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## **DOCTOR OF PHILOSOPHY**

**The population biology of the gooseneck barnacle *Pollicipes pollicipes* (Gmelin, 1790) in the Algarve, southwest Portugal.**

Cardoso, Ana Cristina de Jesus

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**CHAPTER IV: ASPECTS OF THE REPRODUCTIVE BIOLOGY OF  
*POLLICIPES POLLICIPES* (CIRRIPEDIA; LEPADOMORPHA)  
FROM THE SOUTHWEST COAST OF PORTUGAL**

The results in this chapter were presented in a poster at the symposium “ECSA 24 Northern and southern European estuaries and coastal areas” at the University of Aveiro, Portugal, in 1994. Later these results were published by Cardoso, A.C. and A.B., Yule, 1995. *Neth. J. Aquatic Ecol.*, 29:391-396.

#### 4.1 INTRODUCTION

Cirripedes show considerable variability in their breeding activities which has been attributed to environmental and genetic differences (*e.g.* SASTRY, 1975). Reproductive activity varies on a small spatial scale, *e.g.* over an intertidal range (CRISP, 1950, 1959; LEWIS and CHIA, 1981; PAGE, 1984), or on a large spatial scale across different geographic ranges (*e.g.* CIMBERG, 1981), as well as varying temporally (*e.g.* HINES, 1978; LEWIS and CHIA, 1981; PAGE, 1984). The length and timing of the breeding season, weight of the egg masses, and resulting reproductive effort are all subjected to local and geographic variation.

Hines (1978) has grouped cirripedes into five categories based on a spectrum of reproductive patterns: (1) a boreo-arctic pattern in which a single large brood is incubated over winter (*e.g.* *Semibalanus balanoides*, BARNES, 1963; *B. balanus* and *B. hameri*, BARNES and BARNES, 1954; CRISP, 1954, 1956; BARNES, 1957); (2) a pattern shown by a few cold-temperate species which produce a small number of broods in winter and spring (*e.g.* *Verruca ströemia*, BARNES and STONE, 1973; *B. glandula*, BARNES and BARNES, 1956; HINES, 1978); (3) a variable pattern found in several warm-temperature and subtropical species which produce many small broods during summer (*e.g.* *Chthamalus stellatus*, PATEL and CRISP, 1960b; *C. fissus*, HINES, 1978; *B. amphitrite denticulata*, PATEL and CRISP, 1960b); (4) another summer pattern but producing only a few broods (*e.g.* *Tetraclita squamosa*, HINES, 1978); (5) a pattern of continuous brooding throughout the year (*e.g.* *Elminius modestus* and *B. pacificus*, CRISP and DAVIES, 1955; HURLEY, 1973).

Some barnacles show different patterns of reproduction at different geographic ranges. For example *Pollicipes polymerus* has a limited summer breeding season in the cold temperate zone north of Point Conception which increases in length to central California (HILGARD, 1960; CIMBERG, 1973; LEWIS, 1975), while brooding activity in the warm temperate waters south of Point Conception peaks in winter (STRAUGHAN, 1971; CIMBERG, 1973).

The major environmental determinants in the reproductive cycles of a wide variety of animals, including barnacles, are temperature (both absolute level and fluctuations), food (both quality and quantity) and light (both intensity and periodicity). Other

environmental factors such as wave action and salinity may also influence the breeding cycles. Furthermore, there is evidence to show that interaction takes place between these factors so that a change in the critical level of one is accompanied by changes in those of the others (*e.g.* the critical temperature for breeding in *S. balanoides* can be raised by decreased periods of illumination, BARNES, 1963; CRISP and PATEL, 1969). One should also bear in mind that these environmental factors, or levels of one or more of these, may affect diversely the various phases (gametogenesis, copulation, fertilisation, embryogenesis and larval release) of the reproductive cycle (*e.g.* see BARNES, 1959 for a discussion of the temperature conditions at which the diverse phases of the reproductive cycle of *S. balanoides* take place).

The role of temperature, food and light in the breeding activities of several species of barnacles has been studied through field work and laboratory experimentation. There is evidence that barnacles from tropical and warm temperate zones can breed continuously so long as food is available and temperature is sufficiently high, while specimens from cold waters breed in temperate zones mainly or exclusively in cooler months.

Breeding in the former can be induced by providing such animals with abundant food at an appropriate temperature, *e.g.* PATEL and CRISP (1960a) successfully induced several tropical species of operculate cirripedes (*E. modestus*, *C. stellatus*, *B. perforatus* and *B. amphitrite* var. *denticulata*) to breed by raising the temperature and feeding liberally on *Artemia* larvae. On the other hand, only limited success inducing breeding of certain boreo-artic barnacles (*e.g.* *S. balanoides*, Crisp, 1959; BARNES, 1963; CRISP and PATEL, 1969; *B. balanus*, CRISP and PATEL, 1969; CRISP, 1954), beyond the period of natural breeding, has been reported. In these species breeding was not controlled by the conditions immediately prevailing but by those operating over previous months (CRISP and CLEGG, 1960) and Crisp and Patel (1969) suggested the existence of an endogenous rhythm in *S. balanoides* which becomes entrained at one or more points with prevailing seasonal variables.

For several species there is a critical temperature before breeding condition can be attained (*e.g.* 10° to 12° C for *S. balanoides*, 10° to 14° C for *B. balanus* and, about 17° C for *B. crenatus*, CRISP and PATEL, 1969), in others it is a change in temperature

towards an optimum rather than a critical temperature that triggers the onset of breeding (e.g. *P. polymerus*, CIMBERG, 1981; LEWIS and CHIA, 1981). Brooding in *C. fissus* is regulated by food availability rather than water temperature as found by Hines (1978) through laboratory experiments and corroborated by the patterns of reproduction seen in the field at Goleta Point (California) (PAGE, 1984); temperature and photoperiod did not affect the brooding frequencies of this species. In *S. balanoides* kept under laboratory conditions high light and low feeding exerts an inhibitory influence delaying the onset of breeding (CRISP and PATEL, 1969).

Our present knowledge of the reproductive biology of *P. pollicipes* is scarce and, apart from the early studies of Darwin (1851) and Gruvel (1893), it arises from information on the reproductive state of individuals collected at Biarritz (France) (BARNES and BARNES, 1977), the number of animals brooding eggs in a sample taken in the low intertidal region at Cabo Silleiro (Spain) (BARNES and BARNES, 1966), the number of eggs per given dry weight of animal in barnacles from Cabo Silleiro (BARNES and BARNES, 1968) and, from a preliminary study of the reproductive cycle at the south of Douro's estuary (Portugal) (CARVALHO, 1983).

It was the aim of the current study to monitor the biological parameters of the *Pollicipes* population, both in space (different sites, Castelejo and Zavial) and time (over a two year period). The work reported here details that part of the project concerned with the reproductive capacity of two populations and, it examines the breeding patterns from two locations with different environmental conditions. Estimates of the reproductive effort, the annual energy expended on reproduction in terms of percentage of body weight per year were made for *Pollicipes* at the two sites.

## 4.2 MATERIALS AND METHODS

As already described above (see field work) the main sampling programme took place at Castelejo (an exposed beach) and Zavial (a more sheltered beach) between September 1991 and December 1993 and was, from March 1992 onwards, conducted at approximately monthly intervals.

An account of the sampling strategy, the measurements and observations made, is also given above (see field and laboratory work). For each individual, the capitulum

height and the presence of ripe ovaries, fertilised egg masses and seminal vesicles filled with white seminal fluid, was recorded. Dry and ash weights were individually ascertained and, when present, dry egg mass weights were also assessed.

#### 4.3 RESULTS

An adult invertebrate can be defined as one capable of reproduction, *i.e.* possessing functional gonads. Thus barnacles carrying fertilised egg masses or seminal vesicles filled with sperm can be considered adult. From several thousand *P. pollicipes* examined from the Algarve the smallest found carrying egg masses or sperm were 8 mm in capitulum height (approximately 0.3g total wet weight). Certain smaller individuals showed signs of developing ovary and testes but the size of first maturation for *P. pollicipes* in the western Algarve can be considered as 8 mm capitulum height.

Fig. 4.1 shows the percentage of sampled animals brooding egg masses through the sampling period. The data for the Castelejo population is more extensive but the general pattern is comparable with that shown by the Zavial population. From October through to March in both 1992 and 1993 virtually none of the sampled animals carried egg masses at Castelejo. From April through to September between 25% and 55% of the Castelejo barnacles and 15% to 70% of the Zavial barnacles carried fertilised egg masses in 1992 with peak numbers in July. The brooding success in 1993 was less variable but generally lower with only 20-40% of the sampled animals carrying egg masses at either location between April and October. In July 1993 a summer storm swamped the beach at Zavial with sand and buried a large proportion of the *Pollicipes* population. They appear to have been prevented from fertilising although the temporary burial appears not to have killed them. The population at Zavial did, however, continue to bear egg masses in October 1993 while those at Castelejo did not.

Fig. 4.2 shows the correlation between the percentage of brooding adults at both sites and the average monthly air temperature. The significant positive correlation ( $r=0.608$ ,  $df=61$ ,  $p<0.01$ ) indicates greater breeding success at higher temperatures. Indeed very few individuals can be found carrying egg masses when the monthly average drops below 14°C. Changes in average seawater temperatures follow those of

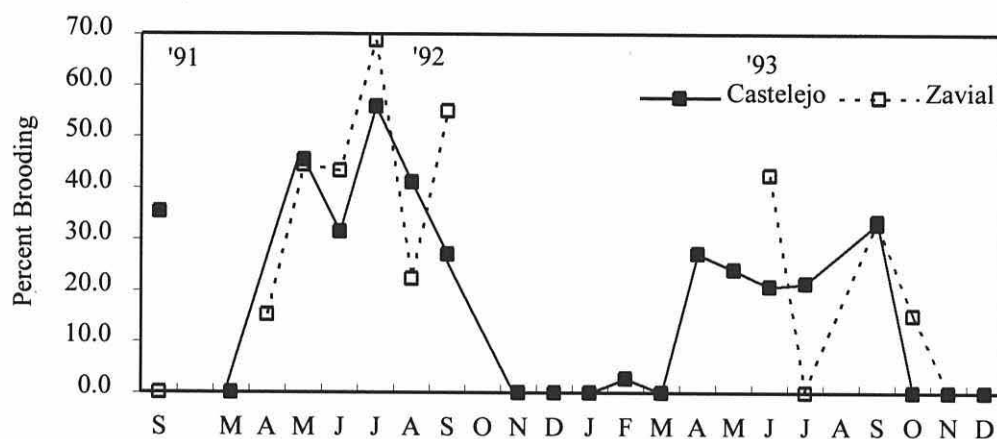


Fig. 4.1 The percentage of *P. pollicipes* adults carrying egg masses (brooding) at Castelejo and Zavial in 1991-93.

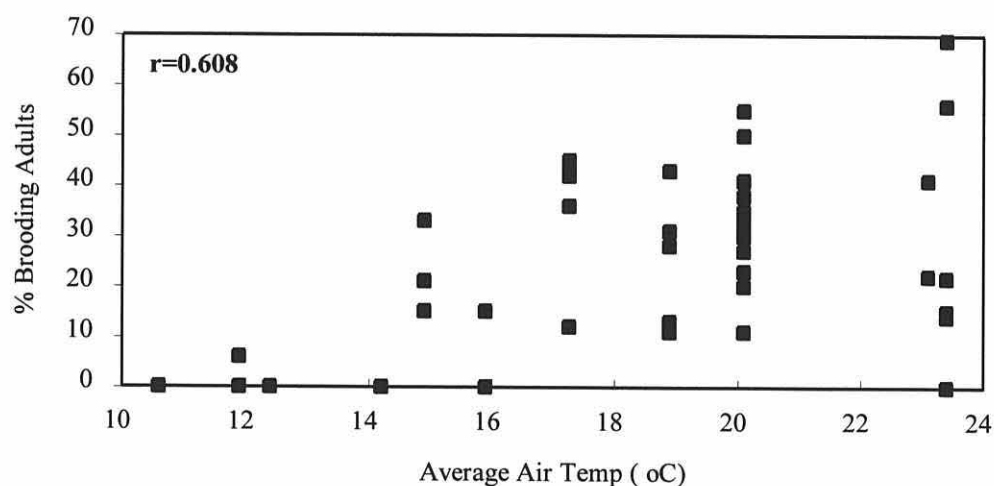


Fig. 4.2 The percentage of *P. pollicipes* adults brooding at Castelejo and Zavial plotted against average monthly air temperature (°C).  $r$ =Spearman's rank correlation.

air temperatures quite closely but with smaller amplitude (see Fig. 4.3). However, the correlation with brooding *P. pollicipes* was not significant ( $r=0.177$ ,  $df=61$ ,  $p>0.05$ ) due to a consistent influx of warmer water in October and November (when few egg masses can be found) following an initial drop in temperature in September.

The percentages of animals containing ovary and sperm were extremely variable and showed no consistent pattern through the year (Fig. 4.4). For example in December 1992 nearly 80% of the animals sampled had ovary at Castelejo yet the same population sampled in January 1993 showed no signs of ripe ovary (see Fig. 4.4a). No egg masses were found in animals at Castelejo from November to January. Fig. 4.5 shows a significant (yet weak) positive correlation between the percentage of animals with ovary and those with sperm ( $r=0.476$ ,  $df=61$ ). Functional ovaries and testes are thus available in the population virtually all year round but fertilisation does not appear to occur during the winter months.

Fig. 4.6 shows a linear, if some-what variable, relationship between dry weight of egg masses and organic (ash free) body weight for animals from Castelejo and Zavial. Animals from Zavial showed a slightly greater investment in eggs per unit body weight (6%) than those at Castelejo (5%) but the difference in slope was not significant ( $F = 0.62$ ,  $df = 1$  and  $101$ ,  $p = 0.434$ ) hence the combined regression has been fitted to the data in Fig. 4.6. The intercept ( $0.24 \pm 0.79$  mg) was not significantly different from zero but then no small animals ( $<25$  mg organic weight) carry egg masses. The slope of the combined regression shows that  $5.5 \pm 0.6\%$  of the organic body weight is invested in eggs.

#### 4.4 DISCUSSION

The two sampling sites are characterised by differences in environmental conditions (see field work). Castelejo, located on the west coast facing the open expanse of the North Atlantic, is subject to intense wave exposure while Zavial faces south and is generally more sheltered. In the summer months the southwest coast of the Algarve experiences an upwelling of nutrient rich, colder water which makes the area very productive. The upwelling is virtually a permanent feature throughout the summer in the sea off Castelejo but its occurrence is much more variable off the south coast.



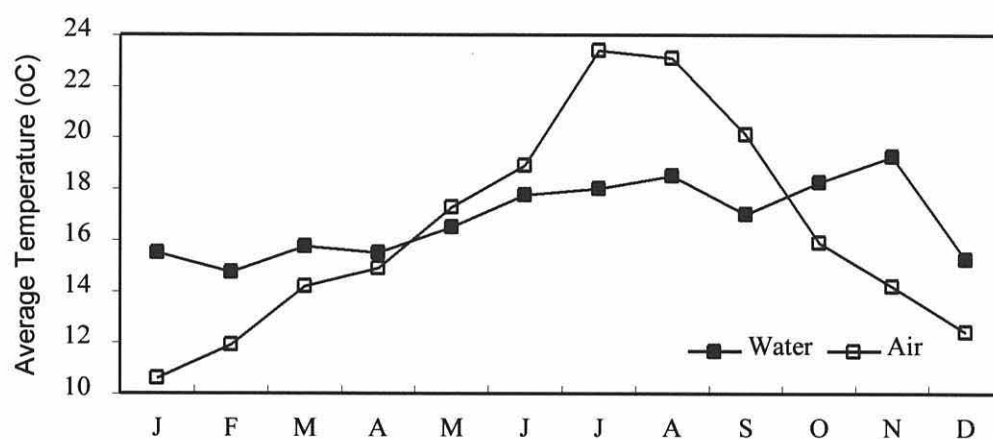


Fig. 4.3 Monthly average surface seawater and air temperatures (°C) around the southwest coast of the Algarve. (Data supplied by D.R.A.R.N. Algarve Hydrometry section, and Paulo Relvas, University of the Algarve).

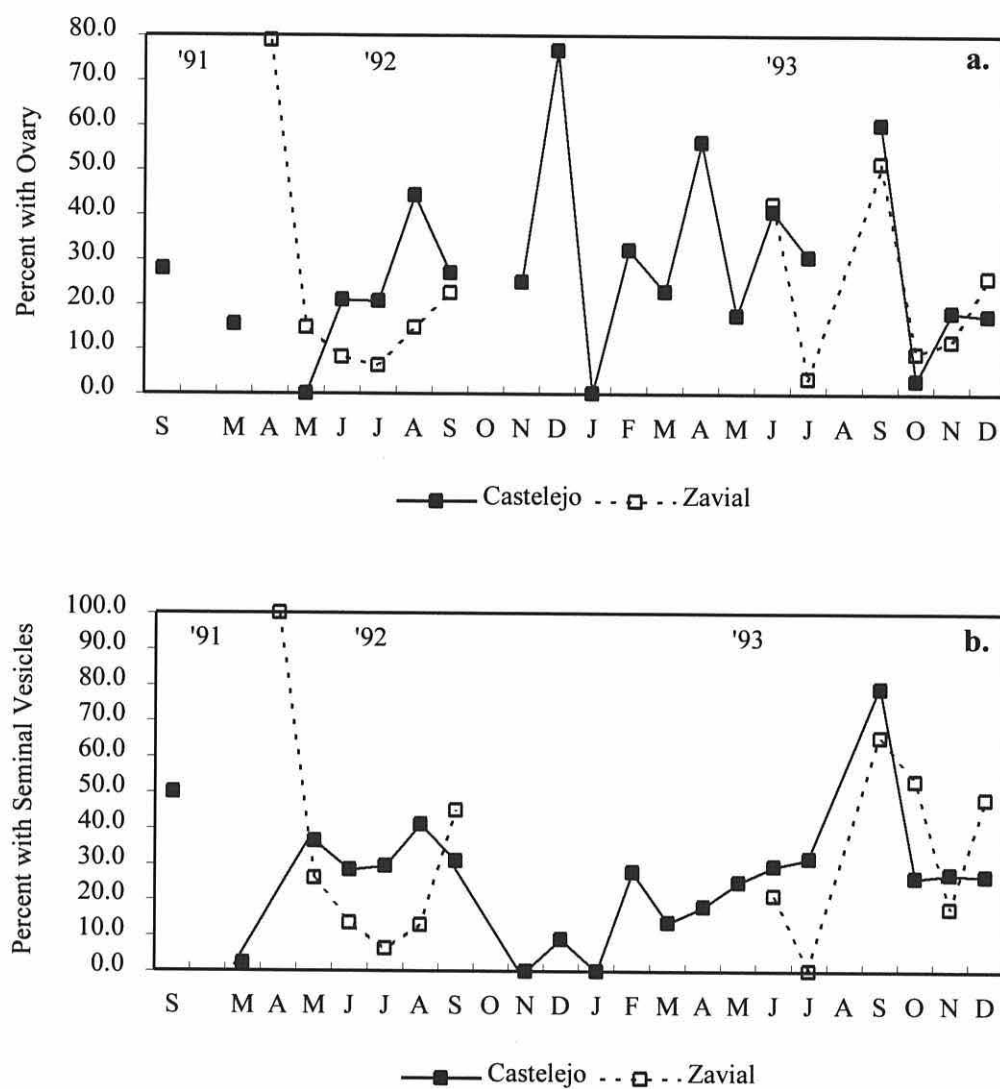


Fig. 4.4 The percentage of adult *P. pollicipes* bearing ovary (a) and with obvious seminal vesicles (b) at Castelejo (n=39 - 823) and Zavial (n=16 - 748) in 1991-93.

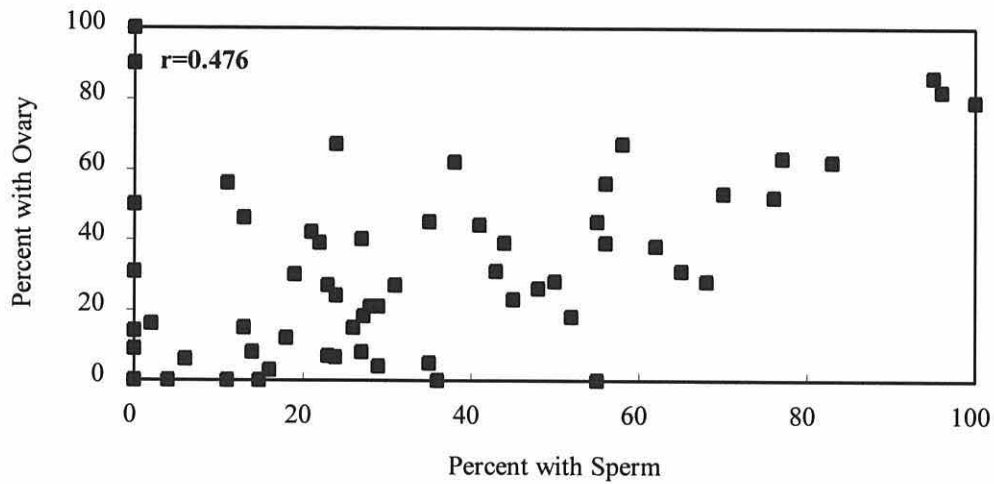


Fig 4.5 Correlation between the percentage of *P. pollicipes* adults bearing ovary and those with obvious seminal vesicles (sperm) at Castelejo and Zavial.  $r$ =Spearman's rank correlation.

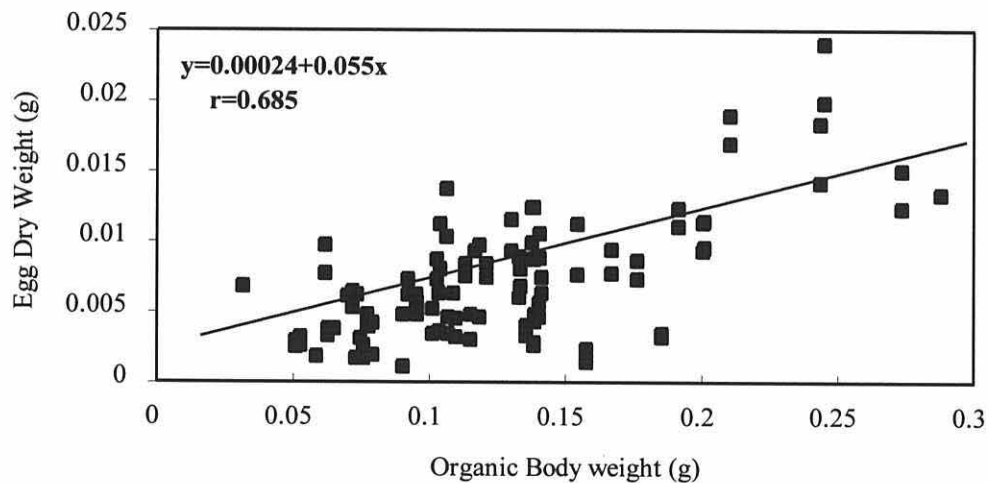


Fig 4.6 Relationship between egg mass dry weight and adult organic (ash-free) dry body weight in *P. pollicipes* from Castelejo and Zavial. The regression equation was fitted by the method of least squares with 103df.

The difference in duration of the upwelling phenomenon should, generally, result in food availability for *P. pollicipes* at Castelejo being higher than that at Zavial. The seawater temperature at Castelejo is roughly 0.5-1.0 °C lower, on average, than that at Zavial which reflects the influence of the sustained upwelling. Although there were minor differences in reproductive patterns between the two sites, none were statistically significant hence differences in environmental conditions between the sites do not appear to affect materially *P. pollicipes* reproductive patterns.

The brooding activity of marine organisms, and of barnacles in particular has been broadly related to temperature and plankton availability (e.g. CRISP, 1954; CRISP and DAVIES, 1955). Although, there is no direct evidence that the onset of brooding in *P. pollicipes* is controlled by temperature, seasonal breeding trends for *P. polymerus* followed seawater and air temperatures at San Juan (LEWIS and CHIA, 1981). The reproductive season for *P. pollicipes* at Biarritz, France, is similar to that shown here for the barnacles in the Algarve and reproductive effort appeared to correlate with environmental temperature (BARNES, 1992). On the southwest coast of the Algarve the percentage of *P. pollicipes* individuals carrying egg masses correlated positively with air temperature but not with seawater temperature. Brooding success was greatest with average air temperatures in excess of 14 °C, during the months of strongest upwelling and presumed food availability. It is difficult to separate the effects of food availability from temperature except to note that highest sea temperature occurred during a month of low air temperature and negligible brooding success. CIMBERG (1981) has reported that temperature controls the breeding of *P. polymerus* to a greater extent than food availability but with the assumption that food resources must be in excess of maintenance to allow gonad development to ripeness. At Castelejo and Zavial ripe male and female gonads were found in *P. pollicipes* adults all year round with great variability between months. There is a significant correlation between the percentage of adults bearing ripe ovaries and those with ripe testes generally showing the contemporaneous development of male and female function so typical of barnacles (e.g. *P. pollicipes*, CARVALHO, 1983; *Mitella* (= *P.*) *polymerus*, HILGARD, 1960). Since high percentages (averaging 30-40% at Castelejo from November 1992 to March 1993) of the population carry ripe ovary through the winter months we can assume that food resources exceed individual

maintenance levels all year round and hence may not directly limit the reproductive capacity.

There is currently no way of knowing if the ripe ovary, noted by its rich yellow colour and copious quantity, observed during the winter months in the Algarve is actually capable of being fertilised. It may well prove that although sufficient energy is available to sustain ovarian development during the winter, the quality of food material may not be sufficient to encourage the final stages of oogenesis necessary for stimulating copulation and egg laying. Ultrastructural investigation of ovarian tissue is currently underway to ascertain the functionality of winter ovary. Temperature and food availability may well control the rate of deposition of gonadal tissue but need not necessarily control the ripening of the gonads to a receptiveness for fertilisation. In the temperate, single brooder, *Semibalanus* (= *Balanus*) *balanoides*, fertilisation is controlled by day length. As the days shorten in the winter so the population begins fertilisation, probably under the control of a neurosecretory system associated with the eyes since fertilisation can be prevented by maintaining a 12h light:dark cycle (e.g. see BARNES *et al.*, 1977). It may be that the opposite is true for *P. pollicipes* and decreasing daylight towards the winter months is a cue to cease copulatory activity.

The fecundity of a population can be compared in terms of number of broods per adult per season, which may vary according to adult size, nutrient conditions, position on the shore and latitude (HILGARD, 1960). Adapting the method of HILGARD (1960), Table 4.1 compares the fecundity of the populations of *P. pollicipes* at Castelejo and Zavial in 1992 and 1993. The number of broods produced by an individual per year was estimated from the number of days in the breeding season (183, April to September inclusive, see Fig. 4.1), the development time for a brood of 25 days (considering the values given by HILGARD, 1960, 25 d for *P. polymerus* at 13-15 °C; LEWIS, 1975, 24.4 d at 13-15 °C for *P. polymerus*; and MOLARES *et al.*, 1994, 25 d at 20 °C for *P. pollicipes*) and the average percentage of the population brooding eggs over the time interval.

In 1992, 3 broods per individual per year were estimated for the populations at both Castelejo and Zavial representing a reproductive effort of 18-19% (proportion of organic weight devoted to eggs). In 1993 the reproductive capacity was reduced to nearly 2 broods at Castelejo and just over 1 at Zavial, just over half the reproductive effort seen

in 1992. The general reduction from 1992 to 1993 may well be due to the lower average temperature during the breeding season in 1993 (18.9 as opposed to 19.7 °C) but the very low performance at Zavial is undoubtedly due to the loss of breeding condition in July 1993 brought about through the influx of sand. HILGARD (1960) estimated 5-7 broods per individual per year in *P. polymerus* while LEWIS and CHIA (1981) report average brood numbers of 2-4.4, very similar to those reported here for *P. pollicipes*. PAGE (1984) reports a more variable situation for *P. polymerus* of between 1 and 11 broods per season with a reproductive effort equivalent to between 4 and 231% of adult biomass.

Reproduction of *P. pollicipes* on the southwest coast of the Algarve thus appears closely linked to the upwelling phenomenon and the rate of deposition of gonadal tissue as determined by environmental temperature. The cues which determine the length of the breeding season remain to be investigated. However, there seems little difference in reproductive patterns between the south and west facing coasts although it is clear that environmentally induced phenomena, such as the influx of sand noted at Zavial, can significantly reduce reproductive output and presumably affect future recruitment.

**Table 4.1**

The fecundity (number of broods per individual per year) and reproductive effort (percentage of organic body weight deposited as fertilised eggs) of *P. pollicipes* at Castelejo and Zavial on the southwest coast of Portugal.

<b>Year</b>	<b>Locality</b>	<b>Estimated number of broods</b>	<b>Reproductive effort %</b>
<b>1992</b>	<b>Castelejo</b>	3	18
	<b>Zavial</b>	3	19
<b>1993</b>	<b>Castelejo</b>	2	11
	<b>Zavial</b>	1	8