Conservation status and updated census of *Patella ferruginea* (Gastropoda, Patellidae) in Ceuta: distribution patterns and new evidence of the effects of environmental parameters on population structure

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Abstract

Conservation status and updated census of Patella ferruginea *(Gastropoda, Patellidae) in Ceuta: distribution patterns and new evidence of the effects of environmental parameters on population structure.*— The Strait of Gibraltar has important populations of the highly endangered patellid limpet *Patella ferruginea.* Between 2006 and 2010, an exhaustive census was carried out in Ceuta. The total coastline was divided into 17 sectors. The coast of each sector was examined by using 10 m transects. For the case of those sectors composed of breakwaters, jetties or islets, no transects were used, and instead, the total number of individuals was recorded. Each individual was measured to the nearest millimetre using a calliper. Moreover, the complete rocky shore length where the species could potentially be present was calculated, and an estimation of the total number of individuals that each sector could host was made. Results indicate that Ceuta could be home to around 44,000 individuals. The species found in Point Benzú, its westernmost limit of distribution on the North African coasts. The largest populations were recorded on the South Bay, with higher Mediterranean influence. Our results indicate that substrate roughness (topographic heterogeneity) and the area's accessibility highly influence the abundance and population structure. Those populations located on high topographic heterogeneity substrates show higher recruitment rates and lower percentages of larger individuals, while medium to low rugosity surfaces presented the opposite pattern. Additionally, easily accessible areas (and frequented by humans) presented smaller average shell sizes. Implications of the results for conservation purposes are discussed.

Key words: Limpet, *Patella ferruginea*, Endangered species, Conservation, Substrate roughness, Strait of Gibraltar, Ceuta.

Resumen

Estado de conservación y censo actualizado de Patella ferruginea *(Gastropoda, Patellidae) en Ceuta: patrones de dsitribución y nueva evidencia de los efectos de los parámetros ambientales en la estructura de la población.*— El Estrecho de Gibraltar presenta importantes poblaciones de la lapa *Patella ferruginea* altamente amenazada. Entre 2006 y 2010, se llevó a cabo un censo exhaustivo en Ceuta. La totalidad de la costa fue dividida en un total de 17 sectores. Se examinó el litoral de cada uno de estos sectores empleando transectos de 10 m. Para el caso de aquellos sectores compuestos por escolleras, espigones o islotes, no se emplearon estos transectos, y se registró el número total de individuos. Cada individuo fue medido por medio de un pie de rey con precisión de un milímetro. Además, se estimó la longitud total de costa rocosa que podría potencialmente presentar individuos y se realizó una estimación del número total de individuos que podría albergar cada sector. Los resultados indican que Ceuta podría presentar en torno a 44.000 individuos. La especie demostró tener en Punta Benzú su límite occidental de distribución en el Norte de África. Las poblaciones más importantes fueron registradas en la Bahía Sur, con importante influencia mediterránea. Nuestros resultados indican que la rugosidad del sustrato (heterogeneidad topográfica) y la accesibilidad de la zona influencian en gran medida la abundancia y la estructura de las poblaciones. Aquellas que se localizan sobre sustratos de alta heterogeneidad topográfica muestran mayores tasas de reclutamiento y menores porcentajes de individuos de gran tamaño, mientras que los sustratos de media a baja rugosidad muestran el patrón contrario. Además, aquellas áreas

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fácilmente accesibles (y frecuentadas por el ser humano) presentan poblaciones con tallas medias menores. Se discuten las posibles implicaciones de los resultados de cara a la conservación de la especie.

Palabras clave: Lapa, *Patella ferruginea*, Especies amenazadas, Conservación, Rugosidad del sustrato, Estrecho de Gibraltar, Ceuta.

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Introduction

The patellid limpet *Patella ferruginea* is an intertidal species endemic to the Mediterranean. It was widely distributed throughout the Western Mediterranean basin during the Pleistocene (Caton–Thompson, 1946; Laborel–Deguen & Laborel, 1991a) and its presence on European and North African coasts was recorded until the end of the 19th century. But it was in the beginning of the 20th century when the species started to suffer clear regression (Laborel–Deguen & Laborel, 1991a; Templado, 2001). Nowadays, the species has almost completely disappeared from European waters (Templado & Moreno, 1997). Its presence has been recorded in Southern Spain (Espinosa, 2006; Moreno & Arroyo, 2008) (where 700 individuals have been located, most of them present in Algeciras Bay). It can also be found on the coasts of Alborán Island (Paracuellos et al., 2003; Templado et al., 2006), North and Western Corsica (Laborel–Deguen & Laborel, 1991a; Curini–Galletti, pers. com.; Rivera–Ingraham et al., pers. obs.), Sardinia (Porcheddu & Milella, 1991; Doneddu & Manunza, 1992; Cristo et al., 2007; Cristo & Caronni, 2008; Rivera–Ingraham et al., pers. obs.), Pantellaria and Egadi Islands (Laborel–Deguen & Laborel, 1991a) and Tuscany (Italian peninsula) (Curini–Galletti, 1979; Biagi & Poli, 1986). In any case, the most important populations are currently located on the North African Coasts: Ceuta (Guerra–García et al., 2004; Espinosa, 2006; Espinosa et al., 2009), Melilla (González García et al., 2006), Chafarinas Islands (Guallart et al., 2006), Morocco (Bazairi et al., 2004), the Algerian isles of Rachgoun (Frenkiel, 1975) and Habibas (Boumaza & Semroud, 2001; Espinosa, 2009) and reaching Cape Bon (Espinosa, 2006) and Zembra Island (Boudouresque & Laborel–Deguen, 1986) (Tunisia).

This regression has been mainly caused by human exploitation (Aversano, 1986; Guerra–García et al., 2004; Moreno, 2004) which takes place in the highly accessible intertidal habitat (Raffaelli & Hawkins, 1996; Haedrich & Barnes, 1997; Rochet & Trenkel, 2003) where the species lives. It is commonly collected to be used as food, as fishing bait because of its muscular foot (Pombo & Escofet, 1996) or even for ornamental purposes, as happens with other big intertidal limpets such *as Lottia gigantea* (Lindberg et al., 1998; Kido & Murray, 2003). The species is presently considered as the most endangered marine invertebrate species on the Western Mediterranean rocky coasts (Laborel–Deguen & Laborel, 1991a; Ramos, 1998), and is protected at a European level (Annex II of Berne Convention; Annex IV of the Habitats Directive; Annex II of Barcelona Convention) as well as by Spanish laws (National Catalogue of Threatened Species; Andalusian Catalogue of Endangered Species).

Little is known regarding the biology of the species (Guerra–García et al., 2004) although many studies have been recently conducted in order to provide more information (*e.g.* Espinosa, 2006; Rivera–Ingraham, 2010). In this sense, the Spanish National Strategy for the Conservation of *P. ferruginea* has also been recently approved (MMAMRM, 2008) with the objective of promoting activities that could contribute to the knowledge of the species and obtain the necessary information to propose adequate conservation measures. One of these objectives is to obtain updated quantitative data regarding the distribution and the conservational status of the species, by developing detailed censuses. Some other authors like Paracuellos et al. (2003) have also pointed out the interest of quantifying the remaining *P. ferruginea* populations. The aim of the present study was to achieve a complete description of the meta-population of *P. ferruginea* in Ceuta, and to estimate the total number of individuals present in the area. Special attention is paid to the influence of substrate roughness and the area's accessibility on the species distribution and population structures.

Material and methods

Study site

The study was conducted in Ceuta, located on the African coast of the Strait of Gibraltar (fig. 1A), which is known to have important *P. ferruginea* populations (see Guerra–García et al., 2004; Espinosa, 2006; Espinosa et al., 2009). The coasts of this city are composed of natural rocky shores, beaches and small rocky islets. We also find many artificial jetties (especially on the South Bay). The city's commercial port has the peculiarity of being connected with the North Bay (through the port's main entrance) and with the South Bay through a moat.

Sampling methods

After the inspection of Ceuta's coastline, all areas presenting natural or artificial rocky shores that could potentially present *P. ferruginea* individuals were recorded. In order to estimate the total number of *P. ferruginea* individuals present in the area, the complete coastline was divided into 17 sectors (fig. 1B, table 1). However, within some of these sectors, some clearly differentiated structures (islets, breakwaters, jetties, etc.) were separately taken into account (refer to table 2). Later, for each of the sectors considered and only for rocky shores, a minimum of five transects (each composed of 10 m) running parallel to the shore were randomly established on the coastline with the help of a metric tape. Each *P. ferruginea* individual located within these transects was measured to the nearest millimetre using a calliper (Guerra–García et al., 2004; Espinosa, 2009; Rivera–Ingraham, 2010). Small individuals are often difficult to detect (Guallart et al., 2006), so special attention was paid to avoid missing this fraction of the population. For those sectors where the census was carried out using transects, the total length of rocky shoreline where the species could potentially be present was calculated by using 1:9,000 maps obtained using Google Earth ©. With this value and the average density recorded, an estimation of the total number of individuals within each sector was obtained. However, for the specific case of walls,

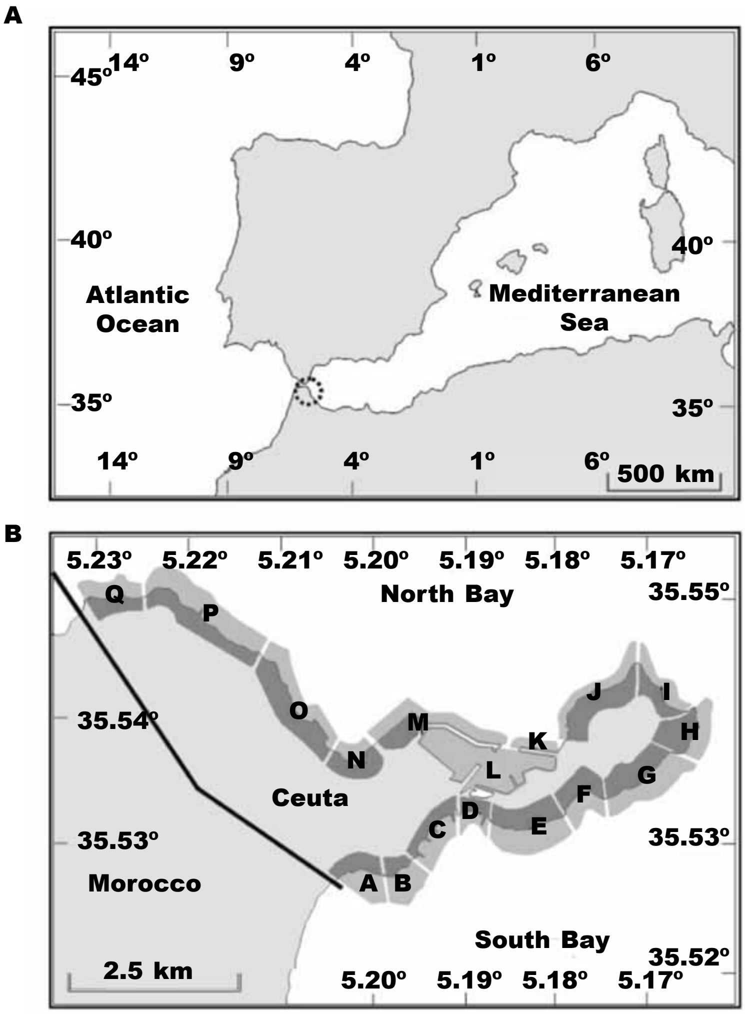

Fig. 1. A. Location of Ceuta; B. Sectors the study site was divided into to estimate the total number of individuals of *P. ferruginea*.

Fig. 1. A. Localización de Ceuta; B. Sectores en los que fue dividida la zona de estudio para la estimación del número total de individuos de P. ferruginea.

jetties, breakwaters and those islets that are not completely submerged during high tide, the total perimeter was measured, again using a metric tape, and a complete census was carried out when possible. The complete coastline was inspected from 2006 to 2010. Additionally, and for each of the prospected locations, some physical parameters were recorded: i) type of substrate (natural/artificial), considering as an artificial substrate any man–made structure, regardless of the origin of the substrate itself (*e.g.* Fauvelot et al., 2009; Bulleri & Chapman, 2010); ii) accessibility by humans, dividing areas into three categories: (a) high, easily accessible areas where it is common to find people collecting intertidal organisms; (b) medium, areas relatively easy to access and where it is not frequent find people at intertidal levels; and (c) low, areas which are difficult or cannot be accessed by land, and where no collection presumably occurs; and iii) substrate roughness or topographical heterogeneity index (THI), calculated as in Blanchard & Bourget (1999): THI = T_r/T_s, where T_r is the actual distance between two points (measured following the substrate's irregularities) and T_s the linear distance between the two same points. Substrates were again classified into three categories: (a) high roughness (THI >1.30); (b) medium roughness (THI = 1.30–1.15); and (c) low roughness (THI < 1.15). It is also important to note that in the present study, the total number of individuals present in Ceuta is considered to constitute a metapopulation, which would be composed of different sub–populations that are genetically connected (see review by Badii & Abreu, 2006).

Table 1. Data corresponding to each of the considered sectors: TR.Total rocky shore length (m); N. Number of individuals recorded; SL. Shore length inspected; T. Total number of individuals

Tabla 1. Datos correspondientes a cada uno de los sectores considerados: TR. Longitud total de la orilla rocosa (m); N. Número de individuos registrados; SL. Longitud de costa inspeccionada; T. Número total de individuos.

Sector	Sector Name	TR	N	SL	T
A	Frontera and P. Pineo	300	195	100	585
B	P. Gordas and P. Brazo	311	2,260	311	2,260
C	Chorrillo and Foso jetties	712	3,518	712	3,518
D	Fuentecaballos	350	2,262	350	2,262
E	Mellizos	1,142	104	100	1,187
F	Sarchal	350	106	100	371
G	Desnarigado	1,710	297	100	5,079
H	Desnarigado–Point Almina	2,201	479	258	4,086
I	Point Almina–Point Sirena	1,271	440	100	5,592
J	San Amaro	959	19	100	182
K	Dique de Levante	555	709	100	3,934
L	Inner port	3,754	4,111	3,754	4,111
M	Dique de Poniente (concrete cube section)	1,156	23	30	886
M	Dique de Poniente (limestone section)	1,115	244	50	5,441
N	Benítez	316	273	100	863
O	Desaladora–Point Bermeja	1,217	351	143	2,987
P	Point Bermeja–Point Blanca	1,138	42	100	477
Q	Point Blanca–Benzú	900	19	100	171
Total		19,457 m	15,452 ind.	6,608 m	43,992 ind.

Statistical analyses

Univariate analyses were carried out using the statistical package SPSS 15.0. One and two–way ANOVA tests were carried out between several physical parameters (nature of substrate (natural/artificial), sector location (North Bay, South Bay or Port) and substrate roughness) and the most common population parameters (density of individuals per size class, adult average shell size, maximum shell size, adult density and total density). Finally, and taking into account that the reduction of data to summary statistics (such as means, medians, etc.) for comparisons can significantly reduce the amount of available information (Sagarin et al., 2007), multivariate analyses were also conducted to compare size distributions among populations, as has been satisfactorily used by other authors (*e.g.* Sagarin et al., 2007; Espinosa, 2009). In order to do this, the total number of individuals for each size class (1 cm intervals) and sector was used. But considering that the total length of shoreline inspected varied considerably between locations, these frequency values were standardized by transforming them to percentages (over the total number of recorded individuals in the sector). Additionally, these data were later transformed to log (x+1) to homogenize variances. An MDS (Multi–dimensional scaling) analysis was carried out using PRIMER–E v.6.0 and based on the UPGMA (Unweigh Pair–Group Method using arithmetic means) method and the Bray–Curtis similarity index (Bray & Curtis, 1957). Moreover, the Kruskal stress coefficient was used to determine ordination (Kruskal & Wish, 1978).

Results

P. ferruginea distribution and abundance

Throughout the study, a total of 6,608 m of Ceuta's rocky shores was surveyed (33.96% of the total rocky shore that could potentially house *P. ferruginea*

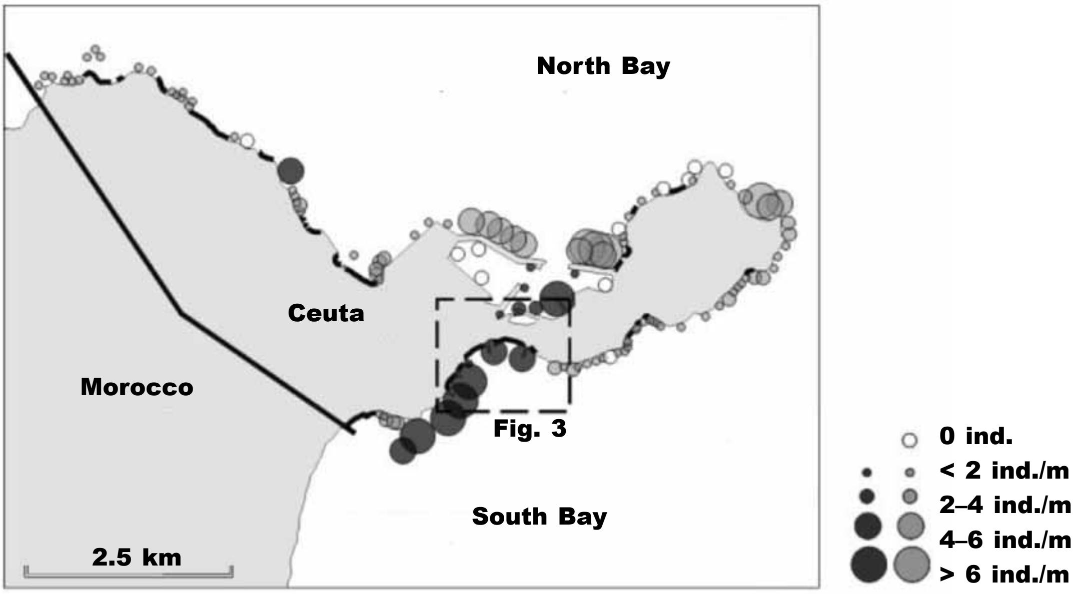

Fig. 2. General distribution of *P. ferruginea* in Ceuta, general view. Circle diameter corresponds to the density of individuals. Coastline sections plotted with thicker lines indicate the location of non–suitable areas (*e.g.* beaches) for the species. Light grey circles indicate the density recorded for each transect established (except for sectors H and I where only five transects are represented due to lack of space), while darker circles represent the density of individuals in an area where a complete census of the coastline was carried out. The discontinuous line indicates the inaccesssible areas of the port.

Fig. 2. Distribución general de P. ferruginea *en Ceuta, vista general. El diámetro de los círculos se corresponde con la densidad de individuos registrados. Aquellas secciones de costa marcadas con trama más gruesa indican la localización de zonas (p. ej. playas) no adecuadas para la especie. Los círculos claros representan la densidad registrada en cada uno de los transectos realizados (excepto para los sectores H e I para los que sólo se han representado cinco por falta de espacio), mientras que los oscuros representan la densidad media total en la zona tras la realización de un censo completo. La línea discontinua indica las zonas inaccesibles del puerto.*

individuals), finding 15,452 individuals. Therefore, we estimated that Ceuta's metapopulation is composed of 43,992 individuals (table 1).

Figure 2 shows how the South Bay of Ceuta is home to more important *P. ferruginea* subpopulations. Although it is frequent to find *P. ferruginea* subpopulations in the North Bay, they became scarcer as we moved towards the Atlantic. In fact, the density of adult individuals (> 25 mm) in the South Bay (4.90 ± 7.46 ind./m) was significantly higher than the average values recorded for subapopulations located in the North Bay (1.44 ± 1.64 ind./m) and inside the commercial port (1.45 ± 2.02 ind./m) ($\chi^2 = 7.51$; $p = 0.023$). It is also interesting to note the spatial distribution of individuals in certain areas such as the artificial breakwaters located in the southern area of the commercial port as well as on the jetties located in the South Bay (fig. 3). It was evident that the maximum densities of individuals were found within the inaccessible areas of Parque del Mediterráneo and the Guardia Civil's base. Jetties also showed important densities, especially in the inner sides of these structures (those oriented towards the moat exit) and preferentially in their endings.

Effect of physical parameters on population structure

Information regarding the subpopulations' size structures is represented in figure 4 and table 2. When taking into account these values and the physical parameters recorded in each sector, the following results were obtained:

Effect of the nature of substrate and sector location

The nature of substrate (natural *vs.* artificial) did not seem to influence any of the above mentioned population parameters. However, a one–way ANOVA test showed that the areas inside the port presented the highest maximum shell size values (8.89 ± 1.16 cm), higher than the values recorded in the North Bay (7.18 ± 1.19 cm) and the South Bay (8.12 ± 1.06 cm) ($F = 4.87$; $p = 0.016$). In fact, it was inside the port

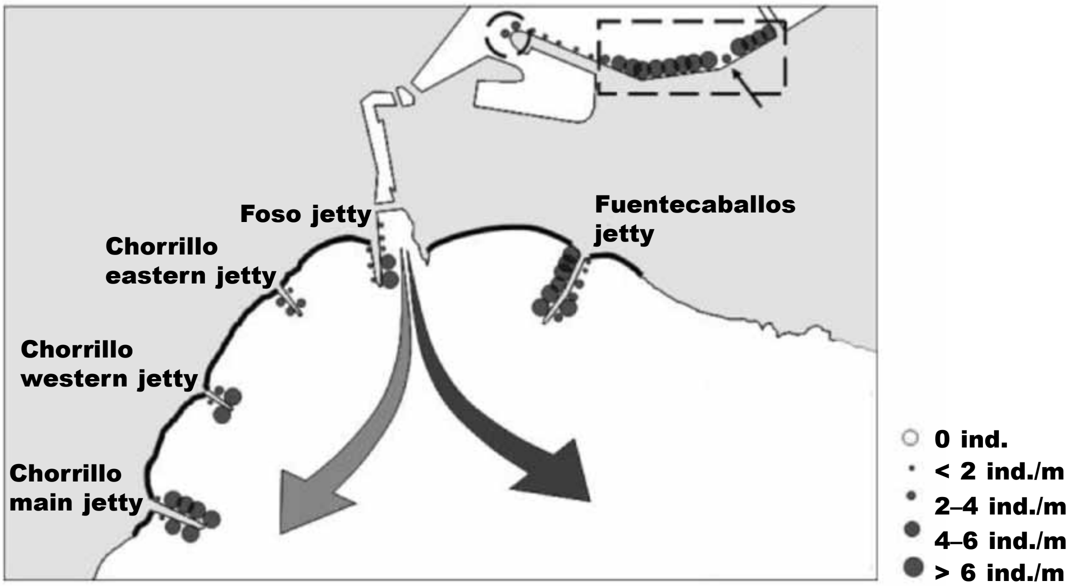

Fig. 3. Density of *P. ferruginea* individuals on the breakwaters of the southern area of the commercial port and on the jetties of the South Bay. The area represented has been completely censused. Circles represent density values grouped in 30 m stretches to visualize the spatial distribution of individuals. The inaccessible areas of the port (Parque del Mediterráneo and the Guardia Civil's base) are surrounded by a discontinuous line. The small arrow indicates the location of a wastewater outfall. Note the important influence of substrate inaccessibility and the presence of the outfall on the density of individuals. The two large arrows indicate the direction of water currents with east winds (light grey arrow) and west winds (right dark grey arrow).

Fig. 3. Densidad de individuos de P. ferruginea *en las escolleras del sur del puerto comercial así como en los principales espigones de la Bahía Sur. Toda el área mostrada ha sido completamente censada. Los círculos representan valores de densidad agrupados en tramos de 30 m para la visualización de la distribución de individuos. Las zonas inaccesibles del puerto (Parque del Mediterráneo y la base del servicio marítimo de la Guardia Civil) estan enmarcadas con una línea discontinua. La flecha indica la localización de un emisario aguas. Nótese la importante influencia de la inaccesibilidad de la zona y la presencia del emisario sobre la densidad de individuos. Las dos flechas grandes indican la dirección de las corrientes de agua con vientos de levante (flecha clara) y vientos de poniente (flecha oscura).*

(within the Guardia Civil's military base) where the largest individual (10.7 cm) was located. No significant differences were recorded between the North and South Bays regarding this parameter.

Effect of substrate roughness and accessibility on population structure

After conducting a multivariate analysis of classification (based on population size structures) figure 5 was obtained. Figure 5A shows how for an 80% similarity, a total of four groups of subpopulations can be differenced: first, sectors P, F, G, K, N, C and D were found, all of them characterized for presenting a clear predominance of small (< 25 mm) and medium (25–50 mm) size individuals, and where the largest individuals (> 50 mm) represented less than 20% of the subpopulation. These subpopulations were subject to medium to high impact by collection, and were also located on medium to high THI substrates (fig. 5B). The second group was composed of sectors L, H, I, A, B, E, M y Q. Subpopulations in these areas were mainly composed of medium and large size individuals, while small individuals (< 25 mm) only represented up to 25% of the subpopulation. Returning to figure 5B, it can be observed how individuals in these areas presented low impact by collection, and most of them were located on medium THI substrates. The cluster analysis detected sector J as significantly different from the rest of the areas considered, which was subject to medium collection impact. But the main characteristic of this area was the atypical substrates found in the area, composed of natural rocks of very low roughness. This was the only area where the largest individuals clearly dominated over the rest (47% of the total subpopulation). Finally, sector O was also clearly segregated from the rest of sectors, and it was the only area where juveniles (< 25 mm) clearly dominated the subpopulation (71%).

Table 2. Summary statistics for *Patella ferruginea* sizes (cm) for each subpopulation considered in the study: Sc. Sector; Sp. Subpopulation; TS. Type of substrate (N. Natural; Ar. Artificial riprap; Asw. Artificial sea wall); D. Density (ind./m); R. Recruit density (ind./m, < 25 mm); As. Average shell size (cm); Ms. maximum shell size (cm); K. Kurtosis († kurtosis is considered significative when its absolute value is greater than 2*SE kurtosis); Kt. Kurtosis type (Pk. Platikurtic; Lk. Leptokurtic); Sk. Skewness (Skew is considered significative when its absolute value is greater than 2*SE Skew); Am. Asymmetry (P. Positive; N. Negative).

Tabla 2. Resumen de las estadísticas de los tamaños de Patella ferruginea *(en cm) para cada subpoblación considerada en el estudio. Sc. Sector; Sp. Subpoblación; TS. Tipo de sustrato (N. Natural; Ar. Escollera artificial; Asw. Muro marino artificial); D. Densidad (ind./m); R. Densidad de reclutamiento (ind./m, < 25 mm); As. Tamaño medio de la valva (cm); Ms. Tamaño máximo de la valva (cm); K. Curtosis († la curtosis se considera significativa cuando su valor absoluto es mayor que el doble de su EE); Kt. Tipo de curtosis (Pk. Platicúrtica; Lk. Leptocúrtica); Sk. Coeficiente de asimetría (la desviación se considera significativa cuando su valor absoluto es mayor que el doble de su EE); Am. Asimetría (P. Positiva; N. Negativa).*

Sc	Sp	TS	D	R	As	Ms	K	Kt	Sk	Am
A	Frontier shoreline	N	2.68	0.28	4.58	8.20	–0.796	–	0.132	–
A	'Pineo' islet	N	6.77	0.18	4.25	7.50	–0.643	–	–0.281	–
B	'Piedras Gordas' islets	N	6.71	1.44	4.12	9.20	–0.866†	Pk	0.092	–
B	'Brazo' islet	N	35.14	5.71	4.68	8.80	–1.157†	Pk	–0.246	–
C	Chorrillo main jetty	Ar	6.86	0.73	4.28	8.60	–0.198	–	–0.082	–
C	Chorrillo western jetty	Ar	6.36	4.03	2.44	6.10	0.554†	Lk	0.899*	P
C	Chorrillo eastern jetty	Ar	1.87	0.91	2.99	7.50	–0.247	–	0.695*	P
C	Foso jetty	Ar	4.31	1.08	3.65	8.70	–0.290	–	0.407*	P
D	Fuentecaballos jetty	Ar	6.46	2.18	3.47	9.30	–0.406†	Pk	0.521*	P
E	Mellizos	N	1.04	0.01	4.42	8.40	1.684†	Lk	1.091*	P
F	Sarchal	N	1.06	0.20	3.47	6.40	–0.326	–	0.581	–
G	Desnarigado	N	2.97	0.75	3.34	7.50	–0.027	–	0.252	–
H	Desnarigado–Point Almina	N	1.86	0.07	4.36	9.70	–0.842†	Pk	0.254*	P
I	Point Almina–Point Sirena	N	4.40	0.84	5.09	9.40	–0.715†	Pk	0.212	–
J	San Amaro	N	0.19	0.04	4.40	6.90	–1.032	–	–0.500	–
K	Dique de Levante	Ar	7.09	2.81	3.10	7.80	–0.534†	Pk	0.372*	P
L	Parque del Mediterráneo	Ar	6.81	1.71	3.67	10.00	0.881†	Lk	1.125*	P
L	Dique del Comercio	Ar	2.61	0.83	3.20	7.60	0.614†	Lk	0.664*	P
L	S. M. Guardia Civil	Ar	2.92	0.35	6.30	10.7	–0.571	–	–0.648*	N
L	Muelle de España	Asw	0.10	0.02	3.84	8.00	–0.268	–	0.573*	P
L	Muelle de Poniente	Asw	0.13	0.01	4.84	9.50	–0.399	–	0.309	–
L	Muelle de Babor	Asw	0.08	0.01	4.85	7.70	–0.546	–	–0.113	–
L	Interior Foso	Asw	0.04	0.01	4.58	8.90	–0.695	–	0.422	–
M	D. Poniente (concrete cube section)	Ar	0.77	0.10	4.81	9.70	–0.846	–	–0.186	–
M	D. Poniente (limestone section)	Ar	4.88	1.18	3.58	6.60	–0.636†	Pk	0.198*	P
N	Benítez	Ar	2.73	1.02	3.00	6.60	–0.903†	Pk	0.167	–
O	Desaladora–Point Bermeja (natural substrate section)	N	0.95	0.26	3.31	6.90	–0.641	–	0.306	–
O	Desaladora–Point Bermeja (breakwater section)	Ar	4.36	3.62	1.68	5.60	2.169†	Lk	1.673*	P
P	Point Bermeja–Point Blanca	N	0.42	0.05	3.69	5.90	0.914	–	–0.299	–
Q	Point Blanca–Benzú	N	0.19	0.01	4.13	7.70	2.122†	Lk	0.627	–

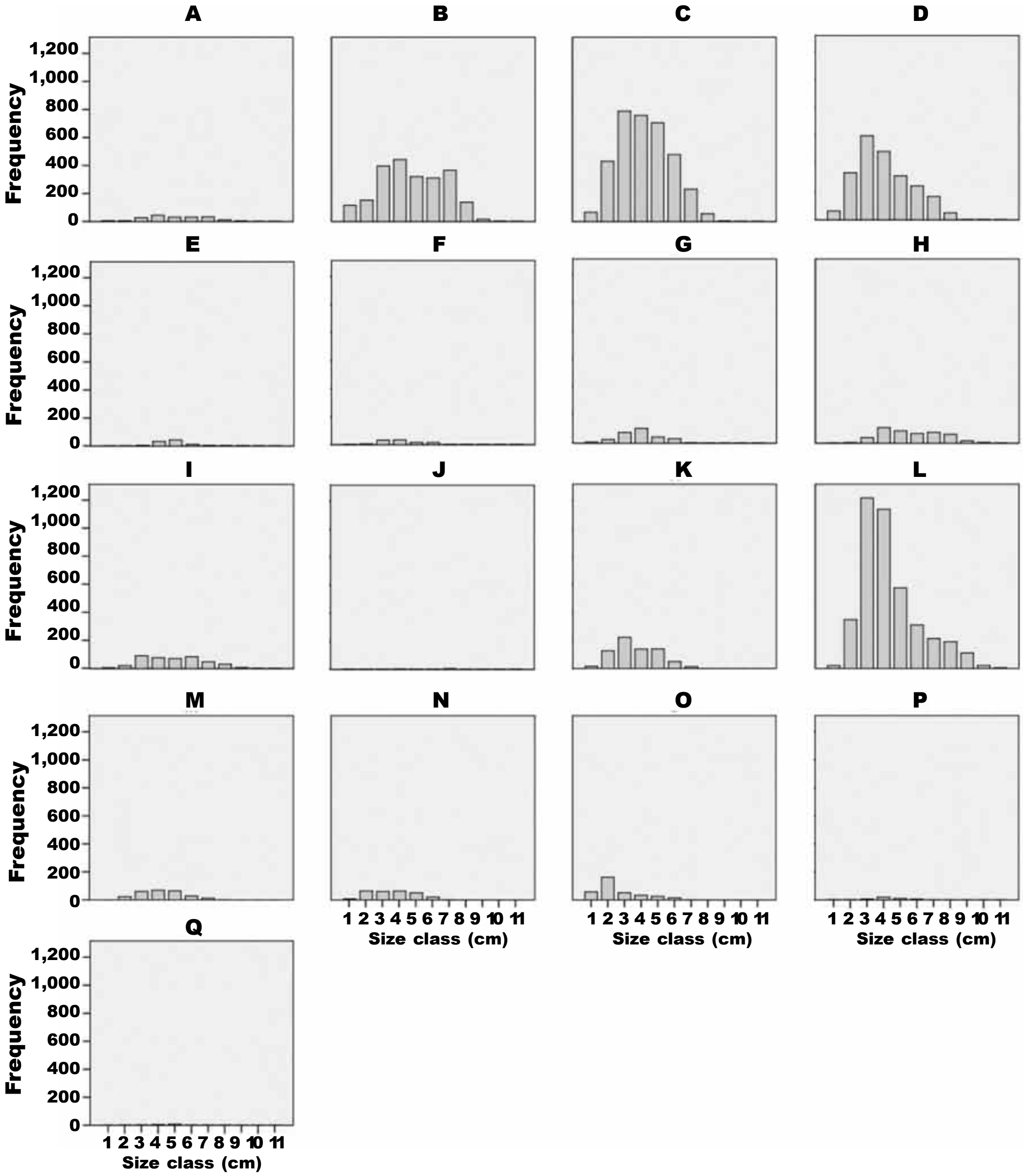

Fig. 4. Size frequencies for each of the sectors considered. Letters correspond to the code used in table 1 and figure 1: 1(0–1), 2 (1–2), 3 (2–3), 4 (3–4), 5 (4–5), 6 (5–6), 7 (6–7), 8 (7–8), 9 (8–9), 10 (9–10), 11 (10–11).

Fig. 4. Frecuencias de tamaños para cada uno de los sectores considerados. Las letras corresponden al código usado en la tabla 1 y la figura 1. (Para las abreviaturas de los tamaños de clase, ver arriba.)

Two–way ANOVA tests were conducted to define the effects of the substrate's accessibility and topographical heterogeneity on population structure and density. Results indicate that adult average shell size was influenced by accessibility (table 3). However, overall adult density was not apparently influenced by either of these two factors. However, figure 6 shows how substrate roughness alone may be influencing subpopulation density and structure. In this figure, the differences in density of small individuals (< 25 mm) among substrates are noticeable, the maximum being observed in high THI surfaces (fig. 6). Substrate

Table 3. Two–way ANOVA results for the influence of the substrate's accessibility and THI (topographical heterogeneity index) on adult average shell size (SS): n.s. Non significance; * *P* < 0.05.

Tabla 3. Resultados del ANOVA de dos factores para la influencia de la accesibilidad y THI (índice de heterogeneidad topográfica) sobre la talla media de los adultos (SS): n.s. No significativo; * P < 0,05.

Source of variation	Mean ± SD (cm)	SS	*F*	*P*
Accessibility		4.043	5.439	0.012*
High	4.04 ± 0.29			
Medium	4.29 ± 0.61			
Low	4.93 ± 0.71			
Substrate THI		0.114	0.153	n.s.
High	4.30 ± 0.87			
Medium	4.65 ± 0.51			
Low	4.81 ± 0.53			
Acc x THI		1.546	1.040	n.s.

roughness may also influence adult average size. In high THI substrates, adult individuals showed an average size of 4.30 ± 0.87 cm, while average values of 4.65 ± 0.51 cm and 4.81 ± 0.53 cm were recorded for subpopulations on medium and low THI surfaces, respectively.

To corroborate the abovementioned results, the specific case of 'Dique de Poniente' was taken into consideration. This sector presents the same physical parameters throughout the area, except for the fact that half of the breakwater is composed of high roughness rocks while the second half was constructed using smooth 3x3m concrete cubes. The density of individuals recorded for the transects in each of these two subareas was compared using a one–way ANOVA, which showed that the area with the highest THI presented significantly higher densities of *P. ferruginea* individuals (4.88 ± 1.82 ind./m) than the cube area (0.77 ± 0.76 ind./m) ($F = 13.24$; $p = 0.01$). Moreover, adult average size in the concrete cube area (5.08 ± 0.40 cm) was significantly higher than that recorded for adults located on the other section of the mole (4.09 ± 0.20 cm) ($F = 22.16$; $p = 0.005$).

Discussion

After inspecting 33.96% of the coast of Ceuta that could potentially present *P. ferruginea* individuals, we estimated that the city is home to around 44,000 individuals. The methodology used in the study has been used successfully by other authors to estimate the total number of individuals in metapopulations, such as that in Habibas Islands (Espinosa, 2009) or Zembra Island (Boudouresque & Laborel–Deguen, 1986). Our estimation is considerably higher than those obtained by other authors who determined that Ceuta holds between 12,000 (Guallart et al., 2006) and 3,704 individuals (Ocaña et al., 2010). Although in the latter cases the sampling effort was considerably lower, during the present study we were able to physically count more than 15,000 individuals, supporting the fact that the aforementioned estimations clearly underestimated the total number of specimens in Ceuta. We can additionally highlight that our estimations can be considered conservative. It is known that the smaller the step (or scale) used in calculating a perimeter, the higher the values and better the estimations obtained (Mandelbrot, 1967). Taking into account that the perimeter of the coastline potentially used by the species has been calculated using 1:9,000 maps, we can suggest that we clearly underestimated this value, and in consequence, the total number of individuals. An additional focus of variability is found in the quantification of the smallest fraction of the population (< 25 mm), which is often difficult to detect (*e.g.* Guallart et al., 2006; Espinosa, 2009). Although censuses were always carried out by the same experienced team (reducing the probability of missing these individuals), a considerable fraction of this variability is induced by the inter–annual differences in recruitment rates that have been recorded in the area (Rivera–Ingraham, 2010) and by the time of the year in which the censuses were carried out (in relation to the species' reproduction period).

The most important *P. ferruginea* subpopulations (regarding density) were, in general terms, located in the South Bay of Ceuta, which is mainly influenced by Mediterranean waters. On one hand, this result may seem surprising, specially taking into account that one of the main problems that *P. ferruginea* encounters is human collection (Laborel–Deguen & Laborel, 1991a, 1991b; Templado & Moreno, 1997; Ramos, 1998), and that the South Bay's coastline is generally very acces-

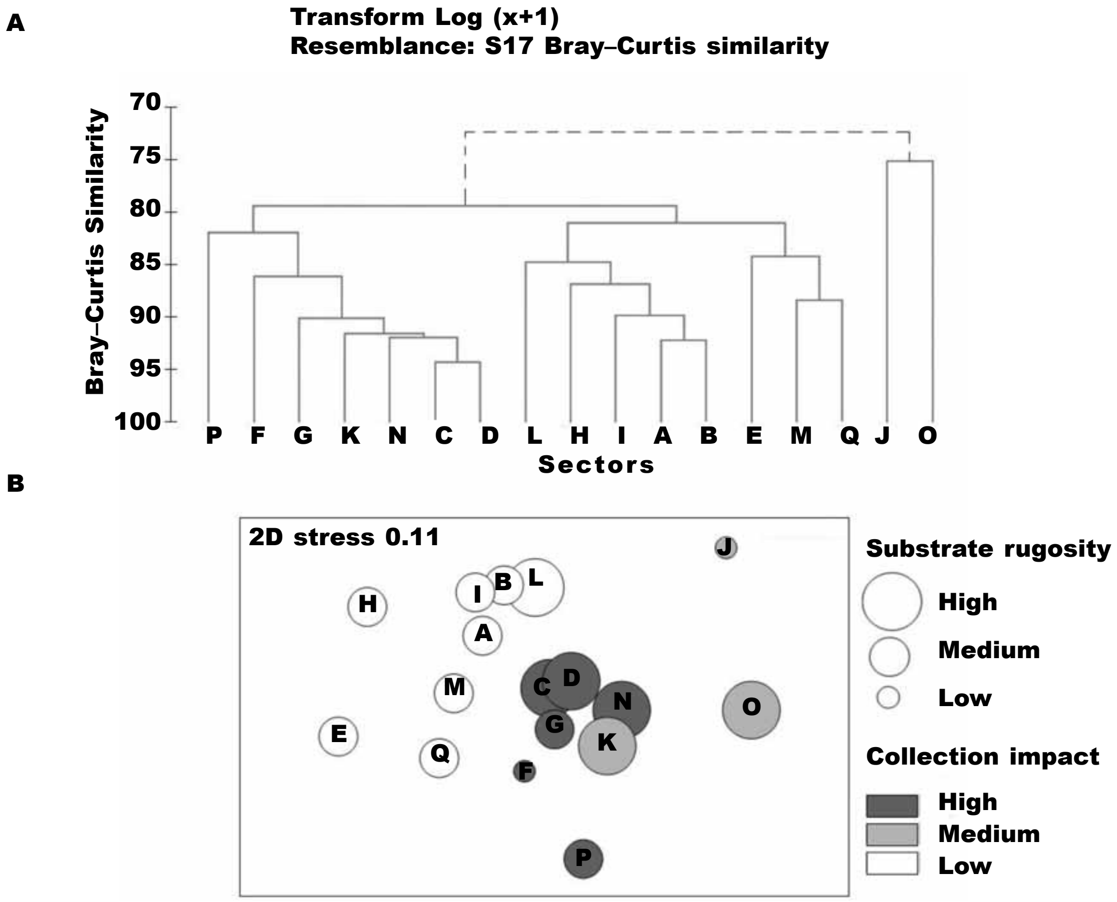

Fig. 5. Multivariate analyses: A. Cluster analysis. Continuous lines indicate significantly different groups (SIMPROF analysis). B. Spatial representation of centroids (MDS) for each sector. Circle diameter is positively correlated with the area's substrate roughness (THI) (Blanchard & Bourget, 1999): High, > 1.30; Medium, 1.15–1.30; Low, < 1.15. Colours are associated with the different grades of impact by collection suffered by individuals in the area (High. Easily accessible areas, where it is common to find people recollecting intertidal macroinvertebrates; Medium. Areas of relatively easy access, although they do not present high impact by collection; Low. Areas with difficult or no access by land to the intertidal fringe, and where no people have been seen).

Fig. 5. Análisis multivariante: A. Análisis de grupos. Las líneas continuas indican diferencias significativas entre grupos (análisis SIMPROF). B. Representación especial de centroides (MDS) para cada sector. El diámetro de los círculos está positivamente correlacionado con el coeficiente de rugosidad del área (THI) (Blanchard & Bourget, 1999): High, rugosidad alta > 1,30; Medium, rugosidad media, 1,15–1,30; Low, rugosidad baja, < 1,15. Los colores están asociados con los diferentes grados de impacto por recolección sufrido por los individuos de cada área (High. Áreas fácilmente accesibles, donde es habitual encontrar personas recogiendo macroinvertebrados intermareales; Medium. Áreas de relativamente fácil acceso, aunque no presentan altas tasas de impacto por recolección; Low. Áreas de difícil acceso o inaccesibles por tierra, donde no se han detectado personas durante todo el estudio).

sible and consequently highly frequented by fishermen. However, these subpopulations became scarcer as we moved towards the Northwestern coasts (with higher Atlantic influence). This seems a predictable pattern, taking into account that we are dealing with a Mediterranean endemic species. This type of distribution pattern has previously been pointed out by several authors (Templado, 2001; Guerra–García et al., 2004; Espinosa, 2006). Guallart et al. (2006) considered that the western limit of distribution of this limpet on the North African coasts could be in Point Blanca, although we recorded considerably important subpopulations reaching Point Benzú (sector Q) (0.19 ind./m) (table 2). Indeed, no individuals have been found in the near

Point Leona or Point Cires, although the former is separated from our sector Q by a long beach, meaning that Benzú could actually constitute the western limit of distribution of this species in northern Africa. On the other hand, the above mentioned authors also indicated that the highest densities were recorded inside the port. However, our results indicate that the densities recorded in the South Bay were significantly higher than those recorded inside the port. In any case, it should be taken into account that the aforementioned authors only inspected the breakwaters inside the port of Ceuta (Parque del Mediterráneo), while the present study considered its complete extension. Vertical and smooth substrates (*e.g.* sea walls) are clearly dominant in the port, and this seriously affected the average density values recorded in the area as the species is not frequent on this type of substrate (pers. obs.).

It is known that *P. ferruginea* is commonly present on artificial rocks (Guerra–García et al., 2004). This is corroborated by the observations and results obtained from the present study. However, one of the main differences we observed between natural rocky shores and artificial structures was related to substrate roughness and the presence of microstructures, which is supported by other authors (see review by Bulleri & Chapman, 2010). Our observations and results indicate that substrate THI may be playing an important role in recruitment processes and in consequence, also on the distribution of *P. ferruginea*. The substrates presenting the highest irregularities showed coefficients higher than 1.30 (using the equation provided by Blanchard & Bourget, 1999) and around 1.017 (Rivera–Ingraham, 2010) using fractal dimensions (Mandelbrot, 1967) [following an adapted method from Beck (2000) and using profile gauges to obtain rock profiles as in Frost et al. (2005)]. Statistical analyses showed that these surfaces presented the highest recruitment rates. It is known that the presence of irregularities in substrates is associated with high recruitment rates (as these structures can enhance settlement and provide shelter for juvenile limpets) (*e.g.* Creese, 1982) and may determine the distribution patterns of intertidal species such as barnacles (Crisp & Barnes, 1954) and gastropods (including limpets) (Beck, 2000; Underwood, 2004). However, it should be taken into consideration that high THI substrates also showed low density of large individuals. This would considerably reduce competition events on these surfaces and could also explain why such important recruitment rates have been recorded. An experimental study approaching the effect of substrate roughness and the density of adult conspecifics on *P. ferruginea* recruitment rates is highly recommended in order to support our observations and results.

Based on this and the abovementioned studies (which support the hypothesis that high numbers of recruits are associated with substrate topographic heterogeneity), an ethological component could also be considered: larvae of many invertebrate species can actively select substrates during the settlement process (see reviews by Woodin, 1986; Butman, 1987; and results obtained by Wilson, 1990). Additionally, similar evidence of the influence of larvae behaviour on settlement has also been pointed out for other limpet species like *Cellana grata* (Williams & Morritt, 1995), *Patelloida pygmaea* (Nakai et al., 2006) *P. caerulea* or *Cymbula nigra* (Rivera–Ingraham et al., 2011b). For *P. ferruginea,* previous studies indicate that settlement may additionally be mediated by chemical cues that are presumably produced by adult conspecifics (Rivera–Ingraham et al., 2011b), which could attract larvae and produce the natural aggregation pattern that has been observed in the species (Espinosa et al., 2006a; Rivera–Ingraham, 2010).

Surprisingly, the substrate's topography also influences the average adult shell size, and those subpopulations located on high THI surfaces had considerably lower average shell sizes than medium and low roughness substrates. *P. ferruginea* is a homing limpet (Espinosa et al., 2008a), and it has already been observed that when individuals cannot continue growing in their home scar because of the presence of unavoidable irregularities, they can move to smoother areas (Espinosa et al., 2008a). However, the impossibility of individuals to move to smoother surfaces may prevent the normal growth of the individuals, which has already been observed in other areas such as Tarifa Island (obs. pers.), explaining our results. On the other hand, smoother substrates (some natural substrates like in 'San Amaro') presented old and low density subpopulations, with the lowest recruitment rates recorded, and where individuals of more than 50 mm of shell length represented high percentages of the subpopulations. The low density values could be the result of low recruitment rates, although individuals could reach large sizes as the substrate's surface lacks relevant irregularities. These patterns have already been observed in other invertebrates (Taniguchi & Tokeshi, 2004) and giant limpet species such as *L. gigantea* (Kido & Murray, 2003). Moreover, these conclusions are additionally supported by the case of 'Dique de Poniente': while the area composed of 3 x 3 m concrete cubes (smooth surfaces) is clearly dominated by other patellid limpets such as *Cymbula nigra* (Rivera–Ingraham et al., 2011a), and presents very low densities of *P. ferruginea* individuals (0.77 ind./m), the limestone area shows an average density of 4.88 ind./m.

Moreover, results indicate that the area's accessibility to humans also plays an important role in determining population density and size structures (fig. 3). The maximum densities were recorded on the artificial breakwaters inside the port (Parque del Mediterráneo and within the Guardia Civil's military base) and at the locally known as 'Piedra del Brazo' islet. The first two sites are restricted access areas composed of high roughness substrates. The latter showed the highest density value recorded in the present study (an also the highest ever recorded for the species), which was established at 35.14 ind./m. It is a 4 x 7 m islet only some meters away from the shore in sector B, only visible during low tide. These areas were also home to some of the largest individuals found. It has been frequently suggested that human collection of organisms reduces population density and preferentially affects the largest fraction of populations. This

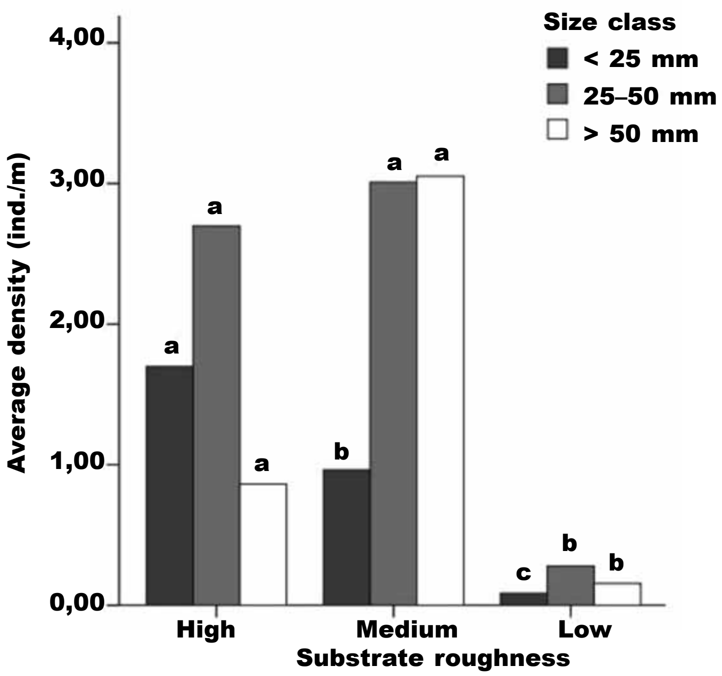

Fig. 6. Average density values recorded for populations located on substrates of high (THI > 1.30), medium (THI = 1.30–1.15) and low (THI < 1.15) roughness (measured using equation provided by Blanchard & Bourget, 1999). Results have been divided into three size classes (< 25 mm, 25–50 mm, > 50 mm). Those values associated with the same letter (a, b, c) and colour belong to the same roughness subset based on a one–way ANOVA and a a posteriori multiple comparison test Student–Neuman–Keuls.

Fig. 6. Valores de densidad medios registrados para las poblaciones localizadas sobre sustratos de rugosidad alta (THI > 1,30), media (THI = 1,30–1,15) y baja (THI < 1,15) (medida usando la ecuación descrita por Blanchard & Bourget, 1999). Los resultados han sido divididos en tres clases de tamaños (individuos < 25 mm, 25–50 mm y > 50 mm). Aquellos valores asociados con la misma letra (a, b, c) y el mismo color pertenecen al mismo subgrupo de rugosidad en base a los resultados de un ANOVA de un factor y un test a posteriori de comparación múltiple Student–Newman–Keuls.

is true for giant limpets such as *Lottia gigantea* (Kido & Murray, 2003), and has already been proven for *P. ferruginea* (Espinosa et al., 2009; Rivera–Ingraham, 2010). Our observations support these results. On the other hand, the largest individuals were again located inside the port, in the Guardia Civil base and 'Parque del Mediterráneo'. The areas' protection status and the fact that people are usually reluctant to collect and consume organisms from port areas (presumably living in more polluted waters) (Doneddu & Manunza, 1992) would determine a low collection rate and favour the survivorship of large individuals (Espinosa et al., 2009).

The subpopulation in Piedra del Brazo can be considered as very mature, in the sense that 49.6% of the individuals recorded exceeded 50 millimetres in maximum shell length, while recruits only constituted 16% of the total subpopulation. The area was surveyed in July 2009, when most of the recruits resulting from the previous reproduction process should be evident (see Rivera–Ingraham, 2010). Additionally, it was quite frequent to find recruits established on the adult shells (foresy), clearly at a considerably higher frequency than the rest of the areas surveyed. It is interesting to comment that after a later inspection in 2010, no growth in the number of small individuals was detected. This suggests that the area has reached its carrying capacity, and that the juvenile fraction of the subpopulation recorded the previous year did not survive, probably because of the lack of available space and the competition for food, which are the limiting factors in intertidal habitats (Branch, 1975a).

The distribution pattern observed in figure 3 also deserves further examination. Individuals were mainly distributed on the sides of the jetties facing the moat's exit. This could be explained by considering the direction of water currents (represented by the large arrows in figure 3) and assuming that the populations inside the port are the main larvae suppliers. Hydrodynamic currents can determine the local distribution and genetic patterns of intertidal organisms (Baus et al., 2005; Casu et al., 2006). As commented above, 20% of the subpopulation located inside the port exceeds 50 mm in shell length, partly thanks to the presence of two inaccessible areas (Parque del Mediterráneo and the Guardia Civil base). As the species delays the timing at which sex change occurs when the density of individuals larger than 50 mm is high (Rivera–Ingraham et al., in press), the port holds some of the largest males and females. It is also known that for *P. ferruginea* fecundity increases with shell size (Espinosa et al., 2006b). In consequence, these 'protected' subpopulations located inside the port may be producing an important number of larvae, which would be exported by tidal currents through the North and South exits of the port. This may be yet another example of the importance of protecting key populations (like the abovementioned) and creating marine reserves for the repopulation of nearby areas, as has been described extensively for many species (*e.g.* Hastings & Botsford, 1999; McClanahan & Mangi, 2000). Furthermore, a large concentration of individuals was detected in all the jetty endings, which could be explained if we consider that the marine currents responsible for larvae distribution, at a microscale level, run parallel to the shore. In this case, the jetty endings could act as larvae traps, and such a heterogeneous coastline may also determine a heterogeneous distribution of individuals.

Finally, it is interesting to comment on the two recently created artificial structures: Fuentecaballos (sector D) and the concrete cube area of Dique de Poniente (Sector M). For the former, a density of 6.46 ind./m was recorded, and the maximum shell length was established at 9.3 cm. Taking into account that this jetty was finished in April 2005 (J. L. Ruiz, pers. com.), and that the census was carried out in March 2010, we could estimate that individuals may present an average growth rate of 1.86 cm/year. On the other hand, the cube area in Sector M, which presents one of the most important *C. nigra* subpopulations in Ceuta (Rivera–Ingraham, 2010), presented *P. ferruginea* individuals with a maximum shell length of 9.7 cm (February 2010). Its construction ended in the early months of 2004 (J. Medina, pers. com.), so we can estimate a growth rate of 1.62 cm/year. It has been found that growth rates in the species highly depend on the age of the individuals, in the sense that smaller/younger individuals show higher growth rates that larger/ older individuals (Espinosa et al., 2008b; Rivera–Ingraham, 2010). Previous studies indicate that individuals located in the North Bay of Ceuta present growth rates of 1.15 and 0.73 cm/year, for initial shell lengths of 2 and 8 cm, respectively (Rivera– Ingraham, 2010), while for individuals in the South Bay, values reach 1.64 and 0.38 cm/year. Our calculations establish that individuals located both in Sector D and the concrete–cube section of Sector M should have developed growth rates significantly higher than the aforementioned values. These differences could be due to the fact that the recorded individuals were probably the first to colonize these newly constructed structures (with abundant microalgae biofilm and almost no fauna). If this was the case, newly settled individuals would have abundant trophic resources at their disposal and these could result in higher growth rates than those for individuals that settle in areas with well developed subpopulations (where individuals would have to compete for space and food) (Branch, 1975b). Furthermore, a shore may contain individuals in very different conditions of wave exposure or emersion. It may be inappropriate to average the population dynamics of such assemblages at the shore scale when demographic rates are likely to vary greatly within shores (Johnson, 2006).

Implications for conservation

In the present study, two main parameters seem to highly determine distribution and population structure in *P. ferruginea*: substrate roughness and the area’s accessibility by humans. The creation of coastal infrastructures has grown in the last decades as a response to the increasing density of humans living by the sea (see Hinrichsen, 1999) to meet port needs and security requirements. The construction of these types of structures can have an important impact on communities settled in nearby areas. Additionally, invader organisms can easily colonize recently created structures, and affect natural/endemic species (see review by Bulleri & Chapman, 2010). Notwithstanding, the results of this study indicate that medium to high roughness substrates (as some materials that are frequently used in the creation of breakwaters and jetties) can favour settlement in *P. ferruginea*. The population structure recorded on newly created structures (such as Fuentecaballos) suggests that artificial moles and jetties created with this type of substrate can constitute a good habitat that may be collecting larvae from nearby areas. It is important to note that these results and evidence cannot be considered as an excuse to promote the creation of civil engineering constructions (which frequently produce fatal effects on species and communities). However, if these type of structures need to be developed we suggest using dolomitic rocks with medium roughness surfaces (1.15–1.30 roughness coefficients) instead of the concrete cubes, which are starting to be more frequently used. This would allow good recruitment rates and the obtainment of large individuals. Additionally, it has been found that these port areas are avoided by fishermen (Doneddu & Manunza, 1992), as organisms in ports are usually associated with polluted waters. Moreover, these breakwaters are usually difficult to access and would be easy to patrol and guard, which could boost the conservation of the species with the collaboration of port authorities with very little cost (García–Gómez et al., 2011). It has been shown that the inaccessibility and guarding of certain breakwaters is a good way to enhance the obtainment of larger individuals (*e.g.* Parque del Mediterráneo, Guardia Civil base, etc.), which additionally contribute in large measure to the reproduction event (Espinosa et al., 2006b).

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