

Intraspecific trade-offs between facilitation and competition in the invasive mollusc *Crepidula fornicata*

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ABSTRACT: We tested the hypothesis that high-density populations of the non-indigenous gastropod *Crepidula fornicata* increase settlement of conspecific recruits (facilitation process), and that this facilitation is balanced by competition processes. To verify our hypothesis, we sampled *C. fornicata* at 2 drastically different densities for 10 yr. We found that at high densities, the number of 1 yr old individuals per square meter colonizing the habitat and individual growth performances were higher in comparison with the low-density condition (Allee effect). In contrast, the production/biomass ratio (P/B), a good indicator of population fitness, was lower at higher densities. We relate this lower P/B ratio to the deficit of young individuals compared to adult biomass. We conclude that the net effect of high density on the conspecific colonization processes of the population is positive, thanks to the higher available hard substrate for larvae (facilitation). However, intraspecific competition also occurs and mitigates this positive effect. Therefore, we suggest that it is particularly important to take into account the 'net' balance between costs and benefits (i.e. what we observe) when analyzing population growth, in order to better understand its dynamics.

KEY WORDS: *Crepidula fornicata* · Facilitation · Competition · P/B ratio · Non-indigenous species · Population dynamics

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INTRODUCTION

Population demography within communities is thought to be strongly shaped by physical disturbances and negative interactions such as competition, predation and parasitism (Hixon et al. 2002). However, other studies have highlighted the importance of positive interactions in population and community dynamics (e.g. Bruno et al. 2003). In particular, one of these interactions is facilitation, generally defined as all non-consumer interactions among 2 or more species (named 'foundation species') that positively affect at least one of the species involved (Bertness & Callaway 1994), often with major cascade effects on recipient ecosystems (Gribben et al. 2009, Gouhier et al. 2011, Yakovis & Artemieva 2017).

Therefore, facilitation occurs when one organism makes the local environment more favourable for another species. This process is mostly described for sessile organisms, which cannot actively escape stress (by locomotion), and consequently profit from the presence of other foundation species mitigating adverse conditions (Bruno & Kennedy 2000, Wonham et al. 2005, Bulleri 2009, Branch et al. 2010).

Facilitation may consist of providing a suitable substrate for other species, as is the case for the gastropod *Batillaria attramentaris* in its introduced range in Washington, USA. Its proliferation, in fact, increases hard substrate surface (shells) for other species, including *Crepidula convexa* (Wonham et al. 2005). In many other cases, facilitation consists of mitigating physical stress, such as reducing wave-related phys-

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ical disturbance either in close vicinity of the foundation species or at a larger scale. Cordgrass *Spartina alterniflora*, for example, modifies cobble beaches nearby by reducing flow speed, stabilizing the sediments and allowing seedlings of other plants to establish (Bruno & Kennedy 2000). *Mytilus edulis* beds, in contrast, break the wave energy and facilitate cockle *Cerastoderma edule* settlement 50–100 m beyond the bed (Donadi et al. 2013). Even though facilitation is often defined as a positive interaction among 2 or more species (Bertness & Callaway 1994), this biotic factor can also act within a single population, in the same way negative interactions such as competition or predation do (i.e. intraspecific competition or cannibalism, respectively). In this regard, Allee effects describe situations where density of conspecifics is positively correlated with population fitness (Courchamp et al. 1999, Stephens & Sutherland 1999), in contradiction with Verhulst's logistic equation, which states mathematically that population size has a negative effect on its own per capita growth rate (Hixon et al. 2002). Furthermore, the Allee effect is often considered as a major mechanism facilitating non-indigenous species expansion, at least when those have already passed the first settlement and dispersal stages (Simberloff & Von Holle 1999, Wonham et al. 2005) or other types of invasions (Shaw et al. 2018). One important output concerns the 'left part' of the theoretical curve of Allee effects, which supports the principle that low conspecific density may lead to population extinction or decreased fitness by genetic inbreeding and loss of heterozygosity or demographic stochasticity (Courchamp et al. 1999). However, few studies focus on the 'central part' of the curve that shows the positive effect on population growth at high conspecific densities (i.e. inverse density dependence), beyond the threshold where negative effects would be expected.

Authors who assessed Allee effects have generally concentrated on life history traits of populations such as density/mortality rate (Leslie 2005, Svanfeldt et al. 2017), growth (Tsai et al. 2010) or reproductive output (Leslie 2005). In the present work, based on a 10-yr monitoring program of a marine benthic population, we propose to estimate a more comprehensive parameter describing population fitness—the production/biomass (P/B) ratio—in conditions of low and high conspecific densities. The P/B ratio is considered a good indicator of energetic flow in an ecosystem (Brey 1990). It typically estimates the percentage of annually renewed biomass, and consequently integrates recruitment success, individual growth and mortality rate. Brey (1990) reviewed different

correlations (or dependences) between P/B ratios and biological features of macrozoobenthic populations, such as age at sexual maturity, lifespan and number of generations. Moreover, the P/B ratio is an indicator of population health. For example, the P/B ratio of a population of the cockle *C. edule* was decreased by 27% in the presence of parasites (Gam et al. 2009). Our study also highlights the need to clarify the definitions of competition and facilitation. In fact, one definition of facilitation states that facilitative or positive interactions are encountered between organisms when at least one of the participants benefits, 'causing harm to neither' (Bruno et al. 2003, p. 120). This definition seems incompatible with the one stating that facilitation appears when the 'benefits exceed the costs' (Stachowicz 2001, p. 237).

Our biological model is the slipper limpet *Crepidula fornicata*, a gastropod that was accidentally introduced in Europe in 1872 from the east coast of the USA (Blanchard 1997), and has been introduced to many coastal areas (Stiger-Pouvreau & Thouzeau 2015). *Crepidula fornicata* appeared in France in the 1940s (Blanchard 1995) and was first recorded in 1969 in Arcachon Bay (Bachelet et al. 1980). These organisms form stacks of up to 12 individuals (Coul 1979). They are protandric hermaphrodites and exhibit planktotrophic development. Larvae need to reach a specific size in order to attain metamorphic competence. Then, they settle on hard substratum, e.g. conspecific live or dead shells (Henry & Lyons 2016). Paradoxically, although its planktonic larvae require a hard substrate to settle, *C. fornicata* is particularly prolific in soft-substrate habitats. Thus, our hypothesis was that we would observe facilitative processes related to the increase of hard substrates (represented by the shells of *C. fornicata*) with increasing *C. fornicata* density in a soft-sediment environment. Conversely, a high density of conspecifics would beget competition, leading to limited growth, higher mortality and less successful recruitment. Our objective was to assess the net effect of density on population fitness using the P/B ratio and the settlement of 1 yr old individuals.

MATERIALS AND METHODS

Study location and sampling

All samples were collected from an intertidal mudflat of Arcachon Bay, France (44° 39' 18" N, 1° 08' 25" W). *Crepidula fornicata* are aggregatively distributed within a narrow band of 450 × 15 m²

along the lowest intertidal levels, which can be reached by foot at ebb tide, when the tidal coefficient is >100 . Salinity and water temperature seasonally fluctuate in the range of 22–32 and 1–25°C, respectively. In this area, patches with a high density of *C. fornicata* (ca. 8 m diameters) are separated by areas in which it is rare. Once a year from 2001 to 2010, during the same period (February–March), 8 quadrats were sampled and washed on a 5 mm mesh sieve. This period of sampling is just before *C. fornicata* begins seasonal reproduction (de Montaudouin et al. 2002, Richard et al. 2006, Bohn et al. 2012) and was selected to ensure that our youngest individuals were ca. 1 yr old. The size of the quadrats was selected according to *C. fornicata* density: four 0.04 m² quadrats were situated in the middle of a patch ('high' density), while four 0.25 m² quadrats were sampled at least 20 m from the closest high-density patch, where *C. fornicata* are rare ('low' density). In order to obtain a clear quantitative difference between 'low' and 'high' treatments, we defined 'low' as those samples characterized by less than 2 kg fresh mass (FM) of live *C. fornicata* per m², and 'high' as those having more than 7 kg FM m⁻². The accuracy of our GPS did not allow us to detect whether high-density patches were at the exact same location each year, but the entire sampling area (see above) was always within the same mudflat.

All applicable institutional and/or national guidelines for the care and use of animals were followed.

Cohort determination

Every *C. fornicata* ($n = 10\,071$) was measured with a calliper (1 mm precision) at the lower edge (straight shell length), and the position in the stack was noted. A prior study has noted the peculiar fact that *C. fornicata* forms stacks with an average of one individual settling per year (Coum 1979). Thus the position of an individual in a stack could provide its age (Deslous-Paoli 1985). An isolated individual (i.e. an individual that is not settled on the top of another) is considered as a stack of one specimen. However, a recent study, performed in the same area as this one, showed that more than one individual per year could settle in a single stack and proposed a model to transform a stack/position matrix into a stack/age matrix (de Montaudouin & Accolla 2017). The R 3.3.1 script of this model (R Core Development Team 2014) is available in de Montaudouin & Accolla (2017). Consequently, we used this model to identify the different cohorts and

calculate population dynamics parameters per year (10 yr from 2001 to 2010) and for each level of *C. fornicata* abundance (low and high).

Population dynamics

Density and mortality

We calculated the mortality rate of every *C. fornicata* cohort (Z , yr⁻¹) for each year Y (2001 to 2010) and for each of the density conditions (low and high *C. fornicata* density) by comparing the density N at age t with density N at age $t-1$. The theoretical density of recruits N_0 (ind. m⁻²) was deduced from the exponential mortality model:

$$N_t = N_0 e^{-Zt} \quad (1)$$

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

Then, we calculated the percentage of 1 yr old individuals as the ratio of the number of 1 yr old individuals to the total number of individuals, and multiplied this by 100. This value is a proxy of the success of recruitment related to the density of adults, ca. 1 yr after settlement.

Individual growth

The 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 (Richardson et al. 2005, Chatziniolaou & Richardson 2008), including examples for *C. fornicata* (Coum 1979, Deslous-Paoli 1985, de Montaudouin et al. 2001, de Montaudouin & Accolla 2017). Its formulation is:

$$L_t = L_\infty (1 - e^{-K(t)}) \quad (2)$$

where L_∞ is the asymptotic shell length (mm) and K is the growth coefficient (yr⁻¹).

For each year Y (2001 to 2010) and each of the density conditions (low and high *C. fornicata* density), we measured growth increment 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 FISAT II software (version 1.2.2, FAO-ICLARM).

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

$$\phi' = 2\log(L_\infty) + \log K \quad (3)$$

Biomass, production and P/B

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

$$\log DM = 2.15 \log L - 4.17 \quad (4)$$

where DM is shell-free dry mass (g) and L is the straight shell length (mm). Dry mass was obtained after dissecting the flesh 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):

$$P = \sum_{t=0}^{t=n} [(N_t + N_{t+1})/2 \times (M_{t+1} - M_t)] \quad (5)$$

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

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

Statistical analysis

All parameters (density N , mortality Z , % of 1 yr old individuals, asymptotic shell length L_∞ , growth coefficient K , growth performance index ϕ' , biomass B , production P , P/B ratio) were compared according to *C. fornicata* sampling conditions (low versus high), using the non-parametric Wilcoxon paired test, with years as paired replicates ($n = 10$ yr). The Wilcoxon paired test was chosen because we sampled the same population of *C. fornicata* each year, with low-density patches being geographically close to high-density patches.

RESULTS

Length–frequency histograms were obtained for each of the 10 investigated years, discriminating high *Crepidula fornicata* density patches from low *C. fornicata* density areas (Fig. 1). Mean density was 4.5 times higher in the high-density condition than in the low-density condition ($W = 2.80$, $p = 0.005$; Table 1). The relative density of 1 yr old individuals was 2.6 lower in the high-density condition than in the low-density condition ($W = 2.80$, $p = 0.005$; Figs. 1 & 2, Table 1). However, the density of 1 yr old individuals was 2.5 times higher in the high-density condition

than in the low-density condition (Table 1). Mortality rate Z was similar for both conditions ($W = 0.10$, $p = 0.919$). Asymptotic length L_∞ was similar in both conditions ($W = 1.38$, $p = 0.169$), but the growth coefficient K was 15 % higher in the high-density condition ($W = 2.80$, $p = 0.005$; Fig. 3). As a consequence, the growth performance index ϕ' was 1.4 % higher in the high-density condition ($W = 2019$, $p = 0.028$; Table 1). Mean biomass and production were 5.4 and 4.2 times higher in the high-density condition than in low-density condition, respectively ($W = 2.80$, $p = 0.005$; Table 1). Conversely, the P/B ratio was 23 % lower in the high-density condition than in the low-density condition ($W = 2.50$, $p = 0.013$; Fig. 4, Table 1).

DISCUSSION

The low- and high-density conditions discriminated 2 drastically different situations of *Crepidula fornicata* biomass and density. The high-density condition displayed density values that are currently found in areas with longer histories of *C. fornicata* invasion (Hily 1991, de Montaudouin & Sauriau 1999, de Montaudouin et al. 2001, Gu erin 2004, de Montaudouin & Accolla 2017), while the low-density condition described a process of colonization (de Montaudouin et al. 2001). Likewise, all parameter values (L_∞ , K , ϕ' , P and B) except the P/B ratio were within the range of what has already been assessed for this species. The P/B ratio, in contrast, displayed particularly low values in both the high- and low-density conditions. Indeed, we obtained values between 0.21 and 0.45 yr^{-1} , while the expected P/B values for invertebrates are usually not smaller than 1.00 yr^{-1} : $P/B = 1.77 \text{ yr}^{-1}$ for molluscs, 1.82 yr^{-1} for filter feeders and 1.00 for molluscan filter feeders (Cusson & Bourget 2005). Moreover, computational models, which provide an estimation of the P/B ratio according to the lifespan or the maximum individual mass (Robertson 1979, Tumbiolo & Downing 1994), give values for *C. fornicata* between 1.18 and 1.28 yr^{-1} ; and P/B ratios previously calculated for *C. fornicata* were usually not $< 0.50 \text{ yr}^{-1}$ (de Montaudouin & Accolla 2017). This discrepancy could be attributed to the rather uncommon position of the *C. fornicata* population: our samples were at the intertidal level, while this species usually lives at the subtidal level (Loomis & Van-Nieuwenhuize 1985).

The comparison of population dynamics parameter values between low- and high-density conditions provided new insight into the facilitation/competition processes of species with particularly high perform-

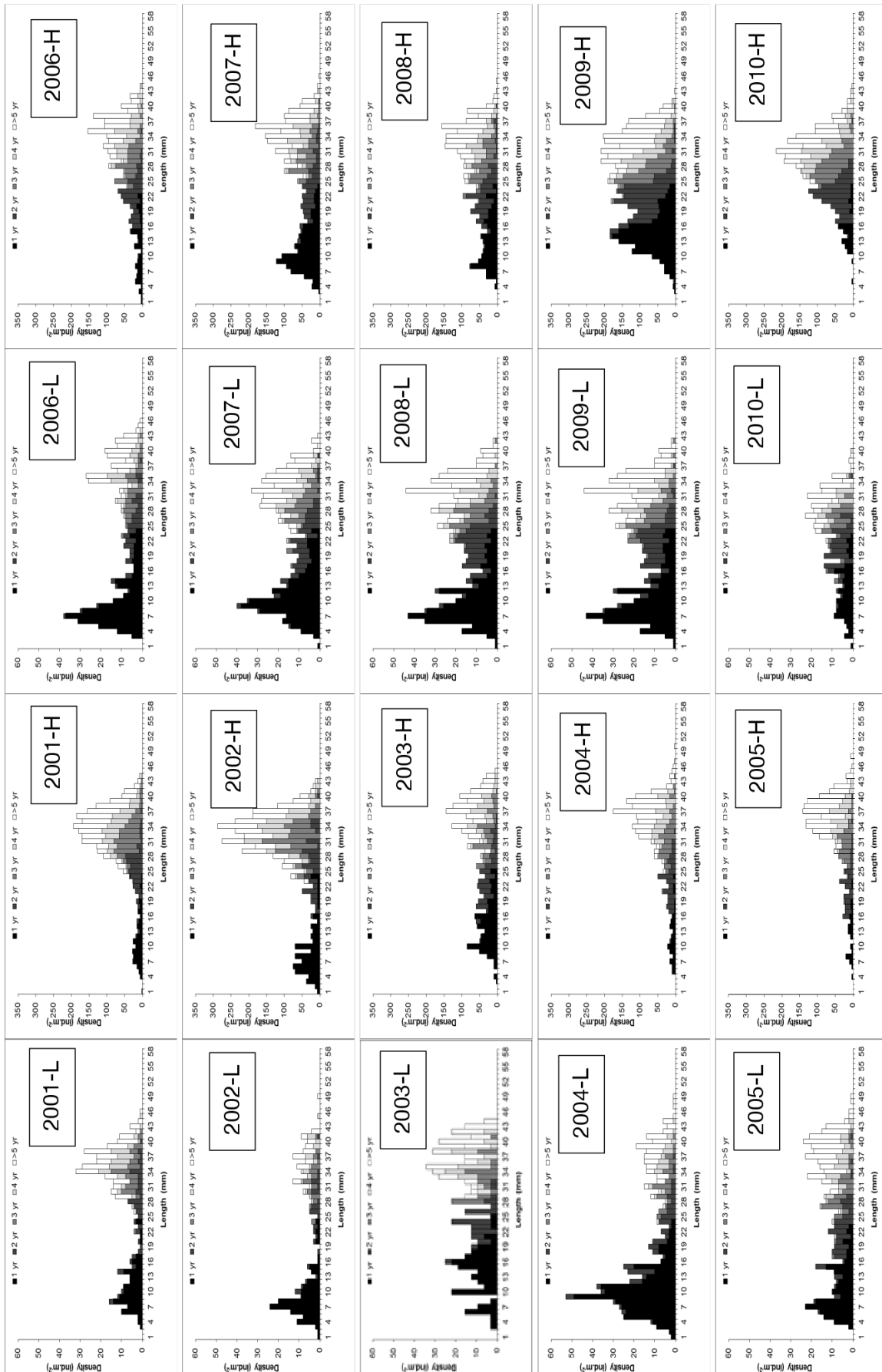


Fig. 1. Shell length–frequency histogram of *Crepidula fornicata* from 2001 to 2010 at the low (L) and high (H) density conditions, and by age

Table 1. Summary of results of Wilcoxon paired tests examining the effect of *Crepidula fornicata* density (low and high) on different population dynamics parameters. **Bold** p-values indicate significant differences ($p < 0.05$)

	Low	High	W	p
Density N (ind. m^{-2})	575 (403–712)	2583 (2084–2891)	2.80	0.005
Mortality rate Z (yr^{-1})	0.44 (0.40–0.47)	0.45 (0.38–0.49)	0.10	0.919
% 1 yr old	38.0 (30.0–47.0)	14.5 (9.0–28.0)	2.80	0.005
Asymptotic length L_{∞} (mm)	39.0 (33.8–41.7)	37.9 (36.1–41.3)	1.38	0.169
Growth coefficient K (yr^{-1})	0.47 (0.42–0.54)	0.54 (0.49–0.59)	2.80	0.005
Growth performance index ϕ'	2.85 (2.76–2.93)	2.89 (2.84–2.92)	2.19	0.028
Biomass B (g DM m^{-2})	47 (39–53)	256 (243–304)	2.80	0.005
Production P (g DM $m^{-2} yr^{-1}$)	19 (13–20)	79 (64–89)	2.80	0.005
P/B (yr^{-1})	0.40 (0.34–0.45)	0.31 (0.21–0.34)	2.50	0.013

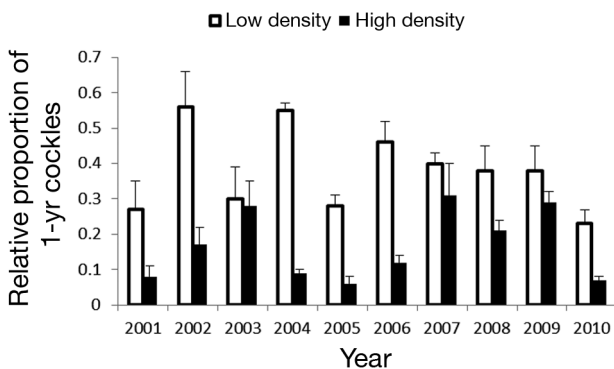


Fig. 2 Mean relative proportion of 1-yr-old (ind. m^{-2} ; +1 SE) *Crepidula fornicata* in the low- and high-density conditions, from 2001 to 2010 ($N = 4$ replicates)

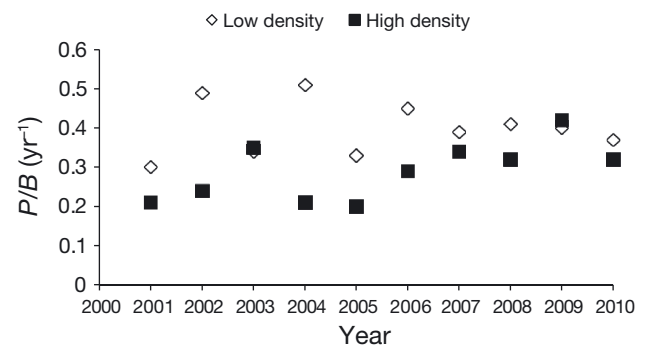


Fig. 4. Mean production/biomass (P/B) ratio of *Crepidula fornicata* in the low- and high-density conditions, from 2001 to 2010

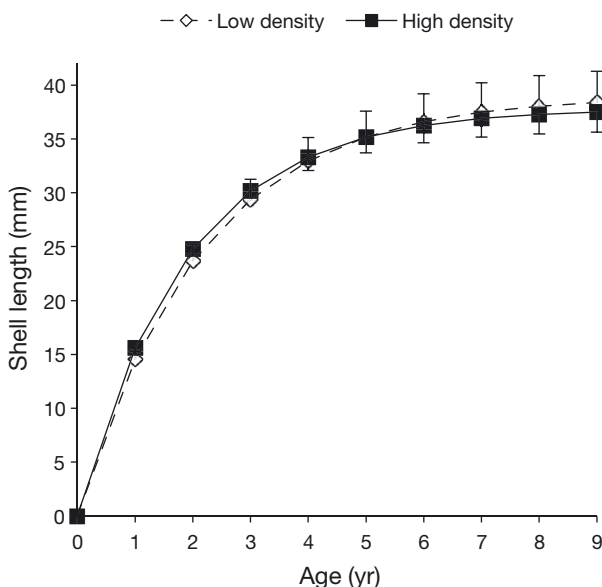


Fig. 3. Modelled growth curve of *Crepidula fornicata* with average von Bertalanffy growth function parameters (2001–2010) in the low- and high-density conditions (see Table 1)

ance, such as invasive molluscs. The well-established density-dependent intraspecific competition concept is not fully valid in the present case. Firstly, and unexpectedly, growth performance was not affected by high density, but on the contrary was slightly stimulated. This result contradicts that of many studies demonstrating that high density of suspension feeders is usually related to stunted growth (Peterson & Black 1987, Peterson & Beal 1989, Jensen 1992, Kamermans et al. 1992). Moulin et al. (2007) observed a higher particle resuspension (i.e. higher available food) during spring tides when fewer stacks of *C. fornicata* were on the bottom. In contrast, in our sheltered study site, current speed is low and resuspension of benthic diatoms, a large part of the *C. fornicata* trophic regime (Riera et al. 2002), could instead be related to bioturbation activity due to the grazing activity of the younger stage (Chaparro et al. 1998) and to the lifting behaviour of the older individuals (Diederich et al. 2015). Thus, the higher the density, the higher the bioturbation and microphytobenthic availability. *Crepidula fornicata* growth can also

be stimulated by the contact of conspecifics (Le Gall 1980), such that high density consequently promotes these processes. Secondly, we were not able to measure competitive effects on shell growth, although there was certainly trophic competition at these high levels of biomass, as observed with another suspension feeder, the cockle *Cerastoderma edule* (de Montadoun & Bachelet 1996). In conclusion, facilitation was the dominant process influencing growth.

The density values of 1 yr old individuals clearly illustrate the antagonistic effects of competition and facilitation. In the low-density condition, 1 yr old individuals comprised on average 38% of the total population (i.e. 219 ind. m⁻² out of 575), which corresponded to a 1 yr old/>1 yr old ratio of 0.61. If we extrapolate this ratio to the high-density condition, we should obtain an average density of 1 yr olds of 1347 ind. m⁻². This would be the pure consequence of a gross facilitation process: the higher the availability of suitable substrate (here, conspecific shell density), the higher the larval recruitment. However, the observed density of 1 yr old individuals was only 375 ind. m⁻² in the high-density condition (14.5% of total density). This could be caused by intraspecific competition and by a consequent alteration of recruitment by suspension-feeding activity of previously settled conspecific adults, as observed for many other marine species (Woodin 1976, Bachelet et al. 1992, de Montadoun & Bachelet 1996). Moreover, cannibalism in suspension feeders has been commonly observed in the laboratory (Young & Chia 1987), and in particular for *C. fornicata* (Pechenik et al. 2004). This relative deficit of younger individuals in the high-density condition explained why the *P/B* ratio was 23% lower than in the low-density condition.

In conclusion, this 10 yr study showed that a 5.4-fold increase of biomass facilitated settlement of 1 yr old individuals ($\times 6.1$), but this facilitation was modulated by strong intraspecific competition ($\div 3.6$). The net result was positive ($\times 1.7$): facilitation (Allee effect) prevails over competition in terms of colonization success in high densities. This self-sustained growth of a population, exacerbated by this peculiarity to live piled up in stacks, is certainly a major reason explaining the success of *C. fornicata* in becoming invasive (Blanchard 2009, Stiger-Pouvreau & Thouzeau 2015), but also the success of other sessile species needing hard substrates to settle in environments dominated by soft bottoms (Diederich 2005, Leslie 2005, Lang & Buschbaum 2010, Svanfeldt et al. 2017). Conversely, we also demonstrated that, even though greater density of *C. fornicata* increases pop-

ulation growth (Allee effect), the *P/B* ratio at high density is diminished, suggesting that a density threshold beyond which fitness is altered has been exceeded in the high-density condition. Our study provides evidence for the importance of examining 'net' balance between costs and benefits (i.e. what we observe) when analysing population growth. This means that a net competition (or a net facilitation) should be scrutinized to evaluate which part is due to costs and which part is due to benefits (Bruno et al. 2003, Leslie 2005).

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