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Testing the abundant-centre hypothesis using intertidal porcelain crabs along the Chilean coast: linking abundance and life-history variation

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ABSTRACT

Aim The abundant-centre hypothesis (ACH) is based on the assumption that physiological constraints limit populations at the edges of their distributional range, yet the geographical variation of physiological performance or life-history traits has rarely been examined. Here we examine the applicability of the ACH in a marine system by testing whether physiological predictions are reflected in large-scale variations of life-history traits.

Location The Chilean coast (18°–42° S), encompassing more than 2500 km along the Pacific coast of South America.

Methods Five porcelain crab species (*Petrolisthes granulosus*, *Petrolisthes laevigatus*, *Petrolisthes tuberculatus*, *Petrolisthes violaceus* and *Allopetrolisthes angulosus*) were sampled on intertidal boulder beaches at 13 sampling sites. For each species and site we evaluated: (1) relative abundance (density), (2) maximum size, (3) size at maturity, (4) sex ratio, (5) proportion of ovigerous females, and (6) presence of recruits. The shape of the spatial distribution of each trait was evaluated statistically against the prediction of four hypothetical models (normal, ramped-south, ramped-north and abundant-edge).

Results The relative abundance and life-history traits showed different spatial patterns among species. Relative abundance (across sites) was fitted by a normal model in only two species. No model fitted the spatial variation in body size and size at first maturity, which showed a slight but monotonic poleward increase in all species. Sex ratio showed a prominent hump-shaped pattern, with females prevailing in the centre of the ranges and males dominating towards the range boundaries; this pattern was statistically significant in three of the five studied species. The proportion of ovigerous females showed no clear latitudinal trends, and mature individuals were observed across most of the geographical range of the species. However, recruits tended to be absent towards the southern (poleward) boundaries of the distribution.

Main conclusions The ACH does not apply to all species equally. The link between abundance and life-history traits is complex and variable among the porcelain crab species studied. Overall, the observed patterns were consistent with the idea that equatorward boundaries might be controlled by physiological restrictions mainly affecting adult survival, whereas poleward boundaries might be shaped by limitations in reproductive output and larval survival. Our results underline the importance of incorporating ecological, physiological and life-history studies in future tests of the ACH.

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INTRODUCTION

The abundant-centre hypothesis (ACH) is based on Brown's principle (Brown, 1984), which predicts that the abundance of a species should be highest at the centre of its geographic range and decline towards the edges (Brown, 1984; Brown et al., 1995; Enquist et al., 1995). This principle is an extension of Hutchinson's niche concept (Hutchinson, 1957), and assumes that living conditions are optimal at the centre of the range, and that local abundance is a reflection of the individual-level success (Brown, 1984; Gilman, 2005). However, recent reviews have shown that many species do not follow Brown's principle and that the abundance pattern of different species varies across their geographic ranges (Sagarin & Gaines, 2002a; Gaston, 2003; Sagarin et al., 2006).

Because the study of geographic patterns of abundance variation offers little insight into the underlying processes that shape the population distribution and range boundaries, several authors have proposed a more integrated framework to study the ACH, including life-history traits, proxies for physiological conditions, biophysical variables, and genetic structure (Caughley et al., 1988; Gilman, 2006a,b; Sagarin et al., 2006; Lester et al., 2007). The factors shaping the abundance distribution and range boundaries should be reflected in the geographic variation of life-history proxies. For instance, low abundances at poleward boundaries often seem to result from recruitment limitation, which can be related to the reduced reproductive capabilities of adults (i.e. prolonged incubation times and short reproductive seasons) and/or the low survival of larvae and juveniles towards the edge (Zacherl et al., 2003; Gilman, 2006a,b; Sanford et al., 2006). In contrast, equatorward boundaries of intertidal organisms are often related to the thermal limitations of adults (Stillman & Somero, 2000; Stillman, 2002; Sorte & Hofmann, 2004; Compton et al., 2007), which may be linked to a number of physiological and life-history traits (Osovitz & Hofmann, 2007), including reduced body sizes (Hummel et al., 2000). Geographic patterns of variation in abundance may also be size-dependent (Wenner, 1972) or differ between sexes, producing a latitudinal gradient in sex ratios (Defeo & Cardoso, 2002).

The Chilean coast offers an excellent model system with which to test these predictions because it has a predominant north–south orientation, which simplifies the biogeographic questions to one dimension (Rivadeneira & Fernandez, 2005). Gradual changes in various oceanographic and climatic conditions are observed along the Chilean coast, which affect intertidal populations (Strub et al., 1998; Fernández et al., 2000; Camus, 2001; Thiel et al., 2007). For instance, upwelling is more persistent throughout the year in northern Chile, but highly seasonal in southern Chile (Montecino et al., 2005). Similarly, sea surface temperature decreases from about 20 °C in northern Chile to < 10 °C in southern Chile (e.g. Hinojosa et al., 2006), possibly causing latitudinal variations in the life-history traits of coastal organisms.

Herein we used five closely related species of porcelain crabs (Anomura: Porcellanidae), which have wide distributional ranges extending over > 20 latitudinal degrees along the Southeast Pacific coast. Porcelain crabs are ideally suited to testing the ACH and the underlying assumptions, because they are very common components on intertidal boulder beaches along the Chilean coast (Castilla & Paine, 1987). In spite of intense human harvesting in coastal ecosystems of Chile (Castilla, 1999; Moreno, 2001), these species are not extracted by coastal gatherers, thus minimizing the effects of human activities on the observed geographic patterns (Sagarin et al., 2006).

Although some information on the intertidal zonation patterns (Viviani, 1969; Emparanza, 2007) and reproductive biology (Antezana et al., 1965; Lardies & Wehrtmann, 1996; Hernáez & Palma, 2003; Gebauer et al., 2007) is available, the large-scale geographic variation in abundance or life-history traits of porcelain crabs along the Southeast Pacific coast has not previously been evaluated. The analysis of published information, however, provides a basic framework with which to predict geographic patterns of variation in the abundance and life histories of porcelain crabs along this coast. A study conducted at a single site in northern Chile (Emparanza, 2007) revealed that the relative abundance of the examined porcelain species fits at least partially with the predictions of the ACH: species close to their geographic boundaries had lower abundances, whereas species closer to their centres of distribution reached either high or low abundances (sensu Enquist et al., 1995; Kiflawi et al., 2000). Other studies provide insights into the patterns of variation in life-history traits and the factors shaping the boundaries of the distribution. For instance, in several species the maximum size seems to increase towards higher latitudes (Hernáez & Palma, 2003), thus supporting the predictions of the temperature–size rule (Atkinson & Sibly, 1997; Angilletta & Dunham, 2003). Locally, adult body size also shows a marked cline across the intertidal zone, decreasing towards the upper intertidal zone, where desiccation risk is more intense (Emparanza, 2007); this suggests that body sizes should also decrease towards the

equatorward boundaries in response to the higher thermal stress (Stillman & Somero, 2000; Stillman, 2002). At the poleward boundaries of the geographic range, different proxies (e.g. annual brood production, fecundity, larval duration) indicate that reproductive output and larval survival could be considerably lower than at the equatorward boundaries (Antezana *et al.*, 1965; Hernáez & Palma, 2003; Gebauer *et al.*, 2007). In addition, physiological constraints might particularly affect female porcellanids, which produce yolk-rich eggs and incubate their broods for several weeks (Lardies & Wehrt-mann, 1996; Hernáez, 2001; Hernáez & Palma, 2003; Lardies *et al.*, 2004; Gebauer *et al.*, 2007). Thus, depending on the shape of geographic variation in the reproductive and other physiological costs, sex ratios may vary monotonically or nonlinearly across the geographic range of a species.

Here, we tested these ideas, analysing the geographic variation in the abundance and life-history traits (maximum size, size at maturity, sex ratio, proportion of ovigerous females, and presence of recruits) of five common intertidal porcelain crabs (*Petrolisthes granulosus*, *Petrolisthes laevigatus, Petrolisthes tuberculatus*, *Petrolisthes violaceus* and *Allopetrolisthes angulosus*) along the Chilean coast (18°–42° S), across *c.* 2500 km and encompassing most of the latitudinal ranges of these species. We hypothesize (1) that geographic variation in abundance should follow the predictions of the ACH, and (2) that geographic patterns in life-history traits should reflect the existence of different mechanisms controlling equatorial (thermal/physiological constraints) and poleward (reproductive/larval constraints) boundaries.

MATERIALS AND METHODS

Data collection

We sampled at wave-exposed boulder beaches (boulders of 10–50 cm diameter) at 13 sampling sites along the Chilean coast (Fig. 1 and Appendix S1 in Supporting Information), encompassing *c.* 25° of latitude. All sites were visited once during austral summer (January and February 2000), and so the recorded patterns must be considered as a 'snapshot'. However, because all studied species are relatively long-lived, temporal variations in abundance should be limited (Sagarin & Gaines, 2002b; Gilman, 2005). Previous studies on *P. laevig-atus* from southern Chile indeed showed very little intra- and inter-annual variability in local abundance (Lardies *et al.*, 2004; Gebauer *et al.*, 2007). Furthermore, because sampling was carried out during a single season (with a time-lag of < 2 months), it may be considered as a representative picture of the system at that given time window, and under the prevailing oceanographic conditions. The snapshot sampling could affect the absolute magnitude of some of the reproductive variables (i.e. the percentage of ovigerous females). This would be especially problematic if, in addition, the timing of the reproductive peaks exhibited a latitudinal gradient, as seen
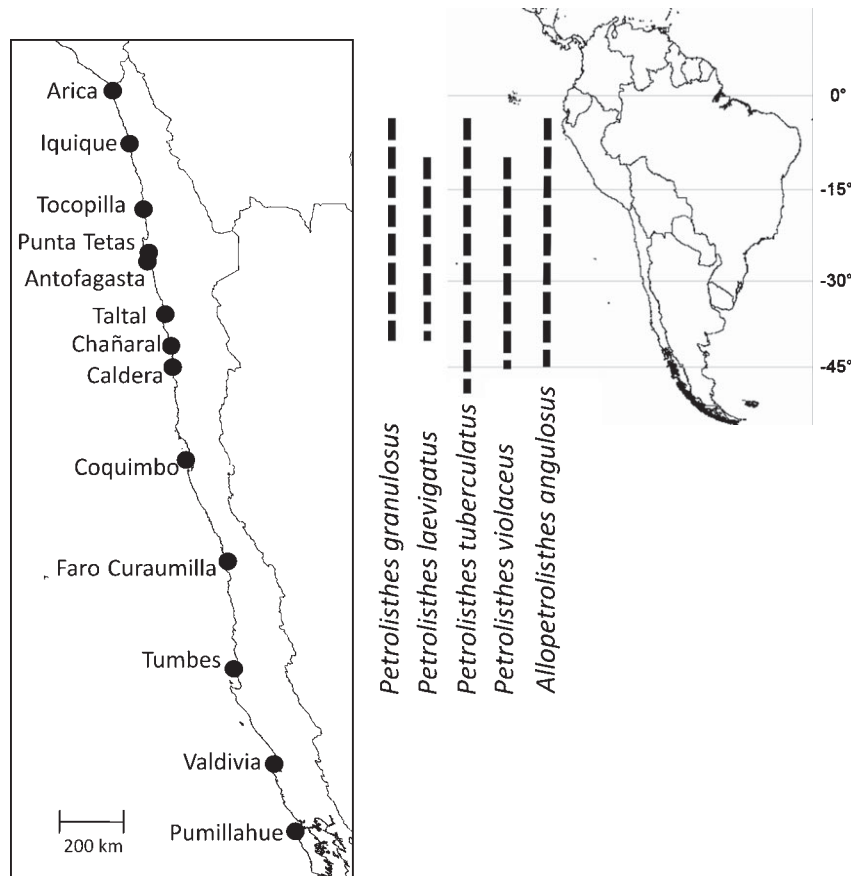

Figure 1 Map of the study region along the Chilean coast, showing the 13 sampled sites (left panel) and the latitudinal ranges of distribution of the five porcelain crab species analysed in this study.

in other species (e.g. Lewis, 1986; Henmi, 1993; Defeo & Cardoso, 2002). However, because most of the littoral porcelain species have year-round reproduction (i.e. there will always be reproductive females, Antezana et al., 1965; Baeza & Thiel, 2000; Baeza et al., 2001, with P. laevigatus being an exception, see below), the reproductive patterns presented herein can be considered representative for most species, even though our snapshot sampling did not enable us to identify temporal variations.

For logistical reasons, we did not explicitly consider vertical variation in species abundance, and sampling was conducted at the mid–low intertidal levels, where the vertical ranges of distribution of the studied species overlap (see Table 1). Although species abundance may vary across the vertical gradient (Antezana et al., 1965; Emparanza, 2007), it is unlikely that this will severely affect the outcome of our analyses, because: (1) despite changes in physical and biological conditions, zonation patterns tend to be stable along the Chilean coast (see Antezana et al., 1965; Viviani, 1969; Villarroel, 1989; Emparanza, 1999, 2007); (2) despite variation in species abundance across the vertical gradient (Viviani, 1969; Villarroel, 1989; Emparanza, 1999, 2007), a study carried out in northern-central Chile showed that this variation is very systematic across sites (Villarroel, 1989); and (3) in most species and sites, maximum abundances are recorded at mid–low intertidal levels (Viviani, 1969; Villarroel, 1989; Emparanza, 1999; but see Emparanza, 2007). These considerations suggest that the large-scale patterns of abundance observed in our study may not be severely biased by the fact that sampling was concentrated at the mid–low intertidal level, although this possibility cannot be entirely dismissed.

At each site, six 0.25-m² replicate quadrat samples were taken along a shoreline of variable extension parallel to the coast (1–5 km) in order to obtain representative samples for that geographic location. Furthermore, at some sites, boulder beaches were relatively small (< 20 m beach length), and in order to avoid local impacts from sampling we had decided a priori to take only one single quadrat sample in these small boulder pockets; consequently, sampling was then spread over a wider extension (up to 5 km) along the shoreline.

Three people conducted the sampling: one held a stopwatch and the sampling tray, while the other two were responsible exclusively for the sampling of crabs. This sampling protocol was followed in order to minimize underestimations caused by individuals escaping. Upon a signal from the time-keeper, the two other people started removing boulders and sampling all crabs that could be reached. Usually one person moved a boulder while the other captured all crabs as quickly as possible and threw them into the sampling tray. This sampling process continued for 60 s and usually it was roughly limited to the area outlined by the sampling quadrat. Individual samples were preserved in 5% formalin. Samples were taken back to the laboratory, where they were washed with freshwater over a 0.25-mm sieve before sorting. All crabs were identified to species level, counted, sexed (according to the presence/absence of the modified male pleopods), and measured (carapace width) with a 0.1-mm-precision caliper. We also recorded the presence of egg masses in females.

Analyses

A total of 14,241 individuals were collected (mean = 1095 individuals per site), and five porcelain species were recorded (P. granulosus, P. laevigatus, P. tuberculatus, P. violaceus and A. angulosus). A summary of the information obtained is given in Table 1. The data were used to estimate several variables for each species at each site: (1) absolute and relative abundance, (2) maximum body size, (3) size at maturity, (4) sex ratio, (5) proportion of ovigerous females, and (6) presence of juveniles. Absolute abundance was estimated as the total number of individuals recorded at each site divided by the total area sampled, and was expressed as individuals m^{-2}. The relative abundance of a species at a given site was estimated as the total number of individuals of this species present, divided by the number of individuals recorded at the site with maximum abundance, in order to facilitate interspecific comparisons (Enquist et al., 1995; Sagarin & Gaines, 2002b). Maximum

Table 1 Summary of the main ecological and biogeographical properties of the five species of porcelain crabs analysed in this study. Vertical distribution refers to the intertidal zone occupied by each species.

Species	Vertical distribution	Total individuals sampled	Median density across sites (Ind. m^{-2})	Maximum density across sites (Ind. m^{-2})	Mean size (minimum–maximum) (mm)	Identification threshold for sex (mm)	Reported range limits (north–south) (°S)	Source for range limits
Petrolisthes granulosus	Mid–high	1506	5.3	292.6	5.0 (0.9–12.0)	5	5–42	1, 2, 4
Petrolisthes laevigatus	Mid–high	1407	0.66	891.3	9.5 (0.9–22.6)	6	5–50	1, 2, 3
Petrolisthes tuberculatus	Low–mid	1082	53.3	188.6	5.9 (1.4–17.9)	6	12–42	2, 4
Petrolisthes violaceus	Low–mid	6890	202.7	968.0	8.3 (1.0–33.6)	6	12–46	1, 2, 3
Allopetrolisthes angulosus	Low–mid	3356	38.0	762.6	7.4 (1.0–18.3)	5	5–46	2, 3

Ind. m^{-2}, individuals per m^2.

Sources: 1, Carvacho (1980); 2, Retamal (1981); 3, Carvacho & Saavedra (1994); 4, this study. Vertical distributions taken from Antezana et al. (1965), Viviani (1969), Villarroel (1989) and Emparanza (2007).

body size was estimated as the 95th percentile of the size frequency distribution, a measure less prone to bias than that of the single largest individual. Similarly, size at maturity was estimated as the 5th percentile of the distribution of body sizes of egg-carrying females. Sex ratio was estimated as the number of females divided by the number of males. Because sexual identification can be uncertain in small individuals, only individuals above a species-specific body size threshold were used (Table 1). This threshold was considered sufficiently large to ensure that sex was correctly identified. Departures from the expected 1:1 ratio were tested statistically using an exact chi-square test, but conclusions should be interpreted with care as the number of individuals showed marked variations across the latitudinal range, and hence the test has a low power at sites with a low number of individuals (e.g. at the edges of the distribution, see Results). The proportion of ovigerous females was estimated as the number of egg-carrying females divided by the total number of females. The presence of juveniles (sexually immature individuals) was used as coarse proxy for recruitment (Zacherl *et al.*, 2003; Gilman, 2006b).

We analysed large-scale trends in the variation of the life-history traits for each species. Because the Chilean coast runs mostly in a north–south direction, latitudinal trends may reflect overall geographic trends. To facilitate interspecific comparisons, we tested whether the life-history traits of a species varied along the relative position of each site over its latitudinal range. This was done separately for each species, using the expression proposed by Enquist *et al.* (1995) and Sagarin & Gaines (2002b):

$$RI = 2(L - S)/R,$$

where RI is the range index, or the relative position of each site across the range (varying between −1 and 1: −1 = northern edge, 0 = centre of range, 1 = southern edge), L is the site location (in degrees of latitude), S is the latitudinal midpoint of the species' range, and R is the latitudinal range (in degrees of latitude). Latitudinal limits of distributions were determined using literature records (Table 1). Most of the species have northern edges of distribution along the coast of Peru, that is, outside the study region. However, the study region encompassed most of the latitudinal ranges of all studied species (53–80%, Fig. 1), so that the observed patterns can be considered as representative. Large-scale patterns of life-history-trait variation (except for the presence of juveniles) were fitted to four hypothetical models, following the procedure developed by Sagarin & Gaines (2002b) (Fig. 2). These models represent the most common abundance patterns of a species throughout its geographic range (Sagarin & Gaines, 2002a; Gaston, 2003; Sagarin *et al.*, 2006). In the first model (normal, Fig. 2a), maximum abundance is expected to follow a normal distri-
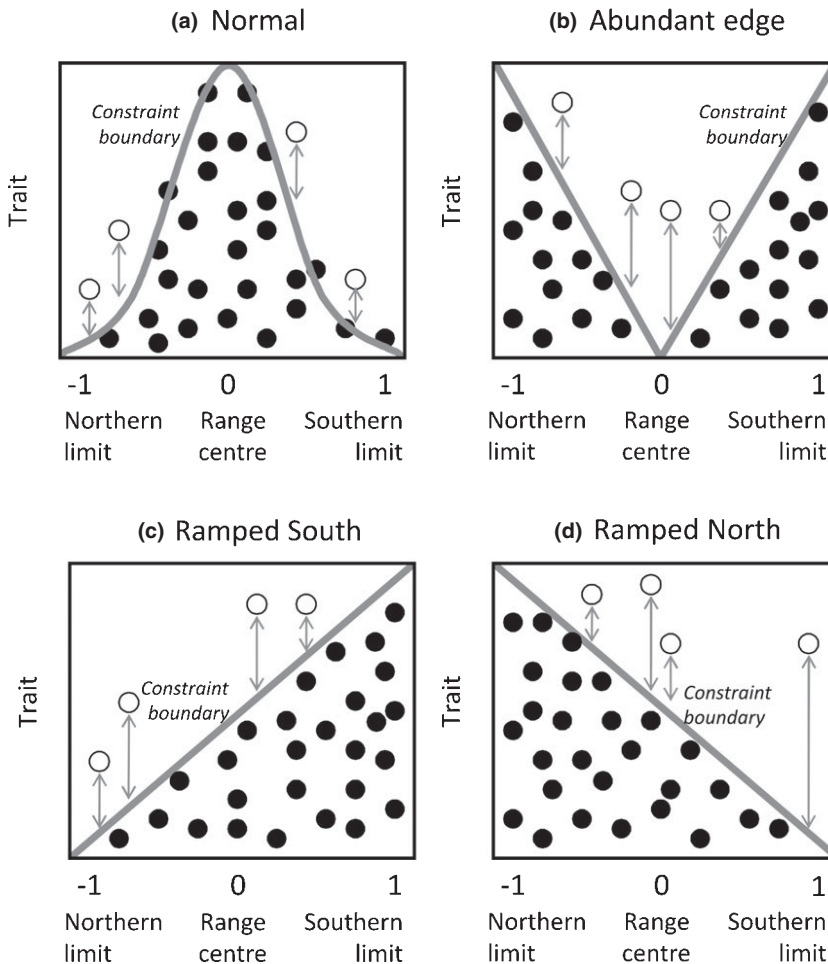

(a) Normal

(b) Abundant edge

(c) Ramped South

(d) Ramped North

Figure 2 Four hypothetical models describing the distribution of abundance/life-history traits along the geographic ranges of species of porcelain crabs (modified from Sagarin & Gaines, 2002a): (a) normal, (b) abundant edge, (c) ramped south and (d) ramped north. The degree of fit of each model to the observed data was evaluated by calculating the sum of squared deviations (SS, deviations indicated by arrows) for sites exceeding the constraint boundary (open dots).

bution, with maximum values being reached at the centre of the range, decreasing to zero towards the northern and southern edges. The second model (abundant edge, Fig. 2b) assumes the inverse pattern, with maximum abundances observed at the edges of the range, and minimum values in the centre. The two remaining models (ramped south, ramped north, Fig. 2c,d) assume that the maximum abundances decline from one range limit to the other and that intermediate abundances are reached at the centre of the range. The degree of fit of each model to the observed data was evaluated by calculating the sum of squared deviations (SS) for sites exceeding the constraint boundary generated by each model (Fig. 2). Values of SS close to 0 indicate good agreement between the model and the observed data. The significance of the observed SS values was evaluated by generating 10,000 randomized values of RI and relative abundance. The fit of the model was considered significant when the observed SS value was lower than the 5th percentile of the randomized distribution. Because *P. laevigatus* was absent from many sites, its latitudinal variation in life-history traits is presented but is not tested against the models. Furthermore, this is the only species with a clear seasonal reproductive cycle, with high proportions of ovigerous females in winter and spring (Lardies *et al.*, 2004; Gebauer *et al.*, 2007), which impedes the analysis of any spatial patterns in the proportion of ovigerous females of *P. laevigatus* in the present study.

Spatial patterns of occurrence of juveniles were analysed using a logistic regression between juvenile presence (1 = present, 0 = absent) and range index. All analyses were carried out using the R software (R Development Core Team, 2007). Simple latitudinal gradients in life-history traits were tested

using Pearson product–moment correlation, with *P*-values corrected for any possible spatial autocorrelation using Dutilleul's method (Dutilleul, 1993) implemented in the sam software (Rangel *et al.*, 2006).

RESULTS

The geographic pattern of density and relative abundance varied among the different species (Fig. 3). For *A. angulosus* and *P. tuberculatus*, the highest densities were found near the centre of their respective geographic ranges; that is, the relative abundance showed a hump-shaped pattern, fitted by a normal model. For *P. violaceus*, the highest densities were found at the northern edge of the geographic range and the abundance pattern was significantly fitted by a ramped-north model. A hump-shaped trend was evident for *P. granulosus*, but the normal model was not significant ($P = 0.08$). For *P. laevigatus*, the most common porcelain species in the southern region, abundance peaked around 40° S, but it was extremely rare in central and northern Chile. No model fitted the distribution, although a ramped-south model fitted significantly after abundance was log-transformed.

In general, maximum size and size at first maturity showed a poleward increase, with larger values being found at the southern edge of the distribution (Fig. 3). However, neither maximum size nor size at first maturity were fitted by any of the hypothetical models for any of the five species; latitudinal trends were also not significant (Table 2). Nevertheless, in all cases the correlation values were positive; assuming binomial probabilities of obtaining positive or negative values ($P = 0.5$), the chances of obtaining only positive correlations were low
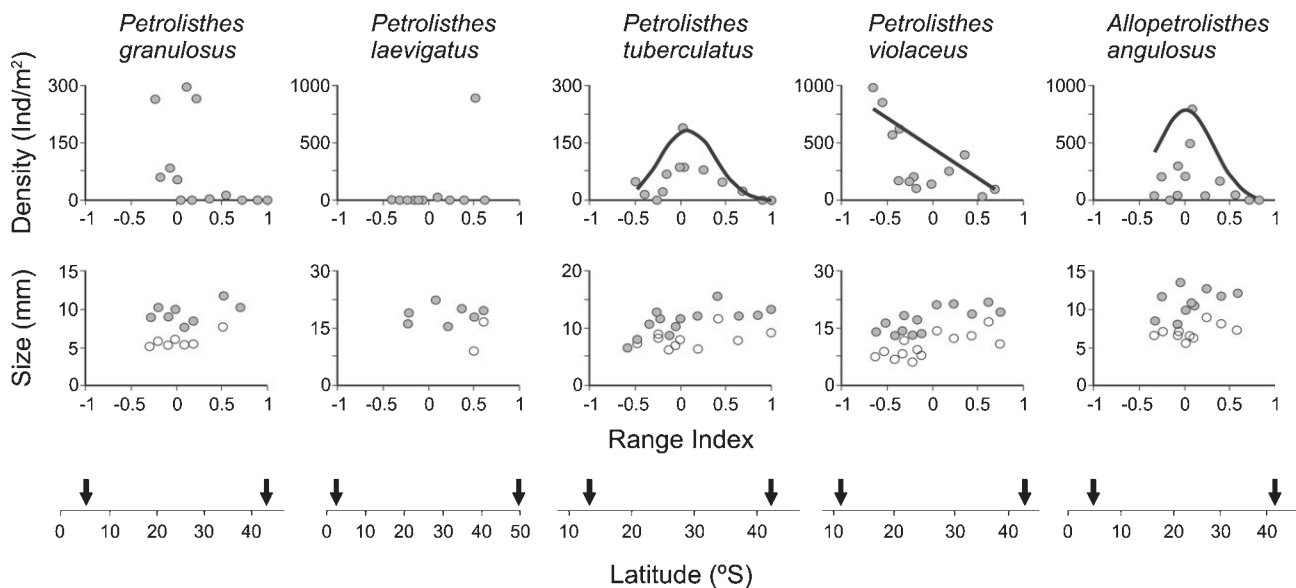

Figure 3 Large-scale variation in the absolute abundance (upper panel) and in the maximum size (filled dots, lower panel) and size at maturity (open dots, lower panel) of the five species of porcelain crabs across their geographic ranges (range index) and latitudinal gradient. The figure also shows the best model fitting the observed patterns (bold lines, see models in Fig. 2 and text for details). The models were not tested for size at maturity of *Petrolisthes laevigatus* owing to the absence of this species at many sites. The arrows indicate the range limits of each species (see Table 1).

Table 2 Latitudinal gradient of variation in maximum body size and size at maturity in all studied species. The significance values of Pearson product–moment correlations were corrected for spatial autocorrelation (Dutilleul, 1993).

Species	Maximum size		Size at maturity	
	Correlation	*P*-value	Correlation	*P*-value
Petrolisthes granulosus	0.44	0.24	0.78	0.07
Petrolisthes laevigatus	0.18	0.66	n.e.	n.e.
Petrolisthes tuberculatus	0.68	0.16	0.39	0.38
Petrolisthes violaceus	0.71	0.16	0.69	0.19
Allopetrolisthes angulosus	0.45	0.35	0.44	0.25

n.e., not estimated.

($P = 0.02$ for maximum size, and $P = 0.06$ for size at first maturity).

Sex ratios showed a consistently hump-shaped pattern, and they were best fitted by a normal model in three out of the four tested species (Fig. 4). In the case of *P. violaceus*, the pattern remained firm even after the maximum sex-ratio value was removed from the analysis. The hump-shaped pattern was also evident in the case of *P. tuberculatus*, but this was not significant, probably because the maximum values of sex ratios were slightly displaced towards the southern portion of the range. The sex ratios were particularly high (biased towards females) at the centre of the distribution, up to five-fold compared with the edges. The bias favouring females was significant in the case of *P. violaceus*, *A. angulosus* and *P. tuberculatus*. Moreover, the highest sex ratios of *P. laevigatus*

(not tested statistically) were recorded very close to the centre of its range.

Ovigerous females were found at the vast majority of sites (77–100%, depending on the species). In the case of *A. angulosus*, the pattern fitted a normal distribution: up to 70% of females carried eggs at the centre of the range, compared with *c.* 13–40% towards the southern and northern edges (Fig. 4). In contrast, no model fitted the observed patterns for *P. violaceus*, *P. tuberculatus* and *P. granulosus*, and the proportion of ovigerous females remained relatively high (30–50%) throughout the study area.

The presence of juvenile recruits was less common – they were recorded in only 31–70% of all sites, depending on the species. The occurrence of juveniles tended to be concentrated at the centre and the northern margins of the geographic distribution (Fig. 4), but the trends were not statistically significant (logistic regression, $P > 0.05$ in all cases). However, no juveniles of any species were recorded at sites close to the southern edges of the distribution (i.e. range index > 0.54). In contrast, juveniles were detected at all sites with a range index < −0.40.

DISCUSSION

Generality of the ACH

Our results provide an empirical test of the ACH, and of its possible connections with geographic variations in life-history traits. Although the ACH has recently been considered more an exception than a rule (Sagarin & Gaines, 2002a,b, 2006;
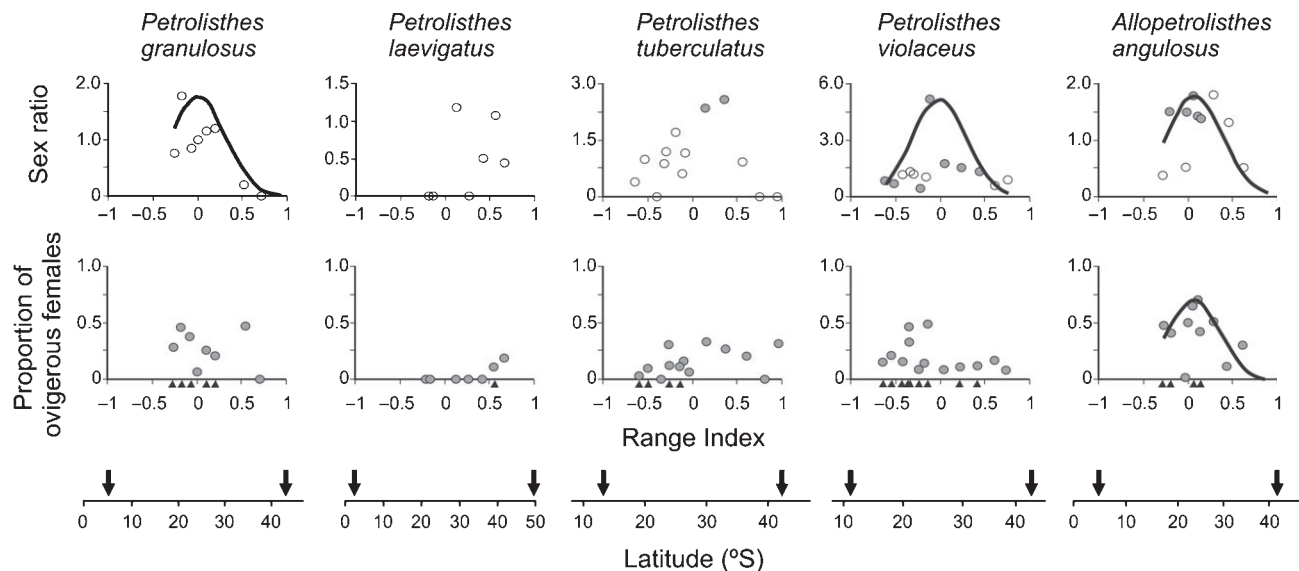

Figure 4 Large-scale variation in the sex ratio (female/males) (upper panel) and in the proportion of ovigerous females (lower panel) of five species of porcelain crabs across their geographic ranges (range index) and latitudinal gradient. In the upper panel, significant ($P < 0.05$) departures from the expected 1:1 ratio are indicated by filled dots, whereas non-significant ratios are shown by open dots. The presence of juvenile individuals is shown (black triangles, lower panel). Also shown is the best model fitting the observed patterns (bold lines, see models in Fig. 2 and text for details). The models were not tested for *Petrolisthes laevigatus* owing to the absence of this species at many sites. The arrows indicate the range limits of each species (see Table 1).

Gaston, 2003; Sagarin *et al.*, 2006), our study has provided empirical evidence that the pattern, albeit not general, is not uncommon in marine species (see also Enquist *et al.*, 1995; Fiori & Defeo, 2006; Fenberg, 2008). Three of the five studied species showed a peak of abundance close to the centre of their ranges and declined in abundance towards the edges, but only in two of them was the pattern fitted by a normal model.

The causes of the lack of generality of the ACH, or more broadly of the multiple geographic patterns of abundance displayed by the species, are poorly understood. The only previous multi-specific study conducted in an intertidal system was unable to offer an explanation for the considerable differences in the abundance pattern exhibited by 12 invertebrate species (Sagarin & Gaines, 2002b). Sagarin & Gaines (2002b) suggested that differences could be the result of species-specific responses to ecological factors or to larval dispersal patterns. In our case, all species are closely related phylogenetically (Stillman & Reeb, 2001) and share similar ecological and life-history traits, and thus any differences in abundance patterns should arise from more subtle variations in their biology. It is interesting to note that the ACH was evident only in small-sized and less abundant species (Table 1), although the trend was not significant in *P. granulosus*. In the large-sized and locally dominant forms (*P. violaceus*, *P. laevigatus*) the ACH did not apply. Although this pattern is based on only five species, it suggests that the less dominant species of the assemblage may be more susceptible to the mechanisms on which the ACH is based.

An alternative explanation is that the reported geographic ranges may not be representative of the realized geographic range at a given moment in time. The realized geographic range might vary in time and oscillate in parallel with the El Niño–Southern Oscillation (ENSO) cycle, as seen for other intertidal species in the region (Martínez *et al.*, 2003; Espoz *et al.*, 2004). An indication that the realized geographic range may differ substantially from the reported geographic range comes from the data on *P. laevigatus*. This species has been reported up to northern Peru at 5° S (Retamal, 1981; Carvacho & Saavedra, 1994), but our data suggest that its realized geographic range limits during the conditions of our study might have been substantially farther south. We did not find this species at several sites near its supposed centre of distribution (25°–30° S), and we found only three very large males at the northernmost site (23° S) at which this species was found in this study. In order to explore whether shifts in the range limits may affect the outcome of our results, we re-ran the analyses using different combinations of northern and southern limits (Fig. 5). For most of the explored combinations of northern/southern limits no model fitted the observed abundance distribution. However, when we assumed that the true northern limit is at 22°–23° S (the observed limit) and the true southern limit is at 54°–55° S (*c.* 4°–5° south of the currently reported limit), abundance followed a hump-shaped pattern, and it was fitted significantly only by a normal distribution model. The simulations also showed that a subtle, yet realistic, variation in the range limits

of *P. violaceus*, *A. angulosus*, *P. tuberculatus* and *P. granulosus* did not affect the validity of our conclusions (Fig. 5). For *P. violaceus*, the ramped-north model prevailed for most of the simulated range, but the abundant-edge model could not be rejected in some cases. However, the SS was always minimized by the ramped-north model, suggesting a better fit.

The lack of support for the ACH may also be caused by bias introduced by our sampling strategy. First, the snapshot sampling assumes that the spatial patterns of abundance (and life-history traits) are robust to temporal dynamics. Second, our sampling did not account for vertical variations in species abundance, assuming that their abundances peaked at the sampled mid–low intertidal fringe. Although we have shown that existing evidence supports these assumptions at least in part (see Materials and Methods), particular site-specific conditions or interspecific interactions might cause local shifts in vertical abundance peaks; new and more exhaustive datasets, encompassing more species sampled throughout their entire geographic range and across the whole intertidal zone, are needed to test this idea further. This will help in gaining an understanding of whether and how the realized geographic range of these intertidal species oscillates depending on the predominant oceanographic conditions.

ACH and sex ratios

Surprisingly, of all the analysed traits besides abundance, the sex ratio was the one showing strongest support for the idea of an 'optimum centre' across the geographic range of the species. Notably, the proportion of females is maximized at the centre of ranges, whereas at both edges of the distributions the populations tended to be dominated by males. Deviations from the expected 1:1 ratio are fairly common in crustaceans in general (Wenner, 1972). Studies on the mole crab *Emerita analoga* from sandy beaches have shown a different latitudinal gradient, with an increasing proportion of males found at the equatorward boundary of the range (Defeo & Cardoso, 2002), but to our knowledge this is the first time that this hump-shaped pattern has been reported at biogeographic scales.

To the best of our knowledge, ontogenetic sex change occurs neither in porcelain crabs nor in closely related clades of anomuran crabs (e.g. squat lobsters, king crabs and hermit crabs, Baeza *et al.*, 2001; Chiba, 2007), and consequently other mechanisms must be responsible for the observed pattern. According to theoretical models, if the survival of both sexes is affected differentially along an environmental gradient, then the sex ratios in the population should depart from the expected 1:1 ratio and vary in a predictable way along the gradient (Charnov *et al.*, 1981). The high sex ratios found at the centre of the ranges may imply either enhanced survival of females, or reduced survival of males, or a combination of both. We hypothesize that the prevalence of females (i.e. lack of males) at the centre of the ranges may result from an enhanced intraspecific competition among males. Intraspecific competition can be intense in porcelain crabs, and at high densities survival may be severely affected (Donahue, 2004,
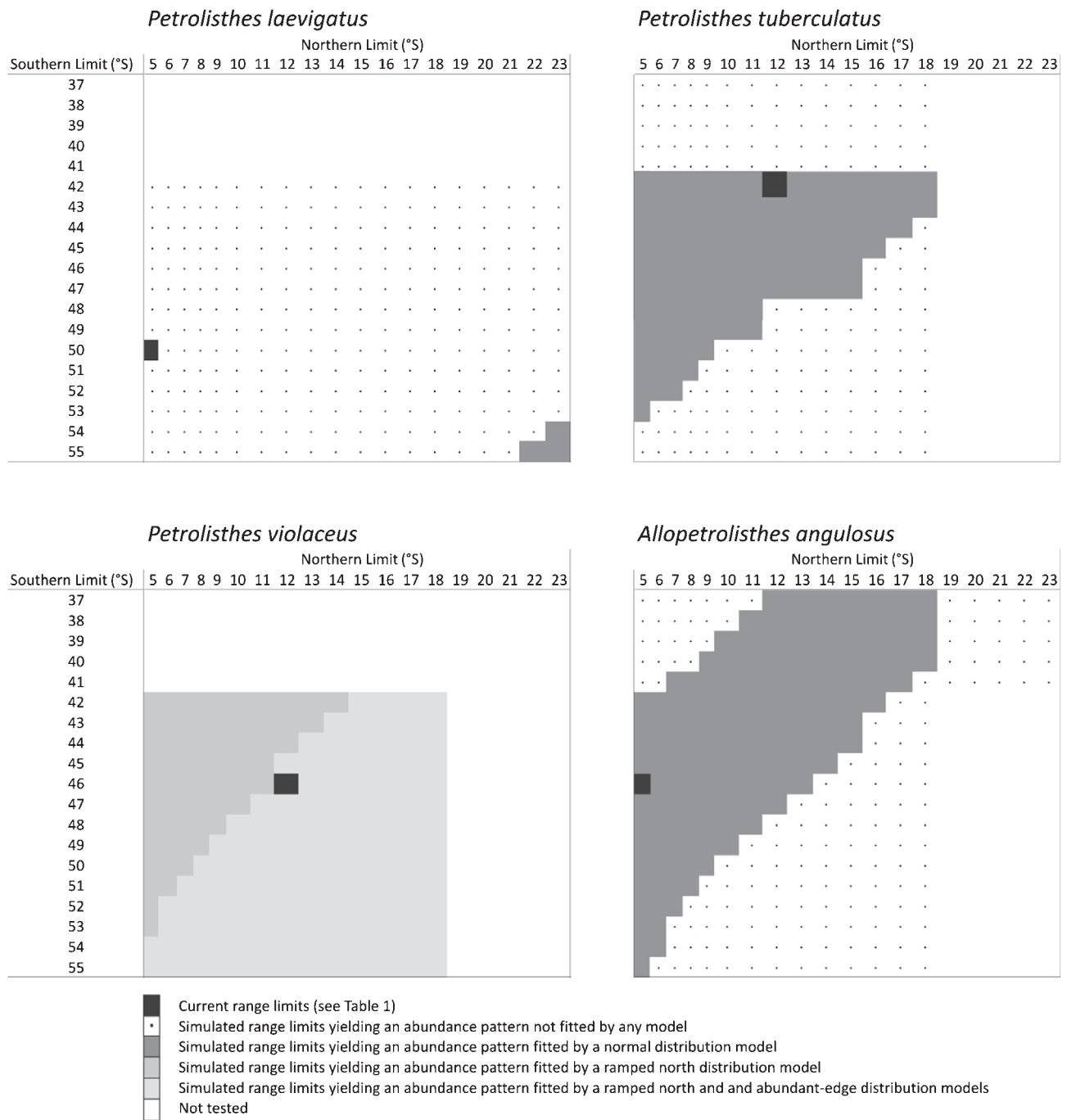
Figure 5 Sensitivity of the conclusions about the shape of the abundance and distribution to changes in the true northern and southern limits. The abundance and distribution patterns generated by each northern/southern limit combination were evaluated against the predictions of four hypothetical models of distribution (Fig. 2, and see Methods for details). No model fitted the abundance distribution of *Petrolisthes granulosus*. Note that in all species but *Petrolisthes laevigatus* the shape of the abundance distribution remained unaffected after even large changes in the precise locations of the northern and southern boundaries.

2006). Because males tend to be highly territorial during courtship (reported for other porcelain species by Molenock, 1975), strong intra-sexual competition among males may reduce their survival at the centre of the range, perhaps by means of agonistic interactions (Rypien & Palmer, 2007). Although male survival appears to be diminished at the centre of the range, at the edges female survival might be suppressed. For instance, high and low temperatures towards the edges of the geographic ranges of our species might raise the costs of egg production and brooding, resulting in diminishing survival of reproductive females. In support of this idea, Fischer & Thatje (2008) reported that the annual number of egg-masses

produced by females of the crab *Cancer setosus* shows a marked hump-shaped pattern along its geographic range on the Southeast Pacific coast, being higher around the centre of the distribution, and declining towards the northern and southern edges. Although suggestive, it is uncertain whether this pattern might also apply to our studied species. Experimental studies are needed to test whether sexes experience differential costs (owing to intra-sexual interactions or costs of egg production and embryo incubation, e.g. Baeza & Fernández, 2002) at the centres or edges of their distributional ranges.

Factors shaping the equatorward boundaries of porcelain species

Even though the connections between abundance and other traits are not absolutely clear, the geographic patterns found for these traits provide some clues about the processes that shape population structure at the edges of the ranges. For instance, our data indicate that populations close to the northern (equatorward) edge tended to have smaller maximum sizes and smaller sizes at maturity, as also seen in other intertidal species (Defeo & Cardoso, 2002; Cardoso & Defeo, 2004). Along the intertidal vertical gradient, smaller adult sizes are often found at higher intertidal levels, a pattern that has been related to higher thermal stress in local-scale studies (Emparanza, 2007). The equatorward edge of the geographic range of marine invertebrates is often limited by thermal stress (Sorte & Hofmann, 2004, 2005; Compton *et al.*, 2007). Indeed, experimental studies have demonstrated that the upper lethal temperatures of several *Petrolisthes* species (*P. violaceus*, *P. tuberculatus* and *P. granulosus*) is *c.* 29–35 °C (Stillman & Somero, 2000; Stillman, 2002), which is very close to the maximum aerial temperatures recorded in northern Peru (Takahashi, 2004). The higher mortality rates associated with smaller sizes and higher temperatures (Defeo & Cardoso, 2002; Cardoso & Defeo, 2004) could also negatively impact adult abundance. The explanation of thermal limitation may apply to the four species exhibiting a decline in abundance towards the northern boundary, but apparently not to *P. violaceus*. Further sampling at the northern geographic range of this species along the Peruvian coast is urgently needed in order to validate the hypothesized processes and mechanisms shaping the equatorward edge of the distribution.

Factors shaping the poleward boundaries of porcelain species

Although the ACH cannot be generalized for all studied species, abundance declined sharply towards the southern edge of their distributions for four of the five species. However, for *P. laevigatus* the southern edge is located far from the study area, and thus it was not possible to evaluate the pattern appropriately. For the remaining four species, the pattern of lower abundances at the southern edges cannot be explained by reduced physiological performance of adults, as hypothesized for the equatorward edge. Indeed, the largest individuals,

a gross indicator of higher individual survival (Gilman, 2005), were commonly recorded close to the southern edges.

The underlying processes shaping the southern boundaries of the distributions of porcelain species could be related to an overall reduction in benthic recruitment. This idea is supported by the lack of juveniles towards the southern edges, despite the presence of ovigerous females across most of the distributional ranges of the studied species. This does not mean that recruitment never occurs at these sites, but that local recruitment may fail more often than in the northern region. Two mutually non-exclusive mechanisms could be causing this limited recruitment in the south: (1) lower reproductive output and/or (2) increasing larval mortality. Lower reproductive output in southern Chile is suggested by several proxies, including fewer eggs produced (Antezana *et al.*, 1965; Hernáez & Palma, 2003; Gebauer *et al.*, 2007), shorter reproductive seasons (Antezana *et al.*, 1965; Lardies & Wehrtmann, 1996; Baeza *et al.*, 2001; Gebauer *et al.*, 2007), prolonged incubation times (Hernáez, 2001; Lardies *et al.*, 2004), and lower larval density in the plankton (Ulloa & Palma, 1998; Mujica, 2007). Furthermore, an increase in larval mortality should also result in an overall reduction of benthic recruitment. High larval mortality as a result of cooler water temperatures might play a key role in shaping the poleward distribution, as seen in other marine species (Zacherl *et al.*, 2003; Gilman, 2006a,b; Sanford *et al.*, 2006). Studies aimed at comparing the intensity of recruitment, reproductive output, and thermal tolerances of larvae across the Chilean coast are needed in order to test these ideas.

Concluding remarks

The ACH, albeit not universal, is a recurring phenomenon, and its value as a biogeographic hypothesis should not be dismissed until further evaluations become available (Sagarin & Gaines, 2002a). By including life-history aspects of the species, new insights into the factors shaping the geographic variation in abundance become evident. Some of our results support the suggestion that physiological constraints (here evaluated by means of demographic proxies) might contribute to the lower abundances near the range boundaries. Future studies may deal more appropriately with the intrinsic complexity of the system by including studies of adult and larval physiology, and the role of larval dispersal, which may be critical in shaping the species' ranges and internal structures of the ranges (see also Sagarin & Gaines, 2002b). We furthermore encourage interannual and seasonal sampling across the geographic range of the organisms of interest, especially in regions strongly affected by ENSO, in order to reveal whether the realized geographic ranges might vary in time.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Geographic coordinates of the study sites.

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BIOSKETCH

Members of the BEDIM laboratory (Biology, Ecology and Diversity of Marine Invertebrates) at Universidad Católica del Norte are interested in the evolutionary ecology and behaviour of marine organisms and their biogeography (http://www.bedim.cl). They have studied a wide diversity of taxa and they often use crustaceans as model organisms. During recent years they have repeatedly travelled the Chilean coast, both by land and by sea, in a quest to understand the processes that shape its marine biogeography.

Author contributions: M.T., C.C., I.H. and J.A.B. conceived the idea; S.B., M.C., C.C., A.C., E.dV., I.H., N.U., N.Va., N.Vz., A.Z. and M.T. collected and processed the samples; P.H. entered and ordered the data; P.H. and M.M.R. analysed the data; M.M.R., P.H., J.A.B. and M.T wrote the paper.

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