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ORIGINAL PAPER

Predicting habitat use and trophic interactions of Eurasian ruffe, round gobies, and zebra mussels in nearshore areas of the Great Lakes

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Abstract The Laurentian Great Lakes have been subject to numerous introductions of nonindigenous species, including two recent benthic fish invaders, Eurasian ruffe (*Gymnocephalus cernuus*) and round gobies (*Neogobius melanostomus*), as well as the benthic bivalve, zebra mussel (*Dreissena polymorpha*). These three exotic species, or ''exotic triad,'' may impact nearshore benthic communities due to their locally high abundances and expanding distributions. Laboratory experiments were conducted to determine (1) whether ruffe and gobies may compete for habitat and invertebrate food in benthic environments, and (2) if zebra mussels can alter those competitive relationships by serving as an alternate food source for gobies. In laboratory mesocosms, both gobies and ruffe preferred cobble and macrophyte areas to open sand either when alone or in sympatry. In a 9-week goby–ruffe competition experiment simulating an invasion scenario with a limited food base, gobies grew faster than did ruffe, suggesting that gobies may be competitively superior at low resource levels. When zebra mussels were added in a short-term experiment, the presence or absence of mussels did not affect goby or ruffe growth, as few zebra mussels were consumed. This finding, along with other laboratory evidence, suggests that gobies may prefer soft-bodied invertebrate prey over zebra mussels. Studies of interactions among the ''exotic triad'', combined with continued surveillance, may help Great Lakes fisheries managers to predict future population sizes and distributions of these invasive fish, evaluate their impacts on native food webs, and direct possible control measures to appropriate species.

Keywords Aquatic species · Benthic · Competition · Exotic species · Fishes · Habitat preference · Nonindigenous species · North America · Species interactions

Abbreviation

NIS Nonindigenous species

Introduction

Biological invasions are an important component of global change in aquatic ecosystems (Sala et al.

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2000). The impacts of invasions on the Laurentian Great Lakes have been particularly profound, with over 160 nonindigenous species (NIS) introduced since the mid-1800's (Ricciardi and MacIsaac 2000; Ricciardi 2001). Over the last century, species introductions through the opening of the St. Lawrence Seaway in 1959 and intercontinental transfers of ballast water have resulted in massive changes in the Great Lakes pelagic food web (Mills et al. 1994; Ricciardi and MacIsaac 2000). Invasive fishes such as sea lamprey, alewife, and rainbow smelt have caused declines in several important commercial fisheries including lake trout, lake whitefish, and yellow perch (Christie 1974; Mills et al. 1994; Crowder et al. 1987).

Changes in the nearshore (areas less than 50 m in depth) benthic ecosystem have received far less attention than changes in the pelagic zone. However, the introductions of Eurasian ruffe (*Gymnocephalus cernuus*), round gobies (*Neogobius melanostomus*), and zebra mussels (*Dreissena polymorpha*) in the Great Lakes during the 1980's and 1990's represent a new wave of NIS that could alter the benthic environment (Ricciardi and MacIsaac 2000). These three species, or ''exotic triad'', are native to the Ponto-Caspian region of Eurasia (Ricciardi and MacIsaac 2000) and were likely introduced in ballast water. Our study focuses on the potential interactions among the ''exotic triad'' because they are all (1) native to nearshore benthic environments, (2) have either become or have the potential to become widespread in the Great Lakes and other North American aquatic ecosystems (i.e., they are invasive), and (3) when established, can numerically dominate benthic communities.

The ''exotic triad'' likely already interact in nearshore benthic ecosystems where they currently co-occur in the St. Louis River estuary in western Lake Superior and Thunder Bay in Lake Huron. With zebra mussels virtually lining the entire Great Lakes perimeter (United States Geological Survey 2002), gobies spreading rapidly throughout all five lakes (Charlebois et al. 2001), and ruffe recently expanding their range into northern Lake Michigan near Green Bay, Wisconsin (Czypinski et al. 2005), it is likely that these species will eventually co-occur throughout much of the Great Lakes nearshore environment.

Following their introduction, members of the ''exotic triad'' have rapidly increased their population sizes in invaded areas and have continued to spread. The high success of these three species suggests that they could cause profound impacts on food webs of invaded systems. Round gobies had become a dominant component of the benthic fish community of the St. Clair River as early as 1992 (Jude et al. 1995), only 2 years after their discovery in the St. Clair River. Furthermore, gobies have reached high densities (5–133 individuals m^{-2}) in Lake Erie (Weimer and Keppner 2000) and southern Lake Michigan (Charlebois et al. 1997; Chotkowski and Marsden 1999). Gobies have also been shown to compete with native fishes for food and habitat and territorial adult gobies have been implicated in the decline of native benthic fishes (Jude et al. 1995; Jude and DeBoe 1996). For example, gobies are similar to native mottled sculpin in size, body form, and use of nests for brooding young, and thereby compete with sculpin for food and nest sites (Janssen and Jude 2001). The aggressive behavior of round gobies also allows them to out-compete resident logperch populations for space and shelter in the Great Lakes (Balshine et al. 2005).

Gobies eat primarily small, soft-bodied benthic invertebrates when young but, by 60–100 mm in size, switch to a diet of mostly zebra mussels (Jude et al. 1995; Ray and Corkum 1997; Carman et al. 2006). In Lake Michigan, gobies have altered the size structure of zebra mussel populations by preying on smaller individuals (Djuricich and Janssen 2001) and changed the structure of benthic invertebrate and algal communities through heavy predation on grazers such as caddisflies and midges (Kuhns and Berg 1999). In a rock transplant experiment, gobies significantly reduced sessile organisms, including zebra mussels and quagga mussels, on cobble in just 24 h, and may have indirectly reduced the abundance of other invertebrates by modifying the microhabitat (Lederer et al. 2006). Due to these impacts and the potential transfer of energy and contaminants from zebra mussels to top predators (e.g., smallmouth bass and humans) (Morrison et al. 2000; Steinhart et al. 2004), round gobies may become a keystone species in the Great Lakes benthic environment (Diggins et al. 2002).

Similarly, Eurasian ruffe had become the most abundant fish in western Lake Superior by 1991, only 4 years after their discovery in Duluth Harbor (Bronte et al. 1998). Increases in ruffe populations in western Lake Superior coincided with declines in population sizes of several benthic forage fishes (Bronte et al. 1998), suggesting increased competition for shared benthic invertebrate food, such as chironomids, oligochaetes, mayflies, amphipods, and caddisflies (Fullerton et al. 1998). Other evidence suggests that ruffe have dietary overlap with yellow perch (Ogle et al. 1995; Sierszen et al. 1996; Savino and Kolar 1996; Fullerton et al. 1998) and that increased fish densities lead to declines in both ruffe and yellow perch growth (Fullerton et al. 2000).

Zebra mussels have also become extremely abundant since their introduction to Lake St. Clair in 1988, with densities from 500 to 10,000 individuals m^{-2} on hard substrates (Nalepa et al. 1995), sometimes making up 90% of the invertebrate community numerically (Steward and Haynes 1994). Zebra mussels have spread secondarily into inland lakes and streams throughout most of the eastern U.S. (Bobeldyk et al. 2005) whereas gobies and ruffe have moved into only a few tributaries of Lake Superior and Lake Michigan (M. Berg, personal communication; Carman et al. 2006). Zebra mussels have had many well documented effects on invaded ecosystems including, but not limited to, (1) decreased phytoplankton and zooplankton abundance, (2) increased abundance of submerged plants and benthic algae, and (3) increased abundances of other benthic invertebrate taxa (see review by MacIsaac 1996). Zebra mussels also modify benthic habitats, which may facilitate the establishment of other NIS associated with zebra mussels, such as the round goby (Jude 2001) and *Echinogammarus ischnus*, an exotic amphipod (Ricciardi 2001). Zebra mussel druses (a ball of loosely attached mussels) increase habitat complexity and have been shown to act as a refuge for some invertebrate species from predation (Reed et al. 2004). In addition, zebra mussels transfer energy from the pelagic food web (i.e., plankton) to the benthos in the form of zebra mussel biomass, feces, and pseudofeces (Stewart and Haynes 1994; MacIsaac 1996; Ricciardi et al. 1997).

While it is important to understand individual species effects on the benthic community, round gobies, Eurasian ruffe, and zebra mussels may act together to have unpredicted community and ecosystem effects. The specific goals of this study were to identify potentially complex interactions among gobies, ruffe, and zebra mussels by asking the following questions. First, do ruffe and gobies use and compete for similar habitat resources? Second, do ruffe and gobies compete for food resources when they coexist? Third, do zebra mussels alter competition for food resources between gobies and ruffe? The study of potential interactions among NIS, as in our study, is less common than studies focusing on interactions between nonindigenous and native species (Simberloff and Von Holle 1999; Ricciardi 2001). Yet, in ecosystems such as the Great Lakes where NIS can dominate entire levels of the food web, a better understanding of the interactions among NIS is necessary to predict their effects on entire food webs.

Methods

Overview

Laboratory experiments were used to determine habitat use and potential competition for food between ruffe and gobies in environments with and without zebra mussels. We hypothesized that gobies would use primarily cobble habitat (Charlebois et al. 1997), but could find refuge in macrophytes (Jude 2001), whereas ruffe would be found over fine sediments (Brazner et al. 1998) as well as in macrophyte refuges (Fullerton and Lamberti 2006). Both gobies and ruffe were expected to prefer soft-bodied invertebrates over hard (e.g., shell-bearing) invertebrates (Ogle et al. 1995; Fullerton et al. 1998; French and Jude 2001; Diggins et al. 2002), except that gobies would eat zebra mussels (Ray and Corkum 1997; French and Jude 2001).

Growth experiments were used to investigate competition between the two invasive fish in environments with and without zebra mussels. In the absence of zebra mussels, ruffe, and gobies were hypothesized to have similar growth rates when alone or together. However, the presence of zebra mussels could serve as an alternate food source for gobies, thereby giving them a competitive advantage over ruffe, which do not readily consume mollusks (Ogle et al. 1995; Fullerton et al. 1998).

Fish collection and care

Ruffe used in laboratory experiments were collected from Duluth Harbor and the Iron River estuary in Lake Superior using bottom trawls. Gobies were collected by hook and line from Calumet Harbor, Lake Michigan. Fish were transferred to the University of Notre Dame, where they were held in aerated flow-through holding tanks (13–16°C, 12 h light:12 h dark), and fed natural food such as rainbow trout eggs and diced squid. Fish were tagged along their lateral side by injecting nontoxic fluorescent paint to assess habitat use and determine fish location under ultraviolet light. Effluent water was double-filtered to prevent release of eggs or larvae. All fish were acclimated to the laboratory environment for at least 1 month prior to use in experiments and held in separate tanks by species.

Habitat experiment

Circular tanks (1 m^2 surface area, 0.3 m in height) served as simulated lake environments for experiments. Tanks were provided with equal areas of cobble (3–6 inches in diameter obtained for a local quarry), artificial macrophytes (~25 strands m^{-2}), and play sand (~2 cm in depth), arranged radially, to determine habitat use by ruffe and gobies. Cobble and macrophytes were underlaid by sand, which covered the entire bottom of the tank. Fish species of matched size (ruffe or gobies) and density (0, 3, or 6 individuals of each species) were factors in the completely crossed factorial design ($n = 4$ per treatment minus the uninformative 0, 0 treatment). For example, 3 gobies (and 0 ruffe), 3 gobies + 3 ruffe, or 3 gobies + 6 ruffe were added to tanks for the low density-goby treatments. In this way, goby and ruffe habitat preference when alone could be compared to habitat preference in the presence of the other species at both low and high densities, without the availability of food. One replicate of each treatment was run in four separate 24-h periods, however fish were completely reassigned to the treatments for each replicate. Habitat use by fish was assessed visually and recorded every 15 min in the light and dark (under ultraviolet light to avoid disturbing fish behavior) during each 8-h trial. Observations were pooled for each trial and the proportion of each species present in each of the habitats was calculated. As these observations are serially correlated, independence was achieved by compositional analysis (Aebischer et al. 1993). Specifically, the ratio of habitat use between habitats was computed (cobble:plant and cobble:sand) and then ln-transformed. Only two of three possible comparisons were used because the third comparison (plant:sand) is duplicative. Prior to analysis, a constant was added to each proportion because of zeros in the data set (Aebischer et al. 1993). These transformed data were analyzed using multivariate analysis of variance (MANOVA; SAS Version 6.12) so that the two ratios could be analyzed simultaneously. Significant differences in habitat use were identified when the resulting Wilk's λ value (similar to a P-value for parametric tests) was less than or equal to 0.05.

Goby–ruffe competition experiment

Growth rates of gobies and ruffe were measured for 9 weeks in the simulated lake environments described above, which had equal proportions of all three habitat types (water temperature, 15°C). Treatments consisted of each species alone (2 ruffe or 2 gobies, *Alone* treatment), both species together at the same total density (1 ruffe + 1 goby, *Replacement* treatment), or both species together at doubled density (2 ruffe + 2 gobies, *Invasion* treatment). These three treatments were chosen to simulate populations when their ranges are completely separate (*Alone*) or when they overlap, which are roughly similar to densities found in the wild that ranged from 1 to 2 ruffe per m^2 in Lake Superior (Ogle 1998) to more than 5 gobies per m^2 in Lake Erie (Weimer and Keppner 2000). When the populations converge, individuals of one species (e.g., gobies) could be replaced by the other species (e.g., ruffe) so that the overall fish density does not increase (*Replacement*) or the total fish density could double with the addition of the invading species (*Invasion*). Thus, each 1-m^2 tank contained one of the three treatments above (n = 3 per treatment). Gobies and ruffe used in the experiment had an initial mean individual mass (±SE) of 11.00±0.26 g and 10.86±0.14 g, respectively. Gobies ranged from 82 mm to 90 mm in total length, and ruffe ranged from 82 mm to 94 mm. Thus, fish used in the experiment were well matched in size. Fish in the *Alone* and *Replacement* treatments were fed a per-capita 6% ration of their body weight of an aquatic annelid (*Tubifex* sp.) each day. Fish in the *Invasion* treatment were fed a 3% ration of *Tubifex* daily. The *Invasion* treatment received a reduced ration to simulate a doubling of fish density while food resources available to fish remained constant. Thus, each individual fish received half the food, on average, that it would have garnered if fish density remained constant. Rations were supplied during the dark when both species were active. The 6% ration is between the maintenance and optimal ration calculated for perch and ruffe at 17–22°C (Fullerton et al. 2000; Hoelker and Temming 1998; Henson and Newman 2000) and was considered to be limiting in this experiment. The 6% ration is also between the maintenance and optimal ration for gobies in laboratory aquaria at an average temperature of 20°C (K. Priemer and C. Bauer, unpublished data).

Fish were weighed weekly over the 9-week study. Mean growth rates of fish (g g^{-1} d^{-1}) were calculated by standardizing the weekly change in blotted wet mass by the blotted wet mass of the individual in the previous week. This approach maximized the number of observations included in the analysis, as some female gobies laid eggs during the experiment. To eliminate the effect of egg release, mean specific growth rate (g g^{-1} d^{-1}) was calculated only for weeks when eggs were not found. We used 2-way ANOVA to test for the effects of fish species and treatment on growth over the entire experiment (SYSTAT 10; SPSS, Inc. 2000) followed by multiple contrast tests (Tukey's HSD). Growth rates of fish (g g^{-1} d^{-1}) were analyzed over time using repeated measures ANOVA (SYSTAT 10; SPSS, Inc. 2000).

"Exotic triad" experiment

We conducted a shorter-term experiment for 1 week to examine how zebra mussels affect fish interactions. Fish treatments were similar to the previous experiment, but were applied to 40-l aquaria held at 16°C after fish were acclimated for approximately 12 h (n = 8 per treatment). Treatments were 2 gobies alone or 2 ruffe alone fed a 6% ration (*Alone* treatment), 1 ruffe + 1 goby fed a 6% ration (*Replacement* treatment), and 1 ruffe + 1 goby fed a 3% ration (*Invasion* treatment). In this experiment, we simulated increased fish density by halving the ration, rather than both doubling the total fish density and halving the ration as in the previous experiment. The fish treatments were held in aquaria with or without live zebra mussels. Each aquarium with zebra mussels received a brick colonized with 50 g blotted wet weight of zebra mussels, resulting in an approximate density of mussels (1,000 m^{-2}) within the range of densities recorded in North American lakes (Nalepa et al. 1995). Zebra mussels were colonized on bricks in the laboratory for 1 week prior to the start of the experiment, which allowed the mussels sufficient time to attach themselves to the brick. Treatments lacking zebra mussels received a bare brick. All other methods and calculations were the same as for the previous competition experiment. Daily growth rates of fish were analyzed using 3-way ANOVA (main factors: fish treatment, fish species, and zebra mussels) followed by Tukey's multiple contrast tests.

Results

Habitat use by ruffe and gobies

In the first experiment, ruffe and gobies used similar habitats in both light and dark conditions (Fig. 1). Neither total fish density, which ranged from 3 to 12 fish m^{-2} (Table 1), nor the relative proportion of ruffe and gobies in the tank affected

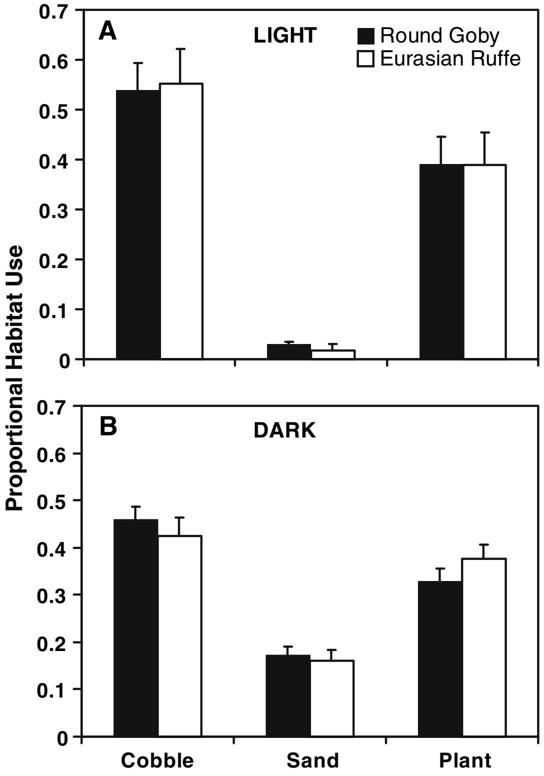

Fig. 1 Mean (+SE) proportional habitat use over all treatments in simulated lake environments during the light (**A**) and dark (**B**)

habitat use (Table 2). Thus, ruffe and goby habitat use in these laboratory experiments was the same when alone as when in the presence of the other species, even at relatively high fish densities (12 fish m^{-2}). Specifically, both ruffe and gobies preferred cobble and plant habitats in the simulated lake environments at all times (Fig. 1), although sand use increased during the dark when the fish were more active (C. Bauer, personal observation). This suggests that they both species prefer complex habitats over sand habitats, but that one species does not exclude the other from its preferred habitat. Observational support for this conclusion includes the fact that ruffe and gobies were often found in close proximity to one another, particularly at the highest fish densities, and were often observed near available refuge, such as cobble interstices and the base of plants.

Growth rates of ruffe and gobies

In the second experiment, goby growth rates were significantly greater than ruffe growth rates (Table 3, fish species $P = 0.014$). However, mean growth rates of gobies and ruffe (g g^{-1} d^{-1} ± SE) were similar in the *Alone* treatment (0.0053±0.0005 and 0.0046±0.0014, respectively), indicating that significantly different growth rates between the species were primarily due to large differences between growth rates of the species (0.0039±0.0011 and 0.0006±0.0004, respectively) in the *Invasion* treatment (Fig. 2). Additionally, the treatment effect was significant (Table 3, Treatment $P = 0.017$), with significantly higher growth rates in the *Alone* (Tukey's $P = 0.025$) and *Replacement* treatments (Tukey's $P = 0.0.34$) than in the *Invasion* treatment (Fig. 2). The interaction of species and treatment was not statistically significant (Table 3, Species * treatment $P = 0.372$), but mean ruffe growth rates (g g^{-1} d^{-1}) were much lower in the *Invasion* treatment (0.0006) than in the *Alone* or *Replacement* treatments (0.0046 and 0.0037, respectively; Fig. 2). In contrast, mean goby growth rates (g g^{-1} d^{-1}) in the *Alone* treatment (0.0053) were similar to growth rates in the presence of ruffe (*Replacement treatment*, 0.0059; *Invasion treatment*, 0.0039; Fig. 2). This laboratory result suggests that gobies may hold a competitive advantage over ruffe since ruffe growth is more

Table 1 Results of multivariate analysis of variance (significance reported as Wilk's λ) used to test effects of fish species and total density on habitat use in the light and dark

Source	Light			Dark		
	df	F	Wilk's λ	df	F	Wilk's λ
Fish species	2, 39	0.3441	0.7110	2, 39	1.9029	0.1627
Total density	6, 78	1.6988	0.1324	6, 78	1.3568	0.2426
Spec * dens	6, 78	0.7143	0.6391	6, 78	1.3267	0.2554

Table 2 Results of multivariate analysis of variance (significance reported as Wilk's λ) used to test effects of fish species and relative species density on habitat use in the light and dark

Source	Light			Dark		
	df	*F*	Wilk's λ	df	*F*	Wilk's λ
Fish species	2, 35	0.0247	0.9756	2, 35	2.0141	0.1486
ER density	4, 70	0.9283	0.4526	4, 70	1.5803	0.1891
RG density	4, 70	0.7241	0.5784	4, 70	0.2025	0.9362
Spec * ER dens	2, 35	0.3810	0.6859	2, 35	0.6254	0.5409
Spec * RG dens	2, 35	0.3361	0.6961	2, 35	0.2975	0.7446
ER * RG	6, 70	1.3739	0.2372	6, 70	1.5885	0.1634
Spec * ER * RG	2, 35	0.2810	0.7567	2, 35	2.2797	0.1173

ER, Eurasian ruffe; RG, round roby

Table 3 Results of analysis of variance showing the effects of fish species, treatment (*Alone, Replacement*, *Invasion*), and their interaction on daily growth rate during the 9-week goby–ruffe competition experiment

Source	df	*F*	P^a
Fish species	1, 12	8.209	**0.014**
Treatment	2, 12	5.867	**0.017**
Species * treatment	2, 12	1.074	0.372

[a] Significant responses are shown in bold

Table 4 Results of repeated-measures analysis of variance showing the effects of time, species, treatment (*Alone*, *Replacement*, *Invasion*), and their interactions on weekly measurements of daily growth rate during the 9-week goby–ruffe competition experiment

Source	df	*F*	P^a
Week	8, 80	4.208	**0.000**
Week * species	8, 80	3.143	**0.004**
Week * treatment	16, 80	1.551	0.103
Week * species * treatment	16, 80	2.020	**0.021**

[a] Significant responses are shown in bold

affected than goby growth when resources are most limiting (*Invasion* treatment), which may be the case in much of the Great Lakes environment. This conclusion is also supported by the significant interaction among time, species, and treatment on growth rates (Table 4, week * species * treatment $P = 0.021$) and the asymmetrically lower growth rate of ruffe over time in the *Invasion* treatment (Fig. 3).

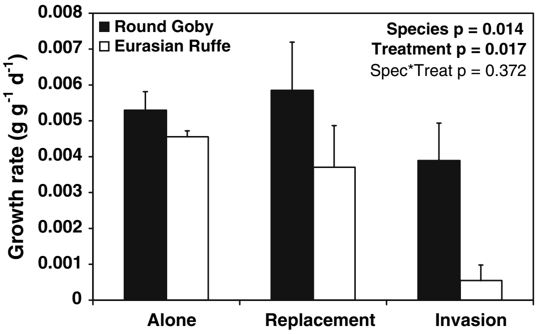

Fig. 2 Mean (+SE) daily growth rates of gobies and ruffe in fish treatments during the 9-week competition experiment. The *Alone* and *Replacement* treatments are significantly different from the *Invasion* treatment (Tukey's $P < 0.05$), whereas *Alone* and *Replacement* treatments are similar (Tukey's $P > 0.05$)

Effect of zebra mussels on ruffe–goby interactions

The final experiment demonstrated that the addition of zebra mussels did not significantly

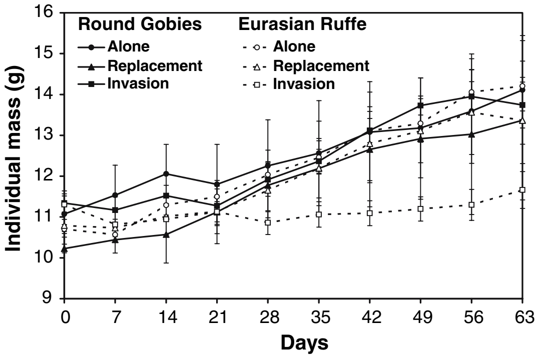

Fig. 3 Mean (±SE) blotted wet mass of fish in each of the treatments during the 9-week competition experiment

affect fish growth in any treatment (mussel $P = 0.558$, Table 5), and no significant interactions were found ($P > 0.05$, Table 5). Very few, if any, zebra mussels were consumed in any of the fish treatments (C. Bauer, personal observation). Growth of both ruffe and gobies was measurable over the 1-week experiment. The two species had similar growth rates (fish species $P = 0.303$, Table 5), but significant differences were found among the different fish treatments ($P < 0.001$, Fig. 4). Similar to the 9-week experiment, fish in the *Invasion* treatment had significantly lower growth rates than in the *Alone* or *Replacement* treatments (Tukey's $P < 0.001$ and $P = 0.005$, respectively).

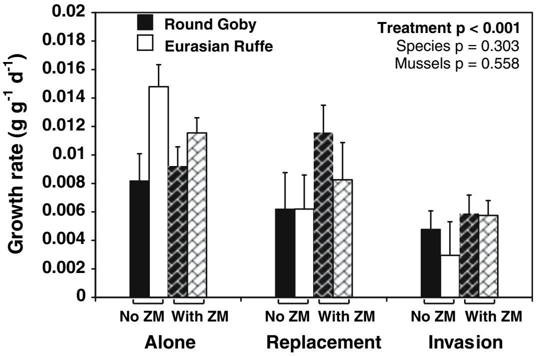

Fig. 4 Mean (+SE) daily growth rates of gobies and ruffe in the presence (With ZM) and absence (No ZM) of zebra mussels during the 1-week "exotic triad" experiment. Main effects of the 3-way ANOVA are presented. The *Alone* and *Replacement* treatments are significantly different from the *Invasion* treatment (Tukey's $P < 0.05$), whereas *Alone* and *Replacement* treatments are similar (Tukey's $P > 0.05$). Interaction terms were not significant

Discussion

Habitat preferences

Ruffe and gobies overlapped substantially in microhabitat use in the simulated lake environments. Generally, both species preferred areas with cobble and plants. We predicted that ruffe would be found primarily over sand as field studies have shown that ruffe are most abundant in deep, dark habitats over simple substrates and may avoid macrophytes (Kalas 1995; Ogle et al. 1995; Brazner et al. 1998). Our laboratory habitat preference study suggests, however, that sand is not a preferred habitat for ruffe when other options exist, as also found by Fullerton and Lamberti (2006). Perceived predation threat in the simulated lake environments resulting from the high water clarity and abundant ambient light during the day may have led ruffe to seek more complex substrate such as plants and cobble.

Table 5 Results of analysis of variance showing the effects of fish treatment, zebra mussels, fish species, and their interactions on daily growth rates of fish during the 1-week "exotic triad" competition experiment

Source	df	*F*	*P*[a]
Fish treatment	2, 83	12.357	< **0.001**
Mussel treatment	1, 83	0.347	0.558
Fish species	1, 83	1.075	0.303
Species * treatment	2, 83	1.819	0.169
Species * mussels	2, 83	1.883	0.174
Treatment * mussels	1, 83	1.184	0.311
Species * treatment * mussels	2, 83	1.550	0.218

[a] Significant effects are shown in bold

If ruffe invade other Great Lakes having greater light transmission than Lake Superior (which is high in dissolved organic carbon that decreases light transmission; Wetzel 2001), ruffe may seek refuge from visually oriented predators in areas with macrophytes or cobble substrates. Our results also suggest that gobies will not be limited to cobble-dominated areas of the Great Lakes, as suggested by Jude (2001), and may become abundant in areas with submerged macrophytes, where they may interact with another NIS, the tubenose goby (Jude 2001). As researchers spend more time sampling macrophyte and cobble-rich areas and population sizes of both ruffe and gobies increase, it may become apparent that these fish are not limited to sand (ruffe) and cobble (gobies) areas. Rather, both species may be commonly found co-existing in more complex macrophyte- and cobble-dominated substrates as observed in this laboratory study.

Competition for food

If ruffe and gobies eventually use similar habitats in the Great Lakes as our laboratory habitat study suggests, interactions between these two fish species, such as territorial aggression, competition for habitat, or competition for food, may be frequent and sometimes intense. Interactions between gobies and ruffe could be important in determining the eventual range and population size of each species. Specifically, our laboratory experiments tested each species' ability to garner limited benthic food resources as measured by fish growth. The intensity of intraspecific and interspecific competition was of similar strength in the 1-week "exotic triad" experiment and when food resources were held constant in both laboratory competition experiments (as evidenced by similar growth rates for both species in the *Alone* and *Replacement* treatments). This result is not particularly surprizing, as the importance of intraspecific competition has been demonstrated in numerous studies (e.g., Lamberti et al. 1983; reviewed by Schoener 1983), including previous work on yellow perch and ruffe (Fullerton et al. 2000).

In our study, however, we also found that gobies may hold a competitive advantage over ruffe in our most food-limited (*Invasion*) treatment over 9 weeks, even in the absence zebra mussels—a potential additional prey source for gobies. In the *Invasion* treatment, goby growth, in contrast to ruffe growth, did not decrease much from levels found in the *Alone* and *Replacement* treatments, despite halving the food ration. This result demonstrates that either (1) gobies interfere with ruffe prey acquisition (interference competition), (2) gobies eat more than their share of the food (exploitative competition), (3) gobies are more efficient foragers than ruffe, or (4) gobies more efficiently assimilate food than ruffe at low resource levels. While it is unclear whether gobies are better at acquiring prey than ruffe, gobies may have an advantage over ruffe because goby neuromasts are more sensitive than species whose neuromasts are contained within canals, such as ruffe (Jude et al. 1995). Ruffe are also thought to have poor movement perception (Ogle 1998). Visual perception of prey may have been important in our tanks since water clarity was high, as is now found in many of the Great Lakes after zebra mussel invasion. Furthermore, ruffe may have a competitive advantage over other fishes only in waters with reduced clarity where ruffe sensory systems are most advantageous (Hoelker and Thiel 1998). In addition, other experiments in our laboratory indicate that the amount of food necessary for standard metabolism, or daily maintenance ration, for gobies is approximately 2% (K. Priemer and C. Bauer, unpublished data), while the daily maintenance ration for ruffe is greater than 3% (Hoelker and Thiel 1998). A combination of these mechanisms likely led to increased goby growth rates relative to ruffe at low resource levels in our 9-week competition experiment.

This finding is significant because even short-term reductions of growth rates can result in decreased population sizes over longer time frames (Persson and Greenberg 1990). Thus, ruffe, which have lower growth rates in the presence of gobies at higher overall fish densities, may have a difficult time establishing sizable populations in areas where gobies are already abundant (currently large areas of the Great Lakes). Establishment of ruffe in areas already invaded by gobies may be especially difficult because overall fish density typically increases in the early stages of invasion. For instance, ruffe may be relegated to less preferred environments (where food resources are more limited or predation pressure is increased), resulting in a scenario that may keep overall ruffe populations low. As a result, the presence of gobies could be an important factor limiting the establishment, distribution, and population size of ruffe in the Great Lakes. Our 9-week competition experiment, which showed that gobies may be competitively superior to ruffe when food resources are limited, provides a potential explanation for the slow invasion of ruffe into the largely goby-dominated environments of the lower Great Lakes.

Correlative evidence also suggests that gobies may be able to displace established ruffe populations in the field. For example, ruffe were introduced into Thunder Bay (Lake Huron) in 1996 and subsequently increased in population size, such that by 1998 ruffe were the most abundant fish caught in the Thunder Bay River estuary (Bowen 2002). However, ruffe populations declined significantly in Thunder Bay in 2000, only 1 year after the establishment of gobies in the estuary (Bowen 2002). This trend of declining ruffe abundance continued during the summer of 2002, when only a few larger adult ruffe were found in the river estuary (A. Bowen, personal communication). By the end of 2002 gobies had replaced ruffe as the most abundant fish found in Thunder Bay River (A. Bowen, personal communication). Low recruitment of ruffe could have many explanations, but it is possible that gobies compete with ruffe for soft-bodied invertebrate food or that gobies consume ruffe eggs or fry (Chotkowski and Marsden 1999; French and Jude 2001). Alternatively, some other environmental factor(s) may currently constrain ruffe in Thunder Bay. Continued monitoring of this river estuary system, as well as nearby areas where ruffe were previously found, may reveal if this inverse relationship between goby and ruffe abundance is real.

Influence of zebra mussels

Zebra mussels could have reduced fish growth in the 1-week competition experiment if zebra mussels increased benthic habitat heterogeneity (which could provide refuge for prey, reduce fish foraging efficiency, and result in lower fish growth rates). Alternatively, zebra mussels could have also increased fish growth rates if they served as a major part of the diet or were incidentally ingested. While we hypothesized that gobies would eat both the soft-bodied worms and zebra mussels available, the presence of zebra mussels did not negatively affect the growth or foraging efficiency of either species. Notably, however, both fish species apparently prefer soft-bodied prey (Fullerton et al. 1998; Diggins et al. 2002; Bauer 2003) such as the worms used in the experiments. Worms may have been abundant enough to make zebra mussel consumption unnecessary, as suggested by Diggins et al. (2002). The use of larger gobies or smaller mussels in laboratory experiments may increase the consumption of zebra mussels, thereby altering the experimental outcome.

Conclusions

Our laboratory experiments investigating competition between gobies and ruffe for habitat and food resources (in the presence or absence of zebra mussels) can be used as an initial basis to predict future habitat use and species interactions in nearshore areas of the Great Lakes. First, our results suggest that while gobies and ruffe do not appear to compete for preferred habitat in the laboratory, they both prefer macrophyte and cobble habitats over sand habitats. Over time, both fish species populations may expand into new habitats, including both cobble and macrophyte-covered areas. This prediction is supported by reports that gobies and ruffe can now be found in some areas of the Great Lakes with extensive macrophyte beds (Jude 2001; G. Czypinski personal communication) and gobies are spreading into open sand in southern Lake Michigan (Clapp et al. 2001). Second, based upon our experiments, gobies may be competitively superior to ruffe in heterogeneous environments even when gobies do not supplement their diet with zebra mussels. Therefore, we predict that ruffe may have difficulty invading areas in the Great Lakes where gobies are well established. It is likely that benthic prey (particularly chironomids and other benthic insects; Ogle et al. 1995; Fullerton et al. 1998; Kuhns and Berg 1999) and native benthic fishes dependent on these insects, will decline in invaded areas. Third, zebra mussels may not alter goby or ruffe growth because zebra mussels do not serve as a preferred food resource for either species. However, if gobies supplement their diet in resource-limited areas with zebra mussels, gobies may gain an additional competitive advantage relative to fishes, both native and exotic, that do not consume zebra mussels.

In summary, vigilant monitoring of these invasive fishes is necessary to determine if competitive exclusion or habitat partitioning will occur and whether the predictions we advance in this paper are supported by field data from the Great Lakes. Laboratory experiments focusing on the mechanisms behind changes in fish populations will also enhance our understanding of the food web consequences associated with these NIS. Increased understanding of the effects of NIS on the Great Lakes benthic food web could be used to better inform policy and management decisions, such as legislation regulating ballast water transport, determining harvest sizes for native fishes, or development of NIS control plans. For example, while efforts to control goby populations through predator stocking or selective harvest may be considered by managers to enhance native fish populations, our results suggest that reduced goby populations may lead to increased ruffe populations. Thus, research findings and management decisions should be integrated to maximize the likelihood that NIS will be controlled and native benthic fish populations will be conserved.

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