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Environmental and demographic factors influence the spatial genetic structure of an intertidal barnacle in central-northern Chile

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ABSTRACT: Understanding the multiplicity of processes producing genetic patterns in natural populations can shed light on the ecology and evolution of species, and help guide effective management and conservation strategies. Here we investigated the role of environmental, demographic, and geographic factors in shaping the spatial patterns of genetic diversity and differentiation of the intertidal barnacle *Notochthamalus scabrosus* along the central-northern coast of Chile (28–34° S). We analyzed genetic data from 7 microsatellite loci genotyped for 300 individuals sampled from 10 sites and combined this information with 8 site-specific environmental (4), demographic (2), and geographic (2) variables using least squares linear regressions, generalized linear models, and matrix regression analyses. We found a strong association between the spatially structured genetic diversity of *N. scabrosus* and patterns of temporal variability in chlorophyll *a*, and among-site differences in seawater temperature and adult abundance. Our results illustrate that population size, partly driven by recruitment success, can leave a signal on genetic structure of this highly dispersive marine species. The significant effect of temperature and chlorophyll *a* stresses that local adaptation may be key to understanding the spatial genetic structure of our model species. Hence, the results of this work represent an advance towards understanding the usually complex causal relationships between environmental variables, gene flow, and genetic diversity patterns of coastal populations.

KEY WORDS: *Notochthamalus scabrosus* · Seascape genetics · Larval dispersal · Coastal oceanography · Marine connectivity

1. INTRODUCTION

Population genetic diversity is important for a range of ecological and evolutionary processes. For example, genetic diversity can determine community structure and primary productivity (Crutsinger et al. 2006). It can be associated with the population growth rate of species (Hughes et al. 2008), and it allows species to adapt to changing environments and fosters persistence over evolutionary time scales (Reed &

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Frankham 2003). Therefore, a strong scientific understanding of the processes that influence spatial genetic variation, genetic diversity, and population structure in nature is of paramount importance to implement efficient conservation and management strategies.

In marine systems, an early paradigm assumed that most organisms were highly dispersive and presented large population sizes, and thus were able to resist genetic divergence at all but perhaps the largest spatial scales. This overly simplistic view was gradually replaced by an increased understanding of hydrographic heterogeneity in the coastal ocean and the advent of molecular genetics, which unveiled many potential causes for genetic structure and speciation in organisms with large dispersal potential (Hellberg 2009, Selkoe et al. 2016). For example, due to the dependence of genetic diversity on population effective size (Ellegren & Galtier 2016), demographic changes along the geographic range of a species can leave a discernible footprint in its spatial genetic makeup. Also, a realistic oceanic environment, especially when there is strong topographic modulation, presents ample opportunities for variation and restriction in effective dispersal distances (Largier 2003, Pringle et al. 2011, Nickols et al. 2015). Geographic distance per se imposes a distance limitation to gene flow, driving increased genetic differentiation with increasing distance between populations, a pattern known as isolation by distance (Wright 1943). Besides the limitation imposed by dispersal between distant populations, phenotype–environment mismatches can impose biological barriers to gene flow (Nosil et al. 2005), producing an isolation by environment, where populations with greater environmental dissimilarity exhibit higher levels of genetic differentiation, blurring or reinforcing patterns generated by geographic distance alone (Wang & Bradburg 2014).

High-resolution molecular and environmental data are now routinely used to assess the influence of landscape-scale environmental characteristics on genetic variation and spatial patterns in natural populations of species. Altogether, the mounting evidence suggests that considerable genetic structure occurs in marine populations around areas where environmental oceanographic factors exhibit strong spatial structure or geographic discontinuity.

The central-northern coast of Chile represents an interesting study system to evaluate the effects of environmental, demographic and geographic factors on genetic diversity and differentiation of marine organisms. Superimposed on what are smooth latitudinal trends in mean sea surface temperature (SST) along this highly productive upwelling ecosystem, there is a marked change in oceanographic regimes that takes place around 30° S. Such geographic discontinuity entails changes in upwelling-driven coastal circulation (Hormazabal et al. 2004, Aiken et al. 2011, Aguirre et al. 2014), as well as prevailing hydrographic conditions, such as SST variability, surface chlorophyll, and nutrient availability (Navarrete et al. 2005, Tapia et al. 2014). Coincidentally, at this same latitude, several studies have reported the occurrence of geographic distribution endpoints of several intertidal and subtidal invertebrate species (Lancellotti & Vasquez 1999, Camus 2001), phylogeographic breaks of several invertebrates and macroalgae (Tellier et al. 2009, Haye et al. 2014), and large changes in population dynamics and abundance of dominant rocky shore species that otherwise extend far beyond this region (Broitman et al. 2001, Navarrete et al. 2005, 2008).

The geographic range of the intertidal barnacle *Notochthamalus scabrosus* (Darwin 1854) spans the 30° S transition zone, and its complete larval development to settlement takes well over 1 mo at the water temperatures typically encountered in central Chile (Venegas et al. 2000). At the same time, the advective nature of coastal flow along central Chile (Aiken et al. 2007) sets the stage for a comparatively high potential for larval dispersal and genetic flow among distant populations of this species, as shown by biophysical models for other long-distance dispersers in the region (Garavelli et al. 2014). Moreover, large variation in larval arrival rates and adult cover have been reported for the central-northern coast, which has been attributed to differences in the temporal regime of upwelling-favorable winds (Navarrete et al. 2005, Lagos et al. 2008). A phylogenetic break in the *N. scabrosus* mitochondrial cytochrome oxidase I gene (mtCOI) around 30° S was reported by Zakas et al. (2009). Although spatially stable, there are significant temporal changes in gene frequencies near the break (~30° 55′ S), presumably related to source–sink dynamics and/or low effective population sizes in this zone (Laughlin et al. 2012). Based on a large-scale circulation model, Ewers-Saucedo et al. (2016) suggested that the genetic break of *N. scabrosus* around 30° S requires differential performance of mtCOI lineages along the coast; in other words, it could not be maintained by dispersal limitation alone. Therefore, the diversity and genetic structure of *N. scabrosus* may respond to multiple causes, such as phylogeography, demography, geographical isolation, and selection pressures driven by environmental variation along the coastline.

This study takes advantage of the genetic information gathered for *N. scabrosus*, based on mtCOI, as well as of a long-term database (5–13 yr) of monthly larval arrival (recruitment) of this species at multiple sites spanning the reported latitudinal break. Together with surveys of adult abundance and satellite-based information of environmental (oceanographic) variables for the region (28–34° S), and the development of neutral microsatellite markers, we assessed the potential influence of nearshore environmental, demographic, and geographic factors on the genetic diversity and population structure patterns of *N. scabrosus*. Using neutral markers of gene flow allowed us to (1) characterize patterns of genetic diversity and the spatial genetic structure in *N. scabrosus* and (2) determine the relative importance of environmental, demographic, and geographic factors for genetic variation between and within populations of this widely distributed barnacle species.

2. MATERIALS AND METHODS

2.1. Hydrography of the study area

The coast of Chile between 18 and 42° S is under the broad influence of the northward flowing Humboldt Current (also called Chile–Peru Current). Close to shore, coastal hydrography is dominated by the dynamics of the Chilean Coastal Current (CCC), a predominantly northward surface stream forced by the prevailing south and southwest upwelling-favorable winds (Aiken et al. 2008, 2011), which intensify during spring and early summer months, and around coastal topographic features (Strub et al. 1998, Tapia et al. 2009, Bravo et al. 2016). Our study area is located in a fairly straight shoreline stretch (Fig. 1) and is exposed to direct wave action (Narváez et al. 2006).

Within the study area, the main upwelling centers are Punta Talca, Punta Toro, Curaumilla, Pichilemu, and, to a lesser extent, Los Molles (Silva & Valdenegro 2003, Wieters et al. 2003, Tapia et al. 2009, 2014). In contrast, the bays of Cartagena, Valparaíso, and Coquimbo remain relatively protected from upwelling (Kaplan et al. 2003, Vargas et al. 2004, Aiken et al. 2008). Four sampling sites (PTal, LMol, Cura, and Pich) were located in active upwelling centers, and 4 sites, namely Temb and Guan (Coquimbo Bay), Mont (Valparaíso Bay), and ECIM (Cartagena Bay), were located in places of weak upwelling. For the 2 remaining sites (Apol and CBaj), records from *in situ* SST suggest that the hydrography of Apol may be similar to that of weak upwelling sites, while CBaj seems to be under the influence of active upwelling (Valdivia et al. 2015).

An important geographic discontinuity in upwelling-favorable winds occurs around 30–32° S (Strub et al. 1998, Thomas 1999, Hormazabal et al. 2004, Navarrete et al. 2005). North of this latitude, equatorward winds are weaker but more persistent throughout the year, while to the south winds are stronger but temporarily more variable (Hormazabal et al. 2004, Navarrete et al. 2005). The change in oceanographic regimes determines or modulates the concentration and temporal variability of surface phytoplankton (Thomas 1999), nutrient regimes (NO_3) of coastal waters (Tapia et al. 2014), and functional structure of benthic communities (Broitman et al. 2001, Navarrete et al. 2005, Wieters et al. 2009).

2.2. Study species

Notochthamalus scabrosus is distributed along most of the rocky coasts of Ecuador, Peru, and Chile (Brattström & Johanssen 1983). In the zone occupied by chthamalid barnacles, *N. scabrosus* inhabits the 3 intertidal elevations, with greater abundance in the middle and upper intertidal zones (Paine et al. 1985,

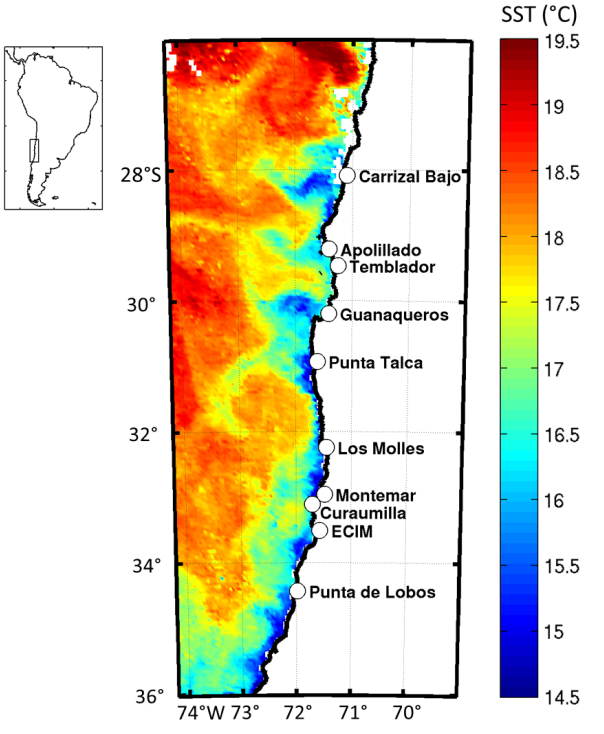

Fig. 1. Central-northern coast of Chile, showing the 10 sampling sites and weekly averages of sea surface temperature (SST) for nearshore areas. ECIM: Estación Costera de Investigaciones Marinas

Shinen & Navarrete 2010). Adults are sessile filter feeding, hermaphroditic brooders. The life cycle of *N. scabrosus* includes a pelagic larval stage that lasts about 37 d at 15–18°C, with 6 naupliar stages with planktotrophic feeding and a cyprid stage competent for settlement (Venegas et al. 2000). Cyprid settlement occurs in pulses of larval arrival to the coast during a few days within the recruitment period, which is mainly concentrated in spring–summer (Tapia & Navarrete 2010).

2.3. Sampling of individuals, DNA extraction, and genotyping of microsatellites

At each of 10 study sites, 30 *N. scabrosus* adults of 3–6.4 mm rostrocranial length were collected from rocky platforms approximately 10–30 m long × 4–8 m wide. Individual barnacles were identified as *N. scabrosus* in the field and were removed from the rock with a scalpel and immediately stored in tubes with 95% ethanol for preservation. Total DNA was extracted using the salt/Proteinase K method (Aljanabi & Martinez 1997) and quantified in a spectrophotometer (Nanodrop).

Seven microsatellite loci were amplified by polymerase chain reaction (PCR). The microsatellite development procedure, the conditions under which the PCRs were performed, and the GenBank accession numbers can be found in Table S1 in the Supplement at www.int-res.com/articles/suppl/m612p151_supp.pdf. Alleles were identified by capillary electrophoresis in an ABI3130 Genetic Analyzer (Applied Biosystems), and the Excel FLEXIBIN macro (Amos et al. 2007) was used to calibrate the reading and allele binning of each locus.

2.4. Genetic polymorphism

The total number of observed alleles (Na), number of private alleles (Pa), and observed (H_o) and expected (H_e) heterozygosity were calculated in GENALEX 6.5 (Peakall & Smouse 2012). Per locus gene diversity (Gd) and standardized allelic richness (Ar) were calculated in the FSTAT software version 2.9.3.2 (Goudet 2001). The Ar index was calculated using the rarefaction method to avoid bias due to differences in sample size (Leberg 2002). To evaluate deviations from the Hardy-Weinberg equilibrium (HWE), Fisher's exact tests were performed for heterozygote deficits at each site–locus combination, and *U*-score tests for global HWE per site through loci and per locus across sites (dememorization 10 000; 100 batches; 10 000 iterations) using the GENEPOP 4.2 software (Rousset 2008). Linkage disequilibrium between all pairs of loci at each site and between each pair of loci across sites was assessed by Fisher's exact tests implemented in GENEPOP with this same parameter set. The inbreeding coefficient F_{IS} by locus and site was quantified with GENETIX 4.05 (Belkhir et al. 2004), and departures from random expectations were assessed by 10 000 permutations. For all multiple comparisons, the nominal level of significance of 5% was adjusted using the false discovery rate (FDR; Benjamini & Hochberg 1995).

To test for large allele dropout and stuttering and to estimate the frequency of null alleles at each site–locus combination following Brookfield (1996: Eq. 4), data were analyzed with the MICROCHECKER software (van Oosterhout et al. 2004).

2.5. Population genetic structure

Global and pairwise genetic differentiation was evaluated calculating θ_{ST} (Weir & Cockerham 1984) and D_{EST} (Jost 2008) indices, respectively, in GENALEX 6.5 (Peakall & Smouse 2012) and running 10 000 permutations to evaluate their significance. Jost's D_{EST} outperforms G_{ST} (the multiallele generalization of F_{ST}) and its relatives (F_{ST}) over a range of sample sizes, including in situations where we have highly variable microsatellite loci with different numbers of alleles (Heller & Siegismund 2009, Gerlach et al. 2010), but it is recommended to compare results between differentiation indices (Leng & Zhang 2011). In all multiple comparisons, sites were used as population units, and the nominal level of significance, 5%, was adjusted using FDR. To identify population relationships in a 2-dimensional space, principal coordinate analyses (PCoAs) of the sites were computed and graphed in GENALEX 6.5 using the θ_{ST} and D_{EST} differentiation indices.

As null alleles can impose error in differentiation estimates (Pompanon et al. 2005), 2 approximations were conducted. First, using MICROCHECKER, we obtained a new database corrected for null alleles. MICROCHECKER adjusts the number of homozygote genotypes to reflect the estimated frequency of null alleles and the likely number of homozygotes given the adjusted allele frequencies and assuming random mating. We then repeated the previous differentiation analysis using the adjusted database. Second, pairwise F_{ST} with and without the null allele correction was estimated with the expectation-

maximization (EM) algorithm (Dempster et al. 1977) with ENA correction to give an accurate estimate of F_{ST} in the presence of null alleles using FREENA software (Chapuis & Estoup 2007). The uncorrected and corrected pairwise F_{ST} were then compared by means of a paired *t*-test.

To estimate the number of genetically differentiated groups, Bayesian-based clustering was used as implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000). STRUCTURE was run using the admixture model, the assumption of correlated allelic frequencies between clusters, with and without the recessive alleles option that accounts for the null alleles (Falush et al. 2003, 2007), and considering sampling site information (Hubisz et al. 2009). From Zakas et al. (2009) and Laughlin et al. (2012), we know that $k = 1$ can be rejected, so all runs were made for k values between 2 and 10. Ten independent runs with 500 000 Markov chain Monte Carlo replicates and a burn-in length of 50 000 were used for each value of k. In order to select the k value that best captures the structure of the data, the statistic Δk, a measure of the second-order rate of change in the likelihood of k (Evanno et al. 2005) was implemented in STRUCTURE HARVESTER (Earl & vonHoldt 2012), and the values of Δk as a function of k were plotted. In CLUMPP 1.1 (Jakobsson & Rosenberg 2007), we merged the results of the 10 runs for each value of k, and DISTRUCT 1.1 (Rosenberg 2004) was used to graphically visualize the results.

2.6. Demographic variables

2.6.1. Recruitment rates

At each site, an estimate of arrival rates of larval *N. scabrosus* was obtained by quantifying recruitment onto 10 × 10 cm Plexiglas plates covered with Safety-Walk™ (3M), an anti-slip surface that provides a heterogeneous substrate for larvae settlement and ensures homogeneity of conditions across plates and sites (Menge 2000). Five replicate collectors were fastened to the rocky substrate with stainless-steel bolts in the mid-upper intertidal zones of rocky platforms exposed to swell. Replicate collectors were replaced monthly, and recruitment rates were standardized to the number of ind. collector^{-1} d^{-1}. The monthly recruitment rates were then averaged to obtain the annual recruitment rates, and these in turn were averaged over the years to estimate the per site recruitment rate. At 8 of the 10 study sites, the collectors were initially deployed in late 1999 or early 2000, whereas at the 2 northernmost sites (CBaj and Apol), recruitment surveys began in mid-2009. The recruitment time series used here covered the period up to December 2013 for all sites.

2.6.2. Adult cover (abundance)

At each site, the benthic abundance of *N. scabrosus* was estimated using 7 to 10 quadrats of 0.25 m^2, located along ca. 20–30 m alongshore transects. Transects were repeated at 3 intertidal elevations (low, mid-, and high intertidal zones) of the same rocky platforms where we deployed larval collectors. The 50 × 50 cm quadrat frame was divided into 25 equal squares with monofilament line, which was used to visually estimate adult abundance of *N. scabrosus* as percentage cover. Cover surveys were conducted approximately every 6 mo. For more details about the field methods, see Broitman et al. (2011).

2.7. Environmental and geographic variables

Environmental heterogeneity imposed by hydrographic conditions such as SST and productivity can directly or indirectly affect population genetic structure in marine organisms (Bekkevold et al. 2005, Mendez et al. 2010, Wei et al. 2013). A multivariate indicator of environmental variability was constructed to test for correlation with the spatial genetic structure of *N. scabrosus*. To this end, spatio-temporal variations in chlorophyll *a* (chl *a*) concentration (mg m^{-3}) and SST (°C) over a period of 10 yr (January 2003 to December 2013) were processed from monthly averages of Aqua MODIS satellite data with a 4 km spatial resolution using MatLab R2014a. Temporal variability in chl *a* and SST across the region was then decomposed by 2 separate principal component analyses (PCAs) of the respective time series, so that scores of sites on PC1 and PC2 (typically called empirical orthogonal functions, EOF1 and EOF2, in the oceanographic literature, as they are carried out in the time domain), were used as multivariate representations of environmental conditions for either SST or chl *a*. In these analyses, the first axis (PC1) is dominated by the seasonal amplitude, with positive/negative values corresponding to sites with strong/weak seasonality. The second mode (PC2) is dominated by higher frequency variability, which in our system is chiefly synoptic variation corresponding to upwelling dynamics (see Wieters et al. 2009, Tapia et al. 2014, Valdivia et al. 2015 for similar

analyses). Latitudinal (Lat) and longitudinal (Lon) positions of each site were used as descriptors of geographic structure.

2.8. Environmental/demographic/geographic–genetic association analysis

Three complementary approaches, i.e. simple linear regressions, multi model selection, and matrix regression, were employed to test for associations among environmental, demographic, and geographic factors with the spatially structured genetic diversity of *N. scabrosus*. The linear regressions and model selection analyses used location (site)-specific data to evaluate the influence of our explicative variables on genetic diversity across sampling sites. The matrix regression analyses used the explicative variables as a proxy of 'seascape resistance' (McRae 2006) to evaluate their effects on among-site genetic differentiation. Our 8 predictive variables were the PC1 and PC2 of chl *a* and SST (hereafter CHLA1, CHLA2, SST1, and SST2), long-term averages of recruitment rates (Rec) and adult cover (Cov), and geographic location (Lat and Lon). The variables Rec and Cov were $\log_{10}$ transformed before analyses to approximate normal distributions.

First, we conducted least squares (LS) linear multiple regression analyses between each metric of genetic diversity (Ar and Gd) and our 8 predictive variables. Second, a sensitivity analysis was performed using generalized linear models (GLMs) to select the best model of variables to explain spatial variation in our metrics of genetic diversity. Because some predictor variables are highly correlated (see Table S3), we examined the impact of collinearity using the variance inflation factor (VIF) before running analyses. The variables Lat, Rec, and SST2 showed high (>10) VIF values, and were removed to minimize VIF values (<5). We then followed a stepwise approach for the sensitivity analysis, which was repeated for the 2 dependent variables (Ar and Gd) in R (R Core Development Team 2017): We (1) ran a full GLM that includes all predictive variables with VIF values <5; (2) examined the scatterplot of residuals versus predicted values (both in terms of the slope of the relationship and in the dispersion of the values) to check for the absence of trends; (3) sequentially removed (one by one) all predictive variables that were not significant ($p > 0.05$); (4) selected the most parsimonious 'suboptimal' GLM through a manual stepwise procedure according to the relative contribution of each factor to the variance explained by the model retaining predictive variables with a relative contribution ≥10%; (5) computed LS means of the dependent variable for each model parameter in order to assess the effect of specific variables on the dependent variables.

As an alternative way to obtain the best subset of explicative variables, we performed stepwise selection (both forward and backward) using the stepAIC function from the 'mass' package in R. This function uses the exact Akaike's information criterion (AIC) as the model selection criterion. Third, we used multiple regressions on distance matrices (MRDM; Manly 1986, Legendre et al. 1994) to estimate the independent effects of explicative variables on *N. scabrosus* among-site genetic differentiation. Briefly, partial regression slopes were estimated using standard multiple linear regression, but the significance of each term was determined by randomly permuting the explanatory variables one at a time while keeping the others constant (Wang 2013). This analysis was implemented using the 'ecodist' package (Goslee & Urban 2007) in R, and significance was based on 10 000 permutations using the genetic distance matrices (θ_{ST} and D_{EST}) as response variables. Each of 8 matrices representing environmental, demographic, and geographic differences among sites were used as the predictor variables. Data were converted into matrices of pairwise distances calculating the absolute differences from site-specific values of each variable following Amaral et al. (2012). Due to its high VIF value (>10), the geographical variable Lat was removed, so a subset of 7 predictor variables was retained for the subsequent analysis.

3. RESULTS

3.1. Genetic polymorphism

The 7 microsatellite loci reached a total of 158 alleles in the 300 individuals of *Notochthamalus scabrosus* genotyped, which ranged from 79 in CBaj to 95 in Temb. In addition, we found 27 private alleles, with the highest number observed at Apol (Pa = 6). In contrast, Pich shared all of its alleles with most other sites. The Ar ranged from 11.0 in CBaj to 13.2 in Temb (mean Ar ± SE = 12.01 ± 0.72), while Gd ranged from 0.77 in ECIM to 0.83 in Apol (mean Gd = 0.81 ± 0.02). Both Ar and Gd indices showed a peak at Guan, Temb and Apol (located around Coquimbo Bay), while the lowest values were found at CBaj and ECIM for Ar, and at ECIM and Mont for Gd (Table S2).

All 10 populations exhibited significant heterozygote deficiency. Of the 70 site–locus combinations, 58 showed a significant deviation from HWE based on Fisher's exact test and after FDR correction, while only 37 had significantly positive F_{IS}-values based on a permutation test (Table S2). Using the corrected database for null alleles, 56 site–locus combinations remained significantly deviating from HWE with the exact test, and 30 site–locus comparisons still had significant $F_{IS} > 0$ with permutation tests (Table S2).

Of the 210 linkage disequilibrium tests performed, none was significant after correcting for false positives (FDR), and none of the global tests for each pair of loci across sites was significant. The estimated frequency of null alleles by site–locus combination varied between 0 and 0.379, with an average frequency of 0.156 (SD = 0.089) across loci and sites (Table S2).

3.2. Population genetic structure

N. scabrosus showed statistically significant global genetic structure ($\theta_{ST} = 0.013$, $p < 0.001$; $D_{EST} = 0.040$, $p < 0.001$). Pairwise θ_{ST} and D_{EST} were significant for 27 and 21 of the 45 comparisons at the nominal level ($\alpha = 0.05$), of which 22 and 15 remained significant after corrections for multiple tests, respectively (Table 1). Significant pairwise comparisons were mostly between sites north of PTal versus sites south of LMol, and the sites with lowest and highest levels of differentiation were Guan vs. PTal (separated by 50.26 km) and Temb vs. Cura (separated by 419.88 km), respectively. CBaj had the highest number of significant pairwise comparisons for both θ_{ST} and D_{EST} (n = 9 and 8, respectively) followed by LMol (n = 7 and 6, respectively; Table 1). The first 2 coordinates of PCoAs with θ_{ST} and D_{EST} values explained 87.62 and 87.88% of total variation, respectively, and revealed similar structuring of sites (Fig. 2). The first axis of the PCoAs separated 2 principal groups, one composed of sites from LMol to the south, the other with the 3 northern sites (Temb, Apol, and CBaj), whilst Guan and PTal were between these 2 groups. Weak separation of sites within these regions was detected along the second PCoA axis, with Temb separated from Apol and CBaj, and LMol and Cura from Mont, ECIM, and Pich (Fig. 2).

Null alleles had some effect on our results: (1) the ENA method gave slightly, but significantly, lower F_{ST} values (average F_{ST} with ENA = 0.00815, SD = 0.00693) than those obtained without correction for

Table 1. Among-site genetic differentiation of *Notochthamalus scabrosus* at 7 microsatellite loci. Analyses were done with (A) the original database and (B) the database corrected for null alleles. Values of θ_{ST} are above the diagonal and D_{EST} values are below the diagonal. CBaj: Carrizal Bajo; Apol: Apolillado; Temb: Temblador; Guan: Guanaqueros; PTal: Punta Talca; LMol: Los Molles; Cura: Curaumilla; ECIM: Estación Costera de Investigaciones Marinas (Las Cruces); Pich: Pichilemu (see Fig. 1). Shaded boxes indicate values significant at the nominal level ($p < 0.05$). Values in **bold** indicate significant values after false discovery rate correction

Study sites	CBaj	Apol	Temb	Guan	PTal	LMol	Mont	Cura	ECIM	Pich
A) Original database										
CBaj	–	0.007	**0.013**	**0.011**	**0.009**	**0.022**	**0.025**	**0.023**	**0.023**	**0.020**
Apol	0.039	–	0.005	0.001	0.005	**0.016**	**0.021**	**0.019**	**0.017**	**0.012**
Temb	**0.065**	0.028	–	0.000	0.004	**0.020**	**0.009**	**0.027**	**0.015**	0.000
Guan	**0.053**	0.009	0.004	–	–0.005	**0.010**	0.005	0.008	**0.008**	0.004
PTal	0.043	0.031	0.023	–0.024	–	0.008	0.007	0.007	0.005	–0.001
LMol	**0.099**	**0.079**	**0.091**	0.043	0.031	–	**0.009**	0.002	**0.009**	0.005
Mont	**0.105**	**0.095**	0.038	0.020	0.024	0.036	–	0.004	–0.004	–0.002
Cura	**0.103**	**0.091**	**0.126**	0.030	0.023	0.009	0.017	–	0.003	**0.009**
ECIM	**0.090**	**0.071**	**0.059**	0.027	0.012	0.035	–0.013	0.015	–	–0.002
Pich	**0.086**	**0.057**	0.001	0.015	–0.004	0.024	–0.008	0.038	–0.005	–
B) Corrected database										
CBaj	–	0.004	**0.010**	0.006	0.011	**0.016**	**0.020**	**0.023**	**0.018**	**0.019**
Apol	0.013	–	0.007	0.001	0.004	0.008	**0.015**	**0.013**	**0.012**	**0.010**
Temb	0.037	0.013	–	0.003	0.009	**0.013**	0.005	**0.024**	0.008	0.001
Guan	0.027	–0.009	–0.012	–	0.007	0.008	0.007	0.008	**0.010**	0.007
PTal	0.010	–0.002	–0.008	–0.045	–	0.011	**0.016**	**0.015**	0.010	0.010
LMol	0.073	0.054	0.060	0.016	0.007	–	0.007	0.004	0.009	0.005
Mont	0.079	0.070	0.018	0.005	0.001	0.019	–	0.007	0.000	0.000
Cura	0.084	0.063	0.105	0.010	0.002	–0.006	0.005	–	0.007	0.006
ECIM	0.068	0.052	**0.039**	0.016	–0.009	0.019	–0.022	0.001	–	0.000
Pich	0.061	0.035	–0.010	0.003	–0.026	0.003	–0.020	0.023	–0.021	–

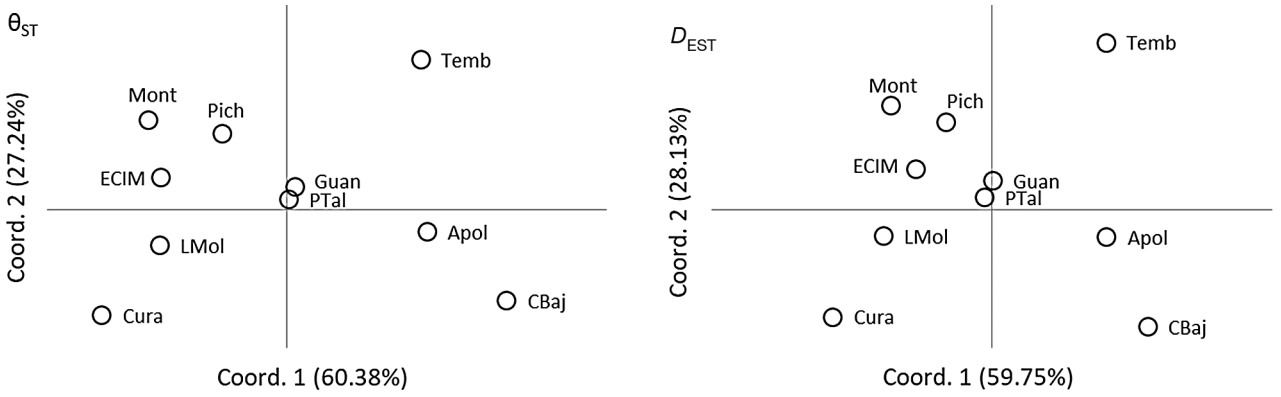

Fig. 2. Principal coordinates analysis calculated by θ_{ST} (left) and D_{EST} (right) values of 10 sites studied. For θ_{ST} and D_{EST} indices, the first 2 axes explain 87.62 and 87.88 % of the total variation, respectively. Site abbreviations as in Table 1

the presence of null alleles (average F_{ST} without ENA = 0.00951, SD = 0.00847; paired t = 3.74, p < 0.001); (2) global structure was lower but still significant with the adjusted database (θ_{ST} = 0.012, p < 0.001; D_{EST} = 0.018, p = 0.001); and (3) there were fewer significant pairwise comparisons after FDR corrections for D_{EST} (only 1 significant comparison) and θ_{ST} (15 of 22 comparisons still significant). However, the main pattern of differentiation between sites north and south of PTal–LMol persisted with the adjusted database, as well as the most and least differentiated pairwise comparisons (Table 1).

The cluster analysis performed using STRUCTURE confirmed the existence of 2 clusters, one south of LMol and the other north of PTal (Fig. 3). For k = 3, a new cluster included CBaj, the northernmost site. According to Evanno's criteria, k = 4 was the most likely number of clusters (Fig. S1). However, no clear spatial pattern could be recovered from the assignment of individuals into these 4 clusters. This may be

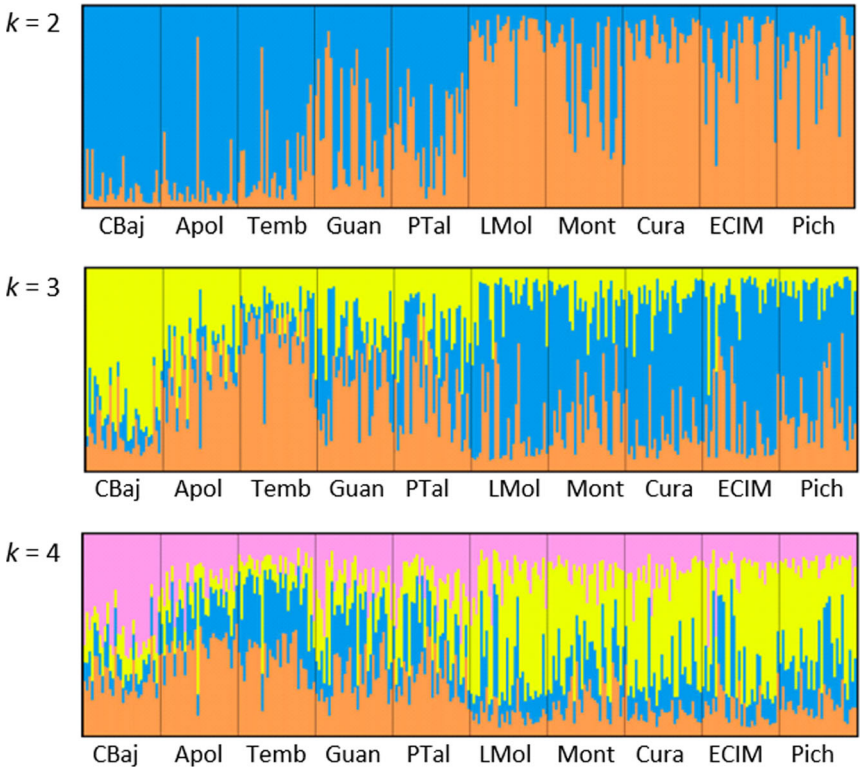

Fig. 3. STRUCTURE assignment of individual *Notochthamalus scabrosus* across all sites into clusters for k between 2 and 4. Colors indicate percentage contribution of individuals to assigned clusters (y-axis), individuals are represented by each line (x-axis); black lines separate sites from which individuals were collected. Site abbreviations as in Table 1

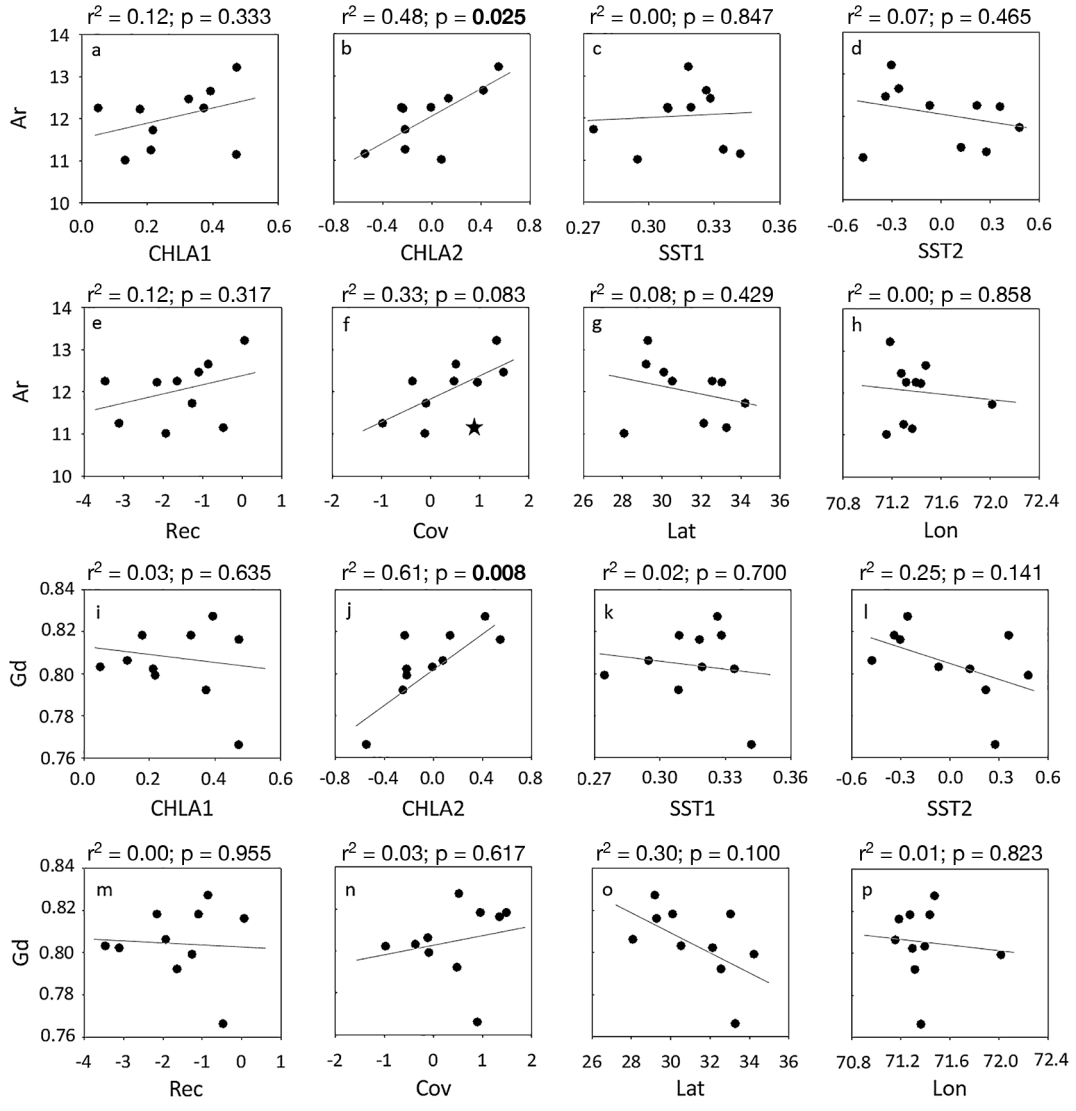

Fig. 4. Results for the linear regressions among 8 predictive and 2 dependent variables. Ar: allelic richness; Gd: gene diversity; CHLA1 (CHLA2): PC1 (PC2) of chlorophyll *a* concentration; SST1 (SST2): PC1 (PC2) of sea surface temperature; Rec: arrival rate of larval *Notochthamalus scabrosus* ($\log_{10}$ transformed); Cov: adult cover of *N. scabrosus* ($\log_{10}$ transformed); Lat: latitude; Lon: longitude. Star in panel f represents the Estación Costera de Investigaciones Marinas (ECIM) site

due to the correlated allele frequencies model, which tolerates differentiation of closely related populations, but is likely to overestimate *k* (Pritchard et al. 2000). The same trends were observed with the full or the adjusted databases (results not shown).

3.3. Demographic/geographic/environmental–genetic association analysis

Linear regressions showed that CHLA2 alone explained 48 and 61% of the total variance in Ar and Gd, respectively, having a significant positive linear relationship with both genetic diversity indices throughout the study region (Fig. 4). Additionally, Cov explained 33% of the variance of Ar, and SST2 and Lat explained 25 and 30% of the variance of Gd, respectively, but these relationships were not statistically significant (Fig. 4).

Statistical control of covariables using GLM model selection identified the variable CHLA2 as the most significant factor explaining variation in both Ar and Gd (Table 2). The second and third best models include the variables CHLA1 and Cov, which is consistent with results of the model selection based on AIC (Table 3), but the fraction of variance explained by these variables was minor in comparison to chl *a*2 (see Table 2).

Table 2. Results of generalized linear modeling (GLM) analyses employed to identify the best fit model for 5 variables explaining genetic diversity of *Notochthamalus scabrosus*. AIC: Akaike's information criterion; Ar: allelic richness; Gd: gene diversity; CHLA1(CHLA2): PC1 (PC2) of chlorophyll *a* concentration; SST1 (SST2): PC1 (PC2) of sea surface temperature; Cov: adult cover of *N. scabrosus* (log_{10} transformed); Lon: longitude; VarExp: variance explained. Values in **bold** are significant ($p < 0.05$)

Initial full model	Best fit models	p	AIC	Test of effects: Variable	Test of effects: p	VarExp (%)
Ar~CHLA1+CHLA2 +SST1+Cov+Lon	Ar~CHLA2+Cov+Lon	0.568	19.38	CHLA2	**0.044**	48.61
				Cov	0.123	15.39
				Lon	0.436	3.74
	Ar~CHLA2+Cov	**<0.001**	18.47	CHLA2	**0.043**	48.61
				Cov	0.127	15.39
	Ar~CHLA2	**<0.001**	20.03	CHLA2	**0.025**	48.61
Gd~CHLA1+CHLA2 +SST1+Cov+Lon	Gd~CHLA1+CHLA2+Cov	**<0.001**	−57.61	CHLA1	0.125	2.96
				CHLA2	**0.010**	67.80
				Cov	0.369	3.97
	Gd~CHLA1+CHLA2	**<0.001**	−58.15	CHLA1	0.173	2.96
				CHLA2	**0.005**	67.80
	Gd~CHLA2	**<0.001**	−57.31	CHLA2	**0.008**	67.80

Table 3. Results of the stepAIC analyses employed to identify the best fit model for 5 variables explaining genetic diversity of *Notochthamalus scabrosus*. Abbreviations as in Table 2

Initial full model	Best fit model	AIC
Ar~CHLA1+CHLA2 +SST1+Cov+Lon	Ar~CHLA2+Cov	22.69
Gd~CHLA1+CHLA2 +SST1+Cov+Lon	Gd~CHLA1+CHLA2	−54.74

Table 4. Results of multiple regression on distance matrices (MRDM). Abbreviations as in Table 2; values in **bold** are significant ($p < 0.05$)

MRDM full model		Coef	p	R^2	*F*	p
θ_{ST} ~CHLA1+CHLA2 +SST1+SST2 +Rec+Cov+Lon	Int	0.007	0.512	0.55	6.445	**0.008**
	CHLA1	−0.006	0.534			
	CHLA2	−0.001	0.953			
	SST1	−0.041	0.629			
	SST2	0.024	**0.002**			
	Rec	0.004	0.401			
	Cov	−0.000	**0.036**			
	Lon	−0.014	0.084			
D_{EST} ~CHLA1+CHLA2 +SST1+SST2 +Rec+Cov+Lon	Int	0.007	0.508	0.55	6.445	**0.007**
	CHLA1	−0.006	0.527			
	CHLA2	−0.001	0.951			
	SST1	−0.041	0.618			
	SST2	0.024	**0.002**			
	Rec	0.004	0.405			
	Cov	−0.000	**0.035**			
	Lon	0.078	0.078			

A different result was obtained from the MRDM analysis, which showed that the spatial structure (differences among sites) in SST2 and Cov had the strongest effects on genetic differentiation, as measured by θ_{ST} and D_{EST}. The overall model showed significant fit to the data ($p < 0.05$), and explained 55% of the total variance (Table 4).

4. DISCUSSION

The extent of effective dispersal and gene flow between populations in the coastal ocean can be much more complex than previously thought (e.g. Pringle & Wares 2007, Teske et al. 2016). In the present study, we found subtle, yet significant levels of genetic differentiation in the intertidal barnacle *Notochthamalus scabrosus*, a species with high dispersal potential. Main differences occurred between sites located to the north and south of the reported phylogeographic latitudinal break at 30° S.

Our results suggest that population genetic diversity in *N. scabrosus* is influenced by environmental regimes manifested in patterns of temporal variability of surface chl *a* concentration, whereas among-site differences in SST fluctuations and benthic abundance of adults appear to be signifi-

cant drivers of population genetic differentiation over space. More broadly, the presence of sites that are both environmentally and genetically differentiated supports the idea of an ecological restriction to population connectivity, despite the long residence of larvae in the water column.

Larval arrival from the plankton can be responsible for local abundance and genetic variability patterns of benthic populations (Iacchei et al. 2013). We found that the temporal variability in surface chl *a* was the most consistent covariable explaining spatial distribution of *N. scabrosus* genetic diversity. This general result is in line with studies showing that patterns of intraspecific genetic diversity of some mobile marine species are associated with variation in chlorophyll concentration (Gaggiotti et al. 2009, Mendez et al. 2010, Amaral et al. 2012). Variability in coastal chl *a* may be viewed as an integrated indicator of the environmental conditions to which invertebrate larvae and onshore adults are exposed, and likely determines both the feeding conditions (i.e. quantity and quality of food) and the larval transport to/off the shore. During upwelling, high food availability can translate into better larval condition and, at the same time, offshore and alongshore upwelling currents can promote the mixing of the offshore larval pool (Barshis et al. 2011). Then, during upwelling relaxation and downwelling events, this well fed/well mixed larval pool can reach local populations. In this manner, sites with constant strong upwelling have few possibilities of larval arrival due to increased larval waste (Roughgarden et al. 1988, Menge & Menge 2013), while on the other hand, sites with constant weak upwelling have more larval retention, therefore their recruitment comes from a poorly mixed larval pool. Other things being equal or homogeneous, high phytoplankton availability in coastal waters during larval development can therefore lead to higher recruitment (e.g. Olson & Olson 1989, Cushing 1990, Menge 2000) and high larval physiological quality that should improve post-settlement survival (Jarrett & Pechenik 1997, Hentschel & Emlet 2000, Phillips 2002) as well as overall juvenile condition (Bertness et al. 1991, Menge et al. 1997, Sanford & Menge 2001). All of these factors may result in the maintenance of genetic diversity from the larval pool. Thus, variable upwelling will maximize larval condition and genetic diversity and, as predicted by the intermittent upwelling hypothesis (Menge & Menge 2013), increase onshore recruitment. Further genetic studies should therefore intensify sampling of recently settled larvae across more diverse upwelling conditions. Indirect evidence about the effect of upwelling/relaxation dynamics on barnacle recruitment (Navarrete et al. 2005, Lagos et al. 2008) and the significant positive cross-correlations between mean chl *a* concentration and *N. scabrosus* recruitment and adult abundance (Table S3) suggest that it is a possible mechanism to explain the genetic pattern in *N. scabrosus*.

Adult cover was used as a proxy of local abundance of *N. scabrosus*, a factor that in linear regressions explained 33% of total variance in allelic richness (although it was not statistically significant; Fig. 4). From examination of Fig. 4f, it seems clear that the site ECIM deviates largely from an otherwise good positive relationship formed by the other 9 sites. Indeed, removing ECIM from the analysis increases the relationship to $r^2 = 0.57$ ($p = 0.019$). The departure of ECIM from the general pattern illustrates well the complexity of determinants of genetic diversity in natural systems and why such univariate relationships between population size and genetic diversity are rarely found in marine environments (but see McCusker & Bentzen 2010). ECIM has some of the historically highest recruitment rates for *N. scabrosus* in the region (Navarrete et al. 2008), yet it displays one of the lowest levels of genetic diversity (in both Ar and Gd indices, Table S2). Furthermore, only at ECIM did individuals have levels of relatedness significantly larger than expected from HWE (Fig. S2).

ECIM is located within Cartagena Bay, an open bay exposed to the southern swell, but in an 'upwelling shadow' where upwelling advection is largely reduced, apparently leading to high phytoplankton concentration (Wieters et al. 2003) and stronger stratification than other sites (Kaplan et al. 2003, Bonicelli et al. 2014). On other shores of the world, low current velocities and water re-circulation, leading to increased local larval retention (McShane et al. 1988), create distinctive patterns of genetic diversity in local populations (e.g. Dupont et al. 2007, Nicastro et al. 2008, Olivares-Bañuelos et al. 2008). Thus, increased larval retention at ECIM, with comparatively low immigration from other populations, as suggested by numerical circulation models (Aiken et al. 2007, Ospina-Alvarez et al. 2018) and observational studies (Bonicelli et al. 2014), may explain the higher genetic relatedness levels observed at this site. The reduced gains of genetic diversity from other sites (poorly mixed larval pool) may be the cause of reduced allelic richness, further supporting the relevance of connectivity patterns on adult population size and genetic diversity.

In natural populations, a genetic discontinuity along a continuously colonized range can arise as a consequence of an environmental discontinuity, either

through selection against migrants or reduced fitness of interlineage hybrids (Nosil et al. 2005). Both mechanisms involve local adaptation in response to selection imposed by divergent biotic or abiotic conditions (Sanford & Kelly 2011, Pflüger & Balkenhol 2014). Our results support the idea that 'environmental distance,' imposed by among-site differences in SST, is a relevant factor to explain genetic differentiation among *N. scabrosus* populations. Indeed, a similar effect has been observed in mammals (Fullard et al. 2000, Amaral et al. 2012), fishes (Han et al. 2012, Diopere et al. 2018), and intertidal and shallow (<5 m depth) coastal invertebrate species (Banks et al. 2010, Wei et al. 2013). Seawater temperature is also one of the most important factors controlling reproduction, development, and growth of ectothermic invertebrates (Pechenik 1987, O'Connor et al. 2007, Byrne 2011). In the case of *N. scabrosus*, such adaptive divergence could be related to selective sorting of competent larvae and/or to post-settlement processes such as temperature requirements for metamorphosis and initial growth, or desiccation tolerance of recruits. Further studies combining genomic tools with high-resolution dispersal models and local experiments with settlers are necessary to discern among the possible mechanisms of population divergence.

5. CONCLUSION

Population genetic structure of *Notochthamalus scabrosus*, as assessed by neutral markers, is characterized by a sharp genetic discontinuity around 30° S, confirming previous conclusions based on mtCOI (Zakas et al. 2009, Laughlin et al. 2012). A modeling study by Ewers-Saucedo et al. (2016) showed that dispersal alone could not generate such genetic discontinuity, and that differential lineage performance in adjacent but divergent environments must be considered. Our results strongly suggest that the environment is indeed influencing the spatial pattern of genetic diversity in *N. scabrosus*. Two main mechanisms could be hypothesized: temporal variability of the food (variation in phytoplankton abundance) and dispersive (upwelling-associated currents) coastal environments favor recruitment from a well fed/well mixed larval pool and therefore increase the allelic richness of benthic populations; and the ecological divergence in coastal ocean temperature may restrict effective dispersal across the 30° S boundary. Such patterns have not been observed in other barnacles, which are traditionally assumed to have large effective population sizes and large dispersal capacity, both of which could override the effects mentioned above. We interpret these results as suggestive that coastal circulation can limit larval connectivity among some populations, generating incomplete barriers to dispersal, which in turns facilitates effects of isolation by environment. Hence, the results of this work advance our understanding of how environmental seascapes can shape patterns of genetic diversity and population differentiation. In particular, our results highlight the importance of further defining the causal relationships between environmental variables and genetic diversity patterns of wild populations in order to guide future region-wide conservation and management efforts.

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