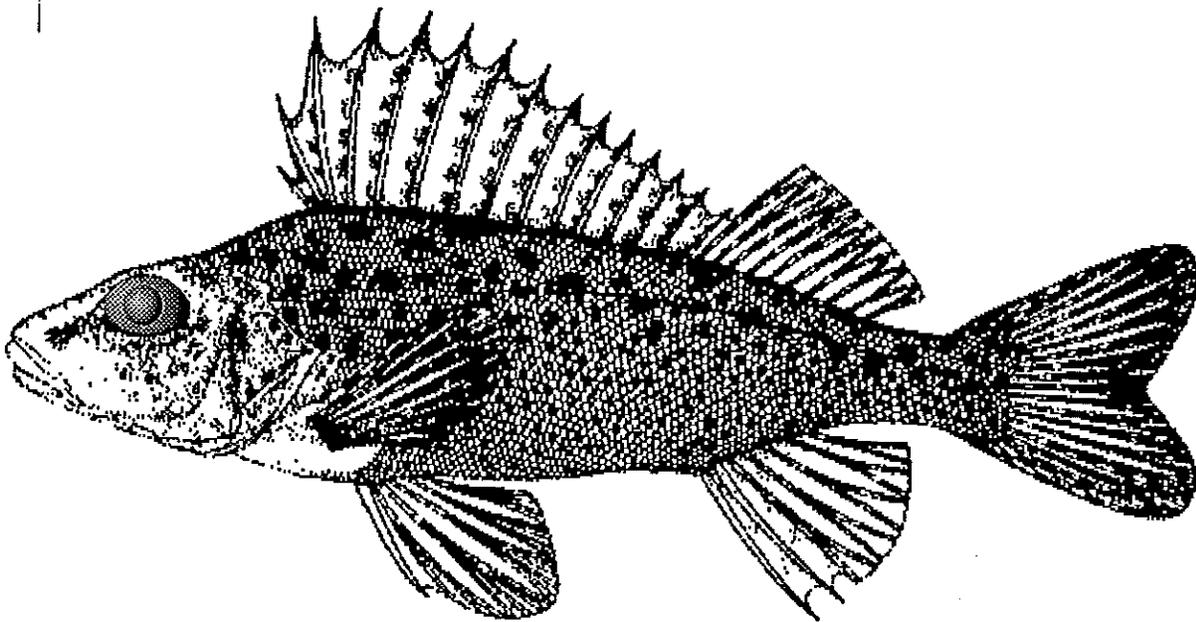


**Ruffe (*Gymnocephalus cernuus*):  
A Review of Published Literature**



**January 1995**

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Wisconsin Department of Natural Resources  
Bureau of Fisheries Management  
Madison, Wisconsin

This review was prepared by Derek Ogle, Department of Fisheries and Wildlife, University of Minnesota, at the request of the Wisconsin Department of Natural Resources. Funding was provided by the the Wisconsin Department of Natural Resources. Copies may obtained from the Bureau of Fisheries Management, Wisconsin Department of Natural Resources, Box 7921, Madison, Wisconsin 53707-7921.

**Ruffe (*Gymnocephalus cernuus*) Literature Review**

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## INTRODUCTION

In the early to mid 1980s, ruffe (*Gymnocephalus cernuus*; Figure 1) were accidentally introduced into the St. Louis River of the Lake Superior drainage (Pratt 1988; Pratt et al. 1992). Apparently introduced through ship ballast, ruffe established a thriving population in the St. Louis River (Selgeby and Ogle 1991, 1992) and by the early 1990s had included several other river mouths of Lake Superior in their range (Pratt et al. 1992; Slade and Kindt 1992). Ruffe are currently not found in any other North American drainage.

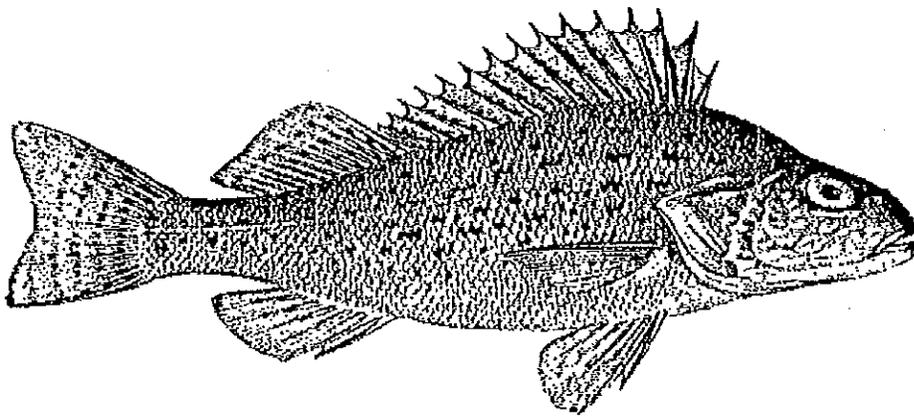


Figure 1. A 92 mm SL ruffe from the Danube River (from Holcik and Hensel 1974).

There is great concern as to what is the best managerial response when an exotic species invades a body of water. This concern is heightened in the case of ruffe in the Laurentian Great Lakes for three reasons. First, in Europe and Asia, ruffe are of very little economic importance but are of great ecological concern. Commercial and recreational harvest is limited due to the ruffe's small size. Furthermore, ruffe are thought to compete with European perch (*Perca fluviatilis*; Bergman 1990; Bergman and Greenberg 1994) and prey on the eggs of native whitefish (*Coregonus lavaretus* and *Coregonus albula*; Pokrovskii 1961; Mikkola et al. 1979; Sterligova and Pavlovskiy 1984; Pavlovskiy and Sterligova 1986; Adams and Tippet 1991). Second, the Great Lakes are of great economic importance. Talhelm (1988) reported that the total (all species) Great Lakes commercial fishery generated \$270 million in total regional economic activity. Third, the Great Lakes management community is still in the midst of understanding and managing other harmful exotic fishes. Most notable in this group is the sea lamprey (*Petromyzon marinus*), which had invaded all of the Great Lakes by 1946 and has been partially blamed for the collapse of some lake trout stocks (Fry 1953; Lawrie 1970; Coble et al. 1990). The United States and Canadian

governments have spent millions of dollars controlling lamprey with chemicals since the late 1940s.

A Ruffe Task Force was appointed by the Great Lakes Fishery Commission in 1991 to determine the best management response to the invasion of the Great Lakes by ruffe. The Task Force immediately concluded that ruffe were "a threat to North American fisheries" and felt that there was a "window of opportunity" to "prevent or delay the spread of ruffe in the Great Lakes and inland waters by containing the species to its current range in western Lake Superior" (Ruffe Task Force 1992; Busiahn 1993). However, opinions about control of ruffe in the Great Lakes fish management community ranged from deployment of all physical, chemical, and biological methods to contain ruffe to beliefs that ruffe are established and will spread regardless of control efforts (Busiahn 1993).

Continuing research and a thorough review of the European and Asian literature will certainly increase our knowledge base and may provide information that could lead to the eventual control of ruffe in invaded waters. This document, and a companion annotated bibliography, provide a thorough review and synthesis of the available European and Asian literature.

#### ACKNOWLEDGMENTS

This work was funded by the Wisconsin Department of Natural Resources. J. Bruner, A. Byla, J. Janssen, R. M. Newman, J. H. Selgeby, and I. J. Winfield have kindly opened their personal libraries or provided partial ruffe literature reviews to me. J. H. Selgeby and A. Byla provided translated materials. Ms. Lalee Kerr, Ms. Sue Stegmier, and several library assistants at the Entomology, Fisheries, and Wildlife library and assistants at the Biomedical and Walter libraries of the University of Minnesota helped locate obscure materials. This review would not have been as complete without all of their efforts. Interpretation of some materials was aided by discussion with colleagues, but all expressions in this review remain those of the author.

I am also thankful to Dr. Ray Newman for encouraging me to pursue a thorough review of the ruffe literature and Dr. George Spangler, my current advisor at the University of Minnesota, for allowing me to follow these interests and divert some of my energies away from my lake trout research to pursue this "tangent."

## LITERATURE SYNTHESIS

### Systematics, Morphology, Evolution, and Genetics

Linnaeus introduced the species as *Perca cernua* in 1758. Ruffe have been variously listed (source in parenthesis listed in Collette (1963)) as *Acerina vulgaris* (Cuvier and Valenciennes 1829), *Acerina cernua* (Kessler 1864); *Acerina fischeri* (Eichwald 1871), *Acerina czekanowski* (Dybowski 1974), *Acerina cernua essipovi* (Burkmakin 1941) and, recently, as *Gymnocephalus cernua* (Collette 1963). *Gymnocephalus* and *cernua* did not match gender so *cernua* was recently changed to *cernuus*. Thus, the currently accepted taxonomic name of ruffe is *Gymnocephalus cernuus* (Bergman 1990a, American Fisheries Society 1991). The ruffe has various local common names (Table 1).

Table 1. Local common names of ruffe.

Country	Common name(s)	Country	Common name(s)
Czechoslovakia	jezdik	Norway	nork, steinpurke
Denmark	horke	Poland	jazgarz
England	stone-perch, pope	Romania	ghibort
Finland	kiiski or kueski	Russia	ersh or jorsch
France	perche goujonnere, Brenille	Sweden	gers
Germany	kaulbarsch	Ukraine	iorzh, bubyr'
Netherlands	kulbaars	Yakut	tas-bas, khakhynai

The general taxonomic nomenclature of ruffe is generally well agreed upon, with the exception of subfamily or tribal membership. Collette (1963) and Collette and Banarescu (1977) placed *Gymnocephalus* in the tribe Percini within the subfamily Percinae (includes *Perca* and *Percarina*). Etheostomatini was the other tribe within Percinae. Page (1985) removed Etheostomatini from Percinae, leaving Percinae with only *Perca* and *Gymnocephalus* (Figure 2). He felt that egg-stranding, thought to be common in *Perca* and *Gymnocephalus*, was vastly different from egg-burying, common in darters. This change is tenuous because I have found no evidence that *Gymnocephalus* produce egg-strands (see Reproduction and Early Life History section). Wiley (1992) proposed that *Gymnocephalus* should be in Etheostomatinae, a subfamily that included all Percid genera except *Perca*. In this organization, *Gymnocephalus* is the basal taxon for all Percids except *Perca* (Figure 2). Coburn and Gaglione (1992) rejected Wiley's proposal because an equally parsimonious relationship with *Perca* and *Gymnocephalus* in the same subfamily could be found by simply including Page's egg-stranding information. Again, the

inclusion of egg-stranding is tenuous, but Coburn and Gaglione's analysis is similar to Collette's, in that *Perca* and *Gymnocephalus* are closely related and probably sister groups. A general nomenclature for ruffe is shown in Table 2.

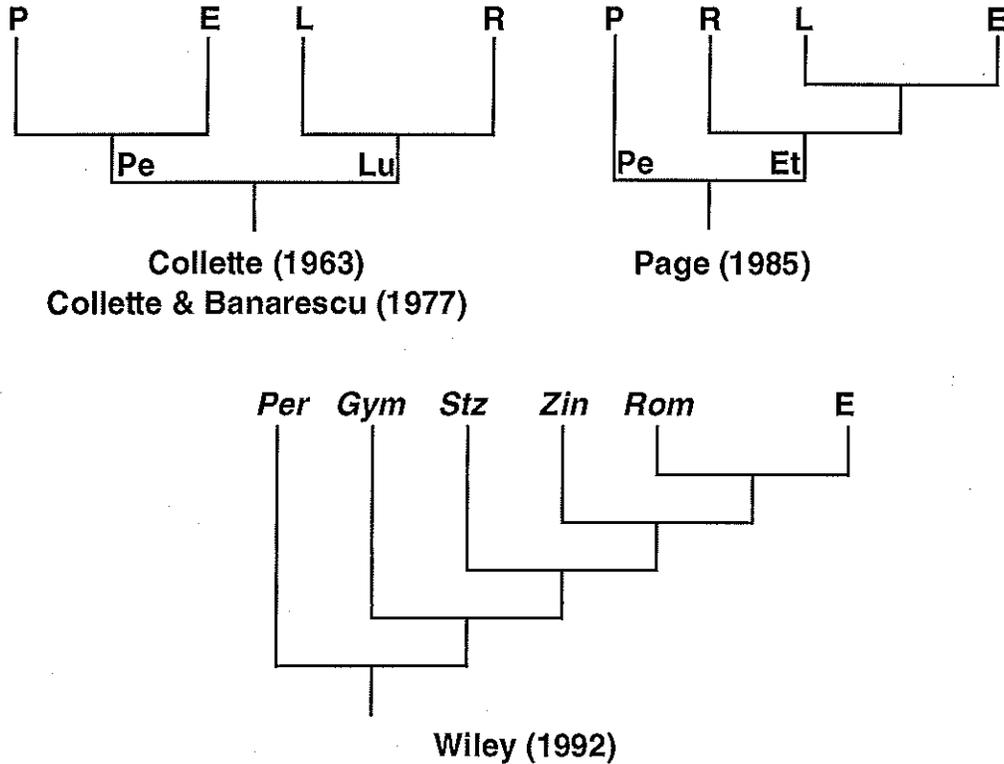


Figure 2. Three cladograms depicting alternative hypotheses of relationships among percids (from Coburn and Gaglione 1992): (A) Collette (1963) and Collette and Banareescu (1977); (B) Page (1985); (C) Wiley (1992). Abbreviations: Et = Etheostomatinae; Lu = Luciopercinae; Pe = Percinae; E = Etheostomatinae; L = Luciopercini; P = Percini; R = Romanichthyini; Gym = *Gymnocephalus*; Per = *Perca*; Rom = *Romanichthys*; Stz = *Stizostedion*; Zin = *Zingel*.

Table 2. General taxonomic nomenclature of ruffe. Note that there is some controversy

Classification	Name
Class	Osteichthyes
Subclass	Actinopterygii
Order	Perciformes
Suborder	Percoidei
Family	Percidae
Subfamily	Percinae
Genera	<i>Gymnocephalus</i>
Subgenera	<i>Acerina</i>
Species	<i>ceruus</i>

Several morphological characters led to the taxonomies described above. Percinae are separated from Luciopercinae by an enlarged anteriormost interhaemal bone, large and well developed anal spines, and a lateral line that usually does not extend onto the caudal fin (Collette 1963). Percini are separated from Etheostomatini by a well developed swimbladder, a compressed body, an auxiliary interneural bone that supports the first dorsal fin, a well developed supraoccipital crest, a strongly serrated preoperculum, small or absent genital papilla, and lack of breeding tubercles (Collette 1963). Characteristics synapomorphic for *Gymnocephalus* are enlarged preopercular spines, a distinctly shorter anterior ramus compared to the ventral ramus, a club-like distal end of the premaxilla, a retrarticular that is distinctly higher than long when viewed medially (Wiley 1992), and hypertrophy of the cephalic lateral-line canals (Collette and Banareescu 1977). In addition, two characteristics found only in *Gymnocephalus* and *Zingel* were a distinctly enlarged foramina of the lower jaw and a reduced or absent articular process. Scales of *Gymnocephalus*, *Percina*, and *Stizostedion* are identical with respect to eight characters observed by Coburn and Gaglione (1992). *Gymnocephalus* appear to have fewer vertebrae than other percids with the exception of *Percarina* and some *Etheostoma* (Collette 1963). Within *Gymnocephalus*, *G. baloni* and *G. cernuus* have a similar number of vertebrae, which are significantly fewer than *G. acerina* and *G. schraetser* (Holcik and Hensel 1974). Based on vertebrate counts (and some coloration differences), Holcik and Hensel (1974) separated *Gymnocephalus* into two subgenera, *Gymnocephalus* and *Acerina* (Figure 3). Elshoud-Odenhave and Osse (1976) thoroughly described the cephalic skeletal and muscular systems of ruffe. A compilation of meristics and morphological characters of ruffe is shown in Table 3. Matkovskiy (1987) determined the relationship between total length and size of several body parts.

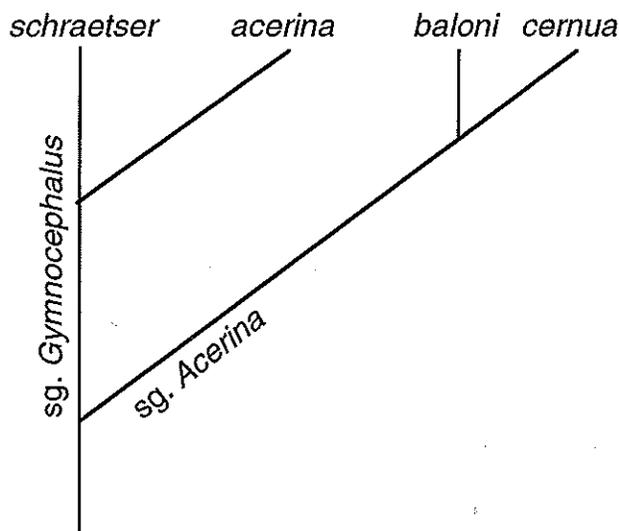


Figure 3. Presumed phylogeny of the genus *Gymnocephalus* (from Holcik and Hensel (1974)).

Table 3. Range of meristic and morphological measures on European or Asian ruffe. Sources are denoted by the following bold letters and are given in the works cited: A = Aleksandrova (1974), B = Berg (1949), C = Craig (1987), Co = Collette (1963), H = Holcik and Hensel (1974), K = Kolomin (1977).

Source	Character	Range	Source	Character	Range
A,B,C,H,K	Dorsal Spines	11-16	A,Co,K	Vertebrae	31-36
A,B,H	Dorsal Soft Rays	10-15	A,B,C,H	Lateral Line Scales	33-42
H	Dorsal Length	49.9-55.6	A,B	Scales below L.L.	5-10
H	Dorsal Depth (soft rays)	12.4-17.4	A,B	Scales above L.L.	10-18
A,B,K	Anal Spines	2-3	A,B,H,K	Gill-rakers, 1st arch	6-14
A,B,H,K	Anal Soft Rays	4-7	H	Interorbital Distance	5.3-7.7
H	Anal Length	10.5-14.4	H	Eye Diameter	6.6-8.8
B	Pectoral Rays	13-17	H	Body Depth	24.1-27.3
H	Head Depth	20.9-24.1	A,B,H	Preopercular Spines	7-16
H	Head Width	21.2-29.6	H	Opercular Spines	1
H	Caudal Peduncle Length	20.1-24.5	H	Predorsal Distance	30.7-34.8
H	Branchiostegal Rays	6-7		Preventral Distance	33.0-38.6
				Minimal Body Depth	7.7-8.9

Different morphotypes of ruffe may exist. "Shallow-bodied" and "deep-bodied" forms of ruffe existed in the same stretches of the Dneiper (Aleksandrova 1974). Differences between littoral- and pool-dwelling populations of ruffe in Syamozero were identified (Kuderskiy 1966). Some of the morphological and meristic characters that differed between the two groups were the number of dorsal rays and spines, scales above and below the lateral-line, opercular spines, vertebrae, and the relative size of the head, snout, eyes, and fins (Aleksandrova 1974).

In addition to different morphotypes, geographical variation in meristic and morphological characters exist (Bilyi 1967; Witkowski and Kolacz 1990). There is a general gradient (longer to shorter) from east (Europe) to west (Siberia) in the following characters: maximum and minimum body depth, predorsal and preanal distance, depth of first dorsal fin, length and depth of anal fin, and length of pectoral fin (Witkowski and Kolacz 1990). Differences may occur over a smaller geographic distance. Ruffe from the Nadym River had a more fusiform body, shallower head, longer snout, and pelvic, pectoral, and dorsal fins positioned more posteriorly than ruffe from the nearby Ob' (Kolomin 1977). Ruffe from the lower Ob' were deeper bodied than the fusiform ruffe from the upper Ob' (Petlina 1967). Morphological differences may be caused by environmental differences among locations (Witkowski and Kolacz 1990). For example, differences between ruffe from the Nadym and Ob' Rivers may be an adaptation to long spawning and overwintering migrations (Kolomin 1977).

Sexual dimorphism in ruffe is present in some characters. The morphological characters that differ between sexes might differ between populations (Petlina 1967). Opalatenko (1967) found that least body depth, head length, pelvic fin length, and upper lobe of the caudal fin length were greater in males than in females (Opalatenko 1967). Petlina (1967) found differences between the sexes in pelvic fin length, eye diameter, head length, body thickness, head depth through the middle of the eye, and preventral, prepectoral, and anal-caudal distance. Sexual dimorphism in 30 morphological and meristic characters was not observed in either "deep-bodied" or "shallow-bodied" ruffe from the Dneiper (Aleksandrova 1974). Opalatenko (1967) found no sexual differences in meristic characters. Furthermore, Shmidtov and Varfolomeyev (1952), Shilenkova (1962), and Biliy (1967) did not observe sexual dimorphism in ruffe.

Ruffe can apparently hybridize with *Perca fluviatilis* and *G. baloni*. *G. cernuus* and *Perca fluviatilis* hybrids are intermediate in appearance between the two parental types but usually more closely resemble the female parent (Kammerer 1907). Hybrids are less active than pure-bred specimens, grow faster, and are more resistant to extremes in temperature, pollutants, and starvation. Male hybrids show no interest in female hybrids and no milt is produced. Female hybrids, though, can successfully reproduce with males from both parental groups. *G. cernuus* and *G. baloni* hybrids are also intermediate in coloration and osteological characters (Holcik and Hensel 1974).

Ruffe have  $2n=48$  chromosomes (Lieder 1964; Nygren et al. 1968; Bozhko et al. 1978; Rab et al. 1987; Klinkhardt 1990). Bozhko et al. (1978) found 2 metacentric, 11 submetacentric, 8 subelocentric, and 3 acrocentric chromosome pairs. Rab et al. (1987) discovered 1 metacentric, 16 submetacentric, 4 subelocentric, and 3 acrocentric chromosome pairs. Mayr et al. (1987) found only one acrocentric chromosome pair (no. 14). Logvinenko et al. (1983) described a diallelic codominant system of inheritance at two independent loci and proposed that these alleles may serve as genetic markers. Nyman (1969, 1975) demonstrated that ruffe have a simple two-allele serum esterase polymorphism and suggested that this information could be used in population investigations. The karyotypes of the four *Gymnocephalus* species are unique at the species level (Rab et al. 1987).

All known *Gymnocephalus* fossils are *G. cernuus* from interglacial deposits in Denmark, Germany, Russia, England, and Poland (Holcik and Hensel 1974). *G. cernuus* are apparently of Paleo-Danube origin (Holcik and Hensel 1974; Rab et al. 1987) and may have arose from *Perca* (Collette and Banarescu 1977; Rab et al. 1987). Collette et al. (1977) hypothesized that the lack of centrarchids in Europe may have allowed for the evolution of the four moderate-sized *Gymnocephalus* species. *G. cernuus* and *G. baloni* appear to be more primitive than *G. acerina* and *G. schraetser*, with *G. baloni* apparently derived from *G. cernuus* (Holcik and Hensel 1974).

Thus, *G. cernuus* may be the basal *Gymnocephalus* species with most speciation due to geographic isolation (Holcik and Hensel 1974).

### Sensory Physiology

Ruffe have an extremely sensitive lateral-line system. Immediately after hatching, the cephalic lateral-line sensors are underdeveloped and can only detect large amplitude vibrations (Disler and Smirnov 1977). By fry stage, the 25 cephalic cupulae (Figure 4) become embedded in canals covered by stretched-skin membranes (Jakubowski 1967). Embedding the neuromasts in canals affords protection while maintaining contact with the water. High sensitivity is maintained by a large number of nerve fibers per neuromast and receptors per nerve fiber (Gray and Best 1989), large size of the lateral-line (Denton and Gray 1988), and by the membrane covering the canal (Denton and Gray 1988). Blinded ruffe could detect water vibrations at a greater distance than other test species (Dijkgraaf 1934). Only deep-sea fishes have similar numbers of nerve fibers and receptors (Von Bekesy 1967; Gray and Best 1989).

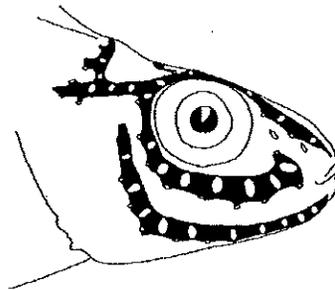


Figure 4. The position of the cephalic lateral-line canals on ruffe (from Kuiper 1967).

The ultrastructure and electrical physiology of the lateral-line system has been actively studied (Jielof et al. 1952; Flock 1967). Ruffe are sensitive to frequencies of 50-150 cycles per second (cps) and are able to distinguish between the low and high end of this range (Kuiper 1967). Van Netten (1991) found that the “hydrodynamic excitation of the cupulae ... can satisfactorily be described with a frequency-dependent combination of viscous and inertial fluid forces, which result from the boundary layer around the cupula.” Gray and Best (1989) and Denton and Gray (1989) described the relative stimulation of each cephalic neuromast as a ruffe passed over a prey source (Figure 5). The stimulus pattern changes as the fish moves over the source. This change in nerve activity should allow ruffe to accurately detect prey. Wubbels (1991) described a phase reversal of the responses of adjacent neuromasts that may allow ruffe to detect and locate a moving object.

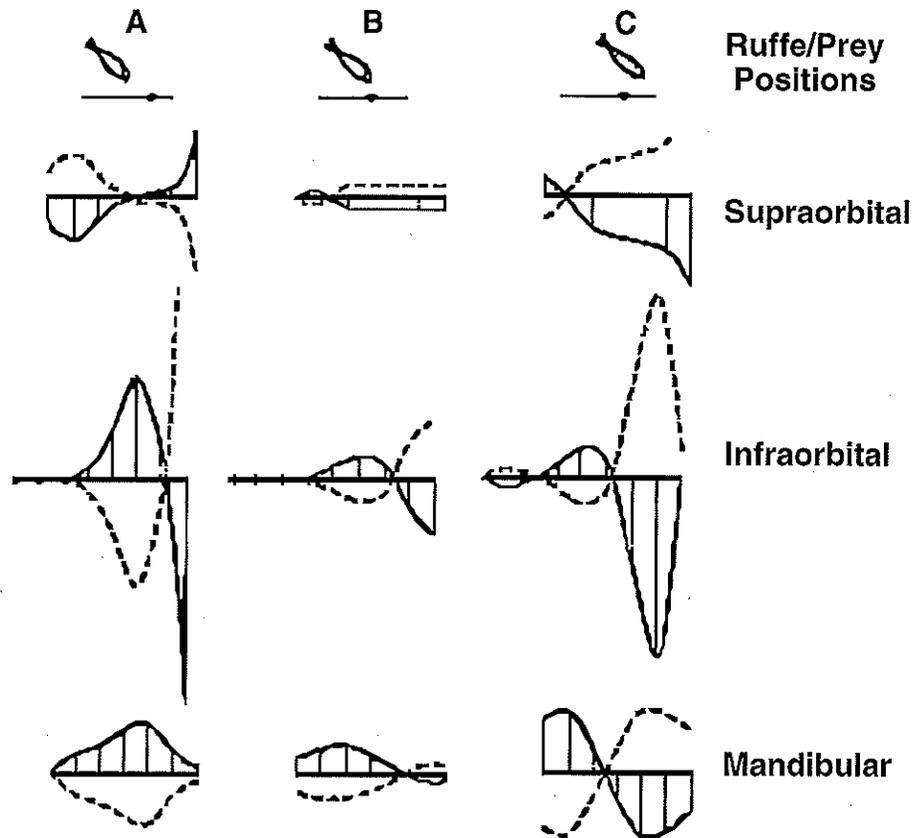


Figure 5. Diagram from Gray and Best (1989) to illustrate changes of stimulus pattern to the head neuromasts. Within each of the three parts (A, B, & C) are three diagrams arranged in a column representing, from top to bottom, the supraorbital, infraorbital, and mandibular canals. Within each diagram the posterior neuromast is the left and the anterior to the right. Each vertical line is proportional to the velocity of liquid at that neuromast, relative to that at neuromast 16, for a transient in one direction; the direction of the line above or below the base indicates the relative direction of the velocity along the canal. A full line outlines the vertical lines; a similar dashed line indicates what the outline would be like for an identical transient of the opposite polarity. The diagram has been calculated for a fish moving forward with its mouth at a constant distance of 10 mm above a 'mud surface' and its body held at 60° to that surface (ruffe/prey positions). The source is taken as being at the surface with its axis of vibration along the surface in the direction of the fish's axis. A, is for a fish 5 mm before reaching the source; B, is when the mouth is exactly above the source; C, is for a position 5 mm beyond the source.

Ruffe possess a retinal tapetum lucidum similar to that of Luciopercini (Ahlbert 1970). The tapetum lucidum is a reflective material found in the dorsal two-thirds of the pigmented epithelial layer of the ruffe retina (Wunder 1930; Harder 1975; Craig 1987). In the dark-adapted state (low light), light is reflected back and forth between the tapetal processes with additional absorption by the rods after each reflection (Harder 1975; Zyznar and Ali 1975; Ali et al. 1977). Ali and Anctil (1968) found a relationship between the developmental state of the tapetum lucidum and habitat use by walleye (*Stizostedion vitreum*) and sauger (*Stizostedion canadense*). Sauger, which have a more developed tapetum lucidum than walleye, prefer more turbid waters. Thus, the presence of a tapetum lucidum aids vision in low-light conditions.

The photoreceptors of ruffe are arranged in an irregular twin cone pattern that varies between row and square configurations (Ahlbert 1970; Collette et al. 1977). The existence of a square pattern is positively correlated with poor movement perception (Ahlbert 1970). The greatest cone density in ruffe is distributed rostrally, suggesting that ruffe are positively adapted for vision in the posterior field and that vision in the anterior field is of lesser importance.

### Geographic Distribution

Originally found throughout Europe and Asia, *G. cernuus* is the most widespread species of the genus. The native range of ruffe included northeastern France, eastern rivers of England, the rivers entering the Baltic Sea, the rivers entering the White Sea, most of Siberia (Figure 6; Wheeler 1974; Collette and Banarescu 1977; Lelek 1987), and the brackish archipelagos of the Baltic Sea (Hansson 1984; 1985; 1987). Ruffe have recently been found in several European water bodies outside of their original distribution. These water bodies include Loch Lomond, Scotland (Maitland et al. 1983), Llyn Tegid, North Wales (Winfield 1992), the Lake District, England (Winfield 1992), a Zurich, Switzerland lake (H. Persat, personal communications), and two new reservoirs on the Drava River, Croatia (H. Persat, personal communications). The expansion of ruffe has probably been aided by the construction of canals (Wheeler 1974) and the use of ruffe as bait for northern pike (*Esox lucius*; Winfield, personal communications).

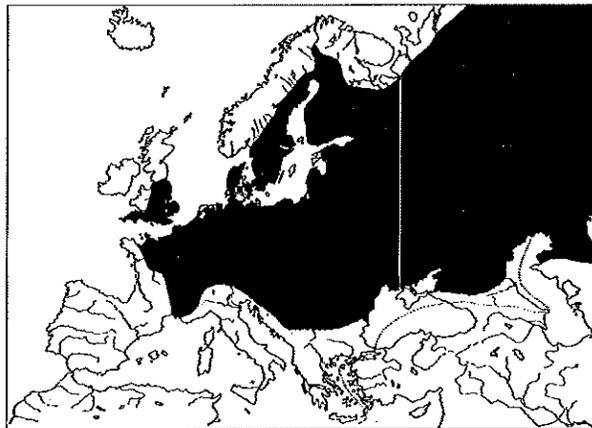


Figure 6. European distribution of ruffe (from Lelek 1987).

### Habitat

Ruffe can tolerate a wide range of ecological and environmental conditions (Johnsen 1965). Ruffe have been found in fresh and brackish (salinities up to 10-12‰; Lind 1977; Pethon 1980) waters; lacustrine and lotic systems; depths from 0.25 m (Van Densen and Hadderingh 1982) to 85

m (Nilsson 1979; Sandlund et al. 1985); montane and submontane areas (Kawecka and Szczeny 1984); and from oligotrophic to eutrophic waters (Leach et al. 1977; Lind 1977; Hansson 1985; Johansson and Persson 1986; Bergman 1991). Although ruffe are found in a variety of conditions, three generalities can be made about ruffe habitat use. Ruffe prefer areas of slow-moving water with soft bottoms that are devoid of vegetation (Johnsen 1965; Lelek 1987), are often associated with the bottom (Holcik and Mihalik 1968; Sandlund et al. 1985; Bergman 1988), and generally increase in abundance with increasing eutrophication. Soft-bottom areas may be preferred because of the location of preferred food items (see Diet and Foraging Behavior section) or because these areas are often associated with deeper or darker areas. Ruffe have developed adaptations for living in dark environments (see Sensory Physiology section).

The abundance of ruffe generally increases with eutrophication until hypereutrophy is reached (Entz 1977; Leach et al. 1977; Hansson 1985; Johansson and Persson 1986; Bergman 1991; Persson et al. 1991; Figure 7). In contrast to ruffe, the abundance of most other percids is greatest in mesotrophic waters (Leach et al. 1977; Ryder and Kerr 1978). Ruffe abundance increased with anthropogenic additions of nutrients in several situations (Heinonen and Falck 1971; Anttila 1973; Hansson 1987; Neuman and Karas 1988), but Peirson et al. (1986) found that ruffe abundance increased after severe nutrient additions were eliminated. Leopold et al. (1986) found no correlation between level of eutrophication and ruffe catch because year-to-year ruffe catch was highly variable. Biro (1977) reported that ruffe abundance declined with increasing eutrophication, but did not state where on the trophic continuum the increase occurred.

There are four possible hypotheses to explain the correlation between increased ruffe abundance and increased eutrophication. First, ruffe forage more efficiently under the reduced light conditions associated with increased algal production (Johansson and Persson 1986; Bergman 1988, 1991). Second, the benthos may increase in abundance and diversity and shift to smaller species in response to the storage of increased energy in the sediment due to eutrophication (Leach et al. 1977). Ruffe are primarily benthic feeders and would presumably be favored by the increased benthic production and shift to smaller species. Third, increased productivity may release predation pressure on ruffe (Bergman 1991). Fourth, ruffe may simply be physiologically more tolerant of eutrophic conditions than other percids.

Ruffe appear to be tolerant of a wide range of temperatures (Bergman 1987). Ruffe have been found to be abundant in water as cold as 0-2°C (Neuman 1979). The upper lethal temperature for juvenile ruffe appears to be 30.4°C, whereas the critical thermal maximum is 34.5°C (Alabaster and Downing 1966 and Horoszewicz 1973, as summarized in Hokanson 1977). The upper lethal temperature for ruffe was near the middle of 9 species tested (Alabaster and Downing 1966). Evidence of stress did not occur below 29.8°C (Horoszewicz 1973). Optimal temperature for larval growth is 25-30°C (Kammerer 1907), whereas optimal growth for age-0 ruffe is 21°C

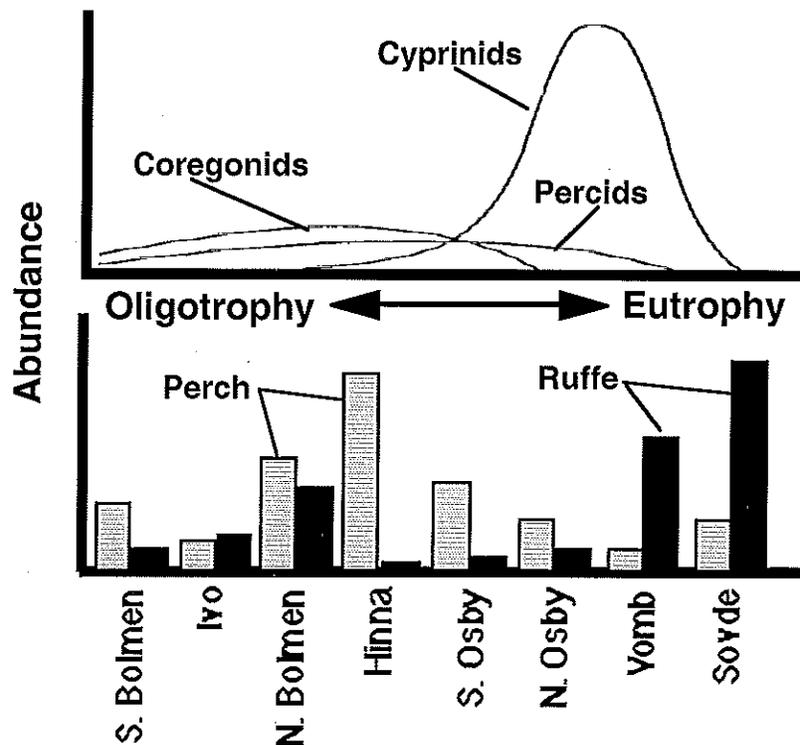


Figure 7. Schematic representation of the relationship between productivity and coregonid, cyprinid, and percid abundance (top panel; from Bergman 1990a) and abundance of perch and ruffe in eight Swedish lakes ordered by increasing chlorophyll a values (bottom panel; from Bergman 1991).

(Edsall et al. 1993). The foraging ability (capture rate, handling times routine swimming performance, and reaction distance) is affected by temperature, but not nearly as drastically as that of perch (Bergman 1987). Nyman (1975) concluded that ruffe may be able to genetically adapt to a wide range of temperatures. In contrast, Hokanson (1977) states that the temperature requirements of *G. cernuus*, *Perca fluviatilis*, and *Perca flavescens* can not be distinguished with the available data.

Ruffe mortalities occur at low levels of oxygen and high levels of toxic chemicals. Ruffe, which prefer oxygen concentrations of 5-6 mg/l (Holcik et al. 1989), died in 1-3 h at oxygen concentrations of 0.69-0.97 mg/l (Holcik 1986). Severe mortalities of ruffe may occur in the anoxic hypolimnion of some lakes (Lelek 1987). Ruffe prolarvae were deformed and died when exposed to 1 mg/l triethyl-stannic chloride solutions (Danil'chenko 1982). Development ends at the prolarvae stage when ruffe are exposed to 10 mg/l silicylanilide, 0.1 mg/l triethyl lead chloride, and 0.1 mg/l pentachlorophenolate of sodium (Danil'chenko and Stroganov 1975). Ruffe eggs are resistant to some toxins that embryos are sensitive to (Danil'chenko 1977).

## Reproduction and Early Life History

Ruffe generally mature at age 2 or 3, at total lengths near 11 or 12 cm (Lind 1977; Maitland 1977; Kolomin 1977; Neja 1988). However, ruffe may mature at age 1 (Fedorova and Vetkasov 1974; Lind 1977; Craig 1987; Neja 1988). For example, in Lake IJssel, 50% of ruffe were mature at age 1 (approximately 7 cm; Willemsen 1977). Early maturity may be a result of warmer waters (Fedorova and Vetkasov 1974; Craig 1987) or high mortality early in life (Lind 1977).

Ruffe are categorized as non-guarding, open substrate, phytolithophil spawners, laying eggs on available submerged plants in clean water habitats, or on other submerged items such as logs, branches, gravel, or rocks (Balon et al. 1977). The summaries of Maitland (Maitland 1977; Maitland et al. 1983) agree with Balon's generalizations, but the review of Collette et al. (1977) did not agree with Balon, as they concluded that ruffe spawn on hard bottoms of sand, clay, or gravel. Available field evidence supports both conclusions. Nadyrn River ruffe lay eggs on submerged vegetation or silted snags at approximately 2 m (Kolomin 1977). In Denmark, ruffe have been found to move from deep areas to shallow areas of stone-sand bottoms, sometimes near vegetation, or into rivers to spawn (Johnsen 1965). In Lake Ilmen, ruffe spawn on firm sand, sand-stone, or clay bottoms in less than 3 m of water (Kovalev 1973; Fedorova and Vetkasov 1974) or, on occasion, ruffe will spawn on plant remains and moss in abandoned smelt spawning grounds (Fedorova and Vetkasov 1974). In summary, ruffe spawn on a variety of substrates at depths of approximately 3 m or less.

Ruffe spawn between mid-April and July (Collette et al. 1977; Hokanson 1977; Neja 1988); beginning when the water warms to 6.0°C and continuing to water temperatures between 12 and 18°C. Nadyrn River ruffe begin spawning in June when the river is ice-free and temperatures are between 6 and 8°C (Kolomin 1977). Lake Ilmen ruffe spawn from mid-April to June when water temperatures are between 6.5 and 13°C (Kovalev 1973; Fedorova and Vetkasov 1974). Ruffe in other Russian waters spawn at temperatures between 6 and 10°C (Berka 1990). Lake IJssel ruffe spawn in May and June at water temperatures of 12 to 18°C (Willemsen 1977). Ruffe in Lake Aydat spawned at temperatures between 15.0°C and 18.0°C. Knowles (1974) reported that ruffe were "ready to spawn at unusual times of the year", presumably late summer and fall. Hokanson's (1977) report that the lowest recorded spawning temperature for ruffe was 11.6°C appears to be erroneous.

Very little other physical or chemical parameters concerning ruffe spawning are reported in the literature. Kiyashko and Volodin (1978) did, however, determine that ruffe eggs will develop normally at pH values between 6.5 and 10.5, one of the widest ranges from a broad set of fish tested.

Available evidence indicates that ruffe eggs are extruded from the female without sticking together, but will, upon contact with the water, become adhesive and stick to the substrate

(Johnsen 1965; Kovalev 1973). Page (1985), however, categorized ruffe as "strand-ers" with "the unique habit of encasing their eggs in long gelatinous stands" and cited Seeley (1886) and Wheeler (1969) as sources. Page did note, though, that other authors did not mention egg-stranding in their ruffe spawning summaries. No other evidence for egg-stranding appears in the literature located for this review.

Ruffe may spawn intermittently, laying eggs in two or more batches (Koshelev 1963; Travkina 1971; Kovalev 1973; Fedorova and Vetkasov 1974; Kolomin 1977; Craig 1987; Neja 1988; Jamet and Desmolles 1994). Koshelev (1963) extensively studied the physiology of intermittent spawning ruffe. Rapid and asynchronous oocyte growth and the lack of a resting stage II oocyte led to batch spawning and longer spawning periods in ruffe. The first batch of oocytes mature in 165 days during winter and spring, whereas the second batch matures in 30 days during summer. Resorption of the first batch of ova does not interfere with growth of the second batch because resorption and growth occur simultaneously. The number and size of eggs is reduced in the second batch (Kolomin 1977). Neja (1988) notes that at one point in time the ruffe contains three types of eggs: (1) small, hyaline, and colorless, (2) larger, opaque, white or pale yellow to yellow and orange in color, and (3) large, partly hyaline, and yellow-orange and orange in color. Only type (2) and (3) eggs will be released in an upcoming spawning event.

The number of eggs laid depends on the size of the female (Neja 1988, Kolomin 1977) and the batch of eggs (Kolomin 1977). Individual absolute fecundity (total eggs per female) was 13,388-82,233 in Lake Dabie (Neja 1988), 6,900-64,665 in Ob' River (Petlina 1967), and 4,220-29,600 in the first batch and 352-6,012 in the second batch in the Nadym River (Kolomin 1977). Maximum absolute fecundity appears to be about 200,000 eggs (Collette et al. 1977; Berka 1990). In contrast to absolute fecundity, the relative fecundity of Lake Dabie ruffe was uncorrelated to body size, gonad weight, or age (Neja 1988). Relative fecundity was between 305-1,540 eggs per g of fish (Bastl 1983; Neja 1988; Jamet and Desmolles 1994). Average gonosomatic index for spawning female ruffe was between 7.11 and 15.6 (Kolomin 1977; Neja 1988; Jamet and Desmolles 1994), with an individual maximum of 27.78 (Bastl 1983). The gonosomatic index for spawning males was between 7.0 and 9.96 (Bastl 1983; Neja 1988; Jamet and Desmolles 1994).

Egg diameter also depends on the size of the female and the batch of eggs. Egg diameters ranged from 0.34 to 1.3 mm (Johnsen 1965; Kovalev 1973; Fedorova and Vetkasov 1974; Disler and Smirnov 1977; Kolomin 1977; Bastl 1983). Bastl (1983) reported that mean egg weight was  $0.45 (\pm 0.05)$  g and mean egg volume was  $0.59 (\pm 0.48)$  mm<sup>3</sup>. Eggs from a first batch are larger (0.90-1.21 mm) than eggs from a second batch (0.36-0.47 mm) and yellow compared to whitish in color (Kolomin 1977).

Gonadal activity in males occurs during spring and autumn waves of spermatogenesis (Butskaya 1980, 1985), with the autumn wave being more important (Butskaya 1985). In the

laboratory, spermatogenesis and the extrusion of ripe sexual products in ruffe are thermo-dependent processes that do not depend on a fixed daylight regime. There is a continuum of effects of temperature on gonadal activity. At extreme temperature ( $< 2^{\circ}\text{C}$  and  $> 18^{\circ}\text{C}$ ), spring spermatogenesis is limited. From 5 to  $15^{\circ}\text{C}$ , the rate of spermatogenesis increases with increasing temperature. From 15 to  $17^{\circ}\text{C}$  individual sensitivity is evident, as shown by a negative effect on spermatogenesis. The number of degree days required for the development of spermatogenesis in overwintering ruffe, prior to the formation of new spermatozooids, was greater under experimental conditions than during spring spermatogenesis in nature. This observation suggests that the gonadotrophic system of males in nature is influenced by the synergic action of additional factors not detected by his experiments, such as photoperiod or temperature (Butskaya 1980). Furthermore, in nature, temperature may interact with other forces to influence the presence of females on the spawning grounds and to initiate spawning conditions in males (Butskaya 1980).

Instances of hermaphroditism in ruffe have been recorded (Knowles 1974; Butskaya 1976). In the Gulf of Finland, approximately 25% of all ruffe gonads had both testicular and ovarian cells (Butskaya 1976). In 85% of these fish, the sexual organs are of a "testicular type." About half of these fish function as "normal" males. In the remaining half, fecundity is varyingly decreased from the "normal" levels down to none. In only 2% of the fish can a changeover to functional hermaphroditism occur. The presence of large numbers of these "inter-sexual" fish did not have a negative influence on overall ruffe reproductive levels.

Ruffe eggs hatch in 5 to 12 days at temperature between 10 and  $15^{\circ}\text{C}$  (Johnsen 1965; Maitland 1977; Craig 1987; Berka 1990). A newly hatched embryo of 3.5-4.4 mm (Fedorova and Vetkasov 1974; Disler and Smirnov 1977) is in a relatively underdeveloped stage, compared to yellow perch (*Perca flavescens*; Disler and Smirnov 1977). The embryo remains sedentary on the bottom for 3 to 7 days until it reaches a size of 4.5 to 5.0 mm, which is the same stage of development as a newly hatched yellow perch embryo (Collette et al. 1977; Disler and Smirnov 1977). Disler (1960) and Disler and Smirnov (1977) described the morphological development of ruffe larvae.

Ruffe have no, or only a brief, pelagic larval stage (Johnsen 1965; Fedorova and Vetkasov 1974; Disler and Smirnov 1977). The onset of active feeding and the later transition to exogenous feeding (diet described in the Diet and Foraging Behavior section) takes place in the benthopelagic layer (Disler and Smirnov 1977), within about one week of hatching (French and Edsall 1992). Larval ruffe are positively phototactic (Disler and Smirnov 1977). At the larval stage, ruffe are secretive and solitary, not forming schools (Disler and Smirnov 1977). For these reasons, ruffe larvae are not highly vulnerable to plankton sampling gear (Disler and Smirnov 1977; French and Edsall 1992).

The temperature requirements of young ruffe have been determined. The lower TL50 for embryos is 10°C and the upper TL50 is 21.5°C (Hokanson 1977). Survival of larval ruffe is poor below 10°C (Hokanson 1977). Optimal growth of larval ruffe occurs between 25 and 30°C (Hokanson 1977), whereas optimal growth of age-0 ruffe was 21°C (Edsall et al. 1993). However, age-0 ruffe grew at temperatures between 7.0 and 24.8°C (Edsall et al. 1993).

## Age and Growth

Female ruffe may reach a maximum age of 11, but male ruffe generally do not exceed age 7 (Kolomin 1977). In most cases, 6 age-groups are sampled (Table 4), but a sizable majority of the fish are young (Fedorova and Vetkasov 1974; Lammens et al. 1990). For example, Fedorova and Vetkasov (1974) sampled 7 age-groups, but 93% of the catch was age 1 or 2 fish.

Most authors used scales to age ruffe (Aleksandrova 1974; Fedorova and Vetkasov 1974; Holker and Hammer 1994). Jamet and Desmolles (1994) found that ruffe produced only one annulus per year and the annulus was formed in the winter. Holker and Hammer (1994) provided a relationship between scale radius and ruffe total length. In some instances, scales have been found to be inadequate for assigning age (Mills and Eloranta 1985). Thus, dorsal spine or otolith sections have been used to assign age (Bast et al. 1983). Aleksandrova (19974) used otoliths as "controls" for scale-assigned ages, but did not mention any discrepancies between the two methods. Doornbos (1979) and Matkovskiy (1987) provided a relationship between otolith length and ruffe total length.

Ruffe are typically less than 20 cm, rarely attain a size greater than 25 cm (Lind 1977; Craig 1987; Lelek 1987; Berka 1990), but may be as large as 29 cm (Moller et al. 1988). Ruffe mature at a young age (see Reproduction and Early Life History section), so most of the overall length is attained in the first or second year (Table 4; Kolomin 1977).

Growth of ruffe is affected by sex, morphotype, water type, intraspecific density, and food supply. Females typically grow faster than males (Table 4; Bast et al. 1983; Berg 1949; Fedorova and Vetkasov 1974; Neja 1989; Holker and Hammer 1994), although, in some instances no difference was observed (Neja 1989). Aleksandrova (1974) determined that growth was different

Table 4 (Next Page). Total length (unless noted) at age of ruffe in selected European investigations. Items with a bold-faced letter were interpreted by the following authors (citations can also be found in those papers): **A** = Aleksandrova (1974), **B** = Boikova (1986), **Ba** = Bast et al. (1983), **H** = Holker and Hammer (1994); **N** = Neja (1989), **W** = Willemsen (1977). Lengths from Neja (1989) were converted to total lengths. Letters in comments are: **a**: known to be back-calculated; **b**: shallow-bodied form in the middle Dneiper; **c**: deep-bodied form in the middle Dneiper; **d**: freshwater; age-10 length is 166; **e**: brackish waters; **SL**: standard length; **FL**: fork length.

Author	Year	Country	Age									Comments		
			I	II	III	IV	V	VI	VII	VIII	IX			
N Adamus et al.	1978	Poland (?)	35	55	72	84	107	125						
Aleksandrova	1974	USSR			108	115	119							b
Aleksandrova	1974	USSR	64	96	98	109	116							c
Aleksandrova	1974	USSR	32	64	91	104	118							a,b
Aleksandrova	1974	USSR	31	59	83	97	104							a,c
H Arzbach	1987	Germany	101	159	190	210	219	236						a
Bast et al.	1983	Germany		97	112	132	162							
Bast et al.	1983	Germany	80	97	112	136	169	186						
Bast et al.	1983	Germany			127	152	177	184						
N Bauch	1963	Germany	60	90	110	120	139							
Berg	1949	USSR		84	97	115								SL, male
Berg	1949	USSR		86	103	123								SL, female
Ba Biro	1971	USSR (?)	56	65	79	107	126							
Fedorova and Vetkasov	1974	USSR	56	73	90	106	117	125						
Holker & Hammer	1994	Germany	101	157	190	207	229	241						b; male
Holker & Hammer	1994	Germany	97	154	177	203	214							a; female
Jamet and Desmolles	1994	France	66	99	119	132	139	144						FL
Ba Johal	1980	Czechoslovakia	66	91	107	117	132	143	151					
Ba Johal	1980	Czechoslovakia	64	89	106	120	136	145	157					
Ba Kijashko	1980	USSR	57	85	101	114	124	133						
H Knowles	1974	Germany	84	121	156	180								a
N Kolander	1969	Poland	89	106	121	137	145	161						
Kolomin	1978	USSR	77	113	121	125	131	141						males
Kolomin	1978	USSR	91	115	122	133	137	155	163	163				females
A Kostyuchenko	1962	USSR	38	79	106	127								a
N Kozlova	1979	USSR ?	63	72	84	99	106	119						
Ba Lind	1977	Finland	41	73	102	118	137	143	148	167	164			d
Ba Lind	1977	Finland		109	126	137	144	154	159	172				e
Lelek	1987	Europe	38	62	78	90	110	112						
H Masatova & Zavela	1988	Czechoslovakia	51	71	85	101								a
Neja	1989	Poland (sl)	72	105	122	137	148	157	162	170	172			a: females
Neja	1989	Poland (sl)	73	106	122	137	148	158	159	157	163			a; males
Neja	1989	Poland (om)	74	101	119	129	143	155	164	176	179			a: females
Neja	1989	Poland (om)	73	99	119	128	137	145						a; males
Neja	1989	Poland (ld)	72	103	122	136	143	156	169	174				a: females
Neja	1989	Poland (ld)	71	99	114	128	135	143	152					a; males
N Neuhaus	1934	Poland	72	92	105	117								
W Neuhaus	1934	Poland	80	120	140	160								
Ba Noack	1978	Germany	70	121	157	178								
Ba Nolte	1939	Germany	91	119	134	160	177							
B Shamardina	1968	Russia	41	52	77	92	105							
Ba Smirnov	1977	Russia	59	80	111	138	157	172	184	194				
B Vasnetsov	1950	Russia	50	81	102									
B Vasnetsov	1950	Russia	37	56	89	117	136							
Willemssen	1977	Netherlands	60	90	100	110								
Willemssen	1977	Netherlands	80	150	180	190								
Willemssen	1977	Netherlands	80	120	140	160								
N Zawisza	1953	Poland (?)	50	81	100									
N Zbigniew	1989	Poland	72	104	122	136	147	157	161	168	168			
N Zbigniew	1989	Poland	71	101	119	133	141	153	162	173				
A Zhukov	1965	USSR	43	83	109	116								a

between shallow- and deep-bodied forms of ruffe. Hansson (1985) found that ruffe growth was reduced in areas where ruffe densities were high. Bergman and Greenberg (1994) showed a clear decline in growth of ruffe in enclosures with increasing densities of ruffe. Ruffe captured in clear and brackish waters tend to grow faster (Neuhaus 1934; Lind 1977; Bast et al. 1983). Poor ruffe growth may also result if the benthos is impoverished (Boikova 1986; Bakanov et al. 1987) or, in one case, largely inaccessible due to oxygen deficiencies (Boikova 1986).

### **Diet and Foraging Behavior**

Ruffe first feed on rotifers and copepod nauplii (Johnsen 1965). Larger cyclopoid copepods, cladocera, and chironomid larvae are important items in the diet of age-0 ruffe larger than about 1 cm TL (Leszczynski 1963; Johnsen 1965; Fedorova and Vetkasov 1974; Collette et al. 1977; Boikova 1986; Boron and Kuklinska 1987). Chironomids have been found in ruffe as small as 10.5 mm (Tolg 1960). Age-0 ruffe larger than 3 to 5 cm generally feed on chironomidae (Leszczynski 1963; Nagy 1988), although Boron and Kuklinska (1987) described a case where mostly microcrustaceans were consumed until the ruffe were 5 cm in length.

The principal prey of juvenile and adult ruffe are chironomids or macrocrustaceans (Table 5). The principal genera of chironomids consumed are *Chironomus* (especially *plumosus*) and *Procladius* (Fedorova and Vetkasov 1974; Boron and Kuklinska 1987; Nagy 1988). The prevalence of chironomids in the diet may decrease with age (Leszczynski 1963; Fedorova and Vetkasov 1974). Other macrobenthos that are prevalent in the diet are Ephemeroptera, Trichoptera, and Hirudinea (Table 5). Ruffe collected from brackish or very deep waters, also feed heavily on macrocrustaceans such as *Pallasea quadrispinosa*, *Pontoporeia affinis*, *Mysis relicta*, *Neomysis integer*, and *Gammarus* spp. (Sandlund et al. 1985; Van Densen 1985; Table 5). For example, Hansson (1984, 1986) found the primary prey of ruffe in brackish waters to be *Gammarus* spp. and *Pontoporeia affinis*, with chironomids important at some locations. Larger ruffe eat some fish (Fedorova and Vetkasov 1974; Kozlova and Panasenko 1977; Bagge and Hakkari 1985). Ruffe of all sizes may eat fish eggs (see Egg Predation subsection in the Community Dynamics section).

The diet of ruffe differs little between lakes with different trophic status or ruffe densities or spatially within lakes. Ruffe fed mainly on chironomids and ephemeropterans in both lakes of moderate and high productivity, although diet breadth was greater in the more productive lake (Bergman 1991). Bergman and Greenberg (1994) determined that ruffe diet consisted of mostly macrobenthos at all levels of ruffe density, with only the contribution of trichopterans and *Pisidium* affected by ruffe density (Bergman and Greenberg 1994). Hansson (1987) and Nilsson (1979)

found ruffe diet to differ little between sampling locations, but Hansson (1984) found differences between locations in a brackish archipelago.

Table 5. Major food items of ruffe in selected European investigations. Citations for items with bold-faced letters are found in the following papers: **B** = Bergman (1987), **Bo** = Boikova (1986), **BK** = Boron and Kuklinska (1987), **J** = Johnsen (1965), **JP** = Johansson and Persson (1986), **N** = Nagy (1988).

Author	Year	Country	Major Food Items
Adams & Tippet	1991	Scotland	Fish eggs, Trichoptera, Crustacea
Aleksandrova	1974	USSR	Chironomidae, Gammarus, Oligochaeta
<b>J</b> Alm	1917	Sweden	Chironomidae, Alona, Cyclopoida
<b>J</b> Alm	1922	Sweden	Chironomidae, Asellus
Appelberg	1990	Sweden	Chironomidae, Asellus
Bagge and Hakkari	1985	Finland (?)	Chironomidae, Mysis, Pallasea
Bergman	1990	Sweden	Chironomidae, Ephemeroptera, Crustacea
Bergman	1991	Sweden	Chironomidae, Ephemeroptera, Crustacea
Bergman & Greenberg	1994	Sweden	Sialis, Chironomidae, Ephemeroptera, Trichoptera
? Berka	1990	USSR	Chironomidae, Amphipoda, Fish eggs
<b>N</b> Bogatova	1963	USSR (?)	Chironomidae
Boikova	1986	USSR	Chaoborus, Cyclopoida, Leptodora, Trichoptera
Boron & Kuklinska	1987	Germany	Chironomidae, Cladocera, Copepoda
<b>JP</b> Brabrand	1983	Norway	Chironomidae, Cladocera
<b>J</b> Brofeldt	1922	Germany	Chironomidae, Asellus, Entomostraca
Fedorova & Vetkasov	1974	USSR	Chironomidae, Crustacea, Fish eggs
Hansson	1984	Sweden	Chironomidae, Amphipoda, Mollusca
Hansson	1987	Sweden	Gammarus, Pontoporeia, Chironomidae
<b>J</b> Hartley	1940	England	Chironomidae, Crustacea
Holker and Hammer	1994	Germany	Neomysis, Crangon crangon, Eurytemora
<b>J</b> Huitfeldt-Kaas	1917	Norway	Pallasea, Mysis, Chironomidae
<b>J</b> Jaaskelainen	1917	USSR	Chironomidae, Pisidium
<b>J</b> Jarnefelt	1917	Finland	Asellus, Trichoptera, Cladocera
<b>J</b> Jarnefelt	1921	Finland	Asellus, Ephemeroptera, Chironomidae
Johnsen	1965	Denmark	Chironomidae, Crustacea, Amphipoda
<b>J</b> Kessler	1868	USSR	Gammarus, Mysis, Pontoporeia
Kolomin	1977	USSR	Chironomidae, Trichoptera, Mollusca
Kozlova & Panasenko	1977	USSR	Chironomidae, Crustacea
<b>J</b> Leszczynski	1963	Poland	Chironomidae
<b>J</b> Levander	1909	Finland	Chironomidae, Gammarus, Corophium
<b>B</b> Meisriemler	1974	Sweden	Chironomidae, Gammarus
<b>J</b> Mohr	1923	Germany	Gammarus, Tubifex, Mysis
Nagy	1986	Germany	Chironomidae, Ephemeroptera, Crustacea
Nagy	1988	Germany	Chironomidae
<b>J</b> Neuhaus	1934	Germany	Asellus, Chironomidae, Corophium
Nilsson	1979	Sweden	Pontoporeia, Mysis, Chironomidae
<b>BK</b> Palle	1965	Denmark	Chironomidae
<b>BK</b> Pliszka & Dziekonska	1953	Poland (?)	Chironomidae
<b>N</b> Schiemenz	1905	German (?)	Chironomidae
<b>J</b> Schneider	1922	Finland	Chironomidae, Trichoptera, Cyclopoida
<b>J</b> Schneider	1922	Estonia	Chironomidae, Trichoptera, Asellus
<b>J</b> Schneider	1922	Estonia	Chironomidae, Limnophilidae, Entomostraca
<b>Bo</b> Shamardina	1967	USSR	Chironomidae, Chaoborus, Cyclopoida
<b>Bo</b> Smirnova	1978	USSR	Chironomidae, Chaoborus, Cyclopoida
<b>J</b> Stadel	1936	Germany	Gammarus, Copepoda
<b>J</b> Tolg	1960	Hungary	Chironomidae, Cyclopoida, Corophium
Van Densen	1985	Denmark	Chironomidae, Amphipoda, Crustacea
Willemsen	1977	Netherlands	Chironomidae, Gammarus

After switching to a diet composed of largely macrobenthos early in life, ruffe diet changes little with size. Bergman (1988) found the diet of three size-classes of ruffe to be similar. Boron and Kuklinska (1987) also did not find any diet differences due to size for age-1 and older ruffe and Jamet and Lair (1991) came to the same conclusion for age-2 and older ruffe. Boikova (1986) identified a slight shift in ruffe diet at 8-10 cm, although the shift is not very evident.

Juvenile and adult ruffe may select chironomids (Leszczynski 1963; Nagy 1986), ephemeropterans (Nagy 1986), and *Sialis* spp. (Bergman 1990b; Bergman and Greenberg 1994), but select against oligochaets (Leszczynski 1963; Nagy 1986) and Hirudinea (Nagy 1986). On a species level, some species of chironomids may be selected against (Nagy 1986). In addition, age-0 ruffe may select larger *Daphnia* and copepods (Van Densen 1985). In contrast, Johansson and Persson (1986) summarized that ruffe are not selective and consume organisms in proportion to the organisms abundance.

Prey items found in the diet can give some indication of ruffe habitat use and feeding behavior. Adult ruffe probably feed in the littoral or sublittoral zones (Leszczynski 1963; Holcik and Mihalik 1968; Boron and Kuklinska 1987; Jamet and Lair 1991). A high percentage of *Chaoborus* in large ruffe led Shamardina (1967) to conclude that large ruffe are in deeper water during the summer than smaller ruffe, a conclusion also made by Bagge and Hakkari (1985). Holcik and Mihalik (1968) felt that ruffe moved to shallow waters to feed in the evening. Ruffe probably feed in soft bottom areas because they penetrate the bottom substrate to capture some prey (Boron and Kuklinska 1987), as evidenced by predation on burrowing chironomids such as *Chironomus plumosus* (Hilsenhoff 1966; Coffman 1978) and *Procladius* spp. (Ford 1962; Coffman 1978). However, high levels of habitat complexity may lead to a reduction in the ruffe predation rate (Mattila 1992). Ruffe in very deep waters typically consume *Mysis relicta*, *Pontoporeia affinis*, and *Pallasea quadrispinosa* (Sandlund et al. 1985).

The feeding behavior and functional morphology of the feeding system in ruffe was described by Elshoud-Oldenhave and Osse (1976). In this paper, the movements and interactions of the cephalic skeletal and muscular systems during a feeding event were described in great detail. The author's developed a general model of teleost feeding from these observations. In addition to the development of this model, interesting observations on ruffe feeding behavior were described.

Ruffe appear to have two types of feeding behavior (Figure 8; Elshoud-Oldenhave and Osse 1976). "Horizontal" feeding occurs when ruffe visually detect the prey in the water column, approach the prey, and suck the prey into it's mouth. "Back-lifting" feeding occurs when a ruffe detects the prey on the bottom, lifts and curves it's body so that the ventral portion of it's head is at a 20-30° angle to the prey, and then sucks the prey into it's mouth. If the ruffe detect the prey visually then it will assume the "back-lifted" position as it approaches the prey. In contrast, if the

ruffe detects the prey with the cephalic lateral-line system then it must swim backwards to get into the "back-lifted" position. Debris captured in the sucking action is expelled through the opercular cavity or spat out. In most cases, a last spitting action follows the final swallowing of the prey.

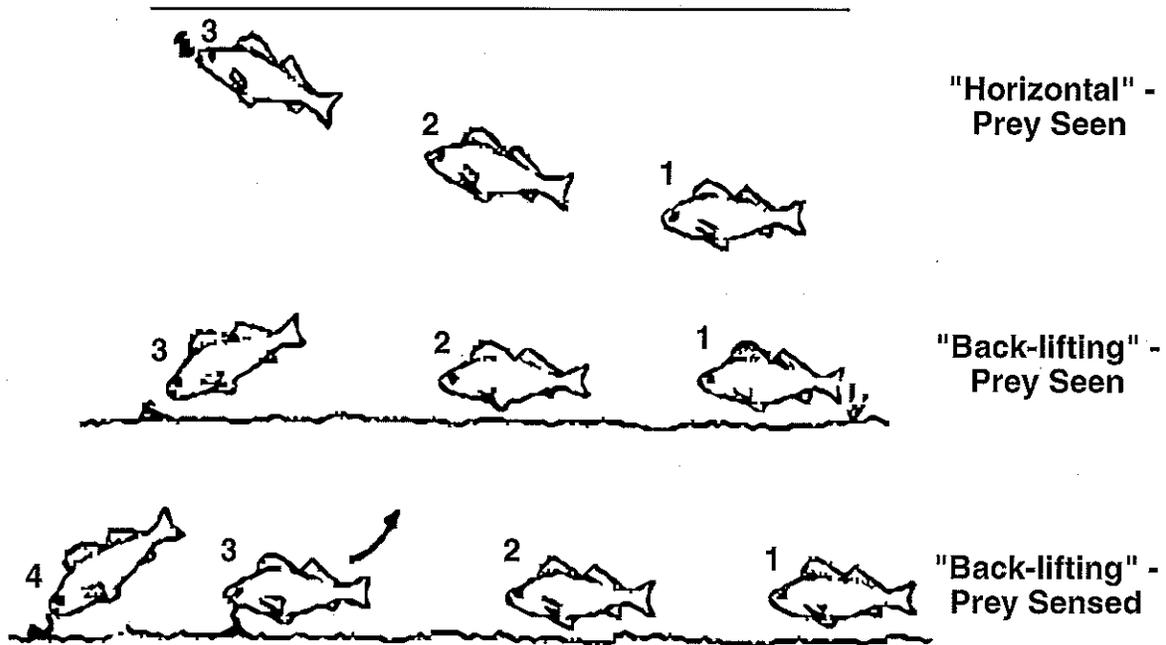


Figure 8. Two types of ruffe feeding -- A = "Horizontal", B = "Back-lifting" -- adapted from Elshoud-Odenhave and Osse (1976).

Ruffe can feed under a variety of conditions but seem to exhibit crepuscular patterns of activity or stomach fullness. Westin and Aneer (1987) found ruffe held in aquariums exposed to natural light levels were generally active during twilight periods with a tendency toward diurnal activity patterns in the winter (Figure 9). Ogle (1992) found adult ruffe to be capable of feeding throughout the 24-h period, but, on some sample dates, adult ruffe did not feed during the day, began feeding at dusk, and continued to feed at night. Jamet and Lair (1991) provided limited evidence that ruffe fed mostly at night. Adams and Tippett (1991) claimed that no diel feeding periodicity was observed for ruffe, but offered no evidence for this conclusion.

The primary sensory system used to detect prey by ruffe appears to be the lateral-line system. The physiology of the extremely sensitive cephalic lateral-line system is discussed in the Sensory Physiology section. Blinded ruffe could localize immobile prey that were made mobile by "involuntary trembling of the hand" (Kuiper 1967). Furthermore, electromagnetic stimulation of nerves attached to the cupulae cause ruffe to "snap for food" (Kuiper 1967). Gray and Best (1989) concluded that the ruffe lateral line is sensitive enough and has sufficient discriminatory power to detect and locate a source 2-5 cm from it's snout. Denton and Gray (1989) also concluded that

ruffe could detect and locate chironomid larvae in the top layers of the bottom substrate using the head canals.

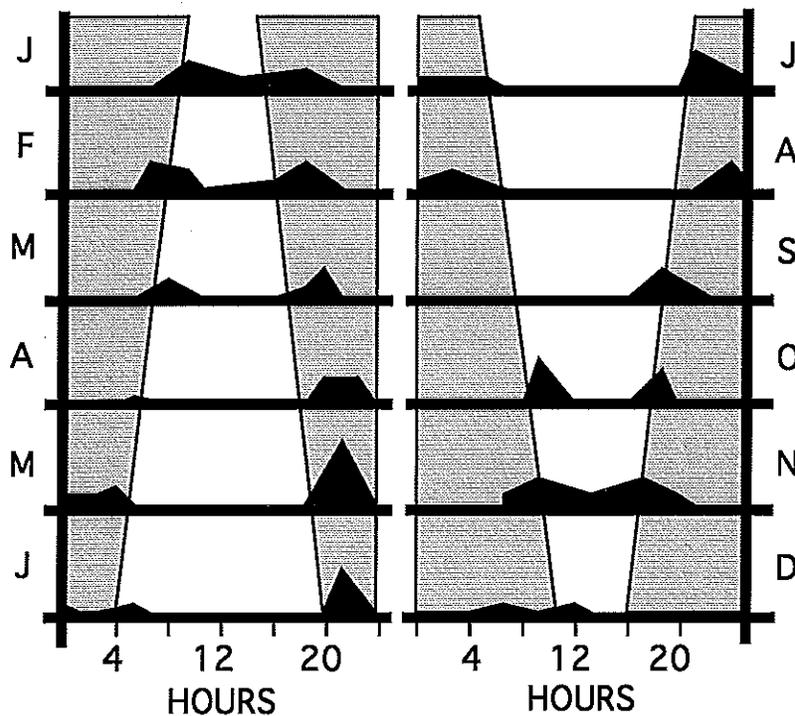


Figure 9. Monthly diel activity patterns of ruffe held in aquaria exposed to natural light levels (from Westin and Aneer 1987)..

Vision may also be used to detect prey by ruffe. The organization of the cone cells in the retinae and presence of the tapetum lucidum (see the Sensory Physiology section) is consistent with the bottom-feeding behavior of ruffe (Ahlbert 1970). Thus, vision may be used to locate prey, even in low-light situations. Ruffe had relatively high levels of choleacetyltransferase and acetylcholine levels in the brain, which is typical of fish with well-developed visual systems (Szabo et al. 1991). However, Ahlbert (1970) suggested that vision might not be that important in ruffe because the ruffe's square cone pattern is related to poor movement perception. Furthermore, Bergman (1987) showed that the reaction distance of ruffe was only 4 cm, compared to 21 cm for perch.

Bergman (1988) provided both field and experimental data to support the conclusion that ruffe are adapted for feeding in low-light conditions. Ruffe were found in all zones of the lake but were most abundant in low-light benthic areas. In the laboratory, the feeding ability (i.e., attack success, capture rate, handling time, and swimming speed) of ruffe was affected little by reduced light levels.

Only one calculation of annual per capita food ration of ruffe appears in the literature. Kozlova and Panasenko (1977) determined that an “average” ruffe consumed approximately 130 g of food per year and 870 g of food per lifetime.

## Community Dynamics

### Egg Predation

Ruffe have been found to prey on fish eggs in both the laboratory (Mikkola et al. 1979; Sterligova and Pavlovskiy 1985; Pavlovskiy and Sterligova 1986) and in the field (Pokrovskii 1961; Balagurova 1963; Johnsen 1965; Titova 1973; Fedorova and Vetkasov 1974; Adams and Tippett 1991; Figure 10). In the one study where an alternative prey was offered (Pavlovskiy and Sterligova 1986), ruffe consumed mostly *Asellus aquaticus* when *A. aquaticus* and *C. lavaretus* eggs were offered in about equal abundance. Several major diet investigations have found egg predation by ruffe to be low or nonexistent (e.g., Johnsen 1965; Hansson 1984; Nagy 1986, 1988; Boron and Kuklinska 1987). Eggs can be identified in the stomachs for 1-3 days (Hanski 1977; Sterligova and Pavlovskiy 1984).

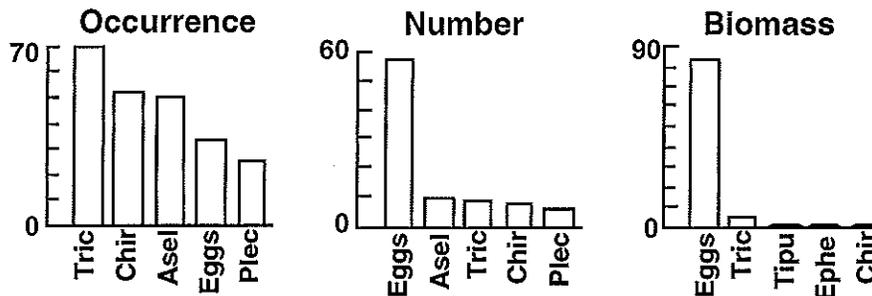


Figure 10. Percent occurrence, number, and weight of prey in Loch Lomond ruffe (from Adams and Tippett 1991).

Ruffe have been implicated in the decline of several *Coregonus* stocks. Pokrovskii (1961) described several cases where *Coregonus* stocks have declined, presumably due to egg predation by ruffe. Unfortunately, Pokrovskii (1961) provided little supportive data and cited documents that are exceedingly obscure. In some instances, 80-90% of spawning *C. albula* eggs were eaten by ruffe which may result in a two or three fold decline in *C. albula* catch. Good catches of *C. albula* occurred in Svaytozero Lake, where the *Tetracotyle* parasite caused a mass mortality of ruffe (Pokrovskii 1961). In other Russian lakes, there was an inverse relationship between the catch of ruffe and *C. lavaretus* in subsequent years (Balagurova 1963; Titova 1973). In Loch Lomond, Scotland, ruffe were found to prey substantially on the eggs of *C. lavaretus* during and immediately after the *C. lavaretus* spawning period (Adams and Tippett 1991). Adams and Tippett

(1991) thought that the rate of predation on the eggs of this stock could be great enough to negatively affect the abundance of *C. lavaretus*. However, ruffe abundance, ruffe consumption rates, and number of *C. lavaretus* eggs laid were not estimated (Winfield 1992). Ruffe have also been found to prey on smelt eggs (Fedorova and Vetkasov 1974).

### *Competition*

In Europe and Asia, ruffe likely compete for food resources with other benthivorous fish, including bream (*Abramis brama*; Boikova 1986), white bream (*Blicca bjoerkna*; Zadorozhnaya 1978), *Coregonus* spp. (Winfield 1992), roach (*Rutilus rutilus*; Duncan 1990), sturgeon (*Acipenser rutherns*; Sokolov and Vasil'ev 1989), smelt, and perch (Thorpe 1977). Only competition between perch and ruffe has been extensively studied. Diet overlap between ruffe and roach is low (Hansson 1984), roach growth was unaffected by ruffe density (Bergman and Greenberg 1994), and ruffe growth and diet composition is not affected by roach (Bergman 1990). However, Duncan (1990) found that the abundance of ruffe increased after perch and roach abundance declined due to a viral infection. A high diet overlap between ruffe and *Coregonus widegreni* (Hansson 1984) and smelt (Bagge and Hakkari 1982) has been observed.

Competition between ruffe and perch is likely high because they consume the same food items and ruffe are generalists in respect with several parameters that dictate habitat use. Perch undergo three ontogenetic diet shift in their lifetime: first they feed on zooplankton, then on benthic macroinvertebrates, and finally fish (Collette et al. 1977; Hartman and Numann 1977; Johansson and Persson 1986). During the benthivorous stage, when perch eat mostly chironomidae and ephemeroptera, diet overlap with ruffe will likely be high. For example, diet overlap between ruffe and small (< 17.5 cm) and large (> 17.5 cm) perch was significant in a Baltic archipelago (Hansson 1984). Furthermore, because the foraging ability of ruffe is more independent of light (Bergman 1988) and temperature (Bergman 1987) than that of perch, ruffe should have a competitive advantage over perch with respect to these parameters (Bergman and Greenberg 1994). Previous studies showed that the presence of roach forced perch to begin feeding on macroinvertebrates at a smaller size (Persson 1986; Persson and Greenberg 1990a, b). However, when ruffe were present, perch did not increase it's consumption of macroinvertebrates (Bergman 1990b), suggesting an affect of ruffe on perch. Bergman and Greenberg (1994) showed that, with increasing ruffe density and constant roach density, that perch included more zooplankton in their diet and their growth correspondingly declined. This is evidence that ruffe and benthivorous-feeding perch compete for food resources.

Intraspecific competition has also been indirectly shown for ruffe. Both Hansson (1985) and Bergman and Greenberg (1994) found ruffe growth to decline with increasing ruffe density.

One of the prerequisites for competition is that a fish can reduce the biomass of available prey. Mattila and Bonsdorff (1989) suggested, based on feeding rates determined in the laboratory, that ruffe should be able to structure the benthic community through predation. However, in a weakly designed experiment, they found no effect of ruffe on the abundance or composition of the bottom fauna in the Baltic Sea. Bergman (1990b) and Bergman and Greenberg (1994) found that *Sialis* spp., a preferred food item of ruffe, were reduced significantly in enclosures containing ruffe. Nagiec (1977) suggested that a depauperate benthos may have been caused by ruffe, bream, or eel.

Ruffe was one of the species used to identify fish "assemblages" in Finland. Salojarvi and Ekholm (1990) classified 33 Finnish lakes based on the percentage catch of 14 common fish, including ruffe. Lakes with a high percentage of ruffe were generally in a cluster labeled "trash fish." The "trash fish" cluster also included a high percentage of roach and a low percentage of pike. The success of stocking *Coregonus lavaretus* was poor in lakes in the "trash fish" cluster. Ruffe formed a small percentage of the catch in lakes in 4 other clusters. Tonn et al. (1990) found that the presence/absence or relative abundance of ruffe was unimportant in discriminating fish assemblages for 113 Finnish lakes.

### *Predators*

In Europe and Asia, ruffe are preyed on by only a few predators. The primary predators of ruffe are pikeperch (*Stizostedion lucioperca*; Deedler and Willemsen 1964; Holcik and Mihalik 1968; Ivanova 1969; Biro 1971; Fedorova 1974; Fedorova and Vetkasov 1974; Bonar 1977; Collette et al. 1977; Marshall 1977; Popova and Sytina 1977; Willemsen 1977) and northern pike (Vollestad 1986; Eklov and Hamrin 1989; Adams 1991; Pervozvanskiy and Bugayev 1992). Eel, perch, burbot (*Lota lota*), white bream, and lake trout (*Salvelinus namaycush*) eat ruffe in small quantities (Johnsen 1965; Ivanova 1969; Popova and Sytina 1977; Rundberg 1977; Willemsen 1977; Kozlova and Panasenko 1978; Zadorozhnaya 1978; Nilsson 1979, 1985; de Nie 1987). Rare instances of cannibalization have been documented (Johnsen 1965). In addition, ruffe are eaten by cormorants (*Phalacrocorax carbo*; Van Dobben 1952), heron (*Ardea cinerea*; Adams personal communications), kingfisher (*Alcedo atthis*; Hallet 1977), and smew (*Mergus albellus*; Doornbos 1979).

The rate of predation on ruffe is affected by the abundance of ruffe or the availability of alternative prey. Pikeperch prefer soft-rayed fish, especially smelt, to ruffe (Deedler and Willemsen 1964; Collette et al. 1977). In some cases, ruffe are eaten in proportion to their abundance, except that larger pikeperch (> 40 cm) may increase their consumption of ruffe (Fedorova and Vetkasov 1974; Bonar 1977). Pikeperch generally consume more ruffe in years of

low smelt abundance (Pihu and Pihu 1974; Popova and Sytina 1977; Samokhvalova 1982; Willemsen 1977). For example, Pihu and Pihu (1974) found that ruffe were 10-15% of the annual ration of pikeperch in years of high smelt abundance but 80-85% of the annual ration in years of low smelt abundance. In the absence of smelt, ruffe and cyprinids are the preferred food of pikeperch (Popova and Sytina 1974; Willemsen 1977). Perch also consume more ruffe in years of low smelt abundance (Popova and Sytina 1977). The diet of northern pike shifted from *Coregonus lavaretus* to ruffe after the introduction and population explosion of ruffe in Loch Lomond (Adams 1991).

Ruffe have a wide array of morphological, physiological, and behavioral adaptations to avoid predation. The most conspicuous of these adaptations are the large dorsal, anal, pelvic, and preopercular spines. Spines have multiple anti-predation adaptations. Spines make a small forage fish appear larger than it actually is, especially to a predator that generally attacks the center of a prey mass (e.g., pike; Webb and Skadsen 1980; Eklov and Hamrin 1989). They also require that a predator swallow the fish head first, therefore, limiting the focus of the attack to the head, increasing the handling time required to maneuver the prey for ingestion, or decreasing retention. Spines may also puncture the throat or stomach linings of the predator (Eklov and Hamrin 1989; Lammens et al. 1990). In addition, ruffe are equipped with a retinal tapetum lucidum, that allows ruffe to exploit low-light twilight conditions (Ahlbert 1970), and numerous lateral-line sensors that are sensitive to large wavelength disturbances from predators (Collette et al. 1977). Finally, cryptic coloration and utilization of benthic habitats may reduce predation (Swenson 1977) as most predators forage in littoral or pelagic areas (e.g. Esocidae, Centrarchidae, some Percidae) and strike prey from beneath ("Twilight theory"; Pitcher and Turner 1986).

### **Parasites and Pathology**

Apparently, 74 species of ruffe parasites have been documented in the scientific literature (J. H. Selgeby, personal communications). Of these, 63 are listed in Table 6. Bykhovskaya-Pavlovskaya et al. (1964) provided a comprehensive list of parasites on Russian fishes. Some parasites were common on ruffe in some instances. For example, 56% of ruffe caught in Lake Paijanne were infected with *Triaenophorus nodulosus* (Bagge and Hakkari 1982), 79% of ruffe in a thermal effluent in the Baltic Sea were infected by *Anguillicola crassus* (Hoglund and Thomas 1992), nearly all ruffe captured by Thomas and Ollevier (1992) were infected by *A. crassus*, and nearly 100% of Lake IJsselmeer ruffe were infected with *Cotylurus variegatus* (Swennen et al. 1979). Some parasites show seasonal fluctuations in infection rates. For example, Jokela et al. (1991) only found *Anodonta piscinalis* glochidia on ruffe from March through May and Izyumova (1958) found the highest prevalence of *Dactylogyrus amphibothrium* on ruffe in winter and spring.

However, Valtonen et al. (1990) found that over 70% of ruffe were infected by *Dactylogyrus amphibothrium* in every month but one. In most situations no pathological effects were observed (e.g., Petrushevski and Shulman 1961; Haenen and Van Banning 1990). However, Johnsen (1965) reported a severe mortality of Esrom So ruffe in 1913 and at a later date due to infection by

Table 6. List of parasites found on ruffe in Europe and Asia. Sources are identified by the following bold letters and are listed in the general works cited: A : Alarotu (1944), B = Bagge and Hakkari (1982), BP = Bykhovskaya-Pavlovskaya et al. (1964); D = Dykova and Lom (1978), F = Faulkner (1989), H = Haenen and Van Banning (1990), HT = Høglund and Thomas (1992), I = Izyumova (1958,1964), J = Johnsen (1965), Jo = Jokela et al. (1991), K = Kashkovski (1982), Ko = Kolomin (1977), P = Petrushevski and Shulman (1961), S = Swennen et al. (1979), T = Thomas and Ollevier (1992), V = Valtonen et al. (1990), W = Wootten (1974), Wi = Willemssen (1968).

Source	Parasite	Area	Source	Parasite	Area
BP	<i>Acanthocephalus anguillae</i>	Intestine	BP	<i>Ergasilus briani</i>	Gill
BP	<i>Acanthocephalus lucii</i>	Intestine	B,H,J	<i>Ergasilus sieboldi</i>	Gill
J	<i>Achteres percarum</i>	Gill	BP	<i>Eustrongylides excisus</i>	Muscle, Intestine
H,HT,T	<i>Anguillicola crassus</i>	Swimbladder	BP	<i>Eustrongylides mergorum</i>	Intestine (?)
W	<i>Anodonta cygnea</i>	Gill	BP	<i>Gyrodactylus cernuae</i>	Gill, Mouth
Jo	<i>Anodonta piscinalis</i>	Gill	BP	<i>Gyrodactylus longiradix</i>	Skin (?)
BP	<i>Apophallus mühlengi</i>	Fin, Gill	BP	<i>Hemiteleopsis marginata</i>	Blood-sucker
BP	<i>Argulus foliaceus</i>	Skin, Gill	BP,D	<i>Henneguya creplini</i>	Gill
BP	<i>Azygia lucii</i>	Stomach, Mouth	BP	<i>Lernaea esocina</i>	Skin, Gill
BP	<i>Bunocotyle cingulata</i>	Stomach, Intestine	BP	<i>Metagonimus yokogawai</i>	Scales, Fin
BP,J	<i>Bunodera luciopercae</i>	Intestine	BP	<i>Myxobolus ellipsoides</i>	Gill, Muscle, Eye, Int. Organs
B,BP,H	<i>Camallanus lacustris</i>	Intestine	BP	<i>Neascus brevicaudatus</i>	Eye
BP	<i>Camallanus huncatus</i>	Intestine	B,H	<i>Nematode spp.</i>	?
BP	<i>Contracaecum squalii</i>	Internal Organs	BP	<i>Neodiplostomulum spp.</i>	?
BP	<i>Corynosoma seimeri</i>	Internal Organs	BP	<i>Neoechinorhynchus rutili</i>	Intestine
BP	<i>Corynosoma strumosum</i>	Internal Organs	BP	<i>Philometra ovata</i>	Body Cavity
S	<i>Cotylurus platycephalus</i>	Pericardium	BP	<i>Phyllodistomum angulatum</i>	Urinary Bladder, Kidney
P,Wi	<i>Cotylurus spp.</i>	?	BP	<i>Phyllodistomum folium</i>	Ureter, Gall Bladder
J,S	<i>Cotylurus variegatus</i>	Swimbladder	BP	<i>Phyllodistomum pseudofolium</i>	Ureter, Kidney
BP	<i>Crowcoecum skrjabini</i>	Intestine	J	<i>Piscicola geometra</i>	Blood-Sucker
BP	<i>Cyathocephalus truncatus</i>	Intestine	BP	<i>Plisiphora acerinae</i>	Intestine
BP	<i>Dactylogyrus hemiamphibothrium</i>	Gill	BP	<i>Pomphorhynchus laevis</i>	Intestine
A,I,K,V,W	<i>Dactylogyrus amphibothrium</i>	Gill	BP	<i>Posthodiplostomum cuticola</i>	Skin, Fin
BP	<i>Diphyllobothrium latum</i>	Liver, Muscle	B,BP,H,J	<i>Proteocephalus cernuae</i>	Intestine
BP	<i>Diplostomulum clavatum</i>	Eye	BP	<i>Pseudoechinorhynchus clavula</i>	Intestine
BP	<i>Diplostomulum flexicaudum</i>	Eye	B,BP,H	<i>Raphidascaris acus</i>	?
BP	<i>Diplostomulum spathaceum</i>	Eye	BP	<i>Rossicotrema denticum</i>	Skin, Fin
F	<i>Diplostomum gasterostei</i>	Eye	BP	<i>Sphaerostoma bramae</i>	Intestine
J	<i>Diplostomus volvens</i>	?	BP	<i>Tetracotyle echinata</i>	?
BP	<i>Echinorhynchus gadi</i>	Intestine	BP,J,Ko	<i>Tetracotyle ovata</i>	Swimbladder, Internal Organs
J	<i>Echinorhynchus angustatus</i>	?	B,BP,H	<i>Triacnophorus nodulosus</i>	Liver
J	<i>Echinorhynchus tereticollis</i>	?	BP	<i>Trichodinella epizootica</i>	Gill
			BP	<i>Trypanosoma acerinae</i>	Blood

*Tetracotyle ovata*. No other fish species died during this episode. Pokrovskii (1961) also noted a mass dieoff of ruffe due to *Tetracotyle* infection. Large dieoffs in IJsselmeer may have been due to *Cotylurus* infections (Swennen et al. 1979).

Abnormalities of the liver and fins of ruffe have been documented. Kranz and Peters (1985) recorded the occurrence of excessive fat deposition in the hepatocytes, localized discoloration, and pale neoplastic nodules in ruffe livers and Peters et al. (1987) observed shrinkage of liver cells, blood clots, tissue necroses, and neoplastic liver nodules in ruffe. In both instances, they related the occurrence of these liver abnormalities to anthropogenic pollutants, specifically PCBs in the latter case. Lindesjoo and Thulin (1983) and Thulin et al. (1988) found instances of fin erosion and curvature in ruffe captured in bleached kraft effluents in the Gulf of Bothnia. Weissenberg (1965) noted that lymphocystis, a viral disease whose symptoms include wart-like proturbences on the fins, jaws, and opercula, was first recognized in ruffe.

### **Introductions in Europe and Asia**

Ruffe have invaded several areas (see Geographic Distribution section), however, only information about the invasion of Loch Lomond, Scotland has been published. Ruffe were first caught in Loch Lomond in 1982 (Maitland et al. 1983). By 1989, ruffe were the most common fish at 2 of 5 sampling locations (C. E. Adams, personal communications) and by 1992 ruffe were the most abundant fish impinged on water intake screens at a power plant (Maitland and East 1989; Figure 11). It is feared that ruffe will have (or have had) an impact on native *C. lavaretus* and perch stocks. The introduction of ruffe to Loch Lomond has already resulted in predation on *C. lavaretus* eggs (Adams and Tippett 1991) and shifted predation pressure by northern pike from *C. lavaretus* (Adams 1991). However, it appears that no efforts to control the abundance or distribution of ruffe within the Loch have been implemented.

Several characteristics of ruffe make them successful invaders of new communities. Taylor et al. (1984) list 12 attributes of exotic species that preadapt them for successful colonization and population growth in novel environments (Table 7). Within "broad physiological tolerances," ruffe can withstand temperature extremes and turbidity and pollution. In addition, they can withstand relatively low oxygen levels and a relatively broad range of salinities. Within "feeding habits and diet," ruffe can feed under a variety of light and temperature conditions and are well-adapted to discourage or avoid predation. In addition, they appear to be strong competitor for benthos. Finally, within "reproductive behavior," ruffe show rapid growth, early maturation, and multiple clutches. From this analysis it is apparent that ruffe are very good colonizers of new environments.

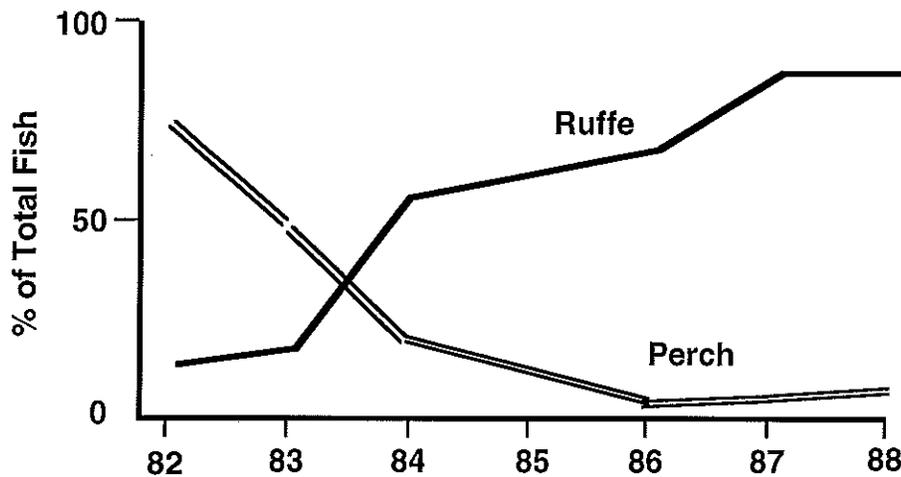


Figure 11. Change in proportional contribution of ruffe and perch to the catch of fish impinged on a water intake screen in Loch Lomond, Scotland (from Maitland 1990).

Table 7. Attributes of exotic species that preadapt them for successful colonization and population growth in novel environments (from Taylor et al. 1984).

<b>I.</b>	<b>Broad physiological tolerances</b>
A.	temperature extremes
B.	low oxygen levels
C.	fluctuations in salinity
D.	turbidity and pollution
E.	drought
<b>II.</b>	<b>Feeding habits and diet</b>
A.	diet composition
B.	feeding schedules
C.	vulnerability to predation
<b>III.</b>	<b>Reproductive behavior</b>
A.	rapid growth and maturation
B.	extended or continuous breeding
C.	multiple clutches
D.	advanced parental care.

The establishment of ruffe in new areas may also be enhanced by instabilities in the invaded community. Lelek (1987) stated that “the ruffe is dominant in unbalanced populations of fishes.” Instabilities in a community may predispose a community for invasion by an exotic species (Christie et al. 1987).

## Management

Intentional or unintentional management efforts to control the abundance of top-level predators (e.g., northern pike and pikeperch) have resulted in lower ruffe abundance. The catch of "undesirable" fish, which include ruffe, bream, roach, small perch, and white bream, was positively correlated to the yield of predatory fish, which include eel, pikeperch, and pike, in some Polish lakes (Bonar 1977). However, it is impossible to determine whether ruffe themselves declined. Stocking of elvers and protective regulations for pikeperch and eel resulted in a 5-7 fold decline in ruffe catches in Lake Vortsjarv (Pihu 1982; Pihu and Maemets 1982). In contrast, intentional or unintentional management efforts resulting in the decline of top-level predators has resulted in increased ruffe abundance. A decrease in predators due to overfishing led to a sudden rise in the abundance of "small coarse fish", including ruffe, in some Russian waters (Popova and Sytina 1977). Ruffe became abundant in London reservoirs following the loss of predatory fish to viral infections (Duncan 1990). A cause-effect relationship is not evident in this case because benthivorous roach also declined (Duncan 1990).

Some management efforts, however, have not resulted in declines of ruffe stocks. In Lake Tjeukemeer, the termination of the gillnet fishery resulted in significantly more and larger pikeperch, but catches of ruffe were not affected (Lammens et al. 1990). Predation on ruffe in Tjeukemeer did not increase, even though pikeperch abundance increased, because the abundance of smelt, the preferred prey of pikeperch, was uncoupled with pikeperch abundance due to migration from an adjoining lake. Thus, pikeperch did not have to switch to the less desirable ruffe. In Lake Vortsjarv, intensive bottom trawling did not result in decreased ruffe numbers (Pihu 1982; Pihu and Maemets 1982).

Legislation against the use of ruffe as bait for northern pike has been used to attempt to control the spread of ruffe to other areas of England (I. J. Winfield, personal communications). This measure has been largely ineffective at restricting the spread of ruffe in England (I. J. Winfield, personal communications).

Ruffe are not specifically mentioned in management plans for several lakes where ruffe are present (Steinmetz 1990; Steinmetz et al. 1990; Van Densen et al. 1990).

It is difficult to reduce the numbers of ruffe with traditional methods (i.e., removal with traditional gear or a top-down approach) because ruffe have several adaptations for compensating for high mortality rates (Lind 1977). As mentioned in previous sections, ruffe may grow quickly, mature early, and spawn more than once in a season. For example, Lelek (1987) noted that ruffe abundance will rebound quickly if water quality improves after severe ruffe mortalities due to low oxygen.

Very few fisheries are prosecuted with the idea of catching ruffe. In the Elbe River, ruffe were an important commercial fishery at the beginning of the 20th century with a catch of 350,000

kg in 1990 (Sterner 1916). By 1965 - 1975, ruffe catch was only 2,500 kg (Holker and Hammer 1994). In Lake Illmen, total mortality was 65% and natural mortality was 42%, leaving 23% of the ruffe being removed by the fishery (Fedorova and Vetkasov 1974). In Tjeukemeer, ruffe are captured in the fishery for baiting long-lines for eel (Goldspink and Banks 1975). Ruffe are caught incidentally in several fisheries.

Some chemicals are selectively toxic to ruffe. Bills et al. (1992) determined that ruffe could be selectively killed by application of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM). Tests in the Brule River, Lake Superior suggested that an average application of 3.2 mg/l selectively killed up to 97% of ruffe and lamprey (*Petromyzon marinus*), but killed very few non-target finfish. Lethal concentrations of TFM were determined for ruffe under a variety of water quality conditions in laboratory experiments.

In some instances, the abundance of ruffe may be limited by benthos production. Ruffe were present in low numbers in Lake Vastra Kyrksundet when it was meromictic (Bonsdorff and Storberg 1990). When the lake became limnic after isolation from the Baltic Sea, benthos production and ruffe biomass increased.

## **Ruffe in the United States**

Ruffe have been the target of intensive studies since they were first identified in the St. Louis River Harbor (SLRH), Lake Superior, United States in the mid-1980s. Unfortunately, little has been published in peer-reviewed journals because of the ruffe's short existence in the U.S. The following subsections will contain brief summaries of what is known about ruffe in the U.S. under the same headings used throughout this review.

### *Systematics, Morphology, and Evolution*

Larval ruffe are distinguished from all native North American percids by (1) "a slightly concave head becoming attenuate at larger length intervals", (2) "a pointed snout with teeth on the maxillary and premaxillary" by 11 mm, (3) "a large dorsally pigmented swim bladder", (4) "a serrated preopercle", and (5) "few postanal myomeres (usually 18-22)" (Simon and Vondruska 1991).

### *Habitat*

Ruffe are found in all habitats of the SLRH (Selgeby and Ogle 1992). Ruffe are found in the deepest channels (8 - 10 m) at ice-out, move into the shallows to spawn, remain in 1-3 m water throughout the summer, and then return to the deeper channels in September and October. Adult

ruffe are generally found in deep, dark waters during the day, move to shallower waters to feed at night, and return to deeper waters at dawn (Ogle 1992). Large numbers of age-0 ruffe were captured in both deep and shallow waters at night, but only in shallow water during the day, although substantially fewer were caught there than during the night (Ogle 1992).

Optimal temperature for growth of age-0 ruffe was at 21°C, with a fundamental thermal niche of 18-22°C (Edsall et al. 1993). However, ruffe grew at all temperatures in the test range (7.0-24.8°C). The fundamental thermal niche for age-0 ruffe corresponds closely to that of walleye, sauger, and yellow perch. Thus, using a relationship developed for walleye, the authors estimated that 58% of Lake Erie, 21% of Lake Huron, 12% of Lake Michigan, 7% of Lake Ontario, and 2% of Lake Superior was optimal growth habitat for ruffe.

### *Reproduction and Early Life History*

Age at maturity has increased since ruffe were first discovered in the SLRH. During the initial years of their invasion of the SLRH (1988 and 1989), nearly 100% of ruffe were mature after one year of life (Selgeby and Ogle 1991, 1992). By 1990 and 1991, only about 85% (Selgeby and Ogle 1992) and in 1992, only about 50% (Selgeby 1993) of age-1 ruffe were mature. Mean absolute fecundity of a 15 cm female ruffe is approximately 45,000 eggs (Selgeby and Ogle 1992).

French and Edsall (1992) described the hatching of artificially fertilized eggs and the development of ruffe protolarvae from the SLRH. Detailed developmental descriptions will not be given here. Fertilized eggs are 0.9-1.2 mm diameter. Newly hatched protolarvae are 2.5-3.2 mm TL. Feeding and swimming begin when the yolk-sac is fully absorbed about 1 week after hatching. Ruffe protolarvae are distinguishable from other Lake Superior percids by having fewer preanal myomeres, the head deflected over the yolk sac, continuous finfold of even width, and a total length of less than 4.0 mm.

### *Age and Growth*

Most ruffe reach about half of their ultimate length after one year of life (Selgeby and Ogle 1991). First year growth of ruffe, though, declined from 1988 through 1991 (J. H. Selgeby, personal communications).

### *Diet and Foraging Behavior*

Ruffe in the SLRH are primarily benthophagous. Age 0 ruffe fed mostly on cladocerans and copepods in early summer and chironomids in later summer and fall. Adult ruffe <12 cm fed mostly on chironomids and other macrobenthos, but also consumed large numbers of

microcrustaceans. Adult ruffe  $\geq 12$  cm fed mostly on chironomids, *Hexagenia* spp., and caddisflies. Ruffe consumed very few fish eggs. Patterns in catch rates and stomach contents weight suggest that all age-0 and adult ruffe (in deeper waters) fed throughout the day. Adult ruffe, though, moved to shallower waters at night to feed most heavily. Local weather systems and spawning activities may have disrupted these patterns. Ogle (1992) also calculated daily rations for adult ruffe (0.004-0.046 g per g of fish) and made the first gastric evacuation calculations for ruffe.

### *Community Dynamics*

Competition between ruffe and native fishes has not yet been tested in the U.S. However, several pieces of evidence suggest that ruffe may have a negative effect on native fishes. First, the diet of ruffe likely highly overlaps that of other benthivores, such as yellow perch, trout-perch (*Percopsis omiscomaycus*), and many others (Ogle 1992). Second, the abundance of nearly every other forage species in the SLRH, including yellow perch, trout-perch, emerald shiners (*Notropis atherinoides*), and spottail shiners (*Notropis hudsonius*), has declined since the introduction of ruffe (Selgeby and Ogle 1991, 1992; GLFC 1992; Selgeby 1993, 1994). These declines, though, can not yet be attributed to ruffe because intensive stockings and restrictive regulations for predator fishes (northern pike and walleye) have been implemented since ruffe were discovered (see management section below).

There is also some indirect indication that ruffe in the SLRH have reduced the available benthos. From 1989 to 1990, the total stomach contents weight declined for all sizes of ruffe, the amount of microcrustaceans (presumed to be of lesser value) in the diet of adult ruffe increased, and smaller sizes of prey were consumed (Ogle 1992). These all suggest that food availability may have been lower in 1990 than in 1989.

Ogle (1992) and Savino (personal communications) investigated the feeding behavior and diet of predators (1989-1991) likely to consume ruffe in the SLRH. Laboratory studies showed that walleye, northern pike, and burbot will eat ruffe, but walleye and northern pike preferred soft-rayed fish to ruffe. Predation on ruffe in the SLRH by most predators remained low, but overall predation increased slightly from 1989 to 1991. Most ruffe eaten were age-0 (1989 and 1990) or were small age-1 fish (1991). The primary predators of ruffe were bullheads *Ictalurus* spp. and northern pike, but yellow perch, smallmouth bass *Micropterus dolomieu*, black crappie *Pomoxis nigromaculatus*, and burbot all ate ruffe. No ruffe were found in the nearly 1000 walleye stomachs examined. Additional work reported in Selgeby (1993), indicated that ruffe were 5-7% of the diet of walleye in 1992 and 1993.

### *Parasites*

Selgeby (personal communications) documented the parasites of St. Louis River ruffe. A total of 22 species were found; 7 were endemic to North America, 5 were endemic to Eurasia, and 10 were of common origin or uncertain taxonomic classification. At least three of the parasites found were new to North America.

### *Management*

Lake Superior fisheries managers feel that a "window of opportunity" existed for containing ruffe in western Lake Superior because of the extremely cold, oligotrophic nature of Lake Superior (Busiahn 1993). During this "window" managers will (1) recommend educational and regulatory actions to prevent "bait-bucket" transfers, (2) develop a ballast water management plan, (3) propose a plan to eliminate reproducing populations of ruffe on the periphery of the range with piscicides, (4) urge further research and surveillance, and (5) evaluate a biological control program (enhance predators) that was undertaken by the states of Minnesota and Wisconsin.

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