

## DIET COMPOSITION AND FOOD CONSUMPTION LEVEL OF RUFFE, *Gymnocephalus cernuus* (L.), IN LAKE PEIPSI

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**Abstract.** Ruffe has little or no value for commercial and recreational fisheries in L. Peipsi today but it plays a very important role in the food web of this large eutrophic lake. The aim of this study was to determine the diet composition and to quantify the food consumption of ruffe in different seasons. In 1995–99 the stomach content of 387 ruffe with a standard length of 29–148 mm was investigated. The diet of ruffe is diverse (including a wide range of invertebrates, fish ova, and detritus). More than 93% of ruffe had consumed benthic animals, mainly chironomids, forming 7.3% of the total number of food items in the stomachs. The frequency of occurrence of zooplankters was 47% (72% numerically). Fish (mainly smelt) eggs were found in 10% of the ruffes' stomachs. The feeding activity of ruffe was significantly lower in winter than in summer. Mean consumption level as the food weight percentage of ruffe's mean body wet weight was  $0.95 \pm 0.05\%$ , with a maximum of 6.8%. As ruffe grew, the weight of consumed food relative to their body weight decreased, although absolute consumed weight increased.

**Key words:** ruffe, diet composition, consumption level, Lake Peipsi.

### INTRODUCTION

Ruffe is a small, bottom-dwelling largely benthivorous percid fish that is found throughout most of central and northern Europe (Winfield et al., 1998). Its distribution has recently expanded through accidental introductions into L. Superior of North America (Simon & Vondruska, 1991) and into many European lakes not inhabited previously by ruffe (Adams & Tippett, 1991; Kålås, 1995; Rösch & Schmid, 1996). Because of its small size and low

economic value, ruffe received little attention in the past. In contrast to the other percids, ruffe has been relatively neglected by fish biologists, and literature data on it are scanty (Winfield & McCulloch, 1995). With the establishment of new ruffe populations and the concomitant threat to native ecosystems, the biology and ecology of ruffe have recently attracted more interest. Interaction and competition between ruffe and other fish species need to be investigated more thoroughly (Rösch et al., 1996).

Studies on the biology of ruffe have revealed that this fish is a "generalist" regarding food and ecological preferences (Bergman, 1991; Adams, 1994). In many lakes ruffe are found everywhere from shallow to the deepest zones (Winfield et al., 1996; Popova et al., 1997). Along the gradient of increasing productivity in lakes, the abundance of ruffe continues to increase (Bergman & Greenberg, 1994). Ruffe feed on a wide assortment of prey under a variety of conditions. Though they are usually benthivorous (Collette et al., 1977; Bergman, 1991; Ogle et al., 1995; Kangur & Kangur, 1996), a predominance of cladoceran zooplankton has also been recorded in the diet (Bergman & Greenberg, 1994; Kålås, 1995). Larval ruffe feed mainly on zooplankton, but even adult fish can ascend from the bottom and consume large cladocerans and copepods (Popova et al., 1997). Ruffe, unlike perch, does not undergo dramatic ontogenetic diet shifts (Bergman & Greenberg, 1994). In eutrophic Lake Aydat (France), ruffe of all age classes consumed insect larvae and pupae (Jamet & Lair, 1991).

Although ruffe is a natural member of the fish fauna in Estonia, being found in at least 41% of the Estonian lakes (Pihu, 1993), relatively little information is available about it. In the largest and, from the viewpoint of fishery, the most important inland waterbody of Estonia, L. Peipsi, ruffe is one of the most numerous benthophagous fishes (Kangur et al., 1998) and has spread quite uniformly throughout the whole lake (Efimova, 1966). Although it has little or no value for commercial and recreational fisheries in L. Peipsi, this species plays a very important role in the food web of the lake.

The aim of this study was to determine the diet composition and to quantify the food consumption of the ruffe of different sexes in different seasons in L. Peipsi. The frequency of occurrence and mean number of food items per individual were used for the description of the diet. Ruffe's possible competition for food with bream and perch is discussed.

## STUDY AREA

Lake Peipsi is located on the border of Estonia and Russia (Fig. 1). With respect to its surface area (3555 km<sup>2</sup>), L. Peipsi in the broad sense is the fourth largest lake in Europe (Jaani, 1996). Lake Peipsi consists of three parts: largest and deepest northern L. Peipsi s.s. (2611 km<sup>2</sup>, mean depth 8.3 m, maximum depth 12.9 m),



southern L. Pihkva (708 km<sup>2</sup>, 3.8 m, 5.3 m), and narrow strait-like L. Lämmijärv (236 km<sup>2</sup>, 2.6 m, 15.3 m) connecting them. Lake Peipsi s.s. is an unstratified eutrophic lake with mesotrophic features, L. Lämmijärv has some dyseutrophic features, while L. Pihkva is strongly eutrophic (Nõges et al., 1996). The whole lake is holomictic–dimictic, revealing unstable summer stratification, but is well aerated by waves and currents down to the bottom. The period of ice cover lasts about five months (December–April). Sand and aleurite prevail in shallow coastal regions, while the bottom of the deep central part is mostly covered with mud. This lake is the most zoobenthos-rich waterbody among North European large lakes (Timm et al., 1996).

Lake Peipsi may be classified as a smelt–bream lake; however, due to eutrophication during recent decades and owing to rearrangement of the fishing strategy, it has developed features of a pikeperch lake (Pihu, 1996; Kangur & Kangur, 1998). According to official data the total catch of fish in the Estonian part of L. Peipsi made up 1680–3610 tonnes per year in 1991–98. Commercial fishes accounting for the highest catches were smelt, *Osmerus eperlanus* (L.); perch, *Perca fluviatilis* L.; pikeperch, *Stizostedion lucioperca* (L.); and bream, *Abramis brama* (L.). The catch of ruffe is recorded together with other small fishes. According to Pihu (1996), ruffe's annual catch in the lake since the 1930s has been in most cases 800–1500 t, with a maximum catch of about 2500 t in 1972. Because of its small size, ruffe has practically no commercial or recreational importance today.

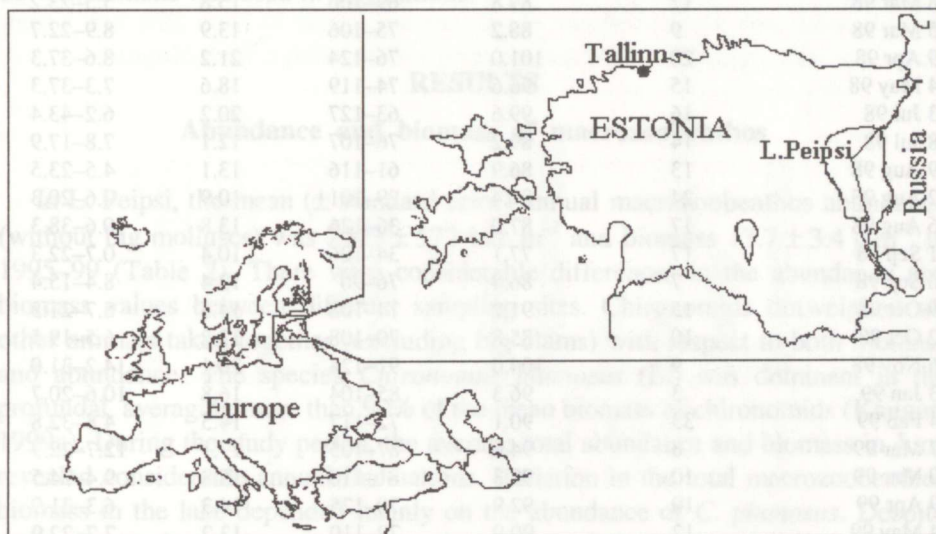


Fig. 1. Location of Lake Peipsi.

## MATERIAL AND METHODS

A total of 387 ruffe (including 227 females, 144 males, and 16 small unidentified specimens) with a standard length (SL) of 29–148 mm were studied from September 1995 to May 1999 (Table 1). The ruffe were sampled once or twice a month during the ice-free period with a bottom seine (mesh size 18–22 mm in the cod-end) or an experimental bottom trawl (mesh size of 12–14 mm). Trawling was carried out in the morning hours. In winter, ruffe were caught by hooks baited with chironomid larvae or earthworms. Sampled fish were weighed (total wet weight, Tw) with an accuracy of 0.1 g; standard length and total length were measured with an accuracy of 1 mm. Thereafter the fish were dissected and

**Table 1.** Date of sampling and measurements of the studied ruffe from L. Peipsi

| Date      | Number of fish | SL, mm |         | Tw, g |           |
|-----------|----------------|--------|---------|-------|-----------|
|           |                | Mean   | Range   | Mean  | Range     |
| 28 Sep 95 | 4              | 87.5   | 80–96   | 10.5  | 9–12      |
| 25 Feb 96 | 6              | 84.2   | 78–90   | 9.8   | 7–11      |
| 8 Aug 96  | 5              | 80.0   | 76–82   | –     | –         |
| 31 May 97 | 27             | 76.7   | 60–112  | 9.4   | 4–28.7    |
| 20 Jun 97 | 12             | 86.4   | 71–103  | 11.4  | 6.2–20.1  |
| 26 Sep 97 | 20             | 84.5   | 51–112  | 11.7  | 2.1–26.5  |
| 6 Jan 98  | 7              | 134.0  | 115–148 | 50.7  | 34.5–66.9 |
| 9 Feb 98  | 13             | 92.1   | 78–111  | 14.9  | 10–25.3   |
| 22 Feb 98 | 9              | 87.2   | 72–97   | 13.0  | 9.4–18.3  |
| 8 Mar 98  | 12             | 89.8   | 69–106  | 15.8  | 5.5–23.2  |
| 25 Mar 98 | 9              | 88.2   | 75–106  | 13.9  | 8.9–22.7  |
| 29 Apr 98 | 20             | 101.0  | 76–124  | 21.2  | 8.6–37.3  |
| 14 May 98 | 15             | 96.6   | 74–119  | 18.6  | 7.3–37.3  |
| 23 Jul 98 | 16             | 99.6   | 63–127  | 20.2  | 6.2–43.4  |
| 28 Jul 98 | 14             | 89.2   | 76–107  | 12.1  | 7.8–17.9  |
| 9 Aug 98  | 13             | 86.9   | 61–116  | 13.1  | 4.5–23.5  |
| 12 Aug 98 | 24             | 81.4   | 29–101  | 10.9  | 0.6–20.3  |
| 26 Aug 98 | 17             | 87.0   | 36–126  | 13.8  | 0.6–38.3  |
| 11 Sep 98 | 17             | 77.1   | 34–106  | 10.4  | 0.7–22.3  |
| 20 Sep 98 | 7              | 86.4   | 76–96   | 12.4  | 8.4–15.4  |
| 9 Oct 98  | 15             | 91.2   | 74–108  | 14.5  | 8.7–21.3  |
| 22 Oct 98 | 10             | 85.8   | 70–108  | 12.2  | 6.5–19.5  |
| 26 Nov 98 | 9              | 104.0  | 91–124  | 20.1  | 14.2–31.0 |
| 13 Jan 99 | 3              | 96.3   | 85–104  | 16.8  | 10.6–20.7 |
| 14 Feb 99 | 33             | 90.1   | 72–117  | 14.5  | 4.8–32.8  |
| 7 Mar 99  | 8              | 94.6   | 87–105  | 17.1  | 12.7–22.9 |
| 10 Mar 99 | 10             | 92.3   | 81–110  | 15.8  | 9.4–24.5  |
| 29 Apr 99 | 10             | 92.9   | 70–125  | 14.3  | 6.3–31.9  |
| 14 May 99 | 12             | 90.9   | 79–110  | 13.2  | 7.7–22.9  |
| 27 May 99 | 10             | 89.4   | 76–101  | 11.5  | 7.5–15.4  |
| Total     | 387            | 89.5   | 29–148  | 14.7  | 0.6–66.9  |



their stomachs were removed. Entire stomach content was weighed on a torsion balance with an accuracy of 1 mg and analysed immediately or preserved frozen ( $-18^{\circ}\text{C}$ ). The weight of stomach content was expressed as fresh weight (mg) per one fish. Prey items or their remains were counted and identified under the microscope. Larval instars of chironomids were identified by head capsule width (Kangur & Kangur, 1978). The frequency of occurrence (FO) of prey, i.e. the percentage of all studied fish in which a certain prey species occurred, and diet composition by prey numbers were calculated. The consumption level was determined as prey wet weight per one gram of fish wet weight in percentages.

For comparing the mean food consumption per individual ruffe with the same body length but of different sex in different seasons *T*-test with unequal variances was employed. The Pearson correlation analysis was used to measure the relationship between the weight of the consumed food and the standard length of ruffe.

The macrozoobenthos of L. Peipsi has been annually studied since 1964 in early June. In this paper data from 1995–99 were used. To estimate macrozoobenthos abundance and biomass the Estonian part of L. Peipsi was monitored at 11–13 sites (3 hauls per sample). All samples were taken by a Boruckij or Zablockij type grab sampler with a  $225\text{ cm}^2$  grasp area. The samples were washed on a gauze sieve with 0.3 mm mesh size, the animals were sorted by the eye, and fixed in 70% alcohol separately as Chironomidae, Oligochaeta, Mollusca, and other small animals (others). Large molluscs (Unionidae, *Dreissena*, and *Viviparus*) were fixed separately and were not included in the total numbers of macrozoobenthos abundance and biomass. The ethanol-fixed wet weight of bottom animals was used in calculations.

## RESULTS

### Abundance and biomass of macrozoobenthos

In L. Peipsi, the mean ( $\pm$  standard error) annual macrozoobenthos abundance (without big molluscs) was  $2703 \pm 572\text{ ind. m}^{-2}$  and biomass  $13.7 \pm 3.4\text{ g m}^{-2}$  in 1995–99 (Table 2). There were considerable differences in the abundance and biomass values between different sampling sites. Chironomids outweighed all other animals taken together (excluding big clams) with respect to both biomass and abundance. The species *Chironomus plumosus* (L.) was dominant in the profundal, averaging more than 90% of the mean biomass of chironomids (Kangur, 1999a). During the study period, the average total abundance and biomass in June revealed considerable annual fluctuations. Variation in the total macrozoobenthos biomass in the lake depended mainly on the abundance of *C. plumosus*. Despite these fluctuations, the community demonstrated notable stability in overall abundance over years: low abundance in some years was followed by a fast recovery to the previous level.

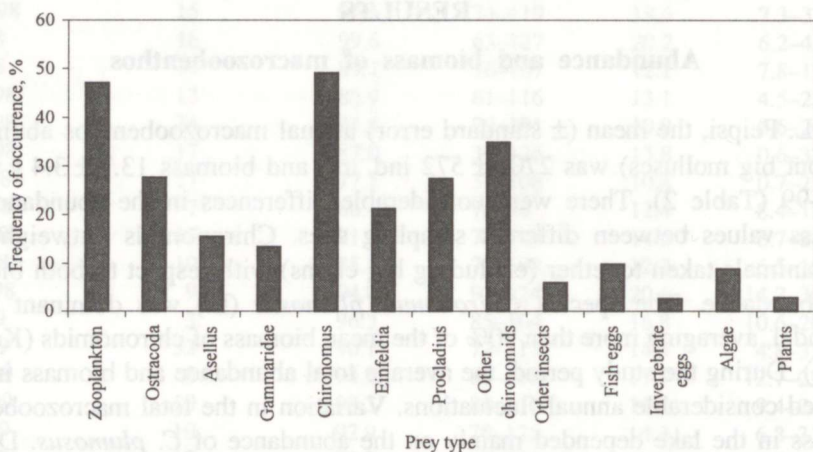
**Table 2.** Yearly mean ( $\pm$  SE) abundance and biomass of macrozoobenthos in L. Peipsi in June 1995–99

| Species or group               | Abundance            |       | Biomass           |       |
|--------------------------------|----------------------|-------|-------------------|-------|
|                                | ind. m <sup>-2</sup> | %     | g m <sup>-2</sup> | %     |
| Chironomidae                   | 1453 $\pm$ 373       | 53.8  | 8.08 $\pm$ 2.31   | 59.1  |
| Oligochaeta                    | 882 $\pm$ 187        | 32.6  | 1.99 $\pm$ 0.33   | 14.5  |
| Mollusca                       | 143 $\pm$ 57         | 5.3   | 2.04 $\pm$ 0.49   | 14.9  |
| Others                         | 225 $\pm$ 27         | 8.3   | 1.57 $\pm$ 0.40   | 11.5  |
| Total (without large molluscs) | 2703 $\pm$ 572       | 100.0 | 13.67 $\pm$ 3.38  | 100.0 |
| Large molluscs                 | 239 $\pm$ 75         |       | 229 $\pm$ 59      |       |

### The composition of the diet of ruffe

Only about 1% of the examined ruffes' stomachs did not contain any food. Ruffe in L. Peipsi fed both on benthos and plankton, and their prey spectrum was broad (Fig. 2). More than 70 different prey types (among them 27 chironomid taxa) were determined in the stomach content of ruffe from L. Peipsi.

The diet of ruffe of SL > 29 mm contained mainly Chironomidae larvae and pupae, Ostracoda, Amphipoda (Gammaridae), Isopoda (*Asellus aquaticus* L.), Pisidiidae, Oligochaeta, Nematoda, Mermithidae, Trichoptera, Ceratopogonidae, invertebrate and fish eggs, and zooplankters (Cladocera and Copepoda). More than 93% of all the examined ruffes had consumed benthic animals, while the frequency of occurrence of fish eggs (mainly smelt) was about 10%. About 47%



**Fig. 2.** Frequency of occurrence of main food items in the stomachs of ruffe in L. Peipsi in 1995–99.



of the ruffe had fed on zooplankters. Analysis of the diet composition of ruffe indicated that zooplankters were numerically the most important prey type and accounted for 72% of the prey items (Fig. 3). Detritus and grains of sand were also often (FO > 40%) found in ruffes' stomachs. Fragments of macrophytes and algae occurred in a few stomachs (FO > 9%).

Chironomid larvae and pupae were the most commonly taken prey, found in 78.6% of the ruffes' stomachs and forming 7.3% of the total number of food items. Of a wide range of chironomid species, *Chironomus plumosus*, *Procladius* spp., and *Einfeldia carbonaria* (Meigen) were predated most frequently (Fig. 2) and abundantly (Fig. 3). Chironomidae were consumed by the ruffe of all examined length groups (SI 29–148 mm). The frequency of occurrence (38.6%) as well as the mean number ( $1.78 \pm 0.25$  specimens) of the fourth-instar larvae of *C. plumosus* per stomach of ruffe were the highest. The maximum number of engulfed fourth-instar larvae of *C. plumosus* per stomach of ruffe (SI 112 mm) was 40. Pupae of this species were heavily predated during the emergence period (from May till September).

Among other insects besides chironomids, larvae of caddis flies (Trichoptera) were consumed most frequently. Of bottom crustaceans, Ostracoda (FO 28%), *Asellus aquaticus* (16%), and Gammaridae (13%) were most heavily predated by ruffe. Small clams, mainly *Pisidium* spp., were also consumed frequently. The frequency of occurrence of this prey type constituted 28%.

Fish eggs were found in 10% of the ruffes' stomachs (11% by number). Fish eggs were most intensively predated in spring. During the short spawning and incubation periods (in April–May) of smelt, ruffe consumed large numbers of its eggs. Some stomachs of ruffe collected on 29 April 1998 and 14 May 1999 were filled with eggs of smelt. The maximum number of this prey item per one stomach, engulfed by a ruffe of SI 116 mm, was 998. In spring ruffe consumed

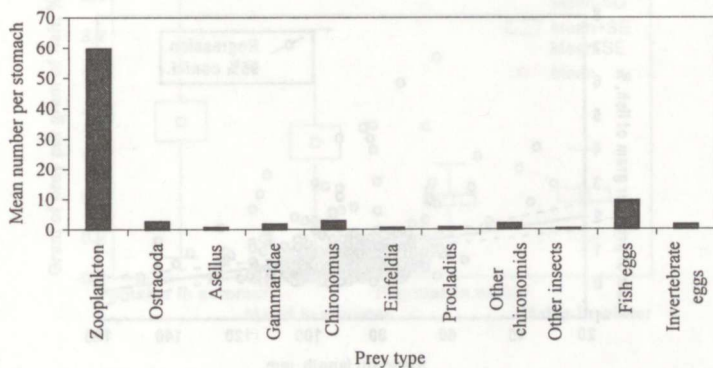


Fig. 3. The mean number of main food items in the stomachs of ruffe in L. Peipsi in 1995–99.

also quite a large number of invertebrate eggs. In late autumn and in winter, ruffe was found to predate on a few whitefish (*Coregonus lavaretus* (L.)) and vendace (*Coregonus albula* (L.)) eggs.

### Food consumption level

The mean weight of the stomach content of all studied ruffe in L. Peipsi constituted  $122.6 \pm 6.9$  mg per stomach. Considering the mean weight of ruffe ( $14.7 \pm 0.5$  g, Table 1), it can be stated that the amount of food taken at one time by ruffe formed on an average at least  $0.95 \pm 0.05\%$  of its body weight. However, consumption estimates may be higher. Maximum food consumption level amounted to 6.8% of the ruffe's body weight.

Smaller ruffe fed more intensively than larger individuals. Consumption levels for bigger ruffe were lower (Fig. 4), although the absolute weight of the consumed food increased with the size of ruffe. Positive correlation between the weight of the stomach content and the ruffe's total body weight was significant ( $r = 0.41$ ;  $n = 371$ ;  $p < 0.01$ ); whereas correlation between consumption level (g prey wet weight per g fish wet weight, %) and the standard length of ruffe was negative but also significant ( $r = -0.28$ ;  $n = 371$ ;  $p < 0.01$ ).

There were some indications that female ruffe fed in summer more intensively than male ruffe (Table 3). We compared the consumption levels of ruffe with an equal body length (SI 70–99 mm) but of different sex. The amount of food eaten at one time by female ruffe made up approximately  $0.89 \pm 0.12\%$  of their body weight, while the respective figure for males was  $0.85 \pm 0.10\%$ . However, differences between the sexes in food intake were not significant at  $p < 0.05$ .

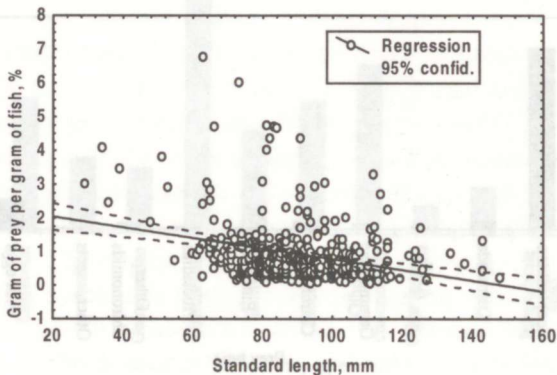


Fig. 4. Consumption level of ruffe of different length groups in L. Peipsi in 1995–99.

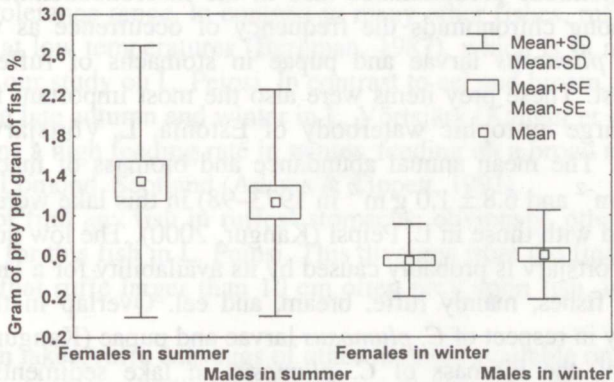


**Table 3.** Seasonal variation in the feeding intensity of ruffe (SI 70–99 mm) in L. Peipsi in 1995–99

|                   | Mean ( $\pm$ SE) parameters of ruffe |                | Total weight of food, mg |
|-------------------|--------------------------------------|----------------|--------------------------|
|                   | SI, mm                               | Tw, g          |                          |
| Summer            |                                      |                |                          |
| Females, $n = 42$ | $88.3 \pm 1.2$                       | $12.4 \pm 0.4$ | $161.1 \pm 24.3$         |
| Males, $n = 40$   | $82.3 \pm 1.2$                       | $10.3 \pm 0.4$ | $110.6 \pm 15.4$         |
| Winter            |                                      |                |                          |
| Females, $n = 35$ | $87.3 \pm 1.2$                       | $12.9 \pm 0.6$ | $67.8 \pm 7.4$           |
| Males, $n = 37$   | $86.2 \pm 1.1$                       | $12.6 \pm 0.5$ | $72.1 \pm 6.9$           |

### Seasonal variations

Ruffe continued to take food in late autumn and winter when the water temperature in L. Peipsi fell below 4°C; however, the consumption level was lower compared with that in summertime. We compared the consumption level of ruffe of SI 70–99 mm in late summer (July–September) and in winter (January–March). In this size group of ruffe the mean weight of food per stomach ( $138.6 \pm 12.0$  mg in summer and  $93.1 \pm 9.8$  mg in winter) as well as the consumption level ( $1.20 \pm 0.14$  in summer and  $0.52 \pm 0.04$  in winter) were significantly higher in summer than in winter ( $T$ -test with unequal variances,  $p = 0.001$ ). The consumption level was lower in winter in case of both sexes (Fig. 5).



**Fig. 5.** Consumption level of ruffe (SI 70–99 mm) of different sexes in summer and winter in L. Peipsi in 1995–99.

## DISCUSSION

The fry of ruffe feed on zooplankton; in autumn it begins to take also zoobenthos (Kangur, 1968; Ogle et al., 1995). According to Newman et al. (1997), one summer old ruffe eat primarily benthic microcrustaceans in early summer, but complement their ration with more macrobenthos later in the same season. In L. Peipsi, the ruffe of different size groups (SI 29–148 mm) were mostly benthophagous. We did not observe significant diet shifts with the growth of ruffe. Chironomid larvae and pupae were the most frequently taken prey by ruffe in L. Peipsi. In the Bautzen Reservoir (Germany) chironomids already dominated in the diet of ruffe of about 25 mm length (Werner et al., 1996). The chironomid-dominated diet of this fish has been found in many other lakes as well (Antipova, 1981; Jamet, 1994; Ogle et al., 1995; Kangur & Kangur, 1996).

Zooplankters dominated in the diet of ruffe in L. Peipsi numerically. The mean zooplankter weight was only 0.004 mg in L. Peipsi in 1992–95 (Haberman, 1996); whereas the mean weight of chironomid larvae made up 5.6 mg (Biomass/Abundance in Table 2). Considering that the zooplankters are very small compared with chironomids, the importance of this prey type as food for adult ruffe is modest in L. Peipsi.

According Newman et al. (1997), ruffe are selective feeders, consuming greater proportions of some taxa relative to their abundance in the benthos. Selectivity was different at different sites; however, the typically high occurrence of chironomids in the diet does not generally appear to be due to strong positive selection for chironomids. Richards et al. (1997) found in an experimental investigation that ruffe reduced significantly ( $p < 0.05$ ) the abundance of Chironomidae and Ceratopogonidae, but did not affect zooplankton populations.

The observed chironomid-dominated diet of ruffe in L. Peipsi is not surprising, because Chironomidae predominated also in the macrozoobenthos of the lake (Table 2). Among chironomids the frequency of occurrence as well as mean number of *C. plumosus* larvae and pupae in stomachs of ruffe in L. Peipsi were the highest. These prey items were also the most important food for ruffe in the other large eutrophic waterbody of Estonia, L. Võrtsjärv (Kangur & Kangur, 1996). The mean annual abundance and biomass of macrozoobenthos ( $844 \pm 63$  ind.  $m^{-2}$  and  $6.8 \pm 1.0$  g  $m^{-2}$  in 1973–98) in this lake were significantly lower compared with those in L. Peipsi (Kangur, 2000). The low quantity of zoobenthos in L. Võrtsjärv is probably caused by its availability for a large number of benthophagous fishes, mainly ruffe, bream, and eel. Overlap in their diet was revealed largely in respect of *C. plumosus* larvae and pupae (Kangur et al., 1999). In L. Võrtsjärv, the biomass of *C. plumosus* in lake sediments was highly correlated with their rate of predation by ruffe in different years. Like in large Estonian lakes Võrtsjärv and Peipsi, *C. plumosus* serves as essential food for many fishes in several European eutrophic lakes: in L. Balaton (Tatrai, 1980), L. Ladoga (Shchashchae, 1985), and L. Tjeukemeer (De Nie, 1987).



According to Fullerton et al. (1997), in laboratory experiments ruffe consumed preferentially individuals of soft-bodied taxa, such as mayflies, chironomids, and oligochaetes, and avoided taxa provided with morphological protection, such as cased caddis flies, snails, and bivalves. This finding contrasts with our data: in L. Peipsi both small clams (mainly *Pisidium* spp.) and cased caddis flies were found in the stomachs of ruffe.

In some lakes ruffe may have an adverse impact on commercial fishery through competitive interactions with perch (Winfield et al., 1998). Ruffe may compete with perch by foraging more effectively on benthos (Henson & Newman, 1997). Trophic interactions of ruffe with other benthophagous fishes in the lake have not yet been studied in detail. The high level of macrozoobenthos biomass in L. Peipsi (Kangur, 1999) indicates that the rich macrozoobenthos resources of this lake are underconsumed, and competition between benthophagous fishes is probably not strong.

A study on L. Võrtsjärv showed that the diet composition of ruffe is more diverse than that of eel and bream (Kangur et al., 1999). Ruffe can compensate for the disappearance of one food object by consuming another, abundant, item. Obviously, ruffe's omnivorous mode of feeding offers it an advantage over the other benthophagous fishes. The results of this study indicate that ruffe can feed on both plankton and benthos in L. Peipsi. Although benthic organisms dominated in the diet by occurrence, zooplankton were also found in the stomachs of ruffe of all length groups. This is in accordance with the findings of Popova et al. (1997) that even adult ruffe can ascend from the bottom and consume large cladocerans and copepods. Kålås (1995) found an introduced population of ruffe in Norway to feed largely on cladocerans rather than on benthic macroinvertebrates, which is more typical of the species.

One of the advantages of ruffe seems to be also its relatively broad temperature tolerance range. In contrast to many other fishes, ruffe can maintain high activity at low temperatures (Bergman, 1987), which is in accordance with the results of our study on L. Peipsi. In contrast to eel and bream, ruffe continued to take food in late autumn and winter in L. Võrtsjärv (Kangur et al., 1999). Also, ruffe maintains a high feeding rate in winter, feeding on a broad range of benthic prey in Loch Lomond, Scotland (Adams & Tippet, 1991).

We did not find any fish in ruffes' stomachs; obviously, other kinds of food are sufficient for this fish in L. Peipsi. This diverges from the findings of Popova et al. (1997) that ruffe larger than 10 cm often prey upon fish, including young conspecifics.

In Estonian lakes, ruffe eats eggs of other fishes if available on their spawning grounds (Pihu & Pihu, 1974). Introduced populations of ruffe in Loch Lomond in Scotland (Adams & Tippet, 1991) and Lake Constance in the European mainland (Rösch & Schmid, 1996) have both been found to consume a large number of whitefish's eggs. Winfield et al. (1996) concluded that egg predation by ruffe can have a significant negative impact on the abundance of adult

*Coregonus* spp. According to the present study, ruffe in L. Peipsi consumed smelt's eggs most intensively during a short period in spring.

In L. Peipsi, the amount of food consumed at one time by ruffe was equal to approximately  $0.95 \pm 0.05\%$  of their body mass (g prey wet weight per g fish wet weight); the maximum consumption level was estimated at 6.8%. Similarly, ruffe's daily rations in L. Superior (North America) ranged from 2 to 7% of wet body weight in July and August (Newman et al., 1997).

Detailed studies on the feeding of benthophagous fishes in L. Võrtsjärv (Kangur et al., 1999) and the present data on the feeding of ruffe in L. Peipsi suggest that the diet of ruffe in L. Peipsi seems to be more diverse. In L. Võrtsjärv, benthophagous fishes (ruffe, bream, and eel) tend to be monophagous, preferring *C. plumosus* as the prey. This is not surprising because in the benthic community of L. Võrtsjärv, *C. plumosus* forms, as a long-term average, 73% of the total biomass of macrozoobenthos (Kangur et al., 1998). Although Chironomidae accounted for a large part of macrozoobenthos in both lakes, the proportion of their biomass compared with that of the other bottom animals was significantly lower in L. Peipsi, and the proportion of chironomids in ruffe stomachs was also lower.

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