Intraspecific trade-offs between facilitation and competition in the non-native 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 *Crepidula* at two drastically different densities for 10 years. We found that at high densities, the number of one-year old individuals per m² colonizing the habitat and individual growth performances were higher in comparison with the low density condition (Allee effect). On the contrary, 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 colonisation 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.

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INTRODUCTION

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Population demography within communities is thought to be strongly shaped by physical disturbances and negative interactions like competition, predation and parasitism (Hixon et al. 2002). However, other studies have highlighted the importance of positive interactions in population and community dynamics (Bruno et al. 2003). In particular, one of these interactions is facilitation, generally defined as all non-consumer interactions among two 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, like reducing wave related physical 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*, instead, break the wave energy and facilitate cockle, *Cerastoderma edule*, settlement

50-100 m towards the coast (Donadi et al. 2013). Even though facilitation is often defined as a positive interaction among two 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). Besides, Allee effect is often considered as a major mechanism facilitating non-indigenous species expansion, at least when those have already overpass 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 generally concentrate on life history traits of populations like 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 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

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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 cockles, *Cerastoderma edule*, was 27% decreased by the presence of parasites (Gam et al. 2009). Our study also aimed to highlight the need of clarifying 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 without "causing harm to neither" (Bruno et al. 2003). This definition seems antagonistic with the one stating that facilitation appears when the "benefits exceed the costs" (Stachowicz 2001).

Our biological model is the slipper limpet, *Crepidula fornicata*, a gastropod which was accidentally introduced in Europe in 1872 from the East coast of the United States (Blanchard 1997), and is introduced to many coastal areas (Stiger-Pouvreau & Thouzeau 2015). *C. 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 where up to 12 individuals are piled up (Coum 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 necessitate a hard substrate to settle, *C. fornicata* is particularly prolific in soft-substrate habitats. Thus, our hypothesis is that we could observe facilitative processes related to the increase of hard substrates (represented by *C. fornicata*'s shells) 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 is to assess the net effect of density on population fitness through the P/B ratio and the settlement of one-year individuals.

METHODS

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Study location and sampling

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All samples were collected from an intertidal mudflat of Arcachon Bay, France (44°39'18.00"N - 1°08'24.62"W). *Crepidula fornicata* are aggregately distributed within a narrow band of 450×15 m² along the lowest intertidal levels which can be reached by foot at ebb-tide, when tidal coefficient > 100. Salinity and water temperature seasonally fluctuate in the range 22–32, and 1–25°C, respectively. In this area, patches with high density of *C. fornicata* (ca. 8-m-diameters) are separated by areas where it is rare. Once a year from 2001 to 2010, during the same period (February-March), eight quadrats were sampled and washed on a 5-mm mesh sieve. 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" those samples characterized by less than 2 kg Fresh Weight (FW) of live *C. fornicata*.m^{-2} and "HIGH" those having more than 7 kg FW.m^{-2}. The accuracy of our GPS did not allow to detect whether high density patches were at the exact same location each year, but the whole sampling area (see above) was always within the same mudflat. This period of sampling is just before *C. fornicata*

138 begins seasonal reproduction (de Montaudouin et al. 2002, Richard et al. 2006, Bohn et al.

139 2012) and was selected to ensure that our youngest individuals were ca. 1-yr old.

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142 **Cohort determination**

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145 Every *C. fornicata* (n = 10,071) was measured with a calliper (1-mm precision) at the lower

146 edge (straight shell length) and the position in the stack was noted. Former studies have noted

147 the peculiar fact that *C. fornicata* forms stacks with an average of one individual per year

148 settling (Coum 1979). Thus the position of an individual in a stack could provide its age

149 (Deslous-Paoli 1985). An isolated individual (i.e. an individual that is not settled on the top of

150 another) is considered as a stack of one specimen. However, a recent study, performed in the

151 same area as this one, showed that more than one individual per year could settle in a single

152 stack and proposed a model to transform a stack/position matrix into a stack/age matrix (de

153 Montaudouin & Accolla 2017). The R 3.3.1 script of this model (Team 2014) is available in

154 de Montaudouin & Accolla (2017). Consequently, we used this model to identify the different

155 cohorts and calculate population dynamics parameters per year (10 years from 2001 to 2010)

156 and per *C. fornicata* abundance (LOW and HIGH).

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159 **Population dynamics**

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161   Density, Mortality

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163   We calculated the mortality rate of every *C. fornicata* cohort (Z , yr^{-1}) for each year Y (2001 to

164   2010) and for each of the density conditions (LOW and HIGH *C. fornicata* density) by

165   comparing the density N at age t with density N at age t-1. The theoretical density of recruits

166   N_0 (ind m^{-2}) was deduced from the exponential mortality model:

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

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

169   Then, we calculated the percentage of 1-year individuals as the ratio of the number of 1-year

170   individuals over the total number of individuals, $\times$ 100. This value is a proxy of the success of

171   recruitment related to the density of adults, ca. one year after settlement.

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173   Individual growth

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175   Von Bertalanffy growth function (VBGF) predicts length as a function of age and is

176   commonly used in gastropod growth analysis with or without seasonal correction (Richardson

177   et al. 2005, Chatzinikolaou & Richardson 2008), including examples for *C. fornicata* (Coum

178   1979, Deslous-Paoli 1985, de Montaudouin et al. 2001, de Montaudouin & Accolla 2017). Its

179   formulation is:

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

181   where L_∞ is the asymptotic shell length (mm) and K the growth coefficient (yr^{-1}).

182   For each year Y (2001 to 2010) and each of the density conditions (LOW and HIGH *C.*

183   *fornicata* density), we measured growth increment by comparing straight shell length at age t

184   and straight shell length at age t-1. The VBGF parameters, L_∞ and K, were assessed using

185   FISAT II software (version 1.2.2, FAO-ICLARM).

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

187   as:

188    $\phi' = 2log(L_\infty) + logK$ (3)

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190   Biomass, Production, P/B

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192   Biomass was calculated from individual shell length with the following equation based on 45

193   specimens ($r^2 = 0.92$) (de Montaudouin & Sauriau 1999):

194    $log\ DW = 2.15\ log\ L - 4.17$ (4)

195   where DW is shell-free dry weight (g) and L the straight shell length (mm). Dry weight was

196   obtained after dissecting the flesh and drying it at 60°C for 48 h.

197   Total annual production P was calculated for $C.\ fornicata$ according to incremental

198   summation method for populations with non-continuous recruitment and distinguishable year-

199   classes (Crisp 1984):

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

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

202   P/B (yr^{-1}) was calculated, dividing production P by mean biomass B, where B is defined as the

203   average $C.\ fornicata$ biomass at year Y.

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205   **Statistical analysis**

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207   All parameters (density N, mortality Z, % of 1-year individuals, asymptotic shell length L_∞,

208   growth coefficient K, growth performance index ϕ', biomass B, production P, P/B ratio) were

209   compared according to $C.\ fornicata$ sampling conditions (LOW vs. HIGH), using the non-

210   parametric Wilcoxon paired test, with years as paired replicates (n = 10 years). Wilcoxon

211   paired test was chosen because we sampled the same population of $C.\ fornicata$ each year,

212   with LOW density patches being geographically close to HIGH density patches.

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RESULTS

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Length-frequency histograms were obtained for each of the ten 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-year individuals was 2.6 lower in the HIGH density condition than in the LOW density condition (W = 2.80, p = 0.005) (Fig. 1 & 2, Table 1). However, the density of 1-year individuals is 2.5 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 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, 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).

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DISCUSSION

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The LOW and HIGH density conditions discriminated two drastically different situations of *Crepidula fornicata* biomass and density. The HIGH density condition displayed density

238 values that are currently found in areas with longer histories of *C. fornicata* invasion (Hily

239 1991, de Montaudouin & Sauriau 1999, de Montaudouin et al. 2001, Guérin 2004, de

240 Montaudouin & Accolla 2017), while the LOW density condition rather described a process

241 of colonization (de Montaudouin et al. 2001). Likewise, all parameter values (L_∞, K, ϕ', P and

242 B) but the P/B ratio are within the range of what is already assessed for this species. The P/B

243 ratio, instead, displayed particularly low values in both HIGH and LOW density conditions.

244 Indeed, we obtained values between 0.21 and 0.45 yr^{-1}, while the expected P/B values for

245 invertebrates are usually not smaller than 1.00 yr^{-1}: P/B = 1.77 yr^{-1} for molluscs, P/B = 1.82

246 yr^{-1} for filter feeders and P/B = 1.00 for mollusc filter feeders (Cusson & Bourget 2005).

247 Moreover, computing models, which provide an estimation of the P/B ratio according to the

248 lifespan or to the maximum individual weight (Robertson 1979, Tumbiolo & Downing 1994),

249 gives for *C. fornicata* values between 1.18 and 1.28 yr^{-1}. *C. fornicata* is usually not <0.50 yr^{-1}

250 (de Montaudouin & Accolla 2017). This discrepancy could be attributed to the rather

251 uncommon position of the *C. fornicata* population: our samples were at the intertidal level,

252 while this species usually lives at the subtidal level (Loomis & VanNieuwenhuize 1985).

253 The comparison of population dynamics parameter values between LOW and HIGH density

254 conditions provided a new insight in the facilitation/competition processes of species with

255 particularly high performances, such as invasive molluscs. The well-established density-

256 dependent intraspecific competition concept is not fully valid in the present case. Firstly and

257 unexpectedly, growth performance was not affected by high density, but on the contrary was

258 slightly stimulated. This result contradicts many studies demonstrating that high suspension-

259 feeders density is usually related to stunted growth (Peterson & Black 1987, Peterson & Beal

260 1989, Jensen 1992, Kamermans et al. 1992). Moulin et al. (2007) observed a higher particle

261 resuspension (i.e. higher available food) during spring tides when fewer stacks of *C. fornicata*

262 were on the bottom. In our sheltered study site, instead, current speed is low and resuspension

263   of benthic diatoms, a large part of *C. fornicata* trophic regime (Riera et al. 2002), could rather

264   be related to bioturbation activity due to the grazing activity of the younger stage (Chaparro et

265   al. 1998) and to the lifting behaviour of the older individuals (Diederich et al. 2015). Thus, the

266   higher the density, the higher the bioturbation and the microphytobenthic availability. *C.*

267   *fornicata* growth can also be stimulated by the contact of conspecifics (Le Gall 1980), such

268   that high density consequently promotes these processes. Finally, we were not able to measure

269   competitive effects on shell growth, although there was certainly trophic competition at these

270   high levels of biomass, as observed with another suspension-feeder, the cockle *Cerastoderma*

271   *edule* (de Montaudouin & Bachelet 1996). In conclusion, facilitation was the dominating

272   process influencing growth.

273   The density values of 1-year old individuals clearly illustrate the antagonistic effects of

274   competition and facilitation. In the LOW density condition, 1-year old individuals were on

275   average 38% of total population (i.e. 219 ind.m^{-2} out of 575), which corresponded to a [1-yr

276   old]/[>1-yr old] ratio of 0.61. If we extrapolate this ratio to the HIGH density condition, we

277   should obtain an average density of 1-yr old individuals of 1347 ind.m^{-2}. This would be the

278   pure consequence of a gross facilitation process: the higher the availability of suitable

279   substrate (here conspecific shells density), the higher the larval recruitment. However, the

280   observed density of 1-yr old individuals was only 375 ind.m^{-2} in the HIGH density condition

281   (14.5% of total density). This could be caused by intraspecific competition and by a

282   consequent alteration of recruitment by suspension-feeding activity of previously settled

283   conspecific adults, as observed for many other marine species (Woodin 1976, Bachelet et al.

284   1992, de Montaudouin & Bachelet 1996). Moreover, cannibalism in suspension-feeders has

285   been commonly observed in the laboratory (Young & Chia 1987), and in particular for *C.*

286   *fornicata* (Pechenik et al. 2004). This relative deficit of younger individuals in the HIGH

287 density condition explained why the P/B ratio was 23% lower than in the LOW density
288 condition.

289 In conclusion, this 10-yr study showed that a 5.4 fold increase of biomass facilitated
290 settlement of 1-year individuals (x 6.1), but this facilitation was modulated by strong
291 intraspecific competition (÷3.6). The net result was positive (x 1.7): facilitation (Allee effect)
292 prevails over competition in terms of colonisation success in high densities. This self-
293 sustained growth of a population, exacerbated by this peculiarity to live piled up in stacks, is
294 certainly a major reason explaining the success of *C. fornicata* in becoming invasive
295 (Blanchard 2009, Stiger-Pouvreau & Thouzeau 2015), but also the success of other sessile
296 species needing hard substrates to settle in environments dominated by soft bottoms
297 (Diederich 2005, Leslie 2005, Lang & Buschbaum 2010, Svanfeldt et al. 2017). Conversely,
298 we also demonstrated that, even though greater density of *C. fornicata* increases population
299 growth (Allee effect), the P/B ratio at high density is diminished, suggesting that a density
300 threshold beyond which fitness is altered has been exceeded in the HIGH density condition.
301 Our study provides evidence for the importance of examining "net" balance between costs
302 and benefits (i.e. what we observe) when analysing population growth. This means that we
303 should stress what is the net competition when costs are high, albeit gross facilitation is
304 present too, or what is the net facilitation when benefits are high in presence of gross
305 competition (Bruno et al. 2003, Leslie 2005).

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310 Acknowledgements

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461   Fig. 1. Shell length frequency histogram of *Crepidula fornicata* from 2001 to 2010 at the LOW and

462   HIGH density conditions, and by age. Black bars concern the 1-yr individuals.

463   Fig. 2. Mean relative proportion of 1-yr ind.m^{-2} (+ 1 standard error) of *Crepidula fornicata* at the LOW

464   and HIGH densities condition, from 2001 to 2010 (N = 4 replicates).

465   Fig. 3. Modelled growth curve of *Crepidula fornicata* with average Von Bertalanffy growth function

466   parameters (2001-2010) at the LOW and HIGH densities conditions (Table 1).

467   Fig. 4. Mean Production/Biomass ratio of *Crepidula fornicata* at the LOW and HIGH densities
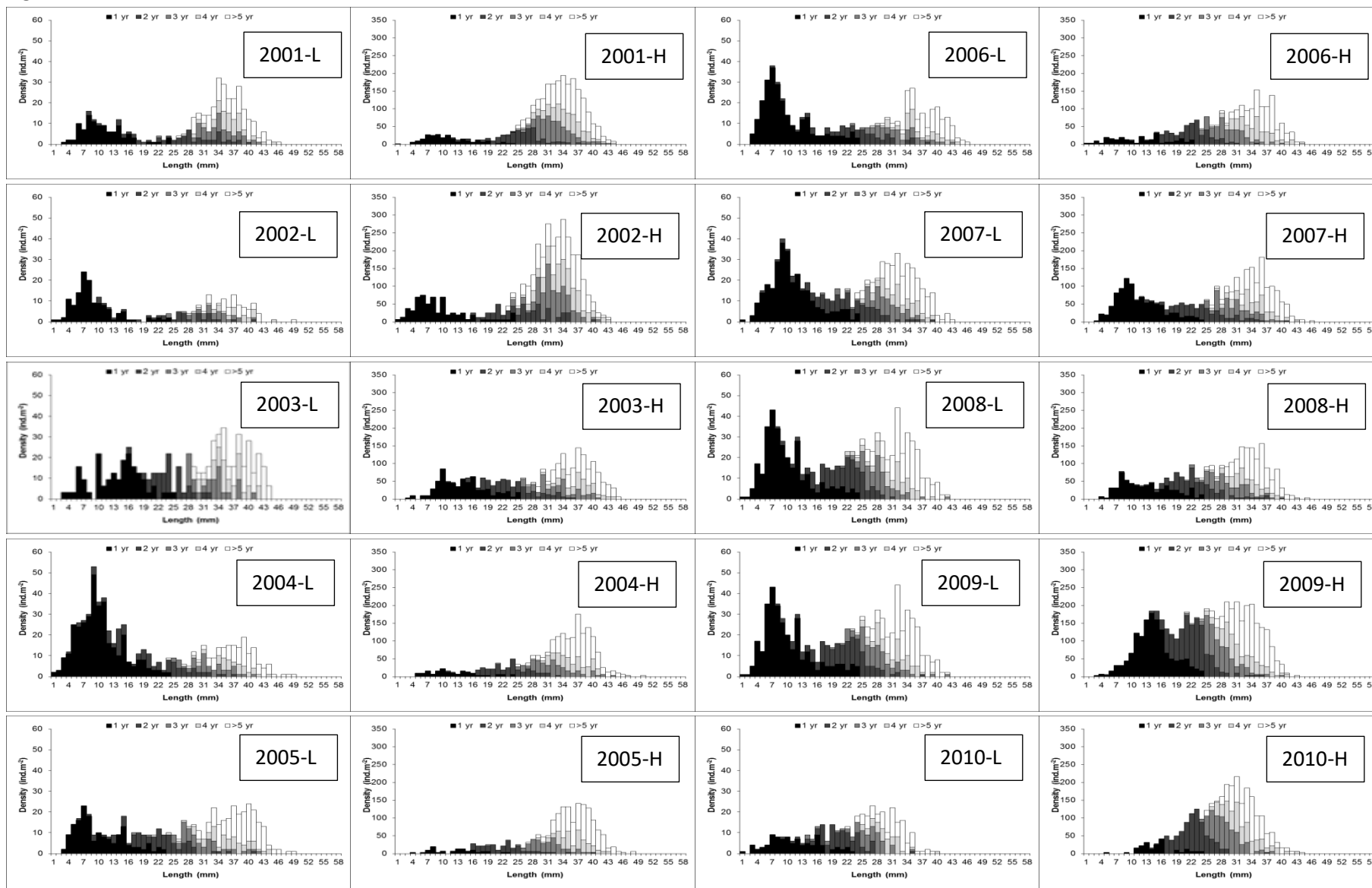
468   condition, from 2001 to 2010.
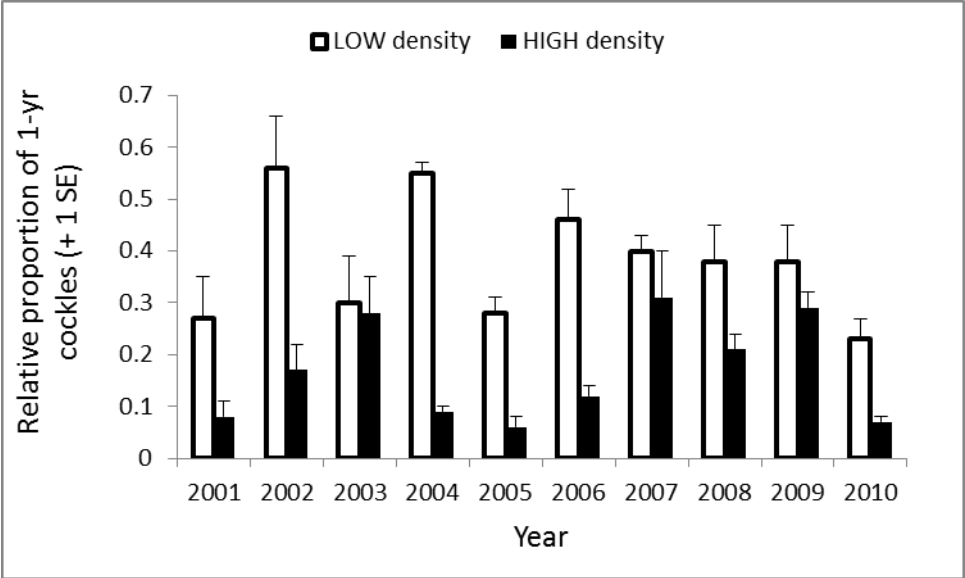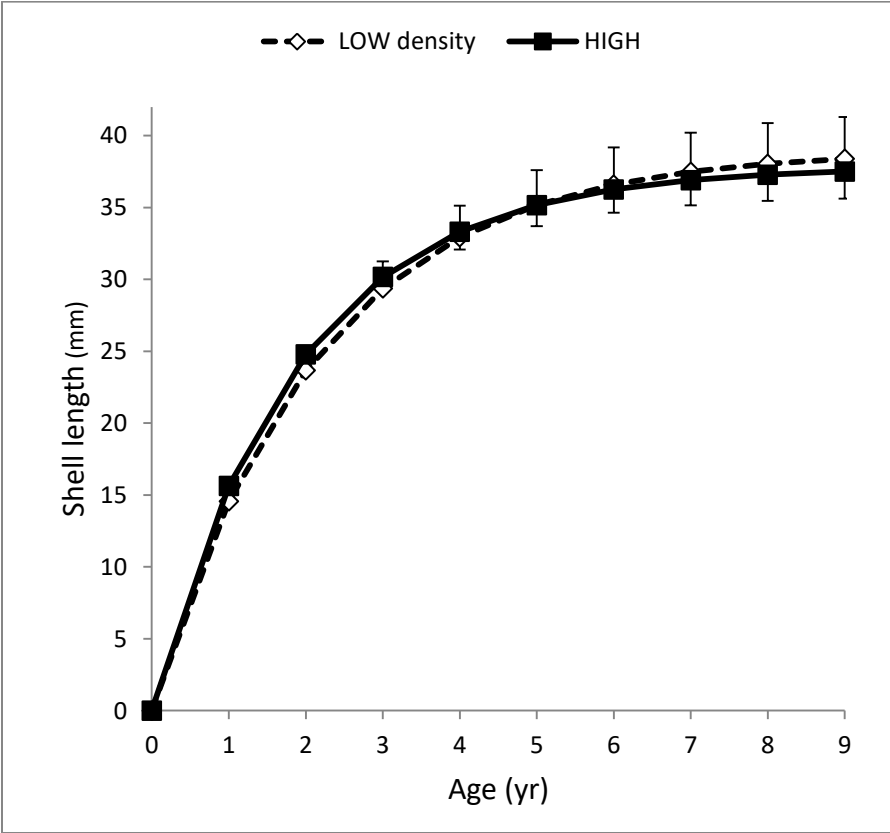
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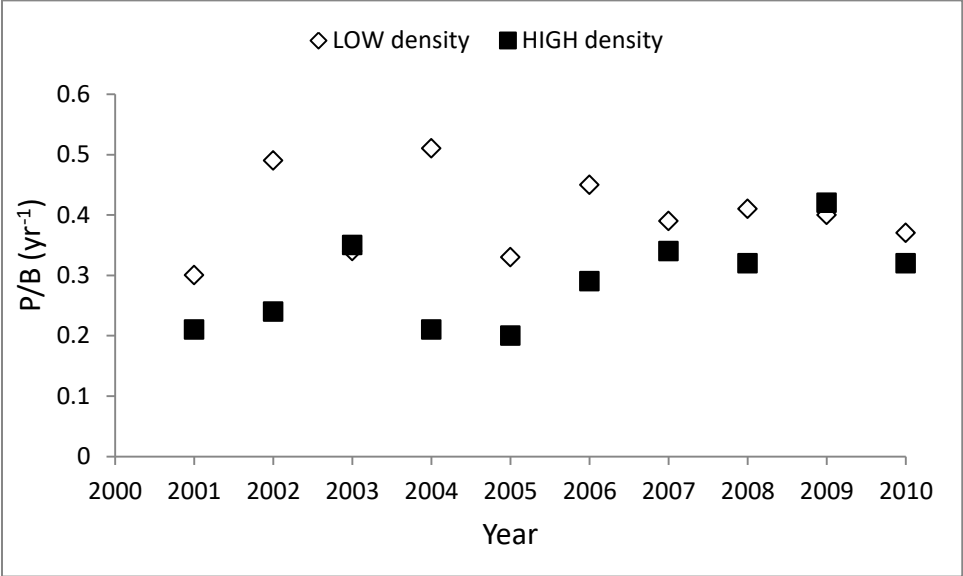Figure 1

Figure 2

Figure 3

Figure 4

Table 1. Summary of results of Wilcoxon paired test examining the effect of *Crepidula fornicata* density (LOW and HIGH) on different parameters of their population dynamics.

	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 $L\infty$ (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 (gDW.m^{-2})	47 (39-53)	256 (243-304)	2.80	**0.005**
Production P (gDW.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**