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CREPIPATELLA DILATATA (LAMARCK, 1822) (CALYPTRAEIDAE): AN EXAMPLE OF REPRODUCTIVE VARIABILITY AMONG GASTROPODS

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ABSTRACT

Reproductive characteristics of a species are often defined from a small number of individuals collected from a single location at one particular time. However, this study reveals that the South American gastropod *Crepipatella dilatata* (Lamarck, 1822) shows an unusually high level of intraspecific variability in some key reproductive characteristics: the number of egg capsules brooded per female, the size of the egg capsules, the number of eggs per capsule and the sizes and size distributions of the uncleaved eggs. Larger females were more fecund than smaller ones, not because they produced more egg capsules, but because they produced capsules of significantly larger size. Such variability was evident not only when considering different populations, but also within a single population sampled in different years, as well as among specimens collected during a single sampling event. Thus our data emphasize the importance of obtaining information from numerous specimens per locality as well as from specimens from different localities and in different years when describing the reproductive characteristics of any particular taxon.

INTRODUCTION

Differences in reproductive characteristics and patterns of development are frequently used in molluscs to distinguish among species and to understand the evolution of reproductive patterns (Gallardo, 1977a, 1979; Collin, 2000, 2003, 2004; Simone, Pastorino & Penchaszadeh, 2000; Véliz, Winkler & Guisado, 2003). In the southeastern Pacific Ocean, for example, *Crepipatella dilatata* (Lamarck, 1822) is sympatric with the morphologically cryptic *C. fecunda* Gallardo, 1979. Both species encapsulate their embryos in transparent egg capsules, which are then incubated in the mantle cavity until hatching (Gallardo, 1977a, 1979). However, the two species differ markedly in their pattern of development: whereas females of *C. fecunda* release planktotrophic larvae (Gallardo, 1979; Chaparro *et al.*, 2005), the offspring of *C. dilatata* complete larval development within capsules, emerging as fully formed juveniles. Indeed, *C. dilatata* and *C. fecunda* are excellent examples of how important reproductive characters can be in recognizing and defining species.

For reproductive patterns to serve as reliable systematic and phylogenetic tools, it is important to know how uniform these patterns are among populations and among years (Collin & Salazar, 2010). *Crepipatella dilatata* (frequently referred to as

Crepidula dilatata) is one of the most studied species in the family, with most of the studies having been performed along the Chilean coast (Gallardo, 1976, 1977a, 1979; Gallardo & Garrido, 1987; Chaparro *et al.*, 1999; Véliz *et al.*, 2003). Even so, those studies have come to a range of sometimes conflicting conclusions, which are addressed here. In particular, there is disagreement about whether the distribution of egg sizes within the egg capsules of this species is bimodal (Gallardo, 1977a, 1979) or unimodal (Penchaszadeh, Pastorino & Cledón, 2002) and about whether there is (e.g. Gallardo, 1976) or is not (e.g. Gallardo, 1977a) a positive relationship between female size and fecundity.

In this paper we have reexamined the egg-size distribution in *C. dilatata* and reexamined in more detail the relationship between female size and fecundity, looking in particular at whether larger individuals increase their fecundity by packaging more eggs per egg capsule, by increasing egg capsule size or by producing more egg capsules per brood.

MATERIAL AND METHODS

A total of 66 female *Crepipatella dilatata* were collected at random from their substrates from two different localities along the

southern Chilean coast in three different years: 30 females from Quempillén (41°52'S, 73°45'W, Chiloé I.) in December 2003, 20 females from Quempillén in October 2004 and 16 females from Bahía Mehuín, Valdivia (39°25'S, 73°13'W) in January 2005. The specimens here studied were found living on small rocks, *c.* 7–12 cm in diameter. As substrate size could potentially restrict the maximum size of female specimens (so that growth could be occurring in height instead of length) the relationship between dry tissue weight and shell length was examined from a subsample of 30 specimens. These variables were found to be positively correlated (see the Results section), so maximum shell length was later used as an estimator of adult size.

The snails were removed from their substrates in the laboratory to obtain the egg masses. For each female, we counted the number of egg capsules per brood mass and measured the capsules at 15× magnification using an ocular micrometer mounted in a stereoscopic microscope, according to the following criteria: H = maximum height without the peduncle; W = maximum width, perpendicular to H (Fig. 1). Taking into account that the egg capsule outline is approximated by two right-angle triangles, the area of each egg capsule was determined as $A = W \times H$.

To examine the size distribution of eggs within broods, capsules were sampled from six brooding females collected in January 2005 from Mehuín. Only capsules containing early embryos (fewer than 128–256 cells) were examined, to avoid

problems associated with potential consumption of nurse eggs by more advanced embryos. Two or three capsules (usually three) were opened from each female and all of the eggs inside were measured at 50× using a dissecting microscope equipped with an ocular micrometer. In total the complete contents of 17 capsules (*i.e.* more than 3,700 eggs) were measured. Means were compared by one-way ANOVA when assumptions of homogeneity of variance were met (Barlett's test). Otherwise, means were compared using the Kruskal–Wallis test followed by Dunn's multiple comparison tests. The relationships between variables (*e.g.* number of egg capsules as a function of female shell length) were examined by regression analysis and ANCOVA.

RESULTS

Capsule and egg production by females from different collections

The females examined in this study ranged between 12.7 and 34.5 mm in shell length (Table 3); females over this entire size range were brooding egg capsules when collected. Females were significantly smaller at Mehuín than at Quempillén (Fig. 2C; Table 3) (Bonferroni's *post hoc* comparisons, $P < 0.01$); the largest individual collected at Mehuín was only 20 mm in shell length. We found a linear relationship ($P < 0.01$) between female shell length and dry tissue weight (Fig. 3).

The number of capsules per spawning mass ranged between 4 and 24 (mean \pm SD = 12.8 ± 5.3 , $n = 60$) and at Quempillén differed significantly between the samples taken 9 months apart (Fig. 2A) (Bonferroni's *post hoc* comparison, $P < 0.01$), even though mean female size in the 2 years did not (Fig. 2C); no other comparisons yielded significant differences.

There was no significant correlation between the number of egg capsules being brooded per female and female shell length when considering either the overall data set ($r^2 = 0.001$, $P = 0.79$) or each of the samples individually (Mehuín: $r^2 < 0.001$, $P = 0.99$; Quempillén 2003: $r^2 = 0.11$, $P = 0.08$; Quempillén 2004: $r^2 < 0.001$, $P = 0.95$) (Fig. 4A; Table 1). This fact is related to the great variability in mean number of egg capsules brooded by individuals within a given size range (Fig. 5).

There was no significant relationship between female dry weight and egg capsule production (Fig. 4B) (overall r^2 for combined data = 0.001; results of two-way ANOVA shown in Table 1). However, the number of eggs per capsule differed significantly for females collected in the three samples (KW = 69.28, $P < 0.0001$) (Fig. 2B). The number of eggs per capsule ranged from 46 at Mehuín to 721 at Quempillén, with a maximum of 4,418 eggs per egg mass.

Relationships between capsule sizes and female sizes

Mean egg capsule surface area varied greatly, not only among females but also among egg capsules produced by any given female, and capsule surface area was reasonably well predicted by female shell length (Fig. 6; Table 2). In this regard, egg capsules ranged in between 2.4 and 4.5 mm in height and between 2.4–5.2 mm in width, resulting in a range of egg capsule areas from 5.76 to 28.08 mm² (Table 3).

Although the number of egg capsules was not correlated with female size, egg capsule surface area was positively correlated with female size ($P < 0.0001$) when all data were combined for analysis (Fig. 6), but not when location was considered as a separate factor (Table 2). Larger egg capsules tended to hold more eggs (Fig. 7), so that larger females produced more eggs.

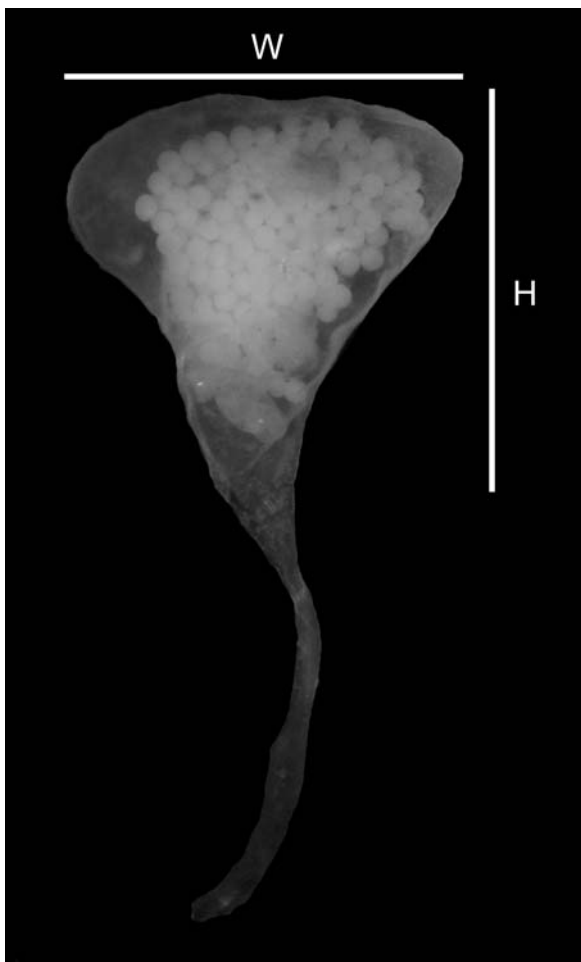


Figure 1. Egg capsule of *Crepipatella dilatata*, showing the dimensions measured (H = height, W = width).

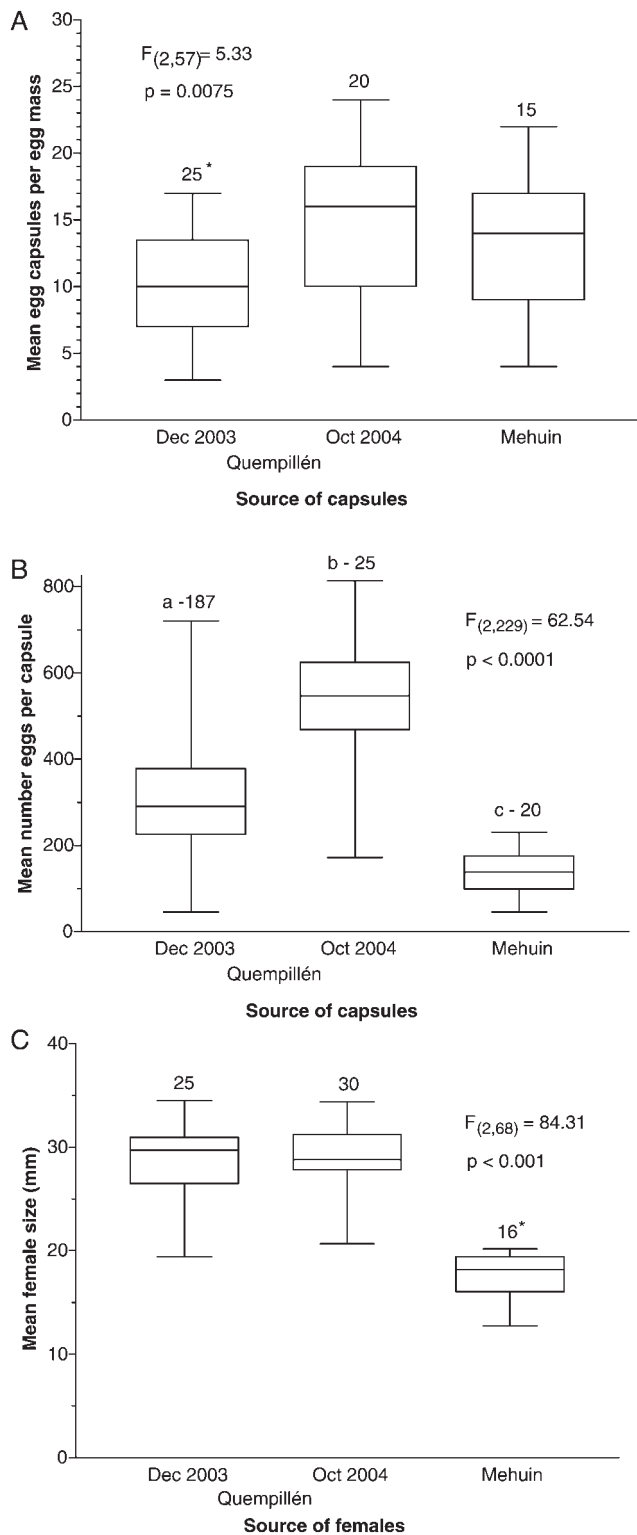


Figure 2. Influence of collection site and year on egg capsule (**A**, **B**) and female (**C**) characteristics of *Crepipatella dilatata*. Number above bars indicates sample size. Different letters above bars (in **B**) indicate means that are significantly different ($P < 0.05$).

Eggs sizes

Uncleaved eggs ranged between 154 and 300 μm in diameter (Fig. 8; Table 3), and the complete range of egg sizes could be found within individual egg capsules. In our samples, the

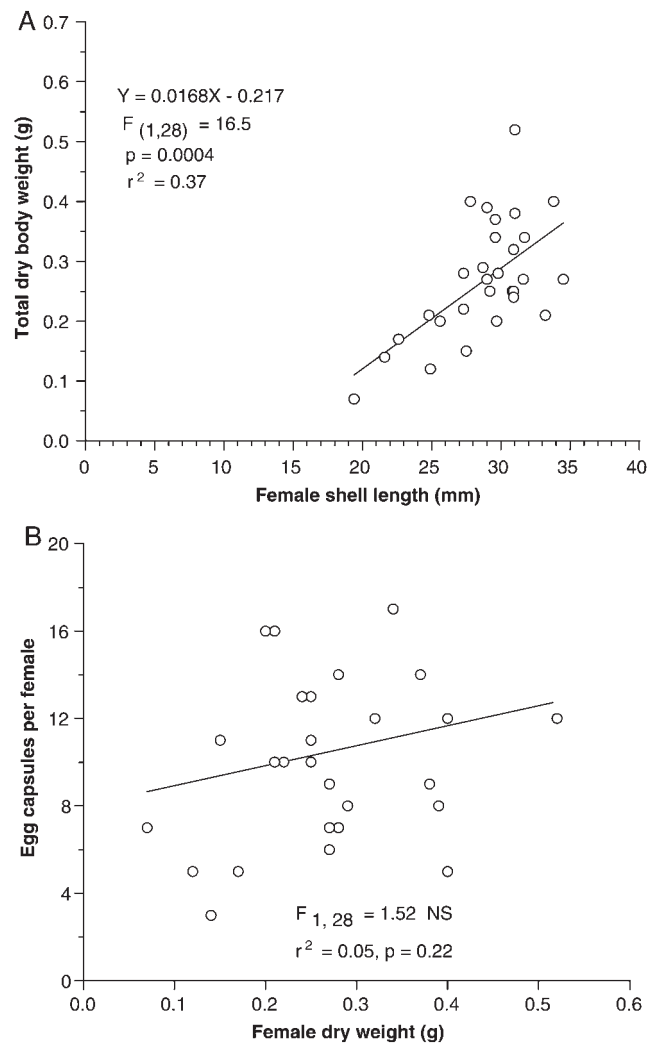


Figure 3. Relationship between female shell length and dry body weight for *Crepipatella dilatata*.

distribution of egg sizes within individual egg capsules followed a unimodal pattern in 19 egg capsules and a bimodal pattern in the other 7 capsules (Fig. 9). When the size distribution was bimodal, the larger eggs (200–300 μm in diameter) were consistently more frequent than the smaller ones (154–200 μm). These two patterns of egg-size distribution were seen not just for capsules obtained from different females, but were in fact equally common for different egg capsules sampled from the same egg mass; i.e. individual egg masses had some egg capsules showing a unimodal egg-size distribution while other egg capsules being brooded by the same female showed a bimodal distribution in egg size.

DISCUSSION

Information presented in this study reveals considerable variation in some key reproductive characteristics of *Crepipatella dilatata*, such as the relationships between female size and the number of brooded egg capsules, the size of those capsules and the number and size of the eggs. The data also illustrate the extent of the variability that can be expected for the family Calyptraeidae with regard to offspring production among females, and among females from different localities. Similarly, Collin & Salazar (2010) have documented considerable

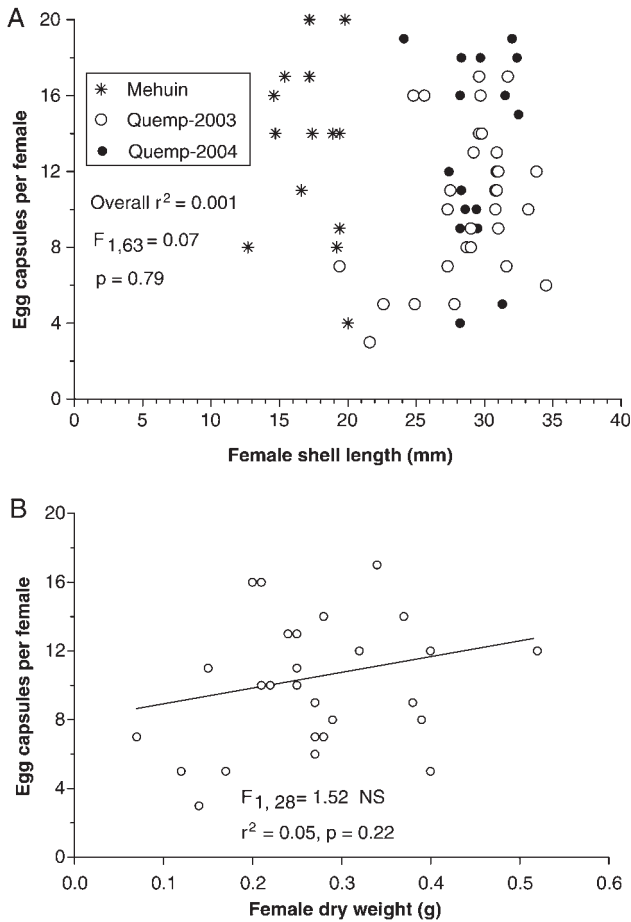


Figure 4. Number of egg capsules of *Crepidatella dilatata* according to shell length of parental specimen (A) and female dry weight (B). Symbols: asterisk, specimens from Mehuín; open circle, specimens from Quempillén, December 2003; filled circle, specimens from Quempillén, October 2004.

Table 1. ANCOVA results (GLM procedure) for the relationship between fecundity and female shell length for *Crepidatella dilatata* (Fig. 4).

Source	df	Type III SS	F	P
Female shell length	1	3.23	0.13	0.72
Sample site-year	2	39.65	0.82	0.45
Interaction	2	16.16	0.33	0.72

variability in egg diameter and in hatchling size and shape for *Crepidula atrasolea* (Collin, 2000) and *Crepidula ustulatulina* (Collin, 2002). Such variability must be considered in subsequent systematic studies of the family.

The number of brooded egg capsules per female ranged in *C. dilatata* from 4 to 29, a considerably wider range than that reported by Gallardo (1979: 22–29 capsules), even though the size range of females examined in the two studies was similar. When examining specimens from Mehuín, Gallardo (1976) found that larger individuals produced more egg capsules per egg mass. This conclusion is not in accordance with our results, even for the specimens from the same locality, nor with those by Gallardo (1977a), based on specimens from Chinguihue; in these other studies, adult size and egg capsule production were not significantly related. Chaparro *et al.* (1999: 266) also reported that “the number of capsules... showed a significant

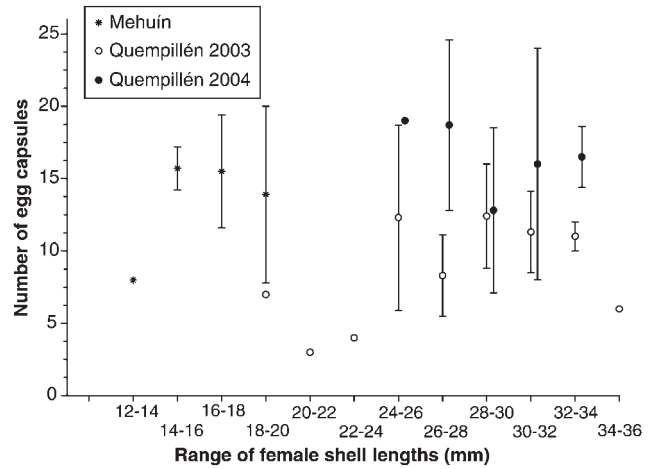


Figure 5. Relationship between female shell length and number of brooded egg capsules per female *Crepidatella dilatata*. Symbols as in Fig. 4.

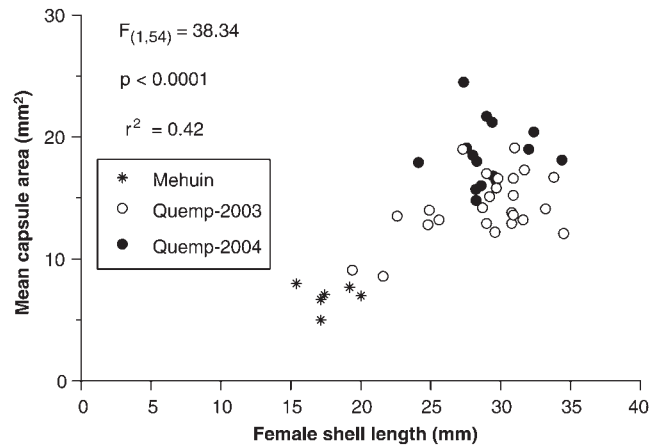


Figure 6. Mean capsule area of *Crepidatella dilatata* according to shell length of females. Females were collected from specimens from Quempillén in two different years, as shown, or at Mehuín. Symbols as in Fig. 4.

Table 2. ANCOVA results (GLM procedure) for the relationship between mean egg capsule surface area and female shell length for *Crepidatella dilatata* (Fig. 6).

Source	df	Type III SS	F	P
Female shell length	1	4.07	0.51	0.48
Sample site-year	2	5.14	0.32	0.73
Interaction	2	2.84	0.18	0.84

relationship with the shell length of female”, but later (p. 267) concluded: “there was not significant relationship between the number of capsules per brood and the shell length”. The lack of a clear relationship between both variables seems to originate in the wide variability exhibited among different females of similar shell length (Fig. 5). Note that a few females might not have finished depositing egg capsules when we sampled them. However, even if we eliminate data for the four individuals producing five or fewer egg capsules, there is still no significant relationship between female dry weight and number of capsules deposited ($F_{1,26} = 0.20$, $P = 0.66$, $r^2 = 0.008$).

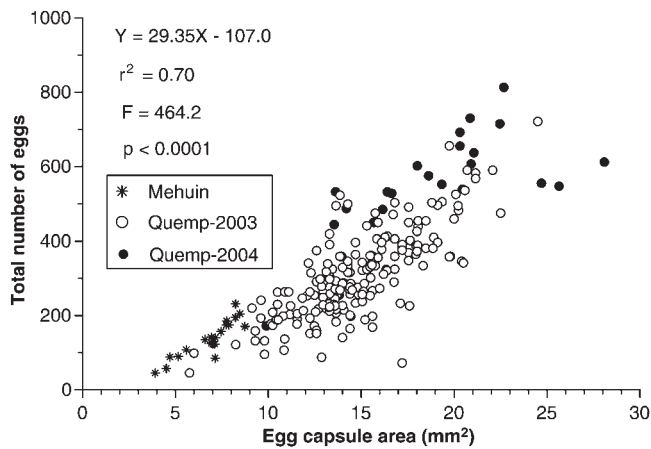


Figure 7. Relationship between capsule area and number of eggs for *Crepipatella dilatata*. Symbols as in Fig. 4.

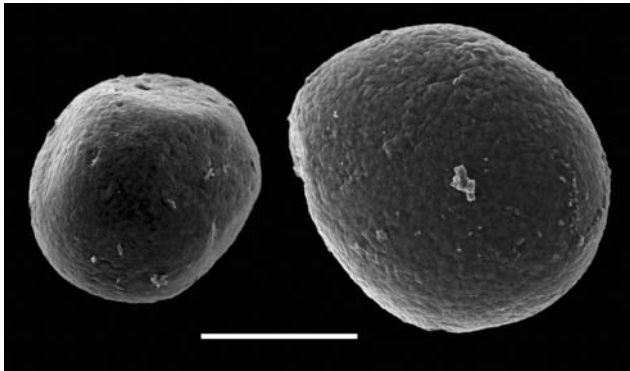


Figure 8. ‘Small’ (left) and ‘large’ (right) uncleaved eggs of *Crepipatella dilatata*. Scale bar = 100 µm.

The size of the egg capsules we examined varied between 2.4–4.5 mm height \times 2.4–5.2 mm width, with the larger females brooding larger egg capsules. In addition, the larger egg capsules contained more eggs. The number of eggs per capsule ranged between 46 and 721. These values show some differences when compared with data from previous studies: 46 is the lowest number of eggs per capsule presently known for the species; the maximum number found in this study (721) is included in the range estimated by Gallardo (1979), but is considerably larger than that reported by Véliz *et al.* (2003) in specimens from Coquimbo Bay (223–363 eggs per capsule).

The sizes of the uncleaved eggs observed in this study (154–300 µm) were slightly greater than the values previously indicated by Gallardo (1977a), who reported the eggs as being 195–263 µm in diameter, but are similar to those indicated by Véliz *et al.* (2003). Regarding egg-size frequencies, the present study indicates that egg size showed a unimodal curve for some capsules but a bimodal distribution in other capsules, with a group of smaller eggs (154–200 µm) and a group of larger eggs (200–300 µm in diameter) within a single egg capsule. The first pattern (unimodal) agrees with the previous findings of Penchaszadeh *et al.* (2002), although those researchers did not indicate how many egg capsules their observations were based on; the bimodal distribution of egg size that we report here agrees with that reported by Gallardo (1977a, 1979), who found this pattern in an egg capsule from Chiquihue Bay and

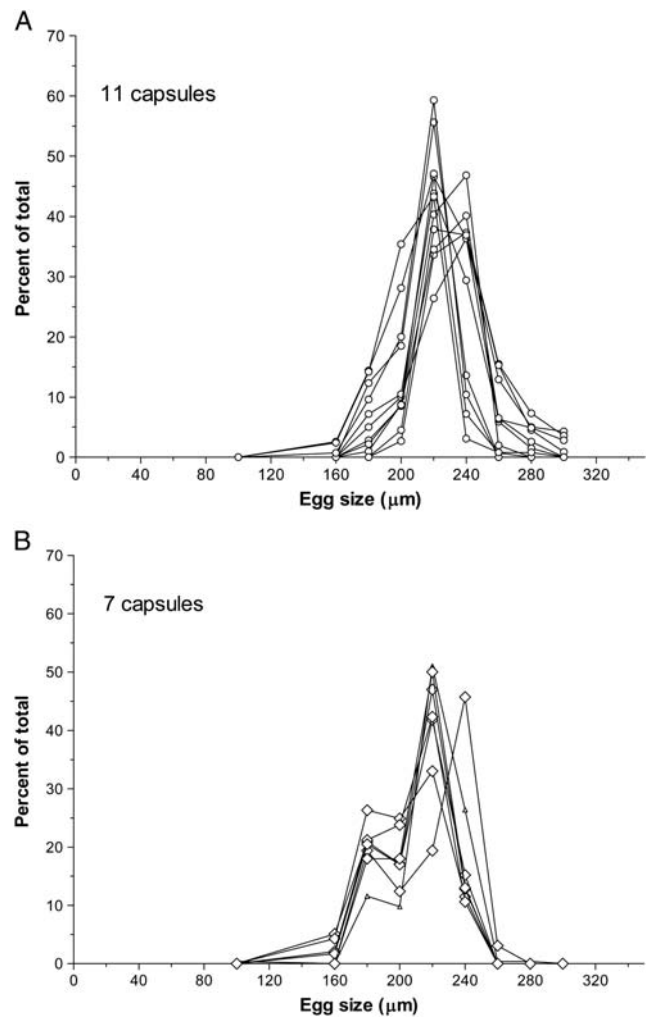


Figure 9. Distribution of egg sizes within egg capsules of *Crepipatella dilatata*. **A.** Capsules showing unimodal egg-size distributions only (11 capsules). **B.** Capsules showing bimodal egg-size distributions only (6 capsules).

in capsules from Mehuín. In the second case, and as indicated by Gallardo (1977a), the smaller eggs were the less frequent.

Our results make clear that the egg-size distribution (unimodal *vs* bimodal) for *C. dilatata* is not uniform among capsules. This in turn suggests that the fate of the eggs in capsules with bimodal size distributions, whether they will develop into embryos or function as nurse eggs, is not determined by egg size. The proportion of nurse eggs within a capsule was similar among capsules and, according to Gallardo (unpublished observations), in bimodal capsules the fate of the initial eggs (nurse *vs* developing ones) is independent of the egg-size group to which they belong. Typically, the egg capsules of this species contain 16–18 nurse eggs per embryo (Gallardo, 1977a).

The variability found in reproductive characteristics of *C. dilatata* is not restricted to the above-mentioned characteristics. Chaparro *et al.* (1999) also reported a great variability in the total number of embryos that develop per egg capsule, ranging between 0 to more than 50. Since selection should maximize the number of embryos per amount of energy invested in the egg capsules themselves it is not surprising that larger capsules tend to support a greater number of developing embryos.

Table 3. Variability presently known in different populations of *Crepidatella dilatata*.

Locality	Female length		Egg size		Capsules per egg mass		Reference
	Range (in mm)	Mean \pm SD	Size (in μm)	Number of capsules	Capsule area (in mm^2)	Mean \pm SD	
Quempillén Dec. 2003	19.4–34.5	28.85 \pm 3.79 (n = 25)	154–300 (n = 9)	3–17 (n = 25)	5.76–24.50	14.77 \pm 3.11 (n = 25)	This study
Quempillén Oct. 2004	29.7–34.4	28.98 \pm 2.74 (n = 30)	154–300 (n = 4)	4–24 (n = 20)	9.90–28.08	18.42 \pm 4.46 (n = 15)	This study
Quempillén	18.0–34.0					14.7 \pm 3.22 (n = 110)	Chaparro <i>et al.</i> (1999)
Mehuín	12.7–20.1	17.45 \pm 2.27 (n = 16)	154–300 (n = 6)	4–12 (n = 15)	3.92–8.75	6.87 \pm 1.39 (n = 6)	This study
Mehuín	12.0–28.0		196–246 (n = 5)	7–20 (n = 34)			Gallardo (1976)
Chinquihue	20.0–50.0	35.13 (n = ?)	195–263 (n = 1)	24–27 (n = 2)			Gallardo (1977a, b, 1979)
Mancera				22–29 (n = 2)			Gallardo (1979)
Coquimbo	18.8–37.0	25.98 \pm 6.27 (n = 57)	173–270 (n = ?)	4–24 (n = 28)			Vélez <i>et al.</i> (2003)

Another variable character is the shell length of the hatching juvenile, which ranges between 0.8 and 1.8 mm (Gallardo, 1976, 1977a, 1979; Gallardo & Garrido, 1987; Chaparro & Paschke, 1990; Chaparro *et al.*, 1999). Provided that eggs sizes are not markedly different among localities (but see Collin & Salazar, 2010), interpopulation variation in the quantity of nutritive material eaten by each encapsulated embryo probably accounts for most of the geographic differences in average hatching size. Attributes like hatching size are of great selective value for marine caenogastropods (e.g. Spight, 1976). Hatching-size frequencies in each population normally follow a normal distribution, as observed for instance by Gallardo (1981) in the case of the muricid gastropod *Chorus giganteus* (Lesson, 1829).

Crepidatella dilatata shows an unusually high level of intraspecific variability in reproductive characteristics, compared with that reported for most other species of the family. For example, various species of *Crepidula* show less variability in the total number of eggs per egg capsule (8.78 \pm 2.48 in *Crepidula adunca* Sowerby, 1825; Collin, 2000); in the range of egg sizes [250–350 μm in *Crepidula adunca* (Collin, 2000) and 136–170 μm in *Crepidula philippiana* Gallardo, 1977 (Gallardo, 1996)]; in the number of embryos that develop per egg capsule; and in the number of hatching specimens (Gallardo, 1996; Collin, 2000, 2003). However, *Crepidula atrasolea* and *Crepidula ustulatulina* show similarly high levels of variability among females (Collin & Salazar, 2010).

In summary, key reproductive characteristics show great intraspecific variability in *Crepidatella dilatata*, not only when considering different populations but also within a single population sampled in different years and even among specimens collected during the same sampling event. Some differences correlate with differences in female size. Such differences in fecundity are not due to differences in the number of egg capsules produced, however, but rather in the size of the capsules, a character that is positively correlated with the number of eggs they each contain. Thus, larger females produce larger egg capsules, and thus a greater number of eggs. The pattern here reported for *C. dilatata* differs from that reported for species of *Crepidula* with direct development such as *Crepidula convexa*, *Crepidula adunca* and *Crepidula philippiana*, where the number of capsules correlates positively with female size (Gallardo, 1996; Collin, 2000; Li & Pechenik, 2007, respectively). The same occurs, however, in the case of *Crepidatella fecunda*, a closely related species with free-living larvae in the life history; this could suggest an advantage taken by this species by evolving a larger adult size (and consequently a greater fecundity per female) than in the case of *C. dilatata*, probably because the developmental stages of *C. fecunda* must confront a major uncertainty of larval recruitment and dispersal, reproductive assurance being thus improved through larger and more fecund females. In addition, in *C. dilatata* (this study), as also reported for *Crepidula adunca* by Collin (2000), there is a positive relationship between capsule size and number of eggs; however, these variables are not correlated in *Crepidula philippiana*, where the mean size of the egg capsules is constant and does not vary with female size (Gallardo, 1996). The development of *Crepidula philippiana* is unusual in that only one embryo develops within each egg capsule (Gallardo, 1977b), so that there would be no selective advantage for this species for females to invest more energy into each egg capsule by making them larger. Furthermore, the number of nurse eggs available for the unique embryo remains more or less constant.

In recent laboratory studies, Collin & Salazar (2010) showed that rearing temperature can produce differences in egg size and hatching size for two *Crepidula* species (*Crepidula atrasolea* and *Crepidula ustulatulina*). Temperature differences might also be, at least in part, the source of variability reported in the

present study for *C. dilatata* from different populations and in different years. However, it is clear that this is not the only source of variation; in fact, this study shows the existence of differences between specimens from the same locality when considering different times of the year and even among specimens within a single sampling. The great intraspecific variability in key reproductive characteristics shown here for *C. dilatata* reveals that previously published information on life histories should be used with caution in systematic studies (see also Collin & Salazar, 2010). Previous papers frequently provided reproductive characteristics of particular species based on only one or a few specimens, and specimens collected from only one locality in one year and one time of year. The evidence provided here for *C. dilatata* and by Collin & Salazar (2010) for two *Crepidula* species shows the importance of obtaining information from numerous specimens per locality, as well as from specimens from different localities and in different years when describing the reproductive characteristics of a particular taxon (Table 3).

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