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Population structure and shell use in the hermit crab, *Clibanarius erythropus*: a comparison between Mediterranean and Atlantic shores

Chiara Benvenuto and Francesca Gherardi

Dipartimento di Biologia Animale e Genetica 'Leo Pardi', Università di Firenze,
Via Romana 17, 50125 Firenze, Italy. E-mail: gherardi@dbag.unifi.it

Two populations of *Clibanarius erythropus* from Mediterranean and Atlantic rocky shores were studied to provide data on morphometry, population structure and shell use under different environmental contexts. Hermit crab sex and size were analysed as well as genus, dimension and status of the inhabited shells. A comparison between the two populations gave particular emphasis to the morphological and eco-ethological plasticity of this hermit species.

INTRODUCTION

It is well known that the intertidal habitat is a high risk zone (Vannini & Chelazzi, 1985). The animal species inhabiting it must be able to avoid or tolerate the stress caused by both abiotic parameters—such as wave action, thermal extremes, dehydration, variation in salinity—and biotic ones, including both marine and terrestrial predators. In such a complex and variable habitat, eco-ethological plasticity plays a primary role, enhancing individual survival (Hazlett, 1988).

Hermit crabs are one of the most successful groups in intertidal areas, as they have been able to modulate their biology and behaviour to match habitat characteristics. The major adaptation seems to be the behavioural patterns associated with living in a shell (Reese, 1969). The shell serves as a moveable shelter allowing the crab to exploit this zone where sheltering is difficult. Apart from the passive protection from predators, the use of shell as a microhabitat affords micro-climatic conditions that can modify the hermit crabs' physiological tolerance (Reese, 1969).

Hermit crabs are dependent on empty shells, which they are generally unable to procure from living snails (for exceptions, see Randall, 1964; Rutherford, 1977). Shell availability may be a limiting factor for hermits, influencing population size (Vance, 1972a), growth rate (Markham, 1968; Fotheringham, 1976) and clutch size (Childress, 1972; Bertness, 1981a). Shell availability depends on the effective abundance of gastropods in the habitat, on their rate of mortality (Scully, 1979) and on intra- and inter-specific competition for shells (Abrams, 1986). Shells either transported away by currents (Vance, 1972a), or buried in the sand (Kellogg, 1976), or broken by predators, cannot be used. Moreover, the gastropod species of the shells which are inhabited by hermit crabs does not always correspond to the more frequent gastropod species of the habitat (Hazlett, 1981; Gherardi, 1991), showing that hermit crab species can choose a shell of a given morphology, size and status. In addition, different hermit crab categories (juveniles, males, non-ovigerous and ovigerous females) show different shell preference (Bertness, 1980; Elwood et al., 1979).

Shells also play an important role in the social structure of hermit crabs (e.g. Hazlett, 1966; Gherardi, 1991; Gherardi et al., 1994). The crab–shell relationship has been the main subject of both eco-ethological studies (see Hazlett, 1981, for a review) and models describing animal assessment and decisions (Elwood & Neil, 1992).

Clibanarius erythropus is a common intertidal Diogenidae living in the Mediterranean, Black Sea and along the Atlantic coast from Brittany to the Azores (Zariquiey Alvarez, 1968). In this study, two populations of the species have been studied, the first inhabiting a Mediterranean rocky shore and the second an Atlantic one, for the purpose of comparing population structures, relative growth and use of shells. The inhabited shells were analysed from a morphological viewpoint and with respect to the gastropod abundance in the areas. Particular attention was given to the morphological and eco-ethological plasticity of this hermit species.

MATERIALS AND METHODS

Samples of *Clibanarius erythropus* were collected in October 1996 during the day, at low tide, along one transect of the Baia Domiziana rocky shore (Monte Argentario, Italy, 46°26′5″N and 11°09′E), preserved in 75% alcohol and then analysed in the laboratory. The study site is protected from wave action and has a small variation of water level (tidal change does not exceed 35 cm). In summer, water temperature averaged 25.1°C.

The gastropod shells inhabited by hermit crabs were identified at the genus level (following D'Angelo & Gargiullo, 1978), weighed (dry weight) using an analytical balance (to the nearest 0.01 g) and measured using a vernier caliper (length along the base-apex axis, width and aperture size). On the basis of the length:width ratio, shells were classified as globose (if the ratio was <2) or elongate (if the ratio was $\geqslant 2$). Similarly, the aperture was defined as round (length:width ratio of the aperture <1)

or elongated (length:width ratio of the aperture $\geqslant 1$). The extent of breakage (0–3) and encrustation (0–3) of the shell was also determined, score 0 being assigned to unbroken (and non-encrusted) shells, score 1 up to 20% degree of breakage (or encrustation), score 2 up to 40% and score 3 more than 40%. Shell architecture was defined on the basis of the degree of spiralization: high (shell length:number of spire ratio $=3$) or low (shell length:number of spire ratio $\geqslant 3$).

When possible, each animal was sexed on the basis of the position of gonopores and weighed using an analytical balance (to the nearest 0.01 g). The shield length (the distance from the tip of the rostrum to the cervical suture in the front hard portion of the carapace) and the length and width of both chelae and propodus and dactylus of the second right pereiopod were measured using an ocular micrometer (to the nearest 0.01 mm). The number of injured specimens (i.e. specimens missing appendages) was also recorded.

Morphometric analysis was based on the comparison of each measure (y) with the independent variable (x), the shield length, considered by many authors as the best index of hermit size because of the ease of measurement and reproducibility of the results even with nearly moulted individuals (Markham, 1968). The logarithmic transformation ($\log y = \log a + b \log x$) of the exponential function $y = a\ x^b$ was used (Hartnoll, 1982) which fits almost all the cases of allometric growth in crustaceans. The value of b defines the type of allometry ($b=1$, isometry; $b<1$, negative allometry; $b>1$, positive allometry). This parameter and the others obtained using the least-squares method allowed us to use statistic standard tests.

The same procedure was followed for samples of hermit crabs collected along the south-west rocky coast of Portugal, south of Sines Cape, in July 1998, along the shores of Burrinho (37°52′30″N and 08°47′30″W) and Nascedios (37°41′N and 08°47′30″W). Data from these two shores were pooled because these did not show any significant difference. Throughout the text, we will refer to the hermit crabs under analysis as belonging to the Atlantic population or to the Mediterranean one.

This Atlantic study site (for simplicity referred to as Sines throughout the text) is often exposed to considerable wave action and great variation of tide (often exceeding three metres). During summer the water temperature averaged 16.8°C. Hermit crabs were collected at low tide along a transect similar to the one followed on the Mediterranean rocky shore. In the case of ovigerous females, egg number was counted and their developmental stage was distinguished on the basis of the presence or absence of eyes.

As suggested by Kuris & Brody (1976) and Gherardi et al. (1994), the overall characteristic of the shells was analysed through a principal component analysis (PCA). This procedure was justified by the assumption that hermit crab choice is not based on a single variable but employs a gestalt of the overall size-related suitability of the shell. Five measures of the shell size were used, i.e. length, width, weight and the aperture length and aperture width. Each shell is associated with a point in a 5-dimensional space in which each dimension represents one of the five shell variables. The first PCA axis is in the direction that captures as much variance as possible along the ordination axis. A second PCA axis is then found orthogonal to the first and accounts for maximal remaining variance, and so on. The result of PCA ordination is a sequence of axes of diminishing importance (Gauch, 1982). Eingenvectors provide a series of loadings showing the extent of the correlation of the original variables with the principal components.

RESULTS

Morphometry

Table 1 shows the type of allometry found plotting the logarithm of various morphological measures against the logarithm of the shield length. Width and length of both chelae showed a negative allometry in all the females. In males from Argentario, the right chela length was isometric and a negative allometry occurred for the dimensions of the left chela and the width of the right one. On the contrary, males from Sines were positively allometric for the length of the chelae and isometric for their width. In general, chelae grew faster with respect to the shield length in males than in the females. A difference between the Mediterranean and the Atlantic populations was found in males (Figure 1), because the latter from Sines showed larger chelae dimensions (Argentario vs Sines: right chela, $t=3.172$, df$=170$, $P<0.01$; left chela, $t=3.049$, df$=170$, $P<0.01$).

Population structure

A total of 786 *Clibanarius erythropus* (551 from Argentario and 235 from Sines) were analysed; 25 crabs with no defined sex (both gonopores absent) were excluded from the analysis. Figure 2 shows the frequency distribution of *C. erythropus* size (shield length) compared between the two populations. In both cases, males were larger in size than the females (Wilks test: Argentario, $G=43.480$, df$=3$, $P<0.001$; Sines, $G=35.981$, df$=3$, $P<0.001$). Females ($G=376.012$, df$=3$, $P<0.001$) and males ($G=63.131$, df$=4$, $P<0.001$) from Sines reached a longer shield size than hermit crabs from Argentario. Size was always positively correlated with weight ($P<0.01$). Males weighed more than females of the same size (Argentario, $r=0.089$ vs 0.134, $t=7.664$, df$=519$, $P<0.01$; Sines, $r=0.119$ vs 0.149, $t=2.511$, df$=230$, $P<0.02$).

Sex ratio (i.e. the percentage of males in the whole population) was 49% in Argentario, which does not differ from the expected 1:1 ratio ($G=0.219$, df$=1$, $P>0.01$), while in Sines was completely unbalanced towards females (36 males vs 199 females, 15.32% vs 84.68%, $G=124.258$, df$=1$, $P<0.001$). Obviously, sex ratio significantly differed between the two populations ($G=85.682$, df$=1$, $P<0.001$), but this result might depend on the different times of collection (see, e.g. the case of *Calcinus tibicen*; Fransozo et al., 1998). In the Portuguese sample, 96.98% females were ovigerous. Clutch size (Figure 3) was positively correlated with female shield length ($r=0.575$, df$=190$, $P<0.01$).

The percentage of the injured specimens was low in both Argentario (3.64%) and Sines (7.48%).

Table 1. *Patterns of relative growth in* Clibanarius erythropus. *Log–log relationships between each analysed morphological character and the shield length.*

	F				M				F≠M
Argentario	df	b	t	allometry level	df	b	t	allometry level	b:t
log (right chela L)	120	0.820	4.060**	–	139	0.961	2.191	=	2.465*
log (right chela W)	120	0.583	12.627**	–	139	0.780	10.762**	–	5.080**
log (left chela L)	120	0.823	4.061**	–	139	0.915	2.982**	–	3.135**
log (left chela W)	120	0.693	10.606**	–	139	0.758	12.93**	–	1.396
log (dactylus L)	90	0.668	6.524**	–	114	0.783	6.668**	–	1.762
log (dactylus W)	90	0.283	26.287**	–	114	0.371	44.346**	–	2.859**
log (propodus L)	90	0.737	6.312**	–	114	0.874	4.993**	–	1.127
log (propodus W)	90	0.485	15.309**	–	114	0.277	95.995**	–	2.159*

	F				M				F≠M
Sines	df	b	t	allometry level	df	b	t	allometry level	b:t
log (right chela L)	196	0.564	6.910**	–	31	1.196	2.481*	+	6.252**
log (right chela W)	196	0.566	9.493**	–	31	0.986	0.268	=	5.772**
log (left chela L)	196	0.575	6.865**	–	31	1.186	2.096*	+	6.032**
log (left chela W)	196	0.462	12.472**	–	31	0.902	1.633	=	6.276**
log (dactylus L)	190	0.583	7.006**	–	31	0.977	0.263	=	4.099**
log (dactylus W)	190	0.301	25.289**	–	31	0.433	20.103**	–	3.136**
log (propodus L)	190	0.525	8.769**	–	31	1.097	2.233*	+	7.081**
log (propodus W)	190	0.434	14.997**	–	31	0.628	10.041**	–	3.392**

	F				M			
Sines	n	b:t	a:t	>	n	b:t	a:t	>
log (right chela L)	318	3.311**	–	Argentario	172	3.172**	–	Sines
log (right chela W)	318	0.288	3.158**	Sines	172	3.970**	–	Sines
log (left chela L)	318	3.274**	–	Argentario	172	3.049**	–	Sines
log (left chela W)	318	4.457**	–	Argentario	172	2.468*	–	Sines
log (dactylus L)	282	1.083	4.196**	Sines	147	2.194*	–	Sines
log (dactylus W)	282	0.461	5.523**	Sines	147	1.72	4.621**	Sines
log (propodus L)	282	3.958**	–	Argentario	147	3.535**	–	Sines
log (propodus W)	282	0.988	1.861	=	147	1.473	1.746	=

b, regression coefficient; *, $P<0.05$; **, $P<0.01$. F, females; M, males; L, length; W, weight; =, isometry; +, positive allometry; –, negative allometry.

Shell use

Table 2 provides a list of the shells more commonly inhabited by hermit crabs in Argentario, compared with the gastropod species present in the study area, collected along a 12 m-long × 1 m-wide transect parallel to the coast. Spearman rank correlation test revealed an absence of correlation ($r_s=0.356$, $t=1.618$, df=18, $P>0.05$), showing that hermit crabs chose their shells and used a depot different from the intertidal habitat one. Females and males occupied the same shell species ($r_s=0.55$, $t=2.464$, df=14, $P<0.05$). On the contrary, in Sines the two sexes did not share the same shell species ($r_s=0.491$, N=7, $P>0.05$).

From a morphological point of view, in both Argentario and Sines, elongated shells were used more than the globose ones (Argentario: 441 vs 134, $G=172.602$, df=1, $P<0.001$; Sines: 212 vs 23, $G=174.827$, df=1, $P<0.001$) by both females and males (Figure 4). In Argentario, sexes did not differ ($G=2.201$, df=1, $P>0.1$), while in Sines females occupied more elongated shells than males did ($G=18.758$, df=1, $P<0.001$). All the shells analysed from the Sines sample presented a low degree of spiralization (234 vs 0, $G=323.701$, df=1, $P<0.001$), while in Argentario highly spiralled shells prevailed (189 vs 386, $G=68.821$, df=1, $P<0.001$), without any difference between sexes ($G=1.838$, df=1, $P>0.1$).

The elongate shape of the shell aperture was preferred in both populations (Argentario: 505 vs 70, $G=370.865$, df=1, $P<0.001$; Sines: 215 vs 19, $G=192.155$, df=1, $P<0.001$). In Sines, shell aperture was wider than in Argentario (Argentario: 188 vs 387, $G=70.225$, df=1, $P<0.001$; Sines: 233 vs 2, $G=302.088$, df=1, $P<0.001$; Argentario vs Sines: $G=370.899$, df=1, $P<0.001$). The degree of breakage (Figure 5) did not differ between sexes in the two populations (Argentario: $G=2.140$, df=3,

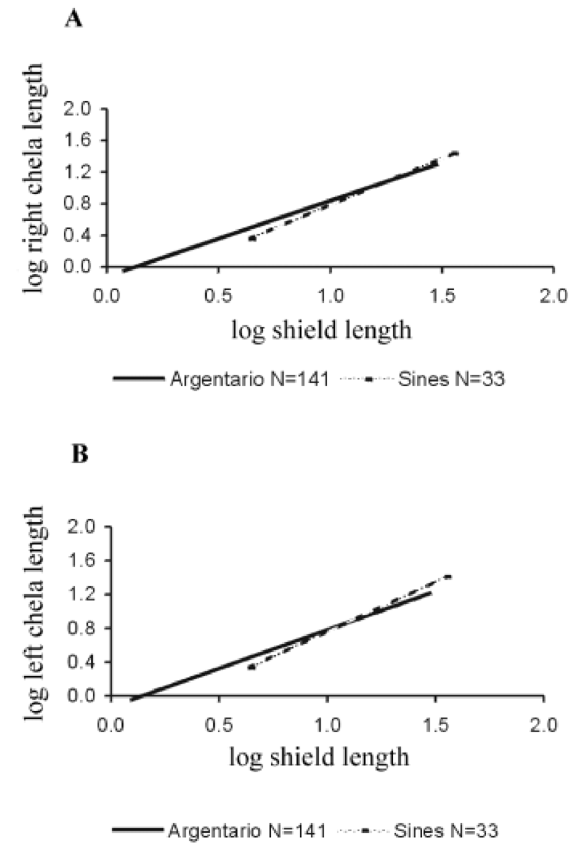

Figure 1. Log–log relationships between the shield length and the length of (A) the right chela and (B) the length of the left chela in *Clibanarius erythropus* males: comparison between Mediterranean and Atlantic populations.

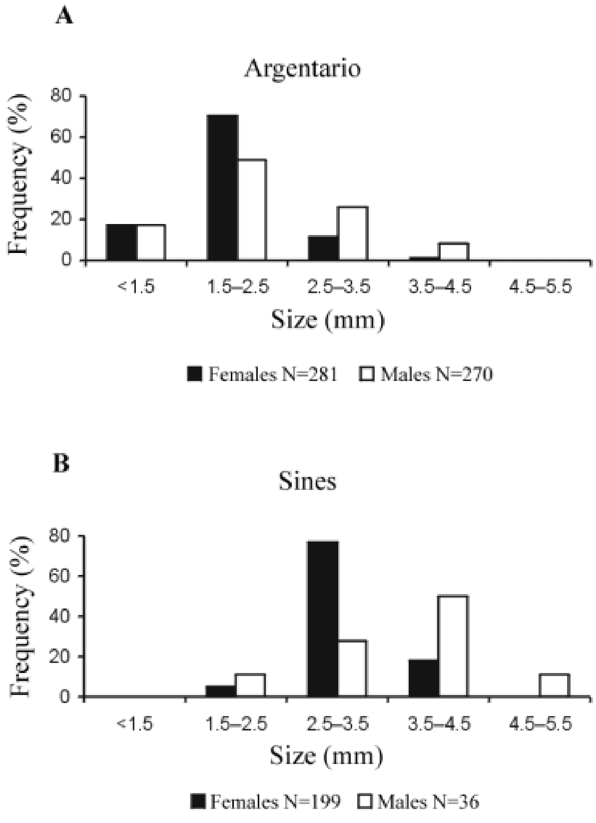

Figure 2. Frequency–size distributions of (A) Mediterranean and (B) Atlantic *Clibanarius erythropus*.

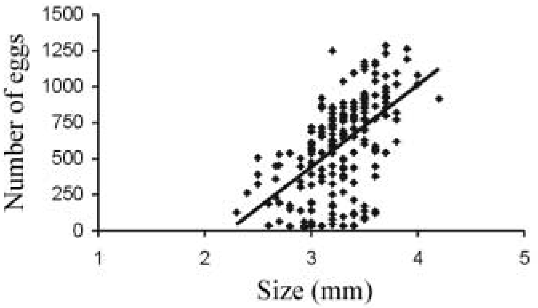

Figure 3. Correlation between shield length and egg number in Atlantic *Clibanarius erythropus* females.

Table 2. *Species composition of shells inhabited by Mediterranean* Clibanarius erythropus*, compared with the gastropods species present in the study area. Percentage values are reported in parentheses.*

	Hermit crabs	Gastropods
Alvania montagui	223 (14.8)	0
Amyclina corniculum	5 (0.33)	0
Bittium reticulatum	8 (0.53)	17 (13.08)
Bulla striata	3 (0.20)	0
Cantharus d'orbignyi	0	1 (0.77)
Cerithium spp.	1028 (68.21)	41 (31.54)
Clanculus jussieui	0	1 (0.77)
Columbella rustica	0	2 (1.54)
Comarmondia gracilis	1 (0.07)	0
Coralliophila sp.	1 (0.07)	0
Gibbula spp.	80 (5.31)	4 (3.077)
Hinia incrassata	3 (0.20)	0
Jujubinus sp.	3 (0.20)	0
Mitra ebenus	4 (0.26)	1 (0.77)
Mitrella scripta	1 (0.07)	0
Monodonta spp.	8 (0.53)	19 (14.61)
Ocenebra erinacea	6 (0.40)	0
Pirella conica	0	1 (0.77)
Pisania maculosa	129 (8.56)	43 (33.07)
Truncularioposis trunculus	4 (0.26)	0
Total	1507	130

$P>0.1$; Sines: $G=2.921$, df=3, $P>0.1$). However, shells occupied by the Argentario population were more heavily broken than those inhabited by the Sines population ($G=102.766$, df=3, $P<0.001$), especially in the females ($G=86.393$, df=3, $P<0.001$). The degree of encrustation appeared to be similar in both sexes (Argentario: $G=2.411$, df=3, $P>0.1$; Sines: $G=5.335$, df=3, $P>0.1$) and populations ($G=0.482$, df=3, $P>0.1$).

In Sines, many empty shells were found on the shore. However, also in this context, shells appeared the most important limiting factor for hermit crabs (Figure 6); empty shells belonged to different gastropod species than those normally used by the hermit crab population and were smaller ($G=498.151$, df=6, $P<0.001$) and lighter ($G=65.876$, df=4, $P<0.001$).

Shell length was positively correlated with the animal size. A comparison between sexes was done (Figure 7), considering the shell length belonging to *Cerithium* spp., which was the genus used most in Argentario. Males inhabited longer shells than similarly-sized females

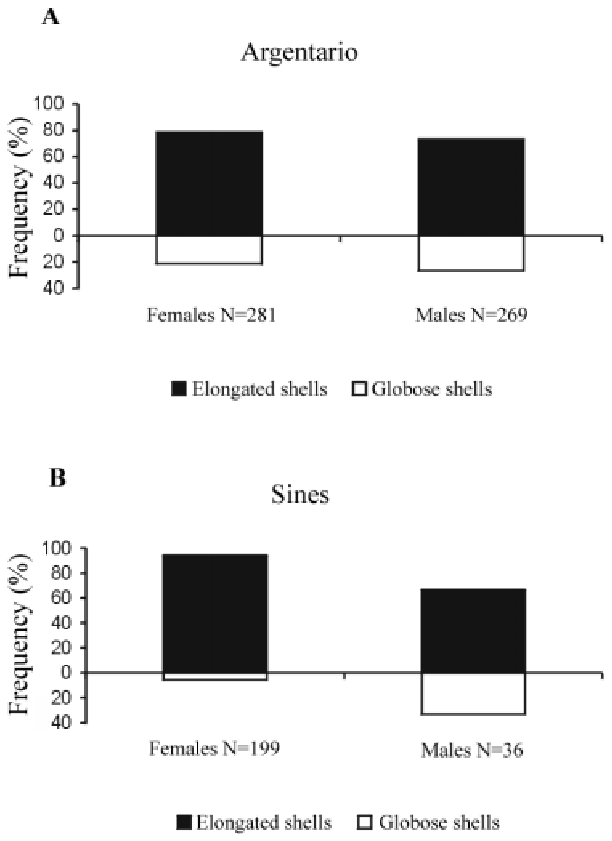

Figure 4. Frequency of the shell types used by females and males of *Clibanarius erythropus* from (A) Mediterranean and (B) Atlantic shores.

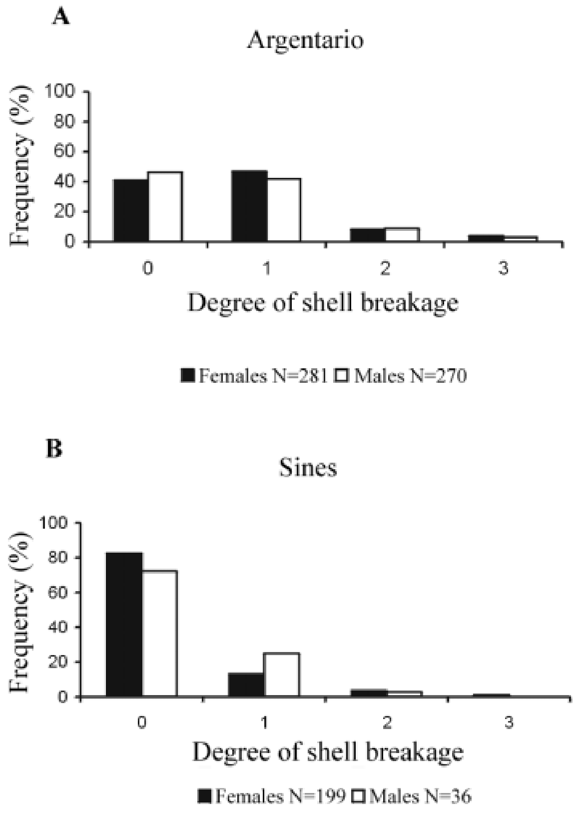

Figure 5. Degree of shell breakage compared among sexes in *Clibanarius erythropus* from (A) Mediterranean and (B) Atlantic shores.

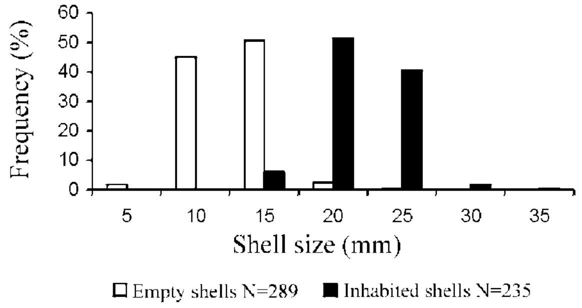

Figure 6. Size–frequency distribution of empty and inhabited shells in Atlantic *Clibanarius erythropus*.

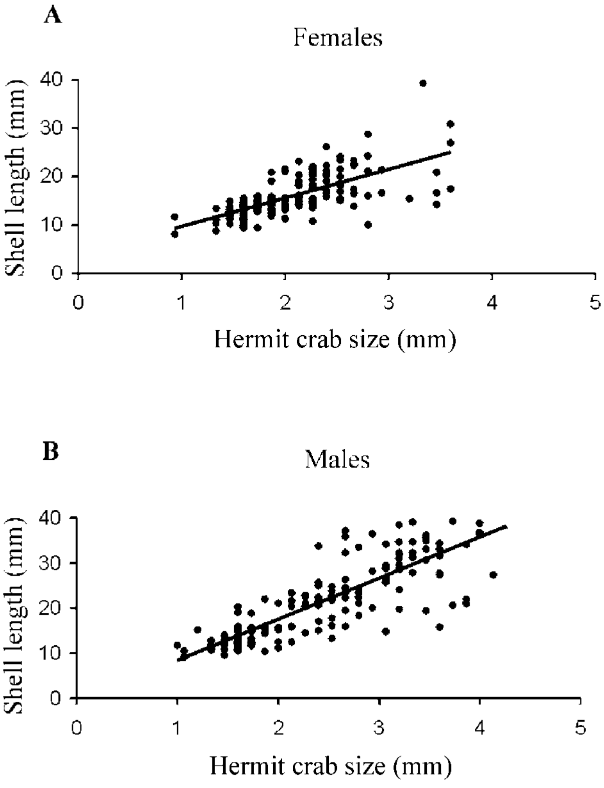

Figure 7. Relationship between Mediterranean *Clibanarius erythropus* hermit crab size (A, females; B, males) and *Cerithium* spp. shell length.

(females: r=0.703, df=190, $P<0.01$; males: r=0.845, df=163, $P<0.01$; females vs males: b, t=4.532, df=353, $P<0.001$). Similar results were obtained for *Nassarius reticulatus* in Sines, where males of all sizes occupied longer shells than the other sex (females: r=0.429, df=185, $P<0.01$; males: r=0.738, df=21, $P<0.01$; females vs males, a, t=3.521, df=207, $P<0.01$).

The weight of the inhabited shells ranged between 0.02–5.93 g in Argentario and 0.14–5.11 g in Sines. In Argentario, both sexes occupied heavier shells than in Sines (Table 3), and males occupied heavier shells than the females. Analysing the genus *Cerithium*, animal size and shell weight were positively correlated in both the females (r=0.814, df=189, $P<0.01$) and the males (r=0.872, df=163, $P<0.01$), with a significantly higher value in the males (b, 0.808 vs 0.649, t=2.977, df=352, $P<0.01$).

Table 3. *Relationship between hermit crab size (shield length) and shell weight.*

Argentario	*r*	df	*P*	b	a
Females	0.794	279	<0.01	0.602	−0.741
Males	0.852	268	<0.01	0.832	1.114
Sines	***r***	**df**	***P***	**b**	**a**
Females	0.264	197	<0.01	0.181	0.229
Males	0.622	34	<0.01	0.767	−1.376

Table 4. *Principal component analysis applied to shell shapes. Eigenvalues given as percentages of the total variance accounted for by each PC.*

	PC I	PC II	PC III	PC IV	PC V
Eigenvectors					
Shell length	0.403	0.786	0.071	0.441	−0.144
Shell width	0.491	−0.280	−0.153	−0.183	−0.790
Aperture length	0.436	−0.142	−0.762	0.122	0.441
Aperture width	0.427	−0.494	0.543	0.476	0.226
Shell weight	0.474	0.199	0.309	−0.728	0.332
Eigenvalue	3.705	0.585	0.463	0.177	0.070
Percentage	74.101	11.694	9.264	3.546	1.395

The PCA allowed us to identify a high correlation between shell shape and crab size when a high diversity of shell species was found in the field samples. The eigenvectors of PC I (Table 4) yielded loadings (correlation coefficients) of the formerly used shell patterns and all these values were highly positively correlated. The PC I accounted for 74.1% of the variance, becoming a synthetic variable that represented the overall size. The PC II accounts for 11.69% of the variance and shows a strong positive correlation with shell length and a lower correlation with shell weight. Shells having a high score on PC II are elongated. The assemblage of shells used by *C. erythropus* showed a clear difference in their general shape relatively to the two study areas.

DISCUSSION

The allometric analysis allowed us to evaluate the variations in the relative growth of the two populations of the same species living in different habitats. In both the Mediterranean and the Atlantic samples a sexual dimorphism was revealed in the right and left chelar propodus growth, for both the length and the width (with the exception of the left chela in the Mediterranean population). As already observed by Gherardi (1991) for the same species and by Manjón-Cabeza & García Raso (1999) for other species, males have more voluminous chelae than females. The functional significance of this sexual dimorphism has been examined in the Brachyura (Hartnoll, 1974). Males get more benefits than costs from having larger chelae, which are used in territorial defence, combat, agonistic display and courtship. In Paguridae and Diogenidae, during sexual behaviour males used chelipeds to perform complex precopulatory behavioural patterns (Hazlett, 1966, 1968), while no significant male–female difference in the use of chelae were found during shell fights (Hazlett & Bossert, 1965; Hazlett, 1966). Other differences in the relative growth of various appendages between the two populations support the idea of a morphological plasticity of this species.

A strong differentiation was found in the growth rate of the two populations. Males of the Atlantic population showed larger chelae than the Mediterranean one, possibly due to a greater interspecific competition. In the Sines area, *Clibanarius erythropus* was found in sintopy with *Anapagurus curvidactilus*, which occupies the same shell species, while in Argentario the only species sharing the same area was *Calcinus tubularis*, a less competitive species (part of the latter species' population occupies empty vermetid tubes; Busato et al., 1998).

Males reached a larger size than females did. The faster growth rate can be due to a greater availability of energy in males (they do not spend energy to produce eggs), to sexual selection (when a male–male competition exists to acquire a sexual partner, the fitness increase with size is faster in males than in the females) and to intersexual competition for shell occupation (Hazlett, 1966; Bertness, 1981b; Abrams, 1988). The Atlantic population reached a longer shield size than the Mediterranean one, possibly because food resources and more voluminous shells (both influencing hermit growth; Bertness, 1981a) are more available.

Sex ratio was strongly unbalanced towards the females in the Atlantic shore, while it was about 50% in the Mediterranean shore. In *Calcinus tibicen*, Fransozo & Mantelatto (1998) recorded a change of sex ratio with season and this may explain the observed difference. In *Clibanarius laevimanus* (Gherardi et al., 1994), *Diogenes brevirostis* (Walters & Griffiths, 1987), *Pagurus granosimanus*, *P. hirsutiusculus*, *P. samuelis*, *P. kennerly*, *P. beringanus*, *P. dalli*, *Elassochirus tenuimanus*, *Paguristes turgidus* (Abrams, 1988), and *C. erythropus* in Sardinia (Gherardi, 1991), females mostly belong to middle-sized classes. These data result in an unbalanced sex ratio at different sizes.

In accordance with the hermit crab literature (Fotheringham, 1976; Bertness, 1981a; Gherardi et al., 1994; Gherardi & Nardone, 1997), in the Atlantic population of *C. erythropus* ovigerous female size was positively correlated with the number of eggs. This showed that also in the females rapid growth can lead to a fitness increase, raising fecundity.

The gastropod species, the shells of which were inhabited by hermit crabs, did not correspond to the more frequent gastropod species found in the habitat, showing that hermit crabs chose their shells and use a different depot than the snails sharing the same habitat (Orians & King, 1964). Elongated shells were preferred both in the Mediterranean and in the Atlantic shores, being lighter and less energetically expensive. Females used elongated shells more frequently, while the heavier globose ones were mostly inhabited by males, especially in those habitats affected by a high predatory rate (Bertness & Cunningham, 1981). An intersexual difference in shell use was found in the Atlantic shore, with females inhabiting mostly *Nassarius reticulatus*. This probably depends on the shell architecture that could afford egg protection (Fotheringham, 1976; Bertness, 1981b). A second hypothesis is that one sex is more successful in obtaining empty shells (Bertness, 1981a), or this may be the result of a different ecology and behaviour.

Both populations preferred shells with an elongated aperture, which made hermit crabs more resistant to predation (Bertness, 1981a). In the Atlantic population, the apertures of the used shells were larger, possibly because in these shores predation is less strong than in the Mediterranean ones. The degree of spiralization varied in the two populations, but this usually depended on the different gastropod genera. In general, highly spiralled shells may hold water, thus protecting hermit crabs from extreme variations in temperature (due to the high specific heat of water), while low spiralled shells confer better protection from predation (Bertness, 1982).

Shell length was positively correlated with animal size. Males inhabited longer shells than the similarly-sized females, possibly because the latter prefer shells with less energy costs. Also, shell weight showed a positive correlation with hermit crab dimensions, with males inhabiting heavier shells than the similarly-sized females. These results confirm the hypothesis that hermit crabs do not use preferred shells and that the majority of the population inhabits shells that are far from being optimal (Vance, 1972b; Conover, 1978).

Shell morphology varies for a number of architectural patterns and to study these patterns singularly can be useful but cannot explain completely all the complex questions of optimal shell choice. The use of principal component analysis may be helpful to describe overall size and shape and stresses the differences in utilization recorded between habitats. Moreover, Gilchrist (1985) demonstrated that the type of shell a hermit crab experiences in the early phases of its life influences the shell preference in the future. As the number of different shells that a hermit crab can explore after metamorphosis is very high, an animal genetically programmed to search for the 'right' shell could certainly be disadvantaged compared with a hermit crab with flexible preference. A behavioural plasticity throughout life allows exploration and use of new shells that will eventually appear in the habitat (Blackstone & Joslyn, 1984). Hermit crabs can evaluate the shells with all their characteristics as a whole and realize an adaptive choice.

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