

## Poor Growth of Rainbow Trout Fed New Zealand Mud Snails *Potamopyrgus antipodarum*

MARK R. VINSON\*

U.S. Bureau of Land Management, National Aquatic Monitoring Center,  
Department of Watershed Sciences, USA

MICHELLE A. BAKER

Department of Biology and Ecology Center,  
Utah State University, Logan, Utah 84322-5210, USA

**Abstract.**—The New Zealand mud snail (NZMS) *Potamopyrgus antipodarum* is rapidly invading North American freshwaters, leading to speculation that native fisheries, especially those involving trout, will be negatively impacted. To assess whether trout would consume NZMSs and could assimilate nutrients from them, we conducted a laboratory <sup>15</sup>N tracer study, a laboratory feeding study, and bioenergetics modeling with rainbow trout *Oncorhynchus mykiss*; we also evaluated 5 years of diet and condition data describing rainbow trout and brown trout *Salmo trutta* collected from a river colonized by NZMSs. The <sup>15</sup>N tracer study showed that rainbow trout consumed and to a lesser extent assimilated NZMSs. Rainbow trout fed <sup>15</sup>N-labeled NZMSs had muscle isotopic signatures that were 80% higher than those of fish fed unlabeled NZMSs and 30% lower than those of fish fed <sup>15</sup>N-labeled amphipods. The feeding study showed that rainbow trout fed an exclusive and unlimited amount of NZMSs lost 0.14–0.48% of their initial body weight per day. Collection of rainbow trout feces showed that 8.5% of the NZMS shells were empty, and these snails were assumed to have been digested; 53.8% of NZMSs passed through the digestive system alive. Bioenergetics modeling showed that starved rainbow trout would have lost between 0.52% and 0.54% of their initial body weight per day, depending on their initial weight. Based on observed fish weight changes during three trial periods, mean modeled digestibility of NZMSs for rainbow trout fed an unlimited supply of the snails (proportion of maximum consumption = 1.0) was 63, 65, and 27%. Field survey data supported our laboratory experiments: we observed a sharp annual increase in the number of brown and rainbow trout consuming NZMSs between 2001 and 2005 in the Green River, Utah, downstream from Flaming Gorge Dam; moreover, the condition of brown and rainbow trout with NZMSs in their guts was significantly lower than that of fish without NZMSs in their stomachs. Our results confirm that North American trout fisheries face potential negative impacts from NZMS invasion.

The New Zealand mud snail (NZMS) *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae) is a small (<7 mm long), operculate freshwater snail (Winterbourn 1970) from New Zealand that has spread throughout the world. Since invading the USA in 1987, it has spread rapidly throughout the western USA (Montana State University 2007). The NZMS flourishes in a variety of aquatic habitats, including springs, rivers, lakes, and estuaries. It has been found across a wide range of water temperatures (0–30°C; Winterbourn 1969; Michaelis 1977; Hylleberg and Siegismund 1987), substrates (Heywood and Edwards 1962; Cogerino et al. 1995; Richards et al. 2001), water depths (Zaranko et al. 1997), productivity levels (Schreiber et al. 2003), and salinities (Winterbourn 1970). In many streams, NZMSs reach high population

densities and out-compete native fauna for space on the substrate and for food (Hall et al. 2003; Kerans et al. 2005). In a study of three rivers in the Greater Yellowstone ecosystem, Hall et al. (2006) found that NZMSs dominated total invertebrate production and had the highest secondary production rates ever measured for a river animal. The NZMSs were responsible for 65–92% of the total invertebrate production in these three rivers (Hall et al. 2006); thus, at these dominant population levels, NZMSs could become the dominant forage base for invertivorous fish.

Conventional wisdom has been that although NZMSs do not directly harm fish, their small, hard shells may not be digestible by North American fishes, resulting in little or no nutritional value gained from eating the snails (McCarter 1986). Studies conducted in Europe generally support this conjecture: NZMSs passed live through the digestive tracts of brown trout *Salmo trutta* (Bondeson and Kaiser 1949), Eurasian perch *Perca fluviatilis* (Dean 1904–1906), and Euro-

\* Corresponding author: mark.vinson@usu.edu

pean plaice *Pleuronectes platessa* (Hertling 1928; Ankel 1929) but not through the digestive tracts of common carp *Cyprinus carpio* (Dean 1904–1906).

The purpose of this study was to evaluate the willingness and ability of trout to consume, digest, and assimilate NZMSs. The four major objectives of the study were to (1) determine whether rainbow trout *Oncorhynchus mykiss* would ingest and assimilate  $^{15}\text{N}$ -labeled NZMSs into their muscle tissue, (2) estimate the digestibility of NZMSs for juvenile rainbow trout by collecting fish feces and using a bioenergetics model to estimate indigestibility, (3) evaluate laboratory growth of juvenile rainbow trout offered an exclusive diet of NZMSs, and (4) determine whether field survey data provide evidence for consumption of NZMSs and reduced condition in rainbow trout and brown trout that feed on NZMSs. Assimilation was defined as the incorporation of digested material into fish tissue, and digestibility was defined as the proportion of ingested material passed across the fish's gut wall. Food that passed through the digestive tract as large discernable particles (for NZMSs, generally whole shells) was considered undigested.

### Methods

*Study design.*—To assess whether trout would consume NZMSs and could assimilate enough nutrients from this source to maintain good condition, we conducted laboratory experiments and bioenergetics modeling and evaluated 5 years of fish diet and condition data from a river colonized by NZMSs. The first laboratory experiment was a stable isotope trace study in which we tracked the movement of  $^{15}\text{N}$  through algae, invertebrates, and fish to determine whether rainbow trout fed  $^{15}\text{N}$ -labeled snails would assimilate  $^{15}\text{N}$  into their muscle tissue. The second experiment evaluated growth of rainbow trout fed an exclusive diet of NZMSs. The Wisconsin bioenergetics model (Hanson et al. 1997) was used to compare growth of rainbow trout fed an unlimited diet of either NZMSs or native amphipods *Hyaella azteca* with growth estimated for starved fish. The ability of rainbow trout to digest NZMSs was evaluated by collecting the feces of fish fed NZMSs during the growth experiment and counting the number of empty, dead, and live snails. These laboratory results were then supplemented with field data on the consumption of NZMSs by brown trout and rainbow trout in the Green River, northern Utah.

*Stable isotope experiment.*—The stable isotope study was conducted between February and July 2004. Filamentous algae *Spirogyra* spp. and diatoms were grown in 19-L glass aquaria (41 cm long  $\times$  20 cm wide  $\times$  25 cm deep) that received 75 mg of  $^{15}\text{N}\text{-H}_4\text{Cl}$

(98 atom percent). After 7 d, more than 100,000 NZMSs and amphipods were each introduced into the aquaria. The NZMSs were also raised in a control aquarium that contained algae and diatoms but was not enriched with  $^{15}\text{N}$ . The NZMSs and amphipods used in the experiment were collected from the Green River downstream of Flaming Gorge Dam. Every few weeks, additional NZMSs and amphipods were collected, placed into alternate aquaria, and allowed to assimilate the heavy isotope before being used as feed.

At the start of the experiment, 27 juvenile rainbow trout (total length = 89–113 mm; weight = 8.7–13.8 g) were marked with passive integrated transponder tags (BioSonics, Inc., Seattle, Washington), measured, and weighed. The fish were placed in a large, flow-through trough at 10°C and were fed the Silver Cup trout diet (Nelson and Sons, Inc., Tooele, Utah) twice daily. After 23 d, 3 fish were killed for analysis as pretreatment controls and 24 fish were evenly and randomly assigned to one of four feeding treatments (6 fish/treatment): (1)  $^{15}\text{N}$ -enriched NZMSs, (2)  $^{15}\text{N}$ -enriched amphipods, (3) nonenriched NZMSs, and (4) commercial fish diet. Fish were fed twice daily. Rainbow trout were fed an amount of food that was consumed in about 5 min (~80 amphipods, 60 pieces of fish food, or 70 NZMSs at each feeding). Twice daily, about 80% of the water and the fish feces in each aquarium were siphoned out and replaced with fresh well water. The feeding trial was run for 84 d beyond the 23-d acclimation period.

Isotope samples were collected from invertebrates before they were moved to the isotope-enriched aquaria (control) and after 23 d in the enriched aquaria (treatment). For treatment and control samples, five replicate samples of  $^{15}\text{N}$ -labeled NZMSs, unlabeled NZMSs, and  $^{15}\text{N}$ -labeled *H. azteca* were prepared and analyzed. Tissue samples were collected from 3 rainbow trout before the feeding trials started and from 24 fish (6 fish/treatment) at the end of the experiment. Fish tissue samples were collected from below the dorsal fin with a 5-mm-diameter dermal biopsy punch (Miltex Instrument Co., Bethpage, New York). Samples were stored on ice and then frozen until processed (Bosley and Wainright 1999).

*Stable isotope laboratory methods.*—The NZMS and amphipod samples were inspected under a microscope. The snails were removed from their shells, cleaned of debris with forceps, rinsed with deionized water, and placed in 5-mL glass vials. Samples were dried for at least 48 h at 65°C (Midwood and Boutton 1998), ground to a fine powder with a mortar and pestle, and packed in 4-  $\times$  6-mm tin capsules. For NZMS analysis, several individuals were pooled until the weight requirement was met. For *H. azteca*, the

weight requirement was met with roughly half of one individual. The  $^{15}\text{N}$  content was measured with a Europa Hydra 20/20 continuous-flow isotope ratio mass spectrometer (PDZ Europa, Ltd., Cheshire, UK) at the Stable Isotope Facility, University of California–Davis. Stable isotope content ( $\delta^{15}\text{N}$ ; ‰, dry weight basis) is defined as:

$$\delta^{15}\text{N} = [(R_{\text{SAMPLE}}/R_{\text{STANDARD}}) - 1] \times 1,000,$$

where  $R_{\text{SAMPLE}}$  is the  $^{15}\text{N}:^{14}\text{N}$  ratio in the sample and  $R_{\text{STANDARD}}$  is the  $^{15}\text{N}:^{14}\text{N}$  ratio in the atmospheric  $\text{N}_2$  standard ( $R_{\text{SAMPLE}} = 0.0036765$ ). Values of  $\delta^{15}\text{N}$  were converted to the isotope mole fraction,  $^{15}\text{N}/(^{14}\text{N} + ^{15}\text{N})$ , by the equation

$$\begin{aligned} &^{15}\text{N}/(^{14}\text{N} + ^{15}\text{N}) \\ &= \{[(\delta^{15}\text{N}/1,000) + 1] \times 0.0036765\} \\ &\div (1 + \{[(\delta^{15}\text{N}/1,000) + 1] \times 0.0036765\}). \end{aligned}$$

To calculate the mass of  $^{15}\text{N}$  in food and fish tissues, the isotope mole fraction was multiplied by the mass of total N in the sample. Differences in the  $\delta^{15}\text{N}$  values for fish food items and fish muscle composition were compared among treatments by using a one-way analysis of variance (ANOVA; SAS Institute 2002).

*Weight change experiment.*—The weight change experiment was conducted between August 2004 and June 2005. Six juvenile rainbow trout (total length = 106–142 mm; weight range = 13.1–38.6 g; mean weight = 29.0 g) were randomly placed in each of two large, flow-through troughs (2 m long  $\times$  0.6 m wide  $\times$  0.3 m deep) supplied with well water at 10°C. Both troughs were stocked with aquatic macrophytes, principally buttercups *Ranunculus* spp., waterweeds *Elodea* spp., and duckweed *Lemna minor*. Invertebrates attached to the macrophytes were removed. One trough was stocked with amphipods, and the other was stocked with NZMSs collected from the Green River downstream from Flaming Gorge Dam. Additional amphipods and NZMSs were added to the troughs every few weeks. Amphipod and NZMS populations remained high throughout the experiment, averaging over 130,000 individuals/m<sup>2</sup>. Fish were weighed approximately weekly to the nearest 0.01 g.

After 108 d (trial period 1), the fish were removed from the troughs and quarantined for 24 h in individual aquaria to allow clearance of digestive tracts. After the quarantine period, we collected feces from each aquarium, placed each sample in a small petri dish with water, and examined the sample under a dissection microscope to tabulate the number of live NZMSs, dead NZMSs, and empty shells. Live snails were very active and easily distinguishable from dead

snails and empty shells. Fish were then placed in a trough of the opposite treatment from that occupied during period 1, and the feeding experiment was run as before for another 107 d (trial period 2). On day 216, the above quarantine, sampling, and aquarium switching procedures were repeated, and the experiment was run for another 98 d (trial period 3). The rate of weight change for an individual rainbow trout was calculated as the slope of the fitted regression line to relative change in weight as a function of days of treatment. For each combination of trial period and treatment, slopes were averaged across all individuals to calculate the mean daily percent change in weight.

*Bioenergetics modeling.*—We used the Wisconsin bioenergetics model (Hanson et al. 1997) to evaluate two scenarios: (1) the expected weight change of starved fish and (2) the indigestibility of NZMSs based on observed weight changes in the three feeding trials. Model scenarios were run for individual juvenile rainbow trout based on their weights at the start of each trial period at 10°C for 108, 107, and 98 d. Physiological parameter values for rainbow trout were from Rand et al. (1993). Percent weight change per day in fish that consumed no food was modeled with the proportion of maximum consumption ( $pC_{\text{max}}$ ) set to 0.0. To estimate indigestibility, we assumed that the rainbow trout were feeding at maximum rates when exposed to an essentially unlimited supply of NZMSs; therefore,  $pC_{\text{max}}$  for this case was set equal to 1.0. We adjusted the estimate of indigestibility in our bioenergetics model simulations until the modeled weight of rainbow trout was within 0.1 g of the observed weight at the end of the trial. The value of  $pC_{\text{max}}$  can range from 0.0 to 1.0, where 0.0 represents no feeding and 1.0 represents feeding at the maximum rate for a given fish size and water temperature. The  $pC_{\text{max}}$  is a product of digestion, assimilation, and other ecological constraints on the maximum feeding rate. Energy densities used in modeling were 675 J/g wet mass for NZMSs (Heywood and Edwards 1962; Ryan 1982) and 1,700 J/g wet mass for *H. azteca* (Cummins and Wuycheck 1971). Dry weight energy values for NZMSs from Ryan (1982) were converted to wet mass by using the conversion values of Heywood and Edwards (1962).

*Field survey of NZMS ingestion by brown and rainbow trout.*—Rainbow trout and brown trout were collected by Utah Division of Wildlife personnel using electrofishing during 1998–2005. Samples were collected each September from two stream reaches (each about 10 km long; sampled on consecutive nights): (1) downstream from Flaming Gorge Dam and (2) downstream from Little Hole. All fish were collected at night between 2000 and 2200 hours. Stomach contents were collected from 50 fish that were randomly

selected at each location in each year. Once collected, fish were anesthetized with tricaine methanesulfonate (MS-222), identified, measured to the nearest millimeter, and weighed to the nearest 0.1 kg; their stomach contents were then removed by pulsed gastric irrigation (Light et al. 1983). Stomach contents were preserved in the field in 95% ethanol and returned to the laboratory, where all invertebrates were identified (generally to genus or species) and counted. The percentage of brown trout and rainbow trout with NZMSs present in their stomachs each year was summarized.

Fish condition ( $K_n$ ) was determined following Ricker (1975):

$$K_n = w/l^b,$$

where  $w$  = weight,  $l$  = length, and  $b$  is the slope of the logarithmic linear regression represented by  $\log_{10} w = \log_{10} a + b \log_{10} l$  ( $a$  = intercept). The  $b$ -value was determined separately for brown trout and rainbow trout from data for all fish collected between 1998 and 2005. To compare  $K_n$  for brown trout and rainbow trout with and without NZMSs in their stomachs, we used a one-way ANOVA test (SAS Institute 2002).

## Results

### Stable Isotope Experiment

The addition of  $^{15}\text{N-H}_4\text{Cl}$  to the aquaria resulted in  $^{15}\text{N}$ -enriched invertebrate tissues after 23 d. Mean  $\delta^{15}\text{N}$  values varied significantly (ANOVA:  $P < 0.0001$ ) among food items: nonenriched NZMSs averaged  $9.9 \pm 0.8\text{‰}$  (mean  $\pm$  SD), enriched NZMSs averaged  $668 \pm 60\text{‰}$ , and enriched amphipods averaged  $1,299 \pm 68\text{‰}$ . On a dry weight basis, the  $^{15}\text{N}$  content of the labeled NZMSs ( $9.8 \pm 0.8 \times 10^{-4}$   $\mu\text{g}/\mu\text{g}$  dry mass) and labeled amphipods ( $9.9 \pm 1.0 \times 10^{-4}$   $\mu\text{g}/\mu\text{g}$ ) did not differ.

At the end of the experiment, mean  $\delta^{15}\text{N}$  of rainbow trout muscle tissue varied significantly among diet treatments (ANOVA:  $P < 0.0001$ ): pretreatment control fish averaged  $11.4 \pm 0.4\text{‰}$ , fish given commercial feed averaged  $10.9 \pm 0.8\text{‰}$ , fish fed unlabeled NZMSs averaged  $12.6 \pm 1.2\text{‰}$ , fish fed  $^{15}\text{N}$ -labeled NZMSs averaged  $69.9 \pm 16\text{‰}$ , and fish fed  $^{15}\text{N}$ -labeled amphipods averaged  $99.6 \pm 10.6\text{‰}$ . The mean  $\delta^{15}\text{N}$  of fish fed  $^{15}\text{N}$ -labeled NZMSs was 80% higher than that of fish fed unlabeled NZMSs and 30% lower than that of fish fed  $^{15}\text{N}$ -labeled amphipods. These results confirm that rainbow trout were able to assimilate NZMSs but at a slower rate than that of *H. azteca* assimilation.

### Weight Change Experiment

The two diet treatments produced opposite trends in rainbow trout growth over all three trial periods

(Figure 1). Fish fed NZMSs lost an average of 0.15, 0.14, and 0.48% of their initial body weight per day in the respective periods, whereas fish fed amphipods gained an average of 0.64, 1.37, and 0.99% of their initial body weight per day during the three periods. During period 3 (98 d), fish fed NZMSs died on days 7, 49, and 70 (i.e., mortality = 3 fish). These results showed that rainbow trout had a difficult time growing or even surviving when fed an exclusive diet of NZMSs in the laboratory. This seemed particularly true for the fish fed NZMSs during period 3, as their weight loss was substantially greater than that during period 1 for the same treatment.

### Snail Digestibility and Survival through Rainbow Trout Digestive Tracts

Rainbow trout were quarantined when switched between food treatments and allowed to naturally void their stomach contents for 24 h. In feces collections, 468 NZMSs were present in 13 fish after trials 1 and 2. Of these 468 NZMSs, 40 (8.5%) were empty shells and were assumed to have been digested, 176 (37.6%) were dead but present in their shells (assumed undigested), and 252 (53.8%) were alive.

### Bioenergetics Modeling

The bioenergetics model predicted that starved rainbow trout would have lost on average 0.52–0.54% of their initial body weight per day, based on initial weights at the start of each trial. This rate of weight loss was more than that observed during periods 1 and 2 and less than that observed during period 3 for fish fed only NZMSs (Figure 1). These findings support our stable isotope results indicating that rainbow trout are able to assimilate some nutrients from NZMSs, because the weight loss of fish in the feeding trials (except in period 3) was less than the model prediction for starved fish. Fish fed only NZMSs for a second time (period 3) lost weight at a greater rate than starved fish did. On the basis of observed weight changes, the bioenergetics model predicted that the digestibility of NZMSs for rainbow trout fed an unlimited supply of NZMSs ( $pC_{\text{max}} = 1.0$ ) averaged 63, 65, and 27%, respectively, for the three periods (Figure 1).

### Field Survey of NZMS Ingestion by Brown Trout and Rainbow Trout

We detected a sharp annual increase in the number of brown trout and rainbow trout consuming NZMSs after 2001, when NZMSs were first collected in the Green River (Figure 2a). The  $K_n$  of brown trout and rainbow trout with NZMSs in their guts was significantly lower than that of fish without NZMSs in their

RAINBOW TROUT FED NEW ZEALAND MUD SNAILS

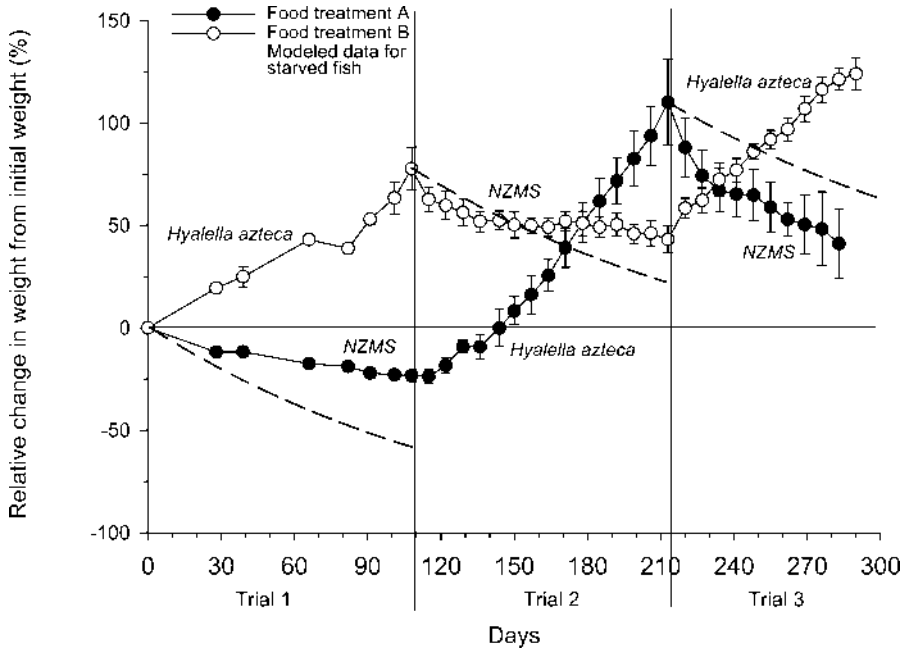


FIGURE 1.—Weight change (relative to initial weight) in juvenile rainbow trout fed native amphipods *Hyalella azteca* or nonnative New Zealand mud snails (NZMSs). Treatments were switched at 108 and 215 d. Group A was sequentially fed *H. azteca*, then NZMSs, and then *H. azteca*. Group B received the opposite treatment sequence. The dashed line describes modeled weight loss over time for starved fish (proportion of maximum consumption,  $pC_{max} = 0.0$ ); the dotted line describes weight loss over time for fish fed an unlimited diet of NZMSs ( $pC_{max} = 1.0$ ) with an indigestibility of 91.5%. Indigestibility was calculated based on fish feces collections. Model calculations were performed using the Wisconsin bioenergetics model (Hanson et al. 1997); parameter specifics are provided in the text.

stomachs (brown trout ANOVA:  $F_{1,576} = 8.26$ ,  $P = 0.0042$ ; rainbow trout:  $F_{1,561} = 12.0$ ,  $P = 0.0006$ ; Figure 2b). Mean ( $\pm$ SE)  $K_n$  was  $0.95 \pm 0.02$  for brown trout with NZMSs in their stomachs,  $1.02 \pm 0.08$  for brown trout without NZMSs,  $0.85 \pm 0.02$  for rainbow trout with NZMSs in their stomachs, and  $1.03 \pm 0.01$  for rainbow trout without NZMSs. These results support the findings of our laboratory experiments in that fish appear to readily consume NZMSs, but the ingestion of NZMSs may reduce condition and growth.

**Discussion**

Using laboratory studies, bioenergetics modeling, and field surveys, we showed that rainbow trout readily ingested NZMSs but appeared to receive reduced nutritional value from them compared with other foods. Fish assimilated some energy from NZMSs; the mean isotopic signature of fish fed  $^{15}\text{N}$ -labeled NZMSs was 80% higher than that of fish fed unlabeled NZMSs, and weight losses for fish fed only NZMSs were less than that predicted for starved fish. However, digestibility of NZMSs was low, averaging only about 9% based on

collection of fish feces; modeled digestibility rates ranged from 27% to 65%. In using the bioenergetics model to estimate the digestibility of NZMSs, the assumption that the rainbow trout were feeding at the maximum rate ( $pC_{max} = 1.0$ ) may not have been valid, particularly during the period 3. The feeding rate during period 3 may have been well below  $C_{max}$ , thereby at least partly explaining the lower digestibility estimate for period 3 relative to periods 1 and 2. Perhaps our estimate of digestibility based on the examination of rainbow trout feces at the end of period 1 was not indicative of digestibility during most of that trial; digestibility might have instead been considerably higher during the trial. This explanation would account for the substantial difference between our estimate of digestibility based on examination of rainbow trout feces and our estimates based on bioenergetics modeling. Also, the digestibility estimate reported by McCarter (1986) was applicable only to snails that passed through the digestive system intact and not to snails for which all soft tissue had been completely digested. Thus, the digestibility reported by McCarter (1986) may have underestimated total digestibility of

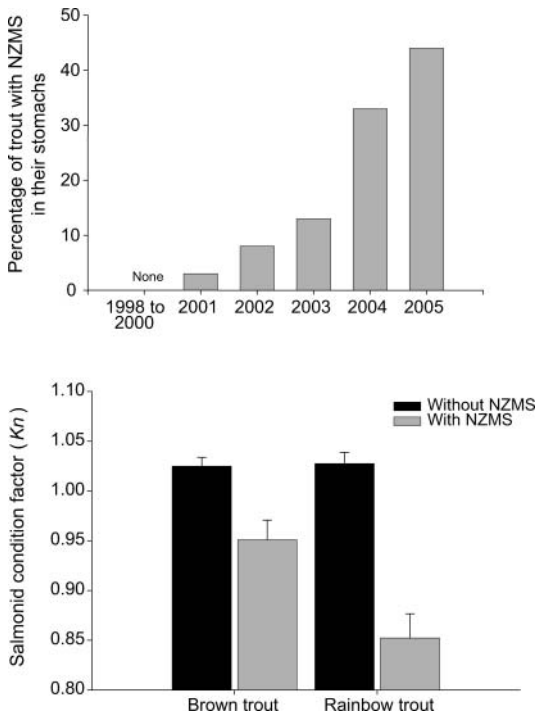


FIGURE 2.—New Zealand mud snail (NZMS) occurrence in brown trout and rainbow trout stomachs and associated condition ( $K_n$ ) of fish collected from the Green River, Utah, downstream from Flaming Gorge Dam after NZMS invasion in 2001: (A) percentage of fish (species combined) that consumed NZMSs and (B) mean ( $\pm$ SE)  $K_n$  of fish that did or did not consume NZMSs.

NZMSs for rainbow trout. Overall, these results indicate that although rainbow trout can assimilate some nutrients from NZMSs, fish growth may be reduced in systems where the NZMS is the dominant food item.

Actual effects of NZMSs on wild trout populations will probably be mediated by the availability of other invertebrate prey and by fish feeding habits. Trout may compensate for a low-energy food item by eating more of the item or switching to higher-energy prey. Data from our field survey showed that brown trout and rainbow trout readily consumed NZMSs in the Green River downstream from Flaming Gorge Dam: the percentage of fish consuming NZMSs increased consistently during each postinvasion year (Figure 2). This increase is probably a response to the increased availability of the snail, which has expanded in abundance and riverine distribution since 2001 (M.R.V., unpublished data). Diet studies conducted in Europe and New Zealand found NZMSs in the stomachs of brown trout (Bondeson and Kaiser

1949), rainbow trout (McCarter 1986), Eurasian perch (Dean 1904–1906), and European plaice (Hertling 1928; Ankel 1929). Data from our field survey showed that the  $K_n$  of brown trout and rainbow trout with NZMSs in their stomachs was significantly lower than that of fish without NZMSs in their stomachs. Although these results should be considered preliminary, they suggest that NZMSs can negatively affect trout populations in areas where they become the dominant food item.

Three aspects of trout life history and behavior are relevant to our results and to the possible effects of NZMSs on wild trout populations. First is a strongly positive correlation between aquatic invertebrate abundance and trout growth, abundance, distribution, and condition (Elliot 1975; Shirvell and Dungey 1983; Wilzbach 1985; Filbert and Hawkins 1995; Johansen et al. 2005). Second, trout typically consume prey in proportion to their abundance in the environment (Bres 1986; Cada et al. 1987; Angradi and Griffith 1990; Hilderbrand and Kershner 2004a). Third, resident trout commonly move throughout river basins (Gowan et al. 1994; Gowan and Fausch 1996; Schmetterling and Adams 2004), and more mobile fish tend to have lower condition than the general population (Gowan and Fausch 1996; Hilderbrand and Kershner 2004b).

The rapid dispersal of NZMSs within basins has been attributed to passive downstream drift on aquatic vegetation and woody debris, upstream movement (Lassen 1975; Haynes et al. 1985), fish stocking operations (Loo et al. 2007), and transport by recreational fishers (Ribi 1986; Loo et al. 2007). Our collection of rainbow trout feces, moreover, showed that the fish themselves may be actively spreading NZMSs throughout river basins. We found that nearly 54% of the snails recovered from fish feces passed through the digestive system alive and would probably be able to reproduce. Haynes et al. (1985) made a similar observation after feeding NZMSs to juvenile rainbow trout (120 mm long). They later recovered 49 snails in fish feces, of which 35 were alive; 10 live young were also recovered within 24 h of being voided. On another occasion, two snails were voided that later gave birth to 28 young. Clearly, the potential is high for trout to increase the distribution of NZMSs in rivers as they transport live snails in their guts to other locations.

Once NZMSs colonize a site, they often numerically dominate stream invertebrate assemblages, and populations exceeding 100,000 individuals/m<sup>2</sup> are regularly reported (Dorgelo 1987; Richards et al. 2001; Hall et al. 2003; Kerans et al. 2005). At these high population densities, NZMSs can substantially modify lower trophic levels (Hall et al. 2006). Our results suggest

that these snails can affect higher trophic levels if they become a dominant component of fish diets. Initial field evidence for this is available from the Green River, where NZMSs were first detected at a site 35 km downstream from Flaming Gorge Dam in 2001, and from New Zealand lakes (McCarter 1986). Since 2001, NZMSs have expanded throughout a 50-km river reach from the dam downstream to the Utah–Colorado state line (Vinson et al. 2006). The presence of NZMSs in brown and rainbow trout stomachs in the Green River has similarly increased (Figure 2). We also detected a significant difference in  $K_n$  between wild fish with NZMSs in their stomachs and those without snails in their stomachs on the date of collection. These results should be considered preliminary because stomach content samples were collected only once annually; nonetheless, the observations were consistent with our laboratory experiments and with observations made in New Zealand (McCarter 1986). McCarter (1986) speculated that trout growth rates in New Zealand lakes are lower for systems in which the predominant trout prey available are small, indigestible mollusks (e.g., hydrobiids) than for systems in which aquatic insects are abundant and mollusks are only a minor dietary component. Monitoring of the population dynamics of NZMSs and the  $K_n$  of brown trout and rainbow trout in the Green River should continue, because this site is one of the few places (Hall et al. 2006) for which pre-invasion data on invertebrate assemblages and trout populations are available (Vinson et al. 2006).

New Zealand mud snails present a substantial challenge to fisheries managers. The snails have exhibited rapid dispersal throughout North America over the last decade (Montana State University 2007). These problems may be exacerbated by the ability of ingested NZMSs to survive passage through fish digestive tracts. This factor may be particularly relevant for trout hatchery and stocking operations (Loo et al. 2007). High-quality, coldwater conditions at trout hatcheries make these facilities highly susceptible for infestation by NZMSs. Once this occurs, snails stowing away in fish digestive tracts could be unwittingly spread to new habitats by trout stocking operations.

We know of no method for eliminating NZMSs once they have become established in the wild. Current efforts to reduce the spread of NZMSs and other aquatic nuisance species center on implementing Hazard Analysis and Critical Control Points plans (USFWS 2007). The plans focus on identifying critical control points at which nontarget species can be removed; documenting risks and methods used to remove nontarget species; and making consistent decisions based on identified risks. Practices to reduce

the spread of NZMSs through fish stocking include (1) regularly surveying hatchery facilities for the presence of NZMSs, (2) maintaining several sets of equipment and decontaminating them between uses, and (3) holding fish for 48 h in tanks known to be free of invasive species before releasing the fish into the wild. Although these techniques should reduce the chance of spreading NZMSs, live snails might still be present in fish digestive tracts, and the development of techniques to reduce this vector is needed.

Future research to assess the effects of NZMSs on native communities include (1) determining the potential distribution of NZMSs in North America (sensu Drake and Bossenbroek 2004) to better identify regions with high potential for invasion and to allow for more focused public awareness programs, (2) quantifying competitive interactions between NZMSs and native invertebrates (sensu Kerans et al. 2005) to determine which habitat types are most susceptible to invasions, and (3) expanding our preliminary work on the Green River to quantify the effects of NZMSs on higher trophic levels in natural systems (sensu Vander Zanden et al. 1999).

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