

Spatial niche differentiation and coexistence at the edge: co-occurrence distribution patterns in *Scurria* limpets

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ABSTRACT: Examining the co-occurrence of taxonomically similar species can provide important information about their niches and coexistence. Segregation at smaller scales can be especially relevant for grazers living at the edge of their geographic distribution, because environmental factors can lead to similar distribution. Related grazer species may show dispersive, i.e. uniform, distribution at small scales (few centimetres) to reduce interference among individuals. We examined intra- and interspecific spatial distribution and habitat use in 2 phylogenetically related intertidal limpets, *Scurria viridula* and *S. zebrina*, at the polar and equatorial edge of their geographic distribution, respectively, and in *S. araucana*, a widely distributed species that overlaps the range of the other 2 species across the southeastern Pacific. *S. viridula* and *S. zebrina* overlapped in a narrow geographic zone (ca. 250 km) and reached relatively similar densities and sizes. Intraspecific spatial structure estimated through autocorrelation and individual-to-individual distances was random for *S. viridula* and variable for *S. zebrina* and *S. araucana*, depending on the scale considered; *S. zebrina* was aggregated at the individual-to-individual distances, while *S. araucana* was mostly random at this scale. Segregated distribution between *S. viridula* and *S. zebrina* was observed at the finer scale, whereas the association with *S. araucana* was random. Abundance of limpets loosely followed major habitats, namely bare rock and the alga *Mazzaella laminarioides*, which showed patchy distributions. We suggest that similarity in population traits between *S. viridula* and *S. zebrina* found in the overlap zone may be compensated by small-scale spatial segregation. Thus, at the edge of their geographic distribution, coexistence between related species may be influenced by spatial niche differentiation driven by habitat suitability or competition.

KEY WORDS: Coexistence · Geographic edge · Grazers · Habitat type · Niche partitioning · Nearest neighbour · Spatial autocorrelation

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INTRODUCTION

Tracking the dynamic distribution of multiple species in space has been key to our understanding of the mechanisms behind species coexistence (Lomolino et al. 2005, Lavergne et al. 2010). Patterns of co-occurrence of taxonomically similar species can provide insights into ecological and evolutionary

processes determining coexistence and species diversity through niche-based mechanisms (MacArthur & Levins 1967, Leibold 1998, Chesson 2000, Mouquet & Loreau 2002). Related species are more likely to have equivalent fundamental niches (i.e. similar environmental requirements) as a consequence of phylogenetic niche conservatism (e.g. Wiens et al. 2010) but segregated realized niches (different spatial

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distributions) owing to biotic interactions (Godsoe 2010). Spatial patterns of abundance around the edge of a species' geographic distribution are important to understand the processes driving range shift dynamics (Goldberg & Lande 2007, Moore et al. 2007, Godsoe 2010) and rapid variation in assemblage structure in the face of changing environmental conditions (Parmesan & Yohe 2003, Lima et al. 2006, Parmesan 2006, Chen et al. 2011). However, dynamic patterns of taxonomic and functionally similar species co-occurrence at the edge of their geographic range remain largely unexplored.

In marine and terrestrial ecosystems, biogeographic distribution patterns are affected by a suite of abiotic and biotic processes, which shape range limits over ecological and evolutionary scales (Case et al. 2005, Sexton et al. 2009, Lavergne et al. 2010). Abiotic factors like habitat structure and temperature stress can constrain range distributions and demographic patterns of both mobile and sessile species in intertidal and subtidal habitats (Wethey 2002, Miller et al. 2009, Mellin et al. 2011, Tam & Scrosati 2011). In addition, biotic factors like competition and predation can contribute to shape the edge of the range and individual spatial distribution patterns of different species (e.g. Wethey 2002, Harley 2003, Firth et al. 2009). In intertidal habitats, in particular, species distributions and coexistence patterns are influenced by the interplay of environmental and biotic interactions operating at the local (centimetres to metres) and larger scales (tens of kilometres) (Denley & Underwood 1979, Menge & Branch 2001, Fraschetti et al. 2005).

Commonly, habitat use, distribution and survival of grazers are largely determined by species-specific tolerance limits (e.g. thermal stress; Garrity 1984, Harper & Williams 2001, Miller et al. 2009) and behavioural preferences of individuals (e.g. Crowe & Underwood 1998, Olabarria et al. 2002, Underwood et al. 2004, Muñoz et al. 2005, Chapperon & Seuront 2011a). Limpets, snails and chitons commonly show behavioural responses to desiccation stress and predation risk, which determines aggregation of individuals inside shelters (e.g. crevices, under algal canopy) or other suitable microhabitats and generates patchiness in the spatial distribution of abundance (e.g. Williams & Morrill 1995, Olabarria et al. 2002, Coleman et al. 2004, Aguilera & Navarrete 2011, Stafford et al. 2011). On the other hand, interference during feeding can result in random or uniform individual distributions of species with similar requirements to reduce deleterious effects of individual encounters (Branch 1975, 1976, Underwood 1976, Iwasaki 1992). A population is randomly distributed

when the position of each individual is independent of other individuals and is uniformly distributed when the distance between neighbouring individuals is maximized (e.g. Clark & Evans 1954, Ludwig & Reynolds 1988). Positive spatial association among con- or heterospecific individuals, however, is considered an aggregated distribution pattern (Fortin & Dale 2005). Similarities in diet, morphology or size can determine competitive symmetries among limpet grazers (e.g. Branch 1975, Iwasaki 1992, Underwood 1992). Contrarily, differences in density, size or behaviour can increase asymmetries and establish competitive hierarchies (Chapman & Underwood 1992, Iwasaki 1992, Marshall & Keough 1994, Boaventura et al. 2003, Aguilera & Navarrete 2012b). Therefore, differences or similarities in individual traits and habitat suitability can influence distribution patterns and population size of grazers modifying their coexistence across spatial scales (e.g. *Patelloida*, Fletcher & Underwood 1987; *Patella*, Firth & Crowe 2008, 2010). Spatial segregation and coexistence at smaller scales are particularly relevant for grazer populations inhabiting the edge of their geographic distribution, where low population size coupled with high temporal variation in demographic patterns is expected (see Sagarin et al. 2006, Fenberg & Rivadeneira 2011). Related grazer species may show dispersive (i.e. uniform) spatial distribution at small scales (few centimetres) to reduce interference among heterospecific individuals. Hence, identifying the spatial scales at which different processes influence species distribution patterns is critical to understand species responses to environment and the potential for coexistence within the assemblage (Fortin & Dale 2005).

On the north-central coast of Chile, a broad transitional zone of species distributions extends between 30° S and 41° S (Camus 2001, Rivadeneira et al. 2002, Hormazábal et al. 2004, Broitman et al. 2011), but a narrow area between 30° S and 32° S concentrates the polar or equatorial range edge of several intertidal species (Rivadeneira & Fernández 2005, Broitman et al. 2011). The overlap of species with disjointed distributions (i.e. parapatry) and the occurrence of several closely related species across a narrow area make this biogeographic transition zone an ideal system to explore ecological processes such as the spatial basis of coexistence (Broitman et al. 2001, Rivadeneira & Fernández 2005, Rivadeneira et al. 2010). Here, we explore the spatial distribution, habitat use and co-occurrence at local scales (centimetres to metres) in 3 congeneric species of intertidal grazers, the limpets *Scurria viridula*, *S. zebrina* and *S. araucana* (Espoz et al. 2004). The first 2 species overlap their polar and

equatorial distribution limits across 30° S to 32° S (i.e. ~230 km), respectively, while the latter spans broadly across the region. *S. viridula* and *S. zebrina* are closely related, display similar behavioural responses and have relatively similar morphology (Espoz & Castilla 2000, Espoz et al. 2004). *S. araucana*, on the other hand, shows clear differences in most traits with the other 2 species. For example, this species has a small size and marked radial ribs which project beyond the shell compared with the other species and is more distant in the scurrinid phylogeny (Espoz et al. 2004). In addition, *S. araucana* showed no active response against their main predator, the sun star *Heliaster helianthus*, while *S. viridula* and *S. zebrina* have an active escape response (Espoz & Castilla 2000). Many *S. araucana* individuals tend to inhabit rock pools, where they show a mostly dispersive distribution pattern and generate home scars in the rock surface (Espoz et al. 2004, M. A. Aguilera pers. obs.). As suggested for other intertidal grazers (e.g. Firth & Crowe 2010), the 2 similar limpet species could coexist in the overlap zone by means of small-scale segregation caused by, for example, differential use of shelters or resting areas. We use 2 different sampling methodologies to determine the spatial distribution of the study species and to identify the scale at which spatial segregation may take place. Thus, we hypothesize that (1) both parapatric species display similar patterns of intraspecific spatial structure (either aggregated or uniform), densities and body size structure; (2) these species show segregated interspecific spatial association, i.e. uniform distribution, at small scales (centimetres to metres) across their geographic overlap zone; and (3) because the focal limpets use different microhabitats, their spatial distributions should be positively correlated to the distribution of different habitat types. We further tested the hypothesis that (4) the third species, *S. araucana*, which broadly spans the overlap zone, shows independent (uncorrelated) local spatial distribution and different habitat use patterns when compared with the other species.

MATERIALS AND METHODS

Intertidal community characterization

The intertidal community of the overlap zone (30° S to 32° S) of the 2 focal species is dominated by the corticated alga *Mazzaella laminarioides* (Santelices 1990, Broitman et al. 2001). Opportunistic algae like *Ulva rigida*, *U. compressa* and *Pyropia columbina* are

abundant in high to middle intertidal levels. The herbivore assemblage inhabiting mid to high intertidal levels is characterized by molluscan species that feed differentially on microalgae and both microscopic and macroscopic stages of algae, as well as small invertebrates (Camus et al. 2008, and see Aguilera 2011 for review). The most abundant species are the chiton *Chiton granosus*, the keyhole limpet *Fissurella crassa*, the littorinid snails *Austrolittorina araucana* and *Echinolittorina peruviana*, the pulmonate limpet *Siphonaria lessoni* and scurrinid limpets (see below) (Broitman et al. 2001, Rivadeneira et al. 2002, Espoz et al. 2004). The overlap zone corresponds to the equatorial range limit of *M. laminarioides*, the bull kelp *Durvillaea antarctica* and the limpet *Scurria zebrina* and to the polar range limit of the chiton *Enoplochiton niger* and the limpet *S. viridula* (Espoz et al. 2004, Rivadeneira & Fernández 2005, Broitman et al. 2011).

Focal species

Throughout the overlap zone, 6 scurrinid species are common: *Scurria viridula*, *S. zebrina*, *S. araucana*, *S. ceciliansa*, *S. plana* and *S. variabilis*. *S. viridula* and *S. zebrina* are the most derived species of the scurrinid clade of Chile and Peru (Espoz et al. 2004) and show conserved behavioural responses to predator attack when compared with an older coexisting patellogastropod species, *Lottia orbigny* (Espoz & Castilla 2000). In addition, adult individuals of these species have relatively similar morphology, making identification in the field difficult (see identification protocol in Supplement 1 at www.int-res.com/articles/suppl/m483p185_supp). *S. viridula* and *S. zebrina* inhabit high to middle intertidal levels (from 1.0 to 2.5 m above mean low water level, MLWL), and their polar and equatorial range edges, respectively, overlap narrowly from 30° S to 32° S (Espoz et al. 2004). *S. araucana* geographic distribution ranges between 15° S and 42° S, thus broadly spanning the overlap zone. It is worth noting that *S. viridula* has expanded its geographic distribution in recent times (Rivadeneira & Fernández 2005, authors' pers. obs.). No information about range shift of *S. zebrina* has been reported in previous studies.

Geographic distribution surveys

To determine geographic co-occurrence patterns of the 3 focal species at local scales, we used long-term

abundance datasets (i.e. 1998 to 2000, 2003 to 2005 and 2009 to 2011) obtained from surveys conducted during austral summer (December to March) and winter (June to August) at 10 sites spanning ~600 km in central-north Chile (Broitman et al. 2011) (see Fig. 1). In these surveys, density of *Scurria* limpets was estimated within 10 to 15, 50 × 50 cm quadrats haphazardly positioned along ~15 m alongshore transects on 2 gently sloping, flat, rocky shore platforms at each study site, ~1.5 to 2.0 m above MLWL.

Small-scale spatial structure

Local spatial structure of grazers was assessed at 2 spatial scales, the quadrat scale (i.e. 900 cm²) and the individual scale (nearest neighbour [NN] distance, i.e. few centimetres). These methodologies allowed us to identify the spatial scale at which environmental or ecological mechanisms determine both intra- and interspecific spatial structure. At the quadrat scale, it was possible to identify processes affecting spatial distribution of abundance across the sampling site. On the other hand, NN distances captured processes operating at the between-individuals scale (e.g. behaviour) that may influence spatial associations at very small spatial scales (Fortin & Dale 2005).

(1) We determined if spatial distribution of the 3 species was aggregated, random or uniform (i.e. dispersion of individuals). To this end, and to quantify interspecific spatial associations, we recorded focal species density at 4 sites across the overlap zone (Guañaqueros, Limarí, Punta Talca and Huentelauquén) by means of 15 to 25, 30 × 30 cm contiguous, i.e. adjoined, quadrats placed along 5 to 10 m transects parallel to the shoreline in the mid-high intertidal zone (1.5 to 2.0 m above MLWL). This sampling protocol is appropriate to describe the spatial distribution of organisms with different distribution pattern in space because it ensures a complete mapping of the study area (Ludwig & Reynolds 1988). In addition, percentage cover of algae, sessile animals and bare rock were estimated in each quadrat. Our spatial sampling unit (i.e. quadrat size; 30 × 30 cm) has been shown as an appropriate scale to characterize the spatial distribution of *Scurria araucana* abundance elsewhere, but spatial patterns occurring at ≤30 cm (900 cm²) can remain undetected (Aguilera & Navarrete 2011).

(2) The analysis described above was complemented by NN individual-to-individual linear distances, which allowed us to detect either aggregation or dispersion at finer, individual-level scales of a few centimetres

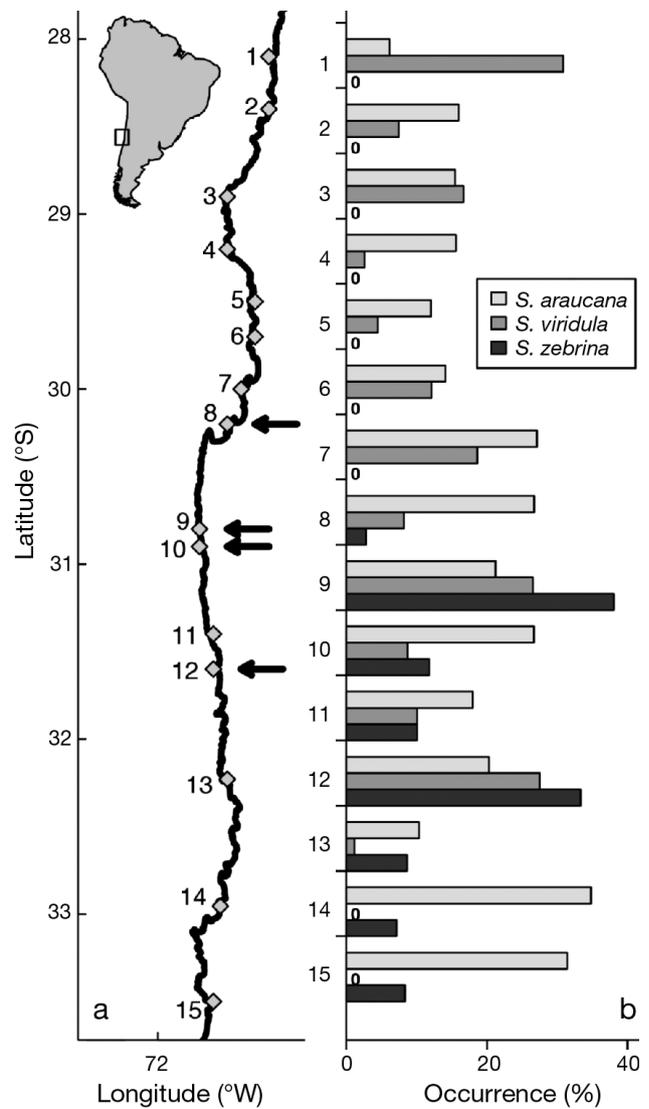


Fig. 1. (a) Sampling sites in central-north Chile, and (b) percentage of occurrence, i.e. percentage of plots where *Scurria viridula*, *S. zebrina* and *S. araucana* were found. Arrows: small-scale sampling sites within the overlap zone (8: Guañaqueros; 9: Limarí; 10: Punta Talca; 12: Huentelauquén)

(e.g. Branch 1976, Underwood 1976, Aguilera & Navarrete 2011). In each site and for each species, we selected two 4 × 2 m areas in which we randomly measured ~260 NN distances of conspecific and 377 NN distances of heterospecific limpets, i.e. from *Scurria zebrina* to *S. viridula* and from *S. viridula* to *S. zebrina*, respectively. Heterospecific distances were estimated separately in 1 of each 4 × 2 m areas selected. This last analysis was not conducted for *S. araucana* due to its low abundances in some sites. In this way, we completely mapped the rocky platforms at the study sites. Surveys were performed during daytime low tides, corresponding to the resting phase of the

Scurria species. Individuals of the focal *Scurria* species tend to use the same home scar after foraging excursions cease, which can be persistent through time (M. A. Aguilera unpubl. data, and see Aguilera & Navarrete 2011 for homing in *S. araucana*). Therefore, the individual spatial distribution should be persistent over daily to monthly temporal scales.

Body size structure

To evaluate interspecific similarity in size structure of focal species, we estimated body sizes of *Scurria viridula*, *S. zebrina* and *S. araucana* in the field by measuring the shell length of all individuals present on the surveyed platforms at each site (see 'Small-scale spatial structure', above). Sampling was conducted during summer and winter in 2010 and 2011 and was aided by a mark-recapture study conducted in Guanaqueros and Punta Talca to ensure correct identification of both adult and juvenile individuals in the field (see Supplement 1).

Data analysis

For the 4 study sites located within the overlap zone, we examined the local spatial structure of each *Scurria* species measured with the 30 × 30 cm quadrats, *Mazzaella laminarioides* and bare rock by using Moran's *I* spatial correlograms (Fortin & Dale 2005). No analyses were conducted for *S. zebrina* at Guanaqueros because of low densities of this species at this site (Fig. 1a). Correlogram data and interpretations were restricted to lag distances shorter than half the transect length, as statistical estimations over longer distance classes have curtailed degrees of freedom (e.g. Rossi et al. 1992). Probabilistic significance of autocorrelation coefficients was determined by means of permutations (Manly 1997), where we randomly shuffled our observed dataset and recalculated the autocorrelation statistic 1000 times for each lag. Significance levels for individual lags were examined after checking whether the correlogram contained at least one significant correlation, with probabilities adjusted with Bonferroni correction for multiple comparisons ($\alpha' = 0.05$ per number of distance classes). As needed, data were normalized to zero mean and unit variance to reduce the effects of outliers. Data of *M. laminarioides* and bare rock were presence-absence transformed. It is worth noting that significance at the shorter distance class considered in our correlograms (i.e. 30 to 40 cm) indicates

that individuals are aggregated at the quadrat scale, while significance at larger distance classes suggests a dispersive pattern of distribution. A random distribution is observed when the correlogram fluctuates around zero or is negative at the shorter distance class considered (Fortin & Dale 2005).

The interspecific spatial associations between focal species estimated through the quadrat sampling method were analysed using cross-correlations (Fortin & Dale 2005). Confidence intervals (95%) of cross-correlation coefficients for different distance lags were estimated through bootstrapping (Manly 1997). To determine habitat use at the 900 cm² scale, we estimated the lag 0 Pearson's spatial correlation (*r*) between each limpet species density and the percentage cover of algae, sessile invertebrates and bare rock across quadrats in each site. Significance was calculated through a *t*-test corrected for the effective degrees of freedom based on lag 1 autocorrelation estimates of Moran's *I* (Dutilleul 1993). No spatial analyses involving *Scurria zebrina* at Guanaqueros were conducted due to insufficient densities of the focal species observed at this site (see Fig. 2a). Analyses were implemented in the software PAS-SaGE v.2 (Rosenberg & Anderson 2011).

We calculated mean conspecific NN distances (i.e. dA , where d is the distance in centimetres from a given individual to its nearest neighbour and A is the total survey area) comparing this measure with the expected (E) NN distance based on a random distribution model: $dE = 1/2\sqrt{\rho}$, where ρ is the density of individuals within the survey area (Clark & Evans 1954). Thus, we calculated the R index = dA/dE , which provides a measure of aggregated (R close to 0), random (R close to 1) or maximum spacing (R close to 2.15 for perfect over-dispersion) distribution (Clark & Evans 1954, and see also Fortin & Dale 2005). The R index provides the general form of the spatial distribution of the focal species, but NN distances are non-independent because of the presence of reflexive points (i.e. when 2 ind. are mutually nearest neighbours; Cox 1981), which complicates tests of statistical significance (Meagher & Burdick 1980). We used a similar approximation as with autocorrelation, where we randomly shuffled our dataset and recalculated the R index 1000 times.

Interspecific NN distances are dependent on conspecific distributions and are difficult to analyse because of the presence of reflexive points (see above) and shared nearest neighbours that occurs when 2 or more points have the same neighbour; thus, we use 2 complementary methodologies for analysis. (1) We visually examined NN distributions and differences

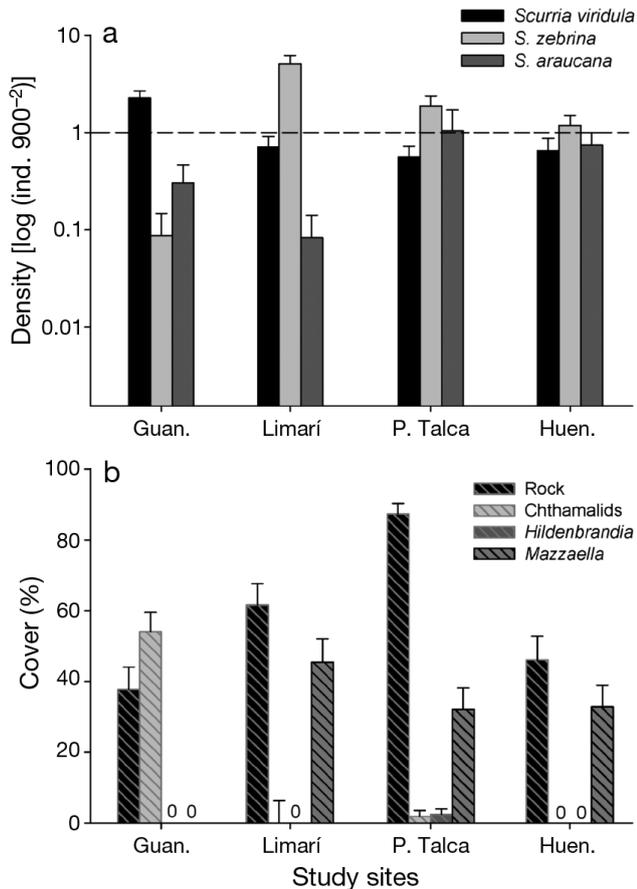


Fig. 2. (a) Density of the focal *Scurria* limpets present in the mid-high intertidal level at 4 sites located in the overlap zone (see Fig. 1), and (b) percentage cover (%) of the most important habitat types recorded in these sites. Note the log scale of the y-axis in (a). Means + SE. Dotted line: 1 ind. 900 cm⁻²

in mean and median heterospecific distances estimated from *Scurria zebrina* to *S. viridula* and vice versa for each study site. (2) We estimated the degree of spatial segregation between species using the method proposed by Pielou (1961) and further improved by Dixon (1994), based on the observed relative abundance of conspecific and heterospecific neighbours. Thus, 2 species are segregated if the ratio of conspecific to heterospecific nearest neighbours is greater than expected by chance and are attracted when this ratio is less than expected (Pielou 1961, Dixon 1994). We used the S_{ij} index proposed by Dixon (1994), based on the observed frequency of conspecific neighbours relative to the expected frequency of each: $S_{ij} = -\log[N_j \cdot (n_{ij}/n_j) \cdot (N_i - 1)^{-1}]$, which corresponds to the simplified measures of interspecific segregation presented by Dixon (1994), where n_{ij} is the number of grazer species i with conspecific neighbour i ; n_{ji} is the number of grazer species i with heterospecific neighbour j ; and N_i and N_j

are the total number of individuals considered of species i and j , respectively. In this case, i corresponds to *S. zebrina* and j corresponds to *S. viridula*. A value of $S_{ij} < 0$ indicates interspecific spatial segregation, $S_{ij} > 0$ indicates an attraction or aggregation and $S_{ij} = 0$ indicates a random pattern. To test the significance of the segregation index, we use Dixon's C statistic (Dixon 1994), which takes into account the presence of both reflexive and shared nearest neighbour points. This test has an asymptotic chi-squared distribution with 2 degrees of freedom (see also Coomes et al. 1999). According to differences in intraspecific patterns between *S. zebrina* and *S. viridula* (see results on NN conspecific distances), we assumed here that $S_{ij} \neq S_{ji}$, and then both indexes and their corresponding tests were estimated.

To test differences in shell length between *Scurria viridula* and *S. zebrina*, we constructed a 2-way contingency table based on the size classes (counts) of the study species recorded at each study site, performing a Pearson's chi-squared exact test.

RESULTS

Geographic patterns

Long-term datasets (i.e. from 1998 to 2011) of surveys conducted at 10 sites across the transition zone showed that *Scurria zebrina* is not present north of 30° S, while the polar distribution edge of *S. viridula* is around 32° S (Fig. 1a). Thus, these species co-occurred for only ~250 km of coastline in central-north Chile (Fig. 1). The limpet *S. araucana* was observed at all study sites north and south of the overlap zone of *S. viridula* and *S. zebrina* (Fig. 1).

Spatial patterns at the overlap zone

Abundance of the focal species was variable across sites in the overlap zone. Densities of *Scurria zebrina* were lowest at Guanaqueros (mean ± SE: 0.087 ± 0.06 ind. 900 cm⁻²) and highest at Limarí (5.083 ± 1.134 ind. 900 cm⁻²) (Fig. 2a). In contrast, density of the limpet *S. viridula* was highest at Guanaqueros (2.26 ± 0.413 ind. 900 cm⁻²), at the northern edge of the overlap zone (Figs. 1 & 2), and relatively constant at the other sites where it occurred (Fig. 2a). *S. araucana* showed the lowest density of the 3 limpets sampled in Limarí (Fig. 2a; 0.080 ± 0.0576 ind. 900 cm⁻²).

Body sizes of *Scurria viridula* and *S. zebrina* sampled between late summer and early winter were

similar across the sites (Fig. 3). Median shell length ranged from 2.3 to 2.8 cm for *S. viridula* and 2.7 to 3.1 cm for *S. zebrina* (see arrows, Fig. 3). Accordingly, shell length was independent of the site and focal species considered (Pearson's χ^2 test: 3.176, df = 2; $p = 0.204$). Maximum shell lengths of *S. viridula* and *S. zebrina* were recorded in Punta Talca, with individuals reaching 6.3 and 5.8 cm, respectively (Fig. 3). Smaller individuals were observed in most sites and ranged from 1.27 to 1.33 cm shell length for both species. *S. araucana* showed small size in all sites compared with the other species, with a median shell length ranging from 1.1 to 1.8 cm (Fig. 3c,f,i).

Intraspecific spatial distribution across different scales

At the quadrat scale (900 cm²), spatial autocorrelation analyses showed that individuals of *Scurria viridula* and *S. zebrina* were not significantly autocorrelated at most distance classes (Fig. 4a,b); thus, both species generally showed random patterns of distribution. At 1 site (Guaqueros), however, *S. viridula* showed an aggregated distribution, with significant autocorrelation at distance classes of ~30 to 40 cm

(Fig. 4a). Spatial abundance distribution of *S. araucana* was aggregated at the smaller distance classes (i.e. 30 to 40 cm) in Guaqueros and Punta Talca but was random at Huentelauquén (Fig. 4c). Abundance of *S. araucana* was very low in Limarí, and the global correlogram could not be appropriately interpreted at this site.

At the individual-to-individual scale, distribution of NN distances to conspecifics showed differences in the individual distribution for *Scurria viridula* and *S. zebrina* in Limarí (Fig. 5a,b). At this site, individual distribution of *S. viridula* was random with an R index of 1.182 (Fig. 5a,b), while for *S. zebrina*, this pattern was aggregated (median NN value = 6.0 cm) with an R index value around 0.0. Contrastingly, individual distribution patterns of *S. viridula* and *S. zebrina* at Punta Talca were random, as confirmed by R index values around 1 for these species. At this site, median NN distances to conspecifics were 15.0 and 9.0 cm for *S. viridula* and *S. zebrina*, respectively (Fig. 5d,e). In Huentelauquén, distances to conspecific neighbours were random for *S. viridula* and aggregated for *S. zebrina*, with median distances of 11.6 and 2.9 cm for these species, respectively (Fig. 5g,h). For *S. araucana*, the conspecific distribution pattern was aggregated in Limarí, with a median NN distance of 6.5 cm

(Fig. 5c). At Punta Talca and Huentelauquén, conspecific distribution was found to be random according to a R index close to 1.0 and with median NN distances of 11.0 cm and 9.0 cm, respectively (Fig. 5f,i).

Interspecific spatial structure across different scales

Spatial cross-correlation between abundances of *Scurria* limpets estimated through the quadrat sampling method showed contrasting patterns between species pairs at the different distance classes considered (Fig. 6). For *S. viridula* and *S. zebrina*, correlograms showed non-significant cross-correlations at small distance classes (30 to 40 cm) and significant positive cross-correlations at distances of ~150 to 180 and 120 to 150 cm at Limarí and Punta Talca, respectively (Fig. 6a,b). At Huentelauquén, we found 1 significant positive cross-correlation at the smallest distance class (i.e. 30 to

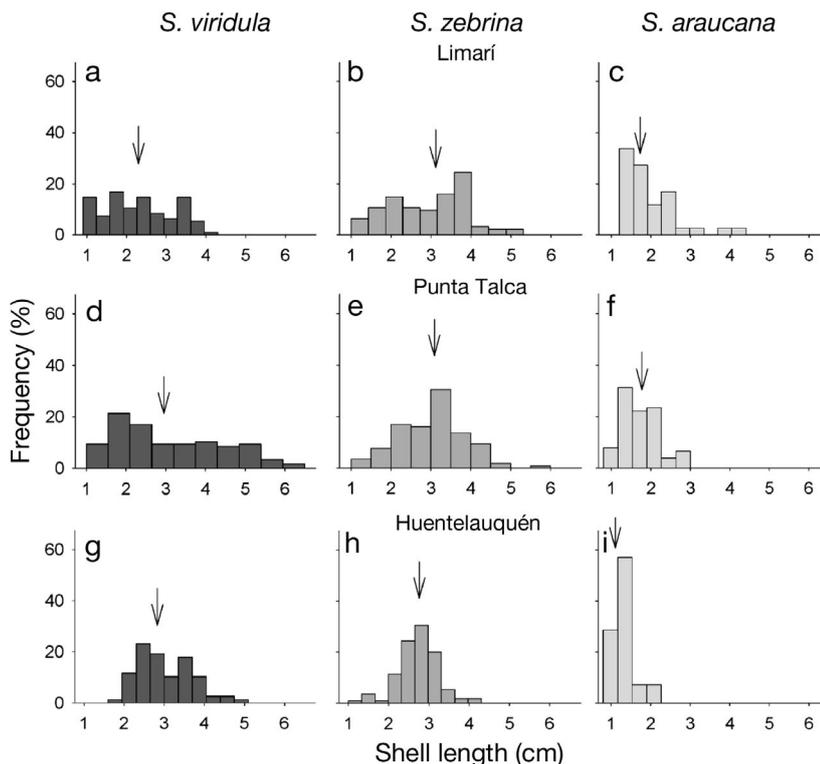


Fig. 3. Shell length frequency (%) for (a,d,g) *S. viridula*, (b,e,h) *S. zebrina* and (c,f,i) *S. araucana* in Limarí, Punta Talca and Huentelauquén. Arrows indicate median length

40 cm, the quadrat level, Fig. 6c). No significant cross-correlations were observed at any site between *S. viridula* and *S. araucana* (○, Fig. 6a,b,c). Similarly, the species *S. zebrina* and *S. araucana* were uncorrelated at all study sites (○, Fig. 6a,b,c). Hence, both

species showed a spatial abundance distribution pattern independent of *S. araucana*.

The analyses using individual-to-individual distances showed that the values of the segregation index were generally in agreement with the observed median and mean values of heterospecific NN distances (Fig. 7). *Scurria zebrina* tended to maintain a segregated pattern from *S. viridula*, with median distances to *S. viridula* neighbours of 27.6, 23.0 and 13.0 cm in Limarí, Punta Talca and Huentelauquén, respectively (Fig. 7a,c,e). The segregation S_{ij} index was negative for all sites, indicating that individuals of *S. zebrina* tended to stay closer (i.e. aggregated) to conspecifics than individuals of *S. viridula* (Fig. 7a,c,e). Accordingly, the test of segregation was significant for all sites (Dixon's C statistic; Limarí: $\chi^2 = 7.174$, $p = 0.030$; Punta Talca: $\chi^2 = 9.031$, $p = 0.010$; Huentelauquén: $\chi^2 = 6.260$, $p = 0.040$; see asterisks in Fig. 7a,c,e). When estimating heterospecific NN distances from *S. viridula* to *S. zebrina*, we found median distances of 13.0, 16.8 and 7.1 cm in Limarí, Punta Talca and Huentelauquén, respectively (Fig. 7b,d,f). The segregation index was negative in Limarí and Punta Talca, indicating a potentially segregated distribution pattern, and positive in Huentelauquén, indicating attraction to heterospecifics, but the test of segregation was not significant for any site (Dixon's C statistic; Limarí: $\chi^2 = 0.905$, $p = 0.640$; Punta Talca: $\chi^2 = 2.756$, $p = 0.250$; Huentelauquén: $\chi^2 = 0.344$, $p = 0.840$; Fig. 7b,d,f).

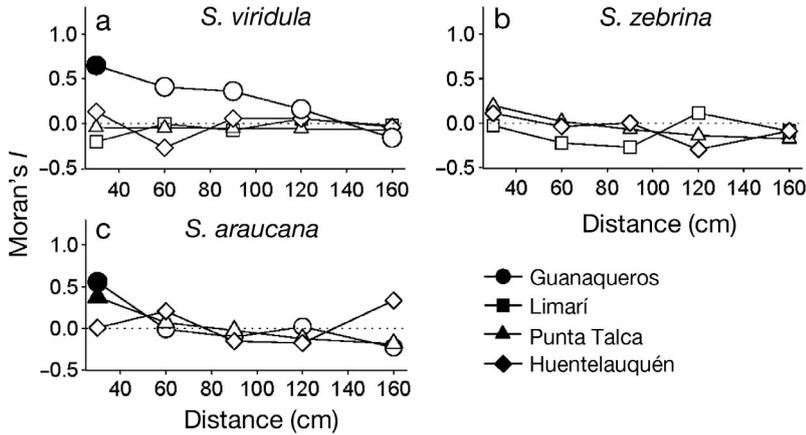


Fig. 4. Moran's I spatial correlograms based on density data for the 3 focal grazers: (a) *Scurria viridula*, (b) *S. zebrina* and (c) *S. araucana*. Symbols: solid = significant correlation ($\alpha = 0.05$) after random permutation test (1000 permutations) and Bonferroni correction, open = non-significant correlation

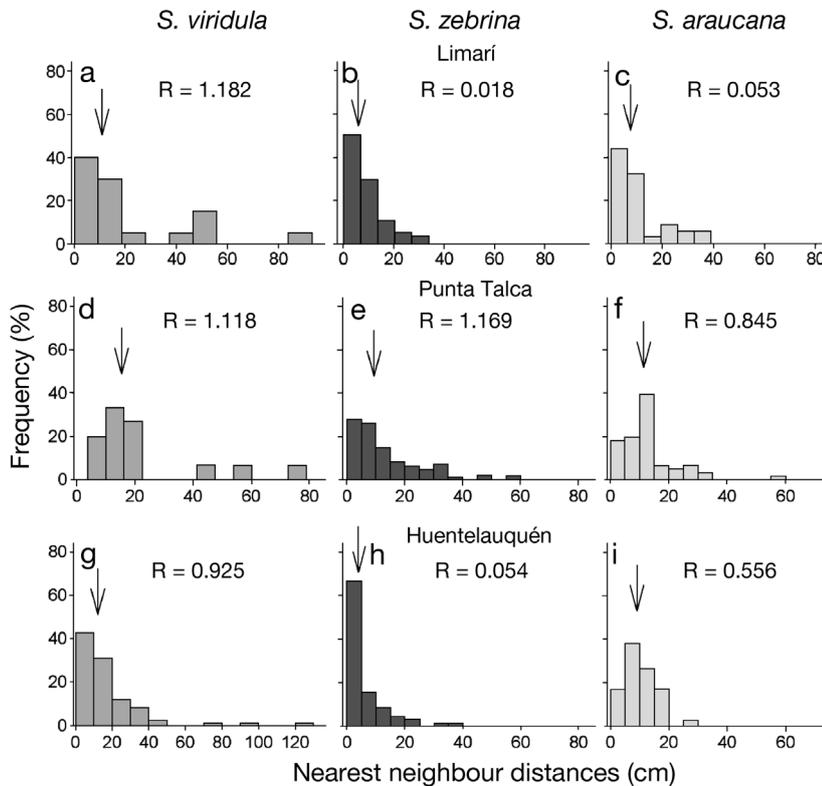


Fig. 5. Frequency (%) histograms of nearest neighbour (NN) linear distances to conspecifics of the 3 study species, (a,d,g) *S. viridula*, (b,e,h) *S. zebrina* and (c,f,i) *S. araucana*, conducted at Limarí, Punta Talca and Huentelauquén. The R index (Clark & Evans 1954) is presented, where values close to 0 indicate an aggregated pattern and those close to 1 indicate a random pattern of distribution. Arrows indicate median nearest neighbour distance

Habitat type and *Scurria* spatial patterns

Spatial correlations between *Scurria* densities and habitat types were variable across sites (Table 1). Strong positive and significant correlation was observed for *Scurria viridula* and bare rock at Guanaqueros, which coincides with a significant negative association with chthamalid barnacles (Table 1). The positive association between *S.*

viridula and bare rock was observed at the other sites, but correlations were generally weak and non-significant. Similarly, *S. zebrina* densities showed a significant positive spatial correlation with *Mazzaella laminarioides* in Limarí, and this pattern was not significant in the other sites (Table 1). No significant correlations were observed between *S. zebrina* densities and bare rock cover at any site (Table 1). *S. araucana* densities showed no significant correlations with any habitat type in any site (Table 1).

DISCUSSION

We showed that *Scurria viridula* and *S. zebrina* coexisted and reached similar densities and body sizes across a narrow geographic zone in central-north Chile, which corresponds to the edge of their geographic ranges. Intraspecific spatial distribution, observed at the quadrat scale (i.e. 900 cm²), was random for *S. viridula* and *S. zebrina* in most sites. However, *S. viridula* intraspecific distribution was aggregated at 1 site (Guañaqueros), where *S. zebrina* showed extremely low densities. In contrast, our observations based on individual-to-individual distances, i.e. NN distances, showed an aggregated distribution for *S. zebrina* at Limarí and Huentelauquén. *S. araucana* showed aggregated intraspecific patterns at the quadrat scale at 2 sites and also at the smaller scale (NN distances) at 1 site, namely Limarí. This agrees only partially with our hypothesis (1) about similarity in abundance and spatial distribution patterns of *S. viridula* and *S. zebrina*. Regarding interspecific distribution, *S. zebrina* segregated from *S. viridula* at the individual-to-individual scale, but this last species showed no clear interspecific pattern. No interspecific spatial association between the species at the edge of their ranges and *S. araucana* was detected at the quadrat scale, in accordance with hypotheses (2) and (4). In general, focal

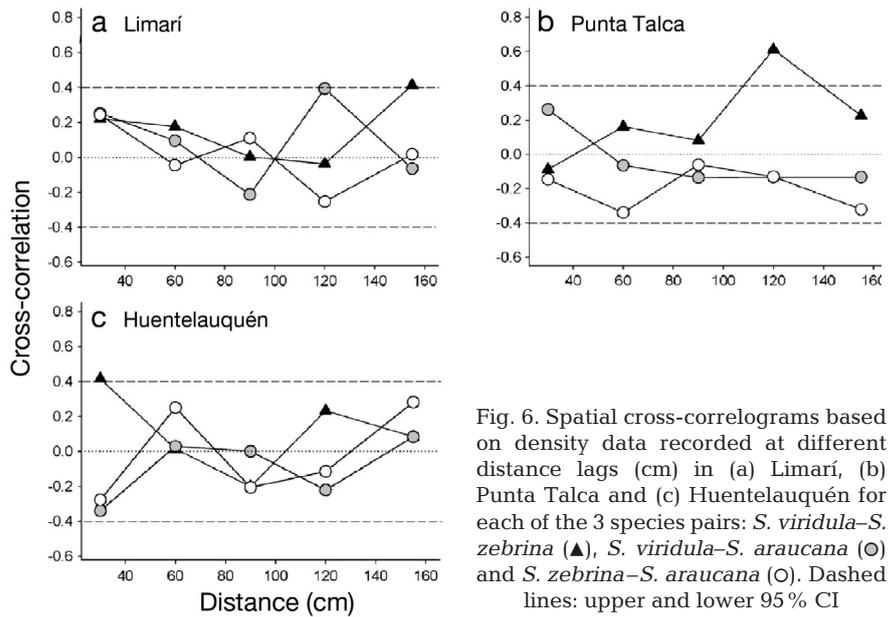


Fig. 6. Spatial cross-correlograms based on density data recorded at different distance lags (cm) in (a) Limarí, (b) Punta Talca and (c) Huentelauquén for each of the 3 species pairs: *S. viridula*-*S. zebrina* (▲), *S. viridula*-*S. araucana* (○) and *S. zebrina*-*S. araucana* (○). Dashed lines: upper and lower 95% CI

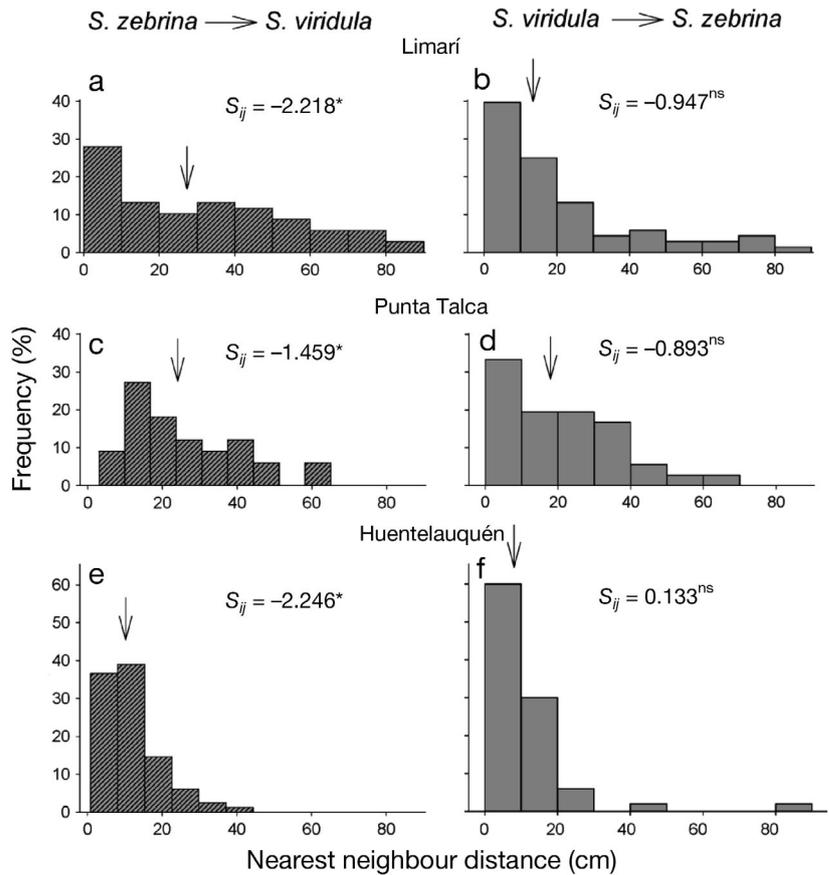


Fig. 7. Frequency (%) histograms of nearest neighbour (NN) linear distances to heterospecifics for *S. zebrina* (denoted by *i*) and *S. viridula* (denoted by *j*) recorded at Limarí, Punta Talca and Huentelauquén. Arrows indicate target heterospecifics from (a,c,e) *S. zebrina* to *S. viridula* and (b,d,f) *S. viridula* to *S. zebrina*. Segregation index is presented in each case (S_{ij} and S_{ji} , respectively). * $p < 0.05$; ns: non-significant. See text for further details

Table 1. *Scurria viridula*, *S. zebrina*, and *S. araucana*. Statistics of Pearson's spatial correlation (r) of limpet abundance and habitat type percent cover ($\log[x + 1]$ -transformed data). *: significant r values ($\alpha = 0.05$) after performing a modified t -test corrected by the degree of autocorrelation in the datasets. -: conditions in which a spatial correlation could not be computed. GUAN: Guanaqueros; LIMA: Limarí; PTAL: Punta Talca; HUEN: Huentelauquén. *M. l.*: *Mazzaella laminarioides*

Species	Habitat type	Site			
		GUAN	LIMA	PTAL	HUEN
<i>S. viridula</i>	<i>M. l.</i>	-	-0.34	-0.005	-0.066
	Bare rock	0.527*	0.231	0.185	0.078
	Barnacles	-0.496*	-	-	-0.163
<i>S. zebrina</i>	<i>M. l.</i>	-	0.415*	0.04	0.029
	Bare rock	0.034	-0.13	0.082	0.012
	Barnacles	0.006	-	-	-0.075
<i>S. araucana</i>	<i>M. l.</i>	-	-0.098	0.175	0.213
	Bare rock	-0.297	0.037	0.038	-0.097
	Barnacles	0.003	-	-	0.178

species loosely resembled the spatial distribution of major habitat types characteristic of mid-high intertidal levels, which showed an aggregated distribution (Fig. S2.1 in Supplement 2), rejecting hypothesis (3). We suggest that broad-scale processes determining species' range edges may also influence intraspecific spatial structures of parapatric species, differentiating them from spatial patterns of species found at the centre of their distribution, and that small-scale segregation may benefit local coexistence. Here, we discuss the importance of interspecific competition for space and habitat suitability in partitioning the spatial niche at the species' edge of geographic distribution and the potential consequences for species range shift.

Geographic range edge and abundance patterns

According to our results, *Scurria viridula* and *S. zebrina* were in most cases more abundant across the overlap zone than outside of it. Increased abundance towards the edge of the range agrees with models indicating increased population size in edge populations (see Sagarin & Gaines 2002 for review) but contrasts with whole-range abundance patterns observed for other limpets and that are consistent with the abundant-centre hypothesis (e.g. *Lottia gigantea*; Fenberg & Rivadeneira 2011). Likely, range edge dynamics of the focal species may help to unravel range shifts as a consequence of climate variability (see Sagarin & Gaines 2002 for review).

There is information suggesting that *Scurria viridula* has expanded its range edge south of 30° S (Rivadeneira & Fernández 2005). Recent gradual changes of

climatic-oceanographic conditions in temperate coasts (Harley et al. 2006, Helmuth et al. 2006, Hawkins et al. 2008), exceptional events like variation in sea surface water salinity and temperature, or sea current intensity seem to influence range shifts of different intertidal species (Lima et al. 2006, Lima & Wetthey 2012, Sousa et al. 2012). However, information about decadal changes in ocean temperature in the study region does not support a poleward range expansion of *S. viridula* (Falvey & Garreaud 2009). No information on distributional range changes has been reported for *S. zebrina* or *S. araucana*. Our results on spatial distribution patterns suggest that *Scurria* limpets have flexible habitat requirements, so that *S. zebrina* and *S. viridula* may display demographic variability in their range edges. *S. zebrina* abundance was positively related to the abundance of the corticated alga *Mazzaella laminarioides* at 1 study site, which also reaches its equatorial edge of the range at the overlap zone (Broitman et al. 2011). Positive herbivore-plant interactions have been established for *S. viridula* and *M. laminarioides* in this zone (M. A. Aguilera, N. Valdivia & B. Broitman unpubl. obs.), but it is unclear whether the alga enhances the abundance or facilitates *S. zebrina* local distribution, providing protection against desiccation or heat stress (discussed below). Recent studies suggest that positive interactions can significantly influence species distribution, especially enhancing fitness at the edge of their geographic distribution (Stanton-Geddes et al. 2012). Thus, further studies should take into account the potential effect of the corticated alga to facilitate persistence of *S. zebrina* populations at the overlap zone.

Intraspecific spatial distribution and habitat use

Gregarious patterns observed in different animal species can be related to food and shelter distribution (e.g. Underwood 1976, Garrity 1984, Chapman & Underwood 1992, Underwood & Chapman 1996, Aguilera & Navarrete 2011), while dispersive (i.e. uniform) spatial distribution can be set by interference competition through changes in individual behaviour (Branch 1975, 1976, Underwood 1976, Iwasaki 1992). We found scarce correspondence of the focal species with the habitat type considered, with *Scurria viridula* using more frequently bare rock patches than other habitat and *S. zebrina* abundance being more related to clumps of the corticated alga *Mazzaella laminarioides*. However, these patterns were not consistent through the overlap zone, suggesting that processes determining small-scale distri-

bution of species could still operate differentially at each site (e.g. Denley & Underwood 1979, Fraschetti et al. 2005). Indeed, spatial distributions, measured at the quadrat scale, of both bare rock and *M. laminarioides* were patchy (Fig. S2.1a in Supplement 2), while those of limpets were mostly random. Thus, spatial distribution of *Scurria* limpets may resemble other local habitat components not considered in our sampling. For example, habitat selection has been directly related to behavioural mechanisms regarding preference and accessibility to areas for foraging and resting (Crowe & Underwood 1998, Olabarria et al. 2002, Underwood et al. 2004). Individual spatial distribution of the focal species could reflect food distribution (Branch 1976), small-scale topography or thermally suitable areas for resting (Garrity 1984). Our surveys were conducted during the resting phase of species, i.e. low tides, when substrate was commonly dry. Previous studies suggest that resting habitats could protect individuals against desiccation, heat stress or dislodgement by waves (e.g. Garrity 1984, Williams & Morrill 1995, Gray & Hodgson 1997, Harper & Williams 2001, Aguilera & Navarrete 2011, 2012b). Individuals of *S. viridula* used flat rock platforms while resting and were rarely seen occupying crevices during the study. The limpet *S. zebrina* is commonly seen resting under *M. laminarioides* canopies, consistent with the positive correlation found with this alga at Limarí. This also agrees with conspecific NN distances that revealed gregarious patterns for *S. zebrina* at Limarí and Huentelauquén. Individual behavioural choice of thermally suitable microhabitats in molluscs can alter their distribution at different spatial and temporal scales (e.g. Garrity 1984, Harper & Williams 2001, Muñoz et al. 2005, Chapperon & Seuront 2011b). *S. viridula* showed a random pattern at resting, but some evidence of gregarious behaviour was observed at 1 site, Guanaqueros, which commonly has higher air temperature than our southern sites (Garreaud et al. 2011). Likely, thermal habitat suitability could be a key factor determining abundance distribution of *Scurria* species, as documented for other intertidal limpets (e.g. *Lottia gigantea*; Miller et al. 2009). Further studies should take into account potential differentiation in thermal stress tolerances between *Scurria* species in an attempt to complement hypotheses about their potential niche partitioning (e.g. Williams & Morrill 1995, Helmuth et al. 2010).

It has been observed that spatial distribution of grazers can account for small-scale distribution of food resources (Aguilera & Navarrete 2007, Johnson et al. 2008, Díaz & McQuaid 2011). Similarity in the

spatial structure of foraging and abundance distributional patterns of focal species could be relevant to species equivalence or redundancy (sensu Walker 1992) in the magnitude of their functional roles. A recent experimental study conducted in the overlap zone showed the consumptive effect of *Scurria viridula* on the algal community (M. A. Aguilera, N. Valdivia & B. Broitman unpubl. data), which is qualitatively similar to the effect observed for *S. araucana* in central Chile (Aguilera & Navarrete 2012a). This suggests that similarity in grazing effects could be more related to specific traits shared by the *Scurria* genus, e.g. radular morphology and spatial behaviour (e.g. Hawkins et al. 1989, Espoz et al. 2004, Lindberg 2007). Likely, similarity in the spatial distribution of *S. viridula* and *S. zebrina* measured at the quadrat scale, i.e. dozens of centimetres to metres, may further enhance functional similarity in roles of these grazers (Walker 1992, Rosenfeld 2002) and influence food distribution in similar ways. Thus, future studies should examine the level of redundancy in effects in these species to determine their potential functional compensation.

Spatial segregation and coexistence

A mostly segregated spatial distribution pattern at small spatial scales was observed between *Scurria viridula* and *S. zebrina* in the study sites, agreeing well with our stated hypothesis. Consistent interspecific segregation of *S. zebrina* from *S. viridula* was observed through the NN distance method, i.e. at the individual-to-individual scale (few centimetres), and contrasted with the quadrat sampling protocol, which did not show a clear indication of interspecific segregation, i.e. negative correlation, at the smaller scales (30 to 40 cm). This can be because the latter method can only reveal the spatial interspecific structure of limpets from distances >30 cm, while average segregation among individuals occurs at scales ranging from 10 to 27 cm. We found no clear indication of segregation when examining NN distances of *S. viridula* to *S. zebrina*, which was probably related to the strong random distributional pattern of *S. viridula* individuals recorded in all sites (see Fig. 5). Nonetheless, we found that 35 and 47% of *S. viridula* individuals sampled in Limarí and Punta Talca, respectively, showed distances >15 cm from *S. zebrina*. Segregation of *S. zebrina* from *S. viridula* occurred at median distances ranging from 10.3 to 27.6 cm, which, based on median shell sizes of individuals between 2.3 and 3.0 cm, seems to be a signif-

icant spatial scale to reduce the probability of interference between individuals when they start foraging activities (Aguilera & Navarrete 2011). Interference competition for space and shelter is common in this intertidal grazer assemblage (Aguilera & Navarrete 2012b). Small-scale spatial segregation between focal species may compensate for the similarities in size and relative densities observed across the overlap zone, thus facilitating coexistence. Alternatively, differences in microhabitat suitability between species could determine small-scale spatial segregation. In a series of field experiments, Firth & Crowe (2010) showed that mortality and growth rates of 2 *Patella* limpets depended on microhabitat type (emergent rock vs. pools). In that study, no interspecific competition was observed, suggesting that differences in small-scale habitat suitability were the main mechanism causing segregation and coexistence at larger scales between those limpets (Firth & Crowe 2008, 2010). Our results showed no consistent differences in habitat use for *S. viridula* and *S. zebriana* but showed relevant small-scale spatial segregation while at rest. Likely, small-scale variation in thermal suitability (discussed above) and/or topography could be relevant for spatial segregation observed in the overlap zone.

Coexistence mechanisms of similar species is one of the main challenges to understand community structure and biodiversity patterns (Leibold 1998, Chesson 2000). Thus, information of species' life histories and their temporal and spatial distribution patterns provides unique information about niche similarity, compensatory potential and potential extinction at regional scales (Leibold 1998, Mouquet & Loreau 2002). We used a biogeographic transition zone to examine intraspecific spatial distribution and small-scale interspecific coexistence mechanisms in 2 highly related species at the edge of their geographic ranges, which can help to predict their range shift potential. If coexistence between these species in the geographic overlap zone is related to spatial partitioning at small scales (centimetres to metres), as our findings suggest, the potential role of differential environmental stress responses and interspecific competition in determining species range shifts at short temporal scales should be a focus of future research (Goldberg & Lande 2007).

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