Diet and Feeding Periodicity of Ruffe in the
St. Louis River Estuary, Lake Superior

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Abstract.—Ruffe *Gymnocephalus cernuus*, a percid native to Europe and Asia, is established in the Lake Superior drainage and could have negative impacts on native fish through competition for forage and predation on fish eggs. We investigated the diet of ruffes in the 4,654-ha St. Louis River estuary in May–October 1989–1990 and the feeding periodicity of ruffes in two adjacent habitats during five 24-h periods in summers 1990–1991. Ruffes were primarily benthophagous. Age-0 ruffes fed mostly on cladocerans and copepods in early summer and midge larvae (Chironomidae) in late summer and fall. Adult ruffes less than 12 cm fed mostly on midges and other macrobenthos but also consumed large numbers of microcrustaceans. Adult ruffes 12 cm and larger fed mostly on midges, burrowing mayflies *Hexagenia* spp., and caddisflies (Trichoptera). Ruffes consumed few fish eggs. Adult ruffes in deeper waters and all age-0 ruffes fed throughout the day as indicated by weight patterns of stomach contents. However, adult ruffes generally moved to shallower waters at night to feed most heavily. Results of this study indicate that ruffes will probably compete with other benthic-feeding fishes such as yellow perch *Perca flavescens* and trout-perch *Percopsis omiscomaycus*.

Ruffe *Gymnocephalus cernuus*, a percid native to Europe and Asia, is firmly established in the St. Louis River estuary and has began to colonize other areas of Lake Superior. In the St. Louis River, ruffe became the most abundant fish captured in bottom trawls in 1991 (Ashland Biological Station, unpublished data) 5 years after first being captured there (Simon and Vondruska 1991; Pratt et al. 1992). Ruffes have recently been collected outside of the St. Louis River estuary in south-shore tributaries to Lake Superior, between the St. Louis River and the Ontonagon River (Michigan), and on the north shore of the lake in Thunder Bay, Ontario (Pratt et al. 1992; T. Busiahn, U.S. Fish and Wildlife Service, personal communication).

Ruffes compete with Eurasian perch *Perca fluviatilis* (Bergman 1990; Bergman and Greenberg 1994) and are thought to compete with a variety of other European and Asian species (Zadorozhnaya 1978; Boikova 1986; Sokolov and Vasil'ev 1989; Duncan 1990; Winfield 1992). Ruffes may compete with a variety of species because their diet is varied and they can feed effectively in a

wide range of environments. In Europe and Asia, ruffe diet varied between locations and was composed primarily of microcrustaceans (Johnsen 1965); chironomid larvae (Johnsen 1965); macrocrustaceans, including *Pallasea* spp., *Pontoporeia affinis*, and *Mysis relicta* (Nilsson 1979; Hansson 1984); or the eggs of powan *Coregonus lavaretus* and vendace *Coregonus albula* (Pokrovskii 1961; Fedorova and Vetkasov 1974; Adams and Tippett 1991). Bergman (1988) found that ruffe feeding efficiency was insensitive to decreasing light levels and was not significantly reduced even in complete darkness. Although complete diel feeding patterns have not been documented for ruffe, ruffes were more active at dawn and dusk (Westin and Aneer 1987) and stomach fullness increased during the night (Jamet and Lair 1991).

Ruffes may also prey on the eggs of native fish. Ruffes have been shown to eat powan eggs in the laboratory (Mikkola et al. 1979; Pavlovskiy and Sterligova 1986) and in the field (Adams and Tippett 1991). Pavlovskiy and Sterligova (1986) and Adams and Tippett (1991) concluded that egg pre-
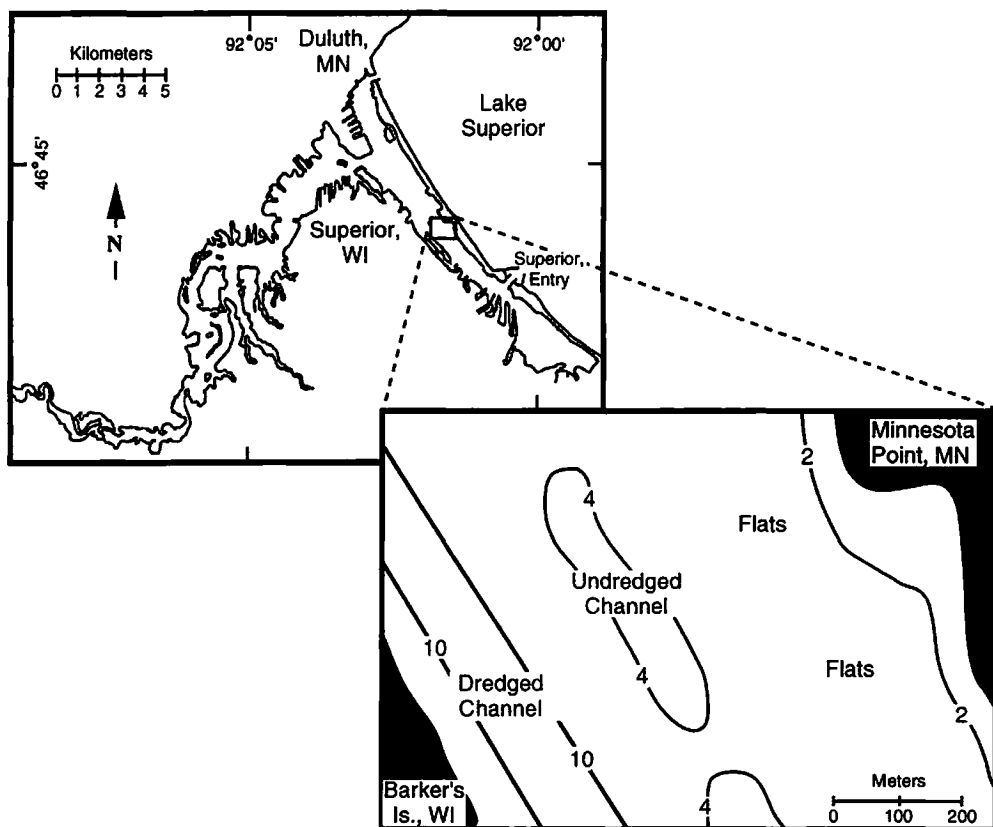
FIGURE 1.—Map of the St. Louis River estuary. The diet of ruffe was described from collections made throughout the entire estuary. The inset shows the location and habitats (flats and undredged channel) where ruffes were collected for analysis of their diel feeding ecology.

dation by ruffes reduced powan abundance. Pokrovskii (1961) found that ruffes may significantly decrease vendace abundance by consuming 80–90% of the eggs deposited by that species.

European and Asian investigations reveal that ruffes possess biological characters that may have a negative trophic impact on native fish. An understanding of the diet and foraging behavior of ruffes on an annual, seasonal, diel, and life stage basis is needed to evaluate the interaction between ruffe and other species in the St. Louis River estuary or in other areas of Lake Superior where ruffes will be found. Foraging characteristics that ruffes have assumed in the St. Louis River estuary must be documented because invading species often express broader flexibility in certain life history characteristics, including diet and foraging behavior (Taylor et al. 1984), than in their native range. In this paper, we describe the diet and diel foraging behavior of ruffes during 3 years (1989–

1991) of their initial colonization of the St. Louis River estuary.

Methods

Monthly and annual diets.—Ruffe diet was described from fish collected every other week from the entire 4,654-ha estuary (Figure 1) in 1989 and 1990. For each collection week, 40 collection locations were chosen randomly within three habitat strata. The three strata were shallow flats (mean depth, 1.9 m; 62.5% of the total surface area), undredged channels (mean depth, 4.0 m; 12.5%), and dredged channels (mean depth, 8.3 m; 25%). The number of locations chosen from each of the three habitats was based on the proportion of the total surface area of the estuary in each habitat. Special collections of ruffe were made in May 1989 near Superior Entry (Figure 1) and in April 1991 throughout the estuary. The April 1991 sample was used only to determine the occurrence of

fish eggs in ruffe stomachs when fish eggs in the estuary would be plentiful.

A 5.2-m lead-line bottom trawl with a 6.4-mm stretched-mesh cod end was used to collect ruffe. The trawl was towed on the bottom for 5 min at 2.6 km/h and each tow covered about 0.06 ha. All ruffes captured in each tow were chilled on ice within 30 min and frozen within 8 h of capture. In the laboratory, up to five ruffes per 1-cm total length (TL) class from all 40 tows made per collection week were measured to the nearest millimeter and weighed to the nearest gram. Stomachs of these fish were removed and preserved in 10% formalin.

Stomach contents from each fish were identified to order or family and enumerated. Inorganic matter and detritus were qualitatively observed to be a small component of the contents and were not quantified. After identification and enumeration, relatively undigested prey specimens of each taxon from ruffes within a 1-cm size-class and collection week were pooled. We determined the mean wet weight of individual prey items for each taxon, size-class, and collection week by dividing the wet weight by the number of organisms in each pooled sample of undigested organisms. We then estimated the total wet weight of each taxon in each stomach by multiplying the number of each taxon found in a stomach by the mean wet weight for an individual of that taxon, ruffe size-class, and collection week. Calculation of total weight of stomach contents in this manner corrects for different stages of digestion (Hyslop 1980) and assumes no weight-selective predation by ruffe within a 1-cm size-class (Weisberg and Janicki 1990). Up to 20 midges and 10 individuals of all other major taxa from the pooled samples of undigested prey were measured to the nearest 0.1 mm (macrobenthos) or 0.05 mm (microcrustaceans). We determined mean length of organisms in each major prey group and all prey combined for each 1-cm ruffe size-class and year by weighting prey lengths by total number of each prey group found in the stomachs. A subsample from the pooled sample of undigested prey specimens was identified to genus or species.

Further analysis of diet was based on ruffes pooled into larger size-classes. Age-0 ruffes, identified from length frequencies, were analyzed separately. Ontogenetic shifts in the diet of age-0 ruffes were not tested because the effect of increasing size of age-0 ruffes could not be separated from seasonal effects on the diet. A contingency table analysis (Hansson 1984) was used to detect shifts in the diet of adult ruffes. To identify the length at which a diet shift occurred, we compared the number of microcrustaceans and macrobenthos in the stomachs of adult ruffes of different pairs of length-groups collected in both years of the study. The first comparison was made between adult ruffes shorter than 10 cm and those 10 cm or longer; seven subsequent comparisons were made by incrementing the separatory length by 1 cm from 11 to 17 cm. A similar analysis was performed for the wet weight of stomach contents. The length corresponding to the greatest difference (i.e., largest G; Crow 1982) was taken as the length at which a shift occurred.

Monthly and yearly diet composition summaries for each size-class of ruffe were based on the percentage of total number and total wet weight of four macrobenthic taxa (Chironomidae, Trichoptera, Ephemeroptera, and Amphipoda) and three microcrustacean taxa (Copepoda, Cladocera, and Ostracoda). An "other" category included less common taxa: Asellidae, Ceratopogonidae, Chaoboridae, Decapoda, fish, fish eggs, Gastropoda, Hemiptera, Hirudinea, Megaloptera, Odonata, and Bivalvia. Both numeric and biomass results are presented because each measure emphasizes different aspects of ruffe diet (Hyslop 1980). Percentage results are difficult to interpret because they are a ratio of two variables. An analysis of variance (ANOVA) model with year and month factors was used to identify possible differences in the total number and weight of prey organisms (i.e., denominators). When month was significant ($P < 0.05$), all pairwise comparisons of months were made with Bonferroni-corrected multiple comparisons with an overall type I error (α) rate of 0.05.

Diel foraging patterns.—Ruffes used to describe diel feeding ecology were collected from an undredged channel (mean depth, 4.2 m) and an adjacent shallow flats area (mean depth, 2.0 m) between Minnesota Point, Minnesota, and Barker's Island, Wisconsin (Figure 1) during 24-h periods beginning on 12 July and 7 August 1990 and on 11 June, 10 July, and 8 August 1991. This location was chosen because it supported high densities of ruffes and because of the proximity of the two habitats. Ruffes were collected from both habitats at 6-h intervals in July 1990 and at 4-h intervals thereafter. An additional collection of ruffes was made near sunset (2100 hours) on 11 June 1991. Ruffes were collected at 1100 and 1500 hours on 5 September 1990 in these two habitats and in a nearby dredged channel (Figure 1) before severe thunderstorms halted further collections. Surface

TABLE 1.—Results of the six ANOVA models that tested for between-year and among-month differences in the total number of prey or wet weight of stomach contents in three size-classes of ruffe. Small adults are shorter than 12 cm; large adults are 12 cm or longer. Numerator degrees of freedom (df) are 1 for each year factor, and 4 with age-0 ruffes or 5 with adult ruffes for each month factor.

Group	Error df	P-values from ANOVA models			
		Total numbers		Total wet weight	
		Year	Month	Year	Month
Age 0	262	0.0002	0.0026	0.0039	<0.00005
Small adult	363	0.2690	0.0594	<0.00005	0.5879
Large adult	411	0.0824	0.0026	0.2075	0.0306

and bottom light intensity were recorded immediately before and after each trawl tow with a Li-cor® LI-189 quantum meter equipped with a LI1925A underwater quantum sensor. The relationship between light intensity and catch of ruffe was tested with the correlation between $\log_e$-transformed surface light measurements and $\log_e$-transformed catch of ruffe.

For each time interval and habitat, up to six ruffes per 1-cm size-class were measured to the nearest millimeter and weighed to the nearest gram. Stomachs were removed and preserved in 80% ethanol within 2 h of capture. Small age-0 ruffes were preserved whole in the field, and stomachs were removed in the laboratory. We determined wet weight of stomach contents by first weighing the intact stomach and then subtracting its weight after its contents were removed. In the diel portion of the study, age-0 and adult ruffes were analyzed separately because types of food consumed, catch patterns, and patterns in the weight of stomach contents differed between the two groups. Adult ruffes were not separated further because size-related differences in catch or weight of stomach content patterns were not observed.

An analysis of covariance (ANCOVA) model was used to determine if the weight of ruffe stomach contents, adjusted by the covariate body weight, differed by habitat or time period. Both stomach contents weight and body weight were square-root transformed to stabilize variance and normalize the residuals from this model. Slopes of the regression of transformed weight of stomach contents on body weight were not significantly different among time periods or habitats (Bonferroni-corrected t-tests). The ANCOVA model included factors for habitat, time period, and their interaction for adult ruffes; only time period was included in the model for age-0 ruffes because few or no age-0 ruffes were collected in some habitats during some time periods. Significant factors were further tested with Bonferroni-corrected multiple comparisons.

Results

Diet

The size at which adult ruffe diet shifted, based on both the number ($G = 7,053$; df = 1) and weight ($G = 1,829$; df = 1) of microcrustaceans and macrobenthos found in stomachs, was 12 cm. Empirical observations suggested the same length (Ogle 1992). Thus, adult ruffes were separated into small (<12 cm) and large ($\geq$12 cm) adults for further analysis.

Age-0 ruffes generally consumed more food, both in numbers of items and weight, as the season progressed (Bonferroni multiple comparisons), but consumed less food in 1990 than in 1989 (Table 1; Figure 2). Small adult ruffes did not exhibit any seasonal changes in the amount of food eaten, but the total weight of food consumed was lower in 1990 than in 1989 (Table 1; Figure 3). Large adult ruffes ate the same amounts of food in both 1989 and 1990, but ate less food in July than in June and August (Bonferroni multiple comparisons; Table 1; Figure 4).

Ruffes fed on microcrustaceans throughout their first summer, but midge larvae became increasingly important to their diets in the fall (Figure 2). Age-0 ruffes, when first collected in late June or early July, fed mostly on copepods (primarily *Megacyclops viridis*) and cladocerans (primarily *Latona setifera*), but also ate small midges (primarily *Procladius* spp.; Figure 2; Table 2). A switch to a more benthic diet dominated by larger prey was indicated by greater numbers of ostracods and the weight of macrobenthos, mostly midges and some mayflies (primarily *Hexagenia* spp.; Ephemeroptera), in stomach contents in late July or early August. The mean size (± 2 SE) of age-0 ruffes during the first week of August declined from 50 (± 6) mm in 1989 to 39 (± 5) mm in 1990.
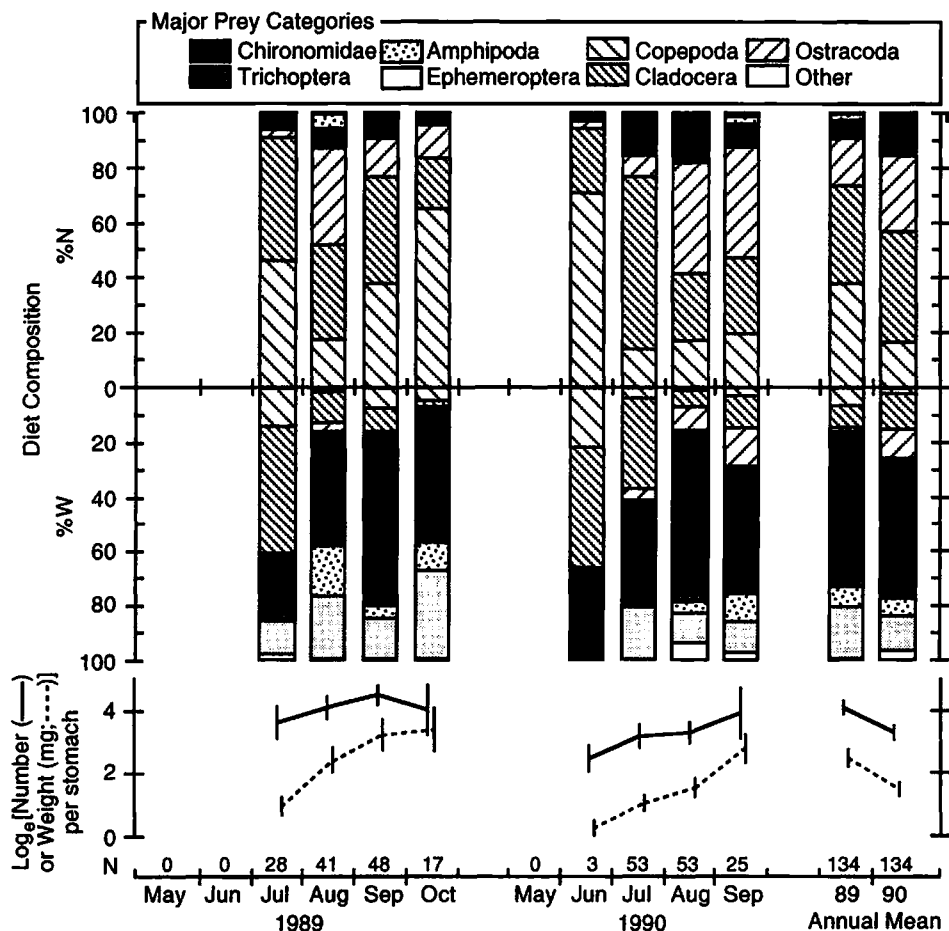
FIGURE 2.—Diet composition of age-0 ruffes. Monthly and annual diet compositions are expressed as the percent total number and total weight of eight major prey categories (upper panel) and as the mean (± 2 SE) log$_e$(number) and log$_e$(weight) of all prey organisms (lower panel). The number of stomachs examined in each period is shown above the abscissa.

Small adult ruffes fed extensively on macrobenthos, although large numbers of microcrustaceans were still consumed (Figure 3). Midges (primarily *Procladius* spp.) were the most prevalent food item by weight in all months but one (Figure 3; Table 2). Mayflies (primarily *Hexagenia* spp.) also formed a substantial portion of the diet's biomass. Weight of microcrustaceans (primarily *Megacyclops viridis*) in the diet was greatest in June and July 1989 and in September 1990. Microcrustaceans, especially copepods early and cladocerans later in the season, dominated numerically in ruffes' diets on all but three dates. Predation on caddisflies (primarily *Phylocentropus placidus*; Trichoptera) by small adult ruffes varied without apparent trend in 1989, but generally decreased through the sampling season in 1990.

Large adult ruffes ate mostly macrobenthos in 1989 and 1990 (Figure 4). Midges (primarily *Chironomus plumosus*), caddisflies (primarily *Phylocentropus placidus*), and mayflies (primarily *Hexagenia* spp.) were the dominant food items, by weight, eaten by large adult ruffes in all months (Figure 4; Table 2). In 1989, large adult ruffes ate mostly midges during 3 months and mayflies during the other 3 months. In 1990, large adult ruffe ate mostly caddisflies in the first 2 months and mayflies during the remaining months. There was no apparent temporal pattern of predation on midges and mayflies by large adult ruffes. However, large adult ruffes ate more caddisflies in early summer and more amphipods (primarily *Gammarus* spp.) in late summer and early fall. Copepods (primarily *Megacyclops viridis*) dominated
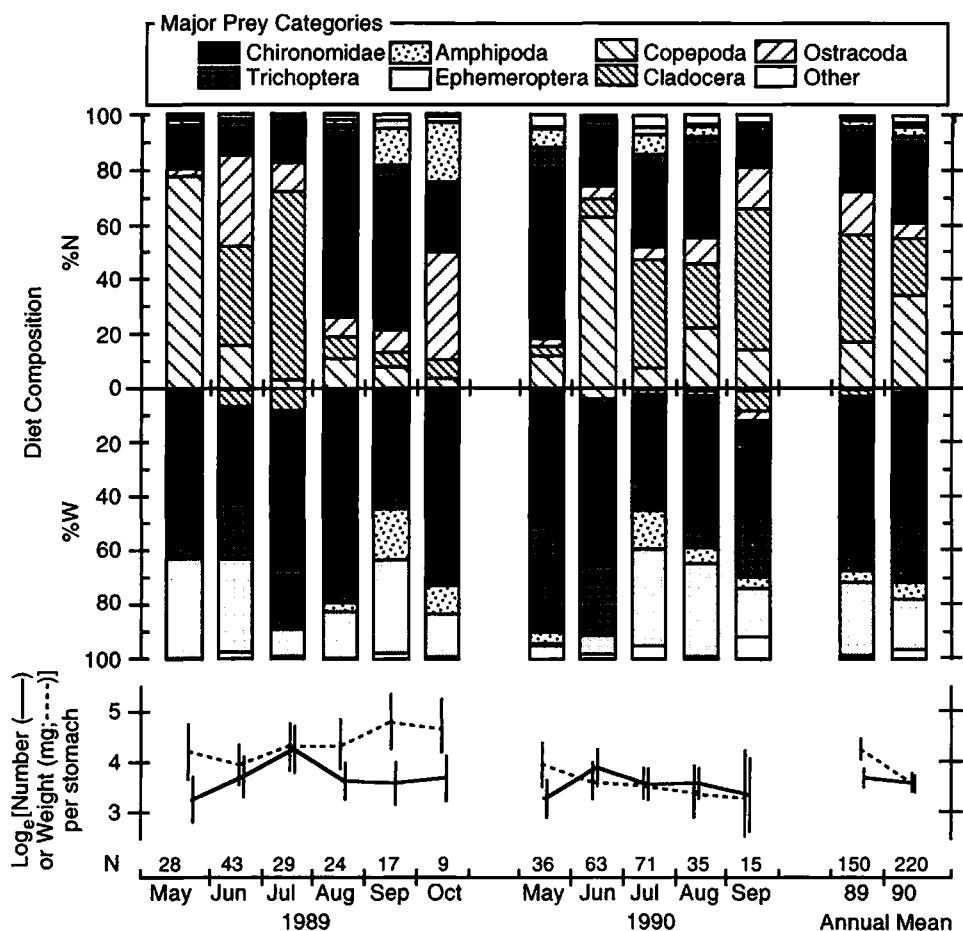
FIGURE 3.—Diet composition of small adult (<12 cm) ruffes. Monthly and annual diet compositions are expressed as the percent total number and total weight of eight major prey categories (upper panel) and as the mean (±2 SE) $\log_e$(number) and $\log_e$(weight) of all prey organisms (lower panel). The number of stomachs examined in each period is shown above the abscissa.

the diet by number during some months, but results were skewed by one or two large adult ruffes.

Ruffes consumed few fish or fish eggs. Fish eggs were found in only 6% of ruffes captured in May and early June of 1989 and 1990. Additionally, only 4% of ruffes captured in April 1991, a time of high egg abundance in the estuary, contained fish eggs. No more than three fish eggs were found in any fish. Two unidentified fish were found in the stomachs of 418 large adult ruffes examined in 1989 and 1990.

The length of each prey consumed increased linearly with increasing ruffe size-class in both 1989 and 1990 (all P for slope, ≤0.0203) with two exceptions. First, ostracod mean length in both years decreased linearly with increasing ruffe size-class ($P \le 0.00005$). Second, the mean length of midges

in 1990 increased linearly with increasing ruffe size-class between 1 and 12 cm ($P = 0.003$ for slope), but remained constant in ruffes larger than 12 cm ($P = 0.2007$). In 1989, the mean length of midges increased linearly through the whole range of size-classes ($P \le 0.00005$) and was very close to values observed in 1990 for size-classes 12 cm or smaller. This is evidence that adult ruffes 12 cm or larger consumed smaller midges in 1990 than in 1989.

Diel Catch and Foraging Patterns

Patterns of the diel catch of age-0 and adult ruffes varied among collection dates. Substantially more age-0 ruffes were captured at night than during the day in both habitats on all collection dates (Figure 5). Some age-0 ruffes were
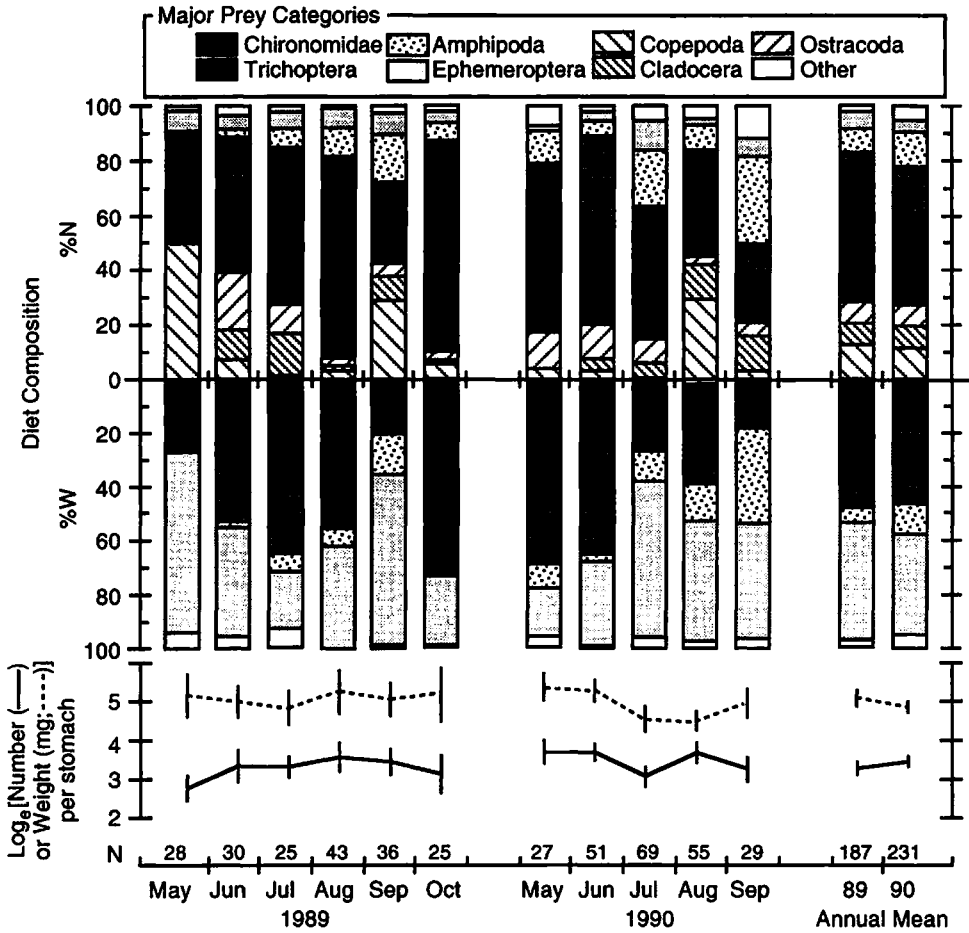
FIGURE 4.—Diet composition of large adult (≥ 12 cm) ruffes. Monthly and annual diet compositions are expressed as the percent total number and total weight of eight major prey categories (upper panel) and as the mean (± 2 SE) $\log_e$(number) and $\log_e$(weight) of all prey organisms (lower panel). The number of stomachs examined in each period is shown above the abscissa.

collected throughout the day in the flats, but such fish were generally captured only during the night or twilight periods in the channel. For adult ruffes in the flats, the greatest catches were made at night in July 1990, August 1990, and August 1991 and just before sunset in June and July 1991 (Figure 6). In June and July 1991, more adult ruffes were caught in the flats at night (at 2300 and 0300 hours) than during the middle of the day (at 1100 and 1500 hours; Figure 6). In the channel, more adult ruffes were caught during the day than at night in July 1990, August 1990, and August 1991, whereas the opposite was true on the other two dates (Figure 6). On 5 September 1990, the date on which severe thunderstorms prevented sampling late in the day, collections of ruffe at 1100 and 1500 hours were low in both the channel

(<50 ruffes per 5-min tow) and flats (<10 per 5-min tow), but high (>150 per 5-min tow) in the nearby dredged channel.

The trawl catch of age-0 ruffes was inversely related to surface light intensity in both the flats and the channel (Figure 7). Catches of adult ruffes were also inversely related to surface light intensity in the flats, but not in the channel (Figure 7). Bottom light levels (micromoles of quanta) during daylight in the channel were 0 μmol$\cdot$cm$^{-2}\cdot$s^{-1} while those in the flats ranged from 0 to 30.3 μmol$\cdot$cm$^{-2}\cdot$s^{-1}, but were generally less than 0.5 μmol$\cdot$cm$^{-2}\cdot$s^{-1}. Bottom light levels at night in both habitats were approximately 0 μmol$\cdot$cm$^{-2}\cdot$s^{-1}.

Age-0 ruffes fed discontinuously on three of four collection dates (ANCOVA; Table 3). A gen-

TABLE 2.—Relative contribution ranks (1 = ≥ 75%, 2 = 25–74%, and 3 = <25%) of a genus or species to the major prey categories identified in the stomach contents of three size-classes of ruffe. Footnotes show other taxa that made up less than 25% of the major prey category for at least one, but not all, of the three size-classes of ruffe. The letter in parentheses following each taxon indicates whether the taxon is primarily benthic (B) or pelagic (P).

Major prey category	Taxon (habitat use)	Age 0	Adult Small	Large
Copepoda[a]	*Megacyclops viridis* (B)	1	1	1
Cladocera[b]	*Latona setifera* (B)	1	1	1
Chironomidae[c]	*Chironomus plumosus* (B)	3	3	2
	Procladius spp. (B)	2	2	3
Trichoptera[d]	*Phylocentropus placidus* (B)	1	1	1
Amphipoda	*Gammarus* spp. (B)	1	1	1
Ephemeroptera	*Hexagenia* spp. (B)	1	1	1

[a] *Acanthocyclops vernalis* (P and B), *Diacyclops thomasi* (P), *Eucyclops prionophorus* and *E. speratus* (B), *Eurytemora* spp. (P).

[b] *Alona quadrangularis* (B), *Bosmina* spp. (P), *Bythotrephes cederostroemi* (P), *Daphnia retrocurva* and *D. ambigua* (P), *Diaphanosoma* spp. (P), *Eurycercus longirostris* (B), *Sida crystallina* (B), *Simocephalus* spp. (B).

[c] *Ablabesmyia annulata* (B), *Coelotanypus* spp. (B), *Cryptochironomus digitatus* (B), *Glyptotendipes* spp. (B), *Harnischia curtilamellata* (B), *Monodiamesa* spp. (B), *Parachironomus* spp. (B), *Potthastia* spp. (B), *Pagastiella* spp. (B), *Polypedilum simulans* (B), *Stictochironomus* spp. (B), *Tanytarsus* spp. (B).

[d] *Neureclipsis bimaculatus* (B), *Oecetis* spp. (B).

eral spatial or temporal pattern of food consumption could not be identified (Figure 8).

Feeding discontinuities across the 24-h period were observed for adult ruffes on four of five collection dates (ANCOVA; Table 4), although patterns of feeding discontinuities differed (Figure 9). On three dates there was a significant interaction between time period and habitat (Table 4), which suggests that the discontinuity patterns differed between fish caught in the two habitats (Figure 9). A feeding discontinuity was detected in fish caught in the flats (ANCOVA; $P < 0.0284$) on all three dates when a significant interaction was observed. In general, mean weight of stomach contents of adult ruffes caught in the flats declined during the day, reached a low near sunset, increased in the first or second sampling period after sunset, and then remained stable throughout the night (Figure 9). On the three dates with a significant interaction effect, the pattern of mean weight of stomach contents of adult ruffes captured in the undredged channel was quite varied (Figure 9); mean weight of stomach contents increased near sunset and remained stable throughout the night in August 1990

(ANCOVA; $P < 0.00005$), remained stable over the 24-h period in June 1991 (ANCOVA; $P = 0.0556$), or declined over the 24-h period in August 1991 (ANCOVA; $P < 0.00005$). A general pattern of weight of stomach contents was not observed for adult ruffes captured in the undredged channel. Overall mean weight of stomach contents was higher in ruffe caught in the flats than in the channels on three of five collection dates (Table 4; Figure 9).

Discussion

During the early years of its invasion of the St. Louis River estuary, the ruffe was primarily benthophagous. Small age-0 ruffes fed on small organisms that lived near the substrate–water interface; larger age-0 ruffes switched to larger, deeper-burrowing organisms. Age-0 ruffes between about 2 and 5 cm fed on *Megacyclops viridis* and *Latona setifera*, which are typically found near the substrate–water interface (Brooks 1959; Hutchinson 1967). Larger age-0 ruffes continued to feed on these same organisms, but also fed on *Procladius* spp., which burrow in the top 2.5 cm of the bottom substrate (Ford 1962; Coffman 1978). Adult ruffes smaller than 12 cm fed primarily on *Procladius* spp. but also consumed burrowing mayflies and microcrustaceans near the substrate surface. Ruffes 12 cm and larger fed primarily on deep-burrowing organisms, such as *Chironomus plumosus, Phylocentropus placidus,* and *Hexagenia* spp., which all burrow up to 12 cm into the substrate (Cole 1953; Hilsenhoff 1966; Edmunds et al. 1976; Wallace et al. 1976; Coffman 1978; Edmunds 1978; Pennak 1978; Wiggins 1978).

In Europe and Asia, ruffes are also primarily benthophagous, but there is little evidence in the literature of shifts in diet like those we observed for St. Louis River ruffes. In their native range, ruffes smaller than 5–6 cm generally fed on microcrustaceans (Johnsen 1965; Collette et al. 1977; Boron and Kuklinska 1987), as did ruffes in the St. Louis River. After European ruffes reached 5–6 cm, their diets varied little and they preyed primarily on chironomids or macrocrustaceans (Johnsen 1965; Collette et al. 1977). The generalization of a static diet throughout most of the ruffe's life is supported by the findings of Boron and Kuklinska (1987) and Bergman (1991), who were unable to demonstrate any shifts in the diet of larger ruffes. It appears that adult ruffes in the St. Louis River estuary feed on a broader set of benthic organisms than is suggested by the European literature.
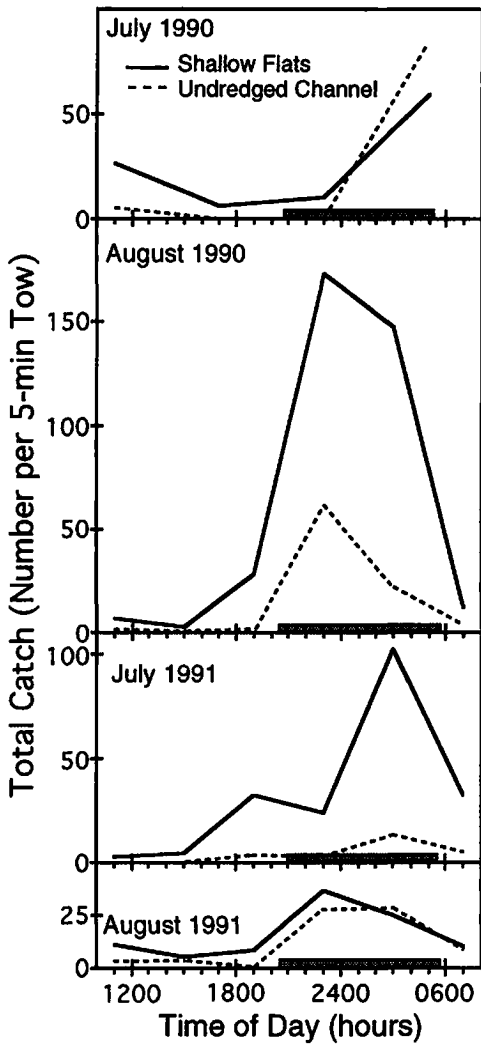
FIGURE 5.—Total catch of age-0 ruffes per 5-min trawl tow in the shallow flats and undredged channel on four collection dates, 1990–1991. The shaded bar on each abscissa indicates the period between sunset and sunrise. Each ordinate has the same scale but a different range.

We found no evidence of substantial egg predation by ruffes, a finding consistent with that of some European studies (Johnsen 1965; Boron and Kuklinska 1987). European studies that documented extensive egg predation by ruffes were either laboratory studies in which ruffes and fish eggs were confined together (Mikkola et al. 1979; Sterligova and Pavlovskiy 1985; Pavlovskiy and Sterligova 1986) or field studies in which ruffes were collected only on the spawning grounds of powan during the spawning season (Adams and Tippett 1991).
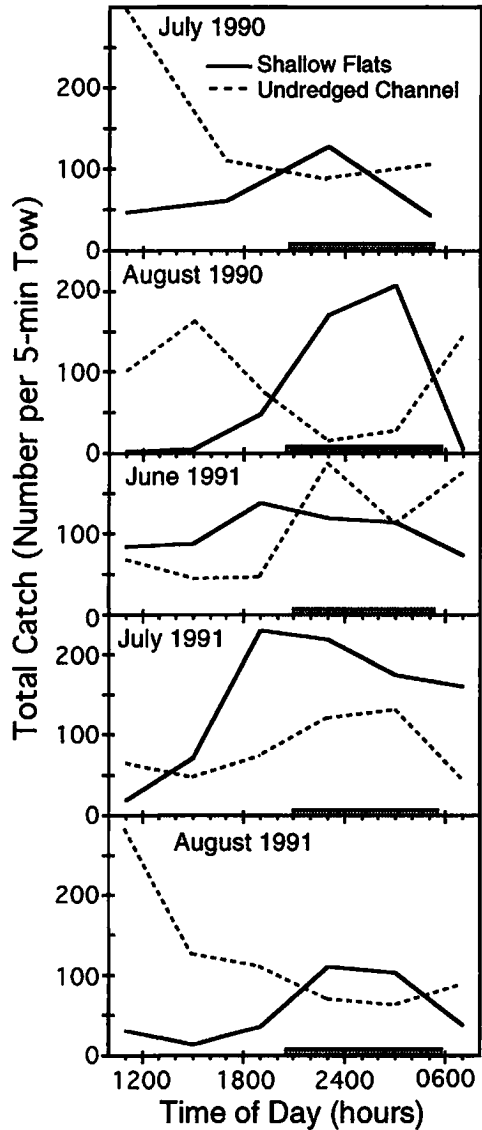

FIGURE 6.—Total catch of adult ruffes per 5-min trawl tow in the shallow flats and undredged channel on five collection dates, 1990–1991. The shaded bar on each abscissa indicates the period between sunset and sunrise. Each ordinate has the same scale but a different range.

Both age-0 and adult ruffes can feed throughout a 24-h period, although adult ruffes may feed much more at night on occasion. Statistically significant discontinuities, but no simple patterns, in food consumption were observed for age-0 ruffes. Adult ruffes captured in the flats on all dates and in the undredged channel on the two 1990 dates generally consumed more food just after sunset and continued feeding, to some extent, throughout the night.
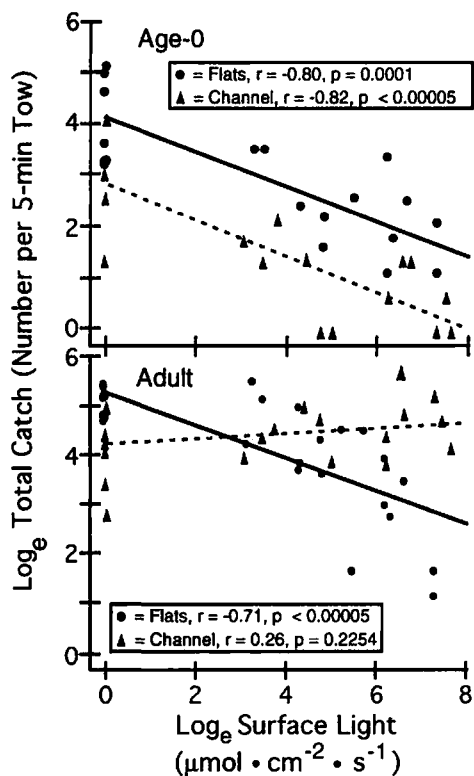
FIGURE 7.—The relationship between catch and surface light intensity (micromoles of quanta) for age-0 (top panel) and adult (bottom panel) ruffes captured in both the shallow flats (solid line) and undredged channel (dashed line) on all dates.

Adult ruffes captured in the undredged channel on the other dates consumed some food over the entire 24-h period.

Catches of adult ruffes differed between habitats and were inversely related to surface light levels. On three of five dates, catches in the shallow flats were greater at night than during the day, and catches in the deeper channel were greater during the day than at night. The relationship observed
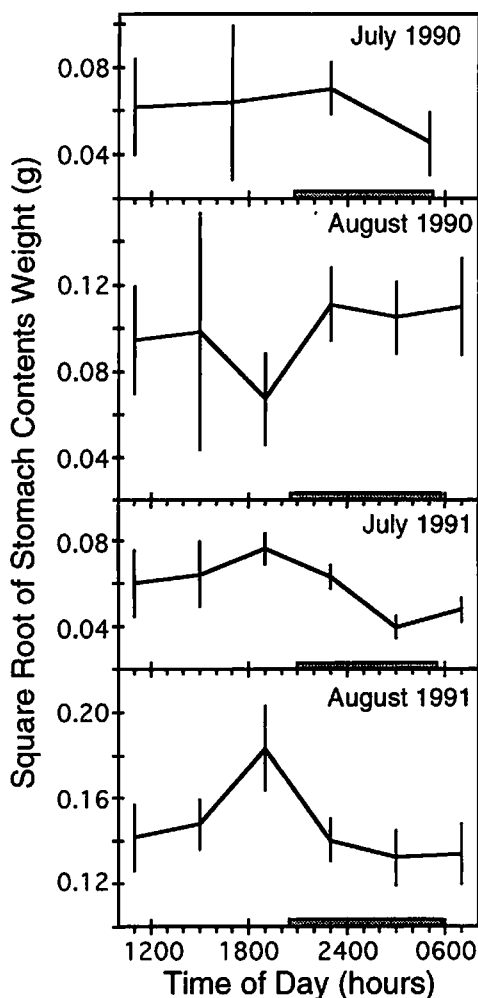

FIGURE 8.—Diel periodicity of weight of stomach contents for age-0 ruffes on four collection dates. For each time period, a least-squares mean and Bonferroni-corrected 95% confidence interval (vertical bar) was estimated with an ANCOVA model with time period as a factor and body weight as a covariate. The shaded bar on each abscissa indicates the period between sunset and sunrise. Each ordinate has the same scale but a different range.

TABLE 3.—Results of the four ANCOVA models to test for differences in weight of stomach contents of age-0 ruffes among time periods on each date. The covariate, fish weight, was highly significant ($P \leq 0.00005$) for each collection date.

Month	Time period		Error df
	P-value	df	
Jul 1990	0.0745	3	15
Aug 1990	0.0401	5	74
Jul 1991	≤0.00005	5	119
Aug 1991	0.0010	5	106

on these dates suggests that migrations of adult ruffes between the two locations may be related to light levels. This behavior is similar to that observed for trout-perch *Percopsis omiscomaycus*, which, like ruffes, possess a retinal tapetum lucidum (Ryder and Kerr 1978). Trout-perch are likely sensitive to high subsurface illumination and avoid light by retreating to deep waters during the day or hiding under boulders or sunken logs (Ryder and Kerr 1978).

TABLE 4.—Results of the five ANCOVA models to test for differences in weight of stomach contents of adult ruffes among time periods, between habitats, and among interactions of the two factors on each date. The covariate, fish weight, was highly significant ($P \leq 0.00005$) for each collection date.

Month	Time period		Habitat		Interaction		Error
	P-value	df	P-value	df	P-value	df	df
Jul 1990	≤0.00005	3	0.0088	1	0.0578	3	188
Aug 1990	≤0.00005	5	0.0001	1	0.0215	5	211
Jun 1991	≤0.00005	5	0.1055	1	0.0109	5	354
Jul 1991	0.1987	5	0.1826	1	0.1219	5	263
Aug 1991	0.0001	5	≤0.00005	1	0.0208	5	243

Local weather conditions or spawning activities may have resulted in catches of adult ruffes in June and July 1991 that differed from those in other months. Ruffes may have sought deeper waters after storms near 1800 hours on 11 June and 10 July 1991. Similarly, 4 h and 8 h before a severe storm in September 1990, many adult ruffes were collected in the dredged channel and few were collected in the flats and undredged channel. Spawning activity, as observed for adult ruffes in June 1991, alters characteristic diel activity patterns in some temperate fishes (Helfman 1981). On 11 June 1991, adult ruffes, which spawn at depths less than 2 m but at unknown times of the day (Johnsen 1965; Fedorova and Vetkasov 1974; Kolomin 1977), could have spawned in the shallow flats during the day and then retreated to deeper waters at night.

The movement patterns of age-0 ruffes were inversely related to light levels, but a spatial pattern could not be found. Large numbers of age-0 ruffes were captured at night in both habitats, and few were caught during the day in either habitat. Age-0 ruffes may have been in shallower waters or suspended off the bottom, above the bottom trawls, during the day. If age-0 ruffes observed in the flats at night were in the dredged shipping channel during the day, they would have had to migrate across the undredged channel to reach the flats (Figure 1). However, as darkness approached, age-0 ruffes were not observed in the undredged channel before they were observed in the flats. More work on diel location of age-0 ruffes is needed, in part, to determine if daytime estimates of age-0 ruffe abundance are being largely underestimated.

The relationship between feeding periodicity, catch, and surface light level provides some insight into the feeding behavior of ruffe. First, catch data suggest that adult ruffes move from the channel to the flats at sunset and reverse this process at sunrise. This observation, coupled with the increased weight of stomach contents at night in the flats, suggests that adult ruffes move to the shallow flats to feed at night. Second, adult ruffes in the shallow flats, where light reached the bottom, generally consumed more food at night than during the day, whereas adult ruffes in the deep undredged channel, where light levels were always at or very near 0 $\mu mol \cdot cm^{-2} \cdot s^{-1}$, fed throughout the 24-h period. These two observations suggest that ruffes continue to feed in dimly lit areas but may suppress feeding in brightly lit conditions. Bergman (1988) has shown that ruffe feeding efficiency is affected little by decreasing light levels, especially when compared to that of the sight-feeding Eurasian perch. Thus, as has been suggested before (Ahlbert 1970; Disler and Smirnov 1977; Bergman 1988), ruffes may rely little on vision for feeding.

Adult ruffes may feed by detecting water currents created by their prey. The three species that adult ruffes fed on most, *Chironomus plumosus, Phylocentropus placidus,* and *Hexagenia* spp., all undulate their bodies to create water currents through their burrows for respiration and feeding (Walshe 1951; Fremling 1967; Wallace et al. 1976). The lateral line system of the ruffe, which is extraordinarily sensitive because of an exceptionally large number of sensory hair cells (Denton and Gray 1989), is capable of detecting these currents (Gray and Best 1989). The sensitive lateral line system could also be used to detect prey under reduced light conditions or at night.

Although definitive evidence regarding competitive interactions with other species is not available, we believe that ruffes may compete with other benthic-feeding fishes such as yellow perch *Perca flavescens* and trout-perch, especially in dark-water systems like the St. Louis River estuary. Ruffe predation on the benthos could reduce the availability of appropriate-sized prey to intermediate-sized yellow perch, which depend on intermediate- and large-sized benthic food items to grow rapidly and attain large sizes (MacLean and Magnuson 1977; Craig 1987; Hayward and Mar-
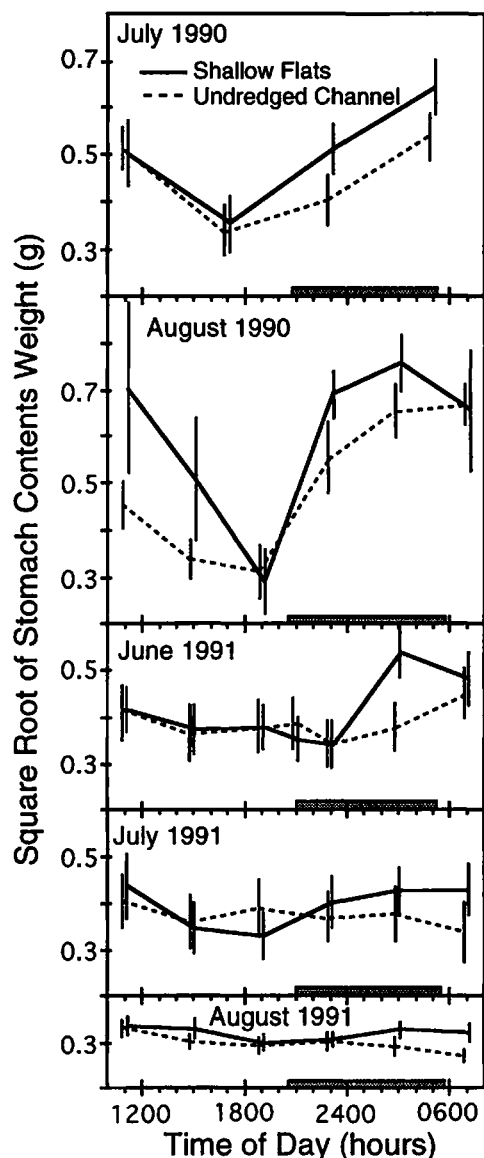
FIGURE 9.—Diel periodicity of weight of stomach contents for adult ruffes in two habitats on five collection dates. For each time period and habitat, a least-squares mean and Bonferroni-corrected 95% confidence interval (vertical bar) was estimated with an ANCOVA model with time period, habitat, and their interaction as factors and body weight as a covariate. The mean and confidence interval for ruffes collected in the two habitats for each collection time have been offset slightly for comparative purposes. The shaded bar on each abscissa indicates the period between sunset and sunrise. Each ordinate has the same scale but a different range.

graf 1987). The effects of ruffe competition on yellow perch may parallel a situation described for slow-growing yellow perch in Lake Erie where the availability of appropriate-sized benthic food items had been reduced by eutrophication (Hayward and Margraf 1987). Direct competition between yellow perch and ruffe may be reduced under some conditions, especially in clear waters, because yellow perch apparently rely on vision to feed mostly during the day (Scott and Crossman 1973). In contrast, competition between ruffe and trout-perch will likely be intense because trout-perch also feed on benthos in shallow waters at night (Hubbs and Lagler 1958; Scott and Crossman 1973). The effects of ruffe on yellow perch, trout-perch, and other native species will likely be greatest in dark-water systems because of the ruffe's superior adaptations for feeding in low-light conditions.

Acknowledgments

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