PROGRESS IN OCEANOGRAPHY

Identifying appropriate spatial scales for marine conservation and management using a larval dispersal model: The case of *Concholepas concholepas* (loco) in Chile

CrossMark

Lysel Garavelli [a,*], David Michael Kaplan [b], François Colas [c], Wolfgang Stotz [d], Beatriz Yannicelli [e], Christophe Lett [a]

[a] *Institut de Recherche pour le Développement (IRD), UMI 209 UPMC UMMISCO, Centre de Recherche Halieutique Méditerranéenne et Tropicale, Sète, France*
[b] *Institut de Recherche pour le Développement (IRD), UMR EME 212 (Exploited Marine Ecosystems), Centre de Recherche Halieutique Méditerranéenne et Tropicale, Sète, France*
[c] *Institut de Recherche pour le Développement (IRD), LOCEAN-IPSL, UPMC, Paris, France*
[d] *Grupo de Ecologia y Manejo, Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile*
[e] *Centro de Estudios Avanzados en Zonas Aridas (CEAZA), Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile*

A R T I C L E   I N F O

A B S T R A C T

Along the coast of Chile, fisheries targeting the marine gastropod *Concholepas concholepas*, commonly named "loco", were highly valuable until the end of the 80s when catches declined significantly. Since the late 90s, a management plan based on territorial-user-rights areas has been implemented, with limited effect on stock recovery. More effective loco conservation and management is impeded by lack of information regarding connectivity via larval dispersal between these individually-managed areas. To develop a regional view of loco connectivity, we integrate loco life history information into a biophysical, individual-based larval dispersal model. This model is used to evaluate scales of loco connectivity and seasonality in connectivity patterns, as well as to partition the coast into largely disconnected subpopulations using a recently developed connectivity-matrix clustering algorithm. We find mean dispersal distances ranging from 170 to 220 km depending on release depth of larvae and planktonic larval duration. Settlement success levels depend quantitatively on the physical and biological processes included in the model, but connectivity patterns remain qualitatively similar. Model estimates of settlement success peak for larval release dates in late austral autumn, consistent with field results and with favorable conditions for larval coastal retention due to weak upwelling during austral autumn. Despite the relatively homogeneous Chilean coastline, distinct subpopulations with minimal connectivity between them are readily identifiable. Barriers to connectivity that are robust to changes in model configuration exist at 23°S and 29°S latitudes. These zones are all associated with important headlands and embayments of the Chilean coast.

© 2014 Published by Elsevier Ltd.

Introduction

Heterogeneous spatial distributions of benthic populations, as well as of anthropogenic pressures on these populations, have significant consequences for conservation and management (Brazeiro and Defeo, 1999; Martone and Micheli, 2012). Identifying adequate spatial scales to set regulations, conduct monitoring and assess conservation efforts involves integrating multidisciplinary and multi-scale biophysical and social information (Orensanz et al., 2005). Biologically relevant scales, such as those of population connectivity and underlying mechanisms driving connectivity, are thought to be of major interest (Green et al., 2009; Ban et al., 2011). Despite its relevance, the scale of population connectivity is an unresolved topic for the majority of marine species. Here we evaluate the spatial structure of population connectivity via larval dispersal of *Concholepas concholepas*, commonly known as "loco", an ecologically-important benthic carnivore that is highly exploited along the Chilean coast (Castilla, 1999).

Although loco has been consumed since pre-hispanic times (Báez et al., 2004), systematic records of loco catch and abundance are only available since the 1960s. During the 80s, loco began to be exported, becoming one of the most valuable benthic fisheries in Chile (Leiva and Castilla, 2002). As a result, fishing effort and landings increased very steeply during this period. Total catch

* Corresponding author. Address: UMMISCO/IRD, av. Jean Monnet – B.P. 171, 34203 Sète Cedex, France. Tel.: +33 499573252.
E-mail addresses: lysel.garavelli@ird.fr (L. Garavelli), david.kaplan@ird.fr (D.M. Kaplan), francois.colas@locean-ipsl.upmc.fr (F. Colas), wstotz@ucn.cl (W. Stotz), beatriz.yannicelli@ceaza.cl (B. Yannicelli), christophe.lett@ird.fr (C. Lett).

fluctuated and then declined at the end of 80s. A three-year fishery closure was implemented, followed by stringent management regulations, to mitigate overexploitation. Despite these efforts, catch levels have never recovered and are currently approximately 12% of the peak level in the 80s (Sernapesca, National Service of Agriculture and Fisheries in Chile, 2012).

The current approach to management of loco populations relies heavily on individually-managed, territorial-user-rights areas referred to as "Management and Exploitation Areas for Benthic Resources" (MEABR). Since the implementation of the first MEABR in 1998, there has been hope that territorial user rights would be more effective than previous loco management based on regional quotas (Bernal et al., 1999). The geographical limits of each MEABR are defined by fishers, and initially coincided primarily with locations of high loco abundance (González et al., 2006). Annual monitoring of each MEABR is used to fix a yearly quota of extraction based on abundance estimates of loco bigger than 10 cm opercular length, the minimum legal size of extraction. Stock assessments are performed primarily by fishers themselves, in conjunction with private consultants and the national fishery authority. In 2011, there were 535 MEABR along the Chilean coast, 392 of which included loco as a target resource (Sernapesca, National Service of Agriculture and Fisheries in Chile, 2012).

In line with institutional proposals in Chile to scale up marine conservation by implementing networks of marine protected areas (MPAs), Gelcich et al. (2008) advised considering MEABR in networks to enhance the conservation of marine species, including loco. A central consideration for the establishment of MPA networks is spatial connectivity between subpopulations (Kaplan, 2006; White and Costello, 2011). Ensuring network connectivity increases population persistence (Botsford et al., 2003) and robustness to climate change (McCook et al., 2009). Therefore, the assessment of potential connectivity between MEABR is a crucial step towards the establishment of a successful regional sustainable management plan integrating individual MEABR.

The life cycle of loco is characterized by a long pelagic larval phase (2–12 months, DiSalvo, 1988; Moreno et al., 1993; Molinet et al., 2005) and an adult benthic phase of low mobility (Stotz and Perez, 1992). Population connectivity of loco is therefore limited to the larval phase, but little information is available regarding spatial scales of loco larval dispersal. This lack of information has been highlighted as an impediment to effective management and conservation (Fernández and Castilla, 2005; González et al., 2006).

To assess larval dispersal in marine populations, three main approaches are currently being used: population genetics, microchemistry of calcifying structures (e.g., otoliths and statoliths) and individual-based larval dispersal models (Leis et al., 2011). The first two of these approaches have previously been applied to study loco connectivity. Using a molecular approach, Cárdenas et al. (2008) concluded that loco correspond to a single taxonomic unit from Peru to southern Chile. This study was followed by a phylogeographical evaluation of genetic differentiation of loco between the three main biogeographical provinces in the Humboldt Current System (HCS) (Cárdenas et al., 2009). Significant differences in population genetic structure associated with biogeographical barriers were not observed, an indication of gene flow over the whole HCS. Manríquez et al. (2012) used differences in trace element composition of statoliths of pre-hatch loco larvae and recruits to assess connectivity between three areas in distinct regions of Chile. At the kilometer scale of individual sampling sites, recruits were not found to have been retained in the area of sampling. At regional scales of order 100 km (between sites), differences in concentrations of elemental signals were observed for sampled pre-hatch larvae and recruits. Although authors could not define the exact origin of recruits, they concluded that there was a strong indication of a lack of dispersal among sampling areas.

While these two studies provide significant information regarding connectivity in loco populations over large and small spatio-temporal scales, they do not measure connectivity over intermediate spatial scales most relevant for management and loco ecology. Biophysical models applied to marine benthic invertebrate species have been widely used to study the influence of larval biology on larval dispersal (Metaxas and Saunders, 2009). In this study, we integrate loco life history information into a biophysical, individual-based larval dispersal model to develop a regional view of loco population connectivity and its consequences for management. We first detail biological and ecological processes involved in early life stages of loco that are relevant for the study of connectivity. We then integrate some of those processes into our larval dispersal model and use it to evaluate the scales of loco population connectivity. Finally, we discuss the implications of our results for management and conservation.

Material and methods

Regional ocean dynamics pertinent for loco dispersal

Loco are distributed along the coasts of the Southeastern Pacific, from central Peru (6°S) to Cape Horn (55.8°S), including the Juan Fernandez Archipelago (Cárdenas et al., 2008). Coasts within loco distribution range are under the influence of two different systems: the Humboldt Current System (HCS) north of ~42–45°S, and the Cape-Horn Current and Interior Chilean Sea to the South. In the coastal HCS, Strub et al. (1998) observed two currents associated with coastal upwelling: a predominantly equatorward surface current (Chile Coastal Current; CCC is poleward in winter; Thiel et al., 2007) and a subsurface poleward current (Poleward Under Current; PUC at 100–300 m depth) (Fig. 1). On time scales of weeks to months, alternating upwelling–downwelling events associated with surface current reversals are driven by coastal wind variability (Rutllant et al., 2004). Although the Chilean coast is rather straight, coastal upwelling varies conspicuously in strength and frequency along the coast, with upwelling centers and upwelling shadows generally being found at and equatorward of headlands, respectively (Figueroa and Moffat, 2000). Mesoscale features, such as offshore spreading filaments, are recurrent near coastal headlands (Marín et al., 2001), whereas cyclonic and anticyclonic eddies develop near the coast due to surface and subsurface topographic features. While filaments and eddies potentially transport coastal organic material beyond upwelling or shelf break fronts into the open ocean (Letelier et al., 2009), other smaller scale eddies and recirculating features also associated with coastal topography may facilitate coastal retention (Yannicelli et al., 2012).

Hydrodynamic model

To simulate oceanic circulation of the HCS, we used the Regional Oceanic Modeling System (in its ROMS «UCLA» version; Shchepetkin and McWilliams, 2005, 2009). ROMS is a free-surface split-explicit model solving the hydrostatic primitive equations using terrain-following curvilinear vertical coordinates. We followed a quasi-equilibrium approach, i.e., the model is forced by monthly climatological means both for atmospheric forcing and open-ocean model boundaries. This approach has been successfully used in previous studies to simulate the mean circulation and the mesoscale spatio-temporal dynamics of eastern boundary upwelling systems (e.g., Marchesiello et al., 2003; Penven et al., 2005; Veitch et al., 2010; Mason et al., 2010). The model was initially implemented over a large domain covering the South-East Pacific (from 15°N to 41°S and from 100°W to the South American coast) with a horizontal resolution of 7.5 km. Surface forcing was
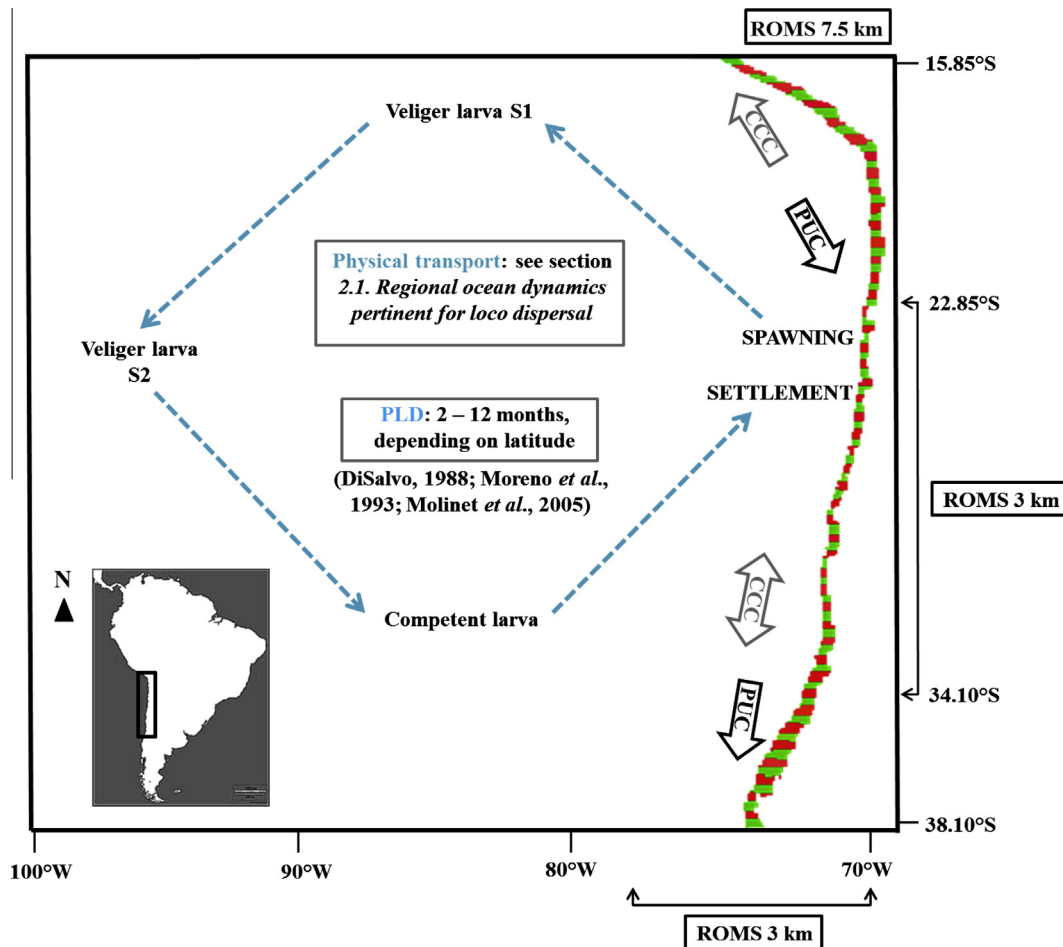
Fig. 1. Schematic representation of loco life history from spawning to settlement mapped on our study area. The three larval stages are planktonic. Dotted blue arrows represent the dispersive stages. The areas used in our larval dispersal model for release and settlement of loco larvae along the coast are shown in red and green. All these areas are potential areas for release and settlement. The two hydrodynamic model (ROMS) configurations outputs that we used as inputs to our larval model differ in horizontal resolution (7.5 km and 3 km) and spatial extent. Elements in gray boxes are those used in the larval dispersal model. PLD = planktonic larval duration; CCC = Chile Coastal Current; PUC = Poleward Under Current. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

from mean-monthly climatologies: heat and freshwater fluxes were taken from COADS (Da Silva et al., 1994), and wind stress is from the QSCAT scatterometer-based climatology SCOW (Risien and Chelton, 2008). Open-boundary forcing was a monthly climatology developed from 2000 to 2006 SODA (Carton and Giese, 2008) products. Using the climatological forcing, the model was run for 13 consecutive years; the first 3 years were considered the model spin-up time and not considered in our analysis. Time series of simulated current velocities were averaged and stored every 3 days. We refer the reader to Colas et al. (2012, 2013) for more details on this simulation and its validation against observations. In order to reach a higher spatial resolution over the northern Chile coastal region we used an offline-nesting approach (Mason et al., 2010), where the 7.5 km resolution, large domain solution (described above) was used to supply lateral boundary information to force a 3 km resolution, smaller domain solution. This smaller domain was embedded within the large regional domain, and extended from 21°S to 35°S and from 78°W to the Chilean coast. This approach allowed the regional and mesoscale structures (eddies) resolved by the 7.5 km solution to be transmitted through the open boundaries of the smaller 3 km model. The higher resolution nested model was run for 6 consecutive years using the same climatological forcing described above for the coarser resolution model. The first 2 years were considered model spin-up time and not considered in our analysis. Time series of

current velocities were averaged and stored every 2 days. As high-frequency wind forcing was not included (hence there were no wind-forced high frequency ocean motions in the model solutions; see the Discussion regarding model limitations), these output sampling frequencies were presumably sufficient to capture mesoscale dynamics resolved by the model (Yannicelli et al., 2012).

Loco life history

To build the individual-based larval dispersal model for loco, we reviewed adult and larval loco life history. Adult loco have been observed on rocky substrates from the intertidal zone down to approximately 40 m depth (Manríquez et al., 2004). Individuals become reproductively mature between 3.5 cm and 7.7 cm opercular length (Castilla and Cancino, 1976; Manríquez et al., 2008), corresponding to approximately 9 and 20 months after settlement, respectively (Stotz, 1997). In central Chile, spawning of loco mainly occurs in austral summer and autumn (Manríquez and Castilla, 2001; Manríquez et al., 2008). After mating, females produce encapsulated eggs that are fixed on rocks until hatching. Eggs hatch after a period of several months (Castilla and Cancino (1976) measured incubation times of 69–128 days at 13.5–14.5 °C), emerging as planktonic larvae that are dispersed before settling into the coastal adult habitat.

There are at least two North–South gradients in reproduction and dispersal that are likely important for connectivity in loco populations. The number of eggs in a capsule is highly variable, ranging from a few hundred to more than 14,000 (Castilla and Cancino, 1976). Fernández et al. (2007) showed that the number of loco embryos per capsule area (mm^2) was lower in northern regions than in southern regions of Chile. This observation was correlated with mean water temperature before egg deposition. Similarly, planktonic larval duration (PLD) has been found to vary depending on latitude. PLD was assessed at around 2–3 months from laboratory studies (DiSalvo, 1988) and between 3 and 4 months from field studies in south-central Chile (39°S) (Moreno et al., 1993). Further south, in fjords and channels (43–44°S), it has been shown that the larval phase may be longer, between 6 and 12 months (Molinet et al., 2005), likely due to lower water temperatures in the region.

Larval dispersal model

The individual-based offline Lagrangian tool Ichthyop 3.1 (Lett et al., 2008) was used to model loco larval dispersal. Virtual loco larvae are advected passively by velocity fields produced by the ROMS hydrodynamic model. At the beginning of each month, 100,000 virtual larvae were randomly released from habitat areas. Locations of each virtual larva (latitude, longitude and depth) are tracked every hour using a forward-Euler advection scheme. Horizontal diffusion was added to represent unresolved horizontal turbulence below the ocean model grid scale following Peliz et al. (2007). Based on our knowledge of loco spawning, habitat areas were defined as sections of 0.25° of latitude (roughly 30 km of coastline) all along the Chilean coast. Habitats areas stretch from the coast to the 500 m isobath. For the 7.5 km and 3 km resolutions ROMS, locations of habitat areas ranged from 15.85°S to 38.10°S and from 22.85°S to 34.10°S, respectively (Fig. 1). Two release depths that encompass the spawning depth ranges of loco were tested: 0–20 m and 40–60 m. We used two values of PLD: 60 days, corresponding to the minimum value found by DiSalvo (1988), and 120 days, corresponding to the maximum value found by Moreno et al. (1993). A period of competency for settlement was also included in the model. DiSalvo and Carriker (1994) observed that loco larvae can delay their metamorphosis for hours to weeks in order to find a suitable habitat to settle. For the gastropod *Crepidula fornicata*, it has been showed that the duration of the competency period can vary from 20 to 30 days (Pechenik and Eyster, 1989). Combining this information, a competency period of about 20 days would seem to be a reasonable assumption for loco larvae and was incorporated into the model. Transport success of larvae to settlement areas was therefore computed between 60 days and 80 days or between 120 days and 140 days. Settlement success was defined as being located in a habitat area at any time during the competency period. Simulations were repeated from January to December during 4 years of ROMS simulations (years 4–7 of the 7.5 km ROMS simulations; years 3–6 of the 3 km ROMS simulations).

Outputs of simulations were represented as connectivity matrices for each spawning depth and PLD. Values of the connectivity matrix C_{ij} were calculated as the percentage of particles released from area j that are transported to area i.

Though it has been demonstrated that another carnivorous gastropod in Chile can adjust settlement timing to take advantage of small habitat patches found among areas of unsuitable sandy habitat (Wieters et al., 2008) and that loco recruitment rates are related to adult abundances, again suggesting larval control of recruitment timing (Martínez and Navarrete, 2002), large, continuous areas of unsuitable habitat may represent a barrier for recruitment and reproduction for locos. To assess the possible effects on connectivity of loco habitat limitation for both spawning and settlement, the percentage of available loco habitat (rocky shore) within each latitudinal band of 0.25° was estimated. First, the length of the coast was calculated from digitized Chilean Military Geographic Institute (IGM) charts 1:250,000. Then, we substracted the length of continuous unsuitable habitat defined as sandy beaches longer than 4 km without any obvious rocky subtidal shelf within each band. Sandy shores were geo-referenced using GoogleEarth 7.1.1.1580. The result was expressed as a percentage of total coastal length per band. For each connectivity matrix, we multiplied the values in each column and each row by the proportion of rocky shore to adjust for limited habitat area for larval production and larval recruitment, respectively.

Connectivity matrices were used to (i) evaluate the similarity between our results and those of Manríquez et al. (2012) which indicated absence of larval dispersal between their northern (23–24°S) and central (33–34°S) sampling areas; (ii) compare and contrast results with and without habitat limitations for larval production and recruitment; and (iii) identify highly independent subpopulations. Subpopulations were identified using a methodology recently developed by Jacobi et al. (2012). This method divides the study area into a finite number of mutually exclusive subpopulations based on minimization of an objective function that calculates larval exchange between potential subpopulations using the connectivity matrix. As larval exchange between subpopulations necessarily decreases when two subpopulations are joined into one, the objective function includes a single tunable parameter that penalizes against regrouping all sites in a small number of subpopulations. In practice, this parameter is varied to produce a series of subdivisions of the study area with different numbers of subpopulations. Jacobi et al.'s (2012) algorithm uses symmetric connectivity matrices, and therefore the connectivity between an area i and an area j was taken to be the average connectivity between these areas $\frac{C_{ij}+C_{ji}}{2}$. The algorithm also allows for an optional normalization of all connectivity matrix columns, which was not used as this would eliminate the effect of habitat area limitation. In a limited number of cases the algorithm identified a single isolated area as a subpopulation. In this case, we regrouped the area with the closest subpopulation. Subpopulations were calculated for connectivity matrices from the 7.5 km resolution ROMS model covering the full area relevant for management. The percentage of larvae exchanged between two adjacent subpopulations (relative to total recruitment originating in the two subpopulations), the percentage of all larvae exchanged between subpopulations and the percentage of self-recruitment for each subpopulation (fraction of settlers originating in the same subpopulation) were calculated.

Results

Distribution of loco habitat

Available loco habitat (rocky shores) is highest in the center of the study domain, dropping along northern and southern edges (Fig. 2). From 19°S to 33°S, sandy shores larger than 4 km are scarce and concentrated in a few embayments, leading to long rocky coastal continuums that are highly favorable for loco populations. By contrast, north and south of this central area, the percentage of available loco habitat varies significantly, with typical values around 60–80%.

Larval dispersal distance

The distribution of distances traveled by loco larvae from spawning to settlement are represented from the larval dispersal model outputs for spawning depth 0–20 m (Fig. 3). For both resolution models, the mean dispersal distance of larval settlers is about
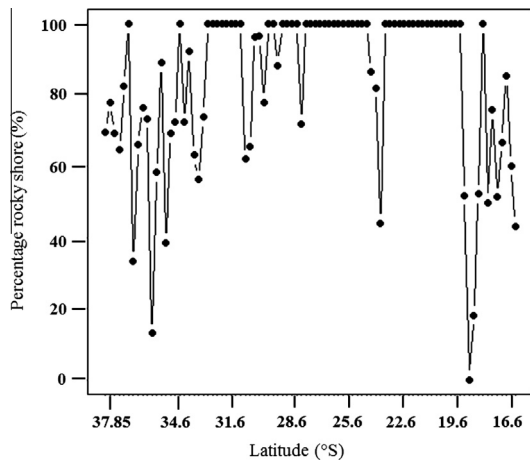
Fig. 2. Percentage of rocky shore representing available habitat for loco every 24 km along the Chilean coast, from 15.85°S to 38.1°S.

170 km for a maximum PLD of 80 days (Fig. 3a and b), whereas it is about 220 km for a maximum PLD of 140 days (Fig. 3c and d). The overall probability of successful settlement is around 2 times greater for the shorter PLD than for the longer PLD. For both PLD values, the number of settling larvae obtained after running the dispersal model over the 7.5 km ROMS outputs was approximately twice that obtained using the 3 km ROMS outputs. Similar patterns are obtained for spawning depth 40–60 m (results not shown).

Connectivity matrices

Connectivity matrices obtained using the 7.5 km ROMS outputs are shown in Fig. 4. Connectivity values are highest on, or close to, the matrix diagonal, indicating that settlement within an area is generally higher than transport among distant areas. At the northern edge of the domain, higher connectivity values are obtained above the matrix diagonal, indicating that virtual larvae are mainly transported to the North for the two spawning depth levels and PLDs tested. In contrast, in the central part of the domain there is a slight larval transport to the South for spawning depth level 40–60 m (Fig 4c and d). For both values of PLD, connectivity values are around 2 times higher for spawning depth level 40–60 m (Fig. 4c and d) than for level 0–20 m (Fig. 4a and b). When limited available habitat for loco is considered, the connectivity values decrease in the northern (to 19°S) and southern (from 33°S) parts of the study area (Fig. 5). Though connectivity patterns from the 3 km resolution ROMS are largely consistent with those from the lower resolution model, two hotspots of high connectivity at 26°S and 29°S are more clearly visible with the 3 km resolution ROMS (Fig. 6).

The northern (23–24°S) and central (33–34°S) areas examined by Manríquez et al. (2012) are represented by squares in Fig. 6. Transport between the two areas is essentially zero for PLD = 80 days regardless of the spawning depth. For PLD = 140 days, ~1 individual in 100,000 is transported on average from the northern area to the central area when spawned at the 40–60 m depth level. In the opposite direction, ~2–3 individuals in 100,000 are transported for the two spawning depth levels.
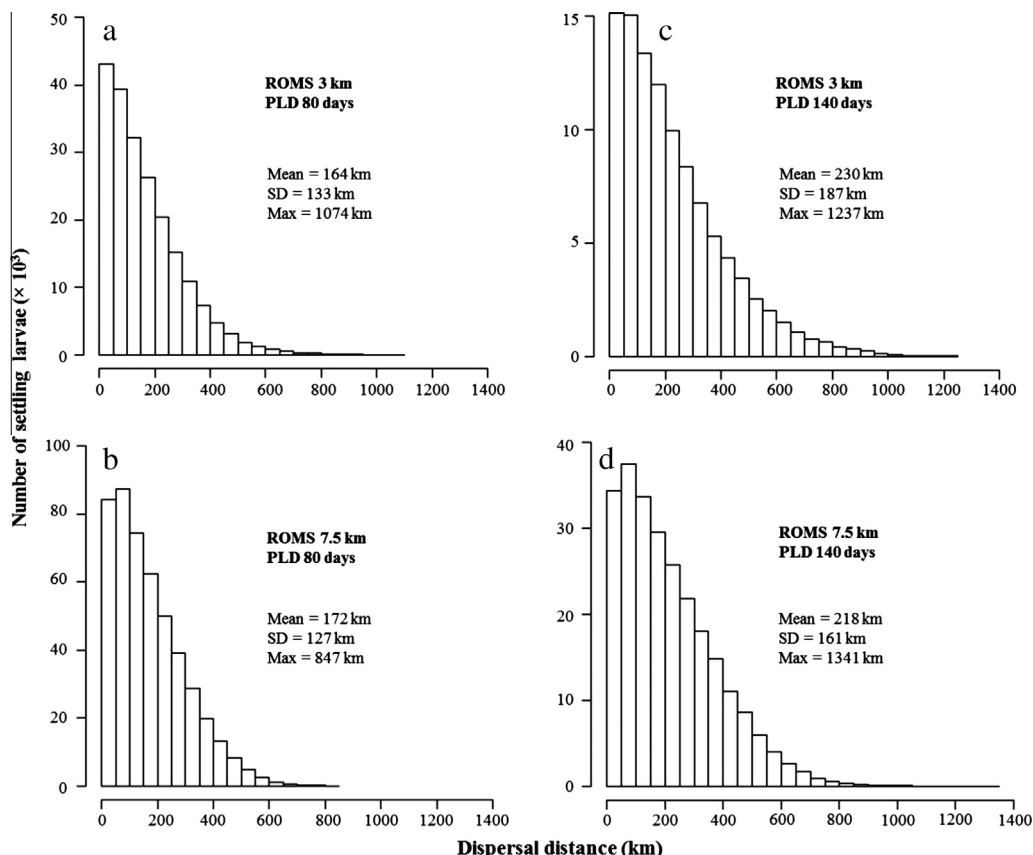

Fig. 3. Distributions of dispersal distances for settled loco larvae for spawning depth 0–20 m after 80 days and 140 days of planktonic larval duration (PLD) for ROMS 3 km (a and c respectively) and ROMS 7.5 km (b and d respectively). Mean, standard deviation (SD) and maximum distance (Max) are indicated.
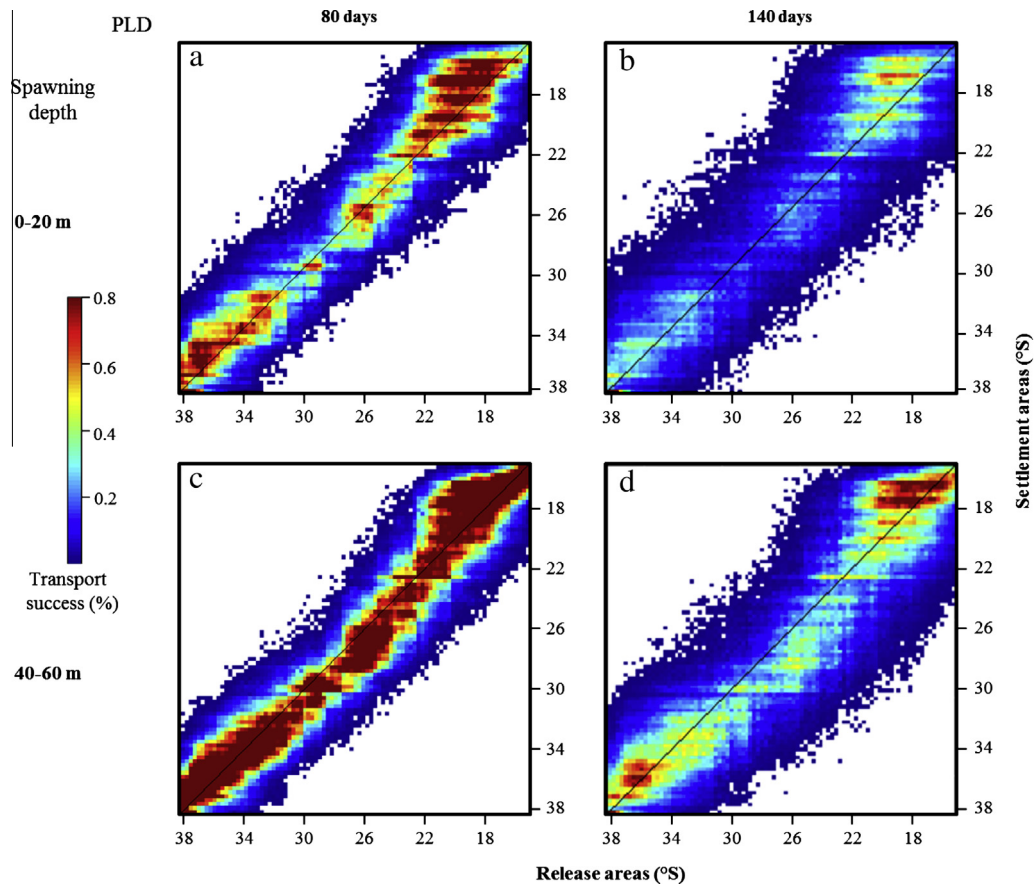
Fig. 4. Connectivity matrices obtained with the 7.5 km resolution ROMS for PLD (planktonic larval duration) = 80 days and spawning depth 0–20 m (a) 40–60 m (c); for PLD = 140 days and spawning depth 0–20 m (b) 40–60 m (d).

Connected clusters

Using the approach of Jacobi et al. (2012), the study area was divided into highly-connected subpopulations for all of the different connectivity matrices (i.e., for each PLD and spawning depth range combination). Results up to six subpopulations are globally consistent for all connectivity matrices assessed. Therefore, we only present those for spawning depth 0–20 m and PLD = 80 days with and without considering habitat availability for loco (Fig. 7a and b, respectively). Beyond six subdivisions, results are inconsistent between connectivity matrices and difficult to interpret.

Without available habitat (Fig. 7a), the separation into two subpopulations occurs at ~29°S, and the separation into three subpopulations at ~23°S. The next separation occurs at ~31°S and the last two separations occur at ~16°S and ~28°S. Increasing the number of clusters from 4 to 6 subpopulations results in self-recruitment values (number of recruited larvae in a subpopulation *i* coming from the subpopulation i) that are low for the 2 small additional subpopulations (20% and 19%) relative to the other subpopulations. Furthermore, percentages of larvae exchanged between adjoining subpopulations (boxed numbers in Fig. 7a) increase considerably. Both these results indicate that the subdivisions at ~16°S and ~28°S are relatively weak.

When habitat is considered (Fig. 7b), a somewhat different partitioning is observed with a separation at ~35°S for 6 subpopulations. From 3 subpopulations, self-recruitment for the northern subpopulations is relatively low (<20%). The percentage of all larvae exchanged between subpopulations reaches 20% for 6 subpopulations when habitat availability is taken into account (underlined numbers at bottom right of each coastline map in Fig. 7), whereas it reaches 15% when habitat availability is not considered. This result suggests that the proposed clustering is stronger when habitat availability is not accounted for.

Seasonality in connectivity

Favorable release areas for loco larval settlement along the coast are mainly located in the North (17–26°S) and South (32–38°S) of the study area (Fig. 8), regardless of PLD or release depth. Although the release of larvae is temporally uniform in the model, the most favorable release months for settlement occur in austral autumn and winter (March–August, Fig. 8). The seasonal pattern is stronger in the South than in the North, and for the surface (0–20 m) than for the subsurface (40–60 m). This results in a weak effect of seasonality in the North at depth. Seasonal patterns are similar for the two values of PLD tested (results not shown).

Discussion

The main objective of our study was to develop a larval dispersal model in order to evaluate the scales of population connectivity for loco in Chile. Our results are globally consistent with previous studies on loco (*C. concholepas*) population connectivity, but also provide significant new information at regional spatial scales. Non-negligible dispersal was observed all along the coast, with mean dispersal distances ranging from 170 to 220 km depending on PLD. This value is similar to, but slightly higher than, the dispersal scale for loco larvae of around 120 km estimated by Kinlan and Gaines (2003) based on a genetic study by Gallardo
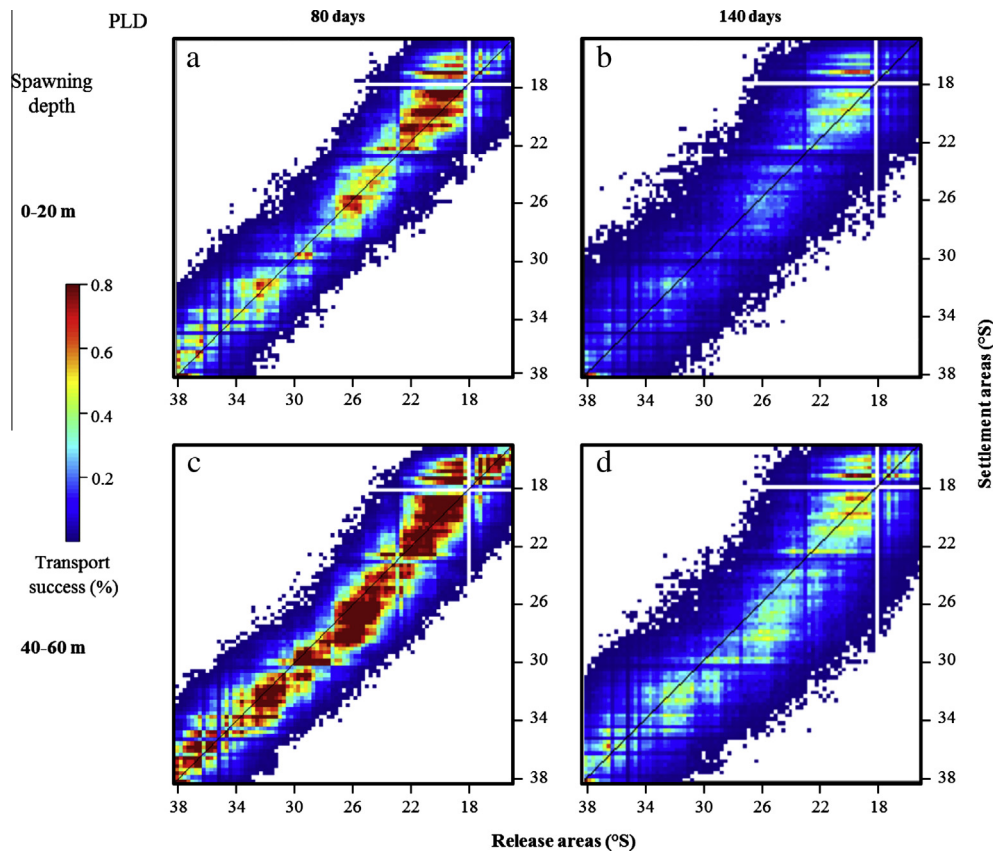
Fig. 5. Same as Fig. 4 but taking into account the limited habitat availability of loco for both release (columns) and settlement (rows).

and Carrasco (1996). Our simulated levels of dispersal are also consistent with little indication of significant larval retention at the scale of kilometers (Manríquez et al., 2012) and low levels of (long-term) genetic differentiation among widely separated loco individuals (Cárdenas et al., 2009).

The clustering analysis to identify highly-independent subpopulations revealed generally consistent patterns across model resolutions and parameter choices. In all cases, a major split occurs at approximately 29°S, and the northern part of the domain is somewhat more highly structured than the southern part (based on earlier split into subpopulations and lower levels of larval exchange between subpopulations). The split at 29°S coincides with a zone characterized by an extensive bay system (Coquimbo, Guanaqueros, and Tongoy bays) and an offshore-oriented current divergence (Hormazabal et al., 2004). This zone is known to represent a climatic and biologic (biogeographic) transition zone in the marine and terrestrial realm (Camus, 2001; Thiel et al., 2007). Coquimbo Bay and areas immediately to the south (~29–31°S) form a subpopulation of loco. This zone has already been described as a particularly high larval retention area (IFOP, INFORME, 2002). The separation at 23°S coincides with the Mejillones peninsula, the most conspicuous surface topographic feature found along the coast of northern Chile, which also coincides with a very narrow continental shelf. These geographic features likely influence connectivity between sites north and south of this zone. Separation at 16°S appears from 6 subpopulations when habitat availability is not considered and from 3 subpopulations when it is considered. At 16°S connectivity values and percentage of loco available habitat are low, which explains the observation of this separation at the beginning of the partitioning. A separation at ~35°S appears when habitat availability is considered. This separation is likely driven by lower levels of rocky-bottom habitat south of this point. Adding habitat along the coast increases percentage of larvae exchanged

between subpopulations in the southern part of the study domain. Surprisingly, subpopulations identified are largely independent of PLD and change only slightly with spawning depth. This, in combination with the fact that some of the identified major barriers to connectivity correspond to known features (like capes and bays) of the Chilean coast, suggest that these results are fairly robust, generic features of coastal circulation in the area.

Whereas connectivity patterns are globally consistent across model resolutions and parameter choices, absolute levels of transport success are sensitive to these factors. Transport success using the higher spatial resolution ocean model was roughly a half of that obtained with the lower resolution model. Oceanographic observations along the Chilean coast highlight the importance of mesoscale processes like eddies, filaments, and meandering currents (Hormazabal et al., 2004) that could cause offshore losses of larvae (Parada et al., 2012). The model resolution at 3 km more accurately reproduces coastal bathymetry and, therefore, coastal mesoscale processes are expected to be better resolved than in the model with a 7.5 km resolution, likely driving reduced transport success. However, as relative patterns are generally more useful than absolute values for assessing connectivity differences, the coherence between connectivity patterns across model resolutions lends support to using the larger (though lower-resolution) domain for management issues.

Some model limitations may impact the level of realism of ocean circulation and connectivity patterns derived from the quasi-equilibrium hydrodynamics model used here. Some of these limitations are already discussed in Parada et al. (2012) and Yannicelli et al. (2012) who used the same approach in the same region for anchovy and squat lobster respectively. First, using climatological monthly-mean forcing precludes high-frequency forced oceanic motions like the alternation of upwelling events and relaxation periods (3–10 days; Rutllant et al., 2004) and inertial motions that could be of importance for the nearshore
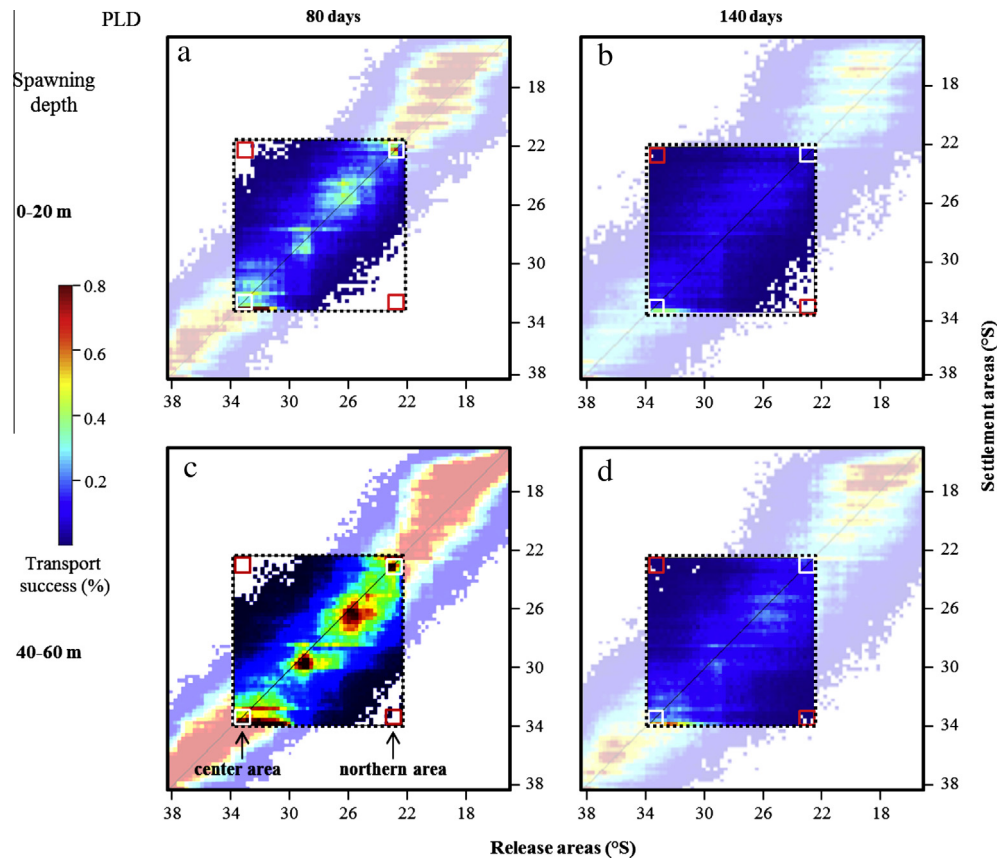
Fig. 6. Same as Fig. 4 with the results obtained using the 3 km resolution ROMS superimposed to those obtained using the 7.5 km resolution. White squares represent retention within the central (33–34°S) and northern (23–24°S) areas sampled by Manríquez et al. (2012) and red squares represent transport from one area to the other. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
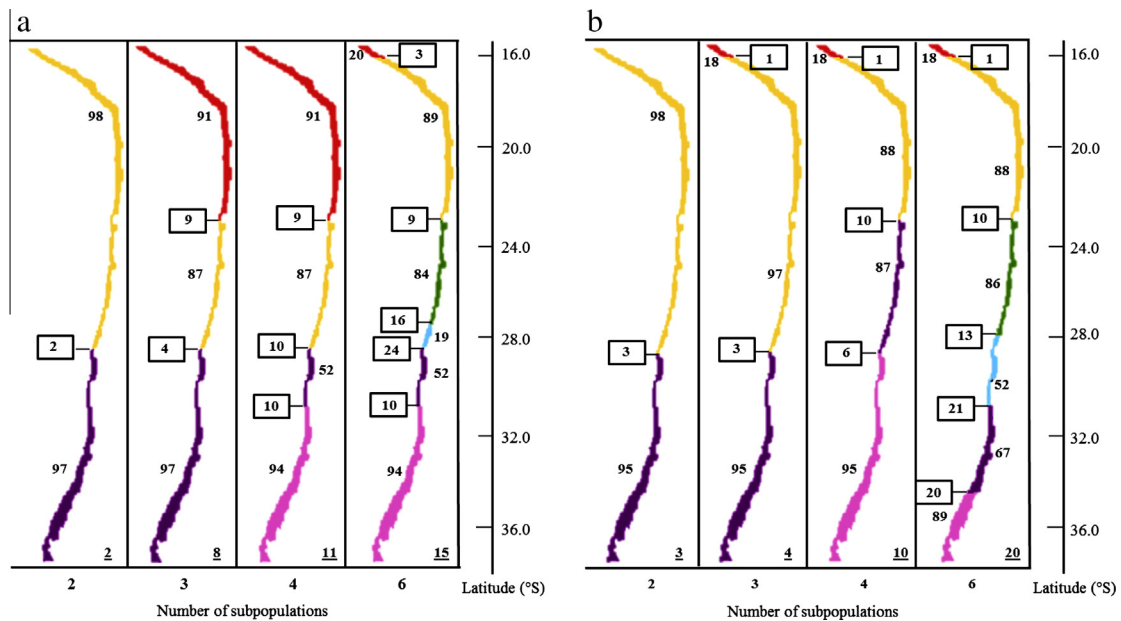

Fig. 7. Partitioning of the loco population into subpopulations successively identified by the method of Jacobi et al. (2012) from the connectivity matrices of (a) Fig. 4a (spawning depth 0–20 m, PLD = 80 days) and (b) Fig. 5a (spawning depth 0–20 m and PLD = 80 days with loco habitat availability). The different values represent the percentage of larvae exchanged between two adjacent subpopulations (numbers in box), the percentage of all larvae exchanged between subpopulations (underscored numbers), and the percentage of self-recruitment for each subpopulation.
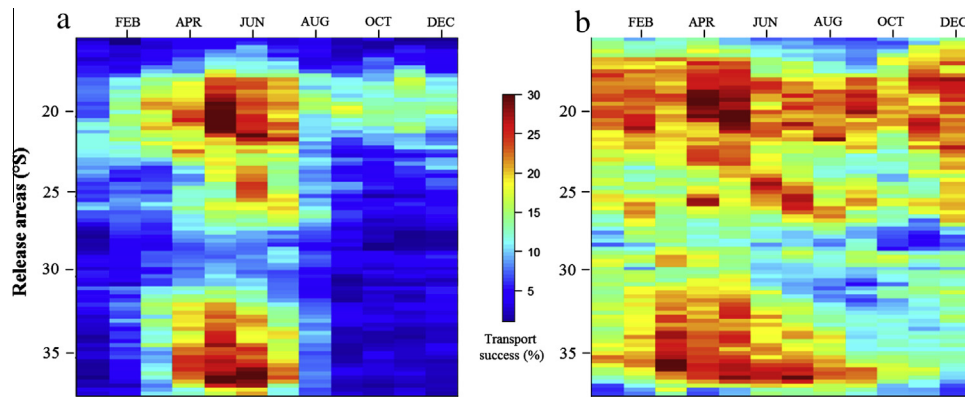
Fig. 8. Transport success of loco larvae in relation to area and month of release for PLD = 80 days and spawning depth (a) 0–20 m and (b) 40–60 m.

transport of larvae (Yannicelli et al., 2006). If this high-frequency forcing was included in the model, then periodic relaxation events may provide increased opportunities for shelf retention leading to higher overall recruitment probabilities (Wing et al., 1998; Kaplan et al., 2003; Gibson et al., 2013). Second, both high-frequency (intra-seasonnal) and low-frequency (interannual, ENSO related) variability are absent in ocean model open boundary forcing. These signals of equatorial origins propagate along the Peru–Chile coast and could also affect the nearshore current system off Chile (Hormazabal et al., 2001; Colas et al., 2008). Other limitations, that we expect to be of secondary importance in the present context and considering our spatial model resolution, are the absence of freshwater run-off and tidal forcing in our simulations. In specific localized areas off central Chile, run-off modulates the nearshore stratification and this may further have an effect on coastal retention processes (Santos et al., 2004), though globally river output is relatively minor in northern and central Chile. Tidal motions are rather weak along the coast of central Chile. It is still unclear whether tidal motions modulate significantly coastal retention in this region or not. However, tides could be taken into account to reproduce a more accurate nearshore advection on short-time scales. Despite these limitations, the oceanographic modeling approach used in this paper has proved to be sufficiently precise to capture the mean characteristics of regional and mesoscale dynamics in many previous studies (e.g., Marchesiello et al., 2003; Penven et al., 2005), reinforcing our level of confidence in the regional scale connectivity patterns we obtained. Nevertheless, these limitations should be addressed in future studies and their potential influence on connectivity patterns investigated.

In our study, we examined the influence of two larval biological processes on connectivity: spawning depth and PLD. Spawning depth influences retention due to opposing surface and subsurface currents. At depth, currents are generally weaker and oriented toward the coast, explaining increased connectivity rates for larvae released at 40–60 m depth than for 0–20 m depth, a result consistent with other modeling works in upwelling systems (Brochier et al., 2008a, 2008b). The increase in southward larval transport for 40–60 m spawning depth coincides with subsurface southward currents (see Appendix Fig. A1). Northward larval transport was expected due to the net northward coastal currents, but this was not observed for the 0–20 m spawning level. The bulk of released individuals were indeed transported north, but these same "northward" individuals were often transported offshore (i.e. away from coastal settlement areas) by offshore Ekman flow along the Chilean coast (Aiken et al., 2011) and by mesoscale features, that are intensified by coastal upwelling (Marín et al., 2001). Our results therefore highlight the importance of onshore subsurface currents and (relatively rare) poleward currents produced by wind relaxation events for loco connectivity.

Increasing PLD produced an increase in mean larval dispersal distance and a decrease in retention, connectivity and global settlement, as in other modeling studies (Lefebvre et al., 2003; Lett et al., 2010; Aiken et al., 2011). In our model, we used a constant PLD value all along the coast, whereas in reality PLD depends on sea temperature (O'Connor et al., 2007). Given the latitudinal extension of the Chilean coast, temperature is one of the characteristics of the marine environment that is particularly variable. From 18°S to 32°S, temperatures in surface waters close to the coast range from 13 °C to 20 °C. Temperature variability is less pronounced in the south of Chile, ranging from 11 °C to 13 °C for latitudes comprised between 32°S and 56°S (Fernández et al., 2000). Experimental data support loco PLD increasing from around 60 days in the northern part of the study area to 120 days to the South, consistent with temperature changes (DiSalvo, 1988; Moreno et al., 1993). This gradient should increase offshore larval losses as one goes from northern to southern Chile.

One important biological process that has not been implemented in our model is larval mortality. Long PLDs such as those described for loco imply high total mortality rates during transport. Data on larval mortality is not available for loco, but a mortality rate of 0.12 d^{-1} has been estimated for the veliger larvae of *Mytilus edulis* (Rumrill, 1990). Assuming such a rate for loco would imply that one larva is 2,000 times more likely to survive 60 days than 120 days, which means that loco larvae spawned in southern Chile could be much more exposed to mortality than those spawned in the North. This effect, combined with increased offshore transport for longer PLDs and reduced loco habitat in the southern part of the domain, suggest that real transport success may be significantly lower in the southern part of the study area than in the North. To our knowledge, there is no available data to confirm this hypothesis, but these results provide a reasonable explanation for increased reproductive investment by adult locos via higher numbers of loco embryos per capsule area towards the South (Fernández et al., 2007), as increased larval production could counterbalance these larval losses. In the central part of Chile, a latitudinal gradient in the abundance of recruits for some benthic invertebrate species has been observed (Navarrete et al., 2005). Testing for such alongshore gradients in loco recruitment is an interesting avenue for future research.

Another important biological process affecting larval dispersal that has not been implemented in our model is larval diel vertical migration (DVM). DVM above and below the thermocline will likely expose larvae to weaker, more southward subsurface currents part of the time and stronger, more northward surface currents at other times. The net effect of this behavior on loco larval dispersal will depend on the details of the DVM and ocean currents. Given the complexity of these processes and our principal objective of examining large-scale connectivity patterns, we

decided not to implement this process in our model. Nevertheless, DVM and larval behavior in general should be examined in future modeling studies based on current knowledge of vertical positioning of loco larvae in the water column.

To perform vertical migration, loco larvae possess a specialized swimming organ, known as a vellum (Ruppert et al., 2003). In southern Chile (43–44°S), the abundance of small loco larvae (stage 1, size between 250 μm and 500 μm, DiSalvo, 1988) was observed to increase in surface water samples at night and to positively correlate with salinity (Molinet et al., 2008). Similar results have been found in laboratory experiments, with the number of larvae moving towards the surface increasing at night (Garavelli et al., unpublished results). For competent loco larvae (1400 μm and 1900 μm; DiSalvo, 1988), vertical migration has also been observed, though the direction of migration has not been consistent between studies. Field studies in central Chile suggested that competent larvae swim to the surface during the day (Poulin et al., 2002). However, other recent field studies in northern and central Chile coupled with laboratory observations indicated the opposite (Manríquez and Castilla, 2011). For larvae between 500 μm and 1400 μm, the behavior remains unknown. Rafting on floating algae or other materials has also been suggested as a mechanism for connectivity in loco populations. This has been suggested for larvae at timescales relevant to population dynamics (Manríquez and Castilla, 2011) and for egg capsules, juveniles and adults for long-distance exchanges over longer timescales (Castilla and Guiñez, 2000).

Spawning for loco in central Chile occurs principally in austral summer and autumn (January–May, Manríquez and Castilla, 2001; Manríquez et al., 2008). Loco eggs are attached to the rocky bottom during 2–3 months (Castilla and Cancino, 1976). Hatching of larvae therefore occurs mainly in austral autumn and winter (March–August), the period identified as the most favorable for larval settlement in our simulations. As PLD for loco larvae is between 2 and 4 months, settlement occurs principally in austral winter and spring in the study area. Aiken et al. (2011) also observed maximum settlement in austral winter in southern Chile from their modeling study. Overall, loco larvae that successfully recruit are transported between austral autumn and spring, and less in summer, the period when intensity of upwelling along the Chilean coast is generally maximal (Thiel et al., 2007) and therefore unfavorable to larval coastal retention. We also observed that the seasonal pattern is less pronounced in the northern part of the study domain than in the southern part, suggesting that seasonality in loco connectivity along the Chilean coast may depend on latitude.

The partitioning of the study domain into subpopulations provides a template for defining regional management units for coordinating MEABR management efforts. Despite its relatively simple coastal geometry, connectivity along the Chilean coast north of 42°S is heterogeneous enough to define rather independent subpopulations. We identified a partitioning into 4 subpopulations having low levels of inter-connectivity and high levels of self-recruitment, suggesting that MEABR within each subpopulation are largely connected, whereas MEABR between subpopulations are rather independent. From a management perspective, the identification of these spatial sub-units imply that: (i) in order to evaluate the performance of the system and state of the fishery, data of individual MEABR need to be integrated over each subpopulation; (ii) identification of productivity hotspots and conservation efforts should be organized at the level of subpopulations; and (iii) environmental and population monitoring should be conducted in at least one location within each zone. Using this partitioning to organize such regional management efforts would provide a compromise between previous large-scale quotas and current small scale user-rights management that is better tuned to loco biology and dispersal. Clearly, considerations other than biology, and in particular societal and economical concerns, need to be taken into account when determining the number of fishery management units. However, our results provide an initial, biologically-optimal partitioning that can then be adapted to societal constraints, highlighting the utility of such a tool for decision support for management of marine resources.
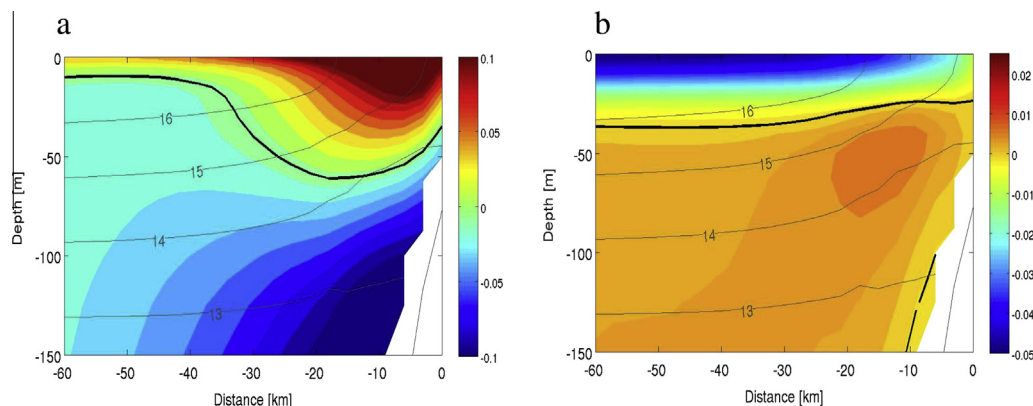
Appendix A

See Fig. A1.

Fig. A1. Vertical sections of annual mean of (a) alongshore and (b) cross-shore velocity components (m/s) averaged between 22°S and 34°S for the 3 km ROMS model. Black contours represent velocity = 0 m/s.

References

Aiken, C.M., Navarrete, S.A., Pelegrí, J.L., 2011. Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate. Journal of Geophysical Research 116, G04026. http://dx.doi.org/10.1029/2011JG001731.

Báez, P., Arata, J., Jackson, D., 2004. El loco *Concholepas concholepas* (Bruguière, 1789) (Mollusca: Gastropoda: Muricidae) como recurso durante el Holoceno Temprano-Medio en Los Vilos, Chile central. Investigaciones Marinas 32, 107–113.

Ban, N.C., Adams, V.M., Almany, G.R., Ban, S., Cinner, J.E., McCook, L.J., Mills, M., Pressey, R.L., White, A., 2011. Designing, implementing and managing marine protected areas: emerging trends and opportunities for coral reef nations. Journal of Experimental Marine Biology and Ecology 408, 21–31.

Bernal, P.A., Oliva, D., Aliaga, B., Morales, C., 1999. New regulations in Chilean Fisheries and Aquaculture: ITQ's and Territorial Users Rights. Ocean & Coastal Management 42, 119–142.

Botsford, L.W., Micheli, F., Hastings, A., 2003. Principles for the design of marine reserves. Ecological Applications 13, S25–S31.

Brazeiro, A., Defeo, O., 1999. Effects of harvesting and density dependence on the demography of sandy beach populations: the yellow clam *Mesodesma mactroides* of Uruguay. Marine Ecology Progress Series 182, 127–135.

Brochier, T., Lett, C., Tam, J., Fréon, P., Colas, F., Ayón, P., 2008a. An individual-based model study of anchovy early life history in the northern Humboldt Current system. Progress in Oceanography 79, 313–325.

Brochier, T., Ramzi, A., Lett, C., Machu, E., Berraho, A., Fréon, P., Hernández-León, S., 2008b. Modelling sardine and anchovy ichthyoplankton transport in the Canary Current System. Journal of Plankton Research 30, 1133–1146.

Camus, P.A., 2001. Biogeografía marine de Chile continental. Revista Chilena de Historia Natural 74, 587–617.

Cárdenas, L., Viard, F., Castilla, J.C., 2008. Paleobiogeography and taxonomy of the genus *Concholepas concholepas* (Lamarck, 1801): a review and new evidences. Revista Chilena de Historia Natural 81, 417–436.

Cárdenas, L., Castilla, J.C., Viard, F., 2009. A phylogeographical analysis across three biogeographical provinces of the south-eastern Pacific: the case of the marine gastropod *Concholepas concholepas*. Journal of Biogeography 36, 969–981.

Carton, J., Giese, B., 2008. A reanalysis of ocean climate using Simple Ocean Data Assimilation (SODA). Monthly Weather Review 136, 2999–3017. http://dx.doi.org/10.1175/2007MWR1978.1.

Castilla, J.C., 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends in Ecology & Evolution 14, 280–283.

Castilla, J.C., Cancino, J., 1976. Spawning behaviour and egg capsules of *Concholepas concholepas* (Mollusca: Gastropoda: Muricidae). Marine Biology 37, 255–263.

Castilla, J.C., Guiñez, R., 2000. Disjoint geographical distribution of intertidal and nearshore benthic invertebrates in the Southern Hemisphere. Revista Chilena de Historia Natural 73, 585–603.

Colas, F., Capet, X., McWilliams, J.C., Shchepetkin, A., 2008. 1997–1998 El Nino off Peru: a numerical study. Progress in Oceanography 79, 138–155.

Colas, F., McWilliams, J.C., Capet, X., Kurian, J., 2012. Heat Balance and eddies in the Peru-Chile current system. Climate Dynamics. http://dx.doi.org/10.1007/s00382-011-1170-6.

Colas, F., Capet, X., McWilliams, J.C., Li, Z., 2013. Mesoscale eddy buoyancy flux and eddy-induced circulation in Eastern Boundary Currents. Journal of Physical Oceanography 43, 1073–1095, http://dx.doi.org/10.1175/JPO-D-11-0241.1.

Da Silva, A.M., Young, C.C., Levitus, S., 1994. Atlas of Surface Marine Data 1994, vol. 1. Algorithms and Procedures, Technical Report. National Oceanographic and Atmospheric Administration. Silver, Spring, MD.

DiSalvo, L.H., 1988. Observations on the larval and post-metamorphic life of *Concholepas concholepas* (Bruguière, 1789). Veliger 30, 358–368.

DiSalvo, L.H., Carriker, M.R., 1994. Planktonic, metamorphic, and early benthic behavior of the Chilean loco *Concholepas concholepas* (Muricidae, Gastropoda, Mollusca). Journal of Shellfish Research 13, 57–66.

Fernández, M., Castilla, J.C., 2005. Marine conservation in Chile: historical perspective, lessons, and challenges. Conservation Biology 19, 1752–1762.

Fernández, M., Jaramillo, E., Marquet, P.A., Moreno, C.A., Navarrete, S.A., Ojeda, F.P., Valdovinos, C.R., Vasquez, J.A., 2000. Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation. Revista Chilena de Historia Natural 73, 797–830.

Fernández, M., Calderón, R., Cancino, J.M., Jeno, K., 2007. The effect of temperature on the development of encapsulated embryos of *Concholepas concholepas* along a latitudinal cline. Marine Ecology Progress Series 348, 229–237.

Figueroa, D., Moffat, C., 2000. On the influence of topography in the induction of coastal upwelling along the Chilean coast. Geophysical Research Letters 27, 3905–3908.

Gallardo, M.H., Carrasco, J.I., 1996. Genetic cohesiveness among populations of *Concholepas concholepas* (Gastropoda, Muricidae) in Southern Chile. Journal of Experimental Marine Biology and Ecology 197, 237–249.

Gelcich, S., Godoy, N., Prado, L., Castilla, J.C., 2008. Add-on conservation benefits of marine territorial user rights fishery policies in central Chile. Ecological Applications 18, 273–281.

Gibson, G.A., Coyle, K.O., Hedstrom, H., Curchitser, E.N., 2013. A modeling study to explore on-shelf transport of oceanic zooplankton in the Eastern Bering Sea. Journal of Marine Systems 121–122, 47–64.

González, J., Stotz, W., Garrido, J., Orensanz, J.M., Parma, A.M., Tapia, C., Zuleta, A., 2006. The Chilean TURF system: how is it performing in the case of the loco fishery? Bulletin of Marine Science 78, 499–527.

Green, A., Smith, S.E., Lipsett-Moore, G., Groves, C., Peterson, N., Sheppard, S., Lokani, P., Hamilton, R., Almany, J., Aitsi, J., Bualia, L., 2009. Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. Oryx 43, 488–498.

Hormazabal, S., Shaffer, G., Letelier, J., Ulloa, O., 2001. Local and remote forcing of sea surface temperature in the coastal upwelling system off Chile. Journal of Geophysical Research 106, 16657–16671.

Hormazabal, S., Shaffer, G., Leth, O., 2004. Coastal transition zone off Chile. Journal of Geophysical Research 109, C01021. http://dx.doi.org/10.1029/2003JC001956.

IFOP, INFORME, http://www.fip.cl/Archivos/Hitos/Informes/inffinal%202002-16.pdf, 2002. Bases biológicas para la evaluación y manejo de metapoblaciones de loco en la III y IV Regiones.

Jacobi, M.N., André, C., Döös, K., Jonsson, P.R., 2012. Identification of subpopulations from connectivity matrices. Ecography 35, 1004–1016.

Kaplan, D.M., 2006. Alongshore advection and marine reserves: consequences for modeling and management. Marine Ecology Progress Series 309, 11–24.

Kaplan, D.M., Largier, J.L., Navarrete, S., Guiñez, R., Castilla, J.C., 2003. Large diurnal temperature fluctuations in the nearshore water column. Estuarine, Coastal and Shelf Science 57, 385–398.

Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84, 2007–2020.

Lefebvre, A., Ellien, C., Davoult, D., Thiébaut, E., Salomon, J.C., 2003. Pelagic dispersal of the brittle-star *Ophiothrix fragilis* larvae in a megatidal area (English Channel, France) examined using an advection/diffusion model. Estuarine Coastal and Shelf Science 57, 421–433.

Leis, J.M., Herwerden, L.V., Patterson, H.M., 2011. Estimating connectivity in marine fish populations: what works best? Oceanography and Marine Biology 49, 193–234.

Leiva, G.E., Castilla, J.C., 2002. A review of the world marine gastropod fishery: evolution of catches, management and the Chilean experience. Reviews in Fish Biology and Fisheries 11, 283–300.

Letelier, J., Pizarro, O., Nuñez, S., 2009. Seasonal variability of coastal upwelling and the upwelling front off central Chile. Journal of Geophysical Research 114, C12009. http://dx.doi.org/10.1029/2008JC005171.

Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., Blanke, B., 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. Environmental Modelling & Software 23, 1210–1214.

Lett, C., Ayata, S.-D., Huret, M., Irisson, J.-O., 2010. Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. Progress in Oceanography 87, 106–113.

Manríquez, P.H., Castilla, J.C., 2001. Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas*. Marine Ecology Progress Series 215, 201–211.

Manríquez, P.H., Castilla, J.C., 2011. Behavioural traits of competent *Concholepas concholepas* (loco) larvae. Marine Ecology Progress Series 430, 207–221.

Manríquez, P.H., Navarrete, S.A., Rosson, A., Castilla, J.C., 2004. Settlement of the gastropod *Concholepas concholepas* on shells of conspecific adults. Journal of the Marine Biological Association of the United Kingdom 84, 651–658.

Manríquez, P.H., Delgado, A.P., Jara, M.E., Castilla, J.C., 2008. Field and laboratory pilot rearing experiments with early ontogenic stages of *Concholepas concholepas* (Gastropoda: Muricidae). Aquaculture 279, 99–107.

Manríquez, P., Galaz, S.P., Opitz, T., Hamilton, S., Paradis, G., Warner, R.R., Castilla, J.C., Labra, F.A., Lagos, N.A., 2012. Geographic variation in trace-element signatures in the statoliths of near-hatch larvae and recruits of *Concholepas concholepas* (loco). Marine Ecology Progress Series 448, 105–118.

Marchesiello, P., McWilliams, J.C., Shchepetkin, A.F., 2003. Equilibrium structure and dynamics of the California Current System. Journal of Physical Oceanography 33, 753–783.

Marín, V., Escribano, R., Delgado, L., Olivares, G., Hidalgo, P., 2001. Nearshore circulation in a coastal upwelling site off the Northern Humboldt current system. Continental Shelf Research 21 (13–14), 1317–1329.

Martínez, P., Navarrete, S.A., 2002. Temporal and spatial variation in settlement of the gastropod *Concholepas concholepas* in natural and artificial substrata. Journal of the Marine Biological Association of the UK 82, 257–264.

Martone, R.G., Micheli, F., 2012. Geographic variation in demography of a temperate reef snail: importance of multiple life-history traits. Marine Ecology Progress Series 457, 85–99.

Mason, E., Molemaker, M.J., Shchepetkin, A.F., Colas, A.F., McWilliams, J.C., Sangra, P., 2010. Procedures for offline grid nesting in regional ocean models. Ocean Modelling 35, 1–15. http://dx.doi.org/10.1016/j.ocemod.2010.05.007.

McCook, L., Almany, G., Berumen, M., Day, J., Green, A., Jones, G., Leis, J., Planes, S., Russ, G., Sale, P., Thorrold, S., 2009. Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28 (2), 353–366.

Metaxas, A., Saunders, M., 2009. Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. The Biological Bulletin 216, 257–272.

Molinet, C., Arévalo, A., González, M.T., Moreno, C.A., Arata, J., Niklitschek, E., 2005. Patterns of larval distribution and settlement of *Concholepas concholepas* (Bruguiere, 1789) (Gastropoda, Muricidae) in fjords and channels of southern Chile. Revista chilena de historia natural 78, 409–423.

Molinet, C., Niklitschek, E., Moreno, C.A., Arévalo, A., 2008. Vertical distribution of early and competent larvae of *Concholepas concholepas* in two systems of Chilean inland seas. Marine Biology 153, 779–787.

Moreno, C.A., Asencio, G., Ibañez, S., 1993. Patrones de asentamiento de *Concholepas concholepas* (Brugière) (Mollusca: Muricidae) en la zona intermareal rocosa de Valdivia, Chile. Revista Chilena de Historia Natural 66, 93–101.

Navarrete, S.A., Wieters, E.A., Broitman, B.R., Castilla, J.C., 2005. Scales of benthic–pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. Proceedings of the National Academy of Sciences of the United States of America 102, 18046–18051.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P., Weiss, J.M., 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proceedings of the National Academy of Sciences of the United States of America 104, 1266–1271.

Orensanz, J.M., Parma, A.M., Jerez, G., Barahona, N., Montecinos, M., Elias, I., 2005. What are the key elements for the sustainability of « s-fisheries » ? Insights from South America. Bulletin of Marine Science 76, 527–556.

Parada, C., Colas, F., Soto-Mendoza, S., Castro, L., 2012. Effects of seasonal variability in across- and alongshore transport of anchoveta (*Engraulis ringens*) larvae on model-based pre-recruitement indicies off central Chile. Progress in Oceanography 92–95, 192–205.

Pechenik, J.A., Eyster, L.S., 1989. Influence of delayed metamorphosis on the growth and metabolism of young *Crepidula fornicata* (Gastropoda) juveniles. Biological Bulletin 176, 14–24.

Peliz, A., Marchesiello, P., Dubert, J., Marta-Almeida, M., Roy, C., Queiroga, H., 2007. A study of crab larvae dispersal on the Western Iberian Shelf: physical processes. Journal of Marine Systems 68, 215–236.

Penven, P., Echevin, V., Pasapera, J., Colas, F., Tam, J., 2005. Average circulation, seasonal cycle, and mesoscale dynamics of the Peru Current System: a modeling approach. Journal of Geophysical Research 110. http://dx.doi.org/10.1029/2005JC002945110.

Poulin, E., Palma, A.T., Leiva, G., Narvaez, D., Pacheco, R., Navarrete, S.A., Castilla, J.C., 2002. Avoiding offshore transport of competent larvae during upwelling events: the case of the gastropod *Concholepas concholepas* in central Chile. Limnology Oceanography 47, 1248–1255.

Risien, C.M., Chelton, D.B., 2008. A global climatology of surface wind and wind stress fields from eight years of QuikSCAT scatterometer data. Journal of Physical Oceanography 38, 2379–2413. http://dx.doi.org/10.1175/2008JPO3881.1.

Rumrill, S.S., 1990. Natural mortality of marine invertebrate larvae. Ophelia 32, 163–198.

Ruppert, E., Fox, R.S., Barnes, R.D., 2003. Invertebrate Zoology. A Functional Evolutionnary Approach, seventh ed. Thomson Brooks/Cole.

Rutllant, J.A., Rosenbluth, B., Hormazabal, S., 2004. Intraseasonal variability of wind-forced coastal upwelling off central Chile (30°S). Continental Shelf Research 24, 789–804.

Santos, A.M.P., Peliz, A., Dubert, J., Oliveira, P.B., Angelico, M.M., Re, P., 2004. Impactof a winter upwelling event on the distribution and transport of sardine (*Sardina pilchardus*) eggs and larvae off western Iberia: a retention mechanism. Continental Shelf Research 24 (14), 149–165.

Shchepetkin, A.F., McWilliams, J.C., 2005. The Regional Oceanic Modeling System: a split-explicit, free-surface, topography-following-coordinate ocean model. Ocean Modelling 9, 347–404. http://dx.doi.org/10.1016/j.ocemod.2004.08.002.

Shchepetkin, A.F., McWilliams, J.C., 2009. Correction and commentary for "Ocean forecasting in terrain-following coordinates: formulation and skill assessment of the regional ocean modeling system" by Haidvogel et al. Journal of Computational Physics 227, 3595–3624. Journal of Computational Physics 228 (24), 8985–9000. http://dx.doi.org/10.1016/j.jcp.2009.09.002.

Stotz, W., 1997. Las áreas de manejo en la ley de pesca y acuicultura: primeras experiencias y evaluación de la utilidad de esta herramienta para el recurso loco. Estudios Oceanológicos 16, 67–86.

Stotz, W., Perez, E., 1992. Crecimiento y productividad del loco *Concholepas concholepas* (Bruguière, 1789) como estimador de la capacidad de carga en áreas de manejo. Investigaciones Pesqueras 37, 13–22.

Strub, P.T., Mesías, J.M., Montecino, V., Rutllant, J., Salinas, S., 1998. Coastal ocean circulation off western South America. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea. John Wiley and Sons, New York, pp. 273–314.

Thiel, M. et al., 2007. The Humboldt current system of northern and central Chile. Oceanographic processes, ecological interactions and socioeconomic feedback. Oceanography and Marine Biology: An Annual Review 45, 195–344.

Veitch, J., Penven, P., Shillington, F., 2010. Modelling equilibrium dynamics of the Benguela Current System. Journal of Physical Oceanography 40, 1942–1964. http://dx.doi.org/10.1175/2010JPO4382.1.

White, C., Costello, C., 2011. Matching spatial property rights fisheries with scales of fish dispersal. Ecological Applications 21, 350–362.

Wieters, E.A., Gaines, S.D., Navarrete, S.A., Blanchette, C.A., Menge, B.A., 2008. Scales of dispersal and the Biogeography of Marine Predator-Prey Interactions. The American Naturalist 171, 405–417.

Wing, S.R., Botsford, L.W., Ralston, S.V., Largier, J.L., 1998. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. Limnology and Oceanography 43, 1710–1721.

Yannicelli, B., Castro, L.R., Valle-Levinson, A., Atkinson, L., Figueroa, D., 2006. Vertical distribution of decapod larvae in the entrance of an equatorward facing bay of central Chile: implications for transport. Journal of Plankton Research 28 (1), 19–37. http://dx.doi.org/10.1093/plankt/fbi098.

Yannicelli, B., Castro, L., Parada, C., Schneider, W., Colas, F., Donoso, D., 2012. Distribution of *Pleuroncodes monodon* larvae over the continental shelf of south-central Chile: field and modeling evidence for partial local retention and transport. Progress in Oceanography 92–95, 206–227.