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An Evaluation of Selective Feeding by Three Age-Groups of the Rainbow Mussel *Villosa iris*

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Abstract.—A tri-algal diet was fed to three age-groups of the rainbow mussel *Villosa iris*: ages 2–3 d, 50–53 d, and 3–6 years. Changes in the relative abundance of each algal species were determined in 5-h feeding trials from feeding chambers and by gut content analyses. All age-groups rejected *Scenedesmus quadricauda* and preferentially selected *Nannochloropsis oculata* and *Selenastrum capricornutum*, principally on the basis of size. Changes in the relative abundance of algae in feeding chambers did not differ significantly among age-groups. Observed differences in the ingested quantities of the similar-sized *N. oculata* and *S. capricornutum* were attributed to other particle-related characteristics. Results indicate that the rainbow mussel can be fed similar-sized algae at all ages in captive propagation facilities. When developing a suitable algal diet for rearing juvenile mussels, one probably need not investigate different species at each stage of development if the algae used are in the 2.8–8.5-μm size range.

Propagation studies of native freshwater mussels (order Bivalvia: family Unionidae) have been used to describe much of their basic life history, including host−fish relationships (Neves et al. 1985; O'Connell and Neves 1999), environmental stress thresholds (Dimock and Wright 1993), and habitat and substrate use (Michaelson and Neves 1995). Dietary studies have not been common, and the nutritional requirements for captive unionids, specifically juveniles, remain undetermined. Algae have been the most popular food source for captive juvenile mussels. Various combinations of algal species have been used to culture juveniles (Hudson and Isom 1984; Gatenby et al. 1996, 1997), and because of their apparent importance in the diet of unionids, algal species have been incorporated into the design of recirculating culture systems as the primary food source (O'Beirn et al. 1998; Tankersley and Butz 2000; Henley et al. 2001).

The importance of algal species as a food source for captive juvenile mussels is probably a compromise between their physical characteristics and their nutritional properties. The lipid content of an algae diet has been directly correlated with juvenile growth (Gatenby et al. 1997). In addition, adult unionids have displayed an ability to sort algae on the basis of their cellular characteristics before ingestion (Paterson 1984; Miura and Yamashiro 1990; S. M. Baker and J. S. Levinton, State University of New York, unpublished data). Possibly, therefore, juveniles also might exhibit a selective response for the cellular characteristics of algae.

Selective feeding may advance during the early developmental stages of juvenile mussels. The primary food source for juveniles may change within the first 2 weeks postmetamorphosis (Yeager et al. 1994), perhaps corresponding with the transition from pedal-feeding to suspension-feeding. This transition is common among bivalves, and almost all juvenile bivalves are believed to have a pedal-feeding stage (Reid et al. 1992). Pedal-feeding by juvenile mussels may extend to 140 d postmetamorphosis (Gatenby et al. 1997). Henley et al. (2001) suggest that accounting for pedal feeding is so important for successful culture that separate culturing strategies should be incorporated for individual stages of grow out. It has not been determined, however, whether different food sources should be used at individual stages of juvenile development.

The purpose of this study was to determine whether selective feeding occurs during early development of captive-reared unionids, a finding that might be useful in the preparation of a suitable algal diet for captive grow out of juvenile mussels. The specific objective of the project was to use three species of algae to determine whether three different age-groups of rainbow mussel *Villosa iris*

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exhibited particle size selection. Particle selection by rainbow mussels was determined at ages 2–3 d, 50–53 d, and 3–6 years by monitoring changes in relative abundance of *Scenedesmus quadricauda*, *Nannochloropsis oculata*, and *Selenastrum capricornutum* in feeding chambers. We then used gut content analysis to verify selective ingestion by the test mussels. Relative abundance of algae within pseudofeces for rejection and in feces for selection was not analyzed, because insufficient quantities were collected for such analyses.

Methods

Specimens of *rainbow mussels* representing three age-groups were tested: age-group I, 2–3 d old (shell length, 280–333 μm); age-group II, 50–53 d old (385–640 μm); and age-group III, 3–6 years old (21–40 mm). These age-groups were chosen on the basis of previously documented transitions from pedal-feeding to suspension-feeding, in which age-group I feeds solely by pedal-sweeping motions (Yeager et al. 1994), age-group II is in a transitional state, and age-group III is an obligate suspension-feeder. Age-groups I and II were obtained from propagated individuals at the Virginia Tech Aquaculture Center, Blacksburg, Virginia. Age-group III was collected from the Little River, Tazewell County, Virginia.

Adult mussels were rinsed with a 50:50 mixture of water from municipal and groundwater sources (hardness, about 150 mg/L) and scrubbed as necessary to remove all epiphytes. Mussels were held in water-filled petri dishes and fed an algal diet of *N. oculata* before use in this study. Immediately preceding the study, all mussels were allowed to purge in water-filled petri dishes without food for 30 h. Water was changed twice during this period.

The feeding chambers used for this experiment were modeled after the jars used for testing selective feeding behaviors in other bivalve mollusks (Shumway et al. 1985; Baker et al. 1998). The 120-mL jars (diameter, 6 cm) were filled with 30 mL of a tri-algal mix (see below). We did not expect individuals of age-groups I and II to clear sufficient algae from the medium to detect individual selectivity, so we relied on a collective removal of algae within the treatment. Therefore, jars of age-groups I and II contained 200 individuals, whereas those of age-group III required only 1 individual. No aeration was supplied to age-groups I and II, thus allowing algae to settle in the jar and preventing juveniles from being suspended in the water column. Slight aeration was added to the jars for age-group III to maintain algal suspension. There were 6 replicate jars for age-groups I and II, 10 for age-group III. To account for different rates of cellular division among algal species during the experiment, six replicates of both aerated and nonaerated control jars containing the algal mix were maintained without mussels. All experiments were conducted simultaneously at 24°C for 5 h in an environmental chamber under normal florescent lighting. Dissolved oxygen was monitored with aYSI Model 58 Dissolved Oxygen Meter (YSI, Yellow Springs, Ohio) to ensure that feeding behavior was not affected by declining oxygen levels.

Algae culture.—The algae *S. quadricauda*, *S. capricornutum*, and *N. oculata* were grown at the Virginia Tech Aquaculture Center. Monocultures were diluted and then combined to obtain an equal abundance of each species within the algal mix, at a cell density of approximately 15,000/mL for each algal species (total, 45,000/mL). *Scenedesmus quadricauda* is a colonial species and, for this experiment, we treated a colony of *S. quadricauda* as a single cell, and the cell diameters given include the colony plus spines. The range of sizes for each species of algae is as follows: *S. quadricauda*, 22.3–44.5 μm; *S. capricornutum*, 3.6–8.5 μm; and *N. oculata*, 2.8–8.1 μm. These sizes were calculated with a calibrated ocular micrometer from measurements of 100 cells.

Relative abundance in the medium.—At the beginning and end of the experiment, the jars were shaken to resuspend the cells and to break up any pseudofeces and feces present; then a 1.5-mL water sample was withdrawn from each jar. These samples were preserved with acid Lugol's solution (Vollenweider 1969), to allow us to quantify the change in relative abundance of algal species at a later date. At that time, we used the mean of 12 hemacytometer counts, made with a light microscope, to calculate the relative abundance of algae per sample. The change in relative abundance for each replicate then was calculated from the difference between relative abundance in the initial and final samples. Arc-sine transformations were performed on proportion data before statistical analysis to satisfy assumptions of normality (MacDonald and Ward 1994; Sokal and Rohlf 1995; Gatenby et al. 1997).

To determine whether juvenile mussels sort particles before ingestion, we used an index for comparing the change in relative abundance of each algal species from 0 to 5 h in the feeding chamber. The index was calculated by subtracting the initial relative abundance from the final relative abun-

TABLE 1.—Changes ± SEs in the relative abundance of *Scenedesmus quadricauda* (Sc), *Nannochloropsis oculata* (Na), and *Selenastrum capricornutum* (Se) in a tri-algal mix fed to rainbow mussels of three age-groups. A negative index value means that the species was selected, a positive value that it was rejected. Asterisks denote significant changes ($P < 0.05$).

Age-group	Sc		Na		Se	
	Index	*P*-value	Index	*P*-value	Index	*P*-value
I	+15.85 ± 4.72*	0.0045	−12.09 ± 4.75*	0.0404	−3.76 ± 5.85	0.5823
II	+18.87 ± 5.89*	0.0125	−10.96 ± 3.41*	0.0180	−7.91 ± 4.00	0.0797
III	+15.65 ± 4.60*	0.0093	−10.17 ± 2.92*	0.0039	−5.49 ± 3.03	0.1210

dance. The index then was tested for each age-group by using a one-sample *t*-test, with the level of significance at $P = 0.05$. If no significant changes were found among the species, then algal species were not selectively consumed. A decline in the relative abundance of an algal species would be noted if it were removed from the medium more often than the other species. Therefore, a significant negative value for the change in relative abundance would indicate that an algal species was selectively consumed. An apparent increase in the relative abundance of an algal species would be recorded if the other species were removed from the medium more often; therefore, a significantly positive value would indicate that a species was rejected.

If we found a significant change in relative abundance for any of the algal species, we compared the change in relative abundance among species to determine whether one algal species was selected in favor of another. To do this, the index of one algal species within a feeding chamber was subtracted from the index of another species within the same feeding chamber. This was done for each replicate, and the difference was tested by a one-sample *t*-test. If there was a significant difference, then one species was positively selected over the other. We repeated this test until the three algal species were compared against each other for each age-group. Sample sizes were 6 for age-groups I and II, and 10 for age-group III.

These same tests were used to analyze for different rates of algal reproduction in the control chambers. No significant change was found for all species; therefore, rates of increase did not differ among the species, and no correction factor was necessary. Sample sizes ($n = 6$) were equal for both aerated and nonaerated controls.

To determine whether selective feeding changed between early developmental stages of juvenile mussels, we tested the change in the relative abundance of one algal species between two age-groups by a two-sample *t*-test. This test was repeated until all three algal species were compared between all three age-groups. If no significant difference was found in any of those tests, then we concluded that age did not affect feeding selectivity.

Gut content analysis.—At the end of the experiment, six randomly selected mussels from each age-group were preserved with acid Lugol's solution for gut content analysis. Mussels were rinsed with distilled water over a 200-μm sieve to remove any uningested particles. The gut contents of age-groups I and II were exposed by crushing them with a fire-blunted pipette in 0.25 mL of distilled water. Gut dissections were performed on age-group III, and a 0.05-mL sample of the ingested particles was taken and diluted in 0.25 mL of distilled water. We used the mean of 18 hemacytometer counts to quantify the relative abundance of ingested but intact algal species from the diluted samples. Arcsine transformations were performed on the proportion data before statistical analysis.

To detect selective ingestion, we calculated the difference between the relative abundances of two ingested algal species in the guts of six specimens per age-group and then tested or compared these differences by using a one-sample *t*-test. If there was a significant difference ($P < 0.05$), we interpreted this as one algal species being selected in favor of another. This test was repeated until all three algal species were compared.

Results and Discussion

Relative Abundance in the Medium

Results of feeding trials indicated that juvenile rainbow mussels possess the ability to feed selectively and presumably to sort particles before ingestion. The negative index for the change in relative abundance of *N. oculata* showed that the mussels strongly selected for this species (Table 1). The relative abundance of *N. oculata* within the medium decreased significantly from time 0–5 h for all age-groups (age-group I, $P < 0.04$; age-

TABLE 2.—Differences between the indexes of change in the relative abundance of *Scenedesmus quadricauda* (Sc), *Nannochloropsis oculata* (Na), and *Selenastrum capricornutum* (Se) in a tri-algal mix fed to rainbow mussels in three age-groups. Asterisks denote significant differences ($P < 0.05$).

Age-group	Na–Sc		Se–Sc		Na–Se	
	Difference	*P*-value	Difference	*P*-value	Difference	*P*-value
I	27.94 ± 7.46*	0.0040	19.61 ± 4.75*	0.0294	8.3 ± 9.55	0.2104
II	29.83 ± 8.75*	0.0048	26.78 ± 9.47*	0.0137	3.10 ± 4.55	0.3036
III	25.82 ± 7.09*	0.0018	21.14 ± 7.22*	0.0134	4.7 ± 3.76	0.1353

group II, $P < 0.02$; and age-group III, $P < 0.004$). The positive index for the change in the relative abundance of *S. quadricauda*, which increased significantly from 0 to 5 h for all age-groups (age-group I, $P < 0.004$; age-group II, $P < 0.01$; and age-group III, $P < 0.004$), suggests that mussels rejected this species (Table 1). Because the indices of *N. oculata* and *S. capricornutum* were significantly lower than that of *S. quadricauda* (Table 2), *N. oculata* and *S. capricornutum* were cleared from the medium with greater efficiency than *S. quadricauda*, suggesting that these species were preferentially selected preingestion. The age-group of the mussels did not affect feeding selectivity or preference (Figure 1).

The observed evidence of selective feeding is probably a function of particle size. The smaller cells of *N. oculata* and *S. capricornutum* (2.8–8.5 μm) were selected over those of the larger colonies of *S. quadricauda* (22.3–44.5 μm). Although no other selective feeding studies for juvenile freshwater mussels have been reported, Yeager et al. (1994) found that gut contents of captive juvenile rainbow mussels consisted mainly of small particles in the 2–5 μm range. Several studies have indicated that particle selection by adult freshwater mussels may be size dependent. Paterson (1984) found that adult *Elliptio complanata* selected particles in the 4–5 μm range. Baker and Levinton (unpublished data) found that adult unionids taken from the Hudson River typically rejected large green algae, such as *S. quadricauda*, as do zebra mussels *Dreissena polymorpha*, in favor of smaller particles (Baker et al. 1998). Adult *Anodonta californiensis* has been shown to select for green algae in the 5–10 μm range (Miura and Yamashiro 1990). In our study, rainbow mussels of all age-groups exhibited particle selection in favor of algal cells in the 2.8–8.5-μm size range.

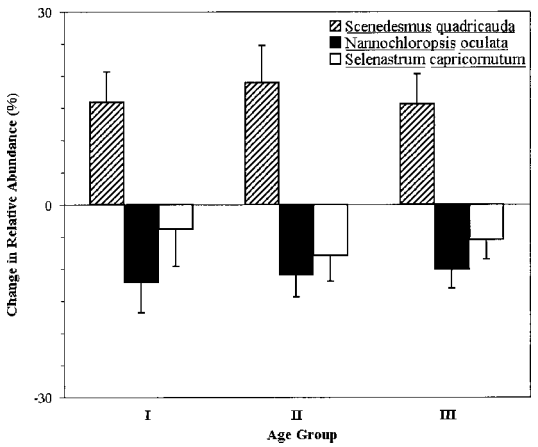

FIGURE 1.—Change in the relative abundance (+SE) of algal species after 5 h in feeding chambers with three age-groups of rainbow mussels. Negative values indicate that the species were selected; positive values indicate that the species were rejected. The changes in the relative abundance of *N. oculata* and *S. capricornutum* were significantly different ($P < 0.05$) from that of *S. quadricauda*. Changes in relative abundance did not differ significantly ($P > 0.05$) among age-groups.

Gut Content Analysis

Mussels appeared to selectively ingest algae in the following order: *N. oculata*, *S. capricornutum*, and *S. quadricauda* (Table 3). *Scenedesmus quadricauda* was not found in mussels of age-groups I and II (Figure 2). This finding is supported by a light micrograph of the arrangement of the digestive tract of a newly metamorphosed (2-d-old) juvenile of *Lampsilis ventricosa* (Lasee 1991). The mouth of this juvenile was approximately 16 μm in diameter, the esophagus approximately 6 μm. The smallest colony length of *S. quadricauda* that we measured was 22.3 μm. Therefore, the mouth and esophagus of newly metamorphosed juvenile mussels were incapable of accommodating algae the size of *S. quadricauda*, and no colonies of *S. quadricauda* were collected in the guts of age-groups I and II. In addition to the size of the suspended particles (Baldwin 1995; Defossez and Hawkins 1997; Raby et al. 1997), various other particle characteristics have been shown to affect feeding behavior of marine bivalves. Chemical cues (Ward and Targett 1989; Ward et al. 1992;

TABLE 3.—The relative abundance of ingested *Scenedesmus quadricauda* (Sc), *Nannochloropsis oculata* (Na), and *Selenastrum capricornutum* (Se) in the guts of rainbow mussels in three age-groups and the *P*-values from statistical comparisons among the ingested concentrations. Significant differences ($P < 0.05$) were found among all algal species for each age group.

Age-group	Relative abundance of ingested algae (%)			*P*-value		
	Sc	Na	Se	Na–Sc	Na–Se	Se–Sc
I	0.00 ± 0.00	86.95 ± 2.88	13.05 ± 2.88	0.0001	0.0002	0.0001
II	0.00 ± 0.00	87.34 ± 3.75	12.66 ± 3.75	0.0001	0.0009	0.0001
III	10.79 ± 1.04	61.72 ± 2.83	27.49 ± 3.12	0.0001	0.0016	0.0031

Baldwin 1995) and electrostatic charge (Solow and Gallager 1990) have been shown to influence capture efficiency and selection by marine bivalves. Selection by juvenile rainbow mussels was seemingly influenced by other particle characteristics, given the observed differences between ingested quantities of *N. oculata* and *S. capricornutum*, which are of similar size.

Large particles the size of *S. quadricauda* were not actively sorted by age-groups I and II and may have been brushed out of the ciliary current after touching the edges of the valve and mantle marginal folds when carried through the pedal gap (Reid et al. 1992). Personal observations of pedal-feeding activities by juveniles of rainbow mussels have confirmed an accumulation of particles at the pedal gap. Similarly, the geometry of the algal cells may have reflected reactions to the hydrodynamic disturbances caused by the currents of mussels during feeding (Gallager 1993). The nonspherical shape of *S. capricornutum* and *S. quadricauda* may have diverted the cells out of the weak current generated by the mussels. The spines of *S. quadricauda* also may have discouraged ingestion. Newly metamorphosed juveniles lack a well-developed buccal cavity (Lasee 1991); therefore, particle sorting by age-groups I and II is most likely passive, but the labial palps may aid in some active selection. The sorting capacity of age-group III is primarily related to the complexity of the gill surface area (cirral structure), which is probably similar to that of other freshwater mussels (Silverman et al. 1997). For zebra mussels, capture and preliminary selection of particles take place on the gills, where large particles such as *S. quadricauda* are moved above the food grooves in a mucus string, whereas smaller particles move deep within the food groove toward the labial palps (Baker et al. 1998).

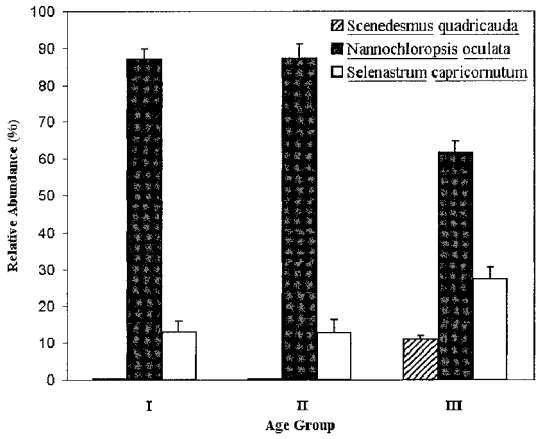

FIGURE 2.—Relative abundance (+SE) of three algal species in the guts of rainbow mussels of three age-groups. Significant differences ($P < 0.05$) were found among all algal species for each age-group. Selective ingestion was not compared among age-groups.

Selective feeding has not been well defined in natural systems, which contain a variety of algae and detritus particles. Parker et al. (1998) reported that gut contents of adult threeridge *Amblema plicata* and pimpleback *Quadrula pustulosa* from the Ohio River revealed ingested particles ranging in size from 4 to 70 μm; moreover, the relative abundance of algal species within the gut was similar to their relative abundance in the external environment. The mussels in that experiment were much larger than rainbow mussels and thus are probably capable of ingesting a wider size range of particles. In our study, gut content analyses showed that *S. quadricauda* was ingested by adult rainbow mussels, but in significantly lower abundance than were the smaller algae (Figure 2).

The ability of rainbow mussels to feed selectively, and presumably to sort particles before ingestion, was documented among the three algal species tested. During early mussel development, particle size may influence selectivity (Sprung 1984), where larger particles (22.8–44.5 μm) are rejected in favor of smaller particles (2.8–8.5 μm), but other factors may also influence feeding behavior and ingestion by juvenile mussels. Although our data show that adult rainbow mussels

may ingest *S. quadricauda* when fed mixed algae, smaller-sized particles dominated the gut contents. Only smaller particles were observed in the guts of rainbow mussel age-groups I and II. Therefore, when developing a suitable algal diet for rearing juvenile mussels, it is probably not necessary to study different species at each stage of development if the algae used are in the 2.8–8.5 μm size range. In addition to size, the nutritional value of the algae and the concentration at which the algae is fed should be considered when developing a suitable algal diet. Gatenby et al. (1997) found that an algal diet high in oils, which may have included polyunsaturated fatty acids, was best for culturing newly metamorphosed juveniles. Algal cell concentrations of up to 10^6/mL may be necessary for maintaining glycogen levels in adult threeridge and pimpleback, as determined by controlled feeding in a laboratory setting for 30 d (Patterson et al. 1999). Gatenby et al. (1997) fed algae at a rate of 3.0×10^5 to 5.0×10^5 cells/mL to achieve excellent survival rates of 66.5% at 45 d post-metamorphosis for juvenile rainbow mussels. These concentrations may be greater than necessary, however, and impractical for use in large-volume recirculating systems. Preliminary experiments suggest that a ration of roughly 30,000 cells/mL should be sufficient for juvenile mussels (Rogers 1999; Henley et al. 2001).

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