Responses of the endangered limpet Patella ferruginea to reintroduction under different environmental conditions: survival, growth rates and life-history

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Responses of the endangered limpet *Patella ferruginea* to reintroduction under different environmental conditions: survival, growth rates and life-history

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Abstract

The mollusc *Patella ferruginea*, endemic to the Mediterranean, is the most endangered marine species of the list of the European Council Directive 92/43/EEC and it is presently under serious risk of extinction. Survival, growth rates and life-history of this species were studied for the first time in this species. A total of 570 specimens (420 introduced in a new habitat and 150 as control) were marked and monitored over a three-year period. Growth rates observed were mainly related to the availability of microalgal food. The mortality rate of transplanted specimens was high (50% mortality immediately after transplant). Seasonality in growth rates was observed in both control and transplanted specimens, with greater growth rates detected in spring-summer (warm season) than in autumn-winter (cold season). Smaller specimens of *P. ferruginea* had the greatest growth rates in comparison with the bigger specimens, therefore the potential ability to adapt in a new habitat was higher for small specimens immediately after removal. An elevated growth rate (appearing as a light-ring in the border of the shell) was detected immediately after translocation, following which growth rate progressively stabilized over time. Using differential equations and the von Bertalanffy model, the longevity of *P. ferruginea* was estimated to range between 8.89 and 35.72 years depending on the environment. Transplantation should not be considered as a conservation measure given the elevated mortality rate.

Keywords: *Patella ferruginea*, conservation, reintroduction, growth, life-history

Introduction

Coastal destruction and harvesting may have led to the extinction of local populations of invertebrates, as well as extinction of entire species (Little & Kitching 1996). The intertidal zone is being progressively squeezed between encroaching onshore developments (Raffaelli & Hawkins 1996) and consequently, many sedentary species inhabiting rocky shores may disappear. The limpet *Patella ferruginea* Gmelin, 1791, endemic to the Mediterranean, is the most endangered marine species of the list of the European Council Directive 92/43/EEC on the conservation of Natural Habitats and of Wild Fauna and Flora, 1992 (Ramos 1998), and it is presently under serious risk of extinction (Laborel-Deguen & Laborel 1991a; Templado & Moreno 1997). Templado (2001) noted that reintroduction of individuals in protected areas that had previously been part of their distributional range would be of great interest. Additionally, the development of civil engineering works is a serious threat to populations of this endangered species. In this sense, as a consequence of the unavoidable enlargement of Ceuta’s harbor (Strait of Gibraltar), we had the opportunity to implement a translocation program to minimize the death of the whole population settled on the breakwaters.

Transplantation of other limpet species such as *P. vulgata* has been reported as a very difficult process (Jenkins & Hartnoll 2001). Hence, the success of transplanting individuals of *P. ferruginea* needs to be assessed, considering the endangered status of the
species. Laborel-Deguen and Laborel (1991c) made some preliminary observations when moving a small population from Corsica to the National Park of Port Cros (continental France). However, individual marking was not carried out in that study and the observations were conducted on population survival as a whole, and without considering growth rates.

Information on distribution, population structure, growth, mortality and reproduction of grazers is required to clarify their role in the dynamics of intertidal communities. Because these characteristics can vary spatially and temporally, comparisons at different places through time allow a greater understanding of the demography of species and variability among populations (Dunmore & Schiel 2003).

Growth rates can be highly variable and are affected by the densities of conspecific and other co-occurring invertebrates, the seasonal supply of food, shore height and substratum complexity (Lewis & Bowman 1975; Underwood 1979; Branch 1981; Creese 1988). Seasonal changes on growth rate are usually related to availability of food (Kenny 1968; Parry 1977; Picken 1980) but are not always linked directly to algal standing stocks (Branch 1981). Nevertheless, given variation with body size, growth rate is not a very useful comparative measure, and the growth coefficient (K) according with von Bertalanffy equation (1957) is a useful comparative index of growth that is not dependent on body size (Branch 1981). This equation has been traditionally used to estimate longevity in patellids. However, the use of other mathematical approaches could be more accurate in elucidating the expected age of patellids.

Mortality rates also vary widely within and among species (Dunmore & Schiel 2003), as they are related not only to species’ life histories (Choat & Black 1979) but also to the characteristics of habitats (Lewis & Bowman 1975; Underwood 1978; Creese & Underwood 1982; Marshall & Keough 1994). The integration of life histories with habitat characteristics, therefore, determines demographic responses to the local environment (Dunmore & Schiel 2003).

The purpose of this study was to examine the responses of the endangered limpet *P. ferruginea* to the removal of individuals and the effect of different environmental conditions on its survival, growth rate and life-history as longevity and ecological strategy.

**Material and methods**

**Study area**

The study was carried out in Ceuta, located on the coast of North Africa in the Strait of Gibraltar (35°53′20″N, 5°18′30″W; Figure 1), which has the greatest densities of *P. ferruginea* in this area, similar to other places in the Mediterranean with well-established populations (Guerra-Garcia et al. 2004).

**Mortality and growth**

The individuals of *P. ferruginea* removed from the study site were transported to aerated aquaria at 20°C. A small area of each shell was scraped with sandpaper, labelled with epoxy resin (Eporai 1127°), and an individual number was stamped directly on the epoxy resin. Missing labels were replaced at each sampling occasion. Individuals that had missing labels were easily identified from their mapped position and from a residual scratch left on the shell from the previous mark. To determine growth rates the lengths of marked individuals were measured periodically (see temporal scale on figures) and the growth rate was standardized monthly. In six different sites (A to F), three replicates of 10 m length each (parallel to the coast) were allocated painting the rocks. Each site was representative of a different environment (artificial/natural substrate and wave exposure) and/or accessibility to humans (see Figure 1 and Table I). Similarly to Moreira et al. (2006), the sampling design did not eliminate potential sources of confounding but was a sensible scheme on the growth and survival of *P. ferruginea* under different situations. A total of 20 marked individuals were introduced in each replicate, with a final number of 60 individuals per site. In order to have a “control” for comparisons, two different plots as those described above were located inside and outside Ceuta’s harbor. The two control plots were located in inaccessible sites to avoid manipulation by humans and subsequent artefacts in the control data. For the controls, all the individuals of *P. ferruginea* present in each of 10 m replicates were marked in the same way as the transplanted individuals. Outside the harbor, the number of individuals for each replicate was 32, 29 and 34 (A2 plot), respectively, whereas inside the harbor the number was 19, 14 and 22 (C2 plot). Therefore, temporal monitoring was conducted on 420 “transplanted individuals” and 150 “control individuals” during the years 2003, 2004 and 2005. Original densities of *P. ferruginea* in each site were A: 0.78 ind. m⁻², B and C: 0.84 ind. m⁻², D: 0.42 ind. m⁻², E: 0.32 ind. m⁻², F: 1.5 ind. m⁻² (Espinosa 2006). Specimens of *P. ferruginea* already existing in these sites were not removed after introducing transplanted specimens, taking into account that intraspecific competition is not severe in *P. ferruginea*, showing growth at extreme densities of 32 ind. m⁻² (Espinosa et al. 2006a).
Microalgal food assessment

To assess the influence of microalgal abundance on growth rates, the chlorophyll concentration of the substratum was estimated. In each monitoring site, three replicates (one for each 10 m replicate) each with a surface of $10 \times 10 \text{ cm}$ was brushed with a stiff toothbrush (Espinosa et al. 2006a). The resulting slurry was treated with 20 ml of 100% methanol to extract the pigments. The samples were frozen and maintained in darkness until analysis (minimum of 48 h) according with the protocol used by Kido and Murray (2003). The samples were filtered through a Whatman GF/C filter and measurements of absorbance were carried out with a spectrophotometer (Pharmacia Biotech Novaspec II). The chlorophyll concentration was calculated according to the formula of Thompson et al. (1999).

$$[\text{chlorophyll}] = 13.0 \times \frac{A_{665}}{V/(d \times V)}$$

where $13.0 =$ constant for methanol, $A_{665} =$ net absorbance of solution at 665 nm, $V =$ final volume of solution (20 ml), $d =$ path length of cell (1.6 cm), $V =$ surface area of sample (100 cm$^2$) and the chlorophyll concentration is expressed in $\mu g \text{ cm}^{-2}$.

Data analysis

Data were analyzed using ANOVA. Data sets were first examined for heterogeneity of variances using the Levene test following logarithmic transformation.

Table I. Sites and types of experimental plots used for temporal and spatial monitoring of P. ferruginea.

<table>
<thead>
<tr>
<th>Sites of plots</th>
<th>Type of substrate</th>
<th>Environmental conditions</th>
<th>Types of plots located</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Artificial breakwater</td>
<td>High hydrodinamism. Inaccessible.</td>
<td>A1 (translocation) + A2 (control)</td>
</tr>
<tr>
<td>B</td>
<td>Artificial breakwater</td>
<td>Low–medium hydrodinamism. Accessible.</td>
<td>B (translocation)</td>
</tr>
<tr>
<td>C</td>
<td>Artificial breakwater</td>
<td>Low–medium hydrodinamism. Inaccessible.</td>
<td>C1 (translocation) + C2 (control) + C3 (translocation)</td>
</tr>
<tr>
<td>D</td>
<td>Horizontal rock surface</td>
<td>High hydrodinamism. Relatively accessible</td>
<td>D (translocation)</td>
</tr>
<tr>
<td>E</td>
<td>Horizontal rock surface</td>
<td>Medium hydrodinism. Accessible.</td>
<td>E (translocation)</td>
</tr>
<tr>
<td>F</td>
<td>Artificial breakwater</td>
<td>Medium hydrodinism. Accessible.</td>
<td>F (translocation)</td>
</tr>
</tbody>
</table>
ANOVA is robust to non-normality (Underwood 1997); therefore, departures from normality were not considered a reason to reject the parametric procedure. Differences among means were examined a posteriori using the Student–Newman–Keuls and Tukey multiple comparison tests. Calculated annual growth rates of limpets from different sub-populations were plotted as a function of initial shell length and subjected to regression analysis to determine growth-rate functions for populations from the different sites. Growth rate regression equations were compared by parallelism and equality test of slopes. A significative regression equation after one year (when the sample size was greater than after two years) was used to estimate the longevity of limpets under different environments, following the method of Kido and Murray (2003). We have used both differential equations and the von Bertalanffy (1957) growth equation to estimate the longevity of P. ferruginea. The maximum expected longevity for this species was estimated following Taylor (1958). Statistical analyses were conducted with the SPSS 12.0 program.

Results

Trophic resource

The chlorophyll concentration was very variable among sites, ranging from 0.011 μg cm⁻² to 0.081 μg cm⁻², indicating substantial inter-site spatial variability (Figure 2). Additionally, high intra-site variability was observed on E and F, as can be seen from the large standard deviations, representative of the patchy distribution of the trophic resources at these sites. On the other hand, A, B, C and D showed higher spatial homogeneity than E and F.

Survival and growth

Translocation operations carried out in Ceuta with P. ferruginea showed a high mortality in the days following the event, with around 50% mortality being obtained (Figures 3–5). However, after this episode, the number became stabilized and the mortality was reduced. Moreover, the individuals transplanted were progressively reduced in number through time. It is important to note that the survival of the individuals transplanted was not related to site-specific variations in wave action, since A1 (outside of the harbor with greater wave action) and C1 (inside the harbor with lower wave action), for example, showed a similar survival, whereas C3 and B (both located inside the harbor) showed lower survival than A1. However, in control plots the individuals located outside the harbor (A2) showed a lower survival than those located inside the harbor (C2) (Figure 3).

When the accessibility by humans was considered, elevated values of this parameter clearly influenced survival rates. In sites E and F (with high human visitation, bathing and fishing activities) the entire population disappeared during the period of monitoring (Figure 5). Sites D and E showed a high mortality in summer periods, whereas in the other sites the greatest mortality events happened frequently in autumn-winter. Control populations

Figure 2. Chlorophyll a in each plot. Data are means (± SD). Results of 1-way ANOVA (n=21): df=5, 15; MS=0.270; F=5.98; P<0.05. The homogeneous groups according to the Tukey test (P<0.05) are indicated with a continuous line: D A B C E F
(A2, C2) showed relatively lower mortality, both outside and inside the harbor. Nevertheless, after one year almost 50% and 40% of the individuals, respectively, had died and, after two years these values were increased to around 80% and 60% (Figure 3).

Figure 3. Survival and growth rate through monitoring time in A1, A2 and C2 plots. Temporal sequence: S=spring; S=summer; A=autumn; W=winter.
The response of individuals according to size was very different between translocation and control plots. Both after one and two years of monitoring the same pattern can be observed (Figure 8): transplanted small individuals exhibited higher survival rates than larger ones, while the control individuals presented the opposite pattern, although these differences were not statistically significant after one year (translocation: $F_{2,56}=0.40$, $P=0.66$, control: $F_{2,15}=0.17$, $P=0.84$) or two years (translocation: $F_{2,38}=0.66$, $P=0.51$, control: $F_{2,15}=0.17$, $P=0.83$), probably due to the great variability.
among individuals and the high standard deviation associated.

Additionally, a peak of growth (appearing as a light-ring in the border of the shell) could be detected in the first few days following translocation in the individuals from the translocation plots, which then progressively stabilized over time (Figures 3–5). On the other hand, control individuals showed a seasonal growth, with
greater growth rates in spring-summer than in the autumn-winter period (Figure 3, Table II). This same seasonal pattern in growth rates could be observed in the transplanted individuals after the stabilization of initial growth. The greatest values of growth rate were achieved in those sites with high chlorophyll concentration (Figure 2), indicating the influence of this trophic resource on growth rate.

**Patterns of growth and longevity**

Significant inverse relationships between growth rate and size were observed both for the transplanted and control individuals after one and two years of monitoring (Figures 6, 7). Hence, smaller individuals of *P. ferruginea* have the greatest growth rates in comparison with the larger specimens and, therefore the potential ability to adapt to a new habitat would be higher in small individuals. Interestingly, the control population inside of the harbor presented practically double the growth rate of the population outside (Figure 6), in parallel with the greater availability of trophic resource inside than outside the harbor (Figure 2). In fact, growth regression equations on control populations showed no parallelism after one year (F1,36 = 6.0509, *P* < 0.05), but after two years parallelism was evident (F1,36 = 0.0843, *P* = 0.77) although not equality of slopes (F2,36 = 21.1421, *P* < 0.001), indicating the same pattern but different growth rates.

**Differential equations**

The regression equations of the control populations after one year of monitoring were summarized as: y = a − bx. If \( h(t) \) is the size of the individual at a given time \( t \) (years) measured in mm, and \( h'(t) \) is the growth rate at that same time, expressed as: \( \frac{\text{variation of size/variation of time}}{\text{time}} \), then, using the regression equation of the control populations \( y = a − bx \), we obtain the following equation: \( h' = a − bh \). The result is a system of equations known as the Cauchy problem for an ordinary linear differential equation of first order and separate variables:

\[
P_c \begin{cases} h' = a − bh \\ h(0) = h_0 \end{cases}
\]

Solving:

\[
\frac{dh}{dt} = a - bh \Rightarrow dh/a - bh = dt \Rightarrow \int \frac{dh}{a - bh} = \int dt + C,
\]

where \( C \) is an integral constant.

\[
\Rightarrow -\frac{1}{b} \ln|a - bh| = t + C \Rightarrow \ln|a - bh| = -b t - b C \Rightarrow a - bh = C_1 e^{-bt},
\]

where \( C_1 \) is an undefined constant.

\[
\Rightarrow h = \frac{a}{b} - C_2 e^{-bt}. \text{It is known that } h(0) = h_0, \text{then } h_0 = \frac{a}{b} - C_1 e^{-b0} = C_1 = \frac{a}{b} - h_0,
\]

replacing:

\[
h = \frac{a}{b} - (\frac{a}{b} - h_0)e^{-bt}
\]

(1)

This function predicts the size of the individual at a given time \( t \). To calculate the time at which a certain individual reached a \( h_1 \) size (in order to predict longevity), i.e. \( t \) being \( h(t) = h_1 \), we replace in Equation (1) to obtain the following algebraic equation:

\[
h_1 = \frac{a}{b} - (\frac{a}{b} - h_0)e^{-b \cdot t} \Rightarrow -(\frac{a}{b} - h_0)e^{-b \cdot t} = h_1 - \frac{a}{b} \Rightarrow e^{b \cdot t} = \frac{h_1 - \frac{a}{b}}{\frac{a}{b} - h_0} \Rightarrow -b^t = \ln\left|\frac{h_1 - \frac{a}{b}}{\frac{a}{b} - h_0}\right| \Rightarrow t = \frac{-\ln\left|\frac{h_1 - \frac{a}{b}}{\frac{a}{b} - h_0}\right|}{b}
\]

(2)

This last Equation (2) allows us to calculate the time at which the individual would be \( h_1 \) (the size for

Table II. *P. ferruginea* mean shell growth rates (mm month\(^{-1}\)) of control populations outside and inside of the harbor for the different seasons. Statistical analyses by 1-way ANOVA for each population. Values followed by the same letter (a,b) belong to the same subset based on Student–Newman–Keuls a posteriori multiple-comparison tests. ***\(P<0.001\) for A2 and *\(P<0.05\) for C2.

<table>
<thead>
<tr>
<th>Season</th>
<th>A2 (control outside)</th>
<th>C2 (control inside)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(n=276)</td>
<td>(n=189)</td>
</tr>
<tr>
<td>Autumn–Winter first year</td>
<td>0.20 ± 0.31 a</td>
<td>0.52 ± 0.56 a</td>
</tr>
<tr>
<td>Spring–Summer first year</td>
<td>0.46 ± 0.37 b</td>
<td>0.88 ± 0.71 b</td>
</tr>
<tr>
<td>Autumn–Winter second year</td>
<td>0.19 ± 0.32 a</td>
<td>0.36 ± 0.44 a</td>
</tr>
<tr>
<td>Spring–Summer second year</td>
<td>0.63 ± 0.49 b</td>
<td>0.77 ± 0.67 b</td>
</tr>
</tbody>
</table>

Results of 1-way ANOVA

<table>
<thead>
<tr>
<th></th>
<th>df</th>
<th>MS</th>
<th>(F)</th>
<th>df</th>
<th>MS</th>
<th>(F)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3</td>
<td>272</td>
<td>20.23(^*)</td>
<td>3,185</td>
<td>0.184</td>
<td>9.02(^*)</td>
</tr>
</tbody>
</table>
which we are calculating the longevity) knowing the initial time at which the individual had a size of $h_0$. Nevertheless, it cannot predict the time necessary to reach the size $h_1$ for any value, since if extreme values are considered, according with the regression equation, the growth may become negative (when the regression line cuts the $x$ axis) and if that was the case, a negative growth is not biologically possible as the logarithm of negative values does not exist. Therefore, if we consider $h_0$ as a size of 0 mm (when born), then the maximum size ($h_1$) for which it is possible to predict the longevity would be: $h' = 0 = a - bh = 0 = h > a/b$. Taking into account that the $a/b$ value was 94.83 outside the harbor, we have selected 90 as $h_1$. Furthermore, this length corresponds to the common largest specimens in Ceuta (personal observation).

Using the regression equation of the control population outside the harbor (A2): $y = -0.0833x + 7.8999$, where $a = 7.8999$, $b = 0.0833$, $h_1 = 90$ mm, the estimated longevity was 35.72 years. For the population located inside the harbor (C2): $y = -0.1736x + 18.215$, where $a = 18.215$, $b = 0.1736$, $h_1 = 90$ mm, the estimated longevity was 11.23 years.

**von Bertalanffy growth equation**

According to the von Bertalanffy expression, we can estimate the longevity of *P. ferruginea* using the following equation:

$$l_t = L_x \left[1 - e^{-K(t-t_0)}\right]$$

where $l_t$ is the length at age $t$, $K$ is the growth rate [as $-\log b$ and $b$ is the slope of Ford–Waldford plot (Waldford 1946)], $L_x$ is the maximum length at which growth is zero [$L_x = a/(1-b)$, where $a$ is the intercept of Ford–Waldford (Waldford 1946)] and $t_0$ is the hypothetical age the limpet would have had at zero length, and is calculated following Pauly (1979) as: $\log(-t_0) = -0.3922 - 0.2752 \log L_x - 1.038 \log K$. The shell length used to estimate the expected longevity was the same as that used for the differential equations ($l_t = 90$mm). $L_x$ was 113.59 for outside (A2) and 119.64 inside (C2) the harbor, respectively, since these values represent the $x$-axis values at which growth is zero. On the other hand, the growth coefficient ($K$) was 0.061 for outside (A2) and 0.1438 inside (C2) the harbor, respectively. Using this approach, we obtained an estimation of longevity of 23.75 years for outside and 8.89 years inside the harbor, respectively.
Finally, according to the expression of Taylor (1958): \( t_{\text{max}} = t_0 + \frac{3}{K} \), the maximum age expected for \( P. \ ferruginea \) \( (t_{\text{max}}) \), using the parameters of the von Bertalanffy growth equation would be 47.17 and 20.04 years for outside and inside the harbor, respectively.

**Discussion**

**Trophic resource**

Differences in primary productivity have been pointed out as a factor that influences the growth rates of intertidal gastropods (Underwood 1984). Many authors have recorded differential growth rates in limpets in relation to different environmental variables (Hatton 1938; Fischer-Piette 1948; Lewis & Bowman 1975; Liu & Morton 1998; Kido & Murray 2003). In this study, the different growth rates observed in the individuals transplanted of \( P. \ ferruginea \) appear related to availability of microalgal food. A and D presented the lowest values of chlorophyll and associated growth rates, whereas B, C, E and F presented the highest values of chlorophyll and, subsequently, the greatest growth rates. However, synergistic factors could be acting, such as for example wave action. In patellids, lower growth rates have been recorded in places subjected to high wave action in comparison with more sheltered sites (Thompson 1980; Branch 1981; Branch & Odendaal 2003). This decreased growth could be due to the high energy invested in tenacity (Houlihan & Newton 1978) or the limited ability to move and, consequently, to graze (Menge 1972, 1978; Lubchenco & Menge 1978; Wright 1978; Quinn 1979). This could be the reason for the higher growth rates obtained inside the harbor than outside.

**Survival and growth**

The individuals of \( P. \ ferruginea \) that were translocated from their original home scars to a new habitat showed initial high mortalities, especially in the first few days, during which time the limpets had to adapt to a new substrate microtopography to avoid desiccation and predation. Laborel-Deguen and Laborel (1991c) recorded high mortalities when they translocated 188 \( P. \ ferruginea \) individuals from Corsica to the National Park of Port Cros in continental France (a protected site), with a survival of 25% after one year and 12% after two years. In the “protected” plots of the present study and, therefore, without human pressure by collecting, the...
results were similar, with a mean survival of 30–35% after one year and 18% after two years for 180 individuals. Furthermore, when plots subject to human activities were considered, survivorship considerably decreased. Laborel-Deguen and Laborel (1990) pointed out the possibility that the marks on the shell could attract unwelcome attention and, therefore contribute to increased collection, as seemed to happen on plots E and F. The influence of collecting and other human pressures on limpet populations has been extensively documented (Branch 1975; Moreno et al. 1984; Hockey & Bosman 1986; Ortega 1987; Lindberg et al. 1998) and also pointed out in P. ferruginea (Laborel-Deguen & Laborel 1991a; Templado & Moreno 1997; Ramos 1998; Templado et al. 2004; Guerra-García et al. 2004), and these observations are supported by our results for plots E and F.

Stress by desiccation can kill limpets, as recorded by Williams and McMahon (abstract in 3rd International Conference on the Marine Biology of the South China Sea, 1998). In this sense, horizontal surfaces suffer from high irradiation and produce high levels of stress in limpets (Williams & Morrill 1995). This could explain the results observed in plots D and E during the summer period. Additionally, the stress derived from reproduction in autumn could be an important determinant of survival in both translocation and control plots. This would present an additional stress on larger, reproductively mature individuals. Significant differences were not observed in survivorship among size classes. However, for both, translocation and control plots, a redundant pattern can be graphically observed: higher survival of small sized individuals in translocation plots and greater survivorship of larger individuals in control plots. Consequently, the adaptative response in translocation operations would be greater in small individuals due to their higher growth rates, whereas larger individuals would be more resistant to predation and have a higher survivorship in natural conditions.

Shell growth rates of P. ferruginea also differed over time, indicating a seasonality in growth rates. This pattern has been previously recorded in the owl limpet Lottia gigantea by Kido and Murray (2003). Similarly to P. ferruginea, this species is protandric, grows to a large size and has one reproductive period in winter.

**Pattern of growth, longevity and life-history**

The growth model observed in P. ferruginea is similar to those recorded in other patellids such as Cellana
P. ferruginea (Dunmore & Schiel 2003) and Lottia gigantea (Kido & Murray 2003). However, Kido and Murray (2003) found that shell growth rates were highly variable and poorly related to size in limpets less than 40 mm in length. Thus, age determination from growth-rate data could be estimated only for populations with many limpets higher than 40 mm in length. Thus, age determination from growth-rate data could be estimated only for populations with many limpets higher than 40 mm, whereas in this study P. ferruginea showed a high correlation between growth rate and size through all different size classes making age determination more accurate. Additionally, few researchers have attempted to determine the ages of limpets (Kido & Murray 2003; see Balaparameswara Rao 1976 for the methodology applied in the limpet Cellana radiata), probably because age determination in most intertidal invertebrates is a difficult task and is usually accomplished by estimating age from growth rates (Murray 2002). Hence, the traditional method based in the von Bertalanffy (1957) growth coefficient applied to P. ferruginea provided values of the same range to those obtained using Cauchy system of differential equations. Nevertheless, in environments with low growth rates, important differences in expected longevity can be observed (23.75 vs. 35.72 years) depending on the method applied. P. ferruginea achieves a great longevity compared with the estimate of 8–10 years obtained by Kido and Murray (2003) for L. gigantea, but in the range calculated for the subantarctic limpet Nacella concinna (Picken 1980). Regardless of the measure of longevity used, P. ferruginea is a long-lived species. This makes it very vulnerable to over-exploitation. Frenkel (1975) recorded sexual maturity at sizes of 19–23 mm for P. ferruginea, and Templado (2001) suggested that sexual maturity would take place at 2–3 years. Using the method applied in the present work, sexual maturity would be estimated to take place at 1.21 and 2.84 years for the control populations settled inside and outside of the harbor, respectively. Therefore, sexual maturity may be brought forward in time in environments where P. ferruginea has a high growth rate (around 1 mm month\(^{-1}\)).

An inverse relationship between growth coefficient (\(K\)) and age has been demonstrated both intra- and interspecifically in limpets (Branch 1981), in particular for P. vulgata, where several authors have often indicated this kind of relationship in different environments (Fischer-Piette 1948; Choquet 1968; Lewis & Bowman 1975; Thompson 1980). A similar trend has measured for P. ferruginea.

The relationship between longevity and productivity also changes both intra- and interspecifically in limpets (Branch 1981), and in our study large intraspecific variability existed in P. ferruginea (Figure 9), dependent on the different environments in which the populations were living. The extreme longevity estimated for P. ferruginea together with its low growth coefficient (\(K\)) and productivity are indicative of a \(K\)-strategist, previously pointed out by Laborel-Deguen and Laborel (1991b) and Templado (2001) based on qualitative observations.

P. ferruginea is protandric and only the largest individuals would be females (Frenkel 1975). However, the larger, more fecund limpets contribute dramatically to reproductive success (Espinosa et al. 2006b). Human pressure can shift the population structure towards higher frequencies of smaller individuals, reducing the proportion of females and leading to reduced gonadal production and lower reproductive success (Kido & Murray 2003) as in other free-spawning invertebrates where high concentrations of gametes are required for fertilization (Levitan 1991; Levitan et al. 1992; Levitan & Petersen 1995; Tegner et al. 1996). In this sense, P. ferruginea is under high human pressure (Aversano 1986; Laborel-Deguen & Laborel 1991a; Templado et al. 2004) and, in Ceuta, the mean shell length has been shown to be affected by anthropogenic disturbance (Guerra-García et al. 2004), with lower mean shell lengths in areas under high visitor impact than in inaccessible areas, inducing a severe decline of the populations.

Conservational implications

The increasing coastal development in recent decades has led to the progressive destruction of coastal habitats and the extinction of several invertebrate populations (Little & Kitching 1996). Ramos (1998) indicated the negative impact of breakwater and harbor constructions on P. ferruginea populations. Relative mortality observed during translocation operations (subtracting the natural mortality) is around 20–30%. The use of artificial cages can reduce this mortality, providing protection against physical stress, predation and wave forces (Espinosa et al. 2006a). P. ferruginea is a species in risk of extinction, severely protected by European and Spanish laws (Directive 92/43/CEE and BOE, 22 June 1999, respectively) and its populations are clearly in regression (Templado & Moreno 1997). In this context, translocation operations are not a conservational measure to be taken into consideration due to the high mortality expected. The preservation of P. ferruginea populations must be conducted by effectively protecting its populations where they are settled, especially in their natural habitats but also in artificial areas with dense and well preserved populations that can maintain genetic diversity. Only in specific cases, repopulation programmes could be
considered (as proposed by Laborel-Deguen & Laborel 1991c), using small numbers from dense populations, that could be reintroduced in areas of considered importance for maintaining inter-populational gene flow, and following the methods proposed by Espinosa et al. (2006a).

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