

RESEARCH ARTICLE

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Yves-Marie Paulet**Reproduction of the invasive slipper limpet, *Crepidula fornicata*, in the Bay of Brest, France**Received: 7 July 2005 / Accepted: 11 October 2005 / Published online: 28 March 2006
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Abstract The reproduction of *Crepidula fornicata* was studied in the Bay of Brest in order to characterise the first step of the reproductive cycle of this invasive species. The survey was carried out from 2000 to 2003 and different parameters were measured, namely, the percentage of the different sexual stages, the straight length of the shell and the percentage of brooding females using a survey of the embryonic development and the fecundity. The juvenile frequency increases generally from mid-June or mid-August, depending on the year. In 2001 and 2003, a first peak was observed as early as May, but it was followed by a rapid disappearance of the individuals. The sex-ratio female/male increased from 0.22 to 0.46 between 2001 and 2003. The sex change between intermediates and females took place mainly in summer and was well marked in 2001 and 2003. The survey of the embryonic development in the egg capsules brooded by the females provided an annual phenology of the laying and hatching processes. The laying period extends from February to September with three to four major periods of egg-laying per year and corresponding hatching periods about 1 month later. Each female lays two to four times per year on average. The first egg-laying concerned fewer females than subsequent ones, except in 2003, and exhibited a higher fecundity. The annual mean of the number of eggs for each stage was not significantly different, thus indicating no significant mortality rate during embryonic development. For the *C. fornicata* population in the Bay of Brest, several

reproductive characteristics tend to highlight its invasive capacity: (1) a long reproductive period, (2) reproduction in a ‘multi-trials’ process equivalent to a spreading out of the risks and (3) a relatively high fecundity.

Introduction

Coastal waters are accumulating species that have been introduced across natural biogeographic boundaries of dispersal in the wake of transoceanic shipping or organism transplantation for aquaculture (Carlton 1985; Ruiz et al. 1997, 2000; Naylor et al. 2001). The rate of introductions has been increasing exponentially since the 1800s (Carlton 2001) and invasive marine species are one of the greatest threats to the world’s oceans (Sala et al. 2000). However, not all species that are introduced establish persistent populations. Only one-tenth becomes established (ten rules, Williamson and Fitter 1996) and only a fraction of these may be considered as problematic species as a result of their ecological or economical effects (Vitousek et al. 1996; Mack et al. 2000; Levin et al. 2003).

The slipper limpet, *Crepidula fornicata*, is an example of an introduced species, which has major effects on its environment. It was accidentally introduced in Europe, primarily in the UK, from the East American coast, at the end of the nineteenth century, probably associated with oyster seeding (Blanchard 1997). The slipper limpet now extends from Spain to Norway and is abundant locally (1,000 individuals m⁻²) in southern England, in The Netherlands (Nienhuis 1992) and especially in France (Blanchard 1997; Connor et al. 1997). In the Bay of Brest, the biomass of *C. fornicata*, estimated at approximately 20,000 tonnes wet weight in 1995 (Chauvaud et al. 2000) and 127,125 tonnes in 2000 (Guérin 2004), is still rising. At high densities, several ecological impacts are documented: (1) bottom silting up related to pseudo-faeces and faeces production (Barnes et al. 1973; Erhold et al. 1998; Thouzeau et al. 2003), (2)

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lowering of native species recruitment by spatial competition processes (*Pecten maximus*, *Aequipecten opercularis*; Thouzeau et al. 2000; Chauvaud et al. 2003a, b), (3) alteration of benthic community structure (Chauvaud 1998; de Montaudouin and Sauriau 1999; Thouzeau et al. 2000), (4) competition for food with other species like *Crassostrea gigas* (Orton 1927; Korringa 1951; Blanchard 1997) and (5) relative protection of the Bay of Brest's eutrophic coastal ecosystem from toxic dinoflagellate blooms (for details see Chauvaud et al. 2000; Ragueneau et al. 2002, 2005).

Invasive species characteristics most cited in the literature are from Lodge (1993): big origin area, ability to disperse, demographic aptitudes (high fecundity, asexual reproduction), competitive aptitudes, potential for adaptation (high genetic variability, phenotypic plasticity) and ecological aptitudes (generalist and/or adapted to humans). The reproductive strategies of the invasive populations are important for understanding the local maintenance of these populations. A good knowledge of the reproduction process of the invasive species is a key step in understanding the success of the installation of the species in its new environment, which can permit, in some cases, the control of the established populations (Myers et al. 2000).

After a number of investigations mainly focussed on invasion consequences and evaluation of threats to coastal ecosystems, studies are now more directed towards the underlying factors implicated in the invasive success, from genetic (Hoagland 1985; Dupont et al. 2003) to ecological through physiological elements, and numerical modelling to foresee the expansion. Among the many biological mechanisms driving the proliferation of *C. fornicata*, reproduction is clearly important, but has been, surprisingly, relatively forsaken in the last decades. Since the end of the nineteenth century, sex-change in this protandrous hermaphrodite has been investigated in native (Conklin 1897; Coe 1935, 1936, 1938a, b, 1948, 1953; Wilczynski 1955; Hoagland 1978; Collin 1995) and introduced areas (Orton 1909, 1950; Le Gall 1980). Nevertheless, reproductive phenology has only been partially investigated. Studies by Chipperfield (1951) and Walne (1956) on estuarine populations in Essex (England), Thielteges et al. (2004) in Sylt Island (Germany) and Coum (1979) in the Bay of Brest provided some basic information on *Crepidula*'s brooding period, while Deslous-Paoli (1985) and Deslous-Paoli and Héral (1986) gave some estimates of potential fecundity for the Marennes-Oléron Bay (France) population.

If the invasion process of *C. fornicata* is to be understood, precise information on the reproduction cycle is required to compare it with the general knowledge on the characteristics of the invasive species. The main objective of this study was to define precisely the different parameters characterising *C. fornicata* reproduction in the Bay of Brest. During a 4-year period (2000–2003), different parameters were measured in the Bay: the sex-ratio, the frequency of the brooding female, the number of eggs per egg-laying, the stages of these

eggs and the size of the females. Within this study, some important key factors for understanding this invasion were defined: the duration of the reproduction, the number of egg-layings per female, the mortality in the egg capsules, the relation between the female straight length and the fecundity during the whole reproduction period. The fact that this bay is a site where extensive environmental research has been and is currently undertaken should increase the chance of understanding this major invasive process.

Materials and methods

Study site

The Bay of Brest is a semi-enclosed marine ecosystem (Delmas 1981) of 180 km² located at the westernmost point of France (Fig. 1). It is connected to shelf waters (Iroise Sea) by a narrow (2 km wide) and deep (40 m) strait. The bay is a shallow basin with 50% of its surface no deeper than 5 m (average depth 8 m). Freshwater inputs are mainly (80%) due to two rivers, the Aulne (watershed of 1,852 km²) and Elorn (watershed of 402 km²). Waters are well mixed by tides; the tidal range reaches 8 m during spring tides, which represents an oscillating volume of 40% of the high tide volume. Nevertheless, most of the water evacuated during ebbing is reintroduced during flooding. The average flushing time is approximately 21 days (Delmas 1981; Delmas and Tréguer 1983). The study site, the so-called Roscanvel bank (30 m deep at high tide; Fig. 1), is characterised by mixed sediments; it was selected for its high density of *C. fornicata* and for the evidence of a new and active colonisation process (about 500 individuals m⁻²; Chauvaud 1998), which provide a unique opportunity to understand the invasive process. Moreover, this station, situated approximately in the centre of the bay, is known to be representative of the mean hydrobiological conditions occurring in the bay: it was a long-term (from the 1980s to 2000) sampling station of the Institut Universitaire Européen de la Mer (IUEM). This site is also a reference point for other species studied by the laboratory, such as *P. maximus*, which is suspected to suffer spatial and/or trophic competition from the invasive species (Chauvaud et al. 2000).

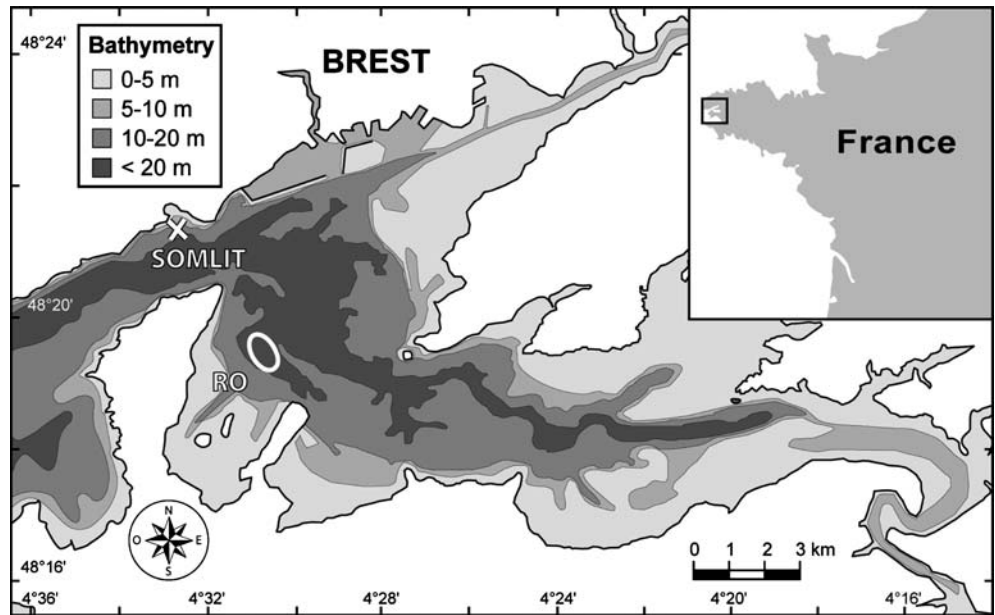
Environmental parameters

The chlorophyll *a* and the temperature were measured in surface water every week at Saint-Anne du Portzic (Service d'Observation en Milieu Littoral (SOMLIT); INSU-CNRS, IUEM, UBO).

Crepidula fornicata sampling

The slipper limpets were sampled by dredging. In 2000, all the individuals found fixed to the external shell face

Fig. 1 Map of the Bay of Brest (France) showing the sampling sites for *Crepidula fornicata* (Roscanvel bank, RO) and for the environmental parameters (SOMLIT)



of ten 3-year-old scallops (*P. maximus*) were collected. From 2001 to 2003, samples were constituted of chains fixed to shells of dead slipper limpets. The 'free' stacks were preferred after 2000, as they were considered more representative of the population because a stack attached to a support becomes free when the first slipper limpet dies. The sampling frequency was monthly during the autumnal and winter periods, and it was done two to three times per month in spring and summer. A number of stacks sufficient to contain a minimum of 30 females in total were analysed at each time, which represented 81–281 individuals for the slipper limpets fixed on the scallops and 62–172 individuals for the 'free' stacks.

Sample treatments

Sexual stage

For every stack, the sexual stage of each *C. fornicata* was noted as follows (adapted from Coum 1979):

- Juvenile: no or a very small penis; gonad not yet developed
- Male: presence of a well-developed penis
- Intermediate: presence of a penis and a vagina
- Female: only vagina

Brooding females

After egg-laying, the eggs protected by capsules are maintained and brooded in the female pallial cavity until hatching. For each female, the presence or absence of egg capsules was noted and, when present, it was

counted. Four egg capsules were picked randomly out of each brood and the eggs were counted to estimate individual fecundity. Since embryonic development was similar in all egg capsules for a given egg-laying, the stage of development of the eggs was assessed for each brooding female. Three developmental stages were assigned from the Chipperfield scale (1951): (1) morula (stages 1 and 2 of Chipperfield), (2) trochophore (stage 3 of Chipperfield) and (3) veliger (stages 4 and 5 of Chipperfield).

Biometric measurements

For each individual, the straight length (biggest antero-posterior length) of the shell was measured with a sliding calliper (± 1 mm).

Data analyses

The significance of the differences between years of the sex percentage means was tested with a non-parametric Kruskal–Wallis test (KW; Statgraphics plus, 95%). To assess the mean annual number of egg-layings per females, the area under the frequency curve of brooding females (Fig. 4) was measured using image analysis (Visilog 5.1.1 software). The differences in the number of eggs in the morula stage and in the straight length of the brooding females between the 4 years of study were tested with non-parametric KW tests (Statgraphics plus, 95%). A KW test was also undertaken between the different stages for each year to test the mortality in the egg capsules. Finally, a powercurve was made between the straight length and the number of eggs in the morula stage with an analysis of variance to test if the model was significant.

Results

Environmental parameters

The coldest surface water temperatures were recorded in January–February and varied between 8.6 and 9.9°C, while the warmest were recorded in late August and varied between 17.1 and 18.7°C, depending on the year (Fig. 2a). The temperature variations (amplitude) were almost the same during the 4 years of study, with the warmest summer in 2003 and the warmest winter in 2001. The deviation from the mean temperature values calculated in the 4-year-study period is represented in Fig. 2b. The spring and summer periods of 2000 and 2002 were colder than the mean seasons, but the autumn and winter of 2002 were warmer. Temperature deviations from the mean values varied between +1.3 and –1.2°C. The first phytoplankton bloom always occurred between late April and mid-May and chlorophyll *a* concentrations varied between 3.8 and 6.4 $\mu\text{g l}^{-1}$ (Fig. 2a). Afterwards, a succession of phytoplankton

blooms of less importance, except for the third bloom in 2002, was observed. The chlorophyll *a* biomass exhibited inter-annual and/or seasonal variations. In particular, (1) the years 2001 and 2003 exhibited a major spring bloom in contrast to 2000 and 2002 and (2) late spring and summer blooms were most pronounced in 2001 and 2002, while chlorophyll *a* biomass regularly decreased from late June in 2003.

Sexual stages distribution

Figure 3a shows variations in the juvenile frequency during the study period. In 2000, only the juveniles present on stacks were taken into account, but not those fixed directly to *P. maximus* shells, in order to avoid any bias due to different substrates. The juvenile frequency increase can be interpreted as the settlement of new recruits. The first increase occurred in May, followed by an abrupt decrease, especially in 2001 and 2003 (see arrows), and a second increase was observed from mid-June in 2001 and from mid-August in the other years. In

Fig. 2 **a** Surface-water temperature (*open diamond*) and chlorophyll *a* concentration (*black diamond*) measured at Saint-Anne du Portzic (SOMLIT) during the 4 years of study (2000–2003). **b** Deviation from the main temperature values calculated in the 4-year study period

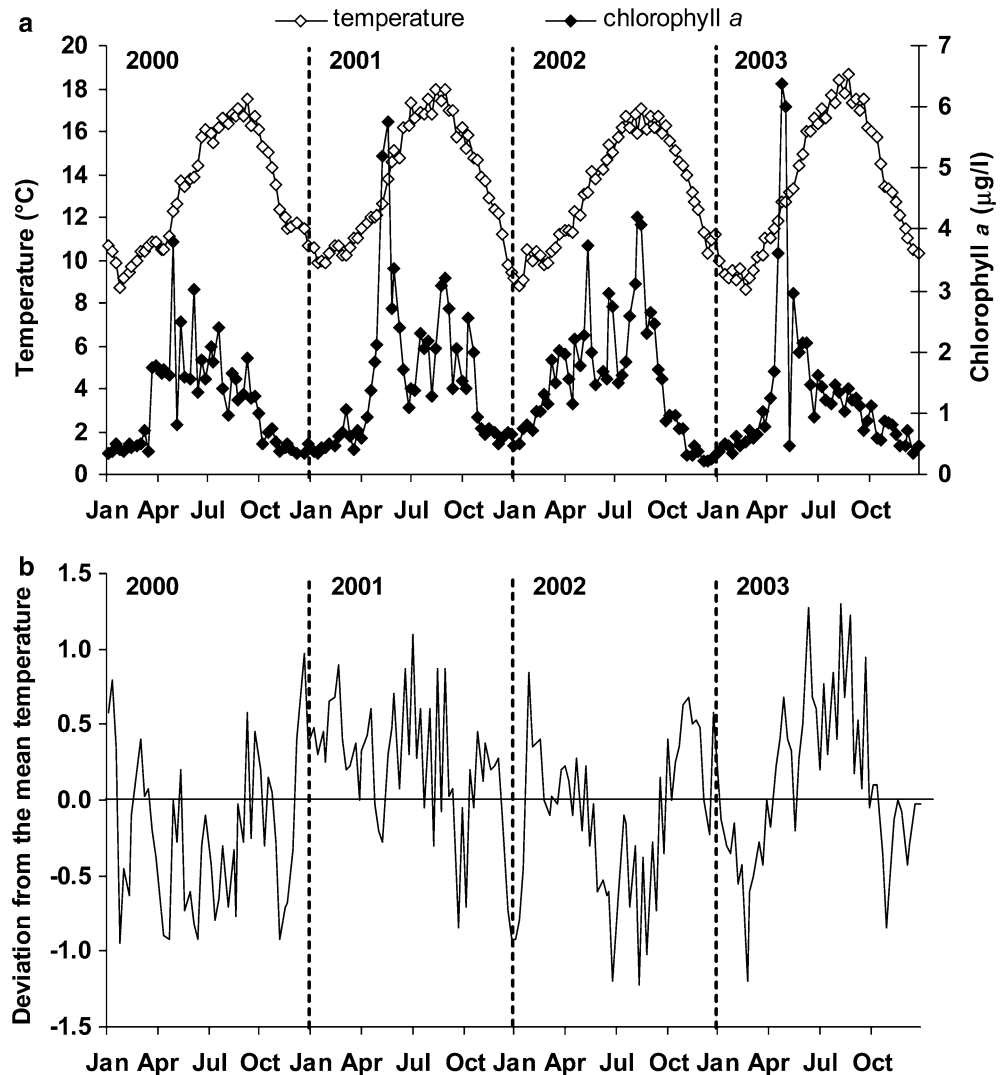
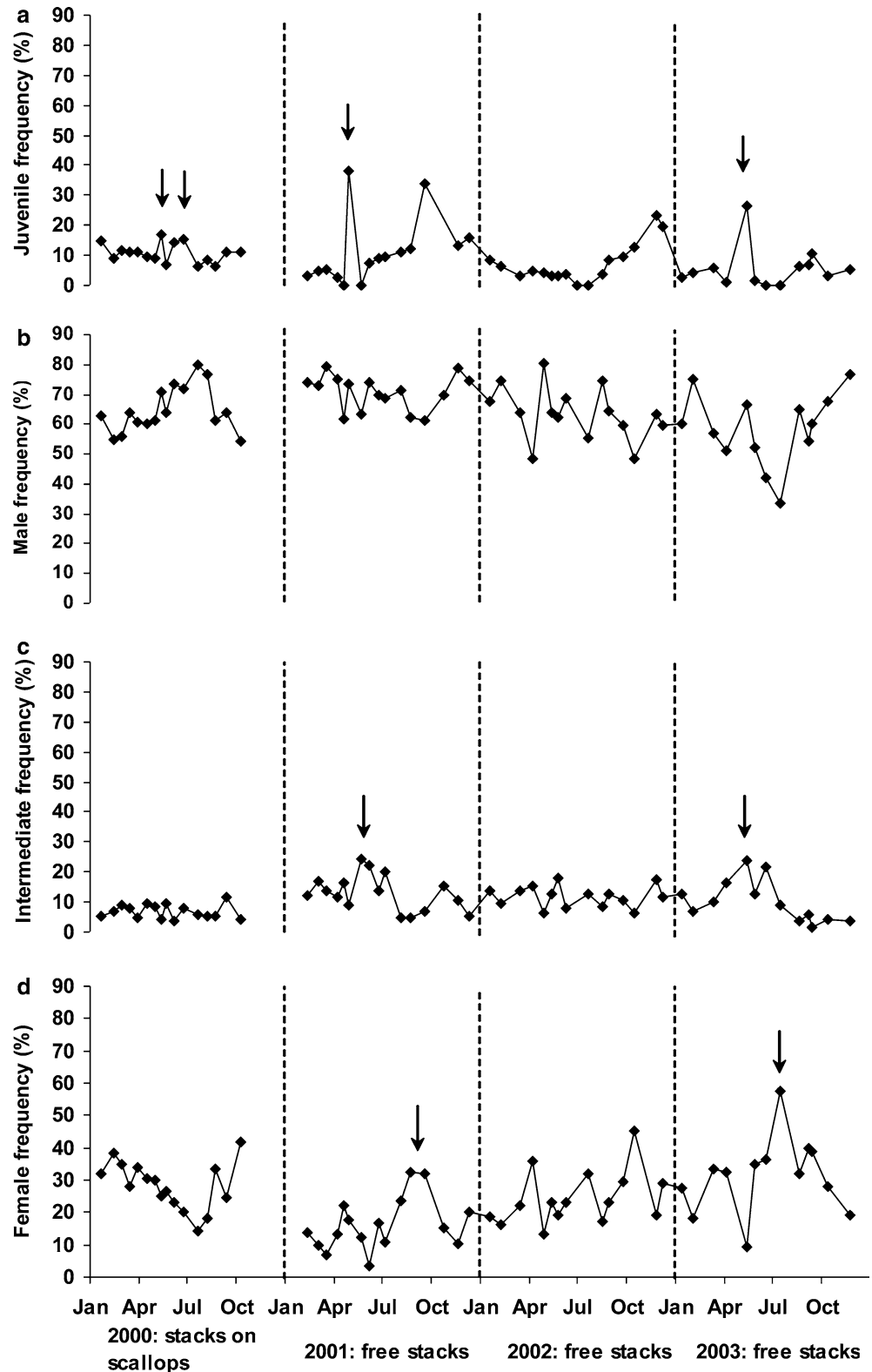


Fig. 3 Frequency of each sexual stage between 2000 and 2003: (a) juvenile frequency with *black arrows* showing particular peaks, (b) male frequency, (c) intermediate frequency and (d) female frequency. For (b–d), the frequencies were calculated without the juveniles. *Arrows* in (c) and (d) indicate the time of the sex-change between intermediate and female in 2001 and 2003

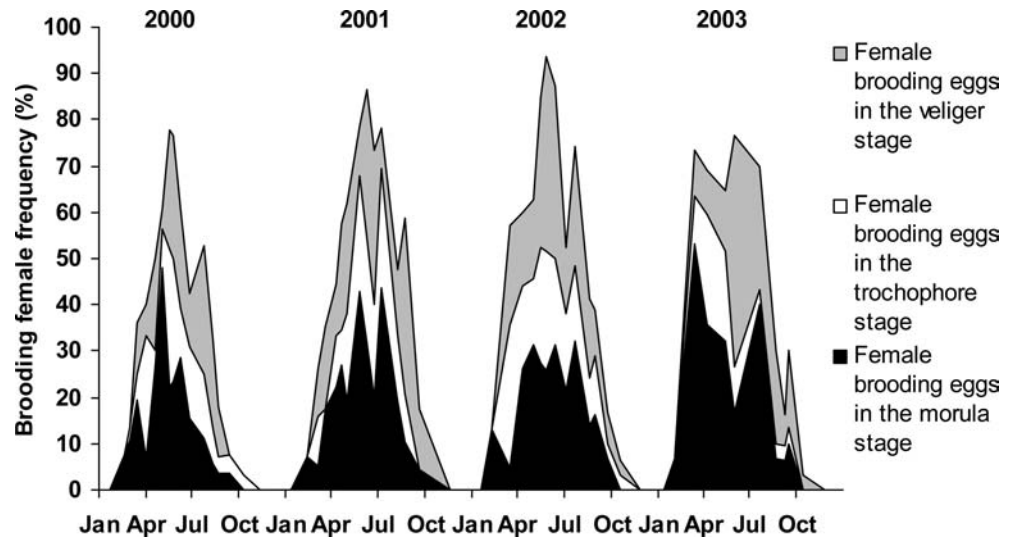


May 2002, no juvenile settlement was recorded. Except during the recruitment periods, the juvenile frequency never exceeded 10%.

Figures 3b–d show frequency variations for the different adult sexual stages after removing the juvenile

numbers from the data. Male frequency (Fig. 3b) was predominant and fluctuated between 30 and 75% (mean $65 \pm 10\%$); no seasonal trends were apparent. However, a significant decrease in the annual mean percentage of males was observed between 2001 and 2003 (2001:

Fig. 4 Frequency of each egg stage (morula, trochophore and veliger) in cumulative percentage between 2000 and 2003 in brooding females. Egg stages are modified from the Chipperfield scale (1951)



$71 \pm 6\%$, 2002: $64 \pm 9\%$, 2003: $59 \pm 12\%$; KW: $P=0.01$). Intermediate stage frequency (Fig. 3c) remained low throughout the study (mean $10 \pm 6\%$) and only two peaks were observed, in spring 2001 and 2003 (see arrows). Female frequency (Fig. 3d) fluctuated between 4 and 58% (mean $25 \pm 10\%$); apart from 2002, a seasonal oscillation can be seen, with a major increase from July to October in 2000, from June to September in 2001 and from May to July in 2003. In 2001 and 2002, a peak of intermediates was observed about 2 months before the female peak (see arrows). Moreover, a significant increase in the female annual mean percentage was found between 2001 and 2003 parallel to the decrease of the male percentage (2001: $14 \pm 7\%$, 2002: $23 \pm 8\%$, 2003: $30 \pm 12\%$; KW: $P < 0.01$). The sex-ratio female/male increased between 2001 and 2003 (2001: 0.22; 2002: 0.38; 2003: 0.46).

Brooding female and embryonic stage frequency temporal successions

The temporal succession of stages in embryonic development is presented in cumulated percentages for the 4 years of study in Fig. 4. In one brood, all the eggs are in the same stage, indicating a strong synchronicity of the reproductive process at the individual level. Each year, the period during which the females laid eggs was of similar duration. For all years, the egg-laying started in the middle of February and stopped at the end of September, when no more morula stages were noticed. Brooding females were never found in November, December or January. Irrespective of the year, the maximum brooding activity occurred in May–June, with approximately 80% of females carrying eggs. The first brooding females, observed in February, always carried eggs in the morula stage and the latest one, after September, carried eggs in the trochophore or veliger stages. By measuring the area under the curve for each year and considering that the brooding occurs for 1 month, as

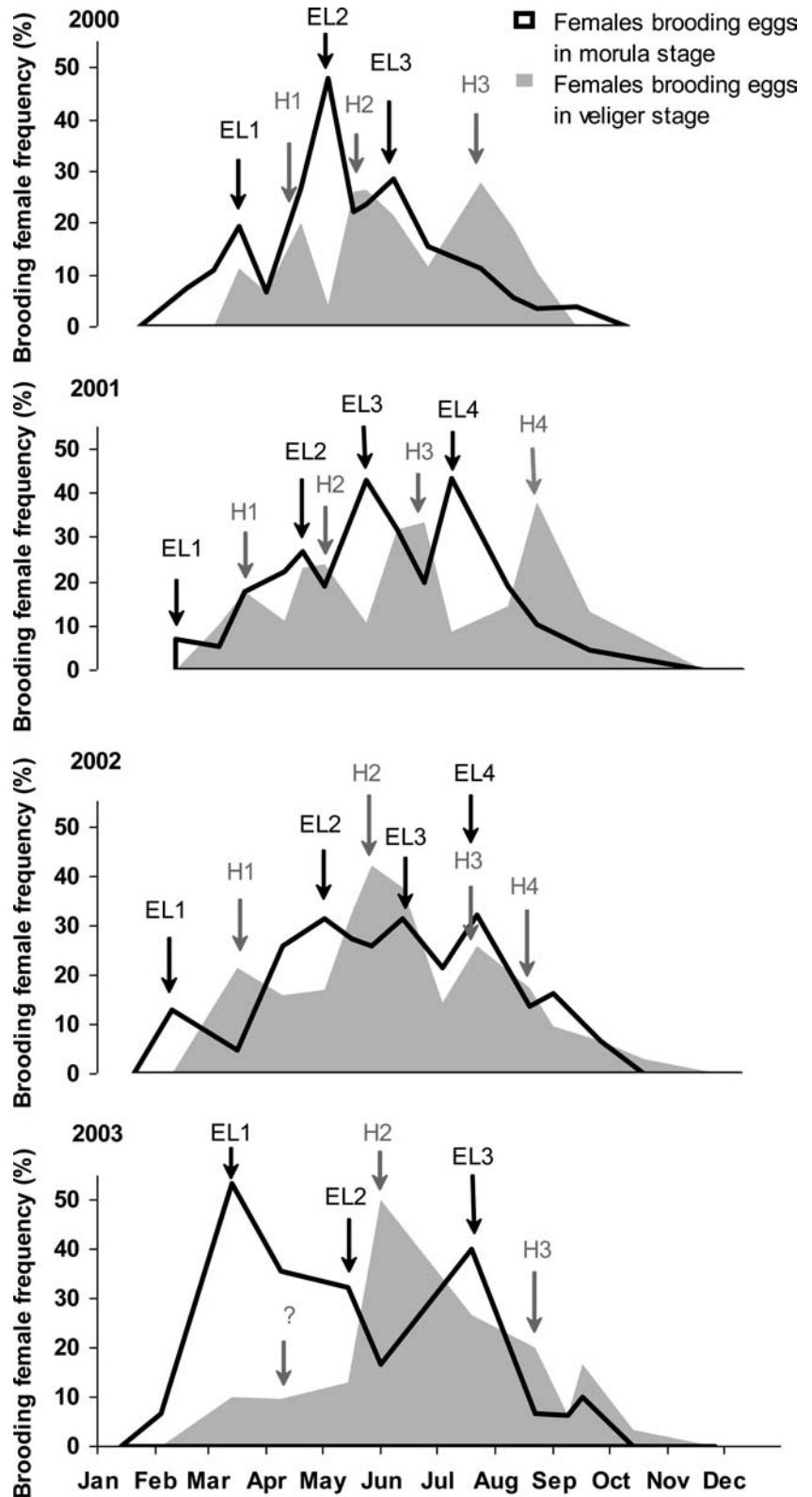
shown in Fig. 5, the mean number of times each female laid can be calculated. In 2000, each female laid on average 2.4 times, vs 3.4 times in 2001, 3.7 times in 2002 and 3.6 times in 2003.

The occurrence of the successive stages revealed several main egg-laying periods (Fig. 5). Each year exhibited between three and four periods of egg-laying (EL) and three or four hatching periods (H) about 1 month later. The first egg-laying usually involved fewer females (7–19%) than the other ones (27–48%). In 2003, observations differed from other years as the most important egg-laying was the first one in February (53% of the females). However, no peak of hatching was observed 1 month later (in Fig. 5, 2003, question mark).

Variations in the number of eggs in the morula stage are presented in Fig. 6. Each year, the number of eggs in the morula stage per brooding female was maximal at the beginning of the year; afterwards, it decreased and remained steady for the rest of the year (KW: from mid-March to mid-September 2000: $P=0.72$; from mid-March to mid-October 2001: $P=0.13$; from mid-April to end of September 2002: $P=0.29$; from mid-May to mid-September 2003: $P=0.20$), with the exception of the beginning of May 2001 and 2002 and the beginning of July 2002, where the values were significantly smaller. Considering the whole year, the mean number of embryos in the morula stage per female varied significantly (2000: $6,740 \pm 5,022$; 2001: $10,102 \pm 6,121$; 2002: $12,019 \pm 6,771$; 2003: $14,695 \pm 7,804$; KW: $P < 0.01$), as well as the mean straight length of the brooding female shells (2000: 34.6 ± 5.6 mm; 2001: 43.6 ± 6.3 mm; 2002: 45.1 ± 5.6 mm; 2003: 46.8 ± 4.3 mm; $P < 0.01$ and P without 2000 < 0.05).

Moreover, a size–fecundity relationship was pointed out by plotting the number of eggs in the morula stage against the straight length for each individual female (Fig. 7). The scatterplot shows the points dispersed in a rough triangular shape of which the upper edge corresponds to the maximum fecundity for a given size. A power type curve, established from the highest egg number values for a given size (black points), constitutes

Fig. 5 Frequency (%) of the female brooding eggs in the morula stage (black line) and in the veliger stage (grey area) for 2000–2003. The black arrows show the periods of egg-laying (EL1–EL4) and grey arrows the periods of hatching larvae (H1–H4). The question mark in 2003 indicates the lack of the first hatching corresponding to the first egg-laying



the best fit between straight length and maximum fecundity ($F = 343.08$; $P < 0.01$).

The annual mean of the number of eggs in each stage is represented in Fig. 8. A KW test was performed for

each year between the three stages of the eggs and no significant differences were observed ($P < 0.05$), indicating that no significant mortality occurred during the development of the eggs in the egg capsules.

Fig. 6 Number of eggs in the morula stage per female between 2000 and 2003

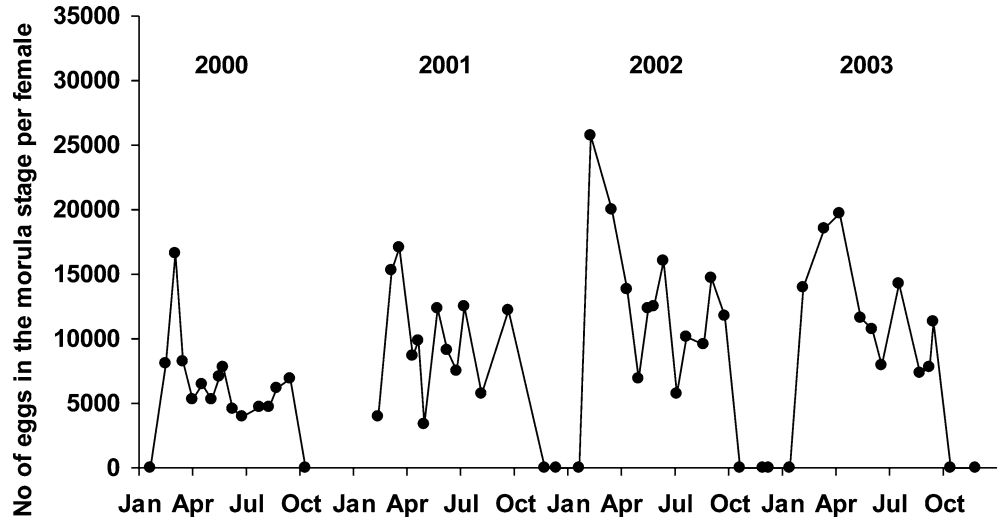
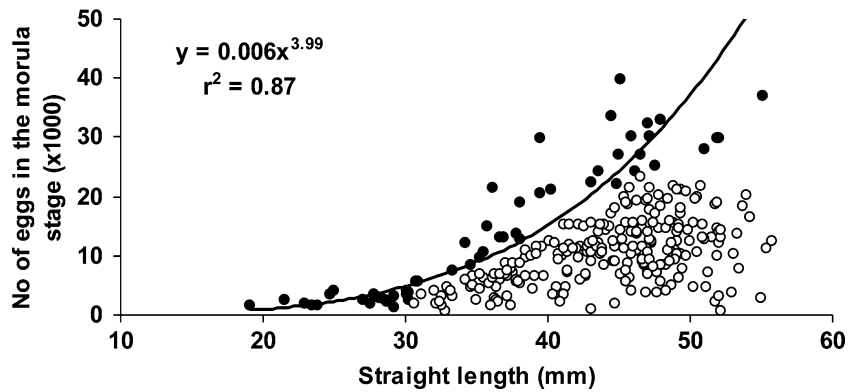


Fig. 7 Relationship between the straight length of the shell (mm) and the number of eggs in the morula stage. The *black circles* represent the maximum fecundity for a specific straight length and the curve is drawn with these points, while the *open circles* represent the relationship between these two parameters for all the females sampled



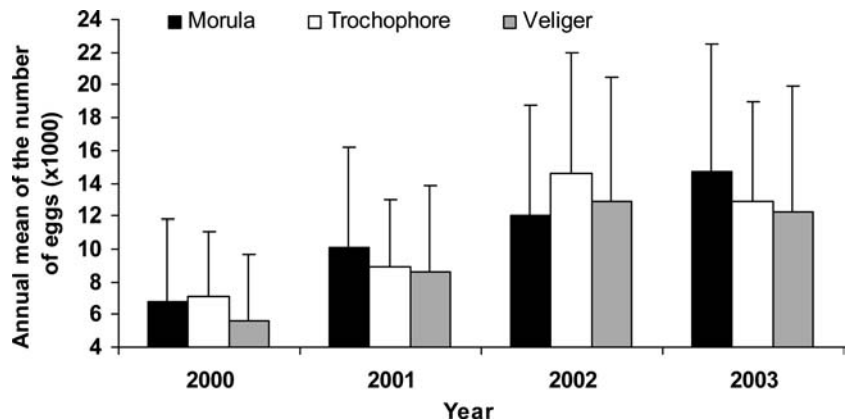
Discussion and conclusions

The set of data obtained on the reproductive biology of *C. fornicata* in the Bay of Brest is unrivalled, both due to its duration (4 years) and also to the extent of reproduction process descriptors measured. It allows a clear picture of the reproductive activity of this invasive species in the Bay of Brest.

In this bay, settlements of new recruits are observed from May to November (Fig. 3a), but the data set does

not allow the precise definition of the different recruitment periods. Deslous-Paoli (1985) showed, for a *C. fornicata* population in the Marennes-Oléron Bay (France), two periods of juvenile settlement per year, the first one in May–June and the second one in October. Coum (1979) also reported two periods of settlement for the Bay of Brest: the first one in May and the second one between mid-August and mid-September. However, Chauvaud (1998) showed five juvenile settlements on plane tiles placed near the sediment–water interface between May and October 1994 in the Bay of Brest. This

Fig. 8 Annual mean of the number of eggs in each stage (morula, trochophore and veliger) for the 4 years of study (2000–2003)



result corresponds well with the periods of hatching defined in the present study. The first arrival of juveniles in May 2001 and 2003 was immediately followed by an abrupt decrease. This could be explained by a high mortality rate or by a sampling method artefact (juvenile losses during dredging). In 2000, the lower juvenile frequency during the recruitment period could be due to the youth of the stacks. In fact, they were not more than 4-year-old because they can only move during the first year of life (Le Gall 1980) and they were fixed on 3-year-old scallops.

Succession in sexual stages showed a relatively 'noisy' signal during the 4-year period. However, between 2001 and 2003, an increase in female frequency was observed parallel to a decrease in male frequency. This could be explained by an ageing of the population even though the latter was always in expansion. The sex-ratio increased between 2001 and 2003 from 0.22 to 0.46, but it was always far from a ratio of 1:1 generally observed in animal populations. However, such a low value has been observed by Wilczynski (1955) in a *C. fornicata* population from the American north-east coast. Moreover, sex-ratio disequilibrium is frequently observed in successive hermaphroditic species (Charnov 1982). Female frequency displays a clear annual oscillation (Fig. 3d), with a maximum observed between July and October. It can be hypothesised that this peak in female occurrence corresponds to a period of intense sexual transformation from male to female. Thus, the individuals changing sex could still participate in reproduction as a female in the same year. This is supported by the peak of intermediates observed in 2001 and 2003 (Fig. 3c) before the females increased. The very low proportion of individuals in the intermediate stage throughout the year expresses the fugacity of this stage and thus the rapidity of the sex change process.

The monitoring of the presence and the developmental stages of eggs gives a good description of the annual phenology of egg-laying and hatching processes (Figs. 4, 5). The laying period starts in mid-February and ends in late September; the percentage of brooding females peaks in May–June every year and is independent of the temperature and chlorophyll *a* concentration. The survey of the developmental stages of the egg (Fig. 5) highlighted three to four major egg-laying events with their corresponding hatchings, depending on the year. The year 2003 differed from the others as the percentage of females participating in the first annual egg-laying was particularly high (about 50% vs less than 20% for the other years). Moreover, hatching corresponding to this intense egg-laying phenomenon was not identified. Two hypotheses can be suggested to account for this disappearance: (1) a slowing-down in the embryonic development (Hoagland 1979), leading to a misinterpretation of the second hatching period which, in fact, would be the first one, or (2) an exceptional mortality rate resulting from a massive egg capsules emission before full-term. This second hypothesis can be supported by the presence of a major phytoplankton

bloom ($6.39 \mu\text{g}$ chlorophyll *a* l^{-1} , Fig. 2) at the end of April 2003. The sedimentation and degradation of this bloom could have caused oxygen depletion (Degobbis 1989), resulting in the release of the egg capsules by the females (Hoagland 1979). One may note that *P. maximus* living at the same site were affected (growth stop) by a bloom of the same species in 1998 (Lorrain 2002). Even if three to four major periods of reproduction were noted, females carrying eggs in the morula stage were observed during the entire period of egg-laying, indicating that the reproductive process was not strictly synchronous. Moreover, no synchronisation was observed inside the stacks. However, there were no brooding female observed during late fall and early winter (November–January), thus indicating a synchronisation for the end of egg-laying and a period of sexual quiescence in winter. Each egg brooding lasted approximately 1 month, as shown by the time spent between a given egg-laying and the corresponding hatching period (Fig. 5, black and grey arrows). This brooding time agrees with the few bibliographic data available (20–30 days; Conklin 1897; Chipperfield 1951). The number of egg-layings per female per year varied during the study period. The smaller value in 2000 could be explained by the youth of the females (individuals fixed on 3-year-old scallops), while increasing values with time corresponded to increasing mean size of the females.

The seasonal variations in the number of eggs per female in the morula stage showed the same trends every year (Fig. 6). The first egg-laying always produced the highest egg numbers. The significant variations observed between years for the number of eggs in the morula stage were correlated with a significant increase of the straight length of the female shell. Our results suggest the existence of a power type relationship between shell size and fecundity (Fig. 7). However, the existence of several spawning events of different intensities per female and per year tempers this pattern. Nevertheless, a relationship linking maximum potential fecundity to size is shown when only the maximum fecundity value relative to a given size class is taken into account. The annual mean of the number of eggs in each stage does not show any significant variations from one stage to the other for a given year (Fig. 8). Such a result highlights the absence of a significant mortality rate during embryonic development inside the egg capsules.

The initial aim of this work on *C. fornicata* was to characterise the reproductive cycle of this invasive species in a European bay where the species proliferation is currently active. The results from the Bay of Brest can be compared to the data available in the literature for the other sites in Europe (Table 1). The duration of the reproductive period is similar along the entire French coast (Lubet and Le Gall 1972; Coum 1979; Deslous-Paoli 1985; Deslous-Paoli and Héral 1986) and also in The Netherlands (Oosterschelde, unpublished data). However, in England (Essex estuaries; Chipperfield 1951; Walne 1956) and in the North of Germany (Sylt Island; Thielges et al. 2004), the reproduction period is

Table 1 Characteristics of the reproductive period of *Crepidula fornicata* in different coastal sites in native and introduced areas

Site	Egg-laying period	Number of eggs per female	Method	Authors
New England coast (USA)	Early summer until about 15 August	13,200	Qualitative observations	Conklin (1897)
Sylt island (Germany)	April–September	No data	Monthly to bi-monthly sampling presence/absence of egg capsules	Werner (1948); Thielteges et al. (2004)
River Blackwater (England)	Early spring to September	2 egg-laying per female	Weekly sampling presence/absence of egg capsules and deduce the number of egg-laying	Chipperfield (1951)
River Crouch (England)	March–September	No data	Monthly sampling presence/absence of egg capsules	Walne (1956)
Banc de Quihot (France)	March–October	No data	Monthly sampling presence/absence of egg capsules	Lubet and Le Gall (1972)
Bay of Brest (France)	March–August	4,600–12,000 (in July)	Sampling every 2 months presence/absence of egg capsules and egg stages	Coum (1979)
Bay of Brest (France)	Mid-February to September	10,102–14,695 (annual mean, February–September); 3–4 egg-laying per female	1–3 samples per month presence/absence of egg capsules, egg stages	This study
Bay of Marennes-Oléron (France)	End of February to October	11,247 (in June)	Monthly sampling presence/absence of egg capsules	Deslous-Paoli (1985); Deslous Paoli and Héral (1986)

reduced to late spring and summer and it begins when the temperature reaches 10°C (Chipperfield 1951), which was also the case in this study. The major factor that seems to limit the duration of the reproduction period is temperature. In England and in northern Germany, very cold winters with ice formation can appear, generating high mortality rates (Thielteges et al. 2004). Reduced reproduction periods in England leads to two egg-layings per female (Chipperfield 1951), vs up to four in the Bay of Brest. The comparison of potential fecundity between the different European banks is difficult since the literature data concern only the major period of egg-laying; during this period, the number of eggs per female is not very different between the sites (Table 1). In the native area, the reproduction period is short (early summer to mid-August; Conklin 1897), even though the temperature may reach 10°C as early as April in Chesapeake Bay (Cronin et al. 2003).

The underlying concept of this study is that certain species more than others exhibit life history traits, which make them potential candidates for invasion. Reproductive modalities are clearly important for understanding the installation success (Myers et al. 2000). For *C. fornicata*, several reproductive characteristics shown in this study tend to highlight its invasive capacity: (1) the annual reproductive period is particularly long (February–September) and females brooding eggs in the morula stage are observed all along this period, indicating a relative independence from immediate environmental conditions such as temperature and chlorophyll *a*; (2) at the individual level, and moreover at the population level, annual reproduction in *C. fornicata* is a ‘multi-trial’ process (two to four egg-layings per female), leading to a sort of spreading out of the risks of failure; and (3) *C. fornicata* shows a relatively high fecundity (10,000–15,000 eggs per brood) compared to other *Crepidula* species: *Crepidula dilatata*: between 3,000 and 10,000 eggs per brood (Chaparro and Paschke 1990); *Crepidula norrisiarum*: about 1,000 eggs per brood (MacGinitie and MacGinitie 1964); *Crepidula philippina*: between 5,500 and 11,000 eggs per brood (Gallardo 1996). These three traits, particularly the first two, are very important for the success of the installation of an introduced species. Some authors like Paulet et al. (1988) working on two populations of *P. maximus* and Newell et al. (1982) working on different populations of *Mytilus edulis* showed the adaptive significance of peaked or extended spawning periods for mollusc species with planktotrophic larvae. They proposed that the extended spawning period could be an adaptation to an unpredictable environment. This ‘spreading out of the risks’ would tend to diminish the probability of weak recruitments since the egg-layings are numerous during the course of the year. Hence, it is likely that at least one of the egg-layings will ‘match’ the environmental conditions and will allow recruitment (see the match/mismatch theory of Cushing 1982). Moreover, *C. fornicata* with an internal fertilisation does not need

a peaked spawning event to increase the probability of gametes fecundation, contrary to the two species cited before, and the brood of the eggs permits a limitation of the mortality. Another biological trait of *C. fornicata* that probably accounts for its invasive success is its 'colonial' way of life with individuals living in stacks composed of adults of the two sexes. In fact, a stack is a reproductive unit that can be considered 'self-sufficient'. Coupling this characteristic with the existence of internal fertilisation, the introduction of one stack in a place devoid of this species might be sufficient to begin an installation process. Recent works, using molecular probes, have demonstrated the reproductive 'self-sufficient' character of a stack (Gaffney and McGee 1992). In the Bay of Brest, Dupont (2004), using genetic probes for paternity tests, has shown that more than 90% of female fertilisations are due to the males present in the stack. This reproduction strategy can be compared to the self-fertilisation of plant species, if a stack is considered as a reproduction unit. The self-fertilisation is considered as a characteristic promoting the invasion (Baker 1965; Brown and Burdon 1987). Moreover, this kind of reproduction unit promotes genetic mixing by the participation of several fathers in reproduction and spermatic storage (Whittier and Limpus 1996). The genetic mixing is also obtained by the settlement of juveniles in the stack originating from the dispersive planktonic larval phase.

Modelling the invasive process requires a precise description of the reproduction cycle in the bay. Even though this study does not provide direct data on the slipper limpet's recruitment, the data on the number of egg-layings per female and the duration of the reproduction period approach this end. The next step is to understand the environmental parameters that may result in recruitment success or failure. All reproductive traits constitute necessary or promoting conditions, but under no circumstances they are solely sufficient for invasions. Colonisation success is the result of the realisation of the entire life cycle of a species, from adult to adult, in an 'open ecosystem' predisposed to receive it. In *C. fornicata*, there is still a lot of work needed to understand the reasons behind its success story in Europe. Concerning its biological potential, some future research should focus on larval life in the field (environmental parameters influence the mortality of the larvae), notably dispersion, nutrition and settlement cues, an aspect poorly documented for this species.

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