The ecology of ruffe, *Gymnocephalus cernuus* (Pisces: Percidae) introduced to Mildevatn, western Norway

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Synopsis

Diet, habitat use, diel and seasonal activity and a number of population parameters were studied on ruffe, *Gymnocephalus cernuus*, introduced to Mildevatn, western Norway. This lake is sited outside the natural range of the ruffe and has a lower fish diversity and a different fish species composition than within its native range. From June through September the ruffe was planktivorous and mainly caught at 4 to 6 m depth in the benthic zone. At other times of year ruffe was feeding on zoobenthos and caught deeper in the benthic zone. Ruffe was mainly day active. Zooplankton feeding during summer is the clearest difference compared to ruffe populations living within its natural range. Presence of large zooplankton organisms available for ruffe is suggested as the main reason for the difference found in food choice. The availability of large zooplankton is probably due to community structure caused by a predator and lack of interspecific competition for zooplankton in the deeper parts of the lake. Piscivorous brown trout, *Salmo trutta*, restrict the habitat of threespined stickleback, *Gasterosteus aculeatus*, to the zone of littoral vegetation, allowing high densities of larger zooplankton species like *Bythotrephes longimanus* to be present in the lake. Brown trout is present only in the upper light and well oxygenated parts of the lake, leaving a refuge for the ruffe, where they can feed on the rich zooplankton community.

Introduction

When introduced to a new and different community, species may change their niche utilization and life history traits (Mittelbach & Chesson 1987, Hindar et al. 1988, Reznick et al. 1990), due to both biotic and abiotic factors (Connell 1975). Competition and predation are shown to be of particular importance (Paine 1966, Diamond 1978, Connell 1983, Schoener 1983, Mittelbach & Chesson 1987, Reznick et al. 1990). The changes in niche utilization and life history traits may occur either immediately after introduction through phenotypic plasticity, or through generations as a consequence of changed selective pressure (MacArthur & Wilson 1967). Genetic changes may also be due to genetic drift if the number of introduced individuals, effectively founding the new population, is small (Mayr 1970).

Many fish are phenotypically plastic (Mittelbach & Chesson 1987), which makes them suited for study of changes in environmental conditions affecting niche utilization and life history traits. Such studies may advantageously be carried out in freshwater lakes where introductions normally happen just once and influx of genes from alien populations of original or introduced species is low or non-existent.

This study describes diet, diel and seasonal activity, habitat use and a number of population parameters of the ruffe, *Gymnocephalus cernuus,* introduced to Mildevatn (lake), Western Norway, a region outside the natural range of the ruffe. This region has a freshwater fish fauna which differs compared to the natural range of the ruffe. A comparative approach is used to investigate possible differences in life history traits, and to evaluate whether the ruffe has modified its niche (time, habitat and diet) in such an ecosystem with a potential reduction in interspecific competition and a potentially changed predation risk. Here I include literature data from a number of ruffe populations from within its natural range. Since no earlier investigation of Mildevatn has been carried out selected data on activity, habitat use and diet of potential competitors and predators, zooplankton abundance and physical and chemical parameters from Mildevatn are also investigated and included in the study site section of this work. These data were necessary to evaluate changes in niche utilization of the ruffe.

The natural distribution of ruffe is restricted to lowland lakes in Central and Eastern Europe including northern France and England, Eastern Scandinavia, rivers entering the Baltic Sea and the White Sea and all Siberia including the Kolyma but excluding the Amur (Collette & Bănărescu 1977). When living within this area the ruffe is generally described as a bottom dwelling, benthivorous species (Johnsen 1965, Collette et al. 1977, Disler & Smirnov 1977, Boroń & Kuklińska 1987). It seems suited to such a life due to a well developed lateral line system, more like that found in many deep sea fishes, which may be used to detect and locate prey in a dark world (Gray & Best 1989).

The ruffe also occur in some lakes far outside its natural range (Maitland & East 1989, Pratt et al. 1992). One example is the lake Mildevatn. Due to geographical causes only freshwater fish able to migrate through seawater occur naturally in the western part of Norway (Huitfeldt-Kaas 1918), where this lake is situated. In this region lakes therefore have a different fish community and fewer fish species than within the natural range of the ruffe. Life history traits may thereby be changed due to altered trade-offs between food intake and factors such as

competition and predation (Mittelbach & Chesson 1987, Reznick et al. 1990). These changes may lead to modifications in both the realized and/or fundamental niche of the introduced species (van Valen 1965). Niche utilization and life history traits of ruffe in Mildevatn could therefore be expected to differ compared to natural populations.

The ruffe is most likely introduced to Lake Mildevatn by man, because its natural distribution in Norway is restricted to the southeastern part of the country (Eggan & Johnsen 1983). The nearest natural population of ruffe is more than 270 km away. However, time and origin of the introduction to Mildevatn is unknown.

Methods

The fish sampling was carried out fourteen times from July 1990 to August 1991 (Table 1). No fish sampling was performed in November 1990 and January and February 1991 due to ice cover. Fish were collected in benthic and pelagic multimesh gillnets of monofilament, with seven mesh sizes (10, 12.5, 16, 19.5, 24, 29 and 35 mm). Benthic nets were 1.5 m deep, had 2.5 m panels and a total length of 17.5 m. Four nets were put together and made up a 70 m long gang, covering the bottom from a depth of 0 to 11 m (Fig. 1). The four nets fished the depths 0–4 m, 4–6 m, 6–9 m and 9–11 m, respectively. The pelagic nets were 6 m deep, had 5 m panels and a total length of 35 m. Two pelagic nets were put out on regular stations, one covered the depth 0 to 6 m, the other the depth 6 to 12 m (Fig. 1). The depth where the pelagic nets were set was 11 to 12.5 m. On each sampling day pelagic and benthic nets were set for three hours around mid day and three hours around mid night. Each fish was individually numbered, and net, mesh size, depth (to nearest meter) for the pelagic nets and time of catch was noted. Where the benthic standard gillnets were set, the shoreline had no vegetation. They gave therefore no good indications of the activity of fish inside the water-lily zone. To monitor this activity some smaller benthic nets were used on all sampling days from 25 April 1991 to 5 August 1991. The small nets were 9 m long, 1.5 m deep and consisted of 9 panels of equal length but

Table 1. Total catch of ruffe from different depths (m) in pelagic and benthic nets at daytime and nighttime during the year.

	Day							Night							Total
	Benthic				Pelagic		Total	Benthic				Pelagic		Total	
	0–4	4–6	6–9	9–11	0–6	6–12		0–4	4–6	6–9	9–11	0–6	6–12		
17 Jul 1990	0	39	0	0	1	3	43	0	2	0	1	0	0	3	46
5 Aug 1990	1	15	0	0	1	0	17	1	1	0	0	0	0	2	19
23 Aug 1990	0	17	0	0	5	0	22	0	0	0	0	0	0	0	22
13 Sep 1990	0	27	0	0	2	0	29	1	1	0	0	0	0	2	31
3 Oct 1990	2	0	11	0	0	0	13	2	0	0	0	0	0	2	15
23 Oct 1990	0	3	16	1	0	0	20	1	0	1	0	0	1	3	23
28 Dec 1990	0	3	3	0	0	0	6	0	1	1	0	0	0	2	8
27 Mar 1991	1	2	10	3	0	4	20	0	3	0	0	0	0	3	23
25 Apr 1991	0	11	14	6	0	13	44	1	0	2	0	0	4	7	51
8 May 1991	0	7	10	26	0	0	43	1	0	1	1	0	0	3	46
27 May 1991	0	2	2	3	0	0	7	2	3	3	1	0	1	10	17
17 Jun 1991	0	2	0	6	0	14	22	3	6	2	1	0	0	12	34
4 Jul 1991	0	10	0	1	2	0	13	2	1	1	0	0	0	4	17
5 Aug 1991	2	16	3	0	1	0	22	1	2	0	0	0	0	3	25
Total:	6	154	69	46	12	34	321	15	20	11	4	0	6	56	377

with different mesh sizes (8, 10, 12.5, 16, 19.5, 24, 29, 35, 43 mm). Two of these nets were set inside the dense vegetated part of the water-lily zone, one parallel and one at a right angel to the shore, and were set for 12 hours from mid day to mid night.
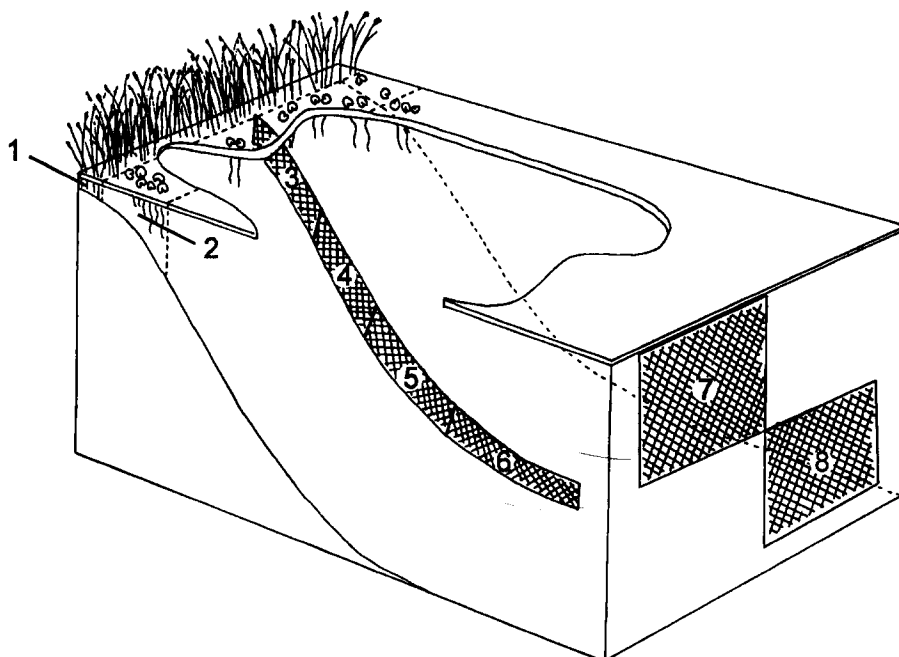
To monitor the activity of the threespined stickle-

Fig. 1. Schematic outline of the study site showing: (1) the common reed zone and (2) the water-lily zone. (3)–(6) benthic nets at 0–4 m, 4–6 m, 6–9 m and 9–11 m, respectively. (7)–(8) pelagic nets at 0–6 m and 6–12 m, respectively.

backs plexiglass fish-traps (Breder 1960) were used. On all sampling days one trap was placed in the transition between the common reed zone and the water-lily zone and a second was placed where the water-lily zone ended. On three occasions, 5 and 23 August 1990 and 27 May 1991, an extra trap was placed 5 m outside the water-lily zone. Traps were out for three hours at daytime and three hours at nighttime. To evaluate eel as a ruffe predator eel traps were used on seven occasions in the period June until October 1991.

Total ruffe standard length (mm), weight (0.1 g) and sex was recorded in the laboratory. Gonadal weight (mg) was also recorded from all sampling days, except 17 July and 5 August 1990. The gonadal status is given as the gonadosomatic index (GSI = $100 \cdot$ weight of gonads (g) $\cdot$ [total body weight $(g)]^{-1}$). As recommended by Andersen (1980) otoliths were used to determine age and for back calculation of growth. Otoliths from 75 fishes within the length range of 69–130 mm sampled in March and April 1991 were used for calculation of the regression between body length and otolith radius, and back calculation of growth. For calculation of the regression I supplemented the material with 30 smaller fish of the length range 25–65 mm sampled in plexiglass fish traps. The regression was calculated to see if the Lea equation for back-calculations of growth could be used directly (Bagenal & Tesch 1978).

The regression between body length (y, mm) and otolith radius (x, mm) for the ruffe population was calculated as:

$$y = 0.91 + 37.8x; n = 105, r = 0.98. p < 0.001.$$

Otolith radius is defined as the length from the centre of the otolith to its posterior end. The Lea equation for back-calculation of growth was not adjusted for deviation from origin since the intercept of the regression line and the y-axis was not significantly different from zero (t-test, p $\sim$ 0.7).

Fifteen ruffe were excluded from analyzes on size, age and gonadal development because they lacked one or more data parameter due to damages from eel or unreadable otoliths.

Stomach contents of the fish were preserved in 90% ethanol. Stomach contents of 178 ruffe subsampled from the total catch were analyzed in the laboratory. The contents were identified, counted and measured under a stereoscopic dissecting microscope. Body length of intact prey individuals was measured. Recognizable heads of prey were counted as individuals and assigned to the same length distribution as comparable intact individuals of the same group from the same period. Length-dry weight regressions from the litterature were then used to calculate dry weight and percent contribution of food items in stomachs. For *Bosmina* spp. and *Holopedium gibberum* regressions are given by Langeland (1982) and for other zooplankton, regressions are given by Bottrell et al. (1976). Regressions for chironomid zoobenthos and non-chironomid zoobenthos follows Hindar et al. (1988) and for *Chaoborus flavicans* in Dumont & Balvay (1979). The regression between body length (L, mm) and dry body weight (W, µg) for a sample of *Bythotrephes longimanus* sampled from Mildevatn in September 1991 was calculated as:

$$\ln W = 3.649 + 1.988\ln L; n = 16, r = 0.95, p < 0.001,$$
range of L: 1.25–2.50 mm.

Dry weight (µg) was obtained by freeze drying the specimens for 24 hours and weighing individuals on a Cahn/Ventron 25 electrobalance. Body length is defined as length from top of the head to the midpoint between the two spikes at the root of the caudal spine.

In the presentation of the ruffe stomach contents *Daphnia galeata, Bosmina* spp., *Bythotrephes longimanus, Holopedium gibberum,* copepods and *Ceriodaphnia* sp. are classified as zooplankton while chydorids, chironomids, *Chaoborus flavicans* larva and pupa, *Ceratopogonidae, Trichoptera* and *Corixidae* are classified as zoobenthos. Stomach contents of brown trout, *Salmo trutta,* and eel, *Anguilla anguilla,* were investigated for remnants of fish.

At mid day on all fishing days and also on 19 February 1991, when the lake was covered by ice, zooplankton was sampled with a 28.5 dm³ Schindler trap at 1, 3 and 5 m depth in the pelagic zone of the lake. Only zooplankton species regarded as important food items for the ruffe are evaluated. Average

density of plankton is calculated as the average of the three samples. All numbers are converted to individuals per m^3.

Temperature, oxygen, secchi disc transparency, conductivity and pH was also monitored at mid day on all fishing days and on 19 February 1991. Temperature (° C) and oxygen concentrations (mg ml^{-1}) was measured at one meter intervals from 0 to 11 m depth using a YSI model 57 oxygen meter and pH and electric conductivity (μ S cm^{-1}) from samples of surface water was measured with a pH meter and a conductivity meter.

The test referred to as the G-test is a 'R × C Test of Independence Using G-Test' (Sokal & Rohlf 1981).

Study site

Mildevatn is a dimictic, mesotrophic lake situated 20 km south of Bergen, Western Norway (60° 15′ N, 05° 15′ E). The surface area of the lake is 9.4 ha and it is elevated 1 m above sea level. Maximum depth is 12.5 m and the mean depth is 4.9 m. The lake has no permanent inlets, but one outlet leading to the sea through the 450 m long creek Vågeelva. The lake has a soft bottom with high organic content.

During the study period the lake was temperature stratified from June through September with a thermocline depth of 4 m and oxygen depletion up to 8 m deep. The oxygen concentrations ranged from 8–11 mg ml^{-1} above the thermocline, 7–4 mg ml^{-1} at 4–6 m depth and 4–0 mg ml^{-1} below 6 m depth. From October until May the water body was homogeneous and well oxygenated except for a reduction in oxygen concentrations in the deeper parts of the lake in February when the lake was covered with ice for a period. In May the thermocline was rebuilding but no oxygen depletion was shown until June. The water was humic with a yellow-brown colour during the study. The electric conductivity and pH of the surface water ranged from 60–100 μS cm^{-1} and 6.6–7.1, respectively. Secchi disc transparency varied between 2.0 and 3.2 m during the year.

Common reed, *Phragmites australis*, occurs in dense stands from shore down to about 1.5 m depth.

This part of the lake is termed the common reed zone (Fig. 1). Outside this zone there is a belt of white and yellow water lily (*Nymphaea alba* and *Nuphar lutea*), and some pondweed, *Potamogeton* sp. This part of the lake is termed the water-lily zone (Fig. 1).

Zooplankton

Bythotrephes longimanus was found in the pelagic zone of the lake from the end of May until October. Average densities ranged from 13 to 130 individuals per m^3 (Fig. 2). Highest densities were found in August 1991 with a maximum density of 320 animals per m^3 in a sample from 5 m depth.

Bosmina spp. had an average density of 4000 to 8000 individuals per m^3 in the pelagic zone, except June to August when the density was lower (Fig. 2). Highest density found was 12 000 per m^3 at 1 m depth on 24 October 1990. Both *Bosmina longi-*
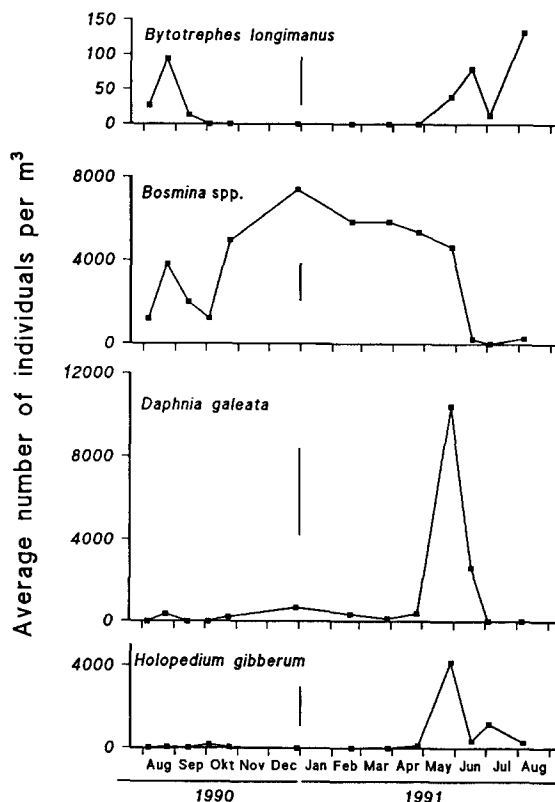

Fig. 2. Abundance of some cladoceran zooplankton species in the pelagic zone during the year.

spina and *Bosmina longirostris* were present in the lake.

Daphnia galeata were found in all samples during the year in the pelagic zone, but at low densities during late summer and autumn. Average densities ranged between 40 and 12 000 individuals per m^3 (Fig. 2). The highest density was found in May and June 1991 with the maximum density of 22 000 animals per m^3 at 3 m depth on 27 May 1991.

Holopedium gibberum was found in the pelagic zone of the lake from April until October with average density of 40 to 4000 individuals per m^3 (Fig. 2). The highest density measured was 11 000 animals per m^3 at 1 m depth on 27 May 1991.

Other zooplankton species found in the pelagic zone were *Eudiaptomus gracilis, Cyclops scutifer, Ceriodaphnia quadrangula* and *Diaphanosoma brachyurum. Chaoborus flavicans* and Hydracarina were occasionally found in the pelagic zone.

Fish species

The fish fauna in Mildevatn consists of brown trout, crucian carp, *Carassius carassius,* eel, ruffe and threespined sticklebacks, *Gasterosteus aculeatus.* One carp, *Cyprinus carpio,* was also caught during this study, and the abundance of this species is presumably low. Carp, crucian carp and ruffe are all introduced species. Juvenile individuals of the flounder, *Platichthys flesus,* live in the outlet of the lake, but a few individuals are also found in the lake.

Brown trout
Of the 69 brown trout caught during the standard gillnet sampling, 49% were caught at nighttime and 51% at daytime; 55% in pelagic nets and 45% in benthic nets. Trout were caught at an average depth of 1.9 m in pelagic nets. Only 15% of trout caught in pelagic nets were caught deeper than 3 m and no one deeper than 6 m. No fish remnants were found in stomachs of trout caught in pelagic nets. In benthic nets most fishes (84%) were caught at 0–4 m deep and none deeper than 6 m. Remnants of sticklebacks were found in 19% of stomachs from trout caught in benthic nets. One juvenile ruffe 40 mm long was also found in a trout stomach. Remnants of

fish were found in trout stomachs in the period May through August only.

Crucian carp
The main part (85%) of the 128 crucian carp caught during the standard gillnet fishing were caught in the pelagic zone on three sampling days in August 1990 and 1991, showing a high pelagic activity at this time of year. At other times of year crucian carp were not commonly found in the pelagic zone. Average catch depth of crucian carp in pelagic nets was 2.7 m and maximum depth was 6 m. Low catches of crucian carp in benthic nets during the year also indicate low activity in parts of the benthic zone with no vegetation. Most fish caught in benthic nets (93%) were caught at 0–4 m, and no fish were caught deeper than 6 m. The small gill nets used in the water-lily zone normally caught approximately 10 crucian carp each. This presumably represents the net catch capacity due to the fact that the net is tangled and unable to catch more fish when about 10 crucian carp are caught. This was the case from 25 April 1991 until 5 August 1991 which was the period when small nets were used. Even if the small nets were deployed for a longer time and for other periods then the standard nets, these catches indicate a high activity of crucian carp inside the water-lily zone also in periods when few or no crucian carps are active in other parts of the lake.

Eel
Of 23 eel caught in eel-traps in the period June until October 1991 one had remnants of ruffe in its stomach. Ruffe injured by eel were commonly found in gillnets, but the importance of eel as predator on living ruffe is uncertain.

Threespined sticklebacks
Threespined sticklebacks were mainly found close to the shore in the vegetation zone. In the period June to September the inner trap always caught more than 20 sticklebacks while the outer never caught more than 2. At nighttime catches were much lower. The catches were also lower at daytime in April, early May, September and early October and no sticklebacks were caught from late October to April. No sticklebacks were caught in the extra
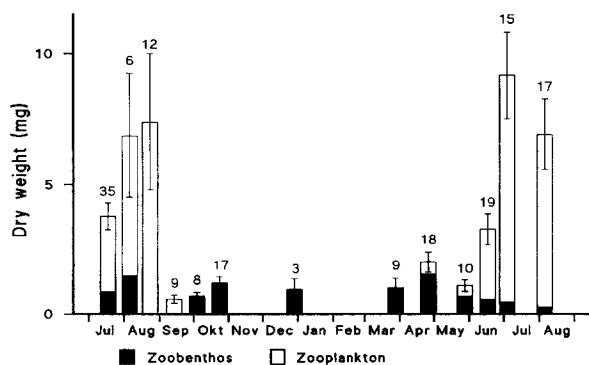
Fig. 3. The diet of ruffe during the year shown as average dry weight of stomach contents. Food groups are zooplankton and zoobenthos. Vertical lines show standard error of total stomach content and number above each bar represent sample size.

trap outside the vegetation zone on the three occasions it was used.

Results

Diet

Zooplankton was the main food item of ruffe from June through September, while zoobenthos was dominating from October through March (Fig. 3). The period April through May represented a transition period where zooplankton gradually replaced zoobenthos in the diet. At the end of April 1991 *Daphnia galeata* represented 22% of the food consumed (dry weight), increasing in importance to 69% in mid June. In July *Holopedium gibberum* and *Bythotrephes longimanus* were dominating. The most important food in August was *Bythotrephes longimanus* which in that month represented from 67% to 96% of food consumed (dry weight). *Bosmina* spp. was the main food in September. In all samples from June, July and August zooplankton made up more than 75% of food consumed (dry weight). From October until April chironomids and *Chaoborus flavicans* were the dominating prey items for the ruffe. In this period zoobenthos made up more than 90% of food consumed (dry weight). Zooplankton was of minor importance in this period, but by number they could represent as much as 53% for *Ceriodaphnia quadrangula* (3 October 1990) and 31% for *Bosmina* spp. (28 December

1990). Except 13 September 1990, the average dry weight of food in stomachs was higher when zooplankton was the dominating food than when zoobenthos was dominating.

Activity and distribution in time and space

The ruffe in Mildevatn is mainly active at daytime, as catches were significantly higher during day in 11 out of 14 sampling events (Binomial test, $p < 0.05$), and 84% of ruffe were caught during day (Table 1). There is, however, a significant difference in the diel activity during the year (G-test, $p < 0.001$), caused by the relatively high nocturnal activity on 27 May and 17 June 1991. When excluding data from these days no significant difference in the diel activity during the year is found (G-test, $p \sim 0.2$).

The catch in benthic nets comprised 86% of total catch, and 54% of the total benthic catch was caught between 4 and 6 m depth. From June until October 84% of ruffe were caught in benthic nets at this depth. Ruffe were caught significantly deeper from October to May, when 73% of the catches in benthic nets were deeper than 6 m (G-test, $p < 0.001$). Furthermore, the ruffe was caught significantly shallower at nighttime than at daytime both for the periods June through September and October through May (G-test, $p < 0.001$). In benthic nets only 6% of the ruffe were caught shallower than 4 m.

In pelagic nets 65% of the ruffe were caught at a depth of 9 to 12 m, only 0 to 3 m above the bottom. No ruffe were caught closer to the surface than 3 m, and 18 ruffe, representing 5% of the total catch were caught between 3 and 9 m.

The catches varied widely during the year, but no clear trend in this variation was found. However, the lowest number of ruffe was caught at the only sampling that was carried out during winter.

Population parameters

Size and age distribution
The total length of the fish ranged from 67 mm to 129 mm for male ruffe and 65 mm to 130 mm for female ruffe (Fig. 4a), the average length of all fishes
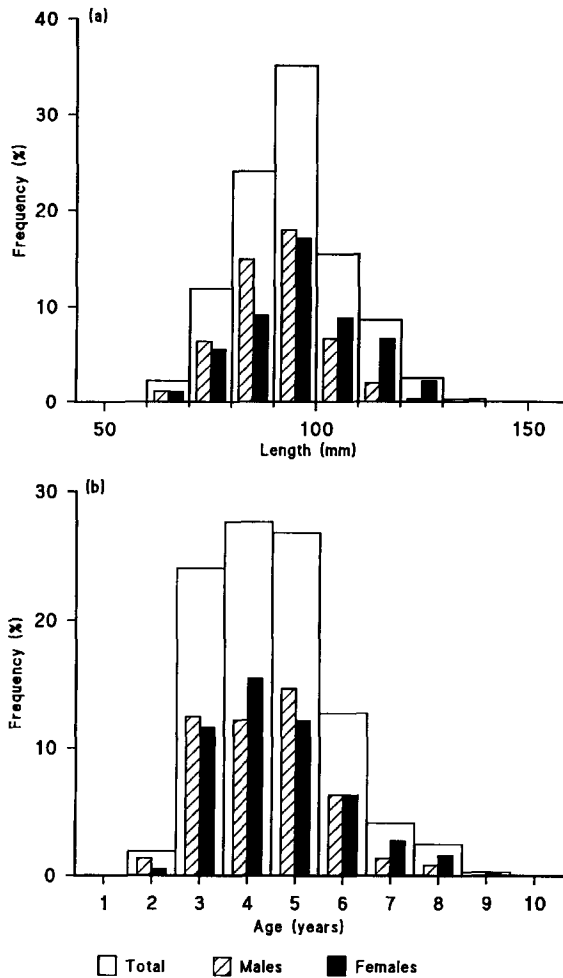
226

Fig. 4. Length (a) and age (b) of ruffe in catches from Mildevatn, n = 362.

Fig. 5. Back-calculated growth of female (dotted line) and male (solid line) ruffe in Mildevatn. Vertical lines show standard deviation, and number of observations are written above and below the lines for females and males, respectively.

being 93.4 mm. The average length of males and females were 90.7 and 95.9 mm, respectively. Independent of age and time of catch female ruffe were significantly larger than males (Three-way main effect ANOVA, $p < 0.01$). There was no significant difference in the length of fish caught during the day vs. night (t-test, $p \sim 0.4$). Fish caught above 9 m depth in the pelagic zone were significantly longer than fish caught with benthic nets (average 105.7 mm vs. 92.9 mm) (Mann-Whitney U-test, $p < 0.001$).

The oldest ruffe caught was nine years old, but only 6.9% of the fishes were older than six years (Fig. 4b). No fish younger than two years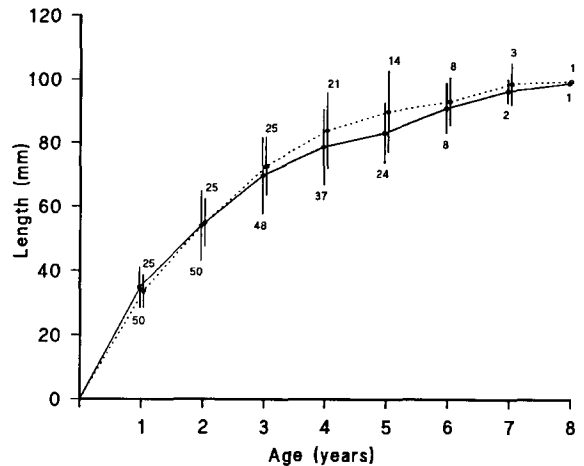 of age were caught. There was no significant difference in the age distribution between male and female ruffe (G-test, $p \sim 0.5$).

Growth

The general pattern of growth seems to be that males grow faster than females their first year of life. From age one until age two females grow faster, and are longer than males when two years old and older (Fig. 5). The length differences among the sexes are, however, small in this limited back calculated material.

Gonadal development

The gonadosomatic index (GSI) is highest for both sexes in the end of April (Fig. 6). The maximum GSI values measured were 5.6 for males and 12.8 for females. For females the GSI then decline until mid July when all fish had finished spawning (Fig. 6a). From Fig. 5 it looks as if males finish spawning before females. This is probably caused by the handling of ripe males that have initiated or forced them to spawn and thereby reduced their GSI. Due to this GSI for males may be underestimated during the whole spawning periode. The male gonad grows fast during September and has its full size in early October (Fig. 6b). The female gonad grows slower and continuously from September to April. The growth then accelerates and the gonad reaches its maximum size at the end of April (Fig. 6a).
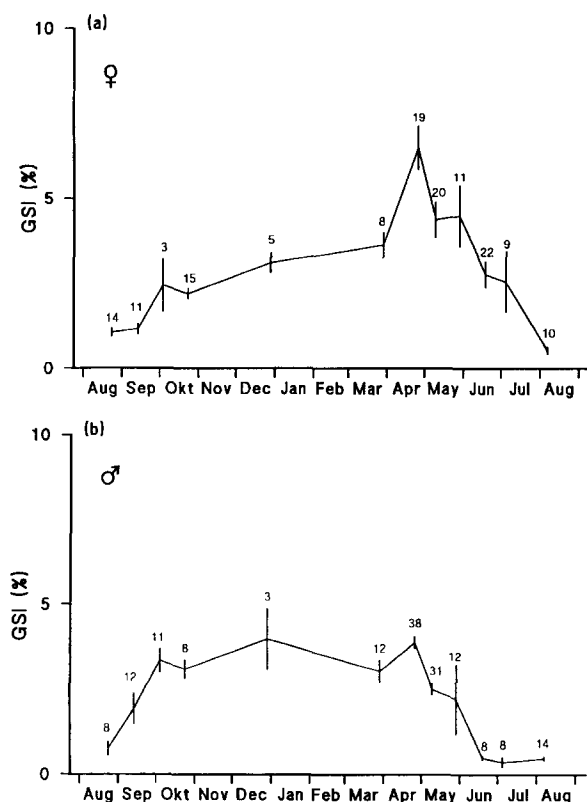
Fig. 6. Gonadosomatic index of (a) female and (b) male ruffe in Mildevatn. Vertical lines show standard error and numbers above the lines show number of observations.

Sex ratio

Of the 362 fish with all data available 178 were males and 184 females. For the total sample of ruffe the sex ratio was not significantly different from 1:1, but the sex ratio was not independent of time (G-test, $p < 0.001$), indicating differences in activity between sexes during the year. The trends in activity are, however, vague. Females tend to be more active in June and July while males tend to be more active from March to June. On 17 July 1990, and 16 June 1991, there were significantly more females in the catches, and 3 October 1990, and 25 April 1991, there were significantly more males (Binomial test, $p < 0.05$).

Discussion

Food and feeding

The dominance of zooplankton in the diet of ruffe in Mildevatn from June through September represents a major difference compared to other populations investigated. Johnsen (1965) lists ruffe diet data from 17 older studies including 18 lakes. Chironomids were the dominant prey species in 10 lakes and among the dominant in 4 more. Other dominant food items were *Gammarus, Asellus* and *Pallasea*. Data from 9 more recent investigations of 13 lakes show that zoobenthos, especially chironomids, are the dominant prey during the summer (Table 2). There is only one exception; among ruffe larger than 100 mm in Lake South Bolmen, Sweden, zooplankton was the dominant food in August. Data from these 32 lakes within the natural range of the ruffe clearly show that zoobenthos is the predominant prey for ruffe and that zooplankton feeding is of little importance. The zoobenthos feeding of ruffe in Lake Mildevatn from October to April is in accordance with what is found within its natural range.

Diel and seasonal activity and distribution

The ruffe in Mildevatn is mainly active at daytime. In Lake Aydat, France, however, the ruffe was found to be predominantly nocturnal (Jamet & Lair 1991). This is to my knowledge the only study that describes diel activity of ruffe. Differences in diel activity of a species can be related to differences in environmental factors (e.g. risk of predation, competition, presence of food) (Curio 1976, Helfman 1986). Mildevatn and Lake Aydat differ in many ways (e.g. diet of ruffe, number of fish species in the lake, potential predators on ruffe, etc.) which may cause differences in diel activity patterns. Since diel activity in ruffe is poorly investigated, it is not known what is the diel rhythm commonly found within the native range of the ruffe, or how it varies. Nor is the diel activity of the donor population of the ruffe in Mildevatn known. It is therefore impossible to conclude that day activity of ruffe in Lake Mildevatn arose after introduction as a response to the new environment. To come any further on this question data from more lakes and/or specific experiments on this topic are needed.

To my knowledge there are no detailed descrip-

Table 2. The diet of ruffe in different parts of Europe.

Locality	Country	Time	Food items of major importance	Reference
Middle Dnieper	Ukraine	Aug	Two morphs of ruffe eating *Gammarus* and chironomids, respectively	Aleksandrova (1974)
Lake Ilmen	Russia	Spring-autumn	Chironomids	Fedorova & Vetkasov (1974)
Lake IJssel	Holland	–	*Gammarus* sp. and chironomids	Willemsen (1977)
Lake Lauwersmeer	Holland	–	*Gammarus* sp. and chironomids	Willemsen (1977)
Lake Vannsjø	Norway	Aug	Chironomids and Ostracoda > 70% volume	Brabrand (1983)
Lake Bjørkelangen	Norway	May-Sep	Zoobenthos, mainly chironomids, 25% zooplankton in June	Vøllestad (1985)
Lake Rødnes	Norway	May–Sep	Zoobenthos, but *Mysis relicta* and *Pallasea quadrispinosa* increase during summer	Vøllestad (1985)
Lake Ødgeren	Norway	May–Sep	Zoobenthos, *Mysis relicta* increase during summer	Vøllestad (1985)
Włocławek Dam	Poland	Jun–Sep	Chironomids predominant > 50%	Boroń & Kuklińska (1987)
Danube River	Slovakia	Summer	Zoobenthos 80%	Nagy (1988)
Lake South Bolmen	Sweden	May–Sep	Zoobenthos, but zooplankton dominates for ruffe > 100 mm in August	Bergman (1991)
Lake Vomb	Sweden	May–Sep	Zoobenthos mainly chironomids	Bergman (1991)
Lake Aydat	France	Jul	Chironomids, Trichoptera, *Chaoborus*	Jamet & Lair (1991)
Mildevatn	Norway	Jun–Sep	Zooplankton	This study

tions on the spatial distribution of ruffe. Sandlund et al. (1985) and Vøllestad (1985) reported that ruffe were rarely caught in pelagic nets in studies of four lakes in eastern Norway, and Bergman (1988) reports that ruffe was only abundant in the benthic habitat in four Swedish lakes investigated. None of the studies above calculate the frequency of activity in the pelagic zone. Also in my catches most of the ruffe were associated with the bottom, but 14% of the ruffe were caught in pelagic nets. Most of them were caught in the lower part from 9 m down to the bottom, but 5% were caught above 9 m, which is clearly in the pelagic zone. The frequency of ruffe in the pelagic zone is, however, so low that I cannot conclude that this population is less closely connected to the benthic zone than those in the works referred.

The ruffe caught above 9 m in the pelagic zone were significantly longer than fish caught in benthic nets. One possible explanation to this is a higher risk of predation from brown trout on small fish in this part of the lake (Werner et al. 1983).

In Mildevatn the ruffe stays deeper during winter than during summer. Similar patterns of distribution are reported by several authors (Johnsen 1965, Sandlund et al. 1985, Vøllestad 1985). It is suggested that this difference in distribution is connected to

spawning (Johnsen 1965, Sandlund et al. 1985), but in my case a change due to the change in diet or reduced oxygen content in the deeper parts of the lake in the summer is also possible. However, no authors have reported that ruffe are relatively more active in the shallower parts of the lake during night like I found in Mildevatn.

Size, age, growth and gonadal development

The ruffe population in Mildevatn shows no clear deviation in size compared to natural Norwegian populations. Ruffe stagnates in growth at lengths of about 10 cm and has an observed maximum length of 13 cm. Four populations from eastern Norway had maximum lengths of 18.3 cm and 14 cm, and stagnation in growth at 14 cm and 11–13 cm, respectively (Andersen 1980, Vøllestad 1985), while Brabrand (1979) reports stagnation in growth at lengths of 7.5 to 8 cm in Lake Vannsjø, eastern Norway.

Huitfeldt-Kaas (1917), Fedorova & Vetkasov (1974) and Andersen (1980) found that female ruffe from the age of two years are larger than male ruffe. This trend is also found in Mildevatn. However, neither Bastl (1964) nor Knowles (1974), both cited in

Andersen (1980), found any such difference between the sexes.

There is a tendency that the ruffe grows older in more northern areas than in the south. Maximum age of ruffe in middle Europe is about six years (Andersen 1980) while three studies from Norway reports 9, 13 and 14 years old ruffe (Andersen 1980, Vøllestad 1985, this study). A complicating factor when comparing age of ruffe is that some authors read scales while others read otoliths for age determination. These methods are not entirely comparable because scales may underestimate the age, especially for older or slow growing fish (Andersen 1980).

The growth pattern of the ruffe in Mildevatn is in accordance with other studies from Norway (Andersen 1980, Vøllestad 1985) with a fast growth during the first 3 years and stagnation at the age of six years, while Brabrand (1979) also from Norway reports stagnation already after two years.

The maturing of ruffe gonads is regulated by temperature (Butskaya 1980). I would therefore expect that the ruffe in middle Europe start spawning earlier than in Scandinavia. Differences are small, however. Spawning takes place from mid April until June in Lake Ilmen (Fedorova & Vetkasov 1974), and from mid April until mid June in the Danube River, Slovakia (Bastl 1988). In Lake IJssel, Holland, the ruffe is spawning in May and June (Willemsen 1977). Andersen (1980) reports spawning in Lake Øyeren, eastern Norway, from mid May until mid July, while Vøllestad (1985) found spawning ruffe from mid June until mid August in three lakes at the eastern part of Norway. The ruffe in Mildevatn is spawning from early May until mid July.

The GSI reported from Danube (Bastl 1988) is 2 to 3 times higher than the GSI of male and female ruffe from Lake Øyeren (Andersen 1980) and Mildevatn. The patterns of gonadal growth during the year for both sexes are, however, identical in Danube (Bastl 1988), Lake Øyeren (Andersen 1980) and Mildevatn.

Why is ruffe planktivorous in Lake Mildevatn?

Diet is the character where I found the clearest difference from what is common for ruffe within its natural range. It is noteworthy that the ruffe, formerly classified as benthivorous, can base its summer diet entirely on zooplankton, and that it feeds on zooplankton even if it is caught near the bottom. Zoobenthos feeding during summer is consistent in virtually all studies of ruffe over a broad environmental range (Johnsen 1965, Table 2). Even if the donor population of the Mildevatn ruffe is not known one may expect that summer diet is changed after introduction. Whether this was a consequence of flexibility or a result of changed selective pressure is not known.

Natural selection favours individuals with the highest lifetime reproduction, which are individuals that can stay alive, and most effectively collect food and convert it to offspring. An individual is therefore expected to optimize the trade-off between maximizing energy intake and minimizing mortality. Under these assumptions the zooplankton feeding in Mildevatn should be due to either higher energy intake per time when feeding on zooplankton and/or lower mortality when feeding on zooplankton compared to the natural range.

I suggest the presence of large zooplankton organisms available for ruffe in Mildevatn to be the main reason making zooplankton the dominant diet of ruffe during summer. Other reasons may, however, also be of importance. The ruffe seems to inhabit the same parts of the lake in Mildevatn as within its natural range and it may therefore be tempting to conclude that it is not influenced by the differences in the communities. However, a reduction in predation risk may have made feeding on zooplankton in the zone immediate above the bottom profitable for ruffe. A change in diet could also have been due to low densities of zoobenthos in Mildevatn. This may have reduced the profitability of zoobenthos feeding. The zoobenthos is unfortunately not investigated in Mildevatn, but the soft bottom of this lake should be a good habitat for zoobenthos. Intensive predation by ruffe or eel on benthos may, though, keep the density at a low level. The zooplankton fauna during summer, however, seems plentiful and of good quality. The most important zooplankton food item for the ruffe during the summer is *Bythotrephes longimanus*. This is a
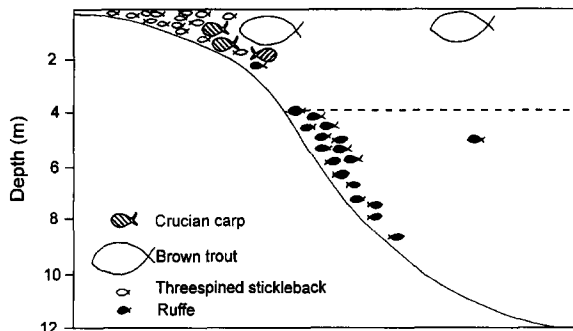
Fig. 7. Distribution of brown trout, crucian carp, ruffe and threespined sticklebacks in the period June through September in Mildevatn, except crucian carp in August which at that time is highly abundant in the pelagic zone. Dashed line represents the thermocline.

species sensitive to predation and only found in lakes with low zooplankton predation intensity (Stenson 1972). Its high abundance in Mildevatn is possibly due to the structuring effect of brown trout on the fish community (Fig. 7). When a large fish predator is present the threespined sticklebacks will hide in the littoral vegetation to avoid predation (Jakobsen et al. 1988). This may explain why threespined sticklebacks are only found within the vegetation in the littoral zone in Mildevatn and are not feeding on the rich plankton community in the pelagic zone. The activity of trout in Mildevatn is restricted to the upper strata of the lake, probably due to high oxygen demands (Moyle & Cech 1982) and need of high light levels to detect prey. In contrast ruffe need less light and are probably less stressed by low oxygen tensions. Experiments have shown that the ruffe can detect and catch zooplankton organisms visually at low light intensities (Bergman 1988). This makes it possible for the ruffe to pick zooplankton from deeper parts of the lake with low risk of predation from the brown trout. Threespined sticklebacks can also tolerate low oxygen concentrations (Wootton 1984) and could potentially utilize the oxygen refuge in the deeper parts of the lake in the same way, but as predators with high light demands (Beukema 1968) they would probably forage inefficiently in the darker parts of the lake. In a hypothetical absence of brown trout the threespined sticklebacks could leave their hide in the vegetation and start exploiting the rich plankton resources in the pelagic zone. Larger zooplank-

ton species as *Bythotrephes longimanus, Daphnia galeata* and *Holopedium gibberum* could thereby be decimated or even eliminated from the lake. Zooplankton feeding would then no longer be profitable for the ruffe. This could also be the probable outcome of the presence of a planktivorous fish species unaffected by the presence of brown trout. An experimental removal of brown trout from Mildevatn would be a test of my suggestion that predation by brown trout is the main structuring effect in the fish community.

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