Relationships between larval nutritional experience, larval growth rates, juvenile growth rates, and juvenile feeding rates in the prosobranch gastropod *Crepidula fornicata*

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Abstract

Planktonic larvae experiencing short periods of starvation or reduced food supply often grow and develop more slowly, have poor survival, fail to metamorphose, metamorphose at smaller sizes, or grow slowly as juveniles. In this study, we examined the impact of short periods of food limitation at various stages of larval development on larval and juvenile growth in *Crepidula fornicata*. In addition, we considered whether juveniles that were stressed as larvae grew poorly because of reduced rates of food collection due to impaired gill function. For 5 experiments, larvae were either starved for several days beginning within 12 h of hatching or were starved for the same number of days following 1 or more days of feeding at full ration (cells of the naked flagellate *Isochrysis galbana*, clone T-ISO, at $18 \times 10^4$ cells ml$^{-1}$). In one experiment, larvae were transferred for 2 or 4 days to seawater with extremely low phytoplankton concentration ($1 \times 10^4$ cells ml$^{-1}$). In all experiments, larvae were returned to full ration following treatment. Control larvae were fed full ration from hatching to metamorphosis. When larvae reached shell lengths of about 900 $\mu$m they were induced to metamorphose and then reared individually at full ration in glass bowls, with phytoplankton suspension replenished daily. Larval and juvenile growth rates were determined by measuring changes in shell length (longest dimension) over time. Juvenile feeding rates were determined by monitoring changes in phytoplankton concentration over 2–3 h at the end of the growth rate determinations. In general, larval growth rates for the first 2 days after the resumption of feeding were inversely proportional to the length of time that larvae were starved. However, larval growth rates ultimately recovered to control levels in most treatments. Starving the larvae caused a significant reduction in initial juvenile growth rates (first 3–4 days post-metamorphosis) in most...
experiments even when larval growth rates had recovered to control levels prior to metamorphosis. Juvenile growth rates were not significantly reduced when larvae were subjected to reduced food availability (1 x 10^4 cells ml^-1), even for treatments in which larval growth rates were compromised. Mean weight-specific filtration rates for juveniles were significantly reduced (p < 0.05) following larval feeding experience in only one or possibly 2 of the 4 experiments conducted. Our data suggest that although larvae of C. fornicata may fully recover from early nutritional stress, the resulting juveniles may exhibit poor initial growth due to impaired gill function, reduced digestive capability, or reduced assimilation efficiency.

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1. Introduction

Phytoplankton concentrations fluctuate both spatially and temporally (e.g., Mackas et al., 1985; Villafane et al., 1995). Moreover, food quality varies considerably among and within phytoplankton species grown under different environmental conditions (reviewed by Pechenik, 1987). Planktonic, feeding larvae may therefore experience some degree of food deprivation during all or part of their development (e.g., Hansson et al., 1990; Fenaux et al., 1994; Harms et al., 1994). In consequence, larval responses to food limitation or starvation have been studied for many years, particularly for crustaceans, molluscs, polychaetes, and echinoderms (e.g., Perron and Turner, 1977; Dawirs, 1984; Anger, 1986; Staton and Sulkin, 1991; Wehrtmann, 1991; Hansen, 1993; Qian and Chia, 1993; Allison, 1994; Anger, 1995a, b; Schuh and Diesel, 1995; McEdward and Qian, 2001; Giménez, 2002; reviewed by Thorson, 1950; Olson and Olson, 1989; Morgan, 1995). In response to low food supply, larvae of at least some species show reduced rates of growth and development (Perron and Turner, 1977; Qian and Chia, 1991, 1993; Wehrtmann, 1991; His and Seaman, 1992; Hansen, 1993; Allison, 1994; Anger, 1995a, b; Eckert, 1995; Basch, 1996; Pechenik et al., 1996a; Qiu and Qian, 1997a, b; Giménez, 2002), poor survival (His and Seaman, 1992; Allison, 1994; Qiu and Qian, 1997a, b; Giménez, 2002), decreased metamorphic success (Qian and Chia, 1993; Eckert, 1995; McEdward and Qian, 2001), and smaller size or lower energy content at metamorphosis (Qian and Chia, 1993; Hart and Strathmann, 1994; Eckert, 1995; Meidel et al., 1999; Miller and Emlet, 1999; McEdward and Qian, 2001; Vaitilingon et al., 2001) or at the onset of metamorphic competence (Pechenik et al., 1996a).

However, the larvae of some species are clearly more sensitive to starvation than others, and the larvae of at least some invertebrate species may never fully recover from the stress of temporary starvation. His and Seaman (1992), for example, found that growth rates of oyster larvae (Crassostrea gigas) never returned to control levels when larvae were starved for more than 5 days under suboptimal environmental conditions (22 °C, 25%o salinity) and then transferred to abundant food. Many of the larvae—up to 100% in groups that had been starved for 7–8 days—eventually died after their transfer to control food concentration. In contrast, mortality of control larvae and those starved for only a few days early in development was negligible. The ability of molluscan larvae to recover from short-term nutritional stress has not been well studied.
It has also become apparent that the detrimental effects of even short-term nutritional stress can extend past metamorphosis in at least some species. In particular, Pechenik et al. (1996a,b) found that juveniles of the gastropod *Crepidula fornicata* grew more slowly if the larvae had been starved or food limited for 3–5 days, indicating that certain processes associated with postmetamorphic development can be influenced by events occurring much earlier in development (Pechenik et al., 1998). Similarly, early juvenile growth rates were significantly reduced in at least some echinoid and polychaete species when the larvae were food-limited (Qian et al., 1990; Miller and Emlet, 1999). Pechenik et al. (1996b) speculated that the reduced juvenile growth rates documented in *C. fornicata* might reflect abnormal development and food-collecting performance of the juvenile gill. Reduced growth rates could also reflect reduced ability to digest or assimilate food, altered nutritional requirements for maximum growth, or increased rates of metabolic expenditure (Withers, 1992). Juvenile growth rates of *C. fornicata* were determined only for the first 3 days following metamorphosis (Pechenik et al., 1996a,b), leaving open the possibility that growth rates might recover to control levels in time.

For this paper, we consider whether short-term food limitation during larval development permanently impairs larval growth in *C. fornicata*, and whether larval sensitivity to food limitation changes during development. In addition, we ask whether the reduced growth rates observed in juvenile *C. fornicata* that were stressed as larvae are associated with impaired gill function and correspondingly reduced rates of food collection. Finally, we ask whether initially depressed juvenile growth rates eventually recover to control levels in this species.

2. Materials and methods

2.1. Experimental design

Six experiments were conducted in total, from 1995–1997, all at 25 °C. Adults of *C. fornicata* were collected from Wickford, Rhode Island and held from 3–8 days until larvae were released. Parameters measured in each experiment are shown in Table 1. Both adults and larvae were fed on the naked flagellate *Isochrysis galbana*, clone T-ISO.

Larvae were exposed to different nutritional regimes in each experiment. In most cases larvae were either starved for a number of days within 12 h of hatching (“Early Treatment”) or were starved for the same number of days beginning after 1 or more days of feeding at full ration on the naked flagellate *I. galbana* (18 × 10⁴ cells ml⁻¹) (“Late Treatment”). No larvae metamorphosed during the starvation periods. Following starvation all larvae were returned to full ration (18 × 10⁴ cells ml⁻¹). In spot checks between daily changes of phytoplankton suspension, cell concentrations never fell below 13 × 10⁴ cells ml⁻¹. In one experiment larvae were not fully starved, but were instead transferred to seawater with a drastically reduced phytoplankton concentration (1 × 10⁴ cells ml⁻¹) and then transferred back to full ration after 1 to 4 days.
When larvae in any given treatment reached mean shell lengths of about 900 µm, they were induced to metamorphose by raising the K⁺ concentration of seawater by 20 mM for 6 h (Pechenik and Heyman, 1987; Pechenik and Gee, 1993). This method of inducing metamorphosis has no detectable effect on juvenile growth rate over the next 3–9 days (Eyster and Pechenik, 1988). Metamorphosed individuals were reared individually in glass bowls containing 45 ml of phytoplankton suspension, which was replenished daily.

To determine larval and juvenile growth rates, larval and juvenile shell lengths (longest dimension) were measured nondestructively at 50°C and 32°C, respectively, using a dissecting microscope equipped with an ocular micrometer. Larvae were positioned to rest on their left sides for all measurements (Pechenik et al., 1996a) until shell growth became linear (Pechenik, 1980). Juveniles were first measured 1 day after metamorphosis was induced and re-measured 3–6 days later. Juvenile growth rates are not influenced by size at metamorphosis in this species (Pechenik et al., 1996c).

At the end of each experiment, juvenile feeding rates were determined using hemacytometers or a Coulter electronic particle counter to monitor the disappearance

<table>
<thead>
<tr>
<th>Experiment number</th>
<th>Food treatments tested</th>
<th>Effects on larval growth rates</th>
<th>Effects on juvenile growth rates</th>
<th>Effects on juvenile feeding rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>(a) Starve at hatching 1–5 days (E1–5), (b) Feed 1st 2 days after hatching and then starve 1–5 days (L1–5).</td>
<td>tested</td>
<td>tested</td>
<td>not tested</td>
</tr>
<tr>
<td>II</td>
<td>(a) Starve at hatching 1–4 days (E1–4), (b) Feed 1st 2 days after hatching and then starve 2 days (L2).</td>
<td>not tested</td>
<td>tested</td>
<td>not tested</td>
</tr>
<tr>
<td>III</td>
<td>(a) Starve at hatching 2 or 4 days (E2, E4), (b) Feed 1st 2 days after hatching and then starve 2 or 4 days (L2, L4). (c) Low food at hatching 2 or 4 days. (d) Feed at full ration 1st 2 days after hatching and then subject to low food 2 or 4 days.</td>
<td>tested</td>
<td>tested</td>
<td>tested</td>
</tr>
<tr>
<td>IV</td>
<td>Starve at hatching for 4 days (E4).</td>
<td>tested</td>
<td>tested</td>
<td>tested</td>
</tr>
<tr>
<td>V</td>
<td>Starve at hatching for 4 or 6 days (E4, E6).</td>
<td>not tested</td>
<td>tested</td>
<td>tested</td>
</tr>
</tbody>
</table>
of food particles from suspension over time. Mean cell concentrations determined by
the two methods were comparable in spot checks. For each measurement, juveniles
were placed individually in small glass dishes in 2 or 4 ml of phytoplankton
suspension (18 \times 10^4 \text{ cells ml}^{-1}) and maintained in dim light in an incubator at 25
^\circ \text{C} for 2–3 h. Phytoplankton concentrations were measured in each dish at the end of
each experiment. Dishes containing phytoplankton in the absence of juveniles served
as controls; control phytoplankton concentrations never changed by more than 5%
during the feeding period. When control juveniles grew noticeably faster than
individuals that had been starved as larvae, we generally conducted feeding rate
determinations on treated individuals several days after making feeding rate determi-
nations on control individuals, so that mean shell sizes would be similar in all
treatments. The mean shell lengths of the juveniles used in feeding rate determinations
are given in Table 2.

Additional experimental details are presented with the results for each series of
experiments. In each experiment on larval growth rates, there were 4 replicates of 6
larvae per replicate. In each experiment on juvenile growth and feeding rates we monitored
10–20 juveniles for each treatment group.

2.2. Data manipulation and analysis

The effects of treatments on mean larval growth rate, mean juvenile growth rate, and
mean juvenile filtration rate were generally compared using one-way analysis of
variance (ANOVA), followed by Bonferroni multiple comparisons tests or Dunnett’s
multiple comparisons tests (to compare results from all treatments specifically against
the control mean) when statistical differences were found. When data did not meet the

Table 2
Mean shell lengths of recently metamorphosed snails (C. fornicata) used in feeding rate studies

<table>
<thead>
<tr>
<th>Experiment number</th>
<th>Mean shell length (µm)</th>
<th>S.D. (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I—Control</td>
<td>1073.5</td>
<td>139 (12)</td>
</tr>
<tr>
<td>I—Early 2</td>
<td>1667.5</td>
<td>71.6 (14)</td>
</tr>
<tr>
<td>I—Early 4</td>
<td>1806.8</td>
<td>87.2 (14)</td>
</tr>
<tr>
<td>I—Late 2</td>
<td>1725.7</td>
<td>96.7 (15)</td>
</tr>
<tr>
<td>I—Late 4</td>
<td>1825.5</td>
<td>72.8 (15)</td>
</tr>
<tr>
<td>III—Control</td>
<td>1389.7</td>
<td>195.5 (11)</td>
</tr>
<tr>
<td>III—Early 1</td>
<td>1303.0</td>
<td>199.4 (7)</td>
</tr>
<tr>
<td>III—Early 2</td>
<td>1277.7</td>
<td>266.8 (7)</td>
</tr>
<tr>
<td>IV—Control</td>
<td>1518.3</td>
<td>54.5 (14)</td>
</tr>
<tr>
<td>IV—Early 2</td>
<td>1665.3</td>
<td>87.3 (13)</td>
</tr>
<tr>
<td>V—Control</td>
<td>1620.3</td>
<td>152.4 (12)</td>
</tr>
<tr>
<td>V—Early 2</td>
<td>1470.9</td>
<td>122.2 (18)</td>
</tr>
</tbody>
</table>

Control individuals were never starved as larvae. Other individuals were starved for 1, 2, or 4 days, beginning
either immediately after release from the adult (“Early”) or after having been fed for 2 days (“Late”).
assumptions required for parametric analysis they were analyzed using nonparametric ANOVA (Kruskal–Wallis tests, followed by Dunn’s post tests for pairwise comparisons). Juvenile filtration rate data were converted from ml filtered h$^{-1}$ juvenile$^{-1}$ to

Fig. 1. Influence of starvation duration and time of initiation of starvation on mean larval growth rates (+ 1 S.D.) of C. fornicata in Experiment I. Larvae were starved for 1–6 days beginning either at hatching ("early" series, panel a) or after 2 days of feeding ("late" series, panel b). For example, for treatment E2 larvae were starved at hatching for 2 days. Larval sizes were determined up to three times at 2-day intervals following the resumption of feeding, to test for recovery of larval growth rate over time. Control larvae (Ctrl) were fed throughout development. The number above each bar shows the number of larvae measured in each treatment. * signifies means that are significantly lower than the control mean ($P<0.05$, Dunnet’s multiple comparisons test).
ml filtered h⁻¹ µg tissue⁻¹ before analysis using the following equation (Pechenik and Eyster, 1989): log tissue weight (µg) = 2.371 log shell length (mm) + 1.133 (r² = 0.96, N = 239 individuals).

3. Results

3.1. Larval and juvenile survival

Larvae were fairly uniform in size when released from the parents. For example, in Experiment I newly released larvae were 427.9 ± 25.3 (S.D.) µm (N = 27). As in previous studies with this species (e.g., Pechenik, 1984; Pechenik et al., 1996a,b), mortality of both larvae and juveniles was generally very low, but we did not record any details.

3.2. Effect of larval starvation on larval growth rates

Starving larvae for as little as 1 day either directly after they were released into the water or after a 2-day pre-feeding period had a substantial effect on subsequent larval growth.
growth rates: mean growth rates were significantly lower over the 2 days following resumption of larval feeding in almost every treatment regardless of whether larvae were starved early or later in development ($P < 0.05$, one-way analysis of variance followed by comparisons with the relevant controls; Figs. 1 and 2). Moreover, starving larvae for 5 or 6 days caused a significantly larger initial reduction in post-stress larval growth rates compared with the results of shorter starvation periods (Bonferroni multiple comparisons following one-way analysis of variance). In Experiment I, for example (Fig. 1): Early, E2 vs. E5: $t = 4.94$, $p < 0.001$; E2 vs. E6: $t = 7.49$, $p < 0.001$; Late, L1 vs. L6: $t = 3.30$, $p < 0.01$). Thus, the larvae of *C. fornicata* were more sensitive to the duration of the starvation period, with respect to short-term effects on larval growth rates after food was restored, than to when in development starvation occurred.

However, larval growth rates eventually recovered to control levels over the subsequent 4–6 days in most of the treatments in which long-term growth patterns were monitored (Figs. 1 and 2). Several notable exceptions were seen in Experiments III, IV, and V, for larvae starved for 4 or more days (Fig. 2).

3.3. Effect of larval experience on juvenile growth rates

In Experiment I, starving larvae early in development for as little as 2 days correlated with significantly reduced ($P < 0.05$) juvenile growth rates of up to 33.3% over the subsequent 3 days (Fig. 3). This was true even for treatments (Early 1, Early 3) in which larval growth rates eventually recovered to those of control larvae that had

![Fig. 3. The effect that timing and duration of starvation during larval development had on mean juvenile growth rate in *C. fornicata* in Experiment I. Each bar reflects the mean (+ 1 S.D.) growth rate of 14 juveniles, except as indicated for the control. * indicates significant differences between means relative to the control mean ($p < 0.05$, Dunnet’s multiple comparisons test).](image-url)
never been starved (Fig. 1). However, we saw no significant effect ($P > 0.10$) of larval starvation on mean juvenile growth rates in that experiment when larvae were fed for 2 days before being starved, even when they were starved as larvae for 5–6 days (Fig. 3).

Starving larvae early in development also caused significant reductions in initial mean juvenile growth rates for at least some treatments in Experiments II–V, as shown in Fig. 4. However, juvenile growth rates eventually recovered to control levels in the two experiments in which growth was monitored beyond the first 3 days after metamorphosis (Fig. 4, Experiments II and III). In one experiment (Experiment III), juvenile growth was significantly ($Dunnett's ~q = 3.6, ~p < 0.01$) accelerated in one treatment relative to the mean growth rate of control juveniles (Fig. 4).

3.4. Effect of exposing larvae to low food concentrations

Juvenile growth rates were not significantly reduced when larvae were subjected to greatly reduced food availability ($1 \times 10^4$ cells ml$^{-1}$) for as long as 4 days,
even when larval growth potential was compromised by the nutritional stress (Fig. 5). Indeed, following one treatment ("Late 2," in which larvae were fed for 2 days and then exposed to low food for 2 days), juvenile growth rates were significantly greater ($P<0.01$, Dunnett’s multiple comparisons test) than those of control animals, and the effect persisted for at least 6 days after metamorphosis (Fig. 5).

3.5. Influence of food limitation on juvenile filtration rates

In Experiments I and III, mean weight-specific juvenile filtration rates were not significantly affected ($P>0.10$) by larval feeding experience (Fig. 6), even when juvenile growth rates had been affected by the food limitation treatments (treatments “Early 2” and “Early 4;” Fig. 3). Mean weight-specific filtration rates were significantly lower for

![Graph showing larval and juvenile growth rates](image-url)

Fig. 5. The effects of reduction in larval food supply on mean larval and juvenile growth rates (+1 S.D.) in *C. fornicata* in Experiment IV. Larvae were held at low food concentration ($1 \times 10^4$ cells ml$^{-1}$) for 2 or 4 days, either immediately after release from the parent ("Early" treatments, E) or after being reared for 2 days at $18 \times 10^4$ cells ml$^{-1}$ ("Late" treatments, L). Larvae (and then juveniles) were then reared at full ration ($18 \times 10^4$ cells ml$^{-1}$) for the rest of the experiment. The number above each bar shows the number of individuals measured in each treatment at each time. Larvae were remeasured at 2-day intervals, while juveniles were remeasured at 3-day intervals. * indicates significantly lower mean growth rate relative to the control mean ($p<0.05$, Dunnet’s multiple comparisons test). # indicates significantly higher mean growth rate relative to the control mean ($p<0.05$).
juveniles in Experiment IV, however \( (p = 0.019) \), and were only marginally insignificant in Experiment V \( (p = 0.051; \text{Fig. 6}) \).

4. Discussion

Few other studies have reported the degree to which larval growth rates recover following short periods of starvation. The work presented here shows that growth rates of larval \( C. \textit{fornicata} \) were suppressed for at least 2 days following limited periods of starvation, but that larval growth rates usually recovered to those of control larvae over the next several days. Similarly, growth rates appear to have rebounded quickly to control levels for larvae of the opisthobranch gastropod \( \textit{Doridella obscura} \) even when larvae were starved for 9 days before feeding was resumed (Perron and Turner, 1977). For oyster larvae (\( \textit{Crassostrea gigas} \)), the results depended on environmental conditions. When oyster larvae were reared until “favorable” conditions (30 °C, 30% salinity), growth rates of treated larvae returned to those of control larvae within 4–5 days, even for larvae that had been starved for 5 days (His and Seaman, 1992). However, under suboptimal conditions of temperature and salinity (22 °C, 25% salinity), larval growth
rates never recovered to those of control individuals if larvae had previously been starved for 5 or 6 days.

The cause of reduced growth rate following the resumption of feeding, and of the subsequent recovery of growth rate, observed for the larvae of *C. fornicata* is unknown. Likely possibilities include temporary reductions in the ability to capture, digest, or assimilate food particles. Periodic observations of larval guts suggested to His and Seaman (1992) that starvation compromised the ability of oyster larvae to properly digest and assimilate food. However, these researchers did not determine larval ingestion rates, which might also have been reduced. Whatever the cause, reduced growth rates might either increase or decrease larval vulnerability to predators, depending on the relationship between larval size and vulnerability (reviewed by Pechenik, 1999). Reduced growth rate might also prolong the time that larvae are exposed to planktonic predators (Thorson, 1950), but only to the extent that growth rates correlate with time required for larvae to become metamorphically competent or with their ability to delay metamorphosis in the absence of suitable substratum (Pechenik and Lima, 1984; Lima and Pechenik, 1985; Zimmerman and Pechenik, 1991; Pechenik et al., 1996a).

The results of the present study confirm previous reports for this species that short periods of starvation during larval development can alter juvenile growth rates for at least the first few days following metamorphosis (Pechenik et al., 1996a,b). As McEdward and Qian (2001) point out, selective mortality caused by starvation can make it difficult to interpret the results of such studies. In our experiments, however, larval and juvenile mortality was consistently low. Thus, any documented differences in growth rates must reflect real effects of food deprivation on individuals rather than selective mortality of individuals with particular genotypes during the starvation period.

A novel finding of this study is that the effect of starvation on mean larval growth rate was not a good predictor of the effect on initial mean juvenile growth rate. In some experiments, juvenile growth rates were reduced even though larval growth rates recovered to control levels. And in some other cases, juvenile growth rates were not significantly reduced even though larval growth rates did not recover to control levels. This lack of correlation between effects on larval and juvenile growth may at least partly owe to the fact that larvae and juveniles collect food by different means: at metamorphosis, the ciliated velum is resorbed and replaced functionally by the ciliated gill (Werner, 1955; Pechenik et al., 1996c).

This explanation assumes that structural or functional abnormalities in the food collecting device is what causes the observed reduction in juvenile growth rate. However, feeding rates were significantly reduced in only 1 (Experiment IV) or possibly 2 (Experiment V) of the 4 experiments in which juvenile growth rates were also reduced (Fig. 6). Such effects on feeding rates could be caused by reduced number of cilia per length of gill filament, reduced cilia length, or reduced ciliary beat frequency. These possibilities are readily testable. Alternatively, reduced feeding rate could derive from effects on more subtle aspects of particle capture—particle capture mechanics have not been worked out for any *Crepidula* species in detail, in comparison with what is now known about the filtration mechanisms of some bivalves (e.g., Riisgård and Larsen, 2000; Silverman et al., 2000; Ward et al., 2000; Medler and Silverman, 2001).
It remains unclear how short periods of starvation during larval life might actually lead to alterations in gill structure or function, since reductions in juvenile growth or feeding rates were often seen even when larvae were starved very early in development, long before gills were formed. Starvation during larval life might somehow interfere with either the timing or the magnitude of transcriptional or translational processes associated with juvenile gill formation much later in development (Pechenik et al., 1998). Alternatively, starvation early in larval life could impact proper gill formation later on if the specific energy stores or materials to be used in gill formation are normally sequestered early in larval life.

The lack of any measurable effect of larval experience on juvenile feeding rates in Experiments I and III might reflect (unmeasured) recovery of juvenile growth rates by the end of the growth period. Feeding rates were measured only after the final measurements of juvenile size were made; feeding rates might have been lower earlier in the recovery period. On the other hand, it may be that reduced feeding rates are not the only cause of reduced juvenile growth. Digestive efficiency or assimilation efficiency could also be affected (Withers, 1992), or the slower growing juveniles might exhibit heightened basal metabolic rates (Hawkins and Day, 1996; Hedgecock et al., 1996). Whatever the mechanism(s), the fact that depressed juvenile growth rates generally recovered to those of control individuals after 4–6 days indicates that the affected processes are merely slowed, rather than completely suppressed. The possible morphological and physiological bases for the significant increases in juvenile growth rates seen in Experiments III and IV (Figs. 4 and 5) following larval starvation or food limitation also remain to be explored.

Some evidence of batch variability with regard to the sensitivity of both larvae and juveniles to the effects of starvation during larval development was noted. In Experiments II and III, for example, larvae starved for either 2 or 4 days grew at rates comparable to those of control larvae by the end of 4 days, but that was not the case in Experiment V (Fig. 2). The causes of this apparent variation in sensitivity remain to be explored.

In a preliminary experiment that we conducted with *C. fornicata* (data not shown), starving the larvae for 5 days late in development (after 12 days of feeding) did not result in significantly decreased mean juvenile growth rates as monitored for the first 4 days following metamorphosis (mean control juvenile growth rates: 109.7 ± 32.8 (S.D.) μm day⁻¹ (N=19); mean juvenile growth rate for individuals starved as larvae: 124.9 ± 25.7 μm/day (N=15); t=0.15, df=31; p=0.18). This is an atypical result in our experience (compared with results of this study, and see also Pechenik et al., 1996a,b). It would be interesting to understand the source of this apparently greater resistance to the carry-over effects of larval experience in these individuals. This issue may be difficult to explore in *C. fornicata*, however, since such insensitivity seems to occur so rarely in this species.

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