J. Great Lakes Res. 24(2):217-227
Internat. Assoc. Great Lakes Res., 1998

Reproduction and Early Life History of Ruffe *(Gymnocephalus cernuus)* in the St. Louis River, a Lake Superior Tributary

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ABSTRACT. Reproduction and early life history of ruffe (Gymnocephalus cernuus,) was investigated during April to July in 1993 and 1994 in the St. Louis River, a western Lake Superior tributary. This study was conducted to assist fishery managers in determining possible interactions among the early life stages of ruffe and other North American percids, and in obtaining information useful in developing control methods targeted at the early life stages of ruffe. Ruffe had a prolonged spawning period that extended from late April to late June with peak spawning in mid to late May when water temperatures were between 12 and 14°C. The majority of ruffe protolarva were captured 1 to 2 weeks after egg deposition between mid May and late June and most were captured in water 0.5-m deep. Onshore-offshore movements were not observed, but diel vertical movements of larval ruffe were observed on several occasions. The greatest chance of ballast water transport of pelagic larval ruffe is between mid May and July. Information on reproduction and early life history in this report will assist fishery mangers in development of ruffe control methods, and assist Great Lakes shipping in ballast water management to prevent the spread of ruffe.

INDEX WORDS: Reproduction, ruffe, Gymnocephalus cernuus, early life history, larval fish, St. Louis River, Lake Superior.

INTRODUCTION

Ruffe *(Gymnocephalus cernuus)* are native to northern, central, and eastern Europe, including northeastern France, England, the rivers entering the Baltic and White seas, and all of Siberia including the Kolyma River but excluding the Amur (Collette and Banarescu 1977). Ruffe have the widest distribution of any percid except the European perch (Perca fluviatilis) (Collette and Banarescu 1977). Ruffe were first discovered in the St. Louis River in 1986 (Pratt 1988, Pratt et al. 1992, Selgeby 1993) and apparently were introduced in ballast water discharged from transoceanic ships (Pratt et al. 1992). There is concern among fishery managers that this exotic species will have negative ecological affects on native fishes of the St. Louis River and North America (GLFC 1992).

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Since ruffe were found in the St. Louis River their range has increased in the Great Lakes. Ruffe have been found along the north shore of Lake Superior as far east as Thunder Bay, Canada, in 1991, along the south shore of the lake as far east as the Ontonagon River, Michigan, in 1994 (Slade *et al.* 1995), and in Lake Huron, near Alpena, Michigan, in late summer, 1995 (Kindt *et al.* 1996). The potential for range expansion of this species in the Great Lakes and North America is high because of the heavy shipping traffic from the Duluth-Superior Harbor (St. Louis River) to other Great Lakes ports (GLFC 1992, Edsall *et al.* 1993).

Ruffe are small benthophagic dwellers of stagnant or slow-flowing water that rely heavily on the lateral line system to avoid predators and to capture prey (Disler and Smirnov 1977). Ruffe prefer waters of moderate to high productivity and have a competitive advantage over European perch in waters with high productivity and low light penetration (Bergman 1988, Bergman 1990). Ruffe are also known to inhabit brackish waters, especially in the Black Sea, where they usually prefer soft mud bottoms that lack vegetation (Johnsen 1965). Ruffe are found in all habitats throughout the St. Louis River (Selgeby and Ogle 1992). They are more abundant in the deepest channels (8 to 10 m) at ice out, in waters 4 to 6 m deep in the summer months, and return to the deepest channels in the fall to overwinter.

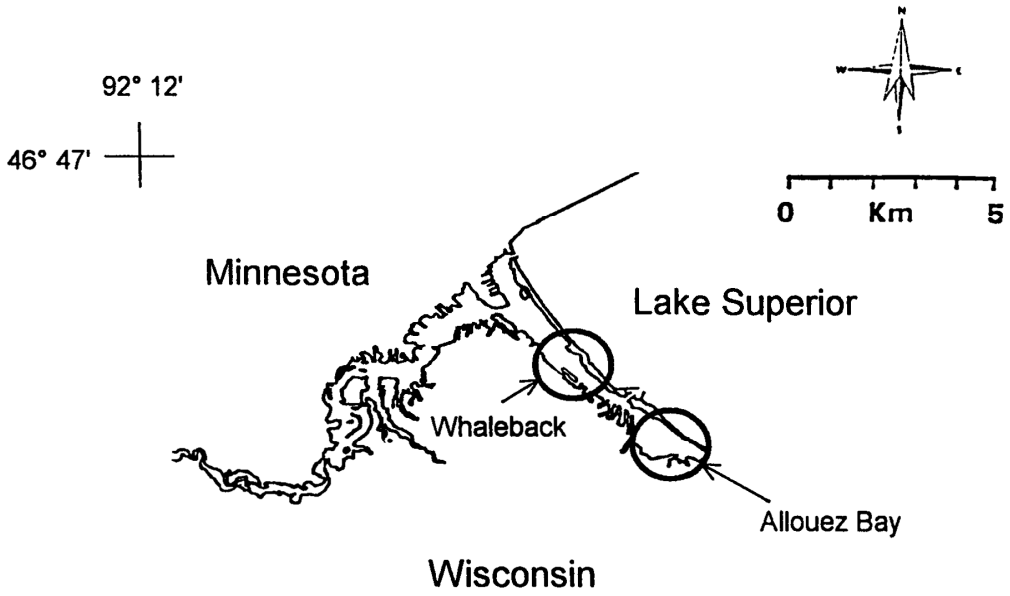

FIG. 1. Ruffe sampling at Allouez Bay and Whaleback in the St. Louis River, Duluth, Minnesota.

Current information on the reproduction and early life history of ruffe in North America is based on laboratory studies (Fairchild and McCormick 1996). Objectives of this study were to determine when and at what water temperature ruffe spawn, to establish the egg incubation period, and to document vertical and horizontal movements of ruffe larvae. Information obtained in this study will provide further insight into the ecology of this exotic species.

MATERIALS AND METHODS

Study Area

Sampling was conducted from 26 April to 9 July 1993 and from 25 April to 12 July 1994 in the lower harbor section of the St. Louis River. Sampling was conducted at Allouez Bay and at Whale-back where major concentrations of ruffe had been found in preliminary studies during 1990 to 1992 (Fig. 1). Water in the St. Louis River is highly stained with organic materials from tributaries upstream. Maximum depth is about 6.0 m upstream and 16.0 m in

the lower harbor sections where the river channel is maintained for shipping (Loy 1963). The Whaleback sample site was located in the lower harbor section of the river. The Allouez Bay sample site was located in the lower section of the river, however it has not been as severely altered as the rest of the lower river. Allouez Bay has a mean depth of about 1.5 m and many woody snags and emergent vegetation are along the shore. One deep pocket in Allouez Bay was once mined for sand and is now between 4 and 5 m deep.

Water temperatures were recorded continuously at each sample site during the sampling periods with Ryan Recording Thermometers[1] that were fastened to stakes driven into the bottom. Each thermometer was positioned 1 m below the surface of the water in water 1.5-m deep. Water temperatures were recorded to the nearest 0.1°C at 20-min intervals in 1993 and at 30-min intervals in 1994. The Allouez Bay thermometer malfunctioned in 1994, and no data were obtained. Mean daily water temperatures and standard errors (SE) were calculated daily.

Collections of adult ruffe were made to determine the initiation and duration of spawning based on gross visual assessment of the gonads. We defined the spawning period as lasting from the first to the last day that female ruffe were observed in running condition. Fish were sampled with a shrimp try-trawl (5.2-m lead-line, 3.81-cm mesh body, 6.2-mm cod end) once weekly in 1993 and three times weekly in 1994. In the laboratory, adult ruffe were measured (nearest 1 mm total length), weighed (nearest 0.1 g), and dissected. Ovaries were removed from female ruffe and weighed to the nearest 0.1 mg in 1993 and 0.001 g in 1994 to determine gonadosomatic index which we used to determine when the majority of female ruffe spawned. Individual ovary and body weights were used to calculate a gonadosomatic index (GSI) for each adult female (Neja 1988, West 1990) where,

$$GSI=(\text{ovary weight} / \text{body weight}) * 100.$$

In 1993, GSI was calculated for a maximum of five females in each 10-mm size class greater than 70 mm, and in 1994 a maximum of 15 females were selected from each 20-mm size class greater than 70 mm. Mean GSI was calculated separately for each sampling date and site. Three-date running averages were calculated for 1994 but not in 1993 when samples were only taken once weekly.

Larval ruffe were collected with a pushnet to determine incubation period, hatching time, and to document horizontal movements after hatching. The pushnet was 1-m square (656 mm mesh) and suspended about 0.5-m in front of a jonboat propelled by a 30-horsepower outboard motor and pushed at about 2 km/h. Larval collections were made at night at Whaleback and Allouez Bay weekly from 20 May to 7 July 1993. Six 3-minute pushnet samples were collected at each site; two each at the 0.5-, 2-, and 5-m depth contours. Larval fish captured were preserved in 95% ethyl alcohol. In 1994, larval sampling was conducted twice weekly at each site from 16 May to 11 July. Pushes were 3 minutes in duration and sampling was initiated at 2300 h each night. Three replicate samples were collected at 0.5-m depth contour intervals from 0.5 to 3 m and at 5 m at Whaleback and from 0.5 to 2 m and at 5 m at Allouez Bay.

We attempted to determine diel vertical migration of larval ruffe using a 0.5-m bongo net (351 mm mesh). In 1993, sampling was conducted during the day on 28 May and 11 June and during the day and night on 21 and 30 June and on 6 July. The net was towed horizontally at about 6.15 km/h for 3 minutes at 1-m intervals from the surface to the bottom. Flow meter readings were recorded at the beginning and end of each tow and the volume of filtered water was calculated. All larval fish collected were preserved in 95% ethyl alcohol. In 1994, day and night collections were made at the Whaleback and Allouez Bay sample sites at weekly intervals from 24 May to 12 July. Sampling was at 1-m intervals from the surface to 7 m at Whaleback and from the surface to 4 m at Allouez Bay. Tow duration was 5 minutes except on May 31 when tows were reduced to 3 minutes to prevent clogging the net with zooplankton.

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[1] *Mention of trade names does not imply endorsement of this product by the federal government.*

Diurnal sampling began at 1100 hours, and nocturnal sampling at 2300 hours. Flow meter readings were recorded at the beginning and end of each tow to determine the amount of water filtered and all larval fish were preserved in 10% formalin.

Larval fish samples were examined under binocular stereoscope at 6 to 12x with percids identified to species, and others to family. Ruffe were removed from the samples and counted. Identifications were based on descriptions by Norden (1961), Auer (1982), Simon and Vondruska (1991), and French and Edsall (1992), and on laboratory reared ruffe reference specimens (J.H. McCormick, Environmental Protection Agency, Duluth, MN; John French, U.S. Geological Survey, Great Lakes Science Center, Ann Arbor, MI). Identity of a subsample of these fish was verified by Nancy Auer (Michigan Technological University, Houghton, MI).

Mean densities of ruffe (number / 100 m^3 of water filtered) were calculated for each depth, date, and sample site for pushnet samples and for each depth, time of day, and sample site for bongo net samples. Random samples of up to 30 ruffe were measured (nearest 1 mm) under a binocular stereoscope with an ocular micrometer at 6x. Mean lengths and SE were calculated for each date, depth, time of day (bongo net samples), and sample site. To determine when newly hatched ruffe were present in the water column, densities of 3 to 5 mm ruffe were calculated for each date and location, for each year, from length frequency and density estimates. Ruffe between 3 and 5 mm had previously been described as newly hatched (Simon and Vondruska 1991, French and Edsall 1992, Kovac 1993, and Fairchild and McCormick 1996).

To detect onshore-offshore movements of larval ruffe after hatching, densities of larval ruffe were compared among depths across time. Density estimates were log (n+1) transformed and compared using ANOVA (a level < 0.05) to detect differences in densities. Tukey's (HSD) confidence levels were used to make multiple comparisons.

To determine if larval ruffe exhibit vertical movements on a diel basis, densities from bongo net samples were log (n+1) transformed and two-way ANOVA (a level < 0.05) was used to compare catches by time of day sampled and among depths sampled. The HSD confidence levels were used to make multiple comparisons. Analysis of variance (α level ≤ 0.05) was used to compare the densities of ruffe among depths during day and night separately. The HSD confidence levels were used to make multiple comparisons among depths.

To determine depth preferences among ruffe of different sizes, mean lengths by date and depth were tested in a two-way ANOVA (α level ≤ 0.05) and Scheffe confidence levels were used to make multiple comparisons (Sokal and Rohlf 1969). Analysis of variance (α level ≤ 0.05) was used to test for significant differences in mean lengths among depths between samples taken during the day and the night. Scheffe confidence levels were used to make multiple comparisons.

RESULTS

The ruffe spawning period in Allouez Bay and Whaleback was about 8 weeks in 1993 and 1994. Female ruffe were observed in running condition between early May and late June in 1993 and between late April and mid June in 1994 when water temperatures were between 5 and 18°C. Based on GSI curves (Figs. 2, 3), the majority of female ruffe spawned during a much shorter period of time. In 1993 and 1994, the majority of females spawned from mid May to the first week of June while water temperatures were between 12 and 14°C and accelerating. A significant negative correlation was observed between mean GSI and water temperature at both locations and years (r-values ranged between -0.82 and -0.93; $p < 0.001$). After the majority of ruffe spawned mean GSI values decreased and continued to decrease through July.

Ruffe larvae hatched over a 6-week period at Al-louez Bay and Whaleback in 1993. Larvae were captured at Allouez Bay from 30 May to 10 July, with peak catch the week of 13 June (Fig. 4). Larvae were captured at Whaleback from 23 May to 3 June with a peak catch the week of 30 May. Most larvae were captured at both sites during the 4 weeks between 23 May and 13 June.

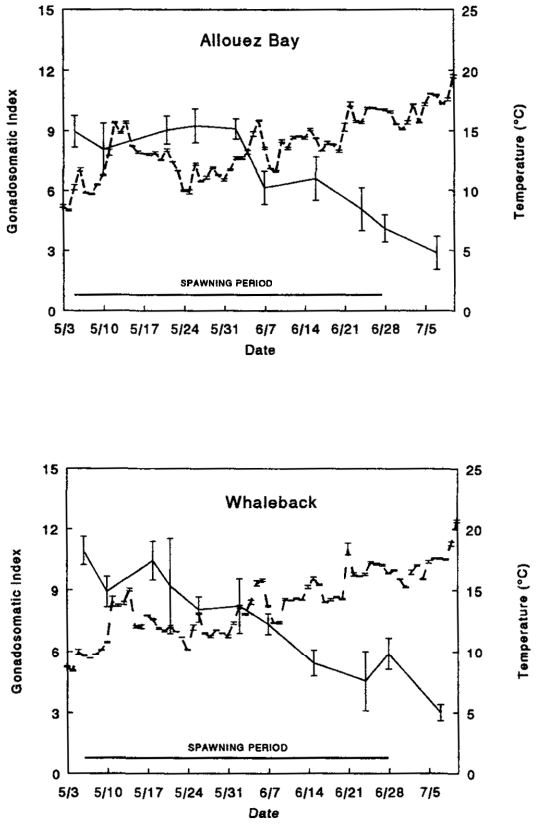
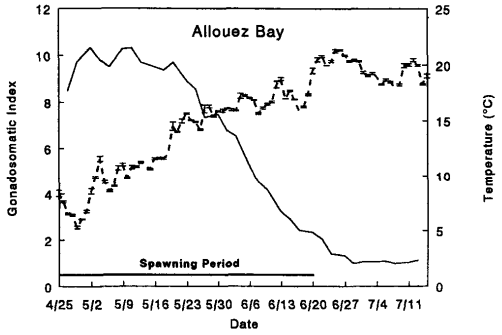


FIG. 2. Mean gonadosomatic index of female ruffe and water temperature (+/- SE) at Allouez Bay and Whaleback in 1993. The dashed line is mean daily water temperature and the solid line is mean gonadosomatic index.

Ruffe larvae were more abundant and were captured earlier in 1994 than in 1993. Larvae were captured from 16 May to 9 July (an 8-week period) at both Allouez Bay and Whaleback in 1994, but most were captured between 16 May and 20 June (Fig. 5). Hatching at Whaleback was bimodal with major hatching events occurring on about 25 May and 15 June.

Horizontal movements of ruffe larvae were not observed at the two sites sampled in 1993. Larval ruffe were first captured in water 0.5 m deep at Whaleback on 24 May (Table 1). Densities of larval ruffe were similar among 0.5, 2, and 5-m depths between 30 May and 3 July (ANOVA; $F = 0.20$; $df = 2, 40$; $p = 0.8201$) and were about the same size (ANOVA; $F = 0.23$; $df = 2, 201$; $p = 0.7971$), indicating no offshore or onshore movements. Observations were similar at Allouez Bay with the exception of larval ruffe first occurring on 1 June over 2- and 5-m of water. (Table 1). Densities were similar among all depths sampled (ANOVA; $F = 0.71$; $df = 2, 38$; $p = 0.7126$) and ruffe were about the same size at all depths (ANOVA; $F = 0.23$; $df = 2,364$; $p=.7911$).

Horizontal movements of larval ruffe were not observed at Whaleback in 1994. Larvae were first captured over all water depths sampled on 16 May (Table 2). The abundance of larval ruffe dramatically increased over 3- and 5-m of water on 21 May but within 5 days these densities rapidly declined. The unusual occurrence of larval ruffe over deep water may have been due to an unusual early spawning in deep water or to wind-blown movement of surface water to these offshore locations. On 25 May, a sharp increase in larval abundance was seen at the 0.5-m depth interval, and subsequently most ruffe were captured over 0.5-m of water through 11 July (ANOVA; $F = 3.43$; $df = 6, 161$; $p = 0.003$). Survival of ruffe larvae seemed to be low at Whaleback. Most ruffe captured there were from 3 to 7 mm and only small numbers of ruffe larger than 7 mm were captured.



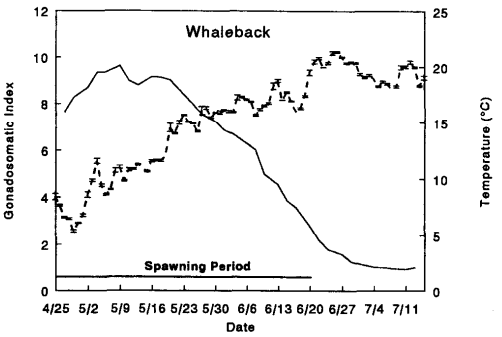
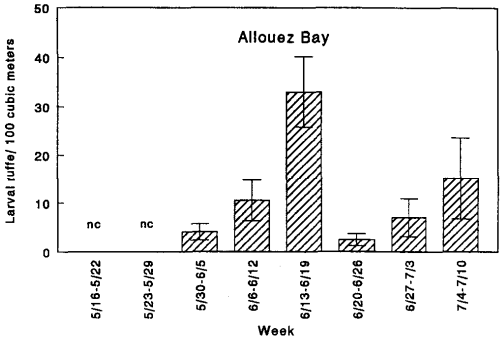


FIG. 3. Mean gonadosomatic index of female ruffe and water temperature (+/– SE) at Allouez Bay and Whaleback in 1994. The dashed line is mean daily water temperature and the solid line is mean gonadosomatic index. Water temperatures recorded at Whaleback are used on both figures.



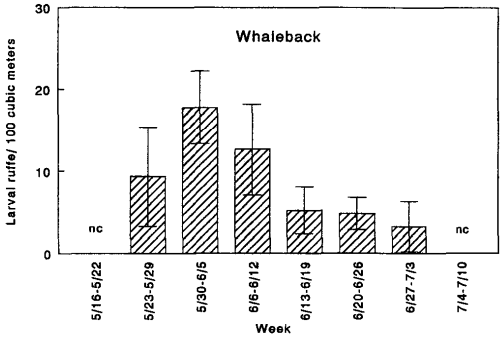
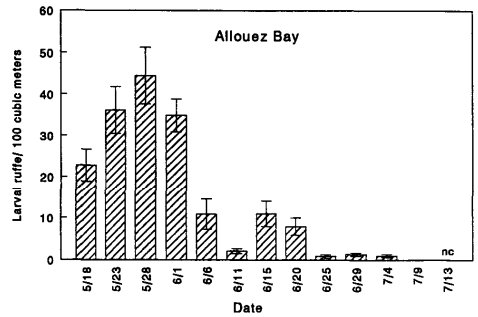


FIG. 4. Mean density of 3–5 mm ruffe (+/– SE) by date captured at Allouez Bay and Whaleback in 1993 (nc = none captured).



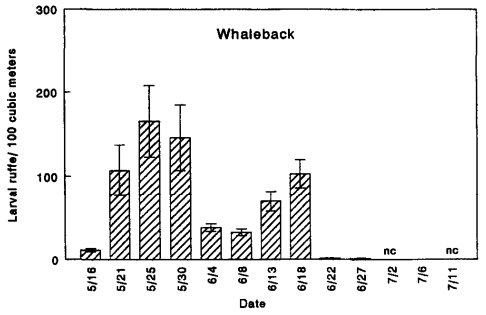


FIG. 5. Mean density of 3-5 mm ruffe (+/– SE) by date captured at Allouez Bay and Whaleback in 1994 (nc = none captured).

TABLE 1. Mean number of larval ruffe captured per 100 meters^3 of water in pushnet collections by depth, date, and location in 1993.

	Whaleback Depth (m)		
Date	0.5	2.0	5.0
May			
19	0	0	0
24	35	0	0
June			
1	21	19	25
7	14	25	12
15	0	4	12
24	10	8	5
28	0	1	10
July			
7	1	0	0
	Allouez Bay		
May			
19	0	0	0
24	0	0	0
June			
1	0	9	8
7	18	26	0
15	45	36	26
23	8	4	6
28	10	11	4
July			
7	33	7	12

TABLE 2. Mean number of larval ruffe captured per 100 m^3 of water in pushnet collections by depth, date, and location in 1994. The 2.5- and 3.0-meter depth intervals were not sampled in Allouez Bay.

	Whaleback Depth (m)						
Date	0.5	1.0	1.5	2.0	2.5	3.0	5.0
May							
16	11	3	21	14	15	10	5
21	17	57	20	21	77	187	374
25	571	133	98	93	160	88	41
30	658	160	155	109	62	64	105
June							
4	69	26	28	17	29	38	62
8	35	61	44	48	18	33	50
13	84	150	130	136	116	58	99
18	196	253	199	197	124	79	37
22	1	4	5	2	3	0	3
27	0	1	3	4	1	1	1
July							
2	0	0	0	0	0	0	0
6	1	0	0	0	1	0	0
11	1	0	0	0	0	0	0
			Allouez Bay				
May							
18	23	17	31	23			9
23	43	29	54	44			47
28	26	29	90	65			94
June							
1	45	80	59	48			74
6	6	11	19	10			67
11	9	13	26	34			152
15	30	16	19	9			28
20	14	31	33	19			21
25	1	2	3	1			4
29	1	3	3	3			6
July							
4	0	7	10	7			5
9	2	1	4	3			0
13	0	1	1	1			0

Larval ruffe were captured over all water depths sampled at Allouez Bay on 18 May, and densities were similar among all depths sampled (ANOVA; $F = 0.98$ $df = 4, 175$; $p = 0.4226$) (Table 2) in 1994. In Allouez Bay ruffe captured over deeper water were significantly larger than the ruffe captured nearshore in shallower water (ANOVA; $F = 24.32$; $df = 4, 2099$; $p < 0.001$; Fig. 6). Ruffe captured nearshore were 3 to 7 mm while most ruffe captured in the offshore areas (5 m) were 7 to 10 mm. However, this was the only time during this study that larger larval ruffe were observed to migrate offshore into deeper water.

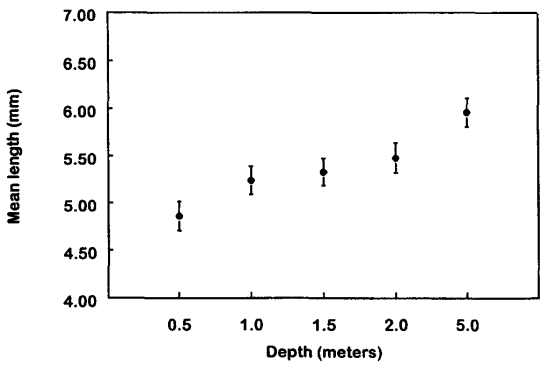


FIG. 6. Mean length of larval ruffe (+/- SE) captured during pushnet collections at Allouez Bay 1994.

Diel vertical movements of larval ruffe were observed on two occasions at Whaleback in 1993. On 21 June, larval ruffe were more abundant in deeper water during the day, and then migrated toward the surface at night (Fig. 7). This pattern was also seen the following week (Fig. 7). Ruffe were about the same size at all water depths during daytime sampling (ANOVA; $F = 1.91$; $df = 6, 304$; $p = 0.078$), but were significantly larger in the upper 1 m of water during nighttime sampling (ANOVA; $F = 5.96$; $df = 7, 269$; $p < 0.001$). This suggests that only the largest ruffe larvae migrated toward the surface.

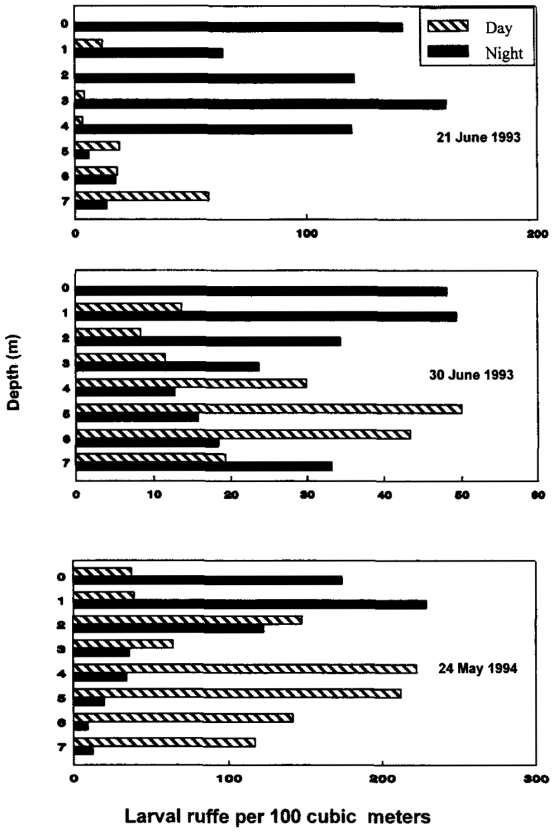


FIG. 7. Number of larval ruffe captured during bongo net sampling at Whaleback.

Diel vertical movements of larval ruffe were observed on one occasion at Whaleback in 1994. Ruffe were more abundant in the deeper waters during the day and migrated towards the surface at night on 24 May (Fig. 7). On the remaining sampling dates, no evidence of diel vertical movements was observed at either location, and ruffe appeared randomly distributed throughout the water column. Larval ruffe were approximately the same size at all water depths during day and nighttime sampling at Allouez Bay and Whaleback in 1994.

DISCUSSION

Time of Spawning

Ruffe in the St. Louis River spawned in late April through late June in 1993 and 1994. This spawning period is similar to that reported for ruffe in their native range in Lake Ilmen, former USSR, and the Danube River, Slovakia (Fedorova and Vetkasov 1974, Bastl 1988). Such a prolonged spawning period probably helps ensure reproductive success. Water temperatures in the St. Louis River during the spawning period ranged from 5 to 18°C, which is a broader range of water temperatures than that reported by Willemsen (1977), who noted that ruffe spawned in Lake IJessel, Holland, when water temperatures were between 12 and 18°C. Most ruffe in the St. Louis River spawned during mid to late May at water

temperatures of 12 to 14°C with peak spawning occurring 2 weeks earlier in 1994 than in 1993, and there was high negative correlation between the mean GSI and water temperature. Our results along with those in the literature suggest that temperatures are favorable for reproduction throughout much of the Great Lakes basin.

The ruffe population in the St. Louis River spawned over a prolonged period of time although it appeared that individual females did not release multiple clutches of eggs. The prolonged spawning period is possibly due to different rates of development of the ovaries among females of different ages. In contrast, Kolomin (1978) reported that female ruffe lay eggs in two clutches in the Nadym River, Yamal-Nenets region of the former USSR, and Hokanson (1977) suggested that the reproductive cycle of ruffe is extremely adaptable to changing environmental conditions. Detection of multiple clutches of eggs being released during spawning was not evident during this study. Perhaps water temperatures in the St. Louis River rise and stabilize too quickly for this to occur. Butskaya (1980) reported that ruffe spawning ended at 18°C because males quit producing viable sperm. In the St. Louis River, water temperatures reached this level by mid to late June in our study. If temperatures had remained lower than 18°C for a longer period of time, multiple spawning events might have occurred.

Most ruffe spawned later than walleye *(Stizostedion vitreum)* and yellow perch *(Perca flavescens)* in the St. Louis River. Our results show that although some ruffe were spawned while walleye and yellow perch were spawning in the St. Louis River, the majority of ruffe spawned later than the other two species. Walleye in the St. Louis River spawned in early April, shortly after ice-out at water temperatures ranging from 5 to 7°C (Schram *et al.* 1992), which is well below temperatures that initiate peak spawning of ruffe. Yellow perch egg strands were discovered in the St. Louis River prior to the major spawning events of ruffe in both 1993 and 1994, and most yellow perch probably spawned 7 to 10 days before the majority of ruffe. This leads us to believe that competition for spawning habitat among these species is unlikely.

Incubation Period and Time of Hatching

Larval ruffe hatch and become pelagic within 1 to 2 weeks after egg deposition and could possibly be entrained in ballast water during the pelagic period. Larval densities sharply increased in pelagic samples between mid and late May during this study when water temperatures were approximately 15°C. In the laboratory, Fairchild and McCormick (1996) observed ruffe hatching 5 to 6 days after fertilization at 16°C and active feeding and swim-up occurring 13 days after fertilization.

Pelagic larval ruffe were captured for approximately 8 weeks. Hatching over a prolonged period of time may help ensure better reproductive success under marginal environmental conditions and may help to explain why ruffe have increased substantially in this system since they first invaded. Pelagic larval ruffe could easily be entrained in the ballast water of ships from the St. Louis River from mid May through mid July, and then transported to other Great Lakes harbors. In 1992, the Ruffe Control Committee (Busiahn 1993) recommended that ballast water from the Duluth-Superior harbor be exchanged over deep offshore waters of Lake Superior in an effort to reduce survival of entrained ruffe and to restrict ruffe to the western basin of Lake Superior. However it is difficult to directly measure the success of this management guideline.

Larval Movements

Onshore-offshore movements of larvae were not observed during this study. Pelagic larval ruffe were captured over all depths sampled for an extended period of time between mid May and the third week of June. Individual larval ruffe remain pelagic for only a brief period of time after hatching and move to the benthic interface approximately 1 to 2 weeks after hatching. After this time ruffe are between 7 to 10 mm and were rarely captured in open water. This suggests that by this size they had moved to the benthic interface and by mid June ruffe greater than 14 mm were readily captured in bottom trawls (Ogle 1992; unpublished data USGS).

Our study revealed that larval ruffe were sometimes more abundant at greater water depths during daytime sampling and more abundant near the surface at night. When diel vertical migrations of larval ruffe occurred, they were likely due to diel vertical migrations of zooplankton, which were being preyed upon by larval ruffe. However, on most occasions diel vertical movements of larval ruffe were not observed and they were scattered among the depths sampled.

The early life history of this species is highly adaptable. This fish has the ability to reproduce over a wide range of water temperatures and the extended spawning and hatching period ensures annual reproductive success over a wide range of environmental conditions. Developing control efforts for the early life stages of this species will be complicated because of the extended spawning and hatching period documented in this study. The complicated yet successful life history may help to explain why ruffe have become firmly established in the St. Louis River (Bronte *et al.* 1998) and other systems outside of its native range. It is almost certain that this species will invade other areas of the Great Lakes and its population in North America will continue to grow.

ACKNOWLEDGMENTS

This study was funded by the Environmental Protection Agency and was part of a Master's thesis submitted by William P. Brown to the University of Minnesota-Duluth. We thank Andy Edwards for his assistance with laboratory work and field collections, and Andy Edwards, Derek Ogle, Chuck Bronte, and Tom Edsall for reviews of earlier drafts of this paper. This article is contribution 1020 of the USGS, Great Lakes Science Center.