HIERARCHICAL ANALYSIS OF SPATIAL DISTRIBUTION PATTERNS OF PATELLID LIMPETS IN THE CANARY ISLANDS

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ABSTRACT

We studied the distribution, abundance and size structure of three limpet species (*Patella rustica*, *Patella candei crenata* and *Patella aspera*) throughout the rocky intertidal zone of the Canary Archipelago. We used a stratified and hierarchical sampling strategy that involved the study of three intertidal zones (high, intermediate and low intertidal) across eight islands with three random locations per island and three randomly selected sites within locations. We did not observe any specimens of *P. candei candei*. For the entire archipelago, the least abundant species was *P. candei crenata* (0.02 ± 0.05 individuals/0.25 m^2, average $\pm$ SD), the species with significantly greatest sizes (26.8 ± 11.08 mm, average $\pm$ SD) and of highest commercial interest. *Patella aspera* (0.08 ± 0.37 individuals/0.25 m^2) and *P. rustica* (0.069 ± 0.16 individuals/0.25 m^2) showed higher abundance, but smaller sizes (21.0 ± 9.21 and 18.1 ± 7.94 mm, respectively). The three zones influence how these species are distributed and these distribution patterns are homogenous among islands. *Patella rustica* was observed to be more abundant in the intermediate zone and *P. aspera* in the lower zone, while *P. candei crenata* showed similar abundance in the low and intermediate zones. This vertical variability is masked by a horizontal variability on small and intermediate scales (10 s to 1000 s of meters), but not among islands (10 s to 100 s of km). This fact can be attributed to the low abundance of the limpet species in the locations studied, as a result of overexploitation of this resource in the Canary Islands. Consequently, there is a need for management and control measures.

INTRODUCTION

Coastal natural resources have been subject to intense human disturbances during the past decades (Castilla, 2000; Thompson, Crowe & Hawkins, 2002). Among these perturbations, the harvest and collection of macroinvertebrates is, without a doubt, one of the main human impacts on the littoral environment (Thompson *et al*., 2002). It is a common activity in the Macaronesian region (Azores, Madeira and the Canary Islands) and is practised at both professional and recreational levels (Moro & Herrera, 2000). Thus, the intertidal shellfish resources of the Canary Islands have a long history of exploitation, having constituted one of the few protein sources of the old native inhabitants (Navío-Vasseur, 2001). At present, the pressures on the Canary Islands intertidal communities have increased due to the rising population of the islands and to the gradual destruction of habitats by alterations of the coast (Aguilera *et al*., 1994), as well as to the lack of legislation on the matter. This over-exploitation may have been the cause of the extinction of *Patella candei candei* d'Orbigny, 1840 in all of the archipelago, except Fuerteventura Island (Núñez, Barquín & Brito, 1994; Núñez, 1995; Corte-Real, Hawkins & Thorpe, 1996; Moro & Herrera, 2000).

Aside from these human induced processes, we must consider the great spatial variability intrinsic to coastal ecosystems (Menconi, Benedetti-Cecchi & Cinelli, 1999; Benedetti-Cecchi, 2001). Its analysis is a key requisite to understanding the ecological processes operating in the intertidal environment, and for explaining the distribution of intertidal populations (Underwood, 1990; Underwood & Chapman, 1996; Menconi *et al*., 1999). The description of vertical and horizontal distribution patterns allows us to assess the natural variability inherent in the population distribution and to define the importance of different sources of spatial heterogeneity (Menconi *et al*., 1999; Benedetti-Cecchi, 2001).

Despite the profusion of studies in intertidal ecology, few quantitative studies have analysed large-scale patterns of distribution (Boaventure, Cancela da Fonseca & Hawkins, 2002). Thus, no study has described and quantified the population structure and spatial distribution patterns of the intertidal natural resources in the different islands that make up the Canarian Archipelago. Consequently, the aim of the present study was to evaluate the status of one of the main shellfish resources, the four species of limpets: *Patella candei candei*, *Patella candei crenata* d'Orbigny, 1840, *Patella rustica* Linnaeus, 1758 and *Patella aspera* Röding, 1798. The taxonomy of the *Patella* species adopted here follows Koufopanou *et al*. (1999) and Weber & Hawkins (2002), although in the Canary Islands the species *P. rustica*, *P. candei crenata* and *P. aspera* are more familiar under the names *P. piperata* Gould, 1846, *P. tenuis crenata* and *P. ulyssiponensis* Gmelin, 1791 (Moro *et al*., 2003). In order to achieve this, the distribution patterns were described for different hierarchically-structured spatial scales spanning five orders of magnitude (from 10 s of m to 100 s of km).

MATERIAL AND METHODS

Study area and sampling strategy

A partially hierarchical (mixed) sampling strategy was selected (Underwood, 1997; Kingsford & Battershill, 1998; Menconi *et al*.,

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1999; Benedetti-Cecchi, 2001), in order to represent the complexity of natural systems (Benedetti-Cecchi, 2001).

Sampling was carried out on intertidal rocky platforms of the seven islands that constitute the Canary Archipelago and in the set of small islets that constitute the Chinijo Archipelago (13–19° W, 27–30° N), during March 2003. These rocky platforms have a smooth slope and are of volcanic origin (mainly basalts), with a width of between 30 and 70 m, and are exposed to a similar degree of wave action. In general, three zones can be recognized in the rocky intertidal of the Canary Islands: high intertidal, intermediate intertidal and low intertidal, following classical zonation schemes (e.g. Steneck & Dethier, 1994; Menconi *et al.*, 1999; Boaventura, Re, Cancela da Fonseca & Hawkins, 2002; Dunmore & Schiel, 2003). The low zone is characterized by a covering of erect corticated macroalgae. The intermediate zone is dominated by the cirripede *Chthamalus stellatus*, whereas the high zone is dominated by a cyanobacterial film (*Cyanophytas*).

On each island, three rocky substrate locations separated by 1–30 km were chosen (Fig. 1), except on El Hierro Island where we added a fourth location. In each location, we randomly selected three sites separated by 10 s to 100 s m. This allowed us to adopt a hierarchically organized perspective spanning five orders of magnitude of horizontal spatial variability (Benedetti-Cecchi, 2001). This design incorporated: islands (10^4–10^5 m), locations (10^3–10^4 m) and sites (10^1–10^2 m). All of the studied locations are easily accessible and collection is not regulated.

In each zone of the three rocky sites within each location, we randomly placed 10 quadrats of 50×50 cm ($0.25\ m^2$) (Kingsford & Battershill, 1998; Liu & Morton, 1998; Takada, 1995, 1996; Menconi *et al.*, 1999; Dunmore & Schiel, 2003), and counted and measured (length to 0.1 mm) all the limpets.

Statistical analysis

The population abundance of each species was analysed separately by means of a mixed ANOVA model to determine differences among the three intertidal zones at the three different spatial scales considered by our sampling design (islands, locations within islands and sites within locations). We thus considered the following factors: (1) Island (fixed and with eight levels corresponding to the eight islands); (2) Zone (fixed, and orthogonal to the previous one, with three levels corresponding to the high, intermediate and low zones); (3) Location (random and nested in the Island factor, with three levels); and (4) Site [random and nested in the interaction term Zone $\times$ Location (Island)] (Underwood, 1997). The model of sources of variation was as follows:

$$X = \mu + I + B + L(I) + S(L(I) \times B) + (I \times B) + (B \times L(I)) + Residual$$

In order to execute balanced analyses we only considered three locations on El Hierro Island. Due to the high heterogeneity of variances (Cochran's test, $P < 0.01$) despite the data transformation, a significance level of $\alpha = 0.01$ was considered instead of 0.05 to avoid type I error (Underwood, 1997). In studies with a considerable volume of data, ANOVA is robust to heterogeneity of variances, if a conservative value of α is used (Underwood, 1997).

For each species we obtained a size-frequency histogram for all specimens found. We tested the possible differences in mean sizes among the three species with a one-way ANOVA, starting with a random selection of 30 specimens of each species, with the intention of executing a balanced analysis (Underwood, 1997).

When some terms of the ANOVAs that included a fixed factor were significant, the SNK *a posteriori* test was applied (Underwood, 1997).

RESULTS

Population abundances

Table 1 shows the average population abundances for the limpet species in each location. *Patella rustica* was the most frequent species, present in 64% of all sampled locations. We found 152 specimens, representing 41.3% of the total limpets. The average abundance of specimens ranged between a maximum of 0.92 individuals/$0.25\ m^2$ (intermediate zone at Taliarte, Gran Canaria) and a minimum of 0.03 individuals/$0.25\ m^2$, corresponding to the observation of a single specimen, which occurred in several studied locations (Table 1). The average abundance for the entire Archipelago was 0.07 ± 0.16 individuals/$0.25\ m^2$ (average $\pm$ SD, Table 1).

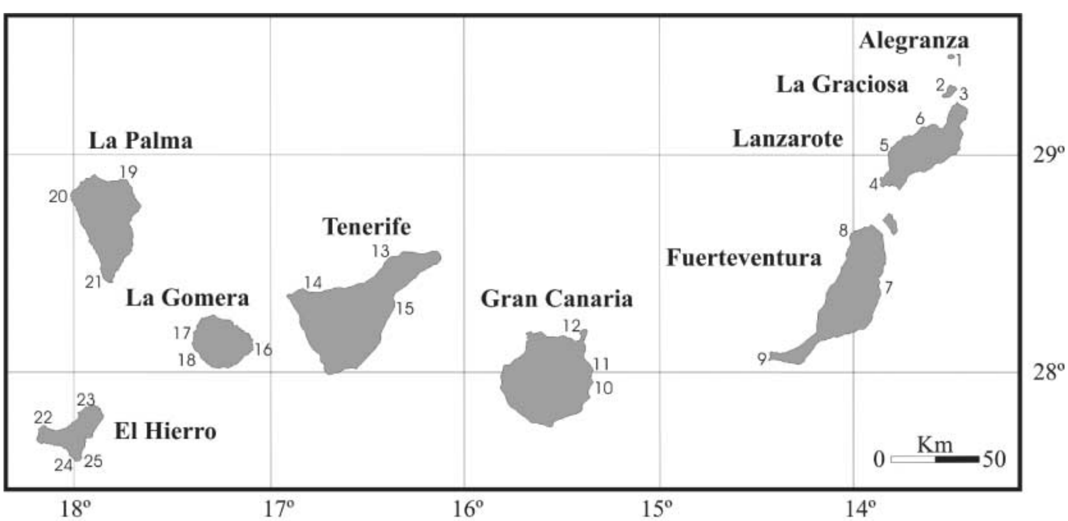

Figure 1. Map of the Canarian Archipelago showing sampling locations. 1, Punta de los Abades; 2, El Corral; 3, Caleta de Sebo; 4, Pechiguera; 5, El Cochino; 6, La Santa; 7, Puerto del Rosario; 8, El Cotillo; 9, Punta Jandía; 10, El Cabrón; 11, Taliarte; 12, La Isleta; 13, Punta del Hidalgo; 14, Caleta de Interián; 15, Malpais de Güimar; 16, Puntallana; 17, Alojera; 18, Valle Gran Rey; 19, Punta Cumplida; 20, Punta Gorda; 21, Punta Larga; 22, Punta Arenas Blancas; 23, Charco Manso; 24, La Restinga; 25, La Restinga, Muelle.

Table 1. Mean density/0.25 m^2 of Patella species recorded at each surveyed location across the Canarian Archipelago.

Island	Location	Zone	*P. rustica*		*P. aspera*		*P. candei crenata*	
			Mean abundance 0.25 m^2	SD	Mean abundance 0.25 m^2	SD	Mean abundance 0.25 m^2	SD
A. Chinijo	Punta de los Abades	High Intertidal	0		0		0	
		Intermediate Intertidal	0		0.0333	0.1889	0.0756	0.2562
		Low Intertidal	0		0.5232	0.6254	0.0714	0.2622
	El Corral	High Intertidal	0		0		0	
		Intermediate Intertidal	0		0		0	
		Low Intertidal	0		0		0	
	Caleta de Sebo	High Intertidal	0		0		0	
		Intermediate Intertidal	0		0		0.0333	0.1889
		Low Intertidal	0		0		0	
	El Cochino	High Intertidal	0		0		0	
		Intermediate Intertidal	0.1785	0.39	0		0.0333	0.1889
		Low Intertidal	0.1785	0.39	0		0	
	La Santa	High intertidal	0		0		0	
		Intermediate Intertidal	0.4285	0.5727	0		0.1785	0.39
		Low Intertidal	0		0		0	
Fuerteventura	Puerto del Rosario	High Intertidal	0		0		0	
		Intermediate Intertidal	0.0333	0.1889	0		0	
		Low Intertidal	0		0.1785	0.39	0	
	El Cotillo	High Intertidal	0		0.0333	0.1889	0	
		Intermediate Intertidal	0		0.0714	0.2622	0	
		Low Intertidal	0.1071	0.3149	0.0333	0.1889	0	
	Punta Jandía	High Intertidal	0		0		0	
		Intermediate Intertidal	0.0333	0.1889	0.0714	0.2622	0	
		Low Intertidal	0		0		0	
Gran Canaria	El Cabrón	High Intertidal	0		0	0.1889	0	
		Intermediate Intertidal	0		0.0333	0.1889	0	
		Low Intertidal	0		0.0333	0.1889	0	
	Taliarte	High Intertidal	0.3214	0.4755	0		0	
		Intermediate Intertidal	0.9212	0.4532	0		0	
		Low Intertidal	0.5003	0.6388	0.9241	0.8529	0	
	La Isleta	High Intertidal	0		0		0	
		Intermediate Intertidal	0.4158	0.5242	0.8562	0.6555	0	
		Low Intertidal	0		2.9252	1.5621	0.1071	0.3149
Tenerife	Punta Hidalgo	High Intertidal	0		0		0	
		Intermediate Intertidal	0.0714	0.2622	0		0.0333	0.1889
		Low Intertidal	0		0		0.2142	0.4178
	Caleta de Interián	High Intertidal	0		0		0	
		Intermediate Intertidal	0		0		0	
		Low Intertidal	0		0		0.0333	0.1889
	Malpaís de Güimar	High Intertidal	0		0		0	
		Intermediate Intertidal	0.2142	0.4178	0.0333	0.1889	0.0333	0.1889
		Low Intertidal	0		0.1071	0.3149	0.0714	0.2622
La Gomera	Puntallana	High Intertidal	0.0714	0.2622	0		0	
		Intermediate Intertidal	0		0		0	
		Low Intertidal	0		0.0333	0.1889	0	
	Alojera	High Intertidal	0		0		0	
		Intermediate Intertidal	0.25	0.4409	0		0.1785	0.39
		Low Intertidal	0		0		0	
	Valle Gran Rey	High Intertidal	0		0		0	
		Intermediate Intertidal	0		0		0	
		Low Intertidal	0		0		0	
La Palma	Punta Cumplida	High Intertidal	0.0333	0.1889	0		0	
		Intermediate Intertidal	0.4285	0.5727	0		0	
		Low Intertidal	0		0		0.0333	0.1889

(*continued on next page*)

Table 1 (*continued*)

Island	Location	Zone	*P. rustica* Mean abundance 0.25 m²	SD	*P. aspera* Mean abundance 0.25 m²	SD	*P. candei crenata* Mean abundance 0.25 m²	SD
	Punta Larga	High Intertidal	0		0		0	
		Intermediate Intertidal	0.6652	0.7122	0		0	
		Low Intertidal	0		0		0	
El Hierro	Punta Arenas Blancas	High Intertidal	0.1071	0.3149	0		0	
		Intermediate Intertidal	0		0.0333	0.1889	0	
		Low Intertidal	0		0.25	0.4409	0	
	Charco Manso	High Intertidal	0		0		0	
		Intermediate Intertidal	0		0		0	
		Low Intertidal	0		0		0	
	La Restinga	High Intertidal	0		0		0	
		Intermediate Intertidal	0.0714	0.2622	0		0	
		Low Intertidal	0		0		0	
	La Restinga-Muelle	High Intertidal	0		0		0	
		Intermediate Intertidal	0		0		0	
		Low Intertidal	0		0		0	
	Overall abundance/0.25 m²		0.0690	0.1666	0.0826	0.3682	0.0153	0.0417

Patella candei crenata was found in 44% of the analysed locations throughout the archipelago, although we only observed 32 individuals (8.69% of the total). The average abundance varied from a maximum of 0.21 individuals/0.25 m^2 (low intertidal in Punta Hidalgo, Tenerife) to a minimum of 0.03 individuals/0.25 m^2, corresponding to the observation of a single specimen at several studied locations (Table 1). It is the least abundant species of the Canary Archipelago, with an average abundance of 0.02 ± 0.04 individuals/0.25 m^2 (Table 1).

Patella aspera was observed in 40% of the surveyed locations throughout the study, with a total of 184 specimens, representing half of the total limpets. The average abundance varied between a maximum of 2.93 individuals/0.25 m^2 (low intertidal in La Isleta, Gran Canaria) and a minimum of 0.03 individuals/0.25 m^2, corresponding to the observation of a single specimen at several studied locations (Table 1). The average abundance for the entire archipelago was 0.08 ± 0.37 individuals/0.25 m^2 (average ± SD, Table 1). It is important to note that 61% of the specimens of this species were observed in one location (La Isleta, Gran Canaria). Without this location, the average abundance for the entire archipelago would drop to 0.03 ± 0.13 individuals/0.25 m^2.

We did not observe any specimens of *Patella candei candei* at any of the locations.

Population spatial distributions

Patella rustica did not show any significant differences in abundance among islands ($F = 1.74$, $P > 0.01$; Table 2), but it did among zones ($F = 10.18$, $P < 0.01$; Table 2), being more abundant in the intermediate intertidal (73.81 %) and maintaining the homogenous patterns among different islands (interaction term Island × Zone, $F = 1.45$, $P > 0.01$; Table 2) and locations within each island (interaction term Location (Islands) × Zone $F = 0.90$, $P > 0.01$, Table 2). However, our study detected variability on a small scale in the distribution of this species (sites within locations, $F = 1.85$, $P < 0.01$; Table 2).

Patella candei crenata likewise did not show significant differences among either islands ($F = 1.26$, $P > 0.01$; Table 2) or locations ($F = 1.16$, $P > 0.01$; Table 2), but only on the smaller sampling scale (sites sampled within locations, $F = 1.86$, $P < 0.01$; Table 2). This species demonstrated the same frequency of occurrence in the low intertidal zone (49.93%) as in the intermediate zone (50.07%), and it was not detected in the high zone. This

Table 2. Results of mixed ANOVA models for each *Patella* species.

	d.f.	*P. rustica* MS	*F*	*P. candei crenata* MS	*F*	*P. aspera* MS	*F*
Island = I	7	1.5680	1.74	0.0081	1.26	0.7960	1.90
Zone = Z	2	4.5500	10.18**	0.0168	2.69*	0.7904	3.76*
I × Z	14	0.6489	1.45	0.0094	1.50	0.4661	2.22*
Location (I) = L(I)	16	0.9032	1.81*	0.0065	1.16	0.4185	4.76**
L(I) × Z	32	0.4470	0.90	0.0062	1.12	0.2103	2.39**
Site (Location (I × Z))	144	0.4991	1.85**	0.0056	1.86**	0.0879	6.03**
Residual	944	0.2705		0.0030		0.0146	

d.f., degrees of freedom. *0.01 < P < 0.05. ** P < 0.01.

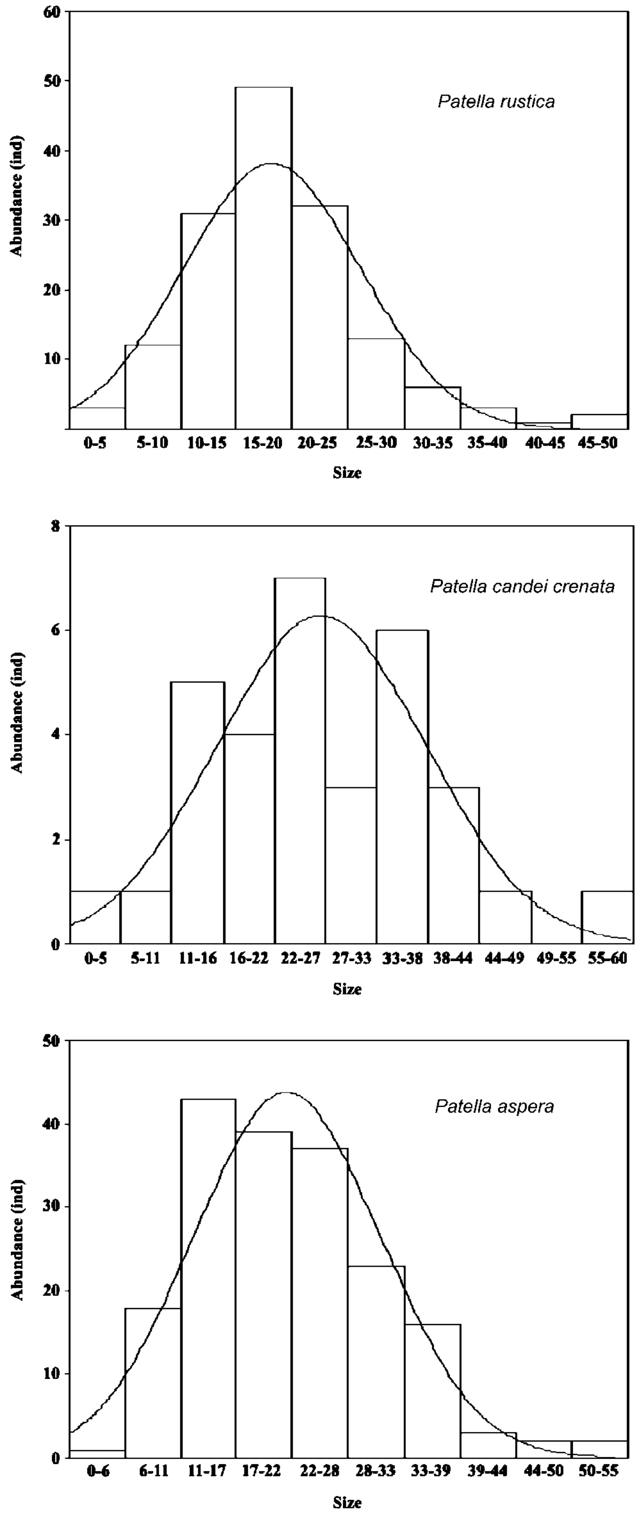

Figure 2. Limpet size distribution in the Canarian Archipelago.

homogenous pattern was maintained among the different islands (interaction term Island × Zone, $F = 1.50$, $P > 0.01$; Table 2) and sampled locations within each island (interaction term Location (Island) × Zone, $F = 1.12$, $P > 0.01$; Table 2).

Patella aspera showed variability among the locations within each island ($F = 4.76$, $P < 0.01$; Table 2), and the sites within each location ($F = 6.03$, $P < 0.01$; Table 2), although differences among islands were not detected ($F = 1.90$, $P > 0.01$; Table 2). This species has showed clear differences among the three intertidal zones, although the ANOVA model did not detect significant values at the $\alpha = 0.01$ significance level for the interaction term Zone × Island ($F = 2.22$, $P > 0.01$; Table 2), and for the main factor Zone ($F = 3.76$, $P > 0.01$; Table 2). Most of the specimens (79.2%) were observed in the low intertidal zone. The remainder were observed in the intermediate intertidal (20.16%) and only one in the high intertidal (0.64%; El Cotillo, Fuerteventura). Within each island, the zone distribution varied for each location, since we detected a significant interaction between both factors (interaction term 'Zone × Location (Island)', $F = 2.39$, $P < 0.01$; Table 2).

Population size distributions

Patella rustica showed an average size of 18.1 ± 7.9 mm (average ± SD, $n = 152$; Fig. 2) for the overall study, with a maximum size of 49 mm. The modal size class 15–20 mm represents a third of the measured specimens (Fig. 2). The average size of *Patella aspera* was 21.0 ± 9.2 mm ($n = 184$; Fig. 2), with a maximum size of 51 mm. Finally, the average size of *Patella candei crenata* was 26.8 ± 11.1 mm ($n = 32$; Fig. 2), with a maximum size of 57 mm. This species was larger than *P. rustica* and *P. aspera* throughout the studied locations in the Canaries (one way ANOVA: $F = 6.68$, $P < 0.05$; Fig. 2).

DISCUSSION

Our results show that the studies on the structure of intertidal populations must consider their distribution in zones throughout a vertical gradient, as well as other variability sources of horizontal variability, which can be of equal or greater importance than the vertical variability. The present study has clarified several questions related to the vertical and horizontal distribution patterns of limpets across the entire Canary Archipelago. Our study has highlighted that the analysed limpet species show vertical zoning, persistent on the different spatial scales in the rocky intertidal environment of the Canary Islands. This vertical variability (Benedetti-Cecchi, 2001) is homogenous among the studied islands. In addition, this vertical variability is masked by horizontal variability on small and intermediate spatial scales (sites and locations separated by 10 s to 100 s m and by 10 s km, respectively), but not among islands (10 s to 100 s km).

No study has analysed the distribution patterns and abundance of intertidal limpets at different spatial scales of the Canary Islands. Other investigations that have analysed spatial distribution patterns on rocky shores of temperate seas have identified multiple sources of horizontal and vertical variability (e.g. Foster, 1990; Archambault & Bourget, 1996; Underwood & Chapman, 1996; Menconi *et al*., 1999; Benedetti-Cecchi, 2001; Boaventura *et al*., 2002). In all these cases, there is an important degree of horizontal variability on small spatial scales, just as we have observed. These differences are not explained by changes in the wave exposure or by large-scale habitat attributes. Thus, various processes have been considered to explain these differences: recruitment variation, behaviour changes, differences in the substratum topography on a small scale, interaction between biological and physical processes, etc. (Cantos *et al*., 1994; Underwood & Chapman, 1996; Menconi *et al*., 1999; Benedetti-Cecchi, Bulleri & Cinelli, 2000). The contribution of each of these processes remains to be quantified, reflecting the lack of understanding of horizontal variability structuring the populations of intertidal grazing invertebrates (Benedetti-Cecchi, 2001).

The main difference between our study and those mentioned above is the absence of significant differences for the largest scale:

variability among islands (10 s to 100 s km). This result is surprising, since important differences exist in the geomorphology of the different islands, and differences are found in oceanographic conditions between the eastern and western islands (Davenport *et al*., 2002) that may produce changes in the abundance and distribution (Menge *et al*., 1997; Menge, 2000; Benedetti-Cecchi, 2001; Nielsen & Navarrete, 2004). We suggest that this may be due to the absence and extremely low abundance of the three studied limpet species in the islands, as a result of overexploitation of this resource. The pooled overall average abundance of limpets throughout the Canary Islands is about two to three orders of magnitude lower that the average limpet abundance recorded for the entire Portuguese coast (Boaventura *et al*., 2002) and some coastal areas of the Mediterranean Sea (Menconi *et al*., 1999).

Our results also suggest the impact of collection of limpets on the size-structure of their populations. Thus, the limpet species that reaches the greatest sizes, *Patella candei crenata*, is the least abundant. This phenomenon can be attributed to the selection of larger limpets by gatherers of intertidal shellfish (Moro & Herrera, 2000), as in other species around the world (Jackson & Sala, 2001). This species, along with *Patella aspera*, is the one of greatest commercial interest in the Canary Islands, although their shortage is beginning to encourage the harvesting of the small *Patella rustica* (Moro & Herrera, 2000). The large endangered species *Patella candei candei* (included in the National Spanish Catalogue of Threatened Species in 'extinction danger') was not found in any of the sampled locations.

A way to estimate the impact of the extraction of these natural resources is by the comparison of protected areas (control) and exploited sites (review by Glasby, 1997). Unfortunately, our study lacks locations suitable as controls. However, the maximum abundance for *Patella aspera* was detected at La Isleta (Gran Canaria) inside a military zone with restricted access. Management measures and control of intertidal shellfishing in the Canary Archipelago are clearly needed, backed by a solid and effective legal framework.

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