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Biology of Ruffe *(Gymnocephalus cernuus* (L.))— A Review of Selected Aspects from European Literature

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Abstract. The focus of this synthesis is the ruffe research conducted in Europe during the last 100 years. Literature data about habitat, feeding ecology, growth, daily ration, production, and commercial value of ruffe from different types of waters were compiled. In some European estuaries, ruffe were formerly an important commercial species. Today, ruffe still have some commercial importance in eastern European countries, e.g., Russia. Ruffe are food generalists with a tendency to feed on benthos, but in tidal estuaries they are rather planktivorous. They have the advantage of being able to select moving prey items under relatively dim light or high turbidity conditions as a result of their excellent near-field sensory resolution. Under these conditions, they are able to compete with other species for zooplankton and small fish. In the clear and less productive waters of many lakes, rivers and reservoirs, ruffe are better competitors for benthic macroinvertebrates than perch and roach. A multivariable consumption model has been developed to allow rough estimates of daily ration in dependence from water temperature and fish size. Although ruffe occur both in freshwater and brackish habitats, they usually grow better in estuaries than in fresh water. Some authors agree that, compared to fresh water, ruffe utilize the better nutritional opportunities in brackish water, which ultimately induces better growth.

INDEX WORDS: Ruffe, habitat, diet, consumption, growth, commercial value, Europe, review.

Introduction

Ruffe have received little attention because of their small size and low economic value. Consequently, the literature about ruffe research in the last 100 years was sparse and a large part consists of gray literature or is written in Russian, German, and other European languages. In general, interest in this species has grown since the introduction of ruffe into new habitats has led to rapid population expansions in Loch Lomond, Scotland (Maitland and East 1989) and in the Great Lakes of North America (Pratt *et. al.* 1992, Busiahn 1993). In the latter, ruffe were considered a serious threat to the delicate predator-prey balance vital to sustaining healthy commercial and sport fisheries across North America (Gunderson 1997). As a result attention was drawn to ruffe for the first time at an International Ruffe Symposium (Ann Arbor, Michigan, 1997). Little has been done previously to synthesize or collate the literature on ruffe. The only reviews known to the authors were restricted to ruffe in Denmark (Johnsen 1965) and Finland (Lind 1977). A bibliography on ruffe is published by Winfield and McCulloch (1995). However, our report does not intend to give a full synthesis of publications on ruffe. The aim is to review selected aspects of ruffe biology, particularly the feeding ecology, food consumption, growth, and former commercial value. The intent of this review is to synthesize the results of other authors, to analyze their findings, identify trends, and compare these findings with the related percid, the European perch *(Perca fluviatilis).*

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Materials and Methods

Relevant research literature was selected according to defined criteria. The following bases were used during the selection process:

- accurate description and appropriate use of methods,
- particular consideration of gray literature and literature from eastern Europe, especially if written in Russian, and
- representative consideration of all types of European habitats inhabited by ruffe.

For intercomparison of feeding ecology, growth, daily ration, production, and commercial value of ruffe, six different habitat types were defined (Table 1):

1) Lakes: small to large stagnant natural waters; fresh water; no currents.
2) Ponds: small and shallow artificial or natural habitats; fresh water; no currents.
3) Reservoirs: artificial habitats of different sizes, mostly built by man-made dams in rivers; fresh water; low currents.
4) Rivers: natural habitats; fresh water; medium—high currents.
5) Tidal estuaries: hypopotamal region of rivers affected by tidal movements; oligohaline—mesohaline waters; low-medium currents.
6) Non-tidal estuaries: Coastal lagoons with out tidal movements; oligohaline—mesohaline waters; no currents.

Feeding Ecology

In several European countries, studies have been conducted on the food of the ruffe in the last century. Most older works give qualitative information about the food composition, without providing further quantitative values (e.g., sample size, number of fishes and prey items). To consider these publications as well, an observation index (Oi) was computed to describe and compare the food diversity of ruffe in different waters. For this approach, each observation of a food category in the diet of a ruffe population in a water was indicated as 1 for occurrence and 0 for absence.

$$Oi\ \% = (ni/Ni) * 100 \qquad (1)$$

ni = number of observations of a food category in the diet of ruffe in all waters belonging to one habitat type

Ni = total number of observations of food categories in the diet of ruffe in all waters belonging to a habitat type

Table 2 summarizes all computed food categories. In most publications, there is information about the food composition for different size classes of ruffe. Three length categories were classified. The class < 5 cm describes the food composition of the 0-Group, the class 5 to 15 cm classifies the same for adult ruffe of most waters, and the class > 15 cm summarizes the food composition of the biggest adults. For the latter the data is primarily from estuaries.

Growth

The data from 48 European waters was summarized. The von Bertalanffy Growth Formula (VBGF) is used to express the growth of fish populations (von Bertallanffy 1957).

$$TL = L_\infty(1 - e^{-K(t - t_0)}) \qquad (2)$$

where TL is the total length at age t, $L\infty$ the asymptotic size, K and t_0 are constants with dimensions l/time. The parameter Ø' in the following equation can be used to compare the growth performance of fish, when their growth is of the von Bertalanffy type (Pauly and Munro 1984, Moreau *et al.* 1986):

$$Ø' = \log K + 2 \log L_\infty \qquad (3)$$

where K is the growth constant and L_∞ the asymptotic length from the VBGF, and Ø' is an index for comparing growth performance of fish in terms of length growth. To compare results obtained by various authors, whenever needed, a standard length (SL) was converted to a total body length (TL) by applying a relationship

$$TL = (SL + 3.904)/0.8596 \qquad (4)$$

based on measurements of ruffe from Szczecin Lagoon, the Odra estuary, and Lake Dabie, all Poland (Neja 1989).

Since information about sample size and distribution does not always exist, unweighted means were used for computation. Although this may result in a statistical bias, the VBGF was applied to describe the growth performance of ruffe populations and the coefficient of correlation was used to provide a better impression of the character of the growth curve. Holker and Hammer (1994) showed for the Elbe Estuary that the growth performance increased during recent decades, but only the current investigations from Arzbach (1987) and Holker and Hammer (1994) present length-at-age data for ruffe older than 4 years. Therefore, to avoid distortion of the results, only data from the age groups I-IV were used for computation of the growth performance for ruffe in tidal estuaries.

Daily Ration

Different approaches have been taken to estimate the quantity of food consumed by ruffe. These approaches fall into two groups; bioenergetic approaches, which integrate the consumption over a relatively long period and measure it by estimating the rate that would give the growth observed over that period (Birkan and Tichomirowa 1982, Thiel 1990); and the estimation of the gastric evacuation rate of food to provide an instantaneous estimate of consumption (Sadoroshnaja and Spanowskaja 1981, Hölker and Temming 1996).

A simple formula of an energy budget was developed by Winberg (1956) who suggested that food consumption could be estimated as:

$$0.8C = P + R \qquad (5)$$

where C is the energy of consumed food over a time interval, P is the energy for growth, and R is the energy used for metabolism over the time interval. For this method, the estimate of metabolic requirements is based on oxygen consumption measurements. Different parameter sets measured at 20°C have been used for this approach, based on the exponential relationship between weight W (g) and standard metabolism Q (mL O_2/h):

$$Q = a * W^b \qquad (6)$$

where a is the oxygen consumption of a fish of 1g, and b the weight (W) specific exponent. Birkan and Tichomirowa (1982) applied the general mean for all fishes, $Q = 0.336 * W^{0.8}$, presented by Winberg (1956). Thiel (1990) used the relationship $Q = 0.561 * W^{0.72}$ based on Melnitschuk's (1978) measurements on fed ruffe. In contrast Tátrai (1977) presented a relationship $Q = 0.307*W^{0.75}$ estimated within 1 hour of the transfer of unfed ruffe into the experimental chamber. Following Mann (1978) these estimates, which refer to unfed and resting fish, must be multiplied by a factor of about 2, in order to account for the higher metabolic requirements of feeding and active fish in the field. Tatrai (1977) suggested a factor of 1.5 for the comparatively sluggish ruffe.

The second approach is based on results from gastric evacuation experiments performed with ruffe fed natural prey. Once the process of gastric evacuation is quantified, these data can be combined with information on the mean stomach content (g) in the field to obtain estimates of the daily ration. Sadoroshnaja and Spanowskaja (1981) used a linear evacuation model (Novikov 1949 and Kogan 1963, cit. in Sadoroshnaja and Spanowskaja 1981). Hölker & Temming (1996) incorporated the effect of temperature and fish weight in a multivari-able version of the exponential evacuation model for ruffe.

All results about the daily ration of ruffe were summarized. In cases where data about ration were missing but stomach content data, fish weight, and temperature were given the daily ration was calculated using the gastric evacuation model derived from Holker and Temming (1996) and the consumption model according to Eggers (1977). All models were fitted with non-linear regression techniques (Levenberg Marquard Algorithm in SPSS for Windows, release 6.1.3).

TABLE 1. Overview of the reviewed papers concerning with (1) distribution and habitat requirements, (2) feeding ecology, (3) growth, (4) metabolism and daily ration, and (5) production and commercial value of ruffe in European waters.

					Reviewed for topic				
Author(s)	Year	Habitat type	Country	Local name of water(s)	1	2	3	4	5
Adams & Tippet	1991	Lake (L)	Scotland	Loch Lomond	x	x		x	
Antipowa	1980	Lake (L)	Russia/ Estonia	Pskov-Chud Lake	x	x			
Antipowa & Konzewaja	1988	Lake (L)	Russia/ Estonia	Pskov-Chud Lake	x	x			x
Arzbach	1997	Lake (L)	Germany	Plußsee	x		x		
Bagge & Hakkari	1982	Lake (L)	Finland	Lake Päijänne	x	x			
Bauch	1954	Lake (L)	Germany	23 different Lakes	x		x		
Bauch	1954	Lake (L)	Germany	Lake Müggel	x		x		
Bauch	1954	Lake (L)	Germany	Lake Sakow	x		x		
Berg	1965	Lake (L)	Russia	Lake Ubinskoje	x		x		
Bergman	1988	Lake (L)	Sweden	Lake North Bolmen	x	x			
Bergman	1988	Lake (L)	Sweden	Lake South Bolmen	x	x			
Bergman	1988	Lake (L)	Sweden	Lake Ivösjön	x	x			
Bergman	1988	Lake (L)	Sweden	Lake Vompsjön	x	x			
Bergman	1991	Lake (L)	Sweden	Lake South Bolmen	x	x			x
Bergman	1991	Lake (L)	Sweden	Lake Vomb	x	x		x	x
Birkan	1983	Lake (L)	Russia	Lake Ladoga	x			x	
Birkan & Tichomirowa	1982	Lake (L)	Russia	Lake Ladoga	x	x		x	
Biro	1971	Lake (L)	Hungary	Lake Balaton	x		x		
Bogatowa	1963	Lake (L)	Russia	Nevel´sko	x	x		x	
Boikova	1986	Lake (L)	White Russia	Glubokoje	x	x			
Brofeldt	1922	Lake (L)	Germany	Lake Müggel	x	x		x	
Federova & Vetkasov	1973	Lake (L)	Russia	Lake Il´men	x	x	x		x
Huitfeldt-Kaas	1927	Lake (L)	Norway	Lake Mjøsa	x	x			
Jamet	1994	Lake (L)	France	Lake Aydat	x	x			
Jamet & Desmolles	1994	Lake (L)	France	Lake Aydat	x		x		
Jamet & Lair	1991	Lake (L)	France	Lake Aydat	x	x			
Järnefelt	1921	Lake (L)	Finland	Lake Tuusala	x	x	x		
Järnefelt	1921	Lake (L)	Finland	Lake Pyhäjärvi	x	x	x		
Johnsen	1965	Lake (L)	Denmark	Esrom Sø	x	x			
Johnsen	1965	Lake (L)	Denmark	Fure Sø	x	x			
Johnsen	1965	Lake (L)	Denmark	Arresø	x	x			
Johnsen	1965	Lake (L)	Denmark	Borre- og Brassø	x	x			
Johnsen	1965	Lake (L)	Denmark	Haderslev Dam	x	x			
Kalas	1995	Lake (L)	Norway	Mildevatn	x	x			
Kangur	1969	Lake (L)	Estonia	Lake Vortsjärv	x	x			
Kangur & Kangur	1996	Lake (L)	Estonia	Lake Vortsjärv	x	x			
Leszczynski	1963	Lake (L)	Poland	Lake Kortowskie	x	x			
Lind	1977	Lake (L)	Finland	Finnish lakes	x		x		
Maitland & East	1989	Lake (L)	Scotland	Loch Lomond	x				x
Meisriemler	1974	Lake (L)	Austria	Neusiedlersee	x	x	x	x	
Mooij *et al.*	1994	Lake (L)	The Netherlands	Lake Tjeukemeer	x			x	
Neja	1989	Lake (L)	Poland	Lake Dabie	x		x		
Pihu & Pihu	1974	Lake (L)	Russia/ Estonia	Pskov-Chud Lake	x	x			
Pokrovskii	1961	Lake (L)	Russia	some Russian lakes	x	x			
Rask & Tuunainen	1990	Lake (L)	Finland	Finnish acidified lakes	x				
Rathcke	1984	Lake (L)	Germany	Alster	x		x		
Rösch & Schmid	1996	Lake (L)	Germany	Lake Constance	x	x			
Sandlund *et al.*	1985	Lake (L)	Norway	Lake Miøsa	x	x			
Shamardina	1968	Lake (L)	White Russia	Lake Glubokoje	x		x		
Tölg	1960	Lake (L)	Hungary	Lake Balaton	x	x			
Van Densen & Hadderingh	1982	Lake (L)	The Netherlands	Bergummermeer	x			x	
Wilkonska	1986	Lake (L)	Poland	Lake Zarnowieckie	x				x
Willemsen	1977	Lake (L)	The Netherlands	Lake Ijssel	x		x		
Winfield *et al.*	1996	Lake (L)	Wales	Llyn Tegid	x	x			
Bergman & Greenberg	1994	Pond (P)	Sweden			x			
Hölker	1992	Pond (P)	Germany	Altengamme	x		x		
Johal	1980	Pond (P)	Czech Republik	Ponedr. Ryb. at Trebon	x		x		
Johal	1980	Pond (P)	Czech Republik	Kanov at Trebon	x		x		
Johal	1980	Pond (P)	Czech Republik	Machovo jezero	x		x		
Bastl	1965	Reservoir (RES)	Slovakia	Orava reservoir	x		x		
Boron & Kuklinska	1987	Reservoir (RES)	Poland	Wloclawek Dam	x	x		x	
Gorjunova *	1956	Reservoir (RES)	Slovakia	Dzeszkazgansk	x		x		
Johal	1980	Reservoir (RES)	Czech Republik	Slapska	x		x		
Kijaschko *	1980	Reservoir (RES)	Russia	Rybinsk reservoir	x		x		
Kijaschko	1981	Reservoir (RES)	Russia	Rybinsk reservoir	x	x			
Masatova & Zaveta	1987	Reservoir (RES)	Russia	Orlik reservoir	x		x		x
Oliva & Vostradovsky *	1960	Reservoir (RES)	Czech Republik	Slapy reservoir	x		x		
Oliva & Vostradovsky *	1960	Reservoir (RES)	Czech Republik	Pastviny reservoir	x		x		
Plewa	1996	Reservoir (RES)	Germany	Bautzen reservoir	x	x			
Sadoroshnaja & Spanowskaja	1981	Reservoir (RES)	Russia	Mozajsk reservoir	x	x		x	
Sadoroshnaja & Spanowskaja	1981	Reservoir (RES)	Russia	Ucinsk reservoir	x	x			
Sadoroshnaja & Spanowskaja	1981	Reservoir (RES)	Russia	Ivan´kovsk reservoir	x	x			
Svetovidova *	1947	Reservoir (RES)	Russia	Ucinsk reservoir	x		x		
Vasnecov *	1950	Reservoir (RES)	Russia	Rybinsk reservoir	x		x		
Werner *et al.*	1996	Reservoir (RES)	Germany	Bautzen reservoir	x	x			
Wielgolsz	1989	Reservoir (RES)	Poland	Wloclawek Dam	x	x			
Aleksandrova	1974	River (RIV)	Ukraine	middle Dnepr	x	x	x		
Kolomin	1977	River (RIV)	Russia	Nadym River	x	x	x		
Johal	1980	River (RIV)	Czech Republic	Berounka	x		x		
Johal	1980	River (RIV)	Czech Republic	Dyje	x		x		
Mikheev & Pavlov	1993	River (RIV)	Bulgaria	Rositsa River	x	x			
Nagy	1982	River (RIV)	Slovakia	Danube	x	x		x	
Nagy	1985	River (RIV)	Slovakia	Danube	x	x			
Nagy	1988	River (RIV)	Slovakia	Danube	x	x			
Zhukov **	1965	River (RIV)	White Russia	upper Dnepr	x		x		
Arzbach	1987	Tidal Estuary (TE)	Germany	Stör	x		x		
Diercking	1984	Tidal Estuary (TE)	Germany	Elbe	x				x
Ehrenbaum	1894	Tidal Estuary (TE)	Germany	Elbe	x	x			
Elliott & Dewailey	1995	Tidal Estuary (TE)	Europe	Europ. Tidal estuaries	x				
Hölker & Hammer	1994	Tidal Estuary (TE)	Germany	Elbe	x	x	x		

Continued

TABLE 1 (Continued). Overview of the reviewed papers concerning with (1) distribution and habitat requirements, (2) feeding ecology, (3) growth, (4) metabolism and daily ration, and (5) production and commercial value of ruffe in European waters (continued).

					Reviewed for topic				
Author(s)	Year	Habitat type	Country	Local name of water(s)	1	2	3	4	5
Hölker & Temming	1996	Tidal Estuary (TE)	Germany	Elbe	x			x	
Knowles	1974	Tidal Estuary (TE)	Germany	Elbe	x		x		
Ladiges	1935	Tidal Estuary (TE)	Germany	Elbe	x	x			
Mohr	1923	Tidal Estuary (TE)	Germany	Elbe	x	x	x		
Möller	1988	Tidal Estuary (TE)	Germany	Elbe	x		x		
Möller	1989	Tidal Estuary (TE)	Germany	Elbe	x				x
Stadel	1936	Tidal Estuary (TE)	Germany	Elbe	x	x			
Thiel *et al.*	1995	Tidal Estuary (TE)	Germany	Elbe	x				
Thiel *et al.*	1997	Tidal Estuary (TE)	Germany	Elbe	x	x			x
Bast *et al.*	1983	Non-tidal Estuary (NE)	Germany	Darß-Zingster Bodden	x		x		x
Bauch	1954	Non-tidal Estuary (NE)	Germany	Darß-Zingster Bodden	x		x		
Chlopnikow	1992	Non-tidal Estuary (NE)	Poland	Vistula Bay	x	x			
Debus & Winkler	1990	Non-tidal Estuary (NE)	Germany	Darß-Zingster Bodden	x	x			
Klinkhardt & Winkler	1989	Non-tidal Estuary (NE)	Germany	Darß-Zingster Bodden	x				
Kozlova ***	1979	Non-tidal Estuary (NE)	Poland/Ruissia	Curonian Lagoon	x				x
Kozlova & Panasenko	1977	Non-tidal Estuary (NE)	Poland/Russia	Curonian Lagoon	x	x			
Lind	1977	Non-tidal Estuary (NE)	Finland	several brackish waters	x		x		
Neja	1989	Non-tidal Estuary (NE)	Germany/Poland	Szczecin Lagoon	x		x		
Neuhaus	1934	Non-tidal Estuary (NE)	Germany/Poland	Szczecin Lagoon	x	x	x		
Neuhaus	1934	Non-tidal Estuary (NE)	Poland	Lebbiner Schär	x		x		
Neuhaus	1934	Non-tidal Estuary (NE)	Poland/Russia	Vistula Bay	x	x			
Neumann	1979	Non-tidal Estuary (NE)	Sweden	Hamnefjärden	x			x	
Nolte	1939	Non-tidal Estuary (NE)	Poland/Russia	Vistula Bay	x	x	x		
Smirnov *	1977	Non-tidal Estuary (NE)	Finland	Gulf of Finland	x		x		x
Thiel	1989	Non-tidal Estuary (NE)	Germany	Darß-Zingster Bodden	x			x	
Thiel	1990	Non-tidal Estuary (NE)	Germany	Darß-Zingster Bodden	x	x		x	x
Vetemaa & Saat	1996	Non-tidal Estuary (NE)	Estonia	Pärnu Bay	x				
Willemsen	1977	Non-tidal Estuary (NE)	The Netherlands	Lauwersmerr	x		x		
Winkler	1989	Non-tidal Estuary (NE)	Germany	Greifswalder Bodden	x				x
Ahlbert	1969			laboratory		x			
Bergman	1987			laboratory		x		x	
De Nie	1996	all types	The Netherlands		x				
Diercking &Wehrmann	1991	all types	Hamburg, Germany		x				
Disler & Smirnov	1977			laboratory		x			
Edsall *et al.*	1993			laboratory				x	
Gray & Best	1989			laboratory		x			
Herter	1953			laboratory		x			
Janssen	1997			laboratory		x			
Lelek	1987	all types	Europe		x				
Melnitschuk	1978			laboratory				x	
Saat & Veersalu	1996			laboratory				x	
Schiemer & Waidbacher	1992	all types	Austria		x				
Tátrai	1977			laboratory				x	
Wunder	1936			laboratory		x			

*Cit. in Bastl 1965, **cit. in Aleksandrova 1974, ***cit. in Bast *et al.* 1983.

TABLE 2. Food items in the diet of European ruffe, which were used for calculation, and summarized food categories as presented in Figures 1 and 2.

ecological group	abbreviation	Counted food categories	Summarized food categories for Figures 1 and 2
Mesozooplankton	MEZ	Copepoda Cladocera	
Macrozooplankton	MAZ	Mysidacea Decapoda	
Zoobenthos	ZOB	Ostracoda Isopoda Amphipoda Chironomid larvae	
		Trichoptera larvae Ephemoptera larvae Megaloptera larvae Ceratopogonid larvae Coleoptera larvae Plecoptera larvae further insects	other insects
		Oligochaeta Polychaeta	Annelida
Nekton	NEC	fishes fish eggs	
Rest	RST	Bryozoa Rotatoria Hydracarina Arachnida Chaoboridae Hirudinea	other taxa
		PLANTS DETRITUS	

Results

Horizontal and Vertical Habitat Use

A comparison of the frequency of occurrence of ruffe in The Netherlands (De Nie 1996) resulted in high frequencies for lakes (70%) and big rivers and estuaries (60%). In small rivers and ponds, lower frequency values between 10-40 % were observed. Stream velocity affects the horizontal distribution of ruffe in rivers. Normally, this percid prefers habitats with lower currents, e.g., backwaters or side channels (Diercking and Wehrmann 1991). However, since ruffe is an eurytopic species (Schiemer and Waidbacher 1992), it can occur with similar frequencies in side and main channels of estuaries as found by Thiel *et al.* (1995) for the Elbe estuary. Due to its relatively high salinity tolerance (Klinkhardt and Winkler 1989, Vetemaa and Saat 1996) ruffe occur in oliogohaline and mesohaline regions of estuaries. The salinity tolerance of ruffe is somewhat higher than that of perch, but the pH-tolerance is lower (Rask and Tuunainen 1990) with a critical level for successful reproduction of around pH 5. Ruffe prefer clean bottom types in deeper water layers with deposits of sand and/or gravel. These substrate types are also used for spawning. Ruffe does not require submerged macrophytes for reproductive success.

In stagnant water bodies such as lakes and reservoirs, ruffe are commonly found in deeper waters than perch. In Lake Mj0sa, Sweden, where perch are restricted to the 0-50 m depth, ruffe are found to 80 m water depth (Sandlund *et al.* 1985). Compared to perch, ruffe prefer lower distances from bottom, lower temperatures, and lower light intensities (Bergman 1988). When stratification of the waterbodies occur, densities of ruffe can decrease rapidly in an anoxic hypolimnion. However, they can recover quickly if the water quality improves (Lelek 1987).

Feeding Ecology

Diet of Ruffe

Chironomid larvae are important food items for ruffe in all water types. With the exception of populations from tidal estuaries they comprise the highest biomass in the food. Copepoda and Cladocera are very frequent in the food of 0-group ruffe, but the frequency decreases for adult ruffe.

Freshwater areas

For almost all freshwater ruffe populations zoobenthos is the predominant prey (Fig. 1). However in some lakes (e.g., Lake Bolmen, Sweden, and Lake Mildevatn, Norway), zooplankton feeding can be found during summer (Bergmann 1991, Kalas 1995). Kalas (1995) stipulates that the availability of large zooplankton to ruffe is the main reason for this difference in food choice. Beside chironomids, the larvae of other insects, mainly Trichoptera and Ephemeroptera, were frequently consumed in fresh water. With increasing body size, they become more important in the diet of ruffe. Fish eggs such as lake smelt roe in spring (Antipowa and Konzewaja 1988) as well as vendace and whitefish roe in late autumn and winter, Pskov-Chud Lake (Russia and Estonia), (Pihu and Pihu 1974) or burbot roe in winter (Alm cit. in Jarnefelt 1921) were only reported from ruffe populations in lakes. In Lake Constance, Germany, (Rosch and Schmid 1996) and Loch Lomond, Scotland, (Adams and Tippett 1991) ruffe switch from insect larvae to coregonid eggs as the main prey during the coregonid spawning season in December and January. Pokrovskii (1961) found that ruffe may significantly decrease vendace abundance by consuming 80-90% of the eggs deposited by that species. In freshwater areas only adult ruffe from lake populations consume fish, such as smelt in Lake Vortsjäry, Estonia (Kangur and Kangur 1996), or Lake Ilmen, Russia (Fedorova and Vetkasov 1974). Detritus was only reported in the diet of lake ruffe, from Lake Tuusula and Lake Pyhajarvi (Finland), (Jarnefeldt 1921), Lake Vortsjarv (Estonia), (Kangur and Kangur 1996) and Lake Constance, (Germany), (Rösch and Schmid 1996).

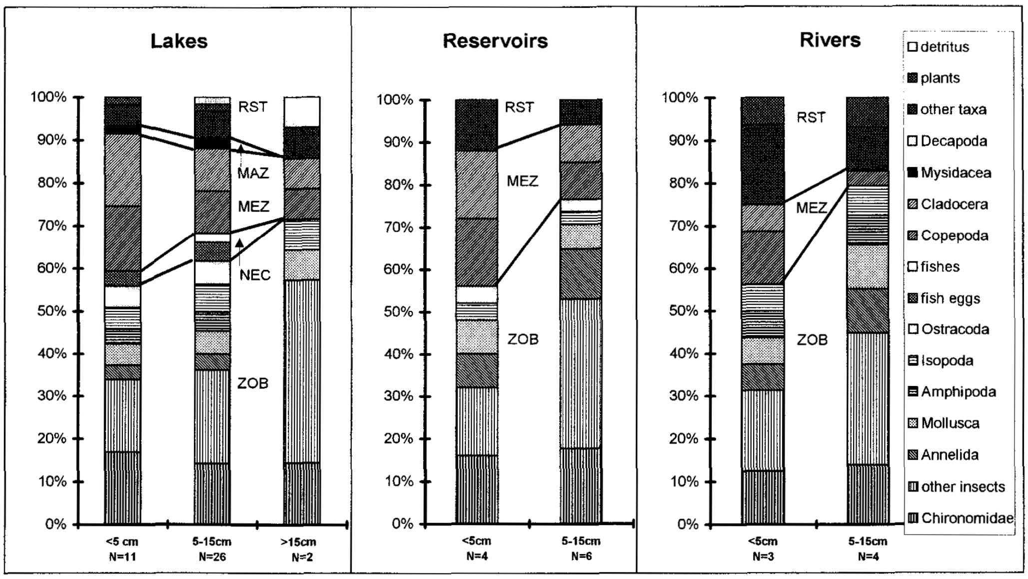

FIG. 1. Food composition of ruffe in freshwater areas using the observation index. The class < 5 cm describes the food composition of the 0-Group, the class 5–15 cm classifies the food composition of adult ruffe in most waters, and the class > 15 cm summarizes the food composition of the biggest ruffe in a few lakes. Abbreviations: Mesozooplankton (MEZ), Macrozooplankton (MAZ), Zoobenthos (ZOB), Nekton (NEC), Rest (RST).

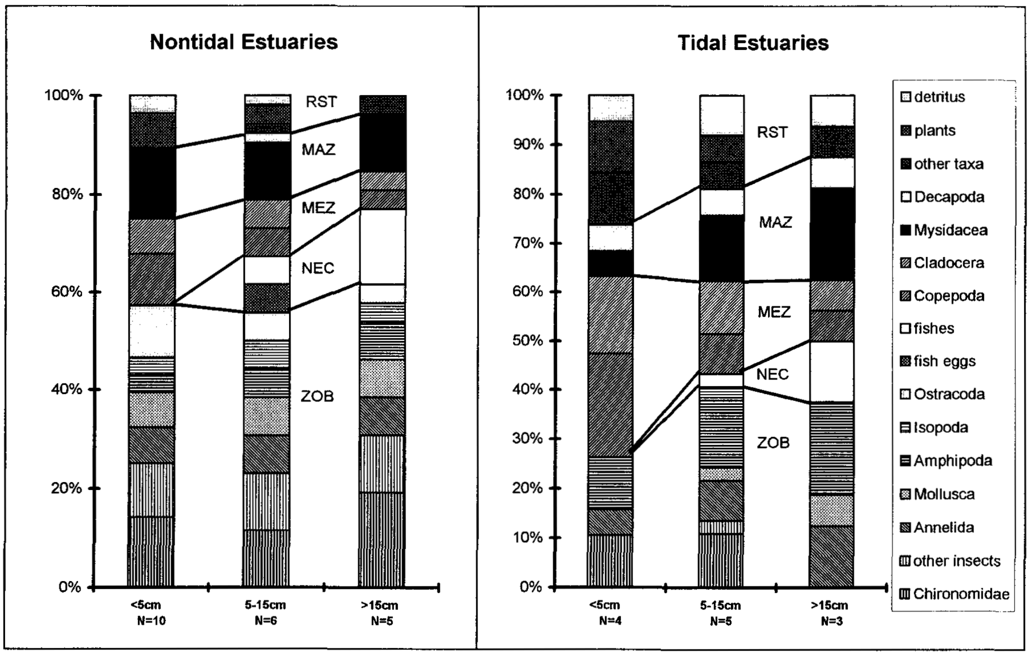

FIG. 2. Food composition of ruffe in freshwater areas using the observation index. The class < 5 cm describes the food composition of the 0-Group, the classes 5–15 cm and > 15 cm classify the food composition of adult ruffe. Abbreviations: Mesozooplankton (MEZ), Macrozooplankton (MAZ), Zoobenthos (ZOB), Nekton (NEC), Rest (RST).

Estuaries

Zooplankton and nekton are much more important as food for populations in estuaries than for ruffe in freshwater areas (Fig. 2). Particularly in tidal estuaries, zooplankton and nekton are more frequent than zoobenthos. As a result of the turbulent character of tidal estuaries, the differentiation into planktonic and benthic organism is problematic. Even Ostracoda and Amphipoda can live in open water (Stadel 1936). In the tidal Elbe River, remarkable amounts of detritus in the stomachs of ruffe (Holker and Hammer 1994, Thiel *et al.* 1997) are found. It remains unclear whether these detritus flocs were actively eaten or if they were accidentally ingested with, e.g., copepods and mysids. Detritus occurring in the Elbe Estuary is important food for copepods and mysids (Bernat *et al.* 1994). In estuaries, insects like Chironomidae, Tri-choptera, and Ephemeroptera were less abundant in the food of ruffe. There are high amounts of meso-zooplankton food items, like Mysidacea and Amphipoda, in the diet of ruffe. Ladiges (1935) emphasized the importance of Copepoda for juveniles in the tidal Elbe River. Thiel *et al.* (1997) reported that ruffe of age groups 0 to 2 in this area fed mainly on zooplankton, especially calanoids and mysids. The latter were significantly selected by ruffe larger than 7 cm (Holker and Hammer 1994). They may be a suitable food item for ruffe because the turbulence of the continuously moving thoracopods of the freely swimming prey can be detected by their excellent near-field sensory resolution. Decapoda, like brown shrimp, are substantial prey too. In estuaries, adult ruffe frequently consume small fishes. In the Elbe River, juvenile smelt (Osmerus eperlanus) and to a less degree gobies (Pomatoschistus microps) were consumed by ruffe (Holker and Hammer 1994). In nontidal estuaries like the Couronian Lagoon, adult ruffe feed on juvenile smelt and perch in addition to meso- and macrozooplankton (Neuhaus 1934, Kozlova and Panasenko 1977). In the Darβ-Zingser Bodden ruffe also feed on nine-spined sticklebacks (Pungitius pungitius, Thiel 1990).

Foraging Ability

The foraging ability of ruffe is less influenced by light than it is for perch (Bergman 1988). Under relatively dim light conditions or at high turbidity, ruffe have an advantage by being able to select moving objects as they have a well-developed lateral system (Disler and Smirnov 1977) and a particularly extensive canal system in the head region (Gray and Best 1989, Janssen 1997). Swimming of ruffe consists of a thrust by the pectoral and caudal fins followed by a glide; prey are detected during the glide phase. Janssen (1997) hypothesizes that the membranes over the openings in the ruffe's lateral line function to reduce non-turbulent, laminar flow "noise" from reaching the neuromasts. In addition to this, the eyes are equipped with a *tapetum lucidum* (Wunder 1936, Ahlbert 1969), which allow prey detection even under extreme low light conditions. The ratio of rods to cones is about 125 to 5 at a distance of 80 µ from the retina. At the same distance only 25 rods to 8 cones are found in perch and a ratio of 74 rods to 4 cones are found in pike perch (Wunder 1936). Herter (1953) shows that ruffe visually prefer objects with a silhouette rich in contrast.

With a reaction distance of about 5 cm (Bergman 1987, Gray and Best 1989) the visual sense organs and the lateral line have an excellent near-field resolution, but over large distances ruffe are comparatively short sighted. In clear and less productive waters of many lakes, rivers and reservoirs, ruffe are therefore a better competitor for benthic macro-invertebrates than perch and roach (Bergman and Greenberg 1994). Here, their sensory system helps them to detect even chironomids living in the sediment. But for zooplankton food, their visual capabilities were less successful than those of perch. The latter had a longer reaction distance (4 to 5 fold that of ruffe) and a higher capture probability (Bergman 1987). As productivity results in increased algae turbidity and hence decreased light penetration, perch and probably a lot of other fish species have a competitive disadvantage in highly productive waters. In such waters, especially in estuaries, ruffe is able to compete with other fish species for zooplankton and even for fish as food.

TABLE 3. Growth parameters of ruffe occurring in different water types. L_∞ is the asymptotic size (cm), K and t_0 are constants with dimensions 1/time. Ø′ has a species-specific value for growth performance.

water type	Ø′	L_∞	K	t_0	N	r^2	mean maximum age
Tidal Estuaries	2,26	25,3	0,28	–0,63	20	0,79	4,6
Nontidal estuaries	2,05	18,7	0,32	–0,57	61	0,82	6,3
Ponds	1,95	14,6	0,42	–0,47	17	0,95	4,1
Reservoirs	1,90	14,5	0,37	–0,30	45	0,84	5,0
Lakes	1,87	19,3	0,20	–0,75	88	0,80	5,3
Rivers	1,85	17,9	0,22	–0,62	28	0,91	5,9

Growth

Table 3 and Figure 3 indicate that the growth performance (0') of ruffe populations from freshwater regions with a 0' smaller than 2 differ very little from each other. Ruffe growth in estuaries is much higher. Here a 0' of 2.05 for ruffe from nontidal estuaries and a 0' of 2.26 for those living in tidal estuaries, namely the Elbe estuary were found.

In the Elbe River, ruffe reaches lengths of about 25 cm (Hölker and Hammer 1994). The same total lengths were found in the Stör River, a tidally influenced tributary of the lower Elbe River (Arzbach 1987). The largest recorded ruffe of this region was 29 cm (Moller 1988). In earlier investigations, ruffe were found to reach maximally 18 cm (Mohr 1923) and 20 cm (Knowles 1974). Currently, ruffe found in the Elbe River are similar in size to those reported by Bast *et al.* (1983), 24 cm in the Darβ-Zingster Bodden, Germany. An earlier investigation in another Baltic coastal region, Vistula Bay (Russia and Poland), Nolte (1939) states that ruffe of 22 cm were frequent in former times, but rarely reach more than 20 cm today. In fresh water, ruffe populations from only Lake Pyhäjärvi, Finland, and some other Finnish lakes (Järnefeldt 1921, Lind 1977) as well as populations from Lake Dabie, Poland, (Neja 1989) reached lengths significantly greater than 15 cm.

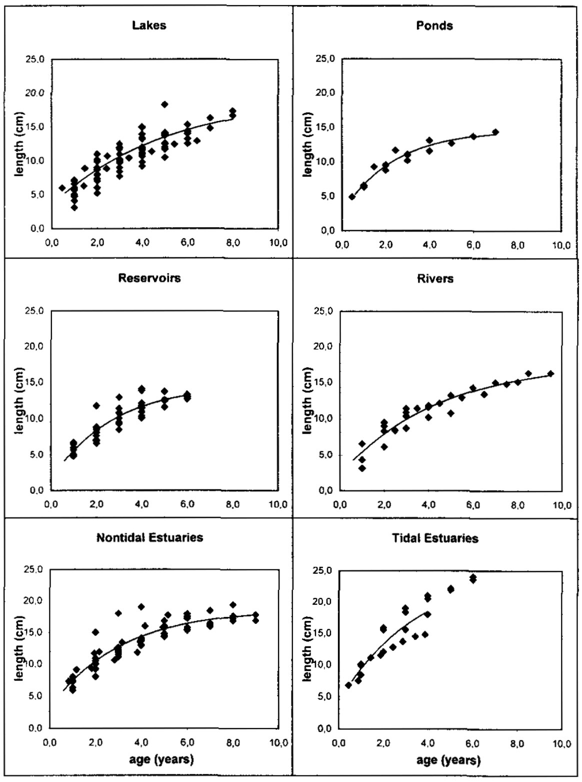

FIG. 3. Comparison of growth performance of ruffe populations in different water types using the von Bertalanffy growth curve (—). Dots represent mean lengths (cm) at age (years) in a water.

Some authors agree that, compared to fresh water, ruffe utilized the better nutritional situation in the brackish water, which ultimately induces better growth (Lind 1977, Bast *et al.* 1983). However, Bakanov *et al.* (1987) could not confirm a significant relationship between the growth rate and the benthic biomass in 20 lakes and 9 reservoirs in Russia, and presumed a stronger influence with temperature. Temperature together with the nutritional situation is an explanation given by Masatova and Zaveta (1987) for the better growth rates. The influence of salinity on the growth of ruffe remains uncertain. Neuhaus (1934) stipulates that ruffe grows better at higher salinities, within the limits of the brackish water environment. Knowles (1974) made similar observations in the Elbe Estuary, but it remains uncertain if this is a physiological reaction or a result of the better nutritional situation in brackish water.

Due to interspecific competition, poor growth has been reported for nontidal Szczecin Lagoon populations (Germany and Poland). This was explained by Neuhaus (1934) as increased competition of ruffe with benthophage bream *(Abramis brama).* Bream populations increased after the fishing techniques and fishing intensity of the region had changed. Differences in the growth performance of ruffe populations were explained by Bast *et al.* (1983) as a result of its competitive ability. In regions of low population density, ruffe seem to grow well. However, if the population density is high or if other benthophage fish are present, competition will occur (Bast *et al.* 1983). Arzbach (1997) found in Lake Plußsee (Germany) significant niche overlap of the food composition between bream and ruffe. As a result of stocking experiments with carp *(Cyprinus carpio)* in an environment with a good nutritional status (Saaler Bodden, Germany), Debus and Winkler (1990) failed to see evidence of competition between carp, bream and ruffe. In contrast to the other two species, ruffe selected chironomid pupae and the larger chironomid larvae. Stadel (1936) considers the Elbe River as an environment with tremendous nutritional resources eliminating competition with other fish species. Therefore, the nutritional status may be seen as a reason for the very good growth of the ruffe populations in the Elbe River.

Metabolism and Daily Ration

About 50% of the data from the literature were based on the bioenergetic approach to estimate the daily ration (Table 4). In Figure 4, all data were separated into five temperature classes for potential regressions. For ruffe larger than 10 g body weight the highest rations were found at 16.5°C. This could mean, that at a temperature around 17°C there is an optimum for food intake for ruffe. Only small ruffe did not feed at significantly higher rations than similar sized ruffe feeding at other temperatures between Il-20°C. More than 1% of their body weight were consumed by ruffe at 5.7°C. To allow easy estimations of daily ration by ruffe a multivariable regression model was developed, where the effects of temperature and fish weight were incorporated:

$$DR\% = a * W^{b} * e^{c*T} \qquad (7)$$

DR is the daily ration in percent of body wet weight, a is a constant, W the predator weight (g wet weight), b the weight coefficient, c the temperature coefficient (1/T), and T the temperature (°C). The DR value of equation 7 is therefore determined as:

$$DR\% = 3.139 * W^{-0.209} * e^{0.059*T} \qquad (8)$$

with 95%-confidence levels of 1.26 to 5.02 for a, -0.266 to -0.152 for b, and 0.024 to 0.094 for c For comparison, a model which describes the daily needs for standard metabolism in % body weight is also derived. Tatrai (1977) computed these needs for the standard metabolism in g wet weight at different temperatures calculated with chironomids as food items and on a metabolism-temperature relationship which was first presented by Krogh (1914). Tatrai's own experiments were done at 20°C. Tatrai's findings were recalculated with the regression model given in equation 7 as:

$$DSt\ \% = 1.114 * W^{-0.276} * e^{0.96*T} \qquad (9)$$

In Figure 5, both models are compared for a ruffe of 10 g fresh weight (eqn. 8-9). The difference between the consumption model (DR %) and the needs for the standard metabolism (DSt %) is that part of the daily food intake which will be used by the fish for excretion, growth, and activity. The temperature optimum is about 18°C.

TABLE 4. Summary of literature dealing with the daily ration of ruffe, * used for recalculation after Hölker and Temming (1996).

Author	Method	Water	N	W (g)	T (°C)
Birkan & Tichomirowa 1982	bioenerg.	Lake Ladoga	21	4.2–80.5	5.0–16.0
Thiel 1990	bioenerg.	Darß-Zingster Bodden	29	0.7–24.9	3.7–18.9
Sadoroshnaja & Spanowskaja 1981	evac.	Mozajskojc	9	3.1–32.1	8.8–19.4
Hölker & Temming 1996	evac.	Elbe River	2	4.4, 172.7	19.7
Thiel 1989	evac.*	Darß-Zingster Bodden	9	0.1–1.1	13.7–18.9
Birkan 1983	evac.*	Lake Ladoga	3	29.3–31.1	15.4–18.5
Nagy 1982	evac.*	Danube	24	8.0–16.0	4.8–23.7
Adams & Tippett 1991	evac.*	Loch Lomond	1	26.6	7.0
Bogatowa 1963	evac.*	Lake Nevel´sko	3	4.0–18.5	20.8

Since an optimum was not considered in the consumption model, the temperature coefficient, c, of 0.059 is low (eqn. 8). The exponential coefficients estimated for gastric evacuation for ruffe with a value of 0.044 has a similar dimension to the temperature coefficient from the consumption model. In comparison, the temperature coefficients for European perch and yellow perch *(Perca flavescens)* for gastric evacuation are approximately three times higher than that of ruffe (Hölker and Temming 1996). Holker and Temming (1996) suggest a crossing-over of the evacuation rate temperature curves, with ruffe evacuating food faster than perch at temperatures below 15°C and vice-versa. A similar crossing-over of activity temperature curves for ruffe and perch was observed by Bergman (1987) at 12°C using fed fish and 15°C using unfed fish. This indicates that ruffe are more active at lower temperatures than perch. Ruffe and perch showed similar prey capture rates and prey handling times in experiments at 4°C. Capture rate of perch increase approximately 6-fold with temperature, while it only doubles in ruffe. Also the prey handling time decreases with increasing temperature much faster in perch than in ruffe (Bergman 1987). Neuman (1979) investigated the relationship between catch and temperature at a cooling water outlet in the Baltic, Sweden, and categorized ruffe as being evenly distributed at medium temperature.

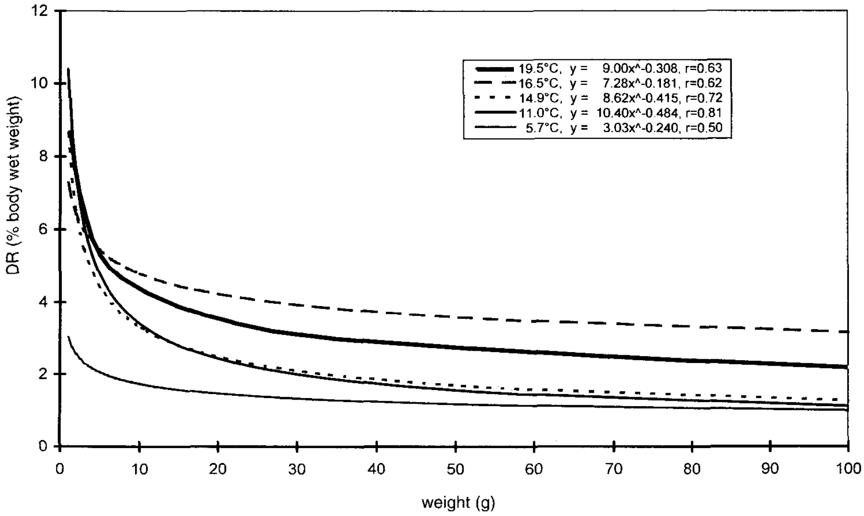

FIG. 4. Daily ration (DR%) of ruffe summarized from literature. Data were separated in five temperature classes represented by their mean values. For each temperature class potential regressions were applied.

The two approaches to estimate the daily ration are either dependent upon growth or the degree of intestine filling. It is interesting to summarize the results from the literature about the temperature dependence of these parameters in comparison with perch. In field studies in Lake Tjeukemeer, The Netherlands, Mooij *et al.* (1994) found that the growth rate in young of the year ruffe was not closely correlated with temperature, whereas growth rate in perch was positively correlated with temperature. These findings compare with the observations of van Densen and Hadderingh (1982) who also observed an increase in the growth rate of perch but not of ruffe in a Frisian lake, The Netherlands, heated by wastewater from a power station. In comparison, Edsall *et al.* (1993) found that, for young-of-the-year ruffe introduced into the Great Lakes basin, the optimum temperature for growth was about 18-22°C. Conversely, Saat and Veersalu (1996) determined the range of ideal temperatures for early development at 9-21°C with an optimum at 15°C. In Lake Muggel, Germany, Brofeldt (1922) found full stomachs in most ruffe during the winter, but only low proportions in perch. Accordingly, Meisriemler (1974) found in the Neusiedlersee, Austria, the highest values of stomach contents in September at about 15°C. During the summer there were high proportions of ruffe with empty or almost empty stomachs. Also Boron and Kuklinska (1987), who attempted to determine the degree of intestine filling with time, revealed that ruffe from Wlo-clawek Dam Reservoir grazed more intensively in autumn than in summer.

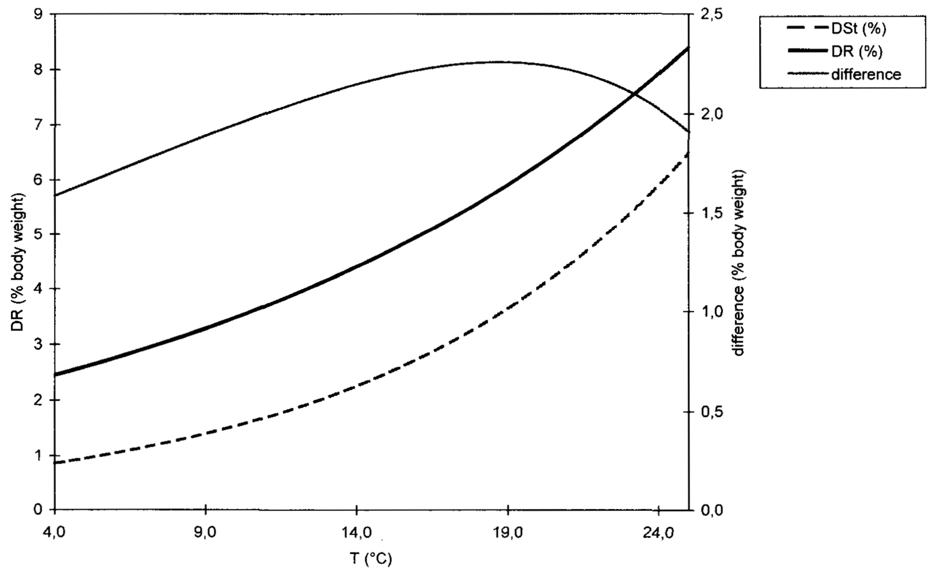

FIG. 5. Comparison of the consumption model for daily ration (DR) and the needs for the standard metabolism (DSt) in % wet weight for a ruffe of 10 g. The difference is that part of the daily food intake, which will be used by the fish for excretion, growth, and activity.

Production and Commercial Value

Today, ruffe is a minor commercial species in Europe. It is rarely used in the fishery and has no commercial value as an aquarium fish. Sometimes, this percid is used as live bait by anglers in western Europe (e.g., Maitland and East 1989). However, in some countries of Eastern Europe, e.g. Russia, ruffe is still a sought-for delicacy (Masatova and Zaveta 1987). Formerly, ruffe catches with commercial importance were taken from nontidal and tidal estuaries, e.g., in the Baltic Sea and in the lower Elbe (Table 5). This must be attributed to the high productivity of ruffe in estuaries. Thiel (1990) estimated annual production values for ruffe amounting to 3.6 kg/ha for age groups 0 to 2 in the Barther Bodden, and Thiel *et al.* (1997) calculated an annual production of ruffe of about 0.7 kg/ha for age groups 0 to 1 in the Elbe estuary.

Although incomplete data are available, it may be estimated that around the turn of the century, 350 tons of ruffe were annually caught in the lower Elbe. During that time ruffe was one of the attractive fishes for the fishermen downstream to the city of Hamburg (Diercking and Wehrmann 1991). The "Sturensuppe," a fish soup, was very popular in this area. Since the mid-1980s, ruffe have not been commercially harvested in the Elbe estuary (Moller 1989, Diercking and Wehrmann 1991). The decline of the ruffe fishery in the Elbe was due to decreased fishing intensity (Möller 1989), but the principal change has been the changing behavior of consumers. Due to its bony flesh, ruffe were no longer accepted.

Mainly gill-nets and stow nets were used in the upper Elbe estuary, whereas otter trawls were used in the outer parts of the Elbe estuary. In the eastern parts of the Baltic, ruffe were mainly caught using otter trawls. Gears mainly used in the southern Baltic were fyke nets, trap nets, and sometimes seines (Bast *et al.* 1983). According to Meyer (1927) mass catches of ruffe in gill-nets were obtained in the Curonian Lagoon during ice cover by attracting ruffe to the gear with loud noises on the ice above the gill-nets. Bast *et al.* (1983) pointed out that ruffe must be regarded as a common by-catch during the rattle fishery for pikeperch which was performed during the winter months in the coastal lagoons of the southern Baltic.

Formerly, ruffe from the southern Baltic Sea was often sold to farmers as food for domestic animals, especially pigs. The main catching areas for ruffe in the southern Baltic were the eastern shallow bays and river mouths (e.g., the Szczecin Lagoon, Vistula Bay, Curonian Lagoon, and the Gulf of Finland). The more western Bodden areas, Darβ-Zingster Bodden and Greifswalder Bodden, were less important catching areas for ruffe. Although the ruffe fishery in the southern Baltic decreased some years later than in the Elbe estuary, it seems to be of minor commercial importance at the moment.

*TABLE 5. Average annual commercial catches of ruffe in several habitat types (indicated by abbreviations in brackets). *cit. in Bast* **et al.** *1983.*

Water	Catch (tons)	Time period	Author(s)
Elbe estuary (TE)	150	1886–1890	Möller 1989
	356	1891–1895	Möller 1989
	380	1896–1900	Möller 1989
	307	1901–1905	Möller 1989
	217	1906–1910	Möller 1989
	150	1911–1915	Möller 1989
	86	1916–1919	Möller 1989
	11	1961–1965	Möller 1989
	6	1966–1970	Möller 1989
	5	1971–1975	Möller 1989
	1	1976–1980	Diercking 1984
	0	1981–1985	Diercking 1984
Gulf of Finland (NE)	1,886	1965–1974	Smirnov 1977*
Curonian Lagoon (NE)	1,540	1926–1931	Neuhaus 1934
	2,708	1930–1938	Bast *et al.* 1983
	442	1969–1977	Kozlova 1979*
Vistula Bay (NE)	150	1926–1931	Neuhaus 1934
	106	1930–1938	Bast *et al.* 1983
Szczecin Lagoon (NE)	318	1901–1910	Neuhaus 1934
	240	1911–1920	Neuhaus 1934
	60	1921–1930	Neuhaus 1934
	49	1930–1938	Bast *et al.* 1983
Szczecin Lagoon (NE) only German part	854	1971–1980	Bast *et al.* 1983
Darß-Zingster Bodden (NE)	12	1930–1938	Bast *et al.* 1983
	28	1972–1977	Bast *et al.* 1983
Greifswalder Bodden (NE)	10	1976–1985	Winkler 1989
Lake Zarnowieckie (L)	143	1960–1982	Wilkonska 1986
Pckov-Chud Lake (L)	1,277	1971–1975	Antipowa & Konzewaja 1988
	471	1976–1980	Antipowa & Konzewaja 1988
	715	1981–1985	Antipowa & Konzewaja 1988
	717	1986–1988	Antipowa & Konzewaja 1988
Lake Il´men (L)	66	1966–1969	Fedorova & Vetkasov 1974
	729	1970–1972	Fedorova & Vetkasov 1974

Generally, the commercial value of ruffe increases eastwards, and in some lakes of Poland and Russia, a ruffe fishery still exists (Antipowa and Konzewaja 1988, Fedorova and Vetkasov 1974, Wilkonska 1986). According to Bergman (1991), production of ruffe increases in lakes along a gradient of increasing eutrophication. With annual catches of more than 700 tons in the 1980s, the Pckov-Chud lake in Russia gives a higher yield than has ever reached in the Elbe estuary. According to Lelek (1987) ruffe can be highly productive in unbalanced populations of fishes, particularly in some reservoirs, gravel-pits, or larger, very slow flowing river reaches. However, no references were found regarding commercial ruffe catches for the river category.

Summary and Conclusions

In summary, high densities, fishery potential and growth performance of ruffe are observed in estuaries. These observations may be explained by the highly productive character of estuaries and by an increased availability of food items like fishes in these turbid waters. Additionally, ruffe have the advantage of being able to select moving objects under relatively dim light conditions or at high turbidity as a result of their excellent near-field sensory resolution. Therefore, ruffe are able to compete with other fish for zooplankton and even for fish as food under low light conditions. In clear and less productive waters such as many lakes, rivers and reservoirs, ruffe are major competitors for benthic macroinvertebrates. For food consumption, ruffe have a temperature optimum between 15-20°C, which probably results in better growth at this temperature range.

From these results it must be concluded that there are three main properties, comprising:

1. ruffe's relatively low water temperature optimum for food consumption compared to the sympatrically occurring European perch,

2. adaptation of foraging ability of ruffe on low light and high water turbidity conditions, and

3. competition ability for macroinvertebrates, zooplankton and fishes in those waters determining density, consumption, growth and production of ruffe in different habitat types.

However, it remains unclear how and with which intensity these properties enable ruffe to compete with other species under different environmental conditions. Therefore, further research is needed to detect the relationships between environmental conditions, biological features of ruffe and its ability to interact and compete with other species. Detailed life history studies of ruffe are needed to analyze if and how biological features of ruffe, of different life history stages change in relation to environmental factors. The key environmental factors for population dynamics of ruffe in each of its life history stages need to be determined.

It is to be expected that in the future, new knowledge of ruffe biology will enable fish biologists to control population dynamics of ruffe, especially in areas of its introduction.

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