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Ecological considerations and niche differentiation between juvenile and adult black limpets (*Cymbula nigra*)

G.A. RIVERA-INGRAHAM, F. ESPINOSA AND J.C. GARCÍA-GÓMEZ

Laboratorio de Biología Marina, Departamento de Fisiología y Zoología, Avenida Reina Mercedes 6, Universidad de Sevilla, 41012, Sevilla, Spain

The endangered patellid limpet Cymbula nigra *is present in the extreme western Mediterranean, yet the species has rarely been the subject of study in this region. The aim of the present research is to describe the ecology, distribution and population structure of the species in an area of the Mediterranean coast of North Africa (Ceuta). Results indicate that the species prevails in waters that have an important Atlantic influence. Furthermore, different shell morphologies are distinguished, and in consequence, a statistical analysis is carried out based on morphometric data. Based on maximum shell length, height/length coefficients and shell morphology, a total of three significantly different morphologies are described. Furthermore, considering physical parameters such as height over seawater level and average substratum inclination, juveniles resulted to be clearly segregated from the two other groups. Additionally, no differences were found regarding the topography of the substrate used by juvenile and adult individuals, although the colonized surfaces are significantly smoother than those where* Patella ferruginea *is present.*

Keywords: *Cymbula*, patellid limpet, intertidal, intraspecific segregation

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INTRODUCTION

Cymbula nigra (da Costa 1771), commonly known as 'black limpet', is mainly distributed along the southernmost coasts of the Iberian Peninsula and from North Africa to Angola (Gofas *et al.*, 1988), being the only representative of the genus in the area. In the scientific literature, we also find references to its presence in the Macaronesian archipelagos: the Azores (Droüet, 1858), Canary Islands (Nordsieck & García-Talavera, 1979) and Cape Verde (Rolán, 2005).

Regarding the Mediterranean distribution of the species, the work of Poppe & Goto (1991) placed the species from the coasts of Tangier to Oran, including the coasts of Ceuta (Templado *et al.*, 2004) and Melilla (Pasteur-Humbert, 1962). On the European coasts, *C. nigra* is also found in the area from Cádiz to Málaga (Spada & Maldonado, 1974; Grandfils & Vega, 1982; Christiaens, 1983; Martínez & Peñas, 1996) although nowadays it is common on the coasts of Granada (personal observation). Additionally, in the last few years, the species has also been reported by Moreno (2006), Peñas *et al.* (2006) and Templado *et al.* (2006) in Alboran Island, although they classify the species as 'rare'.

The species is currently catalogued as an 'endangered and threatened species' (Annex II) by the Barcelona Convention (1993), as 'strictly protected' by the Berne Convention (1995) and as 'vulnerable' by the Andalusian Red List of Threatened Invertebrate Species (Moreno & Arroyo, 2008). Although at present many of the known populations are in clear regression, others seem to be on the increase (Templado *et al.*, 2004). In both cases, because of its classification as an endangered species and the lack of available data, more studies dealing with biological aspects of the species are required in order to establish adequate conservation measures.

Very little is known about the biology of this species. The first written study belongs to Renault & Moueza (1971), who reported data on its ecology as well as providing the first information regarding its reproduction. The reproductive cycle of *C. nigra* was described in more detail by Frenkiel (1975). Grandfils & Vega (1984) recorded the presence of individuals of this species on the coasts of Málaga (southern Spain) and conducted a thorough study of its radular morphology. Later, Espinosa *et al.* (2007) worked on the effects of pollution on different patellid species, among them being *C. nigra*. But most of the acquired data are derived from different genetic studies dealing with the Patellidae family (Koufopanou *et al.*, 1999; Nakano & Ozawa, 2004; Sá-Pinto *et al.*, 2005).

The main objective of the present study is to document the distribution, density and structure of the intertidal populations of the species along the coasts of Ceuta (North Africa, Strait of Gibraltar). Our analysis includes the description of the 3 different morphologies observed, and we conclude by exploring their environment as well as their morphometric characteristics. With this study we aim to assess whether different shell types are linked to niche diversification.

Corresponding author:
G.A. Rivera-Ingraham
Email: grivera@us.es

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MATERIALS AND METHODS

Location of the main populations and population structure

Between July 2007 and March 2009, a general search for the species was carried out along Ceuta's coasts (Figure 1A, B), visiting the most representative intertidal areas of the city, on both the North and South Bays, and including artificial and natural substrata. In each of the areas where *Cymbula nigra* was present, GPS coordinates were registered.

Additionally, in order to obtain a description of the population structure, the registration of the maximum shell length (to the nearest millimetre) of the total number of individuals found in a 100 m transect was carried out when possible, with the help of a caliper and a metric tape. However, for the specific case of the intertidal population of Parque del Mediterráneo (Figure 1C), where one of the most important populations was located, these measurements were taken every 5 m, in order to determine the aggregation pattern of the species. With the total number of individuals registered in the population, the average density per 5-m transect was calculated. Furthermore, the absolute value of the difference between the observed density per 5-m transect and the site's average density was obtained.

Intraspecific differences

After visual inspection of the coasts, three different morphologies may be described: the first, and the easiest to characterize consists of the smallest individuals, with fragile and flat shells characterized by a white and dark striped pattern. They also present a finely lobulated perimeter and radial ribs (Figure 2A); the medium to large individuals comprise the second of these morphotypes, with higher and more solid shells than those belonging to the previous morphotype, although without the striped pattern or at most only present in the outermost area of the shell. They are also characterized by the presence of a lobulated perimeter and radial ribs (Figure 2B). The medium to large individuals also constitute the third and last morphological type. Their shells are extremely solid and high, being almost conical. Here, the striped pattern, lobulated perimeter and the radial ribs are totally absent (Figure 2C).

In order to assess whether these morphotypes were significantly different, morphometric and physical parameters were registered for a total of 105 individuals (35 per each of the observed morphotypes) in Parque del Mediterráneo. For morphometric parameters, the maximum shell length and height were recorded to the nearest millimetre using a caliper. In the case of the physical parameters, the average inclination of the substrate (using a clinometer) and the height over water level were registered. For the latter, a metallic ruler was used with an incorporated bubble level, ending in a long piece of chain. Positioning the metallic structure at the individual's height and perfectly parallel to the ocean's surface thanks to the indications of the bubble level, the chain is dropped until it reaches the water surface. It is then measured to calculate the daily height of the individual.

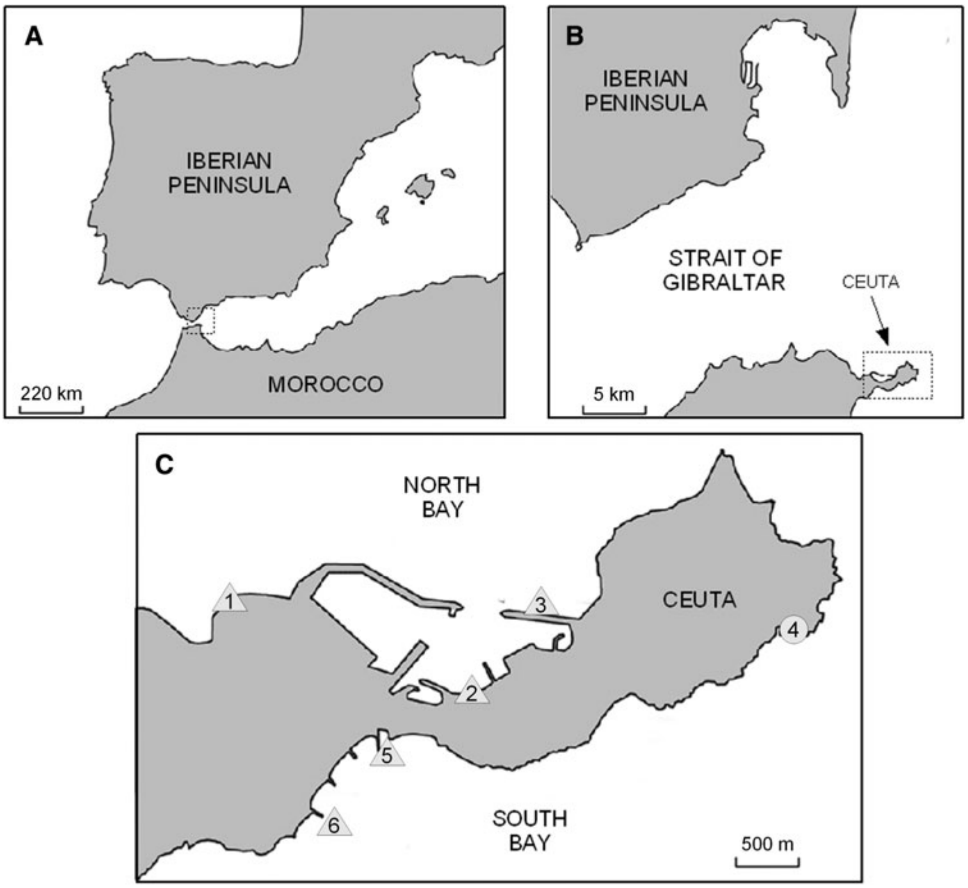

Fig. 1. Locations of the study on Ceuta's coasts, North Africa (Gibraltar area). Each point represents each of the visited locations. Triangles indicate artificial substrate while circles indicate natural substrate. Numbers and location names are correlated in Table 1.

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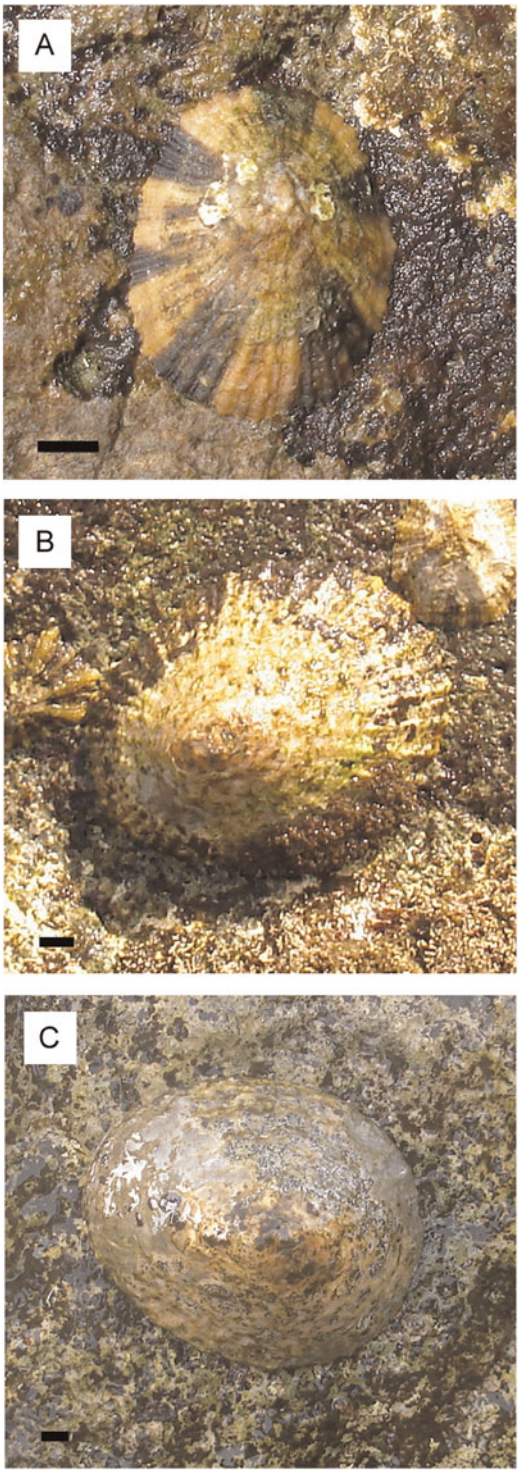

Fig. 2. Representative individuals of the three different *Cymbula nigra* morphologies observed in Ceuta: (A) morphotype 1; (B) morphotype 2; (C) morphotype 3. Scale bars = 1 cm.

These data are later corrected with the tide coefficient for the day, as published in the official tide tables.

Topographic analysis

As previous observations seemed to indicate that *C. nigra* individuals had a clear preference for smoother surfaces than those colonized by other species (such as the endangered limpet *Patella ferruginea*) a study of the topography of the substrata was made. A total of 66 profiles (33 per each of these two species and 11 each for the different *C. nigra* morphotypes) were taken from the rock surface closest to each studied individual during low tide. These profiles, with a maximum length of 13 cm, were later used to calculate the topography of the substrata using fractal dimensions (Mandelbrot, 1967). This methodology entails consecutive recalculations of the total perimeter (P) of each rock profile using progressively smaller steps (λ). This way, starting with a 45 mm step, the total profile perimeter (L) could be expressed as $L = (\lambda^{*}\text{number of used steps}) + (\text{any remaining distance smaller than the } \lambda \text{ used})$. However, it must be kept in mind that in this process, the total number of steps will only be an estimation of the true profile length, as the steps will skip any irregularity smaller than the length of the used step. Therefore, a previous evaluation of the most useful step lengths is necessary. In the case of the present study (rocky shores), steps with lengths between 5 and 45 mm (with 5 mm differences) were used (Beck, 2000).

Having done this, the final fractal dimension for the corresponding profile may be expressed as $Df_n = 1\text{-}M$, where M is the slope of the regression line considering Logλ (Y) and LogL (X).

Statistical analysis

These data were later analysed using SPSS 14.0 statistical software. As with much ecological impact data, the assumptions for parametric statistics were not met (Clarke & Warwick, 2001). While most of our data met the normality (assessed by the Kolmogorov–Smirnov test) and equal variances (assessed by the Levene test) assumptions, parameters such as inclination and height over water level showed slight deviation from equal variances. It is considered possible to undertake parametric analysis even if the equal variances assumption is not met, as long as the number of cases is high and balanced between groups (Underwood, 1997). Taking this into account, one-way ANOVA tests were carried out in order to determine differences between morphotypes based on the above mentioned parameters. Additionally, a *t*-test was undertaken in order to evaluate the aggregation pattern of the species using the same statistical software.

RESULTS

Location of the main populations and population structure

A total of 7 main populations were found during the present study. We can observe that the areas showing the higher density values are Dique de Poniente and Parque del Mediterráneo (artificial breakwaters on the North Bay), which presented an average of 34.1 and 2.96 individuals per metre, respectively. Figure 3 along with Table 1 show the structure of the intertidal populations included in this study. Additionally, in Figure 4, we observe the total number of individuals found in each 5-m interval for Parque del Mediterráneo. Our *t*-test showed that the absolute value of the difference between the observed 5-m frequency

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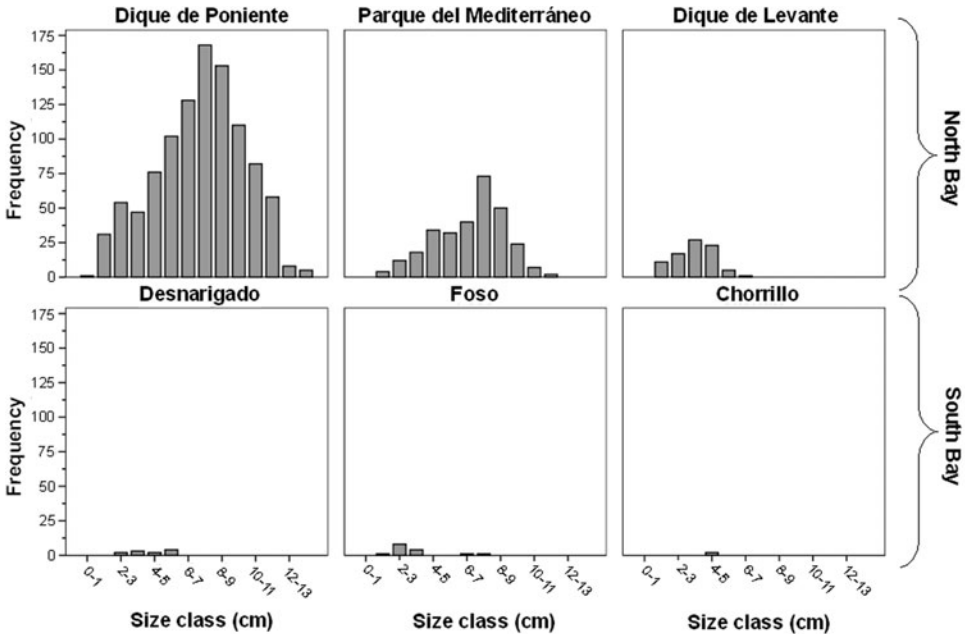

Fig. 3. Structure of the main intertidal populations of *Cymbula nigra* in Ceuta's North and South Bays.

and the expected value obtained from the site's total density is significantly different from 0 ($t = 8.151$; $P < 0.001$). This is evidencing the possibility that there is in fact an aggregation pattern in the species.

Intraspecific differences

An ANOVA test along with a Student–Newman–Keuls *a posteriori* comparison analysis was carried out in order to determine if there were any significant differences between morphotypes. Results can be observed in Table 2. Taking into account parameters such as the maximum shell length and maximum shell height/length (H/L) coefficient, all morphotypes can be statistically distinguished. Posterior regression analysis between maximum shell size and H/L coefficient was carried out, separately for each of the three different morphotypes in order to determine if these could be considered different. While data corresponding to morphotype 1 individuals were positively and significantly correlated, no correlation was found for both of the biggest categories. On the other hand, when pooling the three groups' data, regression proved to be significant (Figure 5).

When analysing the registered physical parameters, only two different morphotypes could be separated (Figure 6; Table 3). On one hand we find the smallest individuals, which are located in significantly more inclined and higher substrata than those individuals belonging to the two bigger size-groups, between which we cannot find any statistical differences regarding these parameters. Further analysis showed how maximum shell length is negatively correlated with height over sea level (Figure 7).

Topographic analysis

When considering the topography of the colonized substrate by calculating the fractal dimensions of the obtained profiles, we observed no significant differences among each of the three considered *Cymbula nigra* morphotypes. On the other hand, when taking into account the results for *Patella ferruginea* we did observe significant differences, confirming how this species colonizes rougher substrata than *C. nigra* (Table 4).

Table 1. Summary statistics for *Cymbula nigra* populations in Ceuta.

Population	Map No.	N	Metres	Density (ind/m)	Mean (cm)	Minimum (cm)	Maximum (cm)	Skew	SE skew	Kurtosis	SE kurtosis	Kurtosis type
Dique de Poniente	1	1023	30	34.1	7.17	1.10	13.30	−0.271*	0.076	−0.474**	0.153	Platykurtic
Parque	2	296	100	2.96	6.67	1.60	11.1	−0.407*	0.142	−0.461	0.282	n.s.
Dique de Levante	3	84	100	0.84	3.41	1.10	6.00	−0.134	0.263	−0.748	0.520	n.s.
Desnarigado	4	11	100	0.11	4.17	2.50	5.90	−0.810	0.661	−1.746	1.279	n.s.
Foso	5	15	100	0.15	3.17	1.80	7.10	1.730*	0.580	2.379**	1.121	Leptokurtic
Chorrillo	6	2	100	0.02	4.60	4.50	4.70	–	–	–	–	–

*, skew is considered significant when its absolute value is higher than 2*SE skew; **, kurtosis is considered significant when its absolute value is higher than 2*SE kurtosis; n.s., non-significant; SE: standard error.

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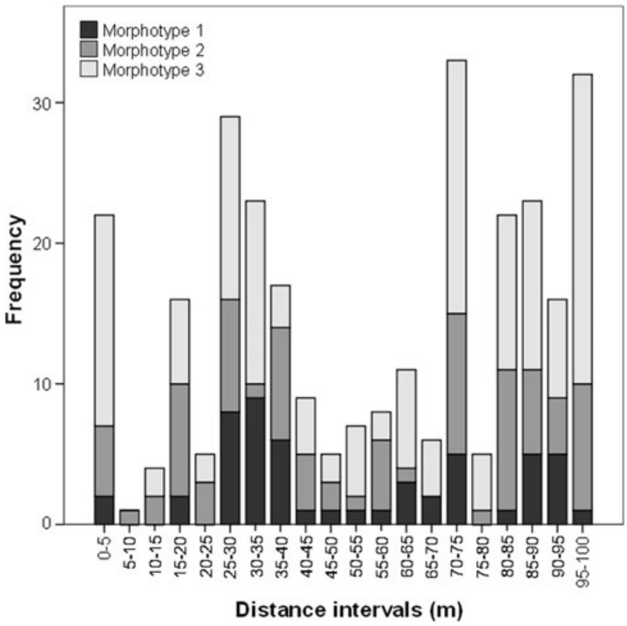

Fig. 4. Distribution of individuals per morphotype for the total of 100 m recorded in the intertidal population of Parque del Mediterráneo (registration in 5-m intervals). The absolute value of the difference between these results and the estimated density for the population is significantly different from 0 (t-test = 8.151; $P < 0.001$).

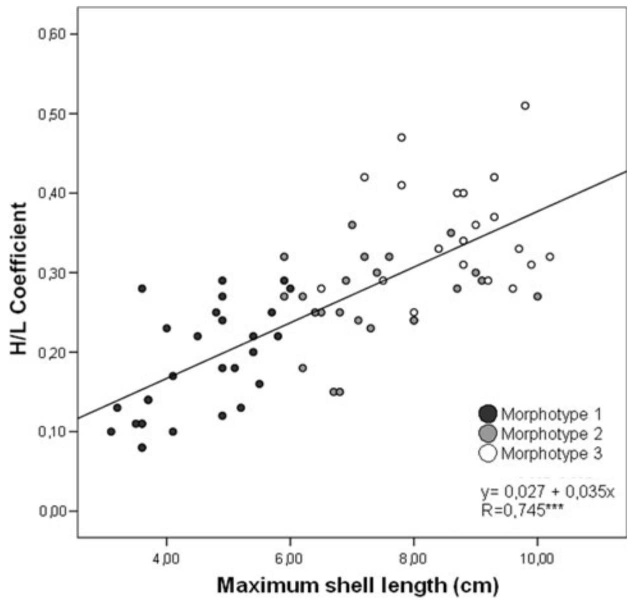

Fig. 5. Linear regression between maximum shell size (cm) and height/length (H/L) coefficient, for the complete pool set of data. ***, $P < 0.001$.

DISCUSSION

Location of the main populations and population structure

Although *Cymbula nigra* is considered a vulnerable species in regional lists of endangered invertebrates, and even 'endangered' and 'strictly protected' at a European level, the species is commonly found on the northernmost coasts of Africa, where the present study was conducted. As seen in our results, *C. nigra* is mainly distributed along Ceuta's northern coasts, where cold waters predominate because of its Atlantic influence. It was on these coasts that the most important populations were found with regards to population density. On the other hand, as we move towards the southern coasts (with a greater Mediterranean influence) the average density of each population drops and they become scarcer.

The two areas demonstrating the highest densities were Dique de Poniente and Parque del Mediterráneo, both being artificial breakwaters located in Ceuta's North Bay. The first is the newer part of the western dyke of Ceuta's commercial port, which consists of 3 × 3 m even-textured cement cubes. It was in this area that the highest density values were recorded (34.1 ind/m) partly influenced by the fact that it is an area difficult to reach by land. This fact along with the topographic results derived from the present study, allows

Table 2. One-way ANOVA results for the influence of maximum shell length (1) and height/length (H/L) coefficient (2) on the different *Cymbula nigra* morphologies. Values followed by the same letter (a, b or c) belong to the same subset based on the Student–Newman–Keuls *a posteriori* comparison test.

Source of variation	Mean ± SD (cm)	df	F	P
(1) Maximum shell length		2	115.93	***
Morphotype 1	4.52 ± 0.89 a			
Morphotype 2	7.36 ± 1.11 b			
Morphotype 3	8.71 ± 0.99 **c**			
(2) H/L coefficient		2	42.17	***
Morphotype 1	0.18 ± 0.07 a			
Morphotype 2	0.27 ± 0.05 b			
Morphotype 3	0.35 ± 0.07 c			

***, $P < 0.001$; SD, standard deviation.

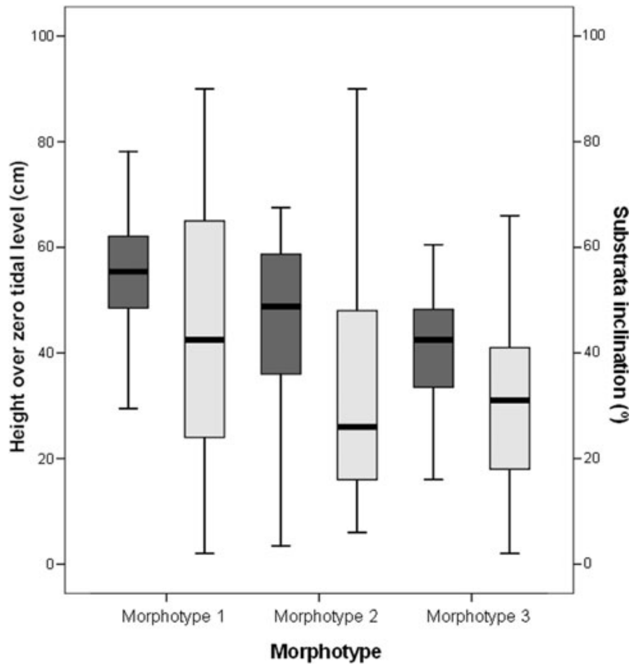

Fig. 6. Distribution of the obtained values corresponding to average substrate inclination and height over zero tide level per each of the observed morphologies. Each box shows the median, quartiles (25 to 75) and extreme values within a category. Black bars correspond to height over zero tide level value, while grey bars correspond to substrata inclination values.

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Table 3. One-way ANOVA results for the influence of the average substrata inclination (1) and height over seawater level (2) for *Cymbula nigra* morphologies. Values followed by the same letter (a or b) belong to the same subset based on the Student–Newman–Keuls *a posteriori* comparison test.

Source of variation	Mean ± SD (°)	df	F	*P*
(1) Substrata inclination		2	3.52	*
Morphotype 1	42.12 ± 25.15 a			
Morphotype 2	33.09 ± 22.52 b			
Morphotype 3	31.45 ± 16.64 b			
	Mean ± SD (cm)			
(2) Height over sea level		2	13.01	***
Morphotype 1	56.05 ± 10.57 a			
Morphotype 2	45.35 ± 16.30 b			
Morphotype 3	41.42 ± 10.44 b			

*, $P < 0.05$; ***, $P < 0.001$; SD, standard deviation.

us to think that this species has not only a clear preference for this kind of artificially smooth substrata but that it can be considered an important competitor in the colonization of these types of surfaces. This is also supported by the fact that on the older part of this western dyke (constructed with typical irregular dolomitic rocks) or even on the near eastern dyke (Dique de Levante, also consisting of irregular rocks), *C. nigra* does not present such important populations as the one located at Dique de Poniente. On the other hand, Parque del Mediterráneo (located inside the port) is another inaccessible area, in this case being private property. At this site the presence of smooth rocks is relatively frequent (which may explain the reason why we also find in this location high densities and big size-classes). Additionally, this area is partly influenced by a periodical municipal waste disposal. The fact that these density values are found associated with a waste dumpage may indicate the species' tolerance for moderately disturbed areas, where the presence of other patellid species, and in consequence interspecific competition, may be significantly lower (see Espinosa *et al.*, 2007).

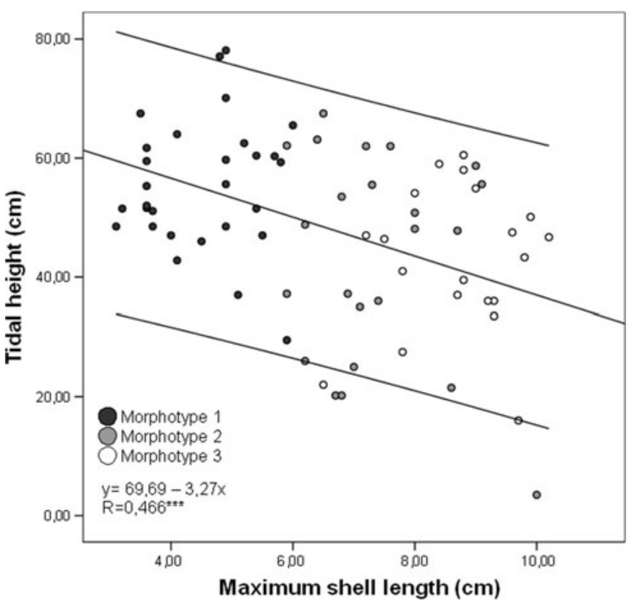

Fig. 7. Linear regression model obtained for maximum shell length and tidal height (cm). ***, $P < 0.001$. Lines represent 95% confidence interval for individuals.

Table 4. One-way ANOVA results for the influence of the species and morphology (for the case of *Cymbula nigra*) on the topography of the colonized substrata, as measured by fractal dimensions.

Source of variation	Mean ± SD (fd)	df	F	*P*
Species		1	5.796	0.019*
Patella ferruginea	1.017 ± 0.014			
C. nigra	1.009 ± 0.009			
C. nigra morphologies		2	0.977	n.s.
Morphotype 1	1.012 ± 0.009			
Morphotype 2	1.006 ± 0.010			
Morphotype 3	1.010 ± 0.009			

n.s., non-significant; *, $P < 0.05$; SD, standard deviation.

On the other hand, we also find a horizontal aggregation pattern, possibly correlated with a chemical larvae attraction system produced by its conspecifics as has been previously suggested for many other invertebrate species since the study of Burke (1984), and even for patellid species such as *Patella ferruginea* (Espinosa *et al.*, 2006).

Intraspecific differences

The three observed morphotypes were statistically different from each other. The registration of morphometric parameters has confirmed the previous observations regarding these morphotypes. Younger individuals (morphotype 1) present radial ribs and a lobulated perimeter, and are easily identified by the white and dark striped pattern. During the growth process, individuals lose this colour pattern and eventually result in a large individual with flat shell (morphotype 2) or develop a highly conical shell where radial ribs and the lobulated perimeter is completely absent (morphotype 3). For the case of Dique de Poniente, almost all of the largest individuals belonged to class 2, while specimens belonging to class 3 were rarely observed. This suggests that the determination of whether a juvenile develops a flat or a conical shell in their adult stage is mediated by physical or biological factors, as happens with many other limpet species such as *Nacella concinna* (Beaumont & Wei, 1991; Nolan, 1991) or *Patella candei* (Corte-Real *et al.*, 1996). On the other hand, when taking into account average substrata inclination and height over water level, we can determine that smaller individuals are segregated from the largest individuals (those belonging to morphotypes 2 and 3), being the latter sharing those preferable substrata, with less rock inclination and nearer to zero tide level, and presumably with more food resources. This change of habitat effectively separates adult and juvenile habitats and may reduce competition as shown in *Patella miniata, P. compressa, P. longicosta* or *P. cochlear* (see review in Branch, 1981). Independently from intraspecific segregation, the species has a clear preference for significant smoother substrata than those colonized by other patellid limpets such as *P. ferruginea*, the other endangered patellid species present in the intertidal coasts of Ceuta. *Cymbula nigra*, and especially the two biggest morphologies which are found at the lowest intertidal levels, have to withstand the highest wave impacts. It is known that flat and smooth surfaces like the ones colonized by these individuals, are the best to help prevent their dislodgement by waves and to enhance their ability to avoid predators (Steneck, 1982). Active substrate selection has also been cited for other limpet species such *Cellana grata* which show a preference for vertical surfaces (Williams & Morritt, 1995) and

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Patelloida pygmaea, which was shown to actively choose the substrate that best adjusted to its shell morphology (Nakai *et al.*, 2006).

Regarding vertical segregation, a negative correlation between maximum shell size and height over tide level is evidenced. This agrees with the Vermeij (1972) model which proposes that low intertidal species (such as *C. nigra*) would present this type of vertical pattern. Thus, recruitment would occur in the higher areas, and this vertical distribution could be explained by a downwards migration during the individual's life history. Other species such as *Patella argenvillei* (Stephenson *et al.*, 1940), *P. intermedia* (Vermeij, 1972) or acmeids like *Acmaea pelta* (Shotwell, 1950) or *A. testudinalis testudinalis* (Stephenson & Stephenson, 1954), which are also low intertidal species, follow this same pattern. In fact, as we have previously mentioned, the two largest morphotypes described here were found in the lower areas, and are mainly present in sub-horizontal rocks. This suggests the possibility that they prefer these areas as opposed to more vertical substrates. In this sense, there might not only be niche segregation between adults and juveniles, but also important competition processes for the occupation of these low and plain rocks. It is in these areas where a high density of the largest individuals is found, each of the individuals defending territories in the *Corallina elongata* belt. This allows us to observe perfectly the garden limits for each individual, which might be positively correlated with shell size (personal observation). Additionally, when recording the height of individuals over water level, some small individuals (belonging to morphotype 1), were found on the lower areas, occupying 'garden' areas surrounded by the largest individuals of the populations (morphotypes 2 and 3). We can assume that these animals may have migrated from upper rock areas to those, perhaps left vacant by other individuals. Moreover, Branch (1975) reported in *Patella cochlear* that the death of an adult limpet leads to an immediate occupation of the vacant scar by juveniles. This would support the theory of high intraspecific competition occurring for more favourable substrates.

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Correspondence should be addressed to:
G.A. Rivera-Ingraham
Laboratorio de Biología Marina, Departamento de Fisiología y Zoología, Avenida Reina Mercedes 6
Universidad de Sevilla, 41012, Sevilla, Spain
email: grivera@us.es

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