

ORIGINAL ARTICLE

Sexual traits plasticity of the potentially invasive limpet *Bostrycapulus odites* (Gastropoda: Calyptraeidae) within its natural distribution in South America

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Abstract

The slipper limpet *Bostrycapulus odites* has recently been reported as an introduced species on the Spanish Mediterranean coast. Another species in the family Calyptraeidae, *Crepidula fornicata*, is a problematic invasive species in the Northeast Atlantic, which makes the closely related *Bostrycapulus* introduction a matter of concern. Information on the biology of *B. odites* in its natural environment can facilitate predictions on where the species could find favourable conditions for settlement and expansion. Size and sex were recorded for individuals in four populations over 2600 km of the Southwestern Atlantic shoreline, in Argentina and Brazil, covering the whole native latitudinal range of this widely distributed species. Animals were collected by hand in the intertidal or by SCUBA in subtidal locations; specimens were examined to determine shell length, sex, and the presence and number of brooded egg capsules in females. Mean shell length for the whole population did not differ significantly among populations. However, this species experiences sequential hermaphroditism (protandry), and the size at sexual maturity (minimum male size) increased significantly with latitude. The fecundity of females at all sites increased with size, and the number of brooded egg capsules as well as the average size of capsules was larger in bigger individual females; however, mean fecundity varied among sites independent of mean female body size. This limpet species modifies its reproductive traits with local conditions, and sexual characters develop earlier in more temperate localities.

Introduction

Several studies have been conducted on the reproductive traits of molluscan populations (such as sex ratio, and spawning seasonality and duration), but almost all of them have been restricted to a single area or population. Localized studies have shown that many species present adaptations to local conditions, e.g. the gastropod *Hexaplex trunculus* from the North Atlantic and Mediterranean Sea (Tirado *et al.* 2002; Vasconcelos *et al.* 2004, 2008; Lahbib *et al.* 2008, 2009), *Buccinum undatum* from the

North Atlantic (Kristensen 1959; Bruce *et al.* 1963; Martel *et al.* 1986), *Concholepas concholepas* from Chile (López & Moreno 1988; Moreno *et al.* 1993, 1998; Peña *et al.* 1994), among others.

Snails in the caenogastropod family Caplytraeidae have distinctive adult shells without the characteristic spiral coiling of typical adult gastropods but with a shelf or partition in place of the body whorl (Bandel & Riedel 1994). Calyptraeids cover a worldwide distribution in shallow marine environments. Several species in this family have been reported as invasive species outside their native

ranges. *Crepidula fornicata*, native to the Western North Atlantic coast, has been introduced in Europe and is a noted pest species especially in England and France (Blanchard 1997). Another slipper limpet, *Bostrycapulus odites*, has been found in the Spanish Mediterranean (Izquierdo *et al.* 2007). This is a small local population that has apparently been established for some time (Collin *et al.* 2010); however, it remains a species of concern as a potential invasive in European seas.

Bostrycapulus odites and *C. fornicata* both form mating 'stacks' where a group of individuals cluster in vertical arrangements and experience sequential hermaphroditism known as protandry. Younger animals, at the top of the stack, are male, and transform to females in later adulthood (Hyman 1967; Fig. 1). The largest and oldest (female) animals, at the bottom of the stack, brood their eggs within the shell. Some *Crepidula* species release swimming veliger larvae, whereas *Bostrycapulus* matures larvae within the brood capsule and releases crawl-away metamorphosed larvae (Parodiz 1939).

The native distribution of *B. odites* covers a wide latitudinal and longitudinal range of the South Atlantic, settling on any hard substrata from Southern Brazil to Patagonia and Argentina, and is also found on South African coasts (Collin 2005). This species previously suffered from the taxonomic obfuscation common to all calyptraeids (Collin 2005). It was formerly referred to as *Crepidula aculeata*; recent work identified this cosmopoli-

tan species as a complex composed of at least eight species, which are substantially different from the rest of the *Crepidula* species (Collin, 2005). It is so different, anatomically and genetically, that the species complex was recognized as belonging to the genus *Bostrycapulus* Olsson & Harbison 1953; The Argentinean population contains a single species named *B. odites* Collin 2005; but has previously been recorded as *Bostrycapulus aculeatus* (e.g. Olsson & Harbison 1953) and *Crepidula aculeata* (e.g. Parodiz 1939; Zenetos *et al.* 2005). No studies have examined the reproductive plasticity of *B. odites*, which is essential for prediction of future reproductive success, colonization of new areas and distribution under modified environmental variables.

The key question in this study was whether *B. odites* modifies its reproductive traits with local conditions.

Material and Methods

Samples of stones with *Bostrycapulus odites* attached were collected across the distribution of the species, to sample the northern and southern extremes of its natural distribution and a middle location, at one site in Brazil and two sites in Argentina (Fig. 2). From north to south, the locations are: Ubatuba, Brazil (23°30' S, 45°W), Mar del Plata (MDP; 38°02'10" S, 57°31'29" W) and San Matías Gulf (SMG; 40°50' S, 54°55' W). In the southernmost location, SMG, we sampled two separate sites, one intertidal at Ria San Antonio Oeste and one subtidal at Playa Orenge (12 m depth).

Each of the four populations occupies a different local environment. The population of Ubatuba inhabits subtidal shallow bottoms; in MDP *B. odites* occupies low intertidal to subtidal hard bottoms at c. 7 m depth; in SMG it can be found on hard and soft bottoms at 12 m depth as epibionts of clams, as well as in the intertidal and subtidal where it forms stacks attached to rocks (Fig. 1).

Animals were collected in groups of 100 by the authors by hand or SCUBA diving (MDP, n = 100; SMG intertidal, n = 100; SMG subtidal, n = 300); at Ubatuba only 18 animals were found owing to their scarce abundance (Table 1). Specimens were preserved in 5% formalin diluted in seawater for morphological examination. All specimens were collected under appropriate permits from the relevant authorities.

Shell length was recorded to the nearest 0.1 mm with a digital Vernier calliper. Simultaneously, individuals were discriminated by sex. The sex of each individual was determined by observation of the penis or ovipositor in preserved specimens. When both characters were observed simultaneously, the individual was classified as intersex, while small individuals with no penis were assumed to be sexually immature juveniles. Brooding

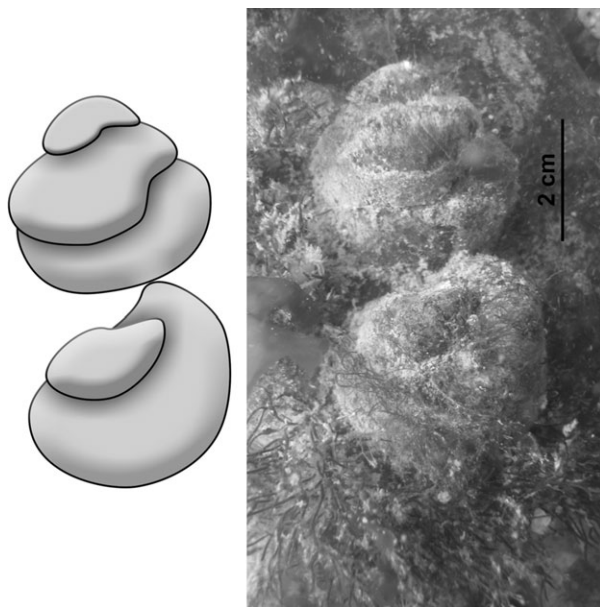


Fig. 1. Photograph and line drawing of *Bostrycapulus odites* forming mating stacks in San Matías Gulf, Argentina, 12 m depth; larger, older specimens at the bottom are female, younger male or immature specimens are at the top.

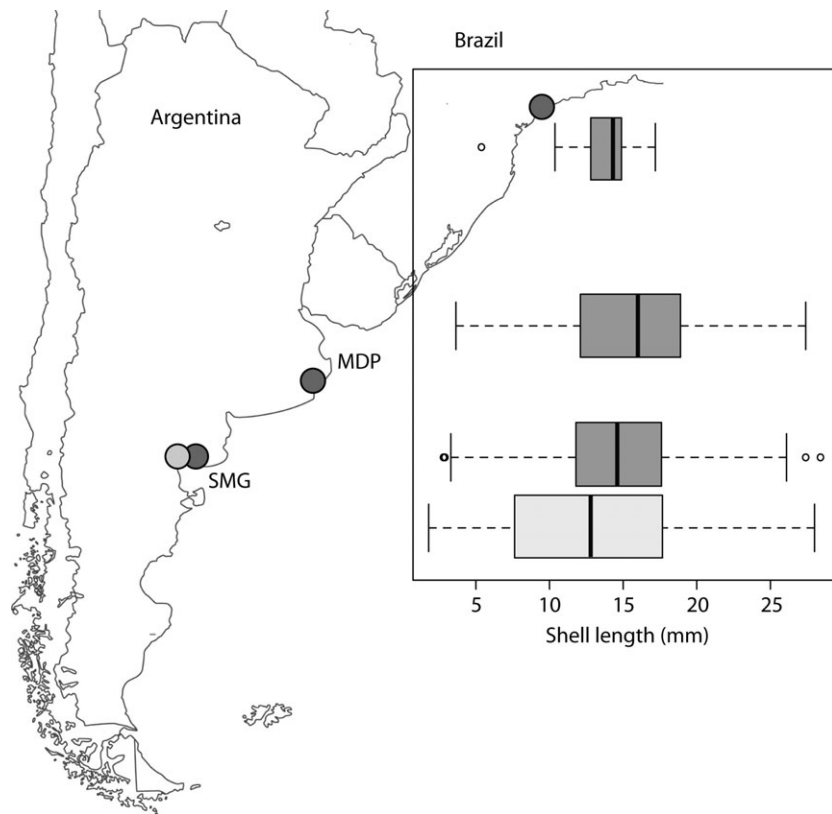


Fig. 2. Map of study area in the SW Atlantic showing location of the sampling sites with total average shell length for the four populations studied at Ubatuba, Brazil; Mar del Plata, Argentina (MDP); and San Matías Gulf, Argentina (SMG). Subtidal populations are in dark grey, the intertidal population is in light grey. Box-and-whisker diagram overlay shows median shell length and inner quartiles.

Table 1. Mean shell sizes of *Bostrycapulus odites*, showing female, male and sexually immature specimens. Differences between specimen numbers within data partitions and the total value are accounted for by intersex specimens (transitioning from male to female), which are not shown. Data are from four sites in three locations in the SW Atlantic, from north to south, Ubatuba, Brazil; Mar del Plata, Argentina (MDP); and San Matías Gulf, Argentina including subtidal (SMG sub) and intertidal (SMG int).

site	shell length (mm)				collecting depth (m)
	female	male	juvenile	total	
Ubatuba	14.28 ± 1.60 (n = 15)	10.07 ± 4.25 (n = 3)	–	13.58 ± 2.62 (n = 18)	3–8
MDP	18.48 ± 3.55 (n = 114)	11.31 ± 3.19 (n = 47)	5.66 ± 1.71 (n = 13)	15.53 ± 5.37 (n = 176)	2–12
SMG sub	18.02 ± 3.26 (n = 155)	12.44 ± 2.19 (n = 141)	4.80 ± 1.51 (n = 19)	14.70 ± 4.59 (n = 318)	3–8
SMG int	17.52 ± 2.88 (n = 205)	8.91 ± 2.15 (n = 129)	4.06 ± 1.06 (n = 61)	12.60 ± 5.84 (n = 399)	0

females were measured separately and the number of capsules per brood (capsule density) was recorded as well as capsule size and capsule length (Fig. 3). When broods were observed to be in the initial or final developmental stage, the number of eggs or number of juveniles per capsule was recorded by counting the whole contents of three capsules (Fig. 3). Egg capsules were counted, measured under a stereoscopic microscope and contained eggs and embryos were counted and measured.

Prior to analysis, the data were tested for homogeneity of variances with the D’Agostino omnibus test implemented in R (R Development Core Team, 2011). As the

data were not normally distributed within all populations, a Kruskal–Wallis test was used to investigate differences in mean size among sample sites, with a non-parametric multiple comparison to determine pairwise differences (Helms & Munzel 2011). To determine the interaction of size and gender we used nested analysis of variance (ANOVA) models on selected transformed data partitions, including zone (intertidal or subtidal in SMG; fixed) and sex (random, nested within zone). To examine interactions of size, fecundity and site we used an analysis of co-variance (ANCOVA) and also followed previous literature on calyptraeids in implementing ordinary least squares (OLS)

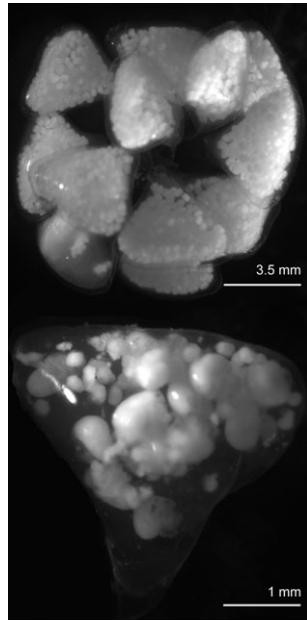


Fig. 3. A brood of egg capsules of *Bostrycapulus odites*, removed from the female shell (top; scale bar = 3.5 mm), and a close-up of one capsule showing developing eggs (bottom, scale bar = 1 mm).

regression analyses (Collin 2000). Finally, local sea surface temperature and daylight hours were plotted to improve the interpretation of differences among population traits. These data were provided from *in situ* data loggers maintained by the National Institute of Fisheries Research and Development (INIDEP) for Mar del Plata and by Institute A. Storni for San Antonio. As the sampling locations were clearly marine, salinity was rather constant and was not taken into account.

Results

Geographical variation in adult size

The mean sizes of animals taken together were significantly different among the four sites considered: Ubatuba, MDP, SMG, and SMG intertidal (Kruskal–Wallis $\chi^2 = 34.89$, $df = 3$, $P < 0.001$). The maximum size of the Brazilian specimens (Ubatuba) was statistically significantly smaller than in MDP (two-tailed $P < 0.01$) but the variance in both the SMG subtidal and intertidal populations masked any statistical differentiation.

In *Bostrycapulus odites*, which experiences a sex change from male to female in mid-adulthood, the parameter of interest to population structure is the size of males and females taken as separate subpopulations. Female shell size reflects maximum potential growth as the sex change is never reversed. Thus, male shell size is the parameter of most interest. The recorded mean male shell length

Table 2. Shell length differences between populations sampled from intertidal and subtidal zones in San Matías Gulf, Argentina, from transformed data analysed by nested analysis of variance (significance is noted: *** $P < 0.005$; ns, not significant).

source of variation	df	MS	F
zone	1	82.43	11.27
sex (zone)	2	7.31	51.86***
residual	396	0.14	
transformation	sqrt(X + 1)		
Cochran's test	ns		

(SL) in Ubatuba, Brazil (23°30' S) was 10.07 mm ($\sigma^2 = 4.25$), in MDP (38°02' S) SL = 11.3 mm ($\sigma^2 = 3.08$) and in the subtidal population in SMG (40°50' S) SL = 12.54 mm ($\sigma^2 = 2.7$). These three populations are significantly different in male shell size (Kruskal–Wallis $\chi^2 = 6.4121$, $df = 2$, $P = 0.041$).

Two populations (intertidal and subtidal zones) were sampled within SMG; a nested ANOVA on transformed data showed no statistically significant differences between the two zones, but the interaction of sex nested at each zone was statistically significant (Table 2). A Tukey's *post hoc* test indicated that this originated from differences in male shell lengths.

The size of animals at sexual (male) maturity was determined as the overlap in size between the largest juvenile specimens and the smallest male specimens, within a tolerance of 0.2 mm. Size at first maturity was significantly different among the three sites (Kruskal–Wallis $\chi^2 = 52.0524$, $df = 2$, $P < 0.001$) and pair-wise comparisons showed that all three sites were different to each other (two-tailed P -values < 0.001 in all). This analysis could not include consideration of the Brazilian data because no juvenile specimens were collected at Ubatuba; however, the smallest adult male specimen was notably smaller than the other, Argentinean, subtidal samples (Fig. 4).

Similarly, the overlap in size range among large male specimens, intersex specimens, and small female specimens, is indicative of the size at hermaphroditic transformation within a population. Size at female transition was not significantly different among the three subtidal sites (Kruskal–Wallis $\chi^2 = 0.9831$, $df = 2$, $P = 0.612$), but all three were significantly larger than at the intertidal site at SMG (Kruskal–Wallis $\chi^2 = 136.3745$, $df = 3$, $P < 0.001$; Fig. 4).

Brood trait comparisons

Among Argentinean populations, the mean number of capsules in each brooding female was significantly different among the three sites, with the highest capsule density at

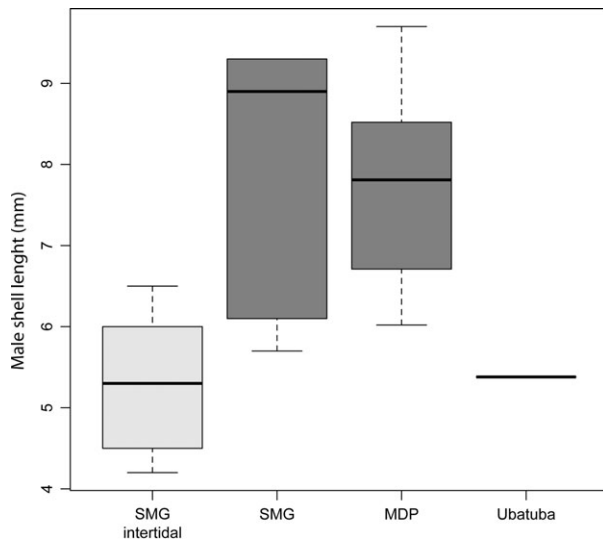


Fig. 4. Box-and-whisker diagram (median and inner quartile dimensions) showing shell length at sexual (male) maturity, taken from the size overlap between large immature specimens and small male specimens at four populations in San Matías Gulf, Argentina (SMG; intertidal in light grey $n = 14$, subtidal population in dark grey, $n = 46$); Mar del Plata, Argentina (MDP, subtidal $n = 25$); and Ubatuba, Brazil (subtidal, $n = 1$).

MDP (Kruskal–Wallis $\chi^2 = 11.96$; $df = 2$; $P < 0.001$). In total, 73 females were found in brooding condition out of 474 mature female specimens collected.

Capsules per brood at MDP ranged from 4 to 22 (mean = 14.7, $\sigma^2 = 4.45$, $n = 25$). At this site brooding females were found every month, but the proportion changed from almost 100% in September and May to <10% in the winter months. Egg capsules ranged from 0.59 to 4.2 mm in length (mean = 3.06, $\sigma^2 = 0.76$) and 0.68 to 5.36 mm in width (mean = 3.7, $\sigma^2 = 0.89$).

The numbers of capsules per brood at the two sites in SMG (subtidal and intertidal) were not significantly different (*post-hoc* pair-wise comparison, two-tailed P -value = 0.52). Intertidal broods contained between 10 and 17 capsules (mean = 12.2, $\sigma^2 = 4.1$, $n = 18$) and from 7 to 20 (mean = 11.1, $\sigma^2 = 3.7$, $n = 30$) in subtidal broods. The mean egg capsule width was 3.40 mm ($\sigma^2 = 0.43$) for intertidal broods and 3.24 mm ($\sigma^2 = 0.67$) for subtidal broods. Brooding females were found at both sites in SMG between October and April, while during the winter months, broods were never found.

In MDP the average number of eggs per capsule was 382, but this was based on a subset of only 11 specimens in suitable condition (without fertilized or developed embryos). By contrast, in SMG subtidal and intertidal specimens the mean numbers of eggs per capsule were much higher (248 subtidal; 253 intertidal). However, all

of the brooding females collected from these two sites were in a suitable condition to count their undeveloped eggs.

In specimens from all three sites the uncleaved eggs measured between 190 and 215 μm in diameter, all of them achieved division until 32 blastomeres but only between 6 and 15 developed to the juvenile stage reaching more than 790 μm in shell length. Each juvenile consumed about 27 nurse eggs before hatching. For specimens in MDP, some of which also contained developing embryos ($n = 7$) and veliger larvae ($n = 5$), the shell length of hatchlings was 800 μm .

Among the total data set for brooding females, there is a significant positive correlation between individual female shell length and the number of capsules per brood (Pearson's correlation co-efficient = 0.351; $P = 0.0026$). Previous workers have used log-transformed data to examine the increase in capsule size with female shell length (e.g. Collin 2000). Applying this approach to our data set showed no significant correlation in the MDP (OLS $r^2 = 0.11$, $P = 0.099$) nor the SMG intertidal populations (OLS $r^2 = 0.035$, $P = 0.46$), but there was a positive log-log correlation in the SMG subtidal population (OLS $r^2 = 0.80$, $P = 0.0079$). There was also a very strong positive linear correlation between female shell length and the average width measured for the individual capsules examined (Pearson's correlation co-efficient = 0.550; $P < 0.001$). This linear correlation was seen in the females in all three sites (Fig. 5). However, the mean capsule counts were significantly different among sites, when controlling for female body size (ANCOVA $F_{2,71} = 6.79$, $P = 0.0020$). This was also true for the mean number of eggs per capsule, which varied among sites independent of female shell length ($F_{2,53} = 8.35$, $P = 0.00073$). The animals from MDP were the most fecund; SMG subtidal animals were the least fecund.

Sea surface temperature and daylight seasonal fluctuations

There is a delay of nearly 2 months between daylight and surface temperature at all locations. Ubatuba, Brazil, presents a daylight seasonal fluctuation of 3 h and a temperature range of 9 °C. In Argentina, MDP fluctuates by 5 h of light and around 10 °C seasonally, while San Antonio differences are 6 h and 15 °C at the lower subtidal and 6.5 °C at 10 m depth.

Discussion

We found a robust correlation between female shell length and capsule count, but, unexpectedly, fecundity varied among sample sites independent of female size. This is partly in conflict with previous studies on

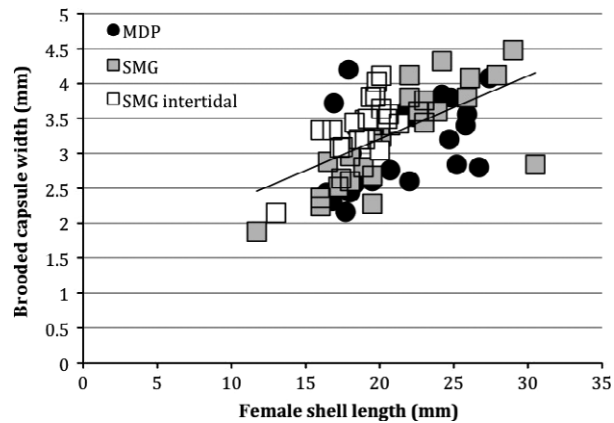


Fig. 5. Comparison of egg capsule size and the shell length of brooding females of *Bostrycapulus odites* in three Argentinean populations: Mar del Plata (MDP, black circles) and San Matías Gulf (SMG) subtidal (grey squares) and intertidal (white squares), showing the least squares line of regression for the total trend across all three populations.

calyptraeids that showed female body size to be a strong predictor of fecundity in *Crepidula* spp. (Hendler & Franz 1971; Collin 2000). Our results allow us to compare life history traits among four conspecific populations separated latitudinally, and to put *Bostrycapulus odites* in context with other members of Calyptraeidae. Subtidal populations of *B. odites* show a general latitudinal gradient, with increasing size at sexual maturity poleward from north to south; however, intertidal populations reach sexual maturity at smaller sizes. Among subtidal populations, size at sexual maturity (as a male) and size at sex change (to female) are both delayed at higher latitudes. Yet, females at our intermediate subtidal site (MDP) are apparently more fecund than the southernmost site (SMG).

Abiotic factors and fecundity

It is relevant to consider the major abiotic differences across this latitudinal gradient that may have greater control over reproductive potential (female fecundity) than individual body size, for example photoperiod, temperature and tidal flux. In Alicante, Spain, where a feral population of *B. odites* is established (Izquierdo *et al.* 2007), temperature fluctuates by 12 °C from summer to winter while daylight changes by 5 h. This is a slightly wider temperature range, but a similar photoperiod, compared with the sites that we sampled in its native range.

Photoperiod appears to be the predominant environmental cue that regulates reproductive tract recrudescence in many species, while secondary cues include temperature and nutrition, which control the timing of breeding

and egg laying through several hormone products (Sternberg *et al.* 2010). Although separated by 2° of latitude, the photoperiod differs between MDP and SMG by 1 h, which is correlated with the observed differences in fecundity.

There is a latitudinal thermal cline of coastal water temperature. The sampled subtidal population at SMG experiences a constrained thermal range. The mean surface temperature at the intertidal site at SMG (mouth of the river Ria San Antonio) ranges from 7 °C in winter to 21 °C in summer. This is very similar to the reported shallow subtidal temperatures in MDP, with a annual thermal range from 8 to 22 °C (Cledón *et al.* 2005). Finally, the temperature in Ubatuba, Brazil, at 3 m depth, ranges from 23 °C in winter to 26 °C in summer. The mean adult female shell size does not differ among these three sites; however, female sizes in the more tropical site at Ubatuba, Brazil, are significantly smaller.

Yet the surrounding water temperature does not determine all reproductive traits in this species, as the MDP and SMG intertidal populations live at the same temperature, but present different spawning seasons and dramatically different sizes at first maturing (Fig. 4). The SMG subtidal and intertidal populations live under different temperature ranges yet share the same spawning season.

On the other hand, the northern part of the Argentinean coast is washed by the last tail of the convergence of the currents of Brazil and Malvinas (Falkland Islands) during austral winter, which is known to increase the phytoplankton availability at the area (Boltovskoy 1999). The basin of San Matías Gulf presents a semi-closed internal circulation (fully described in Morsan *et al.* 2010) that minimizes incoming water masses. This hydrographical containment could enable a comparatively longer spawning season in the SMG populations.

The most substantial difference in environment among the three Argentinean populations is that one location is in the intertidal zone, and is exposed to the air during many low tides. There is a desiccation stress factor added to the fact that the animals cannot filter (breathe and feed) during these periods. A negative impact of emersion on growth rate and consequent differences in size at sex change, brooding female size and maximum final size, should be expected for these populations, and is confirmed by the present results. Yet, the intertidal population has an intermediate (not the minimum) mean fecundity among the three Argentinian populations.

In the SMG intertidal population, females are able to brood egg capsules when they reach 13 mm, which is the shortest shell length among the studied populations. Since these females can reach large SLs, this population has the widest SL range of brooding females of those we studied. The inter-tidal specimens reached maturity more quickly

and changed sex at smaller size, although they reached the same maximum sizes as their subtidal neighbours. Maturity at an earlier size would increase the total lifetime fecundity of individuals in this intertidal population, which may be necessary for coping with a more challenging physical environment.

Another factor speculatively affecting these shallow-water and intertidal populations is anthropogenic pollution. Heavy metal pollution (Pb and Cr) has been reported in Ubatuba, Brazil (Avelar *et al.* 2000). SMG suffers from sewage-induced eutrophication (Teichberg *et al.* 2010), whereas in MDP there are reports of hydrocarbons (Colombo *et al.* 2005), heavy metals (Ferrer *et al.* 1993) and tributyl tin (Cledón *et al.* 2006). Bigatti *et al.* (2009) sampled *B. odites* individuals from our study locations and did not find any sign of imposex effects on this species. They concluded that its hermaphroditism implies a hormone path that would not be affected by tributyl tin, although some females of the congeneric *B. calyptraeformis* in areas of high marine traffic did develop signs of imposex (Li & Collin 2009).

Plasticity in reproductive ability

Many species with wide geographical distributions have been shown to exhibit a variety of reproductive strategies depending upon local conditions. Duration and intensity of gonadic cycles are highly variable within a single species, varying with latitude, but biologically driven by temperature and nutrient availability, and populations may alter their behaviour in different years depending on local conditions (Fretter 1984; Cárdenas & Aranda 2000). For *B. odites* in Argentina, each population spawns from austral spring to late summer at high latitudes but almost all year round at lower latitudes.

When spawning intensity increases, spawning seasons can shorten to improve synchronicity (Cárdenas & Aranda 2000). Such differences can be observed in *B. odites*, since the northern population studied here presents a longer spawning season than the more southern locations, which is not only related to temperature. Site-to-site variation in the timing of reproduction within populations may also be as large as broader-scale temporal and latitudinal variation, particularly at different depths and between subtidal and intertidal populations (*e.g.* Fletcher 1987).

Calyptraeid limpets more broadly exhibit a wide range of life history strategies; stacking and hermaphroditism are not universal within the family but there are several other species that have been studied, mostly from a single locality, that share the generalized life history of *B. odites*. Most other calyptraeids of similar body size and with direct development (brooding crawl-away larvae) have dramatically lower fecundity than *B. odites*; *Crepidula*

convexa individuals have 13–14 eggs per capsule (Hendler & Franz 1971) and *Crepidula adunca* around nine per capsule (Collin 2000), while from our own data *B. odites* had on average 21–28 eggs per capsule across the different sites.

From the present results, if the invasive population of *B. odites* now settled on the Spanish Mediterranean coast continues to colonize new areas, we predict it could expand along the Atlantic coast owing to the similarity in sea conditions (surface temperature range, tidal amplitude and latitudinal location) between the snail's native and invaded shores. Moreover, intertidal populations could develop in macrotidal areas, such as Normandy and the Wadden Sea.

Within its native range, as the females of *B. odites* get bigger, their number of capsules increases, but surprisingly the capsule size gets bigger as well. This means that larger females are even more fecund. This is variable amongst sites independent of female size but populations at higher (more temperate) latitudes would especially have higher fitness and could therefore be more competitive.

A northward direction of expansion implies the potential for competition with the invasive slipper limpet *Crepidula fornicata*, which is already present in Europe. As *C. fornicata* has colonized the shores from the Mediterranean to the mouth of the Baltic sea (Blanchard 1997), both species are already co-existing on the Mediterranean coasts.

Within the European distribution of *C. fornicata*, its optimal environmental range seems to be located on the French coasts and Southern England (Blanchard 1997). Furthermore, Thielges *et al.* (2003) indicated that this species invaded the Wadden Sea around 1934, but the current population density there is considerably lower than on more southerly European coasts.

Several species of Calyptraeidae are notable invasive species and knowledge of the biology of all members of the family is potentially relevant to prevention and control of the spread of invasives. *Bostrycapulus odites* is a species of particular concern. Streftaris & Zenetos (2006) included '*Crepidula aculeata*' (*i.e.* currently *B. odites*) within the 100 worst invasive species of the Mediterranean Sea because of the impact that it has on local diversity. This species is a common member of Hawaiian fouling communities as well as sediment faunas, which implies that it is capable of crawling over certain grain sizes to colonize neighbouring hard surfaces (Coles *et al.* 1999).

Conclusions

Bostrycapulus odites has both the opportunity and the capacity to settle on the extremes of the European

distribution of *Crepidula fornicata*. A small population of this species is already established in Europe (Izquierdo *et al.* 2007) and, although its dispersal potential is limited by its brooding strategy, we have shown here that its fecundity is not entirely dependent upon female body size. *Bostrycapulus odites* thrives in temperate waters and the potential plasticity in reproductive ability demonstrated in populations of *B. odites* in its native range, especially between intertidal and subtidal populations, indicate that this species has an adaptive capacity to local conditions, to maximize its reproductive potential.

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