

A Synopsis of the Biology and Life History of Ruffe

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ABSTRACT. The ruffe (*Gymnocephalus cernuus*), a Percid native to Europe and Asia, has recently been introduced in North America and new areas of Europe. A synopsis of the biology and life history of ruffe suggests a great deal of variability exists in these traits. Morphological characters vary across large geographical scales, within certain water bodies, and between sexes. Ruffe can tolerate a wide variety of conditions including fresh and brackish waters, lacustrine and lotic systems, depths of 0.25 to 85 m, montane and submontane areas, and oligotrophic to eutrophic waters. Age and size at maturity differ according to temperature and levels of mortality. Ruffe spawn on a variety of substrates, for extended periods of time. In some populations, individual ruffe may spawn more than once per year. Growth of ruffe is affected by sex, morphotype, water type, intraspecific density, and food supply. Ruffe feed on a wide variety of foods, although adult ruffe feed predominantly on chironomid larvae. Interactions (i.e., competition and predation) with other species appear to vary considerably between systems.

INDEX WORDS: Ruffe, review, taxonomy, reproduction, diet, parasite, predation.

INTRODUCTION

This is a review of the existing literature on ruffe, providing a synopsis of its biology and life history. A review of the existing literature is needed at this time because the ruffe, which is native to Europe and Asia, has recently been introduced in North America and new areas of Europe. Furthermore, Rosch *et al.* (1996) suggested that "a synopsis of this species is desirable and should be attempted." Currently available synopses of ruffe are incomplete (Rosch *et al.* 1996), in the gray literature (Ogle 1995), or geographically restricted (see other reviews in this volume). In this paper the published information, which was available prior to the convening of this symposium, will be reviewed. The paper will focus on the distribution, taxonomy and nomenclature, evolution and genetics, sensory physiology, habitat, reproduction and early life history, age and growth, diet and foraging behavior, competitors, predators, parasites and pathology, and possible methods for control of ruffe populations.

DISTRIBUTION

Ruffe are native to all of Europe except for along the Mediterranean Sea, western France, Spain, Portugal, Norway, northern Finland, Ireland, and Scotland (Collette and Banarescu 1977, Lelek 1987). In Asia, ruffe are native only in Siberia, but not the Amur River or Transcaucasia (Berg 1949).

Ruffe were accidentally introduced to several areas in the late 1980s and early 1990s. Ruffe are now found in Loch Lomond, Scotland (Maitland *et al.* 1983); Llyn Tegid, Wales (Winfield 1992); Bassenthwaite Lake, England (Winfield 1992); Lake Constance, Germany (Rosch and Schmid 1996); Lake Mildevatn, Norway (Kalas 1995); the Camargue region, France (E. Rosecchi, Station Biologique de la Tour du Valat, pers. comm.); Italy (Chiara 1986); Lake Superior, United States (Simon and Vondruska 1991, Pratt *et al.* 1992); and Lake Huron, United States (T. Busiahn, U.S. Fish and Wildlife Serv., pers. comm.).

TAXONOMY AND NOMENCLATURE

The accepted name for ruffe is *Gymnocephalus cernuus* (American Fisheries Society 1991, Rosch *et al.* 1996). Linnaeus introduced the species as *Perca cernua* in 1758. More recently the ruffe has

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TABLE 1. Summary of meristics for European and Asian ruffe.

Character	Range	Character	Range
Dorsal	XI–XVI, 10–15	Lateral-line scales	33–42
Anal	II–III, 4–7	Scales below lateral line	10–18
Pectoral	13–17	Scales above lateral line	5–10
Opercular spines	1	Branchiostegal rays	6–7
Preopercular spines	7–16	Gill rakers, first arch	6–14
Vertebrae	31–36		

been named *Acerina cernua* and *G. cernua* (Collette 1963). Ruffe have various local common names including jezdič (former Czechoslovakia), horke (Denmark), stone-perch or pope (England), kiiski or kueski (Finland), perche goujonniere or Brenilie (France), kaulbarsch (Germany), kulbaars (Netherlands), nork or steinpurke (Norway), jazgarz (Poland), ghibort (Romania), ersh or jorsch (Russia), gers (Sweden), and iorzh or bubyr' (Ukraine).

The ruffe is a member of the Percidae. Subfamily nomenclature differs among authors. Collette (1963) and Collette and Banareescu (1977) placed ruffe in the tribe Percini with *Perca* and *Percarina*. The tribes Percini and Etheostomatini make up the subfamily Percinae. Wiley (1992) proposed two subfamilies, Percinae and Etheostomatinae. Only *Perca* is in the Percinae and *Gymnocephalus* are the basal taxon for the Etheostomatinae. The subfamily nomenclature of Page (1985) and Coburn and Gaglione (1992) depended largely on their belief that ruffe produce egg-strands, for which no evidence could be found in the literature.

Four species of *Gymnocephalus* have been described, *G. schraetser*, *G. acerina*, *G. baloni*, and *G. cernuus*. Characteristics synapomorphic for *Gymnocephalus* are enlarged preopercular spines, a small (< 1 cm) anterior to ventral ramus ratio, a club-like distal end of the premaxilla, a retroarticular that is distinctly higher than long when viewed medially (Wiley 1992), and hypertrophy of the cephalic lateral-line canals (Collette and Banareescu 1977). Holcik and Hensel (1974) suggested two subgenera, *Gymnocephalus* and *Acerina*, based on vertebral counts and slight color differences. *Gymnocephalus cernuus* and *G. baloni*, with significantly fewer vertebrae, make up *Acerina*.

General morphological descriptions were made by Collette (1963), Aleksandrova (1974), Holcik and Hensel (1974), Collette and Banareescu (1977), Matkovskiy (1987), Nedelkova and Zaveta (1991), and Wiley (1992). Selected meristics from these studies are summarized in Table 1. The following

specific morphological aspects have been described in great detail: the ctenoid scales (Coburn and Gaglione 1992); the cephalic skeletal and muscular systems (Elshoud-Odenhave and Osse 1976); the cephalic lateral line system (Jakubowski 1967, Disler and Smirnov 1977); the eye and optical system (Sroczynski 1981); and the relationship between total length and the size of several body parts (Matkovskiy 1987, Nedelkova and Zaveta 1991).

Morphological differences may exist on several geographical scales and between sexes. Witkowski and Kolacz (1990) suggested that body depth, predorsal distance, preanal distance, first dorsal depth, anal fin length and depth, and pectoral length generally declined from east (Europe) to west (Siberia). Differences in body shape of ruffe within a watershed have also been described (Aleksandrova 1974, Nedelkova and Zaveta 1991). Sexual dimorphism has been observed for some characteristics (e.g., eye diameter; preventral, prepectoral, and anal-caudal distances; head length; and body thickness, summarized by Aleksandrova 1974).

EVOLUTION AND GENETICS

All known *Gymnocephalus* fossils are *G. cernuus* from interglacial deposits in Denmark, Germany, England, Poland, and Russia (Holcik and Hensel 1974). The basal *Gymnocephalus* species may be *G. cernuus*, as *G. acerina* and *G. schraetser* appear more "primitive" and *G. baloni* apparently recently derived from *G. cernuus* (Holcik and Hensel 1974). *Gymnocephalus cernuus* is apparently of Paleodanube origin (Holcik and Hensel 1974, Rab *et al.* 1987).

Ruffe have $2n = 48$ chromosomes (Nygren *et al.* 1968, Klinkhardt 1990). The types of chromosome pairs differ among studies. Bozhko *et al.* (1980) found 2 metacentric, 11 submetacentric, 8 subelocentric, and 3 acrocentric; Rab *et al.* (1987) found 1 metacentric, 16 submetacentric, 4 subelocentric, and 3 acrocentric; and Mayr *et al.* (1987) found only 1 acrocentric. Nyman (1969) and Logvinenko

et al. (1983) described polymorphic serum esterases that could be used in population investigations. The karyotypes of the four *Gymnocephalus* species are unique (Rab *et al.* 1987). Ruffe can hybridize with *Perca fluviatilis* (Kammerer 1907, as cited in Hokanson 1977) and *G. baloni* (Holcik and Hensel 1974). Other aspects of the genetics of ruffe were described recently by Rosch *et al.* (1996).

SENSORY PHYSIOLOGY

Ruffe have an extremely sensitive cephalic lateral-line system with 25 cupulae embedded in bony canals covered with a stretched-skin membrane (Jakubowski 1967). The bony canals afford protection to the neuromasts. High sensitivity is maintained by a large number of nerve fibers per neuromast and receptors per nerve fiber (Gray and Best 1989), the large size of the canals (Denton and Gray 1988), and the membrane (Denton and Gray 1988). The ultrastructure and electrical physiology of this system has been actively studied (Flock 1967, Kuiper 1967, Disler and Smirnov 1977, Gray and Best 1989, Denton and Gray 1989, Van Netten 1991, Wubbels 1991). Disler and Smirnov (1977) described the development of the system during the early life history period.

Ruffe possess a tapetum lucidum in the dorsal two-thirds of the pigmented epithelial layer of the retina (Ahlbert 1970, Craig 1987). The tapetum lucidum aids vision in low-light conditions because it reflects light for additional absorption by the rods (Zyznar and Ali 1975, Ali *et al.* 1977). In addition, the photoreceptors of ruffe are arranged in an irregular twin-cone pattern that varies between row and square configurations (Ahlbert 1970).

HABITAT

Ruffe can tolerate a wide range of ecological and environmental conditions (Johnsen 1965). Ruffe have been found in fresh and brackish (salinity to 10 to 12 ppt) water (Lind 1977); lacustrine and lotic systems; depths from 0.25 m (Van Densen and Haderingh 1982) to 85 m (Nilsson 1979, Sandlund *et al.* 1985); montane and submontane areas (Kawecka and Szczeny 1984), and waterbodies ranging from oligotrophic to eutrophic. Although ruffe are found in a wide variety of habitats, three generalities about habitats used by ruffe can be made: 1) ruffe prefer areas of slow-moving water with soft bottoms that are devoid of vegetation (Johnsen 1965, Lelek 1987); 2) ruffe are associated

with the bottom (Holcik and Mihalik 1968, Sandlund *et al.* 1985, Bergman 1988); and 3) ruffe increase in abundance with increasing eutrophication.

The abundance of ruffe 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). Bergman (1991) showed that the abundance of ruffe generally increased in lakes ordered along a productivity gradient. Ruffe abundance increased with anthropogenic additions of nutrients in several situations (Heinonen and Falck 1971, Anttila 1973, Hansson 1987, Neuman and Karas 1988). In contrast, Leopold *et al.* (1986) found no correlation between level of eutrophication and ruffe catch because of high year-to-year variability in catches. In other cases, ruffe abundance declined with increasing eutrophication (Biro 1977) or ruffe abundance increased after major nutrient additions were eliminated (Peirson *et al.* 1986).

Four possible hypotheses may explain the positive relationship between eutrophication and abundance of ruffe. First, ruffe forage more efficiently under reduced light conditions associated with increased algal production (Johansson and Persson 1986; Bergman 1988, 1991). Second, 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). Benthic-feeding ruffe might be favored by the increased production and shift to smaller species. Third, increased productivity may release predation pressure on ruffe (Bergman 1991). Fourth, ruffe may be physiologically more tolerant of eutrophic conditions than other percids.

REPRODUCTION AND EARLY LIFE HISTORY

Ruffe commonly mature at age 2 or 3 and at total lengths near 11 to 12 cm (Lind 1977, Maitland 1977), although maturity at age 1 has also been reported (Fedorova and Vetkasov 1974, Neja 1988). Early maturity may be a physiological response to warmer waters (Fedorova and Vetkasov 1974, Craig 1987) or a population-level response to higher mortality rates (Lind 1977).

Ruffe exhibit a great amount of variability in spawning characteristics (e.g., habitats and conditions, time of year, egg size). Spawning occurs on a variety of substrates at depths of about 3 m or less. Balon *et al.* (1977) categorized ruffe as non-guard-

ing, open substrate, phytolithophil spawners that deposit eggs on submerged plants in clean-water habitats, or on other items such as logs, branches, gravel, or rocks. Maitland (1977) generally agreed with Balon, but Collette *et al.* (1977) concluded that ruffe spawn on hard bottoms of sand, clay, or gravel. Field evidence can be found to support both conclusions (Johnsen 1965, Kovalev 1973, Fedorova and Vetkasov 1974, Kolomin 1977). Ruffe spawn between mid-April and July at temperatures of 6 to 18°C (Kovalev 1973, Fedorova and Vetkasov 1974, Kolomin 1977, Willemsen 1977, Neja 1988). Ruffe eggs develop normally at pH values of 6.5 to 10.5, one of the widest ranges from a broad set of fish tested (Kiyashko and Volodin 1978).

Ruffe may spawn intermittently, laying two or more batches of eggs (Koshelev 1963, Fedorova and Vetkasov 1974, Kolomin 1977, Neja 1988). The first batch of oocytes matures in 165 days during winter and spring, whereas the second batch matures in 30 days during summer (Koshelev 1963). A mature ruffe ovary 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 (Neja 1988). Only the latter two types will be released during the next spawning season. The physiological details of ruffe that spawned intermittently are given by Koshelev (1963).

Ruffe eggs become adhesive upon contact with water, and stick to the substrate (Johnsen 1965, Kovalev 1973). Page (1985) suggested that ruffe eggs are extruded in "strands," but no evidence for this was found in any other published material.

The number of eggs deposited depends on the batch of eggs and size of the female. The number of eggs per female is 4,000 to 200,000 for the first batch (Kolomin 1977, Collette *et al.* 1977, Neja 1988) and 352 to 6,012 for the second batch of eggs (Kolomin 1977). Relative fecundity was 305 to 1,540 eggs per g of female (Bastl 1988, Neja 1988, Jamet and Desmolles 1994) and appears to be uncorrelated with body weight, gonad weight, or age (Neja 1988). Average gonosomatic index was 7.1 to 15.6 for spawning females and 7.0 to 10.0 for spawning males (Kolomin 1977, Bastl 1988, Neja 1988, Jamet and Desmolles 1994).

Egg diameters were 0.34 to 1.3 mm (Johnsen 1965, Kovalev 1973, Fedorova and Vetkasov 1974, Disler and Smirnov 1977, Kolomin 1977, Bastl 1988). Bastl (1988) reported a mean egg weight of

0.45 (± 0.05 SD) g and volume of 0.59 (± 0.48 SD) mm³. Eggs from the first batch are larger than eggs from the second batch (Kolomin 1977).

Ruffe eggs hatch in 5 to 12 days at 10 to 15°C (Johnsen 1965, Maitland 1977, Craig 1987, Berka 1990). Newly hatched embryos of 3.5 to 4.4 mm (Fedorova and Vetkasov 1974) were underdeveloped, relative to yellow perch (*Perca flavescens*, Disler and Smirnov 1977). The embryos remain sedentary on the bottom for 3 to 7 days until reaching a size of 4.5 to 5.0 mm (Disler and Smirnov 1977). The transition to exogenous feeding takes place in the benthopelagic layer (Disler and Smirnov 1977), about 1 week after hatching (French and Edsall 1992). Larval ruffe are positively phototactic (Disler and Smirnov 1977), but have little or no pelagic larval stage (Johnsen 1965, Fedorova and Vetkasov 1974, Disler and Smirnov 1977). At the larval stage, ruffe are secretive, solitary, and do not form schools (Disler and Smirnov 1977, French and Edsall 1992). Extensive details on the morphological development of ruffe embryos and larvae are provided by Disler and Smirnov (1977), Simon and Vondruska (1991), French and Edsall (1992), and Kovac (1994).

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). The optimal temperature for "early development" is 15°C (Saat and Veersalu 1996). Larval ruffe survival is poor below 10°C (Hokanson 1977). Optimal temperature for larval growth is 25 to 30°C (Hokanson 1977), whereas optimal growth of age-0 ruffe occurs at 21°C (Edsall *et al.* 1993). However, age-0 ruffe grew at temperatures between 7.0 and 24.8°C (Edsall *et al.* 1993).

The only detailed research concerning the reproductive physiology of ruffe that could be found were those of Butskaya (1976, 1980, 1985).

AGE AND GROWTH

Female ruffe may reach age 11, but male ruffe generally do not exceed age 7. In most cases, fewer than six age-groups are sampled (Table 2), with most fish being age 2 or younger. For example, Fedorova and Vetkasov (1974) sampled seven age-groups with 93% of the catch being age 1 or 2.

A firm conclusion about which calcified structure is best for assigning age to ruffe cannot be made. Jamet and Desmolles (1994) found that ruffe produced only one annulus per year on scales (in win-

TABLE 2. Total lengths-at-age (mm; except where noted) of ruffe from selected European and Asian investigations. Superscript letters following the authors' name and publication year indicate interpretations by the following authors: A = Aleksandrova (1974), B = Boikova (1986), Ba = Bast et al. (1983), H = Holker and Hammer (1994), N = Neja (1989), and W = Willemsen (1977). Comments in the Comm. column are abbreviated as follows: FL = fork length, BC = "known to be back-calculated", f = females, m = males, sb = shallow-bodied, db = deep-bodied, fw = freshwater, br = brackish, est = estimated (from graphs or growth equation).

Author	Country	Age										Comm
		I	II	III	IV	V	VI	VII	VIII	IX	X	
Adamus <i>et al.</i> (1978) ^N	Poland(?)	35	55	72	84	107	125					
Aleksandrova (1974)	USSR			108	115	119						sb
Aleksandrova (1974)	USSR	64	96	98	109	116						db
Aleksandrova (1974)	USSR	32	64	91	104	118						BC, sb
Aleksandrova (1974)	USSR	31	59	83	97	104						BC, db
Arzbach (1987) ^H	Germany	101	159	190	210	219	236					BC
Bast <i>et al.</i> (1983)	Germany		97	112	132	162						BC
Bast <i>et al.</i> (1983)	Germany	80	96	112	136	169	186					BC
Bast <i>et al.</i> (1983)	Germany			126	151	176	183					BC
Bauch (1963) ^N	Germany	60	90	110	120	139						
Biro (1971) ^{Ba}	USSR	56	65	79	107	126						
Fedorova & Vetkasov (1974)	USSR	56	73	90	106	117	125					
Holker & Hammer (1994)	Germany	97	154	177	203	214						BC, m
Holker & Hammer (1994)	Germany	101	157	190	207	229	241					BC, f
Johal (1980) ^{Ba}	Czechoslovakia	66	91	107	117	132	143	151				
Johal (1980) ^{Ba}	Czechoslovakia	64	89	106	120	136	145	157				
Kijashko (1980) ^{Ba}	USSR	57	85	101	114	124	133					
Knowles (1974) ^H	Germany	84	121	156	180							BC
Kolander (1969) ^N	Poland	89	106	121	137	145	161					
Kolomin (1977)	USSR (males)	77	113	121	125	131	141					m
Kolomin (1977)	USSR (females)	91	115	122	133	137	155	163	163			f
Kostyuchenko (1962) ^A	USSR	38	79	106	127							BC
Kozlova (1979) ^N	Russia	63	72	84	99	106	119					
Lelek (1987)	Europe	38	62	78	90	110	112					
Lind (1977)	Finland	41	73	102	118	137	143	148	167	164	166	fw
Lind (1977)	Finland		109	126	137	144	154	159	172			br
Masatova and Zaveta (1988) ^H	Czechoslovakia	51	71	85	101							BC
Neja (1988)	Poland (sl)	73	106	122	137	148	158	159	157	163		BC, m
Neja (1988)	Poland (sl)	72	105	122	137	148	157	162	170	172		BC, f
Neja (1988)	Poland (om)	73	99	119	128	137	145					BC, m
Neja (1988)	Poland (om)	74	101	119	129	143	155	164	176	179		BC, f
Neja (1988)	Poland (ld)	71	99	114	128	135	143	152				BC, m
Neja (1988)	Poland (ld)	72	103	122	136	143	156	169	174			BC, f
Neuhaus (1934) ^H	Poland	73	93	106	118							
Neuhaus (1934) ^H	Poland		117	125	135	158						
Noack (1978) ^{Ba}	Germany	70	121	157	178							
Nolte (1939) ^H	Germany	91	119	134	160	177						br
Rosch & Schmid (1996)	Germany	75	103	126	139							est
Sanjose (1984)	Czechoslovakia	65	92	110	133	150						BC
Sanjose (1984)	Czechoslovakia	67	83	126	137	155						BC
Sanjose (1984)	Czechoslovakia	58	76	100	113	144						BC
Sanjose (1984)	Czechoslovakia	51	74	94	116	120	140	154	171			BC
Sanjose (1984)	Czechoslovakia	54	74	85	109	144						BC
Shamardina (1968) ^B	Russia	41	52	77	92	105						
Smirnov (1977) ^{Ba}	Russia	59	80	111	138	157	172	184	194			
Vasnetsov (1950) ^B	Russia	50	81	102								

Continued

TABLE 2. Continued.

Author	Country	Age										Comm
		I	II	III	IV	V	VI	VII	VIII	IX	X	
Vasnetsov (1950) ^B	Russia	37	56	89	117	136						
Willemssen (1977)	Netherlands	60	90	100	110							
Willemssen (1977)	Lauwersmeer	80	150	180	190							
Willemssen (1977)	Zalew Wislany	80	120	140	160							
Zbigniew (1989) ^N	Poland	72	104	122	136	147	157	161	168	168		
Zbigniew (1989) ^N	Poland	71	101	119	133	141	153	162	173			
Zhukov (1965) ^A	USSR	43	83	109	116							BC
Winfield <i>et al.</i> (1996)	U.K.	73	89	105	120	135						FL, est
Winfield <i>et al.</i> (1996)	U.K.		73	86	99	110	121	130	139			FL, est
Winfield <i>et al.</i> (1996)	U.K.			83	98	109	117	123				FL, est
Jamet & Desmolles (1994)	France	66	99	119	132	139	144					FL

ter), but Mills and Eloranta (1985) found scales to be inadequate for assigning age. Aleksandrova (1974) used otoliths as "controls" for scale-assigned ages but did not mention any discrepancies between the two methods. Dorsal spines (Bast *et al.* 1983) and opercula (Winfield *et al.* 1996) have also been used. The relationships between total length and scale radius (Holker and Hammer 1994) and total length and otolith length (Doornbos 1979, Matkovskiy 1987) have been developed.

Ruffe are typically less than 20 cm in total length (TL), rarely exceed 25 cm TL, but may be as long as 29 cm TL (Lind 1977, Craig 1987, Lelek 1987, Berka 1990). Most of the overall length is attained in the first or second year of life (Table 2). Sex, morphotype, water type, intraspecific density, and food supply affect growth of ruffe. Female, deep-bodied, and freshwater ruffe grow slower than male, shallow-bodied, and brackish-water ruffe, respectively (Table 2). A negative relationship between ruffe growth and density has been shown in both the field (Hansson 1985) and in enclosures (Bergman and Greenberg 1994). Slow growth of ruffe may also result if the benthos is impoverished (Boikova 1986, Bakanov *et al.* 1987) or 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 (Johnsen 1965, Fedorova and Vetkasov 1974, Boikova 1986, Boron and Kuklinska 1987, Ogle *et*

al. 1995). Age-0 ruffe larger than 3 to 5 cm generally feed on Chironomidae (Leszczynski 1963, Nagy 1988, Ogle *et al.* 1995), although Boron and Kuklinska (1987) described a case where mostly microcrustaceans were consumed until the ruffe were 5 cm long.

The principal prey of juvenile and adult ruffe are chironomids or macrocrustaceans (Table 3). The principal genera of chironomids consumed are *Chironomus* and *Procladius* (Fedorova and Vetkasov 1974, Boron and Kuklinska 1987, Nagy 1988, Ogle *et al.* 1995, Kangur and Kangur 1996). The prevalence of chironomids in the diet may decrease with increasing size or age (Leszczynski 1963, Fedorova and Vetkasov 1974, Ogle *et al.* 1995). Other macrobenthos prevalent in the diet are Ephemeroptera, Trichoptera, and Hirudinea. 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. (Hansson 1984, 1985; Sandlund *et al.* 1985; Van Densen 1985). Larger ruffe eat some fish (Fedorova and Vetkasov 1974, Kozlova and Panasenko 1977, Bagge and Hakkari 1985). Sierszen *et al.* (1996) used stable isotope analyses to determine that ruffe feed on both plankton and benthos.

Fish eggs (especially those of *Coregonus* spp., but also smelt (*Osmerus eperlanus*)) were eaten by ruffe in the laboratory (Mikkola *et al.* 1979, Sterligova and Pavlovskiy 1984, Pavlovskiy and Sterligova 1986) and in the field (Pokrovskii 1961, Balagurova 1963, Johnsen 1965, Fedorova and Vetkasov 1974, Adams and Tippet 1991, Rosch and Schmid 1996). However, only one of the lab studies (Pavlovskiy and Sterligova 1986) offered an

TABLE 3. Major food items of ruffe from Johnsen's (1965) review and from selected other investigations. Superscript letters following the authors' name and publication year indicate interpretations by the following authors: B = Bergman (1987), Bo = Boikova (1986), BK = Boron and Kuklinska (1987), J = Johansson and Persson (1986), and N = Nagy (1988).

Author	Country	Major Food Items
<i>from Johnsen (1965)</i>		
Alm (1917)	Sweden	Chironomidae, <i>Alona</i> , Cyclopoida
Alm (1922)	Sweden	Chironomidae, <i>Asellus</i>
Brofeldt (1922)	Germany	<i>Asellus</i> , Chironomidae, Entomostracha
Hartley (1940)	England	Chironomidae, Crustacea
Huitfeldt-Kaas (1917)	Norway	<i>Pallasea</i> , <i>Mysis</i> , Chironomidae
Jaaskelainen (1917)	USSR	Chironomidae, <i>Pisidium</i> , Insecta larvae
Jarnefelt (1917)	Finland	<i>Asellus</i> , Trichoptera, Cladocera
Jarnefelt (1921)	Finland	<i>Asellus</i> , Ephemeroptera, Chironomidae
Kessler (1868)	USSR	<i>Gammarus</i> , <i>Mysis</i> , <i>Pontoporeia</i>
Leszczynski (1963)	Poland	Chironomidae
Levander (1909)	Finland	Chironomidae, <i>Gammarus</i> , <i>Corophium</i>
Mohr (1923)	Germany	<i>Gammarus</i> , <i>Tubifex</i> , <i>Mysis</i>
Neuhaus (1934)	Germany	<i>Asellus</i> , Chironomidae, <i>Corophium</i>
Schneider (1922)	Finland	Chironomidae, Trichoptera, Cyclopoida
Schneider (1922)	Estonia	Chironomidae, Trichoptera, <i>Asellus</i> , Cladocera
Schneider (1922)	Estonia	Chironomidae, Limnophilidae, Entomostracha
Stadel (1936)	Germany	<i>Gammarus</i> , Copepoda
Tolg (1960)	Hungary	Chironomidae, Cyclopoida, <i>Corophium</i>
<i>Other Authors</i>		
Adams & Tippet (1991)	Scotland	Whitefish eggs, Trichoptera, Crustacea
Aleksandrova (1974)	USSR	Chironomidae, <i>Gammarus</i> , Oligochaeta
Appelberg (1990)	Sweden	Chironomidae, <i>Asellus</i>
Bagge and Hakkari (1985)	Finland	Chironomidae, <i>Mysis</i> , <i>Pallasea</i>
Bergman (1990)	Sweden	Chironomidae, Ephemeroptera, Crustacea
Bergman (1991)	Sweden	Chironomidae, Ephemeroptera, Crustacea
Bergman & Greenberg (1994)	Sweden	<i>Sialis</i> , Chironomidae, Ephemeroptera, Trichoptera
Berka (1990)	USSR	Chironomidae, Amphipoda, Fish eggs
Bogatova (1963) ^N	USSR	Chironomidae
Boikova (1986)	USSR	<i>Chaoborus</i> , Cyclopoida, <i>Leptodora</i> , Trichoptera
Boron & Kuklinska (1987)	Germany	Chironomidae, Cladocera, Copepoda
Brabrand (1983) ^J	Norway	Chironomidae, Cladocera
Fedorova & Vetkasov (1974)	USSR	Chironomidae, Crustacea, Fish eggs
Hansson (1984)	Sweden	Chironomidae, Amphipoda, Mollusca
Hansson (1987)	Sweden	<i>Gammarus</i> , <i>Pontoporeia</i> , Insecta larvae
Holker & Hammer (1994)	Germany	<i>Neomysis</i> , <i>Crangon crangon</i> , <i>Eurytemora</i>
Jamet (1994)	France	Macroinvertebrates
Johnsen (1965)	Denmark	Chironomidae, Crustacea, Amphipoda
Kangur & Kangur (1996)	Estonia	Chironomidae, Cladocera, Copepoda
Kolomin (1977)	USSR	Chironomidae, Trichoptera, Mollusca
Kozlova & Panasenkov (1978)	USSR	Chironomidae, Insecta larvae, Crustacea
Meisriemler (1974) ^B	Sweden	Chironomidae, <i>Gammarus</i>
Nagy (1986)	Germany	Chironomidae, Ephemeroptera, Crustacea
Nagy (1988)	Germany	Chironomidae
Ogle <i>et al.</i> (1995)	USA	Chironomidae, Ephemeroptera, Crustacea
Nilsson (1979)	Sweden	<i>Pontoporeia</i> , <i>Mysis</i> , Chironomidae
Palle (1965) ^{BK}	Denmark	Chironomidae
Pliszka & Dziekonska (1953) ^{BK}	Poland	Chironomidae
Polivannaya (1974)	Russia	Copepoda, Cladocera, Chironomidae
Schiemenz (1905) ^N	Germany	Chironomidae

Continued

TABLE 3. Continued.

Author	Country	Major Food Items
Shamardina (1967) ^{Bo}	USSR	Chironomidae, <i>Chaoborus</i> , Cyclopoida
Smirnova (1978) ^{Bo}	USSR	Chironomidae, <i>Chaoborus</i> , Cyclopoida
Van Densen (1985)	Netherlands	Chironomidae, Amphipoda, Crustacea
Willemsen (1977)	Netherlands	Chironomidae, <i>Gammarus</i>
Winfield <i>et al.</i> (1996)	U.K.	<i>Bosmina</i> , Chironomidae
Winfield <i>et al.</i> (1996)	U.K.	<i>Asellus</i> , Chironomidae

alternative prey, *Asellus aquaticus*, which ruffe consumed mostly. Several major diet studies found egg predation by ruffe to be low or nonexistent (Johnsen 1965; Hansson 1984; Nagy 1986, 1988; Boron and Kuklinska 1987; Ogle *et al.* 1995), even though eggs can be identified in the stomach for 1 to 3 days after being eaten (Sterligova and Pavlovskiy 1984). Ruffe have been implicated in the decline of *Coregonus* stocks on several occasions (Pokrovskii 1961, Balagurova 1963, Adams and Tippet 1991), but good evidence beyond a correlation has not been provided.

The diet of ruffe differs little due to lake trophic status, within-lake location, or ruffe density. Ruffe fed mainly on chironomids and ephemeropterans in lakes of moderate and high productivity, although diet breadth was greater in the more productive lakes (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. Differences in ruffe diet between sampling locations were observed in some situations (Hansson 1987, Nilsson 1979), but not others (Hansson 1984, Ogle 1992).

In general ruffe change their diet little after switching to feeding primarily on macrobenthos early in life (Collette *et al.* 1977, Rosch *et al.* 1996). This is supported by observations by Bergman (1988) for three size classes of ruffe, Boron and Kuklinska (1987) for age-1 and older ruffe, and Jamet and Lair (1991) for age-2 and older ruffe. However, Boikova (1986) identified a slight shift in diet composition at a length of 8 to 10 cm and Ogle *et al.* (1995) identified a similar shift at a length of 12 cm.

Little information is available regarding prey selection by ruffe. Juvenile and adult ruffe may select chironomids, ephemeropterans, and *Sialis* spp. (Leszczynski 1963, Nagy 1986, Bergman 1990, Bergman and Greenberg 1994), but select against oligochaets and Hirudinea (Leszczynski 1963, 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) concluded that ruffe consume organisms, and Kangur and Kangur (1996) found that ruffe consumed *Chironomus plumosus*, in proportion to their abundance in the benthos.

Adult ruffe probably feed in the shallow littoral zone (Leszczynski 1963, Holcik and Mihalik 1968, Boron and Kuklinska 1987, Jamet and Lair 1991). Holcik and Mihalik (1968) and Ogle *et al.* (1995) concluded that ruffe move from deeper to shallower waters at night to feed. Bagge and Hakkari (1985) suggested that ruffe feed in deeper waters during the summer than during other times of the year. Ruffe appear capable of feeding at all times of day (Bergman 1988, Ogle *et al.* 1995), but on some days may only feed at dusk, night, or dawn (Westin and Aneer 1987, Jamet and Lair 1991, Ogle *et al.* 1995). Adams and Tippet (1991) did not observe diel feeding periodicity by ruffe during winter.

The sensitive cephalic lateral line and visual systems may both be used by ruffe to detect and locate prey. Kuiper (1967) found that ruffe could localize immobile prey that were made mobile by "involuntary trembling of the hand" and that electromagnetic stimulation of nerves attached to the cupulae caused ruffe to "snap for food." Physiological studies indicate that the ruffe lateral line could detect and locate chironomid larvae in the top layers of the bottom substrate at a distance 2 to 5 cm from its snout (Denton and Gray 1989, Gray and Best 1989). The organization of the cone cells in the retinae and presence of the tapetum lucidum are consistent with the bottom-feeding behavior of ruffe in low-light conditions (Ahlbert 1970). Furthermore, ruffe have relatively high levels of choleacetyltransferase and acetylcholine levels in the brain, which are typical of fish with well-developed visual systems (Szabo *et al.* 1991). However, the square cone pattern is indicative of poor movement perception

(Ahlbert 1970) and the reaction distance of ruffe is only 4 cm, compared to 21 cm for Eurasian perch (Bergman 1987).

Elshoud-Odenhave and Osse (1976) described two types of feeding and thoroughly describe the physiology and behavior related to these two types. Backlifting-type feeding occurs when the ruffe senses the prey on the bottom, approaches the prey, lifts and curves the body while above the prey, and sucks the prey into its mouth. Horizontal-type feeding occurs when the ruffe senses the prey floating in the water-column, approaches it from below, and sucks it into its mouth.

The effect of temperature and light on capture rate, handling time, and swimming performance were examined by Bergman (1987, 1988). Handling time decreased, capture rate increased, and swimming performance remained constant with increasing temperature (Bergman 1987). Maximum capture rate and swimming speed decreased with decreasing light levels (Bergman 1988). When compared to Eurasian perch, ruffe were affected less by temperature and light and had a much shorter reaction distance (4 cm compared to 20 cm; Bergman 1987, 1988).

COMPETITORS

Ruffe likely compete for food resources with other benthivorous fish, including bream (*Abramis brama*; Boikova 1986), white bream (*Blicca bjoerkna*; Zadorozhnaya 1978), *Coregonus* spp. (Hansson 1984, Winfield 1992), roach (*Rutilus rutilus*; Duncan 1990), sturgeon (*Acipenser rutherns*; Sokolov and Vasil'ev 1989), smelt, trout-perch (*Percopsis omiscomaycus*; Ogle *et al.* 1995, Sierszen *et al.* 1996), Eurasian perch (Thorpe 1977, Bergman and Greenberg 1994), and yellow perch (Ogle *et al.* 1995). Only interactions between ruffe, roach, and Eurasian perch have been studied extensively. 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 was not affected by roach (Bergman 1990). However, Duncan (1990) found that the abundance of ruffe increased after Eurasian perch and roach abundance declined due to a viral infection. Diet overlap between ruffe and Eurasian perch was substantial in a Baltic archipelago (Hansson 1984) and in Lake Aydat, France (Jamet 1994). Ruffe foraging ability is not as affected by light (Bergman 1988) and temperature (Bergman 1987) as much as Eurasian perch forag-

ing ability; thus, ruffe should have a competitive advantage (Bergman and Greenberg 1994). Bergman and Greenberg (1994) concluded that ruffe and Eurasian perch compete for food resources because an increasing density of ruffe and a constant density of roach (in enclosures) caused Eurasian perch to eat more zooplankton, thus slowing their growth. Evidence for intraspecific competition has also been shown (Hansson 1985, Bergman and Greenberg 1994).

A prerequisite for competition is the ability of a fish to reduce prey biomass. 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. Bergman (1990) 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 (*Anguilla anguilla*).

PREDATORS

In Europe and Asia, ruffe are eaten by only a few predators. The primary predators of ruffe are pikeperch (*Stizostedion lucioperca*; Deedler and Willemsen 1964, Holcik and Mihalik 1968, Biro 1971, Fedorova and Vetkasov 1974, Bonar 1977, Marshall 1977, Popova and Sytina 1977) and northern pike (*Esox lucius*; Vollestad 1986, Eklov and Hamrin 1989, Adams 1991, Pervozvanskiy and Bugayev 1992, Ogle *et al.* 1996). Fish that eat ruffe in small quantities are eel, burbot (*Lota lota*), white bream, lake trout (*Salvelinus namaycush*), small-mouth bass (*Micropterus dolomieu*), black crappie (*Pomoxis nigromaculatus*), bullheads (*Ictalurus* spp.), walleye (*Stizostedion vitreum*), Eurasian perch, and yellow perch (Johnsen 1965; Popova and Sytina 1977; Rundberg 1977; Willemsen 1977; Kozlova and Panasenkov 1977; Zadorozhnaya 1978; Nilsson 1979, 1985; de Nie 1987; Ogle *et al.* 1996). Rare instances of cannibalization have been documented (Johnsen 1965). In addition, ruffe are eaten by cormorants (*Phalacrocorax carbo*; Van Dobben 1952), kingfishers (*Alcedo atthis*; Hallet 1977), and smew (*Mergus albellus*; Doornbos 1979).

The rate of predation on ruffe is affected by the abundance of ruffe and the availability of alternative prey. Pikeperch generally consume more ruffe

in years when the abundance of smelt, their preferred prey, is low (Popova and Sytina 1977, Willemsen 1977). For example, Pihu and Pihu (1974; as cited in Popova and Sytina 1977) found that ruffe were 10 to 15% of the annual ration of pikeperch in years when smelt were abundant and 80 to 85% in years when smelt were scarce. Eurasian perch also consume more ruffe when smelt are scarce (Popova and Sytina 1977). In Loch Lomond, the diet of northern pike shifted from *Coregonus lavaretus* to ruffe after ruffe were introduced and their population expanded (Adams 1991). Walleye, conditioned to eat soft-rayed fish or offered soft-rayed fish as an alternative, consumed few ruffe (Ogle *et al.* 1996).

Ruffe have a wide array of adaptations to avoid predation. The most conspicuous of these adaptations are the large dorsal, anal, pelvic, and preopercular spines. Spines make a small forage fish appear larger than it actually is, especially to a predator that attacks the center of a prey mass (Webb and Skadsen 1980, Eklov and Hamrin 1989). Spines also require the predator to swallow the fish head first, thus limiting the attack to the head and may puncture the throat or stomach lining (Eklov and Hamrin 1989, Lammens *et al.* 1990). In addition, ruffe are equipped with a retinal tapetum lucidum that allows ruffe to see predators in 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 living near the bottom may reduce predation.

PARASITES AND PATHOLOGY

Ogle (1992) compiled a list of 63 parasites of ruffe from the published literature and Bykhovskaya-Pavlovskaya *et al.* (1964) provided a comprehensive list of ruffe parasites in Russia. Only those parasites that were common or had known impacts will be discussed here. The cestodian (a liver parasite) *Triaenophorus nodulosus* (Bagge and Hakkari 1982), the nematode *Anguillicola crassus* (Hoglund and Thomas 1992, Thomas and Ollevier 1992), the monogenean (a gill parasite) *Dactylogyrus amphibothrium* (Izyumova 1958, Valtonen *et al.* 1990) and the fluke *Cotylurus variegatus* (Swennen *et al.* 1979) were common on ruffe in some instances. In most situations, no pathological effects were observed (e.g., Haenen and Van Banning 1990). However, massive dieoffs due to infections by the flukes *Tetracotyle* (Johnsen 1965,

Pokrovskii 1961) and *Cotylurus* (Swennen *et al.* 1979) have been reported. *Dactylogyrus amphibothrium* were apparently transferred to the U.S. with ruffe (Cone *et al.* 1994).

Abnormalities of the liver (Kranz and Peters 1984, Peters *et al.* 1987), fins (Lindesjoo and Thulin 1990, Thulin *et al.* 1988, Weissenberg 1965), and jaws and opercula (Weissenberg 1965) have been documented. Many of the ruffe with abnormalities were collected in polluted waters (i.e., kraft mill effluent, PCB contamination).

POSSIBLE POPULATION CONTROL

It is difficult to reduce the numbers of ruffe because they have several adaptations to compensate for high mortality rates (Lind 1977) and would likely quickly rebound (Lelek 1987). For example, ruffe may grow quickly, mature early, and spawn more than once in a season. Thus, few efforts to control ruffe have been carried out and those that have, have met varied success.

Some intentional or unintentional changes in piscivorous abundance have sometimes resulted in decreased levels of ruffe. Stocking of elvers and protective regulations for pikeperch and eel resulted in a 5- to 7-fold decline in ruffe catches in Lake Vortsjarv, Estonia (Pihu 1982, Pihu and Maemets 1982). A decrease in potential ruffe 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 also became abundant in London reservoirs following the loss of predatory fish to viral infections (Duncan 1990); however, a cause-and-effect relationship is not evident in this case because benthivorous roach also declined. The catch of "undesirable fish," which includes ruffe, was positively correlated to the yield of predatory fish (eel, pikeperch, and pike) in some Polish waters (Bonar 1977); however, it is impossible to determine if ruffe actually declined. In contrast, the termination of the gillnet fishery in Lake Tjeukemeer, the Netherlands resulted in significantly more and larger pikeperch, but catches of ruffe were not affected (Lammens *et al.* 1990). Predation on ruffe did not increase in Lake Tjeukemeer, because the abundance of smelt, the preferred prey of pikeperch, was not linked to pikeperch numbers because smelt immigrate from an adjoining lake. In the St. Louis River, United States, walleye and northern pike were stocked aggressively and their harvest was curtailed in hopes that the two pisci-

vores would keep ruffe numbers low. However, walleye and northern pike consumed few ruffe during the initial invasion period (Ogle *et al.* 1996). In Lake Vortsjarv, intensive removal of ruffe by bottom trawling did not decrease ruffe numbers (Pihu 1982, Pihu and Maemets 1982).

In some instances, the abundance of ruffe may be limited by benthos production. Ruffe were present in low numbers in Lake Vastra Kyrksundet, Finland, when it was meromictic (Bonsdorff and Stenberg 1990); however, ruffe biomass increased when the lake became limnic and benthos production increased.

CONCLUSIONS

Ruffe appear to be remarkably adaptable to a wide variety of conditions as evidenced by the large amount of variability in many of the biological and life history traits examined here. Morphological characteristics varied across large geographical scales, within certain water bodies, and between sexes. Ruffe tolerated a wide variety of conditions including fresh and brackish waters, lacustrine and lotic systems, depths of 0.25 to 85 m, montane and submontane areas, and oligotrophic to eutrophic waters. Age and size at maturity differed according to temperature and levels of mortality. Ruffe spawned on a variety of substrates, for extended periods of time, and in some instances, may have spawned more than once per year. Growth of ruffe varies by sex, morphotype, water type, intraspecific density, and food supply. Interactions with other species (i.e., competition and predation) appeared to vary considerably between systems.

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