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Competition for food between Eurasian perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* [L.]) over different substrate types

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Abstract – Food consumption by Eurasian perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* [L.]) was studied in single and mixed-species treatments in the laboratory, where alternative food resources, chironomids and zooplankton, were offered simultaneously. The effects of structural complexity, which was represented by substrate grain size, and of feeding level on food consumption were analysed. Across all experiments, the outcome of competition between perch and ruffe depended on food abundance and on the structural complexity of the environment. Perch and ruffe both changed their food consumption in the presence of a heterospecific competitor. With high food supply, perch consumed more benthic food than ruffe. With low food supply, the consumption of perch decreased strongly, while that of ruffe remained high on fine sediment. Under all conditions tested, the mechanism of competition appeared to be of interference rather than of exploitative nature. It is suggested that with decreasing lake productivity caused by re-oligotrophication, habitat shifts of both species will occur, which will alleviate interspecific competition. Ruffe will forage over fine sediment and perch over coarse sediment, whereby both species will achieve the highest foraging efficiency under conditions of low food supply.

Key words: perch; ruffe; interference competition; substrate type; food supply

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

The interactions between Eurasian (*Perca fluviatilis* L.) or yellow perch (*Perca flavescens* Mitchell) and ruffe (*Gymnocephalus cernuus* [L.]) have recently been studied with increasing interest, especially by authors from Europe and North America (Bergman 1990, 1991; Bergman & Greenberg 1994; Savino & Kolar 1996; Fullerton et al. 1998, 2000). Ruffe was accidentally introduced into the Laurentian Great Lakes in 1986 (Pratt & Blust 1992) and into many European lakes, e.g., into Lake Constance in the mid-1980s (Berg et al. 1989). In almost all lakes where ruffe appeared as an exotic species, it met with native Eurasian or yellow perch. As ruffe and both species of perch show similar food and habitat preferences (Bergman & Greenberg 1994; Ogle et al. 1995; Ogle 1998), competition between these species is likely to occur. Therefore, concerns arose that non-native ruffe might have negative impacts on the commercially important fisheries for Eurasian and yellow perch.

Perch feed on zooplankton during their first months of life and later add benthic macroinvertebrates to their diet, until they eventually become piscivorous. In Lake Constance, perch feed mainly on zooplankton until the end of October when they reach a total length of 83 ± 4.4 mm (±SE), while chironomids are the main food source for fish larger than

100 mm total length (Wang & Eckmann 1994; Wang 1994).

Ruffe by contrast do not undergo pronounced ontogenetic diet shifts. During their first year of life, they feed on zooplankton and benthic macroinvertebrates (Van Densen 1985; Werner et al. 1996). The consumption of zooplankton by ruffe becomes less important as the fish grow, and above 40 mm body length, they feed almost exclusively on benthic macroinvertebrates (Bergman 1991; Popova et al. 1998). In Lake Constance, age 0 and age 1 (total length 109 ± 22 mm in July) ruffe feed mainly on zooplankton during the day and on benthic invertebrates (mostly chironomids) during the night (Schmid 2000).

Wherever ruffe have become established as an exotic species, changes in the fish community structure have been observed (e.g., Mills et al. 1994; Adams & Maitland 1998), which were probably caused by competitive interactions. Most studies agree that juvenile perch and ruffe are potential competitors for benthic macroinvertebrates (Bergman & Greenberg 1994; Rösch & Schmid 1996; Savino & Kolar 1996; Fullerton et al. 1998). Moreover, experiments in ponds with muddy sediment suggested that perch might be the inferior competitor (Bergman & Greenberg 1994), because with increasing density of ruffe, Eurasian perch consumed less benthic macroinvertebrates and more zooplankton.

To assess diet overlap between ruffe and yellow perch, Fullerton et al. (1998) carried out laboratory experiments in which they studied the preferences of both species for benthic macroinvertebrates. In the mixed-species treatment, the fish expanded their preferences and included more taxa in their diet, while at the same time per capita consumption rate increased as compared with the perch-only treatment. However, as no gut content analyses were carried out, changes in food consumption and diet composition of the two species could not be analysed in more detail.

The motivation for the present study on food competition between Eurasian perch and ruffe was the rapid expansion of the ruffe stock in Lake Constance. After ruffe had been observed for the first time in 1987, by 1996 it had become the most numerous species in shallow littoral areas (Rösch & Schmid 1996). As Lake Constance is actually undergoing a process of pronounced re-oligotrophication, whereby total phosphorus content during spring turnover decreased from >80 μg l^{-1} around 1980 to 12 μg l^{-1} in 2003, food supply for both percid species will decrease in the future and hence, competition for food will likely become more intense than it is today.

In the present study, food consumption of age-0 perch and ruffe was analysed in laboratory experiments. Particular attention was paid to whether the presence of a heterospecific competitor influences the feeding patterns of the two species in qualitative and/or quantitative terms. To avoid confounding results because of different fish densities, mixed-species as well as single-species treatments were conducted with two specimens per tank. This design has the additional advantage that the fish adapt more easily to the experimental conditions. In preliminary trials, one fish alone remained extremely nervous even after 24 h adaptation, and in many cases refused to feed. As both ruffe and perch live in social aggregations, results obtained with two individuals per tank were considered more trustworthy than results obtained with a solitary fish.

As ruffe forage preferentially over soft substrates (e.g., Ogle et al. 1995 and citations therein) where they might have an advantage over perch, substrate type was included as an additional variable in the experimental design. This set-up corresponds to the true situation in large lakes, where perch and ruffe have the possibility to forage over different types of substrate, from sand to pebbles and gravel or even boulders. Furthermore, as exploitative competition will only occur when food supply is limited, experiments were performed with both low and high food supplies. Finally, zooplankton was included as an alternative food resource in addition to macrozoobenthos, because the best-documented response of perch to competition by ruffe was a diet shift to zooplankton (Bergman & Greenberg 1994). Therefore, these two types of prey were offered simultaneously.

With this experimental set-up, the following questions were addressed:

(i) Does the amount and type of food consumed by perch and ruffe depend on substrate type?

(ii) Does the presence of a heterospecific competitor alter the feeding behaviour (amount and type of food consumed), and if so, does the response depend on substrate type?

(iii) Do these consumption patterns change when the level of food supply is lowered?

The final goal of this study was to sketch a scenario how the two percids might compete for food resources in a large lake with varied bottom substrate, where food supply becomes increasingly limited because of re-oligotrophication.

Methods

Experimental set-up

Juvenile perch (72.7 ± 6.4 mm total length, 3.5 ± 0.9 g wet mass; mean ±95% CL) and ruffe (63.3 ± 6.1 mm total length, 2.7 ± 0.8 g wet mass) were caught with a dip net (6 mm bar mesh) in the littoral zone of Lake Constance. The fish were separated by species and acclimated to laboratory conditions in 250 l tanks for up to 1 month. Photoperiod in the laboratory followed the natural day/night cycle and the experiments were carried out during daylight. Temperature during the acclimation period and the experiments ranged from 12 to 20 °C. As short-term food consumption and not growth was to be measured, this temperature range was considered appropriate.

During acclimation, the fish were fed with zooplankton and chironomid larvae. Zooplankton, mainly *Daphnia galeata*, *D. hyalina* and *Bythotrephes longimanus*, were harvested during daytime from the epilimnion of Lake Constance, while chironomid larvae (mainly *Chironomus plumosus*) were purchased from a commercial supplier.

In preliminary trials, the food consumption of both fish species was evaluated with each of the two prey types. Two perch or two ruffe were starved for 24 h in 25 l tanks (25 cm × 45 cm × 25 cm height) without substrate at a temperature of 20 °C. Thereafter they were offered either chironomids or zooplankton *ad libitum* and allowed to feed for 1 h. The dry mass of prey eaten was then determined from gut contents (see below). These preliminary trials were replicated three times for each combination of fish species × prey type. Food consumption of perch was higher than that of ruffe. In terms of dry mass, one perch consumed 17.3 mg chironomids or 17.8 mg daphnids, whereas one ruffe consumed 14.6 mg chironomids (about 25 individuals) or 16.1 mg daphnids (about 250 individuals).

In the experiments with low food supply, twice the amount of zooplankton plus twice the amount of chironomids that had been consumed by one ruffe in the preliminary trials was offered. This should represent a limited food supply of each prey type as prey abundance would decrease during the course of a 2-h experiment and hence search time would increase. Additionally, chironomids would hide in the substrate and thus would not be such an easy prey as those in the tanks without substrate. The amount of food offered in the low food treatments represents approximately 20% of the daily ration for maximum growth of perch at 20 °C and 35% of the daily ration at 12 °C (Hanson et al. 1997). In the experiments with high food supply, 10 times as much zooplankton and twice as many chironomids were offered. The reason for not offering more chironomids under high food conditions was that on sand about 10% of the chironomids did not hide in the sediment and so were an easy prey for both species. By further increasing the abundance of chironomids, a presumed substrate effect on the consumption of chironomids might have been masked.

All experiments were run with two fish per tank, either of the same species (single-species treatments) or one fish from each species (mixed-species treatments). The fish were acclimated in 25 l perspex tanks for 24 h prior to the beginning of the experiment. During this time, no food was offered. The experimental tanks were placed side by side behind a black curtain to avoid any external disturbance, and cardboard barriers optically separated them from each other. One hour before the start of an experiment, the fish were gently corralled by hand into a glass receptacle (15 cm × 10 cm × 15 cm) within the tank to avoid untimely ingestion of prey organisms, and the prey organisms were then released into the tank. After 1 h, most chironomids (except for a maximum of 10%) had hidden in the substrate and the experiment was started by slowly inclining the glass receptacle to set the fish free. In contrast to the preliminary trials, the fish were allowed to feed for 2 h. At the end of this period, the fish were dipnetted from the tanks and immediately killed with 2 mg/l 1,1,1-trichloro-2-methyl-propanol (TCMP). Total length was measured to the nearest millimetre and wet mass determined to the nearest 0.01 g. To slow down digestion of prey, the fish were chilled on ice. After removing the stomach contents quantitatively, they were separated into chironomids and zooplankton and dried for 24 h at 104 °C. After another 24 h in a desiccator, the dry mass of the stomach contents was determined to the nearest 0.1 μg.

The experimental design was full factorial with three factors and two dependent variables. The factors were (i) substrate type (three levels: sand, pebbles, gravel), (ii) type of competition (two levels: intraspecific, interspecific) and (iii) feeding level (two levels: high, low), while the dependent variables were biomass of zooplankton and biomass of chironomids consumed per fish. All treatments were replicated seven times. As data for perch and ruffe in the mixed species treatments were collected from the same aquaria, 18 experimental set-ups were required to combine all factors. In some cases, for unknown reasons, the fish did not feed and were excluded from the analysis. When this happened in several replicates per treatment, the whole experimental series was replicated. The sequence of experiments was randomly determined.

Statistical analyses

The data were $\log_e (x + 0.1)$ transformed to achieve normal distribution and variance homogeneity. Normality of the transformed data was tested with the Kolmogorov–Smirnov test, and variance homogeneity was checked with Bartlett's test. For the evaluation of all effects, a three-way MANOVA was calculated for each fish species separately in Statistica version 5.5, module GLM (StatSoft Inc., 1999).

The multivariate approach was chosen to explore potential interactions between the dependent variables, i.e., the two types of food that were always offered simultaneously. These variables are not statistically independent, because they originate out of the same experimental unit. A significant interaction including the dependent variables would indicate a change in the proportion of the consumed food types in at least one of the treatments.

As higher order interactions describe the consistency of an effect under different levels of another factor, there is no value in the interpretation of the lower-order interactions and the main effects of the whole model (Underwood 1997). Instead, we considered partial models for further evaluation of the data when three-way or two-way interactions were significant.

Relevant main effects of partial models were tested with Tukey's HSD test. Differences between intra- and interspecific competition were followed by linear contrast analyses for each fish species and each factor level combination. The overall significance level was maintained by a sequential Bonferroni adjustment (Rice 1989).

Results

General results

Perch food consumption depended on substrate type only in single-species treatments with high food supply (Fig. 1a; Table 1). Under these conditions, the largest amount of prey was ingested on sand, less on pebbles and even less on gravel. With low food supply, the presence of a heterospecific competitor, as well as the combination of these two factors, the levels of food consumption were independent of substrate type (Fig. 1b–d; Table 1).

Ruffe showed the opposite feeding behaviour. In single-species treatments with high food supply, their consumption was similar on all substrate types (Fig. 1e; Table 2). Low food supply, the presence of a heterospecific competitor, as well as the combination of these two factors, lead to substrate-specific food consumption by ruffe with higher consumption rates on the fine substrates (Fig. 1f–h; Table 2).

Under most experimental conditions, far more chironomids than zooplankton were consumed by both species (Fig. 1a–h). Especially under low food conditions, both perch and ruffe ingested little plankton and the amount ingested did not depend on substrate type in either case (Fig. 1b,d,f,h).

For both species, the overall three-way models were significant for the multivariate approach as well as for the two prey types, plankton and chironomids (Tables 1 and 2). This means that all factors investigated (feeding level, substrate type and the type of competition) and the dependent variables interacted. An interaction of the dependent variables indicates that the fish consumed different proportions of chironomids and zooplankton under certain experimental conditions. To analyse in more detail how these conditions influenced the food consumption of the fish, partial models were considered.

Effects of competition on food consumption

In the single-species treatments with high food supply, the consumption by perch was substrate-specific (Fig. 1a). In the equivalent mixed species treatment, this pattern changed. Perch consumed similar amounts of chironomids over all substrates when ruffe was present (Fig. 1c). The higher consumption of chironomids by perch on gravel was accompanied by an opposite effect in ruffe, which ingested fewer chironomids on the coarser substrates in the mixed-species treatment (Fig. 1g; Table 3). Zooplankton became more important for ruffe and was ingested in similar, or even higher amounts than chironomids, indicating a diet switch under high food condition in the presence of perch (Fig. 1g, Table 2). Only on sand, did ruffe show a consistently high consumption of chironomids, even when food supply was low and when perch was present (Fig. 1g,h).

With low food supply, perch generally consumed less than when there was a high food supply, and food consumption was even more reduced in the presence of ruffe, independent of substrate type (Fig. 1b,d). Ruffe also changed their feeding pattern between intra- and interspecific competition, tending to consume fewer chironomids over the coarser substrates in the mixed-species treatment while their consumption on sand remained as high as in the single-species treatment (Fig. 1f,h, Table 3).

Effects of substrate type on food consumption

Under high food conditions and in the absence of ruffe (Fig. 1a), perch consumed two to three times more chironomids on sand and pebbles than on gravel (Tukey-test, $P < 0.001$ each). Under the same conditions, ruffe consumed similar amounts of chironomids on all substrates (Fig. 1e). Whenever the consumption of chironomids by ruffe was substrate-specific, more chironomids were consumed on sand and less on the coarser substrates (Fig. 1f–h).

The ingestion of zooplankton did not depend on substrate type under low food conditions, either for perch or for ruffe (Tables 1 and 2; Fig. 1b,d,f,h). However, when food supply was high and a heterospecific competitor present (Fig. 1c,g), both species consumed more zooplankton on pebbles and gravel than on sand (Tukey test, $P < 0.01$ for ruffe and $P < 0.05$ for perch).

Under high food conditions and intraspecific competition (Fig. 1a), perch discriminated against plankton on pebbles as compared with the other substrates (Tukey test, $P < 0.05$).

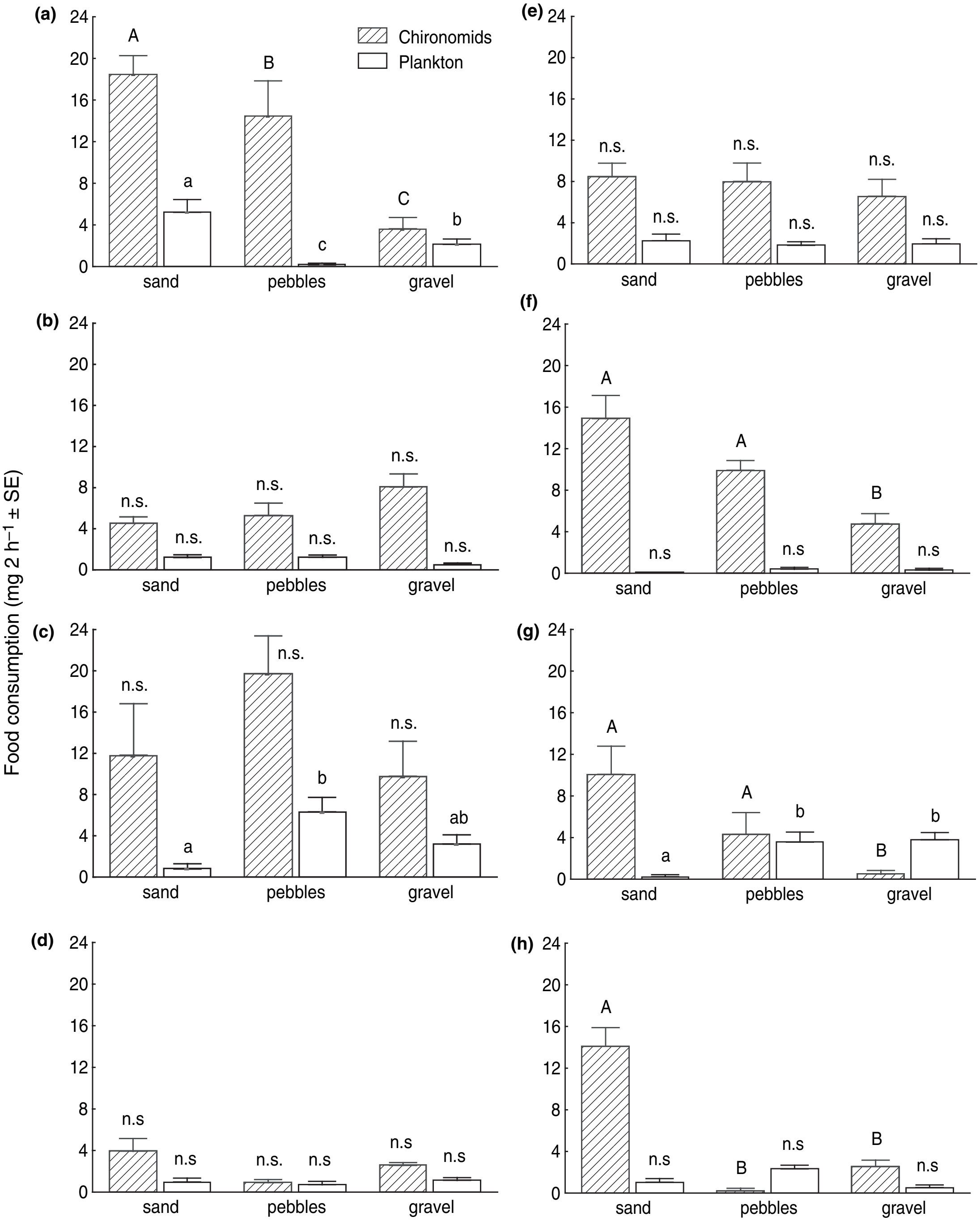

Fig. 1. Consumption of plankton and chironomids (dry mass) by individual perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) over different substrate types: a) Perch, intraspecific competition, high food; b) Perch, intraspecific competition, low food; c) Perch, interspecific competition, high food; d) Perch, interspecific competition, low food; e) Ruffe, intraspecific competition, high food; f) Ruffe, intraspecific competition, low food; g) Ruffe, interspecific competition, high food; h) Ruffe, interspecific competition, low food. Different letters indicate differences in food consumption within the respective one-way model (Tukey test $P < 0.05$). Hatched bars/capital letters: chironomids; white bars/small letters: zooplankton; n.s.: not significant.

Effects of feeding level on food consumption

In the single-species treatments, level of food availability influenced the substrate-specific food consumption patterns of both species, while this was not the case in the mixed-species treatments (Tables 1 and 2). Perch consumed less food with a low food supply (Fig. 1a–d), while the consumption by ruffe remained about the same, irrespective of the feeding level (Fig. 1e–h). Neither perch nor ruffe showed a diet switch from chironomids to zooplankton when food supply was low.

Table 1. Overall model and partial models of food consumption by perch in the laboratory experiments.

	Selection conditions		Multivariate approach				Plankton		Chironomids	
Model	Competition	Feeding level	*N*	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Substrate × competition × feeding level			129	4	7.45	**<0.001**	11.26	**<0.001**	3.80	**0.025**
Substrate × competition		High	57	4	9.08	**<0.001**	16.20	**<0.001**	3.33	**0.044**
Substrate	Intraspecific	High	39	4	20.85	**<0.001**	27.73	**<0.001**	15.33	**<0.001**
Substrate	Interspecific	High	18	4	1.45	0.25	2.14	0.15	1.17	0.34
Substrate × competition		Low	72	4	1.01	0.40	0.88	0.42	1.17	0.31
Competition		Low	72	2	7.72	**<0.001**	0.01	0.94	15.69	**<0.001**
Substrate		Low	72	4	2.21	0.07	0.38	0.68	4.21	**0.019**

Summary results of three-way, two-way and one-way MANOVAS and ANOVAS for the different types of food (plankton, chironomids) under selected experimental conditions are given. The factors were (i) substrate (three levels: sand, pebbles, gravel), (ii) type of competition (two levels: intraspecific and interspecific) and (iii) feeding level (two levels: low food, high food). Significant values are given in bold.

Table 2. Overall model and partial models of food consumption by ruffe in the laboratory experiments.

	Selection conditions		Multivariate approach				Plankton		Chironomids	
Model	Competition	Feeding level	*N*	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Substrate × competition × feeding level			123	4	7.68	**<0.001**	4.62	**0.012**	12.46	**<0.001**
Substrate × competition		High	59	4	3.99	**0.005**	4.85	**0.012**	5.48	**0.007**
Substrate	Intraspecific	High	39	4	0.33	0.86	0.23	0.80	0.53	0.59
Substrate	Interspecific	High	20	4	7.10	**<0.001**	12.19	**<0.001**	11.05	**<0.001**
Substrate × competition		Low	64	4	16.25	**<0.001**	2.35	0.10	39.83	**<0.001**
Substrate	Intraspecific	Low	39	4	5.38	**<0.001**	1.28	0.29	10.36	**<0.001**
Substrate	Interspecific	Low	25	4	18.94	**<0.001**	3.50	**0.048**	58.29	**<0.001**

Summary results of three-way, two-way and one-way MANOVAS and ANOVAS for the different types of food (plankton, chironomids) under selected experimental conditions are given. The three factors were (i) substrate (three levels: sand, pebbles, gravel), (ii) type of competition (two levels: intraspecific and interspecific) and (iii) feeding level (two levels: low food, high food). Significant values are given in bold.

Table 3. Differences in food consumption of perch and ruffe between conditions of intraspecific and interspecific competition (linear contrasts).

Fish	Feeding level	Substrate	*N*	Multivariate *P*	Plankton *P*	Chironomids *P*
Ruffe	High	Sand	21	0.032	**0.009**	0.49
		Pebbles	17	0.10	0.42	0.036
		Gravel	21	**<0.001**	0.14	**<0.001**
	Low	Sand	24	0.044	0.012	0.77
		Pebbles	19	**<0.001**	**<0.001**	**<0.001**
		Gravel	21	0.31	0.50	0.14
Perch	High	Sand	19	0.017	**0.009**	0.22
		Pebbles	19	**<0.001**	**<0.001**	0.41
		Gravel	19	0.017	0.47	**0.003**
	Low	Sand	34	0.21	0.88	0.081
		Pebbles	22	**0.007**	0.25	**0.004**
		Gravel	16	0.10	0.38	0.045

Significant values after a sequential Bonferroni adjustment (Rice 1989) are given bold. Overall significance level for each dependent variable and each fish species is $P < 0.05$.

Discussion

The results show that the feeding patterns of perch and ruffe depend in a complex way on the type of substrate, on the conditions of competition and on the level of food supply. The experimental design, with two fish per tank, allowed different outcomes between the treatments only when there was a marked asymmetry in the effects of intra- and interspecific competition (Underwood 1997). This asymmetry was most pronounced under conditions of high food supply, when perch competed successfully with ruffe. Perch consumed more chironomids than zooplankton on all substrates, whereas ruffe ingested fewer chironomids but a greater amount of zooplankton over coarse substrates. Thus ruffe, as the inferior competitors, showed a diet shift and changed their food preference when exposed to interspecific competition. A similar response was reported for yellow perch (*P. flavescens*), which ingested fewer macroinvertebrates and a higher percentage of microcrustaceans when interspecific competition with pumpkinseed (*Lepomis gibbosus*) increased (Hanson & Leggett 1986).

With high food supply and interspecific competition, perch consumed more chironomids than ruffe on the coarse substrates. Moreover, under these conditions perch consumed more chironomids than when in conditions of intraspecific competition. Hence, for perch, intraspecific competition for food was more severe than interspecific competition with ruffe. The competition must have been based upon interference rather than on exploitation, because in these experiments food supply was high and, at most, 50% of the food was consumed during an experiment.

When food supply was low, the asymmetry between inter- and intraspecific competition was less pronounced. Neither species showed a diet switch, irrespective of the type of competition. This means that under conditions of low food supply, competition for macroinvertebrates between conspecifics and heterospecifics was even stronger and was not alleviated by a diet switch to zooplankton. With interspecific competition, both species consumed fewer chironomids on pebbles and gravel, which suggests that the two species influenced each other in a negative way. Because, on the coarse substrates, neither species could increase its food uptake at the expense of the other, the nature of the competition again seems to be interference rather than exploitative. On sand however, the picture was different. Ruffe consumed more benthic food under low as compared with high food supply with both intra- and interspecific competition. This indicates that ruffe can deal well with interspecific competition on sand and may out compete perch when the food supply is low.

The higher intake of benthic food by ruffe with a low food supply may be caused by the different proportions of benthic prey and plankton at the two feeding levels. The proportion of chironomids to zooplankton was 1:1 in the low food treatments and 1:5 in the high food treatments in terms of biomass and 1:10 and 1:50 in terms of individuals. Ruffe probably spent more time feeding on plankton when relatively more plankton than chironomids was present, i.e., in the high food treatments. When the relative abundance of plankton was lower, ruffe seemed to concentrate more on chironomids, thereby ingesting more chironomids during an experiment in the low food treatments. This might have caused the seemingly paradoxical result of higher food consumption in the low food treatments and probably reflects an optimal foraging strategy in the sense of Werner et al. (1983).

Perch were not negatively affected by ruffe as long as the food supply was high. Under low food conditions however, consumption of perch decreased dramatically, particularly under interspecific competition. For both species, interspecific competition was stronger than intraspecific competition when food supply was low.

Substrate influenced the food consumption of perch only under conditions of high food supply plus intraspecific competition, where the highest food intake occurred on sand. On the coarser substrates, food intake of perch was significantly lower, probably because the chironomids could hide more efficiently in interstitial spaces. Unlike the sand substrate, perch could not dig into the coarse substrates. They therefore needed more time to detect and handle hidden chironomids and thus consumed fewer prey per unit time. The strong effect of habitat complexity on the predation efficiency of perch has been shown in several studies, where structural complexity was represented by submerged macrophytes (Winfield 1986; Diehl 1988; Mattila 1992). The results of the present study suggest that structural complexity should additionally be defined by substrate grain size. Whenever there was substrate-specific consumption of chironomids, most prey items were eaten on sand by both species. This is partly consistent with the results of Fullerton et al. (1998), who observed higher food consumption by both ruffe and yellow perch on sand as compared with cobbles.

The present results, as well as those of other authors, provide insight into the interactions between native Eurasian or yellow perch and non-native ruffe. The application of laboratory data to field situations, however, is subject to a number of limitations. In the first place, perch are visual hunters and depend on good light conditions (Ali et al. 1977; Disler & Smirnov 1977; Helfman 1979), whereas ruffe have a more sensitive lateral line system (Disler & Smirnov 1977; Gray & Best 1989) and are able to feed at low light intensities (e.g., Ogle et al. 1995 and references therein). Bergman (1988) showed that with decreasing light perch, capture rates declined while those of ruffe were less affected, and ruffe were able to feed even in total darkness. The present experiments, carried out under daylight conditions, did not allow ruffe to exploit their advantage over perch with regard to feeding in darkness. However, as ruffe consumed similar amounts of food as compared with perch, and under certain conditions even out competed perch, it is unlikely that the experimental conditions biased the results in favour of perch.

Another abiotic parameter that could also play an important role is temperature. Bergman (1987) reported that with decreasing temperature, prey handling times increased and capture rates decreased for both species, but perch as a thermophilous species was much more affected than ruffe. To take this effect into account, we calculated adjusted consumption rates based on the temperature and density dependence of the capture rates of perch and ruffe according to Bergman (1987). The (M) ANOVA results obtained with these data showed the same effects as the results calculated with the original data. We are therefore convinced that the results of our experiments are not biased by temperature.

The outcome of competition can also depend on differences in body size. In the present experiments, the age-0 perch were bigger than age-0 ruffe. This size difference is, however, characteristic of the situation in Lake Constance, where it can be observed throughout the year (Wang 1994; Rösch & Schmid 1996).

From the results obtained here, a scenario can be sketched how both percids might coexist in Lake Constance and other large lakes in the future, taking into account the effects of decreasing lake productivity. With high food supply, both species will probably coexist on fine substrates, while ruffe will likely be out competed by perch on gravel. Ruffe will therefore forage mainly over sand and pebbles, where their food consumption in competition with perch is higher than over gravel. Perch by contrast may utilise all available substrates, because their food consumption does not depend of substrate type under conditions of interspecific competition and high food supply. With decreasing lake productivity and hence lower food supply, habitat choice of both species will change markedly. Ruffe will forage predominantly over sand, where they are clearly superior to perch. Coarser substrates will then be available to perch, where they can forage under conditions of intra- but not interspecific competition. Through these habitat shifts, which lead to niche separation, both species will be able to achieve the highest foraging efficiency under conditions of low food supply. In summary, the present data demonstrate that the level of food supply and the availability of varied substrate types are crucial for the long-term coexistence of perch and ruffe in large lakes.

It should be noted that this scenario differs from predictions that would emerge from studies where substrate grain size and feeding level have not been considered specifically. During its recent spread, ruffe has colonised large lakes, which are characterised by different types of bottom substrate. Additionally, in several of these lakes, lake rehabilitation measures have already led, or will lead, to decreasing food supply. Therefore, any predictions about the long-term coexistence of both species in such lakes must necessarily be based upon studies that explicitly include these two parameters into the experimental design.

Resumen

1. Hemos estudiado el consumo alimenticio de *Perca fluviatilis* L. y *Gymnocephalus cernuus* (L.) en condiciones de laboratorio. Bajo tratamientos de especies individuales y mezcladas, les ofrecimos, simultáneamente, varios recursos alimenticios alternativos (quironómidos y zooplancton).

2. Analizamos los efectos de la complejidad estructural - representada por el tamaño del sustrato (arena, grava, y guijo) - y del nivel alimenticio, sobre el consumo alimenticio. Pusimos especial atención a la potencial influencia de competidores hetero-específicos sobre los patrones alimenticios de ambas especies, tanto en términos cualitativos como cuantitativos. Además, dado que en un futuro cercano una menor productividad general en lagos debida a re-oligotrofia, probablemente aumente la competición por el alimento en muchos lagos donde ambas especies co-existen, los experimentos se llevaron a cabo bajo niveles de abastecimiento alimenticio alto y bajo.

3. En los experimentos, la aparición de competencia entre *P. fluviatilis* y *G. cernuus* dependió de la abundancia del alimento y de la complejidad estructural del ambiente. El consumo de quironómidos por *P. fluviatilis* dependió del tipo de sustrato a niveles altos de abastecimiento alimenticio pero no a niveles bajos, mientras que en *G. cernuus* observamos lo contrario.

4. Ambas especies cambiaron el consumo alimenticio en presencia de un competidor hetero-específico. A altos niveles de abastecimiento alimenticio, *P. fluviatilis* consumió más bentos que *G. cernuus*. A niveles bajos, el consumo de *P. fluviatilis* decreció substancialmente mientras que el de *G. cernuus* permaneció alto en sedimento fino. Bajo todas las condiciones experimentales analizadas, los mecanismos de competición parecieron ser de interferencia más que de naturaleza explotativa.

5. Finalmente, presentamos un escenario sobre como *P. fluviatilis* y *G. cernuus* pueden competir por alimento bentónico en lagos con variado sustrato de fondo. Sugerimos que a altos niveles de abastecimiento alimenticio, *G. cernuus* forrajee más sobre arena y grava mientras que *P. fluviatilis* puede utilizar todos los sustratos disponibles. Al decrecer el abastecimiento alimenticio por re-oligotrofia, pueden producirse cambios en el hábitat de ambas especies que minimizarán la competencia inter-específica. *G. cernuus* forrajeará básicamente sobre sedimento fino, allá donde sea claramente superior a *P. fluviatilis*. Esta última especie forrajeará predominantemente sobre sedimento más grueso donde se enfrentará a competencia intra- e inter-específica. A través de estos cambios de hábitat, ambas especies podrían alcanzar la mayor eficiencia de forrajeo bajo condiciones de bajo abastecimiento alimenticio.

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