

Two Modes of Development in the Morphospecies *Crepidula dilatata* (Gastropoda: Calyptraeidae) from Southern Chile*

C. S. Gallardo

Instituto de Zoología, Universidad Austral de Chile; Valdivia, Chile

Abstract

In Chinquihue Bay, a sheltered locality in Southern Chile, female *Crepidula dilatata* Lamarck brood egg masses which differ in intracapsular development. In some, all eggs develop and are hatched as free veliger larvae (indirect development). In others, only some of the eggs develop and hatch as young adults (direct development), the rest being consumed as nurse eggs. Two possible interpretations are considered: intrapopulation variation of developmental pattern in a species, and the coexistence of two sibling species. Stages of the intracapsular development are described and illustrated. Fecundity varies according to size of the female. For females brooding eggs with indirect development it is estimated at between 3840 and 85575 embryos per spawn; for females with eggs undergoing direct development, embryo production per egg mass is estimated at between 70 and 812. A comparison is made between females brooding the two kinds of egg masses. Minor differences exist in adult coloration, shape of egg capsules, egg diameters, spawning season and their abundance and distribution in the intertidal. Brooding females with eggs displaying indirect development are significantly larger than those with eggs of direct development. The latter females form chains subtidally but not intertidally as do females bearing eggs with indirect development. On these females with pelagic larvae, chains frequently include sedentary males which reach large sizes. On basal females with direct development, chains contain mostly other females, suggesting that matings are temporary and by errant males. These results are compared with existing information in the literature for other species both in this genus and in other marine invertebrates. It is concluded that two sympatric sibling species with different modes of development are present in the morphospecies *C. dilatata* Lamarck in Southern Chile.

Introduction

The development of benthic marine invertebrates falls within a few basic patterns, as has been established and discussed mainly by Thorson (1946, 1950) and Mileikovsky (1965, 1971). In general, these modes of development may involve a pelagic larval phase, a demersal larva which feeds during its free-living benthic phase, or else direct development in which case the young adult develops without a free larval stage. Different types of development exist in closely related species, and in some cases even in different populations of one and the same species. Such intraspecific variability has been found to occur in relation with geographic, seasonal or other

environmental parameters (Mileikovsky, 1971).

The marine prosobranchs of the genus *Crepidula* are especially appropriate for comparative studies of early development and reproductive behaviour in different populations. Such studies are facilitated in this genus by the sessile habit of the adults and because the females brood egg masses during the intracapsular development of the embryos. Closely related species of *Crepidula*, sometimes coexisting, may differ in type of larval development (Coe, 1949).

Crepidula dilatata Lamarck, is a common species in Chile, with a wide distribution along the Chilean and Argentinian littoral (Parodiz, 1939; Dell, 1971; and Marincovich, 1973 as *Crepipatella dilatata*). Its development has not been known till now. On examining egg masses of *C. dilatata* from localities of North Patagonian

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bays, differences were observed in the mode of development and in other biological features of individuals from these localities. The present study provides information on the reproductive biology of specimens from one chosen locality, and particularly on the existence of two modes of development in *C. dilatata* from one locality. These findings are compared with available knowledge of other species and are discussed as to their adaptive significance. Up to now, the taxonomy of this species has been based on the morphology of the adults, and particularly of the shell (Lamarck, 1822; Parodiz, 1939). Here, I discuss the possibility of two biological species being included in the morphospecies *C. dilatata* Lamarck, from Southern Chile.

Materials and Methods

Crepidula dilatata Lamarck for this study were collected in Chinquihue Bay (41°31'S; 73°03'W), a sheltered locality near Puerto Montt, at the northern end of the Chilean Patagonic channels. A smaller number of specimens came from Tabón Island (41°54'S; 73°08'W), only a few miles south of Puerto Montt, in the Gulf of Ancud.

Monthly collections were made in Chinquihue Bay from May to November 1971 and in some months of 1972 and 1974. The snails were found on stones of muddy sand shores during low tides. The specimens from Tabón Island were obtained at the fish market in Puerto Montt, in October 1971, June 1973 and July 1973, attached as epibionts on the large subtidal edible barnacle *Megabalanus psittacus* and the mytilid *Auilacomya ater*. All specimens were carried to the laboratory in Valdivia, in bowls with sea water, on the substrate to which they were attached. In the laboratory they were detached and inspected foot-up. Sex was determined by the development of the phallus (Hendler and Franz, 1971) or of the oviduct. Mobile individuals were recognized by their displacement or by the activity of the foot on being removed from the substrate. Sedentary individuals were recognized by the weak mobility of the foot on being displaced from the substrate, by the presence of a scar on the substrate, and by the close correspondence between this scar and the edge of the shell.

Egg masses, when present, were also detached and examined in a dish of sea water. The number of brooding females in each sample was recorded and in some cases also the number of capsules per egg mass and the number of eggs and lar-

vae per capsule. Some egg capsules were kept in running sea water to follow the development of the embryos. Counts and measurements of eggs and larvae were made under a stereomicroscope using a micrometer eyepiece. Drawings of the embryos were made in a Leitz Orthoplan microscope with drawing tube. Egg capsules were drawn with a camera lucida.

Results

Patterns of Development

Capsules and egg masses of *Crepidula dilatata* are similar to those of other *Crepidula* spp. (Thorson, 1946; Amio, 1963). Compartment membranes (Hendler and Franz, 1971) are not observed. Females brood their egg masses beneath the ventral face of the neck lappets. The egg capsules are peduncled and their base is cemented to a substrate. On inspecting egg masses, two types of development were clearly recognized. Some females brood egg masses in which the intracapsular development leads to the hatching of large numbers of typical veliger larvae. These females are considered to brood egg masses with indirect development, with a free larval stage. Other females brood egg masses in which the embryos develop to the young adult stage entirely within the egg capsules (direct development). In these females, the capsules also contain non-developing nursery eggs.

Capsules, Eggs and Larvae with Indirect Development

The egg capsules are flattened triangular sacs with rounded vertex, their lateral margins being longer than the distal one (Fig. 1a). A laminar peduncle extends from the proximal vertex of each capsule and anchors it to the substrate or to the propodium in clusters. The fertilized eggs are generally spherical and creamy white in colour. The eggs of one capsule ranged between 204 and 238 μm , the commonest diameter being 212 μm (Fig. 2a). All eggs develop, there are no nurse eggs and "embryonic cannibalism" (Coe, 1949) was not observed. Stages of the intracapsular development are illustrated in Fig. 3 (a-d). This development ends with the hatching of numerous typical planktonic veligers. Some characteristics of these newly hatched veligers are: transparent colourless shell of about 1 whorl and 500 to 560 μm in length; velum formed of 2 well-developed lobules, along the margin of which are

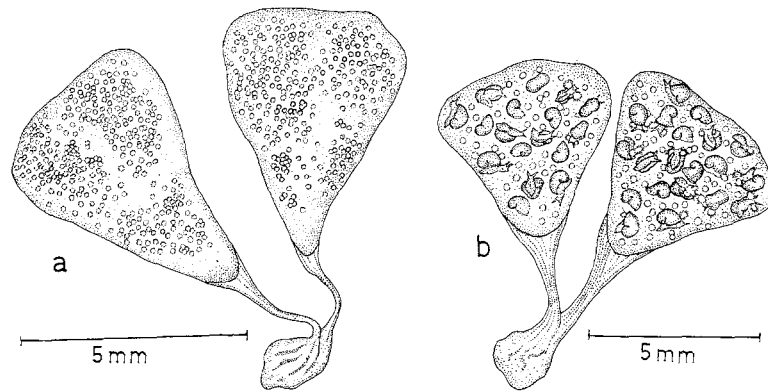


Fig. 1. *Crepidula dilatata*. Egg capsules. (a) Capsules with indirect development containing eggs; (b) capsules with direct development containing advanced embryos and nurse eggs

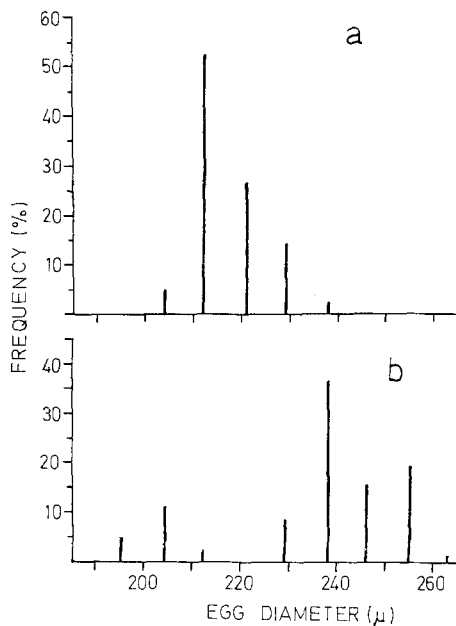


Fig. 2. *Crepidula dilatata*. Egg diameters. (a) Total eggs ($n = 894$) in capsule with indirect development; (b) total eggs ($n = 682$) in capsule with direct development

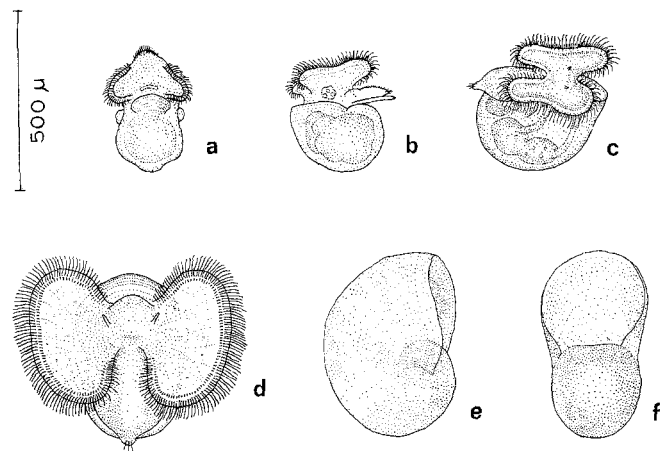


Fig. 3. *Crepidula dilatata*. Indirect development. (a)-(d) Some stages from preveliger to newly hatched veliger; (e), (f) larval shell of newly hatched veliger

spots of dark brown pigment; foot and tentacles scarcely developed. These larvae coincide, except by their larger size, with those described by Werner (1955) in his classic study of the planktotrophic veliger of *Crepidula fornicata*.

Capsules, Eggs and Embryos with Direct Development

The capsules are similar to those described for egg masses with indirect development, except that the three margins are of equal length (Fig. 1b). The eggs are creamy white in colour. The 682 eggs

of one capsule ranged between 195 and 263 μm in diameter, distributed in two size groups (Fig. 2b). The smaller eggs constitute 18% of the total in this capsule; the larger ones constituted 82% of the total. These egg diameters are clearly smaller than in other *Crepidula* species with direct development (Coe, 1949); the latter probably hold enough yolk for complete development up to the benthonic young.

An average of 5 to 6% of the eggs in each capsule develop (Table 1), the others remaining as nurse eggs; this source of food for embryos was not previously known in *Crepidula* spp. There is no rela-

Table 1. *Crepidula dilatata*. Relation between number of nurse eggs and number of embryos per capsule; direct development. Values are means of 10 capsules and standard deviations (SD) from egg masses of 3 brooding females from Chinquihue Bay

Female	Shell length (mm)	No. of nurse eggs/capsule		No. of embryos/capsule		No. of nurse eggs available/embryo	
		Mean	SD	Mean	SD	Mean	SD
1	30	308	45.82	18	5.78	18	5.71
2	30	369	85.34	23	5.73	17	3.96
3	36	352	73.40	24	6.61	16	6.78

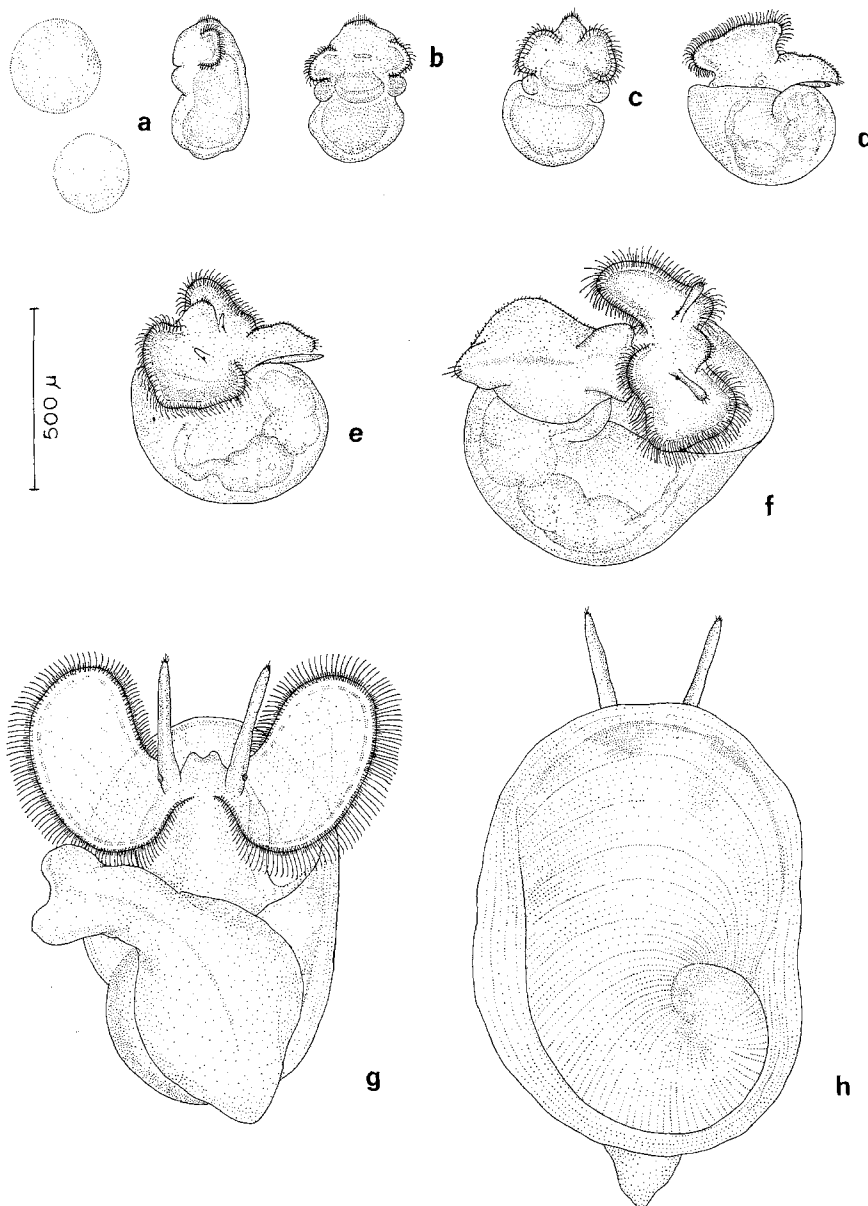


Fig. 4. *Crepidula dilatata*. Direct development. Some stages from preveliger to newly hatched young

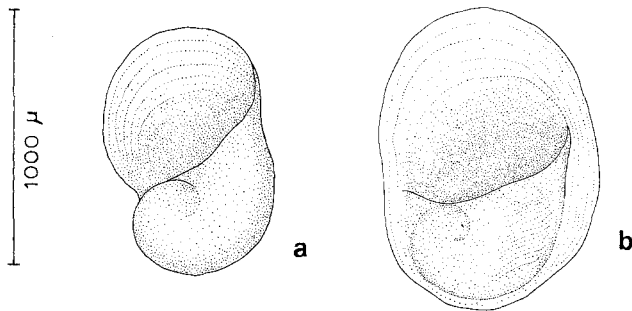


Fig. 5. *Crepidula dilatata*. Direct development. (a) Advanced shell of intracapsular embryo, ventral view; (b) shell of newly hatched young, ventral view

tion between developing or nurse eggs and the size of eggs; cleavage occurs in both large and small eggs. Table 1 shows the estimated number of nurse eggs and of embryos per capsule in 10 capsules with embryos at early stages of development, randomly chosen from the egg masses of three females. During early development, embryos do not yet consume nurse eggs, so the initial number of eggs is still present at this stage. Although the sample is small, it can be seen that the mean number of nurse eggs available per embryo, 16 to 18, is similar in all cases.

Some stages of direct development, from preveliger to the postlarval young, are illustrated in Fig. 4. As intracapsular development progresses the embryos show a gradual growth of the foot, tentacles and shell with final resorption of the velum. The larvae have consumed all or most of the nurse eggs by the end of intracapsular development. Hatching occurs with the rupture of the distal margin of the capsule. At this stage (Fig. 4h) the postlarval young have an active crawling foot and large tentacles. The shell is semitransparent and of a brilliant clear gold colour, with some purplish-brown spots near the anterior margin. The shell measures 900 to 1370 μm in length. The apex and the rest of the spiral become surrounded by a thin growing plate which exceeds to some extent the margin of the spiral (Fig. 5). The internal lip of the early shell will constitute the margin of the septum, a horizontal plate whose margin has not yet become sigmoid as is typical of adult *Crepidula dilatata*.

Differences in Adults

The two patterns of development described above could be explained as in-

trapopulation variation in *Crepidula dilatata*, or else as the coexistence of two sympatric sibling species (Mayr, 1963) of *Crepidula* in Chinquihue Bay. In order to settle this question, differences were investigated in the adults.

Morphological Differences in Females

No clearcut morphological differences distinguish females with one or the other type of development (Fig. 6). The sigmoid margin of the septum, a diagnostic feature of this morphospecies (Parodiz, 1939), is similar in both kinds of females (Fig. 6b,e). Also the radular structure is similar in both kinds of females; the teeth in transverse rows agree with those described by Parodiz (1939) and by Clasing (1972) for *Crepidula dilatata*. Neither in the colour of the gonads are there differences in the two kinds of females. The ovaries vary from creamy-yellow to orange. The most noticeable differences are the size ranges of brooding females (a feature analyzed below) and the colour of the head, neck and shell.

With regard to coloration, the following was observed. In females with indirect development, the interior of the shell is generally white, although in smaller females it may be somewhat violet or pinkish, similar to the shells of females with direct development. The head and neck are usually black dorsally. In females with direct development, the interior of the shell is almost always violet or at least pink. The back of the head and neck is generally white with some yellowish spots, black pigment not being as frequently observed as in females with indirect development. These features are nevertheless very variable and only tendencies can be found, if at all, in the females from Chinquihue Bay.

Reproductive Biology

Size of Brooding Females. In Chinquihue, where both types of development coexist, one of the most suggestive differences in the adults is the size range of brooding females (Fig. 7). In the 206 brooding females with indirect development sampled during this study, the antero-posterior length of the shell ranged from 34 to 65 mm, with a mean of 51.42 mm. In a comparable sample of 86 females with direct development, the range was 20 to 50 mm, with a mean of 35.13 mm. The difference between these means proved to be highly significant ($P \ll 0.0005$, "Student's *t* test", $t =$

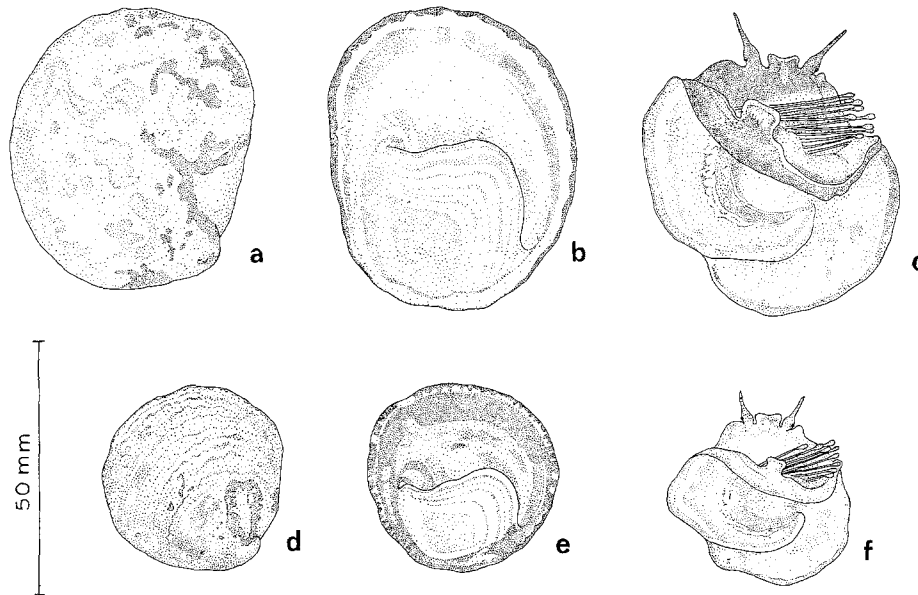


Fig. 6. *Crepidula dilatata*. Morphological characteristics in adults. (a)-(c) External morphology of female with indirect development; (d)-(f) external morphology of female with direct development

11.01). This distribution of brooding females into two significantly different size-groups was observed in all samples collected throughout the spawning season.

Brooding Season. Random samples taken in Chinquihue during various months of 1971, 1972 and 1974 allow an estimation as to the brooding season throughout the year. Field observations during late March and in April 1971, showed that no females were brooding egg masses. Quantitative observations, starting in May 1971 (see Table 2), show that there are brooding females, both of indirect and of direct development, during most months (May through January), declining in the first quarter of the year (late summer and early autumn, in the southern hemisphere). Females with indirect development begin spawning in May, and the highest number of brooding females occurs in July; for females with direct development, both events occur 1 month later. The extended brooding season could be due to successive spawning, as has been shown in other *Crepidula* species (Ishiki, 1936; Hendler and Franz, 1971). It is evident, though, that there is a wide overlap in the spawning and brooding seasons of both kinds of females. The decline of the brooding season corresponded to a decrease in spawning; in other *Crepidula* species this has been attributed to depletion of sperm in the seminal receptacles, exhaustion of the gonads, or to the increasing number of newly mature fe-

males not yet inseminated (Chipperfield, 1951; Hendler and Franz, 1971).

Fecundity. Fecundity of individual females with indirect development is expressed as the total number of eggs or embryos per egg mass. This number was estimated for each female by multiplying the number of capsules per egg mass by the average number of eggs or embryos in 10 of its capsules randomly chosen. These data are based on 28 brooding females of different shell sizes, collected in Chinquihue (see Fig. 8a,b,c). As can be seen, the number of capsules per mass and egg production are size-dependent; the largest females producing more eggs per capsule and more capsules per mass. Correlation coefficients obtained in these cases and their significance are indicated. Total egg production per female, estimated between 3840 and 85575 per mass, is far beyond that reported for other *Crepidula* species with pelagic larvae (Ishiki, 1936; Coe, 1949). For broods with direct development, data on egg production per capsule is available only for three females of middle size (see Table 1). Since only some of the eggs in a capsule develop, fecundity of these females will be expressed as the number of embryos per egg mass; 10 capsules randomly chosen from the egg masses of 22 brooding females with direct development from Chinquihue, were examined to estimate such embryo production (see Fig. 8d,e,f). No signifi-

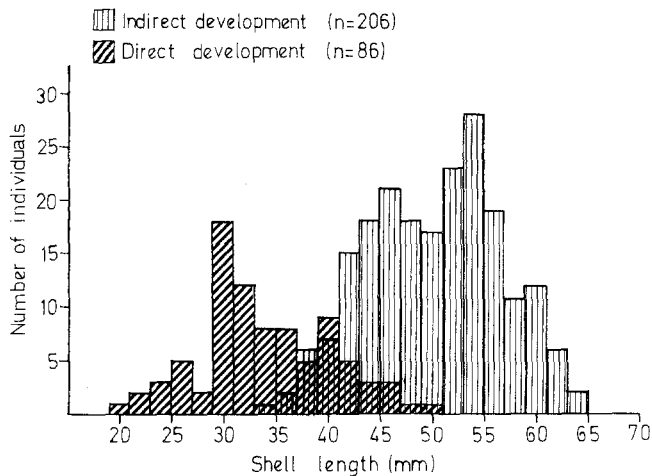


Fig. 7. *Crepidula dilatata*. Shell-length distribution in total brooding females collected at Chinquihue Bay

cant correlation was observed between shell length and number of capsules, nor between shell length and total embryo production (Fig. 8d,f), although in the latter case a greater r value (0.35) was obtained. Total embryo production per mass, estimated as between 70 and 812, is greater than in most *Crepidula* species with this type of development (Coe, 1949) and somewhat similar to that in *C. williamsi* and *C. convexa* (Coe, 1949; Hendler and Franz, 1971).

Sexual Phases and Chain Formation. For the purpose of this study, 4 sexual phases are considered: immature, male, transitional and female. The methods for determining sex and mobility of individuals were as described above.

Small immature individuals move about actively from one place to another, and were found both on females and other substrates. The largest of 36 specimens measured 22 mm in length. The males may be errant or sedentary on the shell of a female or other substrate; 38 sedentary males, found on females with indirect development from Chinquihue Bay, ranged from 8.5 to 49 mm in shell length. No males were present on females with direct development from the intertidal at Chinquihue Bay. Transitional individuals in sexually inactive condition seem to be sedentary or scarcely mobile. They were frequently found on stones; one sedentary individual was attached on an empty larger shell. Nine individuals mea-

Table 2. *Crepidula dilatata*. Frequency of brooding females with indirect and direct development in samples obtained at Chinquihue Bay

Date of collection	No. of females collected	No. of females with indirect development and as % of total sample	No. of females with direct development and as % of total sample
1971			
9.V.	16	1 (6%)	0 (0%)
20.VI.	54	5 (9%)	5 (9%)
19.VII.	35	21 (59%)	3 (8%)
22.VIII.	62	15 (24%)	18 (29%)
21.IX.	35	6 (17%)	6 (17%)
19.X.	30	10 (33%)	6 (20%)
28.XI.	33	7 (21%)	2 (6%)
1972			
28.I.	26	3 (11%)	3 (11%)
12.VIII.	54	19 (34%)	15 (27%)
17.XII.	84	9 (11%)	6 (7%)
1974			
21.VII.	214	110 (51%)	22 (10%)

sured 22 to 52 mm in shell length. Females are always sedentary; as already stated, females with direct development spawn at smaller shell length than females with indirect development and these latter attain a larger size.

Crepidula dilatata form chains by the well known habit in this genus (Orton, 1909, 1912) of attaching themselves in linear series over each another, as illustrated in Fig. 9. It was notable for the intertidal in Chinquihue Bay that chains were found only on females with indirect development, females with direct development being always solitary on rocky substrate. Yet females with direct development from the subtidal of Isla Tabón were found to bear chains, including some sedentary males. In order to determine the sequence of individuals, some entire chains from Chinquihue Bay and Isla Tabón were analysed. The sexual phases of the individuals in the chains are shown in Table 3. It is interesting to note that sedentary males are more frequent on females with indirect development; basal brooding females with direct development bear mostly females or transitional individuals.

Abundance and Distribution of Brooding Females

In Chinquihue Bay, a sheltered locality with muddy sand shores with stones and boulders interspersed, brooding females with indirect development are found in

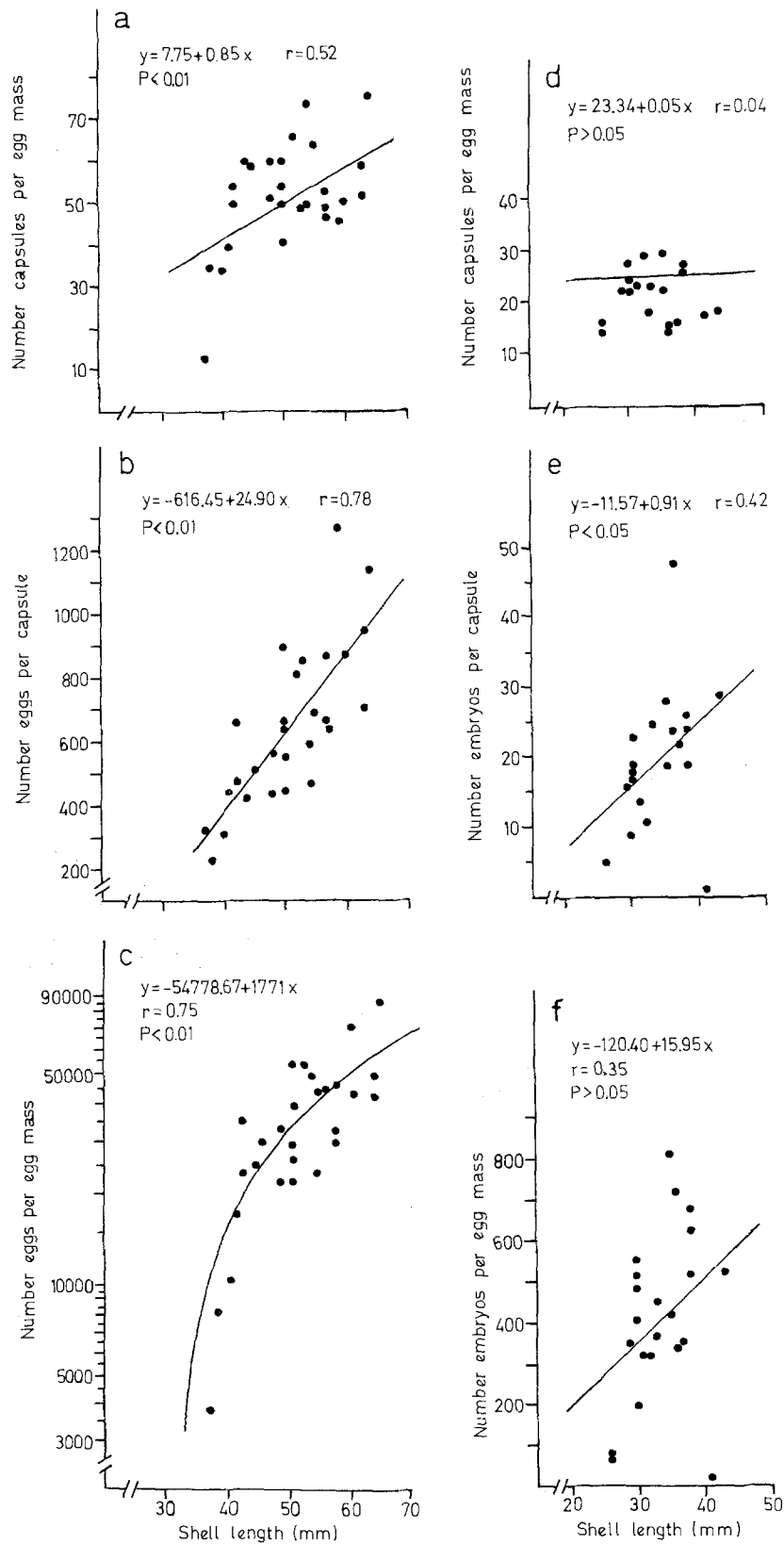


Fig. 8. *Crepidula dilatata*. Data on fecundity in relation to shell length of brooding females. (a)-(c) Females with indirect development ($n = 28$); (d)-(f) females with direct development ($n = 22$)

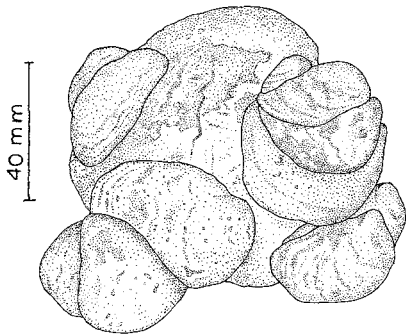


Fig. 9. *Crepidula dilatata*. Typical chains of sedentary individuals on basal female with indirect development. Snails obtained at intertidal in Chinquihue Bay

Table 3. *Crepidula dilatata*. Sequence of sexual phases in chains on brooding females with indirect and direct development. Specimens of indirect development are from intertidal of Chinquihue Bay. Those of direct development are from subtidal of Isla Tabón. Sequence of sexual phases is indicated from basal female upwards

Type of development	No. of chains	No. of individuals in chain	Sequence
Indirect	36	2	♀♂
	12	3	♀♂
	4	3	♀♂♂
	1	3	♀♀♂
Direct	15	2	♀♀
	4	2	♀♂
	1	2	♀ Transitional
	2	3	♂♂♂

the intertidal forming dense groups on all the stones, sedentary, isolated or forming chains. They occur from the mean low-water spring tide level through the upper subtidal, being found by divers at depths of 25 m where they are common epibionts of the edible mytilids *Choromytilus chorus* and *Aulacomya ater*. Brooding females with direct development are less abundant and are found isolated or in groups but with rather discontinual distribution at the intertidal and subtidal of Chinquihue, coexisting on some stones with individuals of indirect development. As already stated, these females without pelagic larvae are also present in the subtidal samples from Isla Tabón, as common epibionts on *A. ater* and *Megabalanus psittacus*, on which they do form chains.

Discussion and Conclusions

Intraspecific variation in modes of development has been reported for marine benthic invertebrates in the form of interpopulation variation, and is believed to represent an adaptation to different local conditions within the species' geographical range (Mileikovsky, 1971). Cases have been described in polychaete and prosobranch populations subjected to different salinities (Rasmussen, 1951, 1956). One case of intrapopulation variation is known in the prosobranch *Polinices triseriata*, which has direct development in years with wet cool summers and semiplanktonic development in years with hot dry summers (Giglioli, 1955). Giglioli believes that both types of development exist simultaneously and that their frequencies vary from year to year according to climatic conditions. Although this has not been confirmed, the possibility cannot be dismissed that certain species could insure their local population's stock by such delicate balance between two modes of development.

However, in cases of differences in patterns of development at one locality, the possibility of a geographical overlap of two similar sibling species (Mayr, 1963) should also be considered. This is the interpretation favored to account for the findings of the present study in the morphospecies *Crepidula dilatata* in Chinquihue, Chile. Present knowledge of the reproductive biology of other species both in this genus and in other marine invertebrates supports this hypothesis. Species of the genus *Crepidula* which scarcely differ in morphology and overlap at one locality have been found to have different modes of development (Coe, 1949). In such cases, females with pelagic larvae reach a larger size than those with direct development. From our observations this is also the case with the two types of brooding females found in Chinquihue Bay throughout the spawning season. It is possible that the two kinds of females found in Chinquihue have different growth rates, as has been shown for other *Crepidula* species with different modes of development (Ishiki, 1936; Coe, 1949); in such cases, species with pelagic larvae grow faster than species with direct development. Furthermore a larger size of females with planktonic larvae is consistent with the requirements of high fecundity (from about 3800 to 85000 larvae per spawn in *C. dilatata*), to cope with the high mortality of these larvae during the pelagic phase. Differences in size of brooding females seem to be significant for the coexistence of two similar or related species

which differ mainly in their modes of development. On this point I agree with the recent assumptions of Menge (1975), who suggests that in seeking causes of patterns of reproductive methods in marine invertebrates, it is essential to consider a complex of interrelated factors; among these, he considers interactions between adults of closely related species. With respect to the role of these interspecific interactions in the evolution of reproductive strategies, he suggests that when (1) competition results in coexistence of closely related species, (2) resource allocation is based on significant differences in size of the competitors, and (3) planktonic mortality is great, then the smaller competitor will "brood" (in the sense of direct development) and the larger will "broadcast" (hatching of pelagic larvae).

Other biological features observed in the morphospecies *Crepidula dilatata* also suggest two coexisting *Crepidula* species in Chiquihue Bay; namely, the local distribution and abundance of brooding females and the well known phenomenon of chain formation and its relation to sexual differentiation. Chain formation has been related to advantages for filter-feeding in *C. fornicata* (Orton, 1912). Yet chain formation relates also to reproduction; classical studies have shown varying degrees of the influence of females on the sexual phase of associated individuals (Coe, 1936, 1938; Ishiki, 1936; Gould, 1952). In some species such as *C. fornicata* and *C. onyx*, basal females often bear sessile males which reach large sizes; permanent association of males with individuals in the female phase tends to accentuate the masculine characters and to prolong the male phase. Such would seem to be the case in *C. dilatata* with indirect development. In other species, such as *C. lingulata*, *C. convexa* and *C. aculeata*, mating is temporary and females are mostly found solitary, rarely with mated males. Such was the case for *C. dilatata* females with direct development at the intertidal in Chiquihue Bay; as already stated, these females do bear chains subtidally, but the overlying individuals were mostly females, suggesting a lability of the male and the transitional phases in this form, when associated with mature females. However, I do not suggest that the sexual behaviour observed in one *Crepidula* species, must necessarily be dependent on its mode of development.

Given the sessile habit of *Crepidula* spp. females and the weak mobility of transitional individuals, the earlier phases in the life cycle are clearly im-

portant for dispersion, at least in species without pelagic larvae. Small immature individuals and young males seem to be actively mobile in all species. As already noted, sedentary males on basal females are of common occurrence in *C. dilatata* with pelagic larvae, while temporary mating by errant males seems to occur mostly in *C. dilatata* with direct development. Hendler and Franz (1971) have discussed the role of the mobile phases in *C. convexa*, a species with direct development. They have assumed the advantage of mobile males to fertilize different females and have stressed the importance of errant individuals in colonizing new substrates in the absence of pelagic larvae. These properties can be assumed to occur in *C. dilatata* displaying direct development, in contrast to the coexistent *C. dilatata* with pelagic larvae.

Such numerous and biologically important differences as described here in similar organisms coexisting at the same locality, strongly support, to the author's mind, the hypothesis of the presence of two sibling species in the morphospecies *Crepidula dilatata* Lamarck, which are sympatric in Chiquihue Bay, Chile. The taxonomic treatment of these populations and a further discussion of the adaptive value of their reproductive strategies (Mileikovsky, 1971; Vance, 1973; Menge, 1975), await the results of research now in progress. They shall be the subject of future reports.

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C.S. Gallardo
 Instituto de Zoología
 Universidad Austral de Chile
 Casilla 567, Valdivia
 Chile