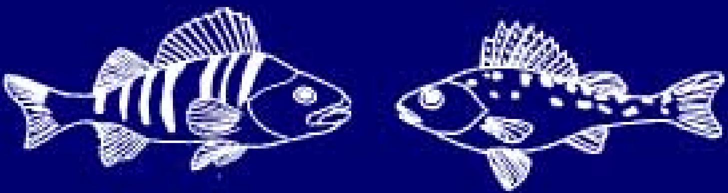
Diana Schleuter

Competition for food between perch (*Perca fluviatilis* L.) and invasive ruffe (*Gymnocephalus cernuus* (L.)) in re-oligotrophic Lake Constance



Cuvillier Verlag Göttingen

Competition for food between perch (*Perca fluviatilis* L.) and invasive ruffe (*Gymnocephalus cernuus* (L.)) in re-oligotrophic Lake Constance

Dissertation

Zur Erlangung des akademischen Grades des
Doktors der Naturwissenschaften (Dr. rer. nat.)
an der Universität Konstanz
Mathematisch-Naturwissenschaftliche Sektion
Fachbereich Biologie

vorgelegt von

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Konstanz, Dezember 2006

Tag der mündlichen Prüfung: 11.5.2007
Referent: Prof. Dr. Reiner Eckmann
Referent: Univ. Doz. Dr. Josef Wanzenböck

Bibliografische Information Der Deutschen Bibliothek
Die Deutsche Bibliothek verzeichnet diese Publikation in der Deutschen Nationalbibliografie; detaillierte bibliografische Daten sind im Internet über http://dnb.ddb.de abrufbar.
1. Aufl. - Göttingen : Cuvillier, 2007
Zugl.: Konstanz, Univ., Diss., 2007

978-3-86727-304-6

Nonnenstieg 8, 37075 Göttingen
Telefon: 0551-54724-0
Telefax: 0551-54724-21
www.cuvillier.de

1. Auflage, 2007
Gedruckt auf säurefreiem Papier

978-3-86727-304-6

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General introduction

Competition for limited resources is one of the most important factors mediating population dynamics and, as a consequence, the distribution and coexistence of species. It is defined as 'The negative effects that one organism has upon another by consuming, or controlling access to, a resource that is limited in availability' (Keddy 2001). In the case of intraspecific competition these effects are strongly density dependent with higher densities leading to reduced growth rates and fecundity (Dash and Hota 1980, Lewis et al. 2001, Lorenzen and Enberg 2002, Thomas and Eckmann 2007). Ontogenetic niche shifts on the other hand can relieve intraspecific competition (Persson and Greenberg 1990, Werner and Gilliam 1984). In the case of interspecific competition, two competing species can only coexist if the competition is not asymmetric or the overlap of the real niches is moderate. Otherwise the superior competitor displaces the inferior (Keddy 2001).

The outcome of competition is strongly influenced by the competitors' abilities and the prevailing environmental conditions. The competitor's abilities are for instance its sensory abilities to detect prey under certain light conditions (Eiane et al. 1997). Other abilities can be its physiological capacities, e.g. to withstand or perform well under certain physical conditions like low temperature or low oxygen content (Bergman 1987) or morphological characteristics, such as a special jaw apparatus to be especially efficient in the exploitation of certain food resources (Liem 1975, Rice and Lobel 2003). Environmental conditions, however, are not stable, but can vary on short- or long-term scales. A short-term variation is for instance the day night cycle, which is coupled to variations in light intensity and temperature. In temperate zones we also find annual variations, which among others affect temperature, water level and nutrient dynamics. A long-term variation in aquatic systems can be the change in trophic status due to eutrophication and re-oligotrophication. This can be observed in Lake Constance and other large pre-alpine lakes (Figure I). Anthropogenic eutrophication increased rapidly from the mid-1950s due to the discharge of untreated or only partially treated sewage, and the run-off of fertiliser, resulting in a change in species composition, increased turbidity or oxygen depletion (Jeppesen et al. 2005, Persson et al.

1991, Wetzel 2001). In the 1960s and 1970s countermeasures were taken such as the installation of sewage treatment plants and the ban of phosphorous-containing detergents. These measures led to decreasing nutrient loads and consequently many of the pre-alpine lakes returned to oligotrophy. With these short- and long-term variations of environmental conditions, however, the advantage that one species gains over another through its particular abilities may also change, affecting which of the competing species is superior.

A stable community composition has often developed over decades or centuries. Some species may have been displaced by their competitors, others may have altered their real niches by changing their habitat or their prey as a consequence of competition (Keddy 2001). When non-indigenous species are introduced into a system, their competitive abilities and their role in predator-prey interactions are key factors determining the fate of both, the non-indigenous and the native species. If a non-indigenous species is capable of establishing a breeding population in its new ecosystem without further intervention by humans, it is in the following regarded as an invasive species. Invasive species can seriously harm and alter the existing community composition and are sometimes a severe threat for the native species (Simon and Townsend 2003). They can, for instance, carry new pathogens, outcompete the native species or heavily prey on them (Lodge et al. 2000, Mooney 2000). The colonisation and establishment of invasive species often follows a so-called boom-bust cycle (Strayer and Malcom 2006). Because natural predators are often missing, invasive species develop high population densities shortly after their introduction, often exceeding sustainable population densities. Intraspecific competition increases, predators may adapt and diseases establish. The population size will decrease again, until it balances at a stable level (Strayer and Malcom 2006, Werner et al. 2005, Wolfe 2002).

Especially in aquatic systems, invasive species have become a prominent problem (Simon and Townsend 2003). Intentional introduction of fish to enrich the present community, to increase yields with commercially attractive species or for bio-manipulation have been popular, disregarding of the price the introduction might have for the ecosystem. The connection of rivers with canals, release of ballast water from ships, the transfer of ships between water bodies especially by tourists, live bait for fishing and to maroon unpopular pets from the aquarium into the wild have rapidly increased the spread of aquatic species (Mooney 2000). Meanwhile, the negative consequences for the native species, such as preying on eggs, outcompeting the native species, or serving as a vector for disease, became apparent. Consequently, the negative impact on the ecosystems and economically negative effects are feared (Lodge et al. 2000). Therefore the mechanisms underlying biotic interactions of invasive and native species have become an important aspect of ecological research to understand and thus predict how invasive species might influence an ecosystem under different environmental conditions (Kolar and Lodge 2001).

This study aims at understanding the mechanisms of competition for food between native perch (*Perca fluviatilis* L.) and invasive ruffe (*Gymnocephalus cernuus* (L.)) in Lake Constance under ongoing re-oligotrophication. In the 1980s the percid ruffe was accidentally introduced into several large lakes, including Lake Superior (USA), Loch Lomond (Scotland) and Lake Constance (Germany) (Maitland and East 1989, Pratt et al. 1992, Rösch and Schmid 1996). In these lakes ruffe rapidly developed high population densities. In Europe Eurasian perch and in North America its sister species yellow perch (*Perca flavescens* (Mitchill)) are commercially important fish species. Therefore fisheries stakeholders feared that ruffe would negatively affect the growth of perch. Both species exploit benthic food sources. Ruffe are specialised benthivorous feeders throughout their life (Hölker and Thiel 1998, Kangur et al. 1999), while the generalist perch undergoes an ontogenetic diet shift and feeds first on zooplankton then on zoobenthos and finally on fish (Radke and Eckmann 2001, Thorpe 1977). Both species occur in the littoral zone of lakes and are assumed to be competitors for food resources (Bergman and Greenberg 1994, Fullerton et al. 1998).

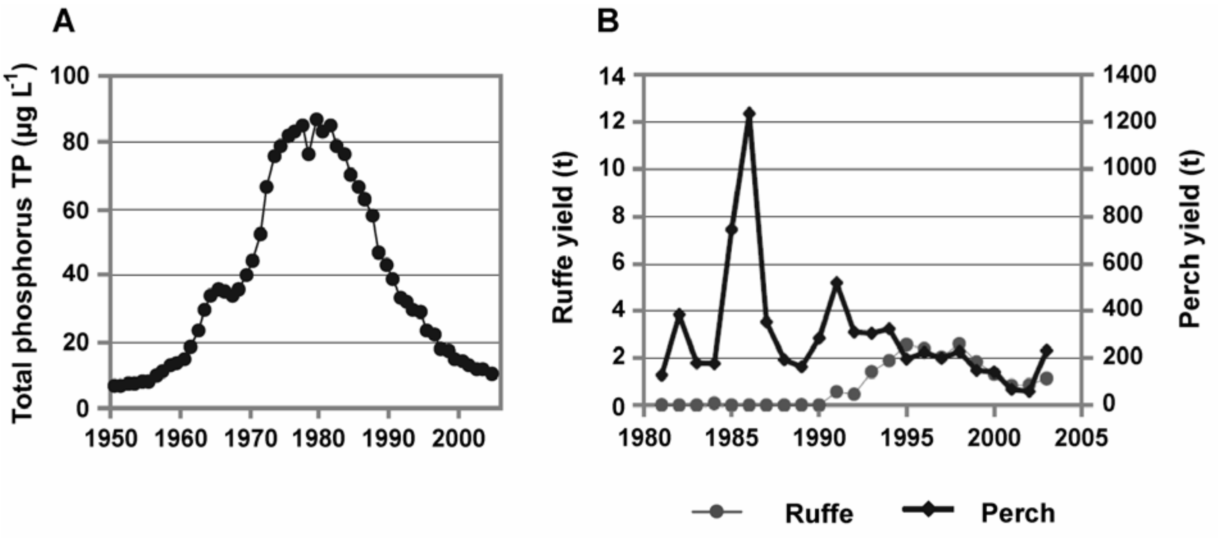

Figure I A Total phosphorus during spring circulation in Upper Lake Constance from 1951 to 2005 (data from IGKB) **B** Yields of perch and ruffe from Upper Lake Constance after the statistics of commercial fishermen from 1980 to 2003 (Source: Rösch and Schmid 2005).

Studies of the fish community composition along the productivity gradient of lakes show that perch is favoured under mesotrophic conditions while ruffe prosper under meso- to eutrophic conditions (Bergman 1991, Jeppesen et al. 2000, Persson et al. 1991). In oligotrophic lakes ruffe is far less abundant than perch or even absent. Ruffe possess a very sensitive lateral line organ and a *tapetum lucidum*, which enables them to feed in a turbid or dark environment (Bergman 1988, Disler and Smirnov 1977, Janssen 1997), conditions expected to increase with increasing trophy (Wetzel 2001). Perch, by contrast, are visually oriented predators, which seem to be in advantage under well-lit, oligotrophic conditions (Diehl 1988, Thorpe 1977). Lake Constance was undergoing re-oligotrophication when ruffe was first detected in 1987. The population developed rapidly and ruffe soon became one of the most abundant fish species in the littoral zone of Lake Constance (Eckmann and Rösch 1998, Fischer and Eckmann 1997a, Rösch and Schmid 2005). Under the mesotrophic conditions at the end of the 1990s ruffe even reached their highest abundances (Figure I). Moreover, during the last 20 years a decline in the growth of perch was observed, which is reflected in reduced perch yields in Lake Constance (Figure I) (Eckmann et al. 2006, Rösch and Schmid 2005). Eckmann et al. (2006) discuss the drastic reduction of nutrient loading accompanied by a decline in zooplankton abundance as main reasons for the decline in growth of perch. Additionally, growth of perch is negatively affected by an increase in pike worm (*Triaenophorus nodulosus*) infections due to a change of the zooplankton community composition towards a higher relative proportion of copepods, the main disease vector (Brinker and Hamers 2005, Eckmann et al. 2006). The competition with ruffe is discussed as an additional explanation, since the decline in growth and yield of perch coincided with the increase of ruffe abundance. Recent observations show, however, declining abundances of ruffe (Reyjol et al. 2005, Rösch and Schmid 2005).

Despite many studies dealing with the competition between perch and ruffe, their competitive abilities and their performance while coexisting in a large oligotrophic lake are not studied in detail so far. The concept of a succession of community composition along a productivity gradient was developed focusing at the low to high productivity gradient. Re-oligotrophication is expected to cause an inverse development of community composition, but the underlying mechanisms are not fully understood. The advantage ruffe may gain over perch due to its sensory abilities under turbid conditions, for instance, appears to be obvious. The decreasing importance of ruffe's sensory abilities with ongoing water clarification, however, cannot fully explain the low abundances of ruffe in oligotrophic lakes.

Concerning Lake Constance some studies regarding the general performances of ruffe and their impact on the native species were carried out. From their field studies and laboratory experiments Rösch and Schmid (1996, 2005) and Schmid (1999) concluded that a negative impact of ruffe on the natural reproduction of whitefish is expected because of egg predation. They assumed further interspecific competition of ruffe with perch to be unlikely, because of perch feeding on zooplankton. They concluded that ruffe had occupied an empty niche. However, the field studies were conducted at the beginning of the 1990s, when Lake Constance was still mesotrophic. Re-oligotrophication has proceeded since then, and due to declining zooplankton abundance perch are likely to include benthos and fish again in their diet as prior to eutrophication. Dieterich et al. (2004a, 2004b) and Dieterich (2004) focused in their experiments on the influence of food availability on the outcome of competition between perch and ruffe over different substrate types. The authors concluded that under natural conditions with limited food resources, ruffe would forage efficiently over fine sediments and perch over coarse sediments.

In this study I conducted laboratory and field experiments to enlighten the mechanisms underlying the interactions between both species under oligotrophic conditions.

In a laboratory study, I investigated the influence of light on the competitive advantage perch and ruffe may gain due to their different sensory abilities under different feeding regimes. In single and mixed species treatments, I fed a limited food ration in three different feeding treatments: food was supplied only during the day, only during the night, or during both, day and night. I measured specific growth rates and analysed the feeding and agonistic behaviour by video recording, to differentiate between exploitative and interference competition. The differences in sensory abilities of perch and ruffe lead to the hypothesis that perch should be the superior competitor in clear, well-lit waters, whereas ruffe should be favoured in an environment with lower light intensity. The results of this study are presented in **Chapter 1**.

The specific growth rates for ruffe I measured in these feeding experiments were up to 3.5 fold as high than growth rates measured by Henson and Newman (2000) under similar conditions. However, both experiments differed in the group size of experimental fish used. Henson and Newman (2000) used only a single ruffe in their experiments, while my experiments were performed with groups of four fish. Further, in preliminary tests for my growth experiments, perch and ruffe both displayed signs of stress and had longer acclimatisation times when only a single fish was in the aquarium. This led to the assumption that there might be a group effect present in both species, which is described for a number of fish species in the literature. Higher oxygen consumption for isolated fish could explain the lower growth rates, as more energy is demanded for the routine metabolism and hence less energy can be invested into growth. To test for a group effect I performed, in cooperation with Susanne Haertel-Borer, respiration experiments with three different group sizes of fish (**Chapter 2**). We used either a single perch or ruffe, or single species groups of four and eight fish. Additionally to the daily oxygen consumption we analysed the activity patterns.

In enclosure experiments I focused on the question whether i. littoral macroinvertebrate communities in a large oligotrophic lake are top-down controlled, ii. fish predation is influenced by competitive interactions, and iii. predatory impacts and competitive interactions are influenced by environmental conditions at the study sites (**Chapter 3**). These experiments were conducted in cooperation with Nicole Scheifhacken, who was responsible for the benthological part of the study. Cages were deployed in the littoral of Lake Constance and stocked with either perch, ruffe, or with both species, or they remained unstocked as controls. Benthos was sampled in each cage before and after the experiments. Fish stomach contents were analysed at the end of experiments. Since environmental conditions in the littoral zone of Lake Constance are very variable, we chose two representative study sites which differ not only in shore morphology and wind exposure but also in benthos abundances and community composition. This enabled us to test the effect of the study site on both predatory impact and competitive interactions.

Parallel to the experiments I accomplished a detailed field study to gain information on the performances of both species in the field and their niche overlap under ongoing re-oligotrophication (**Chapter 4**). The main question concentrated on a possible diet change of perch to include zoobenthos again in its diet, which would result in interspecific diet overlap. I collected data on depth distribution, feeding activity and diet composition at the same two study sites as in Chapter 3. To obtain a fine temporal resolution on a seasonal and diel scale, surveys were carried out monthly from May to October 2004 at three different times of the day. In 2004 line transect scuba diving was performed additionally to the fishing campaigns to gain further information on the species' depth distribution. These data are supplemented by data from additional fishing campaigns I conducted in 2003, 2005 and 2006, to test whether observed patterns were similar over time.

Chapter 1

Competition between perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*): the advantage of turning night into day

DIANA SCHLEUTER AND REINER ECKMANN

Freshwater Biology **51**: 287-297

SUMMARY

1. The outcome of interspecific competition for food resources depends both on the competitors' sensory abilities and on environmental conditions. In laboratory experiments we tested the influence of daylight and darkness on feeding behaviour and specific growth rate (SGR) of two species with different sensory abilities.
2. We used perch (*Perca fluviatilis*) as a visually-orientated, and ruffe (*Gymnocephalus cernuus*) as a mechano-sensory oriented predator and tested their growth rates and behaviour under conditions of interspecific and intraspecific competition. Three different foraging conditions were used: food supplied (i) only during the day, (ii) only during the night or (iii) during both day and night.
3. In perch neither SGR nor feeding behaviour were influenced substantially by interspecific competition during daylight. During darkness their foraging behaviour changed markedly and their access to the food source as well as their SGR were negatively affected by the presence of ruffe.
4. Ruffe's foraging behaviour did not change during either day or night with interspecific competition. During the night ruffe's SGR was higher with interspecific competition, probably due to a release from intraspecific competition and the competitive inferiority of perch during the night.
5. Because of its sensory abilities ruffe feeds predominantly at night, thereby reducing competitive interference from perch.

Introduction

Individuals exploit limited resources against a background of intra- and interspecific competition. The outcome of interspecific competition depends strongly on the sensory abilities and the behavioural plasticity of the species involved. Additionally, an individual's competitive ability may be modulated by environmental conditions, which generally vary across spatial and temporal scales. Light intensity, for example, shows a regular day-night cycle. In aquatic habitats it is additionally affected by turbidity and wave action, and it decreases exponentially with water depth (Wetzel 2001). If two competitors belong to different functional groups such as visual, or mechano-sensory or tactile predators, their competitive success will depend on the competitors' abilities to cope with the particular light conditions and their variation during a 24-h cycle. Eiane et al. (1997) developed a mathematical model describing general competition between fish, as visual and jellyfish as tactile planktivores. Their model demonstrates that the optical properties of the water column are of great importance for the outcome of such competition: visual planktivores outcompete tactile planktivores in clear water with low zooplankton abundance, whereas tactile planktivores gain an advantage with increasing light attenuation. Experimental studies on the influence of the light regime on interspecific competition are, however, scarce.

To elucidate the influence of the light regime in aquatic systems on competition between species with different sensory abilities, we selected two co-occurring percids, namely perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* (L.)), for laboratory experiments. Perch is a mobile, visually-oriented predator (Diehl 1988, Thorpe 1977) that undergoes an ontogenetic diet shift from planktivory through benthivory to piscivory (Collette et al. 1977, Persson 1986, Thorpe 1977). Ruffe in contrast has a very well developed lateral line organ and a light sensitive eye due to a *tapetum lucidum* in the retina (Bergman 1988, Collette et al. 1977, Disler and Smirnov 1977, Gray and Best 1989, Janssen 1997). Ruffe almost exclusively feeds on benthic organisms (Bergman and Greenberg 1994, Collette et al. 1977, Hölker and Thiel 1998, Kangur et al. 1999). The differences in sensory abilities of perch and ruffe leads to the hypothesis that perch should be the superior competitor in clear, well-lit waters, whereas ruffe should be favoured in an environment with lower light intensity. Bergman (1988) demonstrated niche divergence of the two species in Swedish lakes, with perch occurring in the better illuminated zones of the upper littoral and the pelagic, while ruffe were more abundant in deeper zones with lower light intensity, but only in benthic habitat. In Lake Constance, however, both species co-occur in the shallow littoral zone

(Fischer and Eckmann 1997b). This habitat overlap results in a considerable diet overlap, particularly between the juveniles of both species (D. Schleuter unpubl.).

After ruffe was accidentally introduced into large lakes, including Lake Superior (USA), Loch Lomond (Scotland) and Lake Constance (Germany) in the 1980s (Maitland and East 1989, Pratt et al. 1992, Rösch and Schmid 1996), numerous studies have investigated competition between ruffe and perch (or yellow perch *Perca flavescens* (Mitchill)) (Bergman and Greenberg 1994, Dieterich et al. 2004b, Fullerton et al. 1998, Fullerton et al. 2000, Kolar et al. 2002, Savino and Kolar 1996). Nevertheless, the competitive relationship between perch and ruffe is still not fully understood, perhaps partly due to the neglect, in earlier studies, of differences between the two species in their sensory physiology and foraging behaviour during day and night. For example, Fullerton et al. (1998, 2000) conducted 24-h experiments, but with their experimental set-up they could not analyse competition separately for day and night. They found that neither species was a clearly superior competitor. This is in contrast to the results of Savino and Kolar (1996), who observed that ruffe were far more aggressive than perch in laboratory experiments and they assumed that ruffe had a competitive advantage because they spent more time at the feeding station. However, their experiments were carried out only under well lit conditions. The results of Dieterich et al. (2004a, b), who found that perch is the superior competitor on complex substrates (e.g., mussel beds of *Dreissena polymorpha* Pall.), are likewise only representative of daylight conditions. Bergman (1988) has demonstrated, in single species experiments, that food consumption by ruffe is less affected by decreasing light intensity, when compared with perch, but mixed species experiments testing for a competitive advantage of one or the other species as a function of light conditions are still lacking.

Our study investigated the influence of light regime on the competitive abilities of perch and ruffe, assessing foraging efficiency and competitive behaviour of both species in single and mixed species set-ups. Three different foraging conditions were used: (i) fish were fed only during day, (ii) fish were fed only during the night, or (iii) fish were fed during both day and night. We proposed four different scenarios for the outcome of competition between the two species: (I) no competitive advantage for either species, because no competitor is superior either during the day or at night; (II) no competitive advantage for either species, because the competitive superiority of perch during the day is balanced by the competitive superiority of ruffe at night; (III) competitive advantage for one species, because its superiority during either day or night is not balanced by the other species being superior during the other part of the cycle; (IV) competitive advantage for one species, because it is the superior competitor during both phases of the day-night cycle.

Methods

The 1+ perch and 1+ ruffe used in this study were caught in Lake Constance, Germany with a lift net at least five months before the experiments started. The fish were acclimated to laboratory conditions in 100 L aquaria under a natural day-night cycle and they were fed with frozen chironomid larvae.

The experiments were carried out in 72 L aquaria, the bottoms of which were covered with a 2 cm deep layer of sand and pebbles of up to 4 mm particle size. To avoid visual contact between experimental groups, the side walls of the aquaria were covered with black plastic film. The aquaria were supplied with filtered lake water at a rate of 0.4 L min^{-1}, the water temperature was held constant at 19°C, and light from a daylight fluorescent tube was provided from 8:00 to 19:00 local time, so that the room was evenly illuminated with 600 lux. During night, complete darkness (0 lux) was reached through elimination of any source of light. During the experiments the fish were fed with living chironomid larvae, which were obtained from a commercial supplier every week.

To provoke competition for food, fish were fed a suboptimal ration, which was calculated using the model Fish Bioenergetics 3.0 (Hanson et al. 1997). Because the physiology of Eurasian and yellow perch is very similar (Thorpe 1977), the model parameters for yellow perch were considered appropriate for Eurasian perch. Since no bioenergetics model for ruffe was available, the calculations for ruffe were also based on the model parameters for yellow perch. Hence, based on the yellow perch bioenergetics model, 75% ($p = 0.75$) of the maximum daily food ration was provided per day. In the experiments where food was provided during day and night, the daily food ration was separated into two equal halves, otherwise the entire ration was given at one time.

The food was provided in sand filled Petri dishes of 14 cm diameter. The dishes were initially placed in a separate aquarium and each surrounded by a cylinder of gauze, which was slightly taller than the aquarium. Then the weighed (to 0.1 mg) rations of chironomids were poured into the cylinders. The chironomid larvae were allowed to burrow into the sand during daylight or during the night, respectively, then every morning and evening a new feeding dish with the surrounding gauze was introduced into each experimental aquarium. As soon as the chironomids that had not burrowed into the sand (less than 5%) had settled down on top of the sediment, the gauze was removed so that the fish had access to the food source. Differences in borrowing behaviour of chironomids between day and night could not be observed. In treatments where food was provided only once per day, either during the light or the dark period, a sand filled Petri dish without food was introduced in the morning or evening, respectively, a procedure which was adopted to standardise experimental handling across all set-ups. To determine the food consumed during each feeding cycle, the chironomids remaining in the Petri dish at the end of the cycle were picked from the dish by hand and weighed to the nearest 0.1 mg.

The experimental design was fully factorial with two factors at each of three levels: fish species (four perch, four ruffe, two perch plus two ruffe) and feeding regime (only during the day, only during the night, during both day and night). Thus, nine different factor combinations were used, and these were replicated three times, each replicate lasting for three weeks. The treatments were assigned randomly to the aquaria for each replicate.

For behavioural analysis, video recordings were taken of experiments where fish were fed during the day and night with recordings being made for one day during each of the first and the third weeks of the second and third replicates. The aquarium was observed for 24 h, from above, using an infrared sensitive camera and a time-lapse video recorder. At night the visual field of the camera was illuminated with infrared lights ($\lambda > 850$ nm), mounted around the camera lens. In addition to the time lapse recordings, fish behaviour was videotaped through the front wall of the aquarium at 8:00, 8:15, 8:30, 8:45, 9:00, 11:00, 13:00, 15:00, 17:00 for five minutes each time.

For acclimatisation, fish of similar size and weight were transferred to the experimental aquaria one week before an experiment started. To allow for individual analyses of weight gain, fish were anaesthetised with 2-phenoxyethanol (0.3 mL L^{-1}) and marked individually with fin clips. To adapt the fish to the experimental protocol, food was provided in the same way as during the experiments. The experimenter entered the room in the morning and switched on a dim light. The feeding dishes were removed from the aquaria, the fish were gently corralled with gauze frames to the front parts of the aquaria, and the new feeding dishes were put into place. When everything was ready, the gauze frames were removed, the room light was switched on, and the experimenter left the room. In the evening the same procedure was repeated with the room light switched off after the fish were allowed access to the feeding dishes.

On the evening before an experiment started, the fish were anaesthetised, measured to the nearest 0.1 cm and weighed to the nearest 0.1 g, having been starved for 24 h before weighing to ensure that they had empty stomachs (Henson and Newman 2000, Persson 1979). Initial mean standard length of perch was 8.3 ± 0.7 cm, initial mean body mass 8.1 ± 2.0 g (mean ± SD), of ruffe 7.3 ± 0.5 cm and 7.3 ± 1.5 g, respectively. After the three-week experiment the fish were starved for 24 h, anaesthetised and weighed again. The specific growth rate (SGR) for each fish was calculated as: $SGR = (\log_e Y_2 - \log_e Y_1) / \Delta t$, where Y_1 and Y_2 are the initial and final body masses, and Δt is the duration of the experiment in days (Busacker et al. 1990).

The time-lapse video observations were analysed every half hour for 180 s. The variables measured were: frequency of visits to the feeding dish FV (mean number of visits per fish during 180 s), duration of visits to the feeding dish DV (mean time a fish spent at the dish per visit) and total time per fish at the feeding dish TT (mean total time per fish). TT is not simply the product of FV and DV, because the zero values of FV are not included in the calculation of DV. Hence, TT in some cases is lower than the product of FV and DV. Aggressive behaviour was examined from the video recordings through the front wall of the aquarium. Aggression was defined as one fish chasing another with an erect dorsal fin. The number of aggressive acts during five minutes was counted per species. In the mixed species set-ups, aggressive acts against conspecifics and heterospecifics were evaluated separately.

The program JMP 4.0 was used for statistical analysis of the data. All data except for aggressive acts were analysed by one-way ANOVA. In cases of unequal variances, the data were arcsine-transformed (percentage of food consumed) or log-transformed (FV perch). For further comparisons between set-ups (post hoc tests), contrast analysis (ANOVA CA) was used (Bonferroni corrected). Before pooling data across replicates or across time within one experiment, replicates, or time of observation (video recordings during the first or third week of an experiment), were tested as additional factors. For the analysis of food consumption, mean values for an experiment, and for the analysis of feeding behaviour, mean values for the day and the night phases separately were used. Differences between species were tested with t-tests or Kruskal-Wallis ANOVA.

Observations on aggressive behaviour were analysed separately for the first hour after food was given and then for the rest of the day (from 9:00 to 17:00). Differences between inter- and intraspecific competition, single and mixed species treatments and between species were compared with t-tests or Kruskal-Wallis ANOVA.

Results

Both the perch and ruffe adjusted well to the experimental protocol and showed no symptoms of stress after the second or third day of the acclimatisation period. They learnt quickly to look for food in the Petri dishes.

Specific growth rates

The SGRs of perch ranged from 0.28 ± 0.26 (mean ± SD) to 0.42 ± 0.18 in the single species set-ups and from -0.43 ± 0.24 to 0.41 ± 0.34 in the mixed species set-ups (Figure 1.1). The SGRs of the ruffe ranged from 0.69 ± 0.17 to 1.02 ± 0.08 in the single species set-ups and from 0.87 ± 0.15 to 1.43 ± 0.37 in the mixed species set-ups (Figure 1.1). Perch's SGRs were lower in the mixed species set-ups compared to the single species set-ups (one-way ANOVA, $p = 0.020$) and decreasing from the treatment when food was provided only during the day to the treatment when food was provided only during the night (one-way ANOVA, $p = 0.010$). This trend was even more pronounced in the mixed species set-ups: when fed during the day, perch reached growth rates equal to those in the single species treatments (ANOVA CA, $p = 0.931$), but when fed only at night the perch grew less than in all other treatments and lost weight (Figure 1.1). Ruffe, by contrast, grew least when fed only during the day (one-way ANOVA, $p = 0.010$), and they grew better in the mixed species set-up when compared with the single species treatments (one-way ANOVA, $p = 0.003$) (Table 1.1, Figure 1.1).

Table 1.1 Results of one-way ANOVA, testing differences of specific growth rates of perch and ruffe, between species and for each species separately.

Source	d.f.	SQ	*F*-value	*P*-value
Perch				
1-/2-species setup	1	0.401	7.495	0.018
Time of feeding	2	0.753	7.040	0.009
1-/2-species setup × time of feeding	2	0.399	3.732	0.055
Residuals	12	2.195		
Ruffe				
1-/2-species setup	1	0.488	9.106	0.011
Time of feeding	2	0.503	4.692	0.031
1-/2-species setup × time of feeding	2	0.148	1.382	0.288
Residuals	12	1.781		
***Perch, ruffe (single and mixed*)**				
Species	3	6.875	42.818	0.000
Time of feeding	2	0.148	1.384	0.270
Species × time of feeding	6	1.655	5.153	0.002
Residuals	35	9.963		

Thus, the SGRs of perch and ruffe showed opposite trends under interspecific competition. Perch SGR decreased from the day to the night feeding treatment, while ruffe SGR increased. In all treatments the ruffe SGRs were significantly higher than those of perch (t-test, $p < 0.05$) (Figure 1.1).

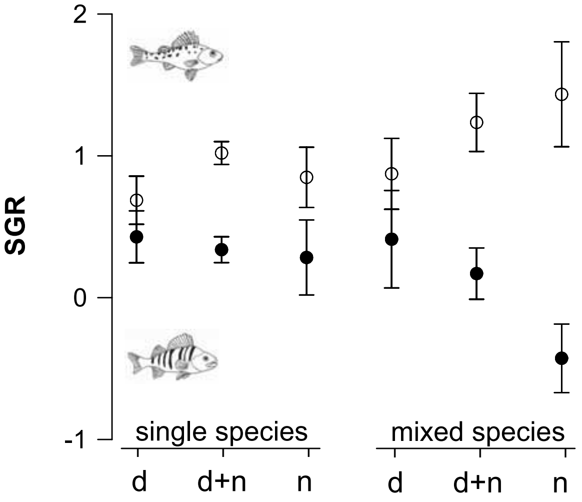

Figure 1.1 Mean (± SD) specific growth rates of perch (closed circles) and ruffe (open circles) in single and mixed species set-ups. d = feeding during the day, d + n = feeding during the day and at night, n = feeding during the night.

Food consumption

The foraging ability of perch was greatly reduced during darkness (Figure 1.2). In the single species treatment, perch consumed nearly all the chironomids (93.3 ± 4.8%; mean ± SD) when food was supplied during the day. However, they consumed significantly less when food was given during the day and night (76.0 ± 8.8%, ANOVA CA, $p = 0.007$), and when food was supplied only during the night (66.2 ± 16.5%, ANOVA CA, $p = 0.000$). In the ruffe and in the mixed species treatments, in contrast, always more than 90% of the chironomids were consumed irrespective of the feeding regime (ANOVA CA, $p > 0.05$) (Figure 1.2).

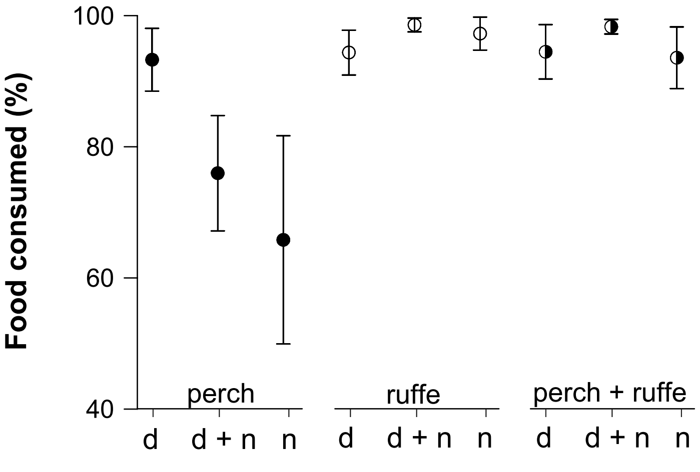

Figure 1.2 Mean (± SD) of the percentage of chironmids consumed in single perch, single ruffe and mixed species treatments. d = feeding during the day, d + n = feeding during the day and at night, n = feeding during the night.

Feeding behaviour

Perch and ruffe showed different feeding behaviours. Perch swam to the feeding dish, inclined the body to pick up the chironomids they had spotted, and returned into a horizontal position in the water column. Quite often, particularly after introduction of the feeding dish, three or four perch approached the dish to feed at the same time. In contrast ruffe swam to the feeding dish and moved slowly around, close to the bottom. In most cases, no more than two ruffe visited the feeding place at the same time.

The different behaviours of perch and ruffe can be described through the variables frequency of visits to the feeding dish (FV) (Figure 1.3A, Table 1.2) and duration of visits (DV) (Figure 1.3B, Table 1.2). For perch, the day values of both variables (mean ± SD) did not differ significantly between the single and mixed species treatments (FV: 2.5 ± 0.7 vs. 2.1 ± 0.5, ANOVA CA, $p = 0.475$; DV: 15.2 ± 7.2 vs. 9.0 ± 3.4 s per fish, ANOVA CA, $p = 0.414$), while the night values did (ANOVA CA, FV: $p < 0.001$; DV: $p < 0.001$).

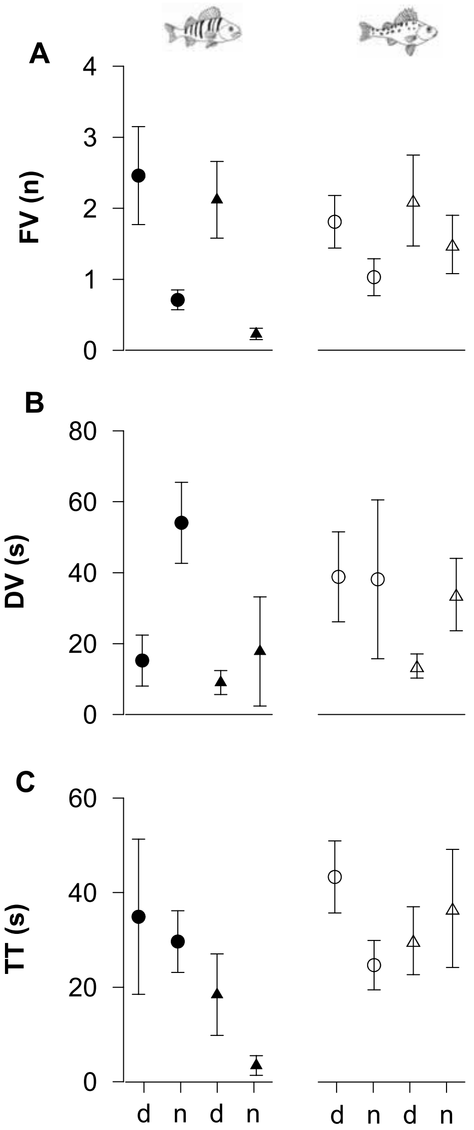

Figure 1.3 Feeding behaviour of perch and ruffe (day + night feeding treatment). **A** Mean (± SD) of the number of visits to the feeding dish per fish per 180 s **B** Mean (± SD) of the duration of visits to the feeding dish per fish per 180 s **C** Mean (± SD) of total time spent at the feeding dish per fish per 180 s. Closed circles = perch in single species set-ups; closed triangles = perch in mixed species set-ups; open circles = ruffe in single species set-ups; ruffe = open triangles mixed species set-ups. d = observation during daytime, n = observation during the night.

Table 1.2 Results of one-way ANOVA, testing differences in feeding behaviour between perch and ruffe. Differences between single and mixed species treatments and the time of day are tested for the number of visits per fish to the feeding dish and time spent there.

Source	**d.f.**	**SQ**	***F*-value**	***P*-value**
Frequency of visits (FV)				
Perch				
Time of day	1	2.287	152.933	0.000
1-/2-species setup	1	0.326	21.823	0.001
Time of feeding × 1-/2-species setup	1	0.197	13.168	0.004
Residuals	12	0.179		
Ruffe				
Time of day	1	1.796	8.583	0.014
1-/2-species setup	1	0.533	2.548	0.139
Time of feeding × 1-/2-species setup	1	0.022	0.106	0.751
Residuals	11	2.302		
Duration of visit (DV)				
Perch				
Time of day	1	2 265.998	21.062	0.001
1-/2-species setup	1	1 803.489	16.763	0.002
Time of feeding × 1-/2-species setup	1	903.754	8.400	0.013
Residuals	12	1 291.045		
Ruffe				
Time of day	1	349.621	2.096	0.176
1-/2-species setup	1	800.678	4.801	0.051
Time of feeding × 1-/2-species setup	1	401.218	2.406	0.149
Residuals	11	1 834.590		
Total time per fish (TT)				
Perch				
Time of day	1	408.242	4.188	0.063
1-/2-species setup	1	1 819.876	18.667	0.001
Time of feeding × 1-/2-species setup	1	94.868	0.973	0.343
Residuals	12	1169.872		
Ruffe				
Time of day	1	129.220	1.671	0.223
1-/2-species setup	1	2.045	0.026	0.874
Time of feeding × 1-/2-species setup	1	13.801	17.031	0.018
Residuals	11	850.824		

When together with conspecifics, perch visited the feeding dish less often during the night than during the day (FV: 0.7 ± 0.1 vs. 2.5 ± 0.7; ANOVA CA, $p < 0.001$), and they spent significantly more time at the feeding place during the night than during daytime (DV: 54.1 ± 11.5 vs. 15.2 ± 7.2 s; ANOVA CA, $p < 0.001$). From the video recordings it was obvious that perch often rested in the feeding dish during the night and sometimes did not move at all during a 180 s observation period.

When together with ruffe, however, the perch visited the feeding dish less often during the night when compared to the single species set-up (FV: 0.2 ± 0.1 vs. 0.7 ± 0.1, ANOVA CA, $p < 0.001$). The time perch spent at the feeding place during nights was similar to the day value, and was significantly lower when compared to the single species set-up (DV: 17.8 ± 15.4 vs. 54.1 ± 11.5 s, ANOVA CA, $p < 0.001$). The total time perch spent at the feeding place did not differ significantly between day and night in the single and mixed species set-ups (Table 1.2). In the mixed species set-up, however, perch tended to spend less time at the feeding dish during the night (TT: 18.4 ± 8.6 vs. 3.5 ± 2.1 s), although the result was not significant (Table 1.2). Altogether perch spent significantly less time at the feeding dish when ruffe were present (Figure 1.3C, Table 1.2).

When comparing the behaviour of these two species it can be seen that in the single species set-ups perch tended to visit the feeding dish more frequently during the day than did ruffe and, in all experiments, perch tended to visit the feeding place less frequently during night. However, the only significant difference was for FV during the night between the mixed species set-ups (t-test, $p < 0.001$) (Figure 1.3A). DVs were generally longer for ruffe than for perch (except for perch during the night in the single species set-up), but they were significantly different only between single species set-ups during daytime (DV: 15.2 ± 7.2 vs. 38.8 ± 12.7 s; t-test, $p = 0.018$) (Figure 1.3B). TT did not differ between species in the single species set-ups (t-test, day: $p = 0.388$; night: $p = 0.329$). When together with ruffe, however, perch TT was significantly lower at night (TT: 3.4 ± 2.06 vs. 36.6 ± 12.5 s.; Kruskal-Wallis ANOVA, $p = 0.021$) (Figure 1.3C).

Aggression

The numbers of aggressive acts (Figure 1.4) did not differ between perch and ruffe in the single species treatments (1.9 ± 1.9 aggressive acts per fish per 5 min for perch vs. 1.8 ± 1.5 for ruffe; Kruskal-Wallis ANOVA, $p = 0.901$) but they decreased for perch and increased for ruffe in the mixed species treatments, although for both species the differences were not significant (Kruskal-Wallis ANOVA, perch: $p = 0.131$, ruffe: $p = 0.855$). When comparing the mixed species set-ups only, perch were less aggressive than ruffe (t-test: $p = 0.050$).

Perch attacked their conspecifics more often than they attacked ruffe (0.9 ± 0.9 vs. 0.3 ± 0.6 aggressive acts; Kruskal-Wallis ANOVA, $p = 0.001$), while ruffe did not discriminate between conspecifics and heterospecifics (1.4 ± 2.1 intra- and interspecific aggressive acts; t-test, p = 0.929). For perch, the number of aggressive acts was similar directly after food supply and later in the day under both experimental set-ups (single species: t-test, p = 0.457; mixed species: Kruskal-Wallis ANOVA, p = 0.491). Ruffe, however, were more aggressive after food supply than later in the day (single species: t-test, p < 0.001; mixed species: Kruskal-Wallis ANOVA, p < 0.001).

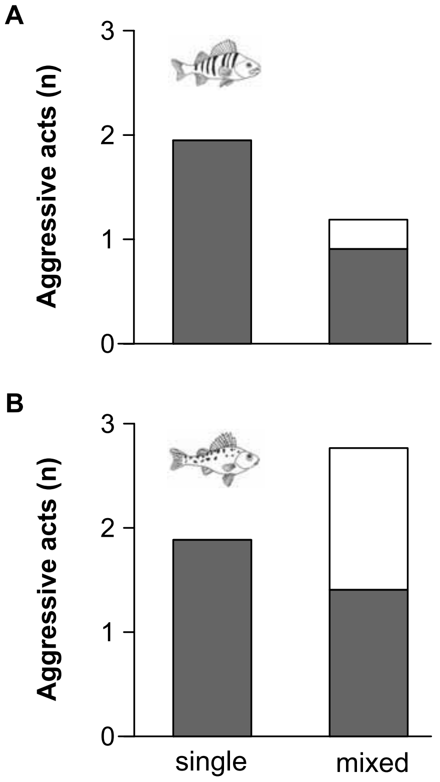

Figure 1.4 Mean number of aggressive acts per fish per 5 min for single and mixed species treatments (day + night feeding treatment). Filled columns show intra-specific aggression, clear columns show interspecific aggression. **A** perch **B** ruffe.

Discussion

The results of this study demonstrate that the outcome of competition for food depends on the competitors' sensory abilities to cope with particular environmental conditions. In the present case, the different abilities of perch and ruffe to detect prey, by visual or mechano-sensory cues respectively, were decisive for the species' feeding success during day and night. During the day neither specific growth rates nor feeding behaviour of perch and ruffe were influenced substantially by interspecific competition. During the night, however, feeding behaviour and specific growth rates of perch were strongly negatively influenced by the presence of ruffe. For ruffe, in contrast, specific growth rates increased with interspecific competition, although there was no significant effect on the variables describing feeding behaviour. Our results therefore supported the hypothesised scenario III, with ruffe being favoured due to its superiority during the night, while perch was an equal but not superior competitor during day.

Several experiments have attempted to understand the feeding behaviour of perch and ruffe in daylight. Our experiments on the feeding behaviour of perch and ruffe in mixed species set-ups did not detect any effect of interspecific competition under daylight conditions, which is similar to the results of Savino and Kolar (1996). Whereas in the experiments of Savino and Kolar (1996) time per visit (DV) and total time (TT) spent at the feeding place decreased for ruffe with interspecific competition, in our study these variables also tended to decrease but the differences were not significant. However, the present study clearly showed how feeding behaviour of both species changed completely during darkness, and that these changes can only be detected when the night is explicitly considered in the experimental design.

Intraspecific competition

In the single species treatments the SGR of perch was reduced when they were fed only at night, most probably due to the small amount of food consumed (66%, cf. Figure 1.2). This is in accordance with the results of Diehl (1988) who observed similar low prey capture rates for perch during darkness. Our behavioural observations revealed reduced activity of perch during the night, with fewer but longer visits to the feeding dish (probably indicating resting behaviour). It is well known from field studies that perch are active during twilight and daytime and that they rest at night (Dörner et al. 1999, Imbrock et al. 1996, Jamet and Lair 1991, Thorpe 1977). Accordingly, field observations of empty stomachs in the morning indicate no food intake during the night (Jamet and Lair 1991, D. Schleuter unpubl. data). In contrast, laboratory studies by, for example, Diehl (1988) and Janssen (1997), like the results presented here, reported food intake by perch during darkness. These observations should, however, be considered as laboratory artefacts caused by the experimental conditions where predators and prey were confined to a rather limited space. Under these conditions it is possible even for a predominantly visually oriented predator such as perch to find prey with its unspecialised - compared with ruffe - lateral line organ (Janssen 1997). For ruffe, which seem to detect their prey with their lateral line organ or through chemoreception rather than through vision, there was no influence of light regime in the intraspecific competition treatments.

Interspecific competition

In the mixed species set-ups the effect of darkness on the feeding behaviour of perch was even more marked than in the single species set-ups. Perch visited the feeding dish even less frequently, but their visits were not longer than during the day because they were chased off by the ruffe. When food was only available during the night, perch seemed unable to consume enough food to meet their daily metabolic costs, leading to negative SGRs. The feeding behaviour of ruffe, in contrast, did not change with competition from perch. Although the total time spent at the feeding dish was the same as for the single species treatments, ruffe achieved higher growth rates in the mixed species treatments. This is probably due to higher food consumption by ruffe under interspecific competition where they consumed at least part of the perch's ration as well. Hence, for ruffe, intraspecific competition had a stronger impact during the night than interspecific competition. In the mixed species set-ups, perch hardly visited the feeding dishes at all during the night, and thus ruffe experienced less competition than in the single species set-ups. Consequently, ruffe gained an additional advantage since they could invest more time in feeding because time needed to defend the food source was reduced.

Bergman (1988), in contrast, observed that the prey capture rate of ruffe decreased with decreasing light level, even though ruffe were less affected by changing light conditions than perch. The discrepancy between these results and our observations is probably due to the different prey organisms used in the two studies. Bergman used two mobile species as prey, *Daphnia magna* and *Chaoborus obsuripes*, while in the present study chironomid larvae were used. The chironomids had buried themselves in the sand where ruffe could easily detect them even in complete darkness by using their lateral line organ while gliding over the sediment (Gray and Best 1989, Janssen 1997).

The fact that both species were equal competitors during the day is surprising. Based upon the model produced by Eiane et al. (1997), perch were expected to be the superior competitor during the day. Furthermore, earlier laboratory studies had shown that perch are more active (Bergman 1987, Bergman 1988, Savino and Kolar 1996) and have higher prey capture rates than ruffe under well lit conditions and at the same temperature (Bergman 1987, Bergman 1988). However, the high capture rates of perch in comparison to ruffe in the studies of Bergman might have been caused also by the readily visible prey types used in her experiments. Savino and Kolar (1996) and Fullerton et al. (2000), in contrast, had already observed that one species was not superior to the other, although Savino and Kolar (1996) observed higher prey capture rates for ruffe. In addition, they measured shorter handling times for ruffe and observed kleptoparasitism. The aggressive behaviour of ruffe is the most likely reason for the lower capture rates by perch. In the present study, ruffe were more aggressive in the presence of perch and addressed their aggression equally to perch and to conspecifics. Perch, in contrast, aimed their aggression mainly at conspecifics, whereby they often restricted their access to the feeding dish. Frequently, the perch chased each other around the feeding dish; meanwhile ruffe were feeding. This kind of interference competition is probably less important in the field, because the daytime activity levels of ruffe were probably higher in our laboratory experiments than under natural conditions. Firstly, the fish had become used to daytime activity, since feeding and handling during acclimatisation to laboratory conditions was mostly conducted during the day, and secondly, the daytime activity of perch might have influenced ruffe activity as well. Most field studies indicate that ruffe mainly feed at night, as can be deduced from full stomachs in the morning and relatively scarcely filled stomachs in evening samples (Jamet and Lair 1991, Ogle et al. 1995). Additionally, low activity of ruffe during daytime was observed in Lake Constance, where ruffe were shoaling under footbridges, macrophytes or artificial reefs, moving very slowly if at all (A. Weber; D. Schleuter, personal observation). However, although agonistic behaviour in nature might be less pronounced compared to laboratory studies, it will still play an important role in competitive interactions, for example during twilight, when both species are active. In previous studies aggressive interactions were often neglected, but we could show the importance of including agonistic behaviour in the analysis of resource competition between perch and ruffe.

In the Swedish lakes sampled by Bergman (1988), perch and ruffe avoided or reduced interspecific competition by the use of different habitats. Perch were found in the lighter, shallower regions of the lake, where they used the pelagic and benthic zones, whereas ruffe were more abundant in the darker parts of the lake where they used the benthic zone. Bergman (1991) and Bergman and Greenberg (1994) suggested that in turbid water ruffe would restrict the access of perch to the common benthic food source, and they showed that ruffe abundance increased with lake productivity.

In Lake Constance both percid species live together in the littoral zone but they have different activity patterns (Fischer and Eckmann 1997b). Perch are active during twilight and during the day, whereas ruffe are active during twilight and at night. Therefore, ruffe can exploit food resources during the night very efficiently, while perch seem to be unable to catch up during day. Food consumption rates of perch during the day might, however, be higher in the field than in our experiments, because the high activity of ruffe during daytime was probably an artefact of the laboratory conditions. However, the results of our night-feeding treatments clearly show that ruffe have an advantage, because their interference competition seems to be greatly reduced due to the resting behaviour of perch during the night. Bergman (1987) found ruffe to be a temperature generalist in comparison to perch. This will play a minor role in Lake Constance, where both species co-occur in the same habitat. In our experiments we used 19°C, which is characteristic of the species' habitat during the growing season.

In conclusion, this study underlines the importance of considering the variability of environmental conditions during the diel cycle when designing laboratory studies aimed at analysing the behavioural mechanisms of resource competition. This is especially important when competitors with different sensory abilities are compared, because competitive success can be strongly dependent on a match between a competitor's sensory abilities and the particular environmental conditions during different periods of the day. For example, the present results demonstrate the advantage that ruffe gain from a sensitive lateral line organ, which allows the fish to avoid interference competition from perch by feeding at night. In contrast to the Swedish lakes, where due to different habitat use of perch and ruffe interference and exploitative competition is reduced (Bergman 1988), in Lake Constance primarily interference competition is alleviated due to different activity patterns.

Acknowledgements

We thank Christine Baderschneider, Anne Berking, Chirstian Bruckner and Oliver Miler for their assistance in the performance of the experiments and the analysis of the video tapes. We further thank Colin Townsend and two anonymous referees whose valuable comments improved the manuscript. This study was supported by the German Research Foundation (DFG) within the Collaborative Research Centre SFB 454 'Littoral Zone of Lake Constance'.

Chapter 2

Respiration rates of Eurasian perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*): lower energy costs in groups

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Transactions of the American Fisheries Society **136:** 43-55

ABSTRACT

The effect of group size on routine metabolic rate (RMR) and activity of the two shoaling percids Eurasian perch (*Perca fluviatilis*) and ruffe *(Gymnocephalus cernuus*) was studied using twin flow intermittent respirometry and time-lapse video techniques. In both species, we found a clear group effect. In isolated fish, oxygen consumption was up to two times as high as in groups of eight fish, with intermediate values in the groups of four fish. RMR was highest during twilight in both species, irrespective of group size. Perch consumed more oxygen and were more active during the day than during the night, whereas ruffe's oxygen consumption and activity were higher during the night than during the day. With increasing group size, the differences between day and night decreased and the diel cycle was less pronounced.

Individual fish may benefit from the presence of conspecifics through a calming effect that reduces their energetic costs. We advise that the social behaviour of a species should be more thoroughly considered when planning behavioural, growth and respiration experiments. As bioenergetic model parameters for many species are based on data gained from isolated fish, we conclude that without considering group size the results of bioenergetic modelling may be severely biased.

Introduction

Environmental factors strongly impact the metabolic costs of animals (Keddy 2001). In fish, these impacts are widely studied through respiration measurements and the influence of abiotic factors such as temperature, salinity, and oxygen depletion on metabolism have been well described (e.g., (Hölker 2003, Ishibashi et al. 2005, Peck et al. 2005, Rao 1968). Among biological factors, the allometry of consumption and respiration are also well analysed (e.g., (Herrmann and Enders 2000, Hölker 2003, Hunt von Herbing and White 2002, Peck et al. 2005). The influence on its metabolism of biotic factors relating to the fish's ecology has, however, rarely been considered. Stress situations such as competition, inadequate habitat or predation risk can increase metabolic costs (Fischer 2000, Huuskonen and Karjalainen 1997, Keddy 2001, Woodley and Peterson 2003). Shoaling, on the other hand, can improve foraging success and reduce predation risk (Magurran 1990, Pitcher 1986, Pitcher and Magurran 1983) and thus may act as a calming, cost reducing factor (Parker 1973).

An influence of group size on their metabolic costs has been found in several fish species (Itazawa et al. 1978, Klyashtorin and Salikzyanov 1981, Parker 1973, Ross et al. 1992, Schuett 1933, Smatresk and Herreid 1980), while it seems to be absent in others (Hölker 2003, 2006, Konchin 1981). Irrespective of these findings, however, growth and respiration rates are often determined in laboratory experiments on single isolated individuals, regardless of the species' social behaviour. The results obtained in these experiments may therefore not be representative of the species' performance in the wild.

Bioenergetic modeling has become an increasingly important tool with which to estimate fish growth or consumption, especially for the management of wild stocks, and the Wisconsin Model (Hanson et al. 1997) has been parameterised for an increasing number of species. Sensitivity analyses have demonstrated that for most species, including yellow perch (*Perca flavescens* (Mitchill)), consumption and respiration parameters are decisive for the model's output (Bartell et al. 1986, Horppila and Peltonen 1997, Kitchell et al. 1977). In a recent evaluation of bioenergetic models for yellow perch Bajer et al. (2003) found strong evidence of deficiencies in estimates of the metabolic rate.

Irrespective of the sensitivity of bioenergetic model outputs to respiration parameters, and the potentially strong group effect on respiration, out of 32 parameter sets listed in Hanson et al. (1997) for different fish species and ontogenetic stages, only 25% are based on respiratory data gained from group experiments (Table 2.1). For solitary species like northern pike (*Esox lucius* L.) respiratory experiments on a single fish are adequate, as experiments with grouped fish would overestimate metabolic rates due to aggressive interactions (Wirtz and Davenport 1976). For shoaling fish species like *Coregonus spp.* or Eurasian perch (*P. fluviatilis* L.), by contrast, respiration rates might be overestimated in experiments with isolated fish. Social behaviour can, however, change during ontogenesis. Reduced metabolic costs were found for example for ayu (*Plecoglossus altivelis* (Temminck and Schlegel)) in visual contact with conspecifics when they were smaller than 9 cm, but when they were larger they started to display aggressive behaviour and metabolic costs increased Umezawa et al. (1983).

In experiments we conducted with Eurasian perch and ruffe (*Gymnocephalus cernuus* (L.)) we also found evidence of a group effect. In preliminary tests for behavioural experiments, perch displayed stressed behaviour, when only a single perch was in the aquaria. When small groups of four fish were used, acclimatisation time was shorter and fish appeared calmer. We further assumed that there is a group effect on the respiration rate of ruffe. Specific growth rates in laboratory experiments with groups of four ruffe (Schleuter and Eckmann 2006), were 3.5 times as high than in comparable experiments by Henson and Newman (2000), who used only single ruffe.

In this study, we therefore focused on the effect of group size on the metabolism of these two shoaling freshwater fish species, Eurasian perch and ruffe. We measured respiration rates and activity in three different group sizes, using single, four and eight fish for both species. With increasing group size we expected decreasing oxygen consumption and activity through a calming effect.

Table 2.1 Sources of input parameter sets for the Wisconsin bioenergetics model for different species and ontogenetic stages of fish, as listed in Hanson et al. (1997). Age: ontogenetic stage the parameter set should be applied to; Source of the parameter set: reference for the model; Source of respiration parameters; Group size in experiments: number of fish used in the respiratory experiments. *n.a.*: original source not available, *RMR*: routine metabolic rate; *SMR*: standard metabolic rate.

Species	Common name	Age	Source of parameter set	Source of respiration parameters	Group size in experiments	Rate measured
Alosa pseudoharengus	alewife	YOY, juvenile, adult	Stewart and Binkowski (1986)	Stewart and Binkowski (1986)	≥ 2	RMR
Chrosomus spp.	dace	adult	He (1986)	*n.a.*	?	?
Clupea harenus	herring	juvenile, adult	Rudstam (1988)	Stewart and Binkowski (1986)	≥ 2	RMR
				Desilva and Balbontin (1974)	9-11	Growth
Coregonus hoyi	bloater chub	adult	Rudstam et al. (1994)	Bernatchez and Dodson (1985)	1	SMR
Coregonus spp.	coregonids	YOY, juvenile, adult	Rudstam et al. (1994)	Bernatchez and Dodson (1985)	1	SMR
Cynoscion regalis	weakfish	age-0	Hartman and Brandt (1995)	Hartman and Brandt (1995)	1	RMR
Cynoscion regalis	weakfish	≥ age-1	Hartman and Brandt (1995)	Hartman and Brandt (1995)	1	RMR
Esox lucius	northern pike	adult	Bevelhimer et al. (1985)	Bevelhimer et al. (1985)	1	RMR
Esox masquinongy	musekellunge	adult	Bevelhimer et al. (1985)	Bevelhimer et al. (1985)	1	RMR
Lates niloticus	Nile perch		Kitchell et al. unpubl.	? (unpublished)	?	?
Lepomis macrochirus	bluegill	juvenile, adult	Kitchell et al. (1974)	McComish (1970)	≥ 1	?
				Pierce and Wissing (1974)	1	RMR
Micropterus dolomieui	smallmouth bass	adult	Shuter and Post (1990)	Shuter et al. (1989)	25	Starvation
Micropterus salmoides	largemouth bass	adult	Rice et al. (1983)	Beamish (1970)	1	SMR
Morone saxatilis	striped bass	≥ age-1	Hartman and Brandt (1995)	Hartman and Brandt (1995)	1	RMR
Morone saxatilis	striped bass	age-0	Hartman and Brandt (1995)	Hartman and Brandt (1995)	1	RMR
Morone spp.	striped bass	larvae	Johnson (1995)	*n.a.*	?	?
Onchorynchus mykiss	steelhead	adult	Rand et al. (1993)	Rao (1968, 1971)	1	SMR
Onchorynchus nerka	sockeye	adult	Beauchamp et al. (1989)	Brett (1965)	1 (age-0 up to 10)	SMR
Oncorhynchus gorbuscha	pink	adult	Beauchamp et al. (1989)	Brett (1965)	1 (age-0 up to 10)	SMR

Species	**Common name**	**Age**	**Source of parameter set**	**Source of respiration parameters**	**Group size in experiments**	**Rate measured**
Oncorhynchus kisutch	coho salmon	adult	Stewart and Ibarra (1991)	Rao (1968, 1971)	1	SMR
Oncorhynchus tshawytscha	chinook salmon	adult	Stewart and Ibarra (1991)	Rao (1968, 1971)	1	SMR
Osmerus mordax	smelt	YOY, juvenile, adult	Lantry and Stewart (1993)	Lantry and Stewart (1993)	1-15	RMR
Perca flavescends	yellow perch	adult, juvenile	Kitchell et al. (1977)	Solomon and Brafield (1972)	1	RMR
Perca flavescens	yellow perch	larvae	Post (1990)	Solomon and Brafield (1972)	1	RMR
Petromyzon marinus	sea lamprey		Kitchell and Breck (1980)	Beamish (1973)	1	SMR
Pomatomus salatrix	bluefish	YOY, juvenile, adult	Hartman and Brandt (1995)	Hartman and Brandt (1995)	1	RMR
Salvelinus namaycush	lake trout	adult	Stewart et al. (1983)	Stewart et al. (1983)	1 (small: 3, very small: 20)	SMR
Sarotheradon spp.	tilapia	adult	Nitihamyong (1988)	*n.a.*	?	?
Stizostedion vitreum	walley	adult	Kitchell et al. (1977)	Solomon and Brafield (1972)	1	RMR
Stizostedion vitreum	walley	juvenile	Madon and Culver (1993)	Madon and Culver (1993)	1-14 depending on body size	RMR
Theragra chalcogramma	walley pollock	adult	Mason et al. unpubl.	*n.a.*	?	?
Theragra chalcogramma	walley pollock	juvenile	Mason et al. unpubl.	*n.a.*	?	?

Methods

The fish used in the experiments were caught in Lake Constance, Germany, with a portable, hand operated lift net (area: 1 m^2; mesh size: 4 mm), at least two months before the experiments started. The fish species were kept separately in 100 L aquaria under the natural day-night cycle. For acclimatisation to experimental conditions, the fish were moved to the experimental room at least two weeks before they were used in the experiments. Until the experiments started they were held in 100 L aquaria under the same day-night cycle and temperature conditions as in the experiments and were fed with live chironomid larvae.

Experimental set-up

Respiration measurements were carried out in an intermittent, twin flow respirometer as described in detail by Fischer (2000). Two circular respiration chambers of transparent Plexiglas (diameter: 29 cm, height: 15 cm, respiratory volume: 9 933 mL minus the fish volume) were placed in parallel in a 1 000 L aquarium (1.5 m × 0.5 m basedimensions) at a constant temperature. A barrier of black polyethylene was placed between the two chambers to avoid visual contact between the two experimental groups. Oxygen saturated water (100%) was supplied from a reservoir above the respiration chambers and the inflow into the chambers was regulated by computer-controlled solenoid valves. Oxygen concentration in the chambers was maintained between 8.6 and 8.2 mg L^{-1}, which corresponded to saturation levels of 96 and 92%, respectively, at the water temperature of 19.4 ± 0.5°C (mean ± SD). Oxygen concentration was measured every 10 s with polarographic oxygen probes (WTW OXY-325). Daylight conditions were provided from 7:00 to 19:00 hours. To simulate twilight, the experimental room was illuminated with a dim light for half an hour before and after the daylight period. During the night, the chambers were illuminated by infrared lights ($\lambda = 910$ nm) to enable 24-h video recording for activity measurements. The microprocessor controlling and recording oxygen, and the video recorder, were outside the experimental room. Thus, the experimenter had to enter the room during the experiment only once a day to feed the fish kept for later experiments.

Three different group sizes of each species were tested (single, four and eight individuals), each in three replicates. The experiments were started in the morning. Experimental fish were chosen randomly from the holding aquaria, weighed and measured to the nearest 0.1 g and 0.1 cm, respectively. Mean total length and mass were 9.5 ± 0.3 cm (mean ± SD) and 7.4 ± 1.0 g in perch, and 9.2 ± 0.5 cm and 8.8 ± 1.6 g in ruffe. The mean body mass of the individual fish did not differ between the groups (ANOVA: $F_{[2, 36]} = 0.521$, $p = 0.599$ (perch); $F_{[2, 36]} = 0.584$, $p = 0.563$ (ruffe)). The fish were then randomly introduced into one of the two respiration chambers through a gate valve in the cover. The fish were fed for the last time 24 h before an experiment started. The respiration of the fish was measured for two consecutive days: the first day was assigned as acclimatisation to the respiration chamber (acclimatisation day); the second day was used as measurement day to determine routine metabolic rate (RMR) as that of an unfed fish with spontaneous activity (Brett 1962, Herrmann and Enders 2000) and standard metabolic rate (SMR), defined as the minimum oxygen consumption for intact, absolutely quiescent, unfed fish (Fry 1971). Each fish was used only once in the experiments. Before and after each experiment, bacterial respiration was measured for at least 2 h during day and during night time for later correction of the respiration rates of the fish. To keep bacterial respiration low (mean bacterial respiration was 15% of total respiration), the chambers were cleaned after each experiment with hydrochloric acid (10%) and all tubes were flushed with ethanol (100%) for at least 15 min.

For activity measurements, each chamber was video-taped from below during the measurement day, with infrared sensitive cameras for 15 s every 16 min during twilight and every 32 min during day and night. The video recordings were analysed by placing a quadratic grid of 5 × 5 squares on the monitor and counting the movements between squares per time, in slow motion replay. A fish's movement was counted as a transition between squares when both eyes had crossed a grid line. In the groups of eight fish, four fish were chosen randomly at the beginning of each sequence and followed individually over 15 s, otherwise all fish in the chamber were analysed. Due to technical problems, we could not analyse the night time activity data for all the replicates with eight ruffe and partly for one replicate each of the single and four fish set-ups of both species.

Data analysis

To calculate respiration rates in $mgO_2\,kg^{-1}\,h^{-1}$, each data set was smoothed in order to eliminate outliers and to reduce system-induced fluctuations of the high-resolution oxygen measurement system (e.g., through sensor accuracy and from electrical interference through the power supply of the laboratory) by a running median procedure over six values (60 s), followed by a running mean procedure over eight values (80 s) (Fischer 2000). Based on these smoothed data, the decrease of oxygen concentration over time was calculated with a running regression analysis over eleven values, each value now representing 110 s. The respiration rates were finally calculated from the slopes of the regressions, corrected for bacterial respiration, and standardised to milligram oxygen per kilogram fish weight per hour, and assigned to the median of the time base of each regression.

The RMR and activity data were analysed for the effects of group size and phase of the day (day, dusk, night and dawn), separately for each species, by analysis of variance (ANOVA). For post hoc comparisons of the means contrast analysis (ANOVA CA) was used. The overall significance level was maintained by a sequential Bonferroni adjustment (Rice 1989). In case the assumption of normality (Kolmogorov-Smirnov test) and equal variances (Bartlett's test) were not met, the non-parametric Kruskal-Wallis test was applied (Bonferroni corrected when used as post hoc test). To test for differences in overall daily respiration between group sizes, we averaged their RMR over 24 h on the bases of hourly medians, except for the twilight conditions, where half-hourly medians were used. This test was computed for the acclimatisation and the measurement day. All other analyses were restricted to the measurement day. The effects of the time of day (day, night, dawn, dusk) and the group size (1, 4, 8) on RMR and activity were analysed comparing the medians of each phase of the day. A multiple linear regression analysis was computed to determine the dependency of the RMR on the activity.

SMR was calculated after Herrmann and Enders (2000) and Hölker (2003) as the median of the lower 10% of the respiration rates (each covering a 110 s period after smoothing) observed during the measurement day of each replicate.

For raw data processing (running mean, median, regression) and calculation of mean respiration rates or activities, the program SAS/IML, and for statistical analysis the program JMP 4.0 were used.

Results

Group size affected both the variance and the frequency distribution of respiration rates throughout the measurement day (Figure 2.1). With decreasing group size, the range of respiration rates was broader and they were more evenly distributed. The frequency distribution of the respiration rates in groups of eight and four perch had a well defined maximum around 180 $mgO_2\,kg^{-1}\,h^{-1}$, whereas the distribution of the single perch rates was broader, showing no clear peak. Maximum respiration rates were 410, 565 and 1 150 $mgO_2\,kg^{-1}\,h^{-1}$ for group sizes of eight, four and one perch, and 80% of the values lay between 109 and 228, 170 and 370, and 73 and 569 $mgO_2\,kg^{-1}\,h^{-1}$, respectively. For ruffe, relative frequencies of respiration rates were similarly influenced by group size. Groups of eight and four ruffe displayed clear peaks in the frequency distributions around 160 and 200 $mgO_2\,kg^{-1}\,h^{-1}$ and highest respiration rates were 456 and 514 $mgO_2\,kg^{-1}\,h^{-1}$, respectively. For single ruffe the distribution was more variable with a less pronounced peak and a maximum respiration rate of 994 $mgO_2\,kg^{-1}\,h^{-1}$. For the different groups of eight, four and one ruffe, 80% of the values fell between 118 and 216, 135 and 269, and 118 and 462 $mgO_2\,kg^{-1}\,h^{-1}$, respectively.

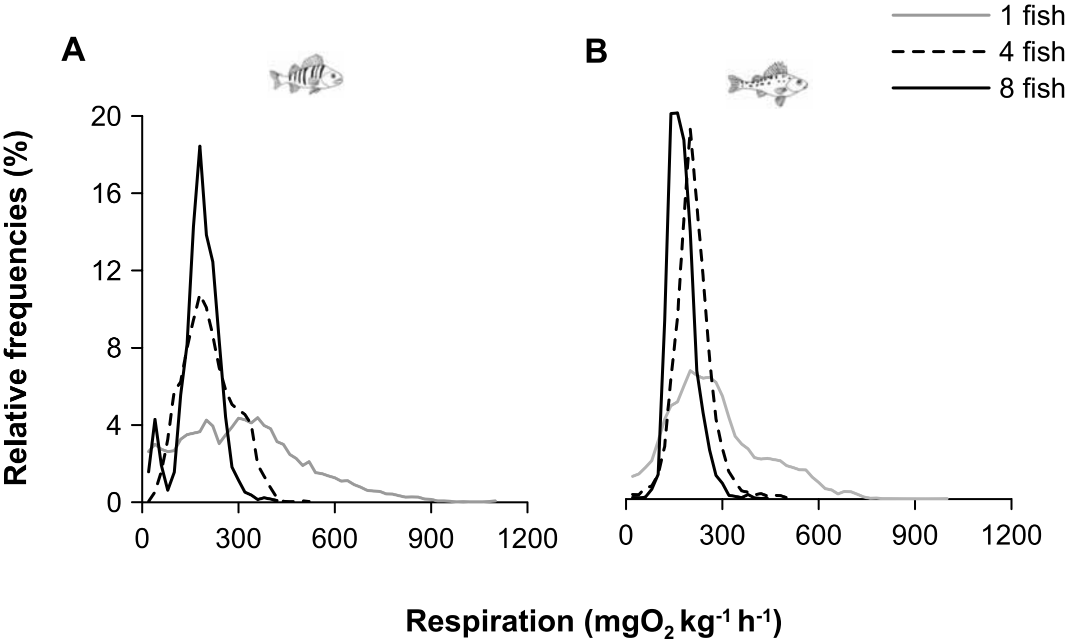

Figure 2.1 Relative frequencies of respiration rates determined for sequential 110 s periods on the measurement day for different group sizes of **A** perch and **B** ruffe. Respiration rates are pooled into classes of 20 mgO_2 per kilogram of fish weight per hour (i.e. 0 to 20 $mgO_2\,kg^{-1}\,h^{-1}$, 20 to 40 $mgO_2\,kg^{-1}\,h^{-1}$, and so forth).

RMR averaged over 24 h differed with group size in both species (Figure 2.2). Mean daily oxygen consumption was always highest for the single fish and lowest, for fish in groups of eight. RMRs for groups of four fish were intermediate. For perch this group effect was significant on both the acclimatisation day (ANOVA: $F_{[2,6]} = 9.837$, $p = 0.013$) and the measurement day (ANOVA: $F_{[2,6]} = 11.238$, $p = 0.009$). For ruffe, by contrast, the group effect was most pronounced on the acclimatisation day (ANOVA: $F_{[2,6]} = 40.246$, $p < 0.001$), with the oxygen consumption of the single fish being more than twice that of a fish in the group of eight. On the measurement day the influence of group size on RMR averaged over 24 h was only significant at the 10% level (ANOVA: $F_{[2,6]} = 4.269$, $p = 0.070$).

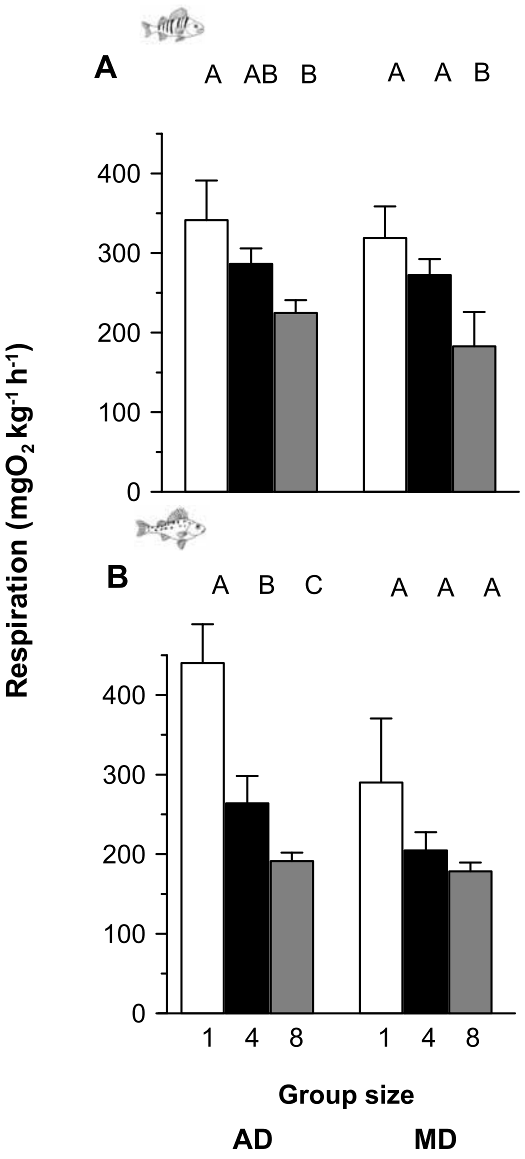

Figure 2.2 Mean ± SD routine metabolic rate (RMR) integrated over one day ($mgO_2\,kg^{-1}\,h^{-1}$) for **A** perch **B** ruffe. AD: Acclimatisation day, MD: Measurement day. Different letters within one day indicate differences of routine metabolic rate between group sizes (ANOVA CA: $p < 0.05$).

For both species, RMR displayed a clear diel cycle (Figure 2.3A) and time of day significantly influenced RMR (Table 2.2). Independent of group size, perch RMRs were lower during the night than during day and twilight (ANOVA CA: $p < 0.05$, Table 2.2). Although oxygen consumption increased slightly during twilight compared to daylight conditions, this increase was not significant. Diel variation of ruffe RMRs, by contrast, depended on group size (Table 2.2). Respiration tended to be lowest during the day and highest during twilight, however, if the ruffe were in a group, the diel cycle was less pronounced. In single ruffe, the diel cycle was more pronounced than in groups of four and eight, and respiration during dawn was significantly higher than during the other phases of the day (ANOVA CA: $p < 0.05$, Table 2.2).

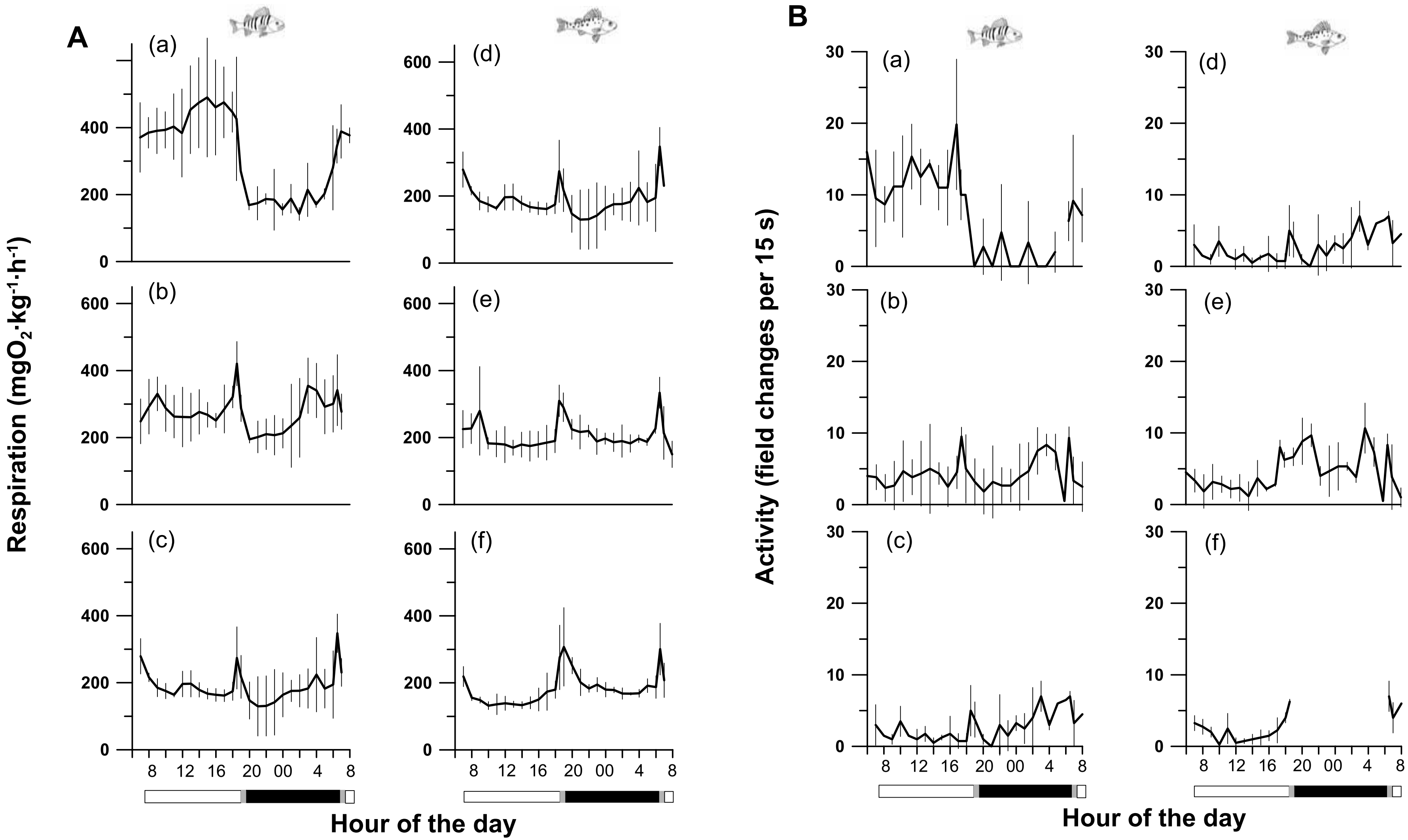

Figure 2.3 **A** Mean ± SD routine metabolic rate (mgO$_2$ kg^{-1} h^{-1}) **B** Mean ± SD of activity (raster changes n per 15 s) of perch and ruffe within different group sizes during measurement day. a-c perch, d-f ruffe; top (a, d) 1 fish, middle (b, e) 4 fish, bottom (c, f) 8 fish. The horizontal bar indicates different phases of the day: white = day, grey = twilight, black = night.

Table 2.2 Results of ANOVA for the effects of the four phases of the day (day, dusk, night, dawn), and the three group sizes (1, 4, 8) on routine metabolic rate (RMR; $mgO_2 kg^{-1} h^{-1}$) and activity (number of field changes per 15 s) during measurement day.

Source	**d.f.**	**SQ**	***F*-value**	***P*-value**
Perch				
Respiration				
Time of day	3	161 803	9.134	0.001
Group size	2	64 964	5.501	0.012
Time of day × group size	6	77 782	2.195	0.084
Residuals	21	124 002		
Activity				
Time of day	3	191.161	8.524	0.001
Group size	2	92.722	6.202	0.008
Time of day × group size	6	166.810	3.784	0.011
Residuals	20	149.500		
Ruffe				
Respiration				
Time of day	3	221 742	21.410	0.000
Group size	2	119 380	17.290	0.000
Time of day × group size	6	93 808	4.529	0.004
Residuals	23	79 404		
Activity				
Time of day	3	123.528	10.343	0.000
Group size	2	292.604	36.748	0.000
Time of day × group size	6	43.896	1.838	0.143
Residuals	20	79.625		

The pattern of activity (field changes per 15 s) during the course of the day (Figure 2.3B) was similar to the pattern of the RMR. In both species, activity was significantly affected by group size and time of day (Table 2.2) with generally highest activity for the isolated fish compared to fish in groups. In perch, activity during the course of the day interacted with group size (Table 2.2): in single perch, activity was highest during the day and at dusk, and lowest during the night (ANOVA CA: $p < 0.05$), while dawn activity was intermediate. With increasing group size, activity was less variable during the course of the day. In groups of four perch, activity tended to be highest during twilight (ANOVA CA: $p < 0.05$; not significant after Bonferroni correction), and did not differ between day and night, while in groups of eight, the fish did not display a clear activity pattern. In ruffe the diel pattern of activity and group size did not interact (Table 2.2). Ruffe were less active during the day (ANOVA CA: $p < 0.05$) and their activity did not differ between twilight and night.

A positive relationship was found between RMR and activity in both species and can be expressed through a linear regression (Figure 2.4). The coefficient of determination (R^2) in perch was 0.62, while for ruffe it was 0.42. These regressions can thus only partly explain the effect of group size on RMR via decreasing activity.

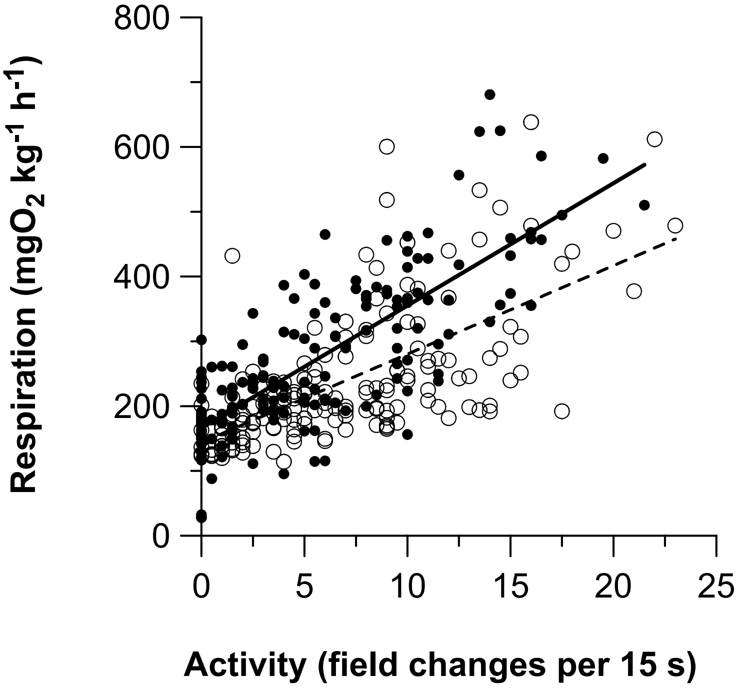

Figure 2.4 Regression between routine metabolic rate and activity. Values are based on the hourly medians of the measurement day. Closed circles, solid line: perch ($Y = 18.88 \times X + 166.37$; $R^2 = 0.62$) open circle, dashed line: ruffe. ($Y = 13.65 \times X + 143.90$; $R^2 = 0.43$)

To test for effects of group size on respiration other than different activity patterns, RMR at low activity levels (very low activity: 0 transitions per 15 s, low activity: 1 to 5 transitions per 15 s) were compared between group sizes, for day and night separately. This comparison between different group sizes still revealed significantly lower RMRs for groups of eight fish (Figure 2.5). During the day, the oxygen consumption of inactive fish (activity level 0) was higher for the isolated fish than in groups of eight, while respiration of fish in groups of four was intermediate. However, these differences were only significant for ruffe, probably due to the small sample size of inactive solitary perch (Kruskal-Wallis test: $\chi^2_{[2,7]} = 4.208$, $p = 0.122$ (perch); $\chi^2_{[2,9]} = 8.827$; $p = 0.012$ (ruffe)). In little active fish (activity level 1), the oxygen consumption for groups of eight was significantly lower compared to the single fish and the group of four for both species (Kruskal-Wallis test: $\chi^2_{[2,34]} = 17.286$, $p < 0.001$ (perch); $\chi^2_{[2,52]} = 16.157$; $p < 0.001$(ruffe)). At night this pattern changed: in little active perch the largest group still had the lowest RMRs, perch in the group of four, however, tended to have highest RMRs, and the single fish were intermediate (Kruskal-Wallis test: $\chi^2_{[2,21]} = 6.803$; $p = 0.033$). Although the trend was similar for inactive perch, group size did not influence respiration significantly (Kruskal-Wallis test: $\chi^2_{[2,30]} = 4.046$, $p = 0.132$). There are no data for ruffe during night, because they were more active during darkness (Figure 2.3B) and thus low activity levels were rarely observed.

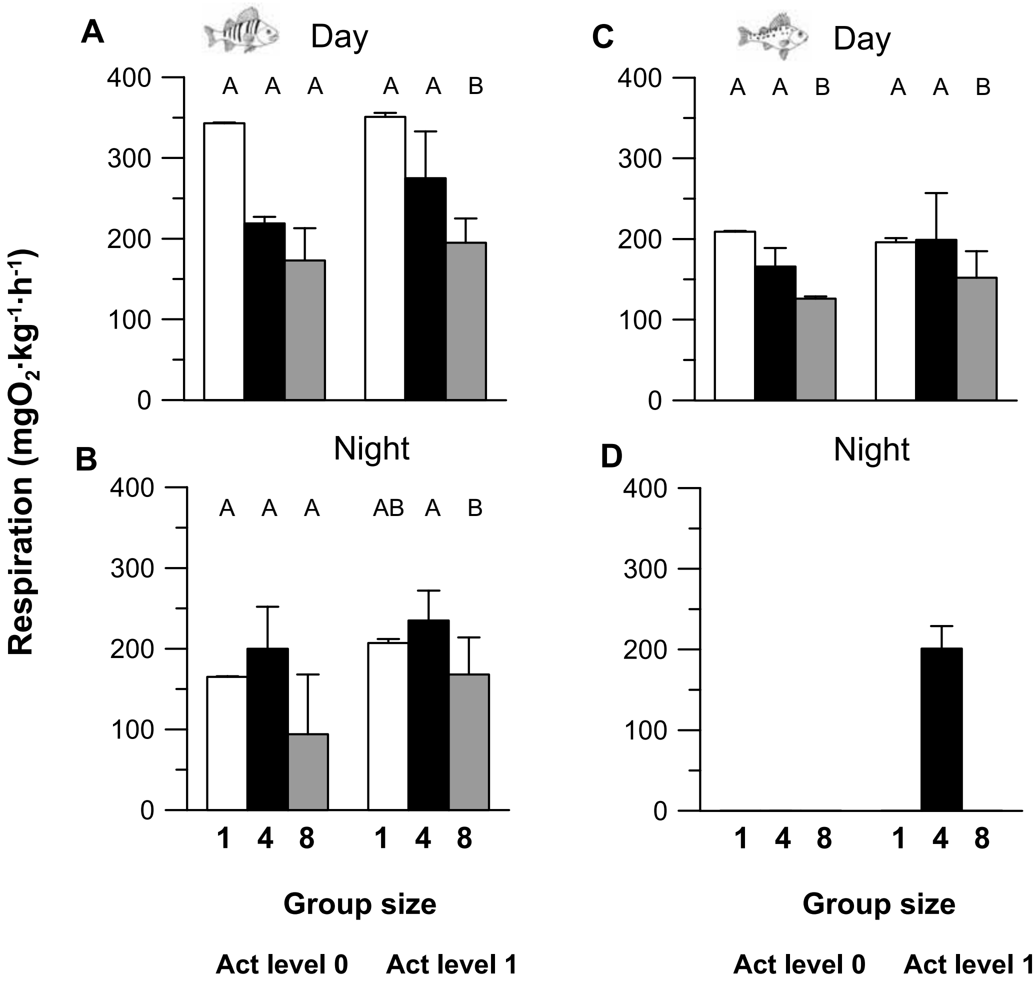

Figure 2.5 Mean ± SD of hourly based routine metabolic rates for different group sizes at the activity level 0 (very low movement, 0 grid line transitions) and the activity level 1 (low movement, 1-5 grid line transitions): **A** perch day **B** perch night **C** ruffe day **D** ruffe night. Different letters within one activity level indicate differences between RMRs of different group sizes within one day (Kruskal-Wallis test: $p < 0.05$).

SMR, the minimum oxygen consumption of an absolutely quiescent, fish, was 36 ± 2 $mgO_2\,kg^{-1}\,h^{-1}$ (mean ± SD) for perch and 90 ± 59 $mgO_2\,kg^{-1}\,h^{-1}$ for ruffe. SMR was derived from the experiments with single fish, because in the experiments with groups of fish respiration rates measured were higher and thus not representative of SMR (perch: 154 ± 40 and 96 ± 67 mg O_2 kg^{-1} h^{-1} for group sizes 4 and 8; ruffe: 118 ± 54 and 108 ± 11 mgO_2 kg^{-1} h^{-1} for group sizes 4 and 8). We hold a methodological bias responsible for this result: With more fish in the chamber the probability that all fish are absolutely motionless at the same time decreases.

Discussion

We found a clear effect of group size on RMR and activity of juvenile perch and ruffe. For both species weight-specific RMR and activity decreased with increasing group size. In isolated fish, metabolic costs were up to two times higher than in groups of eight fish. This confirms the results of Geyer and Mann (1939) who found reduced metabolic rates when placing three perch instead of one in a respiratory chamber. We also demonstrated that this decrease of RMRs is partly caused by decreased activity in groups and, additionally, we found evidence of a calming effect. Decreasing activity with increasing group size was observed by Schleuter (2002), who studied the activity of juvenile perch in groups of 10, 20 and 40 fish in laboratory experiments and the calming effect of group size on respiration rates and activity is also known from other species (respiration: Itazawa et al. 1978, Parker 1973, Ross et al. 1992, Schuett 1933, Umezawa et al. 1983; activity: Anras et al. 1997, Fitzsimmons and Warburton 1992). In our study, respiration was positively correlated with activity, suggesting that the individual fish could benefit from the presence of conspecifics through a calming effect that reduced activity and energetic costs.

Decreased RMRs can, however, only partly be explained by decreased activity (R^2 perch: 0.62, ruffe: 0.42), so an additional 'psychological', calming effect seems to exist. Shlaifer (1939) attributed higher rates of oxygen consumption in isolated fish to 'psychic unrest'. Parker (1973) quoted this term and was the first to describe the soothing effect of groups as a 'calming effect'. As individuals in groups are less vulnerable to predators (Magurran 1990, Pitcher 1986), sedation through the presence of conspecifics is reasonable. As early as 1934, Welty observed, in experiments on group behaviour in fish, that the group had a quietening effect on the individuals. Fright reactions were more common among isolated fish, while fish in groups moved more quietly. In field experiments, sea bass (*Dicentrarchus labrax* L.) not only decreased their activity when in groups, but switched from nocturnal to daytime activity (Anras et al. 1997). The foraging during darkness of a single fish can be explained by predator avoidance behaviour, while grouped fish could calmly forage during daylight. In the experiments done by Fischer (2000), demersal burbot (*Lota lota* (L.)), which were not able to hide in adequate substrate and were thus more exposed to potential, but not actually present, predators, had elevated oxygen consumption rates and, as in our study, oxygen consumption rates were elevated independently from activity.

Several results in our study emphasise the ‘psychological’ calming effect of groups. First, differences in RMRs between different sized groups were more distinct during acclimatisation than on the RMR day. Especially in ruffe, oxygen consumption on the acclimatisation day was elevated more for single and four group fish, while that of eight group fish remained rather similar. This agrees with the findings of Klyashtorin and Salikzyanov (1981) and indicates that stress situations, such as handling and new environments, seem to be better overcome in company. Second, in our experiments, the group effect was still present within a given activity level during daytime, indicating that activity is not the only determinant of respiration. During darkness, however, this group effect did not follow the daytime pattern in perch, as fish in groups of four had the highest RMRs. As it is known for other fish (Shlaifer 1939, Umezawa et al. 1983), the group effect in perch seemed to be induced by visual contact with conspecifics. Field data on the behaviour of perch confirm that perch form shoals during twilight and daytime, but during darkness shoals break up and fish rest on the bottom (Imbrock et al. 1996). For ruffe we cannot confirm the need for visual contact for a group effect at a given activity level, as the fish were mostly active during night time. Nevertheless, we do assume that visual contact is not essential for ruffe because of their very sensitive lateral line organ (Gray and Best 1989, Jansen et al. 2002). Third, the frequency distribution of respiration rates was broader and more evenly distributed in the single fish than in groups of fish, which displayed a nearly dome-shaped frequency distribution at a comparatively low level, and the diel cycle (variability within the course of the day) was more pronounced in the single fish. The high variability and the washy pattern in the frequency distributions are regarded as evidence of anxious behaviour.

The impact of group size on RMR and activity was already recognised in the 1930s, and studies on group effects were resumed at the end of the 1970s and the beginning of the 1980s. Astonishingly, following behavioural and growth experiments, as well as bioenergetics measurements, were still performed on single isolated fish in many cases (Table 2.1), which can give misleading results. Anras et al. (1997) concluded from their experiments, that it is almost impossible to use data gained from isolated individuals as input parameters for bioenergetics models, which are usually applied to model growth or consumption of fish in groups and populations. Nevertheless, the respiration parameter values used in 75% of the parameter sets listed by Hanson et al. (1997) for the Wisconsin model are derived from isolated fish (Table 2.1). In circa 50% RMR was measured, the metabolic rate for which a potential group effect is relevant. In these cases, respiration might be overestimated. As bioenergetic model outputs are very sensitive to the respiration parameters in many species (Bartell et al. 1986, Horppila and Peltonen 1997, Kitchell et al. 1977, Madenjian et al. 2006), the resulting growth or consumption estimates may be severely flawed. The input parameter set for yellow perch listed in Hanson et al. (1997) was derived from Kitchell et al. (1977), who in turn based their model on the respiration measurements of Solomon and Brafield (1972) using isolated Eurasian perch.

With the basic form of the respiration function of this model we calculated the oxygen consumption for perch with our experimental conditions. The calculated oxygen consumption of 262 $mgO_2\,kg^{-1}\,h^{-1}$ exceeds the RMRs we measured for perch in groups of eight fish (182 $mgO_2\,kg^{-1}\,h^{-1}$), that is by 44%. It was, however, similar to the rates measured with four perch (272 $mgO_2\,kg^{-1}\,h^{-1}$) and lower than those measured with isolated perch (318 $mgO_2\,kg^{-1}\,h^{-1}$). Following the model adjustment approach of Madenjian et al. (2006), we changed RA (intercept of respiration model) to fit measured and modelled RMRs. To adjust the modelled respiration rates to the respiration rates measured with eight perch, we had to reduce the value of RA from 0.0108 to 0.0074. Comparing now weight gain modelled with the common and the revised model for perch (duration: 30 days, body mass: 7.4 g, temperature: 19.4°C, prey energy density: 2 213 J g^{-1} wet weight) results in a underestimation of growth by 17% with the common model. The respiratory data in our group experiments may, however, still overestimate respiration in the wild under more natural conditions.

In addition to reduced oxygen consumption, the calming effect of groups should also be reflected in higher growth rates as more energy can be invested in biomass. The higher growth rates of ruffe found by Schleuter and Eckmann (2006) in experiments with groups of four as compared to Henson and Newman (2000), who used isolated fish, can thus at least partly be explained by the lower RMRs we found for ruffe in groups.

In our experiments we could confirm the group effect on RMR and activity for perch already shown by Geyer and Mann (1939), and we have demonstrated it for the first time for ruffe. We conclude that without considering potential group effects on physiological functions, the results of bioenergetics modelling and growth experiments may be severely biased. Social fish like perch and ruffe should be studied in groups. For solitary fish species, however, respiration rates may increase in groups (Wirtz and Davenport 1976). Preliminary experiments are therefore essential to built up bioenergetics models that best reflect the social and ecological characteristics and preferences of the species studied.

Acknowledgements

We thank Myriam Schmid and Pia Mahler for their assistance during the experiments and Myriam Schmid and Matthias Erhardt for their help with the analysis of activity from the video tapes. Hubert Fink and Georg Heine developed the software for the computation of respiration and for the automated video recording, and Franz Hölker gave valuable advice for the analysis. Marry Morris corrected the English. We further thank two anonymous reviewers whose valuable comments improved the manuscript. This study was supported by the German Research Foundation (DFG) within the Collaborative Research Centre SFB 454 ‘Littoral Zone of Lake Constance’.

Chapter 3

Predation effects of the two competitive fish species Eurasian perch and ruffe on littoral benthic communities: the influence of study site and competition

DIANA SCHLEUTER AND NICOLE SCHEIFHACKEN

ABSTRACT

In enclosure experiments we analysed the predation effects of perch and ruffe on benthic communities at two different sites of Lake Constance. We found strong effects of site and sampling date on benthos abundances and composition, but only weak predation effects. Benthos abundances and stomach fullness of perch and ruffe were higher at the exposed site with stony substrate compared to the more protected site with finer sediments. Differences in the benthic community structure were reflected in the composition of the fish diet. However, temporal benthic changes were not related to fish enclosure, and abundances were partly higher at the end of the experiment. We hold strong inherent processes, and a general low availability of benthic organisms to fish predators responsible for the weak predation effects observed.

Fish competition was tested through single and mixed species stocking. With interspecific competition, niche overlap of the two species decreased significantly at both sites. The influence of competition on stomach fullness, however, depended on the study site. At the sheltered site with more limited food resources, intraspecific competition was as strong as interspecific competition in both species. At the exposed site with higher benthos abundances, ruffe was the superior competitor.

Introduction

The effects of fish predation on macrobenthic communities are widely studied in freshwater systems. However, most studies refer on lotic systems, while studies on lentic systems are surprisingly rare and the results and conclusions drawn from these studies differ strongly. Some authors observed clear effects of predation (Crowder and Cooper 1982, Diehl 1995, Mittelbach 1988) while no top-down control was found by others (Baumgärtner and Rothhaupt 2005, Hanson and Leggett 1986, Thorpe and Bergey 1981). In some studies authors concluded variable predation effects, dependent on the macroinvertebrate taxa and size, sampling dates, presence or absence of macrophytes or predator species and density (Cobb and Watzin 1998, Gilinsky 1984, Hershey 1985, Macchiusi and Baker 1991, Persson and Svensson 2006).

Various reasons for these controversial results have been proposed. Prey availability could be the main factor that influences predator success (Boisclair and Leggett 1985). It can be altered by habitat complexity through lower perception of prey organisms or restricted manoeuvrability of predators in vegetation stands (Crowder and Cooper 1982, Diehl 1992, Gilinsky 1984). Further, in response to chemical cues released by potential predators, the behaviour, morphology, and even life history traits of invertebrates can change and result in lower availability (Arnqvist and Johansson 1998, Baumgärtner et al. 2003, Crowl and Covich 1990, Hölker and Stief 2005, Kolar et al. 2002).

In addition to food availability, competition between predators can also influence diet composition and consumption rates (Bergman and Greenberg 1994, Bonesi et al. 2004, Hanson and Leggett 1986, Schleuter and Eckmann 2006). In Lake Constance, Eurasian perch (*Perca fluviatilis* L.) and the invasive fish species ruffe (*Gymnocephalus cernuus* (L.)), are common littoral fish species (Fischer and Eckmann 1997a, Reyjol et al. 2005) which are assumed to be competitors for macrozoobenthos (Bergman 1991, Bergman and Greenberg 1994, Fullerton et al. 1998). Various aspects of intraspecific and interspecific competition for food of Eurasian perch or its sister species yellow perch (*Perca flavescens* (Mitchill)), respectively, and ruffe have been evaluated in several laboratory studies (Bergman and Greenberg 1994, Dieterich et al. 2004a, Dieterich et al. 2004b, Fullerton and Lamberti 2006, Fullerton et al. 1998, Fullerton et al. 2000, Savino and Kolar 1996, Schleuter and Eckmann 2006). Dieterich et al. (2004a, b), for instance, focused on the influence of competition and food availability on food consumption over different substrate types. The authors concluded that under natural conditions with limited food resources, ruffe would forage efficiently over fine sediments and perch over coarse sediments. Fullerton et al. (1998) conducted experiments on the influence of competition on prey selection. They found that compared to the single species treatments, the diet of fish was more diveres in the mixed species treatments.

In the present study, we analysed the predatory impact of these two competitive fish species on the littoral benthic community of Lake Constance, a large, oligotrophic pre-alpine lake. As the littoral is very diverse and differs strongly between sites, we chose two contrasting study sites with differences in shore morphology, substrate types, and wind and wave exposure. We further focused on the influence of the different study sites on the competition between perch and ruffe. We hypothesised, that i. benthic communities are top-down controlled, and expected alterations in size structure and community composition as a result of predatory impact, ii. we assumed fish predation to be influenced by competitive interactions and that iii. both, predatory impact and competitive interactions are influenced by study sites with different wave exposure.

Methods

Study site

The experiments were conducted in Upper Lake Constance, a large, oligotrophic (8 µg P L^{-1} during spring circulation) pre-alpine lake in central Europe (surface: 473 km^2, mean depth: 101 m, maximum depth: 254 m, shoreline: 186 km). Westerly winds prevail throughout the year, with a second less-dominant peak of easterly winds especially in winter (Bäuerle et al. 1998). The littoral zone in Lake Constance is defined as the area of the shore with a maximum depth of 10 m and is restricted to less than 10% of the total lake area (Wessels 1998). It varies greatly, e.g., in width, slope, sediment composition, and wind exposure. We chose two representative, contrasting study sites: Site 1 (sheltered) near Konstanz (Litoralgarten 47°41’26.7’’N, 9°12’18.4’’E) on the south western shore is more sheltered against wind and ferry- and leisure-boat-induced waves owing to its geomorphologic structure and slope; the littoral zone is broad, strong wind events are rare, and the substrate consists of cobble stones loosely embedded within fine sediments with a sparse macrophyte-cover of *Chara* spp. and is thus quite heterogeneous (Schmieder et al. 2004). Site 2 (exposed) near Meersburg (47°41’37.3’’N, 9°16’11.7’’E) on the north eastern shore is highly exposed to westerly winds and ferry- and leisure-boat-induced waves (Bäuerle et al. 1998). The shore is narrow, the substrate is homogenous and consists of coarse stones, and macrophytes are lacking above 5 m (Schmieder et al. 2004).

Experimental design

The experimental design involved two factors with two levels each, fish species (perch and ruffe) and competition (interspecific and intraspecific) plus a control treatment without fish. Three cages each were stocked with either perch or ruffe, both species or no fish (control), i.e. 12 cages were randomly deployed in a block design. The littoral benthic community in Lake Constance fluctuates strongly on small time scales (Baumgärtner and Rothhaupt 2005, Scheifhacken et al. in press). To keep those time effects low, cages were only deployed for one week at each site (July 2004). To ensure a high predation pressure despite the short exposure time, we used high fish densities (12.5 fish per m^2), i.e. 10 perch or 10 ruffe or 5 perch plus 5 ruffe per cage. This density is similar to that used by Gilinsky (1984) as high density treatment (10 fish m^{-2}) and exceeds natural fish densities in the littoral of Lake Constance, which range from 0 to 4.6 fish m^{-2} (S. Stoll, unpublished data). Thus, we could expect predatory impacts on the benthic community and competitive interaction between the fish stocked.

Each cage consisted of a steel frame (1.0 × 0.8 × 0.4 m) covered with 0.8-mm mesh gauze, which allowed water to flow through the cage, but prevented large- and medium-sized macroinvertebrates and fish to enter or leave. The bottom was open to allow fish access to the sediment. The top cover could be opened for benthos sampling and fish removal, and had an additional opening with bayonet coupling (18 cm diameter) for fish stocking. The cages were set by scuba divers at a water depth of 1.0 m along a transect, with 1.5 m between the cages. At this depth cages were not exposed through water level fluctuations and the water column was entirely mixed. The cages were anchored in the sediment with 40 cm pegs at each corner. The bottom edges were sealed with sand-filled sacks of 90 cm length and 20 cm diameter placed on the outside and covered with pebbles. Before fish were introduced into the cages, divers sampled benthos (see next section) and removed any fish or crayfish from the cage bottom with a dip net; the top cover was then immediately closed. Minor perturbations of benthos by divers are likely, but all cages were treated alike, and fast resettlement and uniform redistribution within cages was visually observed.

Benthos

Benthos was quantitatively sampled (25 × 25 cm, $A_o = 625$ cm^2) by scuba divers using a suction sampling device as developed and described by Baumgärtner (2004) and Mörtl (2003). All substrates or macrophytes within the sample frame were transferred into a hand net (200 µm) while the pump ran continuously. This minimised the escape of mobile organisms and allowed further sampling of the upper fine sediment layer. Invertebrates and suspended sediment were retained within a filter inlet (200 µm) and then added to the hard substrate fraction. Benthos in the cages was sampled immediately before fish were introduced into the cages. The sampled area was covered with concrete stones to mark the position and compensate for substrate removal. Benthos was re-sampled at the end of the experiment after fish removal. Benthos outside of the cages at the same depth stratum was sampled additionally at the end of the experiment to detect natural predation pressure.

All samples were brought to the laboratory and processed immediately. Coarse stones were carefully brushed and rinsed within a bowl (200 µm) to remove attached invertebrates, which were stored in 70% ethanol. Fine sediments were repeatedly floated to suspend all invertebrates in the water column. Invertebrates were identified to the species level when possible or to the nearest taxonomic level using a dissection microscope (10 × magnification), counted, and classified into three size classes (small, medium, and large) according to values of (Baumgärtner and Rothhaupt 2003) and standard determination literature. Values of unlisted taxa were based on our own extensive length/dry mass calculations, conforming to their methods.

Fish

The perch (8.5 ± 0.6 cm, mean ± SD) and ruffe (8.0 ± 0.9 cm) used in this study were caught in Lake Constance with a hand lift net nine months before the experiments started and held in 300 L aquaria under a natural day/night cycle. At least two weeks before the experiment started, the fish were transferred to 500 L outdoor tanks for acclimatisation to natural light intensities.

Cages were stocked with fish by gently placing the fish into a Plexiglas tube that protruded the water surface and was docked to the additional opening in the top cover. The fish immediately swam downwards into the cage. The tube was removed, and the opening was sealed with a cap. At the end of the experiment, fish were removed late in the morning to ensure that the visual predator perch had time to feed and that the food ingested by ruffe during the night still remained in the stomach (D. Schleuter, personal observation). A frame with a 4-mm mesh net was placed around the cage. The top of the cage was opened, and the fish were removed by electro fishing. The fish were anaesthetised with a lethal concentration of 1,1,1-trichloro-2-methyl-2-propanol-hemihydrate (2 g L^{-1}). Formalin (10%) was injected into the body cavity to conserve the stomach contents; the fish were then stored in 4% formalin. In the laboratory, stomachs were removed and prey items were identified to the family or genus level. Insect larvae and amphipods were grouped into three size classes as described above. For the calculation of the stomach fullness (dry mass of stomach content (mg)/wet mass of fish (g)) dry mass of prey organisms was calculated using length dry mass regressions of (Baumgärtner and Rothhaupt 2003). Calculations for unlisted taxa were based on our own extensive length/dry mass calculations, conforming to their methods. For *Dikerogammarus villosus* we calculated the length/dry mass regression $y = 0.0016 \times x^{3.2441}$ ($R^2 = 0.98$), with y = dry-weight and x = body-length. For the leech *Erpobdella* spp. we determined the dry weight for the three size classes (big = 0.0098 g, medium = 0.0035 g, small = 0.0011 g).

Data analysis

Total benthos abundance, taxa density, diversity parameters, dominant taxa abundances, and size classes were examined with repeated measurement MANOVA, with site and treatment as factors (Bonferroni corrected). Variances were stabilised with log(x+1) transformation and tested for homogeneity with the Levene test. Tukey HSD post hoc tests were applied when significant effects were detected. For all multivariate calculations, the statistical package SPSS 13.0 was used.

Predation effects on benthos community composition and fish stomach contents were examined with non-metric multidimensional scaling (nMDS) using the PRIMER 6b software package (Clarke and Warwick 2001). Benthos data were log(x+1) transformed to enhance the contribution of less-abundant taxa to overall community composition. Benthos from stomach contents, however, were computed as original data because the same order of magnitude was found in all samples (Clarke and Warwick 2001). Data were displayed in nMDS plots using the Bray-Curtis index for sample similarity calculations. A priori defined groups (site, treatment, and for benthos samples, also date) were tested with ANOSIM permutation statistics against random distribution. Species contribution was analysed using the SIMPER routine. The BVSTEP procedure was used to detect the influential prey items in stomach contents. With this procedure, the smallest possible species subset was determined whose

Bray-Curtis similarity matrix correlates at least at $\rho = 0.95$ (Spearman correlation coefficient) with the similarity matrix for the full set of species.

Stomach fullness within sites was compared with one-way ANOVA and Tukey HSD post hoc tests (Program JMP 4.0), if the criteria of equal variances and normal distributions could be met with log(x+1) transformation. Otherwise, the Kruskal-Wallis test was utilised. Sites were compared using the t-test or the Kruskal-Wallis test.

The selectivity of fish for prey items was calculated using Strauss' preference index (Strauss 1979): $L_i = d_i - e_i$, where d_i is the ratio of food type *i* in the diet and e_i the ratio in the environment. Negative values represent avoidance or inaccessibility, whereas positive values indicate preference for a prey type.

Table 3.1. Species contribution to benthos community composition and average similarity between samples at Site 1 and Site 2 per sampling unit (25 × 25 cm). The Simper routine in PRIMER was used. *SD* standard deviation, cut off by >90%.

Species	**Average abundance N**	**Average similarity (%)**	**SD**	**Contribution (%)**
		Site 1 (sheltered) – Litoralgarten, Konstanz		
Chironominae	597.3	23.5	2.3	47.8
Chironomidae spec.	266.6	7.2	1.2	14.6
Tinodes waeneri	97.6	5.9	0.9	12.0
Tanypodinae	95.3	3.4	1.5	6.9
Ostracoda	145.1	2.5	0.8	5.0
Orthocladiinae	60.2	2.4	1.4	5.0
		Site 2 (exposed) – Meersburg		
Chironominae	1 324.2	39.7	7.8	50.1
Chironomidae spec.	499.2	13.8	5.0	17.5
Tinodes waeneri	450.1	11.6	3.3	14.6
Tanypodinae	188.9	4.5	2.3	5.6
Ostracoda	161.6	4.0	1.9	5.1

Results

Benthos communities

The total benthic community abundance (mean ± SE per sample unit) pooled over both sampling dates and all sites was 4 594 (± 398) (range from 921 to 18 942) individuals. The number of taxa was 19 ± 0.4 (mean ± SE) out of a total of 47 species or higher taxonomic groups. The most abundant taxa were small non-definable Chironomidae larvae (795 ± 86), followed by older larval stages of Chironominae (524 ± 59), Trichoptera *Tinodes waeneri* (298 ± 33), Ephemeroptera *Caenis* spp. (105 ± 13), Oligochaeta (100 ± 16), Orthocladiinae (84 ± 9), Ostracoda (81 ± 27), *Gammarus* spp. (57 ± 10), Tanypodinae (56 ± 13), *Dreissena polymorpha* (19 ± 4), and *Dikerogammarus villosus* (19 ± 4) (Table 3.1, Figure 3.1). Benthic Cladocera (309 ± 71) were only counted at Site 1, after recognising this taxon from stomach contents of perch and ruffe as an unexpected important food source. As a trend, lower abundances of benthic Cladocera were found at Site 2, but quantification for Site 2 was not possible hereafter. However, the rank order of most of the taxa differed between sites and sampling dates. A variety of insect larvae, mainly of caddisflies and mayflies, and other invertebrates such as snails and leeches also regularly occurred, but in low numbers.

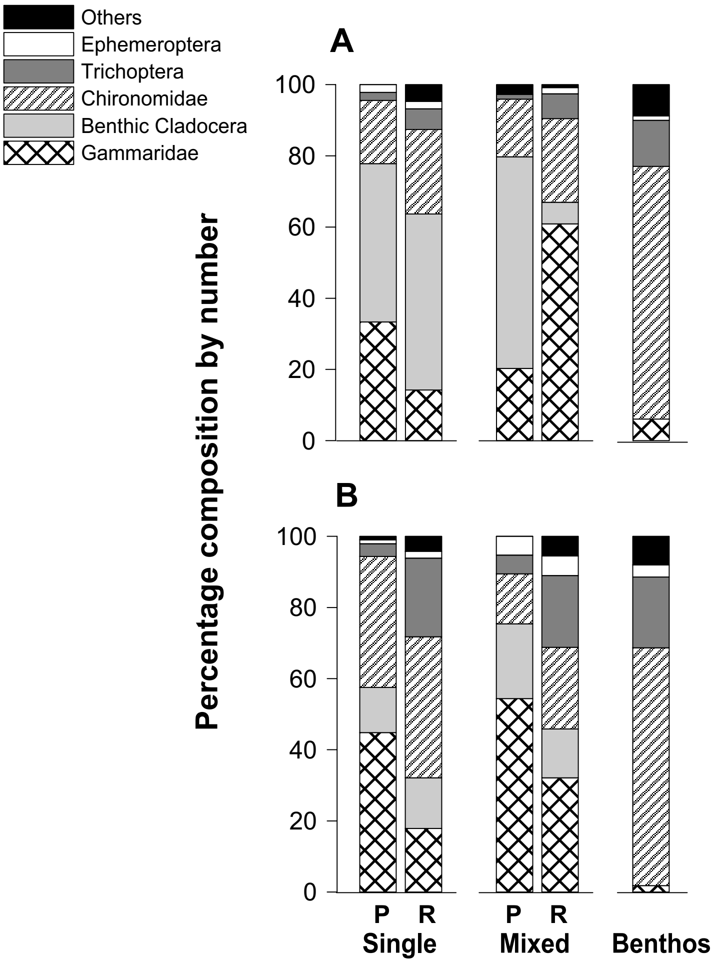

Figure 3.1 Proportion of the main prey types by number found in fish stomachs and in the benthic community (overall average). **A** Site 1 (protected), Litoralgarten, Konstanz **B** Site 2 (exposed), Meersburg. *P* perch, *R* ruffe.

We found strong effects of site and sampling date (beginning/end of experiment) on benthos abundance, number of taxa, diversity parameters (except evenness) and benthos community composition, but only weak predation effects (Table 3.2, Figure 3.2).

Abundances of most taxa were significantly lower at the sheltered Site 1 than at the exposed Site 2 (Table 3.2). Exceptions were Ostracoda, Ephemeroptera without *Caenis* spp., Tanypodinae, and medium-sized Chironominae, which had significantly higher abundances at Site 1. Benthos community composition also showed clear site differences (Global R = 0.748, $p < 0.001$) compared to random distribution (range -0.12 to 0.24) (Figure 3.2A). The variability between samples was considerably higher at Site 1 than at Site 2 and average similarity between all samples was lower at Site 1 (49%) than at Site 2 (79%). Comparison of the two sites revealed a dissimilarity of 37% on average. Chironominae contributed 48% of total abundances at Site 1 and 50% at Site 2 (Figure 3.1), but total abundance was twice as high at Site 2 (Table 3.1).

Surprisingly, abundances were generally higher at the end than at the beginning of the experiment, mainly due to non-definable Chironomidae (small), *Caenis* spp. (small, sum), and zebra mussel *Dreissena polymorpha* (small, sum) (Table 3.2). Significantly lower abundances on the second sampling date were only found for *Tinodes waeneri* (small), *Dikerogammarus villosus* (small), *Caenis* spp. (large), and Orthocladiinae (small). Differences of the benthos community composition were also significant between sampling dates at Site 1 (sheltered) and Site 2 (exposed), but weak (R = 0.324 and R = 0.366, respectively, both $p < 0.001$, treatment data pooled) compared to random distribution (range -0.12 to 0.24) (Figure 3.2A).

Significant treatment effects (Table 3.2, rmMANOVA) were only found for two taxa. Small non-definable Chironomidae (cageless control/cage control $p = 0.027$) had higher values in cageless control samples. Large individuals of *Tinodes waeneri* showed significantly higher abundances in the cages stocked with only perch than in the mixed species cages ($p = 0.003$), the unstocked cages ($p = 0.019$), and the cageless controls ($p = 0.005$), but hardly in the cages stocked with only ruffe ($p = 0.067$). Significant treatment by site or treatment by date interactions were found for only few taxa within specific size classes: *T. waeneri* (large), *Caenis* spp. (medium), Tanypodinae (all sizes), Orthocladiinae (small), Chironomidae non-definable (small), Chironominae (large), and Ephemeroptera with and without *Caenis* spp. (Table 3.2). Treatment effects based on the benthic community composition were also tested, but separately for each site and date (Figure 3.2B, C). However, none of the combinations showed any effect compared to random distribution at both sites (Site 1, Site 2: Global R = 0.214, R = 0.222, range of random distribution -0.30 to 0.30 Site 1; -0.30 to 0.35 Site 2).

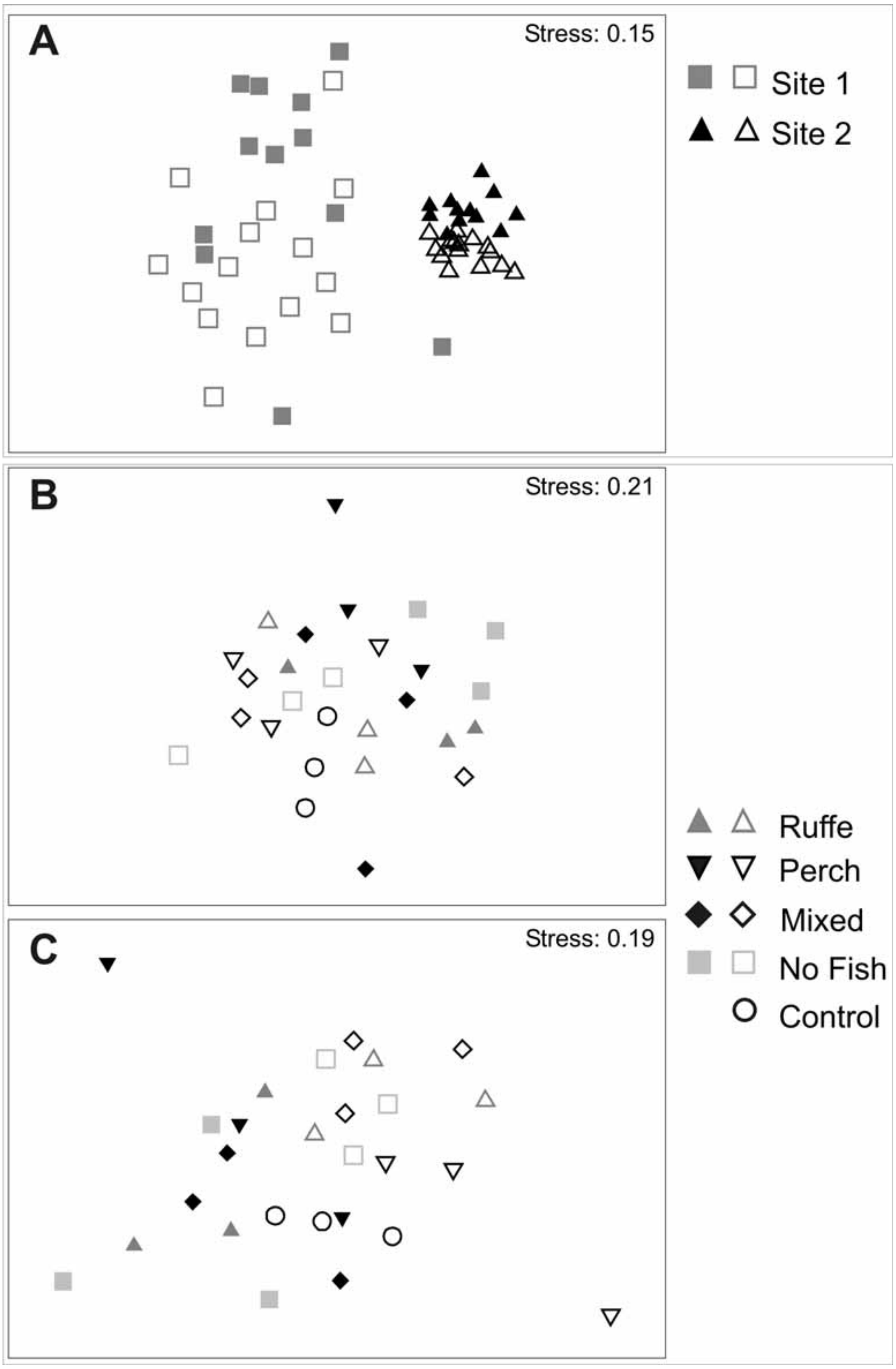

Figure 3.2 nMDS of benthos community composition based on abundance data. **A** Sites 1 (sheltered) and Site 2 (exposed) combined. Site and sampling date are highlighted **B** Site 1, Litoralgarten, Konstanz **C** Site 2, Meersburg. In **B** and **C** treatments are highlighted separately. In **A** to **C**, sampling dates are indicated as follows: filled symbols, experimental start; open symbols, end of the experiment; open circle: control (outside cage at the end of experiment). All data are log(x+1) transformed and standardised to unit N; the Bray-Curtis similarity index was applied.

Table 3.2 Results of repeated-measurement MANOVA on total benthos abundance, number of taxa, diversity and dominant taxa (sum), including three size classes of most taxa. All data were log(x+1) transformed, except taxa and diversity. *S1* Site 1 (sheltered), Litoralgarten, Konstanz; *S2* Site 2 (exposed), Meersburg; *D1* experimental start, week 1, *D2* experimental end, week 2. Categories: *C* unstocked cages, *N* external controls, *R* ruffe only, *P* perch only, *M* (mixed) perch and ruffe together. Only significant results ($p < 0.05$) are shown. Values of the taxa sum are printed in bold.

		Date	**Site**	**Treatment**	**Date × treatment**	**Site × treatment**	**Date × site**	**Date × site × treatment**	**post hoc**	
Abundance	N		0.007						S1<S2	
Number of taxa	S		<0.00				0.001		S1<S2	
Species richness	D		0.003				<0.00		S1<S2	
Shannon diversity	H'_{loge}	<0.00	0.002		0.019				S1<S2;	
Pielou's evenness	J'	0.045					0.007		D1<D2	
Chironominae	sum									
	large		0.027		0.004			<0.00	S1<S2	
	medium		0.002						S2<S1	
	small				0.029					
Orthocladiinae	sum		**<0.00**						**S1<S2**	
	small	0.019	<0.00		0.035			0.033	S1<S2;	
Tanypodinae	sum		**<0.00**						**S2<S1**	
	large				0.007			0.009		
	medium		<0.00						S2<S1	
	small		<0.00		0.013		0.031		S2<S1	
Chironomidae spp.	sum	**0.017**	**<0.00**						**S1<S2;**	
	small	0.009	<0.00	0.032	0.018	0.041	0.030	0.013	S1<S2;	C<N p=0.027
Tinodes waeneri	sum	**0.009**	**0.000**		**0.010**				**S1<S2;**	
	large		<0.00	0.003		0.013			S1<S2	M=N=C=R<R=P
	medium		<0.00						S1<S2	
	small	0.003	<0.00		0.015		0.037		S1<S2;	
Trichoptera excl. *Tinodes*	sum	**0.015**	**0.004**				**0.009**		**S1<S2;**	
Caenis spp.	sum	<0.00	<0.00		0.050		0.009		S1<S2;	
	large	0.002	<0.00				0.001		S1<S2;	
	medium		0.025		0.003	0.021	0.019	0.025	S1<S2	
	small	<0.00	<0.00				0.017		S1<S2;	
Ephemeroptera excl.	sum	**0.013**	**<0.00**				**0.001**	**0.048**	**S2>S1;**	
Dreissena polymorpha	sum	**<0.00**	**<0.00**						**S1<S2;**	
	large									
	medium	<0.00							S1<S2	
	small	<0.00	0.002				0.004		S1<S2;	
Gastropoda	sum	**0.001**							**S1<S2**	
Dikerogammarus villosus	sum									
	large		0.001						S1<S2	
	medium		<0.00						S1<S2	
	small	0.033							D2<D1	
Gammarus spp.	small	0.021	0.045						S1<S2;	
Oligochaeta	sum		**<0.00**						**S1<S2**	
	large		<0.00						S1<S2	
Ostracoda	sum	**0.003**	**0.001**						**S2<S1;**	

Fish

Despite adverse conditions, due to waves from ferry and leisure-boat traffic (especially at the exposed Site 2) and the high water turbidity at the sheltered Site 1 caused by the fine sediments the overall recapture rate was high, with the recapture success lower at Site 1 (perch: 58%; ruffe: 38%) than at Site 2 (perch: 73%; ruffe: 73%). Especially at Site 1 fish could barely be seen, and the escape of some fish could not be prevented. After three sampling rounds electrofishing was stopped. During the experiment at Site 2, one cage stocked with both species was lifted by a storm so that the bottom edges were not completely sealed during the remaining days. Only two perch and one ruffe were recaptured, along with two eels that had invaded the cage. This cage was excluded from further analysis.

At Site 1 (sheltered), perch and ruffe preyed mainly on small Gammaridae, benthic Cladocera, and Chironomidae (percentage composition by number: single species/mixed species: perch 96/96%, ruffe 87/90%) (Figure 3.1A). With interspecific competition, the proportion of benthic Cladocera in the diet of perch was higher (60% compared to 44%) and the proportion of small Gammaridae was lower (20% compared to 33%). For ruffe, in contrast, the proportion of Cladocera was higher with intraspecific competition (49% compared to 6%) and the proportion of small Gammaridae was lower (61% compared to 14%).

At Site 2 (exposed), both fish species preyed on types similar to those at Site 1 (Figure 3.1B). Perch preyed mainly on small Gammaridae, benthic Cladocera, and Chironomidae (single species/mixed species: 94/89%). For ruffe, Trichoptera (22/20%) contribute next to Gammaridae, benthic Cladocera and Chironomidae to the main prey types (91/90%). Both species ingested a higher proportion of insect larvae at Site 2. Especially in the single species cages, more Chironomidae were consumed (Site 1/Site 2: perch: 18/37%; ruffe: 24/39%). The proportion of Ephemeroptera ingested was only slightly higher (up to 5% for both species). Perch consumed also a slightly higher proportion of Trichoptera at Site 2 (up to 4%), but ruffe consumed up to 15% more Trichoptera (ruffe single/mixed: Site 1: 6/7%; Site 2: 22/20%). However, differences between sites were only significant for ruffe in the single species treatment (ANOSIM: Global $R = 0.233$, $p = 0.001$).

In the single species treatments stomach contents of perch and ruffe did not differ (ANOSIM: Global $R = 0.125$; sample range -0.08 to 0.10; Site 1: $R = 0.018$; Site 2: $R = 0.097$) (Figure 3.3A, B), but did differ in the mixed species treatments (ANOSIM: Global $R = 0.243$, sample range -0.16 to 0.22; Site 1 $R = 0.374$, $p = 0.009$; Site 2 $R = 0.275$, $p = 0.024$). The nMDS plot clearly divided perch and ruffe into two separate groups at both sites, even though the variability of stomach contents within species was very high (Figure 3.3C, D). The high variability was also reflected in the relatively low Global R values. However, when we removed the ruffe individual that did not consume small Gammaridae at Site 1 (marked with an asterisk in Figure 3.3C) from the analysis, the ANOSIM results were far more pronounced (Global $R = 0.846$, $p = 0.001$). At Site 1 Gammaridae and benthic Cladocera were found to be mainly responsible for the differences in the mixed species treatment (BVSTEP: $\rho = 0.973$, $p = 0.001$). At Site 2, food items of different size classes caused the differences in stomach contents (BVSTEP: $\rho = 0.955$, $p = 0.001$). Perch fed more on Gammaridae, benthic Cladocera, and small Trichoptera. Ruffe, in contrast, consumed more Chironomidae, especially of medium- and large-size classes, and medium-sized Trichoptera.

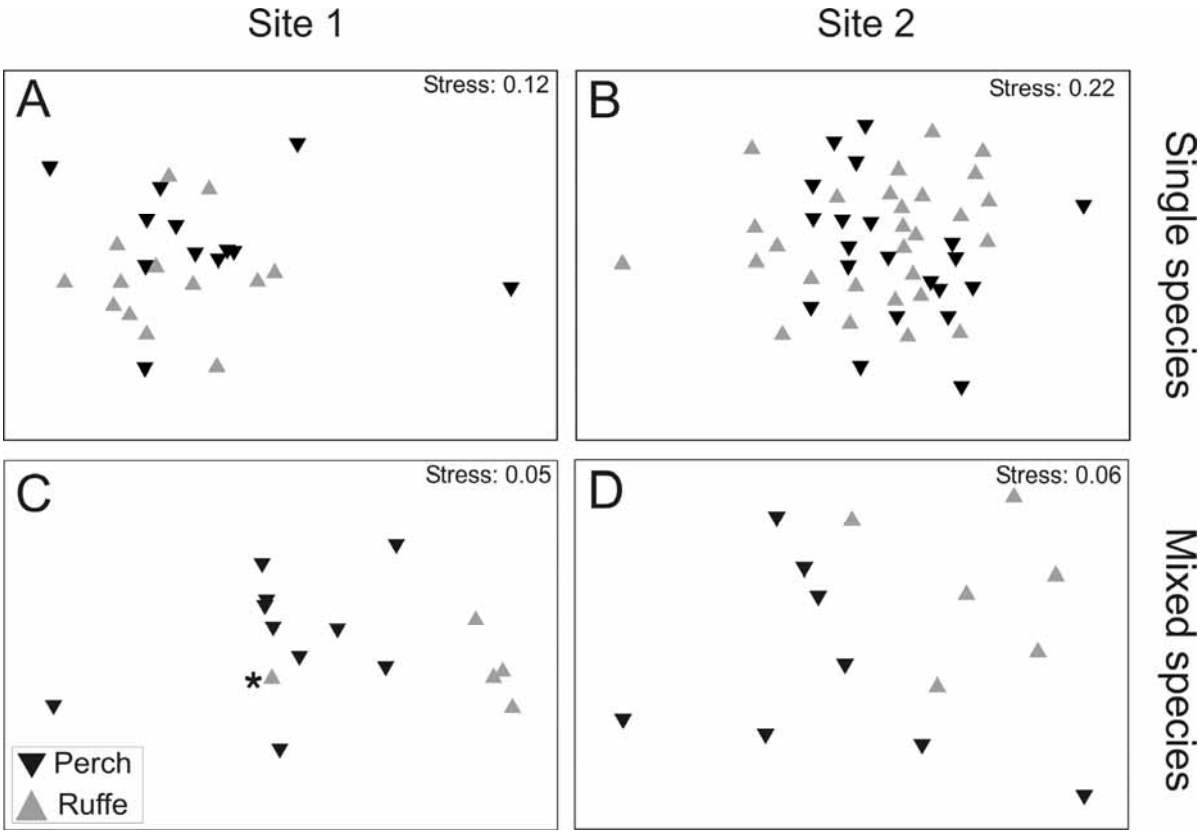

Figure 3.3 nMDS plots of abundance of each prey type in the different size classes in the fish stomachs. The Bray-Curtis similarity index was applied. **A** Site 1 (sheltered), Litoralgarten, Konstanz, single species **B** Site 2 (exposed), Meersburg, single species **C** Site 1, Litoralgarten, Konstanz, mixed species **D** Site 2, Meersburg, mixed species. * in **C** marks the outlying data point of the ruffe stomach contents.

Stomach fullness as a proportion of body weight also differed between species and sites (Figure 3.4). At the sheltered Site 1, stomach content was low for all fish and there were no differences between species and treatments (Kruskal-Wallis: $df = 3$, $\chi^2 = 1.091$, $p = 0.779$). At the exposed Site 2, stomach fullness differed between species and treatments (ANOVA df = 3, F-value = 4.327, p = 0.008). The stomach fullness of perch and ruffe did not differ in the single species treatments. However, in the mixed species treatments, the stomach fullness of perch was significantly lower than that of ruffe ($p < 0.05$). The stomach fullness of perch tended to decrease and that of ruffe to increase from the single to the mixed species treatment, but this result was not significant ($p > 0.05$). Significant differences in stomach fullness between the two sites were only detected for ruffe (single species: Krukal-Wallis, p = 0.012; mixed species: t-test = 0.015).

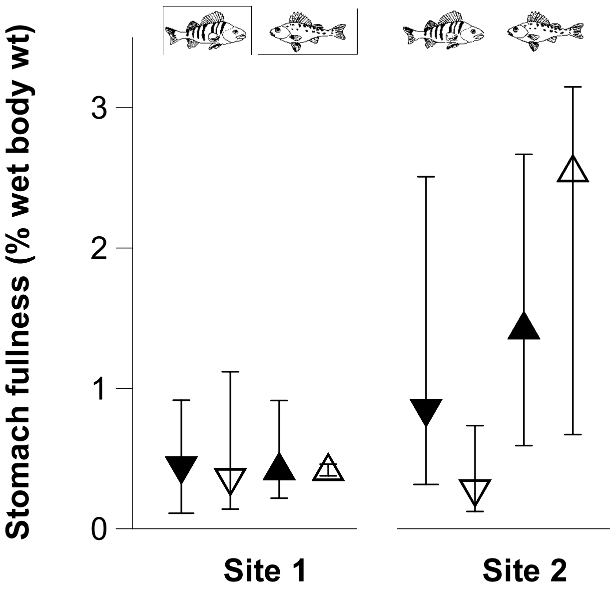

Figure 3.4 Median ± upper and lower quartile of the dry weight of the stomach contents relative to wet body weight. ▼perch single species, ▲ perch mixed species, Δ ruffe single species, ∇ ruffe mixed species. Site 1 (sheltered): Litoralgarten, Konstanz; Site 2 (exposed): Meersburg.

Strauss' selectivity index indicated in most cases an indifferent feeding of both species on specific prey organisms (Table 3.3). However, at both sites, ruffe and perch avoided small insect larvae in all cages (range: -0.21 to -0.59). At Site 1 (sheltered), ruffe further avoided benthic Cladocera in the cages stocked only with ruffe (-0.22 ± 0.14), and positively selected small Gammaridae in the mixed species cages (0.35 ± 0.15). Perch, however, positively selected Cladocera in both, in the single species and in the mixed species cages (0.27 ± 0.12; 0.42 ± 0.29). At Site 2 (exposed), in contrast, ruffe preferred medium-sized insect larvae (0.25 ± 0.11; 0.24 ± 0.15) and perch positively selected small Gammaridae (0.46 ± 0.10; 0.45 ± 0.21), but avoided Oligochaeta in cages stocked only with perch (-0.20 ± 0.04).

Table 3.3 Selectivity of prey items (mean ± SD) using the preference index of Strauss (1979). Negative values represent avoidance or inaccessibility; positive values represent preference of prey items. Values exceeding 0.20 or falling below -0.20 are in boldface.

Group	**Size**	**Ruffe (single species)**	**Ruffe (mixed species)**	**Perch (single species)**	**Perch (mixed species)**
Site 1 (sheltered) – Litoralgarten, Konstanz					
Oligochaeta	small	0.04 ± 0.07	-0.00 ± 0.00	-0.02 ± 0.02	0.01 ± 0,02
Hirudinea	medium	0.06 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mollusca	medium	-0.03 ± 0.02	-0.02 ± 0.02	-0.03 ± 0.02	-0.01 ± 0.01
Insect larvae	small	**-0.21 ± 0.02**	**-0.38 ± 0.07**	**-0.39 ± 0.13**	**-0.47 ± 0.04**
Insect larvae	medium	0.06 ± 0.09	-0.09 ± 0.02	-0.05 ± 0.04	-0.12 ± 0.11
Insect larvae	large	0.03 ± 0.06	-0.05 ± 0.01	-0.02 ± 0.03	-0.02 ± 0.03
Gammaridae	small	0.16 ± 0.11	**0.35 ± 0.15**	0.07 ± 0.10	0.03 ± 0.04
Gammaridae	medium	0.12 ± 0.08	0.13 ± 0.16	0.18 ± 0.06	0.16 ± 0.15
Gammaridae	large	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cladocera	small	**-0.22 ± 0.14**	0.07 ± 0.07	**0.27 ± 0.12**	**0.42 ± 0.29**
Site 2 (exposed) – Meersburg					
Oligochaetae	small	-0.13 ± 0.04	-0.07 ± 0.01	**-0.20 ± 0.04**	-0.07 ± 0.01
Hirudinea	medium	0.00 ± 0.00	0.01 ± 0.03	0.00 ± 0.00	-0.01 ± 0.00
Mollusca	medium	-0.02 ± 0.03	-0.06 ± 0.05	-0.03 ± 0.01	-0.06 ± 0.05
Insect larvae	small	**-0.37 ± 0.09**	**-0.59 ± 0.03**	**-0.54 ± 0.02**	**-0.57 ± 0.05**
Insect larvae	medium	**0.25 ± 0.11**	**0.24 ± 0.15**	0.09 ± 0.17	-0.02 ± 0.00
Insect larvae	large	0.02 ± 0.04	0.04 ± 0.03	0.01 ± 0.04	0.03 ± 0.07
Gammaridae	small	0.00 ± 0.08	0.14 ± 0.25	**0.46 ± 0.10**	**0.45 ± 0.21**
Gammaridae	medium	0.11 ± 0.02	0.12 ± 0.07	0.06 ± 0.06	0.03 ± 0.05
Gammaridae	large	0.01 ± 0.00	0.02 ± 0.03	0.01 ± 0.02	0.00 ± 0.00

Discussion

Spatial variability

Overall benthos abundance, species richness, diversity and community structure clearly differed between the two study sites. Abundances of most of the dominant taxa, and diversity were higher at Site 2. The observed differences in benthos communities between sites were reflected in the fish diet, with higher abundance of Trichoptera (*Tinodes waeneri*) and Ephemeroptera *Caenis* spp. at Site 2 in both, the benthos samples and the fish stomachs. Further, stomach fullness relative to body mass was higher at Site 2 (except perch in the mixed species treatment).

Site 1 (sheltered) and Site 2 (exposed) differ strongly in their morphology, substrate composition, macrophyte and periphyton coverage. These patterns are indirectly caused by hydrodynamic processes, such as wave exposure and water level fluctuations and reflected in the different benthic communities. At the sheltered Site 1 with less frequent disturbance background the environment is more patchy and a fine sediment layer results on top of hard substrates or between the shallow macrophyte-stands of *Chara* spp.. At this more variable Site 1 the variability within benthos samples was also higher. At the exposed Site 2 substrate is homogenous and coarse with absent or only little developed macrophyte-cover. The amount of interstitial refuges is higher at this site and seems to support higher abundances of benthos as well as number of taxa (Lewin et al. 2004). Further, some taxa have certain habitat and substrate preferences: for instance the mayfly *Caenis* spp. feeds mainly on detritus and fine sediments as found at Site 1 (sheltered). Grazers, such as the mayfly *Ecdyonurus dispar* or the caddis flies *Sericostoma personatum/flavicorne* and *Goera pilosa* (Moog 1995), prefer for their feeding more turbulent conditions as found at the wind exposed Site 2. Differences in the benthic communities in nearby shallow littoral sites with differing hydrodynamic regimes were also described by Scheifhacken et al. (in press) during a one-year comparison.

The differences in sediment composition of the two sites could have also influenced the fish stomach fullness. Owing to the finer sediments, turbidity is higher at Site 1, and this, along with lower benthos abundances at Site 1, could be a reason for the lower stomach content of the optically oriented perch (Schleuter and Eckmann 2006, Utne-Palm 2004). However, the low stomach contents of ruffe may be mainly caused by the low benthos abundances, as ruffe can feed in complete darkness using its sensory abilities (Janssen 1997, Schleuter and Eckmann 2006).

Hydrodynamics can, however, also directly impact benthic communities and predator prey interactions. Scheifhacken (2006) found for instance strongly suppressed growth rates and activity of the common freshwater snail *Radix ovata* under experimental wave conditions. The influence on predator-prey interactions is known from lotic freshwater habitats (Hansen et al. 1991, Lancaster 1996, Peckarsky et al. 1990), but as a factor that mediates predator-prey interactions in lentic systems, hydrodynamic forces are still widely ignored. Next to changes in prey behaviour and foraging activities due to turbulence, consumption rates could increase due to higher energy requirements. In addition to higher benthos abundances, this fact might have attributed to higher stomach contents at Site 2 of both fish species in order to compensate for the higher metabolic costs within the exposed habitat. However, the energy requirement of the fish under the different hydrodynamic conditions could not be determined in our experiments.

Date effects

Although we deployed the cages for one week only, we found a strong date effect on benthos abundance and community structure. Abundances were generally higher at the end of the experiment (e.g., non-definable Chironomidae (small), *Caenis* spp. (small, sum), and zebra mussel *Dreissena polymorpha* (small, sum)), leading to a size-class shift from large- to medium- or small-sized individuals, which could not be attributed to fish predation on large individuals, as it occurred also in controls and the abundance of smaller size classes increased. Some aquatic insects could have emerged, which would explain to some extent the lower abundance of large organisms at the end of the experiment. For the accumulation of small-sized individuals we assume drift effects or hatching from eggs to be responsible in most cases. In addition, the observed increase in zebra mussel abundance reflects early instar larvae that recently underwent metamorphosis. These taxa could probably immigrate because of the relatively large mesh size of 0.8 mm of our cages. However, taxa like *Tinodes waeneri* (small), *Caenis* spp. (large), Orthocladinae spp. (small) and *Dikerogammarus villosus* (small) decreased equally in all cages. This might be a result of invertebrate predation (Lancaster et al. 1991), which was an uncontrolled factor in our experiments. A variety of invertebrate predators like flatworms (Hansen et al. 1991) and Chironomidae (Macan 1977) prey on other invertebrates.

Predation

Predatory effects of fish were weak and could only be observed within a few taxa and size classes. This clearly contradicts our hypothesis of expected strong predation effects resulting from a high density fish stocking and the findings of other authors (Crowder and Cooper 1982, Diehl 1995, Mittelbach 1988). However, our results support the findings of others, who found no or only moderate predation effects on benthic communities by perch, ruffe, burbot or cyprinids (Baumgärtner and Rothhaupt 2005, Cobb and Watzin 1998, Okun and Mehner 2005, Persson and Svensson 2006, Scheifhacken 2006).

We expected a great proportion of large-sized prey to be consumed by perch and ruffe within the enclosures (Gilinsky 1984, Mittelbach 1988). We indeed observed a negative selection of small insect larvae and Oligochaeta. In a comparison of the predation effects on benthos abundances between treatments with the fish stomach contents, however, the results revealed some discrepancies. The decrease of small insect larvae in some treatments, for instance, cannot be accredited to fish predation, as they were negatively selected. Since stomach contents could only be sampled at the end of the experiment because of the small fish used and the experimental set-up, we do not know whether the food ingested varied during the experiment. Invertebrate predation might also have contributed to variability. Several studies have shown that vertebrate exclosure leads to an increased invertebrate predation (Crowder and Cooper 1982, Gilinsky 1984, Macan 1977).

Low food availability could be the main reason for the weak predation effects found in our experiments. The benthos exploitation rate depends on differences between potential and available food within the upper layer of soft sediment and on top of hardsubstrates or within the sparse *Chara* spp. stands. A much smaller proportion of food is visible and therefore truly available for foraging fish. Several factors might influence detection and consumption rates, such as colour, contrast, activity or antipredator behaviour of the prey organism (Baumgärtner et al. 2003, Hölker and Stief 2005, Macchiusi and Baker 1991, Utne-Palm 2004), specific fish preference, reactive distance, or gape restriction (De Vries et al. 1998, Mehner et al. 1998, Werner and Hall 1974). Boisclair and Leggett (1985) assumed that only 1% of total benthos biomass is actually available for fish consumption. They found evidence in their comparative study of 21 temperate lakes that daily and annual fish consumption rates of zoobenthos within the upper 5 m of the littoral zone were significantly lower than the reported benthic production/biomass ratios. Maybe weak predation effects might have occurred on top of substrates, but were unlikely to be detected by a quantitative benthos sampling device. The suction sampler also samples the upper interstitial layer of finer sediment, but has the advantage of high precision and repeatability (Baumgärtner 2004, Mörtl 2003).

Our results emphasise low food availability as a reason for weak predation effects. First, both fish species consumed less food than expected, with some stomachs being empty and others containing only a few prey organisms. Fish were recaptured in the late morning, the time of the day when the perch and ruffe stomachs are full (D. Schleuter, personal observation). The low stomach contents could be a result of low availability of preferred benthic food sources. Second, the high amounts of ingested benthic Cladocera (especially at Site 1), allude to low food availability, as they are considered as low-quality food. Hanson and Leggett (1986) documented that the amount of consumed food items eaten by yellow perch (*Perca flavescens*) decreased with increasing perch density and led to an increased ingestion of inferior food. In their study, perch consumed 30 to 50% microcrustaceans when placed under high intraspecific competition, i.e. twice the natural density, and only < 1%

when reared at low or natural densities. Third, in our study small insect larvae and Oligochaeta were negatively selected, although soft bodied organisms are known to be favoured by perch and ruffe (Fullerton et al. 1998). We attribute these results to low availability of the small soft-bodied organisms, which might live buried in the sand or in the interstitial layer, rather than to active avoidance and on the other hand to the better availability of the small Gammaridae, which move over the sediment.

The adaptation of the investigated system to its occurring predators can also lower predation effects. According to Pierce and Hinrichs (1997), there is a difference between systems in which a new fish is introduced and the maintenance of an already existing community. Post and Cucin (1984), for instance, observed dramatic changes in the benthic community of Little Minnow Lake after introduction of yellow perch. In our experiments, however, we used fish that have co-inhabited the littoral benthic community of Lake Constance for the past 20 years.

Competition between perch and ruffe

We found clear evidence for interspecific competition between perch and ruffe for benthic food resources under in situ conditions. Effects of competition between the two species have only been observed under standardised laboratory or mesocosm conditions to date (Bergman and Greenberg 1994, Dieterich et al. 2004a, Dieterich et al. 2004b, Fullerton and Lamberti 2006, Kolar et al. 2002, Schleuter and Eckmann 2006). In our experiments, in the single species treatments no significant difference between the diets of perch and ruffe were found after nMDS analysis. In the mixed species treatments, in contrast, niche overlap decreased, which is what we would expect under competitive conditions (Bergman and Greenberg 1994, Bonesi et al. 2004, Fullerton et al. 1998). However, the diet of the fish within the treatments varied greatly. Therefore, Global R values were lower than expected from the nMDS plots, where each species clearly formed its own group in the cages stocked with both species. If outlying points were removed, the Global R reached high values.

Interspecific competition had strong effects on stomach fullness at Site 2 (exposed). Stomach fullness did not differ between perch and ruffe in cages stocked with a single species. However, in the mixed species cages, the stomach fullness of perch was lower, while that of ruffe was higher. Perch might have been restricted by interference competition, both intraspecific (Schleuter and Eckmann 2006) and interspecific (Savino and Kolar 1996, Schleuter and Eckmann 2006). At Site 1 (sheltered), no differences in stomach fullness between species or treatments were found. This could be caused by the more limited food source at Site 1, thereby generally causing very low stomach contents for both species within both treatments, with a high proportion of benthic Cladocera in the stomach contents (Hanson and Leggett 1986). The high intraspecific competition at Site 1 probably superimposed the effects of interspecific competition. However, we would have expected a higher competitive ability of ruffe at Site 1, and of perch at Site 2 based on substrate preferences and conditions at the two sites (Dieterich et al. 2004a). Furthermore, ruffe should be able to detect prey more easily in the more turbid water at Site 1 because of its sensitive lateral line organ (Eiane et al. 1997, Janssen 1997, Schleuter and Eckmann 2006); conversely, the use of this organ could restrict foraging success in water with high hydrodynamic action, as at Site 2. Additional in situ studies are necessary to further elucidate the influence of these variables on the outcome of competition between the two species.

Conclusions

The contrasting sampling sites led to differences in benthos abundances and benthic community composition. These differences between sites were clearly reflected in the stomach contents of perch and ruffe. At the exposed Site 2, benthos abundances and stomach fullness were generally higher, as were the proportion of Trichoptera and Ephemeroptera. The outcome of competition for food is also influenced by study site. At the exposed Site 2 the stomach fullness of perch decreased with interspecific competition, while that of ruffe increased. At the sheltered Site 1, the stomach fullness was generally low and intraspecific competition was masking effects of interspecific competition. In large lakes like Lake Constance, it is therefore essential to choose study sites carefully, and if possible, to sample more than one representative sites.

Further, our results lead to the assumption that predation effects on benthos is minor in Lake Constance and can be ignored in comparison to inherent benthos seasonal shifts, which were evident after one week only. Therefore, benthos is not likely to be controlled by top-down processes. However, the opposite can be presumed for fish that are likely to be mediated by bottom-up effects of benthos availability that was concluded to be low. A top-down control might only be relevant in systems that have not previously experienced fish predation (Post and Cucin 1984). In systems adapted to fish predation, predation effects are not pronounced enough to alter underlying benthic community structures. Based on the present study with perch and ruffe and a comparable study for juvenile cyprinids in similar habitats (Scheifhacken 2006) we agree with the assumption of (Cobb and Watzin 1998) that this is a common pattern for temperate littoral zone communities of large lakes.

Acknowledgements

R. Eckmann and K.O. Rothhaupt gave very helpful advice during the planning of the experiments and valuable comments, which greatly improved the manuscript. C. Fiek, C. Nitardy, M. Hamitou, J. Hirzig, I. Andernach, C. Berron, A. Fischer, A. Nisch, and R. Blum assisted in the field and laboratory, and the scientific divers of the University of Konstanz, P. Fink, A. Weber, M. Mörtl, N. Müller, and M. Wolf helped with the cage deployment and the benthos sampling. D. Baumgärtner generously provided his cage equipment; members of the Scientific Workshop at the University of Konstanz altered or manufactured the cages. K. Nikoleyczik and J. Behrmann-Godel gave helpful comments on earlier versions of the manuscript.

This cooperation project between ‘Benthos Ecology’ and ‘Fish Ecology’ embedded within the Collaborative Research Centre 454 ‘Littoral Zone of Lake Constance’ was financially supported by the German Research Foundation (DFG).

Chapter 4

Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity

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Ecology of Freshwater Fish **accepted**

ABSTRACT

To elucidate the performances of perch and ruffe in oligotrophic lakes, we carried out a field study in re-oligotrophic Upper Lake Constance. Both these percids used the same habitat, albeit with different activity patterns. Interspecific competition for food was only relevant in summer when both species fed on zoobenthos. Even then, niche overlap was low, while intraspecific diet overlap was moderate to high throughout the season. Perch did not perform fixed, ontogenetic diet shifts, but used a wide range of prey. During spring and early summer, all size classes were planktivorous, then switched to benthivory and cannibalism in summer, and part of the population reverted to planktivory in autumn. Ruffe, in contrast, fed mainly on chironomid larvae and pupae throughout the year. It is suggested that in lakes of low productivity the euryphagous characteristics of perch, including cannibalism, provides a clear advantage over the benthivorous specialist ruffe in two ways: (i) it allows perch to switch to alternative prey types if one prey type becomes scarce, and (ii) it reduces both intra- and interspecific competition for food.

Introduction

The species composition of fish communities in temperate lakes of the northern hemisphere, and the relative proportions of different trophic guilds in the total fish biomass, change in a predictable way along a productivity gradient (Jeppesen et al. 2000, Jeppesen et al. 2005, Olin et al. 2002, Persson et al. 1991). Piscivorous species contribute more to the total fish biomass in oligotrophic lakes, while planktivorous species dominate the fish community under eutrophic conditions (Jeppesen et al. 2000, Jeppesen et al. 2005), resulting in a succession from salmonids to percids to cyprinids with increasing productivity (Persson et al. 1991). Within these taxonomic groups, however, the performance of certain species may differ in response to particular environmental conditions. Among the percids for example, perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* (L.)) respond differently to increasing productivity. Perch attain their highest population biomass under mesotrophic conditions, while ruffe prosper under mesotrophic to eutrophic conditions (Bergman 1991, Jeppesen et al. 2000, Olin et al. 2002).

Since perch and ruffe are potential competitors for benthic food resources (Bergman and Greenberg 1994, Dieterich et al. 2004a, Fullerton et al. 2000, Schleuter and Eckmann 2006), the dominance of one percid species over the other is probably due to its competitive advantage at a certain level of lake productivity. At a given productivity level, either perch or ruffe may be the superior competitor due the species' sensory abilities. Perch, as a visually oriented predator, thrives best under well-lit mesotrophic conditions, but its foraging efficiency is severely reduced under turbid or dimly-lit conditions (Diehl 1988, Radke and Gaupisch 2005). Ruffe, in contrast, may forage efficiently under these latter conditions due to its very sensitive lateral line system and the light-reflecting *tapetum lucidum* in its eye (Collette et al. 1977, Janssen 1997).

Empirical evidence for this concept came from a comparison by Bergman (1991) of perch and ruffe abundances among Swedish lakes of different productivity. She suggested that higher turbidity in the more productive lakes restricted the habitats available for perch and thus decreased their competitive success. Apart from these productivity-related differences in the abundances of perch and ruffe among lakes, a niche divergence within lakes was also attributed to the species' sensory abilities, with perch occurring in well-lit, shallow habitats and ruffe in darker, deeper parts of a lake (Bergman 1988).

The succession from perch to ruffe with increasing lake productivity is thus well documented, and the mechanistic explanation for this pattern, based on foraging efficiency, is well established. The low abundances of ruffe in oligotrophic lakes, however, have received less attention so far, and a mechanistic understanding of why ruffe abundances are low in these lakes is missing. Although it is obvious that the superior performance of ruffe under turbid and dark conditions does not convey any advantage over perch in nutrient-poor, and hence clear and well-lit lakes, this is not a sufficient explanation for the succession from ruffe to perch with decreasing lake productivity. To elucidate the factors that might contribute to lower ruffe abundances in oligotrophic lakes, we studied the performances of perch and ruffe in Upper Lake Constance (ULC), a large lake that has recently returned to oligotrophic conditions.

Ruffe was accidentally introduced into Lake Constance (Figure 4.1) in the 1980s, where it rapidly established large populations despite the lake's ongoing re-oligotrophication (Rösch and Schmid 1996). In warm-monomictic ULC total phosphorous concentration measured during turnover in late winter (TP_{mix}) had increased from the mid-1950s (TP_{mix}<5µg/L) to the late 1970s (TP_{mix}>80µg/L) as a result of anthropogenic eutrophication. This trend was reversed through the installation of sewage treatment plants and the ban on phosphorous-containing detergents, leading to continuously decreasing nutrient loads during the 1980s and 1990s, and consequently a return to oligotrophy (TP_{mix}=7µg/L in 2006). When ruffe became established in ULC in the late 1980s, the lake was still considered to be mesotrophic, and ruffe became one of the most abundant species in the littoral zone by the mid-1990s (Eckmann and Rösch 1998, Fischer and Eckmann 1997b). The increase in ruffe population size coincided with a decrease in the growth rate of perch, the second most important commercial fish species in ULC (Eckmann et al. 2006, Eckmann and Rösch 1998), and stakeholders feared a negative impact of ruffe on perch (Eckmann et al. 2006, Eckmann and Rösch 1998). Recent observations, however, indicate that the population of ruffe is declining (Reyjol et al. 2005).

During the eutrophication of Lake Constance, perch became more limnetic and deviated from their typical ontogenetic diet shift, i.e. from planktivory through benthivory to piscivory in oligotrophic Lake Constance in the 1930s (Nümann 1939), until, in the 1980s, all size classes of perch fed almost exclusively on zooplankton throughout the year (Eckmann et al. 2006, Hartmann 1975, Hartmann and Nümann 1977). Hence, when ruffe became established in ULC, competition with perch for benthic resources was unimportant, and Schmid (1999) concluded that ruffe had occupied an "empty niche" in ULC. With ongoing re-oligotrophication and decreasing zooplankton abundance, however, perch started recently to include benthos in their diet again, so that competition for food with ruffe might start to take effect. The increasing potential for interspecific competition for food between perch and ruffe thus provided a unique opportunity to compare the performances of these two percids in a lake that is gradually advancing towards the lower end of the productivity gradient.

The aim of this study was, therefore, to compare the effects of re-oligotrophication on the foraging performances of, and the competitive interactions between, the two percids perch and ruffe, focussing on the question of which factors may cause the low abundances of ruffe relative to perch under oligotrophic conditions. We carried out fishing surveys in combination with line transect scuba diving and focussed especially on depth distributions, diurnal migration patterns and diet compositions of both species. To account for the possible seasonal patterns in these variables, sampling was performed monthly during the growing season of 2004, when both species occur in the littoral zone.

Methods

Study sites

Upper Lake Constance is a large (473 km²), deep (z_{max} = 254 m, z_{mean} = 101 m), prealpine lake in Central Europe (Figure 4.1). The shoreline is 186 km long, and the littoral zone (from the shoreline to 10 m depth) comprises about 10% of the lake area. Down to a depth of 2.5 - 3 m, the bottom has a more or less gentle slope, depending on the site, while the slope increases at greater depth. Water level fluctuates by about 1.5 m from the lowest level in February to the highest in summer. The main wind direction is from the west throughout the year, but during winter strong north-easterly winds may also occur.

Because littoral width and slope, sediment composition, and wind exposure vary greatly along the shoreline, we chose two study sites on opposite shores with contrasting abiotic conditions (Figure 4.1). Site S_{west} (47°41'26.67''N, 9°12'18.36''E) is characterised by low wind exposure, a broad, gently sloping littoral zone, and heterogeneous substratum with a high fraction of fine sediment. Site S_{east} (47°41'37.25''N, 9°16'11.66''E), by contrast, is more exposed to the prevailing westerly winds, the littoral zone is narrow with a steep slope, and the substratum is more homogeneous, consisting mainly of coarse stones. The benthic communities differ between the two sites, with higher total macrozoobenthos abundance and higher proportions of chironomids, trichopterans and ephemeropterans at the more exposed site S_{east} (Scheifhacken 2006).

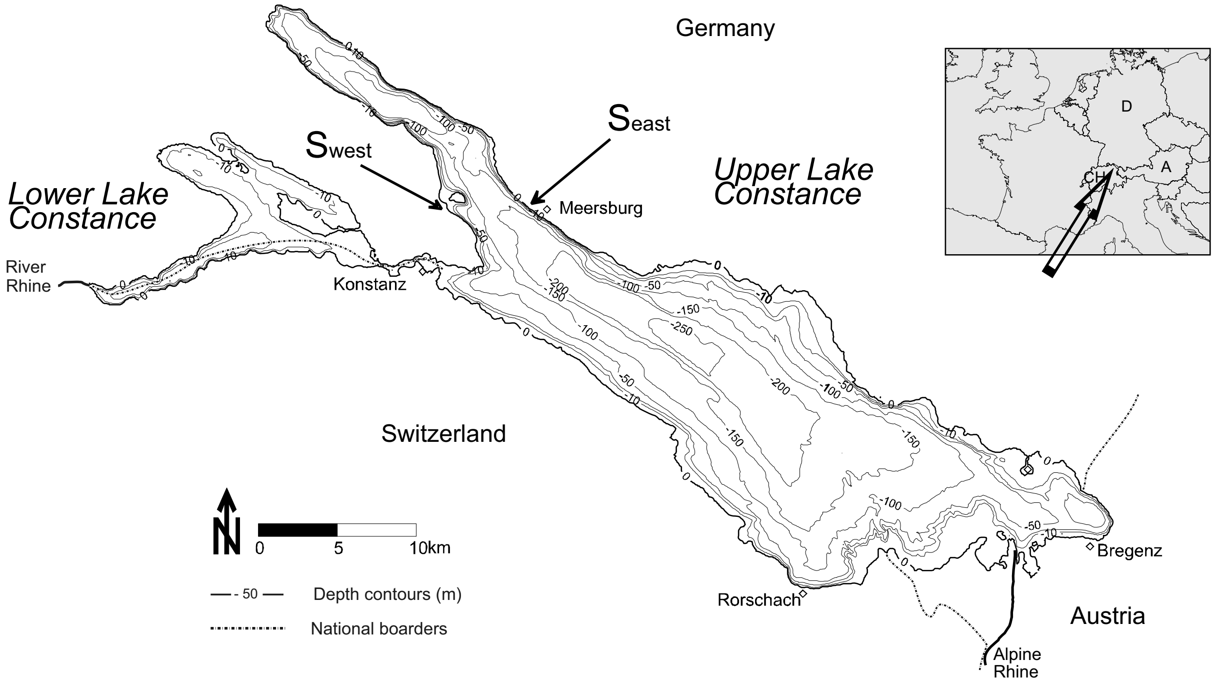

Figure 4.1 Map of Lake Constance, Europe. Study sites S_{east} near Meersburg and S_{west} near Konstanz are indicted.

Fish sampling

Fish were sampled from both sites at the beginning of each month from May through October 2004. Two bottom gill nets (1.6 m deep, 20 m long, mesh sizes 6, 9, 12, 15, 20 mm bar mesh) were set parallel to the shoreline at 2.5 and 10 m depth, respectively. To monitor diurnal changes of fish depth distribution and feeding activity, both nets were exposed three times on each sampling date for 1.5 h during dawn, day, and dusk. A third gill net (1.6 m deep, 10 m long, mesh sizes as before) was exposed perpendicular to the shoreline at less than 2 m depth from August to October at S_{west} and in September and October at S_{east}. Further samples were taken at S_{west} in August and October 2003, and at both sites in September 2005. Additional perch stomach samples were obtained during fishing campaigns in June and August 2006. Water temperature at 1 m water depth and Secchi depth were measured on each sampling date. Fish were removed from the nets immediately after they were lifted and transferred to a lethal dose of 1,1,1-trichloro-2-methyl-2-propanol-hemihydrate (2 g L^{-1}). Formalin (10%) was injected into the body cavity and the fish were stored in 4% formalin for later processing.

Zooplankton

Zooplankton was sampled in 2004 at both sites during the day and after sunset. Triplicate samples from the upper 10 m of water were collected with an Apstein net (mesh size 100 µm) and preserved in 4% sugar-formalin. Each sample was quantitatively flushed into a counting chamber, identified to species level and counted. Copepods and daphnids were grouped into two size classes, ≤ 0.8 mm and > 0.8 mm for copepods, and ≤ 1.6 mm and > 1.6 mm for daphnids, excluding setae and caudal spines, respectively. Total zooplankton abundances were similar between replicates, with a mean coefficient of variation of 0.15 (range: 0.02 to 0.30). Therefore, data for each sampling site were averaged across the replicates and pooled over sampling time.

Fish catch per unit effort

In the laboratory, fish were measured and weighed to the nearest 0.1 cm and 0.1 g, respectively. Perch were divided into three size classes: P_1: ≤ 9.5 cm (maximum total length of 0+ perch in ULC at the end of the year), P_2: 9.5 cm < TL ≤ 13.0 cm (13.0 cm maximum total length of 1+ perch), P_3: > 13.0 cm. Ruffe were divided into two size classes: R_1: ≤ 9.0 cm (maximum total length of 0+ ruffe in ULC at the end of the year), R_2: > 9.0 cm.

The gill net catches were standardized by calculating the catch per unit effort (*CPUE*) as:

$$CPUE = \frac{(A_s/A_u) \cdot Ca}{t}$$

where A_s = area of standard net (15 m^2: area of the smallest net used), A_u = area of the net used (m^2), Ca = actual catch, t = fishing time (h).

Depth distribution and activity

Depth distributions of the fish were described separately for the different fishing times (dawn, day, and dusk) by the relative proportion of *CPUE* from the gill nets set at 2.5 and 10 m depth. Because perch are inactive during darkness and can therefore not be caught by gill nets during the night, depth distributions of fish during the night were analyzed based on line transect scuba diving surveys. These surveys were carried out monthly during day and at night as an alternative method to determine fish distribution. At both sites three parallel ropes were anchored with pegs perpendicular to the shoreline from 10 m to about 0.5 m water depth. The ropes were divided into 10 m sections by numbered marks. Since the inclination of the shore is steeper at S_{east}, this resulted in five sections at S_{east} and seven sections at S_{west}. During the day and after sunset a scuba diver swam slowly along each rope, always starting at 10 m depth, counting all fish along each 10 m section that stayed within 50 cm on both sides of the rope. When fish abundance was too high to be counted ($N = 50$ or higher), it was estimated. For data analysis, fish were separated into those occurring at shallow depth (< 2.5 m water depth: 5 transects at S_{west}, 2 transects S_{east}) and those occurring at greater depth (> 2.5 m water depth: 2 transects at S_{west}, 3 transects S_{east}). Fish counted per transect were averaged over the three parallel ropes at each site. Fish density in shallow water and at greater depth was then calculated by weighting the fish counts in the shallow and the greater depth by the number of transects surveyed in these depth strata (shallow, deep: N fish/ 10 m). Because absolute numbers of fish counted cannot be compared directly with CPUE from gill nets, relative proportions of fish in shallow and deep water were used in Figure 4.5 to compare fish distributions obtained by both methods.

Diet analysis

Stomachs of perch and ruffe were removed, and stomach fullness was assigned to one of three levels: 0 = empty, 1 = medium filled (prey items present, but stomach wall not stretched), 2 = stomach full. Prey items were identified to the family, genus or species level. Copepods and daphnids were grouped into size classes as described in the section on zooplankton. Amphipods were grouped into three size classes (*Gammarus roeseli*: small ≤ 4 mm, 4 mm < medium < 12 mm, large ≥ 12 mm; *Dikerogammarus villosus*: small ≤ 6 mm, 6 mm < medium < 16 mm, large ≥ 16 mm). For all other prey, mean lengths were determined. Dry mass of prey organisms was estimated using length:dry mass regressions for zooplankton from Eckmann et al. (2002) and Laude (2002), and for macrozoobenthos from Baumgärtner & Rothhaupt (2003) and D. Schleuter & N. Scheifhacken (unpubl. data). For prey fish, the mean length of 0+ perch (the most common prey fish) of each monthly catch was determined and converted into dry mass after Hanson et al. (1997).

The stomach content percentage composition by biomass was determined for each size class of perch and ruffe for each sampling date and site. A fish size class was classified as planktivorous, benthivorous or piscivorous if more than 50% of the stomach content dry mass fell into one of these prey categories. When this criterion was not met, a fish size class was assigned to the two trophic guilds which contributed most to the stomach content dry mass. The average dry mass of each type of prey consumed (51 different prey types were considered) was calculated separately for each size class of perch and ruffe for each sampling date and site.

Based on these data, intra- and interspecific diet overlap among the different size classes (perch: P_1-P_2, P_2-P_3, P_1-P_3; ruffe: R_1-R_2; perch-ruffe: P_1-R_1, P_2-R_1, P_3-R_1, P_1-R_2, P_2-R_2, P_3-R_2) was calculated following Schoener (1971):

$$C_{xy} = 1 - 0.5 \cdot \left(\sum \left| p_{xmi} - p_{yni} \right| \right)$$

where C = overlap index ranging from 0 (no overlap) to 1 (complete overlap), p_{xmi} = the proportion of food type i used by size class m of species x, and p_{yni} = the proportion of food type i used by size class n of species y. Index values < 0.05 were considered as zero, values from 0.05 to < 0.25 as low, values from 0.25 to < 0.5 as medium, and values ≥ 0.5 as high diet overlap, and the relative frequencies of the different index levels were calculated.

To evaluate intraspecific diet overlap and individual dietary differences within each size class of each species, up to 10 individuals (minimum 4 individuals) per size class were randomly selected from the August and September samples from both study sites. Fish were chosen from those sampling times, when they were expected to have the fullest stomachs, resulting in perch being selected from the samples taken during day and at dusk, and ruffe being selected from samples taken during dawn. Diet overlaps were then calculated for all possible combinations of two out of 4 to 10 individuals, resulting in 6 up to 45 overlap values. All data were pooled over sampling date and site. Low and medium index values for individual intraspecific diet overlaps were pooled as medium for further analysis.

The selectivity of perch for zooplankton was calculated according to Strauss (1979):

$$L = d_i - e_i$$

where d_i = the proportion of prey type i in the fish diet and e_i = the proportion of prey type i in the environment. L ranges from -1 to $+1$, with $L = 0$ indicating unselective feeding while negative/positive values indicate that a prey type occurs less/more often in the diet than expected under random feeding. Index values < 0.25 were considered as low, values from 0.25 to < 0.5 as medium, and values ≥ 0.5 as strong prey selection.

Results

Temperature, Secchi depth, zooplankton

During the sampling period in 2004, temperature, Secchi depth and zooplankton abundance showed the typical seasonal pattern of lakes in the northern temperate zone (Figure 4.2). Temperatures were around 10 °C in May and peaked in August at around 23 °C. A clear water phase occurred in June, the time when daphnids were most abundant, with Secchi depths of 9.7 m at S_{west} and 7.7 m at S_{east}. Secchi depth was lowest (3.0 m at S_{west} and 3.5 m at S_{east}) in August, after zooplankton abundance had decreased strongly during July. In August zooplankton abundance was low at S_{west}, while it was higher at S_{east} due to the predacious cladoceran *Leptodora kindtii*. A second peak of Secchi depth (about 7.0 m at both sites) and of daphnid abundance occurred in September. Secchi depth increased marginally in October while zooplankton abundance decreased towards the end of the growing season.

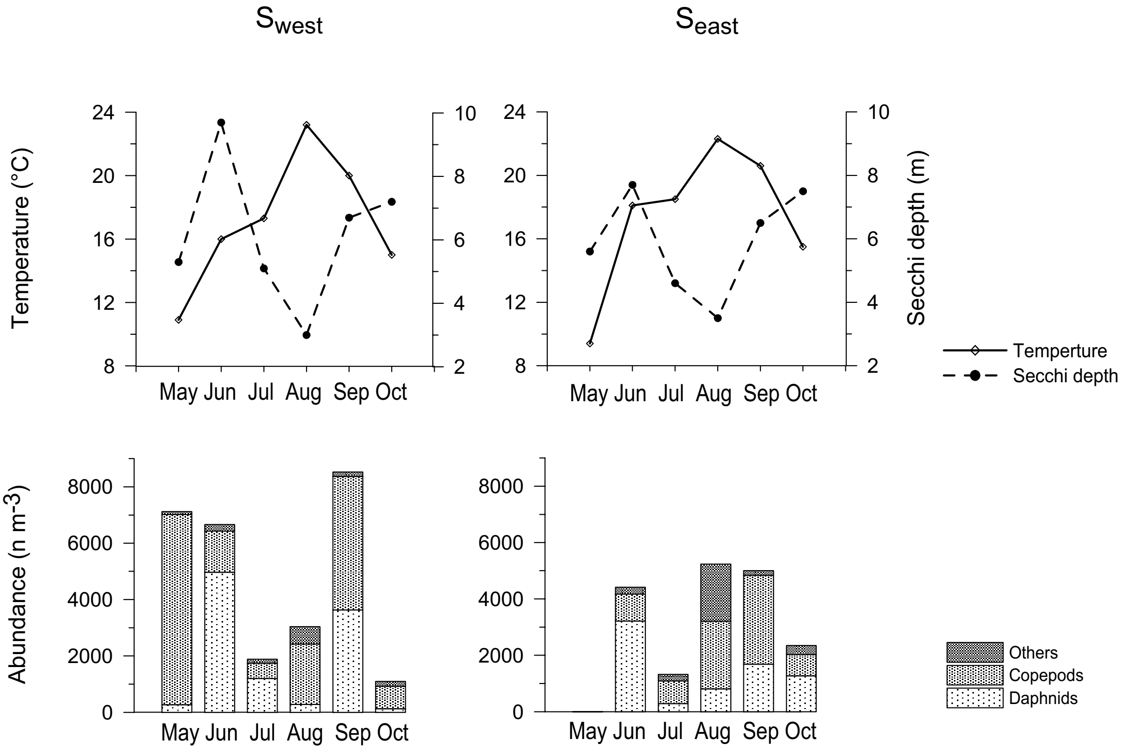

Figure 4.2 Temperature and Secchi depth (upper panels) and plankton abundance (lower panels) at the two study sites during the growing season 2004. Others: *Bythotrephes longimanus*, *Leptodora kindtii*, *Bosmina* spp.

Fish distribution

At both sites perch was the most abundant species and contributed around 70% to the total catch (Figure 3A+B). The relative abundance of ruffe was slightly higher at S_{east} while the relative abundance of cyprinids (mainly dace *Leuciscus leuciscus* (L.) and bleak *Alburnus alburnus* (L.)) was higher at S_{west}. The relative abundances of perch and ruffe based on counts by the scuba divers, by contrast, did not differ between sites. Gill net catches and the total numbers of fish counted by the scuba divers were higher at S_{east} than at S_{west}.

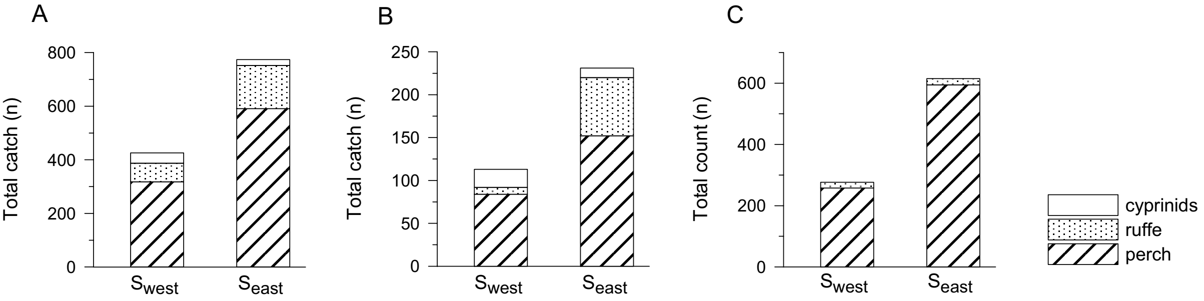

Figure 4.3 Total numbers of fish caught with bottom gill nets exposed at 2.5 m and 10 m water depth at the two study sites in Lake Constance **A** from May to October 2004 and **B** in September 2005; **C** total numbers of fish counted by scuba divers (averaged over the three transect lines ranging from 10 to 0.5 m water depth) at the two study sites from May to October 2004.

During 2004 a pronounced seasonal pattern was apparent in the abundance of perch (Figure 4.4). As the patterns were very similar at both sites, the data were pooled, but the gill net set at less than two meters water depth was not included, as it was only used during the second half of the season. During the first half of the season (May-July), perch abundances were very low. During the second half of the season (August-October) *CPUEs* and diver counts increased until October. This increase was mainly due to the appearance of young-of-the-year (y-o-y) perch, which returned to the littoral zone after completion of their obligate pelagic phase. In the case of ruffe, by contrast, no consistent pattern in its abundance was detected, since *CPUEs* and diver counts differed markedly (Figure 4.4). *CPUEs* were high in May and June but remained low for the rest of the study period. The numbers of ruffe counted by scuba divers, however, increased until August and then decreased towards October. These marked differences were probably caused by an overrepresentation of ruffe in the gill nets during early summer, due to enhanced swimming activity during the spawning season.

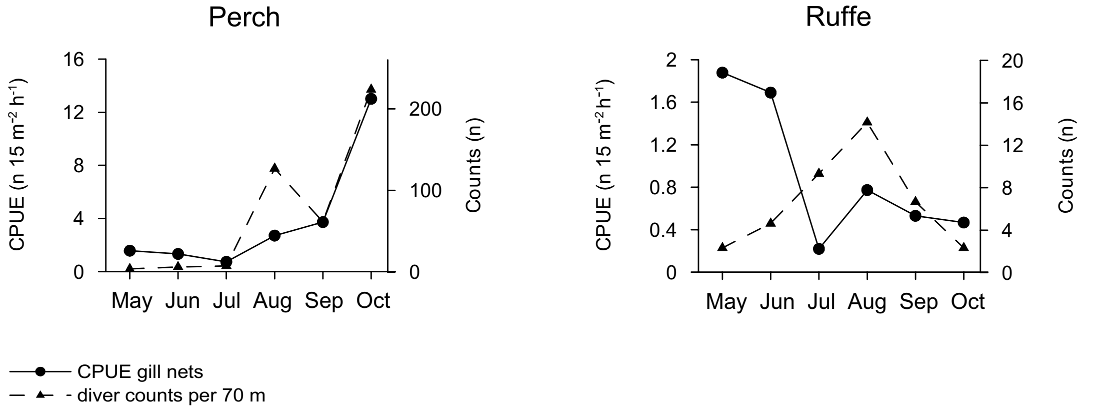

Figure 4.4 Mean *CPUE* and mean numbers of fish counted by scuba divers during 2004 in Lake Constance for perch and ruffe. Data from both sampling sites were pooled.

Both species performed daily horizontal migrations (Figure 4.5). During the day, either no or only a few fish were caught (Figure 4.5B, J, N) or they were mainly caught in the deeper zone (except for perch in August at S_{east}, Figure 4.5F). Additionally, no fish were sighted by the scuba divers during the day except for perch in August and October at S_{east}. During twilight fish were caught at both depths, and at night they were sighted by scuba divers.

In addition to the diurnal changes in depth distribution of perch, seasonal changes in their depth distribution were also apparent, independent of fish size (Figure 4.5A-H). In May, perch were mainly caught at 10 m depth. During summer (June-August) perch increasingly used the shallow littoral zone (higher *CPUEs* at 2.5 m depth) and, during August, some perch were even caught at 2.5 m depth during the day at both sites. In September, the distribution of perch shifted again towards the deeper littoral zone. This seasonal pattern was observed through the gill net catches as well as the line transect diving surveys. Ruffe, by contrast, did not show any seasonal changes in their daily migration pattern (Figure 4.5I-P). During twilight, they were mainly caught at shallow depths, while during the night more ruffe were counted along the deeper transects at S_{east} but not at S_{west}.

Diet

Perch and ruffe had contrasting feeding activities (Figure 4.6). The former fed during the day, as the proportions of medium filled and full stomachs were highest during day and dusk (92/82%). During the night, perch ceased feeding and the relative number of perch with empty stomachs was highest at dawn (62%). Ruffe, by contrast, fed during the night, as 71% of the fish caught at dawn had full stomachs. This proportion decreased to 16% at dusk while the number of ruffe with empty stomachs increased from 4% to 56%.

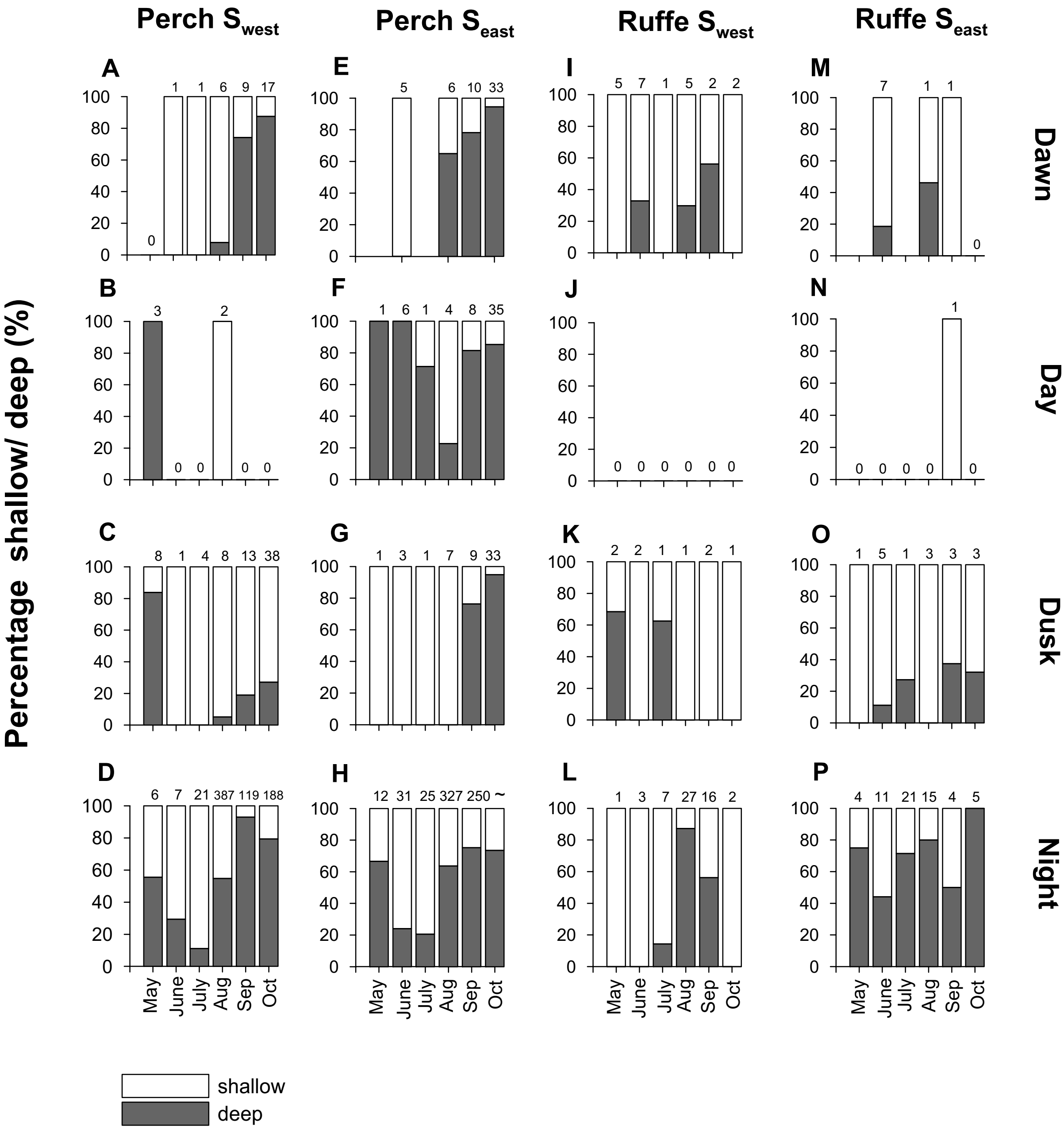

Figure 4.5 Relative depth distribution at different times of the day for perch (**A-H**) and ruffe (**I-P**) at the two study sites in Lake Constance during 2004. For dawn, day and dusk *CPUE* data from bottom gill nets exposed at 2.5 and 10 m depth were used. For the night, scuba diver counts (averaged over the three transect lines ranging from 10 to 0.5 m water depth and weighted by number of transects in the shallow or deep area (N fish/10m)) were used. Numbers at the top of the bars indicate the sum of *CPUE* ($n \cdot 15\ m^{-2} \cdot h^{-1}$) of the shallow and the deep net or the total number of fish counted along the rope (~ = more than thousand). For S_{east}, *CPUE* data are missing for the dawn sampling in May and July.

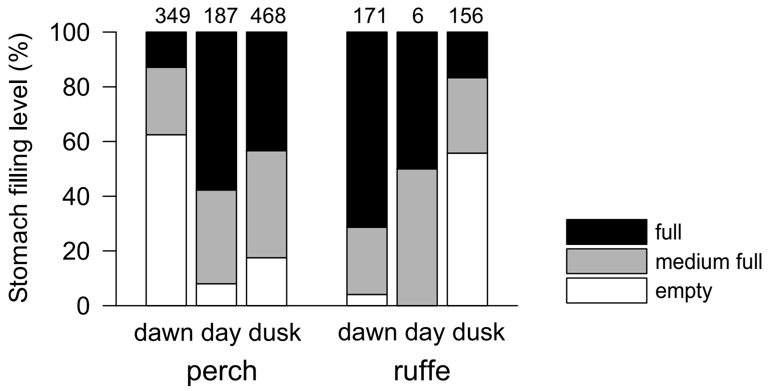

Figure 4.6 Relative amount of perch and ruffe with empty, medium filled or full stomachs. Numbers at the top of the bars indicate number of fish analysed. Data were pooled from May to October 2004.

The diet composition of perch varied strongly during the season (Table 4.1, Figure 4.7). During the first half of the season (May-July) and in October zooplankton was their main food source, while in August zoobenthos and fish dominated in the diet of perch. In September, zoobenthos and zooplankton were of similar importance for small and medium sized perch (zoobenthos 54%, zooplankton 46%), while large perch remained piscivorous. The piscivory of the large perch and of some of the medium-sized perch by late July/early August coincided with the arrival of y-o-y perch in the littoral zone. The observed seasonal pattern in the diet of perch was not only found in 2004, but also in other years (Table 4.1). Ruffe fed nearly exclusively on zoobenthos throughout the entire study period.

The zooplankton ingested by perch strongly depended on the zooplankton community composition (Figurs 4.2B and 7). In May, when the zooplankton community was dominated by copepods, the diet of perch was also dominated by copepods. In June, when daphnids had their highest abundance, perch mainly fed on daphnids. The selectivity indices largely confirm the opportunistic zooplankton consumption by perch: at both sites the mean index values for the different zooplankton taxa were generally low (mostly < 0.25) for all size classes of perch throughout the study period.

The benthic diet of perch included a wide range of organisms, but the most important prey were gammarids (Figure 4.7). In August 2003, *Gammarus roeseli* contributed around 30% to the diet of P_1. In August 2004 and 2006, however, *Gammarus roeseli* was nearly entirely replaced by *Dikerogammarus villosus*, after the introduction of this pontocaspian gammarid into Upper Lake Constance and its rapid dispersal. Pupae of chironomids were the second most important benthic prey of perch. For ruffe, the most important prey were chironomids, either larvae or pupae, followed by the mollusc *Radix ovata* and other insect larvae such as trichopterans and ephemeropterans (Figure 4.7). Gammarids were only occasionally consumed in higher numbers.

Table 4.1 The main prey types of three size classes of perch on each sampling date. A main prey type contributes more than 50% to the dry mass of the fish diet. Data were pooled over both study sites.

Year	Month	≤ 9.5 cm	9.5 cm < x ≤ 13.0 cm	> 13 cm
2003	**August**	benthos	fish	fish
	October	plankton	plankton	plankton
2004	**May**	plankton	plankton	plankton
	June	-	plankton	plankton
	July	-	plankton	plankton
	August	benthos	fish	fish
	September	benthos	plankton	fish
	October	plankton	plankton	fish
2005	**September**	plankton	plankton	fish
2006	**June**	plankton	plankton	plankton
	August	benthos	benthos	fish

The food choices of the two species resulted in medium or high interspecific diet overlap only in August and September (Table 4.2), when perch included benthic organisms in their diet. The only exceptions were medium index values in May at S_{east} for the diet overlap between medium-sized perch and both size classes of ruffe. Overall, the values for interspecific diet overlap between the different size classes of the two species reached values above 0.25 in only 11% (S_{west}) and 17% (S_{east}) of all cases. High diet overlap occurred predominantly between perch < 13.0 cm and ruffe, but as perch grew larger, and eventually became piscivorous, there was hardly any diet overlap between the species. Intraspecific diet overlap among size classes, however, was high throughout the year. The proportion of medium-high or high index values for intraspecific diet overlap in perch was 55% at S_{west} and 38% at S_{east} and occurred mainly in spring and autumn, when perch fed primarily on zooplankton, or in summer among P_2 and P_3, when both size classes fed on fish. For intraspecific diet overlap in ruffe these proportions were even higher, 83% and 67%, respectively.

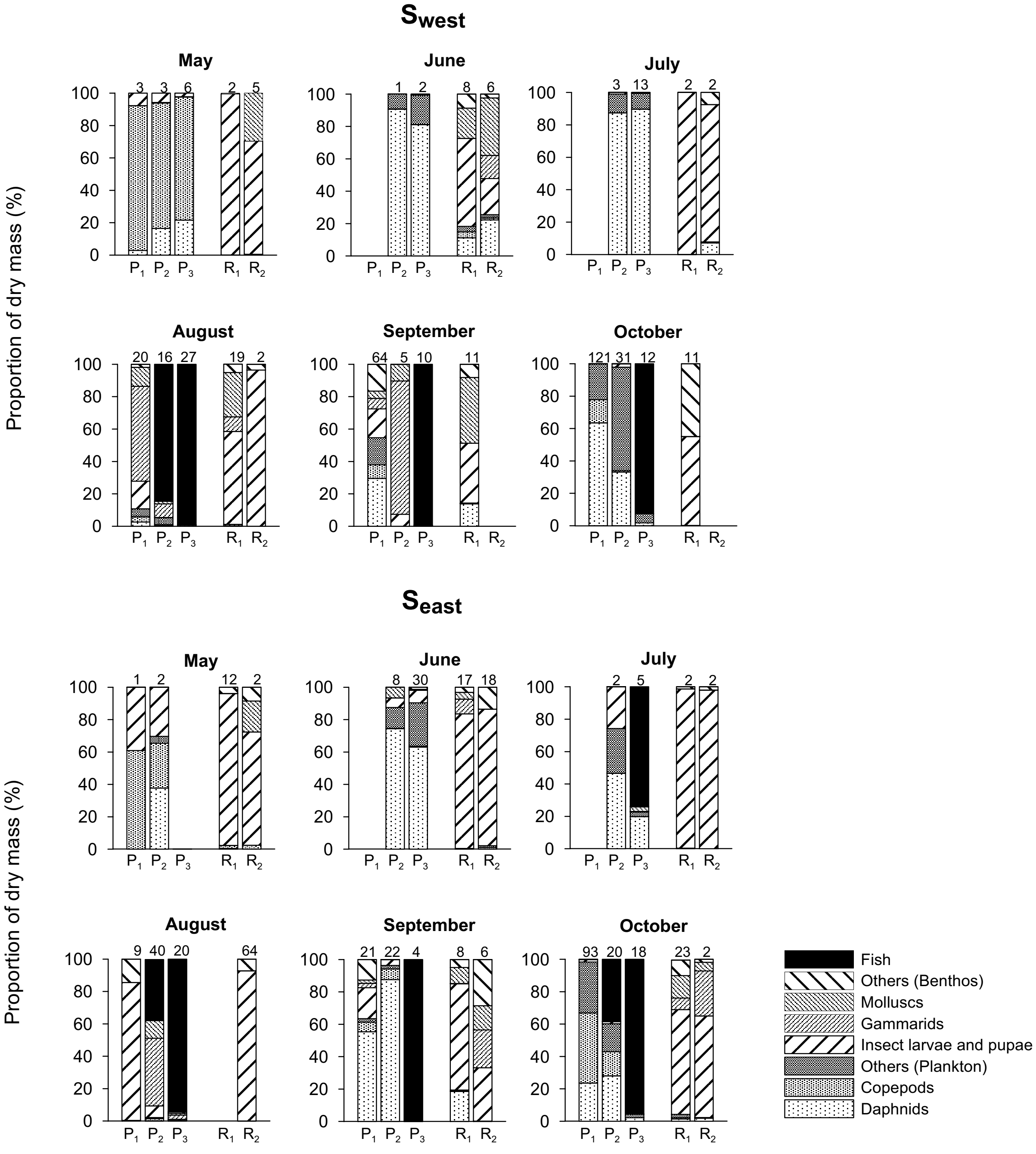

Figure 4.7 Percentage stomach content composition on a dry mass basis for perch and ruffe from both study sites sampled from May to October 2004. Numbers at the top of bars indicate the numbers of fish stomachs analysed. P_1: perch ≤ 9.5 cm, P_2: perch 9.5 cm < TL ≤ 13.0 cm, P_3: perch > 13 cm, R_1: ruffe ≤ 9.0 cm, R_2: ruffe > 9.0 cm.

Table 4.2 Index values after Schoener (1971) for intra- and interspecific diet overlap among different size classes of perch and ruffe at both sampling sites based on 51 different prey types. Bold: high overlap (≥ 0.5); bold italicized: medium overlap ($0.25 \leq C < 0.5$); P_1: perch ≤ 9.5 cm; P_2: perch 9.5 cm $< TL \leq 13.0$ cm; P_3: perch > 13 cm; R_1: ruffe ≤ 9.0 cm; R_2: ruffe > 9.0 cm.

Year	**Month**	**Perch**			**Perch-Ruffe**						**Ruffe**
		P_1-P_2	**P_1-P_3**	**P_2-P_3**	**P_1-R_1**	**P_2-R_1**	**P_3-R_1**	**P_1-R_2**	**P_2-R_2**	**P_3-R_2**	**R_1-R_2**
					S_{west}						
2003	**August**	0.06	0.00	**0.94**	**0.57**	0.06	0.00				
	October	**0.67**	**0.55**	**0.72**	0.14	0.17	0.13	0.03	0.02	0.02	***0.40***
2004	**May**	**0.81**	**0.66**	**0.82**	0.08	0.06	0.02	0.08	0.06	0.03	**0.51**
	June						0.15			0.24	**0.57**
	July			**0.76**		0.01	0.00		0.08	0.08	***0.29***
	August	0.15	0.01	**0.85**	***0.27***	0.08	0.01	0.05	0.00	0.00	***0.28***
	September	0.14	0.01	0.01	***0.25***	0.07	0.00				
	October	**0.50**	0.07	0.07	0.00	0.02	0.00				
2005	**September**	**0.57**			0.12	0.10		0.11	***0.37***		0.04
					S_{east}						
2004	**May**					***0.33***			***0.30***		***0.47***
	June			**0.76**		0.05	0.07		0.05	0.07	***0.45***
	July						0.01			0.00	0.06
	August	0.07	0.01	***0.42***				***0.39***	0.07	0.02	
	September	**0.59**	0.00	0.00	***0.33***	0.22	0.00	0.14	0.01	0.00	***0.29***
	October	**0.53**	0.04	***0.43***	0.06	0.06	0.03	0.04	0.04	0.02	***0.42***
2005	**September**	0.24	0.00	0.00	0.11	0.12	0.00	0.05	**0.55**	0.00	0.17

Diet overlap was also high within both size classes of ruffe (Figure 4.8). Medium index values predominated (71% and 66% of all comparisons), and individual feeding specializations that would result in no diet overlap at all were very rare. Small perch showed a similar pattern to ruffe, with most diet overlaps being medium (50%). However, 25% of the index values were zero, indicating individual feeding specialisations. In medium-sized perch, individual specialisations were even more apparent, resulting in high proportions of zero overlap (50%). In this size class of perch, medium index values hardly occurred, but high index values accounted for 34% of all comparisons. In these cases, perch fed mainly on larger prey such as gammarids, molluscs, and fish, and index values indicated almost complete diet overlap (values > 0.8). Averaged over all size classes of fish, perch consumed more prey items per fish than ruffe, as some perch fed heavily on small zooplankton organisms (up to 2500 organisms per fish). Generally, the bigger size classes within each species consumed less but heavier prey items. This was most pronounced in perch, who could feed on big prey organisms like fish or large gammarids due to their larger gape size.

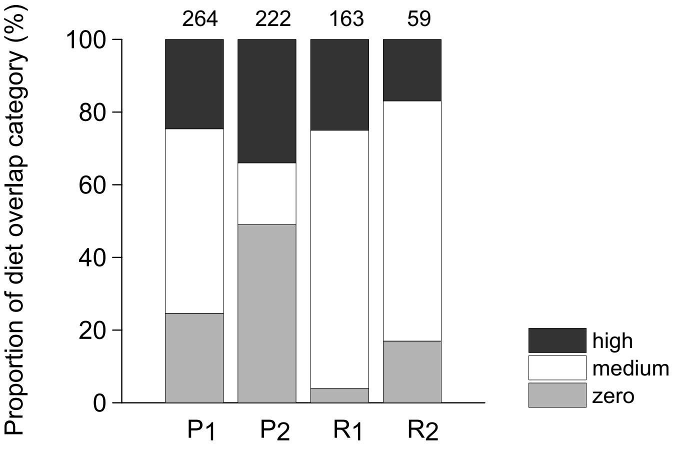

Figure 4.8 Intraspecific diet overlap after Schoener (1971) among individuals, within one size class for perch and ruffe during August and September. Data were pooled over two study sites, years and months. Index values < 0.05 are considered as zero, index values $0.05 \geq C < 0.5$ as medium and index values ≥ 0.5 as high overlap. P_1: perch ≤ 9.5 cm; P_2: perch 9.5 cm < TL $\leq$ 13.0 cm; R_1: ruffe ≤ 9.0 cm; R_2: ruffe > 9.0 cm.

Discussion

Perch and ruffe exhibited clearly contrasting feeding strategies. Ruffe met its reputation as a specialized benthos consumer (Hölker and Thiel 1998, Ogle et al. 1995, Rezsu and Specziar 2006) feeding mainly on chironomid larvae and pupae, irrespective of the sampling date. Perch, in contrast, had resumed its omnivorous feeding strategy in parallel to the ongoing re-oligotrophication of ULC, feeding on zooplankton, zoobenthos and fish. In lakes of low productivity, where food resources are limited and may get exploited rapidly, a euryphagous species like perch has the option to use alternative prey, whereas a food specialist like ruffe has no choice but to react to the reduced food supply through slower growth and/or lower reproductive investment. Furthermore, intraspecific competition also increases with decreasing food availability. Ontogenetic diet shifts and individual feeding specializations, however, which are both characteristic of the food generalist perch (Hjelm et al. 2000, Jamet and Lair 1991, Radke and Eckmann 2001, Rezsu and Specziar 2006), can relieve intraspecific competition (Quevedo and Olsson 2006, Werner and Gilliam 1984). The specialized benthos consumer ruffe, however, is forced into severe intraspecific competition when the food base is reduced, as it does not perform pronounced ontogenetic diet shifts, nor does it show marked individual feeding specialization. After a short plankton feeding stage as larvae, they switch to zoobenthos already with 2 cm body length, with chironimids being their preferred prey throughout their life (Rezsu & Specziar 2006, Hölker & Thiel 1998). In meso- or eutrophic systems, where the food base for benthivorous fish is better, this inflexibility is probably less detrimental, whereas in lakes of low productivity ruffe will likely be at a disadvantage.

Perch nowadays become cannibalistic in ULC at a length of 13 cm at the latest, yet 20 years ago all size classes of perch fed mainly on zooplankton (Becker 1988). The increased importance of cannibalism corresponds with the findings of Jeppesen et al. (2000, 2005) and Persson (1991), who predicted a change from a planktivorous-dominated to a piscivorous-dominated fish community with decreasing lake productivity.

Consuming conspecifics can promote growth and reproduction in various ways because the nutritional requirements of the cannibalistic specimens are best met by conspecifics, since they supply all necessary compounds such as essential amino acids in optimal proportions (Meffe and Crump 1987). Furthermore, with increasing body size it becomes increasingly unprofitable for fish to have to cover their energy needs with small organisms such as zooplankton until the utilization of this resource will finally not allow for a net increase in biomass (Diehl 1993, Mittelbach 1983). If becoming cannibalistic, however, the larger specimens can utilize these energetically unprofitable resources via their transformation by smaller conspecifics into larger, and biochemically more adequate, prey. Cannibals not only benefit from the energy gained by feeding on their conspecifics, but also from reducing competition for shared resources. The substantial impact of cannibalism on population dynamics was shown for perch in a long term study by Persson et al. (2000).

The food choice of perch not only differed between size classes, it also changed during the growth season in a typical pattern. In spring and early summer, perch consumed zooplankton, then switched to zoobenthos in August and consumed zooplankton again in October. Even the medium-sized and large fish, which became piscivorous in August, partly reverted to zooplanktivory in October. At least for the medium sized fish it could be, that the y-o-y outgrew their gape size. Hence, the ontogenetic diet shifts in perch are not as fixed as is often suggested (Hjelm et al. 2000, Jamet and Lair 1991, Rezsu and Specziar 2006); they are reversible, whereby perch can react very flexibly to a changing prey base. The notion that diet shifts are irreversible in perch may arise because field samples are often obtained only during summer, or because studies on food choice have mainly been carried out in lakes of high productivity, where a flexible reaction to changes in the prey base is not provoked (Radke and Eckmann 2001).

The diet shift of perch in ULC from zooplanktivory to benthivory or piscivory in August may be caused either by low zooplankton abundance or by better availability of zoobenthos or fish. In August total zooplankton abundances were indeed low in all study years, but they were even lower in July and October when perch did feed on zooplankton. Similarly, the shift to zoobenthos cannot be attributed to increased zoobenthos abundances, as they are generally lowest in August in the littoral of ULC (Baumgärtner 2004, Scheifhacken 2006). Temperature induced changes in the behaviour of benthic organisms, however, can enhance prey accessibility. Zoobenthos activity probably increases in August due to high water temperature, either through a direct effect on activity or through oxygen depletion in their refuges, forcing at least part of the macrozoobenthos community to abandon these refuges (Newell 1969, Winterbottom et al. 1997). During our study from 2003-2006, temperatures were always highest in August, and as a consequence enhanced prey encounter rates may have triggered a diet shift in perch from zooplankton to zoobenthos. The diet shift of the larger perch to piscivory coincided with the arrival of y-o-y perch in the littoral zone, and with the daytime feeding activity of smaller benthivorous perch.

In contrast to small Swedish lakes where perch and ruffe use different habitats (Bergman 1988), both species used the same habitat in ULC, albeit with partly opposed activity patterns. During the day both species were absent from the shallow littoral zone, but appeared there at dusk and disappeared at dawn. Ruffe arrived in the shallow littoral zone with empty stomachs to feed there during the night until their stomachs were well filled the next morning, whereas perch rested in the shallow littoral zone during the night (Imbrock et al. 1996). Perch fed almost exclusively during the day, which has been observed in other studies as well (Beeck et al. 2002, Jamet and Lair 1991, Schleuter et al. 2007). As both species feed in the warm, shallow littoral zone during summer, the advantage ruffe may gain in the Swedish lakes by being a temperature generalist (Bergman 1987), is of minor importance in Lake Constance.

Despite this noticeable habitat overlap, competition for food between perch and ruffe was only marginal. Even during summer, when the smaller perch (< 13 cm) were benthivorous, interspecific diet overlap reached only moderate values, indicating efficient food partitioning, which was also observed by Rezsu & Specziar (2006). While gammarids contributed most to the diet of perch, ruffe fed predominantly on chironomids. Low interspecific diet overlap, however, can also result from niche divergence due to competition (Bonesi et al. 2004). Bergman and Greenberg (1994) demonstrated that an increased density of ruffe increased perch's consumption of zooplankton and of less preferred prey items. However, perch and ruffe prefer similar, but not completely identical prey (Fullerton et al. 1998) and gammarids are known to be an important prey for perch (Cobb and Watzin 1998, Rezsu & Specziar 2006). Yet, when zooplankton abundances seriously declined in the 1990s, the high abundances of ruffe might have delayed a shift of perch to zoobenthos.

Intraspecific diet overlap between size classes was high for both species throughout the growing season. When perch fed on zoobenthos, intraspecific competition was probably relieved due to individual feeding specializations. Some individuals consumed only one type of prey, and prey types often differed between individuals. This was most pronounced for larger perch, where 50% of all comparisons of individual stomach contents showed no diet overlap at all. Quevedo & Olsson (2006) interpreted the high variability of isotopic composition of perch with a high specialization in resource use, which they considered to be a strategy to reduce intraspecific competition. The long term study of Svanbäck and Persson (2004) confirm these results. They found that individual specialization fluctuated with population density in response to changing resource levels. In ruffe, by contrast, diet variability between individuals was very low and individual diet overlap was mostly moderate to high.

The diel migrations of ruffe in ULC can be attributed to the differences in light intensity and food availability between the shallow littoral and greater depths. In the shallow littoral zone, water transparency is high and macrophyte stands that provide shelter from predators are sparse (Eckmann et al. 2006). Hence, predation risk is lower in the deeper, darker zones. The extremely light-sensitive eyes of ruffe may be an additional reason for them to avoid shallow waters during the day. Ruffe is able to feed at greater depth during the day due to its sensory abilities, but zoobenthos abundances decrease with depth in ULC, and they are already very low at around 10 m depth (Baumgärtner 2004, Mörtl 2003). As a consequence, ruffe have to migrate into the shallow littoral zone at dusk to feed there until dawn. A similar migration pattern was described for adult ruffe in oligotrophic Lake Superior by Ogle (1995). Since prey capture rates of ruffe are low compared to those of perch (Becker 2000, Bergman 1988), the restriction of their feeding time to the night is considered as an additional disadvantage for ruffe in oligotrophic lakes, particularly during summer when nights are short. In more productive, and hence more turbid systems, ruffe may feed continuously during day and night (Hölker and Temming 1996).

Perch also lived in the deeper littoral zone during the day which, in the case of the smaller fish, is probably a behavioural reaction to the lack of, or only sparsely developed, macrophyte cover in the littoral zone. In contrast to ruffe, however, perch mainly fed on zooplankton, which is also abundant at greater depths. During August, when smaller perch preyed primarily on zoobenthos, they also utilized the shallow littoral zone during the day.

The results of this study suggest that competition for food between perch and ruffe in a large, oligotrophic lake is of minor importance. The direct consequences of re-oligotrophication such as higher water transparency, a reduced food base, and the higher prevalence of parasite infection in perch are therefore considered to be the main factors that control the growth and population dynamics of perch and ruffe (Eckmann et al. 2006). Perch reacted very flexibly to seasonal changes in food availability, and they alleviated intraspecific competition through individual feeding specializations. These characteristics may allow them to maintain high population densities in spite of the generally lower food supply in lakes of low productivity. Ruffe, as a zoobenthos specialist, may not revert to other food resources when its food base decreases, and intraspecific competition is intense due to weak individual feeding specializations. And finally, ruffe do not become piscivorous as they grow larger, which is probably their most important disadvantage in lakes of low productivity. With increasing intraspecific competition ruffe is known for a trade-off between gonadal investment and somatic growth in terms of reducing fecundity and increasing size at maturation, which in turn will contribute to declining population densities (Devine et al. 2000). With ongoing re-oligotrophication of ULC, intraspecific competition in ruffe is expected to become more intense, leading to further decreases in their population density, which will then translate into even weaker competition with perch.

Acknowledgements

We thank many students and colleagues, especially Susanne Haertel-Borer and Arnd Weber for their assistance in the field. For the line transect scuba diving we thank the scientific divers of the University of Konstanz. Special thanks goes to Myriam Schmid, for counting the plankton organisms and fish prey items. Christoph Berron, Marc Hamitou, Felix Heindl and Jens Hirzig also helped with stomach analyses. We thank 3 anonymous reviewer and an associate editor, who’s comments helped to improve the manuscript. Marry Morris corrected the English. This study is embedded in the Collaborative Research Centre 454 ‘Littoral Zone of Lake Constance’ financed by the German Science Foundation (DFG).

General discussion and concluding remarks

Many studies on the community succession along a productivity gradient focused on the gradient from low to high productivity. Re-oligotrophication is expected to cause an inverse development of community composition, but the underlying mechanisms are not fully understood. The relative abundances of the two competing percids Eurasian perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* (L.)) both increase and then decrease with increasing productivity. Perch, however, is favoured under mesotrophic conditions while ruffe prosper under meso- to eutrophic conditions. The advantage ruffe may gain over perch under turbid conditions due to its sensory abilities seems to be understood. The mechanisms controlling the distribution going from high to low productivity, however, remain still unclear.

In this thesis I aimed at understanding probable mechanisms underlying the competition between perch and ruffe, and their general performances in a large re-oligotrophic lake. As an initial step I determined the influence of light on the outcome of competition. With ongoing re-oligotrophication water transparency increases and the competitive advantage ruffe may gain through its sensitive lateral line organ over the visual oriented perch under turbid or dark conditions might be of declining importance. In single species experiments Bergmann (1988) and Becker (2000) could show, that in contrast to perch, ruffe can feed during darkness, but mixed species experiments were still missing. In the laboratory growth experiments (**Chapter 1**) I could show that the species competitive superiority strongly depends on the feeding regime. Ruffe is outcompeting perch when food is provided during darkness to the extend that perch looses weight. When food is provided during the day, however, neither specific growth rates nor feeding behaviour of perch and ruffe were influenced substantially by interspecific competition.

The growth experiments described in Chapter 1 entailed further experiments: the specific growth rates for ruffe I measured in these feeding experiments in groups of four fish were 3.5 fold as high than growth rates measured by Henson and Newman (2000) under similar conditions but with isolated ruffe. In cooperation with Susanne Haertel-Borer, I performed respiratory experiments (**Chapter 2**), which clearly demonstrate, that in groups of fish routine metabolism and activity significantly decreased for both species. However, reduced metabolism is not only explained by reduced activity, but also by a ‘psychological’ calming effect.

In a next step I moved to more realistic field conditions. In enclosure experiments in the littoral zone I investigated the competition for benthic resources between perch and ruffe in re-oligotrophic Lake Constance (**Chapter 3**). These experiments I performed in cooperation with Nicole Scheifhacken, who handled the benthological part. The experiments revealed that, if both species are kept together, interspecific competition between perch and ruffe actually occurs: diet composition of perch and ruffe did not differ in the single species cages, but in the mixed species cages the food composition of both species changed and differed significantly. We could further show that for the benthic community bottom-up effects seem to be more important than top-down effects. We hold strong inherent processes of the benthic community and a general low availability of benthic organisms to fish predators responsible for the weak top-down effects.

Finally, in detailed field studies in several consecutive years I could gain information on the general performance of both species and their niche overlap under oligotrophic conditions. I could show that nowadays perch indeed includes zoobenthos again in its diet, as it was the case before eutrophication. Yet, this diet forces it into competition with ruffe (**Chapter 4**). Interspecific diet overlap, however, is moderate and only relevant during summer, when both species feed on zoobenthos. In contrast to interspecific diet overlap, intraspecific diet overlap between different size classes remains high throughout the year. Compared to ruffe diet composition of perch is very flexible and differs not only between different size classes but also follows a seasonal pattern as a reaction to changing food abundances. Ruffe as a specialist in contrast is not able to react to a shortage of food resources. In conclusion, this could be a reason for the (compared to perch) low abundances of ruffe in oligotrophic lakes.

General Discussion

The results of the previous chapters show that the outcome of competition between perch and ruffe and their general performances are influenced by various factors such as light conditions, environmental conditions at the study site, and food availability. In the following these results will be discussed with special emphasis on the environmental conditions in a large oligotrophic lake.

An important factor influencing the outcome of competition between perch and ruffe are the predominant light conditions. In an oligotrophic lake, however, this factor seems to be of minor importance and the high water transparency could even lead to a disadvantage of ruffe. In single species experiments it was demonstrated that ruffe's feeding efficiency is not at all or only slightly influenced by decreasing light intensity or increasing turbidity, while perch is only able to feed efficiently under well-lit conditions (Becker 2000, Bergman 1988, Janssen 1997). However, under well-lit conditions due to high water transparency, perch capture rates are higher than ruffe's. In the laboratory growth experiments (Chapter 1) I could show in mixed species set ups that also the competitive outcome is strongly influenced by the prevailing light conditions. In darkness perch was negatively influenced by the presence of ruffe, to the extend that perch lost weight when food was provided only during the night. These results could reflect the turbid conditions we find in eutrophic systems. Under the well-lit conditions in contrast neither specific growth rates nor feeding behaviour of perch and ruffe were influenced substantially by interspecific competition, which is similar to the results of Savino and Kolar (1996). Hence, compared to turbid lakes neither species would theoretically be disadvantaged nor favoured in a clear lake with high water transparency.

Under natural conditions in an oligotrophic lake, however, ruffe feeds only during twilight and night and is not active during the day, while perch feeds during twilight and day (Chapter 4). The activity of ruffe during the day in the growth experiments might have been enhanced by the particular laboratory conditions (Chapter 1). Day activity of ruffe is known from some field studies, which were conducted in turbid systems (Hölker and Temming 1996, Ogle et al. 1995). In the St. Louis River Estuary of Lake Superior some ruffe fed in deeper regions during day and night, whereas others, which migrated to the shallow littoral zone to feed there heavily during the night, did not feed during the day (1995). The latter behaviour is similar to what we find in Lake Constance (Chapter 4).

This activity pattern in clear lakes may be of disadvantage to ruffe. Bergman (1988) and Becker (2000) demonstrated in their studies that capture rates of ruffe are generally low compared to perch, if perch is not limited by decreasing light intensity. In turbid systems, where ruffe feeds during day and night, it can compensate the lower ingestion rates. However, during summer, when temperatures are high and growth should be best, nights are short and the advantage to be a light generalist vanishes.

Night activity and the daily migration pattern of ruffe in a large oligotrophic lake with high water transparency might be caused by light intensity and food availability. Ruffe seems to prefer crepuscular or dark light conditions probably due to predator avoidance behaviour and maybe due to their light-sensitive eyes (Collette et al. 1977, Hölker and Thiel 1998). In the shallow littoral zone of a large oligotrophic lake, however, water transparency is high and macrophyte-stands as shelter from predators are sparse (Eckmann et al. 2006). Hence, the deeper, darker zones with reduced predation risk provide better chances for survival. Due to ruffe's sensory abilities, feeding would be possible in these areas; however, in the deeper zones of Lake Constance benthic food resources are scarce (Baumgärtner 2004, Mörtl 2003). Below the long-term average of low water level the abundances of zoobenthos continuously decrease with depth and are very low in about 10 m. The highest abundances of benthic organisms ruffe prey on can be found between 0.4 m and 3 m depth. As a consequence, ruffe have to migrate into the shallower littoral zones to feed when light becomes more crepuscular there.

Perch also prefers the deeper littoral zone during the day, probably also as a replay to the absent or only sparse macrophyte-cover in the littoral zone. However, perch might not be as limited as ruffe in its food intake. During spring and autumn, when perch is mainly caught in the deeper zones, it predominantly feeds on zooplankton, which is abundant also in greater depth. The zooplankton-organisms can be spotted by the optical oriented perch because of their contrast against the background of the light from the surface (Eckmann 2004, Köder 2006). During August, when perch prey primarily on zoobenthos, they utilise the shallower littoral zone also during the day.

One factor which was not specifically investigated in the context of this thesis, but which should not remain unmentioned, is temperature. Ruffe is a temperature generalist, what should favour him over perch. Bergman (1987) found that ruffe's foraging ability was far less influenced by different temperature regimes than perch's. As a consequence, ruffe is able to occupy habitats of a wider temperature range. This tolerance against temperature, however, plays a subordinate role during the growing season in Lake Constance, where both species co-occur in the same habitat at temperatures, which are suitable for both species. During winter, however, perch and ruffe use the deeper zones of the lake, where light intensity and temperature are low. During this time, ruffe gains advantage by being a light and temperature generalist (Eckmann 2004).

The environmental condition at different study sites such as substrate composition, wind and wave exposure, and benthos community composition and abundance can also influence the competition between perch and ruffe and the fish species distribution (Chapter 3, 4). The distinct influence of some of these variables, however, remains indifferent. I could show that if perch and ruffe were kept together in a cage, competition actually occurred (Chapter3).

However, the outcome of competition depended on the study site: At the more sheltered, sandy site, with more limited food resources, both, perch and ruffe, had little filled stomachs and intraspecific competition was as strong as interspecific competition. At the more exposed, stony site with higher zoobenthos abundances, in contrast, ruffe was the superior competitor. At this site, total abundance of fish and the relative proportion of ruffe were also higher (Chapter 4). That ruffe performed better at the stony site was surprising, considering the findings of Dieterich et al. (2004a), who showed in their laboratory experiments, that ruffe foraged more efficiently over fine substrates and perch over coarse substrates.

The main reason for the differences in the relative abundances of both species between the study sites could be prey availability. Chironomids and other insect larvae are the preferred prey organisms of ruffe (Chapter 3, Chapter 4, Hölker and Thiel 1998, Kangur et al. 1999, Rezsu and Specziar 2006). The high abundances of these prey organisms at the stony study site may carry higher abundances of ruffe. Additionally, the stronger wave exposure of this site due to the prevailing westerly winds, the close ferry-track and the steep slope could partially contribute to the higher relative abundances of ruffe. Actually, the use of the sensitive lateral line organ while foraging could restrict the foraging success at an exposed stony site due to higher water turbulences (Dieterich et al. 2004b). However, since ruffe is absent in the littoral zone during the day and it forages there during the night only, it may be less exposed to hydrodynamic forces than diurnal species: in summer the relative frequency of occurrence of waves is very high during the day, mainly due to boat traffic, but also due to abating winds in the evening (Hofmann et al. submitted). But additional in situ studies are necessary to further elucidate the influence of these variables.

Food availability is probably also the most decisive factor for the general performances of perch and ruffe in an oligotrophic lake. Both species exhibit very different feeding strategies. Ruffe meets its reputation as benthos specialist and feeds consistent with other studies mainly on chironomid larvae and pupae, irrespective of the sampling date (Chapter 4, Hölker and Thiel 1998, Ogle et al. 1995). Only if zooplankton abundances are high, it can also feed on zooplankton (Kalas 1995). In the case of a shortage of the preferred resources, as it is expected for oligotrophic lakes, it should be difficult for a specialist like ruffe to open up new food resources.

Perch in contrast return with ongoing re-oligotrophication from exclusively planktivory to omnivory and feed again on zooplankton, zoobenthos and fish. They further exhibit a strong seasonal pattern in diet composition independent of fish size. To be a flexible food generalist like perch can be advantageous in oligotrophic lakes like Lake Constance. Food resources get exploited more rapidly, if they are limited; thus the probability that fish are forced to revert on other prey increases. Further, intraspecific competition generally increases with decreasing food availability. Ontogenetic diet shifts and individual food variability, however, can relief from intraspecific competition (Quevedo and Olsson 2006, Werner and Gilliam 1984). Ontogenetic diet shifts with increasing body size can further be supported by an energetic gain (Graeb et al. 2006). With increasing body size it may become unprofitable to cover the energy demand with small sized organisms like zooplankton, especially if abundances are low.

Concluding remarks

Since the beginning of the 1980s the nutrient load of Lake Constance is steadily decreasing. Ruffe was first recorded in 1987 and, despite re-oligotrophication, rapidly developed high population densities (Rösch and Schmid 1996). Already in the mid-1990s it was one of the most abundant fish species in the littoral zone (Eckmann and Rösch 1998, Reyjol et al. 2005). But recently a decline in the population of ruffe is observed.

The increase in ruffe populations in the 1990s coincided with a decrease in the growth of perch (Eckmann et al. 2006). Stakeholders feared that ruffe was negatively impacting perch. However, during this time, perch mainly fed on zooplankton and competition for benthic food resources with ruffe was not occurring. With ongoing re-oligotrophication of Lake Constance perch includes again zoobenthos in its diet, forcing it into competition with ruffe (Chapter 4). Yet, I could show in consecutive years, that interspecific competition is only relevant in August and September, when both species feed on zoobenthos. Even then, interspecific diet overlaps reach only moderate values, indicating efficient food partitioning of perch and ruffe (Rezsu and Specziar 2006). Intraspecific diet overlap between different size classes, however, is high for both species throughout the growing season.

I suggest that in re-oligotrophic Lake Constance rather consequences of re-oligotrophication than interspecific competition are responsible for the reduced growth of perch and the decreasing population densities of ruffe. In the case of perch decreasing food resources and altering zooplankton composition due to re-oligotrophication result not only in increased intraspecific competition but also in higher pike worm infections and can thus lead to decreasing growth rates (Brinker and Hamers 2005, Eckmann et al. 2006). Under the oligotrophic conditions before the eutrophication of Lake Constance, growth of perch was also lower than during eutrophication (Hartmann 1975, 1978). Nevertheless, its flexibility in prey selection as reaction to food availability may enable perch to maintain relatively high stable population densities despite decreasing growth rates and intraspecific competition.

Competition with ruffe may also slightly influence perch. The high abundances of ruffe in the 1990s might have delayed a shift of perch to zoobenthos, when zooplankton abundances seriously declined. Bergman and Greenberg (1994) demonstrated, that an increased density of ruffe increased perch' consumption of zooplankton and of less preferred prey items. Low interspecific diet overlap between species can also resume from niche divergence due to competition (Chapter 3, Bonesi et al. 2004). However, perch and ruffe consume similar bcompletely identical benthic prey (Fullerton et al. 1998).

In ruffe, intraspecific competition increased steadily due to the rapid population development following its introduction and due to ongoing re-oligotrophication. Ruffe as a benthos specialist is not able to open up new food resources such as zooplankton or especially fish. However, when ruffe was introduced to Lake Constance its population density rapidly increased like in other large lakes, although some of these lakes were defined as mesotrophic or oligotrophic (Adams and Maitland 1998, Rösch and Schmid 1996). Such a rapid population development is often typical for invasive species (Strayer and Malcom 2006). Schmid (1999) concluded from his studies on the biology of ruffe in Lake Constance, that ruffe had occupied an empty niche, favouring rapid establishment and population expansion. During this time perch was not feeding on zoobenthos and other abundant benthivorous fish like burbot (*Lota lota* (L.)) prefer other benthic organisms than ruffe (Baumgärtner and Rothhaupt 2005, Wacker 2005). With increasing population size of ruffe, however, intraspecific competition increases and thus growth and reproductive success may decline (Devine et al. 2000, Lorenzen and Enberg 2002, Thomas and Eckmann 2007). Additionally, predators may adapt to the new prey species, and eventually diseases will establish, all leading to a decline of the population size (Wolfe 2002). In the case of ruffe it is known from Loch Lomond, that after the rapid population development, fecundity of ruffe decreased and weight at maturity was higher at high ruffe abundances (Devine et al. 2000). The authors interpret the changing maturity pattern with changing population size and thus intensity of intraspecific competition in terms of changing growth opportunity and a trade-off between gonadal investment and somatic growth. The intraspecific competition and the lower reproduction rates finally led to a smaller population size with intermediate fecundity. In Lake Constance a decline in population size was observed during the last years (Reyjol et al. 2005, Rösch and Schmid 2005), however we could not observe a decline in the growth of ruffe (S.

Haertel-Borer unpubl. data, personal observation). This reproductive strategy of ruffe to maintain high growth rates and to decrease fecundity with increasing intraspecific competition, might also differ from the strategy of perch, which seems to retain fecundity while growth rates decline. However, further research is needed to confirm this hypothesis.

Several factors may interact in causing declining ruffe abundances following rapid population development after invasion in re-oligotrophicating Lake Constance (i) rapid increasing population size, exceeding a sustainable population size (ii) increasing intraspecific competition resulting in decreased growth and reproduction success (iii) increasing competition with other species (e.g., perch which feeds again on zoobenthos) and (iv) ongoing re-oligotrophication, resulting in more limited food resources.

The good growth of ruffe under the turbid conditions is explained by their sensory abilities to feed during darkness. In systems with low water transparency, ruffe often feed during day and night. In oligotrophic lakes with high water transparency and sparse macrophyte-cover, ruffe are restricted to deeper, crepuscular water zones with low zoobenthos abundances during the day. At night they migrate to the shallow littoral zone to feed. The advantage over perch by being a generalist concerning temperature and light conditions is not relevant in this system. As a food specialist, ruffe is even disadvantaged. Perch, as a food generalist, can open up new food resources, if one gets exploited, while ruffe do not have the possibility to switch to zooplankton or fish as main food source, if benthic invertebrates get scarce.

In summary, despite ruffe developed rapidly high population densities after its introduction to Lake Constance, the fear of the fisheries stakeholders did not come true. Schmid (1999) suggested that ruffe had occupied an empty niche. Further, if intraspecific competition is low, ruffe are known to have high fecundities and a low weight at maturation (Devine et al. 2000). Ongoing re-oligotrophication and low fecundity due to high intraspecific competition, contribute now to declining ruffe populations. In oligotrophic Lake Constance, ruffe might be able to sustain low population densities, but it will be of minor importance as a competitor for perch.

Summary

The central issue of this thesis is the understanding of the mechanisms underlying the competition and the general performances of the two percids perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* (L.)) in a large re-oligotrophic lake. Both species are potential competitors for benthic food resources. The visual predator perch is supposed to flourish best under mesotrophic conditions, whereas ruffe with its very sensitive lateral line organ performs best under meso- to eutrophic conditions. In oligotrophic lakes ruffe is far less abundant than perch or even absent. Many studies exist on the competition between perch and ruffe. These studies mostly focus on the gradient from low to high productivity. The competitive relationship between perch and ruffe under ongoing re-oligotrophication, however, has never been studied in detail.

In the 1980s ruffe was accidentally introduced to Lake Constance and developed high population densities, despite the decreasing nutrient loading due to re-oligotrophictaion. The increase in ruffe populations coincided with a decrease in the growth of perch, a commercially important fish species in Lake Constance. In this regard, stakeholders feared that ruffe had a negative impact on perch. However, recent reports refer to declining ruffe abundances. In this study I conducted laboratory, enclosure and field experiments to enlighten the mechanisms of competition and the general performances of both species under oligotrophic conditions.

In the laboratory growth experiments I focused on the influence of light on the competition between perch and ruffe and the advantage one species may gain through their different sensory abilities. In single and mixed species treatments using groups of four fish I could show, that the outcome of competition for benthic food resources strongly depends on the feeding regime. At night, feeding behaviour and specific growth rates of perch were negatively influenced by the presence of ruffe to the extent that perch lost weight when food was provided only during the night. However, when fed only during the day, both species turned out to be equal competitors, as neither specific growth rates nor feeding behaviour of perch and ruffe were influenced substantially by interspecific competition.

The specific growth rates I measured for ruffe in these feeding experiments in groups of four fish were 3.5 fold as high than growth rates known from the literature for isolated ruffe under similar conditions. Respiratory experiments were performed, to test for a possible calming effect in groups of fish, as more energy can be invested in growth, if less energy is demanded for routine metabolism. These experiments clearly showed that in both species routine metabolism and activity decreased for fish in groups compared to isolated fish. However, the reduced metabolism could not only be explained by a reduced activity in groups, but also by an additional ‘psychological’ calming effect. Since many growth experiments and bioenergetics measurements in the literature are still performed with isolated fish, irrespective of the species ecology, these findings could point out that the results can hence seriously be biased.

The enclosure experiments in the littoral zone of re-oligotrophic Lake Constance showed that interspecific competition between perch and ruffe actually occurs if both species are kept in close sympatry. The diet composition of perch and ruffe did not differ in the single species cages, yet in the mixed species cages the diet composition of both species diverged and differed significantly. The outcome of competition and the diet composition of both species were influenced by differences between the study sites and the benthic community composition. Compared to these bottom-up effects, predatory impacts and evidence for a top-down control were weak or even absent, probably due to a low availability of benthic food resources for the fish and strong inherent processes of the benthic community.

The field studies finally revealed that nowadays perch includes zoobenthos again in its diet, as it was the case before but not during eutrophication. Yet this diet forces it into competition with ruffe. However, interspecific competition is only relevant during summer, when both species feed on zoobenthos, while intraspecific diet overlap remains high throughout the year. Compared to ruffe, food choice of perch is very flexible not only between different size classes, it also follows a seasonal pattern. Perch as a food generalist is able to open up new food resources if one gets scarce, which seems to be advantageous in oligotrophic lakes like Lake Constance. Ruffe as a food specialist in contrast is not able to switch to zooplankton or fish as main food resource, if benthic invertebrates get scarce. This marked difference in feeding strategies could explain the relative to perch low abundances of ruffe in oligotrophic lakes.

From the experiments within this thesis I can draw the conclusions that competition between perch and ruffe for benthic food resources actually occurs in Lake Constance. In a large

oligotrophic lake, however, the advantage ruffe as a temperature and light generalist has over perch is of minor importance. In systems with low water transparency, ruffe often feed during day and night. In oligotrophic lakes with high water transparency and sparse macrophyte-cover, ruffe are restricted to deeper, crepuscular water zones with low zoobenthos abundances during the day. At night they migrate to the shallow littoral zone to feed. As a food specialist, ruffe is even disadvantaged as it is not able like the flexible food generalist perch, to open up new food resources if one gets exploited. With ongoing re-oligotrophication, both species will suffer from increased intraspecific competition. Despite decreasing growth rates perch might be able to sustain high population densities, while population densities of ruffe will probably balance at a low level. In my opinion, compared to the consequences of re-oligotrophication, interspecific competition between perch and ruffe might be of minor importance concerning the decline in the growth of perch.

Zusammenfassung

Zentrales Thema dieser Dissertation ist das Verständnis der Mechanismen, die der Konkurrenz zwischen Flussbarsch (*Perca fluviatilis* L.) und Kaulbarsch (*Gymnocephalus cernuus* (L.)) und ihrer Bestandsentwicklung in einem großen, re-oligotrophierenden See zugrunde liegen. Beide Arten konkurrieren potentiell um benthische Nahrungsressourcen. Der visuell orientierte Flussbarsch entwickelt unter mesotrophen Bedingungen seine höchsten Abundanzen, der Kaulbarsch hingegen, der ein sehr sensitives Seitenlinienorgan hat, unter mesotrophen und eutrophen Bedingungen. In oligotrophen Gewässern ist er im Vergleich zum Flussbarsch selten oder fehlt oft sogar ganz. Die meisten Studien und Experimente, die sich mit der Konkurrenz von Fluss- und Kaulbarschen beschäftigen, betrachten den Gradienten von niedriger zu hoher Produktivität. In der Phase der Re-oligotrophierung eines Gewässers wurde die Konkurrenz zwischen Fluss- und Kaulbarsch bisher jedoch noch nicht detailliert untersucht.

In den 1980ern wurde der Kaulbarsch in den Bodensee eingeschleppt und entwickelte trotz der Re-oligotrophierung rasch hohe Populationsdichten. Zeitgleich ging das Wachstum des kommerziell wichtigen Flussbarsches zurück. Daher befürchteten Berufsfischer einen negativen Einfluss des Kaulbarsches auf das Wachstum des Flussbarsches. In den letzten Jahren wurde aber auch ein Rückgang der Kaulbarschabundanzen beobachtet. In dieser Arbeit habe ich Labor-, Käfig- und Freilandexperimente durchgeführt, um die Mechanismen der Konkurrenz und des generellen Verhaltens der beiden Arten unter oligotrophen Bedingungen zu untersuchen.

In Laborexperimenten untersuchte ich, in wieweit Licht die Konkurrenz zwischen Fluss- und Kaulbarsch beeinflusst und welchen Konkurrenzvorteil die jeweilige Art durch ihre unterschiedlichen sensorischen Fähigkeiten hat. In Ein- und Zweiarten-Ansätzen konnte ich zeigen, dass der Ausgang der Konkurrenz stark von der Fütterungszeit abhängt. Nachts wurde sowohl das Fressverhalten, als auch das Wachstum der Flussbarsche negativ durch die Kaulbarsche beeinflusst. Wurde die Fütterung auf die Nacht beschränkt, verloren die Flussbarsche sogar an Gewicht. Wenn hingegen nur am Tag gefüttert wurde, beeinflusste

interspezifische Konkurrenz weder das Fressverhalten noch das Wachstum beider Arten wesentlich.

Die spezifischen Wachstumsraten der Kaulbarsche, die in diesem Laborversuch an Gruppen von jeweils vier Fischen gemessen wurden, erreichten 3,5 mal höhere Werte als Referenzwerte aus anderen Veröffentlichungen, die an einzelnen Kaulbarschen unter ähnlichen Bedingungen gemessen wurden. Da mehr Energie in Wachstum investiert werden kann, wenn weniger für den Routinestoffwechsel verbraucht wird, wurden Respirationsexperimente durchgeführt, um auf einen Beruhigungseffekt durch die Gruppe zu testen. Mit diesen Experimenten konnte gezeigt werden, dass der Sauerstoffverbrauch sowie die Aktivität der Fische in Gruppen stark zurückgingen. Der reduzierte Sauerstoffverbrauch konnte aber nicht ausreichend durch eine geringere Aktivität in der Gruppe erklärt werden, vielmehr gab es Hinweise auf einen zusätzlichen „psychologischen“ Beruhigungseffekt. Diese Ergebnisse zeigen, dass viele Wachstumsexperimente und Messungen zur Bioenergetik angezweifelt werden können, da sie, unabhängig von der Ökologie der jeweiligen Art, an isolierten Fischen durchgeführt werden.

In Käfigexperimenten im Litoral des oligotrophen Bodensees konnte gezeigt werden, dass es zu interspezifischer Konkurrenz zwischen Fluss- und Kaulbarsch kommt, wenn beide Arten zusammen gehalten werden. Die genutzten Nahrungsressourcen beider Arten waren sehr ähnlich, wenn die Käfige nur mit einer Art besetzt waren. Wenn sich aber beide Arten zusammen in einem Käfig befanden, unterschieden sie sich. Der Ausgang der Konkurrenz sowie die Nahrungszusammensetzung wurden stark von den Unterschieden zwischen den Untersuchungsgebieten und in der Benthosgemeinschaft beeinflusst. Verglichen mit diesen bottom-up Effekten, waren die top-down Effekte schwach oder nicht feststellbar. Dies liegt vermutlich an einer geringen Verfügbarkeit der benthischen Organismen für die Fische und der starken Eigendynamik der Zoobenthosgemeinschaft.

Freilanduntersuchungen zeigten schließlich, dass sich der Flussbarsch wie vor der Eutrophierung auch von Zoobenthos ernährt, wodurch es zur Konkurrenz mit dem Kaulbarsch kommt. Während die interspezifische Konkurrenz jedoch nur im Sommer relevant ist, ist die intraspezifische Konkurrenz zwischen den verschiedenen Größenklassen das gesamte Jahr hoch. Im Vergleich zum Kaulbarsch ist der Flussbarsch bei der Nahrungswahl sehr flexibel und unterscheidet sich zwischen den verschiedenen Größenklassen und im Jahresverlauf. Als Nahrungsgeneralist kann der Flussbarsch aufgrund seiner hohen Flexibilität bei der Nahrungswahl auf Veränderungen im Nahrungsangebot reagieren, was in einem oligotrophen See von Vorteil ist. Der Kaulbarsch hingegen kann als Benthosspezialist bei einer

Verknappung der benthischen Nahrungsressourcen schlecht auf andere Nahrungsressourcen ausweichen. Dies könnte ein Grund für die, im Vergleich zu Flussbarschen, geringeren Bestandsgrößen der Kaulbarsche in oligotrophen Seen sein.

Die Ergebnisse der Experimente dieser Dissertation zeigen, dass es im Bodensee zur interspezifischen Konkurrenz zwischen Fluss- und Kaulbarsch kommt. In einem großen oligotrophen See sind aber die Vorteile, die der Kaulbarsch als Licht- und Temperaturgeneralist gegenüber dem Flussbarsch hat, von untergeordneter Rolle. In trüben Gewässern fressen Kaulbarsche oft am Tag und in der Nacht. In oligotrophen, klaren Seen mit geringem Makrophytenbewuchs sind die Kaulbarsche tagsüber jedoch auf Tiefenzonen mit geringer Lichtintensität beschränkt, in denen wiederum die Zoobenthosabundanzen gering sind. Nachts wandern sie dann ins flachere Litoral um zu fressen. Als Nahrungsspezialist ist der Kaulbarsch benachteiligt, da er nicht wie der Flussbarsch auf neue Nahrungsressourcen wie Zooplankton oder Fisch ausweichen kann. Mit fortschreitender Re-oligotrophierung des Bodensees wird die intraspezifische Konkurrenz beider Arten zunehmen. Es ist zu erwarten, dass der Flussbarsch trotz rückläufiger Wachstumsraten hohe Populationsdichten aufrechterhalten kann, während sich die Populationsdichte der Kaulbarsche auf einem niedrigeren Niveau stabilisieren wird. Im Vergleich zu den Konsequenzen der Re-oligotrophierung spielt die Konkurrenz zwischen Fluss- und Kaulbarsch eine untergeordnete Rolle für den Wachstumsrückgang des Flussbarsches.

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Acknowledgements

Many people helped me to accomplish this thesis. Sincere thanks are given to them all!

First of all, I want to thank my supervisor Professor Dr. Reiner Eckmann for providing the topic of this thesis and for his support during the last years. Especially I want to thank him for all the long and very helpful discussion and for the good advice as well in good as in stressful times. His guidance improved my way of working and of course this thesis. I further thank Univ. Doz. Dr. Josef Wanzenböck for his readiness to evaluate this thesis and for being on my defence committee, and Professor Dr. Karl-Otto Rothhaupt for being on my defence committee.

I further thank my co-authors Dr. Susanne Haertel-Borer, PD Dr. Philipp Fischer, and Dr. Nicole Scheifhacken who contributed substantially to parts of this thesis.

The Fish Ecology Group contributed a lot to the last years becoming a good time. I am grateful to everybody in the group, especially to my roommates Petra Klahold and Dr. Jasminca Behrmann-Godel for all their help, the discussions and distractions. The guys from the neighbouring room I want to thank for providing the fridge for always cooled milk, Nik Probst for his assistance in the Vertiefungskurs and Gregor Thomas for his persistence with the sportive lunch program. Phillip Hirsch was helpful with earlier comments on parts of this thesis. The SAS skills I needed, I learned from PD Dr. Philipp Fischer, who was always patiently explaining the program. I am also grateful for many other things I could learn from him, especially concerning the respiration chambers. I greatly thank Dr. Susanne Haertel-Borer, not only for the cooperation in the respiratory experiment, but also for showing me her know-how for the fishing surveys and her support in the field. I profited also from all the scientific discussions and from critical and helpful comments on earlier versions of the thesis. I am very grateful to Myriam Schmid, for assisting in many experiments and especially for counting plankton samples and stomach contents. She also gave me valuable advice for the fish keeping and treatment. Arnd Weber I thank for his help in the field.

I thank all the students who helped me during the experiments, namely Christine Baderschneider, Stefanie Benker, Anne Berkin, Chirstoph Berron, Reiner Blum, Christian Bruckner, Matthias Erhard, Andreas Fischer, Marc Hamitou, Felix Heindl, Jens Hirzig, Katja Lamm, Barbara Leitenmeier, Florian Kundinger, Jasmin Necker, Andreas Nisch and Milene Matos Stangler.

Martin Wolf and the scientific workshop of the University of Konstanz constructed lots of my experimental equipment. Georg Heine, Hubertus Fink and Harald Weber developed software for data logging and processing. Dr. Willy Nagl gave helpful statistical advice.

The scientific divers I thank for their assignment in the field experiments; the night diving during the fishing campaign was sometimes very late.

I thank all the colleges from the Limnological Institute for their support and the nice time at the institute, particularly my fellow PhD students, the secretaries Silvia Berger and Ursula Tschakert, and Jürgen Gans-Thomsen, Beatrix Rosenberg, Alfred Sulger and Christian Fiek for technical support and help in the field.

I am very grateful to my parents, who always supported me during my studies and during this thesis, and to Hilmar for all the hours he spent in helping me in editing this thesis, his patience and all the perfect distractions.

This study was financed by the German Research Foundation (DFG) within the Collaborative Research Centre 'Littoral Zone of Lake Constance' (SFB 454) and the University of Konstanz.

List of Publications

Schleuter, D., and Eckmann R. 2006. Competition between perch and ruffe: the advantage of turning night into day. Freshwater Biology 51: 287-297.

Schleuter, D., Haertel-Borer, S., Fischer, P., and Eckmann, R. 2007. Respiration rates of Eurasian perch (*Perca fluviatilis*) and ruffe: lower energy costs in groups. Transactions of the American Fisheries Society 136: 43-55.

Schleuter, D., and Eckmann, R. accepted. Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. Ecology of Freshwater Fish.

Schleuter, D., and Scheifhacken, N. in preparation. Predation effects of the two competitive fish species Eurasian perch and ruffe on littoral benthic communities: the influence of study site and competition.

Non-reviewed publications

Schleuter, D., and Eckmann R. 2007. Generalist versus Spezialist: Nahrungsvariabilität und Konkurrenz von Fluss- und Kaulbarschen im re-oligotrophierten Bodensee. Deutsche Gesellschaft für Limnologie (DGL) - Tagungsbericht 2006 (Dresden): 140-144.