MODELING REGIONAL DISTRIBUTION AND LOCAL FOOD WEB DYNAMICS OF THE NEW ZEALAND MUD SNAIL (POTAMOPYRGUS ANTIPODARUM)

by

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ABSTRACT

Modeling Regional Distribution and Local Food Web Dynamics of the New Zealand Mud Snail (Potamopyrgus antipodarum)

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Species invasions may cause either significant or nominal ecosystem changes. The effects of invasive species on native communities are difficult to predict, but appear to be related to the life history characteristics of the invaders. The invasive New Zealand mud snail (*Potamopyrgus antipodarum*) persists in a wide variety of aquatic habitats, is parthenogenic, and if kept moist, can survive out of water for several weeks. These characteristics make the New Zealand mud snail well suited for long distance dispersal; as such they may have significant effects on aquatic ecosystems. In this thesis, I addressed two key issues regarding the invasive New Zealand mud snail: 1) potential effects on a local food web using stable isotope analysis and bioenergetic modeling, and 2) prediction of regional NZMS distribution using a factor analysis and GIS to identify sites where public education efforts should be focused. Results from an isotope mixing model suggested that New Zealand mud snails have similar diets as native invertebrates and may thus compete with them. Stomach content analyses revealed that brown trout (*Salmo trutta*) ate and probably assimilated more NZMS than the other fishes. Bioenergetic simulations showed that diets high in NZMS do not meet energy requirements of fish.

Using data from 1327 sites in the western United States, I found that sites likely to be invaded by NZMS were relatively close to population centers and blue ribbon fisheries, had a relatively low elevation, and had a stream order greater than two. This study is considered a first-stage model to identify sites to which NZMS are likely to be transported. I recommend continuing the project into the second-stage, including measurement of biological factors affecting NZMS establishment and local spreading as well as field validation of this first-stage model.

I investigated important issues regarding the NZMS on two scales: local and regional. At the local level, I found circumstantial evidence for negative effects of NZMS on the Green River food web. At the regional level, I created a site suitability map to be used by natural resource managers to effectively and efficiently locate NZMS populations.

(88 pages)

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Tarita K. Harju

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I.

INTRODUCTION

There are four basic stages in a species invasion: transportation (dispersal), release, establishment, and spreading (Kolar and Lodge 2001). Obstacles must be overcome in each stage to have a successful invasion, including ineffective dispersal vectors, environmental resistance, biotic resistance, and demographic resistance (a species' ability to establish with few individuals) (Moyle and Light 1996). Depending on a species' success at each of the four stages of invasion, species invasions may cause either drastic or nominal ecosystem changes (Moyle and Light 1996). The relative effects of invasive species on native communities are difficult to predict, but appear related to the life history characteristics of the invaders and specific characteristics of the food webs they invade (Vitousek 1990). Characteristics common to successful invaders include high reproductive and dispersal rates, parthenogenesis, early maturation, small body size, and being a habitat generalist (Lodge 1993). Habitat characteristics common to invaded environments include low diversity of native predators, recent habitat disturbances, and habitat conditions similar to the invader's native range (Lodge 1993). At least 88 invasive fresh water molluscs are established in the US, including the New Zealand mud snail (*Potamopyrgus antipodarum* Gastropoda: Hydrobiidae, NZMS; OTA 1993).

The NZMS is a small (<5 mm) invasive snail native to New Zealand. Since the mid 1800s the snail has spread from New Zealand to freshwater environments throughout the world, including Australia, Europe, Asia, and North America. The snail was first discovered in the United States in 1987 in the Snake River near Hagerman, Idaho (Bowler 1991). NZMS have several morphological and behavioral traits that make them well- suited for invasions, including a high growth rate, parthenogenesis, viviparity, and lack of parental care (Lodge 1993; Dybdahl and Lively 1995). They also possess an operculum, which allows them to live for several weeks out of the water, if kept moist and sheltered from excessive heat. It has been speculated that recreationists, fish and waterfowl transport NZMS within and between water bodies (Lassen 1975; Bondesen and Kaiser 1949; Haynes et al. 1985). NZMS are able to survive in a variety of aquatic habitats across a wide range of temperatures, substrates, and salinities (Cogerino et al. 1995; Zaranko et al. 1997; Richards et al. 2001; Hall et al. 2003). These traits suggest NZMS have a high likelihood of establishing in new habitats.

Previous studies have shown that NZMS can negatively affect ecosystems. First, they can decrease the availability of primary producers; Winterbourn and Fegley (1989) found depressed periphyton levels associated with NZMS in New Zealand. Hall et al. (2003) found that NZMS population densities in Polecat Creek, Wyoming exceeded 100,000 individuals per square meter, comprised 95% of the total invertebrate biomass, and consumed 75% of the gross primary production. Second, they may outcompete native invertebrates; in a field experiment, negative associations were observed between NZMS and native invertebrates (Kerans et al. 2005). Finally, they may decrease the health of ecosystem predators; in a lab experiment, juvenile rainbow trout (*Oncorynchus mykiss*) continually lost weight when fed only NZMS and when fish voided the snails, 53% of the snails were still alive (Vinson and Baker 2005). Based on these findings, NZMS have the potential to affect the entire food web of an aquatic system.

It is important to recognize possible ecosystem effects of NZMS as well as identify new sites likely to be invaded. Armed with this information, managers can focus efforts to prevent further spread and get an early start on containment and eradication. For my thesis, I investigated the NZMS at two scales: local and regional. At the local scale, I used ^{13}C and ^{15}N stable isotope analysis and bioenergetic modeling to elucidate effects NZMS may have on all trophic levels of the blue-ribbon trout fishery downstream from Flaming Gorge Dam. At the regional scale, I predicted NZMS distribution with an ecological niche factor analysis and GIS, using presence-only NZMS data and predictor variables related to recreationists, the primary NZMS dispersal vector.

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CHAPTER II.

EFFECTS OF NEW ZEALAND MUD SNAILS ON A LARGE RIVERINE FOOD WEB

Abstract

New Zealand mud snails (*Potamopyrgus antipodarum*, NZMS) are invading North American freshwaters and altering native invertebrate assemblages, suggesting adverse effects may be felt by native fish populations. I examined trophic effects of NZMS in the Green River downstream from Flaming Gorge Dam (Utah), based on fish stomach contents, stable isotope samples, and predicted fish growth from observed diets using bioenergetic models. Fish diet differed among 3 salmonid species and a sculpin. Brown trout (*Salmo trutta*) generally consumed and potentially assimilated more NZMS than the other fishes. Overall percentage of fish with NZMS in their stomachs has increased steadily since 2001; in 2005 it varied from 0% (sculpin, *Cottus bairdii*) to 73% (mountain whitefish, *Prosopium williamsoni*). Based on an isotope mixing model, NZMS diets were similar to native invertebrate diets, suggesting the potential for dietary competition. Bioenergetic simulations suggest that diets high in NZMS do not meet energy requirements of fish, resulting in reduced growth and weight loss. Based on the above, I conclude there may be direct and indirect, but species specific, negative effects of NZMS on the Green River food web.

Introduction

Species invasions may cause either significant or nominal ecosystem changes (Moyle and Light 1996). Zebra mussels (*Dreissena polymorpha*) are an example of a non-native species causing substantial ecosystems changes in aquatic habitats. Their invasion into the Great Lakes and Mississippi River Basin has threatened native mussels (Haag et al. 1993), led to a reduction of lake seston (Hebert et al. 1991), and caused biofouling problems for utilities and industry (Nalepa and Schloesser 1993). These detrimental effects have led to preventive measures to curtail their colonization of new habitats (Schloesser and Kovalak 1991, Witte et al. 1992). However, in many instances invasive species integrate with native biota and appear to cause insignificant ecosystem changes or fail to establish altogether.

Effects of invasive species on native communities are difficult to predict, but appear related to the invader's life history and specific native habitat characteristics (Vitousek 1990). Successful invaders are often parthenogenetic, mature early, have a small body size and other r-species characteristics (Lodge 1993). Easily invaded environments include those with low diversity of native predators, recent habitat disturbances, and habitat conditions similar to the invader's native range (Lodge 1993).

The New Zealand mud snail (*Potamopyrgus antipodarum,* NZMS) is a small (<5 mm) snail (Hydrobiidae) native to New Zealand that appears to be a successful invader. Since the mid 1800s the NZMS has spread to freshwaters throughout the world, including Australia, Europe, Asia, and North America. The snail was first discovered in the United States in 1987 in the Snake River near Hagerman, Idaho (Bowler 1991).

New Zealand Mud Snails exhibit traits making them well-suited for invasions, including a high growth rate, parthenogenesis, and viviparity (Lodge 1993; Dybdahl and Lively 1995). They also possess an operculum, allowing them to withstand prolonged periods of desiccation. It is thought that recreationists, fish and waterfowl transport NZMS within and between water bodies (Bondesen and Kaiser 1949; Lassen 1975; Haynes et al. 1985). NZMS are able to survive in a variety of aquatic habitats across a wide range of temperature, substrate, and salinity (Cogerino et al. 1995; Zaranko et al. 1997; Richards et al. 2001; Hall et al. 2003).

Previous studies have shown that NZMS can negatively affect ecosystems. Hall et al. (2003) found NZMS population densities in Polecat Creek, Wyoming exceeded 100,000 individuals per square meter, comprised 95% of the total invertebrate assemblage biomass, and consumed 75% of the gross primary production. In a field experiment, negative associations were observed between NZMS and native invertebrates (Kerans et al. 2005). In a lab experiment, juvenile rainbow trout (*Oncorynchus mykiss*) lost weight when fed only NZMS and when fish voided the snails, 53% of the snails were still alive (Vinson and Baker 2005).

Hence, NZMS have the potential to affect multiple trophic levels of aquatic food webs by grazing primary producers, outcompeting native invertebrates, and reducing quality of fish diets. In this study, I evaluate their role in a large riverine food web, including interactions with other invertebrates and fish.

Food web analyses

Food web studies trace food sources from primary producers to higher trophic levels and are an important tool for understanding ecosystem structure and function. Stomach contents and stable isotope analyses are two common methods for studying food webs. Stomach contents provide information on what an animal has recently ingested, whereas stable isotopes evaluate what food items animals actually assimilate over a longer time period (Rounick and Winterbourn 1986; Rosenfield and Roff 1992; Finlay 2001). Isotope analyses determine naturally-occurring differences between heavier and lighter isotopes ratios to discern trophic structure, especially $^{13}C/^{12}C$ and $^{15}N/^{14}N$ (Coleman and Fry 1991; Finlay 2001). Both techniques have advantages and disadvantages. In this work I used both techniques.

Stable isotope analyses depend on unique isotope 'signatures' of primary producers, which are created through fractionation of ^{13}C and ^{12}C or ^{15}N and ^{14}N. The stable isotope ^{13}C is neither preferentially retained or excreted by a consumer, but certain primary producers show preferences based on photosynthesis (i.e., a C4 plant ≠ a C3 plant ≠ aquatic macrophytes, etc.). Hence, carbon stable isotopes provide a measure of the original carbon source (i.e., you are what you eat). The stable isotope ^{15}N, however is preferentially retained by consumers, because ^{14}N is easier to excrete, so that ^{15}N is enriched

3-5‰ per trophic level (Peterson and Fry 1987). Hence, nitrogen stable isotopes provide a measure of trophic position (Peterson and Fry 1987; Fry 1991). Together, these two isotopes generally allow elucidation of trophic position.

As a rule, when *n* isotopes are used in analyses, *n* +1 food sources can be distinguished using a two source mixing model (Phillips and Gregg 2001). When more than *n* +1 food sources are considered, programs like IsoSource (http://www.epa.gov/wed/pages/models.htm) are used to obtain results (Phillips and Gregg 2003; also see review by Benstead et al. 2006).

My objective was to describe the role and effects of NZMS in the food web of the Green River downstream from Flaming Gorge Dam. To answer this question, I conducted 2 studies: 1) isotope and stomach content analyses to determine dietary overlap between NZMS and native invertebrates and to determine which species were eating NZMS, and 2) bioenergetic modeling to evaluate the effects of consuming NZMS on brown and rainbow trout condition and growth.

Study Area

This study was conducted on a 26 km stretch of the Green River from Flaming Gorge Dam (40˚ 54'N, 109˚ 25' W, 1689 m) downstream to Taylor Flat Bridge in northeastern Utah (Figure 2-1). The pre- and post-dam environments (before and after 1962) have been well described: flow and sediment (Graf 1980; Andrews 1986; Grams 1997; Vinson 2001), channel changes (Lyons et al. 1992;

Grams 1997), water chemistry (Madison and Waddell 1973; Bolke and Waddell 1975), water temperature (Vinson 2001), fish (Woodbury 1963; Vanicek 1970) and invertebrate communities (Woodbury 1963; Pearson et al. 1968; Annear 1980; Vinson 2001). New Zealand mud snails were initially found in the study area in September 2001 (Vinson 2004) and are now found from Flaming Gorge Dam downstream to the Colorado state line (~43 river kilometers).

Methods

Food Web Analysis

Field Collections

Primary producers, detritus, consumer macroinvertebrates, and predator macroinvertebrates were collected in July – August 2005 for carbon and nitrogen isotopic analysis (Figure 2-1). Samples were collected with forceps or latex gloves to prevent contamination and were stored on ice or frozen until processed (Bosley and Wainright 1999).

Non-decomposed terrestrial plants from the riparian zone, aquatic macrophytes, and filamentous algae were collected at each site. Diatoms were removed from sampled aquatic macrophytes by shaking and gentle rubbing in a container of filtered water, and then filtered through pre-ashed Whatman GF/F filters (Angradi 1994). Particulate organic matter was collected in a 50 µm plankton net (12.7 cm diameter, 38.1 cm length) that was set for 5 min in flow adequate to keep the net extended. Particulate organic matter was sieved into 3 size classes: 1) coarse particulate organic matter (CPOM), ≥1 mm; 2) fine particulate organic matter (FPOM), <1 mm to ≥0.25 mm; and 3) very fine particulate organic matter (VFPOM), <0.25 mm to ≥53 µm. Periphyton was scraped from randomly chosen cobbles using a circular template and then condensed on to pre-ashed Whatman GF/F filters. Benthic invertebrates were collected with kick nets from all available habitats at each site and were held live in containers with filtered river water. Filtered river water was exchanged with deionized water after 24 hours of storage. Invertebrate collections were limited to only the most common taxa, determined from Vinson et al. (2006) (Table 2-1).

Fish stomach contents were collected annually in mid-September from 2001-2005. Fish were collected at night, 2000 h to 2300 h, by boat electroshocking from Flaming Gorge Dam to Red Creek Rapid, 18 km downstream. Collected fish were processed by the Utah Division of Wildlife Resources (UDWR) at 2 locations: 1) Tailrace boat launch and 2) Little Hole boat launch. Brown trout (*Salmo trutta),* rainbow trout (*Oncorhynchus mykiss),* mountain whitefish (*Prosopium williamsoni)* and mottled sculpin (*Cottus bairdii)* were identified, measured, weighed, and stomach contents collected by gastric lavage (Light et al. 1983).

Fish tissue samples for stable isotope analysis were collected in September 2005. Isotope tissue samples of each species were collected from subsamples of 3 standard length (SL) size classes (0-250 mm, 251-400 mm, >400 mm). Whitefish <400 mm SL were rarely collected and no mottled sculpin

>110 mm SL were collected. Tissue was collected from the fish dorsum with a 5 mm dermal biopsy punch (Miltex instrument Company, Inc., Bethpage, NY).

Laboratory Processing

Samples for isotopic analysis were inspected under a microscope, identified to the lowest possible level, cleaned of debris with forceps, rinsed with deionized water and placed in 5 ml glass vials. Snails were removed from their shells. Non-fish isotope samples effervesced when exposed to hydrochloric acid (HCl), indicating the presence of calcium carbonate. Therefore, samples were covered with 1M HCl and left undisturbed for 24 hours (Jacob et al. 2005). Samples were then dried for at least 48 hours at 65°C (Midwood and Boutton 1998), ground to a fine powder with a mortar and pestle and packed in 8x5 mm tin capsules. Two mg of plants and 1 mg of fish and invertebrates were required for isotopic analysis. When possible, 1 organism was used to meet the mass requirement, if not multiple organisms were pooled to meet the minimum requirement.

Fish stomach contents were sorted and identified to the lowest possible level (usually genus and species) under dissecting microscopes.

Analytical methods

Isotope composition was measured at the UC Davis Stable Isotope Facility. The average standard error for measurement at the UC Davis facility was 0.009‰. Results were reported in delta (δ) parts per thousand (‰) differences from isotopic standards:

$$\delta^{15}\text{N or } \delta^{13}\text{C} = \left[\frac{\left(R_{\text{sample}} / R_{\text{standard}}\right)}{R_{\text{standard}}}\right] * 1000$$

Where R_{sample} was $^{13}C/^{12}C$ or $^{15}N/^{14}N$ of the organism and $R_{standard}$ was from the Peedee Belemnite marine limestone (^{13}C), or atmospheric nitrogen.

Trophic position, a quantification of trophic level, was calculated for all members of the food web, using the equation:

$$TP = \lambda + \left(\delta^{15} N_{consumer} - \delta^{15} N_{basal}\right) / \Delta N$$

Where *TP* is trophic position, λ is the trophic position of the basal resource and ΔN is the ^{15}N enrichment per trophic level (Vander Zanden and Rasmussen 1999). The gastropod *Physella* was used as the basal resource (^{15}N value of 9.99, λ=2) and a ΔN of 3.4‰ (Minegawa and Wada 1984; Post 2002; Delong and Thorp 2006). Primary consumers, rather than primary producers, are commonly used as the basal resource when calculating TP because they are large bodied and have greater longevity, reducing variability in isotope composition (Cabana and Rassmussen 1996).

I used the IsoSource mixing model (version 1.2; Phillips and Gregg 2003) to determine assimilated food sources. Output from this model identified the range of possible contributions from each source, indicating that source's importance in an organism's diet. IsoSource output is a frequency distribution that shows the proportion of total feasible diet combinations that include each food source at *x*-percentage of the total diet. In order to avoid misrepresentation of frequency distribution results, which are not necessarily normally distributed, the 1st and 99th percentile range of each source was reported, as described in

Phillips and Gregg (2003) to represent the full range of possible contributions from each food source. IsoSource requires that food source isotope values are distinct from each other. Analysis of Variance (ANOVA, using α=0.05) was performed on isotope values to determine whether sources were significantly different. Only significantly different food items were used as inputs for IsoSource.

Three parameters are user defined in IsoSource: increment, tolerance and enrichment of ^{13}C and ^{15}N. Increment specifies the resolution of the probability distribution; i.e., an increment of 1.0% results in the probability distribution being displayed for every 1.0% increase in diet contribution. I used an increment of 2.0% because it provided detailed results with reasonable computational time. Tolerance levels specify the amount of stochastic variation in a specific sample set, and need to be adjusted to represent natural variation in fractionation and sample preparation. For invertebrates, the tolerance was increased until a feasible solution was found, up to a maximum of 1.8 ‰. IsoSource does not automatically account for enrichment between trophic levels, rather ^{13}C and ^{15}N enrichment values for each source need to be specified. I set ^{13}C and ^{15}N enrichment to values commonly observed in the literature for freshwater streams: 0.2‰ and 3.4‰, respectively (Minegawa and Wada 1984; Peterson and Fry 1987; France and Peters 1997).

Because a large number of possible food sources used in Isosource produce results with a low interpretability, limiting or combining the number of potential food sources is a practical way to achieve more interpretable results

(Phillips et al. 2005). This can be done in two ways: *a priori* or *a posteriori* aggregation (Phillips et al. 2005). *A priori* aggregation is used when sources' isotope values are not statistically different and are logically related. *A posteriori* aggregation is used when IsoSource results are vague or indeterminate and sources can be logically grouped. The *a posteriori* method is useful because it allows the unique signatures of each food source to be used as input into IsoSource and is later used to constrain results and aid interpretation (Phillips et al. 2005). Both methods have been simultaneously used (Newsome et al. 2004; Melville and Connolly 2003; Sara et al. 2003) and were necessary to this study.

Analyses of stomach contents (from 2001 – 2005) were limited to the 5 most common prey items in each fish species stomachs per year, which accounted for >90% of the total stomach contents by abundance. The number of fish that consumed at least 1 NZMS and the percent by abundance of total stomach content items that were NZMS was also quantified. Fish with no invertebrates in their stomachs were included in this analysis.

Bioenergetics Modeling

The effects of varying proportions of NZMS in fish diets on fish growth and fish condition were evaluated using the Wisconsin Bioenergetics Model (Hanson et al. 1997). This modeling exercise is intended to be used to compare the relative effects of trout consuming varying levels of NZMS. Parameters need to be defined for the 3 model partitions: 1) fish species, 2) their prey and 3) water temperature.

User defined fish parameters include: fish consumption, respiration, excretion, weight and diet. Brown trout consumption, respiration, and excretion parameter values were taken from Dieterman et al. (2004). Rainbow trout parameter values were from Rand et al. (1993). Initial and final weights, representing growth, used for each species were the mean weight at age 1 and age 2 of fish collected in the study reach in 2004 and 2005 (UDWR, unpublished data). Initial fish diets were based on fish stomach content data for 2005 (Table 2-2).

User defined invertebrate parameters include energy density, digestibility and seasonal abundance. Invertebrate prey energy density values were taken from the literature (Ryan 1982; Hanson et al. 1997; Dieterman et al. 2004) (Table 2-3). Two levels of NZMS indigestibility were modeled: 98% (high) and 82% (low); these were based on digestibility values calculated by McCarter (1986) and Vinson and Baker (2005). The proportion of NZMS in the simulated diet was varied from 0% (late winter) to 100% (summer) (Table 2-4).

Water temperature data were long-term (1994 to 2005) monthly averages for the study reach (Vinson et al. 2006). Temperatures varied from a maximum of 14°C in September to a minimum of 3°C in March.

These input data were used to determine the proportion of maximum consumption (p-value; 0-1) that a fish must feed at to maintain the specified growth rate. This computed p-value was then kept constant for subsequent bioenergetic model runs, and the proportion of NZMS in fish diet was increased by increments of 10% to model the effects of increasing NZMS consumption over

365 days. The ending weight was re-calculated for each dietary increment of NZMS.

Model Analysis

Two comparisons were made using bioenergetic results: 1) change in ending weight as the proportion of NZMS consumption increased and 2) change in Relative Weight (RW) as the proportion of NZMS consumption increased. RW was based on a regression of Log_{10} *Length* and Log_{10} *Weight* using fish from the study area,

$$RW = \left(\frac{WT}{10^{a} * L^{b}} \right)$$

Where *WT* is weight in grams, *L* is length in millimeters, *a* is the slope of the regression and *b* is the intercept. For brown trout, *a* = -3.838 and *b* = 2.539. For rainbow trout, *a* = -3.744 and *b* = 2.508. Relative Weights from bioenergetic simulations were compared to mean age-2 RW from the study area in 2000, the year before NZMS were detected (Utah Division of Wildlife Resources, unpublished data).

Results

Food Web Analysis

My analysis of the Green River food web produced four trophic levels: primary producers, invertebrate herbivores, invertebrate predators, and fish (Figure 2-2a,b). Measured ratios for all taxa and trophic levels are presented in Table 2-5, all data presented here are δ, the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Moss was the most ^{13}C-depleted with a mean value of -36.16 (± 0.33 SE) and a mean ^{15}N value of 8.36 (± 0.31 SE). Periphyton was the most ^{13}C-enriched with a mean value of -12.55 (± 1.16 SE) and a mean ^{15}N value of 3.12 (± 1.14 SE). Terrestrial vegetation species were the most ^{15}N-depleted with a mean ^{15}N value of 1.50 (±0.30 SE) and a mean ^{13}C value of -27.12 (± 0.56 SE). Mountain whitefish were the most ^{15}N-enriched with a mean value of 16.00 (± 0.33 SE) and a mean ^{13}C value of -28.03 (± 0.37 SE).

Algal species had a mean ^{15}N value of 8.16 (± 0.52 SE) and a mean ^{13}C value of -21.08 (± 1.11 SE). Aquatic macrophyte species had a mean ^{15}N value of 8.08 (± 0.30 SE) and a mean ^{13}C value of -25.53 (± 1.89 SE). Consumer invertebrates had a mean ^{15}N value of 9.89 (± 0.14 SE) and a mean ^{13}C value of -27.55 (± 0.17 SE). Predator invertebrate species had a mean ^{15}N value of 11.86 (± 0.20 SE) and a mean ^{13}C value of -26.45 (± 0.23 SE). Brown trout had a mean ^{15}N value of 15.59 (± 0.33 SE) and a mean ^{13}C value of -26.00 (± 0.19 SE). Rainbow trout had a mean ^{15}N value of 14.06 (± 0.45 SE) and a mean ^{13}C value of -25.32 (± 0.42 SE). Mottled sculpin had a mean ^{15}N value of 13.54 (± 0.20 SE) and a mean ^{13}C value of -25.39 (± 0.23 SE).

Terrestrial vegetation species had a mean trophic position of -0.49 (± 0.09 SE). Algae species had a mean trophic position of 1.44 (± 0.09 SE). Diatoms had a mean trophic position of 1.80 (± 0.16 SE). Aquatic macrophyte species had a mean trophic position of 1.46 (± 0.15 SE). Periphyton had a mean trophic position of 0.16 (± 0.29 SE). Organic matter had a mean trophic position of 0.69 (± 0.21 SE). Consumer invertebrate species had a mean trophic position of 1.96

(± 0.04 SE). The five most common prey items in fish stomachs all had a trophic position near 2.0. Predator invertebrate species had a mean trophic position of 2.55 (± 0.06 SE). Mountain whitefish and brown trout had the highest trophic positions at 3.77 (± 0.10 SE) and 3.65 (± 0.10 SE), respectively. Rainbow trout and mottled sculpin had slightly lower trophic positions of 3.20 (± 0.13 SE) and 3.04 (± 0.06 SE), respectively.

Food source inputs in IsoSource for consumer invertebrate diets were FPOM, VFPOM, algae, diatoms, aquatic macrophytes and periphyton. Algae species and aquatic macrophyte species were grouped together *a priori* into algae and macrophyte groups and FPOM and VFPOM were grouped together as organic matter by *a posteriori* aggregation. Moss was excluded as a potential food source because its ^{13}C value was too depleted compared to other sources to be a plausible food item, and there is little evidence in the literature of invertebrate species found in my study area consuming moss. Likewise, terrestrial vegetation was not included because its ^{15}N value was not enriched enough to be a plausible food source (Figure 2-2a). CPOM was not included as a potential food source because most of its components were coarse enough to identify and place in another category, e.g., moss or macrophytes.

Organic matter was the only food source that had a tightly constrained contribution to invertebrate diet. The mean organic matter contribution for all consumer invertebrates combined was 85% (1st percentile= 73%, 99th percentile= 94%, Figure 2-3). Since organic matter is a compilation of primary producers, I used IsoSource to identify important components of FPOM and VFPOM. *A* *posteriori* aggregation showed that both terrestrial and aquatic sources contributed to the make up of organic matter. Terrestrial sources contributed a mean of 54% (1st percentile= 44%, 99th percentile= 72%), and aquatic sources contributed a mean of 46% (1st percentile= 28%, 99th percentile= 56%) toward organic matter.

Analysis of fish diets was constrained to the 5 most common prey items found in stomach content samples and was the same for all fish species: *Hyalella azteca, Baetis tricaudatus,* Orthocladiinae (dominant genera were *Pagastia, Dicrotendipes, Cricotopus/ Orthocladius, Trtenia, Tribelos, Psectrocladius, Prodiamesa,* and *Cardiocladius*)*, Simulium,* and NZMS (Table 2-2). However, the 5 most common prey items were not all statistically distinct in their isotope signatures, a requirement of IsoSource. In pairwise comparisons, *Baetis tricaudatus* isotope signatures were not significantly different from *Hyalella azteca* ($F = 2.41$, $p = 0.1273$) or *Simulium* ($F = 2.74$, $p = 0.1045$). In addition, *Hyalella azteca* were not significantly different from NZMS ($F = 3.71$, $p = 0.0598$). These similarities limit the usefulness of IsoSource, so I relied on stomach content data to determine fish diets. Similarly, predator invertebrate diets included consumer invertebrates whose isotope signatures were not statistically different from each other, so IsoSource could not be used to determine their diet.

Since 2001, when NZMS were first discovered in the study area, the percentage of fish having NZMS in their stomachs increased steadily for all species except sculpin (Figure 2-4; Table 2-6). In 2001, NZMS were only found in brown trout stomachs (8%). New Zealand mud snails were detected in rainbow trout in 2002 and in mountain whitefish in 2003. In 2005, the percentage of mottled sculpin, brown trout, rainbow trout and mountain whitefish that had NZMS in their stomach contents was 0%, 41%, 44%, and 73%, respectively. NZMS have never been observed in sculpin stomachs.

The percent of NZMS found in stomach contents of brown trout with at least 1 NZMS differed significantly among years, ranging from 2.75% in 2003 to 38.86% in 2002 ($F = 5.15$, $p = 0.0012$, yearly n ranged from 43 to 62; Figure 2-5, Table 2-6). The percent of NZMS found in stomach contents of rainbow trout (with at least 1 NZMS) and mountain whitefish (with at least 1 NZMS) did not differ significantly among years. The percent of NZMS found in rainbow trout stomachs ranged from 1.5% in 2003 to 22.0% in 2002 ($F = 1.38$, $p = 0.2759$, yearly n ranged from 35 to 45). The percent of NZMS found in mountain whitefish stomachs ranged from 0.5% in 2003 to 2.11% in 2005 ($F = 0.11$, $p = 0.7536$, yearly n ranged from 3 to 11).

Bioenergetics

Based on data collected in the study area, beginning average weights for age 1 fish in 2004 were 171 g (± 12.96 SE) for brown trout and 192 g (± 7.20 SE) for rainbow trout. Ending average weights for age 2 fish in 2005 were 497 g (± 7.82 SE) for brown trout and 323 g (± 6.31 SE) for rainbow trout. The modeled p-value (proportion of maximum consumption) from bioenergetic simulations, for actual fish diet with high and low NZMS indigestibility was 0.463 and 0.455 for brown trout, respectively, and 0.270 and 0.269 for rainbow trout, respectively.

Modeled p-values were applied to 365-day bioenergetic simulations with varying proportions of NZMS in fish diet. For brown trout, simulated weight change ranged from a weight gain of 404 g with no NZMS in their diets to a mean loss of -60 g for a diet consisting of 100% NZMS (-87 g for high indigestibility and -45 g for low indigestibility; Figure 2-6a). For rainbow trout, simulated weight change ranged from a 141 g weight gain with no NZMS in their diets to a mean loss of -136 g for a diet consisting of 100% NZMS (-148 g for high indigestibility and -123 g for low indigestibility; Figure 2-6b).

For brown trout, RW before NZMS detection in the study area was 0.95 (± 0.02 SE). If their simulated diet contained no NZMS, their RW was 1.12 and if their simulated diet consisted of 100% NZMS their mean RW was 0.21 (0.17 for high indigestibility and 0.25 for low indigestibility; Figure 2-7a). For rainbow trout, RW before NZMS detection in the study area was 0.91 (± 0.01 SE). If their simulated diet contained no NZMS, their RW was 0.92 and if their simulated diet consisted of 100% NZMS their mean RW of 0.15 (0.12 for high digestibility and 0.19 for low indigestibility; Figure 2-7b). This equates to a mean decrease in RW of 0.08, 0.40 and 0.74 for brown trout and 0.24, 0.49, and 0.76 for rainbow trout if their diets consisted of 20, 50 or 100% NZMS, respectively.

Bioenergetic simulations showed that an increase in NZMS consumption resulted in lower growth and eventual weight loss (Figure 2-6). When NZMS comprised between 71% and 81% of brown trout diet, they did not gain weight over the duration of the simulation, and when diet consisted of more than 81% NZMS, brown trout lost weight. This threshold was much lower for rainbow trout;

a diet of 42% NZMS caused them to begin losing weight over the 365 day simulation.

A similar trend was seen with RW comparisons. RW decreased rapidly as NZMS were incorporated into fish diet. An RW of 0.8 is the lower threshold indicating management action may be necessary to improve fish condition (Wright 2000). Brown trout crossed this threshold when between 20% and 30% of their simulated diet was NZMS (Figure 2-7). Rainbow trout crossed this threshold when between 10% and 20% of their diet was NZMS.

Discussion

New Zealand mud snails are affecting the Green River food webs via two primary mechanisms: 1) sharing similar food resources with native invertebrates, and 2) providing poor nourishment to fish, the top trophic level. It is too early to predict how detrimental these effects may be. Only monitoring and assessment will determine if the NZMS eventually dominates the native biota as has happened in Polecat Creek (Hall et al. 2003).

As previously stated, the NZMS has several characteristics that make it a successful invader, but in the Green River, the invasion has been facilitated by a habitat prone to invasion. The Green River, below Flaming Gorge Dam, possesses several features making it susceptible: 1) low native diversity (many of the original aquatic invertebrates were extirpated by early dam operations; Vinson 2001), 2) absence of successful predators, and 3) it is anthropogenically disturbed. Anthropogenic disturbance is perhaps the most important; habitats that have shown severe, large invasion effects are often in human altered environments (Lodge 1993).

Food Web Analysis

Invertebrate Diet Overlap

Organic matter (FPOM+CPOM) was the primary food source of consumer invertebrates and was a mixture of primary producers and detritus. Natural history suggests that substantial diet overlap between *Baetis, Hyalella, Simulium,* NZMS, and Orthocladiinae is atypical. For instance, *Simulium* is a filtering blackfly, suggesting that their food source should only be suspended FPOM. *Baetis* mayflies and Orthocladiinae midges are collector-gathers, so their food source should be settled detritus and benthic algae. *Hyalella* and NZMS are omnivorous and readily eat detritus and biofilm alike (Haynes and Taylor 1984, Pennak 1989). Hence, although isotope signatures show similar food sources, it is possible that these invertebrates feed in separate habitat niches, preventing competition. However, my results provide evidence of the potential for competition, but without a measure of food availability, limitation, and habitat preferences, competition cannot be detected (Schmitt 1996). Because the presence of NZMS in the Green River is still early (6 years), eventual competition and reduction in native invertebrate assemblages may be observed, as in Yellowstone National Park (Kerans et al. 2005).

Fish Consumption of NZMS

The percentage of each fish species that consumed at least one NZMS has steadily increased since 2001 (Figure 2-4). This is likely because NZMS are a relatively new invader to the study area and are still expanding the range of habitats it occupies (Holomuzki and Biggs 1999). If fish showed no dietary preferences and therefore consumed invertebrates in proportion to their availability, it would follow that as NZMS prevalence increases, fish consumption would also increase. However, of the fish that ate NZMS, the proportion of their stomach contents that were NZMS did not steadily increase (Figure 2-5). In other words, even as more fish consumed NZMS, NZMS did not increase as a proportion of individual fish's diet. This suggests that the NZMS is not a preferred food source by all fish. While some fish may actively consume NZMS, it appears that many of them only incidentally consume NZMS or may be actively avoiding them.

In 2002 and 2004 brown trout had relatively high NZMS consumption rates, possibly due to incidentally preying on NZMS in aquatic macrophyte beds. In 2003 their consumption was low for all species. These trends may be indicative of yearly and seasonal trends in NZMS abundance observed in other systems (Heywood and Edwards 1962, Dorgelo 1987, Talbot and Ward 1987, Zaranko et al. 1997). NZMS yearly abundance declines have been associated with a decline in aquatic macrophytes (Heywood and Edwards 1962) and low winter temperatures (Dahl and Winther 1993). Water temperature of the Green river downstream from Flaming Gorge Dam is suitable for NZMS year-round;

however, there are substantial seasonal and yearly fluctuations in aquatic macrophyte densities. Therefore, it is possible that as aquatic macrophytes densities fluctuate, NZMS densities will also change and fish consumption of NZMS will adjust accordingly. The aquatic macrophytes fluctuations would likely not affect native invertebrates because they are within their natural range of conditions.

Bioenergetics

Bioenergetic simulations showed that as consumption of NZMS increased, fish growth decreased, indicating that diets high in NZMS do not meet energy requirements of fish. Both brown and rainbow trout RW's dropped below 0.8, which is low enough to indicate unhealthy populations, with diets of 30% NZMS or more. In Polecat Creek, WY, NZMS comprised 95% of invertebrate biomass (Hall et al. 2003). When connecting Hall et al. (2003) to bioenergetic simulations of fish diet containing 95% NZMS, observed NZMS densities in Polecat Creek are high enough to detrimentally affect fish populations.

Within the study area, bi-annual electroshocking and scale analysis showed that salmonids gained the majority of their weight during the spring and summer (Schneidervin 2006). There were only small amounts of growth in the winter, principally due to lower water temperatures. In 2000, these data showed that brown trout gained 78% and rainbow trout gained 63% of their yearly weight between April and September (Schneidervin 2006). Bioenergetic simulations showed similar trends; brown trout gained 63% of their yearly weight from April to September and rainbow trout gained 61% during the same time period.

Fish must balance the amount of energy allotted for reproduction, growth, and metabolism (Williams 1966). Fish with a higher RW tend to have higher fitness, which indicates additional energy is available beyond that required for growth and metabolism. This additional energy increases the ability of a fish to reproduce (Moyle and Cech 2000; Bagenal 1969). Conversely, if a fish cannot sustain healthy growth and metabolic rates, fitness will decrease. Although bioenergetic simulations showed it was possible for fish in my study area to gain weight when consuming NZMS, they gained less weight than if no NZMS were consumed. The failure of fish to reach potential ending weights (0% NZMS in diet) indicates that potential fitness levels were not achieved.

The hard shell and operculum that NZMS possess provide a good defense against digestion by fish. Not surprisingly, fish gain relatively little energy from consuming NZMS when compared to consuming other molluscs (McCarter 1986). Vinson and Baker (2005) observed live NZMS after being passed through a rainbow trout digestive system. Low digestibility of NZMS combined with bioenergetic simulations suggests that fish fitness decreases as NZMS consumption increases.

Conclusion

NZMS are interacting in the food web of the Green River downstream from Flaming Gorge Dam. Within their trophic level, NZMS consumed similar food resources as native consumer invertebrates. All species of fish besides mottled sculpin consumed NZMS. Since 2001, NZMS have become more prevalent in the study area and are being increasingly incorporated into fish diet. Potential competition with native invertebrates combined with negative effects on fish growth suggests the NZMS are likely to negatively affect the aquatic ecosystem of the Green River downstream from Flaming Gorge Dam.

At least 88 invasive fresh water molluscs are established in the US (OTA 1993). Both NZMS and Zebra mussels are transported by human recreationists and both may substantially alter aquatic ecosystems. Concerns surrounding the zebra mussel are related to their effect on native invertebrates and biofouling and its subsequent economic costs. The potentially high densities of NZMS combined with parthenogenesis, can lead to competitive exclusion, which is cause for serious biological concern. Because of their small body size, the spread of NZMS can easily go undetected, allowing for quick spread over vast areas and biological disruption in unmonitored areas. The NZMS is not expected to have as large of an economic impact, but their damage to aquatic habitats could be severe.

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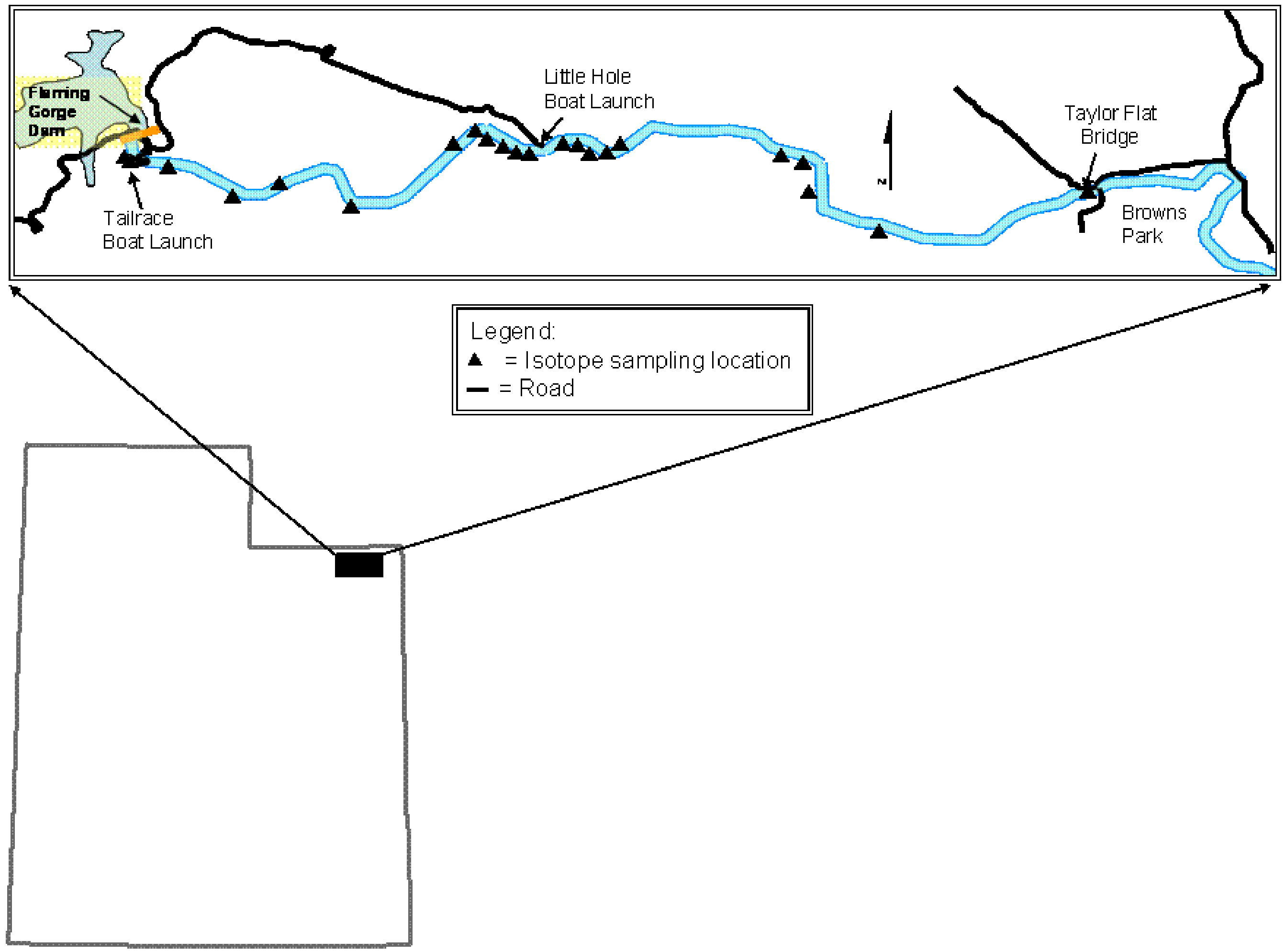

Figure 2-1. The study area spanned 26 km from Flaming Gorge Dam to Taylor Flat bridge in Brown's Park National Wildlife Refuge, UT. Twenty-five locations were sampled for isotope analysis in 2005.

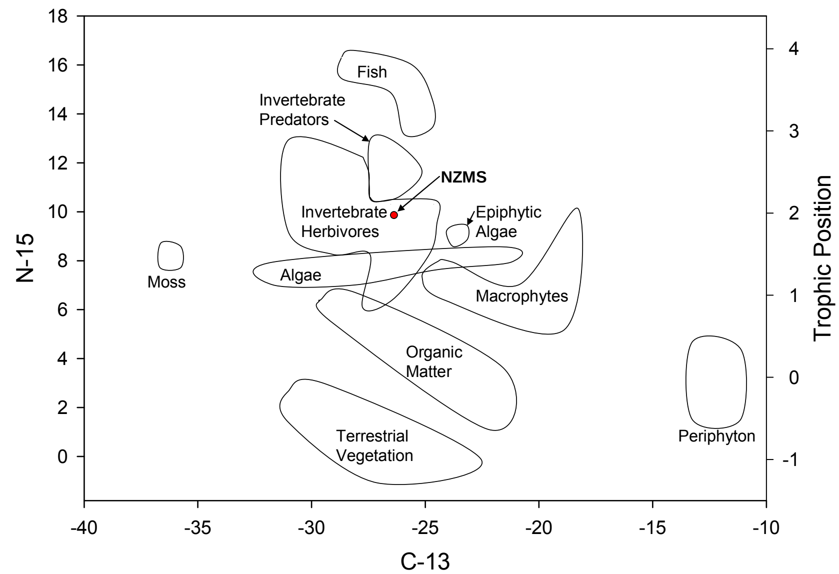

Figure 2-2a. Biplot of ^{13}C and ^{15}N isotope values that represent the food web of the Green river downstream from Flaming Gorge Dam. Samples were collected during summer 2005

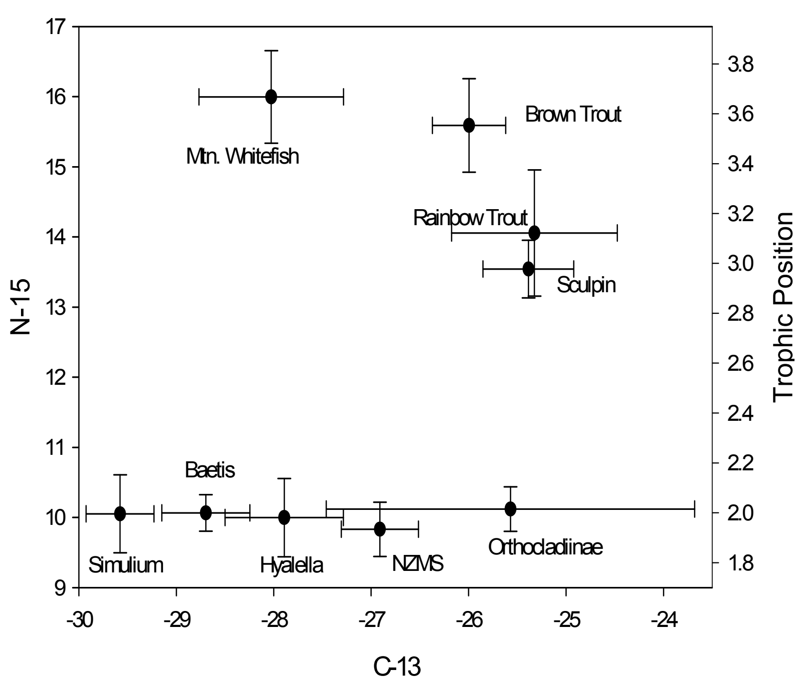

Figure 2-2b. Biplot illustrating the isotope values for fish and their five most common prey items. Sample sizes are shown in Table 2-5. Bars are 95% confidence intervals.

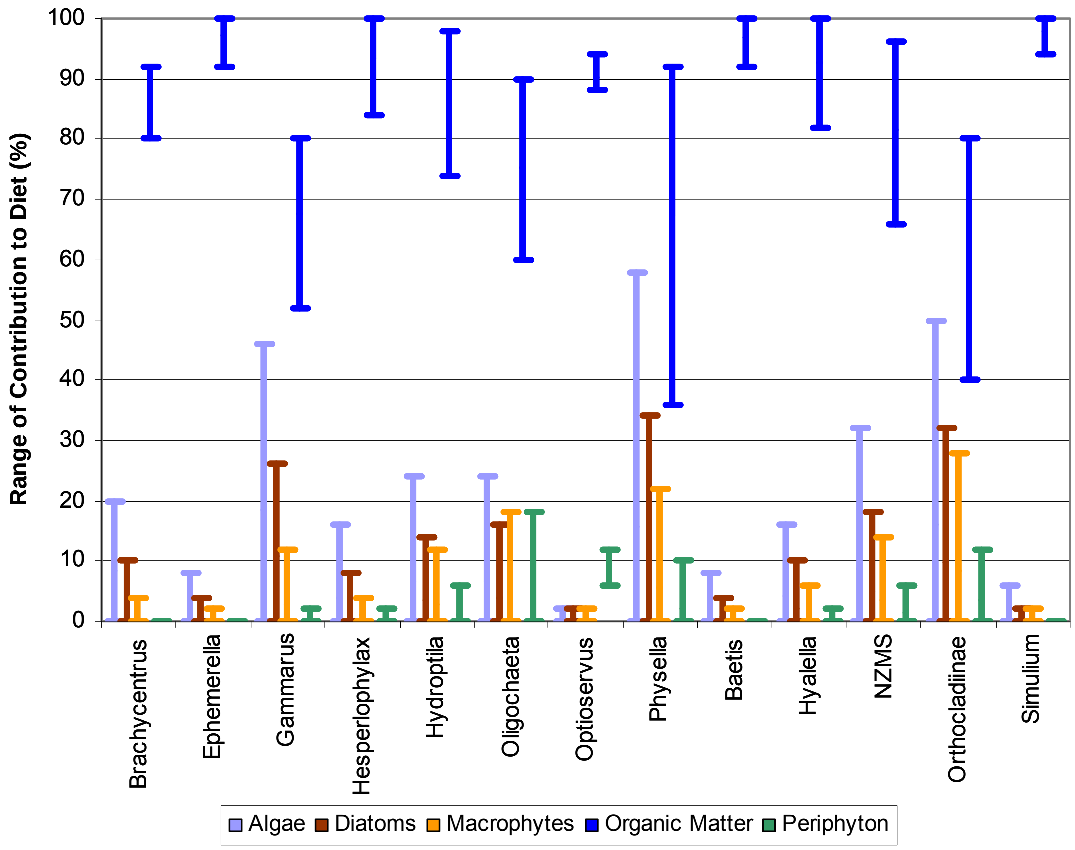

Figure 2-3. Herbivorous invertebrate diet based Isource results using ^{13}C and ^{15}N isotope signatures. Bars are the 1-99th percentile that represents the range of possible contributions for each food source. For all herbivorous invertebrates, organic matter was the most important food source. Samples were collected in summer 2005 from the Green River downstream from Flaming Gorge Dam

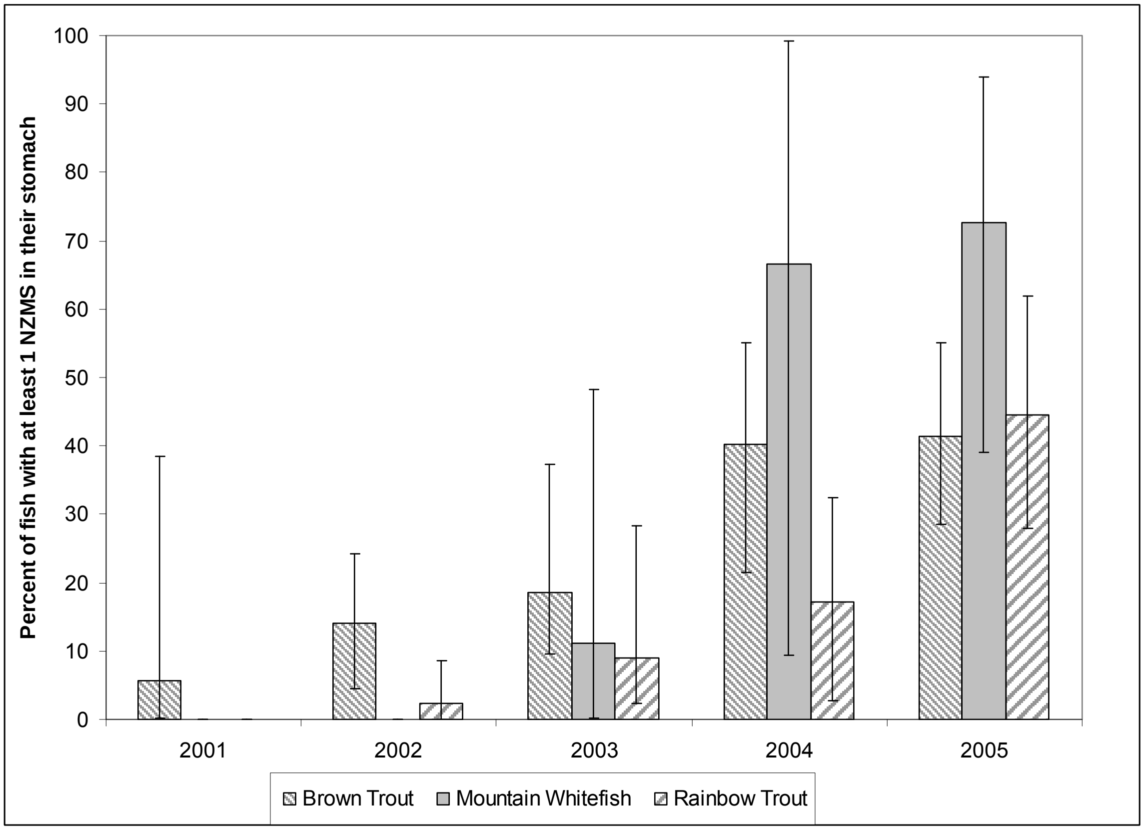

Figure 2-4. The percentage of fish stomachs that contained at least one NZMS. NZMS were first detected in brown trout in 2001 and no sampled sculpin stomach to date contained NZMS. These percentages include fish with no invertebrates in their stomachs. Bars represent 95% confidence intervals. Sample sizes are provided in Table 2-6. Samples were collected in September from 2001-2005 on the Green River downstream from Flaming Gorge Dam.

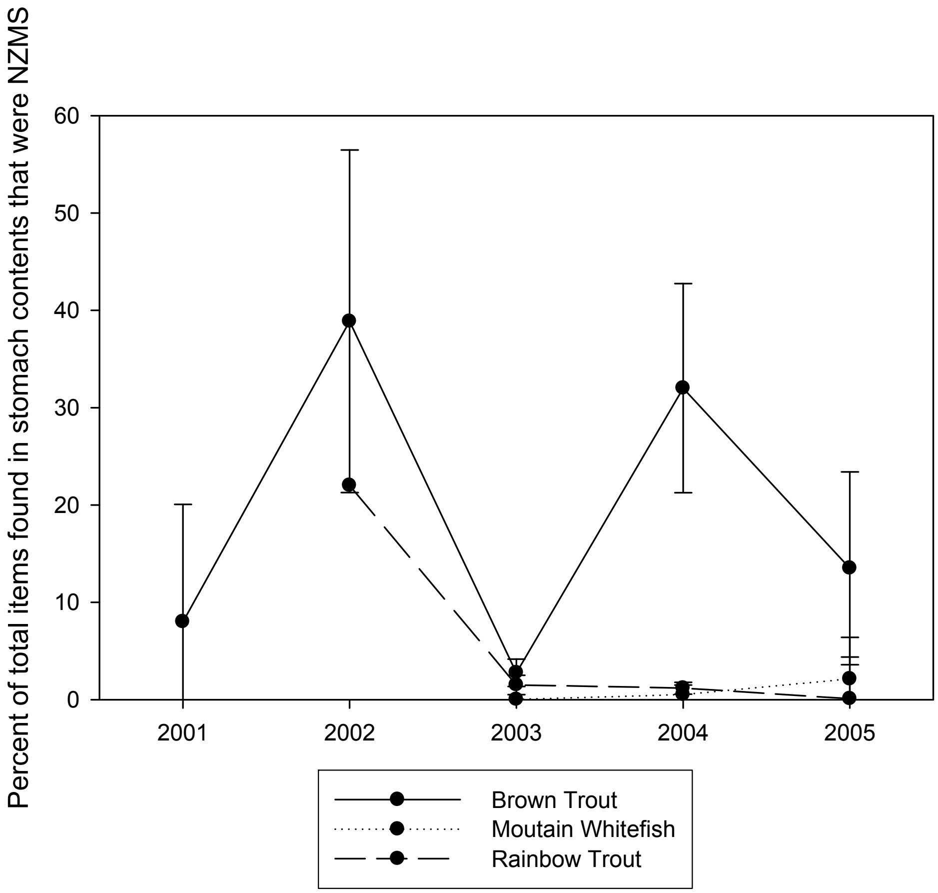

Figure 2-5. The percentage of total diet items by number that were NZMS and associated 95% confidence intervals. Error bars are not present when n=1. Sample sizes are provided in Table 2-6. Fish were included only if they consumed at least one NZMS. Samples were collected in September from 2001-2005 on the Green River downstream from Flaming Gorge Dam.

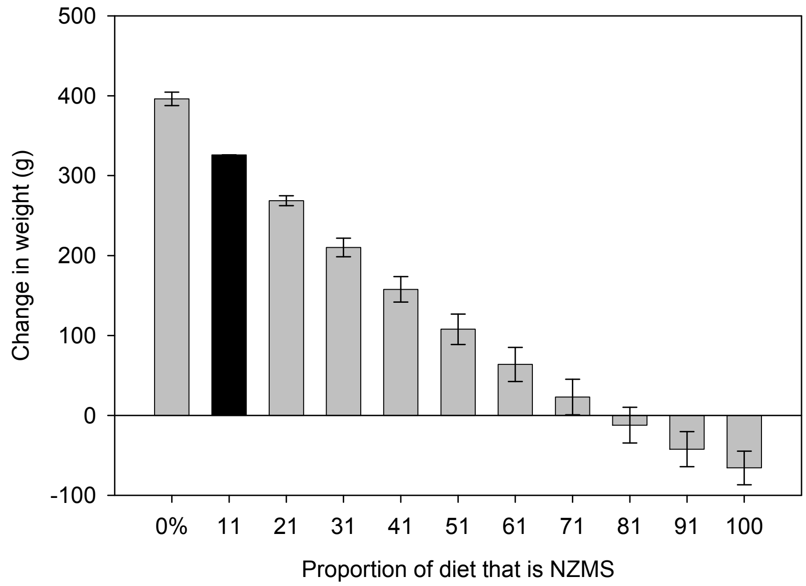

Figure 2-6a. Estimated change in weight for brown trout based on 365 day bioenergetic simulations. Zero on the Y-axis equals fish weight on day one of the simulation. Bars are high(+) and low(-) ranges of digestibility. The black bar represents actual diet.

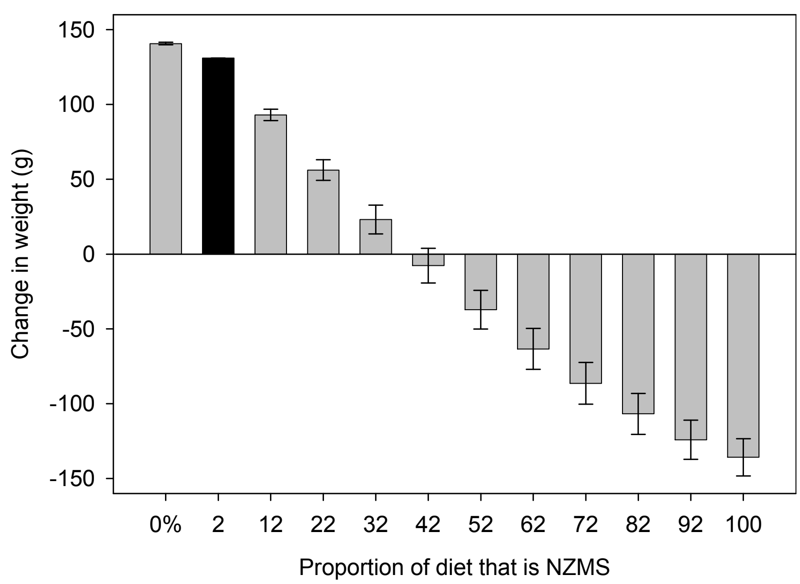

Figure 2-6b. Estimated change in weight for rainbow trout based on 365 day bioenergetic simulations. Zero on the Y-axis equals fish weight on day one of the simulation. Bars are high(+) and low(-) ranges of digestibility. The black bar represents actual diet.

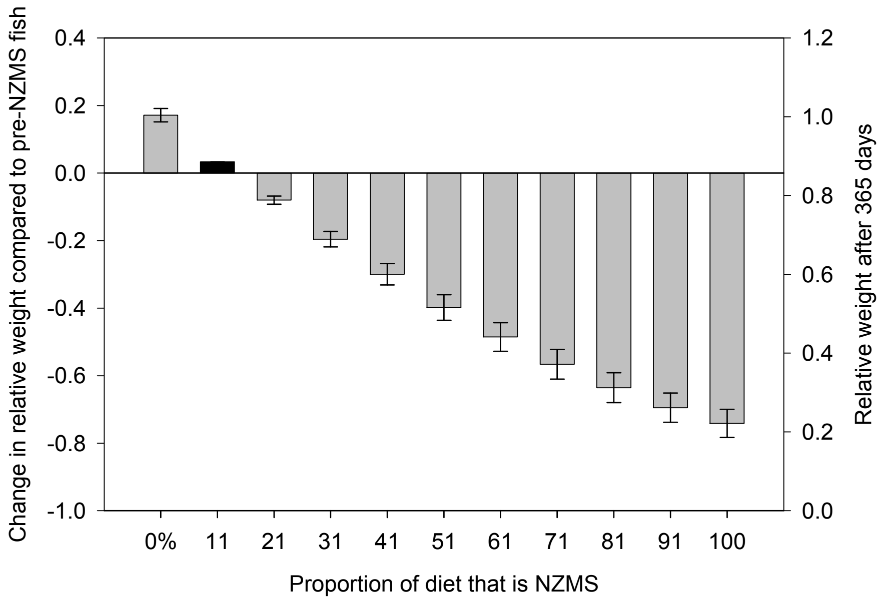

Figure 2-7a. Estimated change in relative weight (RW) based on 365 day bioenergetic simulations for age 2 brown trout. Zero on the left Y-axis represents RW from 2000 (pre-NZMS fish). Bars are high(+) and low(-) ranges of digestibility. The black bar represents actual RW in 2005.

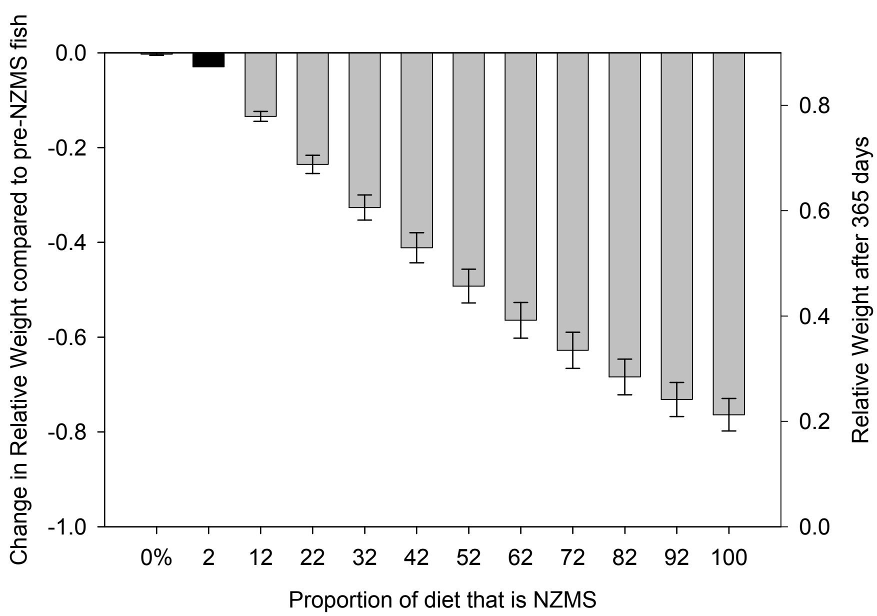

Figure 2-7b. Estimated change in relative weight (RW) based on 365 day bioenergetic simulations for age 2 rainbow trout. Zero on the left Y-axis represents RW from 2000 (pre-NZMS fish). Bars are high(+) and low(-) ranges of digestibility. The black bar represents actual RW in 2005.

Table 2-1. List of invertebrates where more than 100 individuals were collected in the study area since 1994 (Vinson et al. 2006).

Class	Order	Family	Subfamily	Genus	species	Number collected
Malacostraca	Amphipoda	Hyalellidae		*Hyalella*	*azteca*	297659
Branchiopoda	Diplostraca, Cladocera					67771
Insecta	Diptera	Chironomidae	Orthocladiinae			60056
Maxillopoda	Calanoida					57809
Insecta	Ephemeroptera	Baetidae		*Baetis*	*tricaudatus*	31457
Insecta	Diptera	Simuliidae		*Simulium*		16677
Insecta	Coleoptera	Elmidae		*Optioservus*		10108
Insecta	Trichoptera	Hydroptilidae		*Hydroptila*		4862
Arachnida	Trombidiformes					4784
Malacostraca	Amphipoda	Gammaridae		*Gammarus*	*lacustris*	4361
Phylum: Nemata						4292
Insecta	Ephemeroptera	Ephemerellidae		*Ephemerella*	*inermis*	3697
Oligochaeta	Haplotaxida	Tubificidae				2850
Gastropoda	Neotaenioglossa	Hydrobiidae		*Potamopyrgus*	*antipodarum*	2634
Insecta	Trichoptera	Hydropsychidae		*Hydropsyche*		1860
Gastropoda	Basommatophora	Physidae		*Physella*		1588
Branchiopoda	Diplostraca	Daphniidae		*Daphnia*		1572
Insecta	Trichoptera	Brachycentridae		*Micrasema*		865
Insecta	Ephemeroptera	Heptageniidae		*Rhithrogena*		845
Insecta	Diptera	Chironomidae	Tanypodinae			720
Insecta	Lepidoptera	Pyralidae		*Petrophila*		708
Turbellaria	Tricladida	Planariidae				665
Insecta	Plecoptera	Perlodidae		*Isoperla*		367
Insecta	Ephemeroptera	Heptageniidae		*Heptagenia*		323
Insecta	Diptera	Empididae		*Hemerodromia*		304
Bivalvia	Veneroida	Pisidiidae		*Pisidium*		274
Insecta	Odonata	Coenagrionidae				255
Insecta	Trichoptera	Brachycentridae		*Brachycentrus*		241
Insecta	Trichoptera	Limnephilidae		*Hesperophylax*		166

Table 2-2. Trout stomach content results for 2005 from the Green River downstream from Flaming Gorge Dam. Table shows the proportion each prey item comprised of total stomach contents. The five most common prey items accounted for >90% of total diet.

	Fish		
Prey item	**Brown trout (%)**	**Rainbow trout (%)**	**Mountain whitefish (%)**
Baetis	26	34	15
Hyalella azteca	48	41	45
NZMS	11	2	1
Orthocladiinae	11	11	26
Simulium	2	3	13
Total Proportion of Diet	98	91	100

Table 2-3. Invertebrate prey energy density values used in bioenergetic simulations for brown trout and rainbow trout (Dieterman et. al. 2004; Hanson et al. 1997; Ryan 1982). Although NZMS energy was 4500 Joules/gram, percent indigestibility was manipulated to simulate the energy fish were likely to gain from NZMS.

Prey Item	Energy Density (J/g)
Baetis	4705
Hyalella azteca	4429
NZMS	4500
Orthocladiinae	2562
Simulium	2562

Table 2-4. Estimated seasonality profile for NZMS in the study area. In bioenergetic simulations, proportions of NZMS in fish diet were multiplied by these percentages to obtain the seasonal percentage of NZMS available for fish consumption.

Date	**Simulation day**	**Percent of maximum NZMS availability**
1 September	1	100
31 October	60	100
27 February	180	20
29 March	210	0
29 April	240	50
29 May	270	100
31 August	365	100

Table 2-5. Mean carbon and nitrogen δ values, Trophic Position (TP), standard errors (SE) and sample size (n) for isotope collections in summer 2005 from the study area.

			$\delta^{15}N/^{14}N$		$\delta^{13}C/^{12}C$		TP	
	Taxa/size range	**n**	**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
Terrestrial Plants	*Juniperus*	1	0.64	.	-23.36	.	-0.75	.
	Pinus ponderosa	5	0.71	0.4	-25.53	0.6	-0.73	0.12
	Chrysothamnus nauseosus	1	0.11	.	-27.29	.	-0.91	.
	Acer negundo	4	2.09	0.5	-28.13	0.3	-0.33	0.15
	Salix exigua	3	2.63	0.4	-29.97	0.5	-0.17	0.11
Aquatic Primary Producers	*Cladophora glomerata*	5	7.85	0.5	-28.33	2.9	1.37	0.15
	Spirogyra	4	8.37	0.2	-22.02	0.7	1.53	0.06
	Chara	3	6.55	1	-19.94	0.7	0.99	0.29
	Potamogen crispus	5	7.87	0.9	-24.02	2.4	1.37	0.26
	Ranunculus	5	9.41	0.4	-18.81	0.5	1.83	0.12
	Amblystegium riparium (Moss)	5	8.36	0.3	-36.16	0.3	1.52	0.09
	Diatoms	10	9.31	0.5	-23.7	0.6	1.8	0.16
	Periphyton	12	3.12	1.1	-12.55	1.2	-0.02	0.29
Organic Matter	CPOM >1mm	2	3.5	3.2	-22.66	2.2	0.09	0.93
	FPOM .25mm-1mm	3	5.7	0.7	-26.76	0.2	0.74	0.18
	VFPOM 53μm-.25mm	4	6.45	0.5	-28.14	0.5	0.96	0.15
Invertebrate Consumers (Herbivores)	*Simulium*	10	10.05	0.3	-29.58	0.2	2.02	0.08
	Brachycentrus	8	12.07	0.3	-29.21	0.6	2.61	0.09
	Tubificidae	9	8.67	0.5	-25.14	0.3	1.61	0.14
	Ephemerella	10	8.9	0.3	-29.01	0.5	1.68	0.08
	Physella	10	9.99	0.5	-26.34	0.6	2	0.14
	Hyalella	11	10	0.3	-27.89	0.3	2	0.08
	Baetis tricaudatus	12	10.06	0.1	-28.7	0.2	2.02	0.03
	Orthocladiinae	8	10.12	0.2	-25.57	0.9	2.04	0.04
	Gammarus lacustrus	10	11.82	0.3	-27.78	0.4	2.54	0.08
	Hydroptila	4	9.14	0.2	-27.43	2.2	1.75	0.05
	Optioservus	10	6.98	0.2	-26.95	0.2	1.11	0.04
	Potamopyrgus antipodarum	13	9.83	0.2	-26.91	0.2	1.95	0.05
	Hesperophylax	12	10.31	0.5	-28.24	0.7	2.09	0.15
	Oecetis	2	10.17	0.4	-26.38	0.2	2.05	0.11
	Sigara	5	11.68	0.1	-25.83	0.6	2.5	0.01
Invertebrate Predators	Muscidae	8	11.59	0.5	-26.67	0.7	2.47	0.15
	Coenagridae	13	11.89	0.2	-25.67	0.2	2.56	0.06
	Planariida (Flatworms)	10	12.77	0.1	-26.8	0.2	2.82	0.04
Fish	Mottled sculpin *(Cottus bairdus)*	19	13.54	0.2	-25.39	0.2	3.04	0.06
	Rainbow trout *(Oncorhynchus mykiss)*	26	14.06	0.5	-25.32	0.4	3.2	0.13
	Brown trout *(Salmon trutta)*	41	15.59	0.3	-26	0.2	3.65	0.09
	Mountain whitefish *(Prosopium williamsoni)*	11	16	0.3	-28.03	0.4	3.77	0.09

Table 2-6. Percent of fish that consumed at least one NZMS, percent of total diet items that were NZMS (only including fish with at least 1 NZMS in stomach), standard error for the percent of total diet items that were NZMS and number of observations (n). Data is illustrated in figures 2-4 and 2-5. Samples are from the Green River downstream from Flaming Gorge Dam.

	Year	***n***	**Fish that consumed at least 1 NZMS (%)**	**Total diet items that were NZMS (mean %)**	**SE (%)**
	2001	53	5.7	8	6.03
	2002	50	14	38.86	8.8
Brown Trout	2003	43	18.6	2.75	0.7
	2004	62	40.3	32	5.38
	2005	58	41.4	13.49	4.95
	2001	6	0	0	.
	2002	4	0	0	.
Mountain Whitefish	2003	9	11.11	0.01	.
	2004	3	66.7	0.5	0.5
	2005	11	72.7	2.11	1.13
	2001	36	0	0	.
	2002	43	2.3	22	.
Rainbow Trout	2003	45	8.9	1.5	0.5
	2004	35	17.1	1.17	0.31
	2005	36	44.4	0.07	3.17

CHAPTER III.

USING DISPERSAL VECTORS TO PREDICT NEW ZEALAND MUD SNAIL DISTRIBUTION

Abstract

Species distribution models that evaluate long distance dispersal are useful for assessing the risk of invasion by non-native species. New Zealand mud snails (*Potamopyrgus antipodarum*, NZMS) possess numerous traits making them well suited for long distance dispersal, including parthenogenesis, persisting in a wide variety of aquatic habitats, and the ability to live out of water for several weeks. I used the ecological niche factor analysis and GIS to predict potential NZMS distribution using predictor variables related to NZMS dispersal vectors and presence-only data of NZMS invasions. Three factors from the factor analysis described NZMS distribution. Sites likely to be invaded by NZMS were relatively close to population centers and blue ribbon fisheries, had a relatively low elevation and a stream order greater than two. The relationship between NZMS distribution and distance to cities as well as distance to a blue ribbon fishery supports the idea that fisherman are frequently transporting NZMS to new locations. In this study, I considered a first-stage model to identify sites to which NZMS are likely to be transported; I recommend continuing the project into the second-stage including measurement of biological factors affecting NZMS establishment and local spreading as well as a field validation of this first-stage model.

Introduction

The New Zealand mud snail (*Potamopyrgus antipodarum* Gastropoda: Hydrobiidae, NZMS) is a small (<5 mm) invasive snail native to New Zealand. Since the mid 1800s the snail has spread from New Zealand to freshwater environments throughout the world, including Australia, Europe, Asia, and North America. The snail was first discovered in the United States in 1987 in the Snake River near Hagerman, Idaho (Bowler 1991).

NZMS have several morphological and behavioral traits that make them well-suited for invasions, including high growth rates, parthenogenesis, viviparity, and lack of parental care (Dybdahl and Lively 1995; Lodge 1993). They also possess an operculum, which allows them to live for several weeks out of the water if kept moist and not exposed to excessive heat. NZMS are able to survive in a variety of aquatic habitats across a wide range of temperatures, substrates, and salinities (Cogerino et al. 1995; Zaranko et al. 1997; Richards et al. 2001; Hall et al. 2003). It is thought that recreationists, fish and waterfowl transport NZMS within and between water bodies (Lassen 1975; Bondesen and Kaiser 1949; Haynes et al. 1985). NZMS spread has been documented since 1995. Between 1995 and 1997, the number of new occurrences increased at a rate of approximately 79%. Since 1997 the rate of spread has slowed to between 2 and 19% per year (Figure 3-1), potentially due to increased survey efforts. The distance between new sites has increased substantially (Figure 3-2). The distribution of NZMS is important to resource managers as NZMS may outcompete other organisms, threaten native biodiversity and alter ecosystem function (Hall et al. 2003; Kerans et al. 2005).

Geographic information systems (GIS) and statistical tools make modeling species distribution efficient and cost-effective, because information can be projected over a larger study area than can be adequately surveyed. Species distribution models have been used for conserving vital habitat, evaluating species' niche requirements, and assessing the risk of invasion by non-native species (Scott et al. 2002). A variety of invasive species including zooplankton (Havel et al. 2002), crustaceans (MacIsaac et al. 2004), molluscs (Bossenbroek et al. 2001; Johnson et al. 2001; Neary and Leach 1992) cyprinid fishes (Chen et al. 2007), and numerous plant species (e.g., *Lygodium spp, Bromus spp., Poa spp, Lantana spp.*; Underwood et al. 2004, Volin et al. 2004, Goolsby 2004, Robertson et al. 2004) have been modeled to identify sites likely to be invaded as well as the vectors most responsible for their spread. In particular, the distribution of zebra mussels (*Dreissena polymorpha*), which has caused severe economic and environmental consequences, has been successfully modeled using recreational boaters as the primary dispersal vector (Bossenbroek, et al. 2001; Buchan and Padilla 1999; Schneider et al. 1998; Padilla et al. 1996; Johnson et al. 2001; Neary and Leach 1992). In this study, I modeled NZMS distribution using recreational fisherman as the primary dispersal mechanism to predict likely invasion sites.

Numerous predictive models have been used to evaluate species distribution depending on study objectives, assumptions and available data

(Guisan and Zimmerman 2000; Elith et al. 2006; Franklin 1995). These models predict site suitability or probability of species occurrence spatially using presence/absence data. When absence data is not available, either presence-only data is used or pseudo-absence data is generated.

Presence-only data is often the only data available for rare, endangered, or invasive species. When compared to pseudo-absence models, presence-only models tend to be biased towards higher site suitability ratings (Hirzel et al. 2001; Brotons et al. 2004; Engler et al. 2004; Zaniewski et al. 2002). This can be an advantage, to ensure potential suitable habitats are not discounted or overlooked, when considering a species that is still expanding its range (Hirzel et al. 2001), such as the NZMS.

Ecological niche factor analysis (ENFA) is a presence-only modeling technique that uses an environmental envelope to model site suitability (Guisan and Zimmerman 2000). Environmental envelopes compare the attributes of sites occupied by the species to the attributes of the entire study area (Walter and Cocks 1991). The ENFA incorporates the environmental envelope when it uses a factor analysis to determine: 1) the marginality of the species (the mean value for each predictor variable in areas occupied by the species compared to the mean value for each predictor variable in the study area, e.g., the mean elevation the species occupies may be similar to mean elevation in the entire study area or the species may only occupy extreme high or low elevations) and 2) the specialization of the species (the range of values for each predictor variable in areas occupied by the species compared to the range of values for each predictor variable in the study area (Hirzel et al. 2002). Results of the ENFA are applied in BIOMAPPER. BIOMAPPER is a user friendly interface that combines spatial data and multivariate statistics (Hirzel et. al. 2002).

In this study, I modeled site suitability using presence-only data in the ENFA to identify streams in the western U.S. susceptible to invasion by NZMS due to transportation by fishermen. There are four basic stages in a species invasion: transportation, release, establishment, and local spread (Kolar and Lodge 2001). Obstacles must be overcome in each stage for invasions to be successful, including ineffective dispersal vectors, environmental resistance, biotic resistance, and demographic resistance (Moyle and Light 1996). I aimed to create a predictive model of NZMS spread based on its transportation and release vectors. Therefore, predictor variables used in this model were primarily based on human activities, not biological conditions affecting NZMS establishment and further spreading. This approach is likely a good one for NZMS as it has shown little habitat preference in the U.S. Invasions have been reported in all aquatic habitat types, including streams, hot springs, lakes and estuaries (New Zealand Mudsnails in the Western USA, 2006).

Study Area

The site suitability map covers streams in the states of Idaho, Montana, Utah, and Wyoming (104-117º W, 37-49º N). Although NZMS have spread throughout the western U.S., Idaho, Montana, Utah, and Wyoming are the center of invasion and include the majority of known NZMS locations. Landscape characteristics in the region range from desert to alpine with an array of land uses. Elevation ranges from 216 m (710 ft.) on the Snake River, Idaho to 4207 m (13804 ft.) on Gannett Peak, Wyoming.

Methods

Species Occurrence Data

NZMS presence-only data from 1987-2004 were obtained from an online database maintained at Montana State University (Figure 3-3; New Zealand Mudsnails in the Western USA, 2006). These data were either collected by biologists with mollusc identification expertise or the species identification was verified before being included in the database. These data were collected non-probabilistically and thus may have limited inference power; however, non-probabilistic sampling is common and acceptable for surveying species of low detectability (Schreuder et al. 2001). This analysis included 1327 NZMS occurrence records.

Ecogeographical Variables

The following parameters were used as ecogeographical variables (EGV's; predictor variables) of NZMS spread: distance to blue ribbon fishing areas, distance to nearest population center, population density (people/km^2), distance to nearest road, distance to a dam greater than 15.24 m. tall, stream order and elevation (Table 3-1). Distance to blue ribbon fisheries, distance to population center, population density and distance to a road represented the likelihood that a fisherman or recreationist would visit the site, thus increasing the possibility of transporting NZMS. Distance to a dam, stream order and elevation represented both the likelihood of a site being visited and biological conditions affecting the success of a NZMS invasion. Distance to dams is included because NZMS have been found in reservoir tailwater reaches, which are altered habitats left vulnerable to invasive species (New Zealand Mudsnails in the Western USA, 2006). Roads include those paved and unpaved, as defined by the census bureau metadata. Blue ribbon trout streams were defined by a combination of their fish abundance, fishing pressure, esthetics and accessibility based on state agency classifications. Data used to calculate these parameters were obtained from the U.S. Census Bureau and state government web pages (Table 3-1). All calculations performed on raw data to obtain the final EGV's were completed in ArcMap 9.1 (ESRI 2005). All variables were constrained to the streams in the study area and converted to 90 m raster cells before being modeled in BIOMAPPER. A cell size of 90 m was chosen based on existing data and its level of precision.

To test if additional environmental EGV's would improve model quality, I created two ENFA sub-models for the state of Idaho. The first sub-model included only the EGV's used in the original model and the second sub-model included the original EGV's plus annual precipitation and minimum and maximum annual air temperatures (Wai 2006a,b). The choice in environmental EGV's was restricted by the availability of data over the entire study area. There was relatively little difference in model quality between the two sub models (B_{cont} of

0.966 ±0.139 SD and 0.909 ±0.085 SD, respectively for the sub model with only the original EGV's and the sub-model with additional environmental EGV's). Based on the B_{cont} values, correlation matrix, and parsimony, I did not retain the additional environmental EGV's for the final model, which incorporated the entire study area.

ENFA

Ecogeographical variables used in BIOMAPPER must be quantitative and continuous. A box-cox transformation procedure was used to transform variables to a normal distribution to obtain better model predictions. Not all variables could be normalized, but normality is not an explicit assumption of the ENFA.

The ENFA creates uncorrelated factors that represent a combination of correlated EGV's. In the ENFA, the first factor is designed to explain the maximum amount of variance associated with the species marginality and generally is able to include part of the species specialization. The remaining factors explain the remaining variance associated with species specialization, which is all of the variance not explained by marginality.

When interpreting the marginality factor, any variable assigned a positive or negative value indicates that the habitat used by the species is above or below the global mean for that EGV. A higher absolute EGV value indicates that the habitat used by the species has a greater deviation from the global mean for that EGV. When interpreting the specialization factors, any variable assigned a high or low absolute value (e.g., a high absolute vale of -0.8 or 0.8 compared to a low absolute value of -0.1 or 0.1) indicates that the sites used by the species has a highly restricted or wide range for that EGV, respectively. Only the absolute value for each EGV is informative for the specialization factors.

The uncorrelated marginality and specialization factors were used to build a site suitability map. The number of factors used to create the site suitability map was selected to balance parsimony and explained variance with increasing factors. The 'broken stick' method was used as a guide to determine the appropriate number of factors used to describe NZMS distribution. To compute the site suitability map, I used the geometric mean algorithm, which makes no assumptions about the species distribution for each EGV, but does assume that the density of observations is representative of the true distribution (Hirzel and Arlettaz 2003). Site suitability for each cell on the final map is continuous, from 1 to 100, with 100 representing optimal site conditions.

The site suitability model was K-fold cross validated with four partitions. Evaluation indicators were the continuous Boyce index (B_{cont}) and its associated area-adjusted frequency graph. The B_{cont} is based on the Boyce index, which is an assessment of the trend in predicted to expected ratios from low site suitability to high site suitability (Boyce et al. 2002). In this model, predicted values were the number of evaluation points from the left-out partition that were within each site suitability value. Expected values were the number of evaluation points from the left-out partition that were within each site suitability value if evaluation points were randomly distributed across the study area. Boyce index values ranged from -1 to 1, with negative values indicating an incorrect model, a value of 0 indicating the model is equivalent to a random model, and positive values indicate a model consistent with the left-out k-fold presence-only data. To calculate the Boyce index, results were arbitrarily binned according to site suitability. To eliminate results based on arbitrary bin choices, the Boyce index was modified to be continuous (B_{cont}) with a bin size of 20 site suitability units with a moving window across all site suitabilities (Hirzel et al. 2006). B_{cont} values ranged from -1 to 1.

The area-adjusted frequency graph displays the predicted to expected curve as calculated by the Boyce index. Available sites were evenly binned according to their site suitability. For example, there were 4 bins at site suitabilities of 1-25, 26-50, 51-75, and 76-100. The coefficient of variation associated with the predicted to expected curve is a measure of model precision and illustrates which site suitabilities the model was better able to predict.

To further assess the relationship between site suitability and the EGV's, I calculated a separate predicted to available ratio for each EGV based on the cross validated site suitability map. Predicted sites were the number of cells in the study area having a site suitability >50 and available sites were all cells in the study area for each EGV.

To further assess the relationship between site suitability and the EGV's, I calculated a separate 'predicted' to 'available' ratio for each EGV based on the cross validated site suitability map. Predicted sites were the number of cells in the study area having a site suitability >50 and available sites were all cells in the study area for each EGV.

Results

Three factors, which explained 83% of variation, were used to calculate site suitability (Table 3-2). The first factor represented the marginality variation (17% of total variation) and 19% of the variation associated with specialization. Stream order (value of 0.53) was the most important EGV in the first factor; NZMS occurred in streams with above average stream order ($\bar{x}$ =1.88, ±1.28 SD). Closeness to dams (value of -0.45), cities with a population >100,000 people (value of -0.39), and cities with a population > 25,000 people (value of -0.37) were also important predictors. NZMS occurred in streams that were closer than average to these EGV's. The second factor explained 29% of the variation associated with specialization. Distance to cities with a population >100,000 people (value of -0.75) was the most important EGV. The high absolute value of -0.75 indicates the distribution of species occurrences was highly restricted. Elevation (value of 0.45) and distance to cities with a population > 25,000 people (value of 0.43) were also important EGV's. The third factor explained an additional 18% of the variation associated with specialization. Distance to cities with a population >25,000 people (value of -0.82) was the most important EGV. The high absolute value of -0.82 indicates that the distribution of species occurrences was highly restricted. Elevation (value of 0.33) and distance to the nearest road (value of 0.32) were also important EGV's.

The cross validated site suitability map had a B_{cont} of 0.964 (±0.036 SD), indicating a high quality model that was consistent with the jacknifed presence-only data (Figure 3-4). The area-adjusted frequency curve showed a positive relationship with site suitability when binned in 5% increments (Figure 3-5). This curve had few flat or negative slope segments, indicating a relatively strong ability to distinguish between site suitability classes (Hirzel et al. 2006). The standard deviation of the area-adjusted frequency was smaller for poor site suitability; however, the coefficient of variation showed no detectable trend (Table 3-3), thus creating an inconclusive result concerning which sites the model was better able to predict.

Although site suitability was explained by three factors, individual relationships between each EGV and sites with a suitability >50 were informative with regard to the role of fisherman in transporting NZMS (Figure 3-6). Site suitability varied consistently with elevation, stream order, distance to roads, blue ribbon trout fisheries, and large cities. Suitability was highest at mid-elevation high order streams and for sites located close to cities, blue ribbon trout fisheries, and roads. Site suitability did not appear to be influenced by human population density, as it did not have a trend related to site suitability.

Descriptive statistics for sites likely to be invaded by NZMS (site suitability >50) as well as sites unlikely to be invaded by NZMS (site suitability <1) were compiled for each of the EGV's. Average distance to blue ribbon fishing areas was shorter for sites likely to be invaded by NZMS (122.25 km, ± 84.31 km SD) than sites unlikely to be invaded (328.85 km, ±261.04 km). Average distance to dams taller than 15.24 m (50 ft) was shorter to sites likely SD to be invaded by NZMS (28.42 km, ±21.80 km SD) than sites unlikely to be invaded (141.13 km,

±103.80 km SD). Average distance to cities with a population >25,000 people was shorter to sites likely to be invaded by NZMS (56.92 km, ±35.37 km SD) than sites unlikely to be invaded (251.24 km, ±113.32 km SD). Average distance to cities with a population >100,000 people was shorter to sites likely to be invaded by NZMS (173.90 km, ±131.48 km SD) than sites unlikely to be invaded (628.87 km, ±328.53 km SD). Population density was higher at sites likely to be invaded by NZMS (43.35 people/km^2, ±179.5 people/km^2 SD) than sites unlikely to be invaded (0.50 people/km^2, ±8.89 people/km^2 SD). Stream order was larger at sites likely to be invaded by NZMS (3.03 ±2.11 SD) than sites unlikely to be invaded (1.24 ±0.59 SD). Elevation was lower at sites likely to be invaded by NZMS (1146.26 m, ±322.97 m SD) than sites unlikely to be invaded (1498.39 m, ±563.32 m SD). Distance to the nearest road was shorter to sites likely to be invaded by NZMS (222.58 km, ±513.31 km SD) than sites unlikely to be invaded (1628.28 km, ±2989.81 km SD).

Discussion

The three factors used to create the cross validated site suitability map incorporated all EGV's. The most important EGV was distance to cities with a population >25,000 people, as it was strongly incorporated in all three factors. The distance to cities with a population >100,000 people and elevation were also important EGV's, as they were strongly incorporated in two of the three factors. Relationships between each EGV and sites with a suitability >50 indicated that NZMS are likely to be transported to sites that are popular fishing destinations and are close to urban areas at mid elevations. This supports the idea that fisherman are frequently transporting NZMS to new locations. If another vector was primarily responsible for NZMS dispersal, such as waterfowl, rural areas with little fishing pressure would be as susceptible as urban areas. Although stream order was only strongly incorporated into the first factor, I consider it very important because the first factor accounts for all of the species marginality.

Descriptive statistics for sites likely and unlikely to be invaded by NZMS showed basic differences, e.g., areas likely to be invaded were closer to cities and roads than sites unlikely to be invaded. However, standard deviations associated with the mean values were large, probably because site suitability was not calculated from individual EGV's, but from three uncorrelated factors representing a combination of all EGV's.

Non-probabilistic Sampling

Descriptive statistics are affected by the non-probabilistic sampling regime under which the data were collected. Non-probabilistic sampling may not represent the true population, resulting in biased EGV statistics (Overton et al. 1993; Edwards et al. 2004). The species occurrence map shows the highest density of occurrences along the Snake River. Is this because the Snake River is the point of origin for the NZMS and they have spread to nearby suitable sites, or because biologists surveyed more frequently and with higher intensity in the easily-accessed Snake River? If the occurrence points represent sampling effort and not true distribution, then results will additionally be biased. However, the bias does not appear to be large in this case. The National Aquatic Monitoring Center at Utah State University (www.usu.edu/buglab) surveyed 2,456 sites within the study area between 2000 and 2006, and NZMS were found at only 63 of these sites (Vinson unpublished data). No NZMS were found at 1,416 sites that were sampled prior to 2000. These data appear to represent areas where NZMS do not occur or to which NZMS have a low likelihood of being transported. These sites are not considered absence data, however, because it is unknown if NZMS have had adequate opportunity to become established.

Model Predictions

Areas with a high likelihood of invasion (Figure 3-4) are concentrated in the same general regions where NZMS are known to occur (Figure 3-3). Intuitively, this is because characteristics important to the spread of NZMS are similar in areas surrounding known populations. The more useful parts of the site suitability map are areas distant from known populations that are likely to be invaded by NZMS; these include portions of Western Montana, Northern Idaho, Northeastern Utah and a small portion of central Wyoming.

Examples of popular streams help illustrate conditions in which NZMS are likely or unlikely to invade. Streams likely to be invaded by NZMS include the West Fork Bitteroot River, MT; the Big Wood River, ID; Henry’s Fork, ID; the Blackfoot River in Bingham and Caribou counties, ID; the Payette River and it’s tributaries including Big and Little Willow Creeks in Payette and Gem counties, ID; the Weiser River and it’s tributaries including Mann Creek and Crane Creek in

Washington county, ID, and the Bear River, Malad River, and associated canals near Tremonton and Bear River City, UT. These rivers tend to be part of or near blue ribbon fishing areas, to have a stream order larger than two, and to be relatively close to population centers.

Streams unlikely to be invaded by NZMS include the lower Green River in UT, the West Fork Poplar River in northeast MT, the Milk River in Glacier county, MT, and countless first order tributaries across the study area. Few streams with poor likelihood of being invaded have a stream order larger than two, and those that do are relatively distant from population centers and are generally disconnected from blue ribbon fishing areas. In addition, small tributaries are more likely to have intermittent flow and may freeze in the winter; thus they are less likely to be biologically conducive to NZMS survival.

An unexpected result from the site suitability map is the low suitability values for areas near Yellowstone National Park. NZMS have been confirmed at several sites in the area, and due to the recreational popularity of the area, NZMS were expected to continue spreading in the area. However, based on the most important EGV's, the region was not considered suitable because it is relatively distant from a major population center, contains high elevation areas and has primarily low order streams.   However, Yellowstone attracts millions of recreationists each year, a quality not highlighted by the EGV's used in this study that may have affected its likelihood to be invaded by NZMS.

Future Research

The model presented in this study should be considered the first stage in determining site suitability for NZMS. Second-stage modeling should be field oriented, concentrating on factors that affect NZMS survival, community dominance and local dispersal. Second-stage modeling could be accomplished while field validating the first-stage model presented in this paper.

To accomplish field validation of this first-stage model and begin the second-stage model, some percentage of cells (n=2,878,022 90 m cells in the entire study area) could be randomly selected and visited by surveyors to search for NZMS. Surveyors could sample all habitats at a site, including but not limited to slow water, fast water, stream edges, vegetation, and woody debris (Bowler 1991; Richards et al. 2001). In addition to sampling for NZMS presence and abundance, surveyors could take measurements likely associated with NZMS survival, e.g., stream flow, dominant substrate grain size, amount of aquatic vegetation and woody debris present, temperature, water chemistry, land use and invertebrate species richness (Bowler 1991; Hylleberg and Siegismund 1987; Kerans et al. 2005; Holomuzki and Biggs 1999, Schreiber et al. 2003). An extensive second-stage sampling regime could involve monitoring sites for year-round temperature and flow patterns, proximity to known NZMS populations as well as documenting if and when a site was invaded by NZMS.

Conclusion

Within the four state study area, sites suitable for NZMS invasion were primarily characterized as being relatively close to population centers and blue ribbon fisheries, having low to mid elevation and a stream order greater than two. This study focused on predicting NZMS spread based on its dispersal vectors rather than biological factors affecting their survival and community dominance. I recommend continuing this project in the form of a second-stage study that focuses on NZMS establishment and local spreading. However, resource managers and biologists can use the site suitability map to focus efforts to prevent, monitor and control the spread of NZMS. Public education and prevention can be focused in areas with a high likelihood of NZMS invasion.

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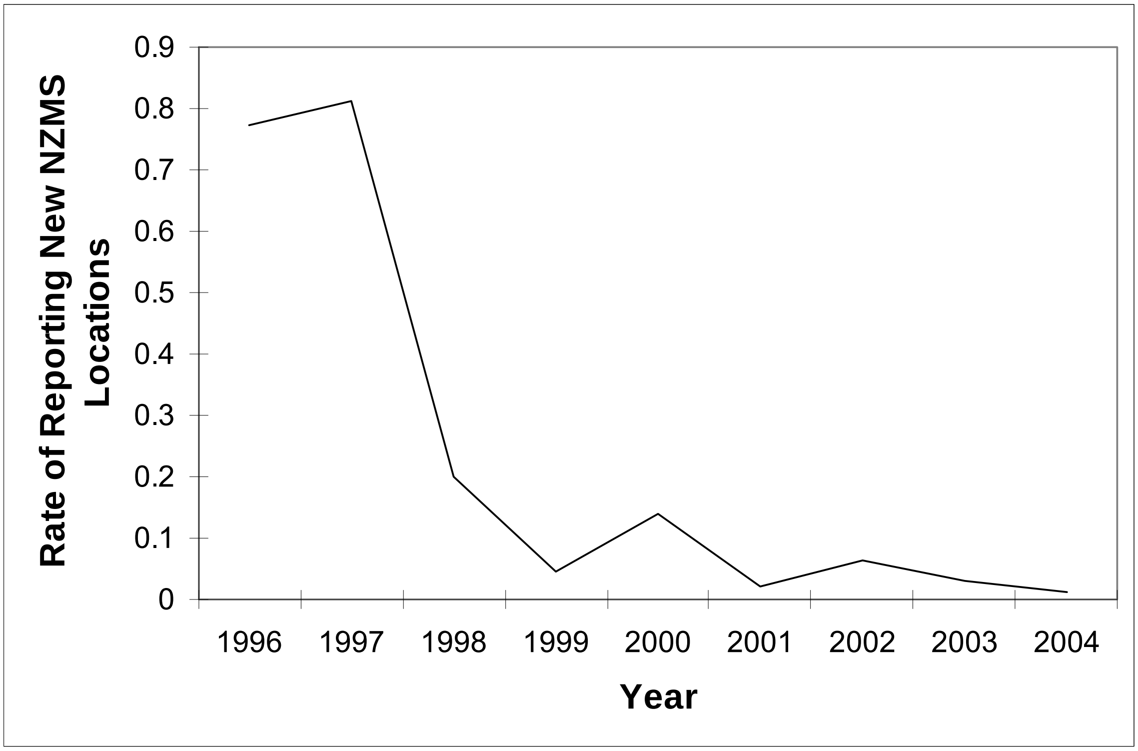

Figure 3-1. Rate (new NZMS locations for a given year divided by the cumulative total number of previously reported NZMS locations) of reporting new populations to the New Zealand mud snail database by year. Data found online at: http://www.esg.montana.edu/dlg/aim/mollusca/nzms/

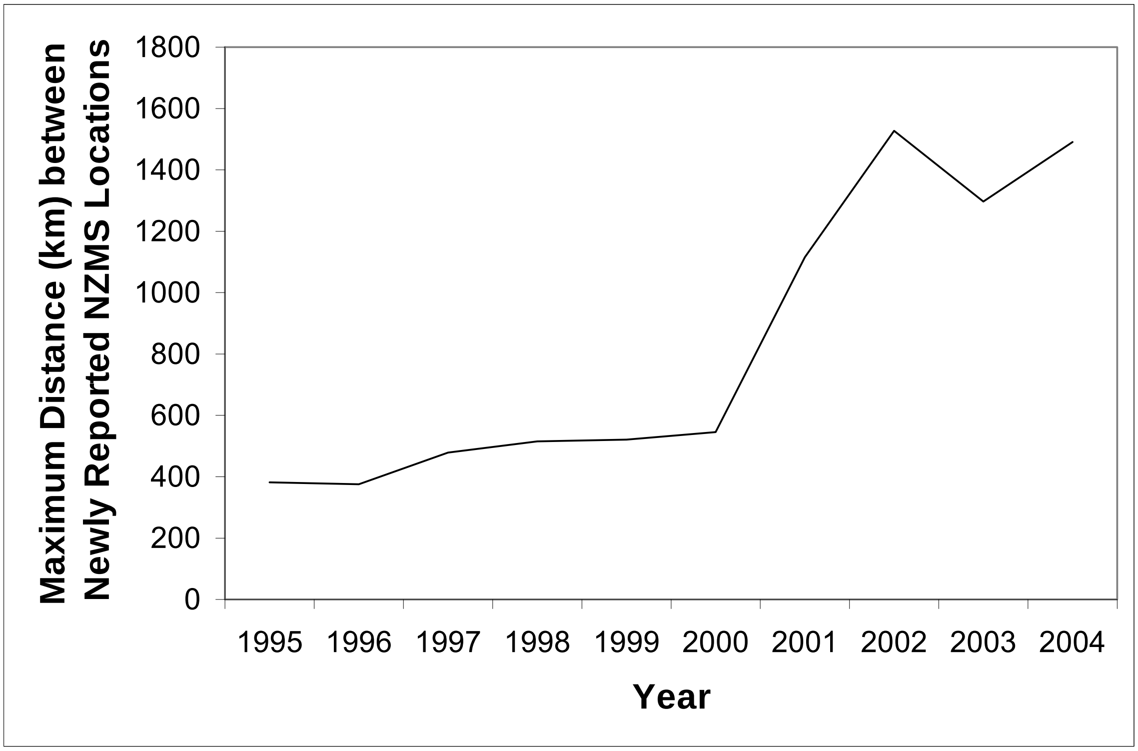

Figure 3- 2. Maximum distance (km) between reported NZMS locations in the United States by year. Data are from the New Zealand mud snail database (http://www.esg.montana.edu/dlg/aim/mollusca/nzms/).

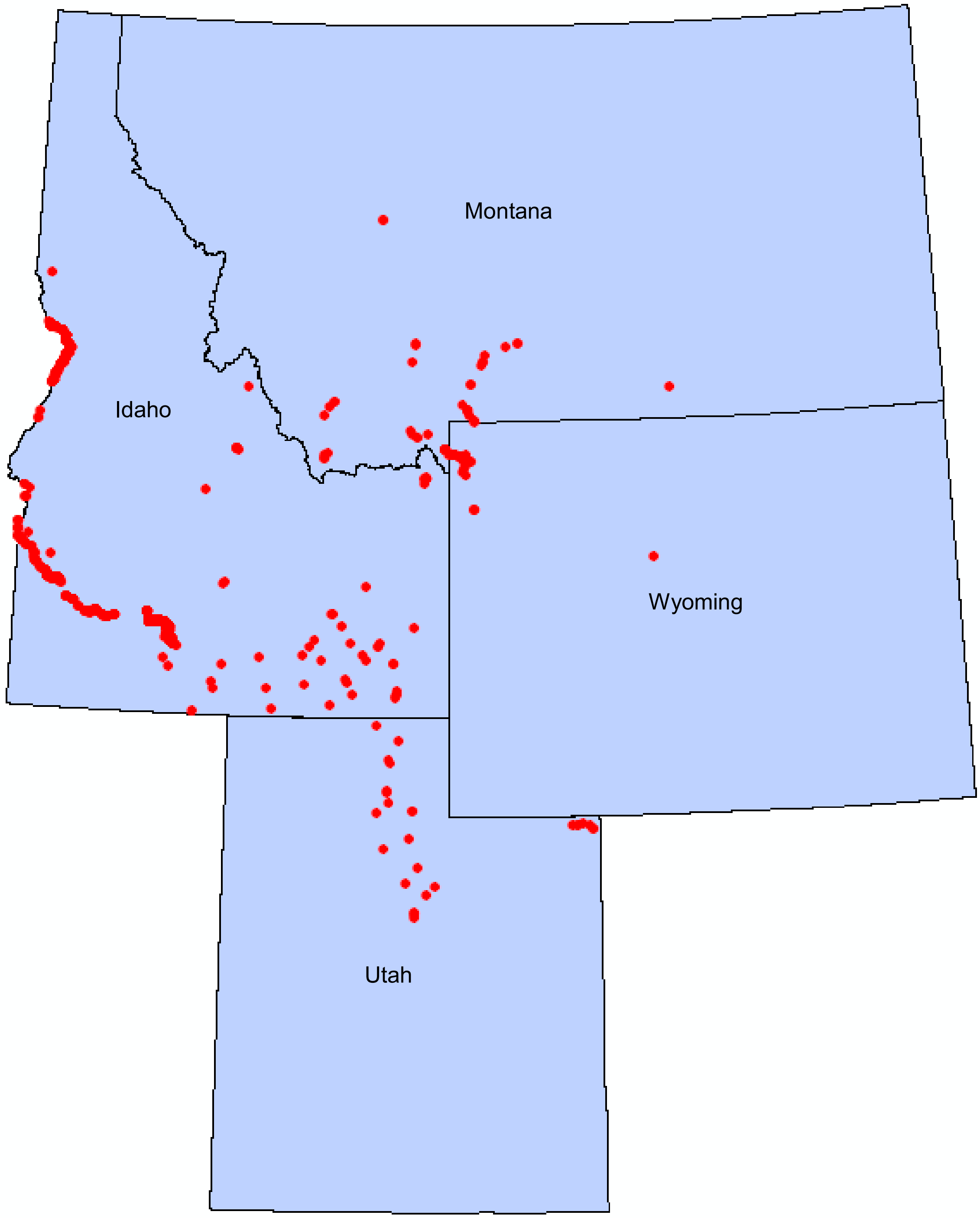

Figure 3-3. NZMS occurrence points used in this study. Data are from 1987-2004 found online at the New Zealand mud snail database (http://www.esg.montana.edu/dlg/aim/mollusca/nzms/).

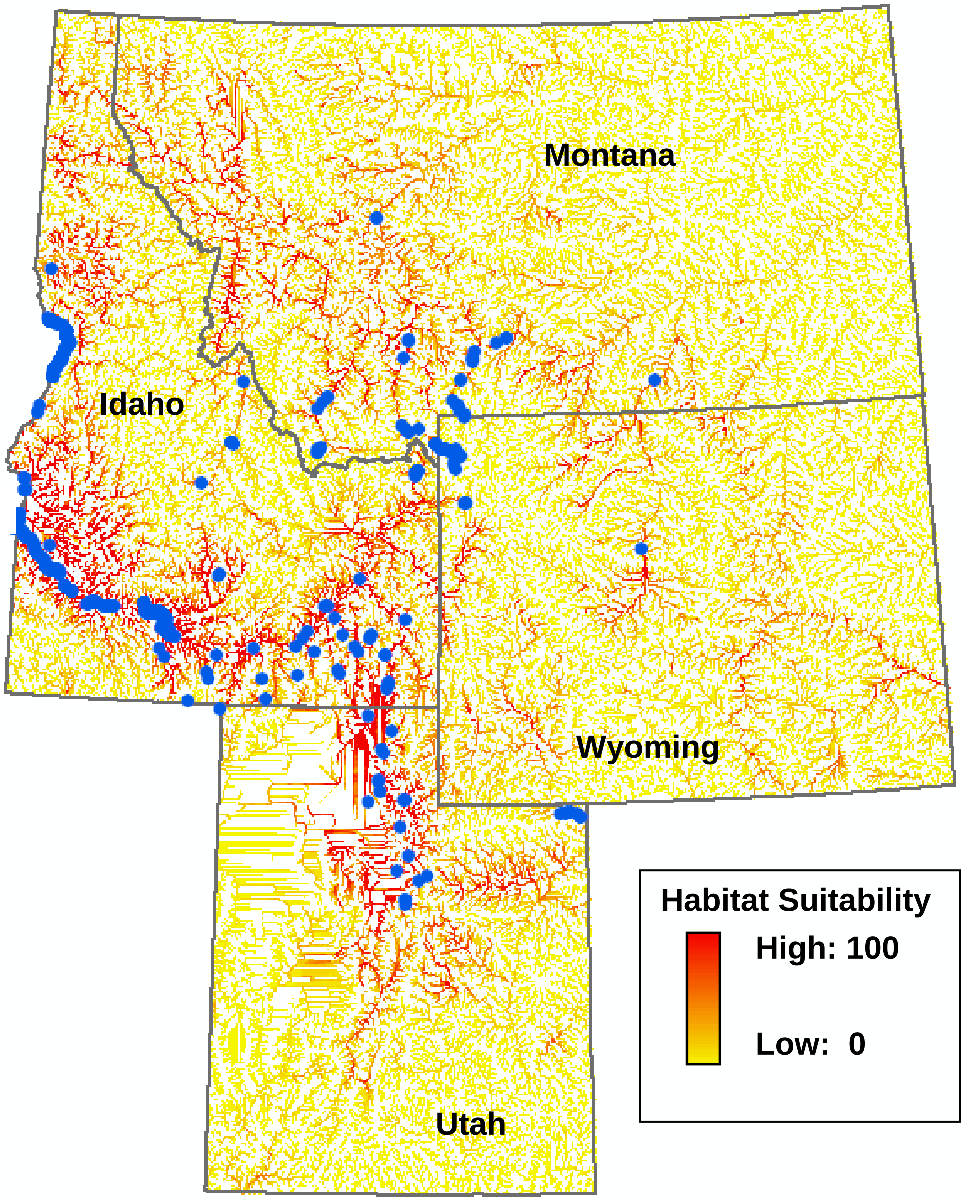

Figure 3-4. Cross validated site suitability map for NZMS based on ENFA model. Blue dots are known locations NZMS populations as of December, 2004. Horizontal lines with a suitability of zero are in the West Desert Region of Utah, where water pathways are not apparent.

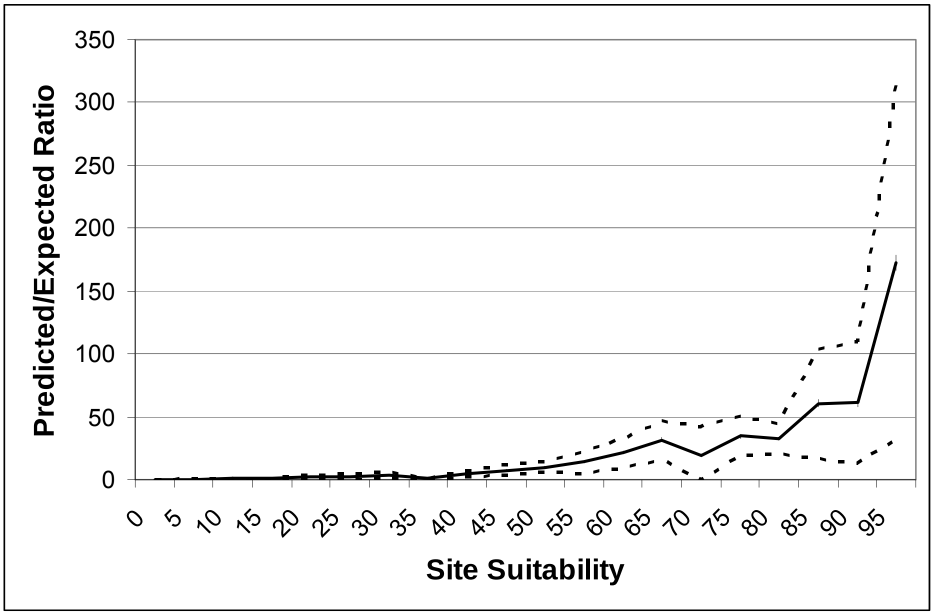

Figure 3-5. Predicted to expected curve showing area-adjusted frequency. Dashed lines are standard deviation. Site suitability is arbitrarily binned in 5% intervals, where 0 represents a poor site suitability for NZMS invasion and 100 excellent site suitability. This graph corresponds to a Boyce continuous index of 0.964, indicating high model agreement with the left-out partition of presence data.

Figure 3-6. Relationship between sites likely to be invaded by NZMS (HS>50) and all EGV's. Predicted to available ratio is the number of cells with HS>50 divided by the total number of available cells for each EGV.

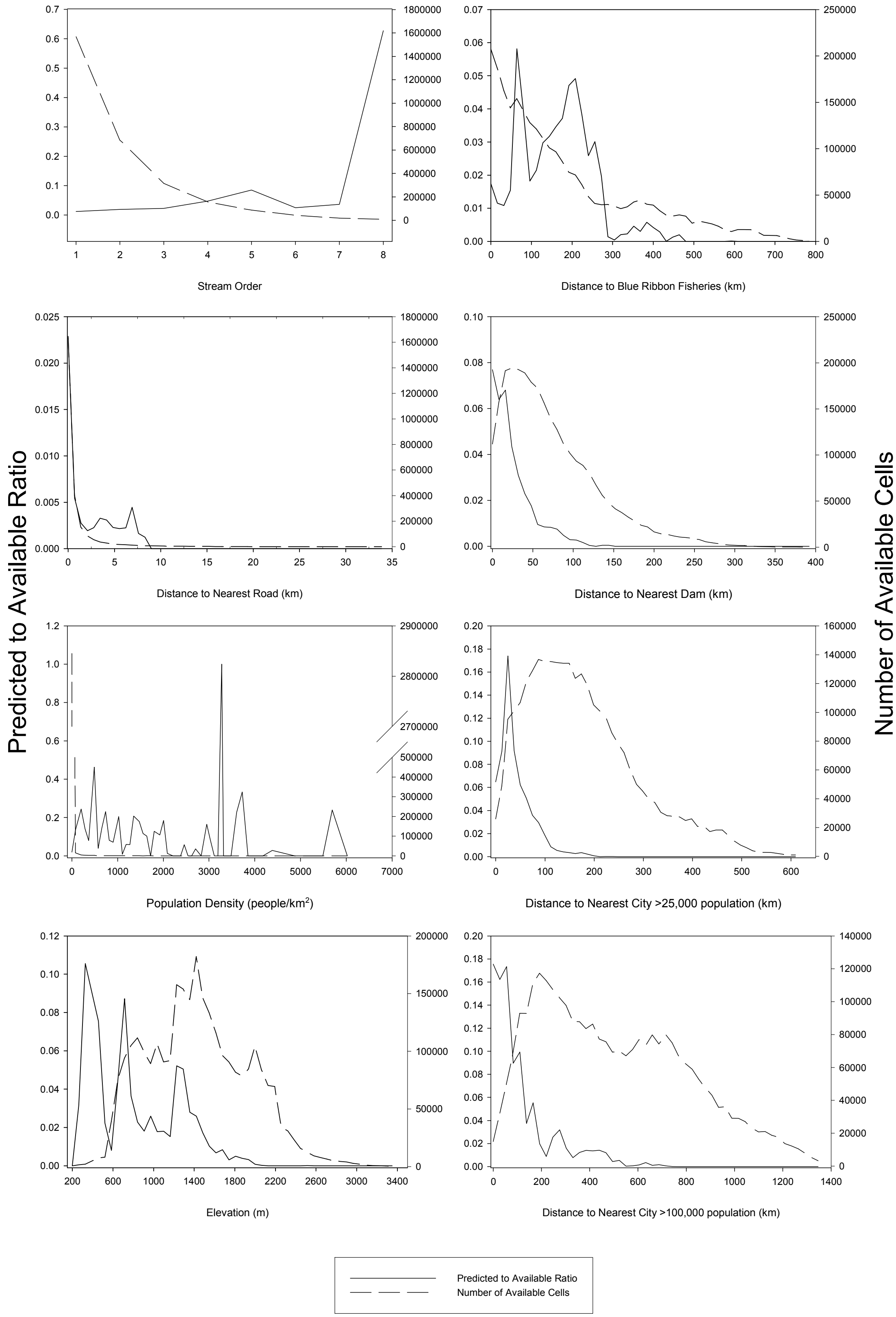
Predicted to Available Ratio
Number of Available Cells
Stream Order
Distance to Blue Ribbon Fisheries (km)
Distance to Nearest Road (km)
Distance to Nearest Dam (km)
Population Density (people/km^2)
Distance to Nearest City >25,000 population (km)
Elevation (m)
Distance to Nearest City >100,000 population (km)
Predicted to Available Ratio
Number of Available Cells

Table 3-1. Ecogeographical variables (EGV's) used in the ENFA and their raw data sources.

Ecogeographical Variable	**Source(s)**	**Range of Values**	**Units**
Distance to nearest city >100,000 population	1	127 - 1373854	meters
Distance to nearest city >25,000 population	1	0 - 621881	meters
Distance to nearest road	1	0 - 34568	meters
Elevation	2,3,4,5	216 - 3414	meters
Distance to nearest dam >15.24 m. tall	6	0 - 400000	meters
Distance to nearest blue ribbon fishery	7,8,9,10	0 - 800000	meters
Population density	1	0 - 10444	people/ km^2
Stream order	2,3,4,5	1 - 8	Strahler method

Sources:
1) http://arcdata.esri.com/data/tiger2000/tiger_download.cfm
2) http://agrc.utah.gov/agrc_sgid/sgidintro.html
3) http://nris.mt.gov/gis/gisdatalib/gisDataList.aspx
4) http://www.sdvc.uwyo.edu/clearinghouse/datalist.html
5) http://inside.uidaho.edu/geodata/popularGISData.htm
6) http://nationalatlas.gov/index.html
7) http://www.wyomingfishing.net/wtf_rivers.htm
8) http://www.wildlife.utah.gov/blueribbon/
9) http://fishandgame.idaho.gov/
10) http://fwp.mt.gov/FwpPaperApps/fishing/class1and2.pdf

Table 3-2. ENFA scores matrix for each EGV. Values in parentheses indicate percent of specialization explained.

EcoGeographical Variable	Factor 1 (19%)	Factor 2 (29%)	Factor 3 (18%)	Factor 4 (13%)	Factor 5 (8%)	Factor 6 (6%)	Factor 7 (4%)	Factor 8 (2%)
Stream Order	0.53	0.12	-0.02	-0.57	0.20	-0.37	-0.07	0.28
Dist. to Dam	-0.45	0.09	-0.06	0.00	0.71	0.03	-0.56	0.09
Dist. to city >100,000	-0.39	-0.75	0.24	-0.42	-0.27	-0.18	0.00	0.21
Dist. to city >25000	-0.37	0.43	-0.82	0.15	-0.23	-0.30	0.00	0.11
Elevation	-0.32	0.45	0.33	-0.34	-0.33	0.12	-0.09	0.47
Population Density	0.25	0.09	-0.15	0.00	-0.44	-0.32	-0.81	-0.13
Dist. to Blue Ribbon Fisheries	-0.20	0.13	-0.15	-0.58	-0.16	0.24	0.10	-0.67
Dist. to nearest Road	-0.16	0.08	0.32	0.17	0.04	-0.75	0.08	-0.42

Table 3-3. Mean area-adjusted frequency ratios (AAF), and associated standard deviation, standard error and coefficient of variation for binned site suitability classes.

Site Suitability Bin	Mean AAF	SD	SE	CV
0	0.101	0.126	0.063	0.624
5	0.417	0.478	0.239	0.573
10	0.985	0.678	0.339	0.344
15	0.982	0.701	0.351	0.357
20	2.183	1.235	0.618	0.283
25	2.794	2.364	1.182	0.423
30	3.282	2.419	1.210	0.369
35	0.614	0.723	0.362	0.589
40	4.667	1.983	0.992	0.212
45	7.479	4.240	2.120	0.283
50	10.030	4.145	2.073	0.207
55	14.179	8.935	4.468	0.315
60	21.480	11.559	5.780	0.269
65	31.823	15.782	7.891	0.248
70	19.062	23.266	11.633	0.610
75	34.754	15.417	7.709	0.222
80	32.677	12.292	6.146	0.188
85	60.581	43.219	21.610	0.357
90	61.461	48.523	24.262	0.395
95	172.741	141.798	70.899	0.410

CHAPTER IV.

CONCLUSION

To fully understand a species invasion, research must be conducted on all four basic stages: transportation (dispersal), release, establishment, and spreading. When an invasive species is established in an area it is also important to identify their potential effects on native species, as well as develop strategies to prevent their further spread. In this thesis, I addressed two key issues surrounding the invasive New Zealand mud snail (*Potamopyrgus antipodarum* Gastropoda: Hydrobiidae, NZMS): 1) Potential effects on a local food web, and 2) Prediction of NZMS distribution to identify sites where public education and control efforts should be focused to have the greatest effect on preventing further spread of NZMS.

To examine local ecosystem effects of NZMS, I analyzed fish stomach content samples and stable isotope samples from all trophic levels in the aquatic food web of the Green River downstream from Flaming Gorge Dam. In addition, I modeled fish diet with varying levels of NZMS to further elucidate how NZMS may affect trout. An isotope mixing model showed that NZMS tissue was isotopically similar to the tissue of several native invertebrates, suggesting they may be competing for resources. Since the introduction of NZMS in 2001, an increasing number of brown trout, rainbow trout, and mountain whitefish have consumed NZMS. Although NZMS were not found in sculpin stomach contents. Bioenergetic simulations showed that trout gained less weight as their consumption of NZMS increased, and weight loss occurred with high levels of NZMS consumption. These results indicated strong circumstantial evidence of negative effects of NZMS on the Green River fish and invertebrate populations.

Predicting sites likely to be invaded by NZMS was accomplished by combining predictor variables representing NZMS dispersal vectors and presence-only data from invaded. I used the ecological niche factor analysis to reduce the predictor variables down to three factors describing NMZS marginality and specialization. The resulting site suitability map characterized locations likely to be invaded by NZMS as close to population centers and blue ribbon fisheries, with a low to mid elevation, and having a stream order greater than two.

Although managers should focus on sites with a high likelihood of invasion when deciding where to concentrate NZMS mitigation efforts, further research can greatly improve the quality of this model. I recommend field validating results from this study and concurrently collecting biological data related to NZMS establishment to better define areas susceptible to NZMS invasion.

Two important but difficult questions to answer surrounding any invasive species are ‘will the invasive species negatively affect native species?’ and ‘where will the invasive species spread to next?’. My research combined these two questions into one project. I created a site suitability map to be used by on-the-ground professionals so they can efficiently prioritize where to survey for NZMS populations and where to focus efforts. Once managers have located new NZMS populations, they can use my research concerning NZMS effects on trout and invertebrates to assess what the likely impacts on native assemblages may be.