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

4

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31 **ABSTRACT:** Understanding the multiplicity of processes producing genetic patterns in  
32 natural populations can shed light on the ecology and evolution of species, and help guide  
33 effective management and conservation strategies. Here we investigated the role of  
34 environmental, demographic, and geographic factors in shaping the spatial patterns of  
35 genetic diversity and differentiation of the intertidal barnacle *Notochthamalus scabrosus*  
36 along the central-northern coast of Chile (28–34° S). We analyzed genetic data from 7  
37 microsatellite loci genotyped for 300 individuals sampled from 10 sites and combined this

38 information with 8 site-specific environmental (4), demographic (2), and geographic (2)  
39 variables using least squares linear regressions, generalized linear models, and matrix  
40 regression analyses. We found a strong association between the spatially structured genetic  
41 diversity of *N. scabrosus* and patterns of temporal variability in chlorophyll *a*, and among-  
42 site differences in seawater temperature and adult abundance, which in turn was related to  
43 overall recruitment levels. Our results illustrate that population size, partly driven by  
44 recruitment success, can leave a signal on genetic structure of this highly dispersive marine  
45 species. The significant effect of temperature and chlorophyll *a* stresses that local  
46 adaptation may be key to understanding the spatial genetic structure of our model species.  
47 Hence, the results of this work represent an advance towards understanding the usually  
48 complex causal relationships between environmental variables, gene flow, and genetic  
49 diversity patterns of coastal populations.

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

52

## 1. INTRODUCTION

53 Population genetic diversity is important for a range of ecological and evolutionary  
54 processes. For example, genetic diversity can determine community structure and primary  
55 productivity (Crutsinger et al. 2006). It can be associated with the population growth rate of  
56 species (Hughes et al. 2008), and it allows species to adapt to changing environments and  
57 fosters persistence over evolutionary time scales (Reed & Frankham 2003). Therefore, a  
58 strong scientific understanding of the processes that influence spatial genetic variation,  
59 genetic diversity, and population structure in nature is of paramount importance to  
60 implement efficient conservation and management strategies.

61 In marine systems, an early paradigm assumed that most organisms were highly  
62 dispersive and presented large population sizes, and thus were able to resist genetic  
63 divergence at all but perhaps the largest spatial scales. This overly simplistic view was  
64 gradually replaced by an increased understanding of hydrographic heterogeneity in the  
65 coastal ocean and the advent of molecular genetics, which unveiled many potential causes  
66 for genetic structure and speciation in organisms with large dispersal potential (Hellberg  
67 2009, Selkoe et al. 2016). For example, due to the dependence of genetic diversity on  
68 population effective size (Ellegren & Galtier 2016), demographic changes along the  
69 geographic range of a species can leave a discernible footprint in its spatial genetic makeup.  
70 Also, a realistic oceanic environment, especially when there is strong topographic  
71 modulation, presents ample opportunities for variation and restriction in effective dispersal  
72 distances (Largier 2003, Pringle et al. 2011, Nickols et al. 2015). Geographic distance per  
73 se imposes a distance limitation to gene flow, driving increased genetic differentiation with  
74 increasing distance between populations, a pattern known as isolation by distance (Wright  
75 1943). Besides the limitation imposed by dispersal between distant populations,  
76 phenotype–environment mismatches can impose biological barriers to gene flow (Nosil et  
77 al. 2005), producing an isolation by environment, where populations with greater  
78 environmental dissimilarity exhibit higher levels of genetic differentiation, blurring or  
79 reinforcing patterns generated by geographic distance alone (Wang & Bradburg 2014).

80 High-resolution molecular and environmental data are now routinely used to assess  
81 the influence of landscape-scale environmental characteristics on genetic variation and

82 spatial patterns in natural populations of species. Altogether, the mounting evidence  
83 suggests that considerable genetic structure occurs in marine populations around areas  
84 where environmental oceanographic factors exhibit strong spatial structure or geographic  
85 discontinuity.

86 The central-northern coast of Chile represents an interesting study system to  
87 evaluate the effects of environmental, demographic and geographic factors on genetic  
88 diversity and differentiation of marine organisms. Superimposed on what are smooth  
89 latitudinal trends in mean sea surface temperature (SST) along this highly productive  
90 upwelling ecosystem, there is a marked change in oceanographic regimes that takes place  
91 around 30° S. Such geographic discontinuity entails changes in upwelling-driven coastal  
92 circulation (Hormazabal et al. 2004, Aiken et al. 2011, Aguirre et al. 2014), as well as  
93 prevailing hydrographic conditions, such as SST variability, surface chlorophyll, and  
94 nutrient availability (Navarrete et al. 2005, Tapia et al. 2014). Coincidentally, at this same  
95 latitude, several studies have reported the occurrence of geographic distribution endpoints  
96 of several intertidal and subtidal invertebrate species (Lancellotti & Vasquez 1999, Camus  
97 2001), phylogeographic breaks of several invertebrates and macroalgae (Tellier et al. 2009,  
98 Haye et al. 2014), and large changes in population dynamics and abundance of dominant  
99 rocky shore species that otherwise extend far beyond this region (Broitman et al. 2001,  
100 Navarrete et al. 2005, 2008).

101 The geographic range of the intertidal barnacle *Notochthamalus scabrosus* (Darwin  
102 1854) spans the 30° S transition zone, and its complete larval development to settlement  
103 takes well over 1 mo at the water temperatures typically encountered in central Chile  
104 (Venegas et al. 2000). At the same time, the advective nature of coastal flow along central  
105 Chile (Aiken et al. 2007) sets the stage for a comparatively high potential for larval  
106 dispersal and genetic flow among distant populations of this species, as shown by  
107 biophysical models for other long-distance dispersers in the region (Garavelli et al. 2014).  
108 Moreover, large variation in larval arrival rates and adult cover have been reported for the  
109 central-northern coast, which has been attributed to differences in the temporal regime of  
110 upwelling-favorable winds (Navarrete et al. 2005, Lagos et al. 2008). A phylogenetic break  
111 in the *N. scabrosus* mitochondrial cytochrome oxidase I gene (mtCOI) around 30° S was  
112 reported by Zakas et al. (2009). Although spatially stable, there are significant temporal  
113 changes in gene frequencies near the break (< 30° 55' S), presumably related to source–sink  
114 dynamics and/or low effective population sizes in this zone (Laughlin et al. 2012). Based  
115 on a large-scale circulation model, Ewers-Saucedo et al. (2016) suggested that the genetic  
116 break of *N. scabrosus* around 30° S requires differential performance of mtCOI lineages  
117 along the coast; in other words, it could not be maintained by dispersal limitation alone.  
118 Therefore, the diversity and genetic structure of *N. scabrosus* may respond to multiple  
119 causes, such as phylogeography, demography, geographical isolation, and selection  
120 pressures driven by environmental variation along the coastline.

121 This study takes advantage of the genetic information gathered for *N. scabrosus*,  
122 based on mtCOI, as well as of a long-term database (5–13 yr) of monthly larval arrival  
123 (recruitment) of this species at multiple sites spanning the reported latitudinal break.  
124 Together with surveys of adult abundance and satellite-based information of environmental  
125 (oceanographic) variables for the region (28–34° S), and the development of neutral  
126 microsatellite markers, we assessed the potential influence of nearshore environmental,

127 demographic, and geographic factors on the genetic diversity and population structure  
128 patterns of *N. scabrosus*. Using neutral markers of gene flow allowed us to (1) characterize  
129 patterns of genetic diversity and the spatial genetic structure in *N. scabrosus* and (2)  
130 determine the relative importance of environmental, demographic, and geographic factors  
131 for genetic variation between and within populations of this widely distributed barnacle  
132 species.

## 133 2. MATERIALS AND METHODS

### 134 2.1. Hydrography of the study area

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

143 Within the study area, the main upwelling centers are Punta Talca, Punta Toro,  
144 Curaumilla, Pichilemu, and, to a lesser extent, Los Molles (Silva & Valdenegro 2003,  
145 Wieters et al. 2003, Tapia et al. 2009, 2014). In contrast, the bays of Cartagena, Valparaíso,  
146 and Coquimbo remain relatively protected from upwelling (Kaplan et al. 2003, Vargas et al.  
147 2004, Aiken et al. 2008). Four sampling sites (PTal, LMol, Cura, and Pich) were located in  
148 active upwelling centers, and 4 sites, namely Temb and Guan (Coquimbo Bay), Mont  
149 (Valparaíso Bay), and ECIM (Cartagena Bay), were located in places of weak upwelling.  
150 For the 2 remaining sites (Apol and CBaj), records from *in situ* SST suggest that the  
151 hydrography of Apol may be similar to that of weak upwelling sites, while CBaj seems to  
152 be under the influence of active upwelling (Valdivia et al. 2015).

153 An important geographic discontinuity in upwelling-favorable winds occurs around  
154 30–32° S (Strub et al. 1998, Thomas 1999, Hormazabal et al. 2004, Navarrete et al. 2005).  
155 North of this latitude, equatorward winds are weaker but more persistent throughout the  
156 year, while to the south winds are stronger but temporarily more variable (Hormazabal et  
157 al. 2004, Navarrete et al. 2005). The change in oceanographic regimes determines or  
158 modulates the concentration and temporal variability of surface phytoplankton (Thomas  
159 1999), nutrient regimes (NO<sub>3</sub>) of coastal waters (Tapia et al. 2014), and functional structure  
160 of benthic communities (Broitman et al. 2001, Navarrete et al. 2005, Wieters et al. 2009).

### 161 2.2. Study species

162 *Notochthamalus scabrosus* is distributed along most of the rocky coasts of Ecuador,  
163 Peru, and Chile (Brattström & Johanssen 1983). In the zone occupied by chthamalid  
164 barnacles, *N. scabrosus* inhabits the 3 intertidal elevations, with greater abundance in the  
165 middle and upper intertidal zones (Paine et al. 1985, Shinen & Navarrete 2010). Adults are  
166 sessile filter feeding, hermaphroditic brooders. The life cycle of *N. scabrosus* includes a  
167 pelagic larval stage that lasts about 37 d at 15–18°C, with 6 naupliar stages with  
168 planktotrophic feeding and a cyprid stage competent for settlement (Venegas et al. 2000).

169 Cyprid settlement occurs in pulses of larval arrival to the coast during a few days within the  
170 recruitment period, which is mainly concentrated in spring–summer (Tapia & Navarrete  
171 2010).

### 172 **2.3. Sampling of individuals, DNA extraction, and genotyping of microsatellites**

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

179 Seven microsatellite loci were amplified by polymerase chain reaction (PCR). The  
180 microsatellite development procedure, the conditions under which the PCRs were  
181 performed, and the GenBank accession numbers can be found in Table S1 in the  
182 Supplement at [www.int-res/articles/suppl/m123p456\\_supp.pdf](http://www.int-res/articles/suppl/m123p456_supp.pdf). Alleles were identified by  
183 capillary electrophoresis in an ABI3130 Genetic Analyzer (Applied Biosystems), and the  
184 Excel FLEXIBIN macro (Amos et al. 2007) was used to calibrate the reading and allele  
185 binning of each locus.

### 186 **2.4. Genetic polymorphism**

187 The total number of observed alleles ( $N_a$ ), number of private alleles ( $P_a$ ), and  
188 observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosity were calculated in GENALEX 6.5 (Peakall  
189 & Smouse 2012). Per locus gene diversity ( $G_d$ ) and standardized allelic richness ( $A_r$ ) were  
190 calculated in the FSTAT software version 2.9.3.2 (Goudet 2001). The  $A_r$  index was  
191 calculated using the rarefaction method to avoid bias due to differences in sample size  
192 (Leberg 2002). To evaluate deviations from the Hardy-Weinberg expectations (HWE),  
193 Fisher's exact tests were performed for heterozygote deficits at each site–locus  
194 combination, and  $U$ -score tests for global HWE per site through loci and per locus across  
195 sites (dememorization 10000; 100 batches; 10000 iterations) using the GENEPOP 4.2  
196 software (Rousset 2008). Linkage disequilibrium between all pairs of loci at each site and  
197 between each pair of loci across sites was assessed by Fisher's exact tests implemented in  
198 GENEPOP with this same parameter set. The inbreeding coefficient  $F_{IS}$  by locus and site  
199 was quantified with GENETIX 4.05 (Belkhir et al. 2004), and departures from random  
200 expectations were assessed by 10000 permutations. For all multiple comparisons, the  
201 nominal level of significance of 5% was adjusted using the false discovery rate (FDR;  
202 Benjamini & Hochberg 1995).

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

### 206 **2.5. Population genetic structure**

207 Global and pairwise genetic differentiation was evaluated calculating  $\theta_{ST}$  (Weir &  
208 Cockerham 1984) and  $D_{EST}$  (Jost 2008) indices, in GENALEX 6.5 (Peakall & Smouse  
209 2012) and running 10000 permutations to evaluate their significance. Jost's  $D_{EST}$   
210 outperforms  $G_{ST}$  and its relatives ( $F_{ST}$ ) over a range of sample sizes, including in situations

211 where we have highly variable microsatellite loci with different numbers of alleles (Heller  
212 & Siegismund 2009, Gerlach et al. 2010), but it is recommended to compare results  
213 between differentiation indices (Leng & Zhang 2011). In all multiple comparisons, sites  
214 were used as population units, and the nominal level of significance, 5%, was adjusted  
215 using FDR. To identify population relationships in a 2-dimensional space, principal  
216 coordinate analyses (PCoAs) of the sites were computed and graphed in GENALEX 6.5  
217 using the  $\theta_{ST}$  and  $D_{EST}$  differentiation indices.

218 As null alleles can impose error in differentiation estimates (Pompanon et al. 2005),  
219 2 approximations were conducted. First, using MICROCHECKER, we obtained a new  
220 database corrected for null alleles. MICROCHECKER adjusts the number of homozygote  
221 genotypes to reflect the estimated frequency of null alleles and the likely number of  
222 homozygotes given the adjusted allele frequencies and assuming random mating. We then  
223 repeated the previous differentiation analysis using the database adjusted by the frequency  
224 of null alleles. Second, pairwise  $F_{ST}$  with and without the null allele correction was  
225 estimated using the expectation-maximization (EM) algorithm (Dempster et al. 1977) with  
226 ENA correction to give an accurate estimate of  $F_{ST}$  in the presence of null alleles using  
227 FREENA (Chapuis & Estoup 2007). The uncorrected and corrected pairwise  $F_{ST}$  were then  
228 compared by means of a paired  $t$ -test.

229 To estimate the number of genetically differentiated groups, Bayesian-based  
230 clustering was used as implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000).  
231 STRUCTURE was run using the admixture model, the assumption of correlated allelic  
232 frequencies between clusters, with and without the recessive alleles option that accounts for  
233 the null alleles (Falush et al. 2003, 2007), and considering sampling site information  
234 (Hubisz et al. 2009). From Zakas et al. (2009) and Laughlin et al. (2012), we know that  $k =$   
235 1 can be rejected, so all runs were made for  $k$  values between 2 and 10. Ten independent  
236 runs with 500000 Markov chain Monte Carlo replicates and a burn-in length of 50000 were  
237 used for each value of  $k$ . In order to select the  $k$  value that best captures the structure of the  
238 data, the statistic  $\Delta k$ , a measure of the second-order rate of change in the likelihood of  $k$   
239 (Evanno et al. 2005) was implemented in STRUCTURE HARVESTER (Earl & vonHoldt  
240 2012), and the values of  $\Delta k$  as a function of  $k$  were plotted. In CLUMPP 1.1 (Jakobsson &  
241 Rosenberg 2007), we merged the results of the 10 runs for each value of  $k$ , and DISTRICT  
242 1.1 (Rosenberg 2004) was used to graphically visualize the results.

## 243 **2.6. Demographic variables**

### 244 **2.6.1. Recruitment rates**

245 At each site, an estimate of arrival rates of larval *N. scabrosus* was obtained by  
246 quantifying recruitment onto  $10 \times 10$  cm Plexiglas plates covered with SafetyWalk<sup>TM</sup> (3M),  
247 an anti-slip surface that provides a heterogeneous substrate for larvae settlement and  
248 ensures homogeneity of conditions across plates and sites (Menge 2000). Five replicate  
249 collectors were fastened to the rocky substrate with stainless-steel bolts in the mid-upper  
250 intertidal zones of rocky platforms exposed to swell. Replicate collectors were replaced  
251 monthly, and recruitment rates were standardized to the number of ind. collector<sup>-1</sup> d<sup>-1</sup>. The  
252 monthly recruitment rates were then averaged to obtain the annual recruitment rates, and  
253 these in turn were averaged over the years to estimate the per site recruitment rate. At 8 of  
254 the 10 study sites, the collectors were initially deployed in late 1999 or early 2000, whereas

255 at the 2 northernmost sites (CBaj and Apol), recruitment surveys began in mid-2009. The  
256 recruitment time series used here covered the period up to December 2013 for all sites.

### 257 2.6.2. Adult cover (abundance)

258 At each site, the benthic abundance of *N. scabrosus* was estimated using 7 to 10  
259 quadrats of 0.25 m<sup>2</sup>, located along ca. 20–30 m alongshore transects. Transects were  
260 repeated at 3 intertidal elevations (low, mid-, and high intertidal zones) of the same rocky  
261 platforms where we deployed larval collectors. The 50 × 50 cm quadrat frame was divided  
262 into 25 equal squares with monofilament line, which was used to visually estimate adult  
263 abundance of *N. scabrosus* as percentage cover. Cover surveys were conducted  
264 approximately every 6 mo. For more details about the field methods, see Broitman et al.  
265 (2011).

## 266 2.7. Environmental and geographic variables

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

## 286 2.8. Environmental/demographic/geographic–genetic association analysis

287 Three complementary approaches, i.e. simple linear regressions, multi model  
288 selection, and matrix regression, were employed to test for associations among  
289 environmental, demographic, and geographic factors with the spatially structured genetic  
290 diversity of *N. scabrosus*. The linear regressions and model selection analyses used location  
291 (site)-specific data to evaluate the influence of our explicative variables on genetic diversity  
292 across sampling sites. The matrix regression analyses used the explicative variables as a  
293 proxy of ‘seascape resistance’ (McRae 2006) to evaluate their effects on among-site genetic  
294 differentiation. Our 8 predictive variables were the PC1 and PC2 of chl *a* and SST  
295 (hereafter CHLA1, CHLA2, SST1, and SST2), long-term averages of recruitment rates  
296 (Rec) and adult cover (Cov), and geographic location (Lat and Lon). The variables Rec and  
297 Cov were log<sub>10</sub> transformed before analyses to approximate normal distributions.

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

316 As an alternative way to obtain the best subset of explicative variables, we  
317 performed stepwise selection (both forward and backward) using the stepAIC function  
318 from the ‘mass’ package in R. This function uses the exact Akaike’s information criterion  
319 (AIC) as the model selection criterion. Third, we used multiple regressions on distance  
320 matrices (MRDM; Manly 1986, Legendre et al. 1994) to estimate the independent effects of  
321 explicative variables on *N. scabrosus* among-site genetic differentiation. Briefly, partial  
322 regression slopes were estimated using standard multiple linear regression, but the  
323 significance of each term was determined by randomly permuting the explanatory variables  
324 one at a time while keeping the others constant (Wang 2013). This analysis was  
325 implemented using the ‘ecodist’ package (Goslee & Urban 2007) in R, and significance  
326 was based on 10000 permutations using the genetic distance matrices ( $\theta_{ST}$  and  $D_{EST}$ ) as  
327 response variables. Each of 8 matrices representing environmental, demographic, and  
328 geographic differences among sites were used as the predictor variables. Data were  
329 converted into matrices of pairwise distances calculating the absolute differences from site-  
330 specific values of each variable following Amaral et al. (2012). Due to its high VIF value  
331 (>10), the geographical variable Lat was removed, so a subset of 7 predictor variables was  
332 retained for the subsequent analysis.

### 333 3. RESULTS

#### 334 3.1. Genetic polymorphism

335 The 7 microsatellite loci reached a total of 158 alleles in the 300 individuals of  
336 *Notochthamalus scabrosus* genotyped, which ranged from 79 in CBaj to 95 in Temb. In  
337 addition, we found 27 private alleles, with the highest number observed at Apol (Pa = 6). In  
338 contrast, Pich shared all of its alleles with most other sites. The Ar ranged from 11.0 in  
339 CBaj to 13.2 in Temb (mean Ar =  $12.01 \pm 0.72$ ), while Gd ranged from 0.77 in ECIM to  
340 0.83 in Apol (mean Gd =  $0.81 \pm 0.02$ ). Both Ar and Gd indices showed a peak at Guan,

341 Temb and Apol (located around Coquimbo Bay), while the lowest values were found at  
342 CBaj and ECIM for Ar, and at ECIM and Mont for Gd (Table S2).

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

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

### 354 3.2. Population genetic structure

355 *N. scabrosus* showed statistically significant global genetic structure ( $\theta_{ST} = 0.013$ ,  $p$   
356  $< 0.001$ ;  $D_{EST} = 0.040$ ,  $p < 0.001$ ). Pairwise  $\theta_{ST}$  and  $D_{EST}$  were significant for 27 and 21 of  
357 the 45 comparisons at the nominal level ( $\alpha = 0.05$ ), of which 22 and 15 remained  
358 significant after corrections for multiple tests, respectively (Table 1). Significant pairwise  
359 comparisons were mostly between sites north of PTal versus sites south of LMol, and the  
360 sites with lowest and highest levels of differentiation were Guan vs. PTal (separated by  
361 50.26 km) and Temb vs. Cura (separated by 419.88 km), respectively. CBaj had the highest  
362 number of significant pairwise comparisons for both  $\theta_{ST}$  and  $D_{EST}$  ( $n = 9$  and 8,  
363 respectively) followed by LMol ( $n = 7$  and 6, respectively; Table 1). The first 2 coordinates  
364 of PCoAs with  $\theta_{ST}$  and  $D_{EST}$  values explained 87.62 and 87.88% of total variation,  
365 respectively, and revealed similar structuring of sites (Fig. 2). The first axis of the PCoAs  
366 separated 2 principal groups, one composed of sites from LMol to the south, the other with  
367 the 3 northern sites (Temb, Apol, and CBaj), whilst Guan and PTal were between these 2  
368 groups. Weak separation of sites within these regions was detected along the second PCoA  
369 axis, with Temb separated from Apol and CBaj, and LMol and Cura from Mont, ECIM,  
370 and Pich (Fig. 2).

371 Null alleles had some effect on our results: (1) the ENA method gave slightly, but  
372 significantly, lower  $F_{ST}$  values (average  $F_{ST}$  with ENA = 0.00815, SD = 0.00693) than  
373 those obtained without correction for the presence of null alleles (average  $F_{ST}$  without ENA  
374 = 0.00951, SD = 0.00847; paired  $t = 3.74$ ,  $p < 0.001$ ); (2) global structure was lower but  
375 still significant with the adjusted database ( $\theta_{ST} = 0.012$ ,  $p < 0.001$ ;  $D_{EST} = 0.018$ ,  $p =$   
376 0.001); and (3) there were fewer significant pairwise comparisons after FDR corrections for  
377  $D_{EST}$  (only 1 significant comparison) and  $\theta_{ST}$  (15 of 22 comparisons still significant).  
378 However, the main pattern of differentiation between sites north and south of PTal–LMol  
379 persisted with the adjusted database, as well as the most and least differentiated pairwise  
380 comparisons (Table 1).

381 The cluster analysis performed using STRUCTURE confirmed the existence of 2  
382 clusters, one south of LMol and the other north of PTal (Fig. 3). For  $k = 3$ , a new cluster  
383 included CBaj, the northernmost site. According to Evanno’s criteria,  $k = 4$  was the most  
384 likely number of clusters (Fig. S1). However, no clear spatial pattern could be recovered

385 from the assignment of individuals into these 4 clusters. This may be due to the correlated  
386 allele frequencies model, which tolerates differentiation of closely related populations, but  
387 is likely to overestimate  $k$  (Pritchard et al. 2000). The same trends were observed with the  
388 full or the adjusted databases (results not shown).

### 389 **3.3. Demographic/geographic/environmental–genetic association analysis**

390 Linear regressions showed that CHLA2 alone explained 48 and 61% of the total  
391 variance in Ar and Gd, respectively, having a significant positive linear relationship with  
392 both genetic diversity indices throughout the study region (Fig. 4). Additionally, Cov  
393 explained 33% of the variance of Ar, and SST2 and Lat explained 25 and 30% of the  
394 variance of Gd, respectively, but these relationships were not statistically significant (Fig.  
395 4).

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

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

## 405 **4. DISCUSSION**

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

412 Our results suggest that population genetic diversity in *N. scabrosus* is influenced  
413 by environmental regimes manifested in patterns of temporal variability of surface chl *a*  
414 concentration, whereas among-site differences in SST fluctuations and benthic abundance  
415 of adults appear to be significant drivers of population genetic differentiation over space.  
416 More broadly, the presence of sites that are both environmentally and genetically  
417 differentiated supports the idea of an ecological restriction to population connectivity,  
418 despite the long residence of larvae in the water column.

419 Larval arrival from the plankton can be responsible for local abundance and genetic  
420 variability patterns of benthic populations (Iacchei et al. 2013). We found that the temporal  
421 variability in surface chl *a* was the most consistent covariable explaining spatial distribution  
422 of *N. scabrosus* genetic diversity. This general result is in line with studies showing that  
423 patterns of intraspecific genetic diversity of some mobile marine species are associated with  
424 variation in chlorophyll concentration (Gaggiotti et al. 2009, Mendez et al. 2010, Amaral et  
425 al. 2012). Variability in coastal chl *a* may be viewed as an integrated indicator of the  
426 environmental conditions to which invertebrate larvae and onshore adults are exposed, and

427 likely determines both the feeding conditions (i.e. quantity and quality of food) and the  
428 larval transport to/off the shore. During upwelling, high food availability can translate into  
429 better larval condition and, at the same time, offshore and alongshore upwelling currents  
430 can promote the mixing of the offshore larval pool (Barshis et al. 2011). Then, during  
431 upwelling relaxation and downwelling events, this well fed/well mixed larval pool can  
432 reach local populations. In this manner, sites with constant strong upwelling have few  
433 possibilities of larval arrival due to increased larval waste (Roughgarden et al. 1988, Menge  
434 & Menge 2013), while on the other hand, sites with constant weak upwelling have more  
435 larval retention, therefore their recruitment comes from a poorly mixed larval pool. Other  
436 things being equal or homogeneous, high phytoplankton availability in coastal waters  
437 during larval development can therefore lead to higher recruitment (e.g. Olson & Olson  
438 1989, Cushing 1990, Menge 2000) and high larval physiological quality that should  
439 improve post-settlement survival (Jarrett & Pechenik 1997, Hentschel & Emlet 2000,  
440 Phillips 2002) as well as overall juvenile condition (Bertness et al. 1991, Menge et al. 1997,  
441 Sanford & Menge 2001). All of these factors may result in the maintenance of genetic  
442 diversity from the larval pool. Thus, variable upwelling will maximize larval condition and  
443 genetic diversity and, as predicted by the intermittent upwelling hypothesis (Menge &  
444 Menge 2013), increase onshore recruitment. Further genetic studies should therefore  
445 intensify sampling of recently settled larvae across more diverse upwelling conditions.  
446 Indirect evidence about the effect of upwelling/relaxation dynamics on barnacle recruitment  
447 (Navarrete et al. 2005, Lagos et al. 2008) and the significant positive cross-correlations  
448 between mean chl *a* concentration and *N. scabrosus* recruitment and adult abundance  
449 (Table S3) suggest that it is a possible mechanism to explain the genetic pattern in *N.*  
450 *scabrosus*.

451 Adult cover was used as a proxy of local abundance of *N. scabrosus*, a factor that in  
452 linear regressions explained 33% of total variance in allelic richness (although it was not  
453 statistically significant, Fig. 4). From examination of Fig. 4f, it seems clear that the site  
454 ECIM deviates largely from an otherwise good positive relationship formed by the other 9  
455 sites. Indeed, removing ECIM from the analysis increases the relationship to  $r^2 = 0.57$  ( $p =$   
456  $0.019$ ). The departure of ECIM from the general pattern illustrates well the complexity of  
457 determinants of genetic diversity in natural systems and why such univariate relationships  
458 between population size and genetic diversity are rarely found in marine environments (but  
459 see McCusker & Bentzen 2010). ECIM has some of the historically highest recruitment  
460 rates for *N. scabrosus* in the region (Navarrete et al. 2008), yet it displays one of the lowest  
461 levels of genetic diversity (in both Ar and Gd indices, Table S2). Furthermore, only at  
462 ECIM did individuals have levels of relatedness significantly larger than expected from  
463 HWE (Fig. S2).

464 ECIM is located within Cartagena Bay, an open bay exposed to the southern swell,  
465 but in an 'upwelling shadow' where upwelling advection is largely reduced, apparently  
466 leading to high phytoplankton concentration (Wieters et al. 2003) and stronger stratification  
467 than other sites (Kaplan et al. 2003, Bonicelli et al. 2014). On other shores of the world,  
468 low current velocities and water re-circulation, leading to increased local larval retention  
469 (McShane et al. 1988), create distinctive patterns of genetic diversity in local populations  
470 (e.g. Dupont et al. 2007, Nicastro et al. 2008, Olivares-Bañuelos et al. 2008). Thus,  
471 increased larval retention at ECIM, with comparatively low immigration from other  
472 populations, as suggested by numerical circulation models (Aiken et al. 2007, Ospina-

473 Alvarez et al. 2018) and observational studies (Bonicelli et al. 2014), may explain the  
474 higher genetic relatedness levels observed at this site. The reduced gains of genetic  
475 diversity from other sites (poorly mixed larval pool) may be the cause of reduced allelic  
476 richness, further supporting the relevance of connectivity patterns on adult population size  
477 and genetic diversity.

478 In natural populations, a genetic discontinuity along a continuously colonized range  
479 can arise as a consequence of an environmental discontinuity, either through selection  
480 against migrants or reduced fitness of interlineage hybrids (Nosil et al. 2005). Both  
481 mechanisms involve local adaptation in response to selection imposed by divergent biotic  
482 or abiotic conditions (Sanford & Kelly 2011, Pflüger & Balkenhol 2014). Our results  
483 support the idea that ‘environmental distance,’ imposed by among-site differences in SST,  
484 is a relevant factor to explain genetic differentiation among *N. scabrosus* populations.  
485 Indeed, a similar effect has been observed in mammals (Fullard et al. 2000, Amaral et al.  
486 2012), fishes (Han et al. 2012, Diopere et al. 2018), and intertidal and shallow (<5 m depth)  
487 coastal invertebrate species (Banks et al. 2010, Wei et al. 2013). Seawater temperature is  
488 also one of the most important factors controlling reproduction, development, and growth  
489 of ectothermic invertebrates (Pechenik 1987, O’Connor et al. 2007, Byrne 2011). In the  
490 case of *N. scabrosus*, such adaptive divergence could be related to selective sorting of  
491 competent larvae and/or to post-settlement processes such as temperature requirements for  
492 metamorphosis and initial growth, or desiccation tolerance of recruits. Further studies  
493 combining genomic tools with high-resolution dispersal models and local experiments with  
494 settlers are necessary to discern among the possible mechanisms of population divergence.

495

## 5. CONCLUSION

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

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861 *Ser* 394:165–177 doi:10.3354/meps08265

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

A	CBaj	Apol	Temb	Guan	PTal	LMol	Mont	Cura	ECIM	Pich
CBaj	–	0.007	<b>0.013</b>	<b>0.011</b>	<b>0.009</b>	<b>0.022</b>	<b>0.025</b>	<b>0.023</b>	<b>0.023</b>	<b>0.020</b>
Apol	0.039	–	0.005	0.001	0.005	<b>0.016</b>	<b>0.021</b>	<b>0.019</b>	<b>0.017</b>	<b>0.012</b>
Temb	<b>0.065</b>	0.028	–	0.000	0.004	<b>0.020</b>	<b>0.009</b>	<b>0.027</b>	<b>0.015</b>	0.000
Guan	<b>0.053</b>	0.009	0.004	–	–0.005	<b>0.010</b>	0.005	0.008	<b>0.008</b>	0.004
PTal	0.043	0.031	0.023	–0.024	–	0.008	0.007	0.007	0.005	–0.001
LMol	<b>0.099</b>	<b>0.079</b>	<b>0.091</b>	0.043	0.031	–	<b>0.009</b>	0.002	<b>0.009</b>	0.005
Mont	<b>0.105</b>	<b>0.095</b>	0.038	0.020	0.024	0.036	–	0.004	–0.004	–0.002
Cura	<b>0.103</b>	<b>0.091</b>	<b>0.126</b>	0.030	0.023	0.009	0.017	–	0.003	<b>0.009</b>
ECIM	<b>0.090</b>	<b>0.071</b>	<b>0.059</b>	0.027	0.012	0.035	–0.013	0.015	–	–0.002
Pich	<b>0.086</b>	<b>0.057</b>	0.001	0.015	–0.004	0.024	–0.008	0.038	–0.005	–

870

B	CBaj	Apol	Temb	Guan	PTal	LMol	Mont	Cura	ECIM	Pich
CBaj	–	0.004	<b>0.010</b>	0.006	0.011	<b>0.016</b>	<b>0.020</b>	<b>0.023</b>	<b>0.018</b>	<b>0.019</b>
Apol	0.013	–	0.007	0.001	0.004	0.008	<b>0.015</b>	<b>0.013</b>	<b>0.012</b>	<b>0.010</b>
Temb	0.037	0.013	–	0.003	0.009	<b>0.013</b>	0.005	<b>0.024</b>	0.008	0.001
Guan	0.027	–0.009	–0.012	–	0.007	0.008	0.007	0.008	<b>0.010</b>	0.007
PTal	0.010	–0.002	–0.008	–0.045	–	0.011	<b>0.016</b>	<b>0.015</b>	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	<b>0.039</b>	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	–

871

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

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

878

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

stepAIC test		
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

882

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

MRDM full model		Coef	p	R <sup>2</sup>	F	p
$\theta_{ST} \sim$ CHLA1+CHLA2+SST1+SST2	Int	0.007	0.512	0.55	6.445	<b>0.008</b>
+Rec+Cov+Lon	CHLA1	-0.006	0.534			
	CHLA2	-0.001	0.953			
	SST1	-0.041	0.629			
	SST2	0.024	<b>0.002</b>			

	Rec	0.004	0.401			
	Cov	-0.000	<b>0.036</b>			
	Lon	-0.014	0.084			
<hr/>						
	$D_{EST} \sim$					
CHLA1+CHLA2+SST1+SST2	Int	0.007	0.508	0.55	6.445	<b>0.007</b>
+Rec+Cov+Lon	CHLA1	-0.006	0.527			
	CHLA2	-0.001	0.951			
	SST1	-0.041	0.618			
	SST2	0.024	<b>0.002</b>			
	Rec	0.004	0.405			
	Cov	-0.000	<b>0.035</b>			
	Lon	0.078	0.078			

885

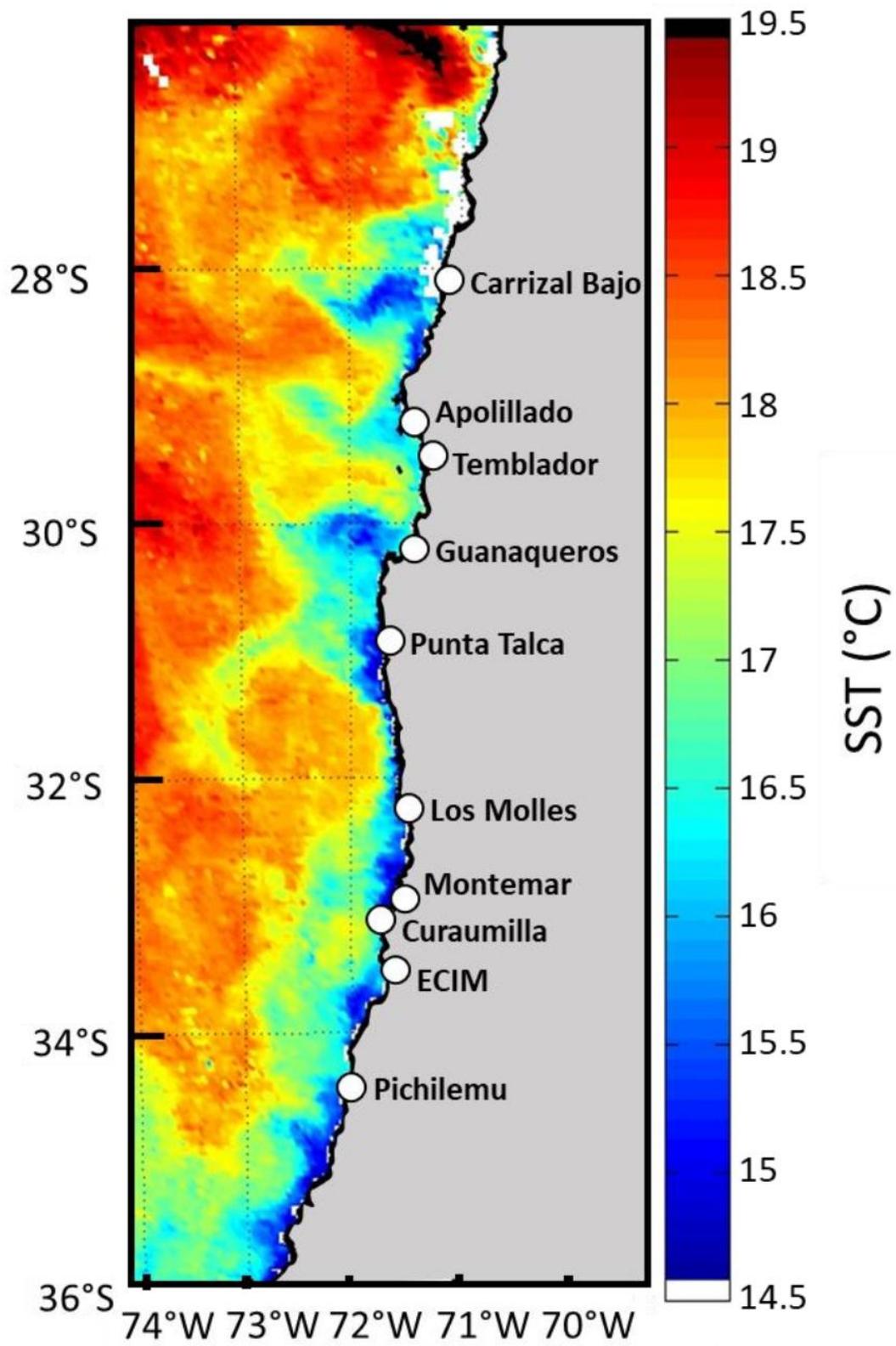
886 Fig. 1. Central-northern coast of Chile, showing the 10 sampling sites and weekly averages  
887 of sea surface temperature (SST) for nearshore areas. ECIM: Estación Costera de  
888 Investigaciones Marinas

889 Fig. 2. Principal coordinates analysis calculated by  $\theta_{ST}$  (top) and  $D_{EST}$  (bottom) values of 10  
890 sites studied. For  $\theta_{ST}$  and  $D_{EST}$  indices, the first 2 axes explain 87.62 and 87.88% of the  
891 total variation, respectively. Site abbreviations as in **Table 1**

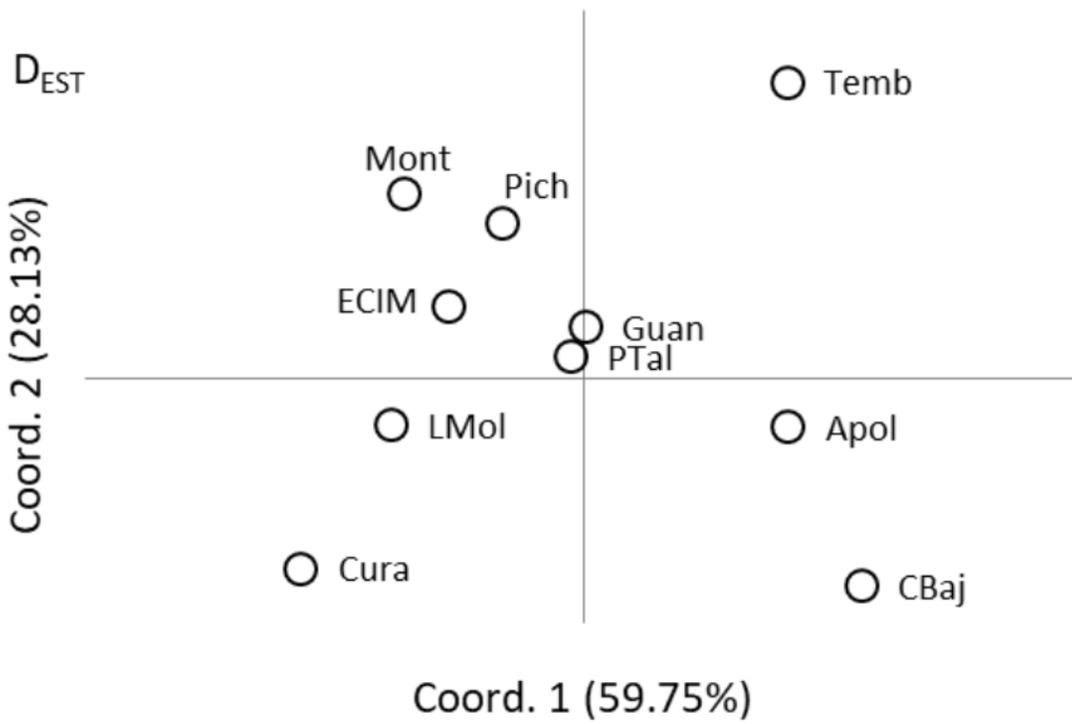
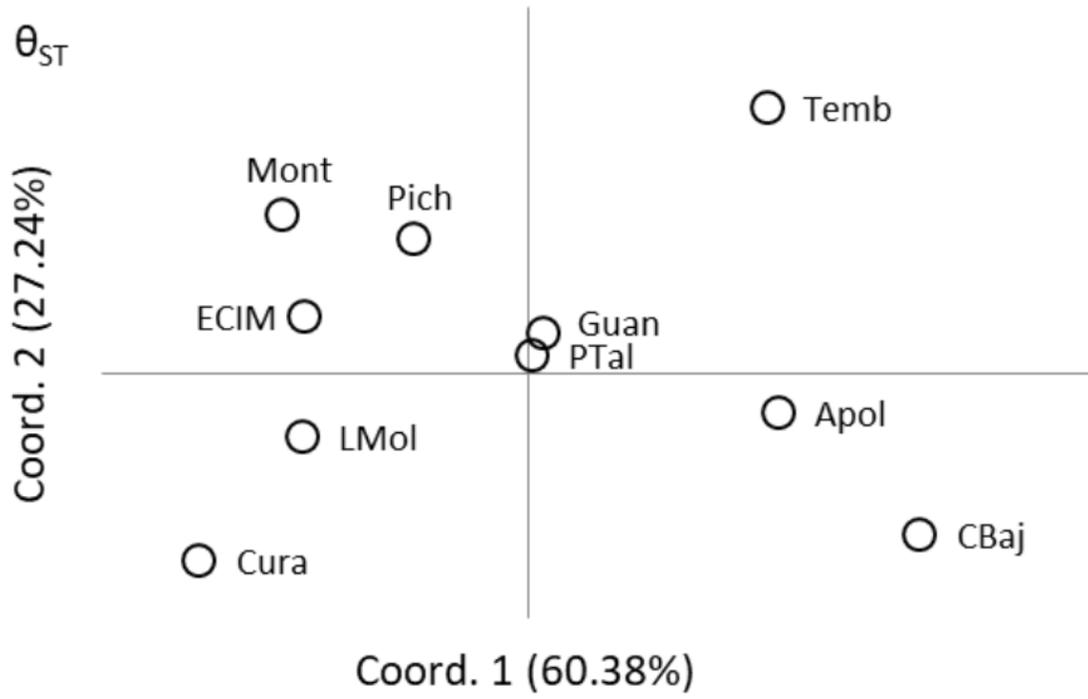
892 Fig. 3. STRUCTURE assignment of individual *Notochthamalus scabrosus* across all sites  
893 into clusters for  $k$  between 2 and 4. Colors indicate percentage contribution of individuals  
894 to assigned clusters (y-axis), individuals are represented by each line (x-axis); black lines  
895 separate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

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

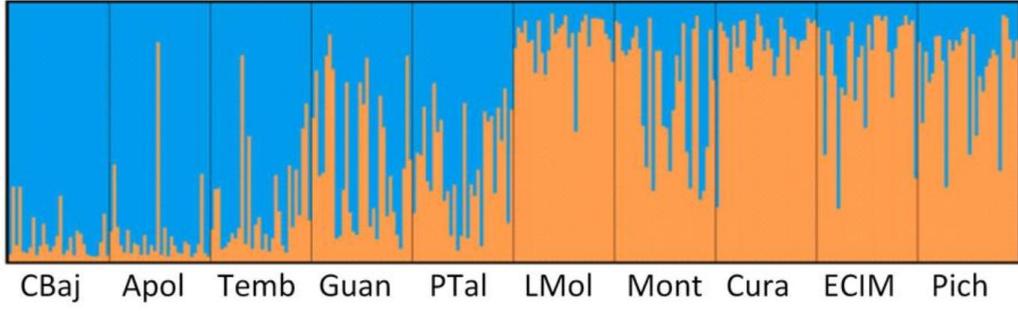
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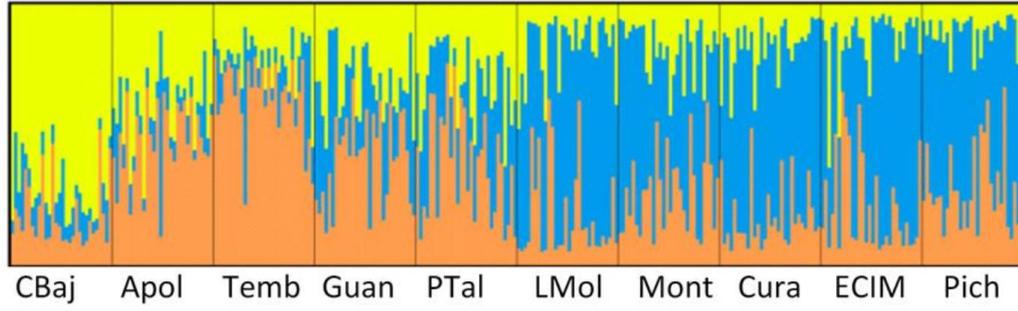
903  
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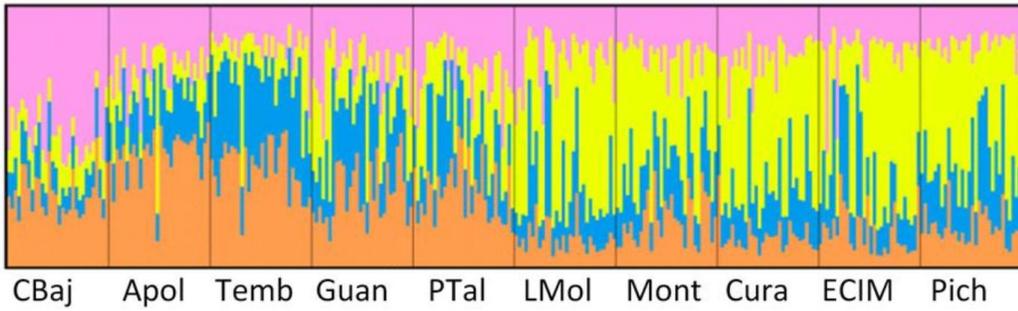
$k = 2$



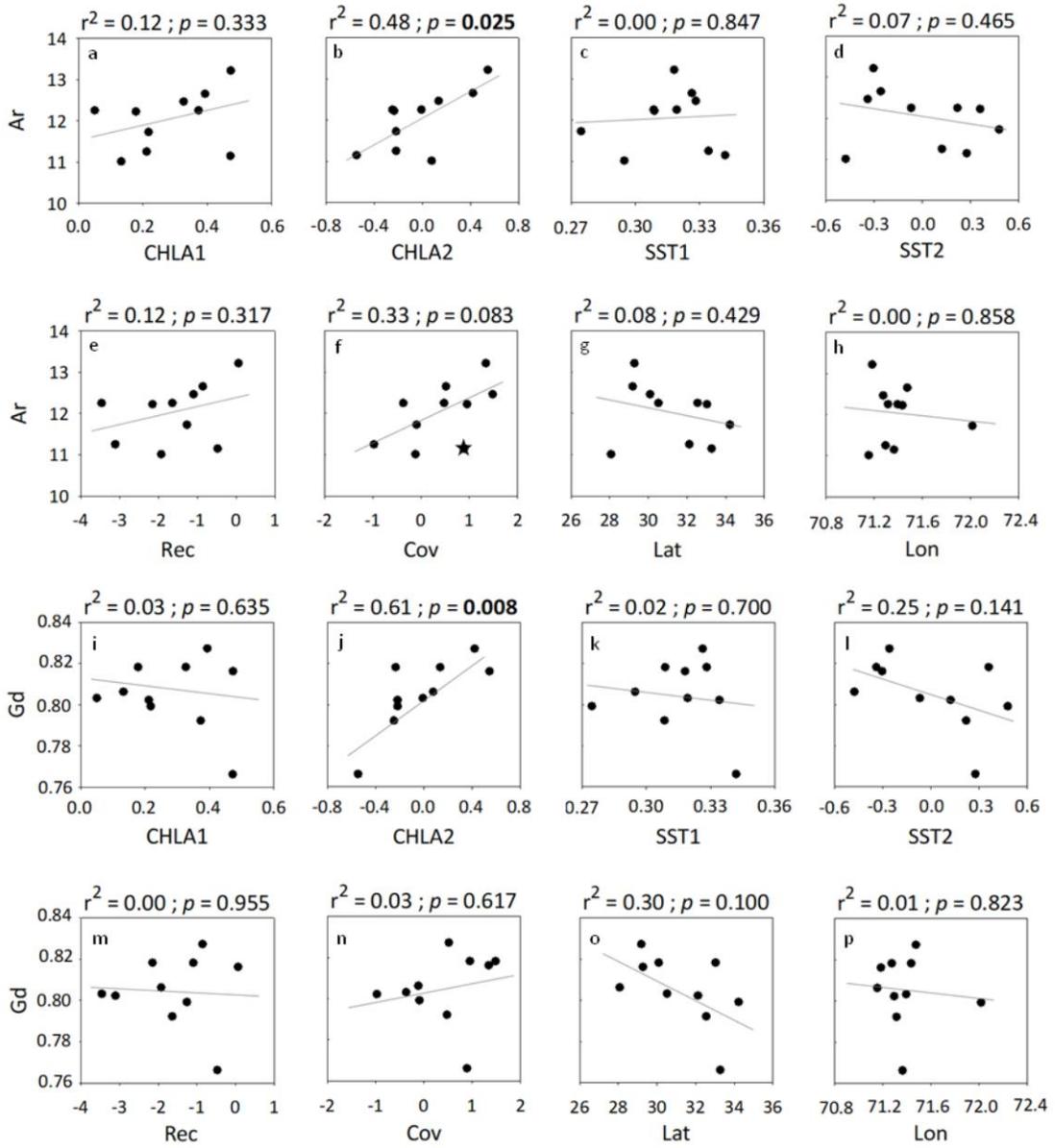
$k = 3$



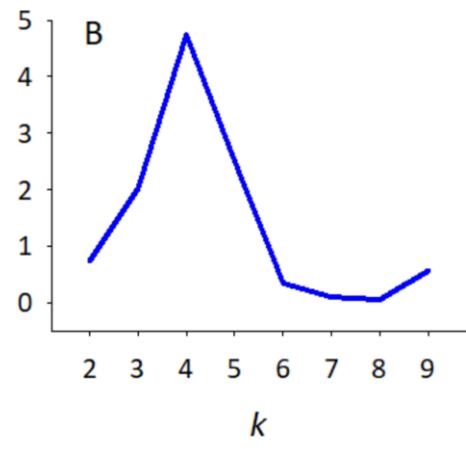
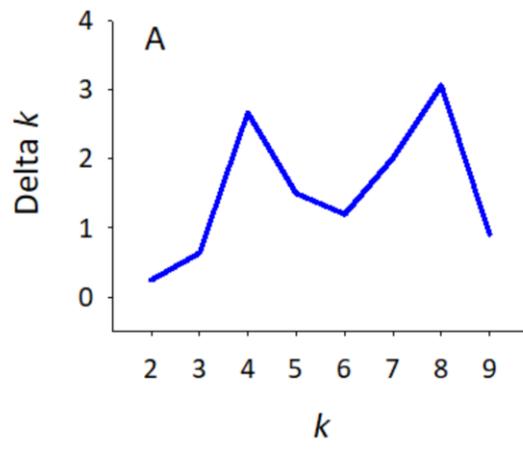
$k = 4$



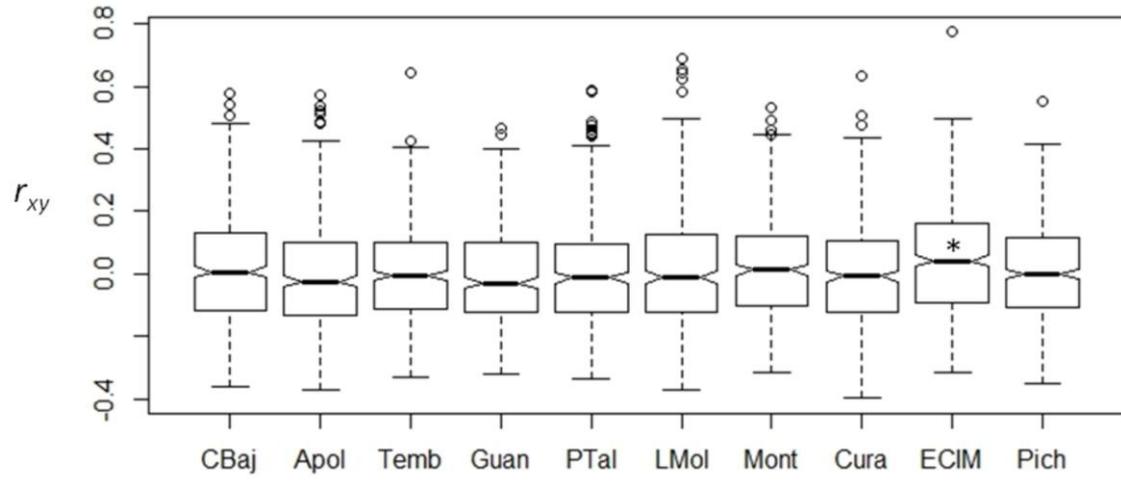
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912 Figure S1  
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915 Figure S2