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Research Article

Is apparent low productivity of the invasive marine mollusc *Crepidula fornicata* Linnaeus, 1758 related to biased age determination?

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Abstract

The slipper limpet *Crepidula fornicata* Linnaeus, 1758 is a major exotic invader of East North Atlantic coasts. Individuals live on top of each other and form stacks with the youngest on the top. Earlier studies reported that one individual typically settles per year. If true, it is a simplified means to provide a "shell length-age" relationship for population dynamics studies, especially Production/Biomass ratio (P/B) assessment. However, estimated P/B ranges between 0.15 and 0.45 yr⁻1 seem low compared to those of closely-related marine invertebrates and considering the invasiveness of *C. fornicata* in coastal habitats. In this study, we placed artificial substrates ("tiles") for one year in the middle of a *C. fornicata* colony and measured settlement. We sometimes observed more than one individual settling per stack in a year: 4% of stacks were composed by 3 individuals, 27% by 2 individuals and 69% were single specimen. On this basis, we formulated a model to better link the position of each *C. fornicata* within a stack to its age. In addition, the *C. fornicata* population was annually sampled for 5 years. Then, population dynamics parameters, density at recruitment, mortality rate, growth performance, production and P/B were estimated. We compared two cases: (i) individual age was defined by its position in stacks; (ii) individual age was corrected by the model. Recalculation moderately increased growth performance expectation (+2 to 8% per year) but greatly enhanced production and P/B (ca. 1.2 to 2.6-fold per year). Recalculated P/B values ranged from 0.55 to 0.72 yr⁻¹. While still low, they were more consistent with published values for similar large marine invertebrates, in particular for invasive species.

Key words: Mollusc, population dynamics, production, non-indigenous species

Introduction

The slipper limpet *Crepidula fornicata* Linnaeus, 1758 is a filter-feeding gastropod mollusc and is one of the most invasive animal species along European coasts (Blanchard 2009; Guérin 2004; Stiger-Pouvreau and Thouzeau 2015). This ecosystem engineer can strongly alter its habitat by modifying the hydro-dynamics at the sediment/water interface (Moulin et al. 2007), changing biogeochemical fluxes (Martin et al. 2006; Ragueneau et al. 2002), and increasing biodeposition (Deslous-Paoli et al. 1987; Ehrhold et al. 1998; Ragueneau et al. 2005). Consequently, associated community structure and diversity are significantly altered (Chauvaud 1998; de Montaudouin et al. 1999; de Montaudouin and Sauriau 1999; Guérin 2004; de

Montaudouin et al. 2017). Therefore, the study of *C. fornicata* population dynamics is of great ecological interest and in particular the estimation of its Production/Biomass ratio (P/B), which is often considered as a good indicator of population vitality and energetic flow in an ecosystem (Brey 1990). Indeed, P/B typically estimates the percentage of biomass that is renewed annually.

Calculation of the production (P) of a population requires distinguishing between cohorts (typically age classes) and monitoring their growth and mortality. One of the major difficulties is to identify distinct cohorts within a population. Indeed, the relatively long reproduction period of *C. fornicata* (Bohn et al. 2012; Richard et al. 2006), its high individual growth rate (de Montaudouin et al. 2001;

Deslous-Paoli 1985; Wall et al. 2013), and its long lifespan make cohort analysis by shell-length histograms almost impossible (Coum 1979), except in the early post-recruitment period when the peak of juveniles can be monitored for few months (Guérin 2004). Thus, the age determination for *C. fornicata* usually is not performed by shell-length histogram analysis but by one of two alternative methods. The first method is based on shell rings, which is time-consuming, complicated (due to presence of false annuli), and difficult to implement at large temporal and spatial scales (Coum 1979; Deslous-Paoli 1985). However, it is a precise method once one accounts for the "false rings" (Garcia 1993). The second method takes advantage of the peculiar fact that *C. fornicate* forms stacks where up to 12 individuals are piled up (Coum 1979) (Figure 1). This method was proposed by Deslous-Paoli (1985), who suggested that in average one individual per year settled in a *C. fornicata* stack. Thus, the position of an individual in a stack could provide its age. He obtained similar results when comparing Von Bertalanffy growth function parameters assessed with these two methods, and concluded that his hypothesis was valid. Deslous-Paoli method was utilized more recently in Arcachon Bay, France, to calculate P/B of different *C. fornicata* subpopulations (de Montaudouin et al. 2001). These authors compared their P/B (most of them ca. 0.30 yr^{-1}) with the few published results, i.e. 0.45 yr^{-1} in Bay of Marennes-Oléron (France) (Deslous-Paoli 1985) and 0.15–0.33 yr^{-1} in Rade de Brest (France), where age was calculated by ring method and was consequently expected to be exact (Coum 1979). The similarity of results between all these studies seemed an argument to consider that the strategy "one position in a stack = one year" could be safely used.

However, the high reproductive output of *C. fornicata* in its native area on East coast of North America (Wall et al. 2013) as well as in its introduction area in Europe (Blanchard 2009; Stiger-Pouvreau and Thouzeau 2015) appears inconsistent with low P/B values (0.15–0.45 yr^{-1}). For marine invertebrates P/B usually ranges from 1.96 to 3.37 yr^{-1} (Cusson and Bourget 2005; Dolbeth et al. 2005). According to the literature review of Cusson and Bourget (2005), P/B = 1.77 yr^{-1} for molluscs, P/B = 1.82 yr^{-1} for filter feeders and P/B = 1.0 yr^{-1} for mollusc filter feeders. Moreover, their lifespan-based-model results suggest a P/B ca. 0.5 yr^{-1} for molluscs. Other reviews on gastropod species showed that P/B values ranged between 0.53 and 5.80 yr^{-1} (Banse and Mosher 1977; Robertson 1979; Rybarczyk et al. 2003). For invasive aquatic molluscs species, P/B values are typically > 1 yr^{-1}; e.g., *Crassostrea gigas* (Thunberg, 1793) (Arizpe 1996); *Dreissena polymorpha* (Pallas,

Figure 1. Photography of a tile colonized by *Crepidula fornicata*. On the top left, two stacks tucked on a common substrate. The right stack has its last settled individual on the right side. Photo by XDM.

1771) and *D. bugensis* (Andrusov, 1897) (Johannsson et al. 2000); *Perna viridis* (Linnaeus, 1758) (García-L et al. 2005); and *Potamopyrgus antipodarum* (Gray, 1843) (Cross et al. 2010). Computing models, which give an estimation of P/B according to *C. fornicata* lifespan or to the maximum individual weight, provide values between 1.18 yr^{-1} (Robertson 1979) and 1.28 yr^{-1} (Tumbiolo and Downing 1994).

Experimental results (Le Gall 1980) and different field observations (e.g., involving hard substrates which had been recently immersed) suggest that more than one *C. fornicata* individual per year could settle on a stack. Thus, the present study aimed at 1) quantifying this settlement rate; 2) adjust Deslous-Paoli theory in order to transform a "position/stack" database into a "age/stack" database; and 3) compare population dynamics parameters, including P/B, between the Deslous-Paoli (1985) method and this study's method. Our expectation is that previous studies (de Montaudouin et al. 2001; Deslous-Paoli 1985) underestimated the annual rate of *C. fornicata* settlement and that our correction will provide more accurate P/B ratio for this species.

Material and methods

Our first objective was to estimate the likelihood of *C. fornicata* to form stacks of several individuals within a single year ("tile experiment" section). To determine the probable age of each individual in a stack, we wrote a program transforming "stack-position" matrix in "stack-age" matrix ("cohort determination" section). The program was used to evaluate the consequences of our hypothesis (i.e. "more than one individual per year settles in a stack") on different population parameters from five sampling campaigns, including P/B ("population dynamics" section).

The first individuals of *Crepidula fornicata* to settle on a hard substrate form the primary stack. Other individuals can settle on this primary stack, forming secondary stacks. In the present study, no distinction was made between primary and secondary stacks. For example, if a juvenile was fixed on the side of a five-individuals primary stack, we considered two stacks, one made of five individuals and another made of one individual.

In situ "tile" experiment

We provided a hard substrate to *C. fornicata* to evaluate its propensity to make stacks of several individuals in less than one year. In February 2006, three roof tiles were placed in a 1-m equilateral triangle, in the middle of a *C. fornicata* colony, parallel to the shoreline at +0.3 m above low tide level. This natural population is heterogeneously distributed, with density and biomass ranging from 341 to 2338 ind.m^{-2}, and 33 to 256 g shell-free dry weight.m^{-2}, respectively (de Montaudouin et al. 2001). The placement of tiles was repeated three times at 100 m intervals along the shore (i.e., a total of 9 tiles). Each of these clay dome-shaped tiles was 50-cm long and 21-cm wide (Figure 1). The selected site, named "La Canelette", is a semi-sheltered mud flat (median grain size = 100 μm; silt and clay = 39% of sediment dry weight) situated in the inner part of Arcachon Bay (44º39′21.06″N; 1º08′27.40″W). Tidal regime is semi-diurnal and the sampling site could be visited by foot only at ebb tide, when coefficient was over 95. Salinity and temperature of water annually range from 22 to 32 and from 1 °C to 25 °C, respectively. The experiment was performed from 1st February 2006 to 18th February 2007 and the site was visited regularly on seven occasions. Each time, tiles were photographed to document stack development. Every *C. fornicata* (N = 1,036) was measured with callipers (1-mm precision) at the lower edge (straight shell length) and the position in the stack was noted. Considering that *C. fornicata* individuals can crawl until 5 yr old (Le Gall 1980) and that maximal shell length at 1-yr old is 25 mm (Le Gall 1980; Guérin 2004), individuals > 25-mm shell length were discarded from the analysis. These large organisms certainly came from the surrounding population.

Within a year, the percentages of one-individual (p1), two-individual (p2) and three-individual (p3) stacks were determined. This means that there is a percentages p2 (respectively p3) of two (respectively three) *C. fornicata* settling one above the other in one year. As previously argued, we also defined 25 mm as a reference value of the maximum shell length (SL) of an organism of one year.

Cohort determination

In the whole text, an isolated individual, i.e. an individual that was not settled on the top of another, was considered as a stack of one specimen. A model was formulated [using R 3.3.1 (R Core Team 2014), Appendix 1] to transform a stack/position matrix into a stack/age matrix ("recalculated data method"). Indeed, the goal was to have a matrix in which columns refer to individual ages. For this purpose, we created a matrix M (*stack × position*) representing the samples: each row refers to a stack, while columns define organism positions in stacks. Every cell contains the individual straight shell length (Figure 2). Organisms that were found alone (rows of M with a length value only in the first column) were considered to be one-year-old and copied in the first column of a new matrix A (*stack × age*). Moreover, since one-year-old individuals had to be ≤ 25 mm, a control step was performed to check if the first column of A contained unacceptably large organisms. If it was the case, the row was shifted over one column and split into two rows, letting then the first column empty (Figure 2).

Then, referring to the results of the *in situ* experiment, we choose randomly among the remaining rows of M and defined: i) a percentage *p3* of rows in which 3 individuals appeared in the same stack within one year; ii) a percentage *p2* of rows in which 2 individuals appeared in the same stack within one year; iii) a percentage *p1* of rows in which 1 individual appeared in the stack within one year. These rows were then split and new rows were formed, in order to have every organism of 1 year old under one another, in the same column. For example, starting from a row *j* of M representing a stack in which 2 organisms settled in the same year (entries m_{j1} and m_{j2} of M), two new rows were written in the matrix A: the former had the value of the first column equal to the one of the first column of
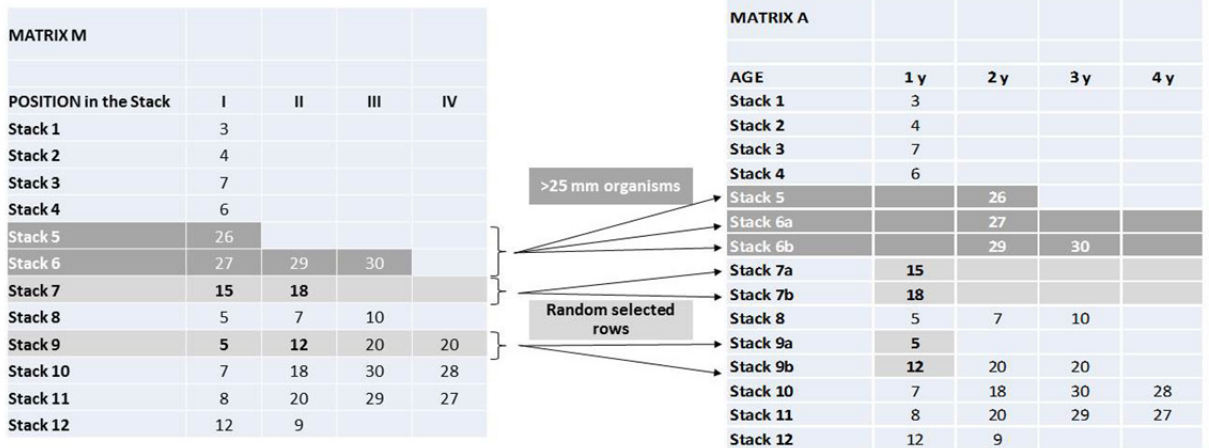
Transformation M ⟶ A

Figure 2. Length-age matrix recalculation scenario. The matrix M contains individual lengths in each stack (e.g. in stack 12 the first position is occupied by an organism of 12 mm and the second position is occupied by an organism of 9 mm). All the organisms found alone are considered to be 1 year old (y) (stacks 1 to 5). However, if individual length is larger than 25 mm, the organism is shifted in the second column (stack 5 and 6). Then, there are 10 stacks with at least one individual of 1 y (and with length < 25mm). Let's define 20% the percentage of stacks in which two individuals appear within the same year. Consequently, two stacks will have each two individuals of 1 y. We choose randomly these two stacks among the rows 6 to 11. The organisms of 15 and 18 mm of the stack 7 are therefore both 1 y and form two "new" stacks in the Matrix A (stacks 7a and 7b). The same process is considered for the organisms of 5 and 12 mm, stack 9 (lengths in bold). We progressively drew a second matrix A where each column contains the length of an individual of a defined age. Finally, this is also done iteratively for the cases in which three individuals appear in the same year.

M (m_{j1}); the latter had the value of the first columns equal to the value of the second column of M (m_{j2}). Every column of A refers now to individual ages: the first column contains the one-year-old organisms, the second contains the two-years-old organisms, etc. Once this modification was done for the organisms of one-year-old, the process was performed for subsequent years. The new matrix A provided the data used to calculate abundance, mortality, growth, and production per cohort.

Population dynamics

The population of *C. fornicata* was sampled once a year (October) between 2012 and 2016. At each occasion, ten 0.1-m² Van-Veen grab samples were performed, stacks were gently sieved on a 5-mm mesh (since smaller individuals are stuck to larger shells), and *C. fornicata* shells were measured as previously described. Parameters of population dynamics (abundance, mortality, recruitment, growth, production, P/B) were assessed and compared using both methods: 1) there was one individual settling on a stack per year (labelled "raw data method"), and 2) there were more than one individual settling in a stack per year (labelled "recalculated data method").

Abundance, mortality, recruitment

From the *C. fornicata* abundance per cohort, the mortality rate (Z, in yr^{-1}) was calculated for each year Y (2013 to 2016), by comparing the abundance N at age t with abundance N at age t-1. The theoretical density of recruits N_0 (ind m^{-2}) was deduced from the single exponential mortality model:

$$N_t = N_0 e^{-Zt} \qquad \text{(Eq. 1)}$$
$$dN/dt = -ZN \qquad \text{(Eq. 2)}$$

where N_t is the number of individuals of a cohort at age t (yr) and N_0 the number of individuals at age 0.

Individual growth

Von Bertalanffy growth function (VBGF) predicts length as a function of age and is commonly used in gastropod growth analysis with or without seasonal correction (Chatzinikolaou and Richardson 2008; Richardson et al. 2005), including examples for *C. fornicata* (Coum 1979; de Montaudouin et al. 2001; Deslous-Paoli 1985), as:

$$L_t = L_\infty (1 - e^{-K(t)}) \qquad \text{(Eq. 3)}$$

where L_∞ is the asymptotic shell length (mm) and K the growth coefficient (yr^{-1}).
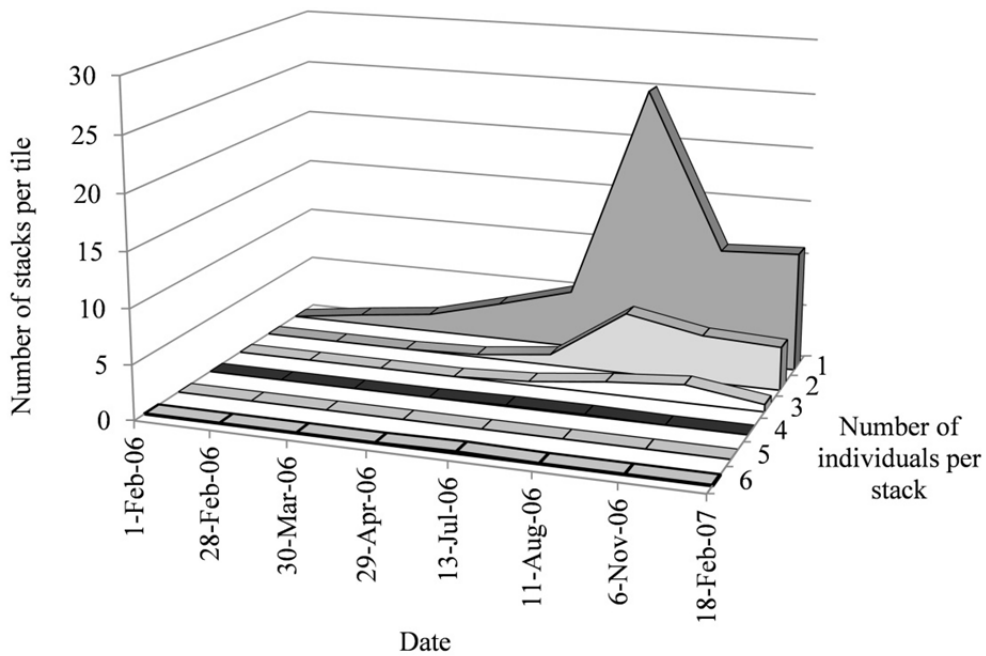
Figure 3. Number of stacks per tile during field experiment, according to the number of individuals per stack (from 1 to 6 individuals).

For each year Y (2013 to 2016), growth increment was measured by comparing straight shell length at age t and straight shell length at age $t-1$. The VBGF parameters, L_∞ and K, were assessed using Appeldoorn's method (Gayanilo et al. 2005) and FISAT II software (version 1.2.2, FAO-ICLARM).

A growth performance index ϕ' was also calculated using K and L_∞ (Pauly and Munro 1984), as:

$$\phi'=2log(L_\infty) + logK \qquad \text{(Eq. 4)}$$

Biomass, production, P/B

Biomass was calculated from individual shell length with the following equation based on 45 specimen ($r^2 = 0.92$) (de Montaudouin and Sauriau 1999):

$$Log\ DW = 2.15\ log\ L - 4.17 \qquad \text{(Eq. 5)}$$

where DW is shell-free dry weight (g) and L the straight shell length (mm). Dry weight was obtained after separating the flesh from the shell and drying it at 60 °C for 48 h.

Total annual production P was calculated for *C. fornicata* according to incremental summation method for populations with non-continuous recruitment and distinguishable year-classes (Crisp 1984):

$$P = \sum_{t=0}^{t=n}[(N_t + N_{t+1})/2 \times (W_{t+1} - W_t)] \qquad \text{(Eq. 6)}$$

where N_t is *C. fornicata* abundance at age t (yr) and W_t is individual dry weight at age t (g).

P/B (yr^{-1}) was calculated, dividing production P by mean biomass B, where B *is* defined as the average of total *C. fornicata* biomass at year Y and $Y-1$.

Results

Recruitment and P/B of C. fornicata on tiles

The individuals with a shell length larger than 25-mm (26–41 mm) represented 18% of the total number of organisms settled on tiles and were discarded from further analysis (see Material and methods). Some rare small individuals recruited or crawled on tiles in late February 2006, but settlement significantly started in July with a peak in August (Figure 3). At this period, the density was 40.2 ind tile^{-1} (386 ind m^{-2}). At experiment completion, in February 2007 (i.e. one year after the tiles were disposed on the mudflat), the density dropped to 21.0 ind tile^{-1} (200 ind m^{-2}) and the average number of stacks per tile was 16 (vs. maximum of 32 in August) with p1 = 69% consisting of a single individual, p2 = 27% of two individuals, and p3 = 4% of 3 individuals.
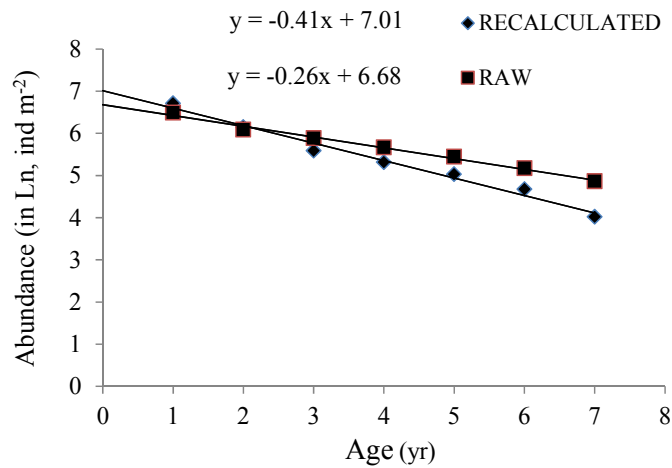
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Figure 4. Average mortality curve (excluding 2015 data) of *Crepidula fornicata* from "raw" and "recalculated" database. Mortality rate Z (in yr^{-1}) is the negative value of the slope coefficient.

Table 1. Annual population dynamics parameters of *C. fornicata* population from 2013 to 2016, with raw database (raw) and recalculated (rec) data base. Each year refers to the dynamics of each cohort (or position in the stack) in the past 12 months (e.g. 2013 is 2012–13, etc.). Some data for 2015 were discarded (see text). Biomass and production were based on shell-free dry weight.

		2013raw	2013rec	2014raw	2014rec	2015raw	2015rec	2016raw	2016rec
Total abundance N_t	ind m^{-2}	1365	1365	1755	1755	2078	2078	2353	2353
Mortality rate	yr^{-1}	0.24	0.28	0.64	0.93	X	X	0.25	0.29
Abundance at recruitment N_0	ind m^{-2}	809	1103	2287	3528	X	X	968	1103
Asymptotic length L_∞	mm	35.20	35.02	43.75	40.56	35.14	X	34.11	35.24
Growth coefficient K	yr^{-1}	0.48	0.60	0.18	0.34	0.52	X	0.51	0.55
Growth performance index ϕ'	No unit	2.77	2.87	2.54	2.75	2.81	X	2.77	2.83
Total biomass B	gDW m^{-2}	97.1	97.4	71.7	72.5	137.9	139.3	164.6	165.5
Production P	gDW m^{-2} yr^{-1}	33.6	49.6	23.6	61.0	55.2	67.5	67.3	83.3
P/B ratio	yr^{-1}	0.39	0.57	0.28	0.72	0.53	0.64	0.45	0.55

Population dynamics

As expected, average density (1188 ind m^{-2}, SD = 425 ind m^{-2}) was not affected after the recalculation on raw data base. In fact, our method considers the possibility that individuals in second or further position in the stack could have settled during the same year of individuals settled on top. Therefore, the global effect is to "drag" individuals toward younger ages than those expected when hypothesizing that only one individual per year settled in a stack. The result was a sharper slope of the abundance curve corresponding to an increased (× 1.6) mortality rate Z, and a higher calculated abundance at recruitment N_0 (Figure 4, Table 1). Year 2015 was discarded because it provided erroneous results (i.e. negative mortality) due to an increase of old adult density. This could be due to strong current or storms accumulating *C. fornicata* stacks in our sampling station.

The recalculation method resulted in a greater amount of large individuals in the first 4 age classes, even though the condition Lmax = 25 mm for one-year-old individuals is imposed. Thus, the global result was to slightly accelerate growth prediction (here, a higher K in recalculated scenario) but with no important effect on asymptotic length L_∞ (Figure 5) and finally only a 2.2 to 8.3% increase in the growth performance index ϕ' according to the year (Table 1).

There also was a strong increase of production (× 1.5, on average) and of P/B ratio. In fact, the recalculation method caused an increase of the abundance of individuals at their maximal growth period (0 to 3 years-old), resulting in an increasing of production P during the 0 to 2 years-old period (Figure 6). Biomass B, on the other hand, was not affected (Table 1).

Discussion

The tile experiment demonstrated that more than one *C. fornicata* individual per year could settle on a stack. When the proportions having multiple recruits were accommodated, the recalculation method slightly modified VBGF parameters, mainly by accelerating growth the first year. On average, shell length of 1-yr
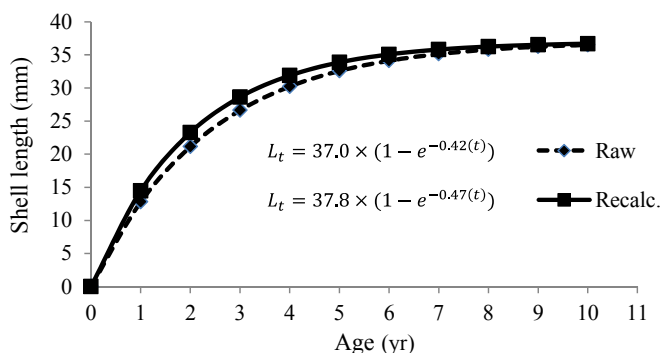
Figure 5. Modelled growth curve of *Crepidula fornicata* with average Von Bertalanffy growth function parameters (2013–2016) (Table 1), from "raw" and "recalculated" database.
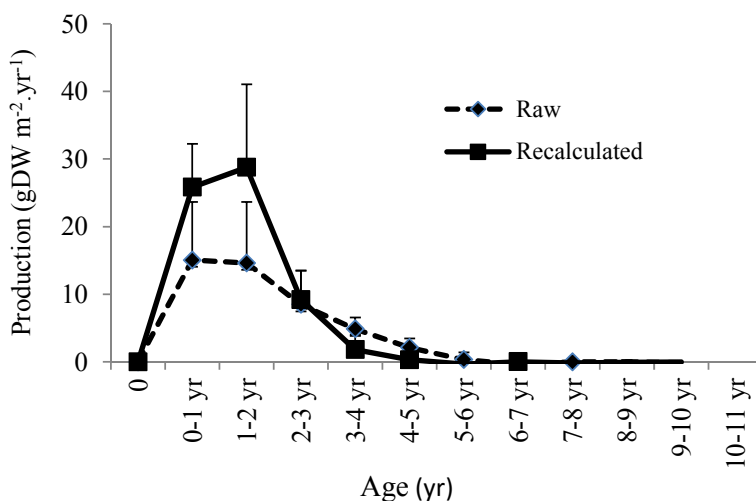
Within the figure:

$$L_t = 37.0 \times (1 - e^{-0.42(t)})$$

$$L_t = 37.8 \times (1 - e^{-0.47(t)})$$

Figure 6. Average annual production (g shell-free DW.m^{-2}.yr^{-1}, + 1 standard deviation) per age of *Crepidula fornicata* from "raw" and "recalculated" database.

old *C. fornicata* increased from 12.8 to 14.5 mm after recalculation. However, shell growth depends on numerous factors including, but not limited to, environmental effects, conspecific density, and type of association (conspecific alive substrate or inert substrate, etc…). The consequence is very high growth rate variability during the first year (Le Gall 1980). Le Gall (1980) showed that the shell length variance between 0^+ and 1^+ cohort increased from 5.5 to 90.4 mm². Moreover, comparing K and L_∞ is hazardous because these parameters are strongly related in VBGF; thus, we preferred to calculate a growth performance index ϕ (Pauly and Munro 1984). In our study, recalculation had a moderate effect on ϕ' (2.82 vs. 2.72 in raw data) and provided values which were similar to those calculated from other studies; e.g., 2.90 by growth-ring analysis (Coum 1979); 2.78 by growth-ring plus cohort analysis (Deslous-Paoli 1985); 2.78 to 2.89 by cohort analysis (de Montaudouin et al. 2001); and 2.81 by δ^{18}O and δ^{13}C isotope-ratio analysis of shells (Richard 2005).

Finally, Deslous-Paoli (1985) showed that there was no important difference in comparing growth parameters when using annual shell rings technique (considered here as the exact method) or when using "one rank in the stack = one year" theory (considered as the alternative method). Our conclusion is that our method just slightly increased values of growth performance parameters in the first year of *C. fornicata* life.

Conversely, taking into account that more than one individual can settle in a stack in one year dramatically increased production (1.6-fold) and P/B ratio (1.5-fold), matching the expectations suggested by the life-history features of *C. fornicata*.

Crepidula fornicata is considered to be unusual, even in its native geographical range (Wall et al. 2013). First, its particular characteristic to form stacks reduces mortality by predators, which have difficulty in handling their prey (Thieltges 2005; Thieltges et al. 2004). Then, the reproductive strategy (Beninger et al. 2016; Brante et al. 2016; Carrillo-

Baltodano and Collin 2015), the high larvae supply (Bohn et al. 2013; Valdizan et al. 2011), and the wide seasonal period of recruitment (Bohn et al. 2012; Richard et al. 2006) should ensure high population turn-over. Moreover, the adaptive qualities of *C. fornicata* enable it to live in a range of harsh environments (Bashevkin and Pechenik 2015; Breton and Huriez 2010; de Montaudouin and Sauriau 1999; Diederich and Pechenik 2013; Mestre et al. 2013). Finally, *C. fornicata* has few parasites (Pechenik et al. 2001; Thieltges et al. 2006). Consequently, low P/B calculated in previous works (Coum 1979; de Montaudouin et al. 2001; Deslous-Paoli 1985) appear in contradiction with such successful species and its invasive status in European waters (Blanchard 2009; Stiger-Pouvreau and Thouzeau 2015). Our recalculation method partly corrects this bias and places P/B ratio of *C. fornicata* closer to the values for other large macrobenthic species, although still lower (see Introduction). In our study, however, the percentage of stacks of more-than-one individual per year was assessed for but a single year and at but one site. The experiment should certainly be repeated elsewhere and adapted in other situations. Here, we considered (from tile experiment) than 69% of "stacks" consisted in isolated individuals, 27% were made of two individuals and 4% of 3 individuals. In contrast, Le Gall (1980), in cages including hard artificial substrate and placed in a natural environment for one year, only 20% of stacks consisted of single recruits with 26%, 36% and 18% of stacks having 2, 3 and 4 individuals, respectively. Naturally, our recalculation method using these percentages would provide even higher production and P/B values than those we provided.

In conclusion, the low previous P/B ratios reports, which seemed in contradiction with *C. fornicata* population characterisitics, appear to be an artefact related to the underestimation of the numbers of recruits. The method that we formulate corrects some of this bias. However, settlement experiments need to be conducted at a variety of sites spanning a wide range of environmental conditions and over multiple years to better capture effects of variable conditions on the numbers of multiple recruit stacks and the effects on production estimates.

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Supplementary material.

Appendix 1. R code of the program formulated to transform stack/position matrix in stack/age matrix.

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