FACULTATIVE PLANKTOTROPHY IN THE TROPICAL ECHINOID *CLYPEASTER ROSACEUS* (Linnaeus) AND A COMPARISON WITH OBLIGATE PLANKTOTROPHY IN *CLYPEASTER SUBDEPRESSUS* (Gray) (CLYPEASTEROIDA : ECHINOIDEA)

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Abstract: Larval development to metamorphosis and early juvenile growth and survivorship were examined in *Clypeaster subdepressus* (Gray) and *C. rosaceus* (Linnaeus). *C. subdepressus* has an obligatorily planktotrophic larva that metamorphoses after 16 to 28 days at 27 °C. The larva of *C. rosaceus* can, but need not feed prior to metamorphosis, which occurs after 5 to 7 days at 27 °C. Feeding by larvae of *C. rosaceus* does not change the time to metamorphosis but does increase size at metamorphosis, early juvenile growth and may increase juvenile survivorship relative to unfed larvae. Size at metamorphosis increases in larvae of *C. rosaceus* that feed for several days after they are competent to metamorphose, but there may be a limit to this increase because the condition of the rudiment degenerates after a period of time. The development of *C. rosaceus* may represent a transition between planktotrophy and lecithotrophy. This intermediate state has advantages for the juvenile stage that are not included in the trade of fecundity against risk to offspring usually considered in life history discussions of developmental mode of marine invertebrates.

Key words: Echinodermata; planktotrophy; larvae; pluteus; juveniles; metamorphosis; *Clypeaster rosaceus*; *Clypeaster subdepressus*

INTRODUCTION

Most marine invertebrates with planktonic larvae produce numerous small eggs that develop into planktotrophic larvae or produce fewer large eggs that become lecithotrophic larvae. Planktotrophic larvae require particulate food to develop and metamorphose. Lecithotrophic larvae have enough yolk reserves to develop and metamorphose without additional food. Some lecithotrophic larvae may possess the structures that enable them to feed but usually are assumed not to feed (e.g. Jablonski & Lutz, 1983). An advantage attributed to planktotrophy is less parental investment per offspring, thus resulting in a greater number of offspring. Advantages of lecithotrophy are a shorter planktonic period which reduces exposure to dangers such as predation or dispersal away from appropriate settling areas. Based on relations between egg size, time of larval

development, and mortality rates, models by Vance (1973) and Christiansen & Fenchel (1979) predict concentrations of species at these two extremes and suggest that only these extremes are evolutionarily stable for species with planktonic larvae.

A pattern of larval development that may be more widespread than is recognized by current classification schemes (see for review Mileikovsky, 1971; Jablonski & Lutz, 1983) is one in which a larva has enough yolk reserves to develop and metamorphose but may also feed while in the plankton. Vance (1973) and Chia (1974) called this form of development facultative planktotrophy. Thorson (1946) alluded to these larvae in his discussion, "Planktotrophic larvae with short planktonic periods". Thompson (1958) first showed that larvae of the nudibranch *Adalaria proxima* can feed, but feeding is not required to reach metamorphosis. Hadfield (1972) reported the same for another nudibranch larva, *Phestilla sibogae*.

This developmental pattern seems to incorporate the advantages and disadvantages of both planktotrophy and lecithotrophy. A facultatively feeding larva can augment nutritive stores that may allow an extended competent period, the time at the end of the larval phase when the larva is capable of metamorphosis. Additional nutritive reserves may also contribute to post-metamorphic growth and survivorship. A disadvantage of facultative feeders is reduced offspring number relative to obligate planktotrophs, though this disadvantage may be balanced by the increased offspring number relative to lecithotrophs. If faculative feeders allocate time and food reserves to construction of larval structures not needed by a lecithotroph, there are costs relative to lecithotrophs. The models of Vance (1973) and of Christiansen & Fenchel (1979) do not explain these intermediate patterns of development.

In this report, I examine possible advantages of facultative planktotrophy by comparing development of the echinoids, *Clypeaster rosaceus* (Linnaeus) and a congener, *C. subdepressus* (Gray). As adults, these species occur in back-reef sand environments and sea-grass beds throughout the Caribbean and tropical west Atlantic. Larvae of *C. rosaceus* are shown to be facultative planktotrophs. Larvae of *C. subdepressus* are shown to be obligate planktotrophs. This comparison shows the differences that ample yolk reserves make for development of a larval body and rudiment. To examine whether there are advantages to facultative planktotrophy of *C. rosaceus*, an intraspecific comparison of development is made between larvae that were fed and those not fed. Specifically, I report the effects of larval feeding on larval development, size at metamorphosis, juvenile growth and survivorship.

MATERIALS AND METHODS

In October 1983, adults of *C. rosaceus* and *C. subdepressus* were collected from Caribbean back-reef, sea-grass habitats at Taiantupo, San Blas Islands, and Isla Grande, Republic of Panama. Adults were maintained in aquaria with recirculated water. Shell fragments from the nearby Pacific Ocean were used as aquarium substratum.

Spawning was induced by rigorous shaking of adults. Eggs were rinsed three times in filtered sea water (1–3 μm pore size) and fertilized with a dilute sperm solution. Diameters of 25 eggs from each female were measured at 40 ×, to the nearest 2.5 μm. All eggs were measured in a drop of sea water and without a coverslip to avoid distortion by compression. Because eggs were approximately spherical, only one axis, parallel to the ocular micrometer, was measured for each egg. The organic content in glucose equivalents was determined for eggs of one individual of *C. rosaceus* with the methods of Strathmann & Vedder (1977). Five samples of approximately 1350 eggs each were assayed. The organic content of eggs of *C. subdepressus* was not determined.

All larval cultures were raised in finger bowls filled with membrane-filtered sea water (0.45 μm pore size) at 26–27 °C and according to the methods of Strathmann (1971), with exceptions described below. Larvae were fed a mixture of algal cells of *Dunaliella tertiolecta, Cryptomonas* sp. and *Isochrysis* sp. separated from the algal culture medium (Alga-Gro, Carolina Biological, Inc.) by centrifugation and suspended in filtered sea water. Two larval cultures of *Clypeaster subdepressus* and five cultures of *C. rosaceus* were reared through metamorphosis. No attempt was made to measure food concentrations or clearance rates. The nomenclature used for the larval arms is that of Mortensen (1921).

The effect of larval nutrition on time to metamorphosis for *C. rosaceus* was examined in two studies. In the first, 900 sibling larvae were divided into 18 stock bowls. Larvae in nine bowls were fed; the others were not fed. On each sampling day, the stock bowls were combined within each treatment, experimental larvae were randomly chosen, and the pooled stock cultures were split again into multiple bowls. On Days 4 through 9 after fertilization, 84 larvae from each treatment were placed in seven replicate bowls (12 larvae per bowl) with a prepared substratum (see below) that induced metamorphosis. Eight hours later each bowl was checked and the number of completely and partially metamorphosed juveniles and number of larvae searching the substratum were counted. Partially metamorphosed juveniles were identified by intact larval arms on the aboral surface of the juvenile. A searching larva was recognized by tube feet extending from the vestibular opening of the larva. Any larvae remaining in experimental bowls were discarded. Less than 3% of the total number of larvae in the stock bowls were unaccounted for at the end of the experiment.

The substratum that induced metamorphosis was prepared from shell fragments and water from aquaria that contained adult *Clypeaster*. A shell/water mixture was shaken by hand for 1 to 2 min and the supernatant was filtered through glass fiber filters to collect the suspended material. The damp filters were quartered and put into bowls for settlement tests. For each test new filters were prepared immediately before introducing larvae.

In the second experiment with larvae of *C. rosaceus*, the effects of larval food on cumulative settlement were examined. This experiment differed from the previous one because larvae were given a relatively longer time to settle and to metamorphose on a more natural substratum. Eight-day-old sibling larvae from fed and unfed treatments

were placed in bowls with shell fragments from aquaria containing adult *Clypeaster* (eight bowls per treatment, five larvae per bowl). Metamorphosed individuals were counted and removed at ≈ 1-day intervals for 6 days.

To test the effects of food on size at metamorphosis of *C. rosaceus*, a total of seven sibling cohorts of larvae were reared through metamorphosis. Sibling cohorts came from four different females. ("Cohort" is used to refer to sibling larvae or juveniles that are the same age.) For this study, sibling larvae between the prism and four-armed stages (2 days after fertilization) were isolated in covered finger bowls containing 100 ml of 0.45 μm filtered sea water, with or without food. The sea water in the bowls was changed daily. Bowls containing the larvae of the "food treatment" were supplied with an ample supply of food after each water change.

To examine the consequences of pre-metamorphic nutrition on post-metamorphic growth and survivorship, six cohorts of juveniles (from four separate larval cultures) were kept in finger bowls and given algal food and/or filters prepared as indicated above. For each cohort, there were two bowls that contained juveniles from fed or unfed larvae respectively. These juveniles were counted and measured subsequently. Test diameter and the longest over-all diameter from spine tip to opposite spine tip (called "test + spine diameter") were measured. Changes in these size parameters are considered growth.

Statistical procedures were carried out according to Sokal & Rohlf (1969).

RESULTS

INTERSPECIFIC COMPARISON OF DEVELOPMENT: SIZES AND RATES

The eggs of *Clypeaster rosaceus* had a diameter nearly twice those of *C. subdepressus* (Table I), equal to an approximately six-fold difference in egg volume. The eggs varied little in diameter within a species. The eggs of both *C. rosaceus* and *C. subdepressus* were negatively buoyant like those of other planktotrophic species of echinoids (Emlet *et al.*, in press). A content of 1.20 μg/egg (SD 0.19, $n = 5$ samples) organic matter (as glucose equivalents) was measured for one *C. rosaceus*. The density of organic matter was calculated to be 100.5 μg/mm^3.

The development of *C. subdepressus* was typical for echinoids with planktotrophic pluteus larvae (Fig. 1). *C. rosaceus* also formed a pluteus that developed through the eight-armed stage (Fig. 2). Even though both species followed similar patterns of morphogenesis, the interspecific comparison of development clearly illustrates the consequences of increasing yolk on developmental rates and on more subtle morphological characteristics such as changes in larval arm length and overall body size (Table II).

Early development until the feeding pluteus stage was faster for *C. subdepressus* than for *C. rosaceus* but slower subsequently (Table II). Larvae of *C. subdepressus* began feeding by the middle of the second day after fertilization. Larvae of *C. rosaceus*

TABLE I

Egg diameters (in μm) of *Clypeaster* species: N is 25 eggs for each female.

Female No.	Mean diameter (μm)	SD
C. rosaceus		
1	281	3.4
2	278	4.6
3	266	6.3
4	287	5.0
5	286	3.2
6	283	5.7
Mean (of 6 means)	280.3	7.7
C. subdepressus		
1	155	4.2
2	150	3.4
Mean (of 2 means)	152.6	3.5

captured and ate algal cells by the end of the second day. The pluteus of *C. rosaceus* added arms rapidly (Table II) and was completely formed including vibratile lobes by the fifth day after fertilization (Fig. 2J). Development of *C. subdepressus* slowed after the four-armed stage and the larvae did not reach their full size until approximately 10 days after fertilization (Fig. 1J). The total developmental time from fertilization to metamorphosis for *C. rosaceus* was less than half that of *C. subdepressus* (Table II).

The larva of *C. rosaceus* was opaque yellow, probably because of widely distributed yolk material, while the pluteus of *C. subdepressus* was transparent except in the gut and rudiment region of the larval body. In both species, red pigment cells appeared in the gastrulae and became concentrated in larvae in patches or rows near the ciliated band and tips of the arms. The pluteus of *C. subdepressus* reached a greater length and had longer arms than *C. rosaceus*, but the body regions of the two larvae were similar in size (Table II).

In both species the juvenile rudiment developed after the 8-armed stage was reached; the larval body did not grow further and usually shrank (Figs. 1K, and 2L). At or about the time of competence, resorption of the larval arms began and they often shortened to half their greatest length before metamorphosis occurred (Figs. 1L and 2M). The tips of the arms swelled, probably with tissue derived from the resorbed regions of the arms.

Morphological changes in the larvae continued until most of the larval body region was occupied by the bulging, globular juvenile rudiment. Fed larvae of *C. rosaceus* were kept for 22 days after fertilization and were still capable of metamorphosis when last tested on Day 20. A comparison of rudiments was made in 8-day-old larvae from one culture and 22-day-old larvae from another culture. The number and length of juvenile spines in the rudiment was compared for six competent larvae from each age group. Rudiments of 8-day-old larvae contained 14–16 spines that were 90–120 μm long; rudiments of 22-day-old larvae contained 6–14 spines that were 50 to 100 μm long.
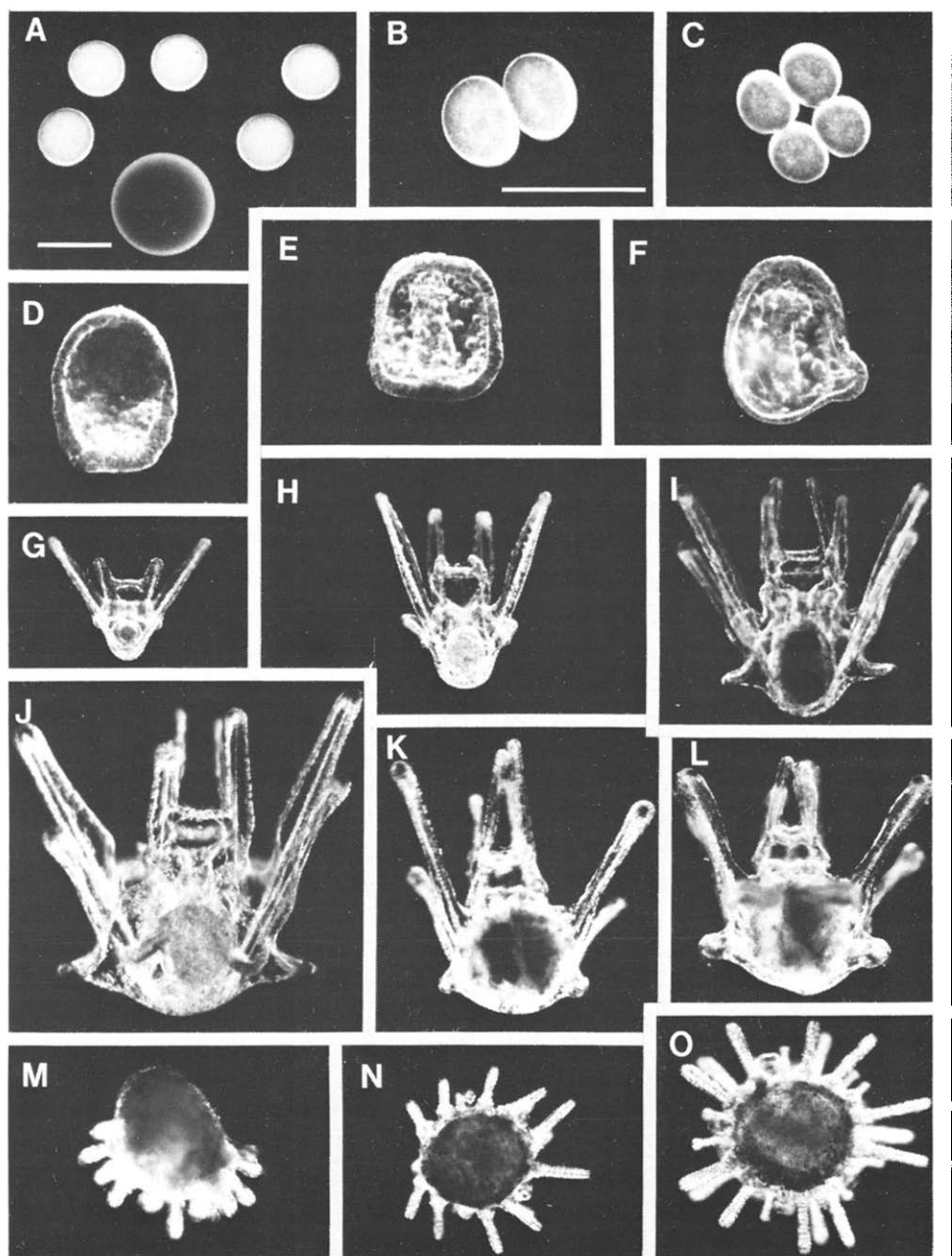
Fig. 1. Stages of development of *Clypeaster subdepressus*: A, five unfertilized ova of *C. subdepressus* and one ovum of *C. rosaceus*; note the greater opacity of the larger egg of *C. rosaceus*; B, 2-cell stage, the fertilization envelope is present but not visible; C, 4-cell stage; D, early gastrula with flattened vegetal plate and invaginating 1° mesenchyme; E, late gastrula with mesenchyme; F, prism stage; G, 4-armed pluteus; H, early 6-armed pluteus; I, 8-armed pluteus; J, full-sized 8-armed pluteus; K, 8-armed pluteus with juvenile rudiment developing in the body region; L, competent larva with shrinking larval arms and a well-developed rudiment; M, lateral view of a newly metamorphosed juvenile; N, aboral view of a juvenile 1 day after metamorphosis; O, juvenile 3 days after metamorphosis; both scale bars, 200 μm; A,G–O are all the same magnification; B–F are the same, greater relative magnification; all plutei G–L are shown in a ventral view, except J, which is a dorsal view.
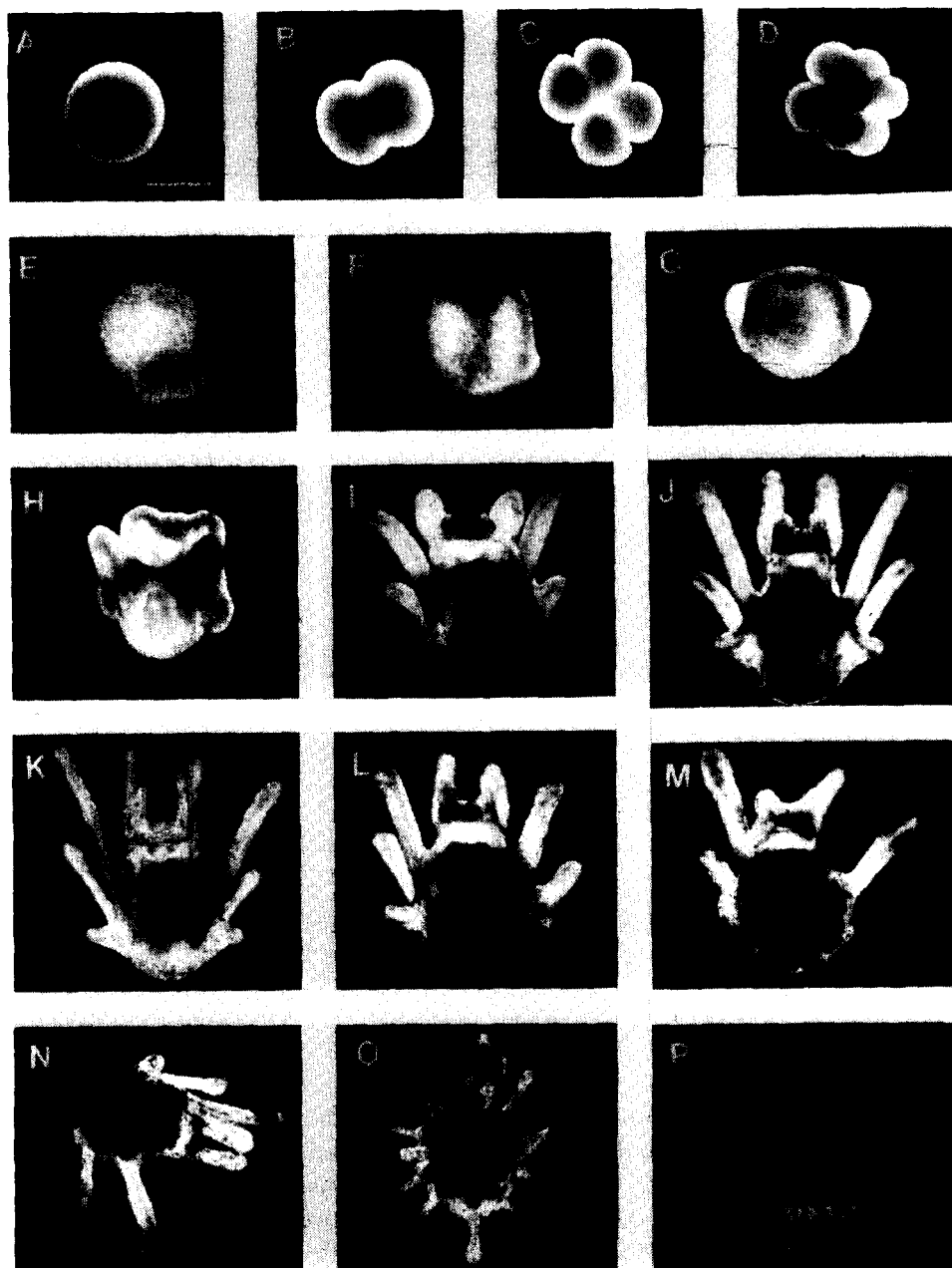
Fig. 2. Stages of development of *Clypeaster rosaceus*: A, unfertilized ovum; B, 2-cell stage surrounded by fertilization envelope; C, 4-cell stage; D, 8-cell stage; E, early gastrula, similar stage to Fig. 1D; F, early prism, with flattened oral surface facing away from view; G, late prism; H, 4-armed pluteus with mouth and anus visible; I, 6-armed pluteus; J, 8-armed pluteus; K, 8-armed pluteus with juvenile rudiment beginning to form in body region; L, competent larva; M, competent larva with bulging rudiment and shortened larval arms; N, larva flaring arms as a sign of response to substratum; O, aboral view of a partially metamorphosed juvenile, with rudiment everted and with oral hood and larval arms still intact; P, lateral view of a later stage, partially metamorphosed juvenile with larval arms still intact; the early juveniles of *C. rosaceus* are indistinguishable in appearance from those of *C. subdepressus* (e.g. Fig. 1M–O); all photos are the same magnification; scale bar, 200 μm; plutei in H–M are shown in ventral view.

RICHARD B. EMLET

TABLE II

Developmental schedule and larval characters for *Clypeaster rosaceus* and *C. subdepressus* at 26–27 °C: –,
no data; except where indicated, stage times are a representative compilation from notes on five cultures
of *C. rosaceus* and two cultures of *C. subdepressus*.

Stage	Time from fertilization to stage in hours (days, in parentheses)	
	C. subdepressus	*C. rosaceus*
Fertilization	0	0
Two-cell	–	1
Four-cell	2	2
Eight-cell	–	2
Sixteen-cell	–	3
Non-motile blastula	–	9
Hatched blastula	–	12
Early gastrula	14	16
Late gastrula	20	25
Late prism	24	29
Early four-armed	–	37
Late four-armed	43	(2)
Six-armed	(4)	(3)
Eight-armed	(10)	(4)
Metamorphosis	(16, 18[a])	(5[a], 7[b])
Larval character		
Larval color	transparent	yellow
Total length[c]	1000 μm	720 μm
Post-oral arm length[d]	590 μm	425 μm
Body length[e]	570 μm	520 μm

[a] Minimum time for two cultures of *C. subdepressus* and one culture of *C. rosaceus*.
[b] Representative time at which most of cohort is competent.
[c] The total length was measured from the posterior median line to the tip of the postoral arm in 8-armed
stages.
[d] The length of the postoral arm (in 8-armed stages) was measured from its tip to where it joins the body
region.
[e] The body length was measured along the median line from the posterior end to the anterior side of pre-oral
hood (8-armed stage).

Fewer and shorter spines in older larvae suggests that there is a degeneration of the
rudiment and may indicate a limit to the competent period, or alternatively that there
were culture effects. The latter possibility seems unlikely as both cultures were equally
well cared for and no other differences were noticed between cultures.

In one culture of *C. subdepressus*, some larvae metamorphosed on Day 16 after
fertilization. Other larvae from the same culture but not yet competent (as judged by
the partially developed juvenile rudiment) were fed for 12 more days before being
introduced to substratum on Day 28 after fertilization. There was no significant
difference in the test diameters at metamorphosis for these two groups (n = 17 and 15,
respectively; t = 0.131; P = 0.897). In a second culture of *C. subdepressus* minimum
time to metamorphosis was 18 days.

EFFECTS OF FOOD ON DEVELOPMENT AND GROWTH OF *C. ROSACEUS*

There were no noticeable differences in the time of appearance or length of larval structures between larvae of *C. rosaceus* from fed and unfed treatments. Their larval bodies appeared similar in size, as did the time of formation of the juvenile rudiment. Fed larvae were more opaque in the body region than unfed larvae.

In the experiment that examined the effect of food on time to metamorphosis, on Day 5 after fertilization only 4 of 84 fed larvae metamorphosed while none of the unfed larvae metamorphosed. Numbers of both fed and unfed larvae that metamorphosed increased thereafter so that by Day 7, 70% of both fed and unfed larvae metamorphosed. On Days 6, 7, 8, and 9 the total number of larvae metamorphosing was always slightly higher for the unfed larvae (Fig. 3a). If totals of partially and completely metamorphosed individuals are compared, the total numbers metamorphosing in fed and unfed treatments are even more similar (Fig. 3b). Thus the effect of food on time to metamorphosis appears to be minimal for the cohort of sibling larvae examined.
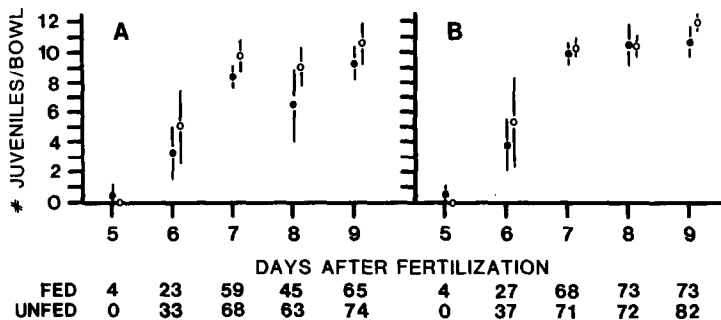

Fig. 3. Effects of feeding larvae and larval age on number of juveniles metamorphosing for *Clypeaster rosaceus*: A, only completely metamorphosed juveniles were counted; B, partially and completely metamorphosed juveniles were counted; ●, mean number/bowl of juveniles from fed larvae; ○, mean number/bowl of juveniles from unfed larvae; each mean is determined from seven bowls that contain 12 larvae each, and the bars are 1 SD around the mean; the bottom rows of numbers are the total number of metamorphosed individuals counted (out of 84 possible) on each day for each treatment.

Because bowls of larvae within each food treatment were pooled prior to sampling for response to inducing substance, information on variation due to food treatments is confounded with that of replicates and analysis with inferential statistics is not valid. The standard deviation bars shown in Fig. 3a,b represent variation due to sampling from the large stock of larvae within each treatment and variation among the multiple induction containers. However, the seven to nine bowls that were used in each food treatment reduce the probability that differences between food treatments are due to replicates.

In the study that examined effects of feeding by larvae on cumulative settlement, total numbers of metamorphosed larvae in each treatment did not diverge until the last days of the census (Fig. 4). On the 6th and last day of the experiment (14 days) after fertilization), there were 39 juveniles from fed larvae and 31 juveniles from unfed larvae. For this last census, the number of juveniles per bowl from fed larvae is not different from the number of juveniles from unfed larvae (Mann–Whitney, two-tailed, $P = 0.08$, $n = 8$ bowls per treatment). These two studies on the effect of food on time to metamorphosis suggest that the developmental schedules of cohorts of larvae of *C. rosaceus* are not changed by larval nutrition.
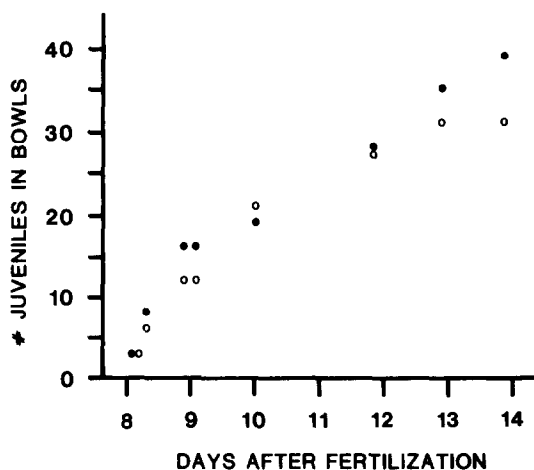

Fig. 4. Effects of food on cumulative metamorphosis where only completely metamorphosed juveniles of *Clypeaster rosaceus* are counted: ●, total number of juveniles from fed larvae; ○, total number of juveniles from unfed larvae; totals were determined from the sum of eight bowls containing five larvae each from each treatment.

The test diameters of juveniles newly metamorphosed from fed larvae were significantly greater than those of unfed larvae (Fig. 5A, $P < 0.001$, *t*-test, for comparisons between treatments in each of seven cohorts). For two of these cohorts enough measurements of test plus spine diameter were made to compare sizes between juveniles from fed and unfed larvae. These also show a significantly larger size for juveniles from fed larvae (Fig. 5B, $P < 0.001$, *t*-test). There is an effect of larval age at metamorphosis on the test diameter at metamorphosis for the fed treatments. There is a significant positive correlation between days after fertilization (6, 8, 9) and test diameter for the fed treatments but not for the unfed treatments (Spearman $r_s = 0.284$, $P = 0.001$, $n = 135$ individuals for fed treatments, and $r_s = -0.0824$, $P = 0.181$, $n = 125$ individuals for unfed treatments). The effects of female parent, food and age (days after fertilization) on test size at metamorphosis were also examined in a three-way ANOVA for five cohorts of larvae from two different female parents. One cohort of larvae
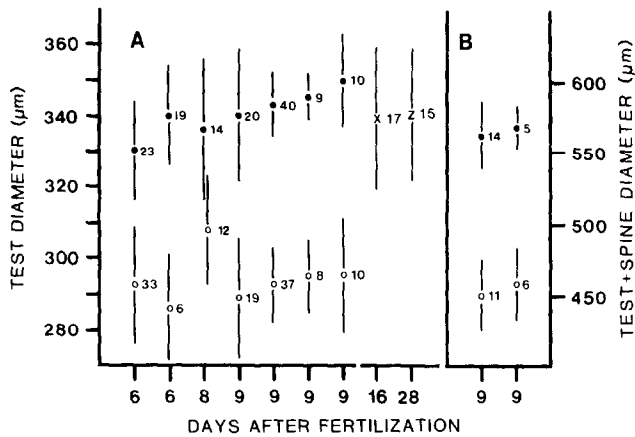
Fig. 5. Effects of feeding larvae on test diameter (A) and test plus spine diameter (B) at metamorphosis: ●, juveniles from fed larvae of *Clypeaster rosaceus*; ○, juveniles from unfed larvae of *C. rosaceus*; X, Z, juveniles from 16- and 28-day-old fed larvae of *C. subdepressus*, respectively; symbols are mean sizes in μm, bars are 1 SD around the mean, and numbers are sample sizes.

(consisting of the fed and unfed treatments) from each female was introduced to substratum on Day 6 and the other three cohorts on Day 9 after fertilization. Test diameters were measured 8 to 12 h after larvae were introduced to the substratum. The effect of female parent is not significant ($F = 2.16, P = 0.144$) but the effects of food and day on test diameter are both significant (food, $F = 339.5, P < 0.001$; day, $F = 4.22$, $P = 0.042$). Second and third order interactions terms are not significant.

The test diameter at metamorphosis for fed larvae of *C. rosaceus* is similar to that of *C. subdepressus* (Fig. 5A).

GROWTH AND SURVIVORSHIP OF JUVENILES

Juveniles from fed larvae of *C. rosaceus* increased in test diameter and test plus spine diameter for 7 to 12 days after metamorphosis (Fig. 6). Juveniles of unfed larvae did not increase in test diameter beyond 5 days or test plus spine diameter beyond 8 days after metamorphosis. Juveniles of *C. subdepressus* that metamorphosed on 16 and 28 days after fertilization grew similarly to those from fed larvae of *C. rosaceus* (Fig. 6).

After these initial growth periods, test diameter remained constant, and test plus spine diameter tended to stay constant or to decline slightly for the remaining time that the juveniles survived. Due to the irregular sampling of juveniles, it was not possible to determine if juveniles of *C. rosaceus* from older larvae grew faster than those from younger ones. Though the juveniles were provided with mixed algal cells for food or filters with suspended material or sand grains, none survived beyond ≈ 30 days after metamorphosis. As time progressed after metamorphosis all juveniles appeared to be starving. Their tests became increasingly transparent and their movements much slower.
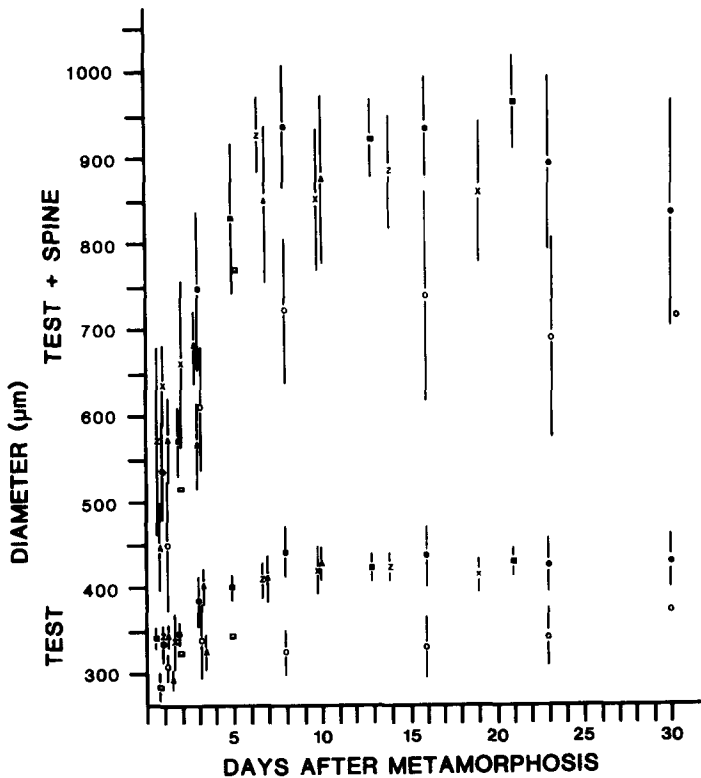
Fig. 6. Growth of juveniles from fed and unfed larvae of *Clypeaster rosaceus* and from fed larvae of *C. subdepressus*: the lower set of points is test diameter and the upper set is test plus spine diameter; ●, ▲, ■, and ○, △, □, are means from corresponding batches of fed and unfed larvae of *C. rosaceus*, respectively; X,Z are means from larvae of *C. subdepressus* in the same cohort, that metamorphosed 16 and 28 days after fertilization, respectively; bars are 1 SD and are included on means from sample sizes ranging from 4 to 21; most sample sizes are between 10 and 20; means without bars have samples sizes of 2 or 3.

There were no apparent differences in rate of development of the Aristotle's lantern in juveniles from the two treatments of *C. rosaceus*. At the time of metamorphosis, the juvenile rudiment contained numerous calcareous plates of the test and spines, including usually two to four sphaeridia, but no jaw apparatus. The oral region was covered with an opaque brown-pigmented tissue. Observations with crossed-polarized light showed that the teeth and pyramids appeared by 24–48 h after metamorphosis and by 4 days the teeth measured 40 μm in length and were each comprised of two primary plates. Seven days after metamorphosis most of the brown pigment was gone, but the lantern was not functional (i.e. movable). By 10 days, the lantern moved, but a buccal opening did not appear for 2 more days. Twelve days after metamorphosis, juveniles from both fed and unfed groups of larvae possessed mouths, moving lanterns, and teeth longer than 100 μm.

Survivorship of juveniles from fed larvae of *C. rosaceus* was greater than for juveniles from unfed larvae (Table III). Juveniles from fed larvae lived longer than juveniles from unfed larvae in three cohorts (Table III, Cohorts 1, 2, 3). For two other cohorts (nos. 4, 5) juveniles from the two treatments lived the same time. In only one cohort (no. 6) did juveniles from unfed larvae out-live those from fed larvae. Time to 50%

TABLE III

Survivorship of juveniles of *Clypeaster rosaceus* from the treatments of fed and unfed larvae.

Day after metamorphosis	Fed (larvae) (No. alive)	Unfed (larvae) (No. alive)	Time (days) to 50% mortality	
			Fed (larvae)	Unfed (larvae)
Cohort 1			14.5	5
1	21	18		
3	21	18		
7	21	0		
10	19	0		
20	0	0		
Cohort 2			29[a]	2
1	19	6		
2	19	3		
5	19	3		
13	15	0		
21	12	0		
Cohort 3			15	7
1	9	8		
13	7	0		
17	2	0		
19	0	0		
Cohort 4			33.5	26
1	16	12		
3	16	12		
8	16	12		
16	15	12		
23	13	9		
30	12	2		
41	0	0		
Cohort 5			10.5	20.5
1	11	5		
9	11	5		
12	1	5		
19	1	3		
26	0	0		
Cohort 6			17	12
2	12	13		
7	12	13		
15	8	3		
22	0	1		

[a] This value was extrapolated by assuming constant mortality based on mortality in the last sample interval. All other values were interpolated.

mortality was determined for each treatment in the six cohorts by interpolation assuming a constant (linear) mortality between sample days (Table III). In one case only (Cohort 2, juveniles from fed larvae) 50% mortality never occurred during the study and this value was extrapolated assuming constant mortality from the last sample interval. In five of six cohorts, the time to 50% mortality was less for juveniles from unfed larvae (Wilcoxon paired-sample test, two-tailed, $n = 6$, $P = 0.10$). A lack of significant difference at the $P = 0.05$ level is probably due to the small number of cohorts.

DISCUSSION

INTERSPECIFIC COMPARISONS

The development of *C. rosaceus* is essentially identical to that of obligatorily planktotrophic species of echinoids (e.g. Mortensen, 1921). This was unsuspected because the eggs are large and yolky compared those of obligate planktotrophs. The major developmental differences are that the larvae of *C. rosaceus* have a shorter total developmental time from fertilization to metamorphosis and do not require food to reach metamorphosis.

The density of organic material in eggs of *C. rosaceus* (100.5 μg/mm^3) is the lowest reported for echinoderm eggs (reviewed in Emlet *et al.*, in press). Strathmann & Vedder (1977) found density of organic matter decreased with increasing egg size for eight planktotrophic species of echinoderms. The density of organic matter in eggs of *C. rosaceus* falls on a line that is an extension of the regression line established by Strathmann & Vedder (1977). In contrast, data from Turner & Lawrence (1979) and Lawrence *et al.* (1984) show no change in organic density with egg size for echinoderms with small eggs. Lawrence *et al.* (1984) found an up to two-fold greater organic density in the large eggs of lecithotrophic species compared to small eggs of planktotrophic species. The low value for organic density in eggs of *C. rosaceus* suggests that there may be a J-shaped curve for concentration of organic matter over the range of egg sizes in echinoderms.

The eggs of *C. rosaceus* have six times greater volume than eggs of its planktotrophic congener, *C. subdepressus*, but this volume difference may not reflect total energy differences. If the density of organic matter in eggs of *C. subdepressus* (not determined) is similar to other echinoderms that have equivalent egg sizes, it would be expected to be twice that in eggs of *C. rosaceus*. This would suggest that the six-fold difference in egg volume, reflects only a three-fold difference in organic content.

The comparison of development between the two *Clypeaster* species shows the plausibility of the assumption of the Vance (1973) model, that much of the variation in developmental patterns of benthic invertebrates is the result of the trade between parental investment and risk to offspring. Because juveniles of the two species of *Clypeaster* are close to the same size at metamorphosis, time spent feeding in the plankton should not be influenced by selection affecting juvenile size at metamorphosis.

Assuming that mortality rates are constant across stages for the two species and that the number of eggs that can be produced is inversely proportional to the egg volume, then the number of juveniles at metamorphosis for a species should be proportional to

$$(1/\text{egg volume})e^{-Td},$$

where T is developmental time in days to metamorphosis and d is the instantaneous mortality rate. For *C. rosaceus* and *C. subdepressus*, T was chosen to be 7 and 16, respectively. The egg volumes are proportional to the cubes of egg diameters, 280 μm and 150 μm respectively. If the number of metamorphosing juveniles (per reproductive effort) are to be the same with each type of development, the two expressions should be equal and the instantaneous mortality rate at which equality occurs can be calculated.

$$(1/150^3)\,e^{-16d} = (1/280^3)\,e^{-7d}.$$

Taking the natural logarithm of both sides and solving for d, we obtain

$$\ln(150^3/280^3) = -d(16 - 7)$$
$$-1.873 = -d(9)$$
$$d = 0.21/\text{day}.$$

An alternative calculation that takes into account the rough estimate of differences in organic content of eggs of the two species yields a balancing mortality rate of $d = 0.11/\text{day}$. In either case, a rather high mortality could be sustained by the planktotroph during its longer period in the plankton and the end result would still be the same number of juveniles as for the facultative planktotroph (or a lecithotroph under similar circumstances). The mortality rates calculated appear reasonable because both higher and lower mortality rates than this have been estimated for larvae of benthic invertebrates and copepod nauplii in some coastal waters (see for summary Strathmann, 1982; Chaffee & Strathmann, 1984).

Egg diameters for 17 species of clypeasteroids (including the two above) were compiled from the literature and from personal communication with H. Lessios (Table IV). The distribution of egg diameters is skewed toward smaller sizes with a median of 120 μm, mode of 100 μm, and range from 90 to 300 μm. Both *C. subdepressus* and *C. rosaceus* have diameters larger than the median. The egg of *C. rosaceus* is one of the largest reported for clypeasteroids and is similar to that of *Peronella japonica* (Table IV). *P. japonica* is known to lack a feeding larva in development, though the developmental stages do show remnant larval arms and spicules prior to metamorphosis (Mortensen, 1921).

There may be other echinoids that have a facultative planktotrophic development. Two cold-water spatangoids in the genus *Brisaster* are known to have large eggs and feeding larvae. Runnström (1929) found it odd that a large egg gave rise to a feeding larva in *Brisaster fragilis*. Strathmann (1979) reported that a feeding larva of *B. latifrons* develops from a 345-μm diameter egg with developmental time of 2 months. He pointed to the oddity that such a large egg does not result in a larger than average juvenile at

RICHARD B. EMLET

TABLE IV

Egg diameters (in μm) of species of Clypeasteroida.

Species	Egg diameter	Reference
Arachnoides placenta	110	Feliciano, 1933
Astriclypeus manni	190	Mortensen, 1921
Clypeaster humilis	100	Mortensen, 1937
Clypeaster japonicus	115	K. Dan, unpubl., in Harvey, 1956
Clypeaster rosaceus	280	Emlet, this paper
Clypeaster subdepressus	152	Emlet, this paper
Dendraster excentricus	120	Snyder, 1925
Dendraster laevis	124	Emlet, pers. obs.
Echinarachnius parma	145	Harvey, 1956
Echinocyamus pusillus	100	Theel, 1892
Encope stokesii	114	Lessios, pers. obs.
Fibularia ovulum	90	Mortensen, 1937
Fibularia nutriens	brooder[a]	Clark, 1909
Laganum depressum	100	Mortensen, 1938
Leodia sexiesperforata	178[b]	Lessios, pers. obs.
Mellita quinquiesperforata	150	Caldwell, 1972
Peronella japonica	276	K. Dan, unpubl.; Harvey, 1956
	≈ 300	Okazaki & Dan, 1954
Scaphechinus tenuis	100	Onoda, 1938

[a] Egg size is unknown, but Clark reports spherical embryos ≈ 500 μm in diameter in the aboral brood chamber.

[b] Crozier (1918) reports an egg diameter of 260 μm for this species.

metamorphosis, and he mentioned that this larva might be a facultative planktotroph. These observations on the development of *B. latifrons* and *Clypeaster rosaceus*, point out that echinoid eggs with diameters that range from 280 to 350 μm should not be assumed to develop into non-feeding, lecithotrophic larvae. Harvey & Gage (1984) have recently reported egg diameters in this size range for three species of deep water pourtalesiids and developmental studies are needed to clarify their type of development.

EFFECTS OF FEEDING LARVAE

In a strict sense, facultative planktotrophy as a type of development refers to the larval stages alone, yet food eaten by larvae could have an effect on the early juvenile period. Feeding by the larvae of *C. rosaceus* may be required for the juvenile to survive in nature. Juveniles from fed larvae have ≈ 15% larger test diameters and 20% larger test plus spine diameters after metamorphosis than unfed larvae (Fig. 5). Juveniles from fed larvae grow for a longer period after metamorphosis and in general survived longer than juveniles from unfed larvae (Fig. 6, Table III). In contrast, food eaten by lecithotrophic larvae of the gastropod *Conus pennaceus* did not increase survivorship of juveniles relative to those of unfed larvae (Perron, 1981).

The advantages conferred by metamorphosing at a larger size might include reducing

susceptibility to predators or starvation and placing an animal higher on a growth curve. Highsmith (1982) has shown that early stage juveniles of the sand dollar *Dendraster excentricus* are eaten by the tanaid *Leptochelia dubia*, and when sand dollars reach ≈ 1.5 mm in total length they are no longer eaten by the tanaids. It is widely accepted that many macroscopic invertebrates show exponential growth rates, that is instantaneous growth rates are proportional to body size (e.g. Yamaguchi, 1975, 1977). Thus, facultative feeding by larvae of *Clypeaster rosaceus* may give the juveniles a "head start" at settlement. However, because none of the *Clypeaster* juveniles lived longer than 30 days and stopped growing before this, it is not possible to fully evaluate how effectively larval food aids juvenile growth.

Another advantage to retaining the ability to feed in lecithotrophic development may be to extend the competent period. Extending the competent period may be an advantage if larvae are not near an appropriate site for settlement (Doyle, 1975; Obrebski, 1979; Jackson & Strathmann, 1981). Fed lecithotrophic larvae of *Conus pennaceus* and *Phestilla sibogae* live longer in culture than unfed larvae (Perron, 1981; Kempf & Hadfield, 1985). Whether this advantage also applies to *Clypeaster rosaceus* is uncertain. Fed competent larvae were still capable of metamorphosis 14 days after they became competent. Extension of the competency period is probably limited, however, because the number and length of spines in the juvenile rudiment of competent larvae (from different cultures) dropped between 8 and 22 days after fertilization. These observations were not extended to longer time intervals or to unfed larvae. The degeneration of the rudiment in *C. rosaceus* is in marked contrast to the finding that there is no difference between growth of juveniles from larvae of *C. subdepressus* that reached competence over different time intervals. Highsmith and Emlet (unpubl. data) have found that larvae of the clypeasteroids, *Dendraster excentricus* and *Echinarachnius parma* can remain competent to metamorphose for at least 6 and 3 wk, respectively, and that juveniles from delayed larvae had slower growth rates.

Contrary to the prediction of the Vance (1973) model, that extremes of planktotrophic and lecithotrophic development are the evolutionarily stable ones, advantages may exist for intermediates like the facultative planktotroph. The increased size and growth at metamorphosis and survivorship after metamorphosis for larvae of *Clypeaster rosaceus*, which retain the ability to feed, may explain why this intermediate condition is found. On one hand, validity of assumptions of the Vance (1973) model are supported by the interspecific comparison between the two *Clypeaster* species; on the other hand, the demonstrated effect of facultative feeding by larvae of *C. rosaceus* on size and survivorship of newly metamorphosed juveniles indicates that non-larval components of a life history could influence developmental mode.

Is *Clypeaster rosaceus* evolving toward non-feeding lecithotrophy? This question cannot be answered here, but the development of a feeding larva with sufficient reserves for survival through metamorphosis is clearly consistent with the hypothesis of a gradual morphological change from feeding to non-feeding larval development. A larva like that of *Peronella japonica* (Table IV) would be the next step. With an abbreviated develop-

ment of $2\frac{1}{2}$ days to metamorphosis at 28 °C (Okazaki, 1975), *P. japonica* grows only two larval arms and the larval digestive system never differentiates (Mortensen, 1921). A comparison of developmental times of *P. japonica* (28 °C) and *Clypeaster rosaceus* (27 °C) shows that the formation of the pluteus body adds roughly 4 days to the developmental time for *C. rosaceus*. These 4 days are the cost of time in the plankton for facultative planktotrophic development relative to a non-feeding lecithotrophic development. The development of *C. rosaceus* offers the paradox of potentially adaptive traits in what may be a transitional larval form. More understanding of the morphogenetic basis of varying developmental patterns and the selective forces operating to stabilize or disrupt intermediate forms of larval development is needed to solve this paradox.

In addition to reports mentioned in the Introduction that show some lecithotrophic nudibranch larvae with the ability to feed, there are other reports with similar findings for other groups. Crofts (1938) reports food in the gut of lecithotrophic *Haliotis* larvae, which, as archeogastropods, lack a metatroch and ciliated food groove (Strathmann, 1978). Berg & Alatalo (1982; see also Alatalo *et al.*, 1984) report that the larvae of the bivalve *Codakia orbicularis* can feed, but that feeding has little or no effect on time to metamorphosis. Allen (1961) describes the development of another bivalve, *Pandora inaequivalvis*, with a lecithotrophic larva that has a short pelagic life. He states that the large egg gives the larva additional food reserves that makes planktonic feeding of secondary importance, though it is not possible to tell if food is eaten or has an effect on development. Knowlton (1973) described the abbreviated development of the snapping shrimp, *Alpheus heterochaelis*, that can feed, but feeding is not required to reach a post larval stage. The evidence for facultative feeding varies greatly in all of these studies and none examine the significance of supplementing egg nutrition. However, these studies indicate that facultative feeding may be wide-spread across phyla, and they provide cases that need further investigation.

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