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Relationship between larval and juvenile growth rates in two marine gastropods, *Crepidula plana* and *C. fornicata*

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Abstract Previous studies on various marine mollusc species have shown that both larval and juvenile growth rates are substantially heritable, but few workers have examined the extent to which larval and juvenile growth rates covary. We examined the relationship between larval and juvenile growth rates in seven laboratory experiments conducted between 1986 and 1993, using the prosobranch gastropods *Crepidula plana* Say and *C. fornicata* (L.). In most experiments larvae were reared individually, measured twice non-destructively to determine larval growth rate, allowed or stimulated (daily 5-h exposure to 20 mM excess K^+ in seawater) to metamorphose, and then measured at least twice after metamorphosis to determine juvenile growth rates. Generally, there was no significant ($p > 0.10$) relationship between larval and juvenile growth rates, suggesting that in these two species selection can act independently on the two stages of development. A positive correlation ($p = 0.007$) between larval and juvenile growth rates was observed for *C. fornicata* in one experiment, but only for offspring from females maturing the most rapidly in laboratory culture. Even for these larvae, however, variation in larval growth rate explained <2% of the variation in juve-

nile growth rate, so that larval and juvenile growth rates are at most only weakly associated in this species.

Introduction

The influence of environmental factors on larval (reviewed by Pechenik 1987) and juvenile (e.g., Kirby-Smith 1972; MacDonald and Thompson 1985; Brown 1988; Rice and Pechenik 1992) growth rates have been much studied for many marine molluscs. For any given set of environmental conditions, larval and juvenile growth rates vary considerably among individuals; this variation is substantially heritable both before and after metamorphosis (Innes and Haley 1977; Newkirk 1978; Newkirk et al. 1981; Mallet et al. 1986; Strömngren and Nielsen 1989; Rawson and Hilbish 1990; Hadley et al. 1991; Hilbish et al. 1993). However, few studies have considered the extent to which larval and juvenile growth rates covary; that is, the extent to which relative growth rates among larvae predict relative post-metamorphic growth rates. In addition to its obvious practical application in aquaculture operations, the extent to which larval and juvenile growth rates are coupled, either positively or inversely, will influence the degree to which selection can bring about shifts in growth rates in either stage (Ebenman 1992; Stearns 1992; Hilbish et al. 1993).

Hilbish et al. (1993) discuss the common assumption that variations in larval and juvenile growth have a common genetic basis. For example, Haley and Newkirk (1977) and Newkirk et al. (1977) suggest that juvenile growth rates in the eastern oyster, *Crassostrea virginica*, may be increased by selecting for fast-growing larvae, based on measurements of spat shell length made 9 mo after the larvae metamorphosed. Larval growth rates were not directly determined in that study; rather it was assumed that the first larvae to metamorphose grew the fastest. However, we now know that rates of shell and biomass growth may be easily

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uncoupled from rates of morphological or physiological differentiation (Pechenik et al. 1990; Zimmerman and Pechenik 1991). In contrast to reported results for the eastern oyster, larvae of the hard-shell clam *Mercentaria mercenaria* (Heffernan et al. 1991) and of the bay scallop *Argopecten irradians concentricus* (Heffernan et al. 1992) grew more slowly when juveniles were selected for rapid growth, implying an inverse relationship between larval and juvenile growth rate. Finally, Hilbish et al. (1993) could find no significant genetic covariance between shell length of 10-d-old larvae and 9-mo-old juveniles of the hardshell clam, *M. mercenaria*, suggesting that larval and juvenile growth rates vary as independent traits in this species.

One difficulty with previous studies is that larval and juvenile growth rates were assessed for populations rather than for individuals, with generally undocumented but probably high mortalities occurring between measurements in the different life history stages; differential mortality of faster or slower-growing individuals at different points in development would clearly skew the results.

The most direct way of assessing the relationship between rates of pre-metamorphic and post-metamorphic growth would be to monitor both traits on the same individuals as they develop and grow. Many marine molluscan larvae are too small and survive too poorly in laboratory culture to make this approach feasible. In this study we were able to make such measurements on larvae and juveniles of *Crepidula plana* and *C. fornicata*, taking advantage of their large shell size at hatching (shell length $\sim 300 \mu\text{m}$ for *C. plana* and $\sim 450 \mu\text{m}$ for *C. fornicata*), their high larval survivorship (typically 95% or greater) in laboratory culture (Pechenik 1980, 1984; Pechenik and Lima 1984; Zimmerman and Pechenik 1991), and their rapid larval and juvenile growth (about $75 \mu\text{m d}^{-1}$ and $150 \mu\text{m d}^{-1}$, respectively, at 25°C – Pechenik 1984; Lima and Pechenik 1985; Pechenik and Eyster 1989; Zimmerman and Pechenik 1991). In addition, competent larvae of both species will eventually metamorphose “spontaneously” on clean glassware (Pechenik 1980, 1984) or can be reliably induced to metamorphose by elevating the K^+ concentration of seawater by 20 mM for about 5 h (Pechenik and Heyman 1987; Pechenik and Gee 1993), so that juveniles can be readily obtained from all larvae reared. In the present study, we report the extent to which larval and juvenile growth rates are coupled in *C. plana* and *C. fornicata*.

Materials and methods

General approach

Studies were conducted at intervals between 1986 and 1993. Adults of *Crepidula plana* Say and *C. fornicata* (L.) were collected near Nahant, Massachusetts or Wickford, Rhode Island, USA and fed the

unicellular protist *Dunaliella tertiolecta* (clone DUN) in the laboratory until larvae were released. The planktotrophic veliger larvae were fed the unicellular protist *Isochrysis galbana* (clone T-ISO) at about $18 \times 10^4 \text{ cells ml}^{-1}$, and transferred to clean containers with fresh food suspension daily. Larval shell lengths (hereafter referred to as larval “size”) were determined nondestructively at $50 \times$ or $63 \times$ twice during the larval stage. In some experiments larvae were cultured through spontaneous metamorphosis, whereas in other experiments metamorphosis was induced by increasing seawater K^+ concentration (Pechenik and Heyman 1987; Pechenik and Gee 1993); treatment with excess K^+ did not alter post-metamorphic growth rate of *C. fornicata* in previous experiments (Eyster and Pechenik 1988).

After larvae metamorphosed, the juveniles were transferred to larger dishes, and shell lengths were measured at least twice several days apart. The volume of phytoplankton suspension provided to both larvae and juveniles was selected to maintain phytoplankton concentrations above about $10 \times 10^4 \text{ cells ml}^{-1}$ between water changes, so that individuals were always growing at maximal rates.

Three types of experiment were performed, as described below. In the Series I experiment, larvae were sorted into three size groups 6 d after emergence and reared in those groups through spontaneous metamorphosis. In Series II and III experiments, larvae were reared individually beginning the day following larval release; metamorphosis was either spontaneous or induced, as discussed below.

Series I experiment, *Crepidula plana*

Adult *Crepidula plana* were collected near Nahant, Massachusetts, and held in the laboratory until one female released larvae 4 d later. Sixty-four larvae were reared in 4-liter batch culture at 23 to 25°C and then measured after 6 d. Based on these measurements, the larvae were divided by size into three groups whose members differed significantly ($p < 0.05$, one-way analysis of variance) in mean shell length. Because larvae of *C. plana* are highly uniform in size at hatching (Pechenik 1980, 1984; and unpublished data), differences in mean larval size on Day 6 reflect differences in mean larval growth rates. The larvae in each group were reared together in 150 ml of seawater, with daily changes of water and glassware until all individuals metamorphosed “spontaneously.” Juveniles were measured within 12 h of metamorphosis and then reared individually in 150 ml of phytoplankton suspension for the next 9 d; juvenile shells were remeasured 3, 6, and 9 d after metamorphosis.

Series II experiments, *Crepidula plana* and *C. fornicata*

Five experiments were conducted, four with larvae of *Crepidula plana* and one with larvae of *C. fornicata*. For each experiment, 15 to 38 larvae were measured 1 d after they emerged from an egg mass and then reared individually at 24 to 25°C in dishes containing 150 ml of phytoplankton suspension until they either metamorphosed spontaneously (three experiments) or were triggered to metamorphose on Day 9 or 10 by elevating seawater K^+ concentration by 20 mM (two experiments). The resulting juveniles were reared individually for up to 14 d and measured periodically, as described above, to assess post-metamorphic growth rates.

Series III experiment, *Crepidula fornicata*

This was part of a larger study investigating heritable variation in duration of the precompetent period and how that trait covaries with other key life-history traits (Hilbish et al. in preparation). Juvenile *Crepidula fornicata* (about 2 to 4 mm shell length) were collected near Wickford, Rhode Island in October 1992, paired, and

reared to maturity on the flagellates *Dunaliella tertiolecta* (clone DUN) and *Isochrysis galbana* (clone T-ISO) in recirculating seawater at the Belle W. Baruch Institute, University of South Carolina. Seawater in the system was replaced with freshly collected seawater about once a week. The first larvae were released on 28 December 1992, and the last larvae used in this study were released 4 mo later. Larvae were harvested within 12 h of emerging from their egg masses. From each spawning, 12 larvae were reared individually at 20°C in 10 ml of phytoplankton suspension in six-well plastic tissue culture plates (Becton Dickinson and Co.). Each larva was measured on Day 1 and remeasured on Day 4, with Day 0 being the day of harvesting. Beginning on Day 5 or 6, larvae were tested daily for metamorphic competence in 20 mM excess K^+ (5 h incubations) until all larvae metamorphosed (Pechenik and Heyman 1987; Pechenik and Gee 1993). Because few larvae metamorphosed on the first day of testing, the size at which larvae metamorphosed on subsequent days estimates the size at which they became competent to metamorphose. Juveniles were measured at metamorphosis and 4 d later. In this way, we measured early larval and early juvenile growth rates for offspring from 122 mated pairs of adults, each producing one set of larvae.

The data were analyzed by multiple linear regression according to the following model:

$$\begin{aligned} \text{Juvenile growth rate} = & \alpha + \beta_1 (\text{larval growth rate}) \\ & + \beta_2 (\text{larval size on Day 1}) \\ & + \beta_3 (\text{size at metamorphosis}) \\ & + \beta_4 (\text{days to competence}) + \epsilon, \end{aligned}$$

where α = a constant and ϵ represents random error.

The data were also analyzed using a mixed model multiple regression (SAS PROC MIXED), in which random effects due to family of origin were accounted for as a separate source of random error. This is characterized as an estimate of variance due to the additional normally distributed error term. Finally, the data were reanalyzed using a model that examines the possible cumulative effect of repeated daily testing for metamorphic competence. To accomplish this, 11 timing variables were added to the model, defining the cumulative event effect for a given day of testing for competence. The j th dummy variable was defined as 1 when day of testing $\leq j$ for $j = 1, 2, \dots, 11$, and 0 otherwise. Data for Days 12 and 13 were collapsed into the 11th category due to low sample size.

Results

Series I experiment, *Crepidula plana*

No larvae or juveniles died or were lost during this experiment, although some shells were damaged in handling and could not be measured. Larval growth rates differed significantly ($p < 0.0001$) among the three different "treatment" groups (Fig. 1, left-most set of bars; all means differ significantly from each other, $p < 0.05$, by Bonferroni's a posteriori comparisons). Nevertheless, there were no significant differences ($p > 0.10$) in mean juvenile growth rates among the treatment groups, whether growth was assessed for the first 3, 6, or 9 d after metamorphosis (Fig. 1). Within each treatment group, juvenile growth rates were also statistically equivalent for all three measurement periods ($p > 0.10$ for all treatment groups).

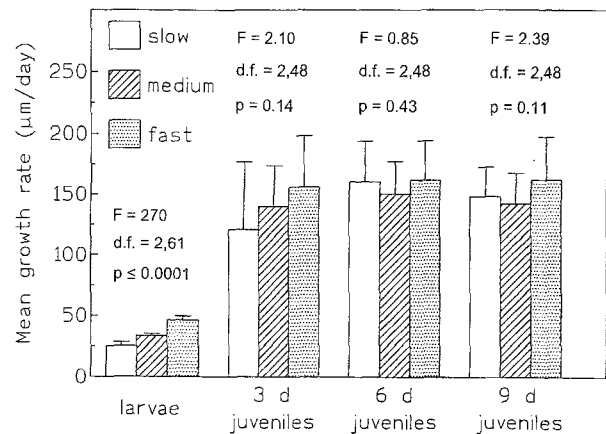


Fig. 1 *Crepidula plana*. Correspondence between larval and juvenile growth rates for 64 larvae reared at 23 to 25°C in Series I experiment. Larvae were sorted on Day 6 into one of three groups [slow-growing (mean shell length \pm SD = 452.2 $\mu\text{m} \pm 17.6$, $N = 9$); medium-growing (mean shell length = 501.1 $\mu\text{m} \pm 11.1$, $N = 30$); fast-growing larvae (mean shell length = 578.8 $\mu\text{m} \pm 20.1$, $N = 25$). Juveniles were measured at spontaneous metamorphosis after 18 to 21 d in culture, $N = 8$ to 27), and 3, 6, and 9 d later. Newly metamorphosed individuals ranged from 1098 $\mu\text{m} \pm 100$ for slow-growing larvae ($N = 8$) to 1133 $\mu\text{m} \pm 142$ for fast-growing larvae ($N = 25$).

Series II experiments, *Crepidula plana* and *C. fornicata*

Mortality or loss of individuals during these experiments never exceeded 5%. There was no significant correlation between larval and juvenile growth rates in any of the five small-scale experiments (15 to 38 larvae) in which larvae and juveniles were reared individually (Table 1). The data for the second experiment using *Crepidula plana* (Fig. 2) are typical, with both larvae and juveniles showing a wide range of growth rates among individuals. As before, juvenile growth rates were statistically equivalent ($p > 0.10$, one-way analysis of variance) within each experiment regardless of when juvenile sizes were assessed (Table 2), suggesting that juveniles of both species grew at constant rates for at least the first 2 wk of post-metamorphic development.

Series III experiment, *Crepidula fornicata*

Larvae were released from 122 females over a 4-mo period. They exhibited considerable variation in duration of the precompetent period, as determined by the number of days larvae were tested before responding to excess K^+ (Fig. 3). Only 0.6% of tested larvae (6/1053 larvae) metamorphosed during their first exposure to excess K^+ , indicating that most larvae became competent to metamorphose after we initiated testing. About 80% of the 1053 larvae tested became competent by Day 6 of testing (Fig. 3). The average larva metamorphosed after 5.3 ± 2.0 (SD) days of testing. The precompetent period thus lasted for 5 to 19 d.

Table 1 *Crepidula plana* and *C. fornicata*. Relationship between larval and juvenile growth rates for larvae and juveniles reared individually in five experiments (Series II). Data are means \pm SD. Four experiments were conducted using *C. plana* and one experiment was conducted using *C. fornicata*. In all cases, growth rates were measured as increases in shell length over 8 to 9 d. Value of “*p*” addresses the question, “Is the slope of the line relating larval and juvenile growth rates significantly different from zero?” * indicates metamorphosis triggered with excess K^+ (NS not significant)

Species	Mean larval growth rate $\mu\text{m d}^{-1}$	Days to metamorphosis	Mean shell length at metamorphosis	<i>N</i>	Mean juvenile growth rate $\mu\text{m d}^{-1}$	<i>N</i>	r^2	<i>p</i>
<i>C. plana</i>	54.7 \pm 8.0	22.7 \pm 8.3	1159.8 \pm 113.4	19	127.2 \pm 62.1	19	0.0004	0.93 NS
<i>C. plana</i>	50.6 \pm 14.4	19.0 \pm 4.4	1246.9 \pm 71.6	22	154.0 \pm 32.4	22	0.011	0.64 NS
<i>C. plana</i>	56.4 \pm 14.5	9.6 \pm 1.6*	1095.4 \pm 128.6	38	139.9 \pm 56.4	36	0.024	0.36 NS
<i>C. plana</i>	68.9 \pm 7.2	8.6 \pm 0.6*	977.9 \pm 81.2	30	156.9 \pm 26.4	29	0.031	0.36 NS
<i>C. fornicata</i>	70.8 \pm 19.8	30.0 \pm 7.9	1062.3 \pm 115.8	15	110.5 \pm 56.5	15	0.002	0.86 NS

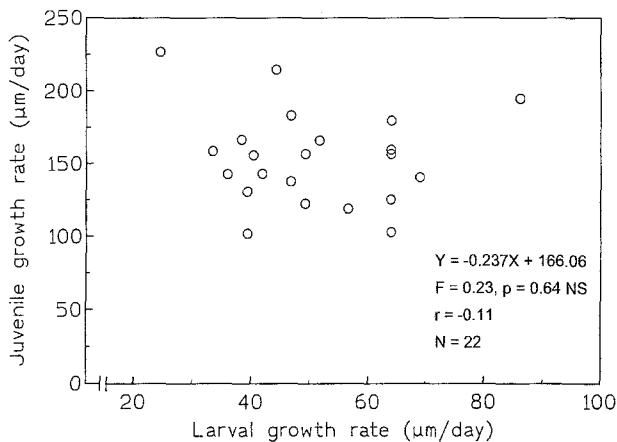


Fig. 2 *Crepidula plana*. Representative relationship between larval and juvenile growth rates for 22 ind reared at 25°C in one Series II experiment (*C. plana*; see Table 2, second experiment). Juvenile growth rates are based on shell length at spontaneous metamorphosis and 8 d later. Mean time (\pm SD) to spontaneous metamorphosis was 19.0 d \pm 4.4 (*N* = 22) and mean shell length at spontaneous metamorphosis was 1246.9 μm \pm 71.6 (*N* = 22)

To assess uniformity of culture conditions and uniformity of larval and juvenile performance during the study, the data were arbitrarily divided by month of release (Table 3). The “January” period includes larvae released between 28 December 1992 and 31 January 1993; 40% of the larvae included in the study were released in this first month of reproductive output.

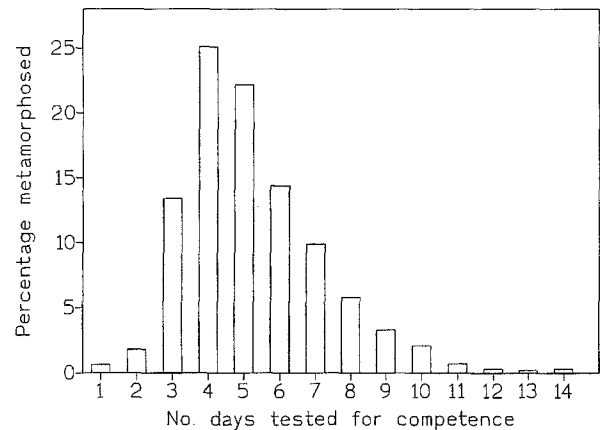


Fig. 3 *Crepidula fornicata*. Proportion of larvae metamorphosing over 14 d in Series III experiment. Beginning 5 to 6 d after emergence, larvae were exposed to 20 mM excess K^+ in seawater for 5 h each day to assess competence. 1053 larvae were tested

Larval growth rates were determined for over 1300 ind, and juvenile growth rates were determined for 950 of those individuals. Loss of individuals during the study primarily reflects unbiased handling errors; natural mortality of larvae and juveniles was $<1\%$.

Larvae released in different months did not differ significantly in the duration of their precompetent period ($p > 0.10$, Scheffe’s and Bonferroni’s a posteriori pairwise comparisons). However, larvae released in the

Table 2 *Crepidula plana* and *C. fornicata*. Juvenile growth rates at 25°C (Series II). Data are mean growth rates ($\mu\text{m d}^{-1}$) \pm SD (*N*). Day of second measurement = number of days after metamorphosis. *F*-value assesses whether juvenile growth rates changed significantly with time (ND not determined; NS not significant)

Species	Day of second measurement			<i>F</i>	<i>df</i>	<i>p</i>
	4–5 d	8–9 d	12–14 d			
<i>C. plana</i>	113.8 \pm 56.2	127.2 \pm 62.1	137.6 \pm 47.2 (17)	0.79	2,48	0.46 NS
<i>C. plana</i>	158.6 \pm 34.6	154.0 \pm 32.4	155.3 \pm 36.8 (22)	0.11	2,63	0.90 NS
<i>C. plana</i>	ND	139.9 \pm 56.4	152.7 \pm 47.2 (36)	0.81	1,68	0.35 NS
<i>C. plana</i>	158.0 \pm 23.4	156.9 \pm 26.4	156.3 \pm 33.1 (29)	0.23	3,111	0.87 NS
<i>C. fornicata</i>	83.9 \pm 53.5	110.5 \pm 56.5	129.2 \pm 55.0 (15)	2.57	2,42	0.09 NS

Table 3 *Crepidula fornicata*.

Number of individuals measured in samples of 122 families of larvae released over four 1-mo intervals and cultured through metamorphosis to Day 4. Most losses of individuals reflect handling errors

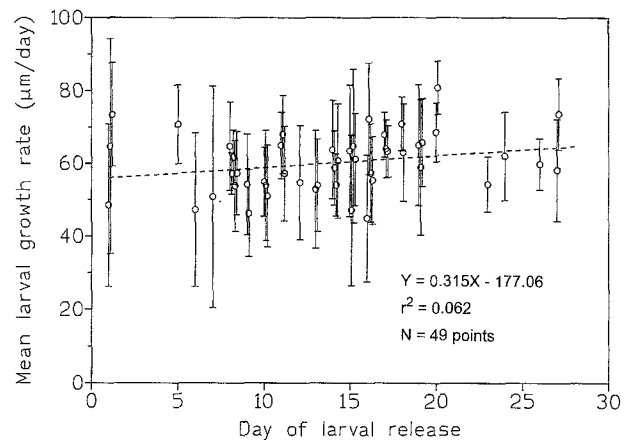
Parameter measured	January	February	March	April	Total number
Day 1 larval size (μm)	534	194	392	204	1324
Larval growth rate, Day 1–4 ($\mu\text{m d}^{-1}$)	526	188	390	203	1307
Shell length at competence (μm)	451	150	285	167	1053
Juvenile growth rate, metamorphosis to Day 4 ($\mu\text{m d}^{-1}$)	421	133	254	142	950

Table 4 *Crepidula fornicata*. Influence of larval release date on measured developmental parameters. *Underlining* at the bottom of each column summarizes results of Scheffé's a posteriori comparisons, grouping months for which there were no significant differences among means

Time of larval release	Initial no. larvae	No. families	Mean larval shell length on Day 1 ($\mu\text{m} \pm \text{SD}$)	Mean larval growth rate ($\mu\text{m d}^{-1} \pm \text{SD}$)	Mean shell length at competence (μm)	Mean juvenile growth rate ($\mu\text{m d}^{-1} \pm \text{SD}$)
A. Jan	534	49	444.9 \pm 46.1	60.3 \pm 15.3	941.5 \pm 118.7	140.0 \pm 36.7
B. Feb	194	19	488.9 \pm 38.2	61.4 \pm 16.9	997.0 \pm 157.9	123.7 \pm 34.2
C. Mar	392	35	479.9 \pm 51.0	64.1 \pm 12.1	994.2 \pm 142.9	121.9 \pm 36.8
D. Apr	204	19	476.1 \pm 29.4	61.8 \pm 12.1	1002.8 \pm 129.8	120.2 \pm 31.4
			$F = 72.7$ $df = 3, 1320$ $p = 0.0001$ <u>A BCD</u>	$F = 5.65$ $df = 3, 1303$ $p = 0.0008$ <u>ABD C</u>	$F = 15.69$ $df = 3, 1052$ $p = 0.0001$ <u>A BCD</u>	$F = 21.4$ $df = 3, 946$ $p = 0.0001$ <u>A BCD</u>

first month (28 December 1992 to 31 January 1993) did differ significantly ($p < 0.05$) from those released later in the study with respect to mean initial larval size, mean size at competence, and mean juvenile growth rate; these larvae were generally smaller on Day 1, became competent at a smaller average size, and grew more quickly after metamorphosis (Table 4). Larval growth rates for individuals released early in the first month did not differ significantly ($p > 0.05$) from those for individuals released later in that month (Fig. 4), suggesting that culture conditions did not deteriorate during the course of the study. Note also that average larval growth rates varied little from one month to the next (Table 4). Yet, juveniles produced earlier in the first month grew significantly faster than those produced later in that month (regression analysis, slope of the regression line differed significantly from zero: $F = 5.99$, $df = 1,47$; $p = 0.02$); in particular, mean juvenile growth rates were generally higher than average for larvae released in the first 10 to 14 d of the study. In the following paragraphs, we consider the results with and without the January data included.

Data on the relationship between larval and juvenile growth rates were based on multiple measurements from 950 *Crepidula fornicata* individuals (Table 3). Grouping the data for all 122 families of larvae, individual larval growth rates varied between ~ 15 and $100 \mu\text{m d}^{-1}$, and individual juvenile growth rates varied between ~ 15 and $225 \mu\text{m d}^{-1}$ (Fig. 5). Larval and

**Fig. 4** *Crepidula fornicata*. Influence of larval release date on mean larval growth rate (\pm SD) in Series III experiment. Data represent growth rate measurements on 526 larvae released 28 Dec 1992 to 31 Jan 1993 from 49 females

juvenile growth rates were not significantly correlated ($p > 0.10$; Fig. 5).

The multiple linear regression model considers how well larval size on Day 1, larval growth rate to Day 4, days to competence, and size at competence predicted individual juvenile growth rate to Day 4 after metamorphosis. Larval shell length on Day 1 and duration of the precompetent period (Fig. 6) were significant contributors to the predictive capacity of the model

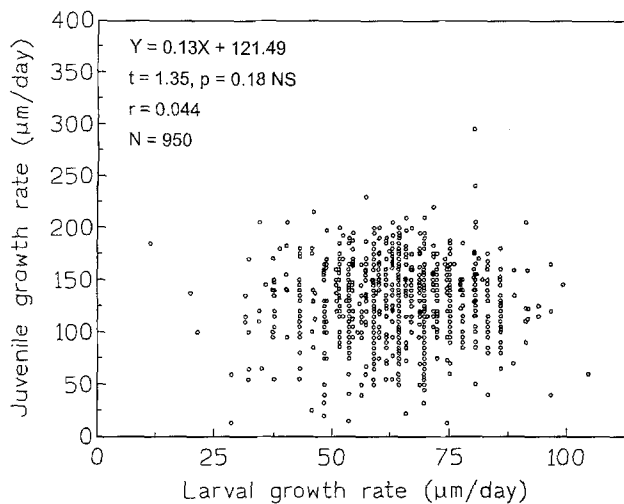


Fig. 5 *Crepidula fornicata*. Correlation between larval and juvenile growth rates for all individuals reared in Series III experiment (28 December 1992 to 30 April 1993) [20°C , 18×10^4 phytoplankton cells ml^{-1} (*Isochrysis galbana*, clone T-ISO)]. $N = 950$ ind released from 122 females

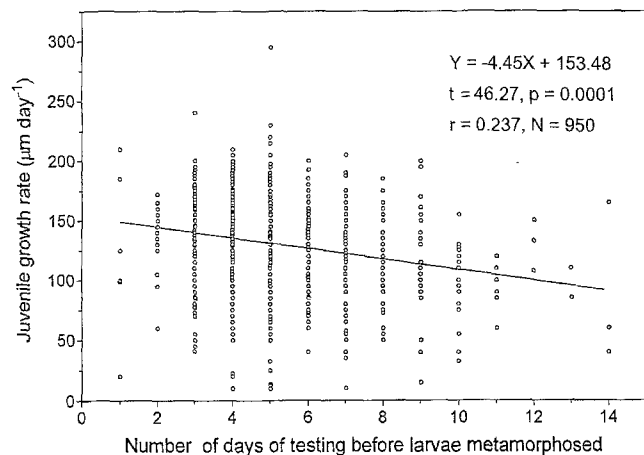


Fig. 6 *Crepidula fornicata*. Relationship between juvenile growth rate and duration of the precompetent period, as determined from the number of days of testing for metamorphic competence (Series III experiment). Testing for competence began 5 to 6 d after larvae hatched. Competence was assessed by exposing larvae for 5 h daily to 20 mM excess K^+ in seawater. Each circle represents data from 1 ind ($N = 950$)

($p < 0.05$; Table 5), but larval growth rate and size at competence were not ($p > 0.10$; Table 5).

Larval growth rate contributed significantly to the predictive capacity of the multiple linear regression model ($p \leq 0.05$) for larvae released during the first month of the study (Table 6). The correlation between juvenile growth rate and larval growth rate for these larvae was significant ($p = 0.007$), although variation in larval growth rate explained $< 2\%$ of the variation in juvenile growth rate ($r^2 = 0.017$) (Fig. 7). When data for the first month's larvae were excluded from analysis,

Table 5 *Crepidula fornicata*. Multiple linear regression model for predicting juvenile growth rates. Each variable has 1 *df*. $N = 950$ to 1324, including data from all months; see Table 3 (NS not significant)

Variable	Coefficient (SE)	<i>t</i>	<i>p</i>
Intercept	176.43 (14.85)	11.88	0.0001
Larval growth rate	0.07 (0.10)	0.71	0.4804 NS
Days to competence	-4.63 (0.68)	-6.793	0.0001
Shell length at competence	0.0004 (0.010)	0.04	0.9690 NS
Larval size on Day 1	-0.06 (0.02)	-2.33	0.0201

Table 6 *Crepidula fornicata*. Contribution of larval growth rate to the prediction of juvenile growth rate, analyzed for four different periods of larval release. All variables were incorporated into the model, but only the coefficients for larval growth rate are shown (N number of larvae; NS not significant)

Month of larval release	<i>N</i>	Coefficient for larval growth rate (SE)	<i>t</i>	<i>p</i>
January	421	0.329 (0.148)	2.233	0.026
February	133	-0.135 (0.215)	-0.629	0.531 NS
March	254	0.206 (0.229)	0.895	0.372 NS
April	142	-0.017 (0.244)	-0.069	0.945 NS

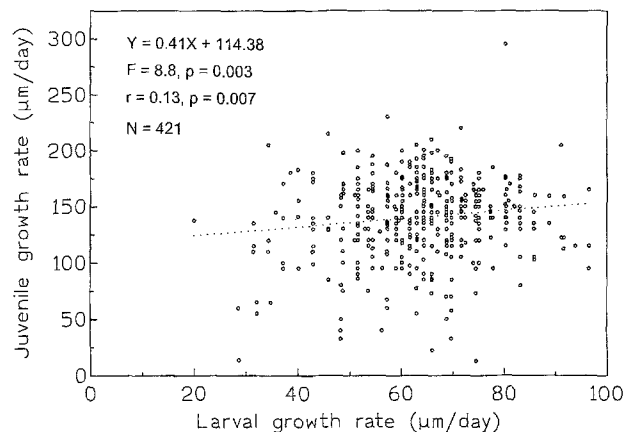


Fig. 7 *Crepidula fornicata*. Relationship between larval and juvenile growth rates for larvae released only through January 1993 ($N = 421$) in Series III experiment. Each circle represents data from 1 ind

only age at competence remained a significant contributor to the multiple linear regression model (Table 7).

The mixed multiple regression model produced slightly different results in that larval growth rate was a mildly significant predictor of juvenile growth rate when all data were included in the analysis ($p = 0.044$, $N = 950$); as before, however, the significance of the relationship depends entirely on data from individuals released during January (Table 8). The parameter

Table 7 *Crepidula fornicata*. Results of multiple linear regression for predicting juvenile growth rates. Results shown here differ from those presented in Table 5 in that larvae released in the first month (28 Dec 1992 to 31 Jan 1993) were excluded from analysis (NS not significant)

Variable	Coefficient (SE)	<i>t</i>	<i>p</i>
Intercept	158.250 (22.41)	7.15	0.0001
Larval growth rate	-0.043 (0.130)	-0.33	0.738 NS
Days to competence	-4.004 (0.796)	-5.029	0.0001
Size at competence	-0.007 (0.012)	0.58	0.562 NS
Larval size on Day 1	-0.039 (0.034)	-1.138	0.256 NS

estimating the random effects error variance ($\hat{\sigma}_{fam}^2$) decreased from 307 to 212 when larvae released in January were excluded from analysis. With or without the January data, variability due to family of origin was less than one-third of the variability due to random error.

In both models, no statistically significant cumulative effect of daily testing for metamorphic competence was detected for data collected in January ($p > 0.10$ for all coefficients, $N = 421$). Mildly significant ($p \sim 0.03$ to ~ 0.07) cumulative effects were observed for three of the 11 coefficients when analyzing the entire data set, and when the January data were excluded from analysis; even then, there was no pattern of significance consistent with the notion of toxic effects associated with daily testing for competence.

Discussion

Our data for *Crepidula plana* and *C. fornicata* generally follow the results obtained by Hilbish et al. (1993) for the bivalve *Mercenaria mercenaria*, showing that larval and juvenile growth rates vary independently. In general, larval growth rates were poor predictors of early juvenile growth rates for both gastropod species tested in this study. Larval growth rate was also a weak predictor ($r^2 = 0.025$) of the size at which larvae of *C. fornicata* became competent to metamorphose, confirming previous indications that the onset of

competence and metamorphosis for various mollusc species are not controlled by larval shell size or growth rates (Pechenik and Lima 1984; Eyster and Pechenik 1987; Pechenik and Heyman 1987; Coon et al. 1990; Zimmerman and Pechenik 1991; Davis 1994).

Our data indicate that the shell length at which larvae of *Crepidula fornicata* become competent to metamorphose is a poor predictor of juvenile growth rate, extending previous results for this species (Pechenik and Eyster 1989).

In all analyses for the major data set (Series III experiment), duration of the precompetent period was a significant predictor of juvenile growth rate, with each additional day corresponding to a decrease of about $4 \mu\text{m d}^{-1}$ in juvenile growth rate (Tables 5, 7, 8; Fig. 6). This result could be an artifact of repeatedly exposing larvae to excess K^+ ; Eyster and Pechenik (1988) found that a single treatment with excess K^+ did not alter juvenile growth rates of this species, but they did not examine the effects of multiple treatments. Alternatively, decreased juvenile growth rate may reflect the effects of daily starvation (5 h d^{-1}) while larvae were exposed to excess K^+ ; starving precompetent larvae of *C. fornicata* for several days reduces post-metamorphic growth rate (Pechenik et al. 1996). Finally, the effect could be genuine: larvae that take longer to become competent to metamorphose may exhibit reduced growth as juveniles. Additional experiments will be necessary to distinguish among these three possibilities. However, analyses of existing data suggest that the effect is genuine. If the decreased growth rate was an artifact of K^+ toxicity or reflected detrimental effects of daily short-term starvation periods, we would expect to see a cumulative effect on post-metamorphic growth rate with each additional day of testing. However, cumulative effects consistent with these hypotheses were not seen in the cumulative effect dummy variables; the few instances in which we obtained p -values between ~ 0.03 and ~ 0.07 probably reflect random chance events.

Probably our most surprising result is that the data collected for *Crepidula fornicata* larvae released during the first month in the Series III experiment differed

Table 8 *Crepidula fornicata*. Results of mixed model multiple linear regression predicting juvenile growth rates; random effects due to family of origin are accounted for as a separate source of random error. Intercept and coefficients are estimated with and without the "January" data. All data: $N = 950$; without January data: $N = 529$ (NS not significant)

Variable	All data			No January data		
	Estimated value of coefficient	<i>t</i>	<i>p</i>	Estimated value of coefficient	<i>t</i>	<i>p</i>
Intercept	154.57	8.76	< 0.0001	160.55	6.57	< 0.0001
Larval growth rate	0.22	2.01	0.044	0.07	0.47	0.64 NS
Days to competence	-3.51	-4.90	< 0.0001	-3.397	-3.95	0.0001
Size at competence	-0.009	-0.89	0.375 NS	-0.01	-0.58	0.57 NS
Larval size on Day 1	-0.026	-0.82	0.410 NS	-0.04	-0.94	0.35 NS

from those collected for larvae released during the following three months of that study. If we had collected individuals as adults, the early-releasing adults would have been conditioned more in the field and less in the laboratory, while adults releasing larvae later in the study would have been conditioned more in the laboratory and less in the field. Bayne et al. (1975) showed that the conditions under which mussels complete gametogenesis can influence larval growth rates. However, this is unlikely to be a factor in our study. Coe (1936) found no functional males of *C. fornicata* with shell lengths less than 3 to 5 mm, and the smallest functional females he found were 16 mm long (Coe 1936). Since we collected individuals that were no more than 4 mm long for our study, few, if any, individuals were reproductively mature males when collected, and none could have begun the transformation to female until after they were in the laboratory. Individuals spent at least 10 wk in the laboratory and grew to several times their initial size before releasing any larvae, so that all females (and at least most of the males) completed gametogenesis in the laboratory.

A more likely explanation for the different characteristics of larvae released in the first month is that individuals maturing earlier may have produced larvae that exhibited, for some unknown reason, life-history characteristics different from those produced by females maturing later. In any event, the data raise the possibility that under some as yet unspecified conditions, larval growth rates can be statistically significant, although very weak, predictors of juvenile growth rates in *Crepidula fornicata*, with faster larval growth associated with faster juvenile growth.

It is easier to explain the lack of correspondence between larval and juvenile growth rates seen in most of our data than to explain the positive relationship seen for individuals released in the first month of the Series III study. Both larvae and juveniles of *Crepidula fornicata* are suspension feeders and can be reared in the laboratory on unialgal diets. At metamorphosis, however, the larvae exchange one food-collecting organ, the velum, for an ontogenetically unrelated food-collecting organ, the gill (Werner 1955). There is no a priori reason to assume that individuals sporting a particularly effective velum will also develop an unusually effective gill, so that larval and juvenile shell growth rates could well be under separate genetic control (Hilbish et al. 1993), unless ciliary functional characteristics in all tissues have a common genetic basis.

One intriguing explanation for our data is that under most circumstances larval and juvenile growth rates for *Crepidula fornicata* may be determined primarily by rates of food collection, which are altered at metamorphosis as one food-collecting device is replaced by another, but under some circumstances may be primarily determined by physiological characteristics

(e.g. digestive enzyme efficiency or basal metabolic rate) that might not change at metamorphosis. The hypothesis seems testable.

In summary, the data from all three series of experiments suggest that larval and juvenile growth rates are generally not correlated in either *Crepidula plana* or *C. fornicata*, and that any selective forces acting on larval growth rates in these species will generally operate independently of those acting on growth in the juvenile stage. In some circumstances, however, larval and juvenile growth rates may be positively correlated for *C. fornicata*. In our study, a weak ($r^2 = 0.017$), but significant, correlation was apparent for the offspring of the most rapidly maturing individuals.

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