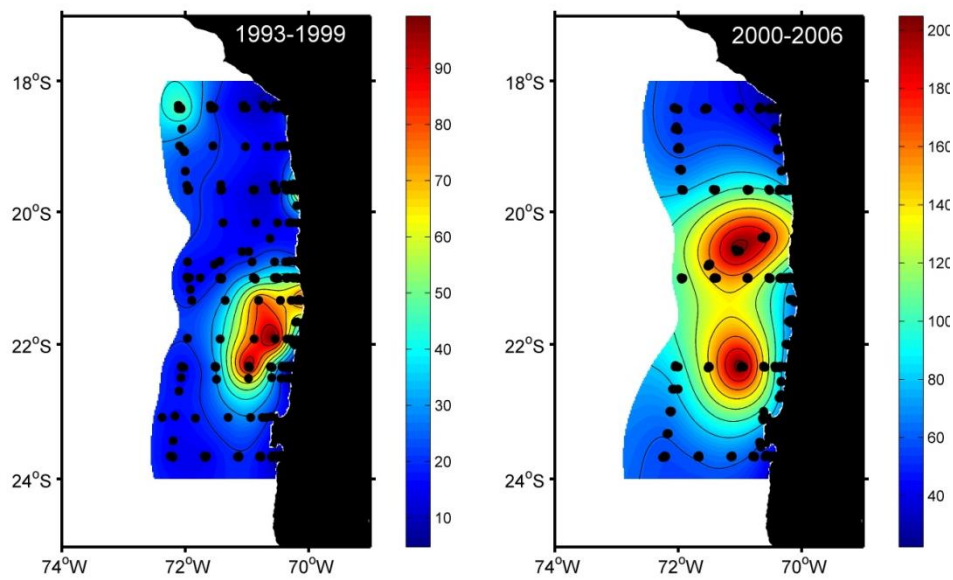


Figure 3. Observed distribution of jack mackerel larvae eggs off Northern Chile in which the initialization of the biophysical model is based.

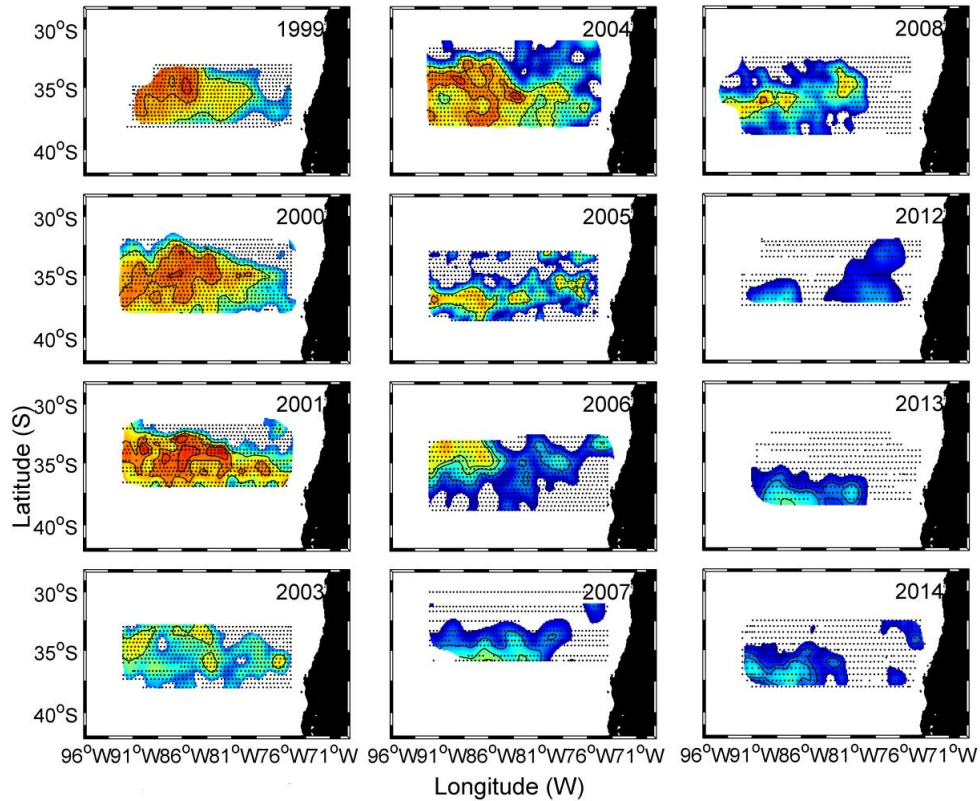


Figure 4. Observed distribution of jack mackerel larvae in the oceanic zone off South-Central Chile in which the initialization of the biophysical model is based.

2.6. Diel vertical migration

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

2.7. 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 modelled and observed data ($R^2 = 0.93$; 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 5a, b), however revealed some differences in the coastal region, which could be related to upwelling dynamics.

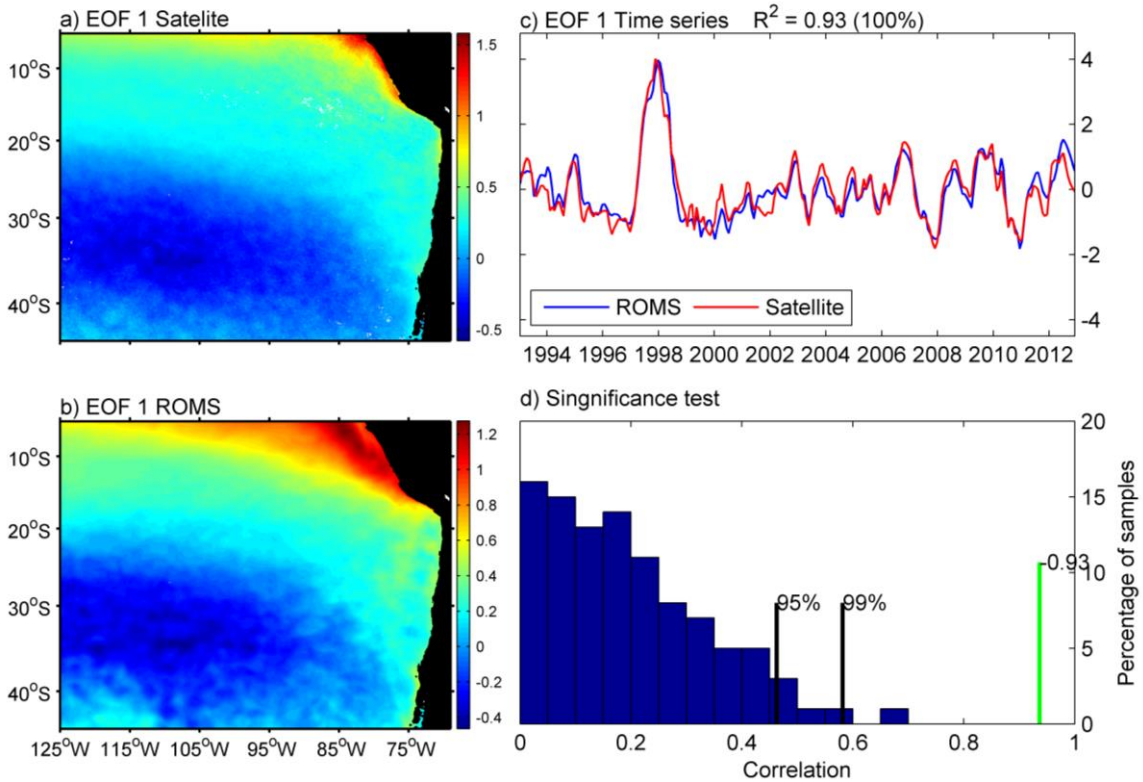


Figure 5. Summary of the validation of the hydrodynamic model. EOF's first mode of variability for Sea Surface Temperature. Spatial domain for a) Pathfinder satellite data and b) OFES model. c) 1994 – 2012 time series for Pathfinder satellite and OFES model data. Significance of correlation between time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

3.2. Simulated juvenile distribution and drifting patterns

The distribution of modelled juvenile jack mackerel (120 days old) from Peru spawning area is showed in Figure 6. The results revealed two scenarios for the spatio-temporal patterns of drifting pathways and the related connectivity. When spawning region is located in coastal northern Peru, as in the period 1994-1999, high levels of offshore advection is registered, reaching up to 500 km offshore. In the other hand, when the spawning area is located in the southern area off coastal Peru, as reported since 2000, high levels of coastal retention and transport southward is observed promoting higher connectivity with the main spawning area described above. Thus, evaluating the dispersion matrices the results revealed that the spawning region off Peru is connected to northern Chile with connection levels over 40% for 2001, 2002, 2009 and 2013 spawning seasons. In addition, inside the

spawning area it was observed retention levels over 50% for 1994,1997 and 2005 spawning seasons. High offshore advection ($>50\%$) was observed during 1995, 1998 and 1999. Finally, lower connectivity with the oceanic area off northern Chile were registered with average levels around 18%.

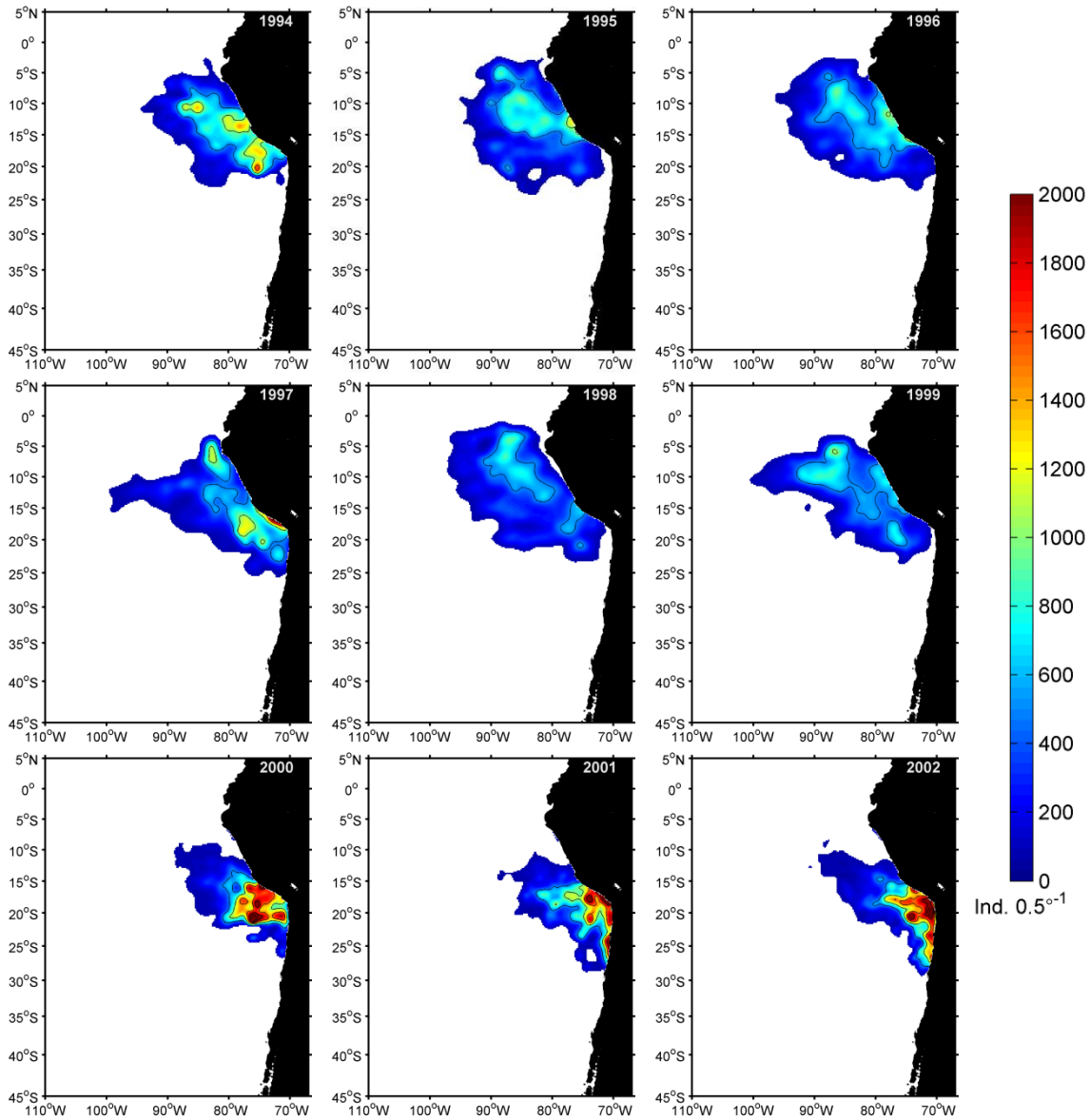


Figure 6. Spatial distribution of modelled juvenile jack mackerel (120 days old) originated from the spawning area located in the coastal region off Peru.

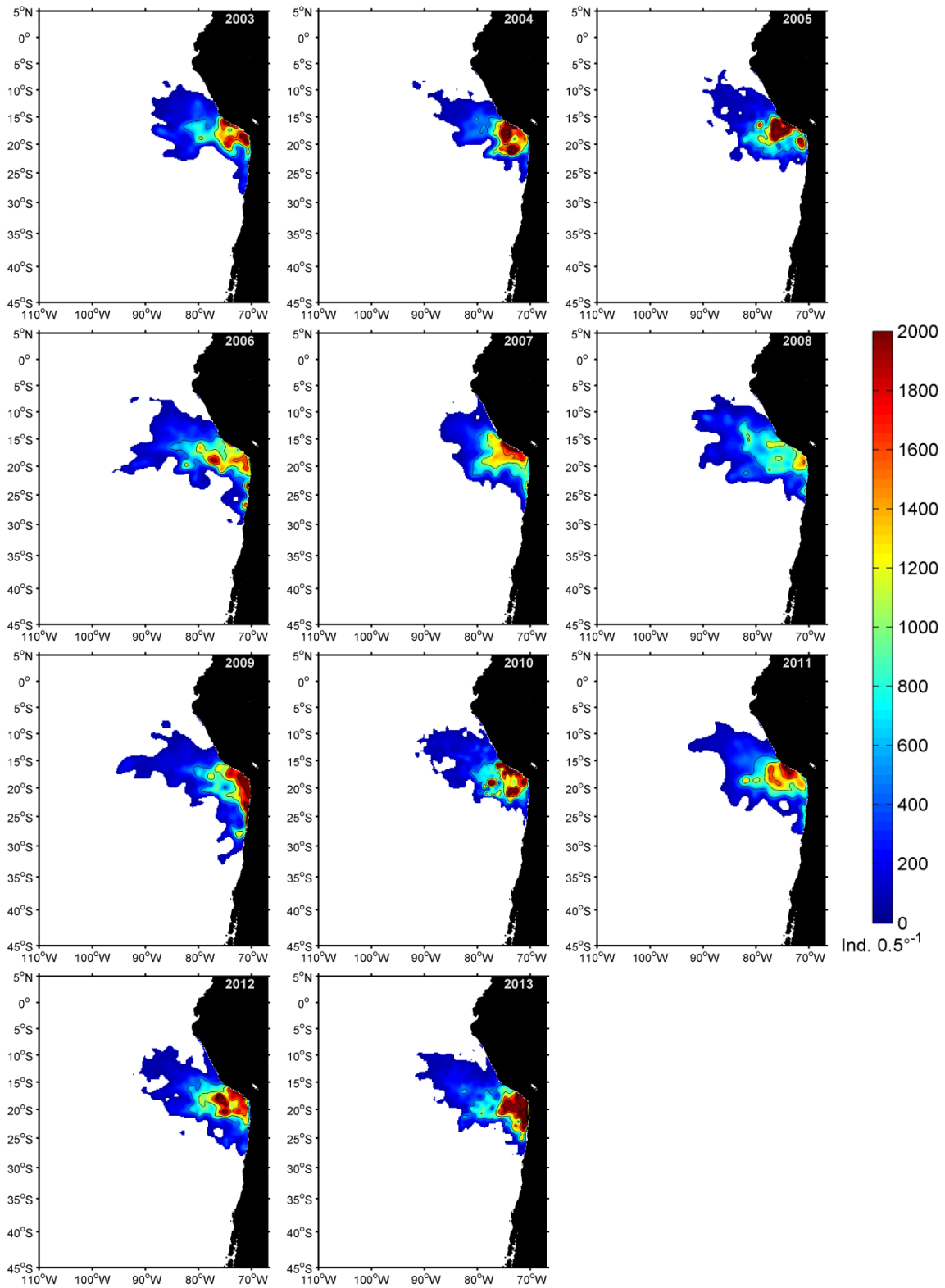


Figure 6 (cont.). Spatial distribution of modelled juvenile jack mackerel (120 days old) originated from the spawning area located in the coastal region off Peru.

The spatial distribution of modelled juvenile jack mackerel originated from the spawning area located in coastal northern Chile is showed in Figure 7. This area is characterized by high retention levels for all the study period. However, during 2004 results showed an advective process that generated an offshore dispersion of modelled individuals. On the other hand, in the reproductive seasons of 2002, 2003 and 2013 a higher coastal southward dispersion was observed, nevertheless the hydrodynamics of this area promotes high nearshore retention levels. The results associated to the dispersion matrices revealed that the spawning region off northern Chile has high levels of retention, which was mainly observed during 2000, 2001, 2005, 2007 and 2010 with retention levels over 85%. This zone was connected to coastal region off southern Peru, which was empathized during 1998, 1999 and 2004 with dispersion levels over 30%. In addition, offshore dispersion was observed, specially in 1995, 1998, 2005 and 2013 ($>20\%$).

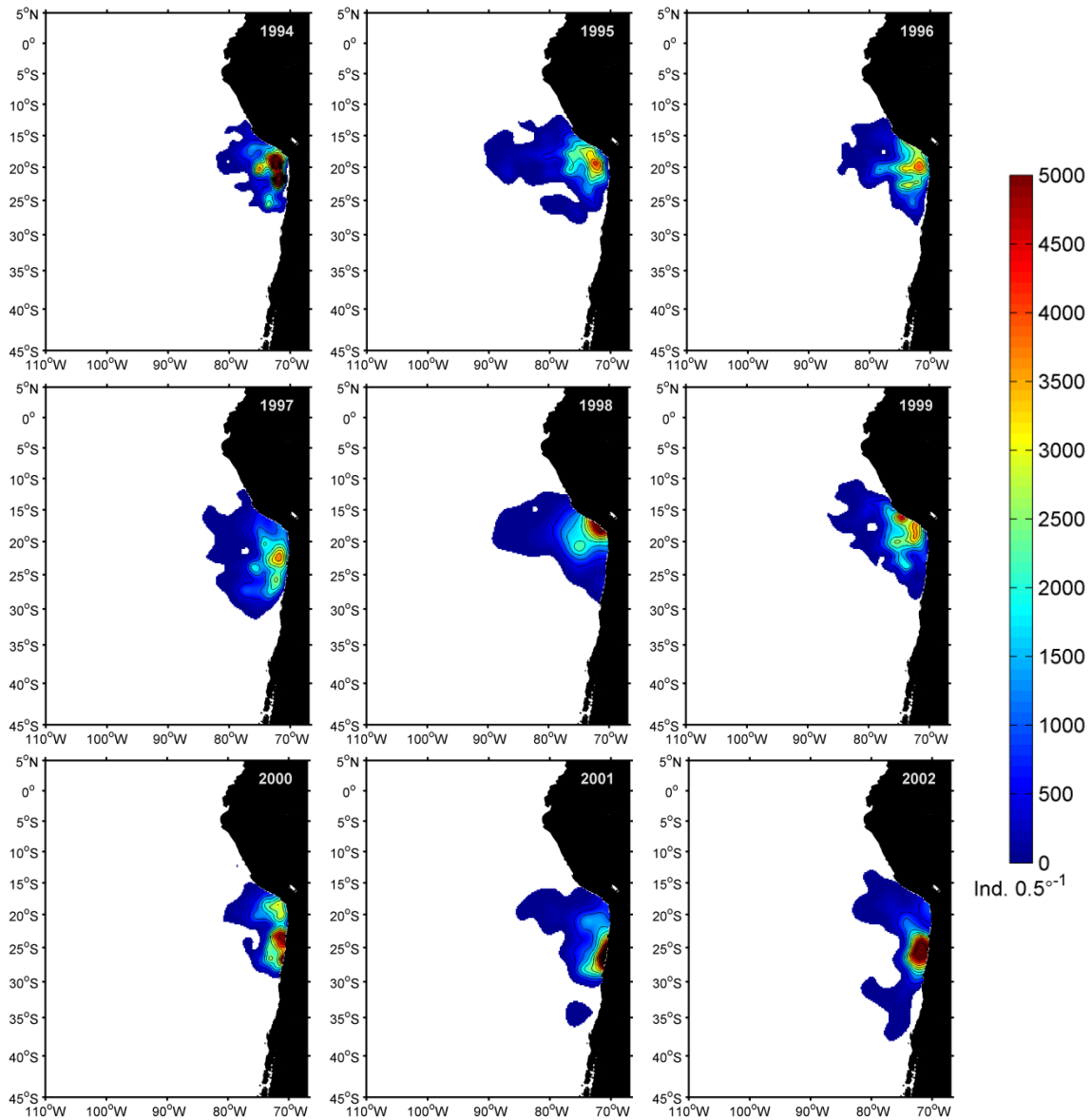


Figure 7. Spatial distribution of modelled juvenile jack mackerel (120 days old) originated from the spawning area located in the coastal region off northern Chile.

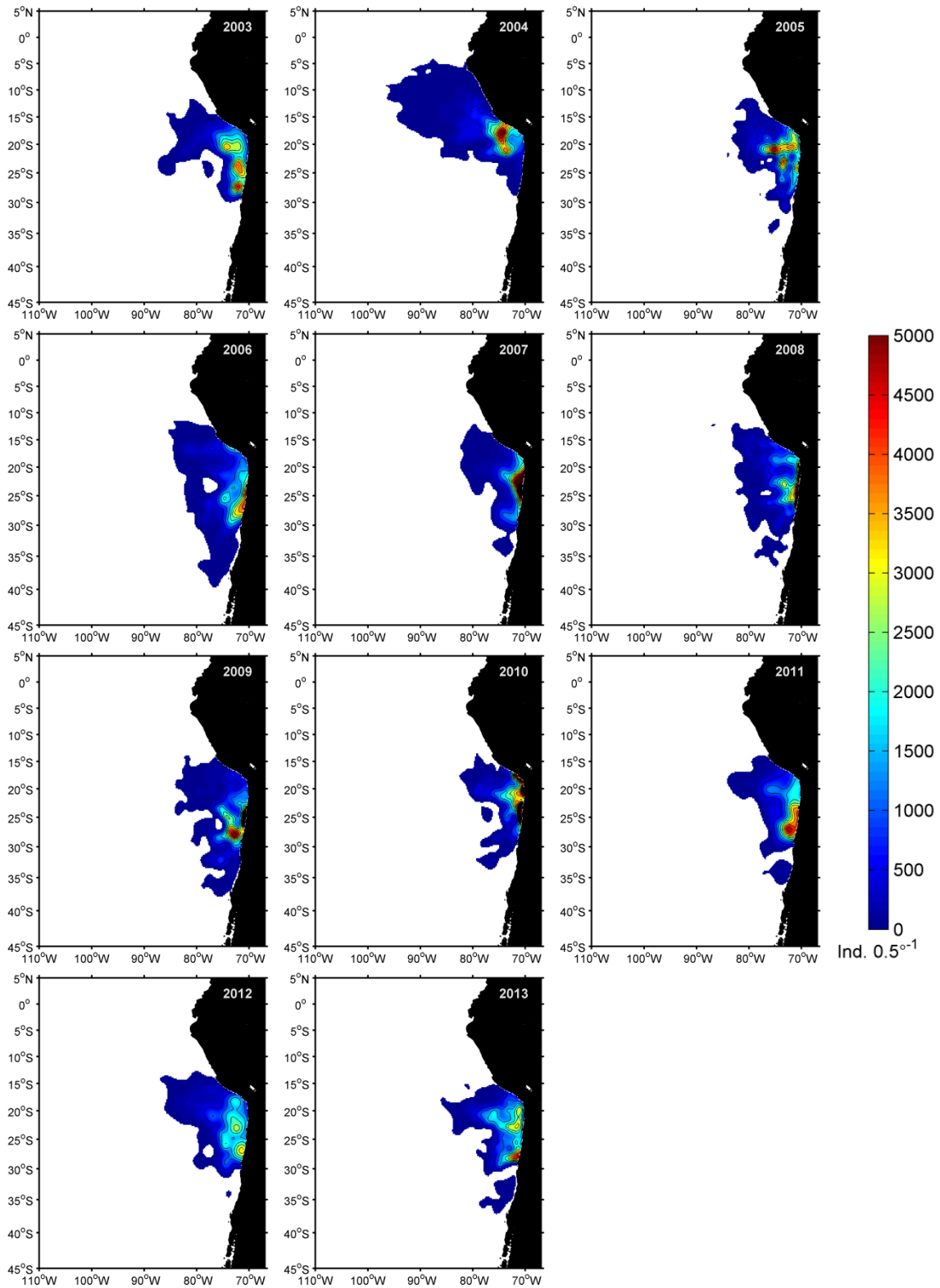


Figure 7 (cont). Spatial distribution of modelled juvenile jack mackerel (120 days old) originated from the spawning area located in the coastal region off northern Chile.

The spatial distribution of modelled juvenile jack mackerel originated from the main spawning area located in oceanic central-southern Chile is showed in Figure 8. The spatial pattern showed a main dispersion to the northeast, specially of those individuals reaching 80°W promoting connectivity with the nursery grounds. In addition, a proportion of the individuals are retained in the oceanic region. The dispersion matrices revealed connectivity with the nursery ground in all the study period with average levels of 25%. In addition, this spawning area showed high retention levels in 2005, 2006, 2008, 2012 and 2013 (>80%). Results also showed low connections with coastal region off central-southern Chile (around 3%).

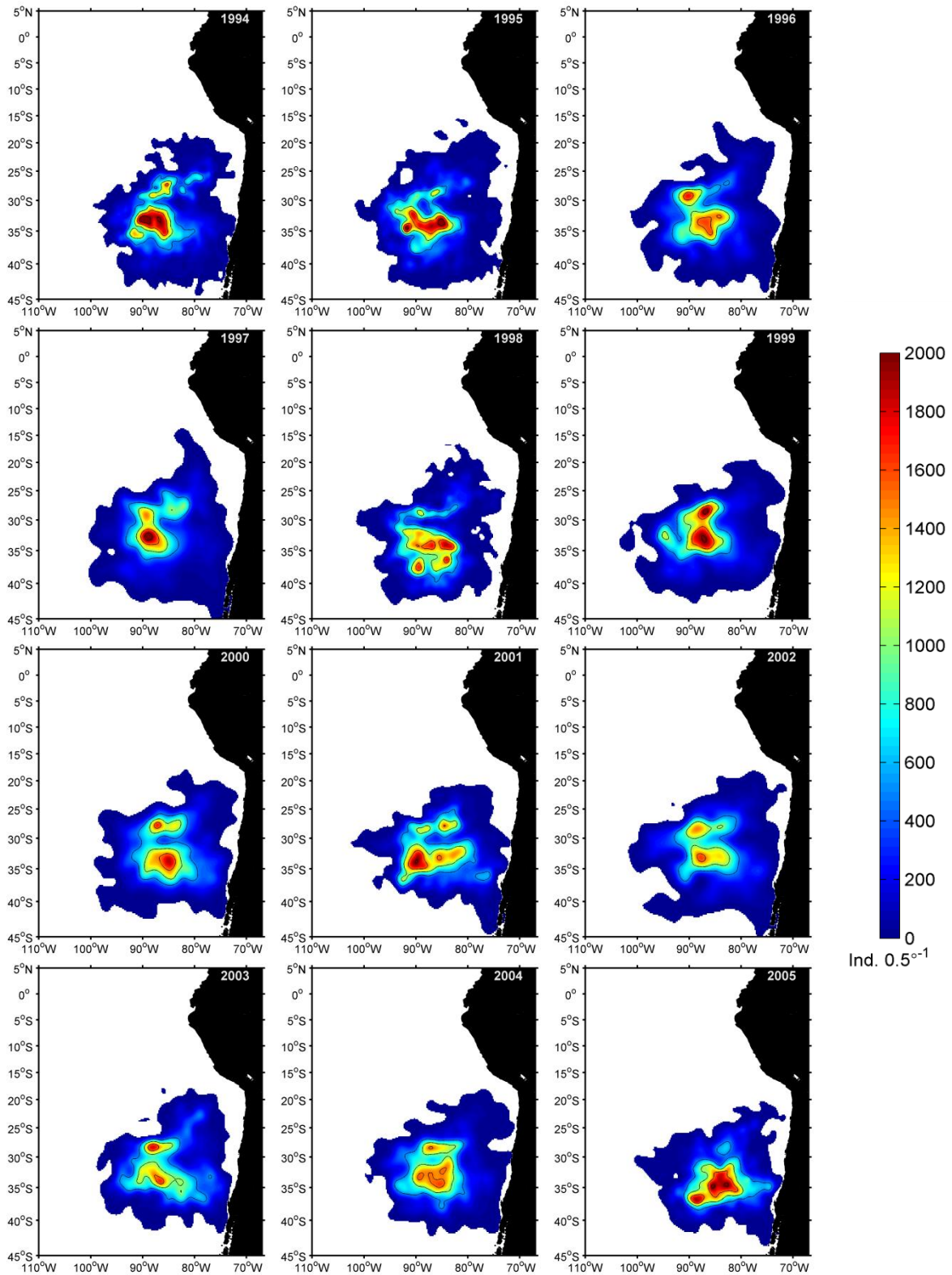


Figure 8. Spatial distribution of modelled juvenile jack mackerel (120 days old) originated from the main spawning area located in the oceanic region off central Chile.

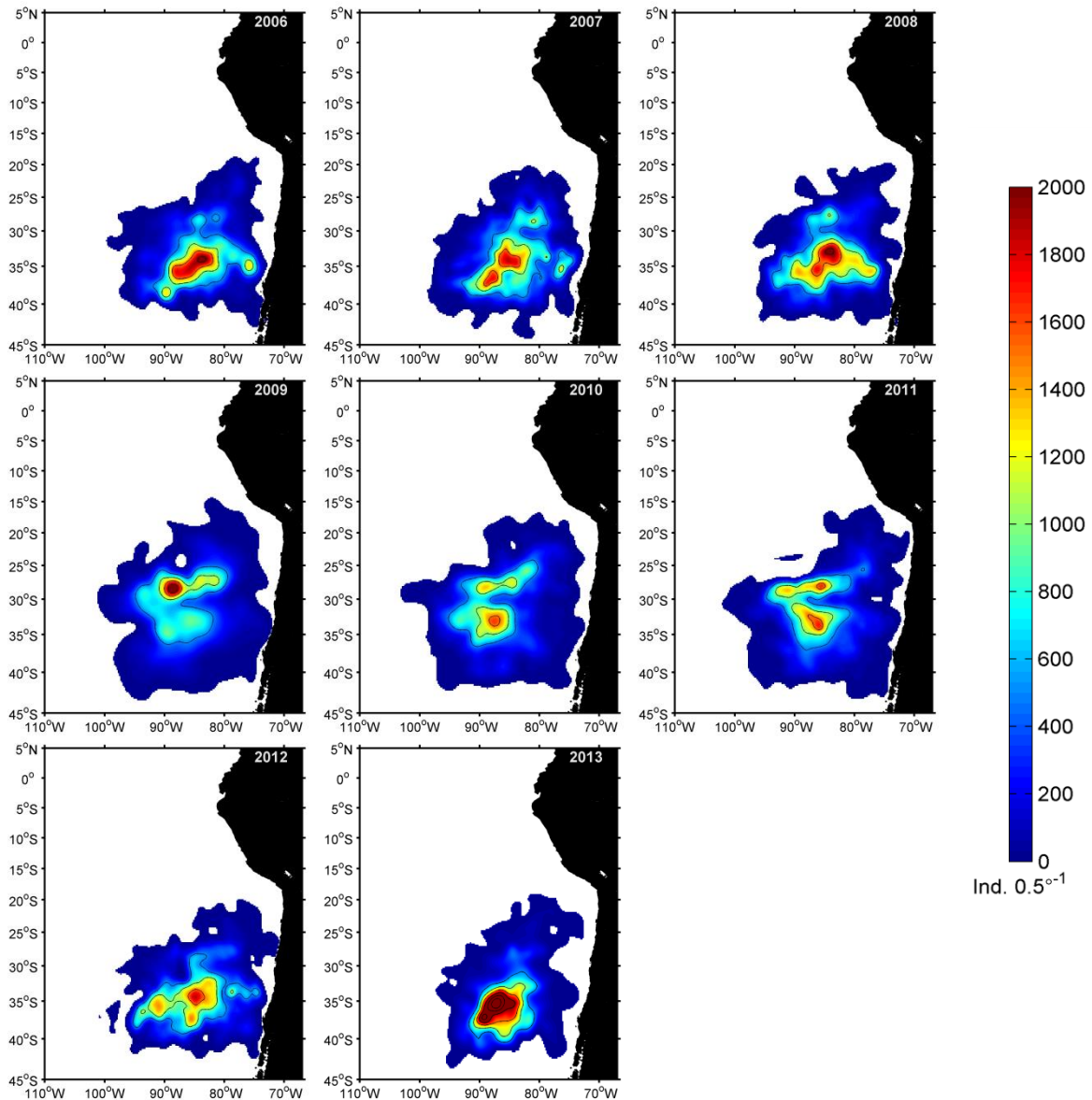


Figure 8 (cont.). Spatial distribution of modelled juvenile jack mackerel (120 days old) originated from the main spawning area located in the oceanic region off central Chile.

The overall spatial distribution of modelled juvenile jack mackerel originated from the three considered spawning areas and for all the study period (1994-2013) is presented in the Figure 9. This result revealed, that nevertheless the interannual variability in the dispersion patterns, there is a continuous distribution of juveniles from oceanic area off central Chile to coastal Peru, with higher densities observed in the coastal region between 15° and 25°S. This findings are consistent with the spatial distribution of jack mackerel recorded by

acoustic surveys carried out within Chilean waters (Figure 10) which have been mainly recorded northward of 25°S. Nevertheless, eventually the recruits can be recorded southward in small patches as during El Niño 1997-1998. A detailed distribution of recruits from acoustic surveys is showed in Figure 11.

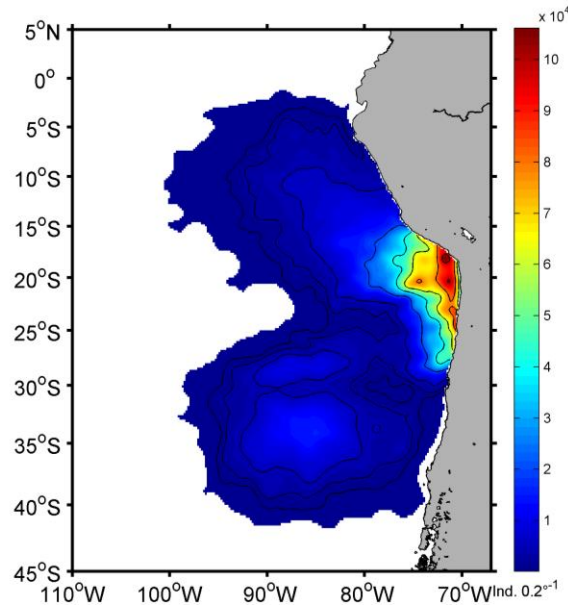


Figure 9. Overall distribution of juvenile jack mackerel (120 days old) from biophysical modelling of three spawning areas (Peru, northern Chile and oceanic central Chile) from 1994-2013.

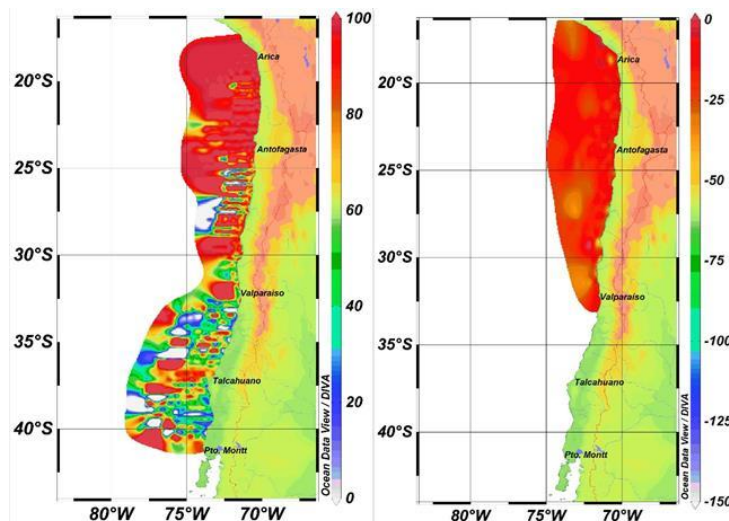


Figure 10. Spatial distribution of jack mackerel recruits recorded by acoustic surveys carried out in Chilean waters (left panel) and mean depth of the recruits (right panel).

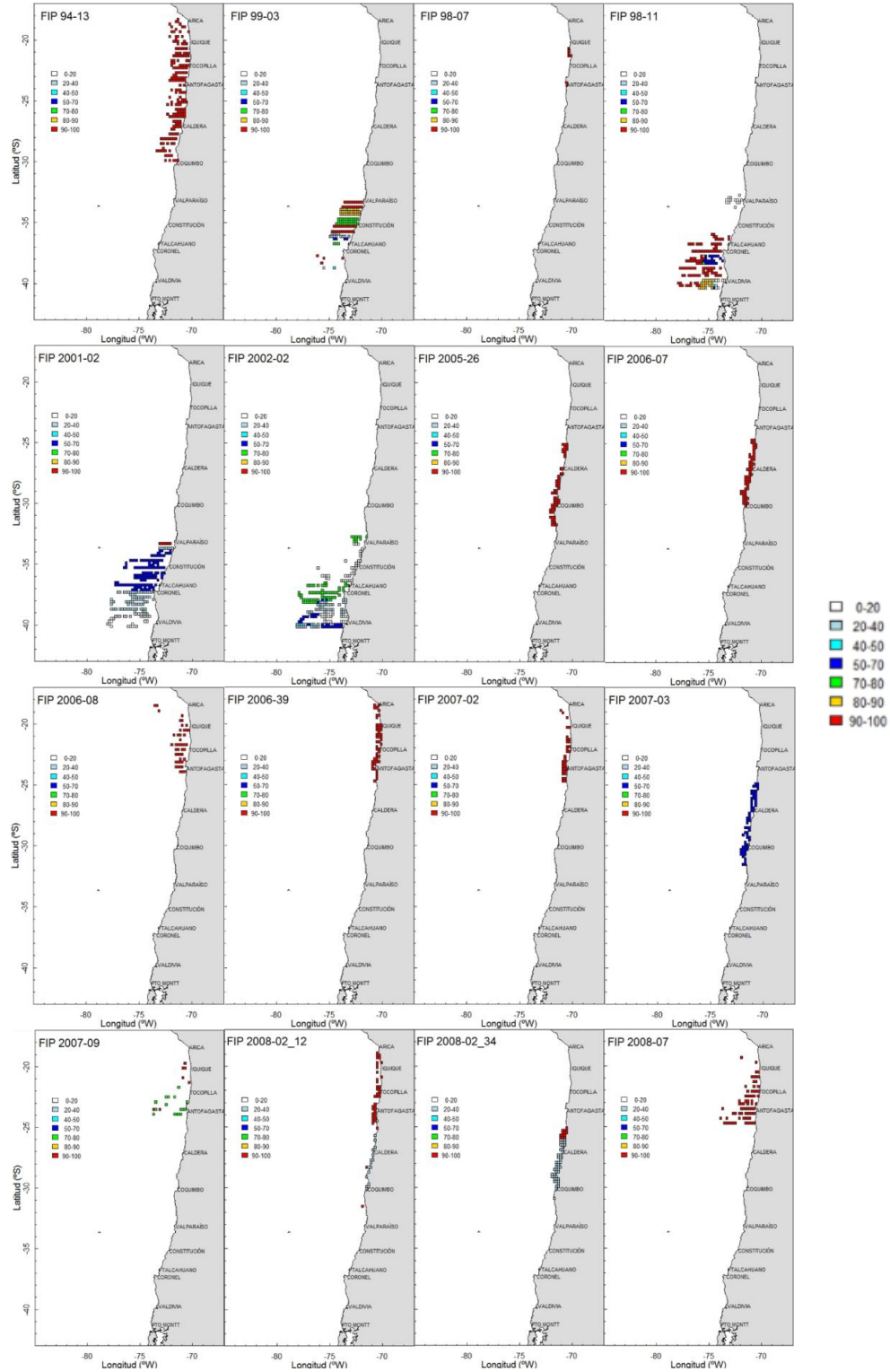


Figure 11. Spatial distribution of jack mackerel recruits from acoustic surveys carried out in Chilean waters from 1993-2013 (as percentage of recruits from acoustic bins).

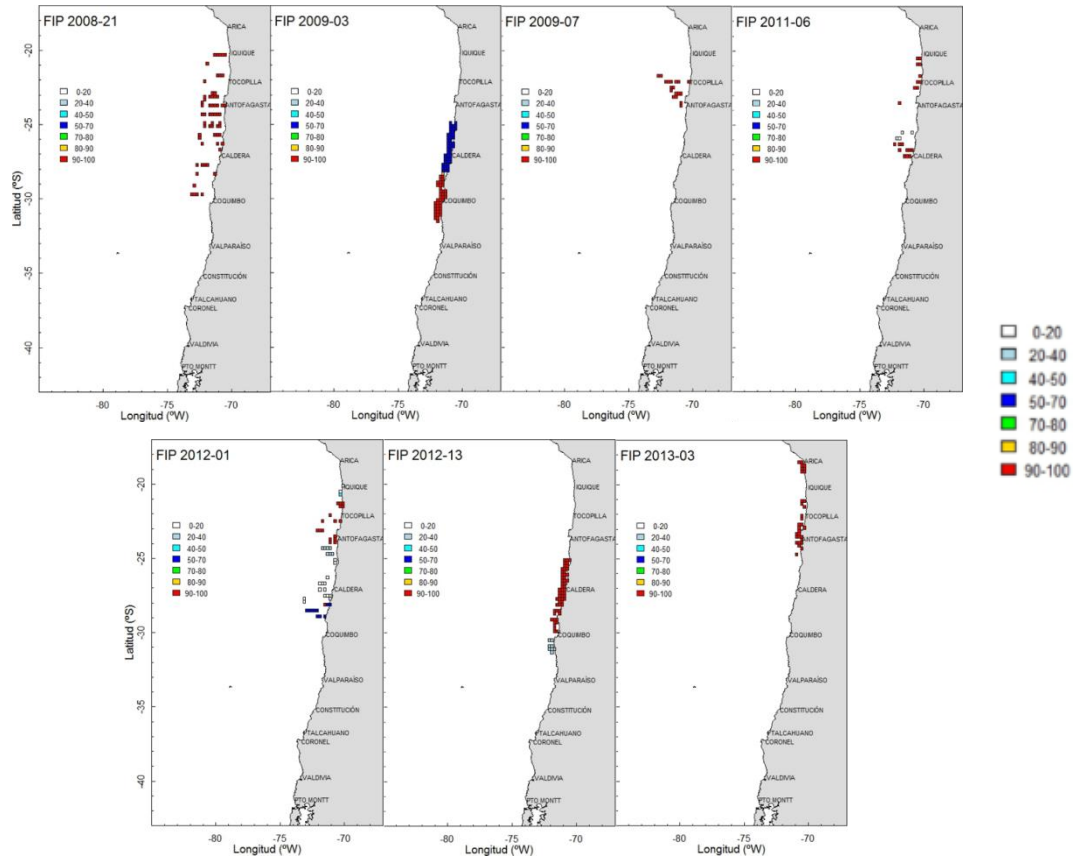


Figure 11 (cont.). Spatial distribution of jack mackerel recruits from acoustic surveys carried out in Chilean waters from 1993-2013 (as percentage of recruits from acoustic bins).

3.3. Physical drivers for jack mackerel transport process

In order to understand the main physical factors affecting the transport and dispersion of Jack mackerel in the southeastern Pacific, the spatial-temporal dynamic of sea surface temperature (SST), wind (wind stress, Ekman transport), geostrophic currents, and the variability of Subtropical front and mesoscale structures (cyclonic and anti-cyclonic eddies) were analyzed through monthly climatology and Empirical Orthogonal Frequencies (EOF) analysis.

3.3.1. Nursery ground (northern Chile)

Monthly climatology of surface Ekman transport off northern Chile (curvature zone) shows a seasonal pattern with maximum values in spring-summer, and minimum in autumn-winter (Figure 12). This area was characterized by a minimum transport compared with the south-central Peru, verifying a less dynamic recruitment area in the northern Chilean coast. In this region, the warm tongue from the equator during spring-summer shows Ekman flow in the same direction, being trapped in the curvature zone of northern Chile.

The spatial structure of the first EOF mode of SST (98.2%) shows the complex dynamics of northern region, evidencing the narrow strip associated with upwelling off Peru, besides the warm and coastal tongue and its displacement towards the Peru-Chile curvature. To observe the evolution of SST along the coast, Figure 13 shows a SST seasonal variability, and the presence of warmer waters in the curvature area (18-22°S).

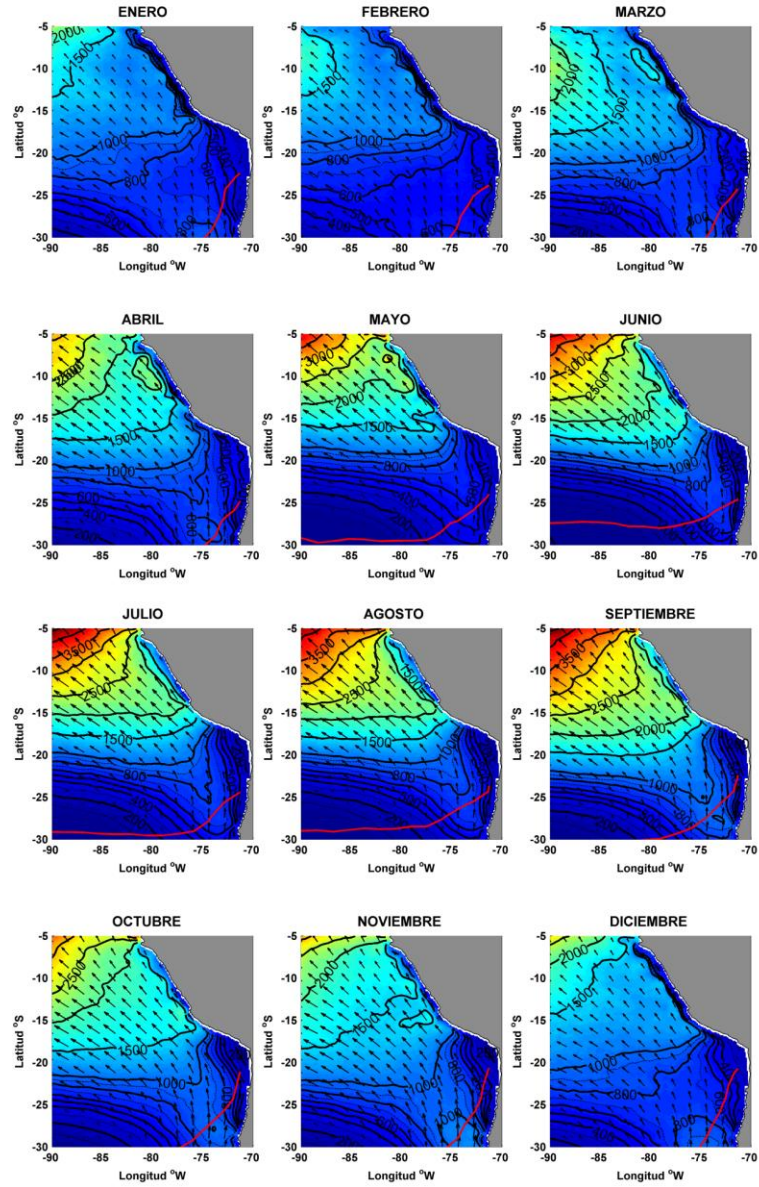


Figure 12. Climatology of Ekman transport (m^2/s) for coastal northern Chile and southern Perú.

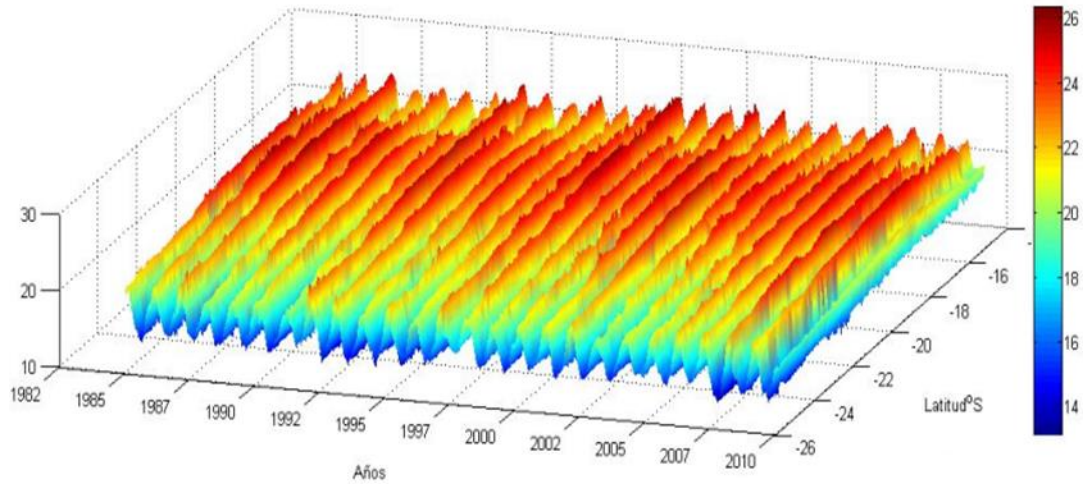


Figure 13. Hovmöller time-space diagram of SST along the coast of northern Chile.

3.3.2. Spawning region (oceanic area off central Chile)

The surface circulation pattern associated with the subtropical gyre, suggests a physical connectivity pattern for jack mackerel population, promoting high ocean-coast connectivity, as showed in Figure 14a. Likewise, meridional distribution of geostrophic velocity zonal average at 95°W (Figure 14b), shows higher values ($\sim 12 \text{ cm s}^{-1}$) centered at 37°S (winter) and 36°S (summer), according to the spatial variability of South Pacific Current (SPC).

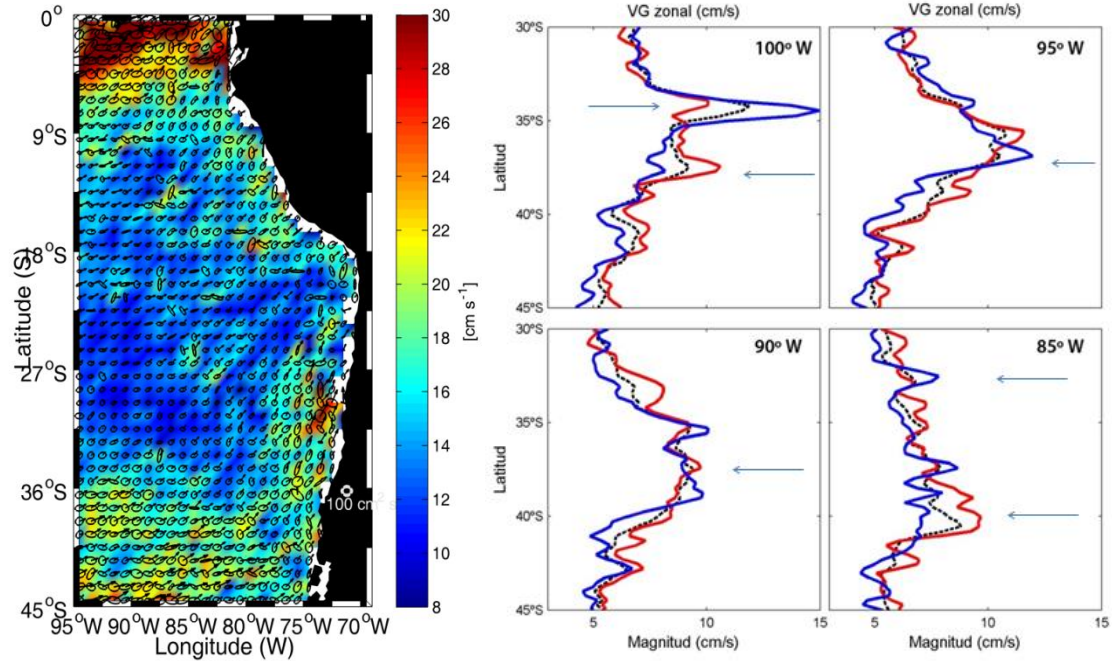


Figure 14. a) Surface circulation pattern in southeastern Pacific ocean (left panel), b) meridional distribution of zonal average of geostrophic velocity (1992-2011) at 100°W, 95°W, 90°W and 85°W (right panel).

Monthly climatology of subtropical front (STF) and South Pacific Current (SPC) show a clear seasonal/meridional variability to the north (winter) and south (summer). Coastward from 90°W a zonal variability was observed and the STF/SPC dividing into a north current branch becoming part of Chile-Peru Current System (northward to 37°S) and another branch to southeast forming the Cape Horn Current. The STF and SPC are zonally coupled to about 90°W where the STF is divided northwest associated with the northern branch stream.

Interannual variability of STF limits (Figure 15) for 1960-2009 time-series, showed a southward displacement of $\sim 5^\circ$ latitude between 1975-1987. Subsequently, it moves northward reaching 30°S (northern boundary) and then again back to south between 1996-2002 (excepting during El Niño 1997-1998 where changes to the north). Better consistency between the northern and southern limits was observed at 88°W (a relatively constant separation between limits). Approaching to the coast (82°W) boundaries were more

separated showing an independent behavior. Despite the above, in both 88°W and 82°W, interannual fluctuations follow similar patterns, especially from the late 80s.

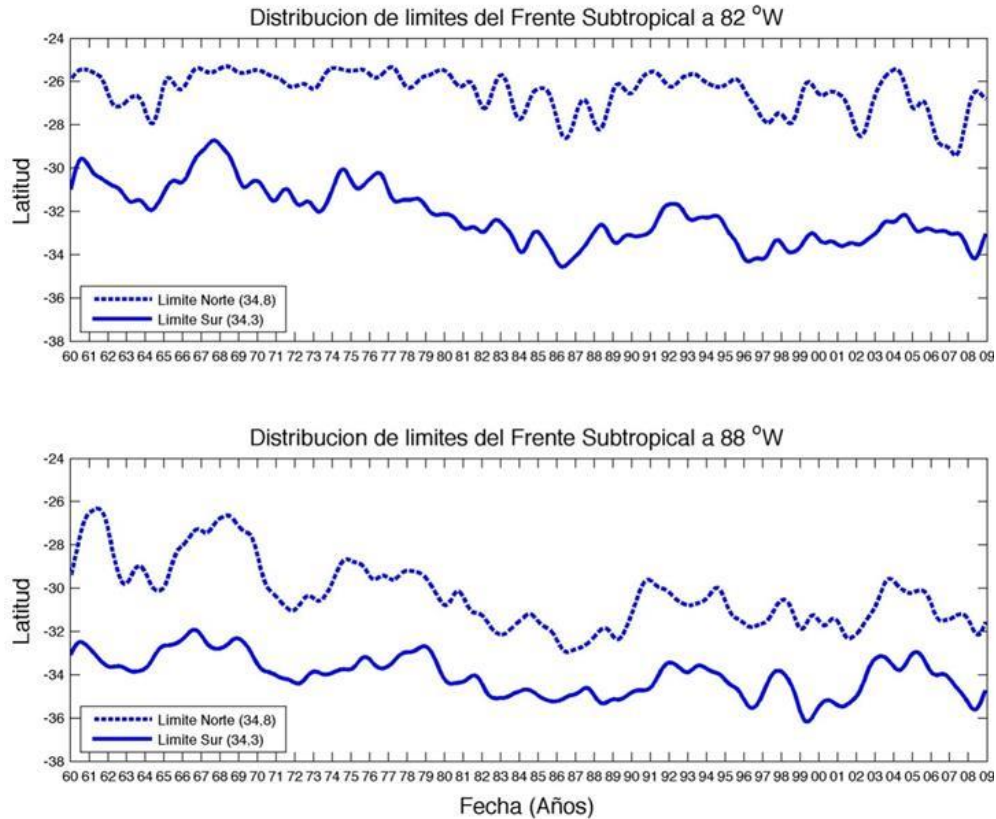


Figure 15. Inter-annual meridional variability of north/south limits of Southtropical Front at 88° and 82°W, defined by the position of 34.8 and 34.3 surface isohalines (Source: hydrography SODA 226).

Figure 16a shows the interannual evolution of the meridional fluctuation of STF (in blue) and the average latitude of spawning (red dots). The location of STF shows an strong interannual meridional variability; however a high level of consistency was observed for November (maximum reproductive of Jack mackerel), showing a high impact on the spatial correlation of spawning and STF (Figure 16b) revealing spatial correlation of $R^2 = 0.64$, which quantitatively confirms the association between the location of FST and oceanic spawning area and Jack mackerel as had been previously proposed (Núñez *et al.* 2008, Cubillos *et al.* 2008, Vásquez *et al.*, 2013).

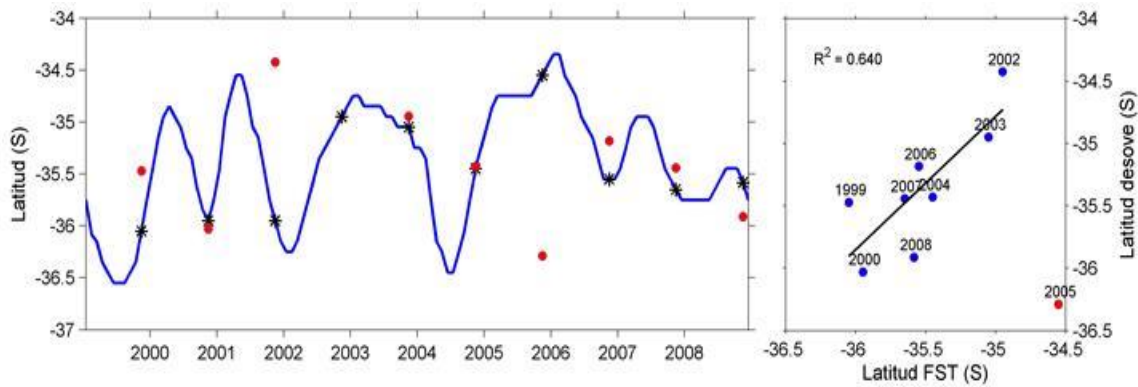


Figure 16. a) Seasonal/meridional displacement of STF and average meridional location of Jack mackerel spawning. Asterisk shows November months used for regression analysis. b) Linear regression between the average location of the STF of November and average latitude annual of Jack mackerel spawning off central Chile.

The monthly climatology of zonal/meridional Ekman transport (0-50 m depth) showed a flow to the coast in $\sim 35^\circ$ S, which is divided into the coastal zone consistent with the geostrophic flow northward. This is verified as a unexplored variable for transport variability of early development stages of Jack mackerel from the oceanic spawning region towards the coast. The central oceanic region (spawning area) was delimited according to the wind stress zero isolines, in both zonal ($\tau_x = 0$) and meridional components ($\tau_y = 0$) (Figure 17, left panel). This approach reveals that near the intersection τ zero isolines, the effect of surface wind is very weak, increasing when these isolines are separated as they approached the coast ($< 85^\circ$ W).

Monthly climatology of SST shows the greatest variations of isotherms in spring-summer, which are consistent with the spatial variations of wind stress, revealing that maximum variations of isotherms deflection occur where wind stress is more intense. Also, Ekman transport exhibits a significant effect on isotherms deflection in spring-summer time and, mainly eastward 80° W (Figure 17 right panel). Within limits of zonal and meridional $\tau=0$, it is verified the oceanic Jack mackerel spawning region, which is consistent with spatial distribution of minimum wind effort induces zonal non-deflection isotherms (Figure 18) revealing a suitable (less dynamic) habitat favorable to spawning process towards the open waters off central Chile. Despite of interannual/meridional variability in the study area, the

isotherm of 16° C is always verified within the region delimited by $\tau=0$. This isotherm has been established as a southern boundary of jack mackerel oceanic spawning region off central Chile (Evseenko *et al.* 1987, Cubillos *et al.* 2008).

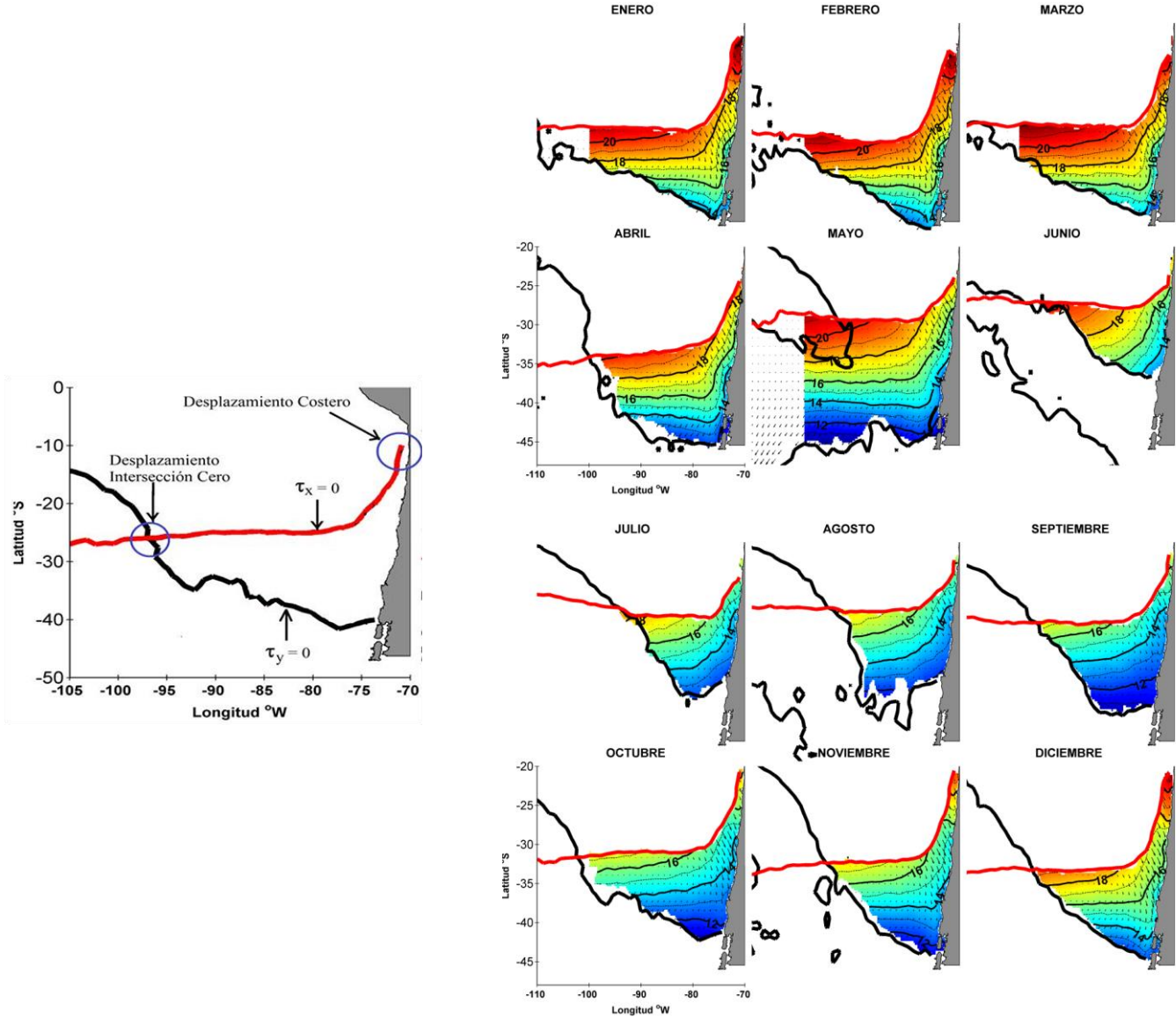


Figure 17. Left panel: Intersection of zonal (red contour) and meridional (black contour) wind stress zero ($\tau_x = \tau_y = 0$), respectively. Blue circles show the intersection displacement. Right panel: Spatial distribution of SST and Ekman transport in the spawning oceanic region off central Chile (area inside of Tau-0 zonal and meridional isolines).

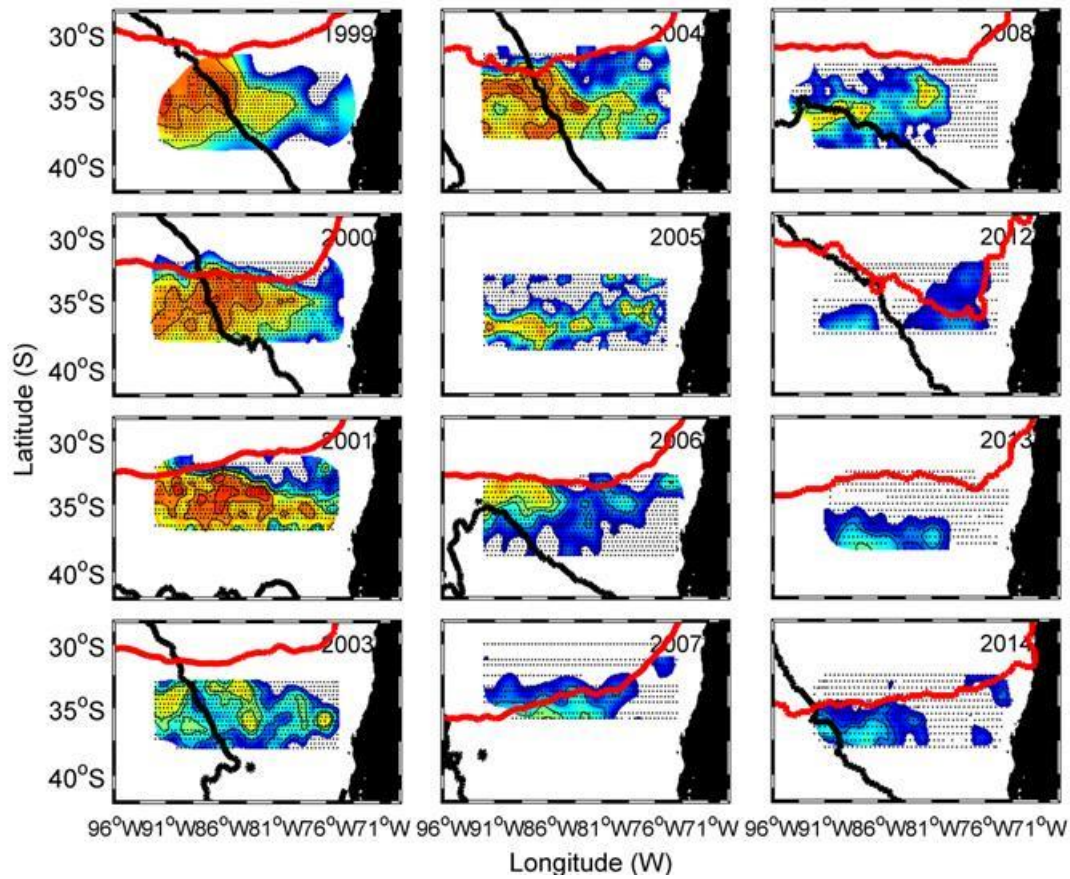


Figure 18. Intersection of zonal (red contour) and meridional (black contour) wind stress zero ($\tau_x = \tau_y = 0$), associated to Jack mackerel spawning area for 1999-2013 (No data for 2005).

3.3. Biophysical recruitment dynamics: a comparative approach

In order to obtain a recruitment index based on biophysical modeling, the number of individuals who reached the modelled nursery ground from the main spawning area, was integrated to obtain an index of biophysical recruitment. The time series 1994-2014 of this index is shown in Figure 19a where it is compared with the index of egg density (MPH) and recruitment index from the stock assessment (SPRFMO joined model). Biophysical index of recruitment (IBM in the figure) showed a strong relationship with the SPRFMO stock assessment recruitment index. The adjusted R squared for the linear regression model was 0.66, and IBM recruitment index as predictor is significant at the 0.001 level (Figure 19b). Furthermore, the results show that the incorporation of a biophysical model 11%

improvement in prediction of next year recruitment compared to use of the indicator based on egg density.

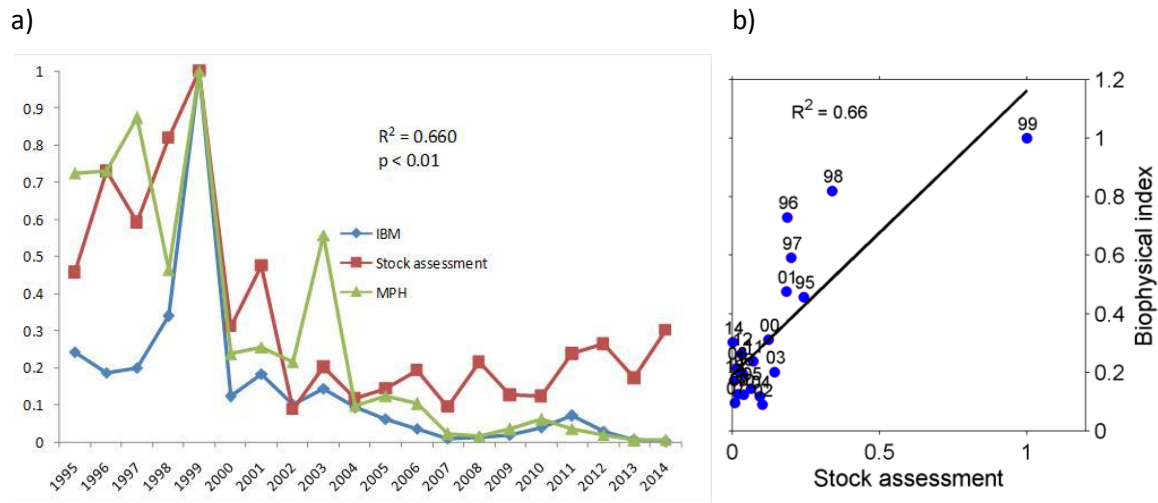


Figure 19. a) Time series of biophysical recruitment index (IBM), Egg Production Index (MPH) and Index recruitment from an age-structured statistical model (expressed as abundance of age group 1); b) Linear regression between the index of biophysical recruitment and the Index recruitment from

3.4. Conceptual model for jack mackerel population in the southeastern Pacific

Based on the background of the life history of jack mackerel and the results of biophysical modeling of this study (considering feeding, spawning adults, migration from nursery ground to adults fraction, spatial location of the nursery ground, connectivity of spawning and nursery grounds) schemes for the conceptual model of the population structure of jack mackerel in the southeastern Pacific is presented. A separation for warm and cold weather periods is considered, which coincide with periods of high and low abundance and/or population expansion and contraction respectively, as well as for the years of major El Niño events in the region. It is proposed that in the southeastern Pacific inhabiting a jack mackerel population widely dispersive through its early life history. In addition this population inhabits a system that has no physical barriers that promote segregation or isolation in discrete population units. The results support the current hypothesis of "unique

population or patchy population" distributed in coastal waters of Peru and Chile and in open ocean waters as well

Figure 20 summarizes the population structure scheme proposed in this study. The main elements that give rise to this scheme are:

- Two areas of distribution of adult feeding fish (A_{north} and A_{south}) temporarily separated from each other in the topographical angle of Arica during the summer months, however there are connections between them through fish migrations along the coast from south to north in the autumn-winter. Also, through migration of spawning fish in the spring to the spawning area both from the north (Peru, northern Chile) and south (south-central Chile and open ocean), to an area where mixing of the adult specimens in both areas (A_{north} and A_{south}) occurs and from the spawning area to the north and south feeding areas. The existence of two distribution areas of adult fish and connections between them are similar for both periods in question, however, are reduced (disappear) coastal connections to the north along the coast and from the spawning area to the north. Finally, connections from the northern area to the spawning area and from the spawning area to the southern area in the years of El Niño are enhanced.

- The continuous spawning area extending from the coastal waters of Peru, northern Chile to south-central Chile to the open ocean (where it reaches its highest expression). In addition, a synchrony of spawning fish that are incorporated into spawning process that begins in July-September from the coasts of Peru and ends in December-January off central-southern Chile.

- The main nursery ground of jack mackerel during the first 2 years (until the age of sexual maturity) is located in coastal waters of northern Chile and southern Peru (15° - 30° S). This area can present decadal spatial variations (in warm climatic period displaced to southern Peru and in cold climatic period with preferential location in northern Chile), interannual (with displacements of centers of gravity northward in the years of La Niña and southward in El Niño years) and seasonal (during summer in a coastal location and during winter and an expansion to the open sea). The existence of connections between different spawning zones of jack mackerel and the main nursery ground is confirmed, both through the process

of transport of eggs, larvae and juveniles (biophysical modeling) and active migration of juvenile fish older than 4 months (data from field observations). In this nursery ground the jack mackerel recruitment occurs at different levels of abundance which depends on the annual reproductive success.

- The active migration of annual recruits jack mackerel from the main breeding area to the areas of distribution of adult fish present interannual and decadal variability in the proposed schemes. During the warm climate regime they predominate towards coastal and ocean waters of the north-central Peru; and expand to the south-west (south-central Chile and the open ocean) during El Niño years. During cold climate regime, entries of new recruitments to the areas of distribution of adult fish are more regularly and more abundant to the south (south-central Chile and open water) than to Peruvian waters, independent of the conditions La Niña or El Niño. The entry of fish into Peruvian waters appear as irregular pulse, probably associated with the enhancement of coastal flows cold waters of the Humboldt Current in certain years. However, in the years of El Niño in the proposed conceptual scheme, the outputs of recruits from the nursery are quite similar to those detected in the period of cold climate regime.

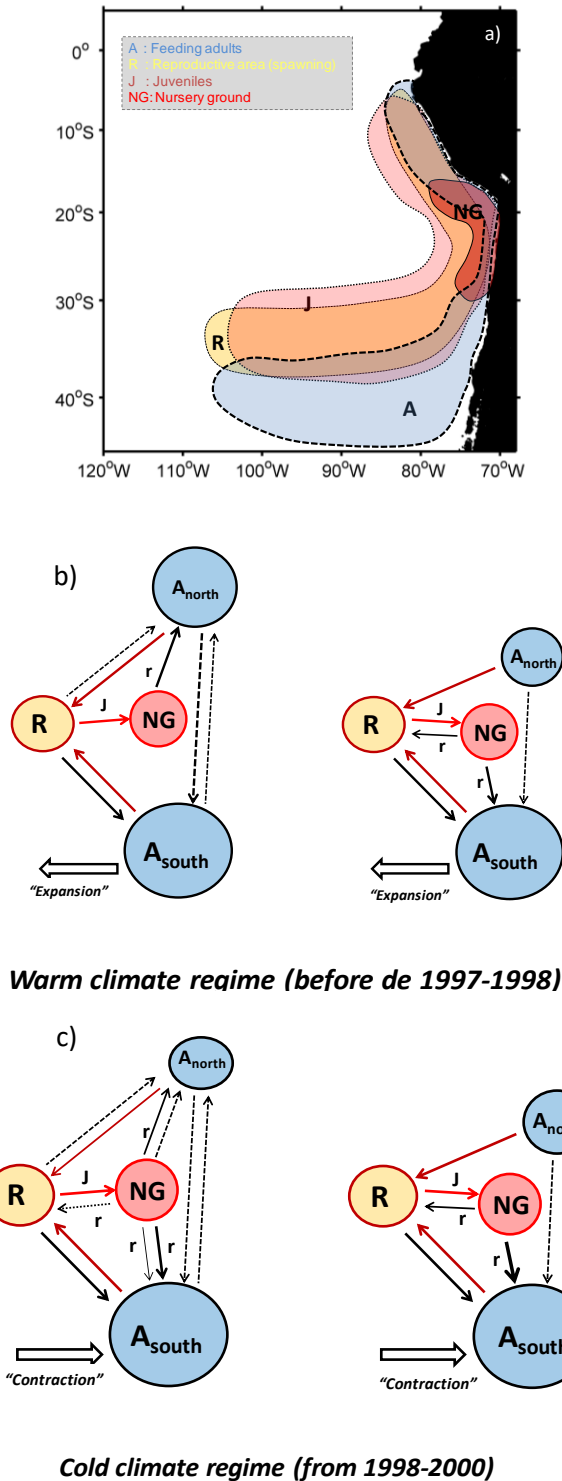


Figure 20. Conceptual model for the population structure of jack mackerel incorporating the findings of this study: a) spatial scheme of the different fraction of life cycle under a scheme of unique population; b) scheme of connections between population fractions under a warm regime (before 1997-1998); c) scheme of connections between population fractions under a cold regime (after 1997-1998)

4. Concluding remarks

- The main physical drivers associated to dispersion and transport processes (Ekman transport and geostrophic currents) revealed that i) the nursery area (situated in northern Chile and southern Peru) shows particular dynamic conditions characterized by low levels of wind stress, low kinetic energy and warmer waters which promotes a suitable area for the survival of juvenile jack mackerel to recruitment; ii) the main spawning area located in oceanic area off central Chile is overlapped with the STF, low wind induced turbulence and currents dynamic that promotes the connectivity between oceanic and coastal regions; iii) in southern Peru there is a less dynamic environment, while in the north increases the Ekman offshore transport associated with upwelling processes; iv) the used hydrodynamic model reproduces the main oceanographic spatio-temporal features of the southeastern Pacific.
- All spawning areas modelled (Peru, northern Chile coast, ocean area off central Chile) are connected to nursery ground through the physical mechanisms that promote transport and retention described above. The overall spatial distribution of modelled juvenile jack mackerel originated from the three considered spawning areas and for all the study period (1994-2013) revealed that nevertheless the interannual variability in the dispersion patterns, there is a continuous distribution of juveniles from oceanic area off central Chile to coastal Perú, with higher densities observed in the coastal region between 15° and 25°S. This modelled distribution of juvenile jack mackerel is consistent with the acoustic records of jack mackerel recruits in Chilean waters in all the study period.
- Biophysical index of recruitment showed a strong relationship with the SPRFMO stock assessment recruitment index. The adjusted R squared for the linear regression model was 0.66, and IBM recruitment index as predictor is significant at the 0.001 level. Furthermore, the results show that the incorporation of a biophysical model 11% improvement in prediction of next year recruitment compared to use of the indicator based on egg density.

- Based on the background of the life history of jack mackerel and the results of biophysical modeling of this study a new scheme for the conceptual model of the population structure of jack mackerel in the southeastern Pacific it is proposed: in the southeastern Pacific inhabiting a jack mackerel population widely dispersive through its early life history. In addition this population inhabits a system that has no physical barriers that promote segregation or isolation in discrete population units. The results support the current hypothesis of "unique population or patchy population" distributed in coastal waters of Peru and Chile and in open ocean waters as well.

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