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Sex Change, Reproduction, and Development of *Crepidula adunca* and *Crepidula lingulata* (Gastropoda: Calyptraeidae)

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Abstract. This paper describes the reproduction and development of *Crepidula adunca* and *Crepidula lingulata* from San Juan Island, Washington, USA. Both species were sampled every 2 months to determine the reproductive season and to measure the relationship between adult size and sex, capsule number, egg number, and brood weight. Development of each species is described briefly based on the broods obtained from these samples. As expected for protandrous hermaphrodites, females were larger than males, in both species. *Crepidula adunca* is an intertidal species that is usually found in stacks of two animals. This species reproduces all year, and embryos develop directly into crawl-away juveniles. *Crepidula lingulata* is a solitary subtidal species that produces planktotrophic veliger larvae in the summer. These veligers have distinctive pigmentation on the velum and settle 4 weeks after hatching at a shell length of 750 μm. Experiments show that associations with conspecifics do influence sex change in *C. lingulata:* males kept with females were less likely to change sex than those kept alone or with other males.

INTRODUCTION

Snails in the family Calyptraeidae (Caenogastropoda), slipper limpets (*Crepidula* Lamarck, 1799), cup and saucer limpets (*Crucibulum* Schumacher, 1817), and hat shells (*Calyptraea* Lamarck, 1799), are marine, suspension feeding, protandrous hermaphrodites that brood their young (Hoagland, 1977). Calyptraeids' sedentary lifestyles and diversity of developmental modes make them ideal animals with which to investigate the evolution of life histories (Hoagland, 1977, 1984, 1986; Warner et al., 1996); development (Coe, 1949; Hoagland, 1986); and the evolution of sex change (Coe, 1938a, b, 1942; Hoagland, 1978; Collin, 1995). *Crepidula* species exhibit a variety of "social" habits: some species form semi-permanent stacks of many individuals, others make small stacks or pairs, and some do not stack. Life history theory predicts that these different strategies may affect size at sex change, so that at the population level, solitary species have one optimal size at sex change, while those that stack show overlap in the sizes of males and females (Charnov, 1982; Collin, 1995). Additionally, Coe (1938b) stated that stacking species change sex in response to conspecifics while solitary species do not. However, these aspects of *Crepidula* biology have been examined empirically for only a few species (e.g., Warner et al., 1996).

Crepidula species are also well known for the great diversity in developmental modes found among closely related species. In fact, there is almost as much variation in developmental mode among species of *Crepidula* as there is among all caenogastropods: Some species have planktotrophic development, some are lecithotrophic, some develop directly from large eggs, and some develop directly from small eggs by consuming nurse eggs. Basic information on life history, reproduction, and development has been compiled for 22 species of *Crepidula* (Hoagland, 1986). There are detailed data on New England species such as *Crepidula fornicata* (Linnaeus, 1758), and *C. plana* Say, 1822 (Ament, 1979; Hoagland, 1986; Conklin, 1897; Franzen & Hendler, 1970; Pechenik & Eyster, 1989); and Coe (1942, 1949) made observations on the natural history of some Californian species. However, little is known about most species outside North America (but see Pilkington, 1974; Gallardo, 1977), or species in the Northeast Pacific and Florida. Despite the fact that development mode is unknown for about half the currently recognized species, it is known for more species of *Crepidula* than for species in any gastropod genus other than *Conus* (Kohn & Perron, 1994; A. J. Kohn, personal communication).

I studied the life history and development of two *Crepidula* species with different development types from San Juan Island, Washington state. The first aim of the study was to describe the relationship between size, intraspecific associations, and sex in these species, and to test the following hypotheses: (1) at the population level, solitary species have one optimal size at sex change, while those that stack show overlap in the sizes of males and females (Charnov, 1982; Collin, 1995), and (2) associations with conspecifics affect sex change in stacking species but not in non-stacking species. The second aim of this study was to measure life history and reproductive characteristics,

Table 1

Collection dates and number of animals collected.

Species	Collection date	Number of males	Number of females	Number of transitionals	Number of juveniles	Total number of animals
C. adunca	January 18	137	68	0	53	258
	April 5	64	25	1	28	118
	June 17	74	45	6	18	146
	August 27	90	68	3	6	167
C. lingulata	February 17	97	111	3	2	213
	April 14	60	70	0	4	134
	June 11	70	76	1	0	147
	August 13	88	76	1	2	167

such as the relationship between female size and fecundity, frequency of brooding, duration of development, duration of planktonic period, and size at settlement, which are all important parameters in models of life history evolution (e.g., Caswell, 1981; Havenhand, 1993; Rowe & Ludwig, 1991). The third aim was to briefly describe the development and embryology of these species.

MATERIALS AND METHODS

All snails for this study were collected along the coast of San Juan Island (48°34′N, 123°2′W), San Juan County, Washington, USA, between January and August 1996. Specimens of *Crepidula adunca* Sowerby, 1825, were collected attached to shells of *Calliostoma ligatum* (Gould, 1849) from the mid-intertidal zone at Deadman's Bay on the west side of San Juan Island. All other animals were collected, attached to small rocks, with SCUBA from a depth of 20–30 meters in Shady Cove on the east side of San Juan Island. Animals were sampled every 2 months, as tides and weather permitted. Sampling dates and the number of each species collected are presented in Table 1.

Within 2 days of collection, the lengths of all animals were measured to within 0.1 mm with calipers, sex was determined on the basis of presence/absence of the penis and female genital papilla, and their broods were collected and observed live. For *C. adunca* I counted all the embryos in every capsule whenever possible. However, freshly laid eggs sometimes clumped together in such a way that they could not be counted. For *C. lingulata* I counted all the embryos in a subset of four arbitrarily selected capsules from each brood (and report the average). In all cases the total number of capsules per brood was recorded. Dry weight was measured for arbitrarily selected adults and egg capsules in which the embryos had not begun to secrete a shell. Because the dry weight of individual eggs was too low to be measured accurately, average egg weight was calculated for *C. adunca* by dividing the total capsule weight by the number of eggs in that capsule. Because this measure of "egg size" includes extra-embryonic material, it more accurately reflects female investment per offspring rather than absolute egg size. However, calyptraeid egg capsule coverings are extremely thin and probably contribute little to the total weight of the capsule. Egg diameter of uncleaved eggs and shell length at both hatching and settlement were measured with an ocular micrometer on a compound microscope.

I performed an experiment to determine if association with conspecifics effects sex change. Males whose shell length fell within the range of size overlap between males and females were randomly assigned to a beaker with one of three treatments: alone, with another smaller male, or with a female. The water was changed every day and the microalgae *Rhodomonas, Isochrysis,* and *Dunaliella* were provided *ad libitum.* After 3 months the animals were measured and sexed.

To determine the duration and frequency of brooding, adult animals were maintained in running seawater tables (at 10–12°C) at Friday Harbor Laboratories. Animals attached to glass bowls and the sides of the sea table, through which broods could be observed.

Calyptraeid development can be observed without removing the embryos from the transparent capsules. Encapsulated embryos were observed with a dissecting microscope, and excapsulated embryos were viewed with a compound microscope using both bright and dark field illumination. In preparation for examination with scanning electron microscopy (SEM), embryos were relaxed in 7.5% $MgCl_2$, fixed directly in 1% OsO_4 in distilled H_2O, dehydrated in a graded series of EtOH, and dried by transferring them from 100% EtOH to Hexamethyldisalizine (HMDS). The HMDS was allowed to evaporate, the specimens were mounted on a stub, sputter coated with gold and palladium, and viewed with a JEOL JM35 SEM.

Larvae of *C. lingulata,* the only indirect developer in this study, were reared to metamorphosis. After hatching, larvae were transferred to 0.45 μm filtered seawater in glass custard dishes that were kept partially immersed in running seawater tables at ambient sea temperature (11–12°C). The initial larval density of approximately 1/mL

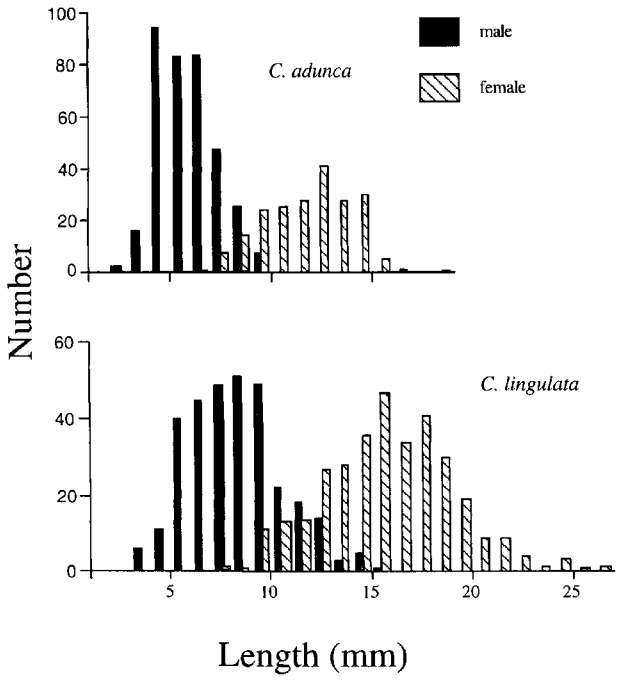

Figure 1

Histograms of the relationship between size and sex for (a) *Crepidula adunca,* (b) *C. lingulata.*

was reduced to around 1/5 mL after 2 weeks. Larvae were fed *Isochrysis galbana* and *Rhodomonas* sp. *ad libitum,* and the water was changed every 2–3 days. When the larvae were 25 days old and had begun to grow a cap-shaped shell, I tested a subset of the most advanced individuals for competence to metamorphose. I exposed five to 10 larvae to either adult conditioned seawater (seawater in which adult animals were kept for 24 hours), a biofilmed dish (dishes that previously had been kept fully submerged in running seawater for at least a week), or adult shells.

The Prussian blue method (W. B. Jaeckle, unpublished method) was used to detect embryonic nutrient uptake. Embryos were carefully excapsulated, incubated in a 1 mg/mL solution of ferretin or iron dextran in seawater for 1–2 hours. They were then relaxed, fixed in 10% formalin, rinsed, and stained with HCl and potassium ferrocyanide solutions. In the presence of iron (from the ferretin or iron dextran) a blue product is formed. Staining was clearly visible with whole mount light microscopy.

Voucher specimens are on deposit at the Field Museum of Natural History in Chicago (*Crepidula adunca:* FMNH #285002; *C. lingulata:* FMNH #285019)

Table 2

Results of sex change experiment.

Treatment	*C. adunca*		*C. lingulata*	
	changed	no change	changed	no change
solitary	0	19	10	2
both males	2	14	12	1
male and female	1	12	3	7

RESULTS

Relationship between Size, Sex, and Intraspecific Associations

The relationship between shell length and sex for *Crepidula adunca* and *C. lingulata* is shown in Figure 1. Females are generally larger than males, but there is overlap between the distributions of male and female lengths: 23.5% of the total size range of reproductive individuals for *C. adunca,* and 37.5% for *C. lingulata.* Juveniles (generally < 3 mm) were not included because their shells were often broken when they were removed from the substrate and could not be measured accurately.

The distribution of male and female sizes did not vary with sampling date in *C. lingulata* (one-way ANOVA, males: $P > 0.5$, n = 315; females: $P > 0.5$, n = 332). However, in *C. adunca* male size did vary with date (one-way ANOVA: $P < 0.005$, n = 363), but female size did not (one-way ANOVA: $P > 0.25$, n = 206). The overall size distribution did not vary with sampling date for any species (one-way ANOVA, *C. adunca:* $P > 0.15$, n = 569; *C. lingulata:* $P > 0.5$, n = 647). An analysis using a non-parametric ANOVA produced similar results.

The frequency of intraspecific associations varied among the species studied here. *Crepidula lingulata* seldom form stacks (2% of all individuals formed stacks of one male and one female). *Crepidula adunca,* on the other hand, commonly forms stacks of two individuals: 48% of males and 78% of females occurred in stacks. Only 8.8% of *C. adunca* stacks included three adult individuals. In all stacks of three there were two males attached separately to one female. In most cases the stacks appeared to be permanent because the male shells fitted tightly on the female shell, often leaving a mark.

Sex Change Experiments

After 3 months, *C. adunca* in the sex change experiments had no visible shell growth, had not laid eggs, and there was high mortality (about 15%), suggesting that culture conditions were suboptimal. The number of *C. adunca* males that changed sex was too small to determine if there is an effect of conspecifics on sex change (Table 2). *Crepidula lingulata,* on the other hand, did well under these conditions, showing visible shell growth, and several produced egg masses. Chi-squared analysis of this data show that there is an effect of treatment (Pearson χ^2 $P = 0.001$; likelihood ratio χ^2 $P = 0.0005$), with males that were paired with females less likely to change sex

Table 3

Number and percent of females brooding.

Species	January–February	April	June	August
C. adunca	45/68 (66%)	14/25 (56%)	26/45 (58%)	30/68 (44%)
C. lingulata	1/111 (0.9%)	26/70 (37%)	46/76 (61%)	47/76 (62%)

than those that were paired with a male or those that were kept alone. Those that changed sex were larger than those that did not (t-test, $P < 0.001$), but there was no significant difference in size among treatments (Kruskal-Wallis test $P = 0.168$). In several of the paired male treatments both males changed sex.

Reproduction and Brooding

The Puget Sound calyptraeid species display a variety of reproductive seasons. *Crepidula adunca* appears to brood throughout the year, whereas *C. lingulata* reproduces in the summer (Tables 3). The number of brooding *C. adunca* females did not differ between stacked and solitary individuals (Chi-squared test: $\chi^2 = 0.07644$, n = 206, df = 1, $P > 0.5$).

I examined the effect of female body size on several reproductive parameters, using shell length as a proxy for adult body size. Ordinary least squares regression of the Ln (dry body weight) on the Ln (shell length) shows that shell length is a good predictor of body weight for both *C. adunca* (b = 2.929, n = 102, $R^2 = 0.92$, $P < 0.005$) and *C. lingulata* (b = 2.50, n = 121, $R^2 = 0.90$, $P < 0.005$) (Figure 2). I used a type I regression because I am most interested in using shell length as a predictor of reproductive parameters (e.g., Collin, 1995). Reduced Major Axis slopes can be calculated from the data given above and in Table 3. There is no difference between the sexes in the relationship between length and dry weight. The relationship between female length, number of capsules, eggs per capsule, and total eggs per brood is summarized in Table 3 and Figure 2. All measures of reproductive output except egg weight in *C. adunca* clearly increase with female length. However, female size accounts for only 10–40% of the variation in any of these parameters (r^2 in Table 4). In neither species did the number of eggs per capsule vary with developmental stage.

There is considerable variation in the size of embryos within any capsule for *C. adunca*. There sometimes appears to be as much as a twofold difference in diameter of blastulae within a capsule, and there is also considerable variation in size of later embryos. Some females also have embryos that are larger than those of other females. Unfortunately, the irregular shape of the embryos makes it difficult to quantify the differences especially among embryos at different stages.

Descriptions of Development

C. adunca

Development is synchronous within and among capsules. The large eggs, 250–350 microns in diameter, cleave equally and almost synchronously. A small polar lobe formed during the first two cell divisions. It may have been present during subsequent divisions, but the size of the eggs made it difficult to see it with any certainty. The first cleavage division takes about 24 hours; in intact capsules incubated at 12° C the second cleavage follows after 18 hours. Third cleavage is unequal and forms four clear micromeres that are easily hidden in the furrows between the macromeres. Later in cleavage, a mound of small, clear micromeres can be seen at the animal pole. After 5 days the pile of micromeres has still not yet begun to grow around the macromeres. Gastrulation occurs by epiboly, as micromere proliferation continues until the large yellow macromeres are completely covered by small clear cells.

Because the embryos are large and opaque, it is difficult to observe the details of development with light microscopy. SEMs of the external morphology of several stages are illustrated in Figure 3 and complement the histological analysis of Moritz (1939). Dense patches of cilia around the mouth, in the area of the head vesicle, located dorsally between the tentacles, and on the foot anlage develop before any of these features are clearly visible with light microscopy (Figure 3a). In the living embryos, the cilia covering the head and foot beat toward the mouth. The eyes appear as faint pigmented spots before any of the other external features. A cluster of six to eight embryonic kidney cells are visible on either side of the large ciliated mouth (Figure 3a). Each cell has a dense covering of microvilli (Figure 4). Incubation in ferretin followed by staining with the Prussian blue reactions shows that the embryonic kidneys take up protein but not polysaccharides from the external medium from this stage until the kidney cells disappear, shortly before hatching. The shell first appears over a flattened area on the posterior dorsal side of the embryo, while the head and foot anlagen are still small and indistinct. It slowly enlarges until it is a miniature version of the virtually bilaterally symmetrical adult shell. At no time is there a coiled embryonic shell. One of the most conspicuous characteristics of the mid-stage embryo, the head vesicle, a trans-

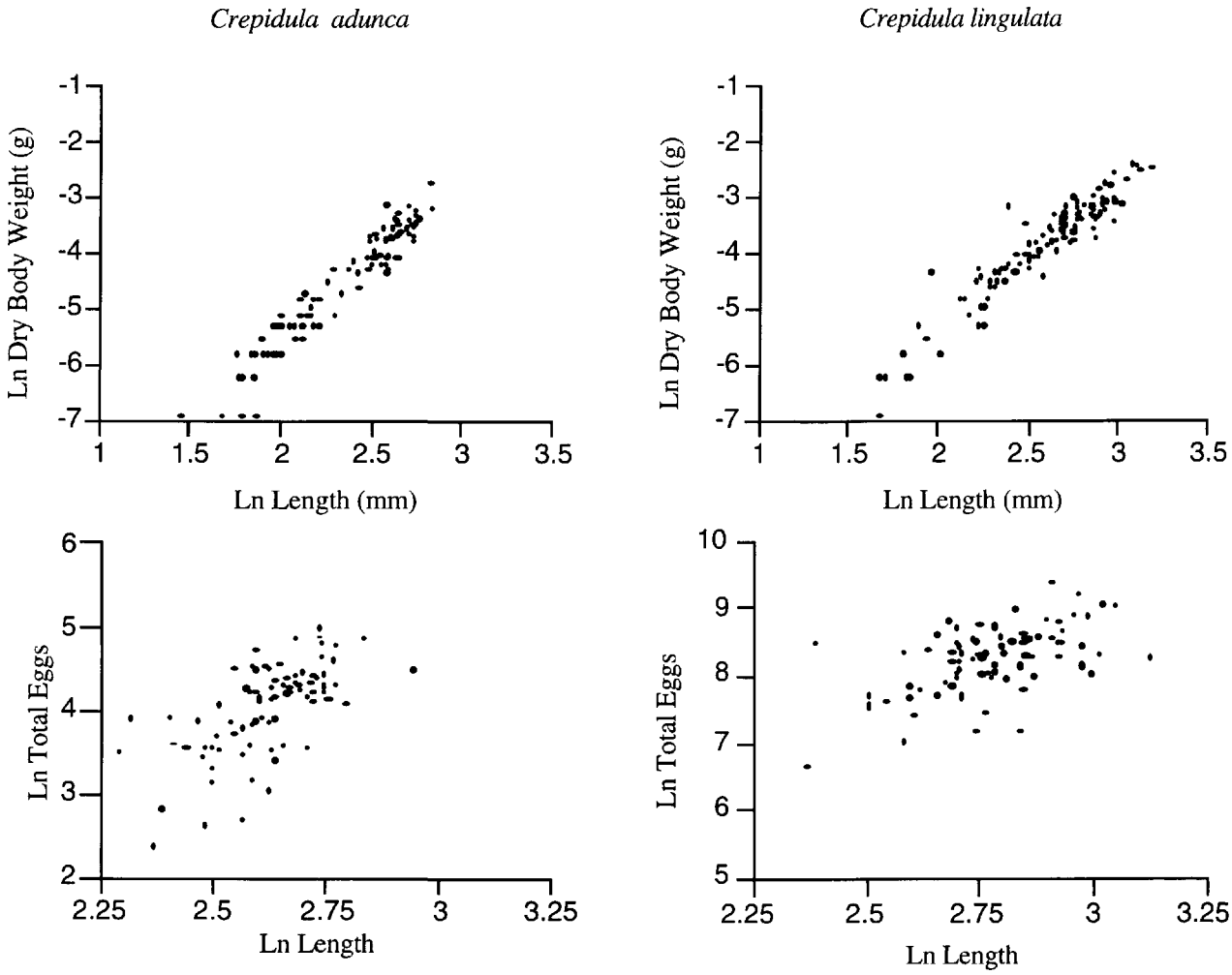

Figure 2

Scatter plots of the relationship between shell length and dry weight and shell length and total number of embryos per brood for *Crepidula adunca* and *C. lingulata*.

Table 4

Relationship between shell length and reproductive parameters.

				Ordinary Least Squares Regression Statistics of Ln(reproductive parameters) on Ln (length)			
Species	variable	mean	SD	n	m	r^2	*P*
C. adunca	total eggs	64.56	29.4	85	2.96	0.413	< 0.000001
	number of capsules	7.14	2.0	105	1.46	0.284	< 0.000001
	average eggs/capsule	8.78	2.48	83	1.42	0.308	< 0.00001
	average egg weight	0.06 mg	0.25	17	−0.32	0.002	> 0.5
C. lingulata	total eggs	4283	2019	81	1.87	0.295	< 0.00001
	capsule number	13.56	4.682	107	0.94	0.101	< 0.001
	eggs/capsule	281.2	88.93	81	1.35	0.370	< 0.00001
	average weight/capsule	0.55 mg	0.20	63	1.22	0.215	< 0.005

Table 5

Comparative life history data.

Species	Stacking	Reproductive season	Egg size (μm)	Egg number mean (SD)	Development type	Brooding duration	Hatching size	Planktonic period	Length (μm) at settlement mean (SD)
C. adunca	y	year round	262–315	64.8 (29.3)	direct	~120 days	1.5–2.7 mm	—	—
C. lingulata	n	summer	150	4283 (2020)	planktotrophic	24–33 days	275–363 μm	29–45 days	745.2 (82.4)

parent, densely ciliated, fluid-filled sac extends from the head between the tentacles. The head vesicle shrinks (Figure 3c) and disappears before hatching. A small ciliated ridge, the highly reduced velum, is present around the base of each tentacle (Figure 3). The foot differentiates slowly from a ventral bump and at no time is there an operculum. The shell develops pigment before it has reached its full size, and the body also becomes pigmented at this time. The embryos hatch when all the yolk has been absorbed. The embryo differentiates directly into the juvenile body without displaying any larval or embryonic specializations other than the head vesicle and embryonic kidneys. My observations of the development of *C. adunca* agree with the few observations of *C. adunca* by Conklin (1897), who focused on the early development of *C. fornicata.*

The number of embryos per capsule is independent of developmental stage. Embryos hatch without assistance from their mother at shell lengths of 1.5–2.7 mm. Hatchling shell length differed significantly between two broods for which I had sample sizes sufficient to estimate statistical parameters (mean = 2.6 mm, n = 11, SD = 0.17 and mean = 1.8, n = 13, SD = 0.10; t-test $P < 0.05$), and the lengths for a third brood were 1.76–1.98 mm. A mean hatching length of 2.6 mm is unusually large for this species. Hatchlings have no osphradial filaments, but the gills, food pouch, and radula are well developed, and pigmentation is the same as the adults. Hatchlings are able to collect and ingest suspended algal cells from the water column, and juveniles did not use their radulae to feed from the substrate.

I could not determine the duration of incubation from single broods because females attached to glass did not lay eggs. However, broods kept in dishes at 12° C took about 4 months to hatch.

C. lingulata

The embryonic development of *C. lingulata* is the same as the development of *C. fornicata* described by Conklin (1897) and, in fact, SEM micrographs of *C. lingulata* and *C. fornicata* embryos are indistinguishable. The eggs are 150 μm in diameter, there are no nurse eggs, and all the embryos within a sac developed synchronously. Cleavage proceeds as in *C. adunca.* Gastrulation is by epiboly with some invagination (Figure 5); the gastrula is flattened, unlike those of the direct developing species, in which it remains spherical. The embryo gradually elongates along the animal-vegetal axis (Figure 6) and the foot, head vesicle, velum, and mouth form as in the other species. It is difficult to distinguish these features with light microscopy but they are clearly visible in SEMs (Figure 6). Unlike those with direct development, the embryonic kidneys of *C. lingulata* are made up of only a single cell located on each side of the embryo (Figure 6), and the operculum develops in synchrony with the shell.

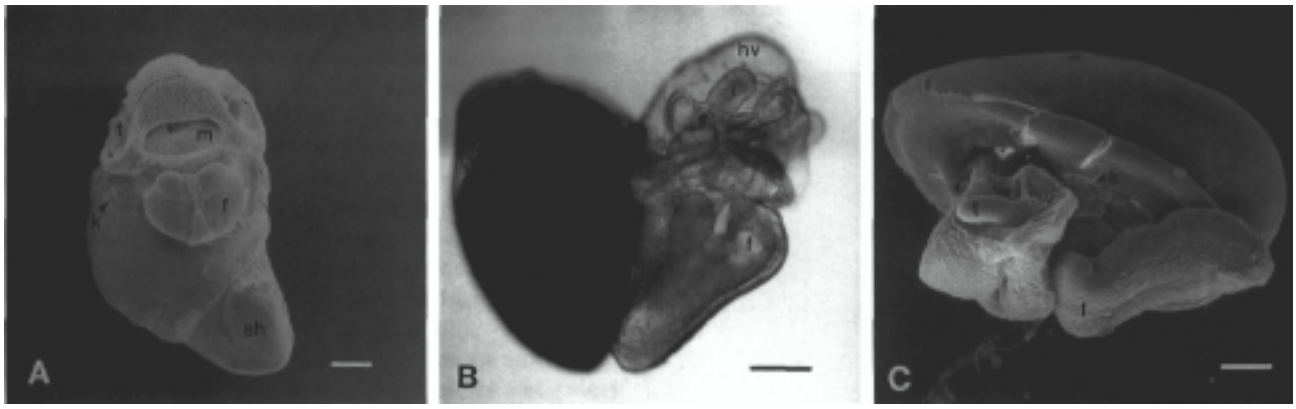

Figure 3

Development of *Crepidula adunca:* A. SEM of an early embryo in which little structure would be visible with light microscopy. The extensive ciliation over the anterior of the embryo beats into the large mouth. The tentacles are visible on either side of the mouth, and the head vesicle is beginning to bulge between them. The embryonic kidneys are visible to the left of the mouth, and the foot anlage is beginning to differentiate and has a distinctive medial stripe of cilia. The posterior constriction (bottom right) marks the area that is covered by the shell at this stage B., C. Light micrograph and SEM of a later stage in which the head vesicle is well developed, as are the shell and foot. The large visceral yolk mass does not extend into the head vesicle in B, and the head vesicle has collapsed in C. The reduced velum is visible in C. around the base of the tentacles; the ciliation is not distinct from the overall ciliation of the head vesicle and mouth. The embryonic kidneys are visible behind the velum. f, foot; hv, head vesicle; k, embryonic kidneys; m, mouth; sh, shell; t, tentacle; v, velum. Scale bar = 100 microns.

Broods laid in the lab took between 24 and 33 days to hatch at 11–12°C. Those that took longest were laid in spring, while those with the shortest development time were laid later in the summer. Individual females produced at least three broods during the summer, and it took

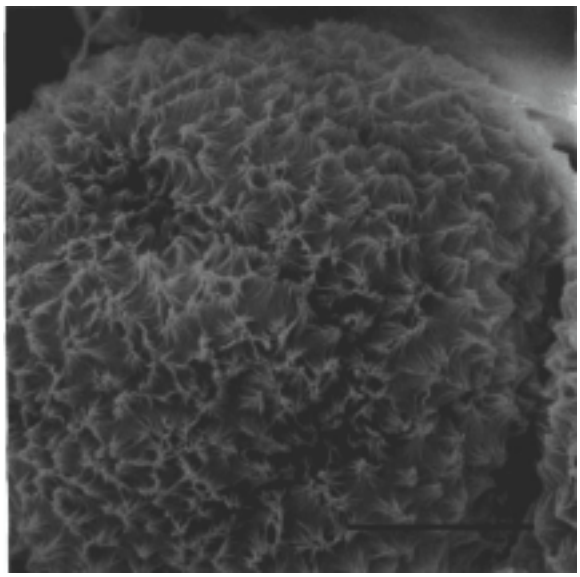

Figure 4

Scanning electron micrograph of *Crepidula adunca* embryonic kidney showing the dense microvilli. Scale bar = 10 microns.

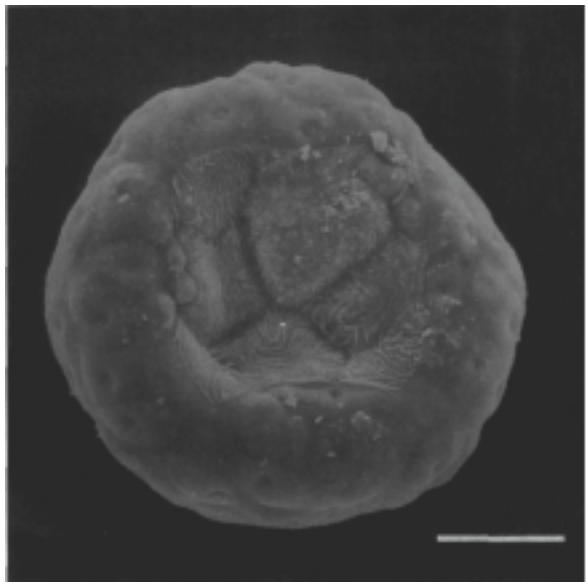

Figure 5

Scanning electron micrograph of a *Crepidula lingulata* gastrula, showing the vegetal cross furrow and the slight invagination as the micromeres grow around the macromeres. Scale bar = 50 microns.

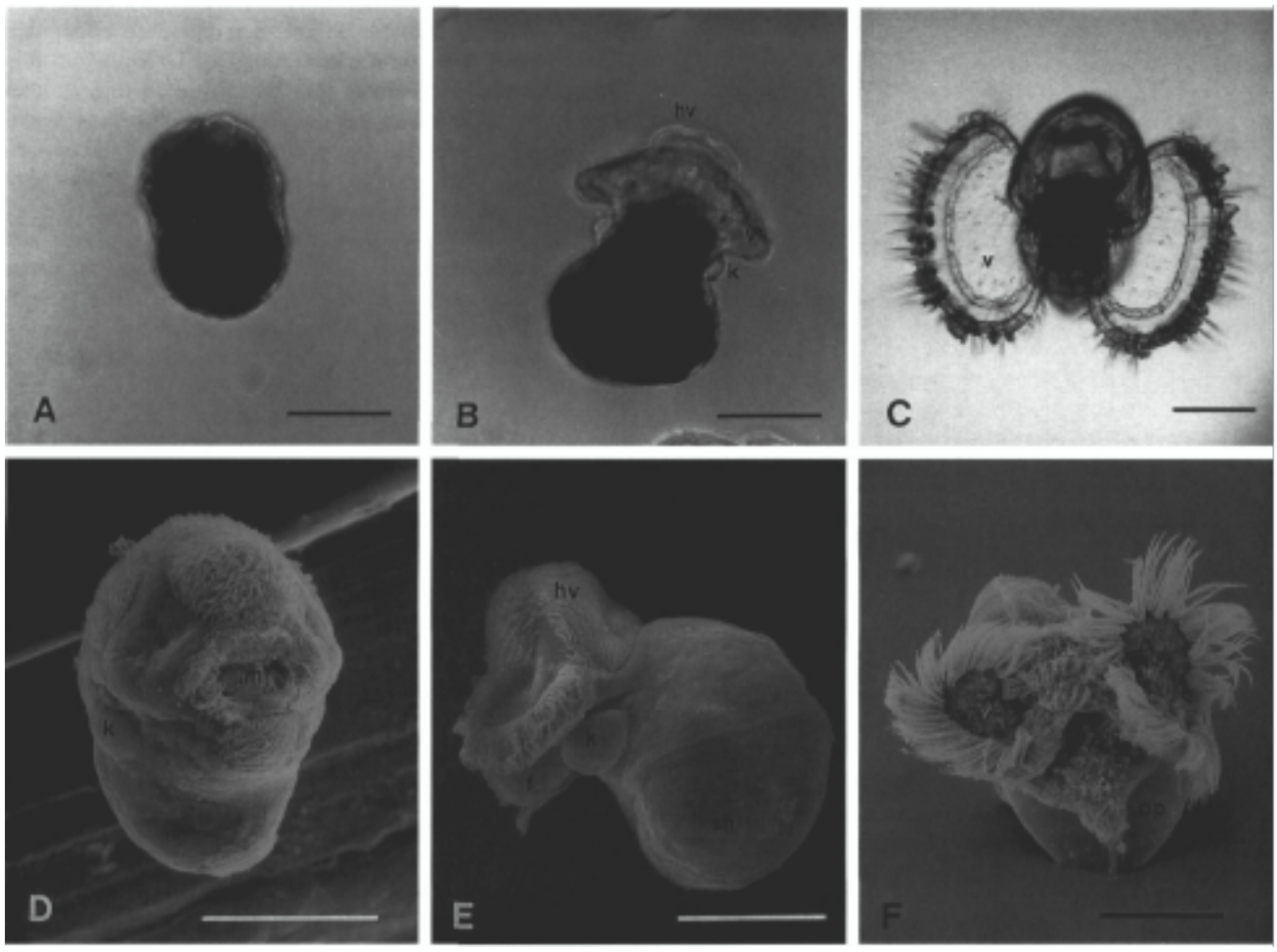

Figure 6

Light micrographs (A, B, C) and SEMs (D, E, F) of three developmental stages of *Crepidula lingulata*. A and D show early embryonic stages in which the beginnings of most major structures are just visible in the SEM, but little can be seen with light microscopy. B and E show a mid-stage embryo with obvious, well-developed head vesicle, embryonic kidneys, foot with operculum (E), and a shell that covers about half the yolk. C is a recently hatched veliger, and F shows an embryo just prior to hatching. The head vesicle and embryonic kidneys have disappeared, and the velar cilia are well developed. f, foot; hv, head vesicle; k, embryonic kidney; m, mouth; op, operculum; sh, shell; v, velum. Scale bar = 100 microns.

as few as 5–7 days after one brood hatched for another brood to appear.

At hatching, the planktotrophic larvae are about 300 μm in shell length. The embryonic shell is smooth, transparent, and planspiral or slightly left-handed. Anatomically they resemble larvae of *C. fornicata* (Werner, 1955): the eyes, tentacles, velum, operculum, heart, and foot are well developed, and the head vesicle and embryonic kidneys have disappeared. There are distinctive deep red stripes which run parallel and proximal to the food groove on the anterior and posterior curves of each velar lobe. On the lateral edge of the velum, proximal to the food groove, are up to three opaque white spots. The number of spots varies among larvae within a single brood. The only other pigmentation is the black pigment on the intestine near the shell apex. As the shell grows, it becomes clearly right-handed and develops widely spaced rows of very fine granular sculpture (Figure 7). After 25 days at 11–12°C the larvae begin to grow limpet-shaped shells, and the velum shrinks. None of these veligers settled when they were exposed to biofilmed substrates, adult-conditioned seawater, or conspecific shells. However, after 27 days, some larvae did settle when exposed to biofilmed substrate. Larvae settled at an average shell length of 745.2 μm (n = 10, SD = 82.4). There was considerable variation in the size of the veligers in any one culture, and animals continued to settle in response to biofilmed substrates over the next 18 days, while none settled

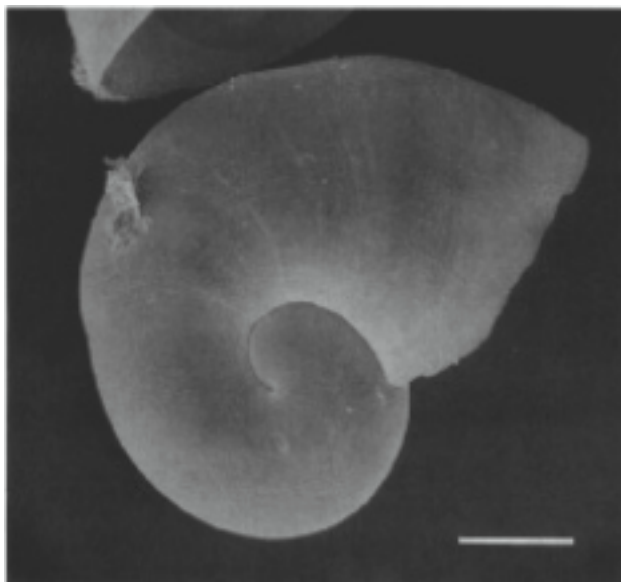

Figure 7

Scanning electron micrograph of the shell of a 3-week-old *Crepidula lingulata* larva. The arrow marks the embryonic/larval shell boundary. Scale bar = 100 microns.

in clean glass dishes. I was not able to determine how much longer the veligers would remain competent to settle or if they would eventually settle spontaneously in clean dishes. Fretter (1972) described the details of metamorphosis for this species.

DISCUSSION

The effects of the proximity of conspecifics on the size at sex change in *Crepidula* have long been of interest to biologists (Coe, 1938b; Collin, 1995; Warner et al., 1996). Coe (1938b) and Warner et al. (1996) have shown that sex change in gregarious species like *C. fornicata* and *C. norrisiarum* Williamson, 1905, is the result of conspecific associations. Juveniles kept alone often bypass the male phase and differentiate directly into females (Coe, 1938b). Males kept in association with females change sex later than those kept with other males. The sex of solitary species was not thought to be effected by conspecifics (Coe, 1938b). If this is true, then variation in stack composition is expected to result in more overlap in the size distribution of the two sexes in populations of species that form stacks. And solitary species are expected to show a more constant size at sex change, resulting in little overlap in size between the sexes (Collin, 1995).

However, the results of this study suggest that this is not the case. There is considerable size overlap between males and females of both stacking and non-stacking species. If anything, the overlap of male and female size in the stacking species is less than in the non-stacking species. This may be due to the demonstrable effect that conspecifics have on the sex change of *C. lingulata*. It is possible that individuals that live close to one another have the same effect on their associates' sex as stackmates do in stacking species. It is clear from the experiments described herein that associations among non-stacking species can have an effect on their sex.

Unlike the situation in other invertebrate groups and even in other mollusks, there is large intraspecific variation in egg size in *C. adunca*. *Crepidula adunca* eggs observed in this study ranged between 262–315 μm for one female. This size range is close to the egg diameter of 240 μm reported by Strathmann (1987) for Friday Harbor. However, Hoagland (1986; citing Coe, 1949) and Conklin, (1897) gave an egg size of 400 μm for *C. adunca* in California. Unfortunately, it is difficult to find uncleaved eggs, and therefore this variation in egg size cannot be partitioned into variation among capsules, females, and geographic regions. Size at hatching is also highly variable in *C. adunca*. The mean hatchling shell length can differ by as much as 60% between broods. Such variation in hatching size is common in gastropods that compete for nurse eggs in the egg capsules (Rivest, 1983; Hadfield, 1989), but is uncommon in invertebrates that, like *C. adunca*, develop to hatching without obvious exogenous food supplies.

It is becoming a paradigm in studies of the evolution of development that changes in larval or embryonic function (e.g., feeding to non-feeding, or pelagic to benthic) are correlated with often drastic changes in the mechanisms and sequence of developmental events (Emlet, 1991). For example, at the turn of the last century, Lillie (1895) explained the modification of cell sizes in unionid bivalve cleavage patterns as an embryonic "adaptation" to producing the specialized glochidium larva. Recent studies, focusing mostly on echinoids, have highlighted changes in larval skeleton, cleavage patterns, gastrulation, and ciliation in congeners associated with a shift from feeding to non-feeding development (e.g., Henry et al., 1992; Wray, 1996). Contrary to the pattern observed among echinoderms, early development in *Crepidula* seems to be conserved in the face of changes in egg size and mode of development. There are few morphological differences between direct and indirect developers that are not the direct result of differences in the amount of yolk or the reduction of larval feeding and swimming structures. However, *C. adunca* develops multiple embryonic kidney cells, whereas indirect developers like *C. lingulata* and *C. fornicata* (Conklin, 1897) have only one cell on each side of the body. Additionally, the operculum does not develop in direct developers (it is absent in all adult calyptraeids). Further studies aimed at determining if other selective pressures such as nurse egg feeding and albumin absorption have produced changes in calyptraeid development will further our understanding of adaptations in gastropod development.

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