Received: 7 March 2018 | Revised: 23 October 2018 | Accepted: 3 November 2018

DOI: 10.1111/jbi.13492

RESEARCH PAPER

WILEY Journal of Biogeography

Coastal biophysical processes and the biogeography of rocky intertidal species along the south-eastern Pacific

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Funding information
Fondo Nacional de Desarrollo Científico y Tecnológico, Grant/Award Number: 1140841, 1140862, 1181300; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: Banting Postdoctoral Fellowship; ICM Nucleus MUSELS

Editor: Michelle Gaither

Abstract

Aim: We assess the spatial distribution of a suite of coastal biophysical characteristics and how their variability is related to the distribution and geographic range of a diverse assemblage of coastal benthic species with different larval dispersal strategies.

Location: South-eastern Pacific (SEP) coast between 18°20′S and 42°35′S.

Methods: Biophysical variability was assessed using chlorophyll-a concentration, sea surface temperature and the signal of turbid river plumes derived from MODIS onboard the Aqua satellite. We established the dominant spatial components using wavelet and coherence analysis, and evaluated the biogeographic structure of 51 rocky intertidal species sampled over ~2,600 km along the SEP using multivariate classification and regression trees.

Results: Biogeographic breaks detected here were consistent with recent biogeographic classification schemes. Distribution breakpoints for species with lecithotrophic larvae clustered around 30°S. We observed a previously unreported break in the distribution of species with planktotrophic larval dispersal strategies around 35°S. These breaks are related to coherence in the spatial structure of sea surface temperature, chlorophyll-a and river outflow over different temporal scales. Regions with similar biophysical characteristics, and the breaks the separate them, are in striking agreement with the biogeographic patterns revealed by the multivariate classification trees.

Main conclusions: Our results reconcile patterns of biogeographic structure reported for other groups of species along the SEP coast. We suggest that river outflow, a poorly studied coastal environmental forcing, may play an important role in determining the geographic distribution of rocky shore species, probably through its effects on larval dispersal patterns.

KEYWORDS
biogeographic provinces, larval dispersal, MODIS, multiscale coherence, river outflows, rocky shore invertebrates

1 | INTRODUCTION

Understanding how environmental variability drives species distribution patterns remains a central challenge for biogeography (Lathlean, McWilliam, Ayre, & Minchinton, 2015; Sutherland et al., 2013). An important link between biogeographic structure and environmental variability is demonstrated by the spatial and temporal structure of the physical processes that determine propagule dispersal, particularly in the ocean (Burgess, Baskett, Grosberg, Morgan, & Strathmann, 2016). The export of young away from parental populations through planktonic larval dispersal is a process that maintains marine metapopulation connectivity across the geographic range of most benthic species, particularly for species with gregarious and sessile adults (Kinlan, Gaines, & Lester, 2005; Shanks, Grantham, & Carr, 2003). During the critical pelagic dispersal stage, marine larvae can either feed on planktonic resources (planktotrophic) or rely on their internal nutritional reserves (lecithotrophic); larval development rates depend chiefly on water temperature and other oceanographic variables (such as Cowen & Sponaugle, 2009; Treml, Roberts, Halpin, Possingham, & Riginos, 2015; Vargas et al., 2016). However, many benthic organisms hatch larvae that do not exhibit a planktonic dispersal stage but instead their larvae develop directly in the benthos, either inside egg masses or brooded by adults; larval supply for these direct developers is even more tightly linked to local environmental conditions (Sanford & Kelly, 2011; Strathmann, 1985). Thus the interactions between larval dispersal and the physical-biological processes that control larval development are key determinants of the biogeography of marine ecosystems (Broitman, Aguilera, Lagos, & Lardies, 2018; Fenberg, Menge, Raimondi, & Rivadeneira, 2015; Pelc, Warner, & Gaines, 2009).

The biogeographic structure of coastal communities worldwide is tightly linked to nearshore circulation processes; major biogeographic breaks coincide with large coastal topographic features that generate divergent flow patterns (Blanchette et al., 2008; Bustamante & Branch, 1996; Fenberg et al., 2015; Pappalardo, Pringle, Wares, & Byers, 2015). Eastern Boundary Upwelling Systems (EBUS), such as the California, Benguela and Humboldt Current Systems, are the result of wind-driven upward transport of cold, oxygen-poor, low pH and nutrient-rich subsurface waters, which fuel strong primary productivity in the nearshore. In turn, surface waters and much of this productivity are advected offshore (Carr & Kearns, 2003; Strub, Mesias, Montecino, Rutllant, & Salinas, 1998). Upwelling circulation is also characterized by energetic mesoscale circulation features that create a dynamic mosaic of oceanographic conditions along the coastline (e.g. Chaigneau, Le Texier, Eldin, Grados, & Pizarro, 2011). Environmental variability associated with coastal upwelling can alter the rate and the spatial distribution of larval recruitment to benthic populations (Broitman et al., 2008; Connolly, Menge, & Roughgarden, 2001; Lagos, Castilla, & Broitman, 2008; Metaxas & Saunders, 2009; Pfaff, Branch, Wieters, Branch, & Broitman, 2011) and the strength and direction of ecological interactions (Kroeker et al., 2016; Navarrete, Wieters, Broitman, & Castilla, 2005). Despite the impact of biophysical processes on the spatial distribution of benthic species, their role as determinants of biogeographic structure in the Humboldt Current System and elsewhere has received limited attention (Fenberg et al., 2015; Pappalardo et al., 2015).

The biogeographic structure of marine temperate biota within the south-eastern Pacific (SEP) has been subject of numerous studies over the last four decades (Brattström & Johanssen, 1983; Camus, 2001; Hayden & Dolan, 1976; Lancellotti & Vásquez, 1999; Thiel et al., 2007; Viviani, 1979). Several syntheses reveal the existence of two major biogeographic provinces recognized along the SEP, the Peruvian and the Magellan provinces, with a large transitional area between 30°–32°S and 42°S (Brattström & Johanssen, 1983; Camus, 2001; Thiel et al., 2007), although the specific location and number of breaks are likely taxon-dependent. In general agreement with the biogeographic classification above, spatial clustering in changes in the genotype frequencies of several species has been noted along the region for species with planktonic larval dispersal (Haye et al., 2014). This break, from 30°S to 32°S, is located at the northern edge of the transitional area and also matches a spatial transition in rocky shore community structure and larval delivery patterns (Navarrete et al., 2005; Tapia, Largier, Castillo, Wieters, & Navarrete, 2014; Valdivia, Aguilera, Navarrete, & Broitman, 2015). The southern edge of the transitional area around 42°S is associated with the northern range limit of many species of marine algae and dispersal-limited invertebrates (Guillemin et al., 2016; Montecinos et al., 2012), and is located near the northern extent of the ice sheet at the Last Glacial Maximum. Hence the presence of several biogeographic breaks in species with particular larval dispersal strategies, and the relative position of the breaks between them, suggest that interactions between dynamic environmental processes over different spatial and temporal scales may alter propagule dispersal patterns across the region.

Multiple environmental processes shape the biogeographic structure of coastal ecological communities along Eastern Boundary Upwelling Systems (Blanchette et al., 2008; Bustamante & Branch, 1996; Navarrete et al., 2005). However, only a surprisingly long-term average upwelling-related variables seem to explain a large fraction of the biogeographic structure along the Pacific coast of North America when species are grouped by larval dispersal strategy (Fenberg et al., 2015). Other studies have also attempted to provide links between proxies of temporal variation in environmental processes and ecological dynamics. For example, Menge and Menge (2013), showed earlier that the upwelling magnitude explains about 50% of the variance in ecological processes such as the rates of larval recruitment of benthic invertebrates (mussels and barnacles) and phytoplankton blooms along the coast of Oregon, California and New Zealand. Similar approaches examining the spatial structure of temporal variability of temperature and larval recruitment rates over the mesoscale have yielded comparable results along the coast central Chile (Navarrete et al., 2005; Valdivia et al., 2015). These approximations have relied on long-term average data that do not incorporate the rich temporal dynamics of the biophysical processes characteristic of coastal upwelling ecosystems (Strub et al., 1998; Tapia et al., 2014). Capturing temporal patterns across spatial scales in key environmental processes that influence larval dispersal should provide important insights into the mechanisms driving biogeographic structure along coastal zones. We hypothesized that variability of a limited set of coastal biophysical characteristics link patterns of biogeographic structure and larval dispersal across multiple species. To test this, we assessed the relationship between the spatial distribution of environmental variability and the biogeographic structure of a broad assemblage of intertidal invertebrates with different larval dispersal strategies.

2 | MATERIALS AND METHODS

2.1 | Satellite data

We used 14 years (2003–2016) of satellite-derived chlorophyll-a (Chl-a), sea surface temperature (SST) and remote sensing reflectance at 555 nm [Rrs(555)] from the MODIS sensor on NASA's Aqua satellite (http://oceancolor.gsfc.nasa.gov/). All composites correspond to 8-day averages (level 3) with a spatial resolution of 4 × 4 km. We used Chl-a and SST as proxies of oceanographic forcing (e.g. Aravena, Broitman, & Stenseth, 2014) and [Rrs(555)], a proxy of turbid river plumes (e.g. Mendes, Saldías, Gómez-Gesteira, Vaz, & Dias, 2017; Petus et al., 2014; Saldías, Sobarzo, Largier, Moffat, & Letelier, 2012) to assess multiscale regimes of biophysical variability along the SEP. All satellite data were averaged in the cross-shore direction (100 km next to the coast) across the area illustrated in Figure 1a with the non-spatially averaged long-term mean SST. We used only the best quality data, removing pixels with land contamination. We calculated the spatial variation in the seasonal cycles as the long-term average of the monthly means across all latitudinal bands.

2.2 | Biogeographic analysis

To assess biogeographic changes in the species composition of intertidal communities along the south-eastern Pacific (SEP, between 18°20′S and 42°35′S), our analysis relied on information compiled through a systematic sampling of 55 wave-exposed rocky intertidal field sites, regularly spread between 18°20′S and 42°35′S (Figure 1a). Species inventories were carried out between 1998–2000 (see Rivadeneira, Fernández, & Navarrete, 2002 for sampling details) and are presented in Jaramillo (2004). Species sampling was focused on the diverse set of mobile invertebrate intertidal consumers, a total of 51 species, including chitons, gastropods, sea urchins and sea stars, a number that is in good agreement with local and regional diversity patterns (Rivadeneira et al., 2002). Additionally, we reviewed the primary scientific literature to determine the dispersal mode of each species in the dataset. The list of species and their developmental modes is provided in Appendix S1. To determine the biogeographic structure of the assemblage and the effect of different dispersal strategies on the spatial distribution of species we used a method namely Multivariate Classification and Regression Trees (mCART; De'Ath, 2002). mCART performs a recursive partitioning of a quantitative variable under the control of a set of quantitative or categorical explanatory variables (Borcard, Gillet, & Legendre, 2011). The result is a tree composed of subsets of leaves (sites) with similar species composition (i.e. biogeographic units) and different from other subsets. In our case, the recursive partitions are driven by the latitude of each site, which acts as a constraint on the formation of the biogeographic units (e.g. Fenberg et al., 2015). The mCART analyses were carried out using the Bray–Curtis similarity index after Hellinger's transformation for presence-absence data (Fenberg et al., 2015). The number of partitions of the tree was determined using cross-validation that gives the simplest tree within one standard error of the best (but more complex) tree; the fit of the model was assessed using the pseudo-R^2 measure (100% cross-validated error) (Borcard et al., 2011). Analyses were carried out for all species, and for species with planktotrophic and lecithotrophic larval development separately. The mCART analyses were conducted using the 'mvpart' library (De'ath, 2006) implemented in the R statistical language (R Development Core Team, 2018).

2.3 | Wavelet analysis

To account for the non-stationarity that characterizes the dynamics observed in nature we used wavelet analysis. By analyzing spatial (alongshore) series through time, wavelet analysis quantifies the evolution of different periodic components in space and/or in time and also any potentially transient associations between components (Cazelles, Chavez, de Magny, Guégan, & Hales, 2007; Cazelles et al., 2008). In this study we used the Morlet wavelet, which is defined by:

$$\psi(t) = \pi^{(-1/4)} \exp(-i\omega_o t) \exp - \left(-\frac{t^2}{2}\right)$$

This wavelet is the product of a complex sinusoidal $\exp(-i\omega_o t)$ multiplied by a Gaussian envelope $exp(-t^2/2)$, where ω_o is the central angular frequency of this wavelet. We applied wavelet decomposition to spatial series. With this wavelet we are able to compute the local Wavelet Power Spectrum of a spatial series, that gives the repartition of the periodic components (variance) along the space domain (Cazelles et al., 2007). Moreover, to quantify the association

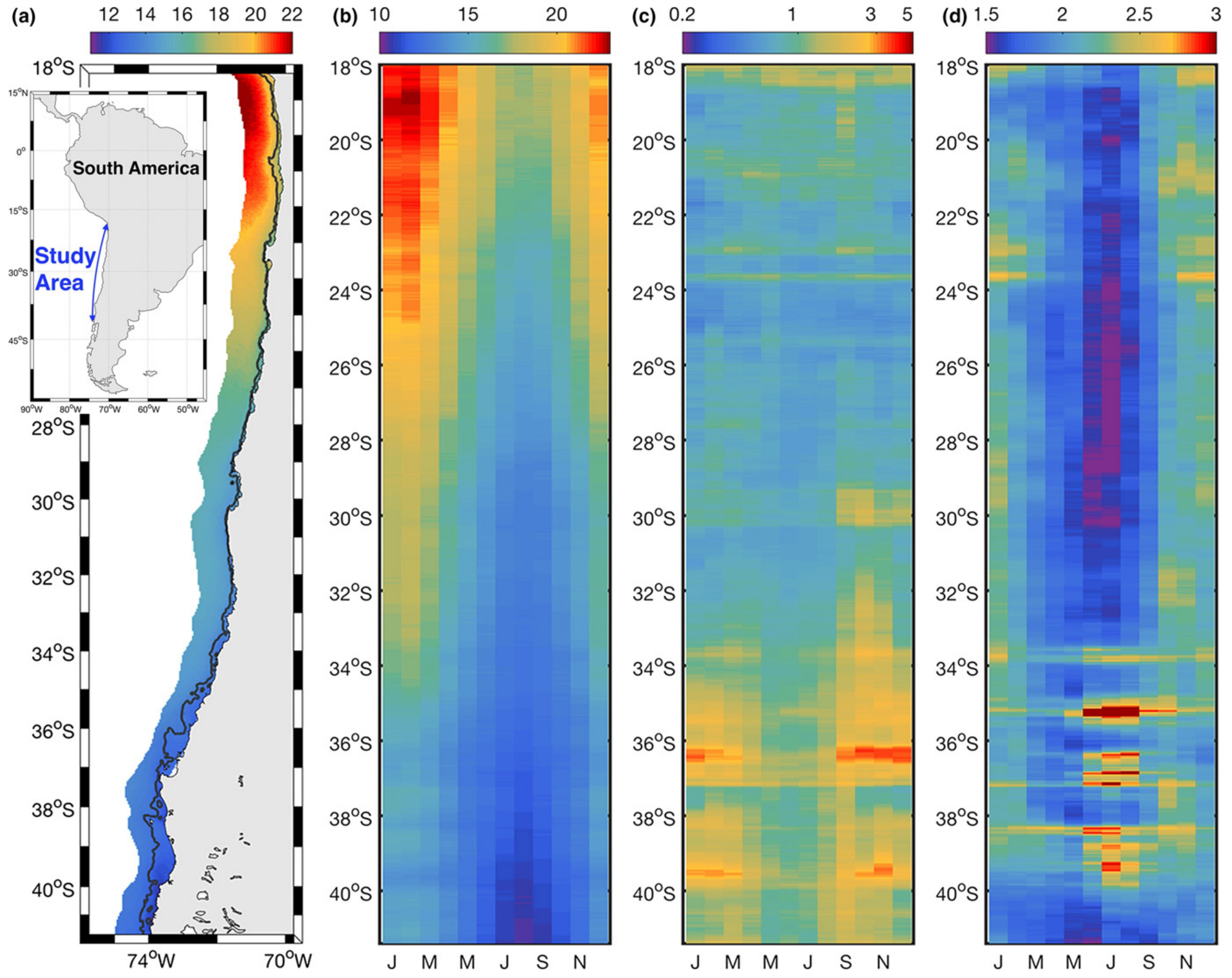

FIGURE 1 Map and spatial climatologies of the three proxies of biophysical variability along the South East Pacific coast, between 18–45°S. (a) Study area, with black line showing the coastline and the coloured offshore section showing the distribution of mean SST over a coastal band of 100 km, the region used to extract the data used for climatology. The thick black line corresponds to the 200-meter isobath. The embedded map in Fig (a) shows the location of our study area in western South America. The remaining panels show the long-term (2003–2016) monthly climatological values (represented from January to December along *x*-axis) of (b) sea surface temperature (°C), (c) chlorophyll-a (log10 mg m-3) and (d) turbid river plumes [Rrs(555) (sr-1)]

between two non-stationary environmental spatial dynamics we performed a Wavelet Coherence analysis defined as:

$$R_{x,y}(\alpha,\tau) = \frac{||<W_{x,y}(\alpha,\tau)>||}{||<W_{x,x}(\alpha,\tau)>||^{1/2}||<W_{y,y}(\alpha,\tau)>||^{1/2}}$$

where a is the period, τ the space index, the angle brackets around terms indicate smoothing, $W_{x,x}(a,\tau)$ is the wavelet transform of the explanatory variable $x(t)$ (SST), $W_{y,y}(a,\tau)$ is the wavelet transform of the response variables $y(t)$ (Chl-a or [Rrs(555)]) and $W_{x,y}(a,\tau)$ is the cross-wavelet transform between $x(t)$ and $y(t)$ (Cazelles et al., 2007).

To assess the significance of wavelet statistics (both for Wavelet Power Spectrum and Wavelet Coherence) we determined the 5% and/or the 10% significance level through an adapted bootstrapping scheme to rule out random processes (Cazelles, Cazelles, & Chavez, 2014). Wavelet Coherence provides a test for phase locking (i.e. simultaneous oscillation on the same frequency) between SST, Chlorophyll-a and [Rrs(555)] (therefore turbid river plumes) spatial series pairs. For operational purposes, we define the regional scale as the longest spatial scale that can be resolved by the approximately 20° of latitude considered in our study, which is 1/4 of that length (i.e. 5° of latitude). We define the mesoscale as structures that are nested within the regional scale, thus extending over 1–3° of latitude. Wavelet analyses were performed using the algorithm developed Cazelles et al. (2007).

3 | RESULTS

3.1 | Environmental patterns

The analysis of satellite imagery highlighted different latitudinal patterns for SST, Chl-a and turbid river plumes. MODIS SST showed an inverse latitudinal gradient in magnitude and seasonality; SST values decreased towards higher latitudes and a large seasonal oscillation was present at low latitudes (Figure 1b). Spatial trends were generally positive for Chl-a and turbid river plumes, with an increase in magnitude towards higher latitudes. The 14-year climatology showed clear latitudinal heterogeneity in the seasonal pattern of Chl-a, with localized areas of high year-round concentration and discrete seasonal maxima equatorward of known coastal upwelling centers (Morales, Hormazabal, Andrade, & Correa-Ramirez, 2013). The topographic dependence of primary productivity was apparent around Peninsula Mejillones (~23°S), Punta Lengua de Vaca (30°S) and Punta Lavapie (37°S), while a peak approximately 40°S was located where the continuous coastline dismembers into the Patagonia fjord system (Figure 1c). The climatology of turbid river plumes showed scant year-round runoff north of 35°S. Local peaks around Peninsula Mejillones may correspond to enhanced aeolian flux of terrigenous sediment (Flores-Aqueveque et al., 2010). The activity of major Andean rivers is evident south of 35°S, where seasonal maxima shift from late austral spring towards winter months (June–August), especially south of 35°S (Figure 1d).

3.2 | Biogeographic structure

Biogeographic analysis of species composition across the 55 rocky shore sites along the Chilean coast showed distinct community composition patterns throughout the broad region examined. Large geographic scale (i.e. thousands of km) mCART analysis showed two breaks and three geographical partitions, with a pseudo-R^2 of 0.54 for all macroinvertebrate species. The biogeographic breaks were observed between sites located around 31°S and 35°S and revealed three biogeographic sub-units (Figure 2a). We observed different patterns of spatial structure of species composition as a function of larval type. Species with lecithotrophic larval development presented one geographic partition (Figure 2b). One group was distributed between 18–31°S, and second group that included all sites between 31.5–42°S. Again, the mCART analysis had relatively low performance (pseudo-R^2 = 0.38). Finally, the classification including only the species with planktotrophic larval development identified a break in biogeographic structure located at 35°S (Figure 2c), generating two large biogeographic sub-units associated with this type of strategy, with pseudo-R^2 = 0.44. Cluster analysis of the biogeographic structure of all groups (i.e. for all species and for groups with different dispersal mode development strategy) using the presence/absence matrix revealed important differences (Figure 2).

3.3 | Biophysical variability

The wavelet analysis is scale-specific and thus allows tracking the changes in the dominant modes of variability across the different spatial scales (or bands) of interest high power in the local spectrum of different spatial bands indicates areas in space associated with high spectral energy in the variable examined at those specific spatial scales. SST showed two significant periods: a mesoscale period of 1–1.5°, observed between 37–41°S, and a regional period of 6–8° that dominated variability between 25–40°S (Figure 3a). The local Wavelet Power Spectrum for Chl-a showed a mesoscale spatial structure with periods of 3° between 35–42°S (Figure 3b). Turbid river plumes showed two significant periodic mesoscale components in the local Wavelet Power Spectrum: 1–2° between 34–37°S and ~42–44°S, and 4° from 37–42°S (Figure 3c). The presence of different significant oscillations that were offset in spatial scale for all satellite fields indicates the occurrence of processes that operate simultaneously at local and regional scales.

3.4 | Modes of biophysical variability

Areas of strong and significant coherence in Figure 4 indicate areas where the spatial dynamics between environmental variables is similar (stronger). Coherence between turbid river plumes and SST signals (Figure 4a) was significant over long spatial scales south of 35°S (4–5°) and north of 30°S (6–7°). The spatial breakdown in Wavelet Coherence between 35°–30°S corresponded to a broad area of mesoscale coherency over shorter scales (1–3°) extending between 35–29°S. Localized areas of significant coherence (1–2°) were observed around upwelling centers (PM, PLV and PL; see map in Figure 4). Wavelet Coherence between Chl-a and SST (Figure 4b) was significant at different spatial scales, which were distributed in space with a pattern of Wavelet Coherence akin to the one observed between turbid river plumes and SST. A mesoscale breakdown in coherence (1–4°) was apparent around 32°S, with a similar breakdown south of 40°S. The Wavelet Coherence between turbid river plumes and Chl-a showed multiple mesoscale spatial coherence (1–4°) over longer scales. However, coherence for the 2–4° band was absent around 35°S (Figure 4c).

4 | DISCUSSION

Our results show that the biogeographic structure of rocky intertidal invertebrates along SEP matches the coherence in the spatial structure of several biophysical proxies. The concordance is likely reflecting a combination of historical and ecological processes that are usually underpinned by barriers to dispersal (Blanchette et al., 2008; Morrone, 2010). Consistently, our results support the importance of species' dispersal strategies shaping differences in biogeographic patterns. Theoretically, the biogeographic structure of dispersal-limited species should be influenced mainly by small-scale processes, such as local adaptation, while species with broad dispersal capacities are likely influenced by regional-scale processes such as geology, climate or oceanographic processes (Fenberg et al., 2015; Haye et al., 2014; Sanford & Kelly, 2011). The existence of a biogeographic break between 30°–32°S at the SEP has been shown by several studies (Camus, 2001; Thiel et al., 2007), and is associated with coastal circulation processes related the location of the South Pacific Anticyclone; upwelling-favourable conditions prevail year-round equatorward of around 30°S (Rahn, Rosenblüth, & Rutllant, 2015).

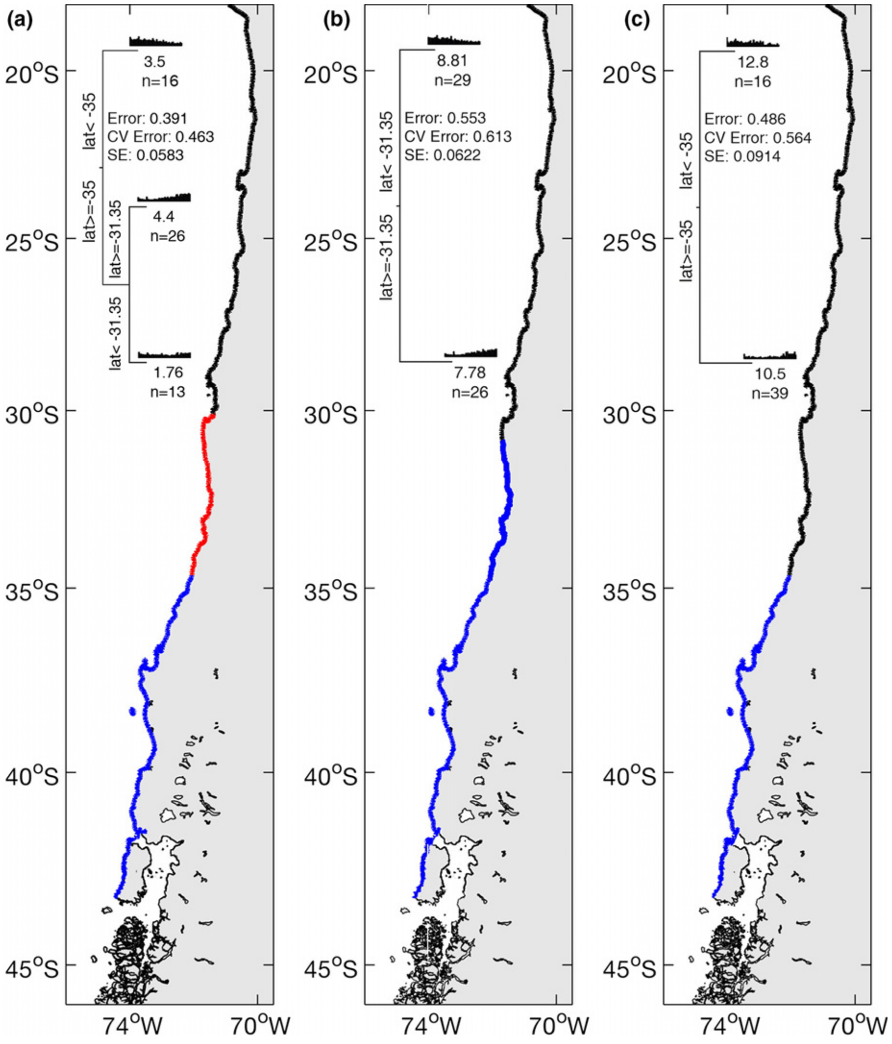

FIGURE 2 Biogeographic structure of intertidal rocky shore communities along the SEP 18–42°S). Multivariate classification tree showing site partitioning according to (a) Species composition (all species, *N*: 51). (b) Species with a lecithotrophic development strategy (*N*: 28). (c) Species with a planktotrophic development strategy (*N*: 20). Different colours represent different biogeographic units defined by the mCART analyses (presented in the insets)

Our analyses confirm the presence of a break around 30°S, only for lecithotrophic species, while the break for planktotrophic species is observed further south, around 34.5°S. The break in coherence over the mesoscale (e.g. 1–3°) between all variables examined from 30 to 35°S, could highlight the spatial coincidence of the location of the first large Andean rivers (32.5°S and 33.5°S, see below) and the major upwelling center at Punta Lengua de Vaca (30°S).Together, our results reconcile the potential of multiple biophysical processes, taking place over different spatial scales and interacting with larval dispersal strategies as important drivers of biogeographic structure.

Phylogeographic studies of organisms with broad distributions and prolonged (i.e. months) planktotrophic larval durations around 30°S on the Chilean coast have not provided evidence for geographic barriers to population connectivity. For example, the carnivorous snail *Concholepas concholepas* (Cárdenas, Castilla, & Viard, 2009) and the widely distributed Humboldt squid *Dosidicus gigas* (Ibáñez et al., 2011) did not show any population genetic structure associated with the barriers discussed above. Equivocal patterns have been observed among species with shared ecological strategies and lower dispersal capabilities. One case is the study of the barnacles *Jehlius cirratus* and *Notochthamalus scabrosus*. Both species have relatively short (i.e. weeks) planktotrophic larval stages, only *J. cirratus* does not show a break in phylogeographic structure between 28–30°S, while the latter shows a break around 30°S (Ewers-Saucedo et al., 2016; Zakas, Binford, Navarrete, & Wares, 2009). The lack of universal concordance between dispersal strategy (and presumed length of the pelagic larval stage) and distribution pattern is also seen in the large kelps *Macrocystis pyrifera* and *Durvillaea antarctica*. These species have similar microscopic propagules and share a circumpolar distribution through their rafting capacity, yet *D. antarctica* reaches its equatorward distributional endpoint at 30°S, while *M. pyrifera* spans it (Santelices & Meneses, 2000). Taken together, the distinct distribution patterns of a broad assemblage of species with planktotrophic and lecithotrophic dispersal strategies suggest that several drivers are shaping the biogeographic structure of the broad transition zone south of 30°S (Camus, 2001). The limited number of species with direct development in our field data (three species, see Appendix S1) makes our analysis difficult to interpret due to the lack of statistical power (data not shown).

In addition to the general agreement with the presence of a biogeographic break around the 30°–32°S area, our analyses support the presence of a new break in the distribution of species with

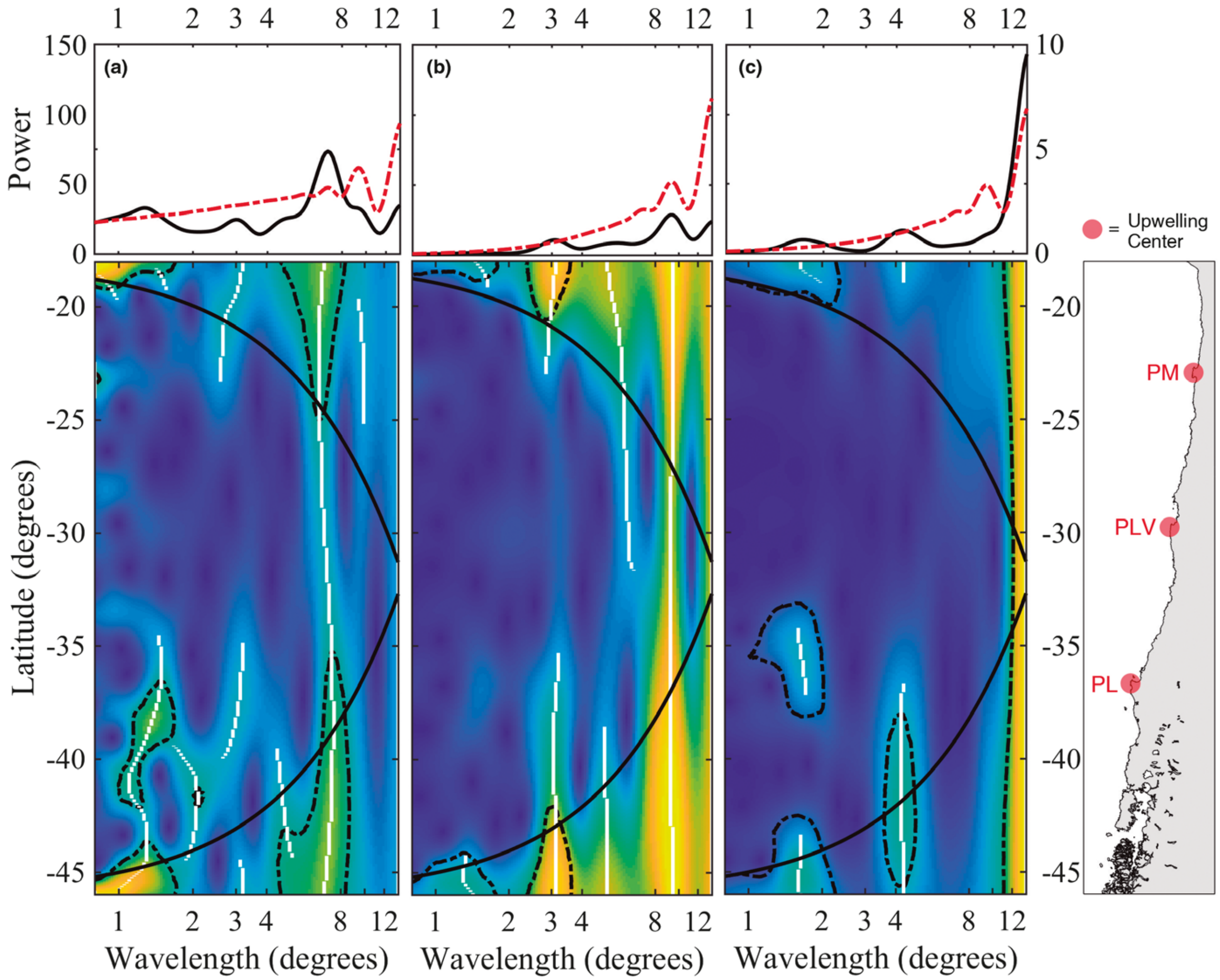

FIGURE 3 Wavelet decomposition of climatology spatial series showing the wavelet power spectrum (WPS) for (a) sea surface temperature, (b) chlorophyll-a and (c) turbid river plumes. The upper panels present the Global Wavelet Power Spectrum along the SEP sector examined, with the red dot-dashed line showing a 95% confidence interval obtained by adaptive bootstrapping. Note the presence of significant structure at small spatial scales for the three variables examined. The lower panels present the local Wavelet Power Spectrum across the SEP sector examined. The black dot-dashed lines indicate the 95% and 90% significant areas obtained by adapted bootstrapping (Cazelles et al., 2014) and the cone of influence (solid black lines) indicate the wavelet domain where computations are not influenced by edge effects (see Cazelles et al., 2008). The colours are coded from yellow (high-power values) to deep blue (low-power values). Spatial periods on the *y*-axis are on log2 scale and expressed in degrees of latitude. The map on the right of the lower panels is provided as a visual aid. Red circles represent large upwelling centers along SEP. PM: Peninsula Mejillones; PLV: Punta Lengua de Vaca; PL: Punta Lavapié

planktotrophic larval development located around 35°S, in relation to river outflow (Figure 3c). This break has also been described for other benthic invertebrates (Lancellotti & Vásquez, 1999), although based on data collected at coarse spatial scales (3° latitude). The transition area south of Punta Lengua de Vaca down to 35°S is an area of intense mesoscale variability (Aguirre, Pizarro, Strub, Garreaud, & Barth, 2012; Hormazabal, Shaffer, & Leth, 2004; Rahn et al., 2015), where eddies and plumes transport primary and secondary coastal productivity offshore (Correa-Ramirez, Hormazabal, & Yuras, 2007; Morales et al., 2007). The well-defined sectors of mesoscale and sub-mesoscale biophysical coherence we observed along this transition region highlight the importance of larval strategies that minimize offshore advection around areas of intensified offshore transport. In turn, alongshore structure in oceanographic conditions and limited dispersal potential create a mesoscale environmental mosaic where local adaptation can take place, particularly for dispersal-limited species (Sanford & Kelly, 2011).

The importance of processes over ecological scales, similar mosaic-like patterns may be underpinned by dispersal limitation driven by geological processes (Luttikhuizen, Campos, van Bleijswijk, Peijnenburg, & van der Veer, 2008). The novel break around 35°S is located in the region where three major Andean rivers (Mataquito, Maule and Itata) discharge freshwater and associated terrigenous material into the adjacent Pacific Ocean, and where we observed elevated seasonal variability in the nearshore (Figure 1d; Saldías et al., 2012; Saldías, Shearman, Barth, & Tufillaro, 2016). River

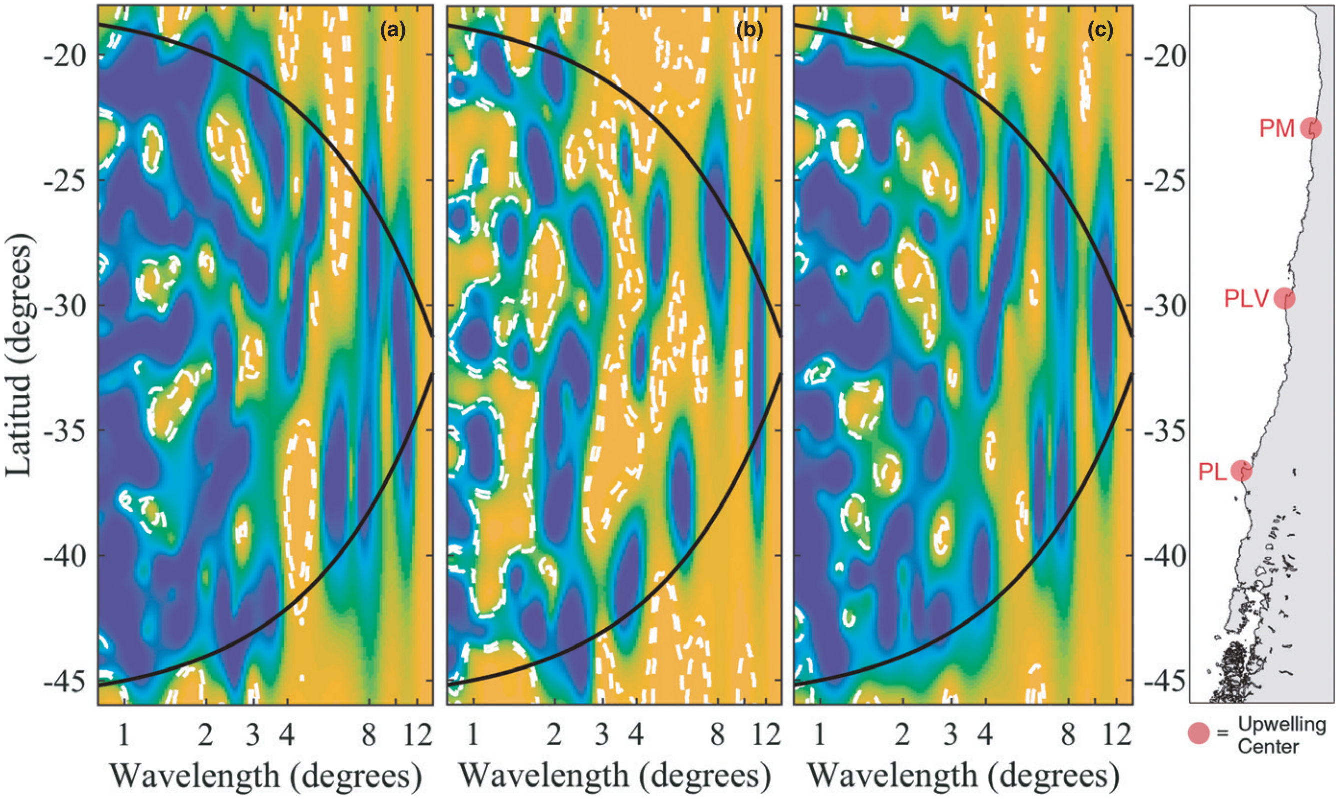

FIGURE 4 Wavelet Coherence between (a) turbid river plumes and sea surface temperature. (b) chlorophyll-a and sea surface temperature and. (c) turbid river plumes and chlorophyll-a. The white dashed lines indicate the 95% and 90% significant areas obtained by adapted bootstrapping (Cazelles et al., 2014) and the cone of influence (solid black lines) indicates the regions where the wavelet computations are not influenced by edge effects (see Cazelles et al., 2008). The colours are coded from yellow (high-coherence) to violet (low coherence). Spatial periods of coherence on the *y*-axis are on log2 scale and expressed in degrees of latitude. The map on the right of the lower panels is provided as a visual aid. Red circles represent large upwelling centers along SEP. PM: Peninsula Mejillones; PLV: Punta Lengua de Vaca; PL: Punta Lavapié

discharge to the coastal ocean can maintain extensive time-varying low salinity plumes (e.g. Saldías, Largier, et al., 2016; Warrick, Mertes, Washburn, & Siegel, 2004), a process that has been shown to limit the dispersal of planktonic larvae along the coast, acting as biogeographic barrier for benthic organisms (Dong et al., 2012). River discharge suggests a mechanistic interpretation for the biogeographic structure we detected in the intertidal assemblage of the SEP. Large rivers originating in the Andes Range south of 33°S drain into the Pacific Ocean during winter-spring months, the period with highest river discharges and largest plumes, as shown in satellite imagery (Saldías et al., 2012). Turbid rivers bear high loads of dissolved nutrients and dissolved inorganic carbon, which impact different traits of adult and larval stages of intertidal species on the open coast (Pérez, Lagos, Saldías, Waldbusser, & Vargas, 2016; Ramajo et al., 2016; Vargas et al., 2016) and the population dynamics of coastal zooplankton (Buttay et al., 2017). Similarly, river outflows can influence primary production through changes in the nitrogen/potassium ratio, which can cascade into the structure of coastal food webs (Balls, 1994; Careddu et al., 2015). Freshwater discharge in estuary ecosystems can also influence the distribution, survival and physiology of multiple species (Lockwood & Somero, 2011; Mion, Stein, & Marschall, 1998; Möller, Castello, & Vaz, 2009). Thus the mechanistic relationship between the biogeographic structure of rocky shore communities and the multiple effects of river discharges along the transitional zone deserves further attention (Dong et al., 2012).

A recent study of the determinants of biogeographic structure of rocky shore communities along the California Current System used a comparable ecological dataset and coarse gridded averages of multiple environmental variables (Fenberg et al., 2015). Their results highlighted the importance of larval development type together with a reduced set of oceanographic variables as predictors of biogeographic structure. A similar, yet more simplified approach was taken by Belanger et al. (2012), who showed that global-scale biogeographic schemes of the distribution of shallow marine benthic faunas can be predicted accurately by a small set of routinely available variables such as temperature, productivity and salinity.

The existence of a large transitional area between 30–32°S to 42°S separating the Peruvian and Magellan marine biogeographic provinces, has been recognized for several decades (Brattström & Johanssen, 1983; Camus, 2001; Lancellotti & Vásquez, 1999; Thiel et al., 2007). However, recent studies report a rather different biogeographic structure for the SEP. For instance, Spalding's global classification scheme (Spalding et al., 2007) recognizes a single biogeographic province from Northern Peru to Chiloé (6°S to 42°S), and several ecoregions defined solely based on expert criteria (Sullivan Sealey & Bustamante, 1999). A recent study (Costello et al., 2017) also found different limits for biogeographic provinces at SEP, with major breaks at 9°S, 25°S and 50°S. Interestingly, breaks proposed by these latter studies are not consistent with the spatial structure of the biophysical variables analyzed. Firmer generalizations could be achieved by future studies expanding the number of taxa, clades, habitats and the geographic scope of the analyses.

Using long-term statistics of multiple environmental variables allows the reconstruction of static scenarios that highlight the effects of historical processes. However, larval dispersal strategies evolved as strategies that allow the dispersive larval phase to exploit dynamic spatiotemporal niches (Strathmann, 1985). The spatial patterns of biophysical variability revealed by our analyses (Figure 4a,b) highlight some shared aspects of the biogeographic structure of the California Current System and Humboldt Current System, for example the paucity of breaks in the distribution of species with planktotrophic larvae around major biogeographic breaks, Point Conception in the California Current System and Punta Lengua de Vaca in the Humboldt Current System, where they are limited to species with poleward boundaries (Gaines et al., 2009). Similarly, the distribution breaks of species with planktotrophic larvae south of 35°S is in agreement with the presence of river plumes and changes in SST as the results of Fenberg et al. (2015), who found that salinity and precipitation were good predictors for breaks in the distribution of species with this mode of larval development.

5 | CONCLUSIONS

Our results help to reconcile the ecological dynamics along Eastern Boundary Upwelling Systems and the pervasive presence of biogeographic structure along these important ecosystems. We suggest that the coastal biogeography of the SEP is similar to other coastal ecosystems such as the California Current System, which are structured by dynamic oceanographic processes. Coastal upwelling circulation seems to maintain regions with similar biophysical variability provides distinct opportunities for different larval development modes. River runoff may also underlie relationships between precipitation and the distribution of species with a planktotrophic dispersal strategy. Taken together, our results emphasize the importance of understanding how different larval dispersal strategies exploit different environmental patterns to understand better the dynamic nature of coastal biogeography along coastal upwelling ecosystems worldwide.

ACKNOWLEDGEMENTS

C.L., G.S.S. and B.R.B. were partially supported by the Millennium Nucleus Center for the Study of Multiple-Drivers on Marine Socio-Ecological Systems-MUSELS funded by MINECON NC120086. G.S.S. is supported by an NSERC Banting Postdoctoral Fellowship. P.A.H., M.M.R. and B.R.B. acknowledge support from FONDECYT grants 1140862, 1140841 and 1181300, respectively. We thank Patricio H. Manríquez, Alfonso Benítez and four anonymous reviewers for their constructive comments.

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BIOSKETCHE

Carlos Lara is a marine ecologist interested in the study of environmental variability using remote sensing tools, and the effects of biophysical forcing on the spatio-temporal synchrony of coastal communities.

Author contributions: C.L., B.C., M.M.R., P.A.H. and B.R.B. conceived the idea. C.L., M.M.R. and G.S.S. provided data. C.L., G.S.S., M.M.R. and B.C. analyzed the data. All authors contributed to interpreting the results and writing the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Lara C, Saldías GS, Cazelles B, Rivadeneira MM, Haye PA, Broitman BR. Coastal biophysical processes and the biogeography of rocky intertidal species along the south-eastern Pacific. *J Biogeogr*. 2019;00:1–12. https://doi.org/10.1111/jbi.13492