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).

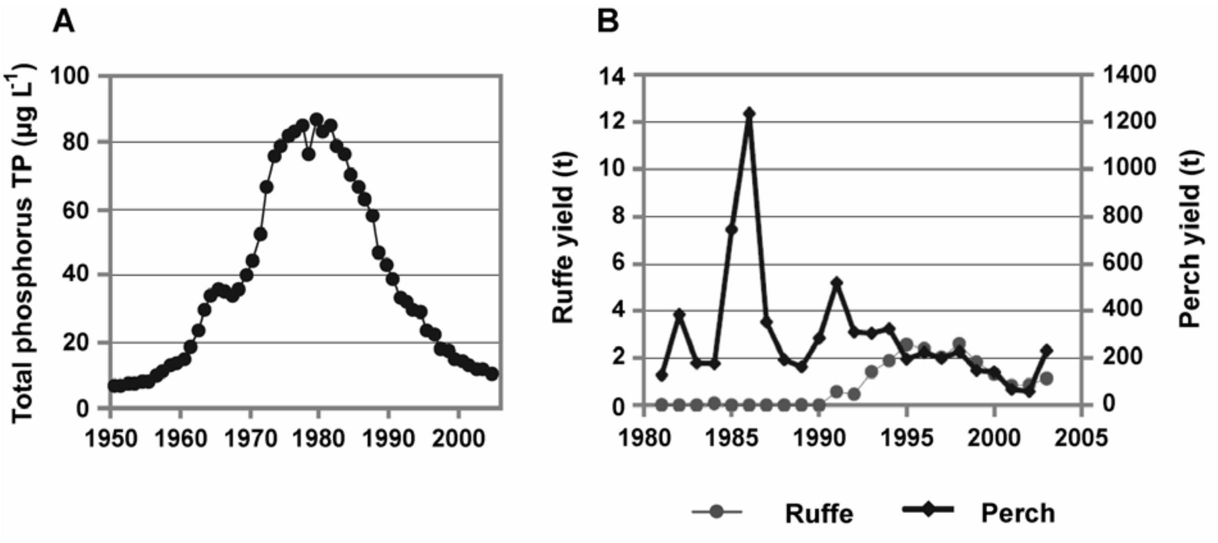

Figure I **A** Total phosphorus during spring circulation in Upper Lake Constance from 1951 to 2005 (data from IGKB) **B** Yields of perch and ruffe from Upper Lake Constance after the statistics of commercial fishermen from 1980 to 2003 (Source: Rösch and Schmid 2005).

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

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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