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Assimilation of micro- and mesozooplankton by zebra mussels: A demonstration of the food web link between zooplankton and benthic suspension feeders

Abstract—We tested the hypothesis that rotifer species in the micro- and mesozooplankton are a potential food source for zebra mussels. We labeled phytoplankton with ^{14}C, fed them to two species of rotifers (140–210 μm length) that were previously found abundantly in the Hudson River and had declined following a zebra mussel invasion, and estimated the assimilation of carbon. Assimilation efficiencies were found to be ~37.4–54.0%. Combined with our feeding experiments, the data on rotifer densities before and after the invasion allowed us to calculate the energy budgets for zebra mussels. Before zebra mussels dominated the Hudson River in 1992, the absorption of energy from rotifers was about two to three times higher than that necessary to maintain its routine metabolic rate and contributed about 0.349–0.662 J h^{-1} to mussel growth and reproduction, conferring a positive scope for growth. Since the zebra mussels became abundant in the Hudson River, assimilation of rotifers is still sufficient to explain ~16.4–23.1% of the mussels' routine metabolic rate. Therefore, rotifers play a conceivably large role in the energy budget of zebra mussels, whether at high rotifer concentrations (before the invasion) or at low rotifer concentrations (after the invasion). This is the first quantitative evidence for a trophic link between benthic bivalve mollusks and larger micro- and mesozooplankton that might extend to marine systems where bivalves can derive nutrition from microzooplankton, including planktonic invertebrate larvae. Combined with other recent results, this study documents a benthos–zooplankton trophic loop, demonstrating potentially strong top-down control by dense bivalves on aquatic systems.

Filter-feeding bivalve populations exert keystone effects on the plankton of the coastal oceans (Prins et al. 1998) by filtering large volumes of water, severely depleting the phytoplankton, and by selectively feeding and thus altering the species composition of the phytoplankton. Overexploitation by humans in some waterbodies and invasions of exotic bivalves into others have resulted in major reorganizations of aquatic ecosystems. No change has been stronger than those caused by the invasion of the zebra mussel, *Dreissena polymorpha,* into lakes and rivers of North America, which has resulted in strong alterations in the composition of the plankton, resulting in strong ecological impacts (Nalepa and Schloesser 1993). The zebra mussel, *D. polymorpha,* was first likely introduced into Lake St. Clair and the North American Great Lakes near Detroit, Michigan, in 1986; it then spread into major basins, including the Mississippi, St Lawrence, and Hudson drainages. The expansion of zebra mussel distribution has induced significant abiotic and biotic changes mediated either directly or indirectly (MacIsaac 1996).

The invasion of the tidal freshwater Hudson River in 1991 by the exotic zebra mussel has caused large changes in several components of the Hudson's food web. Zebra mussels have strongly depleted Hudson River phytoplankton standing stocks (Caraco et al. 1997) and have altered the species composition of the phytoplankton. Selective feeding by zebra mussels might have been instrumental in the shift in phytoplankton dominance from blue-green algae to diatoms (Baker et al. 1998; Bastviken et al. 1998). Zebra mussels can also clear microzooplankton such as rotifers from suspension, and rotifer loricae have been found in zebra mussel guts (MacIsaac et al. 1991). The zebra mussel's invasion of the Hudson ecosystem has decreased the microzooplankton, particularly rotifers (Pace et al. 1998), as they have in other lakes and rivers (Jack and Thorp 2000; Thorp and Casper 2002).

Planktonic rotifers form an important constituent in the diets of many aquatic predators, such as other rotifers (*Asplanchna*), insect larvae (*Chaoborus*), cyclopoid and calanoid copepods (*Diacyclops, Epischura*), malacostracans (*Mysis*), and particulate-feeding and filter-feeding fish (Stemberger and Gilbert 1987). Zebra mussel invasions have been implicated in other rotifer declines (MacIsaac et al. 1991), and they appear to be the agent of decline of microzooplankton and mesozooplankton, such as rotifers, in the Hudson River ecosystem. However, we know of no quantitative evidence of carbon assimilation that would provide a trophic link between zooplankton and zebra mussel nutrition, or any other bivalves, even though other larger zooplankton have also been found in the guts of marine bivalves (Shumway et al. 1987). Over the last 6 yr, it has been shown that bivalves are not solely herbivores, but omnivores. Bacteria, nanozooplankton, and microzooplankton, such as heterotrophic flagellates (~4 μm) and ciliates (~20 μm), can be ingested and assimilated (Kreeger and Newell 1996, 2001; Le Gall et al. 1997), and they have been shown to be quantitatively important in the diet of many suspension feeders, such as the ribbed mussel, *Geukensia demissa* (Kreeger and Newell 2001). In this experiment, we discovered a strong nutritional dependence of zebra mussels on larger micro- and mesozooplankton with lengths from 140 to 210 μm, forming an extensive benthic–zooplankton (BZ) trophic link that could alter our understanding of aquatic, estuarine, and coastal food webs.

Experimental design—We directly tested the possibility of a BZ loop between larger zooplankton and bivalves by feed-

ing radiolabeled cultures of common Hudson River rotifers to zebra mussels. The rotifers *Lepadella ovalis* (~140 μm long and 0.198 μg mass) and *Brachionus calyciflorus* (~210 μm long and 0.313 μg mass) were used in the study. We chose small and large species in order to get an idea of the range of rotifer biomass available for exploitation, because available data have been expressed only in terms of numbers of rotifers per unit water volume. In the first study, the shell length of the mussels was 11.4 ± 0.05 mm, and the rotifer *B. calyciflorus* was used. In the second experiment, *L. ovalis* was fed to mussels of 13.7 ± 0.14 mm length. Both the mussels (usually 6–10) and rotifers were placed in a 1-liter beaker with 500 ml filtered (GF-C) Hudson River water.

Rotifers were labeled as follows. On the first day, 370 kBq of ^{14}C (NaH^{14}CO$_3$, in distilled water) was added to 500 ml of microalgal suspension; the initial concentration of freshwater microalgae (*Kirchneriella* sp.) was usually $2.0–5.0 \times 10^5$ cells ml^{-1}. Three days later, the microalgae were uniformly labeled (Wang and Fisher 1996). Rotifers were added to the ^{14}C-labeled microalgal suspension, and 2 to 3 h later, labeled rotifers were collected by filtering through a 64-μm net sieve. The filtered rotifers were then washed twice with distilled water for 15 to 20 min. The total time rotifers were handled, including filtering and washing, was ~27–32 min, which was substantially longer than the rotifer gut passage time of ~20 min (Starkweather and Gilbert 1977). The rotifers therefore had time to evacuate their guts of labeled microalgae. The rotifers were transferred to a 50-ml beaker with filtered (GF-C) Hudson River water. Because we wanted the bivalves to be exposed to labeled rotifers only, it was important to avoid smaller debris. Under microscopic examination, only intact rotifers were found in the suspension. The only likely debris, rotifer fecal pellets, were small enough to readily pass through the 64-μm sieve (mean ± SD fecal pellet dimensions of the larger rotifer species, *B. calicyflorus*: width = 11.5 ± 2.3 μm, length = 17.7 ± 4.8, $n = 16$). The radioactivity of the rotifer species *B. calyciflorus* and *L. ovalis* in the two experiments were 0.483 and 0.412 Bq, respectively. The experiment using *B. calyciflorus* had four rotifer concentrations—0.2, 1, 2, and 8 individuals ml^{-1}—each with four replicates. The experiment using *L. ovalis* had two concentrations—0.2 and 2 individuals ml^{-1}, representing the two rotifer densities in the Hudson River before and after, respectively, the zebra mussel invasion (Pace et al. 1998)—each with six replicates. To achieve the appropriate rotifer density needed, different volumes of suspension were added at time zero to each replicate of each treatment. Rotifer densities were readjusted to time-zero levels after 15 min (Roditi and Fisher 1999). Just before the "hot" rotifers were added into the beaker, $1.0–2.0 \times 10^5$ individuals ml^{-1} "cold" *Kirchneriella* sp. were suspended in 500 ml filtered Hudson River water. Zebra mussels were collected after the 30-min pulse feeding. The radioactivity of ^{14}C was determined with a Tri-Carb 2100TR liquid scintillation analyzer.

The assimilation efficiency was calculated as

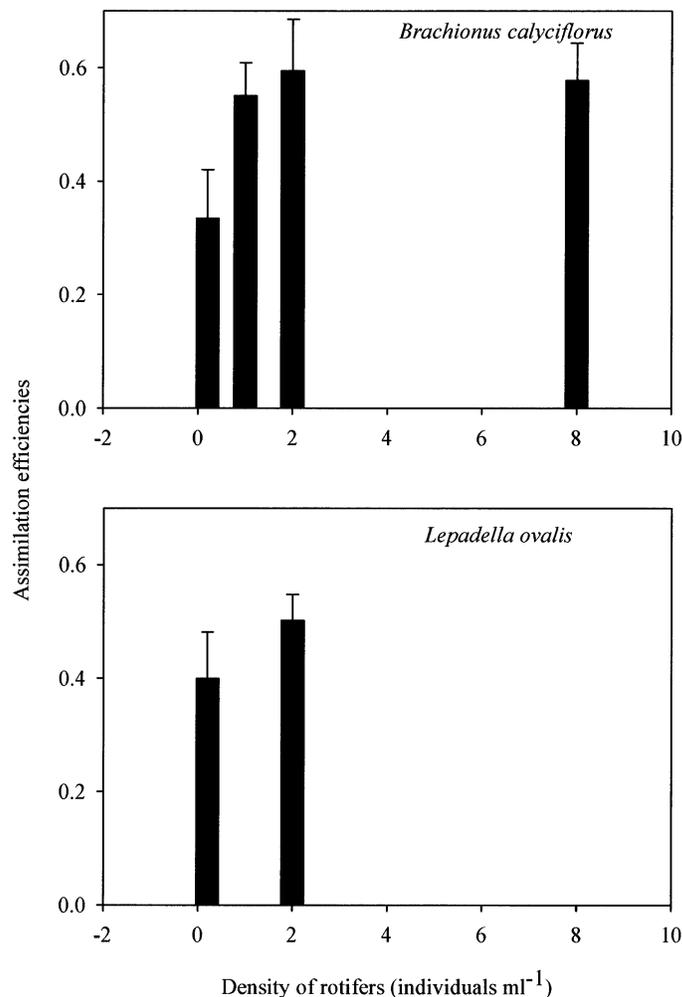$$AE(\%) = \frac{^{14}C_{tissue}}{^{14}C_{tissue} + \ ^{14}C_{feces}} \times 100$$

Fig. 1. Assimilation efficiencies ± SE of zebra mussels on two rotifer species, *B. calyciflorus* ($n = 4$) and *L. ovalis* ($n = 6$), at different rotifer densities.

where $^{14}C_{tissue}$ is the ^{14}C radioactivity in the tissue after 72 h of depuration, and $^{14}C_{feces}$ is the ^{14}C radioactivity in the cumulative feces collected during 72 h of depuration. With this method, we assumed that the respiratory loss of ^{14}C was negligible within the first 24 h (Wang and Fisher 1996). The formula for filtration rate (FR, individuals h^{-1}) was FR = [DPM$_{mussel}$/DPM$_{rotifer}$] × 2. DPM$_{mussel}$ is disintegrations of ^{14}C (min^{-1}) of each mussel immediately following the 30-min radioactive feeding period; DPM$_{rotifer}$ is the disintegrations (min^{-1}) for each rotifer (Roditi and Fisher 1999). Measurements of FR for each replicate were standardized to the FR of a 20-mg "standard" mussel (Bayne 1976). Absorption rate was calculated as FR × AE (assimilation efficiency converted to J h^{-1}). The routine metabolic rate of a 20-mg mussel is 0.322 J h^{-1} (Madon et al. 1998), and the average energy value of rotifers from the pooled data is 22.4 J mg^{-1} ash-free dry weight (Yúrera et al. 1997).

AEs of zebra mussels on *B. calyciflorus* varied between ~34 and 59% and on *L. ovalis* from ~40 to 50% (Fig. 1). For the two densities (0.2 and 2 individuals ml^{-1}), we used a two-factor analysis of variance to analyze the influence of

Table 1. Two-factor ANOVA of zebra mussel assimilation efficiencies on rotifers.

Source	df	MS	F	p
Rotifer species	1	0.001	0.032	0.859
Rotifer density	1	0.158	5.669	0.030*
Species density	1	0.030	1.066	0.317
Error	16	0.028		

* $p < 0,05$.

rotifer species and density on mussel assimilation efficiency. It can be seen from Table 1 that rotifer density has a significant effect on assimilation efficiency, but rotifer species has no significant effect. The average AE of zebra mussels on the two rotifer species at 2 individuals ml^{-1} (54.0%) was greater than that at 0.2 individuals ml^{-1} (37.4%). Rotifer loricae were found in mussel feces, but further investigation is needed to elucidate the mechanism of capture on the gills, transfer to the palps, and ingestion. MacIsaac et al. (1991) found rotifer loricae in zebra mussel guts.

Figure 2 demonstrates a strong linear relationship between absorption rate and rotifer density. Using this relationship, we were able to compare absorption with the routine metabolic rate of a standard 20-mg mussel (Madon et al. 1998). We do not know the relative proportions of rotifer species and size ranges, so we have calculated a range of possible energy balances based on complete dominance by the small rotifer *L. ovalis* and by the large rotifer *B. calyciflorus*. Before zebra mussels dominated the Hudson River in 1992, the absorption of energy from rotifers was about two to three times higher than necessary to maintain its routine metabolic rate. Using the extremes of the possible rotifer size range, we can estimate that rotifers potentially contributed ~0.349–0.662 J h^{-1} to mussel growth and reproduction, conferring a positive scope for growth (Table 2). After the zebra mussels became abundant, the assimilation of rotifers still explained ~16.4–23.1% of the mussels' routine metabolic rate, depending on rotifer size. Therefore, rotifers play a conceivably large role in the zebra mussel energy budget, whether at high rotifer concentrations (~2 individuals ml^{-1}—just before the zebra mussel invasion) or low rotifer concentrations (~0.2 individuals ml^{-1}—after the zebra mussel invasion). Because ciliates are also quite common, there is a conceivably larger contribution of mesozooplankton to the nutrition of zebra mussels. Given the high clearance rates of Hudson
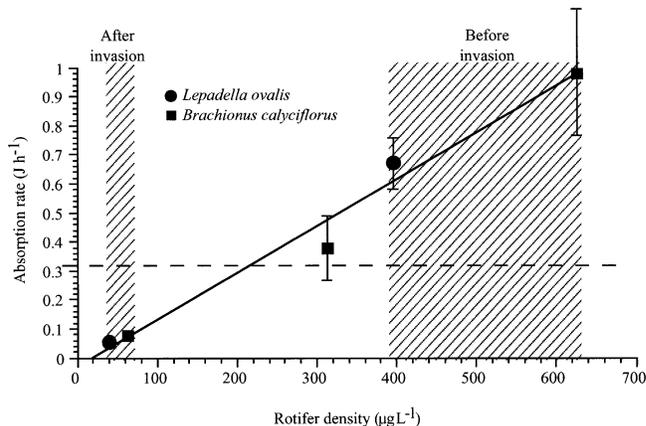

Fig. 2. Relationship between rotifer mass in the water and energy absorbed by zebra mussels from rotifers (data ± SE for two species, as indicated). Values above the dashed horizontal line represent a positive energy balance. Shaded areas show the range of likely rotifer density, in terms of mass, before (right shaded bar) and after (left shaded bar) the invasion. The left and right border of each shaded bar is calculated from estimates of minimum and maximum rotifer body size, respectively, in the Hudson. The intersection of the shaded area with the least squares fit regression line allows the calculation of an energy balance of a 20-mg (soft-tissue dry mass) zebra mussel (value of regression minus 3.22). The dashed line indicates the routine metabolic rate of 3.22 J h^{-1}.

River water (Roditi and Fischer 1999), zebra mussels are probably the dominant grazers of mesozooplankton.

The maintenance of both high larval and adult zebra mussel abundances despite the decline of phytoplankton standing stock raises the conundrum of how such high benthic grazer density can be maintained when the phytoplankton food supply is depleted. The disparity between mussel abundance and apparent food supply has stimulated speculation on what can make up for the deficit. Primary productivity in the Hudson River has been lower since the zebra mussel invasion, and the standing stock of phytoplankton has also been severely depleted (Caraco et al. 1997). During 1993, the amount of carbon required by the zebra mussel population was estimated to be ~120–150 g C m^{-2} yr^{-1}, which is far larger than the concurrent rates of phytoplankton production, estimated to be ~50 g C m^{-2} yr^{-1} (Strayer et al. 1996). This discrepancy is large enough to require accounting. Zebra mussels might derive their nutrition from bacteria and detri-

Table 2. Energy budget of zebra mussels (standardized to 20 mg dry weight) when feeding on rotifers. Routine metabolic rate (RMR) of 0.322 J h^{-1} was from Madon et al. (1998). $n = 4$ for *B. calyciflorus* and $n = 6$ for *L. ovalis*. AR, absorption rate; SFG, scope for growth. Data are mean ± SE.

Rotifer species	Rotifer density (individuals ml^{-1})	AR (J h^{-1})	AR/RMR × 100	SFG (J h^{-1})
B. calyciflorus	0.2	0.074±0.020	23.1±6.141	−0.248±0.020
	1	0.378±0.109	117.5±33.934	0.056±0.109
	2	0.983±0.217	305.5±67.302	0.662±0.217
	8	3.972±1.352	1,233.5±419.961	3.650±1.352
L. ovalis	0.2	0.053±0.053	16.4±1.621	−0.269±0.005
	2	0.671±0.088	208.3±27.343	0.349±0.088

tus as well as phytoplankton or other food resources. Zebra mussels apparently do not prefer bacteria as food. In the Hudson River, bacterial abundances have approximately doubled since zebra mussels arrived, which makes it clear that direct consumption by *Dreissena* is a minor process (Findlay et al. 1998). In the Ohio River in situ experiments, there was no significant difference among treatments with and without zebra mussels (Jack and Thorp 2000). Some of the missing C resources (70–100 g C m^{-2} yr^{-1}) might come from dissolved organic carbon (DOC) (Roditi et al. 2000) or microzooplankton (MacIsaac 1996; Pace et al. 1998), including perhaps feeding on their own planktonic larvae. Roditi et al. (2000) have studied the role of DOC in making up the deficit. They estimated a DOC absorption efficiency of 0.23% (^{14}C-labeled DOC), which could contribute 50% of the carbon demand of zebra mussels in the Hudson River. DOC probably is becoming more and more important in supporting the growth of zebra mussels while the rotifer and phytoplankton biomass declines. The studies on dissolved organic matter (DOM) have shown that uptake of free amino acids and sugars usually could meet 13–24% of the measured energy expenditure of mussels (Hawkins and Bayne 1992).

Our results suggest that feeding on zooplankton could be a major source of nutrition of newly invading and current zebra mussel populations. In past ecological studies, the trophic linkage between zooplankton, probably some mussel larvae, and bivalves usually has been ignored, and the role of crucial water column groups in the nutrition of suspension filter-feeding bivalves could therefore have been greatly underestimated.

It is usually thought that the link between fish and zooplankton is a cornerstone in the integration of predator and nutrient control pathways in aquatic ecosystems. In aquaculture, rotifers are used as food for fish larvae because of their high essential fatty acid content (e.g., eicosapentenoic [20:5n-3] and docosahexenoic [22:6n-3] acids; Oltra et al. 2000). The Hudson River is a specific case that gives us a window of opportunity to reveal this same trophic dependence of mussels on mesozooplankton. This dependence would apply not only to the Hudson River estuary, but also to many rivers and lakes that have been invaded by zebra mussels. In these cases, micro- and mesozooplankton have also declined dramatically (Pace et al. 1998; Jack and Thorp 2000; Thorp and Casper 2002) following the invasion of the zebra mussel.

Field sampling and in situ enclosure experiments (Pace et al. 1998; Jack and Thorp 2000; Thorp and Casper 2002) have shown that micro- and mesozooplankton declined following a zebra mussel invasion, and microcosm studies have demonstrated the ability of zebra mussels to clear rotifers from suspension in the laboratory (MacIsaac et al. 1991). Our present quantitative assimilation analysis demonstrates the nutritive value and absorption rate of rotifers by the mussels. Therefore, there is a strong trophic link between zebra mussels and mesozooplankton. Our results will likely extend to coastal and estuarine marine suspension feeding environments as well. The classic model of phytoplankton feeding by bivalves and most recent subsequent research have overlooked the BZ loop. This discovery and the other discoveries

of trophic linkage between flagellates, ciliates, and benthic suspension feeders (Kreeger and Newell 1996, 2001; Le Gall et al. 1997) have substantially changed our understanding of trophic dynamics in aquatic and coastal environments, of their effects on shellfish stocks, and on the sustenance of zebra mussel and other bivalve invasions. Invasions by zebra mussels could be sustained by micro- and mesozooplankton. Consequently, the indirect effect of major declines of zooplanktivorous fishes could result because zebra mussels apparently are strong competitors for food. The overexploitation by humans of bivalves and the declines of planktivorous fish and other benthic suspension feeders might have increased microzooplankton, which could have led to nuisance blooms of zooplankton-feeding gelatinous zooplankton in estuaries and coastal seas (Newell 1988; Zaitsev 1992). Marine bivalves also might be sustained significantly by feeding on the larvae of marine invertebrates. The BZ loop could play a major role in estuarine food webs, expanding the notion (Newell 1988) that dense populations of bivalves are a strong top-down force in estuarine and coastal ecosystems.

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