Shell use by the hermit crab *Calcinus californiensis* at different levels of the intertidal zone

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SUMMARY: The gastropod shell use of the hermit crab *Calcinus californiensis* was studied at Troncones, Guerrero, México. Hermit crabs were captured at two different levels of the intertidal zone, in wave-protected and wave-exposed sites. *C. californiensis* occupied shells of 18 gastropod species. At both wave-action sites, *Cantharus sanguinolentus* was the most occupied shell. *Columbella* sp. was used more by females than by males, and *Nerita scabricosta* was more used by males. The frequency of use of the shells was different between the different wave sites. *N. scabricosta* and *Columbella* sp. were occupied more at the wave-protected than at the exposed sites; *C. sanguinolentus* and *Stramonita biserialis* were occupied more at the exposed sites. The hermit crabs at the wave-exposed sites occupied heavier and thicker shells compared with the crabs from the protected sites. The Olmstead-Tukey diagram showed eight shell species as dominant in the wave-protected sites, and seven in the wave-exposed sites. Ten shell species were rare in the wave-protected sites, and six in the wave-exposed sites. The rare shells occupied by the hermit crabs were relatively heavier than the dominant shells in both site types. Our results suggest that the shell weight is important in sites that are greatly affected by the hydrodynamics.

Keywords: gastropod shell, hermit crab, *Calcinus californiensis*, waves, Olmstead-Tukey, intertidal.

RESUMEN: USO DE CONCHAS POR EL CANGREJO ERMITAÑO *CALCINUS CALIFORNIENSIS* EN DIFERENTES NIVELES DE LA ZONA INTERMAREAL. – El uso de conchas de gasterópodo por el cangrejo ermitaño *Calcinus californiensis* fue estudiado en Troncones, Guerrero, México. Los cangrejos ermitaños se capturaron en dos niveles diferentes de la zona intermareal, en sitios protegidos y expuestos al oleaje. *C. californiensis* ocupó conchas de 18 especies de gasterópodo. *Cantharus sanguinolentus* fue la concha más ocupada considerando ambos sitios. *Columbella* sp. fue más ocupada por las hembras que por los machos y *Nerita scabricosta* fue más ocupada por los machos. La frecuencia de uso de las conchas de las diversas especies difirió entre ambos sitios. *N. scabricosta* y *Columbella* sp. fueron más ocupadas en la zona protegida al oleaje que en la zona expuesta; *C. sanguinolentus* y *Stramonita biserialis* fueron más ocupadas en los sitios expuestos. Los cangrejos ermitaños ocuparon conchas más pesadas y más gruesas en la zona expuesta al oleaje que en la zona protegida. El diagrama Olmstead-Tukey mostró como dominantes las conchas de ocho especies en la zona protegida del oleaje y siete en el sitio expuesto; como raras las conchas de diez especies en la zona protegida y seis en la expuesta. Las conchas agrupadas como raras en ambas zonas fueron relativamente más pesadas que las conchas agrupadas como dominantes. Los resultados sugieren que el peso de las conchas es un factor importante para los ermitaños en las zonas con alta influencia hidrodinámica.

Palabras clave: gasterópodos, cangrejos ermitaños, *Calcinus californiensis*, oleaje, Olmstead-Tukey, intermareal.

INTRODUCTION

Hermit crabs occupy empty gastropod shells for protection against predators (Vance, 1972) and physical stress (Reese, 1969). The strong association between hermit crabs and shells influences almost all aspects of hermit crab biology (Fotheringham, 1976; Bertness, 1981a; Hazlett, 1981; Angel, 2000; Yoshino *et al*., 2004). Hermit crabs show preferences for particular gastropod shell species and sizes (Hazlett, 1981); however, because shells are a limiting resource for most populations (Fotheringham, 1976; Kellogg, 1976), the

shell occupancy in a natural population is commonly explained by shell availability (Scully, 1979). The shell occupancy along an intertidal gradient can depend on the environmental conditions, the size of the hermit crab, reproductive stage, sex, and previous experience (Bertness, 1981a; Asakura, 1995; Elwood *et al*., 1995; Yoshino and Goshima, 2001; Alcaraz and Kruesi, 2009).

The intertidal zone is a challenging environment regularly exposed to waves by the advance and retreat of the tides; in this environment, the most important factors that determine the fauna distribution are desiccation, wave action, and predation (Bustamante *et al*., 1997; Blamey and Branch, 2009). Life forms in this habitat must be well adapted to the drastic environmental changes associated with tidal activity to avoid their being washed away by the water flow. Waves play an important role in determining the distribution of species and populations in the intertidal zone; therefore, hermit crabs are directly affected by hydrodynamic stress, which is an important factor determining shell use and preference (Scully, 1979; Hahn, 1998). Differences in hydrodynamic stress in the intertidal zone may also affect hermit crabs through indirect but related factors that shape the community composition, for example, predatory pressure is an important factor (Rotjan *et al.,* 2004). Predation by invertebrates and birds changes along the intertidal gradient and is greater in protected sites than in those exposed to wave action (Menge, 1978; Robles *et al*., 2001).

The hermit crab *Calcinus californiensis* Bouvier, 1898 is a common species in the intertidal zone and shallow waters of the eastern Pacific (Poupin and Bouchard, 2006). At Troncones, Guerrero this species inhabits the intertidal rock pools exposed to different levels of wave action. In this study, we determined the shell occupancy of *C. californiensis* at different levels of wave action.

MATERIALS AND METHODS

The study was carried out in the intertidal rock pools at Troncones, Guerrero, México (17°47'16''N; 101°44'17''W) in March and August 2008. Hermit crabs were captured during low tides in two different areas of the intertidal zone: wave-protected and wave-exposed sites. The wave sites were established according to the water speed, estimated as the mean of the highest speeds reached in 5 minutes, as described by Argüelles *et al*. (2009). The wave-protected sites were rock pools, relatively close to the shore (no more than 5 m from the highest tide-mark) with a mean maximum water speed of 1.0 cm s^{-1} (range from 0.3 to 2.0 cm s^{-1}). The wave-exposed sites were at a site approximately 25 m from the shore with a mean maximum speed of 57.3 cm s^{-1} (range from 22 to 178 cm s^{-1}). The water speed was measured during the sampling using a flow meter (Global Water, precision ± 0.1 cm s^{-1}). The water speed measurements were taken as close as possible to

the substrate in which the crabs were collected. The mean depth of the water column at each collection site was estimated as the average water level during 5 minutes as described by Argüelles *et al*. (2009). The water temperature, oxygen concentration, types of sediment, bottom configuration, degree of air exposure, and presence or absence of algae were recorded.

Sampling was carried out using 0.25 m^2 quadrants. All rocks and crevices were searched for hermit crabs. All hermit crabs and vacant gastropod shells were collected by hand and taken to the field laboratory. For each sampling period (March and August), sixteen sites were searched for hermit crabs, with eight quadrants sampled at the protected sites and eight at the wave-exposed sites.

All crabs were removed from their shells by heating the apex of the shell (Kellogg, 1977). Crabs were measured for shield length and chelae length using a digital caliper (±0.01 mm) and weighed on a plate balance (OHAUS, ±0.1 g). The sex of the hermit crabs was determined by identifying the position of the genital pores by using a stereoscopic microscope. Shells were dried (24 h, 60°C), weighed using a plate balance, and measured for shell length, width and aperture (length and width). All the gastropod shells were identified according to Morris (1969), Keen (1971), Abbott (1996), and Skoglund (2001). The shell weight/shield length ratio was used as an index of the relative weight of the shell in relation to the crab (Mantelatto and Dominciano, 2002; Turra and Leite, 2004).

The frequency of shell occupancy of the six most occupied shells in the wave-protected sites and wave-exposed sites was compared in the two sampling periods (March and August) by a chi-square test (χ^2). Since the data from the two sampling periods were similar (see results), they were grouped for further analysis. The shell species occupied at the sites, the sex distribution, the shell species occupied by sex, and the sex ratio were compared using chi-square tests. The shell weight/shield length ratios of the shell species occupied at the protected and exposed sites were compared with an ANOVA analysis using shell species and the collecting zone as factors and the shell weight/shield length ratio as the independent variable. Significant differences between them were tested with a Student's *t*-test. The shell weight/shield length ratio was also related to the frequency of use of each shell species at the two site types. Linear regressions between shell weight and shell length were made for each shell species found at each wave-site. The slopes and elevations were compared with an ANCOVA analysis to estimate morphometric differences between the shells occupied at the two wave sites.

The shell occupancy data were plotted with a Olmstead-Tukey diagram. In this diagram, the frequency of occurrence of the gastropod shell species (number of quadrants in which a particular shell species was found) is graphed versus their abundance (total number of individuals in all quadrants, log (n+1) transformed

TABLE 1. – Total number (*n*) and percentage (%) of gastropod shell species occupied by the hermit crab *Calcinus californiensis* at Troncones, Guerrero.

Shell species	males		non-ovigerous females		ovigerous females		total	
	n	%	*n*	%	*n*	%	*n*	%
Cantharus gemmatus (Reeve, 1846)	8	2.7	0	0	0	0	8	1.2
Cantharus sanguinolentus (Duclus, 1833)	67	22.5	23	28.4	84	31.1	174	26.8
Cerithium maculosum Kiener, 1841	6	2.0	0	0	3	1.1	9	1.4
Cerithium menkei Carpenter, 1857	5	1.7	1	1.2	5	1.9	11	1.7
Columbella sp. Sowerby, 1832	37	12.4	19	23.5	53	19.6	109	16.8
Engina tabogaensis Bartsch, 1931	0	0	1	1.2	6	2.2	7	1.1
Leucozonia cerata (Wood, 1828)	12	4.0	3	3.7	9	3.3	24	3.7
Mancinella speciosa (Valenciennes, 1832)	35	11.7	11	13.6	27	10.0	73	11.3
Mancinella triangularis (Blainville, 1832)	35	11.7	10	12.4	27	10.0	72	11.1
Mitra lens Wood, 1828	5	1.7	1	1.2	0	0	6	0.9
Mitra tristis Broderip, 1836	1	0.3	0	0	0	0	1	0.2
Natica chemnitzii Pfeiffer, 1840	1	0.3	0	0	0	0	1	0.2
Nerita scabricosta Lamarck, 1822	33	11.1	4	4.9	15	5.6	52	8.0
Opeastosoma pseudodon (Burrow, 1815)	5	1.7	0	0	1	0.4	6	0.9
Phos sp. Montford, 1810	1	0.3	0	0	1	0.4	2	0.3
Plicopurpura pansa Gould, 1853	2	0.7	0	0	1	0.4	3	0.5
Stramonita biserialis (Blainville, 1832)	44	14.8	7	8.7	38	14.0	89	13.7
Turritella banksi Reeve, 1849	1	0.3	1	1.2	0	0	2	0.3
Total	298	100	81	100	270	100	649	100

(Olmstead and Tukey, 1947; Argüelles-Ticó *et al.*, 2010). The vertical line dividing the diagram (Fig. 4) shows the shell species present in less than 50% of the quadrants on the left side, and the shell species present in more than 50% of the quadrants on the right side. The horizontal line dividing the diagram shows the most occupied shells in the top part and the least occupied shells in the bottom part. Thus, dominant shells are those most commonly used by the hermit crabs and which are more abundant. Frequent shells are less abundant than the mean abundances, but more frequent than the mean frequencies. Occasional shells occur infrequently at the different sampling sites, but show a high abundance. Rare shells show lower than mean abundances and frequencies.

RESULTS

The bottom configuration of all the sampling sites was mainly composed of volcanic rocks. Macroalgae were not present at either site type. Water temperature in March and August were 27.9 ± 2.9°C and 28.6 ± 3.2°C and no significant differences were found between the exposed and protected sites ($F_{(1,30)}$=0.39, P>0.05). Salinity was 35±1 in both sampling periods and wave sites (P>0.05). No sampling site was exposed to air. A total of 649 individuals were obtained in the study with 298 (46%) males, 81 (12%) nonovigerous females, and 270 (42%) ovigerous females (Table 1). The abundance of the six most occupied shell species in the wave-exposed and protected sites was similar for March and August ($\chi^2_{(0.05,5)}$=9.5; P>0.05), therefore data from both sampling periods were grouped for further analysis. Males were 7% larger and 39% heavier than nonovigerous females ($t_{(2,642)}$=3.1, P<0.01; $t_{(2,642)}$=3.9, P<0.001). Females were more abundant than males in both wave-action sites, and the male-female ratio of the two site types was 1:1.2 ($\chi^2_{(0.05,1)}$=66.5; P<0.001). However,

more females were found at the exposed sites (1:1.7, $\chi^2_{(0.05,1)}$=21.9; P<0.001), but the abundance of males and females was similar in the wave-protected sites (1:1, $\chi^2_{(0.05,1)}$=1.6; P>0.05). Ovigerous females were more abundant in the wave-exposed sites than in the protected ones ($\chi^2_{(0.05,1)}$=11.4; P<0.001; Fig. 1).

Calcinus californiensis occupied a total of 18 different gastropod shells. Combining data from the two wave-action sites, *Cantharus sanguinolentus* (Duclus, 1833) was the most occupied shell, followed in order by *Columbella* sp. Sowerby, 1832 and *Stramonita biserialis* (Blainville, 1832; Table 1). After *C. sanguinolentus,* which was the most occupied shell of all, the shell most occupied by the females was *Columbella* sp. ($\chi^2_{(0.05,1)}$=11.2; P<0.01). *Nerita scabricosta* Lamarck, 1832 was the shell most used by males ($\chi^2_{(0.05,1)}$=25.0; P<0.01). No empty shells were found at the sites.

The use of the six most-occupied shell species was different in the two wave-action sites ($\chi^2_{(0.05,5)}$=67.0; P<0.001). *N. scabricosta* and *Columbella* sp. were oc-
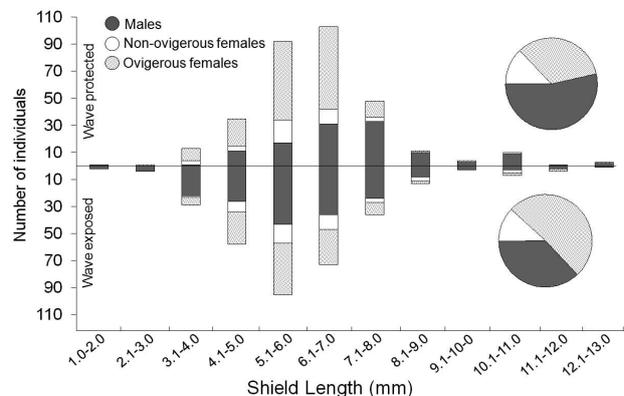

FIG. 1. – Size-frequency distribution for the individuals of the hermit crab *C. californiensis* collected in the wave-exposed and protected sites. The pie diagrams indicate the composition of sexes at the two types of sampling sites.
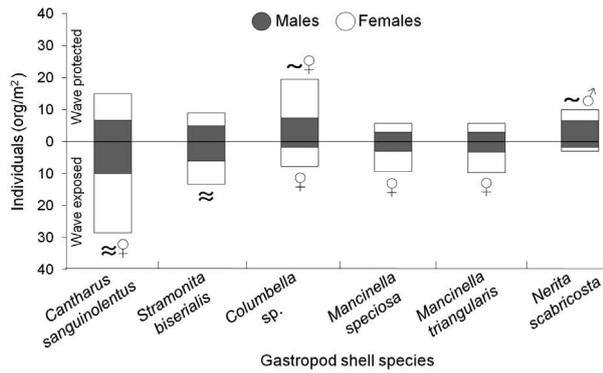
FIG. 2. – Gastropod shell species most used by males and females of the hermit crab *C. californiensis* in the wave-protected and the wave-exposed sites. Males and females show significant differences in shell use by males and females in each site type (*P*<0.05), ~ and ≈ show significant differences in shell species occupancy in the wave-protected and wave-exposed sites (*P*<0.05).
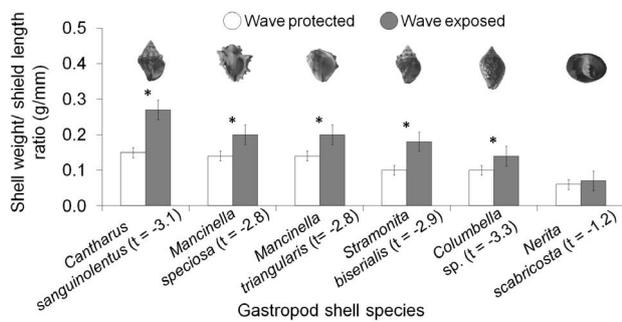

FIG. 3. – Shell weight/shield length ratio of the most occupied shells by the hermit crab *C. californiensis* in the wave-protected and wave-exposed sites. Mean values and standard errors are shown; Student's *t*-test values are shown in parenthesis; * = Significant differences at *P*<0.01.

cupied more in the wave-protected than in the exposed sites ($\chi^2_{(0.05,1)}$=21.2, *P*<0.001; $\chi^2_{(0.05,1)}$=26.1, *P*<0.001), whereas *C. sanguinolentus* and *S. biserialis* were occupied more in the exposed than in the protected sites ($\chi^2_{(0.05,1)}$=17.5, *P*<0.001; $\chi^2_{(0.05,1)}$=4.3, *P*<0.05; Fig. 2).

The shell weight/shield length ratio showed that the hermit crabs in the wave-exposed sites are likely to occupy relatively heavier shells compared with the crabs inhabiting the protected sites ($F_{(12,643)}$=4.89, *P*<0.01;
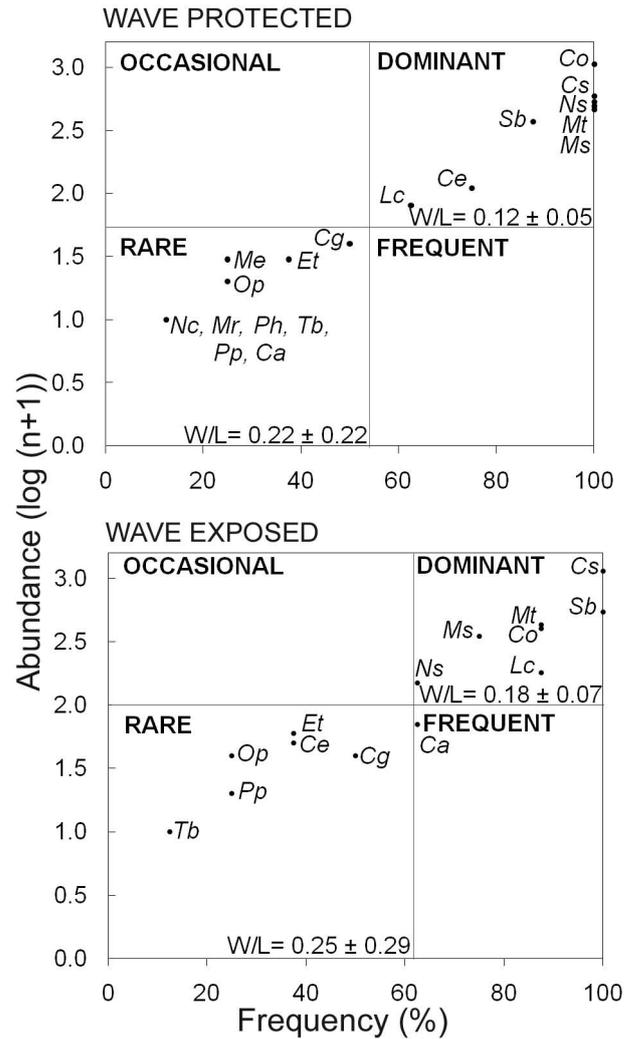

FIG. 4. – Olmsted Tukey diagram showing the frequency and abundance of the different gastropod shell species used by the hermit crab *C. californiensis* in the wave-protected and exposed sites. W/L, mean shield length/shell weight ration of all the shells grouped into each category (±SE). *Cg, Cantharus gemmatus*; *Cs, Cantharus sanguinolentus*; *Ca, Cerithium maculosum*; *Ce, Cerithium menkei*; *Co, Columbella* sp.; *Et, Engina tabogaensis*; *Lc, Leucozonia cerata*; *Me, Mitra lens*; *Mr, Mitra tristis*; *Ms, Mancinella speciosa*; *Mt, Mancinella triangularis*; *Nc, Natica chemnitzii*; *Ns, Nerita scabricosta*; *Op, Opeastosoma pseudodon*; *Ph, Phos* sp.; *Pp, Plicopurpura pansa*; *Sb, Stramonita biserialis*; *Tb, Turritella banksi*.

TABLE 2. – Linear regressions between shell weight and length for each shell species of both site types.

| Shell species | Regression equations | | ANCOVA | | | | |
	Protected	Exposed	df	Slopes t	P	Elevations t	P
Cantharus sanguinolentus (Duclus, 1833)	y=0.101x-0.803 (R²=0.78; *P*< 0.01)	y=0.096x–0.561 (R²=0.57; *P*<0.01)	156	4.0	<0.01	6.8	<0.01
Columbella sp. Sowerby, 1832	y=0.108x-1.314 (R²=0.64; *P*<0.01)	y=0.092x–1.050 (R²=0.56; *P*<0.01)	111	3.9	<0.01	182.6	<0.01
Nerita scabricosta Lamarck, 1822	y=0.069x-0.440 (R²=0.89; *P*<0.01)	y=0.067x–0.359 (R²=0.76; *P*<0.01)	57	2.8	<0.01	76.0	0.04
Stramonita biserialis (Blainville, 1832)	y=0.132x-1.568 (R²=0.74; *P*<0.01)	y=0.141x–1.582 (R²=0.54; *P*<0.01)	83	1.4	0.16	823.0	<0.01
Mancinella triangularis (Blainville, 1832)	y=0.105x-0.861 (R²=0.74; *P*<0.01)	y=0.081x–0.376 (R²=0.56; *P*<0.01)	151	2.4	0.02	260.2	<0.01

Fig. 3). The shell weight/shield length ratio of the hermit crabs inhabiting the wave-exposed sites and occupying *C. sanguinolentus*, *Mancinella speciosa* (Valenciennes, 1832), *Mancinella triangularis* (Blainville, 1832), *S. biserialis*, and *Columbella* sp. was higher than the ratio of the hermit crabs occupying these shells in the protected sites (Student's *t*-test values are shown in Fig. 3). The slopes and elevations of the regressions between shell weight and shell length were different for both wave-action sites, except for *S. biserialis* (Table 2). The data show that the hermit crabs occupied shells that were heavier in relation to their length in the wave-exposed sites compared with the protected sites.

The Olmstead-Tukey diagrams show shells of eight species as dominant in the wave-protected sites vs. seven in the exposed sites. *Cerithium menkei* Carpenter, 1857 is shown as dominant in the protected wave-action sites and is shown as rare in the wave-exposed sites. No frequent shells were found for the protected area. Instead, *Cerithium maculosum* Kiener, 1841, a rare shell in the protected sites, is a frequent shell in the wave-exposed sites. Ten shells are shown as rare in the wave-protected sites and six in the exposed sites (Fig. 4). The mean shell weight/shield length ratio calculated for the grouped dominant shells was higher for the shells of the exposed sites than for those at the wave-protected sites ($t_{(2,614)}$=-10.2, $P<0.001$; see Olmstead-Tukey diagram in Fig. 4); this ratio was similar for the rare shells of the protected and exposed sites ($t_{(2,28)}$=-0.4; $P>0.05$). The weight/shield length ratios of the rare shells were higher than the ratios of the dominant shells of the protected and exposed-wave sites ($t_{(2,328)}$=-6.5, $P<0.001$; $t_{(2,314)}$=-3.7, $P<0.01$ respectively).

DISCUSSION

Temperature, substrate composition, and air exposure have long been recognized as major factors governing the ecology of rocky shores (Bustamante *et al.,* 1997). Our study showed no differences in any of these factors when the wave-exposed and protected sites were compared. The wave action and depth were different at the various sampling sites; therefore, these factors and others related to them, such as predation intensity, could explain our results. The gastropod assemblages in the intertidal area could also explain the hermit crab shell use. However, the intensity of the water flow generated by waves on this shore, the high mobility of these hermit crab species in the intertidal area (personal observation), and the fact that the gastropod distribution does not match the hermit crab shell occupancy, suggest that this is unlikely. For example, in this respect the shells of *Stramonita biserialis* are mainly occupied in the wave-exposed sites while the gastropods are mainly residents of the protected zone; or the shells of *Nerita scabricosta*, which are used at both the different wave-action sites (although with difference frequencies) but the gastropod is never found in sites with intense hydrodynamic action (personal ob-

servation). In addition, some shell species used by the hermit crabs in Troncones do not all come from gastropod inhabitants of rocky shores, for example *Cerithium maculosum*, *Mitra tristis* Broderip, 1836, and *Natica chemnitzii* Pfeiffer, 1840 inhabit estuaries and coastal lagoons (Keen, 1971; Landa-Jaime, 2003). Therefore, it is not likely that the gastropod assemblage explains the shell occupancy by crabs at different levels of the intertidal area.

More females were found in the wave-exposed than in the wave-protected sites. The differences in the sex distribution in the two site types reveals that the sex ratio found at a specific sampling site may not represent the overall population, but rather, it could be determined by the microhabitat conditions. Similar results have been reported for the hermit crab *Clibanarius antillensis* (Stimpson, 1859), an inhabitant of intertidal rocky pools of the Gulf of Mexico, in which although the abundance of males and females was similar considering all transects sampled, females were more abundant in the wave-exposed sites than in the protected sites (Argüelles *et al.*, 2009). Different proportions of the sexes have been reported for various hermit crab populations. For instance, females being more abundant than males has been reported for the species *Coenobita scaevola* (Forskäl, 1975; Sallam *et al.*, 2008) and *Clibanarius vittatus* (Bosc, 1802; Sant'Anna *et al.*, 2006), whereas a higher proportion of males has been reported for *Pagurus exilis* (Benedict, 1892; Terossi *et al.*, 2006) and *Paguristes calliopsis* Forest and Saint Laurent, 1968 (Biagi *et al.*, 2006). In contrast, a similar proportion of males and females has been reported for *Dardanus insignis* (De Saussure, 1858; Ayres-Peres *et al.*, 2008). Variations in the sex ratio between seasons have been reported for *Clibanarius longitarsus* (De Haan, 1849; Litulo, 2005), *C. vittatus* (Lowery and Nelson, 1988), and *Diogenes nitidimanus* Terao, 1913 (Asakura, 1995), though in our study similar sex distribution patterns were found in the different wave-action sites in March and August.

Ovigerous females were more abundant in the wave-exposed sites compared with the wave-protected sites. Similar results have been reported for several species of the hermit crab, such as *C. antillensis* (Argüelles *et al.*, 2009). The movement of ovigerous females to sites with greater hydrodynamic forces could be explained by the increased importance of evading predators when females are more vulnerable. This behaviour is shown by female spiny lobsters, which exhibit an aggregation pattern when bearing eggs (Kelly *et al.*, 1999). Thus, although the risk of dislodgement is greater in the wave-exposed sites, the risk of succumbing to predators at these sites can be lower for the intertidal species, as has been reported for the bay scallop *Argopecten irradians* (Lamarck, 1819), the hard clam *Mercenaria mercenaria* (Linnaeus, 1758; Powers and Kittinger, 2002), and the intertidal hermit crabs *Pagurus* sp., *Clibanarius albidigitus* Nobili, 1901, and *Calcinus obscurus* Stimpson, 1859 (Bertness, 1981b). Alterna-

tive explanations suggested for the large abundance of ovigerous hermit crabs in sites with high wave action are the better aeration of the egg masses and the more efficient dispersal of the hatching crustacean larvae at these sites (Powers and Kittinger, 2002).

The shell use differed between sexes and between the sites with different degrees of wave exposure. The distribution of the organisms in the intertidal zone may be determined by their ability to avoid being dislodged from the substrate by the lift and drag forces of the breaking waves (Lau and Martinez, 2003). The resistance to dislodgement has been positively associated with animal size in intertidal crabs (Lau and Martinez, 2003). Although in our study the size of the hermit crabs did not vary among the wave-action sites, the most occupied shell in the wave-exposed sites was *Cantharus sanguinolentus*, which was the heaviest shell in relation to the crab. In contrast, *N. scabricosta* and *Collumbella* sp. have the lightest shells and were the least occupied in the wave-exposed sites, but highly occupied in the protected sites. In addition, our data show that for almost all the shell species, hermit crabs occupy shells that are relatively heavier in the wave-exposed sites compared to when the same species is used in the protected sites. Similarly, it was found for *C. antillensis* that the shell weight and shape (shell weight/exposed surface area ratio) determine the occupancy in an intertidal gradient of breaking waves. The frequent use of the heaviest turbinate shells at sites with high hydrodynamic forces, relative to the occasional use of lighter turriculate and globular shells has been discussed as an advantage for coping with the hydrodynamic forces of the breaking waves (Argüelles *et al.*, 2009). The frequent use of heavier shells in sites subjected to greater wave action has also been reported for *Calcinus seurati* Forest, 1951 by Hahn (1998), who suggested that heavier shells may provide an advantage in sites where the water flow represents an environmental challenge. The occupancy of heavier shells in wave-exposed sites could be because the resistance to dislodgement is proportional to the net vertical force of the animal, determined by the weight minus buoyancy and lift (Martinez *et al.,* 1998; Martinez, 2001). Therefore, the advantages of occupying heavy shells in wave-exposed areas can be described in terms of hydrodynamics.

The use of shells with a higher ratio between shell weight and shield length in the wave exposed sites can be explained by hermit crabs occupying relatively larger shells for a particular hermit crab size (outsized shells) and/or by using thicker and heavier shells. The linear regressions between shell weight and shell length suggest that the hermit crabs of the wave-exposed sites occupy heavier and thicker shells than the crabs at protected sites. Contrary to our findings that hermit crabs occupy heavy shells in the wave-exposed sites, gastropods generally exhibit heavier shells or thick-shelled morphs on protected shores (Trussell, 1996; Edgell and Rochette, 2008). Polymorphism and variation in shell

thickness in intertidal gastropods has been commonly reported in the literature, where shell thickness trends to parallel the gradients of wave exposure and predation intensity (Menge, 1978; Trussell, 1996; Carlson *et al.,* 2006). Thicker-shelled morphs, which are resistant to being broken by predatory crushers (Avery and Etter, 2006), could be advantageous for gastropods and crabs at sites with high predator intensity; nevertheless, shell thickness is especially important for snails inhabiting wave-protected sites because of the large abundance of predatory gastropods in this area, which do not prey on crabs (Lam, 2002). However, for hermit crabs, the antipredatory benefit of occupying heavy shells might be counterbalanced by the higher energetic costs of locomotion, because the overall cost of moving would be higher for the more active hermit crabs than the commonly slow-moving snails (Donovan *et al.,* 1999). Therefore, whereas thicker shells can be advantageous for the survival of gastropods, heavy shells can be highly costly in terms of energy for crabs. For hermit crabs the cost of carrying a heavy shell in wave-action sites could be compensated by the hydrodynamic benefits. However, the lighter shell morphs of gastropods inhabiting wave-exposed sites could be supported by the strength needed by marine gastropods to remain attached to the substrate (Rilov *et al.,* 2004; Bromley and Heinberg, 2006), which diminishes the lift forces and decreases the relative importance of the shell weight as a hydrodynamic advantage. Nevertheless, specific functional, predatory, and hydrodynamic experiments need to be made to understand the opposing patterns of shell thickness developed by gastropods and used by hermit crabs in the intertidal zone.

The shell weight/shield length ratio values shown in the Olmsted-Tukey diagram also show that the dominant shells of the wave-exposed sites are heavier than the dominant shells of the protected sites. Moreover, the shell weight/shield length ratios of the rare shells of both wave-action sites are almost two times higher than the ratios of the dominant shells. Therefore, it seems that the lightest shells at Troncones beach are the most used by *Calcinus californiensis*. The heaviest shell species might provide advantages at sites with high wave–action though their occupancy might be energetically costly for locomotion (Herreid and Full, 1986).

The differences in shell use in the different wave-action sites were also associated with differences in shell occupancy between sexes, which can be explained by the different requirements to maximize fit. Some of these explanations are based on the advantages provided by the different shell species and their size in terms of the shell volume for egg production and body growth, manoeuvring, and the cost of locomotion (Gherardi, 1991; Osorno *et al.*, 1998). In our study, *Columbella* sp. was the shell most occupied by females, suggesting that the shell of this species could be relatively advantageous for them, especially in the wave-protected sites. This shell type is relatively

light, as shown by its weight/shield ratio (see Figure 3). It has been documented that females occupy lighter shells than males, for instance *P. exilis*, *D. insignis*, and *Clibanarius erythropus* (Latreille, 1818; Terossi *et al*., 2006; Ayres-Peres *et al*., 2008; Caruso and Chemello, 2009). Some authors suggest that the use of heavy shells may limit reproduction and growth in hermit crabs, for example in *C. obscurus*, *Clibanarius albidigitus* Nobili, 1901, and *Pagurus* sp. (Bertness, 1981b), *Coenobita compressus* Herbst, 1791 (Osorno *et al*., 1998), and *C. vittatus* (Sant´ Anna *et al*., 2006). In particular, ovigerous females of *C. antillensis* occupy relatively lighter shells than males, even though their size is similar (Turra and Leite, 2004).

An alternative explanation for the high proportion of females and ovigerous females occupying *Columbella* sp. might be due to its narrow aperture. Botelho and Costa (2000) proposed that the narrow shell aperture of some shells (such as *Mitra* sp.) might be advantageous for ovigerous females because they would not be so easily preyed on by crabs that prey by inserting their chelipeds into the gastropod shells (Borjesson and Szelistowski, 1989).

Nerita scabricosta is also a relatively light shell and frequently occupied in the wave-protected sites, mainly by males. Its advantage could be that males tend to be more active than females because of their active searching for females and the manipulations during copulation (Turra, 2005). It is important to carry a light shell for manoeuvrability and the lower energetic cost of locomotion (Herreid and Full, 1986; Osorno *et al*., 1998). This last point could also explain the higher abundance of males in the wave-protected sites, where the energetic cost of locomotion and the effort to avoid being dislodged would be lower compared to the cost of living and moving in high flow environments (Miller, 2007; Branch *et al*., 2008). The use of globular shells by male *C. erythropus* is frequent and is associated with the large size of these shells, as males grow larger than females in this species (Caruso and Chemello, 2009). Differences in the shell-species occupation between sexes have also been reported for the semiterrestrial hermit crab *C. scaevola* (Sallam *et al*., 2008).

Tide pools are challenging environments, regularly exposed to waves by the advance and retreat of the tides, consequently tide-pool life forms must be well adapted to the drastic environmental changes associated with tidal activity to avoid being washed away by the waves. In addition, other physical, chemical, and biological factors are modulated by the tides and waves, and interact in a complex manner to determine the distribution of the organisms in this zone. In this study, we found that the distribution of the hermit crabs, the shell-species occupancy, the weight of the shell used in relation to the crab size, the shell morph and its thickness, and the sex distribution differed between wave-protected and exposed sites. This is the first study that demonstrates that hermit crabs not only

occupy heavier shell species under high hydrodynamic action, but that hermit crabs occupy heavier and thicker shells of the same species under these conditions. Our study suggests the importance of occupying relatively heavier shells in environments exposed to wave action.

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