

Reproduction of *Patella depressa* Pennant, 1777 on the central Portuguese coast

S. Brazão, D. Boaventura, S. Morais, L. Narciso and P. Ré

Imar/Laboratório Marítimo da Guia, Faculdade de Ciências de Universidade de Lisboa, Estrada do Guincho, P-2750-374, Cascais, Portugal. E-mail: dianab@fc.ul.pt

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ABSTRACT

The reproductive cycle and the sex ratio of the limpet *Patella depressa* Pennant, 1777 were studied on two rocky shores of the central coast of the Portugal, over a period of one year. The gonads were examined and their stage of development was assessed. The gonads of *P. depressa* were found to develop mainly from September/October to December, and between February and April. The spawning peaks occurred in January and between May and August. From June to August the gonads seem to go into a resting phase. In *P. depressa* the sex proportions seem to be approximately equal, suggesting the absence of sex reversal in these limpets. High wind speed under optimum conditions of air temperatures appears to induce spawning in this species.

Keywords: Limpet, *Patella depressa*, reproduction, sex ratio, spawning.

RESUMEN

Reproducción de Patella depressa Pennant, 1777 en la costa central portuguesa

Estudiamos el ciclo reproductor y la proporción de sexos de la lapa *Patella depressa* Pennant, 1777 en dos litorales rocosos de la costa central de Portugal. Examinamos las gónadas y valoramos su fase de desarrollo. Encontramos gónadas de *P. depressa* desarrollándose principalmente desde septiembre/octubre hasta diciembre y entre febrero y abril. Los picos de puesta aparecieron en enero y entre mayo y agosto. Las gónadas parecen permanecer en una fase de reposo desde junio hasta agosto. En *P. depressa* la proporción de sexos parece ser aproximadamente uno, lo que sugiere la ausencia de inversión sexual en estas lapas. Bajo condiciones óptimas de temperatura del aire, la alta velocidad del viento parece inducir la puesta en esta especie.

Palabras clave: Lapa, *Patella depressa*, reproducción, proporción de sexos, puesta.

INTRODUCTION

There are many references in the literature to studies on the reproduction of intertidal gastropods, especially of temperate limpets, e.g., *Patella vulgata* Linnaeus, 1758 (Orton, 1920, 1928, 1946; Orton, Southward and Dodd, 1956; Blackmore, 1969; Baxter, 1983; Bowman and Lewis, 1986; Guerra and Gaudêncio, 1986), *Patella ulyssiponensis* Gmelin,

1791 (Thompson, 1979; Bowman and Lewis, 1986; Guerra and Gaudêncio, 1986) and *Patella depressa* Pennant, 1777 (Orton and Southward, 1961; Bowman and Lewis, 1986; Guerra and Gaudêncio, 1986).

P. depressa is a southern species which extends from north Africa, along the Atlantic coasts of Europe to southwest England and Wales (Orton and Southward, 1961; Campbell, 1976; Fretter and

Graham, 1962, 1976; Guerra and Gaudêncio, 1986; Hayward, Nelson-Smith and Shields, 1996). In Portugal, *P. depressa* is common throughout the eulittoral zone along the entire coast, replacing *P. vulgata* as the dominant intertidal limpet on exposed and sheltered shores (Guerra and Gaudêncio, 1986; Boaventura *et al.*, 2002).

Limpet spawning, resulting in the shedding of eggs and sperm directly into the sea, is apparently related to the occurrence of winds and rough weather (Orton, Southward and Dodd, 1956). After a period in the plankton, the short-lived free-swimming larvae (planktotrophic veliger larvae) settle at low levels on the shore or in damp crevices. As they grow, they slowly move upshore and inhabit different levels on the shore (Fretter and Graham, 1962, 1976; Branch, 1985; Guerra and Gaudêncio, 1986; Little and Kitching, 1996). *P. depressa* is seen as a summer breeder in Britain. Sexes are separate throughout life, and fertilization is external. Gonads begin to develop in spring and spawning takes place from July to September, possibly linked to wave action, combined with maximal temperatures occurring during these months (Orton and Southward, 1961; Fretter and Graham, 1962, 1976; Hayward, Nelson-Smith and Shields, 1996). According to Guerra and Gaudêncio (1986), the reproductive behaviour of this species is different, and changes along the Portuguese coast.

In the present study, the sex proportions and reproductive cycles of the limpet *P. depressa* were investigated on two rocky shores of the central region of the Portuguese coast. An attempt has been made to find out the exact spawning period, and to explore the influence of local meteorological factors on spawning.

MATERIALS AND METHODS

Reproductive cycle

The study of the reproductive cycle was made using limpets collected from two shores on the central region of the Portuguese coast, Avencas (38° 41' N, 09° 21' W) and Cabo Raso (38° 42' N, 09° 29' W), between July 2001 and September 2002. Monthly samples of 100 individuals were taken from upper mid shore levels in the morning during low water of spring tides. Only limpets measuring

above 20 mm shell length were included in the study of the reproductive cycle, since animals over this size always had gonads that could be clearly distinguished throughout the year, either in a developing or spawning stage (Orton, Southward and Dodd, 1956).

After sampling, all limpets were immediately frozen at -20 °C. Later, the shell length of each individual was measured with a vernier calliper to the nearest mm, and both the sex and gonad stage were assessed by cutting away the foot from most of its attachment to the visceral mass and shell, and turning it forward. The gonad lies on the ventral surface of the visceral mass in both sexes (Orton, Southward and Dodd, 1956). The exposed gonad was macroscopically analysed and classified according to the scheme of gonad stages described by Orton, Southward and Dodd (1956) for *P. vulgata*. According to Orton, Southward and Dodd (1956) there are no secondary sexual characters in *P. depressa*. Therefore, the sexes could be distinguished by direct examination of the gonad. The male gonad is pinkish white or cream, and the female gonad is green or brown. The neuter gonad shows a discrete reddish-brown kidney-shaped structure. Developing and spawning stages were separated more subjectively. Spawning males were recognised by the purplish tinge of the gonad, whilst spawning females could be distinguished only by the looseness of the eggs in the ovary, (Orton, Southward and Dodd, 1956). In order to assess the state of sexual maturity in each monthly sample, a Mean State of Development (MSD) was determined for individuals with a shell length longer than 20 mm, using the same method adopted by Orton, Southward and Dodd (1956) for *P. vulgata*. Using the data thus obtained, four variables were calculated in order to describe the progression of the reproductive cycle of the two population samples: MSD and the proportion (as percentage) of individuals in the resting, developing and spawning stages.

Sex ratio

Approximately 1 000 individuals were examined from each of the stretches of shoreline, at Avencas and Cabo Raso, between September 2001 and February 2002. As far as possible, 100 specimens were examined in each 5 mm size-group. On the

shore, all specimens were collected from a 2 m² area each month. Limpets were measured with a vernier calliper, and the sex was determined by observation of the gonad colour. Individuals with a shell length of less than 10 mm sometimes could not be sexed, as they do not possess a discernible gonad.

Spawning stimuli

Data from maximum and minimum air temperature and wind speed at Avencas and Cabo Raso, for each sampling date, were obtained from Portugal's Institute of Meteorology.

RESULTS

Reproductive cycle

The reproductive cycle of *P. depressa* from July 2001 to September 2002 is shown in figures 1 (Avencas) and 2 (Cabo Raso).

In Avencas (figure 1), gonad development occurred between October and December, and continued between February and April. The spawning period occurred in the summer (July/August 2001 and between May and August 2002); however, a secondary peak in spawning activity was observed in January. A short resting phase was observed between June and August at the same time as the number of individuals, either neuter or in the resting phase, increased. This resting phase was followed by a new development period in September.

At Cabo Raso (figure 2), several peaks of spawning occurred during the study period. Gonad development took place between September and December 2001, and also between February and April 2002. Most spawning occurred between May and August 2002, although secondary peaks in spawning activity appeared to occur in October, January and March. A resting phase was also visible in the summer (May/June), followed by a new development period in September.

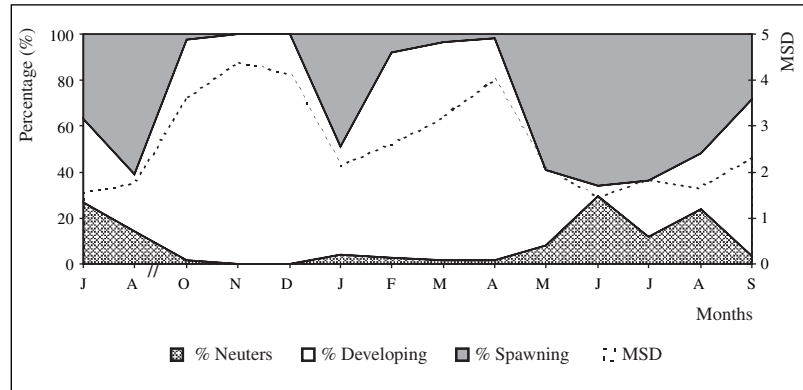


Figure 1. The reproductive cycle of *P. depressa* from Avencas: mean state of development and percentages of the population in the resting, developing and spawning phases

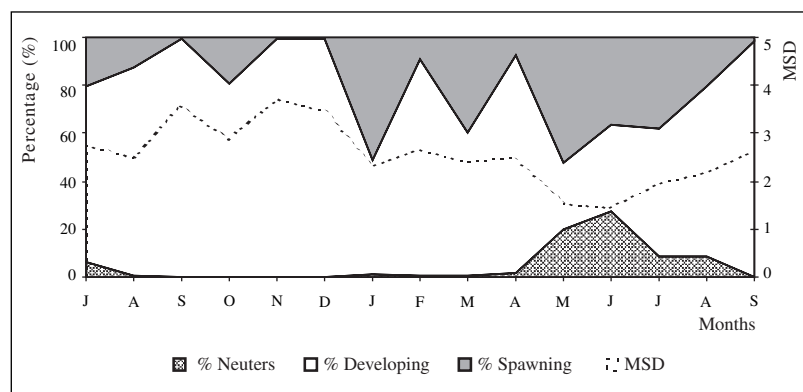


Figure 2. The reproductive cycle of *P. depressa* from Cabo Raso: mean state of development and the percentages of the population in the resting, developing and spawning phases

From both figures, it can be seen that *P. depressa* has a short resting phase during the summer, when the number of neuters increases, but never corresponds to more than 25% of the population. This phase begins in May/June and extends up to July/August in some individuals. The resting phase is followed by a long period of gonad development, over autumn/winter (September/October to December), during which the gonad increases steadily in size until it becomes fully mature. A rapid change from the developing to the spawning condition takes place sometime in January (Avenças) and in January and March (Cabo Raso). Winter/spring gonad development (from February to April) is followed, once more, by a summer resting period.

An annual pattern in the variation of MSD was apparent throughout the study period (see figures 1 and 2). The MSD reached a maximum, at Avenças, between October and December 2001 and from February to April 2002, and at a minimum in July, August 2001 and between May and August 2002. At Cabo Raso, the MSD followed a similar trend, having the highest values been found between the periods of September-December 2001

and February-April 2002, and the minimum between May and July 2002.

Sex ratio

The proportion of males, females and neuters found in the various size-classes of *P. depressa* (total of 1 203 individuals for Avenças and 1 429 for Cabo Raso) is shown in tables I and II, and presented graphically as the percentages of neuters, males and females in figures 3 and 4. All of the samples examined for sex proportions showed the presence of males and females simultaneously, in nearly all size-classes.

From figures 3 and 4 it can be seen that *P. depressa* seems to be immature up to 10-15 mm, and that complete differentiation of the sexes in both populations is reached at a shell length of approximately 16-20 mm. Individuals of both sexes were found over the same size range, i.e., 11-15 mm to 36-40 mm in Avenças and 6-10 mm to 31-35 mm in Cabo Raso. The bulk of the breeding population was found to be between 26-30 mm at Avenças

Table I. The proportions of sexes in *Patella depressa* from Avenças (N = 1 203)

Size-Group	Sex				Percentage		
	Neuter	Males	Females	Total	Neuter	Males	Females
0-5	15	–	–	15	100.0	–	–
6-10	69	5	5	79	87.3	6.3	6.3
11-15	98	36	28	162	60.5	22.2	17.3
16-20	15	95	49	159	9.4	59.7	30.8
21-25	5	145	120	270	1.9	53.7	44.4
26-30	8	209	154	371	2.2	56.3	41.5
31-35	1	72	57	130	0.8	55.4	43.8
36-40	–	14	3	17	–	82.4	17.6
Total	211	576	416	1 203	17.5	47.9	34.6

Table II. The proportions of sexes in *Patella depressa* from Cabo Raso (N = 1 429)

Size-Group	Sex				Percentage		
	Neuter	Males	Females	Total	Neuter	Males	Females
0-5	23	1	1	25	92.0	4.0	4.0
6-10	142	34	16	192	74.0	17.7	8.3
11-15	123	87	71	281	43.8	31.0	25.3
16-20	27	124	148	299	9.0	41.5	49.5
21-25	2	228	168	398	0.5	57.3	42.2
26-30	–	124	99	223	–	55.6	44.4
31-35	–	5	6	11	–	45.5	54.5
Total	317	603	509	1 429	22.2	42.2	35.6

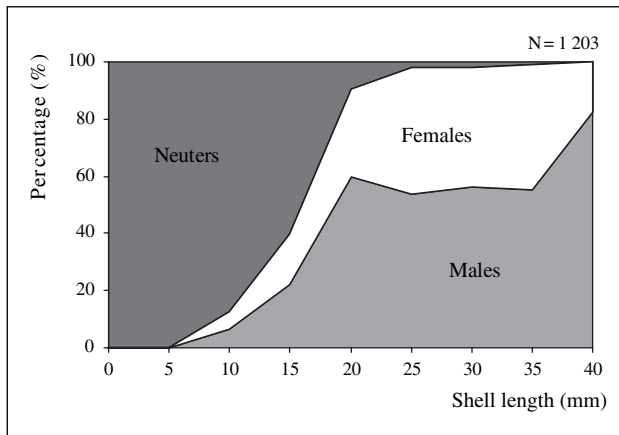


Figure 3. Sex proportions in *P. depressa* from Avencas

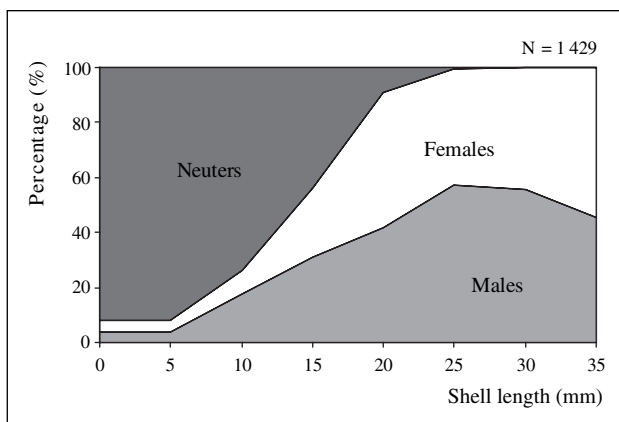


Figure 4. Sex proportions in *P. depressa* from Cabo Raso

(table I) and between 21-25 mm at Cabo Raso (table II). In the 6-15 mm size-classes, practically all specimens were neuter, representing 17.5 % of the Avencas population, and 22.2 % of Cabo Raso's.

Despite the tendency for a higher number of males than females, the percentage of the two sexes did not differ significantly in nearly any size-classes, making up 48 % (35 % of females) of the total limpets at Avencas (table I) and 42 % (36 % of females) at Cabo Raso (table II). The Avencas sex ratio was higher than that of Cabo Raso. The overall sex ratio during the period of study, and considering only males and females, was 1.41:1 for Avencas and 1.20:1 for Cabo Raso.

Spawning stimuli

Figure 5 shows the maximum and minimum air temperature and wind speed, at Avencas (figure

5A) and Cabo Raso (figure 5B), for each sampling date.

Figure 5 suggests that air temperature is a possible stimulus for spawning, since the different peaks of spawning tended to coincide with maximum air temperatures. This trend was more obvious at Avencas, where the spawning peaks (August 2001, January and June/July 2002 in figure 1) coincided with peaks of increasing higher temperatures. At Cabo Raso (see figure 2), the spawning peaks of January (minimum air temperature peak), March, May 2002, and even the small peak in October tended to match with high temperatures peaks. The same trend was observable when comparing wind speeds and spawning. January and July (but not August and June) spawning peaks at Avencas seemed to coincide with increasing periods of high-wind speed, whereas at Cabo Raso the October, June, July and August spawning peaks coincided with high wind speeds.

DISCUSSION

The reproductive cycles of *P. depressa* from Avencas and Cabo Raso reveal interesting similarities. This species showed a gradual gonad development, beginning in September/October and extending up to February-April. Spawning (corresponding to a drop in MSD values) peaked in the summer, but earlier partial spawnings seemed to occur in January at Avencas, and in January and March on Cabo Raso. A short resting phase was also observed in summer, at the same time as the number of neuter individuals increased and the MSD values decreased. Throughout the breeding cycle, the MSD followed the annual developing/spawning tendencies in both populations.

The spawning activity of *P. depressa* in the present study was similar to that found by Guerra and Gaudêncio (1986) in the central region of the Portuguese coast. These authors described spawning as taking place several times during the year, and breeding being asynchronous. Neuter, developing, and spawning gonads were found in almost every monthly sample. Lewis (1986) and Orton and Southward (1961) also reported a *P. depressa* tendency for multiple spawnings.

The most obvious differences between the *P. depressa* breeding cycle at Avencas and Cabo Raso

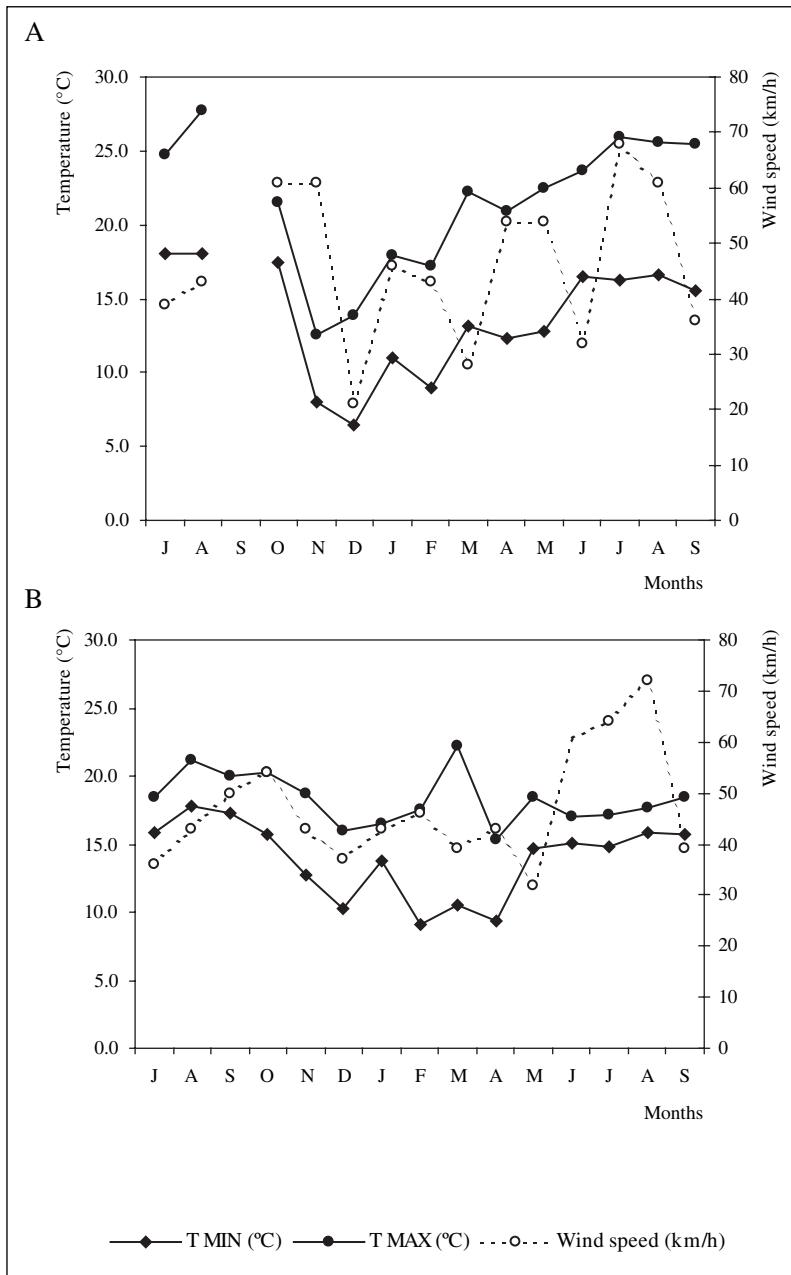


Figure 5. Maximum and minimum air temperatures and wind speed obtained from Avencas (A) and Cabo Raso (B) (data from Portugal’s Institute of Meteorology)

were in the number of spawning peaks: for Cabo Raso, several peaks were observed throughout the year. Bowman (1985) had suggested that early spawnings are characteristic of exposed shores more severely affected by storms, whilst more sheltered populations tend to accumulate gametes to be released at a later major spawning. The two populations studied here seem to conform to this pattern, since Cabo Raso (with lower MSD values) is definitely a more exposed shore than Avencas.

In the central region of the Portuguese coast, the resting phase was short and occurred in sum-

mer. The same phenomenon has also been reported for these limpet species in the north of Portugal (Ribeiro, 2002). Orton, Southward and Dodd (1956), while studying the breeding of *P. vulgata*, observed a prolonged resting phase from January to June, whereas Orton and Southward (1961) found that the resting phase in *P. depressa* is not so prolonged as in *P. vulgata* and occurs in early spring.

The most obvious differences among *P. depressa* and *P. vulgata* and *P. ulysiponensis* are the period of spawning and the seasonal pattern of the reproduc-

tive cycle. In the British Isles, *P. vulgata* is regarded as a winter breeder, usually spawning in late autumn (Orton, 1920, 1928, 1946; Orton, Southward and Dodd, 1956; Blackmore, 1969; Baxter, 1983; Bowman and Lewis, 1986; Guerra and Gaudêncio, 1986); *P. ulysiponensis*, on the other hand, is seen as a summer breeder that matures in May, with spawning occurring in late September (Thompson, 1979; Bowman and Lewis, 1986; Guerra and Gaudêncio, 1986); *P. depressa* is also considered a summer breeder, for which spawning takes place in July, August and early September (Orton and Southward, 1961; Bowman and Lewis, 1986; Guerra and Gaudêncio, 1986). The results of the present study indicate that in the central region of the Portuguese coast, *P. depressa* seems to be a summer breeder, although secondary peaks were observed both at Avenças and Cabo Raso. These differences in breeding behaviour are probably related to the diverse morphology, habitat, distribution and latitudinal differences showed by each species.

Despite a tendency for a higher number of males than females in the examined samples, the sex proportions seem to be approximately equal at both sites. Consequently, a change of sex appears not to take place in *P. depressa*, unlike *P. vulgata*, a protandrous hermaphrodite species in which small individuals are predominantly male, and the proportion of females gradually increases with age (Orton, 1928; Dodd, 1956; Garwood, 1987; Little and Kitching, 1996).

The conditions controlling breeding and spawning in *Patella* spp. are not entirely known. According to Lewis (1986), spawning in *Patella* spp. involves an environmental trigger. Orton, Southward and Dodd (1956), as well as Orton and Southward (1961), reported that high wind speed, associated with stimulation by wave action, may induce spawning in *P. vulgata* and *P. depressa*. They found that strong onshore winds could act as a mechanical trigger, and even stimulate spawning before the limpets reach their maximum maturity, resulting in earlier spawning. The same phenomenon also occurred in the present study, where spawning peaks tended to coincide with a rise in air temperature, linked with high wind speeds. Guerra and Gaudêncio (1986), working on the same species but along the entire Portuguese coast, also observed this tendency, but only with regard to wind speed. According to these authors, air temperature seems to have no influence on spawning. However, Orton and Southward

(1961) found that air temperature is a possible stimulus for spawning in *P. depressa*.

In conclusion, in *P. depressa* the gonads develop from September/October to December and between February and April, and spawning occurs predominantly in the summer months. The sexes in this species are uniformly distributed in nearly all size-groups, suggesting a nonexistence of sex reversal. Finally, high air temperatures and wind speed appear to induce spawning in this species.

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