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Predation on Ruffe by Native Fishes of the St. Louis River Estuary, Lake Superior, 1989–1991

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Abstract.—The ruffe *Gymnocephalus cernuus*, an exotic Eurasian percid, recently became established in the St. Louis River estuary, Lake Superior, after accidental introduction. Management actions (catch regulations and stockings) were enacted in 1989 to increase the density of top-level predators in the estuary, and thus to increase predation on ruffe. We conducted a field and laboratory study to determine if, and to what extent, native piscivores consume ruffe. Stomachs of 3,669 predators were examined in 1989–1991. Ruffe occurred in 6.7% of burbot *Lota lota*, 5.8% of bullheads *Ictalurus* spp., 4.7% of smallmouth bass *Micropterus dolomieu*, 2.6% of northern pike *Esox lucius*, 2.6% of black crappies *Pomoxis nigromaculatus*, and 1.3% of yellow perch *Perca flavescens* (4.5% after 1989) captured during the 3-year study. No ruffe were found in 967 stomachs of walleyes *Stizostedion vitreum* examined. Ruffe were 22.7% of the diet (by weight) of bullheads (during the only year bullheads were captured) and 0.1–17.9% of the diet of northern pike. Ruffe were 0.9–24.5% of the diet of smallmouth bass that contained fish, 1.5–6.9% of yellow perch that contained fish, and 0.0–10.9% of black crappies that contained fish. Most ruffe eaten were age-0 or small age-1 fish. In the laboratory, walleyes that were first fed soft-rayed prey or that were also offered soft-rayed prey consumed very few ruffe, whereas walleyes that were first fed spiny-rayed yellow perch or were also offered yellow perch consumed about equal numbers of ruffe and yellow perch. Northern pike and burbot consumed about equal numbers of ruffe and yellow perch in the laboratory. It is unlikely that predation will effectively control the initial expansion of ruffe in other areas of the Great Lakes because native predators initially consume few ruffe, especially if more preferred soft-rayed prey are available.

Ruffe *Gymnocephalus cernuus* (formerly *Acerina cernua*), a percid native to Europe and Asia, were accidentally introduced into the St. Louis River estuary of Lake Superior in the early 1980s, presumably through ballast water discharge from transoceanic ships (Simon and Vondruska 1991; Pratt et al. 1992). Ruffe were first discovered in the St. Louis River in 1986 and positively identified in 1987 (Pratt et al. 1992). A ruffe population was established in the estuary by 1988 and has increased dramatically since then (Pratt et al. 1992; Mills et al. 1993). The potential North American range of ruffe is thought to extend from the Great Plains to the eastern seaboard and north into Canada (Busiahn 1993), the Great Lakes being prime areas for colonization (Busiahn 1993; Edsall et al. 1993).

Ruffe may harm native fish and fauna of the St. Louis River estuary, Lake Superior, and the other Great Lakes (Edsall et al. 1993; Mills et al. 1993). Their diet in the St. Louis River estuary suggests that ruffe may compete with yellow perch *Perca flavescens*, trout-perch *Percopsis omiscomaycus*, and other benthic-feeding fishes (Ogle et al. 1995).

European studies indicate that ruffe may compete with European perch *Perca fluviatilis*, a close relative of the yellow perch. In enclosures in small Swedish ponds, the growth of Eurasian perch declined and the amount of zooplankton in their diet increased when ruffe density was experimentally increased (Bergman and Greenberg 1994). In Loch Lomond, Scotland, the relative abundances of ruffe and Eurasian perch were inversely related (Maitland 1990; Adams and Tippett 1991). In addition to competition for food, egg predation by ruffe has been implicated in the decline of some populations of powan *Coregonus lavaretus* (Balagurova 1963; Pavlovskiy and Sterligova 1986; Adams and Tippett 1991) and vendace *C. albula* (Pokrovskii 1961). Thus, expansion of ruffe in the Great Lakes may have serious ecological and economic impacts on existing fish communities (GLFC 1992; Edsall et al. 1993).

Local resource agencies began an intensive management plan in an attempt to limit the density of ruffe in the St. Louis estuary and to discourage the dispersal of ruffe from the estuary (Busiahn 1993). As part of this plan, piscivores were stocked and restrictions were imposed on the harvest of native piscivores. In 1989 and 1990, an average of 631 fry of walleye *Stizostedion vitreum*, 13 fingerling walleye, and 6 subadult northern pike *Esox lucius* were stocked per hectare in the 4,654-ha estuary. In 1989, daily creel limits were reduced from six to two walleyes and from five to two northern pike. The minimum length limit on walleye was also increased from 305 to 381 mm.

The effectiveness of predators in controlling ruffe has varied in Europe. Populations of ruffe and other forage species declined after the abundance of zander (pikeperch) *Stizostedion lucioperca* and northern pike increased in some Polish lakes (Bonar 1977) and after regulations restricted the harvest of zander in an Estonian lake (Pihu and Maemets 1982). Increases in ruffe abundance following declines of predatory fish in some Russian (Popova and Sytina 1977) and English (Duncan 1990) waters also indicate that predatory fish may regulate ruffe abundance. However, in Lake Tjeukemeer, increased zander abundance caused by termination of the zander fishery did not result in a decreased abundance of ruffe because the abundance of European smelt *Osmerus eperlanus*, the preferred prey of zander, was high and unaffected by zander abundance (Lammens et al. 1990).

In this paper, we describe the extent to which native predators consumed exotic ruffe in the St. Louis River estuary and the ability of three large piscivores (walleye, northern pike, and burbot *Lota lota*) to consume ruffe under artificial conditions. These two pieces of information provide a basis for evaluating the effect of predation on ruffe during the species' early years in the St. Louis River estuary, and they also provide a baseline with which future determinations of predator diet can be compared.

Methods

Field Study

Several gears were used to collect an adequate number of predators from the estuary during the open-water seasons of 1989, 1990, and 1991. In each year, we collected predators regularly with two main gears. Every other week during all three years, we towed a 5.2-m-lead-line bottom trawl for 5 min at 2.6 km/h at 40 locations selected randomly from throughout the estuary. More details about this gear and selection of locations were given by Ogle et al. (1995). On weeks when we did not trawl, we set fyke nets (25-mm-bar mesh) for approximately 24 h at four locations or electrofished (pulsed DC) at night along a predetermined length of shoreline in Allouez and Superior bays (Figure 1). We set fyke nets only in 1989 and 1991 and electrofished only in 1990. To obtain additional samples, we conducted two intensive sampling efforts in 1989 and obtained stomach contents from fish collected by cooperating management agencies for other purposes in all three years. The two intensive efforts were conducted in Allouez and Superior bays with an 11.2-m-lead-line bottom trawl towed for 5 min at 4.0 km/h and fyke nets (as described above). In addition, we obtained predators from experimental gill nets (1.8 m deep and 15.2 m long with mesh bar measures of 19, 25, 32, 38, and 51 mm, hung at 50%) set in 1989 and 1990, from an open-water creel survey in 1989, and from fyke nets (same as described above) set at additional locations in November 1989. All walleyes, northern pike, smallmouth bass *Micropterus dolomieu*, and black crappies *Pomoxis nigromaculatus* collected in all three years, all yellow perch over 150 mm total length (TL) collected in 1990 and 1991, all bullheads (primarily *Ictalurus melas*, but some *I. nebulosus*) collected in 1991, and all burbot collected in 1989 from these gears were used for complete diet analysis. Altogether, we collected 1,925 predators with regular sampling, 480 predators with intensive sampling, and 400 predators with the other gears just described. In addition, we included all yellow

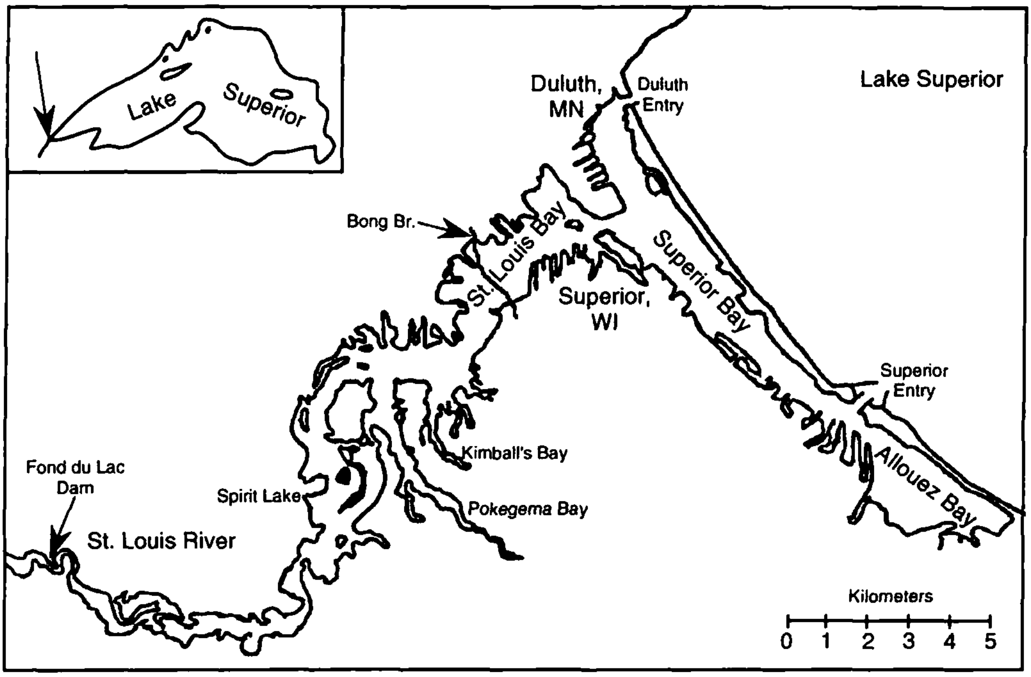

FIGURE 1.—Map of the St. Louis River estuary, Lake Superior.

perch over 110 mm captured in 1989 and all bullheads over 160 mm captured in 1990 for the purpose of evaluating predation on ruffe only (i.e., these analyses were not included in the general diet description). These samples brought the number of predator stomachs examined for ruffe to 3,669.

Individual predators were measured (TL ± 1 mm) and their whole stomachs or stomach contents were removed and preserved in 10% formalin. Stomach contents were flushed (by a method similar to that of Seaburg 1957) from live fish and whole stomachs were removed from all dead fish (which were mostly from gill nets and the creel survey). Stomach contents were identified, counted, and weighed wet (±0.1 g). Invertebrate prey were identified to family or genus but were pooled for summarization. Fish prey were identified to species or family (in the case of small centrarchids and ictalurids) with the aid of reference fish specimens, body parts (e.g., otoliths and preopercles), and meristics (Ogle 1992). Prey fish that were largely intact were measured (TL ± 1 mm). The wet weight at time of ingestion for intact prey fish was estimated from length–weight equations derived from forage fish collected in routine trawl catches or from literature values (Ogle 1992). When partially digested prey fish could not be measured for length, their weight was estimated as the mean weight of measurable specimens of that species found in stomachs collected during the same month. Ruffe found in stomachs were classified as age-0 or age-1 and older based on TL.

Diet composition of predators caught in the field was summarized as the percent of total wet weight at time of ingestion. Diet composition summaries for species thought to be primarily piscivorous (walleyes, northern pike, and bullhead) were based on identifiable invertebrates and fish, whereas summaries for species thought to be less piscivorous (smallmouth bass, yellow perch, and black crappie) were based on only identifiable fish each year. To ensure adequate sample sizes for describing the diet of each predator, all stomach samples collected in the same year were pooled. Walleyes captured in the 11.2-m bottom trawl in May 1989 were not included in the diet summaries because they were collected earlier that year than in 1990 and 1991, and they were on their spawning migration from Lake Superior. These walleyes contained nearly 97% (by number) rainbow smelt *Osmerus mordax*, which had also congregated for spawning near Superior Entry.

Laboratory Study

The ability of walleyes, northern pike, and burbot to consume ruffe was tested in trials with only

TABLE 1.—Numbers and sizes of predators sampled in the St. Louis River estuary, 1989–1991, and numbers, ages, and sizes of ruffe found in stomachs of those predators. Age and size are summarized for all measurable ruffe observed in predator stomachs collected during all 3 years. Total lengths (TL) are in millimeters.

Predators					Ruffe consumed					
		Sample size			Year			Age		Mean TL (SE)
Species	Mean TL (range)	1989	1990	1991	1989	1990	1991	0	≥1	
Walleye	419 (180–758)	524	203	240	0	0	0	0	0	
Northern pike	606 (251–1,015)	262	40	275	2	1	12	2	13	114 (8)
Burbot	553 (333–830)	60	0	0	5			4	1	86 (18)
Bullheads	256 (190–441)	0	383	742		11	80	11	80	81 (2)
Smallmouth bass	300 (173–468)	47	36	89	1	4	3	5	3	53 (6)
Yellow perch	238 (169–335)	491	75	126	0	8	4	9	3	43 (5)
Black crappie	280 (184–335)	20	17	39	0	1	3	4	0	28
All predators		1,404	754	1,511	8	25	102	35	100	79 (2)

ruffe, and the preference for or against ruffe was tested in trials with ruffe and alternative prey. For walleye only, these two tests were conducted with predators that were first fed either soft- or spiny-rayed prey. Predators were acclimated and tested in circular tanks that were 0.5 m deep and either 1.5 m in diameter (walleye and burbot) or 2.5 m in diameter (northern pike). Water temperatures in the tanks were 11–12°C. Yellow perch, which are common in the St. Louis River, were selected as the alternative spiny-rayed prey. Lake trout *Salvelinus namaycush* and rainbow trout *Oncorhynchus mykiss* were used as soft-rayed alternative prey because they were readily available and easily maintained in the laboratory. During tests, a known number of prey, in excess of possible daily consumption rates (3–5% of predator biomass), were measured (TL ± 1 mm) and added to each test tank. The number of prey eaten was recorded and prey were replenished daily to the same density.

Four tanks containing three or four walleyes (450–600 mm TL) per tank were provided ruffe and alternative prey. Walleyes in two of the tanks were tested first on spiny yellow perch (mean TL ± SE, 112 ± 4.9 mm), then on ruffe (84 ± 2.2 mm), and finally on a combination of ruffe and yellow perch (the same sizes as in the single-prey tests). Walleyes in the other two tanks were tested first on soft-rayed lake trout (123 ± 5.0 mm), then on ruffe (120 ± 12.5 mm), and finally on a combination of lake trout and ruffe. Walleye in the first set of tanks were given an additional choice of large (137 ± 5.4 mm) and small ruffe (85 ± 3.7 mm) during weeks 11 and 12 of the trials.

Individual northern pike (N = 2; 600 and 750 mm) and burbot (N = 6; 380–550 mm) were tested similarly, but only with ruffe (150 ± 8.8 mm for northern pike; 93 ± 2.4 mm for burbot) and yellow perch (150 ± 8.8 mm for northern pike; 115 ± 3.8 mm for burbot). In addition, a choice of large (145 ± 7.6 mm) and small ruffe (84 ± 4.8 mm) was offered to each northern pike. The second northern pike quit feeding during weeks 9–12. It was subsequently offered yellow perch for 3 weeks, during which time it fed consistently and was then retested on a combination of yellow perch and ruffe for an additional 3 weeks. One burbot died during the mixed-prey species test and data from that fish are not included in this analysis.

Comparisons among treatments in the experiments for walleye (two tanks) and northern pike (two individuals) were based on the mean number of fish consumed per predator per day over each weekly interval. Sample sizes were too small for meaningful statistical analysis. For the experiments with burbot, the median number of fish consumed per burbot per day over the entire 14-d experiment was the response tested.

Results

Consumption of Ruffe and Diet Composition in the Field

All predators examined from the estuary except walleyes consumed some ruffe (Table 1). Ruffe occurred in 6.7% of burbot, 5.8% of bullheads, 4.7% of smallmouth bass, 2.6% of northern pike, 2.6% of black crappies, and 1.3% of yellow perch (4.5% after 1989) captured during the 3-year study. No ruffe were found in 967 walleye stomachs examined (Table 1). Northern pike and bullheads generally consumed age-1 and older ruffe, whereas the other predators consumed mostly age-0 ruffe (Table 1). However, bullheads consumed only age-0 ruffe in 1990 and small age-1 ruffe in 1991.

TABLE 2.—Percentages of total prey weight in stomachs of walleyes, northern pike, and bullheads contributed by identifiable prey items. This summary is restricted to stomachs with identifiable food. The total numbers of stomachs examined are reported in Table 1.

	Walleye			Northern pike			Bullheads
Prey items	1989 (N = 142)	1990 (N = 89)	1991 (N = 35)	1989 (N = 112)	1990 (N = 16)	1991 (N = 81)	1991 (N = 248)
Ruffe	0.0	0.0	0.0	0.1	17.9	11.7	22.7
Yellow perch	19.1	2.3	32.1	21.3	53.3	38.7	13.6
Black crappie	6.9	2.6	2.9	6.2	0.0	17.5	7.0
Walleye	0.0	0.0	0.0	6.8	0.0	2.6	0.0
Etheostomatinae	0.0	6.7	0.0	0.0	0.0	0.0	0.3
Trout-perch	0.1	0.0	0.0	0.8	16.9	0.7	8.9
Other spiny-rayed fish[a]	1.8	1.3	0.0	4.5	0.0	0.0	0.3
Ictaluridae	17.2	24.7	11.1	0.2	0.0	2.7	0.6
Emerald shiner	11.8	30.9	15.1	5.2	9.2	4.3	1.9
Spottail shiner	13.4	9.2	23.4	2.1	0.0	11.2	37.1
Rainbow smelt	25.0	11.3	3.8	4.1	0.6	0.0	0.0
Catostomidae	0.2	0.3	0.0	47.5	0.0	10.2	0.1
Other soft-rayed fish[b]	2.8	0.0	2.8	0.9	0.0	0.0	3.5
Invertebrates	1.6	10.9	8.8	0.3	2.1	0.4	4.0

[a] Rock bass *Ambloplites rupestris*, smallmouth bass, white perch, and unidentified Centrarchidae.
[b] Alewife *Alosa pseudoharengus*, common shiner *Luxilus cornutus*, and golden shiner *Notemigonus crysoleucas*.

Northern pike consumed larger ruffe than burbot and bullheads, and these three species consumed larger ruffe than the other predators (Table 1). Ruffe were more than 10% (by weight) of the complete diet of northern pike in 1990 and 1991 and of bullheads in 1991, which was the only year that the diet composition of bullheads was determined (Table 2). In addition, ruffe were more than 10% of the piscine diet of smallmouth bass in 1990 and 1991 and of black crappies in 1990 (Table 3). The relatively high percentage of ruffe in the diet of northern pike and black crappies in 1990 was due to a single ruffe found in relatively few samples of both predators.

Walleyes fed mostly on emerald and spottail shiners *Notropis atherinoides* and *Notropis hudsonius* in all three years, but varied their consumption of other prey among years (Table 2). The other major prey eaten by walleyes were ictalurids in all three years, yellow perch in 1989 and 1991, and rainbow smelt in 1989 and 1990. Invertebrates, mostly burrowing mayflies *Hexagenia* spp., were about 10% of walleye diets in 1990 and 1991, but only 2% in 1989. Walleye consumed mostly small ictalurids (mean, 55.3 mm TL; SD, 19.5), which have hardened soft rays (Hubbs and Lagler 1958), but a wide range of sizes of spiny yellow perch (mean, 111.8 mm; SD, 33.9).

Northern pike fed primarily on catostomids and yellow perch in 1989, and yellow perch and a va-

TABLE 3.—Percentages of total prey weight in stomachs of smallmouth bass, yellow perch, and black crappies contributed by identifiable prey items. This summary is restricted to stomachs with identifiable fish. The total numbers of stomachs examined are reported in Table 1.

	Smallmouth bass			Yellow perch		Black crappie		
Prey items	1989 (N = 11)	1990 (N = 20)	1991 (N = 27)	1990 (N = 20)	1991 (N = 37)	1989 (N = 8)	1990 (N = 2)	1991 (N = 6)
Ruffe	0.9	21.4	24.5	6.9	1.5	0.0	10.9	3.0
Yellow perch	35.9	10.1	0.0	0.0	5.4	11.3	0.0	0.0
Black crappie	16.3	2.7	18.4	0.0	13.8	7.3	0.0	93.9
White perch	0.0	0.0	0.0	0.0	0.0	0.0	28.3	0.0
Etheostomatinae	10.6	18.2	6.3	10.0	1.7	0.0	0.0	0.0
Trout-perch	1.4	17.5	4.6	13.6	7.2	0.0	0.0	0.0
Other Centrarchidae	4.9	0.4	2.9	0.0	0.0	25.4	0.0	0.0
Walleye	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.1
Ictaluridae	2.1	0.0	0.0	0.0	0.0	10.0	0.0	0.0
Emerald shiner	0.0	11.0	11.2	55.7	20.5	10.7	60.7	0.0
Spottail shiner	14.0	18.7	24.3	13.8	51.0	25.9	0.0	0.0
Other soft-rayed fish[a]	13.8	0.0	7.9	0.0	0.0	9.4	0.0	0.0

[a] Alewife, golden shiner, and rainbow smelt.

riety of other items in 1990 and 1991 (Table 2). The other major prey eaten by northern pike were ruffe and trout-perch in 1990 and black crappies, ruffe, spottail shiners, and catostomids in 1991. Among the major spiny fish besides ruffe, northern pike consumed medium-size to large yellow perch (mean, 133.4 mm; SD, 41.0) and small black crappies (mean, 105.4 mm; SD, 31.3).

Bullheads fed primarily on spottail shiners, ruffe, and yellow perch (Table 2). In August–September of 1991, many age-0 black crappies were captured in the fyke nets along with many bullheads that contained only age-0 black crappies. This suggests that bullheads may have consumed the abundant small black crappies in the fyke nets and that the consumption of black crappies by bullheads was overestimated. In addition to the age-0 black crappies, bullheads consumed intermediate-size spiny yellow perch (mean, 95.6; SD, 33.0).

Smallmouth bass ate mostly spiny-rayed fish, and ruffe was a prominent noninvertebrate food item in 1990 and 1991 (Table 3). Yellow perch consumed mostly emerald shiners in 1990 and spottail shiners in 1991 (Table 3). Large black crappies ate mostly centrarchids *Lepomis* spp. and spottail shiners in 1989, emerald shiners in 1990, and age-0 black crappies in 1991 (Table 3). More than 90% of the fish eaten by yellow perch and smallmouth bass and 100% of the fish eaten by black crappies were less than 100 mm TL.

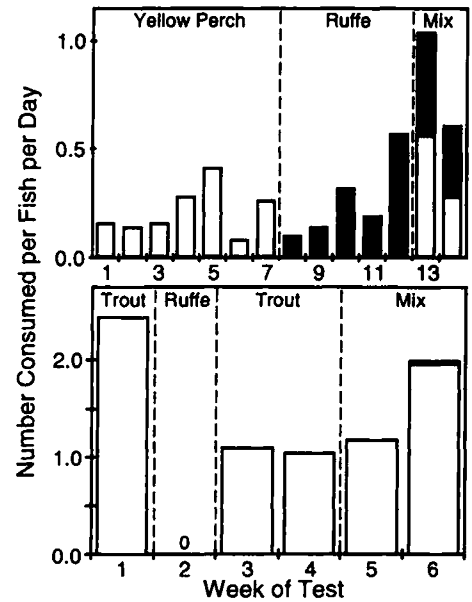

FIGURE 2.—Mean consumption rate per individual per day by walleyes during each week of predation tests with yellow perch, ruffe, or a combination of yellow perch and ruffe (top) or with trout, ruffe, or a combination of trout and ruffe (bottom). A choice of large and small ruffe was offered in weeks 11 and 12 during the yellow perch–ruffe series. Filled bars are consumption rate of ruffe and open bars are consumption rates of alternative prey.

Consumption of Ruffe in the Laboratory

Walleye consumption of ruffe in laboratory tanks was affected by the walleye's previous feeding experience and the type of alternative prey offered. Walleyes that were first fed soft-rayed fish (trout) consumed no ruffe when only ruffe were offered and very few ruffe when both ruffe and trout were offered (Figure 2). Walleyes that were first fed yellow perch consumed ruffe offered alone at a rate similar to the rate observed for yellow perch alone and consumed ruffe and yellow perch at similar rates when both prey were offered (Figure 2). When presented equal numbers of small and large ruffe, 0.33 small and 0.03 large ruffe were consumed per walleye per day.

Northern pike tested in the laboratory gave varied results. Both pike consumed about equal numbers of ruffe and yellow perch when each prey was offered alone (Figure 3). The first pike consumed no ruffe when yellow perch were simultaneously offered. The second pike consumed no food when both ruffe and yellow perch were first offered, but consumed both prey when they were offered a second time. When given a choice of prey size, both northern pike ate only large ruffe.

Burbot ate similar numbers of ruffe and yellow perch in single- and mixed-prey species tests ($P > 0.10$). In single-prey species tests, burbot ate a median (95% confidence interval) of 0.32 (0.14–0.50) yellow perch and 0.36 (0.07–0.71) ruffe per day. In mixed-prey species tests, burbot ate 0.43 (0.28–0.64) yellow perch and 0.14 (0.00–0.50) ruffe per day.

Discussion

Bullheads and northern pike probably exerted the greatest overall predation pressure on the ruffe population in the St. Louis River estuary. The field study indicated that bullheads, burbot, piscivorous smallmouth bass, and northern pike were the primary consumers of ruffe. Overall predation by bullheads was likely greatest because they are abundant in the estuary (Ashland Biological Station, unpublished data). Overall predation by burbot and smallmouth bass was likely low because burbot inhabit the estuary for only a short time (Schram 1983) and smallmouth bass have low

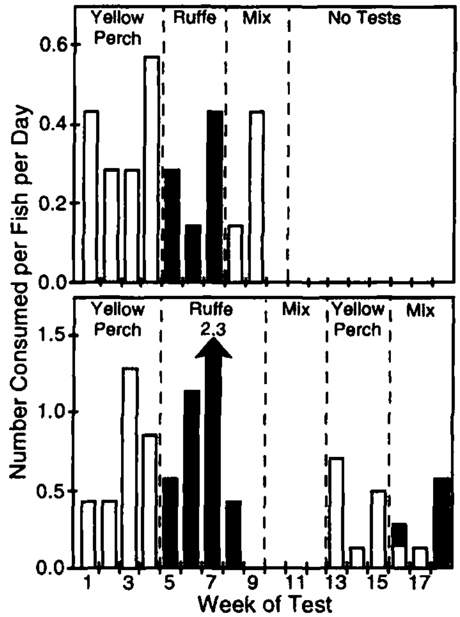

FIGURE 3.—Mean consumption rate per individual per day by the first (top) and second (bottom) northern pike during each week of predation tests with yellow perch, ruffe, or a combination of yellow perch and ruffe. A choice of large and small ruffe was offered to the first northern pike in weeks 5–7 and to the second northern pike in weeks 8 and 9. Filled bars are consumption rate of ruffe and open bars are consumption rates of alternative prey.

abundance (Ashland Biological Station, unpublished data). Overall predation on ruffe by northern pike was probably high because the resident population of northern pike is large, even though some fish may leave the estuary for short periods (J. Spurrier, Minnesota Department of Natural Resources, personal communications). Predation by walleyes was not detected in the St. Louis River estuary, even though we examined 967 walleye stomachs. Furthermore, most adult walleyes only reside in the estuary for a few months during and following the spawning season (Schram et al. 1992). Yellow perch and black crappies consumed some ruffe, but overall predation was likely low because piscivorous size-classes of these predators were not abundant (Ashland Biological Station, unpublished data).

The field results suggest that some predators, especially walleyes, may have selected other prey over ruffe. Ruffe increased from the seventh most abundant species captured in the routine bottom trawl samples in 1989 to the second most abundant fish captured in 1990 and 1991 (Ashland Biological Station, unpublished data). This increase in rank of ruffe in the bottom trawl catches was due to both an increase in ruffe abundance and a decrease in the abundance of yellow perch and small forage fish (GLFC 1992). Furthermore, more small ruffe, which the field study and laboratory experiments suggest are preferred by most predators (except northern pike), became available as large year-classes of ruffe were produced and body growth of ruffe declined (Ashland Biological Station, unpublished data). However, over the same time, the percentage of ruffe in the diet of most predators remained low or was lower than percentages of less abundant prey. For example, walleyes did not consume ruffe during the study, and northern pike consumed much less ruffe than they did yellow perch in the last two years of the study.

The ruffe's large dorsal, anal, pelvic, and preopercular spines may deter predation by walleyes, but may have less of an effect on northern pike. Spines are an effective antipredator adaptation because they increase the apparent size of the prey, limit the attack to the prey's head, and may puncture the predator's throat or stomach lining (Eklov and Hamrin 1989). In the field, walleyes consumed both soft-rayed and spiny fish, although the spiny fish were generally small. In the laboratory, walleyes consumed fewer yellow perch and ruffe than soft-rayed trout, very few ruffe when trout were present, and more smaller than larger ruffe, results consistent with an aversion to spines. However, walleyes in the laboratory readily consumed ruffe when they were previously fed yellow perch. Thus, walleyes can be conditioned to eat ruffe, but they seem to prefer soft-rayed prey to ruffe. When ruffe were first introduced into the St. Louis River estuary, soft-rayed emerald and spottail shiners were abundant there (Ashland Biological Station, unpublished data). The availability of these prey may be one reason why no walleye stomachs from the estuary contained ruffe. Northern pike also consumed both spiny- and soft-rayed prey in the field, but the spiny prey were larger than those consumed by walleyes, which suggests that spines deter northern pike less. Furthermore, both laboratory and field evidence suggest that northern pike prefer larger ruffe.

In addition to the ruffe's spiny armor, its habitat preferences may reduce the probability of encounter between it and predators. Age-1 and older ruffe stay near the bottom (Ahlbert 1970; Bergman 1988) of deeper, darker waters during the day and of shallower littoral areas at night (Ogle et al. 1995). This behavior would reduce encounters with predators that feed by sight in good light, such as northern pike, smallmouth bass, black crappies, and yellow perch (Scott and Crossman 1973). Furthermore, northern pike generally feed on pelagic prey in shallow littoral areas during the day, as indicated by the large proportion of yellow perch and shiners in their diet and by reports in the literature (Hart and Hamrin 1988; Savino and Stein 1989). In contrast, there should be a high probability of encounter between age-1 and older ruffe and predators that are active at twilight or night, such as walleyes (Scott and Crossman 1973) and bullheads (Darnell and Meierotto 1965).

The spatial and temporal overlap between age-0 ruffe and piscivorous predators in the St. Louis River estuary is difficult to predict because the diel distribution of age-0 ruffe is largely unknown. Contact between age-0 ruffe and crepuscular or nocturnal predators, such as walleyes and bullheads, should be high because age-0 ruffe are also near the bottom at night in both shallow littoral areas and in deeper channels (Ogle et al. 1995). The day-time distribution of age-0 ruffe has not been adequately determined (Ogle et al. 1995).

Even if the encounter rate between ruffe and a predator is high in low-light conditions, predation may be low because the sensory system of ruffe is exceptionally sensitive. Their tapetum lucidum (Ahlbert 1970; Craig 1987) should help ruffe see predators in twilight, when predators such as walleye typically have an advantage over their prey. Their sensitive lateral line system (Disler and Smirnov 1977; Denton and Gray 1989) should help them detect movements of active predators in low or no light (Collette et al. 1977).

Evidence from this study suggests that predation on ruffe in the St. Louis River estuary by native predators may increase in the future, even though predation on ruffe remained low or increased only slightly for some predators during this study. First, if ruffe continue to increase in density, their growth will be reduced (Hansson 1985; Bergman and Greenberg 1994) and they will remain small longer; most predators apparently prefer small ruffe. Second, continued predation by native predators on mostly native prey may reduce the abundance of the preferred native prey, leading to an increase in the number of ruffe consumed. Both of these scenarios would be accompanied by undesirable changes in the estuary's community.

No matter how predation on ruffe changes in the future, the results of this study indicate that predation is unlikely to effectively control ruffe during early stages of colonization elsewhere in the Great Lakes. Native predators will likely consume few ruffe initially, especially if more preferred alternative prey (e.g., soft-rayed fish or yellow perch) are available.

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