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PRIMARY RESEARCH PAPER

Distribution ranges of the acorn barnacle *Perforatus (=Balanus) perforatus* (Bruguière, 1789) in the NE Atlantic are influenced by reproductive parameters

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Abstract The acorn barnacle *Perforatus perforatus* has a defined breeding temperature range and reproductive season that varies geographically. This study aims to investigate the influence of reproductive parameters of *P. perforatus* in species distribution ranges in the NE Atlantic. The hypothesis tested is that the breeding season of *P. perforatus* off NW Portugal begins earlier and is longer than at the northern distribution limit of this species, and that fecundity is higher in terms of number of broods per individual per breeding season. The span of the breeding season and fecundity indices were assessed based on the presence and maturation of ovigerous lamellae and correlated with temperature. Results showed that the breeding season in the NW Portuguese coast lasts over 10 months (February–November) and the number of broods was determined to be 9.2 ind/year. Temperature seems to be a primary factor determining the breeding season, but other factors, such as food availably, light and photoperiod, are also of great importance. However, the higher quantity of embryos produced in NW Portugal is not reflected in a higher abundance of settled adults in rocky shores. Contrarily, the species is particularly abundant in artificial substrata offshore.

Keywords Barnacles · Span of breeding season · Fecundity indices · Reproduction · Temperature · Number of broods per individual · Critical breeding temperatures · Climate change

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Introduction

As adults, barnacles (Cirripedia) are exclusively marine sessile crustaceans that function as filter feeders in rocky shore ecosystems and compete for space with molluscs such as limpets and mussels. The occurrence, abundance and latitudinal distribution of barnacle species depend on the climatic regime, and temperature is a crucial factor determining their reproductive success (Norris & Crisp, 1953; Patel & Crisp, 1960a; Barnes, 1989; Southward, 1991; Poloczanska et al., 2008). Namely, the number of broods, timing and extent of the breeding season are species-specific parameters that define barnacles as being either boreo-arctic or temperate-tropical species. Boreo-arctic species (e.g., *Semibalanus balanoides* and *Balanus balanus*) produce a single annual brood, gonadal development occurs during summer and early autumn, and embryos incubate during the winter (Barnes, 1963). In contrast, the pattern corresponding to tropical and temperate barnacles (e.g., *Perforatus perforatus* and *Chthamalus montagui and C. stellatus*) is characterised by a defined breeding season with multiple broods (Norris & Crisp, 1953; Burrows et al., 1999; Herbert et al., 2003; Macho et al., 2010). However, other cirripedes (e.g., *Austrominus modestus* and *Amphibalanus amphitrite*) are strongly eurythermal, having a broad distribution range (comprising various continents) and breeding over a wide range of temperatures. *Perforatus perforatus* is found on a wide range of hard substrata along wave-exposed shores and in ria-type estuaries in the lower half of the littoral zone, (Evans, 1947; Norris & Crisp, 1953; Herbert et al., 2003; Macho et al., 2010) and also in the sublittoral zone (Herbert et al., 2003; Neal & Yule, 1994). It commonly inhabits semi-exposed and shady rock surfaces, crevices and overhangs that reach the mid tide level zone (Evans, 1947; Herbert et al., 2003). *P. perforatus* occurs naturally along the NE Atlantic seashore from SW Wales to West Africa, ranging between 31°N and 52°N and 9°W and 41°E (Choi et al., 2013), as well as in the Mediterranean Sea. However, in the English Channel, at the northern limit of its distribution, the species has extended its range eastwards in response to rising sea temperatures following the severe winter of 1962–1963 (Crisp, 1964; Herbert et al., 2003). The intolerance of adults to low air temperatures also defines the geographic limits of the northern edge of the distribution of the species (Herbert et al., 2003). Also, an increase in occurrence has been noticed in artificial substrates, including piers, breakwaters, marinas and sea defences that produce embayed zones and may facilitate colonisation (Herbert et al., 2003). More recently, *P. perforatus* was found to have been spread globally (e.g., the East China Sea and Sea of Japan) through discharges of ballast waters, fouled ship hulls (Torres et al., 2012; Choi et al., 2013) and plastic flotsam (Rees & Southwards, 2009), and in the NE Atlantic and the North Sea, it represents one of the most important species involved in biofouling (Fragoso & Icely, 2009; Kerckhof et al., 2010).

Previous studies show that *P. perforatus* only breeds over a limited range of temperature and has a defined breeding season that varies according to geographic location (Patel & Crisp, 1960a; Macho, 2006; Macho et al., 2010). In the present study, the reproductive parameters of *P. perforatus* on the NW coast of Portugal, the centre of the natural distribution of *P. perforatus*, were compared to those at the northern limit of the species distribution, as well as to those of other cirripedes species of the NE Atlantic coast. It is predicted that the higher temperatures at the lower latitudes of the NW coast of Portugal determine the reproductive parameters of *P. perforatus* and the abundance of adults on the rocky shores.

Considering previous work on the effects of temperature on breeding in marine organisms, this study aims to test the hypothesis that the breeding season of *P. perforatus* on the NW Atlantic coast of Portugal begins earlier and is longer than that at the northern distribution limit of this species; and that the species has higher fecundity in terms of number of broods per individual per breeding season.

Materials and methods

Adult *Perforatus perforatus* were collected fortnightly at Praia da Memória beach (41°13′47.17″ N; 8°43′21.33″W), Porto, Portugal during low spring tides over 23 months, from August 2013 to June 2015. In total, 1839 adult barnacles were collected and sample size was 60–70 individuals when possible. The location was selected due to the abundance of *P. perforatus,* the morphology of the beach, easy access and proximity to a reference area with low levels of contamination (Cunha et al., 2005). At Praia da Memória beach, there is approximately 1 km of rocky shorefront and the intertidal zone is quite wide at low tide. Barnacles were collected by hand using a small hammer and a chisel from the low intertidal zone shady rocks, in crevices and beneath overhangs. Juvenile barnacles were excluded from the study by selecting individuals whose apical diameter along the rostro-carinal axis was >5 mm (Iwaki & Hattori, 1987) and 10 mm for the basal diameter (Herbert et al., 2003). During January and February, samples were only collected once a month due to the severe weather and sea conditions.

Mean monthly seawater temperatures were provided by the Hydrographic Institute of the Portuguese Navy (Portugal; http://www.hidrografico.pt). Sea temperatures were obtained from an ondograph buoy situated approximately 10 km north and 20 km west (41°19′00″N; 8°59′00″N) of the sampling point (Praia da Memória).

The examination and isolation of mature ovigerous lamellae was performed immediately upon arrival at the laboratory. The presence/absence of lamellae in all individuals was recorded to determine the fecundity index (F_i; %), i.e., the average percentage of the population with embryos over the year, and the relationship between this parameter and temperature. The number of broods (N_B) released per individual per year was determined by applying the formula (Burrows et al., 1992):

$$N_B = L_B / L_E$$

L_B = number of days that an individual spends carrying embryos, given as $L_B = \Sigma\, P_B \times \Delta t$), where P_B is the average proportion of the population carrying embryos during the sampling interval (F_i/100), and Δt is the time interval between consecutive samplings.

L_E = the number of days needed for complete embryo development from oviposition to larval release. LE is 6 days and at 14.5°C and 4 days at 20°C.

The time that individuals spend carrying eggs was corrected for the mean seawater temperature during each sampling interval, assuming a linear relationship between temperature and the time spent carrying broods, based on the values provided by Patel & Crisp (1960a) for this species at 14.5 and 20°C.

The length of the breeding season was defined by counting the number of months in which ovisacs were present in the pallial cavity of adult females, and the optimum breeding temperature corresponded to the highest observed fecundity indices. It was not possible to accurately determine the minimum and maximum critical breeding temperatures since individuals were always observed carrying ovisacs at the minimum and maximum temperatures recorded during the 2 years of sampling. Therefore, we could only determine that the true values of those two temperatures are below and above the minimum and maximum recorded temperatures, respectively.

Results

A total of 1839 adult barnacles were collected and examined, and the mean sample size was 57.5 ± 25.6 ind/sampling (mean ± standard deviation of the mean). The target sample size was 60–70 individuals when possible, and at least 19 individuals were sampled when the weather conditions were not favourable (Fig. 1).

The fecundity indices calculated for adult *P. perforatus* collected between August 2013 and June 2015 are presented in Fig. 1. The presence of ovigerous lamellae was first observed in February, and the maximum fecundity was observed in late April of 2014, when 52% of the individuals presented mature ovigerous lamellae in the pallial cavity. Lamellae are pale yellow and turn to dark orange in the final developmental stage, as they become larger and stiffer. All specimens presented 2 lamellae bilaterally, and mature individuals with lamellae were found from 5 mm apical diameter. During autumn and winter, lamellae were scarce or absent, corresponding to a fecundity index below 20% from September to February or actually nil in various samples (Fig. 1).

The fecundity indices were correlated with the seawater temperature during the month of sampling, as well as 1, 2 and 3 months earlier. A second-order polynomial function was fitted to data, and the best coefficient of determination ($R^2 = 0.39$) was obtained when the fecundity data were modelled as a function of seawater temperature 2 months before sampling date (Fig. 2; Table 1). Accordingly, the highest fecundity index was observed when the mean seawater temperature was 14.9°C. The minimum critical breeding seawater temperature was below 12.6°C, and the maximum was above 19.7°C, the lowest and highest temperatures registered during the sampling period, respectively (Fig. 1).

The number of broods per individual per year (N_B) for *P. perforatus* was calculated to be 9.18 based on the P_B determined for each sampling interval (the values in Fig. 1 transformed into proportions) and the duration of the interval between samplings (days).

Discussion

The breeding season of *P. perforatus* on the NW Portuguese coast starts in February and ends in November. Previous studies have determined that this species breeds during the summer months in England, from the middle of June to August (Norris & Crisp, 1953; Patel & Crisp, 1960a, b) and, more recently, from May to September (Herbert et al., 2003). In NW

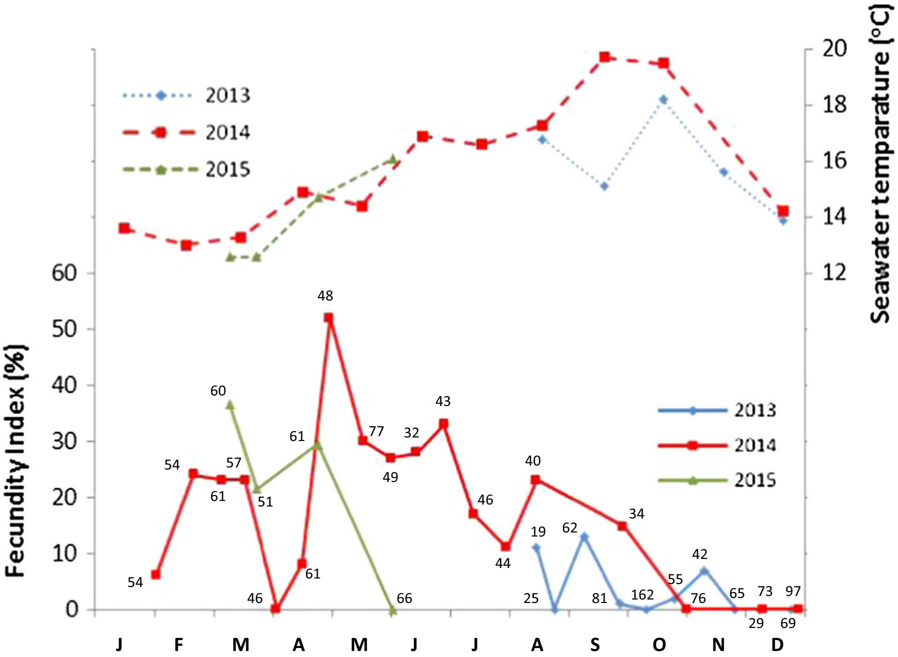

Fig. 1 *Perforatus perforatus* fecundity index (*below*) and monthly mean seawater temperature (*above*) throughout the year. The fecundity index was calculated as the percentage of individuals presenting ovigerous lamellae on the pallial cavity and determined over 23 months, from August 2013 to June 2015. The small numbers near the fecundity curves indicate sample size

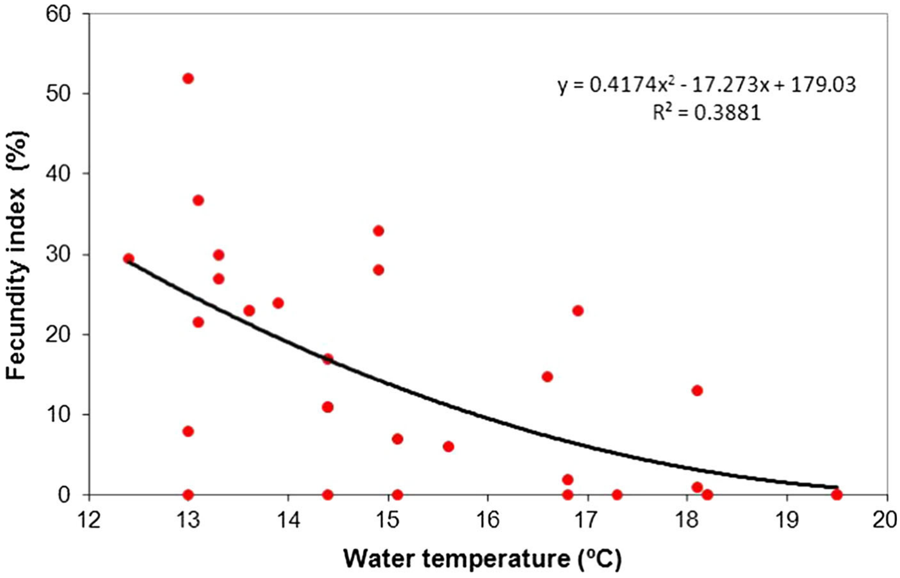

Fig. 2 A second-order polynomial regression model was used to describe fecundity ($n = 32$) as a function of the water temperature 2 months prior to the fecundity assessment. The coefficient of determination (R^2) of the model was 0.388

Spain breeding occurs from March to November (Macho, 2006; Macho et al., 2010) and in April in the Mediterranean, becoming less frequent later in the season (Lochhead, 1936) (Table 2). In summary, the breeding season begins earlier in Portugal (in late winter) followed by Spain and Italy (in spring) and then only in late spring and summer further north, i.e., South Wales and the English Channel, which indicates a strong relationship between temperature and the beginning of the breeding period. This corresponds to

Table 1 Parameters of the second-order model that correlates fecundity (F) to seawater temperature (T) in the month (M) when fecundity was determined, 1 month before (1 M), 2 months before (2 M) and 3 months before (3 M)

Fecundity versus seawater temperature	Model	R^2
M	$F = 0.2249\ T^2 - 8.8914\ T + 97.039$	0.06
1 M	$F = 0.2232\ T^2 - 10.801\ T + 126.99$	0.34
2 M	$F = 0.4174\ T^2 - 17.273\ T + 179.03$	0.39
3 M	$F = 0.3498\ T^2 - 15.045\ T + 160.32$	0.32

$N = 31$

the prediction of Orton (Orton, 1920) that in the northern hemisphere, reproduction occurs progressively later toward the species northern edge of its geographic range.

In addition to the higher air and water temperatures observed further south, food availability is a factor that may also explain the earlier occurrence of the breeding season in NW Portugal by nearly 4 months relatively to South Wales and the English Channel (Table 2). Along the W coast of Portugal, the Canary/Iberian upwelling occurs from March to October (Wooster et al., 1976; Fiúza, 1983) and is responsible for the high productivity in the area at that time. Towards the end of the 20th century, the onset of the upwelling season has occurred progressively earlier in Portugal (Lemos & Pires, 2004), nearly corresponding to the beginning of the *P. perforatus* breeding season in February. In the English Channel, two major blooms are identified. The first occur from mid-April to mid-May, and the second, of slightly lower maximum chlorophyll concentration but longer duration, from early July to late September (Southward et al., 2005; Ward et al., 2011). The major role played by effective feeding on breeding success was confirmed in starved *P. perforatus* and *C. stellatus* (Patel and Crisp, 1960a). Also, in another barnacle species, *Amphibalanus* (as *Balanus*) *amphitrite,* the breeding potential at any given temperature is known to be regulated by food concentration (Desai et al., 2006).

On the NW Portuguese coast, the fecundity index peaks appear in April and May (corresponding to a seawater temperature of 14.9°C), 2 months after the lowest temperatures of the year (12.5°C in February). The time required from oocyte proliferation to the first brood has not been determined experimentally in *P. perforatus*. However, according to our data, it seems to be approximately 2 months of development, since the fecundity index is better correlated with seawater temperature 2 months before each sample was collected than with the temperature at the sampling time (Fig. 2). In contrast, Patel & Crisp (1960a) determined that, in most cases, *P. perforatus* is able to breed 2–3 weeks after being kept at temperatures above the minimum critical temperature for breeding, which is less time than inferred from our data. The minimum critical breeding temperatures of 15–16°C considered by Patel & Crisp (1960a), at which they performed their laboratory experiments, may explain the shorter duration of ovary development than observed in the field in NW Portugal, where the minimum critical breeding temperature appeared to be less than 12.6°C (Fig. 1).

Additionally, the minimum critical breeding temperature (15–16°C) determined by Patel & Crisp (1960a) in the laboratory corresponds to the optimum breeding temperature determined through field sampling in NW Portugal in this study (14.9°C). These differences might be due to the experimental context (laboratory vs field) and other factors associated with the life cycle of the species besides temperature. Although temperature has been invoked as the most important factor determining the onset of reproduction, breeding period length and breeding success (Orton, 1920), and other environmental factors, such as food availability (Olive, 1981), photoperiod (Garwood & Olive, 1982; Clark, 1988), hydrodynamics or gamete growth rates (Clark, 1988) have been recognised as equally important and can also modulate the reproductive response to temperature in invertebrates. Temperature might regulate the embryonic development directly, but the time of fecundity is more likely connected to food availability rather than temperature per se, influencing the start of the breading season and gamete production (Patel & Crisp, 1960a). Food

Table 2 Reproductive parameters of the most abundant cirripedes present at the SE Atlantic rocky shores of Portugal, NW Spain, South England and south Wales

Species	Location	Breeding season	Optimum temperature for breeding	Lowest critical breeding temperature	Maximum critical breeding temperature	Broods per year	Embryos duration (days)	Reference
Perforatus perforatus	South Wales and English Channel	June–Aug (3)	22–23°C	15–16°C	30°C	2.3 (14.5°C) 3.5 (20°C)	6 (14°C) 4 (20°C)	Patel & (1960a , b) Norris & Crisp (1953)
	Ria de Arousa NW Spain	Mar–Nov (9)						Macho (2006), Macho et al. (2010)
	NW Portugal	Feb–Nov (10)				9.8		Present publication
	Naples Italy	Apr-						Lochhead (1936)
Chthamalus sp	South Wales and English Channel	May–Sep (5)	24–25°C	15–16°C	32°C		21 (15°C)	Crisp (1950); Patel & Crisp (1960a)
	South Ireland	Aug–Feb (7)						O'Riordan et al. (2004)
	Plymouth	May–Sep (5)				1–4.4	22.8 (15°C)	Burrows et al. (1992)
	Ria de Arousa and Oviedo, NW Spain	Mar–Nov (9)						Macho et al. (2010)
	SW Portugal	Apr–Dec (9)						O'Riordan et al. (2004)
	W Mediterranean	Feb–Apr (3)						Crisp et al. (1981)
	NE Italy	May–Dec (8)						
Pollicipes pollicipes	Ria de Arousa NW Spain	May–Nov						Macho et al. (2010)
	SW Portugal	April–Oct				1-4		Cruz & Araújo (1999), Cruz (2000)
Amphibalanus Amphitrite	South Wales and English Channel	–	22–32°C	15°C	>31°C			Patel & Crisp (1960a), (1963); Anil (1991)
Austrominius modestus	South Wales and English Channel	Throughout the year	22–25°C	8–9°C	>30°C			Patel & Crisp (1960a) Crisp & Davies (1955)
	Ria de Arousa NW Spain	Throughout the year				18–22		Macho (2006), Macho et al. (2010)

availability may justify the lag of time of about 2 months observed between the rise of temperature and fecundity, as discussed above.

The minimum and maximum critical temperatures for breeding in this species, as well as the duration of ovary development from ovule proliferation to first brood, need to be further investigated and specifically targeted in future studies of *P. perforatus,* since there are significant differences between the values previously determined in the laboratory (Patel & Crisp, 1960a) and the values determined from the field in the present study.

The duration of embryonic development in *P. perforatus* was 6 days at 14.5°C and 4 days at 20°C in the English Channel (Herbert et al., 2003). These short periods of time allow for multiple broods during the breeding season. The number of broods estimated from two different locations in the southern UK at those two temperatures was 2.3 and 3.5 broods per individual per year, respectively (Herbert et al., 2003). In the present study in Portugal, the estimated number of broods was 9.2 per year, a consequence of the mean temperatures being above the minimum critical breeding temperature for a longer time, being 2.5–4 times higher than in the southern UK.

The higher number of broods and fecundity indices observed in NW Portugal should be positively related with the abundance of the species on the shores, if the only parameter determining recruitment was egg abundance. However, the analysis of *P. perforatus* abundance data from surveys on the W coast of Portugal (Santos, 1994, 2000) and the English Channel (Crisp & Southward, 1958) did not indicate a higher abundance of this barnacle in Portugal as would be expected from the fecundity parameters. On the contrary, none of the 35 sampling sites in Portugal, analysed from 1992 to 1999, had an abundance of *P. perforatus* greater than 0.01 ind/cm^2, while many of the sites in southern England reached values well above that. Moreover, despite these low abundance values in natural substrates on rocky shores along the west coast of Portugal, this barnacle is very abundant on artificial substrates and mollusc shells in offshore aquaculture farms in southern Portugal (Fragoso & Icely, 2009). This indicates that other factors contribute to the lower abundance of natural populations of *P. perforatus* along the Portuguese coast and higher abundances on artificial substrates. Many factors other than egg abundance are involved in larval and post-settlement survival and recruitment, including food availability, larval transport, predation, competition, the availability of suitable settlement sites and settler dislodgment among others, and may act in combination. Along the coast of western Portugal the Canary/Iberian upwelling system displaces coastal surface waters offshore from March to October (Wooster et al., 1976; Fiúza, 1983), which in some cases contributes to offshore dispersal pathways and in others to near-shore retention depending on the diel vertical migration of plankton (Marta–Almeida et al., 2006; Peliz et al., 3). Morphologically the north-central Portuguese coast is primarily a low-lying coastal plain with sand dunes and beaches, from which rock outcrops occasionally emerge. Therefore the standing spawning biomass may be decreased, due to the reduced area of rocky shore that serves as habitat for adults, in contrast to southern England. The transport of larvae offshore by the upwelling currents may also explain the higher abundance of adult *P. perforatus* on offshore aquaculture structures (Fragoso & Icely, 2009). Variation in larval supply may contribute to explain the differences in the abundance of *P. perforatus* on the Portuguese coast compared to southern England (Underwood & Fairweather, 1989; Miron et al., 1995). Moreover, this area is one of the most energetic in the world with very high hydrodynamic forces (Barbosa et al., 2005) that may contribute to the low settlement and high mortality rates of recruits due to strong wave exposure. Additional factors that may influence the abundance of adult *P. perforatus* on the W Atlantic border, to be considered in future research, are the causes of mortality in larval, post-settled and juvenile individuals due to differences in shore conditions, predation, competition and fitness, among others. Another fact that needs to be considered is the subtidal abundance of the species. The habitat of this species may extend into the sublittoral zone and recruitment in Wales and South England may be also dependent on individuals from shallower or deeper waters. However, sublittoral surveys performed in the final of 20th century have failed to locate *B. perforatus* along the southeast coast of England (Herbert et al., 2003). Regarding the abundance of *P. perforatus* in subtidal zone of the Portuguese coast, at the best of our knowledge no data could be found.

Conclusions

This study indicates that the breeding season of *P. perforatus* on the NW Atlantic coast of Portugal begins earlier than at the northern distribution limit of this species, which is in accordance with Orton's (1920) rules. The time span of the breeding season is longer along the NW coast of Portugal compared to those near the distribution limit of the species. The optimal breeding temperature determined is 14.9°C, and the minimum and maximum critical breeding temperatures were found to be below 12.6°C and above 19.7°C, respectively. The longer breeding season along the NW coast of Portugal gives rise to 2.5–4 times more broods per individual per year than in South Wales and the English Channel. Therefore, the hypothesis proposed was confirmed by our observations. However, the larval cycle, settling and post-settlement of this species deserves further investigation as the higher quantity of embryos produced in NW Portugal seems to be not reflected in a higher abundance of settled adults in rocky shores.

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