Distribution and activity patterns in an intertidal grazer assemblage: influence of temporal and spatial organization on interspecific associations

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ABSTRACT: In consumer assemblages, the organization of individual foraging behavior, as well as spatial distribution, can largely determine environmental risks, and the intensity of intra- and interspecific interactions. We characterized distributional and behavioral patterns of the most common benthic grazers coexisting in the rocky shores of central Chile: the chiton *Chiton granosus*, the pulmonate limpet *Siphonaria lessoni*, the scurrinid limpet *Scurria araucana* and the keyhole limpet *Fissurella crassa*. *C. granosus* and *F. crassa* were strictly nocturnal foragers whereas *S. lessoni* foraged during daytime. Most *S. araucana* individuals foraged at night, but daytime foraging was also common. The spatial distribution at resting varied from aggregated for *C. granosus* and *S. lessoni* to a more dispersive pattern for *F. crassa* and *S. araucana*. *C. granosus* dispersed slightly from aggregation when foraging whereas *S. lessoni* foraged in tight conspecific aggregations. Foraging excursions varied from over 60 cm in *F. crassa* to less than 7 cm in *S. araucana*. Homing behavior ranged from extreme fidelity in *F. crassa* to low fidelity in *S. lessoni*. Positive associations were observed between *C. granosus* and *F. crassa* during resting and foraging whereas negative associations were observed between these species and *S. lessoni*. These general patterns varied little between 2 sites separated by a few kilometers. Interspecific competition might be important in structuring this guild, but it may affect only some species pairs. Direct interference in the use of shelter or while foraging, rather than food exploitation, seems the most likely mechanism. The marked differences in individual behavior among species, despite ample diet overlap, might translate into different functional effects, which should be explored in future experiments.

KEY WORDS: Activity rhythm · Foraging behavior · Interspecific association · Molluscan grazer · Spatial distribution

INTRODUCTION

Theoretical and experimental studies on animal movement and activity patterns have been developed for a variety of species in an attempt to explain and/or empirically relate the spatial distribution of mobile animals to their food resources, environmental conditions, interspecific interactions and, more recently, ecosystem function (Schmitz 2008). A general finding is that,

beyond phylogenetically constrained ('hard-wired') responses (see Webb et al. 2002), landscape heterogeneity as well as long- and short-term changes in resource distribution can influence the organization of foraging in herbivores (see Fletcher & Underwood 1987, Legendre & Fortin 1989, Chapman & Underwood 1992, Rossi et al. 1992, Tilman & Kareiva 1997). But although behavior is a highly labile trait, different species typically exhibit characteristic and contrasting

behavioral patterns (Palmer 1995). Thus, beyond individual and within-species variation, species can adopt different strategies to cope with the same general landscape of environmental and resource (e.g. food, shelter) heterogeneity (Pulliam 1989, Chapman & Underwood 1992, Legendre et al. 1997, Schmitz 2009). These behavioral patterns will in turn have effects on predation risks perceived by individuals, on the spatial patterns they exert on their resources, and on intra- and/or interspecific interactions within their guild.

Within guilds of grazing mollusks, which commonly are the most diverse taxa in temperate and tropical rocky shores (Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Rivadeneira et al. 2002, Coleman et al. 2006), strikingly different activity and movement patterns have been observed among coexisting species (e.g. Branch 1981, Hawkins & Hartnoll 1983 for review). These behavioral repertoires can generate differential patterns of distribution and abundance in the guild (Underwood & Chapman 1996, Chapman 2000, Olabarria et al. 2002) and account for differences in specific grazing impacts, which cannot be inferred from their diets alone (Branch 1981, Chapman & Underwood 1992, Jenkins et al. 2005, Coleman et al. 2006). Comparatively few studies have evaluated how activity and movement patterns relate to intra- and interspecific spatial distributions and how these patterns vary when individuals are actively foraging or resting. This type of information can shed light on the biotic and/or abiotic processes that structure these assemblages and provide the basis for elaborate hypotheses about the role of species in ecosystem function (e.g. Schmitz 2009). For instance, species that present different foraging activities (e.g. diurnal versus nocturnal) are less likely to compete for shelter or engage in direct interference when grazing (Carothers & Jaksic 1984, Loreau 1992), although they could still compete for a common food resource (Jaksic 1982, Carothers & Jaksic 1984). Conversely, a species could compete and interfere with one species while foraging and with a different species or set of species while seeking shelter. Thus, the degree of spatial or temporal overlap during resting and foraging conditions within the guild can be very informative about interspecific interaction strength between species pairs, assemblage structure and the consumption pressure the species exert on their prey.

The coast of central Chile is characterized by a semidiurnal tidal regime of ~1.70 m amplitude and the predominance of rocky shores directly exposed to wave action (Castilla 1981, Finke et al. 2007). Approximately 10 to 24 species comprise the intertidal mollusk grazer assemblage along the coast of Chile (Rivadeneira et al. 2002), with roughly 7 to 9 common species coexisting locally at mid to high intertidal levels (Otaíza & Santelices 1985, Santelices et al. 1986). Extensive analysis of stomach contents and grazer abundance conducted at a site in central Chile showed ample overlap in the diet of the most common species (Santelices et al. 1986), with all species consuming epilithic, green and crustose (calcareous and fleshy) algae. Slight differences in diet between species were partly related to morphological differences in their radula (as suggested by Steneck & Watling 1982), but also to habitat and behavioral differences (Santelices et al. 1986). Slight differences in diet, together with large differences in body size and biomass, can lead to marked differences in the impact these species can have on algal assemblages (see Wieters et al. 2003, Aguilera & Navarrete 2007). Furthermore, previous studies (e.g. Santelices et al. 1986) and field observations suggest patchiness in the micro-scale (cm) spatial distribution of some species, apparently related to the spatial structure of the habitat. Further research on grazer diets conducted by Camus et al. (2008) at multiple sites in northern Chile has highlighted the high frequency (>40%) at which invertebrate items are included in the diet of most grazer species (see also Otaíza & Santelices 1985, Aguilera 2005, Aguilera & Navarrete 2007), including a high representation of individuals of other herbivores within the same guild (Aguilera 2005, Camus et al. 2008). This high level of intraguild predation (sensu Polis & Holt 1992), together with low levels of cannibalism (Camus et al. 2008), suggest that interspecific interactions within the grazer guild might be more important and more complex than previously envisioned.

In the present study, we examined the spatial patterns of distribution and activity of the 4 most common grazer species present in central Chile, which inhabit the mid–low to the high intertidal zone (i.e. 0.5 to 3.0 m), in order to evaluate the spatial and temporal (i.e. behavioral) associations within the molluscan assemblage. We also evaluated the level of variation in activity and spatial patterns between sites located a few kilometers apart and compared them to among-species variability. Considering the ample diet overlap among the 4 species, and potential patchiness in the distribution of some species at micro-scales, we hypothesized that, if interspecific interactions are important: (1) species should exhibit different patterns of diel foraging activity; (2) those that do overlap in activity rhythms should exhibit negative spatial associations while foraging and resting, unless they use different resting microhabitats (e.g. flat surfaces versus crevices); and (3) there should be no spatial associations between gregarious and non-aggregated species during resting, but they could exhibit negative (or positive) associations while foraging.

MATERIALS AND METHODS

Grazer assemblage and study sites. The study was conducted at 2 sites located in central Chile, Pelancura (33° 33′ S, 71° 37′ W) and Las Cruces (32° 43′ S, 71° 38′ W), which are separated by ~5 km. Pelancura is an extensive rocky shore directly exposed to the prevailing southwestern swell. Las Cruces, where most observations were conducted, is located ~500 m south of the marine reserve of the Estación Costera de Investigaciones Marinas (ECIM). This stretch of coastline faces toward the south–southeast whereas Pelancura faces west, and so the latter receives more direct breaking waves than Las Cruces. The sites show a similar intertidal species composition, which conforms well to the general pattern reported for other sites in central Chile (see Santelices et al. 1986, Fernández et al. 2000, Broitman et al. 2001). The most common molluscan herbivores at the mid intertidal levels are chitons (~2 species; Otaíza & Santelices 1985, Aguilera & Navarrete 2007), scurrinid limpets (~2–4 species; see Espoz et al. 2004), fissurellid limpets (~3–4 species; see Oliva & Castilla 1986) and a pulmonate limpet species. In this study we concentrated on the 4 most abundant species in terms of total biomass: the chiton *Chiton granosus*, the pulmonate limpet *Siphonaria lessoni*, the scurrinid limpet *Scurria araucana* and the keyhole limpet *Fissurella crassa*. Additional observations were also conducted on *Scurria ceciliana*, which, in certain habitats (i.e. mussel beds), can be more abundant than *S. araucana*. Because *F. crassa* is commercially exploited, abundance of large adult individuals is generally low at open-access shores compared with in reserves (Oliva & Castilla 1986). Therefore, we also recorded the behavior of large individuals inside the ECIM marine reserve.

Spatial distribution. To quantify grazer density, we counted all individuals in fifty 30 × 30 cm quadrats, haphazardly positioned along 15 m transects at mid-intertidal levels at each study site in October and November 2007, and again in April 2008 at both study sites.

To determine whether individuals were randomly distributed (i.e. spatially independent), aggregated or more uniformly distributed over the platforms, we followed 2 approaches. The first approach was density based. We positioned contiguous quadrats of 3 different sizes (15 × 15 cm, 30 × 30 cm and 50 × 50 cm) along 15 m transects parallel to the shoreline in the mid intertidal zone of Las Cruces and counted the number of individuals of all target species in each quadrat. These preliminary surveys gave us information about the quadrat size ('grain') that was most appropriate to describe distributional patterns of the focal species through autocorrelation analyses (e.g. Fortin & Dale

2005). Briefly, when autocorrelation using the first distance class is not significant (random distribution of grazers in space) or is negative, it is considered an indication that the sampling unit size is larger than the spatial pattern, or that the quadrat size scale includes more than one process (Fortin 1999). Thus, 50 × 50 cm quadrats were considered uninformative for all focal species (results not shown). Quadrats 15 × 15 cm in size were informative only for *Scurria ceciliana*, whereas 30 × 30 cm quadrats were appropriate for all focal species (see 'Results'). Hence, we conducted surveys using 30 × 30 cm quadrats during daytime low tide and the subsequent night-time low tide on the same rocky platforms (45 quadrats for each phase). In addition, the percentage of rock encompassed by crevices was measured using a 30 × 30 cm quadrat with 81 intersection points. A similar procedure was conducted at Pelancura, but for simplicity we present correlograms for Las Cruces only.

The second approach was based on linear interindividual (nearest neighbor, NN) distances (see Clark & Evans 1954, Pielou 1961). Previous studies have used this sampling procedure to describe spatial patterns and interspecific associations in mobile grazers (see Branch 1976, Underwood 1976, Levings & Franks 1982). We delimited 4 adjacent 3 × 3 m areas at Pelancura and Las Cruces and then randomly sampled individuals of each species, measuring the linear distance (cm) to the closest conspecific during the day in one area and at night in the other area (number of individuals sampled for each area: 25 *Fissurella crassa*, 150 *Siphonaria lessoni*, 90 *Chiton granosus* and 50 *Scurria araucana*). In the third and fourth 3 × 3 m areas we recorded NN distances to heterospecific individuals during the day and at night, respectively (individuals sampled for each area: 23 *F. crassa*, 200 *S. lessoni*, 80 *C. granosus* and 52 *S. araucana*). In this manner, we obtained independent data sets for intra- and interspecific NN distances during the day and at night. We measured distances when individuals were motionless, either resting or feeding. Thus, the distribution of individuals could change over time but, through random sampling throughout a tidal cycle, we could compare foraging and resting phases.

Activity rhythms. *Field:* Observations to characterize activity rhythms were conducted at Las Cruces in December 2007 and April to October 2008, and in November and December 2007 and April to June 2008 at Pelancura. A total of 50 adults (100 for *Siphonaria lessoni*) of each species (mean length ± SD: *Chiton granosus* = 5.5 ± 0.37 cm; *Fissurella crassa* = 7.1 ± 3.9 cm; *Scurria araucana* = 2.6 ± 1.2 cm; *S. lessoni* = 0.97 ± 0.07 cm) were marked with bee tags carefully glued directly to the shell (fifth-plate of chitons), without dislodging the individuals from the substratum and caus-

ing as little disturbance as possible. Then, we monitored the number of active (foraging) and inactive (resting) individuals at 15 min intervals for ≥3 h during 2 to 3 consecutive days/nights.

Laboratory: Because of the difficulty of observing individuals during high tides on wave-exposed platforms, we also quantified the activity of individuals under laboratory conditions. Approximately 10 to 12 (20 for *Siphonaria lessoni*) individuals of each species were collected during low tides at Las Cruces and placed in separate 'arenas' at the ECIM laboratory. Experimental arenas consisted of 40×40 cm concrete blocks with a $20 \times 8 \times 4$ cm crevice carved in the center to provide shelter. The arenas were surrounded with a 10 cm high fence made of coarse plastic mesh to prevent animals from abandoning the blocks, and the units were randomly placed inside separate aquaria with running seawater and air. High and low tides were simulated by completely immersing and completely exposing arenas to air following the natural tidal cycle observed at the time of experiments. Food was provided ad libitum in the form of a mix of *Ulva* spp. and fronds of the corticated alga *Mazzaella laminarioides*, which were directly glued to acrylic plates and affixed to concrete blocks. Microalgae were allowed to settle and grow on the block, thus providing an additional source of food. The number of individuals inside the experimental arenas was chosen according to the natural density of individuals observed in the field when animals are resting: 6 *Chiton granosus*, 10 *S. lessoni*, 2 *Scurria araucana* and 2 *Fissurella crassa*. There were 2 replicates per species. We recorded the number of active individuals at 3 h intervals throughout the day and night for 7 consecutive days.

Displacement and homing behavior. To describe the spatial extension of displacement of individuals while foraging and to quantify the degree of homing behavior (resting place fidelity), we used 2 different but complementary methodologies. First, we recorded changes in the position of marked individuals (the same individuals as those used for assessing activity rhythms in the field) using triangulation in an *x–y* coordinate system (Focardi & Chelazzi 1990). To this end, we fixed a 5 m measuring tape to a gently sloping 13 m platform located at Las Cruces and registered the position of individuals along this *x*-axis. With another measuring tape, extended perpendicular to the first axis, we recorded the position of the individuals along the *y*-axis. The position of individuals was recorded every 12 h, according to the resting–foraging phases observed for most species, during diurnal and nocturnal low tides for 7 consecutive days. Displacement was calculated as the minimum Euclidean distance (diagonal) between consecutive positions. The activity phase for nocturnal foragers (see 'Results') was defined

as the change in position between the diurnal initial location (D_j), the nocturnal location (N_j), and the following diurnal location (D_{j+1}) (Focardi & Chelazzi 1990). For diurnal foragers, the initial location was nocturnal (N_j).

Second, to obtain more precise estimates of displacement and homing behavior, we recorded the distance (paths) traveled by marked individuals (the same individuals as those used for assessing activity rhythms in the field) at intervals of 15 to 30 min for 3 to 5 h during the low tide, over 5 to 7 consecutive days. The distance traveled was measured from the site where individuals were observed inactive at the first low tide (resting site), which was marked with epoxy and considered as a ~5 cm diameter around the individual, in the case of solitary individuals, and as an oval ca. 5 to 10 cm in diameter around a clump of individuals in the case of aggregations. Observations were conducted during 2 separate weeks in April 2008 for *Scurria araucana* and *Siphonaria lessoni* (Las Cruces), and during 2 separate weeks in April 2009 for *Chiton granosus* and *S. lessoni* (Las Cruces). For *Fissurella crassa*, observations were conducted during 1 wk in October, November and December 2008. Because most *F. crassa* marked at Las Cruces were lost (probably to human gathering), we conducted observations on this species inside the ECIM marine reserve. Although studies on other systems have shown seasonal variation in behavioral patterns (e.g. Gray & Hodgson 1997), we did not detect differences in spatial patterns, activity rhythms or displacement distances among surveys or in comparison with previous studies by Serra et al. (2001) on *F. crassa* inside the ECIM marine reserve or by Aguilera & Navarrete (2007) on *C. granosus* on other exposed platforms. Therefore, data from different surveys were pooled for analyses (see below). With this information we computed an index of relative homing error (RHE) (Focardi & Chelazzi 1990) as: RHE = HE/L, where HE corresponds to homing error (i.e. D_j minus D_{j+1} for nocturnal foragers, and N_j minus N_{j+1} for diurnal foragers), and L = length of foraging excursion. Animals with RHE = 0 exhibit a strong homing performance and RHE = 1 a complete dispersive pattern.

Data analysis. The spatial structure of grazer density was analyzed using Moran's *I* spatial correlograms (Sokal & Oden 1978, Fortin & Dale 2005) separately for each species and day/night surveys. As recommended (Rossi et al. 1992, Erlandsson et al. 2005), we only interpreted distances less than half the transect length because correlograms do not represent significant information at lags longer than this scale because of the decrease in degrees of freedom (few distance pairs) (Legendre & Fortin 1989). To determine whether autocorrelation coefficients were significant at α = 0.05, we used bootstrapping (Manly 1997), which com-

pares the autocorrelation statistic (Moran's *I*) calculated for the observed data with the distribution of values obtained by randomly sampling the data set and recalculating the coefficients 1000 times. Before examining individual significance values in the correlogram, we performed a global test by checking whether the correlogram contained at least one significant correlation after probabilities were adjusted using a Bonferroni correction for multiple tests ($\alpha = 0.05$/number of distance classes). Before analyses, data were normalized to zero mean and unit variance to remove outliers. To evaluate the degree of positive/negative spatial association among grazer species and between grazers and crevices (percent cover at the 30×30 cm scale), we used simple Pearson linear correlations (r).

In general, NN distances are difficult to analyze by conventional statistics because of non-independence due to the existence of reflexive NN pairs (i.e. when 2 points are mutual nearest neighbors; see Cox 1981). Moreover, changes in mean or median distance between conditions (day/night) or species can occur because of changes in distribution or density, which makes it difficult to interpret results of null hypothesis tests. Therefore, we first visually examined the distribution of conspecific NN distances between the resting and foraging phases, among species and between the 2 sites. We determined the general form of the spatial distribution by calculating the mean NN distance (*dA*, where *d* is the distance in cm from a given individual to its nearest neighbor and *A* is the total survey area) and compared it with the expected (*E*) NN distance based on a random distribution model: $dE = \frac{1}{2}\sqrt{\rho}$ where ρ is the density of individuals within the survey area (Clark & Evans 1954). Thus, the *R*-statistic = *dA*/*dE* provides a measure of the level of aggregation (*R* close to 0) or random (*R* close to 1) or uniform (*R* close to 2.15 for perfect overdispersion) distribution (Clark & Evans 1954, see also Fortin & Dale 2005). Because no large differences were observed between sites (see 'Results'), for the sake of space we present NN distribution figures for Las Cruces only.

Interspecific NN distances are also complex to analyze because the expected distance between 2 species, in the absence of any interaction, depends on the distributions of the 2 intraspecific distances (Dixon 1994). Therefore, we used 2 complementary approaches. First, we visually examined NN distributions and changes in the median and mean intra- versus interspecific distances during resting and foraging. Second, we estimated the degree of segregation between all possible pairs of species during resting and foraging following the general method of NN abundance proposed by Pielou (1961). The method is based on the relative abundance of conspecific and heterospecific neighbors within a certain distance from focal individ-

uals. Thus, 2 species are segregated if the ratio of conspecific to heterospecific nearest neighbors is greater than expected by chance and attracted when the ratio is less than expected. The S_{ij} index proposed by Dixon (1994), based on the observed frequency of conspecific neighbors relative to the expected frequency of each species was calculated as: $S_{ij} = \log(n_{ii}/n_{ij})/(N_i - 1)/N_j$, where n_{ii} is the number of grazer species *i* with conspecific neighbors *i*, and n_{ij} is the number of grazer species *i* with heterospecific neighbors *j*, N_i and N_j are the total number of grazers considered of species *i* and *j*, respectively. Thus, $S_{ij} < 0$ indicates interspecific spatial segregation, $S_{ij} > 0$ an attraction and $S_{ij} = 0$ a random pattern. A 2 df significance test proposed by Dixon (1994), which takes into account reflexive points, was used to test whether the observed segregation index was different from randomly labeling species positions.

To determine differences in grazer activity in the laboratory trials between immersed individuals (high tide) and those exposed to air (low tide), we conducted a 2-way ANOVA on log + 1 transformed proportions of active animals, considering tide condition and grazer species as fixed factors. Log transformation was necessary to achieve homoscedasticity. For this analysis, we only considered those records in which animals were observed active during the daily phase of activity.

Position of individuals between successive field surveys in the *x*–*y* coordinate system allowed us to estimate orientation of grazer displacements while foraging. Thus, circular statistics (i.e. mean, variance and concentration; Batschelet 1981) were computed with Oriana version 3.0 (Kovach Computing). Mean values are presented ± SE.

RESULTS

Spatial distribution

The grazers *Chiton granosus*, *Siphonaria lessoni*, *Scurria araucana* and *Scurria ceciliana* were the most abundant species in terms of number of individuals at mid intertidal levels at the 2 study sites (Fig. 1), whereas the larger keyhole limpet *Fissurella crassa* was found at much lower densities. Small-bodied species of chitons, snails and limpets, pooled together as 'other grazers' (*Austrolittorina araucana*, *Nodilittorina peruviana*, *Chiton cumingsi*, *C. barnesii* and *Onchidiella* sp.) accounted for 48.2 and 49.6 % of overall molluscan grazer density at Las Cruces and Pelancura, respectively.

Contiguous quadrat sampling revealed different spatial patterns among species and, in some cases, marked diel variability within species. Only small differences in spatial distribution patterns were observed
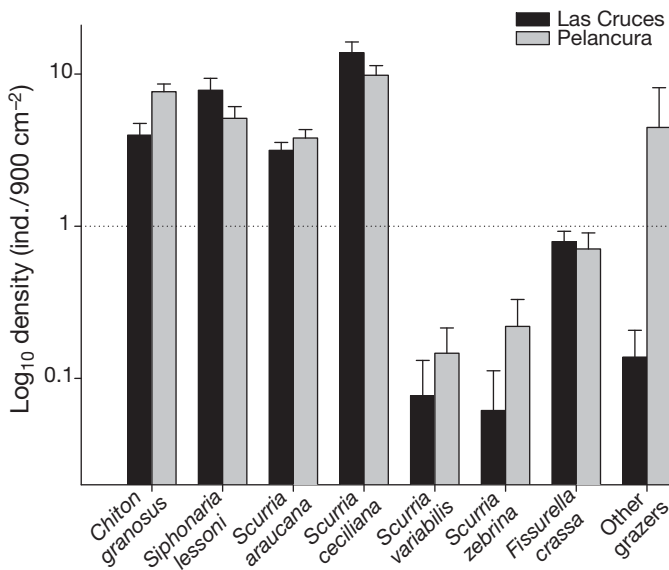
Fig. 1. Benthic grazers (means + SE) measured with 30 × 30 cm contiguous quadrats in the mid-intertidal zone of Pelancura and Las Cruces. 'Other grazers' is the pooled number of small or rare mollusk species at the mid-intertidal level (*Austrolittorina araucana*, *Nodilittorina peruviana*, *Chiton cummingsi*, *C. barnesii* and *Onchidella* sp.). Dotted line: density of 1 ind./900 cm^2

Table 1. Pearson linear correlations (r) between molluscan grazer densities, and between grazer density (ind./900 cm^2) and crevice cover (%) measured in 30 × 30 cm quadrats, for day and night low tides at Las Cruces (first line) and Pelancura (second line). Significant correlations (p < 0.05) are in bold

Siphonaria lessoni	*Scurria araucana*	*Fissurella crassa*	Crevice	
Day				
0.075	−0.104	**0.495**	**0.560**	*Chiton*
−0.090	0.031	**0.327**	0.326	*granosus*
	0.454	−0.179	**0.395**	*S. lessoni*
	0.261	−0.110	**−0.107**	
		0.177	−0.204	*S. araucana*
		−0.055	−0.151	
			0.113	*F. crassa*
			0.216	
Night				
−0.269	0.136	**0.348**	−0.028	*C. granosus*
−0.038	0.031	**0.220**	0.217	
	0.102	**−0.372**	0.157	*S. lessoni*
	−0.001	−0.108	0.012	
		0.188	0.274	*S. araucana*
		0.227	0.226	
			−0.162	*F. crassa*
			−0.066	

between sites (Table 1). Here we describe the correlogram-based patterns observed at Las Cruces and note the differences with Pelancura. During daytime at Las Cruces, the distribution of *Chiton granosus* while resting (see below) was patchy at the scale of the smallest distance class (30 to 60 cm; Fig. 2b) and no other significant structure was observed at other spatial scales (Fig. 2a,b). The distribution of *C. granosus* during daytime was significantly positively correlated with the distribution of crevices along the same platform at both sites (Table 1). At night, *C. granosus* individuals spread out slightly, showing a patchy distribution at ~90 cm as they left the crevices to forage (scale where correlogram crosses from positive to negative autocorrelation values, see Fig. 2b). In this case, a positive correlation was observed at ~300 cm (Moran's *I* = 0.298, p = 0.0069), which is probably the mean distance between aggregations of feeding individuals. Nonsignificant correlations were observed during this phase between *C. granosus* and crevice cover at both sites (Table 1). Consequently, a weakly negative, although non-significant, correlation between day and night quadrat densities was observed in this species (Fig. 2a). In the case of *Siphonaria lessoni*, daytime correlograms, when individuals were actively foraging, showed weak spatial aggregation over scales of ~250 cm (Fig. 2d). We interpret this as the scale separating aggregations of individuals. A generally similar trend was observed at nighttime, when they were usu-

ally found resting inside crevices, but the scale of aggregations was reduced to ~30 cm (Fig. 2d). Significant positive correlations between day and night quadrat densities also suggest that individuals have similar spatial distributions while resting and foraging (see Fig. 2c). Furthermore, this pulmonate limpet showed a significant positive correlation with crevice cover during daytime at Las Cruces, but this correlation was negative at Pelancura during this phase. Correlations in this species were non-significant but positive during nighttime at the 2 sites (Table 1). In the case of *Scurria araucana*, the correlogram for daytime observations, when individuals were largely resting, showed a spatial structure similar to that of *S. lessoni*, with aggregations of ~250 cm. At nighttime, the spatial distribution appeared to be random, without indication of aggregation at the smallest (30 cm) spatial scales (Fig. 2e,f), and there was no significant association with crevice cover at either site (Table 1). The most contrasting spatial patterns were observed in *Fissurella crassa*, which showed no significant structure at any spatial scale, either during daytime or nighttime observations (Fig. 2h).

Spatial interspecific associations among grazers were consistent between study sites for most species pairs (Table 1). The density of *Chiton granosus* and *Fissurella crassa* showed a strong positive correlation both during daytime, when they were resting in crevices, and during nighttime, when they were forag-
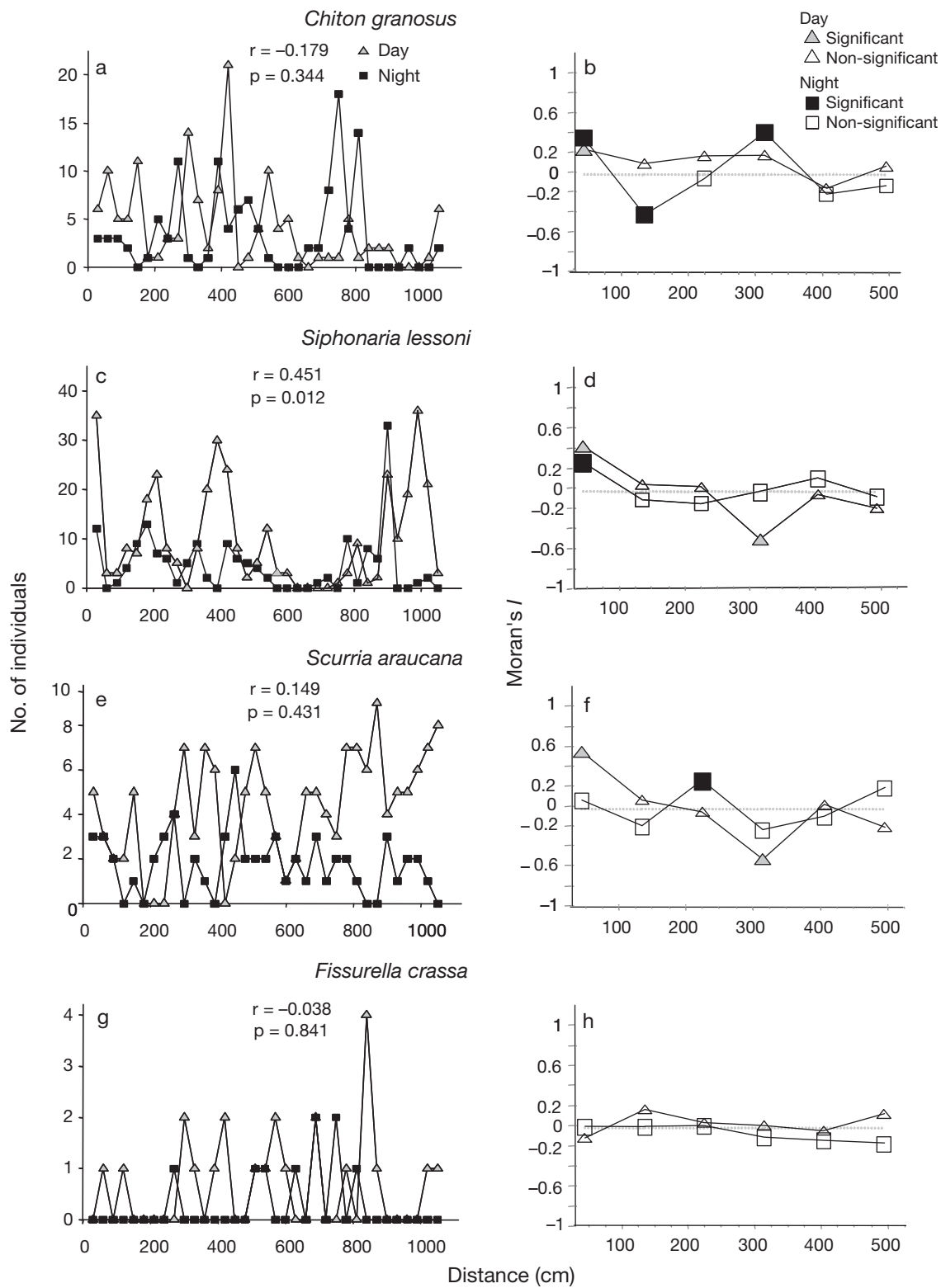
Fig. 2. Density of species along the wave exposed platforms (a,c,e,g) and corresponding Moran's *I* spatial correlograms (b,d,f,h) of the 4 molluscan grazer species: *Chiton granosus*, *Siphonaria lessoni*, *Scurria araucana* and *Fissurella crassa*. Density was measured with 30 × 30 cm quadrats in the mid-intertidal zone at Las Cruces. Pearson's correlation coefficients and significance levels between day and night sampling are also presented. Solid symbols in correlograms indicate significant correlations ($\alpha = 0.05$) after random permutation tests (1000 permutations) and Bonferroni correction. See text for details

ing (Table 1). Similarly, the density of *Scurria araucana* was strongly and positively associated with the density of *Siphonaria lessoni* during daytime, but the relationship disappeared during nighttime when *S. lessoni* was resting (Table 1). In contrast, *F. crassa* was negatively, but weakly, associated with *S. lessoni* during daytime and particularly at nighttime at the 2 study sites. Correlations between the other species fluctuated in direction between daytime and nighttime observations. Non-significant correlations were observed between *S. lessoni* and *C. granosus* and between *S. lessoni* and *S. araucana* at the 2 study sites (Table 1).

In general, Euclidian NN distances among conspecifics changed between the foraging and resting phases for most species (Figs. 3–6, panels d and h). In the case of *Chiton granosus* and *Siphonaria lessoni*, we observed a high frequency of individuals in contact with each other (distance zero, median NN = 0) during the resting phase (87.9 and 57.1% for daytime and nighttime observations, respectively). Consequently, the *R*-statistic (Clark & Evans 1954) indicated a significantly aggregated distribution for both species, although it was slightly stronger in *C. granosus* than in *S. lessoni* (Figs. 3 & 4, compare panels d and h). When foraging at night, *C. granosus* spread out from the aggregations, increasing the median distance between individuals to 3.54 cm, which was also reflected in the *R*-statistic, but they still conformed to an aggregated distribution (Fig. 3h). In contrast, *S. lessoni* did not substantially change NN distances when foraging and the *R*-statistic showed virtually no change (see Fig. 4h). Thus, the NN distances for the chiton and pulmonate limpet are in general agreement with the quadrat-based analyses, suggesting the existence of tight aggregations in these species at the scale of quadrat size (ca. 30 cm) and significant spatial structures again at around 300 cm, probably reflecting patchiness of aggregations. In the case of *Scurria araucana*, few individuals were in contact with each other (<10% zero distances), the median distance was ~5.4 cm (Fig. 5d) and the *R*-statistic showed values that suggested a nearly random distribution. When foraging, the median distance increased to 7.0 cm, but the *R*-statistic still conformed to a nearly random distribution (Fig. 5h). The positive correlation (aggregated pattern) at the scale of quadrat size and the spatial structure at scales of ~250 cm shown by the quadrat-based correlogram (see Fig. 2f) were not
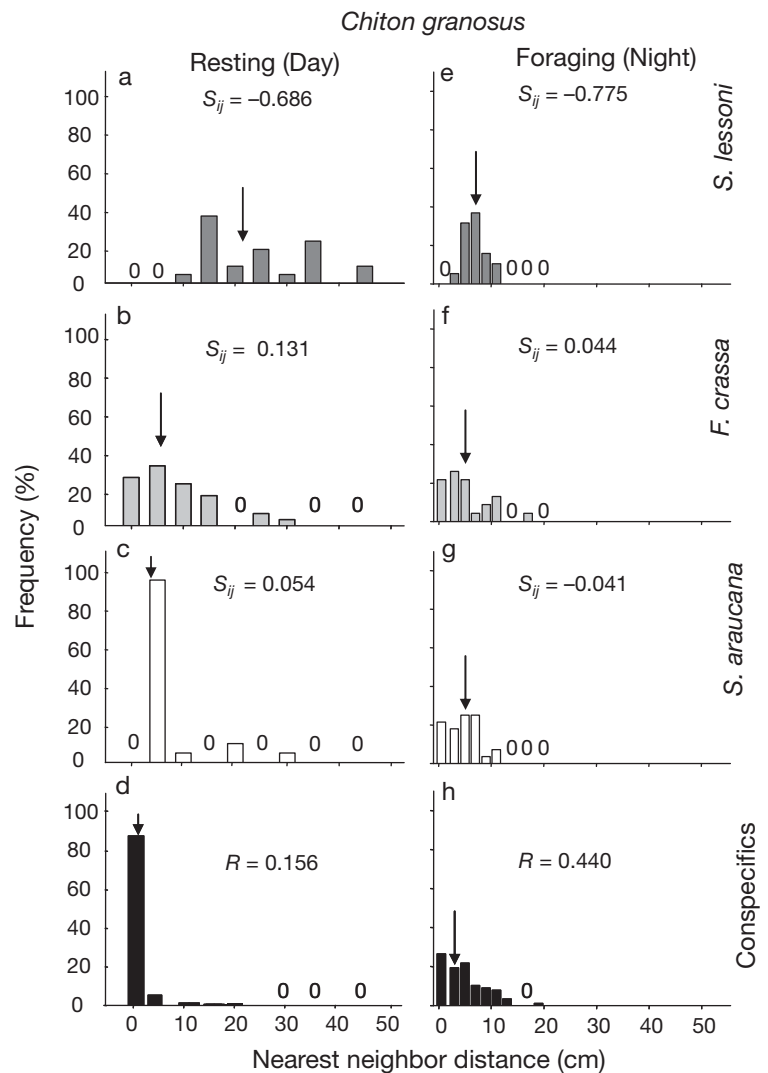

Fig. 3. Frequency distribution of nearest neighbor (NN) distances (cm) for the chiton *Chiton granosus* at mid-intertidal levels at Las Cruces during resting (a–d) and foraging (e–h). Distances to individuals of other grazer species and to conspecific individuals are shown in different panels. Arrows indicate the median NN distance. The segregation index (S_{ij}; see Dixon 1994) is presented for all heterospecific comparisons, where negative values indicate segregation and positive values indicate attraction. The *R*-statistic (Clarke & Evans 1954) is presented for conspecific NN distances, where values close to 0 indicate aggregated pattern whereas those close to 1 indicate a random pattern of distribution. Full species names in Fig. 1

apparent when measuring individual distances. The frequency of individuals in contact with each other was also low (16.6%) in *Fissurella crassa*. Individuals of this species tend to be at a median distance of 5.5 cm apart during resting (mean = 12.6 ± 2.24 cm) and the *R*-statistic showed a nearly random distribution (Fig. 6d). However, while foraging, the inter-individual distance increased to a median of 28.0 cm (mean = 30.7 ± 2.87 cm) and the *R*-statistic showed a more uniform distribution (Fig. 6h).
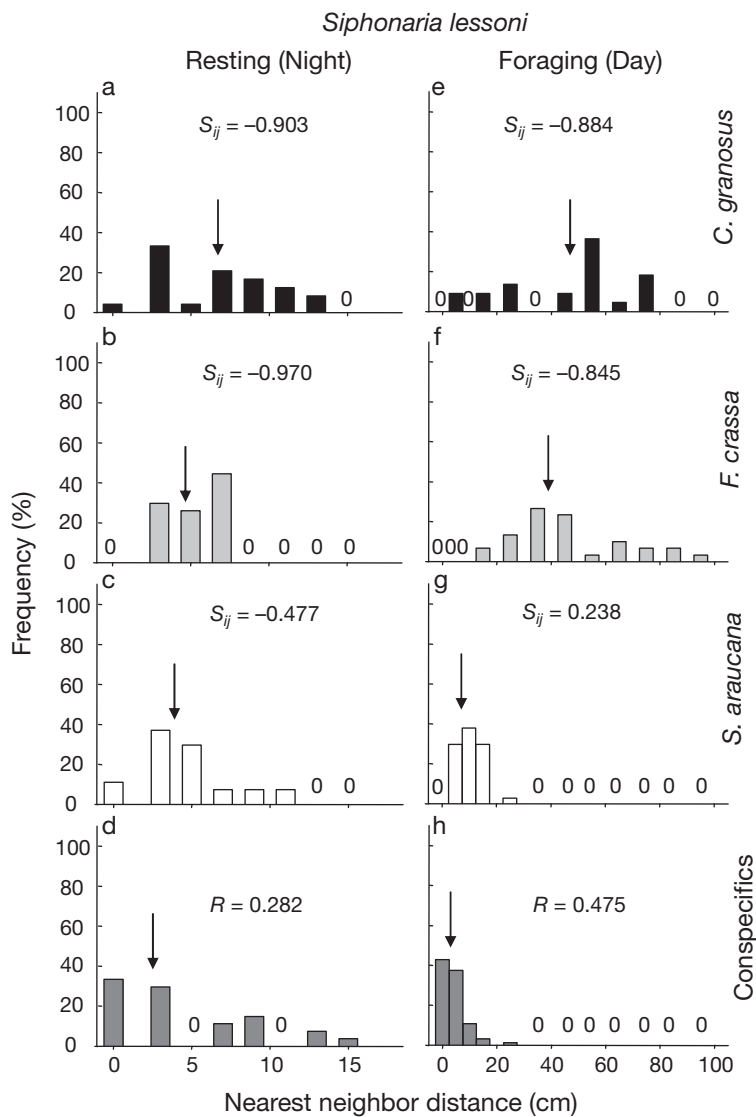
Fig. 4. Frequency distribution of nearest neighbor distances (cm) for the pulmonate limpet *Siphonaria lessoni* at mid-intertidal levels at Las Cruces during resting (a–d) and foraging (e–h). See Fig. 3 legend for details. Full species names in Fig. 1

diel difference was similar to that observed in Las Cruces (Table 2).

The values of the S_{ij} segregation index (Dixon 1994) were in general agreement with observed differences in median heterospecific NN distances. In the case of *Chiton granosus* during the resting phase (Fig. 3, left panels), the median distances to *Scurria araucana* and *Fissurella crassa* (Fig. 3b,c) were only slightly larger (median = 3.5 and 5.0 cm, respectively) than distances to conspecifics (median = 0 cm, see Fig 3b–d), whereas distances to *Siphonaria lessoni* (Fig. 3a) were over 25.0 cm larger than those between conspecifics (compare Fig. 3a and 3d). Similarly, S_{ij} values showed a high level of segregation between resting *C. granosus* and *S. lessoni* and a slight attraction of *C. granosus* to *S. araucana* and particularly *F. crassa*. When *C. granosus* individuals were foraging (Fig. 3, right panels) and tended to be slightly more dispersed (median = 3.15 cm; Fig. 3h), interspecific distances to *S. araucana* and *F. crassa* were further reduced (median = 4.2 and 4.4 cm, respectively). Distances to *S. lessoni* in this activity phase were also shorter than when individuals were resting (compare Fig. 3e and 3h), but remained larger than distances to other species (Fig. 3f,g). Similarly, the segregation index showed larger segregation from *S. lessoni* and attraction to *F. crassa*. Resting *S. lessoni* were observed in close proximity to *S. araucana* and *F. crassa*, although they were never in direct contact with the latter (Fig. 4b,c). The S_{ij} index showed high segregation from *F. crassa* and low levels of segregation from *S. araucana* (Fig. 4b,c), but because of low sample size (n = 40), the estimated index for *F. crassa* must be interpreted with caution. In agreement with observations on chitons as the focal species, the distances between *S. lessoni* and *C. granosus* were much larger than to conspecifics (Fig. 4a) and the S_{ij} index suggests strong segregation between these species. Interestingly, because active (foraging) *S. lessoni* showed an aggregated distribution, interspecific distances to foraging *F. crassa* increased slightly and the S_{ij} index suggested strong segregation during this activity phase (Fig. 4). In the case of the limpet *S. araucana* as a focal species, we observed only slight changes in median interspecific distances during resting or foraging (Fig. 5). The S_{ij} index suggested a pattern of segregation from *C. granosus* and *F. crassa* during resting and foraging, respectively (see Fig. 5a,c,e,g), and from *S. lessoni* only when resting (Fig. 5b). *F. crassa* tended to stay in close proximity to *C. granosus* at resting, even closer than the

In general, the spatial distribution of grazers between the study sites tended to be consistent for each species (Table 2), with generally slight variations in the *R*-statistic, probably attributed to slight differences in density (see Fig. 1) and micro-scale habitat conditions between these sites. The species *Chiton granosus* and *Siphonaria lessoni* had aggregated patterns of distribution and similar diel differences at Las Cruces and Pelancura whereas *Scurria araucana* conformed to a nearly random distribution and *Fissurella crassa* to a more uniform distribution at both sites (Table 2). The largest difference between sites was observed in *S. lessoni*, which exhibited a stronger nighttime aggregation at Pelancura than at Las Cruces, but the general
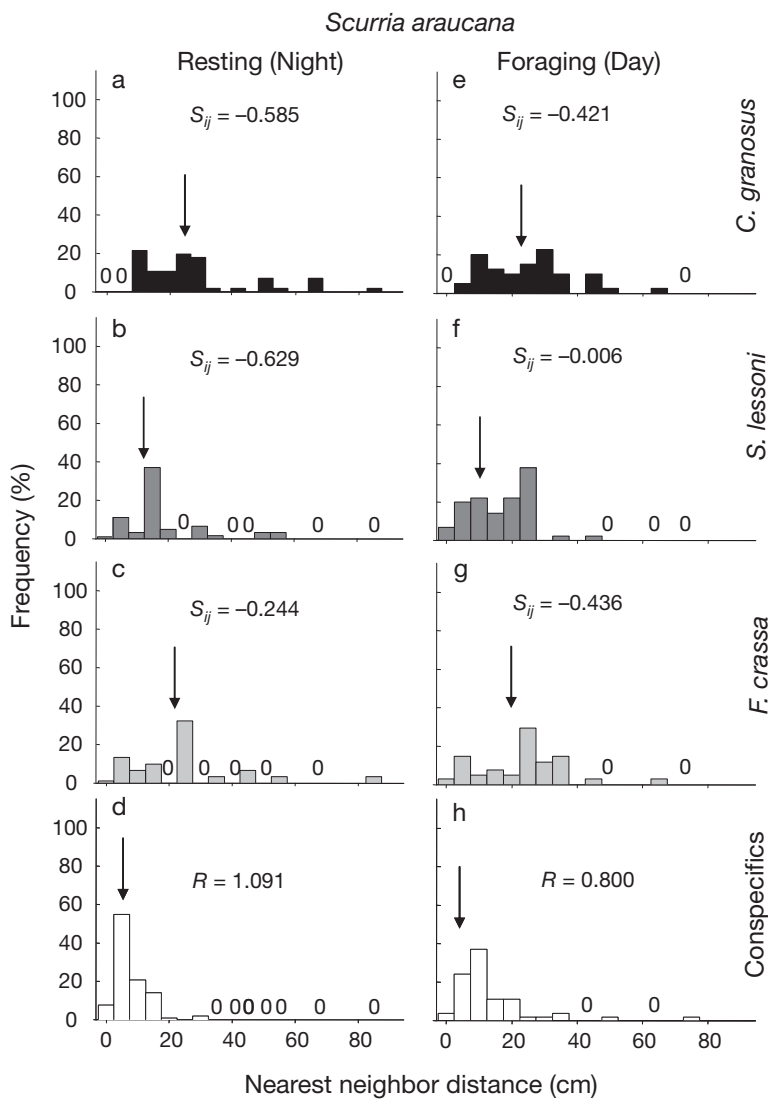
Fig. 5. Frequency distribution of nearest neighbor distances (cm) for the scurrinid limpet *Scurria araucana* at mid-intertidal levels at Las Cruces during resting (a–d) and foraging (e–h). See Fig. 3 legend for details. Full species names in Fig. 1

individuals found active during day or night low tides (Fig. 7). Averaging across surveys and sites, neap–spring tidal cycle had no effect on grazer activity, except for a slight increase in the diurnal activity of *Scurria araucana* during neap tides compared with spring tides (Fig. 8a,b). *Chiton granosus* and *Fissurella crassa* showed well-defined cycles of nocturnal activity and resting during the day whereas *Siphonaria lessoni* exhibited daytime activity (Fig. 8a,b). In general, chitons were active between 20:00 and 04:30 h, both during spring and neap tides. *F. crassa* showed peak activity after sunset, around 19:00 h and between 03:00 and 05:00 h in the morning, and *S. lessoni* were active at dusk, around 05:30 h, as well as during mid-morning and afternoon low tides. Although we could not make detailed high tide observations, movement and foraging of *S. lessoni* clearly decreased with incoming tides. *S. araucana* showed the most variable activity rhythm: this species exhibited both day and nighttime activity, particularly during neap tide (Fig. 8a).

Laboratory results showed similar day/night activity patterns to those observed in the field (Fig. 8c) and only slight differences between low (emersion) and high (immersion) tides (Fig. 8d). The largest differences between field and laboratory observations were observed in *Scurria araucana* and *Siphonaria lessoni*. The former was slightly more active during daytime than nighttime hours in the laboratory than in the field and slightly more active when immersed than when exposed to air (Fig. 8c,d). In the case of *S. lessoni*, individuals were mostly active during daytime, as observed in the field, but on some occasions activity extended to early nighttime hours (~20:00 h) in the laboratory (see Fig. 8c). No differences in activity were observed in this species when immersed or exposed to air (Fig. 8d). Consequently, a 2-way ANOVA showed no significant differences between activity in immersion and air exposure for any of the species (Table 3).

median distance to conspecifics (median = 0.5 cm to *C. granosus* versus 5.5 cm to conspecifics; Fig. 6). In accordance, the segregation index showed attraction between these species during this activity phase (Fig. 6a). At night, when *F. crassa* were foraging, distances to conspecifics increased (Fig. 6h) and distances to heterospecifics decreased considerably, rendering a pattern of attraction with all other grazers (Fig. 6e–g).

Activity rhythms

Daily activity of the 4 focal species recorded in the field were remarkably similar between sites in terms of diel variation in activity as well as in the percentages of

Displacements and homing behavior

Through discrete (changes in position between consecutive low tides) and semi-continuous (every 15 min for 3 h on 5 consecutive days) observations, we characterized patterns of displacement and distances traveled of each species (Fig. 9). Both types of measure-
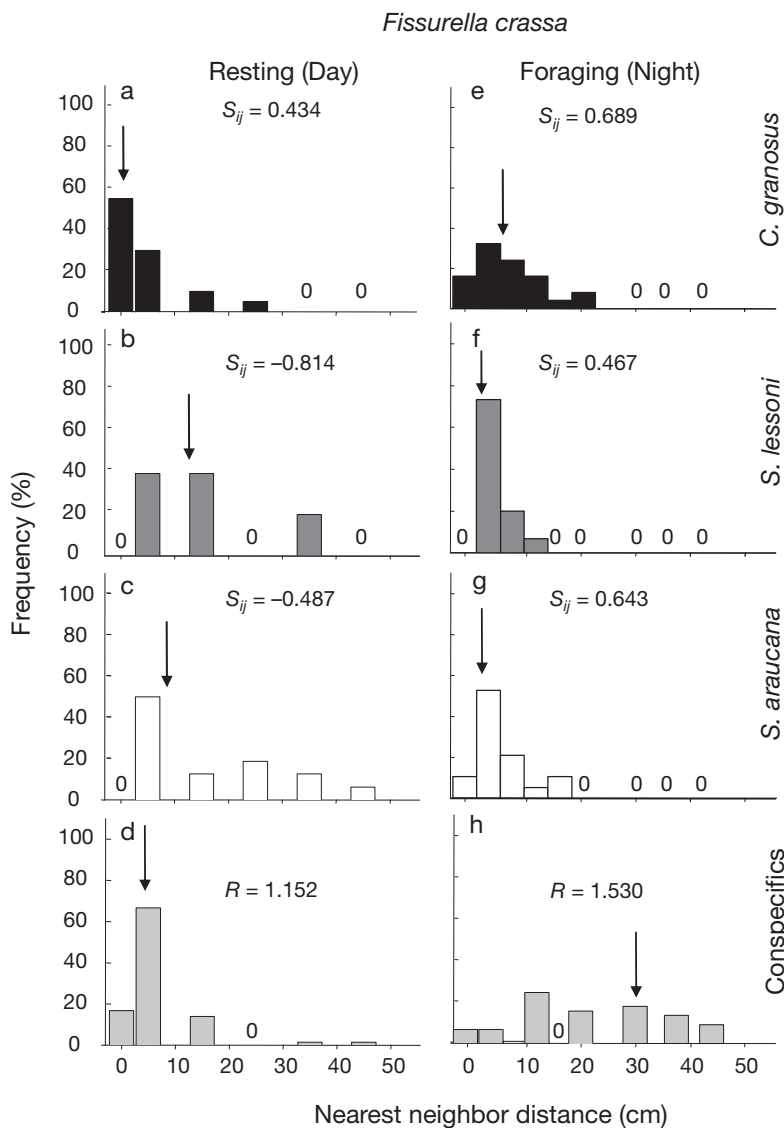
Fig. 6. Frequency distribution of nearest neighbor distances (cm) for the keyhole limpet *Fissurella crassa* at mid-intertidal levels at Las Cruces during resting (a–d) and foraging (e–h). See Fig. 3 legend for details. Full species names in Fig. 1

During foraging excursions, individuals showed a predominant angle of orientation (Raleigh's z = 11.09, 6.48 and 7.26 for *Chiton granosus*, *Siphonaria lessoni* and *Scurria araucana*, respectively, p < 0.001). The statistic could not be calculated for *Fissurella crassa*. The 0–180° axis (insets in Fig. 9a–c) corresponded to the sea–land axis on the platforms and 0 and 110° to the main direction of incoming waves. The mean displacement vectors of *C. granosus*, *S. araucana* and *S. lessoni* were 115.6 ± 11.3°, 123.6 ± 12.9° and 183.6 ± 15.2°, respectively, suggesting that the first 2 species oriented foraging toward incoming waves whereas *S. lessoni* foraged away from incoming waves (Fig. 9a,b,d insets).

Contrasting patterns of homing behaviors were observed among species. *Fissurella crassa* exhibited a remarkably tight and persistent homing behavior over the 3 mo of observations (RHE = 0.0; Fig. 9d). Other species exhibited more moderate homing behavior, with the majority of individuals returning to their homes after foraging excursions (*Chiton granosus* and *S. araucana*; Fig. 9a,c). In the case of *Siphonaria lessoni*, ~48% of individuals returned to their original position after foraging whereas the rest relocated to different resting sites from day to day (Fig. 9b).

DISCUSSION

Our results show that the spatial distributions of grazers varied among species, from aggregated for *Chiton granosus* and *Siphonaria lessoni* to a much more dispersive pattern for *Fissurella crassa* and *Scurria araucana* (Table 4a). In most cases, individuals dispersed slightly from aggregation when foraging, except for *S. lessoni*, which tended to forage in conspecific aggregations. A strong positive association was observed between *C. granosus* and *F. crassa* during resting (day) and foraging (night) whereas a consistent negative association (segregation) was observed between these nocturnally active species and the diurnally active pulmonate *S. lessoni* (Table 4b). Only slight differences in spatial distribution and activity patterns were observed between sites. Distance of foraging excursions varied widely, from over 60 cm in *F. crassa* to less than 7 cm in *S. araucana*, the most sessile of the 4 species studied. Homing behavior also changed among grazers, from extreme fidelity in

ments gave similar results. We used the more extensive discrete observations based on the *x*–*y* grid to estimate orientation angles, but as this method tended to underestimate the extension of foraging bouts, we used semi-continuous observations to estimate excursion distances and homing behavior. Mean displacement distances were 60.1 ± 5.2 cm in *Fissurella crassa*, 54.2 ± 5.9 cm in *Chiton granosus*, 24.6 ± 3.7 cm in *Siphonaria lessoni* and only 6.5 ± 3.9 cm, with a maximum displacement of 16 cm, in *Scurria araucana* (Fig. 9c). In the case of *F. crassa* and *C. granosus*, ~8.0% of individuals moved beyond 100 cm while foraging (Fig. 9a,d) whereas only 5.3% of *S. lessoni* individuals reached this distance (Fig. 9b).

Table 2. *R*-statistic of aggregation for conspecific nearest neighbour distances recorded at Las Cruces and Pelancura during daytime and nighttime low tides. Values close to 0 indicate an aggregated pattern whereas values close to 1 indicate a random pattern of distribution. Values close to 2.149 (the theoretical maximum) indicate an even and widely spaced distance among individuals

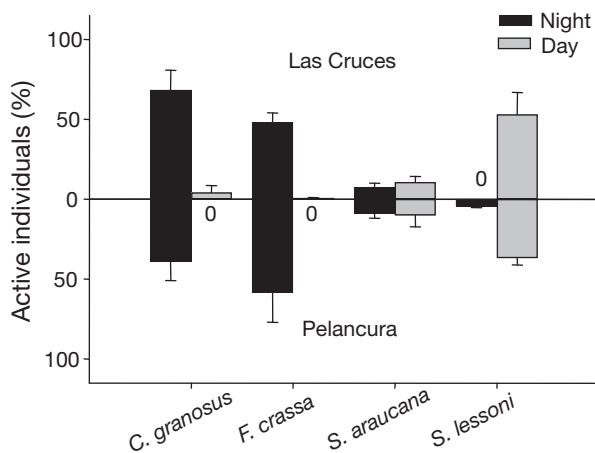|	Las Cruces	Pelancura
Chiton granosus		
Day	0.173	0.013
Night	0.415	0.440
Siphonaria lessoni		
Day	0.367	0.459
Night	0.274	0.032
Scurria araucana		
Day	0.982	1.198
Night	1.376	1.058
Fissurella crassa		
Day	1.280	1.660
Night	1.161	1.532

Fig. 7. Activity (% of individuals, mean + SE) of *Chiton granosus*, *Fissurella crassa*, *Scurria araucana* and *Siphonaria lessoni*, recorded at nighttime and during the daytime at Pelancura and Las Cruces. A total of 50 individuals of each species (100 for *S. lessoni*) were marked with numbered bee tags glued to the shell and activity was recorded during December 2007 and from April 2008 to October 2008 in Las Cruces, and during November and December 2007 and through April 2008 to June 2008 in Pelancura

F. crassa to moderate fidelity in *C. granosus* and comparatively low fidelity in *S. lessoni*. Overall, our predictions, based on the assumption that interspecific competition was an important process structuring spatial and behavioral patterns in the guild, were only partially held. Thus, taken together, results suggest that interspecific interactions could be important in this guild, but that they involve some and not all species. Here we discuss whether differences in activity patterns of the small-bodied *S. lessoni* might result

from interference with the large *F. crassa* and whether spatial segregation might help reduce interference competition with chiton aggregations for the use of shelters.

Individual spatial distribution and behavioral patterns

Spatial patterns of distribution have been studied using different methodologies (e.g. Chapman & Underwood 1992, Underwood & Chapman 1996, Fortin & Dale 2005), which place emphasis on different aspects and driving processes of the spatial distribution. We utilized 2 common methodologies, one based on the distribution of density (quadrat-based) and one based on distances among individuals (NN distances). In all species but *Scuria araucana*, significant autocorrelation values at the smallest scale (i.e. 30×30 cm quadrats) corresponded well with the highly clumped distribution of distances among individuals detected with the NN method. In the case of *S. araucana*, the quadrat method indicated spatial aggregation within the 30 cm quadrat scale, but inter-individual distances, measured at much finer scale, did not show an aggregated pattern. Similarly, we observed non-significant autocorrelation values for *Fissurella crassa*, which is usually indicative that the grain size used (30×30 cm) was not appropriate to detect the spatial structure in this species, but our results using larger (50×50) or smaller (15×15 cm) quadrats also failed to show significant spatial structure at day or night. It could also be indicative that densities are too low to correctly interpret the correlograms (Fortin & Dale 2005), or that the spatial structure is significant only at much larger spatial scales. In this case, as in the case of *S. araucana*, the NN method might be more informative than the quadrat method. Thus, the 2 methods operate at different scales and thereby capture different processes (see Fortin & Dale 2005), one (NN) focuses mostly on individual decisions that generate spatial associations, usually over small spatial scales, and the other on processes affecting the spatial distribution of abundance, usually over larger spatial scales. Description of spatial patterns must therefore be explored with diverse methodologies (e.g. Legendre & Fortin 1989, Legendre et al. 1997, Fortin 1999) to gain insight into the potential processes underlying natural landscapes.

We observed changes in the spatial distribution of most grazers studied between resting and foraging phases (summarized in Table 4a). Chitons commonly aggregate inside crevices at day and disperse slightly when foraging at night. Dispersion during foraging may be the result of quasi-random search for food by individuals, but it may also reduce intraspecific com-
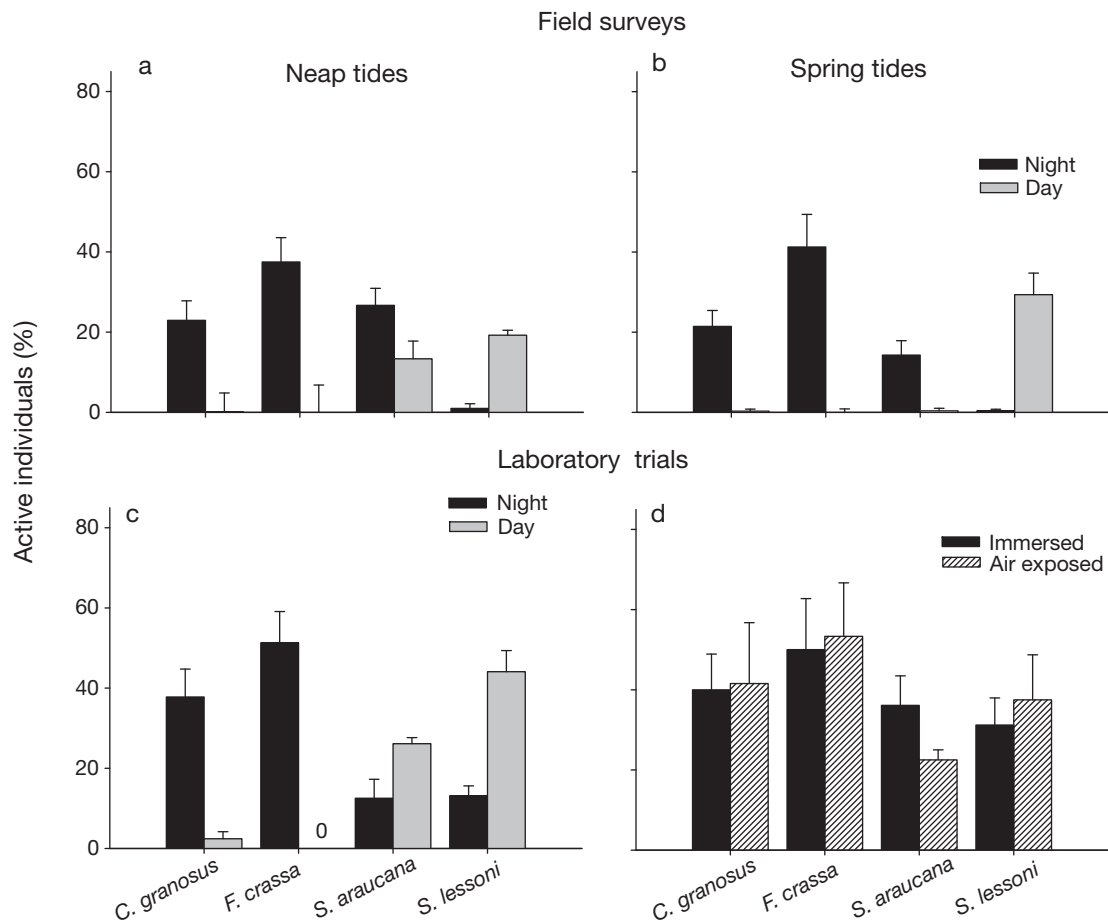
Field surveys

Fig. 8. Activity (% of individuals, mean +SE) of *Chiton granosus*, *Fissurella crassa*, *Scurria araucana* and *Siphonaria lessoni*, recorded in the field at mid-intertidal levels at Las Cruces and Pelancura (pooled data) during (a) neap and (b) spring tides, and in laboratory trials at ECIM during (c) daytime and nighttime hours and (d) immersed in water and exposed to air

Table 3. 2-way ANOVA comparing activity of grazers in laboratory trials, with condition (immersed in water versus exposed to air) and species (4 species) as fixed factors

Source	df	MS	*F*	p
Condition	1	0.012	0.31	0.590
Species	3	0.046	1.15	0.385
Condition × Species	3	0.010	0.27	0.844
Residual	8	0.322		

petition among individuals, probably reducing interference during food acquisition (Schoener 1983, Folmer et al. 2010). However, the other gregarious species, the pulmonate limpet *Siphonaria lessoni*, maintained an aggregated distribution when foraging during daytime hours. We observed tighter aggregations at Las Cruces than at Pelancura in *S. lessoni* during the active phase, which can be related to differences in density or perhaps to small-scale variation in topography between sites. However, the spatial patterns recorded still conform to an aggregated distribu-

tion at both sites. This may also account for the stronger correlation with crevice cover at Las Cruces than Pelancura, which suggests that aggregations tended to be near crevices even when animals were foraging. It is possible that in this species, unlike in chitons, there is a net benefit to foraging in tight groups (e.g. reducing predation risks; Coleman et al. 2004), but this possibility must be further evaluated experimentally. The distribution while foraging may also reflect other individual processes. Indeed, we observed *S. lessoni* individuals commonly engaging in cross-copulation during the activity phase (see also Hodgson 1999).

Like chitons and *Siphonaria lessoni*, *Fissurella crassa* utilizes crevices when resting during the day but, contrary to the former species, their spatial distribution is dispersive, which is reinforced by their generally low density (see Oliva & Castilla 1986). During the foraging phase, the distribution of keyhole limpets tends to be more uniform, which could be related to the large foraging displacements (60.1 ± 5.2 cm) and perhaps
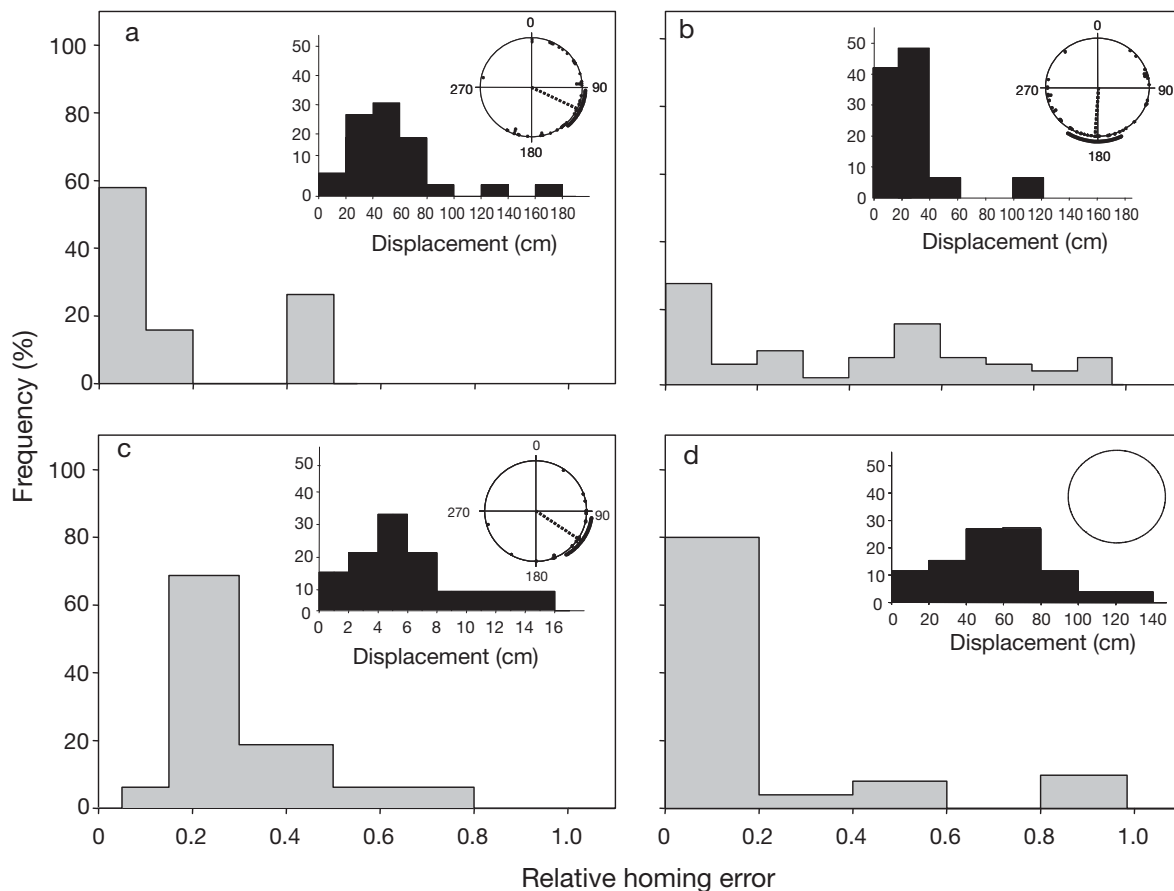
Fig. 9. Frequency distribution of relative homing error (RHE) of (a) *Chiton granosus*, (b) *Siphonaria lessoni* and (c) *Scurria arau-cana*, recorded through semi-continuous sampling in Las Cruces, and (d) *Fissurella crassa*, recorded inside the ECIM marine reserve. Values of RHE close to 0 show perfect homing behavior whereas those close to 1.0 show dispersive excursions. For *S. lessoni*, pooled data of 2 separate assessments were considered for this analysis. Insets show the distribution of displacement lengths (cm) and the polar graph shows the distribution of individual orientation (not estimated for *F. crassa*) recorded through discrete positioning of animals during 7 consecutive days on an *x–y* plane at Las Cruces. Means and SD (dashed lines) of orientation angles are also shown in the polar graphs. Each individual is represented by one data point

to intraspecific interference among foraging individu-als. Although the short displacements at foraging (ca. 7.0 cm) by *Scurria araucana* did not permit differ-entiation of spatial distributions between day and night, the observed interindividual segregation in this species may also be an indication of intraspecific inter-ference, but in this case for spatial territories (see Stim-son 1970, Branch 1976, 1981). Most individuals of this limpet species feed on microalgae in the neighborhood of the homing scar, in a manner which resemble 'gar-dener' limpets on the South African coasts (Branch 1981, McQuaid & Froneman 1993). However, although most grazers show some level of homing behavior (dis-cussed below) and individual home scars are common in flat platforms for *S. araucana*, we did not observe aggressive encounters in the field in any of the species studied. Thus, further experiments are needed to eval-uate the effect of intraspecific interference on the dis-

tribution of *F. crassa* and *S. araucana* and determine whether it sets homing strategies in these species.

All species show some level of homing behavior, but individuals of *Fissurella crassa* had the highest fidelity to resting places (see also Serra et al. 2001). Because *F. crassa* individuals commonly rest solitarily, they may have individual-specific trail recognition cues (e.g. mucus trails) to ensure the return to the same home (Chelazzi et al. 1988, Davies & Hawkins 1998). In turn, gregarious grazers *Chiton granosus* and *Siphonaria lessoni* might be able to use trails from different individuals to return home after foraging excursions (Chelazzi et al. 1987). This could account for the high variability in estimates of the homing indices for these species. Unfortunately, our semi-discrete information on individual positions does not allow us to examine the use of specific trails by individuals. Differences in mechanisms used to return to fixed homes be-

Table 4. (a) Intraspecific spatial and activity patterns during daytime (D) and nighttime (N). (b) Interspecific spatial patterns for the grazers during resting (R) and foraging (F) phases. Spatial patterns were estimated according to nearest neighbour distances and quadrat-based methods. +: positive association; –: negative association; 0: non-significant association. Species: *Chiton granosus*, *Siphonaria lessoni*, *Scurria araucana* and *Fissurella crassa*

a) Intra-specific spatial and activity

Species	Spatial pattern		Activity phase	
	D	N	D	N
C. granosus	Aggregated	Dispersed	Resting	Foraging
F. crassa	Dispersed	Dispersed	Resting	Foraging
S. lessoni	Aggregated	Aggregated	Foraging	Resting
S. auracana	Dispersed	Dispersed	Foraging–resting	Foraging–resting

b) Interspecific spatial patterns

Species	*C. granosus*		*F. crassa*		*S. lessoni*	
	R	F	R	F	R	F
F. crassa	+	+				
S. lessoni	–	–	–	–		
S. auracana	0	0	0	0	–	+

tween solitary and gregarious species deserve further attention.

Marked differences in day and night activity rhythms were observed among species (see Table 3a). Chitons and *Fissurella crassa* have well-defined nocturnal activity, which contrasts with the diurnal activity of *Siphonaria lessoni*. In contrast, the limpet *Scurria araucana* showed activity in both diurnal and nocturnal hours. It has been suggested that nocturnal activity is an adaptive response of intertidal grazers to avoid thermal stress and/or visual (diurnal) predators (Branch & Cherry 1985, Little 1989, Chelazzi et al. 1987). Diurnal activity can expose intertidal species to high thermal and desiccation stresses at low tides, which occur toward the sun summit (Finke et al. 2007). Resting in moist and shaded crevices could then significantly reduce these stresses (Branch & Cherry 1985, Williams & Morritt 1991, Harper & Williams 2001). If environmental stress is the main driver of nocturnal grazers, then one should expect the diurnal pulmonate limpet *S. lessoni* to be more tolerant of temperature and desiccation conditions than keyhole limpets and chitons, as has been shown in other pulmonate species (Branch & Cherry 1985, Marshall & McQuaid 1991, 1994). Perhaps the tight aggregations observed while foraging are partly a behavioral response to sustain activity under harsh conditions. But these propositions must be further evaluated. It has also been previously hypothesized that interspecific competition for food has selected for diurnal or nocturnal activity in grazers (Little 1989). According to Little (1989), when competition for food is low, nighttime feeding should be

common, whereas when competition for food is high, diurnal activity should predominate. This hypothesis assumes that nocturnal activity is the most suitable time to forage because of low desiccation or other stresses and, therefore, inferior competitors (usually those of smaller body size) would be forced to feed during the more stressful daytime hours. Thus, the diurnal activity of *S. lessoni* may be related to historical interspecific competition with the nocturnal grazers *C. granosus* and *F. crassa*, but as we hypothesize below and has been suggested before (Carothers & Jaksic 1984), interference in the use of crevices (shelters against desiccation) or while feeding on individual plants, instead of food exploitation, might be the most relevant mechanism. Unfortunately, our laboratory experiments show that activity rhythms in these species are rather fixed; therefore, it is difficult to directly test the hypothesis of 'competition past' (sensu Connell 1980) on activity patterns. Individuals of the limpet *S. araucana* showed more plastic diel activity. They might be able to partition the time individuals spend foraging during day and night to compensate for seasonal or short-term changes in environmental conditions, such as rock moisture or wave action (Gray & Hodgson 1997, Ng & Williams 2006), or in response to predation risks. Although this species does not display active escape responses in the presence of predators (Espoz & Castilla 2000), future experimental studies could examine whether individuals respond to the presence of predators by changing diel activity rhythms. We have shown that changes in activity patterns in this grazer assemblage were small or nonexistent between sites separated by a few kilometers, but an interesting and unresolved issue is whether these patterns remain the same at regional or biogeographical scales, where environmental and ecological scenarios change more significantly. The question is whether behavioral patterns in this molluscan assemblage are hard-wired responses, largely determined by ancestry (see Lindberg 2007 for patellogastropods), or whether they are dependent on the local environmental condition to which species could rapidly adapt. As we consider below, information on the variation of grazers' behavior between communities separated by hundreds to thousands of kilometers could shed light on these issues.

It is well known that distributional and behavioral strategies of grazers can have important consequences

on the spatial distribution of food resources (Chapman & Underwood 1992, Johnson et al. 2008). Distributions of molluscan grazers at the micro scale and homing can greatly account for spatial autocorrelation or patchiness in food distribution (Johnson et al. 2008). Our results on spatial patterns show that gregarious grazers during resting also tend to maintain aggregated patterns during foraging (although more loosely in *Chiton granosus*), which concentrates grazing activity at 30 to 45 cm around shelters. Moreover, our results on the orientation of grazers showed that *C. granosus* and *Siphonaria lessoni* revisited the same algal patches in successive foraging bouts, which could further reinforce a highly patchy distribution of grazing intensity (M. A. Aguilera & S. A. Navarrete unpubl. data). The sedentary behavior and dispersed distribution of *S. araucana* guarantees a spatially patchy grazing by this limpet, but their real effects on maintaining homing scars must still be experimentally demonstrated. In contrast, grazing impact by *F. crassa* must be more spatially extended and more uniform over space. Thus, despite their relatively similar food diets (Santelices et al. 1986, Camus et al. 2008), the impacts of these species on the algal assemblage and therefore their functional roles (Schmitz 2008) might still be quite different.

Spatial and temporal interspecific association

The observed segregated spatial association during resting and foraging between the gregarious species *Siphonaria lessoni* and *Chiton granosus* (summarized in Table 4b) is only partly in line with our predictions. Chitons and *S. lessoni* have different diel foraging activities and also they commonly aggregate in different crevices during resting in the mid to high intertidal zones, which could be a direct consequence of interference through aggressive behavior (not seen) or crowding effects inside crevices as animals leave or enter the shelters, as seen among other gregarious species (Branch 1976). Thus, segregation in activity does not seem sufficient to reduce and completely eliminate spatial segregation (see Carothers & Jaksic 1984). Differences in body size (chitons are larger than *S. lessoni*) might produce asymmetry in this interaction (i.e. strong differences in the magnitude of effects between the species), but our data cannot resolve this issue. It is interesting that *S. lessoni* tends to forage during the day at a distance ~30 cm further from its own resting sites, which also accounts for positive spatial association with crevices during this phase, and ~45 cm from aggregations of resting chitons, which could be related to food shortage in areas adjacent to chiton crevices (Aguilera & Navarrete 2007) and there-

fore the possibility of exploitative competition for food between these species occurring at very small spatial scales. Segregation during both resting and foraging between *S. lessoni* and solitary *F. crassa* was also apparent. The small body size of *S. lessoni* compared with *F. crassa* might determine strong asymmetry in encounters when acquiring food, or during the brief times when individuals overlap during initiation and termination of foraging. Indeed, a study in southern Chile has suggested the existence of strong interspecific competition between *S. lessoni* and another large keyhole limpet, *Fissurella picta* (Godoy & Moreno 1989), and direct interference might be one of the mechanisms. Again, these spatial patterns and observations reinforce the idea that diurnal activity in *S. lessoni* could be an evolutionary response to reduce encounters with larger nocturnal foragers. In this context, it is interesting to note that the same species has been reported as having nocturnal activity in the Atlantic Patagonia, where large grazers and, therefore, potential competitors are virtually absent (see Olivier & Penchaszadeh 1968, López-Gappa et al. 1996). Further observations over biogeographic scales, together with carefully designed transplant experiments, could shed light into the potential for competition to set patterns of diel activity. We observed positive spatial association between chitons and *F. crassa* during both resting and foraging (see Table 4b). Contrary to our predictions, these species utilize the same microhabitats during resting (i.e. crevices) and also forage at the same time (see Table 4a). This suggests that competition (e.g. interference) between these species is less intense than among conspecific individuals. Taken together, our results suggest that interference competition driven by shelter use and modulated by differences in body size may determine the spatial and temporal organization of some of the grazers in the guild. This interaction may also translate into changes in the distribution of the algae consumed by these species. Further experiments should thus examine grazer effects under different contexts of interspecific coexistence.

Although detailed manipulative experiments are needed to elucidate whether activity and spatial distributional patterns are modified by competitive interactions, our study provides information regarding the most likely and important type of interactions in this grazer guild, interference competition, and the species that might be most affected. Similarly, results demonstrate that, despite high diet overlap (see Santelices et al. 1986), there are sharp and sometimes conspicuous interspecific differences in spatial distribution, mobility and foraging behavior, which could very likely translate into important differences in the functional roles played by each grazer species in algal assemblages and the entire community. This information

sheds light on the roles played by individual behavior and competitive interactions in shaping functional structure in the molluscan grazer assemblage (see Branch 1981), both at ecological and evolutionary scales.

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