

Influence of larval traits on dispersal and connectivity patterns of two exploited marine invertebrates in central Chile

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ABSTRACT: Environmental variability can influence larval development rates and affect critical processes in the dynamics of natural populations, such as dispersal distances and connectivity, when modulated by different larval traits. Knowledge of connectivity patterns in marine populations is fundamental for defining population viability and progressing with management and conservation goals. Here, we developed a biophysical, individual-based larval dispersal model to assess the effect of oceanographic variability and biological traits (i.e. larval diel vertical migration [DVM] and temperature-dependent larval development [PLD]) on recruitment success, dispersal distance, and alongshore connectivity patterns. We selected 2 species exploited by Chilean artisanal fisheries: *Loxechinus albus* (PLD: 20 d) and *Fissurella latimarginata* (PLD: 5 d). A sensitivity analysis was used to examine the effect of intrinsic (DVM and PLD) and extrinsic (release depth, latitude, and timing) processes. Release location and timing of release explained respectively 24.30 and 5.54 % (*F. latimarginata*) and 34.8 and 4.19 % (*L. albus*) of the variability observed in recruitment success, and 23.80 and 6.94 % (*F. latimarginata*) and 26.10 and 19.60 % (*L. albus*) of the variability observed in dispersal distance. Most recruitment to local populations was allochthonous, presenting low levels of self-recruitment and local retention, including species with short PLD. Similar geographic patterns of source and destination strengths were observed in both species, showing a geographic mosaic of source and sink populations with relatively higher importance towards the northern region of the study area. Our findings allow us to identify primary determinants of recruitment success and dispersal distance for 2 important exploited species in Chile.

KEY WORDS: Numerical model · Individual-based model · Source-sink dynamics · Larval migration · Larval behavior · Management

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1. INTRODUCTION

The complex processes affecting the movement of individuals within and among subpopulations (Crooks & Sanjayan 2006) are crucial to comprehending the regulation and persistence of wild populations (Possingham & Roughgarden 1990). In marine ecosystems, life cycles involving very short pelagic larval phases (Cowen et al. 2006) impose major challenges to understanding patterns of connectivity among local

sites and the potential 'subpopulation' structure. A wide variety of plastic larval attributes (e.g. physiological, nutritional, behavioral features), adult reproduction patterns, and the physical characteristics of the fluid environment (e.g. ocean currents) have been identified as the primary determinants of population connectivity and successful onshore recruitment (Levin 2006, Werner et al. 2007, Cowen & Sponaugle 2009, Metaxas & Saunders 2009, Morgan 2014, Ospina-Alvarez et al. 2018). Recruitment of

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coastal marine populations depends on 2 sources of larval supply: those provided by the population itself (self-recruitment or autochthonous recruitment), and those originating from a population other than where the recruitment is evaluated (allochthonous recruitment). Moreover, marine coastal populations are often spatially fragmented or highly heterogeneous throughout space due to natural or human-caused habitat patchiness (e.g. Halpern et al. 2008) or because of highly spatially structured management and conservation schemes (Fogarty & Botsford 2007, Gaines et al. 2010a,b, Defeo & Castilla 2012). This further confounds our understanding of marine metapopulation dynamics, evoking an urgent need to improve our knowledge of determinants of larval dispersal and connectivity under realistic scenarios that capture the complexity of the biophysical processes involved. With this foundation, we can then set a template for the design of conservation and management strategies for marine species (Garavelli et al. 2014).

Diverse approaches have been applied to study connectivity in marine species (Levin 2006, Cowen & Sponaugle 2009, Munguia-Vega et al. 2014). Since it is impractical to follow small, highly diluted larvae in vast water masses (but see Worcester 1994), micro-chemical and genetic markers have been applied to infer general spatio-temporal patterns of connectivity among specific subsets of populations (Hedgecock et al. 2007, Thorrold et al. 2007, Carson et al. 2010, 2011). However, none of these methods can reproduce the 'connectivity matrix,' defined as the quantitative pattern of connection among all locations within a region and over some ecologically or evolutionarily relevant period of time (Hedgecock et al. 2007). The character of this connectivity matrix determines the dynamics, resilience, persistence, and subpopulation structure of a metapopulation (Aiken & Navarrete 2011, Jacobi & Jonsson 2011, Jacobi et al. 2012) as well as possibilities of species coexistence in metacommunities (Aiken & Navarrete 2014). Spatially explicit, coupled hydrodynamic individual-based models (SEIBMs) are useful tools to recreate 'realistic' scenarios of dispersal and therefore evaluate the effect of biological attributes and environmental features (Aiken et al. 2007, Werner et al. 2007, Cowen & Sponaugle 2009, Metaxas & Saunders 2009, Garavelli et al. 2016).

The potential realism of connectivity matrices derived from SEIBMs depends on how well these tools reproduce key hydrodynamic features of the coastal ocean and how they accommodate basic features of larval behavior and general larval performance while developing in the ocean. Temperature is one of the main factors affecting larval performance through

its effects on most biological rates, particularly that of larval development (planktonic larval duration [PLD]; Hoegh-Guldberg & Pearse 1995, Gillooly et al. 2002, O'Connor et al. 2007, Zhang et al. 2015, 2016). Inter-annual, seasonal, and intra-seasonal variability in water temperature can thus deeply affect larval development rates and, consequently, onshore larval recruitment (Hart & Scheibling 1988). The interaction between larval behavior (e.g. diel vertical migration [DVM]) and environmental conditions (e.g. buoyancy fronts, vertical currents) has also been deemed critically important in modulating larval dispersal and eventual recruitment (Paris & Cowen 2004, Woodson & McManus 2007, Metaxas & Saunders 2009, Morgan 2014). Indeed, larvae can move vertically across water layers and modify their swimming behavior in response to fluctuations in flow velocities and direction (Metaxas & Saunders 2009, Ospina-Alvarez et al. 2012). DVM sometimes increases larval retention of coastal species near the shore (Aiken et al. 2011), and likely increases the chances of self-recruitment (Morgan 2014), though this is not always the case (Ospina-Alvarez et al. 2018). DVM appears particularly important in areas influenced by oceanographic conditions that favor baroclinic circulation (coastal upwelling, estuarine tidal currents) (Poulin et al. 2002, Aiken et al. 2011, Sundelöf & Jonsson 2012). In coastal upwelling areas, the concentration of some species' larvae below the Ekman layer has been linked to DVM, which seems to prevent offshore transport during upwelling events that could otherwise entrain larvae at the upwelling front and transport them to offshore waters (Peterson 1998, Morgan et al. 2009). However, larvae remaining in surface waters can be moved towards the shore during upwelling relaxation events (Roughgarden et al. 1991). The inclusion of larval biological traits when examining dispersal and onshore recruitment through biophysical models is therefore essential, since it provides a better representation of the spread of connectivity patterns that may be expected. In turn, it allows us to better inform species-specific or ecosystem-based management plans.

Management and conservation plans for many exploited species are still based primarily on estimates of adult abundance without explicit consideration of replenishing patterns (Szuwalski et al. 2015). Moreover, the spatial scales of regulatory measures (e.g. spatial regulation of fishing effort) on natural resources are not usually coupled with spatial scales of dispersal and recruitment success (Botsford et al. 2001, Gaines et al. 2010b, White & Costello 2011). Processes affecting the spatial distribution of popula-

tion sources and sinks (sensu Roughgarden & Iwasa 1986), produced by fluctuations in adult fecundity or heterogeneous circulation for instance, are still poorly evaluated, despite their pivotal importance in metapopulation dynamics and persistence (Roughgarden et al. 1985, Roughgarden & Iwasa 1986, Salomon et al. 2010). We must therefore move toward the explicit spatial consideration of interplay among processes operating during the larval phase coupled with adult distribution and reproduction patterns (Watson et al. 2011, Aldana et al. 2017, Fernández et al. 2017). This will be necessary if we are to inform management and conservation plans.

From conceptual and applied perspectives, the central coast of Chile is an exceptional model to examine how connectivity through changes in larval dispersal depends on extrinsic (environmental) and intrinsic (biological) factors. A number of exploited species exhibiting a wide range of larval traits inhabit this coastal border, and their larvae are exposed to spatially heterogeneous advective and thermal conditions, induced primarily by upwelling variability (Strub et al. 1998, Aiken et al. 2008). Another condition fundamental to our consideration is the mosaic of regulatory and territorial management areas that generate spatial patterns of adult mortality and abundance, which in turn determine total reproductive output along the coast (Blanco et al. 2017). Specifically, we hypothesized that the species with shorter larval development times would have increased overall onshore recruitment, increased self-recruitment, shorter dispersal distances, and lower sensitivity to temperature-induced variation in PLD. We also hypothesized that, in both study species (see next paragraph), DVM would be a major determinant of recruitment success by way of reducing dispersal distances and increasing larval retention. Furthermore, we predicted that it would alter spatial patterns of connectivity as compared to buoyant (passive) behavior. The simultaneous identification of critical areas for larval production and onshore recruitment may help us to identify local sources within the regional metapopulation, where there is a great deal of potential to contribute to marine conservation and management (Tognelli et al. 2009). We hypothesized here that, as a result of their different PLDs, the 2 species would have contrasting spatial patterns of connectivity.

To advance in this direction, we developed a SEIBM to first assess the interplay between larval biological traits (DVM, temperature-dependent PLD) and spatio-temporal variability in hydrodynamic processes while larvae are in the water column, larval

dispersal distance, and recruitment success (see Table 1 for definitions). Second, we characterized patterns of potential connectivity (see Table 1) and, using empirical information of abundance and estimates of reproductive output, we estimated the 'realized connectivity' to identify the most important areas in terms of spawning, settlement, increased self-recruitment, retention, and sources/sinks. We focus on 2 rocky-reef invertebrates as models of heavily exploited species by artisanal Chilean fisheries: the keyhole limpet *Fissurella latimarginata*, and the red sea urchin *Loxechinus albus*. It is worth nothing that these 2 species have contrasting planktonic larval traits.

2. MATERIALS AND METHODS

2.1. Model species and the fisheries management system

Two management regimes have regulated benthic artisanal fisheries in Chile for ~25 yr: a co-management system based on territorial use rights for fisheries (TURFs) and open access areas (OAAs; no entry restrictions based on territorial use rights). In both of these management strategies, traditional fishery restrictions apply (size limit, closed reproductive season). As a result, high heterogeneity in adult sizes and density is observed (Gelcich et al. 2012), which can lead to large variability in propagule production (Manríquez & Castilla 2001, Blanco et al. 2017). This spatial variability in spawning areas interacts with the heterogeneous hydrodynamic conditions characterizing this upwelling-influenced region.

The 2 harvested species used as models in our study inhabit wave-exposed rocky shores from the lowest intertidal zone down to 30 m depth. Both species are free spawners, releasing their gametes into the water column where fertilization occurs. Three days after fertilization, the echinopluteus larvae of the urchin *Loxechinus albus* start feeding (Arrau 1958) and develop in the plankton between 20 and >33 d (González et al. 1987). Competent larvae can remain in the plankton several days before reaching suitable settling habitat (Bustos et al. 1992). In contrast, larvae of the limpet *Fissurella latimarginata* are lecithotrophic, developing in the plankton for 5 to 10 d before settling (Chavez 2004). Three days after fertilization and prior to a short period of encapsulated development, a free-swimming veliger larva develops in the plankton (Pérez et al. 2007, Reynoso-Granados et al. 2007).

2.2. Ocean dynamics in the region

The study region (31.50°S to 36.00°S , 71.50°W to 74.00°W), located within the coastal region of the Humboldt Current System (HCS), is characterized by the Chile Coastal Current (CCC), which flows primarily northward close to the coast forced by the southerly wind (Strub et al. 1998, Aiken et al. 2008). This wind likewise produces the upwelling of cold, sub-superficial, nutrient-rich waters near the shore, a process strongly modified by coastal topography (Strub et al. 1998, Rutllant et al. 2004, Aiken et al. 2008, Tapia et al. 2009). In austral winter months south of 35.00°S , the CCC flows mostly poleward (Thiel et al. 2007) (our Fig. 1A). Superimposed upon the mean flow, there is a relatively energetic mesoscale eddy field, fed by baroclinic instability of the upwelling fronts (Letelier et al. 2009, Aguirre et al. 2012, 2014, Hormazabal et al. 2013). In the region of interest, the seasonal cycle is strongly marked and coastal upwelling occurs predominantly during spring and summer (Narváez et al. 2004, 2006).

2.3. 3D HYCOM hydrodynamic model

To reproduce the pattern of circulation in the study region, we used the HYbrid Coordinate Ocean Model (HYCOM) (www.hycom.org), available in a $1/12^{\circ}$ resolution for the region. HYCOM is a hybrid isopycnal coordinate ocean model (i.e. isopycnal in the stratified open ocean, fixed 10 m depths in the unstratified surface layers, and terrain-following in shallow coastal waters) that allows for better simulations of both coastal and open ocean features than those of fixed-coordinate systems (Chassignet et al. 2007). The model is data-assimilative, using real-time observations of the ocean surface obtained by satellite altimetry as well as vertical profile information from CTDs, the ARGO observation program, and other sources (www.hycom.org). The HYCOM reanalysis used in our study provides a unique 20 yr record that effectively reproduces the upwelling and instability processes that dominate mesoscale variability in central Chile (Aiken 2017, Ospina-Alvarez et al. 2018). Aiken (2017) provides a comparison of HYCOM and an unconstrained Regional Ocean Modeling System

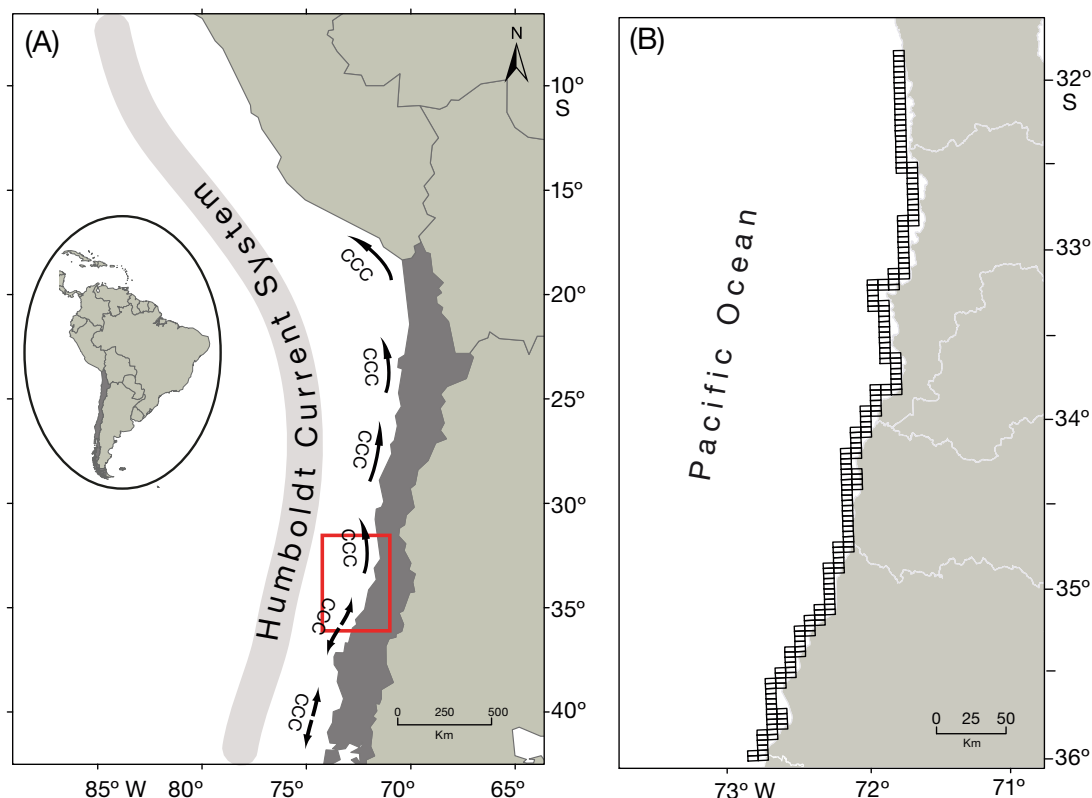


Fig. 1. (A) Overview of the Chile Coastal Current (CCC) in the Humboldt Current System. Red outline: study domain (31.50°S to 36.00°S , 71.50°W to 74.00°W). Inset: South America. (B) Study domain. Black unfilled rectangles: grid cells (2 km of latitude \times 4 km of longitude) into which particles mimicking larvae were released in the spatially explicit individual-based model (SEIBM)

(ROMS) model for the region of the Humboldt Upwelling Ecosystem (HUE) considered in our study, showing that the circulation reproduced by HYCOM is close to that of ROMS simulations, effectively simulating the regional-scale ocean variability as well as surface and subsurface circulation (e.g. polar undercurrent) observed in the HUE. It is important to note, however, that HYCOM suffers from an occasional false surface current that flows around 30° S (Aiken 2017), which is apparently caused by a numerical artifact of the atmospheric model used to provide the wind fields (Allan Wallcraft pers. comm.). This problem occurs to the north, outside the domain used in our study.

The netCDF HYCOM files were downloaded from the HYCOM consortium, transformed to ROMS format, and coupled with Ichthyop software for offline particle tracking (see Section 2.4).

2.4. SEIBM

A SEIBM was developed to reproduce larval transport in the realistic ocean reproduced by HYCOM and assess the importance of 2 key larval biological traits with regard to recruitment success and dispersal

distance: temperature-dependent pelagic development time and vertical swimming behavior, associated to the natural variability imposed by spatio-temporal variability in hydrodynamic circulation (Table 1). Particles mimicking larvae were released in each coastal grid cell of 0.02° (2 km) of latitude and 0.12° (4 km) of longitude at the surface (first 30 m water column) (Fig. 1B). These cells were also used to define successful ‘onshore’ recruitment.

Offline particle (larvae) tracking and statistics were conducted using a customized version of the open-source modeling tool Ichthyop (Lett et al. 2008) (www.ichthyop.org) on the hydrographic fields produced by the HYCOM model described above (Section 2.3). We used a reflective boundary condition at the coast and applied a filter to remove particles that stopped moving for >1.5 consecutive days, which were considered beached. This filter ensured that larval transport had occurred before tallying onshore recruitment. To establish the appropriate number of particles to be released, we performed repeated model runs in which we increased the number of released particles (1000, 5000, 10 000, 15 000, 20 000, 50 000 and 100 000), calculated the average \pm SD of onshore recruitment, and determined the point at which the average stabilized (Brickman & Smith

Table 1. Constants and parameters set to the spatially explicit individual-based model (SEIBM) configurations. PLD: planktonic larval duration

Constants	<i>Fissurella latimarginata</i>	<i>Loxechinus albus</i>
Transport duration (PLD _{fixed} scenarios)	5 + 5 d	20 + 5 d
Temperature-dependent PLD equation (PLD _{Temp} scenarios) ^a	$L_{t+dt} = L_t + GR \cdot (T) \cdot dt$	$PD_{t+dt} = PD_t + K \cdot (T) \cdot dt$
Record frequency	24 (0.5 d)	48 (2.5 d)
Time step (s)	1800	1800
Lethal temperatures (upper/lowest)	23°C/7°C	23°C/7°C
Lag before target depth	Onset of vertical behavior, subsequent to hatching, was set at 3 d	
Vertical migration	Based on sunset/sunrise, depth at daytime: −30 m; depth at nighttime: −1 m	
Parameters		
Studied domain (recruitment)	31.5° S to 36.0° S	
Date	Dates of spawning were set to: 5 th , 10 th , 15 th , 20 th , 25 th , and 30 th every month	
Months	Spawning season (Sep, Oct, and Nov)	
Years	2010, 2011, 2012, and 2013	
Depth	Larvae were uniformly released between 0 and 30 m	
Release	20 000 particles with random release	
Scenarios	Behavior	PLD
LAG + PLD _{fixed}	Passive Lagrangian transport	Fixed
LAG + PLD _{Temp}	Passive Lagrangian transport	Temperature-dependent
DVM + PLD _{fixed}	Diel vertical migration	Fixed
DVM + PLD _{Temp}	Diel vertical migration	Temperature-dependent
^a See Supplements 1 & 2 for explanations of the temperature-dependent PLD equations		

(Table continued on next page)

Table 1. Continued

Variables	Abbrev.	Definition	Estimation
Recruitment success	RS	Number of virtual larvae that are successfully transported and are found on an onshore recruitment area (initial number is constant) at the end of PLD + competency	Number of particles recruited
Dispersal distance	DD	Orthodromic distance (i.e. the shortest distance between any 2 points on the surface of a sphere) traveled from the spawning (release) to successful coastal recruitment locations in km	Distance traveled by recruited particles
Potential connectivity	PC	Hydrodynamic connectivity or also, connectivity due to marine currents	Probability of larval transport between 2 local settlement areas
Realized connectivity ^b	RC	Bio-physical connectivity. Connectivity due to marine currents and modulated by the morphological, physiological, and behavioral characteristics of organisms and the characteristics of the origin and settlement habitats	The product of potential connectivity, egg production, and habitat availability
Realized source strength ^b	RSS	Larvae released at a particular location that will disperse and successfully recruit anywhere in the metapopulation (also known as the 'footprint' of a given location)	Estimated by the sum of the corresponding column of the realized connectivity matrix
Realized destination strength ^b	RDS	The strength of a site to have larvae delivered to that same site	Estimated by the sum of the corresponding row of the realized connectivity matrix
Local retention	LR	Conditions the self-persistence of individual sites and defined as the ratio between locally produced recruitment and local egg production	Estimated by the diagonal element of the connectivity matrix
Relative local retention	RLR	Ratio between local retention and all recruitment of local origin	Estimated by the diagonal element of the connectivity matrix divided by the sum of the corresponding column
Self-recruitment	SR	Ratio between local recruitment (larvae successfully recruiting in the release latitude) and recruitment of all origins at a site	Estimated by the diagonal element of the connectivity matrix divided by the sum of the corresponding row
Total non-local recruitment	TNR	The number of recruits in a site (e.g. latitude) that were released from different sites to the one in which they recruit	Estimated by the difference of the sum of the corresponding row of the connectivity matrix and the diagonal elements of the connectivity matrix
Allochthonous recruitment	AR	Ratio between non-local recruitment (larvae that are successfully recruited at a latitude other than that at which they were released) and recruitment of all origins at a site	Estimated by the difference of the sum of the corresponding row of the connectivity matrix and the diagonal elements of the connectivity matrix divided by the sum of the corresponding row of the connectivity matrix or, simply, 1 – self-recruitment

^bVariables calculated only for the scenario DVM + PLD_{Temp}

2002). A total of 20 000 released particles were then used in all spawning events. The HYCOM fields were interpolated in time and space in the SEIBM to determine the values of the environmental state vari-

ables at any individual location. One timestep represents 1800 s, and the simulations were run until the nominal larval PLD time plus a period of competency for settlement of 5 d were completed.

We reproduced adult spawning throughout the spring season by releasing virtual larvae uniformly distributed along the coast every 5 d from September to November for 4 consecutive years (2010–2013). Since each release event represented a spawning of 20 000 larvae, 1 440 000 larvae were released in total (20 000 virtual larvae per release date \times 6 dates $\text{mo}^{-1} \times 3 \text{ mo yr}^{-1} \times 4 \text{ yr}$). This approach makes several assumptions about the larval release process. First, the modeled species (keyhole limpet and red sea urchin) are broadcast spawners that release eggs and sperm into the water where fertilization occurs. This process takes place over periods of minutes to hours and is not included in our model, therefore assuming that pelagic life starts at time zero with a fertilized egg. Second, the spatial location of the spawning fraction is identical for both model species along the central Chile coast, from 31.50°S to 36.00°S. Third, the spawning locations do not change over time, i.e. the adult spawning population is insensitive to environmental or recruitment variability at the resolution scale.

Using the coupled SEIBM model, we explored the effects of (1) temperature-dependent development times and (2) larval behavior. Connectivity matrices from the circulation model were used to calculate 'realized' connectivity (sensu Watson et al. 2010), considering the pattern of larval production (based on oocyte production, Blanco et al. 2017) and suitable habitat availability (see also Table 1). Specifically, we simulated 4 scenarios for each species: (1) passive Lagrangian transport (LAG) and fixed (temperature-insensitive) PLD (5 d for *F. latimarginata* and 20 d for *L. albus*), labelled LAG + PLD_{Fixed}; (2) fixed PLD and DVM from 0 to 30 m depth (DVM + PLD_{Fixed}); (3) LAG and species-specific temperature-dependent PLD (LAG + PLD_{Temp}); and (4) larval DVM and temperature-dependent PLD (DVM + PLD_{Temp}) (Fig. 2). Successful recruitment was tallied as the number of larvae found in the coastal cells at the end of the fixed or temperature-dependent PLD.

2.5. Larval traits

As explained in the previous paragraph, 2 basic larval behaviors were explored in the models. In the LAG scenario, the virtual larvae are assumed to be neutrally buoyant and behave as passive particles that track water movement in the vertical and horizontal velocity components. This scenario assumes that whatever movement larvae have while developing in the water column, they are not capable of over-

coming ocean current velocities. In the DVM scenario, larvae display typical DVM, moving to deeper waters down to 30 m during daytime and up to the surface (1 m) at night, following the sunset/sunrise schedule. Maximum depth was based on limited observation of *L. albus* and other invertebrate species (Tremblay & Sinclair 1990, Molinet et al. 2010). Many invertebrate larvae perform DVM, though not all do (McLaren 1963). Unfortunately, DVM observations are not available for the model species and, therefore, we contrast putative DVM against LAG behavior. In the model, larvae of both species start DVM 3 d after release, which accounted for the 3 d period of pelagic intracapsular development of *F. latimarginata* trochophore larvae (Reynoso-Granados et al. 2007). Similarly, since sedimentation velocity was equal to or higher than ciliary movement velocity for early larval stages (blastula and gastrula) of *L. albus* (McDonald 2004), we considered that DVM started at the echinopluteus stage, which appears, on average (depending on temperature), 3 d after fertilization (pers. obs.).

Since there is evidence that severe growth retardation of eggs and larvae of most temperate invertebrates and fish as well as high mortality (Rumrill 1990) occurs at temperatures $<7^{\circ}\text{C}$ and $>23^{\circ}\text{C}$, we considered larvae exposed above or below these thresholds for $>0.5 \text{ h}$ (1 timestep) dead. Since these threshold temperatures are rarely observed in central Chile, this mortality source had virtually no consequences on the patterns reported here, but imposing these restrictions prevented inclusion of spuriously long or short larval development times in the PLD_{Temp} condition. This temperature-induced mortality was imposed in addition to and independent of 'larval waste' produced when larvae are found too far from appropriate settling habitat by the end of the competency period.

The universal effects of temperature in determining larval development times were incorporated in Ichthyop through the positive effects of temperature on larval growth (which in turn reduced development times). The strategy for parameterization differed between the 2 species. For *F. latimarginata*, the time to complete PLD under the realistic variable-temperature encounter in the ocean model was based on the general model by O'Connor et al. (2007), using a linear mixed effects model (with temperature and species as fixed and random components) and a database of 74 species: 72 species from O'Connor et al.'s (2007) database, direct laboratory observations of PLD vs. temperature for *F. latimarginata* from Chavez (2004), and our own

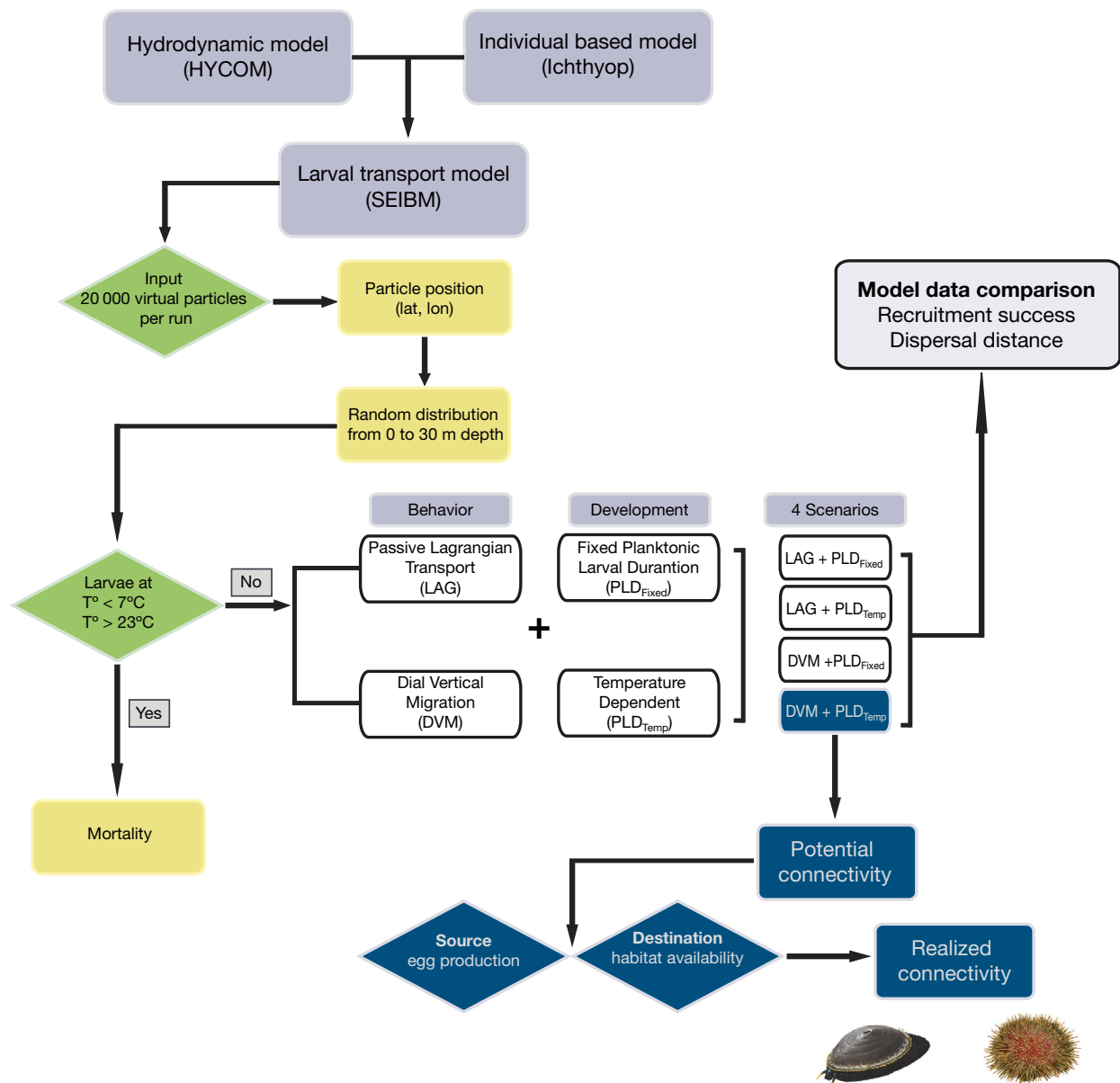


Fig. 2. Flow diagram of the spatially explicit individual-based model (SEIBM) for *Fissurella latimarginata* and *Loxechinus albus* along the central Chilean coast

observations for *L. albus* (this study). Fixed parameters for the model were slightly different than previously reported by O'Connor et al. (2007) (see our Supplement 1 at www.int-res.com/articles/suppl/m612p043_supp.pdf) because of the added species. The beta parameter for *F. latimarginata* ($\beta = 1.81$) was therefore estimated, taking into account fixed and random effects. In the case of *L. albus*, parameterization of temperature effects on larval development times was obtained through laboratory rearing experiments. Considering the developmental characteristic of echinopluteus larvae, we used

the proportion of time larvae remained in each developmental stage, with respect to total developmental time, following the same method used by Hinckley et al. (1996) (see our Supplement 2).

2.6. Analysis of model results

To obtain mean field approximations, we performed 48 simulations for each model species (3 months \times 4 years \times 2 particle behaviors \times 2 larval growth patterns). The analyses on these simulations

were conducted using a multifactor analysis of variance from the generalized additive model (GAM). In these analyses, we evaluated the effect on recruitment success and dispersal distances of (a) larval behaviors (LAG vs. DVM), (b) fixed PLD (5 d for key-hole limpets and 20 d for red sea urchins) vs. temperature-dependent PLD (PLD_{Temp}), and (c) initial conditions: (1) depth of larval release (6 levels, intervals of 5 m from 0 to 30 m), (2) release latitude (16 levels, intervals of 0.3° , from 31.50°S to 36.00°S), and (3) release date (day/month/year). A GAM with quasi-Poisson family error distribution was used for both dependent variables (recruitment and dispersal distance). To compare recruitment success and dispersal distance between years, behavior and temperature-dependent PLD scenarios, and interaction terms, we used a generalized linear model (GLM) analysis with a quasi-Poisson family error distribution. The choice of the most appropriate link function and error distribution was made based on residual analyses. We tested the goodness of fit of the model with a chi-squared test based on residual deviance and degrees of freedom (significance level: 0.05). All statistical analyses were performed using R software v.3.1.3 (R Core Team 2013).

From the potential connectivity matrix, we calculated 3 retention indicators following Lett et al. (2015): (1) local retention (LR) (the diagonal element of the connectivity matrix), which is the number of recruits that recruited back to the origin (Table 1), (2) relative local retention (RLR), which is the local retention weighted by all larvae produced at that site that successfully recruited anywhere in the domain (the diagonal element of the connectivity matrix divided by the sum of the corresponding column), and (3) self-recruitment (SR), which is the fraction of the total larvae produced at a site that recruited back to the origin weighted by the total number produced at that site (the diagonal element of the connectivity matrix divided by the sum of the corresponding row) (Table 1). These metrics were calculated using the R package ConnMatTools (Kaplan & Andrello 2016). In addition, we calculated (4) the total non-local recruitment (TNR) as the sum of all recruits imported to a latitude from other latitudes (the difference between the row sum of the connectivity matrix and the corresponding diagonal element of the connectivity matrix; Table 1), and (5) allochthonous recruitment (AR), which was defined as the proportion of non-local larvae recruited at a latitude (TNR) over the total larvae recruited at that latitude (Table 1). Thus, $AR = 1 - SR$. We also recorded the origin of recruits (north or south of target location) (Table 1). Each of

these metrics was compared among scenarios using a GLM analysis with a quasi-Poisson family error distribution.

2.7. Potential and realized connectivity

A multi-annual (2010–2013) mean connectivity matrix was obtained for each of the 4 modeled scenarios. These matrices contained all needed information for metapopulation dynamics and time-varying processes (Aiken & Navarrete 2014), but they can be visualized as representing potential connectivity before spatial variation in larval production since habitat availability and adult abundance are taken into account. Thus, a realized larval connectivity can be estimated using potential connectivity weighted by relevant biological and environmental information (following Watson et al. 2010) (our Table 1).

To estimate larval production along the shore, we assumed that all eggs produced become viable larvae. Modeled egg production, expressed as the number of oocytes m^{-2} , for each model species was obtained from information on adult density, size structure, sex ratio, and size-specific fecundity (oocytes per female of a given size), which are available for 8 sites along the study area (Blanco et al. 2017). Following the egg production model described in Blanco et al. (2017), we used the spatial distribution of suitable habitat (hard bottoms) and fishing regime (no-take marine protected areas [MPAs], TURFs, and OAAs), which affected size distribution and adult density (through harvesting), to obtain estimates of egg production for both model species in each release cell.

Realized connectivity was then calculated by multiplying the potential connectivity matrix by egg production and, subsequently, adjusting the proportion of available rocky habitat. Realized connectivity matrices were calculated only for the scenario with DVM and PLD_{Temp} because they probably represent the more realistic larval attributes of the species (DVM: Molinet et al. 2010; temperature-dependent PLD: Bustos et al. 1992, Chavez 2004). Following Watson et al. (2010), we calculated realized source strength of each location (its 'footprint'), summing all released larvae per location (sum across columns) that reached a settlement location in the realized connectivity matrix (Table 1). In the same way, we calculated the realized destination strength of each location, summing the fractions of recruited larvae per location (sum across rows) in the realized connectivity matrix (Table 1). To compare the spatial struc-

ture of potential and realized connectivity matrices, we conducted a Mantel test using the R package ‘ape’ (Paradis et al. 2017). The information from the connectivity matrix was used to construct direction linkage from release locations to larval recruitment locations. The potential connectivity matrix defined the strength of connectivity.

3. RESULTS

3.1. Recruitment success

Recruitment success ranged between 12.5 and 32.2% in the species exhibiting shorter PLD (*Fissurella latimarginata*), across all scenarios, and was lower in the species with longer PLD (*Loxechinus albus*), ranging from 3.2 to 6.3% (Table 2).

Significant effects of release latitude, release depth, release date, larval behavior, and temperature-dependent PLD were observed on recruitment suc-

cess in both model species ($p < 0.001$). Release latitude explained most of the variability in recruitment success in both species (24.30% in *F. latimarginata* and 34.80% in *L. albus*) (Table 3), rendering similar spatial patterns of recruitment success for both species and across the 4 modeled scenarios (Fig. 3). Three small shoreline sections (latitudes) concentrated >80% of recruitment success: (1) 34.8% of all *F. latimarginata* and 17.7% of all *L. albus* recruitment (averaged across scenarios) was concentrated between 31.5°S and 32.5°S, (2) 33.2% of *F. latimarginata* and 60.6% of *L. albus* recruitment occurred between 33.0°S and 33.5°S, and (3) 12.15% of *F. latimarginata* and 8.09% of all *L. albus* recruited to the shore was observed between 34.0°S and 34.5°S (Fig. 3). South of 34.5°S, recruitment success was low in both species (8.96% in *F. latimarginata* and 7.76% in *L. albus*) (Fig. 3).

The spatial pattern of recruitment success was similar in the 4 modeled scenarios for both species (Fig. 3), highlighting the importance of topography-

Table 2. Summary of model results obtained for all 4 modeled simulation scenarios for *Fissurella latimarginata* and *Loxechinus albus*: passive Lagrangian transport (LAG) + fixed planktonic larval duration (PLD_{fixed}), LAG + species-specific temperature-dependent PLD (PLD_{Temp}), virtual larvae with diel vertical migration behavior (DVM) + PLD_{fixed}, and DVM + PLD_{Temp}. For recruitment success, results were obtained by calculating the mean from each simulation (each spawning month and year, 12 simulations per scenario), and for the other measures, results were obtained by calculating the mean from all virtual larvae recruited in each experiment. SE: standard error

	LAG + PLD _{fixed}	LAG + PLD _{Temp}	DVM + PLD _{fixed}	DVM + PLD _{Temp}
<i>F. latimarginata</i>				
Mean dispersal distance ± SE (km)	57.10 ± 0.11	75.84 ± 0.21	54.92 ± 0.09	64.09 ± 0.12
Median dispersal distance (km)	48.50	66.59	46.23	56.15
Maximum dispersal distance (km)	323.79	327.03	274.36	243.97
Minimum dispersal distance (km)	0.00	0.04	0.01	0.03
Larval waste + Mortality (%)	74.44	87.50	67.77	75.72
Recruitment success (%)	26.56	12.50	32.23	24.28
Local retention (%)	2.64	1.79	2.33	1.49
Relative local retention (%)	4.74	3.39	4.83	3.57
Self-recruitment (%)	5.25	4.39	5.34	3.53
Total non-local recruitment (%)	97.36	98.21	97.67	98.51
Allochthonous recruitment (%)	94.75	95.61	94.66	96.47
Average time to recruit (d)	5.83	8.03	5.70	8.10
<i>L. albus</i>				
Mean dispersal distance ± SE (km)	49.41 ± 0.49	56.96 ± 0.59	76.98 ± 0.41	70.29 ± 0.40
Median dispersal distance (km)	21.29	26.45	53.66	58.49
Maximum dispersal distance (km)	407.44	409.56	378.59	383.50
Minimum dispersal distance (km)	0.02	0.01	0.34	0.07
Larval waste + Mortality (%)	96.19	96.85	93.74	93.99
Recruitment success (%)	3.81	3.15	6.26	6.01
Local retention (%)	6.13	5.13	1.17	1.81
Relative local retention (%)	3.60	4.58	0.50	0.77
Self-recruitment (%)	4.45	4.42	1.84	3.52
Total non-local recruitment (%)	93.87	94.87	98.83	98.19
Allochthonous recruitment (%)	95.55	95.58	98.16	96.48
Average time to recruit (d)	22.92	23.28	22.67	22.23

Table 3. Analysis of deviance for the generalized additive models (GAMs) with quasi-Poisson error structure applied to the spatially explicit individual-based model (SEIBM) output for the dependent variables, number of larvae recruited, and dispersal distance for *Fissurella latimarginata* and *Loxechinus albus*. Deviance explained (DE) was calculated for each factor individually (GAM: dependent variable ~ term + spline(term)). Note that the sum of DE of each factor is not equal to the total DE obtained for the model. Depth: corresponds to release depth (0–5, 5–10, 10–15, 15–20, 20–25, and 25–30 m); Release latitude: from 31.5° S to –40° S; Date: corresponds to release date (day/month/year); df: degrees of freedom; edf: effective degrees of freedom; PLD: planktonic larval duration

<i>F. latimarginata</i>				
Recruitment success ~ PLD + behavior + depth + spline(release latitude) + spline(date)				
R^2 (adj.) = 0.36; Total DE = 37.30 %				
Parametric terms	df	F	p	DE (%)
PLD	1	1246.87	<0.01	3.95
Behavior	1	664.40	<0.01	2.46
Release depth	5	37.93	<0.01	0.82
Smooth terms	edf	F	p	DE (%)
Spline(release latitude)	8.98	807.70	<0.01	24.30
Spline(release date)	8.99	183.80	<0.01	5.54
Dispersal distance ~ PLD + behavior + depth + spline(release latitude) + spline(date)				
R^2 (adj.) = 0.35; Total DE = 35.70 %				
Parametric terms	df	F	p	DE (%)
PLD	1	719.70	<0.01	3.25
Behavior	1	121.10	<0.01	0.09
Release depth	5	140.60	<0.01	2.95
Smooth terms	edf	F	p	DE (%)
Spline(release latitude)	8.98	652.30	<0.01	23.80
Spline(release date)	8.94	214.20	<0.01	6.94
<i>L. albus</i>				
Recruitment success ~ PLD + behavior + depth + spline(release latitude) + spline(date)				
R^2 (adj.) = 0.35; DE = 42.40 %				
Parametric terms	df	F	p	DE (%)
PLD	1	22.51	<0.01	0.10
Behavior	1	573.42	<0.01	3.84
Release depth	5	16.75	<0.01	0.03
Smooth terms	edf	F	p	DE (%)
Spline(release latitude)	8.98	672.81	<0.01	34.80
Spline(release date)	8.99	89.45	<0.01	4.19
Dispersal distance ~ PLD + behavior + depth + spline(release latitude) + spline(date)				
R^2 (adj.) = 0.39; DE = 39.10 %				
Parametric terms	df	F	p	DE (%)
PLD	1	2.51	0.11	9.33×10^{-3}
Behavior	1	121.72	<0.01	1.23
Release depth	5	35.15	<0.01	1.50
Smooth terms	edf	F	p	DE (%)
Spline (release latitude)	8.97	269.90	<0.01	26.10
Spline (release date)	8.83	172.70	<0.01	19.60

and hydrography-driven dispersal on the spatial patterns of recruitment. Dispersal was asymmetrical and north-skewed across the region, generating patterns of connectivity strongly biased toward northern sites for both species (Fig. 3, higher recruitment above the matrix diagonals). In the case of *L. albus*, the LAG scenarios allowed increased connection toward southern sites from the place of origin (Fig. 3, recruitment below the matrix diagonals) in comparison to the DVM scenarios, for which only northward connectivity was observed (Fig. 3).

Recruitment success also varied significantly over time. Release date explained 5.54 % of variability observed on recruitment success in *F. latimarginata* and 4.19 % in *L. albus* (Table 3). Larval biological traits considered in this study (PLD and behavior) also had significant effects on recruitment success in both species, but explained <3.95 % of the variance (Table 3). See Supplement 3 for comparative results between model scenarios.

3.2. Spatial patterns of larval retention from variability in connectivity

Most indicators of larval retention show the relative contribution of local populations to the regional metapopulation (Fig. 4). First, total non-local recruitment (TNR) and allochthonous recruitment (AR) were high across most local populations and generally higher than self-recruitment (SR) at most latitudes (Fig. 4), highlighting the importance of interpopulation recruitment subsidies and their effect on local population dynamics. Interestingly, this broad pattern was stronger for *F. latimarginata* and its shorter PLD than for *L. albus* (top and bottom panels in Fig. 4). In the case of *F. latimarginata*, LR, SR, and relative local retention (RLR) showed a mosaic structure across the region and all larval trait scenarios, with a slight regional (latitudinal) trend of increased interpopulation connectivity towards the northern end of the region (Fig. 4). In the case of *L. albus*, stronger regional patterns were observed in all indicators of larval local retention and self-recruitment (LR, RLR, SR) as well as TNR and AR, with generally higher values towards the northern end of the region, across larval trait scenarios and regardless of geographic (north/south) origin (Fig. 4). Note that most of TNR was northward in both species (>80 % in all *F. latimarginata* scenarios and >60 % in *L. albus*) (Fig. 5). Southward TNR was <10 % in all scenarios for *F. latimarginata* (Fig. 5B).

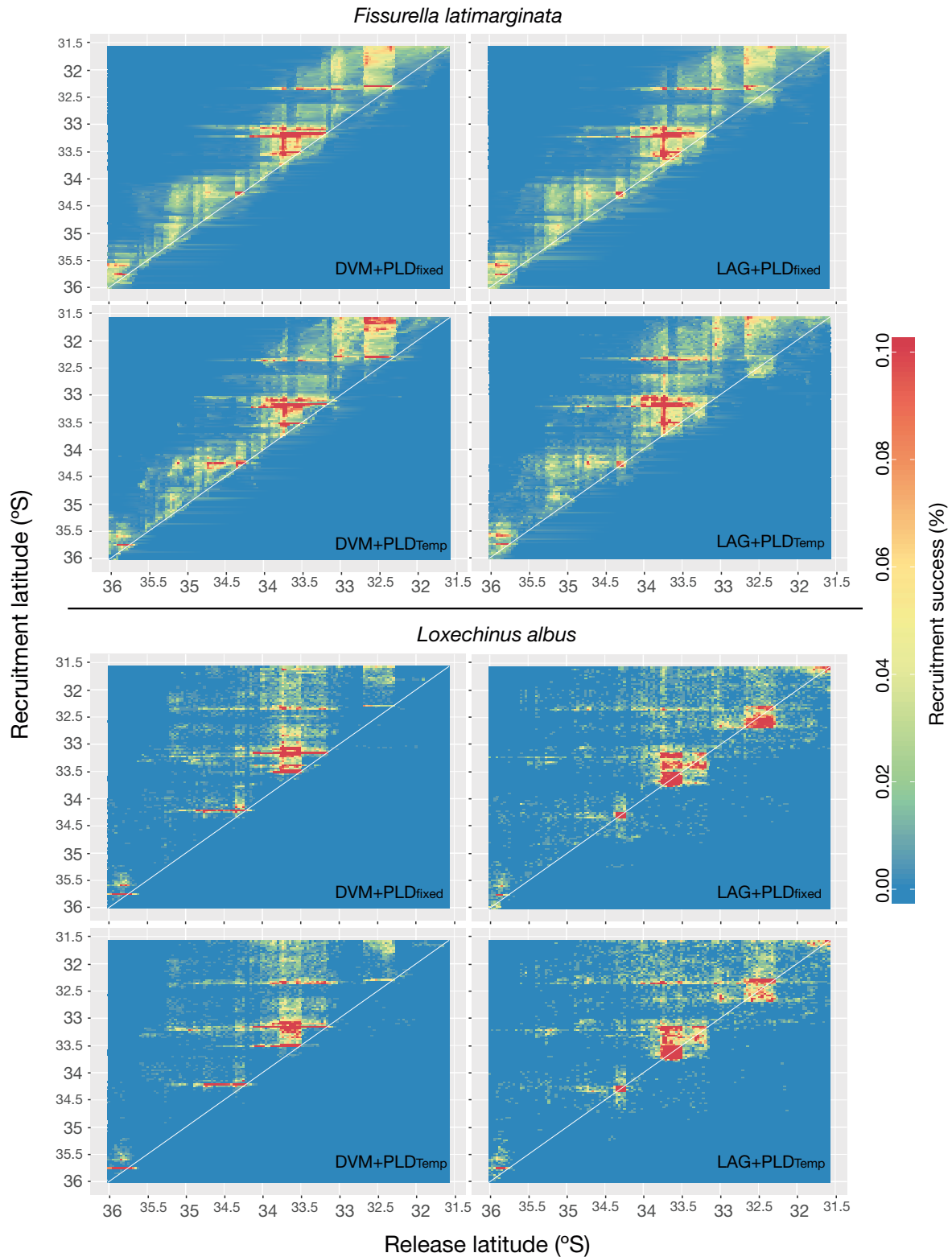


Fig. 3. Potential connectivity matrices obtained from HYCOM coupled with Ichthyop Lagrangian particle (larval) tracking model, for *Fissurella latimarginata* (upper panel) and *Loxechinus albus* (bottom panel), showing mean accumulated recruitment from 2010 to 2013 during spring (Sep–Nov). The 4 simulation scenarios: diel vertical migration (DVM) + fixed planktonic larval duration (PLD_{fixed}), passive Lagrangian transport (LAG) + PLD_{fixed}, DVM + PLD based on species-specific temperature-dependent PLD (PLD_{Temp}), and LAG + PLD_{Temp}. Color scale: percentage of total recruited virtual larvae with respect to total number of virtual larvae released from all locations

3.3. Dispersal distances

As expected, dispersal distances were generally longer for *L. albus* than for *F. latimarginata* (Table 2), but in some years (2013), this pattern reversed, with *L. albus* mean dispersal distances being lower than those of *F. latimarginata* across all larval traits (Supplement 3). Consequently, we observed that release year had a significant effect on dispersal distance in both species ($\chi^2 = 26\,214.9$, $df = 3$, $p < 0.01$ for *F. latimarginata*; $\chi^2 = 42\,066$, $df = 3$, $p < 0.01$ for *L. albus*). Averaging the 4 years of simulations showed increased mean dispersal distances in the much shorter-PLD species, *F. latimarginata*, under some larval trait scenarios (Table 2, Supplement 3). Beyond the inter-annual variation, the date of release had significant effects on mean dispersal and explained 6.94 % of model variability in *F. latimarginata* and 19.60 % in *L. albus* (Table 3). Behavior (DVM or LAG) was statistically significant in both model species, although the variance explained was extremely low (0.09 % in *F. latimarginata* and 1.23 % in *L. albus*) (Table 3). PLD was statistically significant in the model, though only

for *F. latimarginata*, explaining 3.25 % of model variability (Table 3).

Release latitude, release date, and depth of release also had significant effects on mean dispersal distances of both model species ($p < 0.001$). The factor explaining the greatest variance in dispersal was release latitude (23.80 % in *F. latimarginata* and 26.10 % in *L. albus*) (Table 3). The geographic pattern of dispersal distances was similar among larval trait scenarios and also generally similar between species (Fig. 6). Mean *L. albus* dispersal distance was negative in some latitudes (at 36.0° S, between 34.4° S and 34.8° S, and between 33.6° S and 33.8° S), yet only in LAG scenarios, indicating southern connectivity (Fig. 6F,H). However, mean dispersal distance was always positive in DVM scenarios (Fig. 6E,G).

3.4. Realized connectivity

Significant differences in the spatial structure of connectivity were observed between potential and 'realized' connectivity in both species (Mantel test;

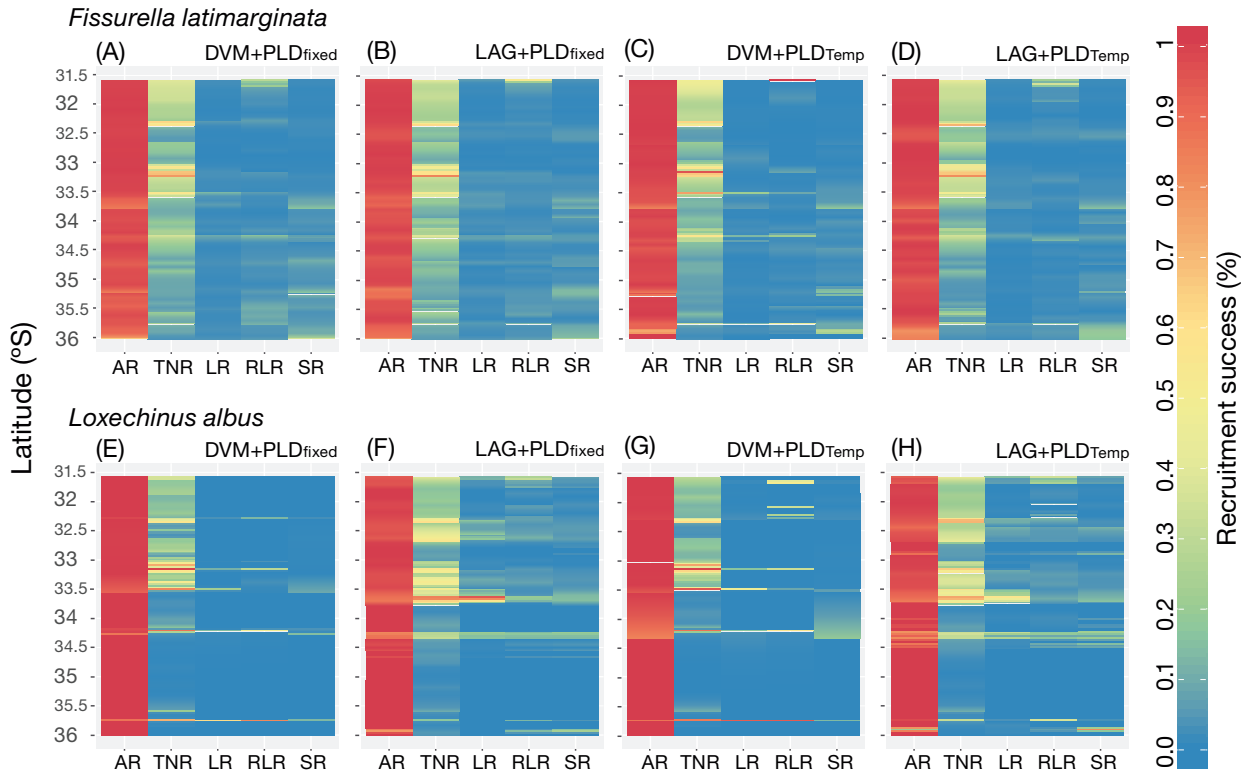


Fig. 4. Potential connectivity metrics calculated for (A–D) *Fissurella latimarginata* and (E–H) *Loxechinus albus* across the study area. AR: allochthonous recruitment; TNR: total non-local recruitment (for the latitudinal variability in total non-local recruitment, we log-transform and sum 1 in TNR in all latitudes); LR: local retention; RLR: relative local retention; and SR: self-recruitment (see Table 1 for definitions). See Fig. 3 for explanation of the 4 simulation scenarios. Color scale: percentage obtained for the metrics calculated

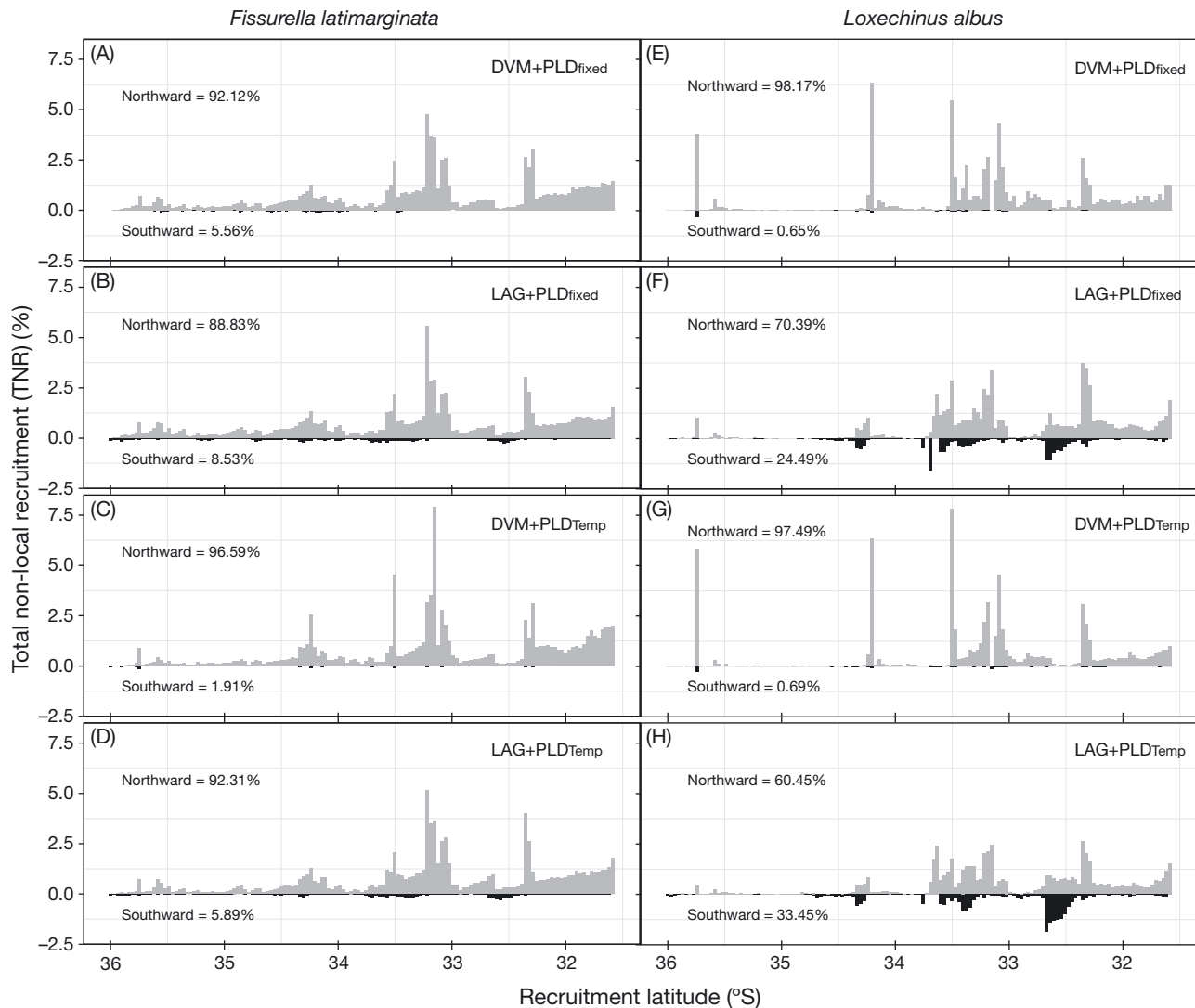


Fig. 5. Spatial variability of total non-local recruitment (larvae that were released in a different latitude than where they were recruited) across latitude showing the northward (positive values in gray bars) or southward (negative values in black bars) origin of the settling larvae (A–D) *Fissurella latimarginata* and (E–H) *Loxechinus albus*, under 4 simulation scenarios (see Fig. 3 for explanation of scenarios). Also shown are the percentage of recruited larvae that moved northward and the percentage that moved southward

$p < 0.001$). This result indicates that the spatial patterns of reproductive output and available habitat have a clear influence on realized connectivity among local populations over the timescales examined in this study. However, the latitudes with high levels of successful recruitment were consistent between species (Fig. 7). The most important source locations for overall recruitment in the metapopulation (considering the DVM and PLD_{Temp} scenarios) were observed between 32.3°S and 32.6°S and between 33.2°S and 33.6°S for *F. latimarginata* (Fig. 7A). Very similar results were obtained for the longer-PLD species, *L. albus*, with the most important realized source loca-

tions between 32.4°S and 32.5°S, and between 33.2°S and 33.5°S (Fig. 7B). Therefore, for both species, we identified the same geographic region as main source locations (between 33.0°S and 33.5°S, and at 32.5°S) for the metapopulations (Fig. 7C). These latitudes contributed 72% to the overall recruitment. The most important realized larval destination (locations receiving larvae from multiple source populations) were found mainly at the northern end of the study area for both species, between 33.0°S to 33.2°S, and north of 32.2°S (Fig. 7D–F). These latitudes contributed 94% to the overall recruitment in the study region.

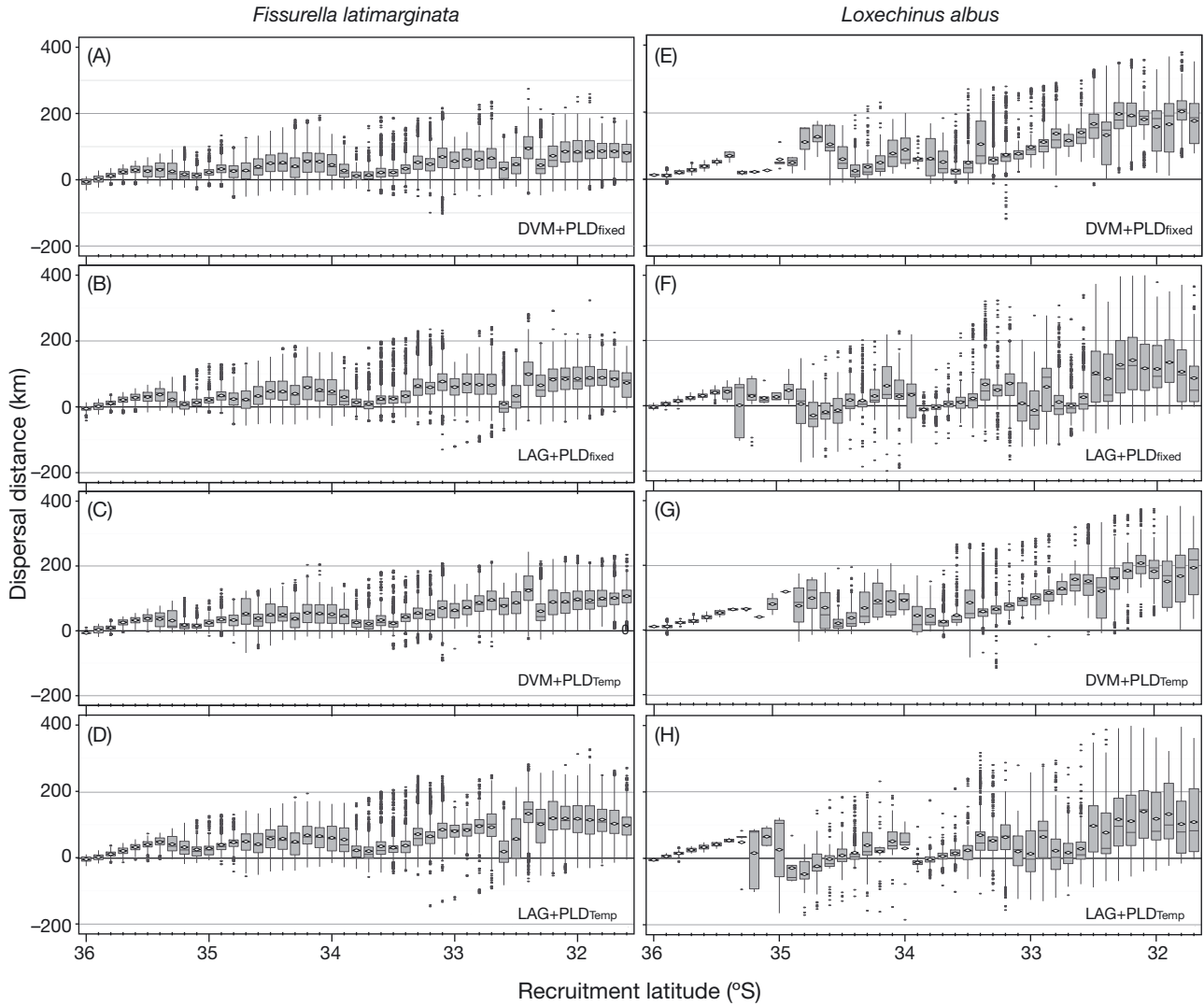


Fig. 6. Box plots showing dispersal distance traveled by virtual larvae of (A–D) *Fissurella latimarginata* and (E–H) *Loxechinus albus* that successfully recruited at a given latitude under 4 different scenarios (see Fig. 3 for explanation of scenarios). Diamond: mean; horizontal line inside box: median; box: 50 % of data (inter-quartile range); whiskers: 1.5 times the inter-quartile range; points: outliers

4. DISCUSSION

4.1. Main findings

Globally, our results allow us to conclude that extrinsic factors, oceanographic processes, geographical position, and timing of spawning are the main determinants of population connectivity patterns for both invertebrate species modeled, regardless of larval biological traits. Larval swimming behavior, as modeled in this study (DVM), had a significant albeit minor influence on most response variables examined. However, in both species, DVM enhanced recruitment success as compared to passive Lagrangian particles (LAG). When larval duration

was allowed to vary (PLD_{Temp}), larval duration had significant but comparatively minor effects on the response variables, and the direction of the effect changed between species and even between modeled years. Within the studied area of central Chile, most recruitment to local populations was allochthonous, presenting low levels of self-recruitment and local retention at the scale of a latitudinal degree, even for the heavily harvested, short-PLD *Fissurella latimarginata*. Our analyses also show the existence of a geographic mosaic of potential sources and sink populations across the region, with few regional breaks and weak latitudinal trends that suggest increasing importance of ‘realized sources’ and ‘realized destinations’ towards the northern end of the

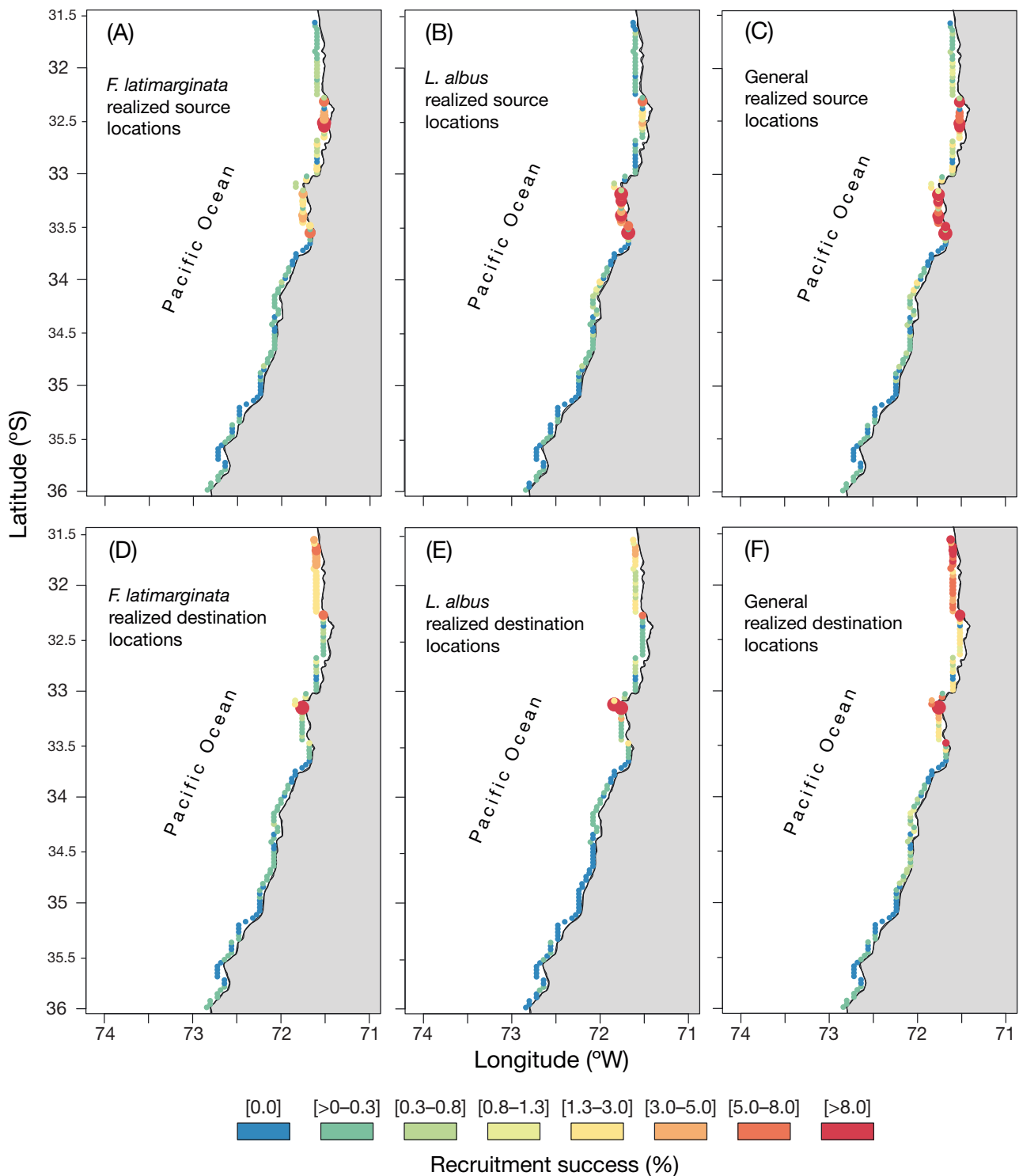


Fig. 7. Metrics for the realized connectivity matrix, calculated weighting the potential connectivity matrix with the modeled egg production and, subsequently, adjusted by the proportion of available rocky habitat. (A–C) Realized source strength of each location, estimated by sum of all the fractions of released larvae per location (sum across columns) of the realized connectivity matrix, for (A) *Fissurella latimarginata*, (B) *Loxechinus albus*, and (C) both model species. (D–F) Realized destination strength of each location, estimated by sum of all the fractions of recruited larvae per location (sum across rows) of the realized connectivity matrix, for (D) *F. latimarginata*, (E) *L. albus*, and (F) both model species. Color scale shows (A–C) the percentage of larvae recruited that were released in each location, or (D–F) the proportion of larvae recruited in each location from all larvae released in the study domain

domain (central Chile) for both modeled species. We next discuss the extent to which these patterns can be used as a template for management and conservation planning in the region and acknowledge the broad contribution of these results to our views of larval dispersal in the ocean.

4.2. Processes driving larval dispersal in a realistic ocean

The identification of the release location and date of larval release as the primary determinant of recruitment success is consistent with studies from other geographic regions (Parada et al. 2008, Brochier et al. 2009, Ospina-Alvarez et al. 2015). Several modeling studies have shown that spawning locations, dates when spawning occurs, and the number of adult reproductive individuals are the main factors explaining recruitment variability (Parada et al. 2008, Brochier et al. 2009, Ospina-Alvarez et al. 2015). However, the comparative analysis of 2 species showing a remarkably similar pattern of source and destination strengths between species with contrasting developmental times suggests that habitat and hydrography outweigh larval traits like DVM and larval development times. Thus, it is important that future studies consider longer timescales encompassing ‘anomalous’ years (e.g. El Niño) and a finer spatial scale using models able to capture small-scale coastal dynamics like eddies (e.g. high spatial resolution or nested models). Our simulations also show that most of the recruitment success for both species is concentrated at 3 locations that coincide with topographic headlands (Fig. S7 in Supplement 4), though our results are constrained by model resolution (latitudinal bands of 2 km). Several studies developed in the study region have shown that topographic effects are more important than variation in wind-driven offshore Ekman flux that intensifies upwelling around these points (Figueroa & Moffat 2000, Aiken et al. 2008). Therefore, coastal topography can play a critical role in determining locations with higher/lower recruitment success by modifying the intensity of oceanographic processes such as upwelling circulation. It also seems to affect realized dispersal distances. Several studies have shown that temporal and spatial variability in upwelling circulation can affect larval recruitment through: (1) retention of water masses and larvae in bays (upwelling shadows), usually found downstream of capes and headlands (upwelling centers) (Graham & Largier 1997, Poulin et al. 2002, Aiken et al. 2008), (2) collision of

upwelling fronts with exposed shore locations during upwelling relaxation events (Roughgarden et al. 1988, 1991, Wing et al. 1995, Shanks et al. 2000), and (3) complex stratified alongshore and cross-shore circulation patterns generated during relaxation (Kirincich et al. 2005, Kirincich & Barth 2009). Whichever the mechanism, our model results suggest that topography plays a major role in defining recruitment patterns and determining inter-annual persistence across this upwelling region, which is generally supported by empirical observations of intertidal invertebrate recruitment along central Chile and Oregon (Lagos et al. 2005, Wieters et al. 2008), utilizing patterns of purple sea urchin (*Strongylocentrotus purpuratus*) recruitment along the coast of California (Ebert & Russell 1988) as evidence. As we discuss in Section 4.3, these findings are of great importance for the applicability of territory-based protection schemes and spatial management (e.g. TURFs, protection of reproductive adults, MPAs).

Despite the persistence of the spatial pattern of sources and sinks, our results showed high inter- and intra-annual (Fig. S5 in Supplement 3, and Fig. S8 in Supplement 4, respectively) variability in mean dispersal distance and recruitment. Upwelling intensifies during austral spring and early summer, coincident with peak spawning for most species (Reitzel et al. 2004) and therefore producing high variability in alongshore transport (Aguirre et al. 2012). Byers & Pringle (2006) noted a discrepancy between the warmest boreal month and dates with the highest larval release, which occurs earlier in the year (spring months). They proposed that spring release could be a tradeoff in which development may be slower, but mean currents—and thereby advection—are minimal and diffusion-driven circulation variability is maximal. Indeed, in our simulation, larval development time (under PLD_{Temp}) during the spawning season was longer than published experimental development times (González et al. 1987, Chavez 2004). In highly advective environments, like most coastal oceans and especially in upwelling shores, spawning over several months or the entire year enhances retention probability by increasing the variety of currents encountered (Byers & Pringle 2006). Therefore, larvae released at different times of the year will contribute differently to metapopulation dynamics simply because of temporal variability in hydrodynamic features (see also Ayata et al. 2010). However, it is uncertain to what extent the tradeoffs among development times and recruitment success play a role in spawning strategies of marine invertebrates. Energetic constraints on female reproduction, mating

behavior, or availability of food for developing larvae clearly are important determinants of spawning timing as well (Leslie et al. 2005, Lester et al. 2007). Thus, reproduction during spring months could be a reproductive-larval dispersal tradeoff for many marine invertebrates inhabiting nearshore environments.

Regardless of this large difference in the magnitude of recruitment success between species (attributable to differences in PLD), the spatial pattern of connectivity was consistent between species and also among scenarios (Fig. 3). This is not entirely surprising considering that release location was the main factor explaining the variability in recruitment and dispersal distances. Many studies have shown apparently high self-recruitment in shorter-PLD species. For instance, Ayata et al. (2010) report higher larval exchange almost twice as great between adjacent populations for a PLD of 2 wk than PLD of 4 wk. In contrast, our results showed high allochthonous recruitment (>90%, Table 2) in both modeled species, with high exchange rates between non-adjacent locations. This suggests that timing and location of release may have greater impact on population connectivity than reproductive adult demography.

4.3. Consequences for conservation and management

Despite the short duration of our simulations and relatively coarse spatial resolution (limited by the availability of the HYCOM product), our modeling results offer important insights for future management and conservation studies. First, despite the large differences in PLD, the pattern of sources and sinks and the specific locations of recruitment success along the shore were very similar between the 2 species (at the scale of latitudinal bands) and remarkably persistent among years. This means that territory-based planning to protect species (MPAs) could be effective for sets of species with contrasting development times (White & Costello 2011). Our finding that the best spawning and recruitment locations remain the same despite inter-annual variation in recruitment success indicates that protection of these sites for either fisheries benefit or conservation value, respectively, may be an effective strategy, at least over ecological timescales. Thus, frequent rotation of areas, as suggested for some species (Game et al. 2009), may not be necessarily the best strategy. Second, increasing PLD expectedly reduced recruitment, attributable to increased larval waste, and mean dispersal distances surpassed most scales of manage-

ment instruments (e.g. TURFs; White & Costello 2011), even in the short-PLD species. The observed importance of allochthonous recruitment throughout the region for both species provides relevant results to inform management and conservation. On one hand, this means that most marine reserves will never be large enough to protect self-maintained populations of threatened species, even those with low dispersal potential. For this and many other reasons (Gaines et al. 2010a, Aiken & Navarrete 2011), a network of reserves is necessary to guarantee species persistence. On the other hand, connectivity among TURF management areas is inevitable, even for these short-PLD exploited species, calling into question the single-TURF management approach followed so far in Chile (Tognelli et al. 2009, Gaines et al. 2010b) and highlighting the importance of regional management plans and cooperation among TURFs (White & Costello 2011). Third, although details of larval behavior and the environmental effects on larval development are important when it comes to study-specific determinants of dispersal and recruitment, they appear to play minor roles in comparison to spatio-temporal variation in coastal ocean circulation. Therefore, while further species-specific information in larval biology will allow us to improve model representations of connectivity (Sponaugle et al. 2006, Werner et al. 2007, Metaxas & Saunders 2009, Morgan 2014), it pays to improve the resolution of our models of coastal circulation in the short term (e.g. Nickols et al. 2012), especially in regions of the world for which basic physical information (e.g. bathymetry, high-resolution winds) are not available.

The analysis of realized connectivity further suggests the importance of the northern domain of our study area, where the most relevant realized source (between 32.40° S and 32.60° S, and between 33.20° S and 33.60° S) and destination locations (between 33.00° S and 33.20° S) were identified. In fact, the northern region of the domain (central Chile) hosts a high proportion of rocky habitat and a large number of TURFs. Therefore, it will be interesting to explore the relative importance of habitat distribution or effective management on the observed patterns. Previous studies have also described high recruitment potential using models (Aiken et al. 2007) and observed recruitment (Navarrete et al. 2008) in central Chile. This highlights the need to increase effective protection (e.g. no-take reserves) in this region.

It is clear that model limitations preclude us from providing more specific advice, and we propose that future studies should address these limitations. First, the spatial model resolution (2 × 4 km model cells)

does not allow us to adequately resolve the coastal boundary layer (Nickols et al. 2012), nor to link recruitment observations with the co-management system of TURFs, which usually are smaller than 1–2 km long. Second, we only modeled 4 years (because of the availability of the HYCOM product at the time of this study), and longer timescales are necessary to capture potentially meaningful ecological variation. Third, we only consider mortality due to losses by advection and temperature limit thresholds. However, other mortality causes may be important, such as predation, food availability, and other density-dependent and density-independent factors (e.g. riverine plumes: Grimes & Kingsford 1996, oxygen concentration: Auel & Verheye 2007, Thomsen et al. 2016). Fourth, the effect of climate change on larval recruitment needs to be analyzed carefully, as it can have important effects both on intrinsic larval factors (e.g. hatch size, settlement size, swimming and feeding behavior) (Peck & Hufnagl 2012, Peck et al. 2012, Llopiz et al. 2014) and extrinsic factors, such as warming events and other processes that can also significantly impact recruitment, e.g. ocean acidification (Kurihara 2008), and in upwelling regions, climate change will produce zonal changes in upwelling strength (Wang et al. 2015).

In general, our findings provide relevant and new information to inform spatial patterns of management and conservation of 2 harvested target species in one of the most human-impacted regions of Chile. Despite the model limitations, the modeling approach used here allowed us to identify primary determinants of recruitment success and dispersal distances for 2 important species exploited by artisanal fisheries in Chile. It also permitted us to make broad recommendations for management and conservation in one of the most productive but also heavily exploited coastal regions in the world.

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