Interactions among Zebra Mussel Shells, Invertebrate Prey, and Eurasian Ruffe or Yellow Perch

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ABSTRACT. *The exotic zebra mussel,* Dreissena polymorpha, *is established in all of the Laurentian Great Lakes and may affect benthivorous fishes by increasing the complexity of benthic substrates and changing energy flow patterns within the food web. Native yellow perch,* Perca flavescens, *and the non-indigenous Eurasian ruffe,* Gymnocephalus cernuus, *are benthivores that may compete for limited food resources. As ruffe spread to areas with more dense zebra mussel populations, the zone of interaction among zebra mussels, yellow perch, and ruffe will increase and intensify. In the laboratory, the effect of zebra mussel shells on the ability of these fishes to forage on amphipods* (Gammarus pseudolimnaeus) *and chironomids* (Chironomus plumosus) *was examined in light and darkness. In 12 h, ruffe consumed more amphipods than did similar-sized yellow perch, particularly in darkness on bare cobble, and in light within zebra mussels. Amphipods decreased activity more in the presence of ruffe than yellow perch. More amphipods were found in zebra mussel shells than in bare cobble, whether or not fish were present. In darkness, when ruffe consumed more amphipods on bare cobble, amphipods became more associated with zebra mussel shells. Although ruffe consumed more amphipods than yellow perch, perch consumed more chironomids than ruffe on bare cobble. The presence of zebra mussel shells altered the relative consumption of invertebrates in some substrate-light combinations. Experiments such as these help to improve understanding of the direct and indirect effects of predation between and among native and non-indigenous species that may exert structuring forces on the nearshore communities of the Great Lakes currently or in the future.*

INDEX WORDS: *Benthic macroinvertebrates, Eurasian ruffe,* Gammarus, *Great Lakes, habitat complexity, predation, yellow perch, zebra mussels.*

INTRODUCTION

Ecosystem engineers like zebra mussels (*Dreissena polymorpha*) that alter the quantity and quality of habitat and food resources available to other species may influence the impact of newly-establishing exotic species in the Great Lakes. Zebra mussels have colonized much of the hard substrate in the Great Lakes (and even some soft substrates, Jarvis *et al.* 2000) and have also spread to many rivers and inland lakes. Where abundant, they have dramatically altered trophic interactions and eco-logical function (Nalepa and Fahnenstiel 1995). Zebra mussels have increased water clarity by reducing phytoplankton density (MacIsaac *et al.* 1991, Leach 1993) and primary productivity (Fahnenstiel *et al.* 1995), altered the community structure of benthic algae (Lowe and Pillsbury 1995), increased the abundance and depth of macrophytes (Skubinna *et al.* 1995), and altered nutrient availability from their nutrient-rich feces and pseudofeces (Stewart *et al.* 1998).

Changes in the Great Lakes ecosystem facilitated by zebra mussels have effectively concentrated energy flow into the benthic region from the pelagic region (MacIsaac *et al.* 1992). Several studies have shown dramatic increases in the density and biomass of benthic macroinvertebrates, particularly annelids, gastropods, amphipods, and chironomids in

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and around zebra mussel beds (Dermott *et al.* 1993, Stewart and Haynes 1994, Botts *et al.* 1996). Gammarid amphipods, in particular, can be limited by availability of interstitial habitat (Adams *et al.* 1987), and increases in this habitat may explain observed increases in amphipods after zebra mussel establishment (Ricciardi *et al.* 1997, Stewart *et al.* 1998, González and Downing 1999). If nutrients and food resources are limited, concentrating energy in the benthos may benefit benthic fish at the expense of pelagic feeders.

Yellow perch (*Perca flavescens*) support large commercial and recreational fisheries in the Great Lakes and are currently the focus of much research and media attention because of several consecutive years of recruitment failure in Lake Michigan (Shroyer and McComish 2000). Zebra mussels and yellow perch co-occur in the St. Louis River estuary (Lake Superior) with Eurasian ruffe (*Gymnocephalus cernuus*), a nonindigenous benthivorous fish introduced into North America in the mid-1980s (Pratt *et al.* 1992). Because ruffe are primarily riverine fishes in their native range (Ogle 1995), ruffe may spread not only to the other Great Lakes (Fullerton *et al.* 1998), but also to large river systems and connected inland lakes. Any effect of zebra mussels on interactions between ruffe and yellow perch will likely increase as the range in which these three species occur in sympatry grows, particularly as ruffe spread to areas with higher zebra mussel densities than occur in Lake Superior.

Because they both are primarily benthivorous by age 1+ (Ogle *et al.* 1995) and they prefer similar types of prey (Fullerton *et al.* 2000), competition between yellow perch and ruffe has been suggested, and laboratory experiments have confirmed competition for limited food resources is possible (Savino and Kolar 1996, Fullerton *et al.* 2000). Adaptations of ruffe, such as a well-developed lateral line system (Janssen 1997), night-adapted vision (Ahlbert 1975), and well-developed spines to deter piscine predators (Ogle 1995) confer benefits of ruffe over yellow perch. Indeed, relative to yellow perch, ruffe detected prey at a further distance (Janssen 1997) and have become quite abundant in waters where yellow perch were formerly abundant in Lake Superior.

Given their differential feeding adaptations, however, competition between ruffe and yellow perch may be affected by the presence of zebra mussels. For instance, clear water ecosystems should benefit yellow perch since they are typically found in such habitats (Weaver *et al.* 1997), whereas turbid

ecosystems should benefit ruffe (Bergman 1987, Rosch and Schmid 1996). Similarly, interstitially complex substrates should benefit yellow perch since they typically forage among macrophytes (Weaver *et al.* 1997), whereas ruffe are often found over open mud habitats (Ogle 1995). Because zebra mussels alter these two important factors affecting foraging success (water turbidity and foraging habitat complexity), potentially in favor of yellow perch, the presence of zebra mussels might mitigate competition between these fishes, particularly if the fishes differ in their ability to locate and consume macroinvertebrates associated with zebra mussel colonies.

Although it is intuitive that increased abundance and biomass of benthic invertebrates within zebra mussel beds would benefit benthivorous fishes, studies to date have not shown a clear benefit (Jennings 1996, Thayer *et al.* 1997). These findings may be explained, in part, by the physical structure of zebra mussel shells. Macroinvertebrates such as amphipods may become very closely associated with zebra mussel shells, effectively reducing activity, remaining less visible to predators, and deriving a physical refuge from predation in zebra mussel beds (Stewart *et al.* 1998). Such a reduction in activity is a common response of invertebrates to the presence of fish predators (Kolar and Rahel 1993). Consequently, although more abundant, macroinvertebrates might be less available to fish in the presence of zebra mussels or would be less profitable due to higher energetic costs. The effect of zebra mussels on benthivorous fishes would therefore depend, in part, on the ability of each fish species to locate and consume macroinvertebrates within zebra mussel beds.

In addition to differential abilities of fishes to remove invertebrates from the interstices of zebra mussel shells, benthic invertebrates may recognize potential predators differentially. If indigenous and nonindigenous benthic invertebrates that did not coevolve with ruffe cannot recognize ruffe by visual or chemical cues, then ruffe may derive more benefit than indigenous benthivorous fishes from invertebrates associated with zebra mussels. The overall goal of this project was to determine if zebra mussels differentially modified the consumption of invertebrates by ruffe and yellow perch. To accomplish this goal, a set of experiments was conducted that 1) examined the behavioral responses of macroinvertebrates to the presence of ruffe and yellow perch to determine if activity level helped explain consumption patterns, 2) compared consumption of macroin-

vertebrates (amphipods and chironomids) by ruffe and yellow perch on substrates with and without zebra mussels in light and dark conditions, and 3) quantified substrate use of amphipods in presence and absence of ruffe and yellow perch.

METHODS

General Experimental Methods

Ruffe were collected from the St. Louis River estuary (Duluth, Minnesota) of Lake Superior, and yellow perch that were raised in ponds and had consumed natural prey were obtained from a hatchery in Michigan. Fish species were held separately for at least 30 days after collection in 240-L tanks at 17°C on a 12-h light:12-h dark cycle and were fed redworms (terrestrial oligochaetes). Amphipod and chironomid species that were readily available were used in experiments. *Gammarus pseudolimnaeus* were collected from a northern Indiana river, and were held in the laboratory at 17°C in aerated buckets with leaf debris. Typically considered lotic, *G. pseudolimnaeus* is found throughout the Great Lakes region including in the Great Lakes proper (Holsinger 1976). Individuals 8 to 12 mm were used—a manageable size for fish and a range encompassing sizes of *G. fasciatus*, common in the Great Lakes (up to 14 mm; Pennak 1978), and *Echinogammarus ischnus*, a nonindigenous gammarid found in Lakes Erie (Witt *et al.* 1997), Michigan (Nalepa *et al.* 2001), and Ontario (Dermott *et al.* 1998). A species with holarctic distribution, *Chironomus plumosus* is common throughout the Great Lakes basin (Cook and Johnson 1974), and is found in zebra mussel beds in Lake Michigan (M. Berg, personal communication). Live *C. plumosus* were purchased commercially and were held at 8°C.

Artificial cobble substrates were created for use in all experiments by molding concrete into uniform hemispherical shapes (10 cm diam). Cobbles were soaked in water for 1 week to leach out residual compounds. On half of them, zebra mussel shells were attached over the entire surface using silicone sealant. To prepare mussel shells, live zebra mussels were collected from a southern Michigan lake, dried, and mussel tissue was removed before filling shell valves with silicone sealant. The sealed shells were sorted into size categories: small (10 to 15 mm shell length), medium (15 to 20 mm), and large (25 to 30 mm) and were attached to the cobble with silicone at a high (140 zebra mussels/cobble = 40 large, 70 medium, and 30 small) or low density (80 zebra mussels/cobble

= 20 large, 40 medium, 20 small). When three low-density and three high-density cobble were placed in a 40-L aquarium, a density of 4,400 zebra mussels/m^2 was simulated (a density found in the field, Nalepa and Fahnenstiel 1995). After attaching zebra mussels, cobbles were soaked for 24 h to leach out residual compounds.

To provide additional substrate for invertebrates, water-soaked vermiculite (3 to 5 mm) was added to aquaria, which were then filled with well water. Six cobble (either 6 cobbles without zebra mussels or three low density and three high density zebra mussel cobbles) were placed on the settled vermiculite. After 24 h (to allow for water clearing and for temperature to stabilize at 19 to 20°C), 20 chironomids (133/m^2) were added, followed at 1-h increments by 50 amphipods (334/m^2), and then one fish (either yellow perch or ruffe). Ruffe (9.5 ± 0.3 g, 102 ± 1 mm TL; mean ± 1 SE) and yellow perch (9.1 ± 0.3 g, 82 ± 1 mm TL) were similar in mass. At the end of an experiment, remaining invertebrates were retrieved by rinsing cobble and vermiculite over a 0.25 mm sieve. Experiments were run separately in the light and dark. Separate experiments were conducted to assess amphipod activity, consumption of invertebrates, and zebra mussel shell use by invertebrates.

Amphipod Activity

Substrate type (cobble with or without zebra mussels), predation pressure (no fish, yellow perch, or ruffe), or light level (light or dark) were simultaneously tested to determine if they influenced the swimming activity of amphipods (n = 3 replicates per treatment combination). Because amphipod behavior was the focus of the study, only the threat of fish predation was needed. Thus, observations of amphipod movement began immediately after adding the fish, before the fish was acclimated to experimental conditions. Analogous experiments examining behavior of prey with uncaged predators in the laboratory are found in the literature (Rahel and Kolar 1990, Kolar and Rahel 1993, MacKenzie and Greenberg 1998). In addition, adding predators or prey to a formerly predator-less or prey-less experimental arena is a typical method of conducting such behavioral experiments (Ware 1972, Wahl and Stein 1988, Kolar and Rahel 1993, Einfalt and Wahl 1997). Amphipod activity in a 1-h period was quantified by visually scanning each aquarium every 2 min and counting the amphipods observed moving or swimming. In dark treatments, a black light was shone briefly above each aquarium to quantify movement.

Similar observations were not possible for chironomids because they were well-hidden in the substrate.

A 3-factor ANOVA was used to assess if the proportion of amphipods moving (corrected through the observational period using the number of amphipods recovered and observed predation events) varied with substrate, light level, and predation pressure. Proportional data were arcsine square-root transformed before conducting ANOVA. All statistical analyses were conducted using SAS (SAS Institute 1991) after testing for normality, independence, equal variance, and linearity using the Guided Data Analysis option in SAS.

Consumption of Invertebrates

To assess whether consumption of chironomids and amphipods varied with substrate type (cobble with or without zebra mussel), predation pressure (no fish, yellow perch, or ruffe), or light level (light or dark), invertebrates and fish were sequentially added at 1-h intervals as previously described (n = 3 each treatment combination). After 12 h (allowing for acclimation and feeding), macroinvertebrates were recovered and counted to determine mortality rates. Midway through the experiment, amphipods were observed consuming chironomids, which was confirmed by gut analysis. Because amphipod predation of chironomids could not be distinguished from fish predation, and because it may have differed among fish treatments, the number of unrecovered chironomids was compared between treatments (without normalizing for fish mass). To determine whether chironomid consumption (combined predation by fish and amphipods) differed among treatments, a 3-factor ANOVA (light, substrate, and fish species) was used followed by contrasts for specific treatments.

It was assumed that all unrecovered chironomids from the control treatments were consumed by amphipods (based on complete recovery of chironomids in trials lacking amphipods after 12 h). The 3-factor ANOVA model above was used to assess if substrate or light affected amphipod consumption of chironomids in fishless treatments.

To assess fish consumption of amphipods, the mean number of amphipods missing from fishless controls of the same treatment combination of light level and substrate type was subtracted from the number of amphipods recovered from each replicate. Analysis of fish predation on amphipods (number of amphipods consumed/g fish wet mass) was otherwise the same as for chironomid data.

Data were first $\log_{10}$-transformed to meet the ANOVA assumption of linearity.

Zebra Mussel Shell Use by Invertebrates

To assess substrate choice by invertebrates, vermiculite was first added to each aquarium, then three bare cobbles were added to one side, and then two high-density cobbles and one low-density cobble with zebra mussels were added to the other side (density of $4,356/m^2$ in zebra mussel portion). Chironomids, amphipods, and fish (no fish, yellow perch, or ruffe) were added as in prior experiments. After 1 h, aquaria were divided with a tight-fitting Plexiglas divider to separate invertebrates in bare cobbles from those in cobbles with zebra mussels. Each side was then siphoned separately, and invertebrates within each substrate were retrieved (cobbles were rinsed as in previous experiments) and counted (n = 5).

Two-factor ANOVAs using light level (dark or light) and species (control, perch, or ruffe) as main effects were conducted to determine whether invertebrates altered their substrate type use in the presence of fish. Contrasts were used to compare specific treatments.

RESULTS

Amphipod Activity

Prior to adding fish, many amphipods were observed swimming or lingering on the substrate or aquarium walls. As fish were added, these amphipods frequently scurried for cover (a behavior not induced by inserting an empty fish net into aquaria). After this quick adjustment, amphipod activity remained reduced by 10 to 95% compared to treatments without fish (Fig. 1). Since fish were not acclimated to tank conditions, they showed little interest in prey; a total of four gammarids were observed being consumed across all 36 trials. Little predation occurred, as confirmed by similar numbers of invertebrates recovered with (49.3 ± 0.3 gammarids and 19.1 ± 0.1 chironomids) and without fish (49.6 ± 0.2 gammarids and 19.0 ± 0.2 chironomids) (ANOVA $F_{1, 34} = 0.85$, P = 0.36, and $F_{1,34} = 0.26$, P = 0.61, respectively).

After adding fish, amphipods were seldom seen in the zebra mussel treatments, whereas they were often observed clinging to cobbles or burrowing into the vermiculite in the bare cobble treatments. Overall, amphipod activity was lower in zebra mussels than in bare cobble (Fig. 1; 3-factor,
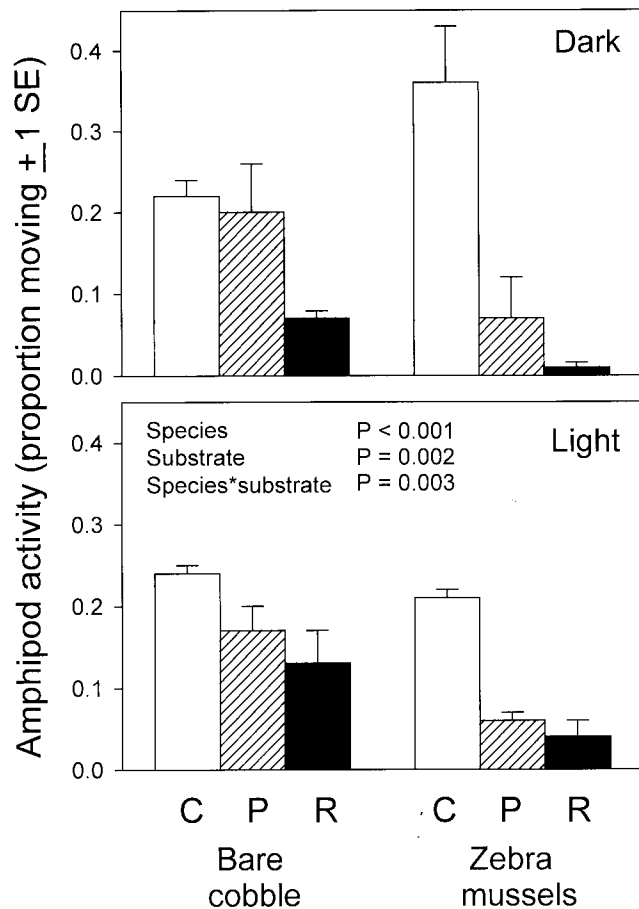
FIG. 1. *Swimming activity of amphipods in the absence of fish, with ruffe, or yellow perch (n = 3) at different light levels (dark or light) and on different substrate (bare cobble or cobble with zebra mussels). Significant P-values from 3-factor ANOVA are indicated. C = fishless control; P = yellow perch; R = ruffe.*

ANOVA, $F_{1, 24} = 11.7$, $P = 0.002$), as well as lower with ruffe than with yellow perch (Fig. 1; 3-factor ANOVA; $F_{2, 24} = 33.4$, $P < 0.001$). Because amphipods were more active in the fishless treatments in zebra mussels, but were less active with fish in zebra mussels, there was significant interaction between species and substrate (3-factor ANOVA, $F_{2, 24} = 7.27$, $P = 0.003$). Light did not affect amphipod activity (3-factor ANOVA; $F_{1, 24} = 0.01$, $P = 0.94$).

Consumption of Invertebrates

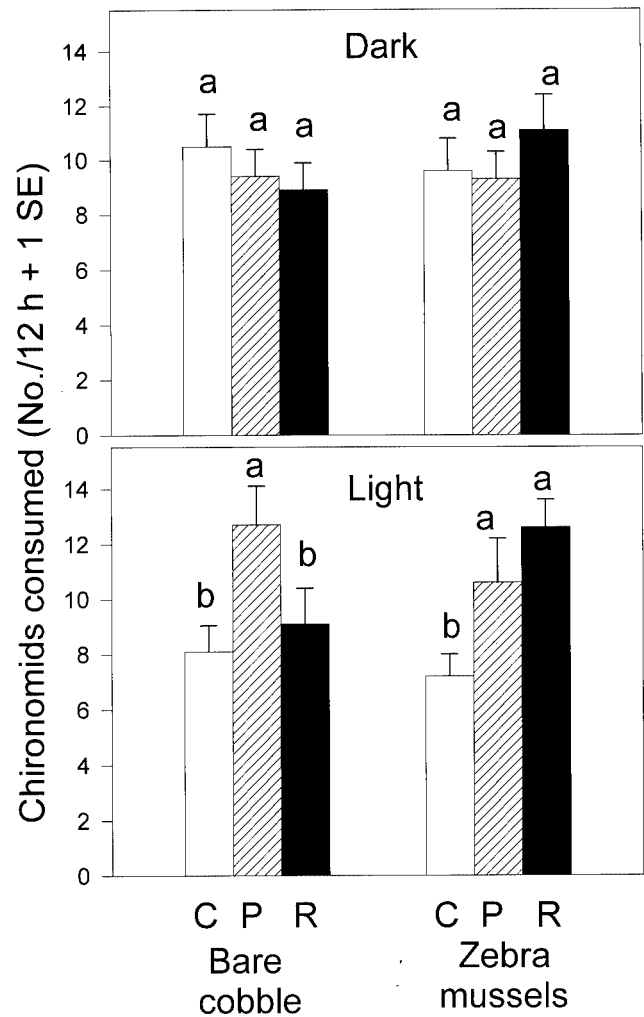Based on main effects in the 3-factor ANOVA, neither fish species, nor substrate type, nor light

FIG. 2. *Number of chironomids consumed by amphipods and fishes in the light and dark on substrate of either bare cobble or cobble with zebra mussels over 12 h (n = 11). Significant differences detected within each bar grouping (light and substrate combination) are indicated with different letters. C = control; P = yellow perch; R = ruffe.*

level affected the number of chironomids recovered from trials. However, there were significant interaction effects between light level and species ($F_{2, 124} = 4.58$, $P = 0.01$) and between substrate type and species ($F_{2, 124} = 3.62$, $P = 0.03$). Contrasts revealed that a fish predation effect was detectable in the light. On bare cobble, perch predation was detectable ($P < 0.01$) and was higher than that of ruffe ($P = 0.03$). On zebra mussel shells (Fig. 2), preda-
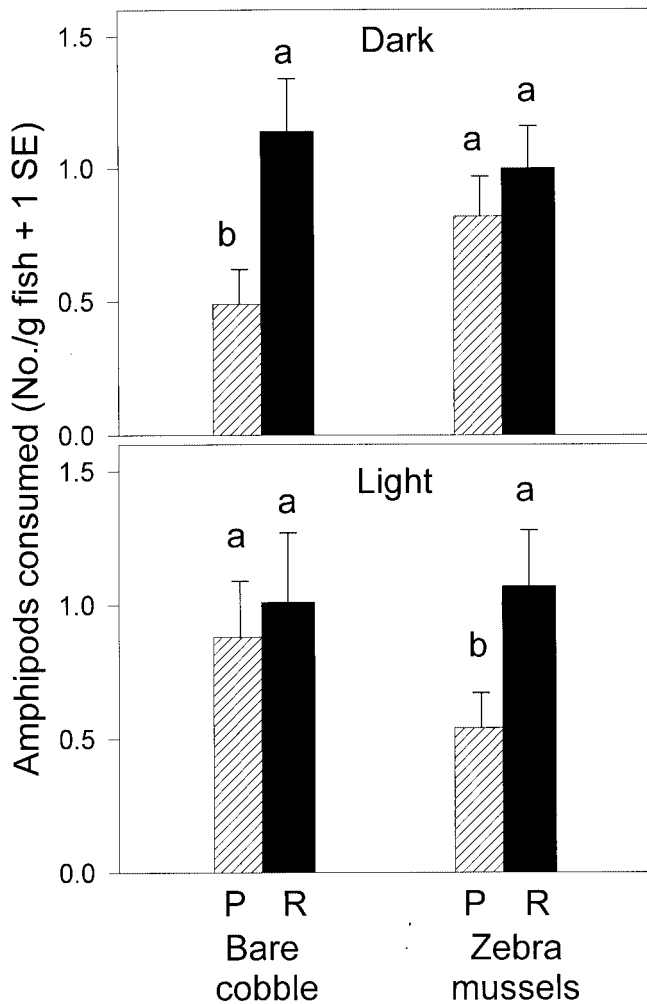
sumption of amphipods. No interactions were significant. Contrasts revealed that in the dark on cobble, ruffe consumed more amphipods than did yellow perch (Fig. 3; P = 0.02). Also, in light on zebra mussels, ruffe consumed more amphipods than did yellow perch (P = 0.04).

Zebra Mussel Shell Use by Invertebrates

Overall, the recovery rate of chironomids was relatively low (15 to 75%), probably due to predation exerted primarily by amphipods. Chironomids had no substrate preference ($F_{1, 16} = 0.00$, P = 1.00) in the absence of fish (Fig. 4). When fish were pre-
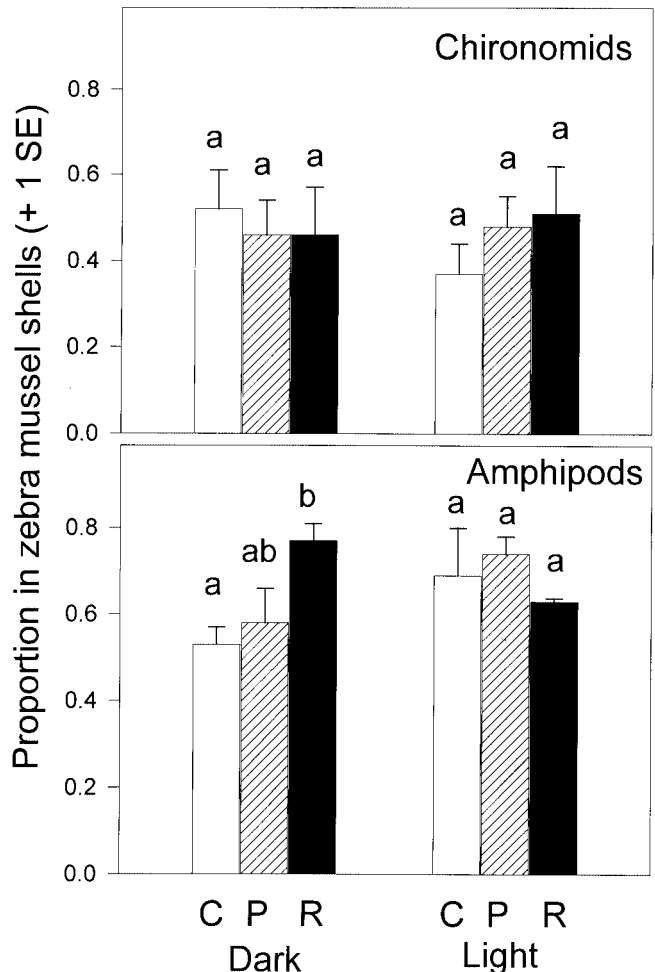

FIG. 3. *Mass-specific consumption of amphipods by fish in the light and dark on substrate of either bare cobble or cobble with zebra mussels over 12 h (n = 11). Significant differences detected within each bar grouping (light and substrate combination) are indicated with different letters. P = yellow perch; R = ruffe.*

FIG 4. *Proportion of chironomids and amphipods found in cobble with zebra mussels in each treatment (C = control; P = yellow perch; R = ruffe) after 1 h access to both bare cobble and cobble with zebra mussel shells (n = 5). Asterisk indicates significantly more use of zebra mussel cobbles than bare cobble in the presence of fish.*

tion by both perch (P = 0.03) and ruffe (P < 0.01) was detectable and similar (P = 0.23).

Contrasts between fishless treatments also showed that amphipods consumed similar numbers of chironomids regardless of substrate type (Fig. 2; cobble, P = 0.13; zebra mussels, P = 0.13) and light level (Fig. 2; light, P = 0.57; dark, P = 0.59).

Overall, ruffe consumed more amphipods than did yellow perch (Fig. 3; $F_{1, 80} = 8.07$, P < 0.01). Neither light level ($F_{1, 80} = 0.04$, P = 0.84) nor substrate alone ($F_{1, 80} = 0.08$, P = 0.78) affected con-

sent, chironomids did not significantly alter their substrate use. Use of cobble with or without zebra mussels did not differ with species ($F_{2, 24} = 0.11$, P = 0.89) nor light level ($F_{1, 24} = 0.12$, P = 0.73).

More amphipods were found in zebra mussels than in bare cobble both without fish (2-factor ANOVA; $F_{1, 16} = 9.19$, P = 0.008) and in their presence (3-factor ANOVA; $F_{1, 48} = 81.43$; P < 0.001). Although the proportions of gammarids in zebra mussels were similar between fish species (2 factor ANOVA; $F_{2, 24} = 1.10$, P = 0.35) and light level (2 factor ANOVA; $F_{1, 24} = 2.44$, P = 0.13), there was significant interaction between these two main effects. While the proportion of gammarids found within zebra mussels without fish and with yellow perch was higher in light than dark, the reverse was true when ruffe were present (2 factor ANOVA; $F_{2, 24} = 4.13$, P = 0.03).

Contrasts showed that in the dark, amphipods preferred zebra mussels to bare cobble with ruffe than without fish (P = 0.06). No other contrasts differed between treatments (all P > 0.13). Recovery of amphipods was high (92 to 100% in all replicates) and no predation activity was observed.

DISCUSSION

It was expected that the increased habitat complexity provided by zebra mussel shells would reduce successful foraging of both fishes. Many studies have shown that predation efficiency of fish declines in habitats that are structurally complex (Savino and Stein 1982, Tonn *et al.* 1989; but see González and Downing 1999 who found similar consumption rates of yellow perch in cobble with live zebra mussels and in bare cobble). In a similar study, Mayer *et al.* (2001) found that in light, yellow perch consumed fewer amphipods in zebra mussels than they did on bare sediments—although they attribute differences in foraging rates more to light level than on the structural complexity provided by zebra mussels. Furthermore, it was expected that zebra mussel shells to more negatively affect the foraging rate of ruffe, which feed primarily over mud (Ogle 1995), than yellow perch, which feed over a variety of substrates (Danehy and Ringler 1991). Contrary to the predictions, the presence of zebra mussel shells did not consistently affect consumption rates. Overall, ruffe consumed more amphipods than did yellow perch, but this response was not universal. Rather, the presence of zebra mussel shells affected predation more subtly

by altering the relative consumption of invertebrates in some substrate-light combinations.

In darkness, ruffe and yellow perch consumed similar numbers of prey among zebra mussel shells, but ruffe consumed more in bare cobble. These findings are consistent with the original hypothesis that ruffe would have higher consumption rates on simpler substrate. In addition, ruffe have dark-adapted vision (Ahlbert 1975), a sensitive lateral line system (Gray and Best 1989), and nocturnal feeding habits (Jamet and Lair 1991, Ogle *et al.* 1995). These adaptations may account for higher consumption rates on bare cobble in darkness. In the light, however, ruffe and yellow perch consumed similarly in bare cobble (akin to Savino and Kolar 1996 where ruffe and yellow perch consumed similar numbers of chironomids in simple substrate), but ruffe consumed more in zebra mussels. These findings are contrary to the hypothesis that yellow perch would consume more prey on complex substrate. Where they are native, ruffe co-occur with zebra mussels, and perhaps they are adapted to foraging in zebra mussels beds occasionally (although these particular ruffe had no previous contact with zebra mussels).

Invertebrate prey often reduce activity in response to predator presence (Kolar and Rahel 1993). It is possible that amphipods were less active in zebra mussels than in bare cobble because of the interstitial habitat the shells provided. It is interesting that amphipods responded more strongly to ruffe than to yellow perch even though *G. pseudolimnaeus* and ruffe were not sympatric. Williams and Moore (1985) reported reduced activity by *G. pseudolimnaeus* after the addition of fish, regardless of whether or not the fish typically consumed them. They suggested that *G. pseudolimnaeus* responded behaviorally to a basic fish secretion or exudate. The results support this hypothesis. Treatments in which amphipods reduced their activity more with ruffe than with yellow perch (bare cobble in light and zebra mussels in darkness) were the same treatments in which ruffe consumed more amphipods than yellow perch. Thus, even though amphipods acted to minimize their risk of predation where they perceived a higher predation threat, they were still consumed more than when perceived predation risk was lower.

It is difficult to interpret consumption of chironomids by ruffe and yellow perch in these experiments because of the unexpected predation on chironomids by amphipods. Amphipods typically eat periphyton and are considered omnivorous scav-

engers that rarely attack and eat live macroscopic prey (Pennak 1978). Adults of some species can become opportunistic predators if sufficient prey are present (Thorp and Covich 1991). In these experiments, amphipod predation on chironomids accounted for much of the chironomid consumption, since fish predation was not detectable in darkness. In light on bare cobble, yellow perch consumed more chironomids than ruffe—the only time when yellow perch had higher consumption rates than ruffe in these experiments.

In their native range, ruffe are competitively superior to European perch (*P. fluviatilis*) in consuming benthic organisms. When they co-occurred with high densities of ruffe, European perch increased their consumption of zooplankton (Bergman and Greenberg 1994). Bergman (1990) suggested that European perch were competitively "sandwiched" between a competitively superior planktivore (roach, *Rutilus rutilus*) and a benthivore (ruffe). Like European perch, yellow perch increased their consumption of zooplankton in the presence of a competitively superior benthivore (pumpkinseed sunfish, *Lepomis gibbosus*; Hanson and Leggett 1985). If ruffe continue to spread in North America and they are able to outcompete yellow perch for benthic organisms, yellow perch may become similarly "sandwiched" between the nonindigenous white perch (*Morone americana*) and ruffe in the lower Great Lakes and invaded river systems. White perch already inhabit the lower Great Lakes and some inflowing rivers, have higher consumption rates than yellow perch (Parrish and Margraf 1990), and eat primarily zooplankton in Lake Erie (Parrish and Margraf 1990). Thus, as ruffe spread to other Great Lakes, particularly to Lake Erie and southern Lake Michigan where both yellow perch and white perch are more abundant than in Lake Superior, yellow perch may become competitively squeezed between better planktivorous (white perch) and benthivorous (ruffe) specialists.

The presence of zebra mussels in the lower Great Lakes may help to mitigate the impacts of ruffe on yellow perch or other fish species as they expand their range. Ruffe are adapted to low light conditions and are found in turbid water where light penetration is low (Bergman 1987, Rosch and Schmid 1996). Since their establishment, zebra mussels have increased water transparency, and decreased phytoplankton abundance and productivity (MacIsaac *et al.* 1991, Leach 1993), allowing an increase in the abundance and depth occupied by macrophytes (Skubinna *et al.* 1995). Combined,

these effects have altered the Great Lakes ecosystem where zebra mussels are abundant to more closely resemble the preferred habitat of yellow perch than that of ruffe. Currently, it is unknown whether ruffe will be able to invade the rivers and inland lakes of North America. Because they have broad environmental tolerances (Ogle 1995) and are abundant in many large river systems in Eurasia (Ogle 1995) with similar physio-chemical conditions, ruffe may eventually inhabit many rivers and inland lakes in North America. As they become established in new areas, ruffe will interact with native and exotic species. As evidenced by the prior interactions among sea lamprey, alewife, and rainbow smelt in the Great Lakes, exotic species can be powerful forces structuring aquatic communities, and such interactions will likely play a significant role in the future.

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