

# **Community structure, diet and growth of fish in two shallow lakes of different macrophyte colonization**

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## Summary

Shallow lakes display a strong dichotomy between two opposing stable states which differ in turbidity and abundance of submerged macrophytes and can be described as alternative equilibria. Environmental conditions largely differ between opposing stable states, since macrophytes provide a structured habitat and resources for fish and their prey, and turbidity affects the interactions between piscivorous fish and prey fish, as well as between fish and their planktonic or benthic prey. The clear-water, macrophyte-dominated state, as well as the turbid phytoplankton-dominated state, are stabilized by numerous feedback mechanisms between biotic and abiotic components in which fishes are important operational components of each ecosystem. Characteristic differences in species and biomass composition of fish as well as differences in their habitat and resource utilization contribute to the reinforcement of oppositional states, and may further result in a different system response to the increased influx of allochthonous carbon expected with climate change. Omnivorous fish, with their flexible feeding habits including pelagic zooplankton and benthic macroinvertebrates in the littoral zone, are expected to play an especially crucial role in sustaining the clear-water regime under more allochthonous conditions.

The aim of this thesis was to analyze and compare the fish community structure, the spatial and temporal dispersal of fish, as well as the diet and growth of omnivorous fish in a clear, macrophyte dominated and a turbid, phytoplankton dominated lake. Studies were carried out at two shallow lakes with similar fundamental characteristics, but opposite stable state.

Fish community structures were analyzed by gill netting and electro fishing. We expected profound differences in species and biomass composition of fish due to the fundamental differences in turbidity and macrophyte colonization between the lakes.

Furthermore, we conducted several gill net fishing experiments in the littoral and in the pelagic zone, by day and by night, to analyze the spatial and temporal dispersal of fish in both lakes. We hypothesized that temporal differences in the dispersal of fish between the habitats would be more pronounced in the clear lake, where macrophytes intensify the contrast between the habitats, than in the more uniform turbid lake.

Analyses of gut content, stable isotopes and growth were carried out to determine whether the contribution of benthic macroinvertebrates to the diet of omnivorous fish is highest in

the vegetated lake, and whether an elevated consumption of macroinvertebrates promotes the growth of omnivorous fish.

In 2010, our investigations revealed few differences in fish community structure or in the temporal and spatial dispersal of fish between the lakes. Stable isotope and gut analyses indicated that seasonal shifts in resource utilization by omnivorous fish were different in each lake, but there was no general difference in the consumption of macroinvertebrates. We observed, however, a more rapid growth of omnivores in the slightly more eutrophic, turbid lake. It is important to note that 2010 was an unusual year for these lakes, since a severe fish kill over the previous winter (attributed to a particularly long period of ice cover) had strongly reduced the total fish biomass and altered the species composition, thus affected the feeding and growth conditions of surviving fishes in each lake. Comparable data from 2007 showed the expected, profound differences in fish community structure between the lakes. Furthermore, back calculations revealed an opposite pattern of growth of omnivores during the previous years, when the mean annual length increment was three times lower than in 2010, following the fish kill. Overall, our analyses in 2010 were strongly affected by the fish kill, which equalized the conditions in both lakes, although the lakes continued to display major differences in turbidity and macrophyte colonization. Furthermore, the fish kill changed the initial situation for the TERRALAC project, which is currently being conducted at the study lakes, and investigates the effect of increased influx of organic carbon from terrestrial catchments on food webs of shallow lakes expressing alternate biological regimes.

## Zusammenfassung

Flachseen kommen ausschließlich in zwei gegensätzlichen Zuständen vor, die sich in ihrer Trübung und im Vorkommen submerser Makrophyten unterscheiden und als alternative Gleichgewichtszustände beschrieben werden können. Die Umweltbedingungen in Seen entgegengesetzter Zustände unterscheiden sich grundlegend, da Wasserpflanzen ein strukturiertes Habitat sowie Ressourcen für Fische und Wirbellose bieten und Trübung die Wechselwirkungen zwischen Raubfischen und ihren Beutefischen, sowie zwischen Fischen und ihren planktischen oder benthischen Beutetieren beeinflussen. Sowohl der klare, durch Makrophyten dominierte, als auch der trübe phytoplanktondominierte Zustand sind durch zahlreiche Rückkopplungsmechanismen zwischen biotischen und abiotischen Komponenten stabilisiert, wobei besonders Fische eine wichtige funktionelle Komponente innerhalb des jeweiligen Ökosystems darstellen. Die charakteristischen Unterschiede in der Arten- und Biomassezusammensetzung der Fische sowie Unterschiede in deren Habitat- und Ressourcennutzung tragen zur Selbstverstärkung entgegengesetzter Zustände bei und könnten zu einer unterschiedlichen Reaktion des jeweiligen Systems auf den erhöhten Eintrag allochthonen Kohlenstoffs führen, wie er als Folge des Klimawandels erwartet wird. Omnivore Fische sind sehr anpassungsfähig in ihrer Ernährungsweise, da sie sowohl pelagisches Zooplankton als auch Invertebraten des Litorals fressen. Man vermutet, dass sie aufgrund dieser Eigenschaft eine besonders wichtige Rolle bei der Erhaltung des Klarwasserzustands bei gleichzeitig hohem Eintrag allochthonen Materials spielen könnten.

Ziel der vorliegenden Arbeit war die vergleichende Analyse der Gemeinschaftsstruktur der Fische, der räumlich-zeitlichen Verteilung der Fische, sowie der Ernährung und des Wachstums omnivorer Fische in einem klaren, makrophytendominierten und einem trüben, zooplanktondominierten Flachsee. Die beiden Untersuchungsgewässer wurden so ausgewählt, dass sie sich nur durch Trübung und Makrophytenbesiedelung, nicht jedoch in fundamentalen Eigenschaften (wie z.B. Volumen, Trophie,..) unterschieden.

Die Gemeinschaftsstruktur der Fische in den Untersuchungsgewässern wurde mittels Kiemennetz- und Elektrofischung analysiert, wobei wir annahmen, dass sich die Unterschiede in Trübung und Makrophytenbesiedelung in Unterschieden in der Fischartenzusammensetzung widerspiegeln würden.

Die räumliche und zeitliche Verteilung der Fische zwischen dem Litoral und dem Pelagial

der beiden Flachseen wurde durch wiederholte Kiemennetzbefischung sowohl tagsüber als auch nachts analysiert. Wir nahmen an, dass zeitliche Unterschiede in der Verteilung der Fische zwischen den Habitaten im klaren See, mit seinen unterschiedlich strukturierten Habitaten, deutlicher ausgeprägt sind, als im eher einheitlichen, trüben See.

Mit Hilfe der Untersuchung von Darminhalten, Analyse stabiler Isotope, sowie Wachstumsanalysen wurde der Frage nachgegangen, ob der Anteil benthischer Makroinvertebrate an der Ernährung omnivorer Fische im klaren See höher ist als im trüben See und ob sich erhöhter Konsum von Makroinvertebraten positiv auf das Wachstum der Omnivoren auswirkt.

Unsere Untersuchungen im Jahre 2010, zeigten nur geringe Unterschiede in der Fischartengemeinschaft und der räumlich-zeitlichen Verteilung der Fische zwischen den beiden Seen. Die Analyse stabiler Isotope und der Darminhalte zeigte zwar Unterschiede in der saisonalen Verschiebung des Nahrungsspektrums Omnivorer zwischen den Seen, nicht jedoch einen allgemeinen Unterschied in deren Konsum benthischer Makroinvertebraten. Dennoch beobachteten wir ein schnelleres Wachstum omnivorer Fische im geringfügig eutropheren, trüben See. Das Jahr 2010 war jedoch ein sehr außergewöhnliches Jahr, da ein schwerwiegendes Fischsterben im vorherigen Winter (aufgrund einer außergewöhnlich langen Eisbedeckung) die Gesamtfischbiomasse drastisch reduziert und die Artenzusammensetzung stark verändert hatte, was folglich die Ernährungs- und Wachstumsbedingungen der überlebenden Fische in beiden Seen stark veränderte. Dies belegen Vergleichsdaten aus dem Jahr 2007, die den erwarteten deutlichen Unterschied in der Fischartenzusammensetzung zwischen beiden Seen zeigen. Ebenfalls zeigten Wachstumsrückberechnungen, dass der mittlere jährliche Längenzuwachs Omnivorer in den Vorjahren nur knapp ein Drittel des Längenzuwachses im Jahr 2010 betrug und das Wachstum in den beiden Seen unterschiedlichen Gesetzmäßigkeiten folgte. Insgesamt waren unsere Untersuchungen im Jahr 2010 stark durch das Fischsterben beeinflusst, da es die Umweltbedingungen für Fische in den beiden Seen angeglichen hatte, auch wenn die Seen weiterhin deutliche Unterschiede in der Trübung und der Makrophytenbesiedelung aufwiesen.

Des Weiteren wurde durch das Fischsterben die Ausgangssituation des TERRALAC – Projektes verändert, welches im Anschluss an diese Untersuchungen an den Seen durchgeführt wurde und die Auswirkungen eines erhöhten Eintrags organischen Kohlenstoffs aus dem terrestrischen Einzugsgebiet auf das Nahrungsnetz von Flachseen gegensätzlichen Systemzustandes erforscht.

## 1 Introduction

Shallow lakes cannot simply be considered shoal versions of deep lakes, as the functioning of shallow lakes is largely different from that of their deep counterparts. By definition, shallow lakes must be sufficiently shallow to allow enough light penetration to the bottom sediments to potentially support photosynthesis of higher aquatic plants over the entire basin (Wetzel 2001). Accordingly, the impact of macrophytes on the biological community is potentially larger in shallow lakes than in deep lakes, where plant growth is restricted to a relatively narrow marginal zone. Another difference to deep lakes is that shallow lakes do not stratify for long periods, since the low vertical dimension of the water body physically prevents a thermal isolation of water layers, which are frequently and thoroughly mixed by winds (DeGroot 1981). The resulting intense sediment-water interaction leads to a faster rate of nutrient recycling and higher primary production at equal nutrient loading in shallow lakes than in deep stratified lakes, where a considerable portion of total nutrients is trapped in the hypolimnion and does not contribute to primary production (DeGroot 1981; Guy et al. 1994). Their high nutrient efficiency makes shallow lakes more vulnerable to eutrophication, which is why the majority of previously clear-water temperate shallow lakes have shifted to the turbid regime during the last century (Irvine et al. 1989; Sand-Jensen et al. 2000; Korner 2002). Accordingly, the most prominent characteristic of shallow lakes might be the strong dichotomy of visual appearance. In contrast to deep, stratified lakes where turbidity follows a smooth function of nutrient concentration, shallow lakes do either occur as clear waters with abundance of submerged macrophytes or as turbid phytoplankton dominated waters. The existence of two strongly contrasting states without intermediate situations in between is addressed by the theory of alternative equilibria in shallow lakes (Scheffer et al. 1993).

These alternative states are stabilized by numerous feedback mechanisms, whereas the basic interaction in the feedback system is between aquatic macrophytes and planktonic algae, which compete for nutrients and light (Scheffer et al. 1993). In the turbid state, suspended algae prevent light from reaching the sediments, thereby inhibiting the growth of submerged vegetation. In the clear state, rooted aquatic macrophytes remove nutrients from the sediments, thus reducing the availability of the dissolved nutrients required for algal growth in the open water (VanDonk et al. 1990). Further feedback loops include the direct inhibition of algal growth by allelopathic substances released by aquatic plants

(Wiumandersen 1987; Hilt & Gross 2008), as well as the stabilizing effect of macrophytes on the water column and sediments, which results in reduced turbidity as a consequence of increased sedimentation and decreased resuspension of particles and nutrients (James & Barko 1990; Horppila & Nurminen 2005; Barko & James 1998). In addition to these interactions between primary producers, higher consumers, and especially fish, directly or indirectly impact different trophic levels, playing a crucial role in the interplay between abiotic and biotic components (Scheffer 1993; Jeppesen et al. 1997; Wright & Phillips 1992; Northcote 1988). Although the amount of energy and carbon flux to the fish trophic level is small, fish are an important ecological component; their community structure, as well as their habitat and diet preferences, largely impact the structure, function and stability of a lake ecosystem.

The community structure of fish is largely influenced by the abundance of macrophytes, which provide additional habitat and resources, as well as by turbidity, which affects predator-prey interactions. The state of a lake is therefore reflected in its fish biomass and species composition, which may potentially further reinforce the current state by way of various feedback loops, identified by the feeding modes described below.

Benthivorous fish such as bream (*Abramis brama*) usually dominate the fish community of turbid shallow lakes (Persson et al. 1991), where they mainly feed on macroinvertebrates which inhabit the unvegetated sediments (Lammens 1984; Lammens et al. 1987). Experimental studies have shown that the feeding efficiency of bream increased with decreasing macrophyte density (Diehl 1988). Accordingly, they are the superior foragers in unvegetated turbid lakes and reinforce the turbid state by mechanically disturbing the sediments in their search for benthic food (Meijer et al. 1990, Breukelaar et al. 1994).

Herbivorous fish such as rudd (*Scardinius erythrophthalmus*) primarily feed on submerged macrophytes and filamentous algae (Prejs & Jackowska 1978), and consequently are more abundant in clear, vegetated lakes. The mechanism by which they may reinforce a clear-water state is not fully understood, though there is evidence that their method of feeding (by plucking of individual leaves) may stimulate production in some macrophytes (Prejs 1984). There are currently no studies which reveal that native herbivorous fish of the temperate zone have precipitated the shift of a lake from a clear-water to the turbid state.

The abundance of piscivores such as pike (*Esox lucius*) and perch (*Perca fluviatilis*) is positively correlated with the abundance of submerged macrophytes (Grimm & Backx 1990; Persson et al. 1991). Both species are optically oriented predators whose foraging

efficiencies are affected by turbidity (Casselman & Lewis 1996; Diehl 1988), and their recruitment as well as their growth is positively influenced by the availability of richly vegetated habitats (Bry 1996; Grimm & Klinge 1996; Persson & Eklov 1995). In contrast, pikeperch (*Sander lucioperca*), which show the opposite pattern (profiting from turbid situations), are typically rare in shallow lakes (Persson 1991). Piscivorous fish generally exert a positive effect on lake transparency as they indirectly reduce the predation pressure on zooplankton by reducing the biomass of planktivorous fish. Piscivores also release zooplankton from predation pressure as planktivorous fish reduce their activity level in the presence of predators (Jacobsen et al. 1997) or switch to alternative food sources as a consequence of restricted habitat use (Persson 1993).

Planktivory is a common feeding mode during the early ontogenetic stages, but few species feed exclusively upon zooplankton as adult fish (VanDensen 1985; Hartley 1947; Persson 1986). Planktivorous fish occur in turbid as well as in clear lakes, where they reduce zooplankton populations and further affect the size structure of the zooplankton community by preferentially feeding on large individuals (Hrbacek et al. 1961; Shapiro & Wright 1984). Thereby zooplankton-feeding fish cause turbidity by releasing phytoplankton from grazing pressure, especially because the remaining small-sized zooplankton are less effective filterers (Brooks & Dodson 1965). In the littoral zone of clear lakes, the foraging of planktivorous fish for zooplankton is hampered by submerged macrophytes (Timms & Moss 1984; Diehl 1988). According to this refuge effect of macrophytes, zooplankton populations can be sustained at higher levels in clear lakes than in sparsely vegetated turbid lakes, thus the turbidity-promoting effect of planktivorous fish is higher in turbid lakes.

Omnivorous fish such as roach (*Rutilus rutilus*), perch and ruffe (*Gymnocephalus cernua*) feed on zooplankton as well as on the benthos (VanderZanden & Vadeboncoeur 2002; Jones & Waldron 2003; Holker & Thiel 1998). In consideration of the fact that zooplankton is one of the most variable food components, and competition for zooplankton by young-of-the-year fish can be high (Luecke et al. 1990; Jeppesen et al. 1997; Cryer et al. 1986), omnivorous fish strongly depend on alternative food sources. Macroinvertebrates represent a valuable and nutritional prey and their abundance is positively correlated with the abundance of submerged macrophytes, which provide additional habitat and resources for invertebrates (Cyr & Downing 1988; Jeffries 1992; Kornijow et al. 1990). Accordingly, in clear-water vegetated lakes, additional macroinvertebrate food sources can sustain the high biomasses of omnivorous fish species, but the biomass of omnivorous fish may

also be high in turbid lakes, due to the abundance of chironomids which colonize the un-vegetated sediments (Blindow et al. 1993). Regardless, a high biomass of omnivorous fish is always attended by a potentially high grazing pressure on zooplankton (Jeppesen et al. 1997), whereas the interaction between zooplankton respective to macroinvertebrates and plankti-benthivorous fish is hampered by submersed macrophytes in clear lakes (Diehl 1988; Kornijow 1990). In short, while the role of omnivorous fish is complex and not yet completely understood, their function in the feedback system of a lake appears to be strongly correlated with their diet.

The function of fishes as operational components in the feedback system of a lake depends on their abundance, but is further regulated by their activity and habitat use (Werner & Peacor 2003; Schmitz et al. 2004). Shallow lakes consist primarily of two habitats with differing resource densities and predation risks. The littoral zone with its structural diversity offers refuge from predation and provides a variety of food resources such as zooplankton and macroinvertebrates as well as non-animal resources such as algae and detritus. On the other hand, the pelagic zone can be more profitable for planktivorous fish, although also offering a higher risk of predation. According to Gauthier & Boisclair (1997), habitat use is a trade-off between food resource utilization and predator avoidance. However, some fish species (e.g. pike, tench and rudd) display a strong general preference for the littoral habitat (Craig 2008; Kennedy & Fitzmaur 1970; Holker et al. 2007), while other species, especially those which feed partly or entirely on zooplankton, have been shown to exhibit diel habitat shifts (Wurtsbaugh & Li 1985; Haertel & Eckmann 2002; Holker et al. 2007). For example, foraging of roach for zooplankton is more efficient in the pelagic zone (Winfield 1986; Persson 1987), but as omnivorous fish, roach can also feed on benthic macroinvertebrates or non-animal resources in the littoral zone (Diehl 1988; Prejs 1984). In predator-exclusion experiments, roach displayed a preference for open water habitats (Jacobsen et al. 1997), whereas in enclosure experiments which included diurnal piscivorous perch (which forage in the open water), roach moved into the vegetation during daytime (Eklov & VanKooten 2001). Conversely, in the presence of pike (which stayed mainly within or near macrophyte beds), roach almost exclusively used the open-water habitat (Eklov & VanKooten 2001). In the presence of both diurnal predators, roach used vegetated areas during the daytime, and foraged in the pelagic zone during the twilight and overnight (Eklov & VanKooten 2001; Haertel et al. 2002). These examples show that some species are highly flexible; thus their habitat use, which is closely linked with resource use and further affects their ecosystem function, is

difficult to predict. The contrast in food availability and predation between the littoral and the pelagic zone is, however, modulated by submerged macrophytes, and differences in the spatial and temporal dispersal of fish are therefore generally expected to be highest in clear-water, richly vegetated lakes, rather than in turbid lakes.

Omnivorous fish feed on zooplankton as well as on the benthos, and potentially undertake diel habitat and diet shifts which further complicate the estimation of their function in the feedback systems of a lake. In Central European shallow lakes, perch and roach are the most abundant omnivorous fish (Persson et al. 1991), whereas they widely differ in their ability to exploit the different resources under turbid or vegetated conditions (Diehl 1988; Radke & Gaupisch 2005). While both species strictly feed on zooplankton during their early ontogenetic stages, the diet of older roach may consist of zooplankton and macroinvertebrates as well as non-animal resources including detritus and algae. Especially large individuals have been shown to specialize on large invertebrates such as caddis fly larvae, zebra mussels, or freshwater snails if available (Hellawell 1972). Perch generally display a smaller feeding niche width in which they are restricted to a carnivorous diet, but undertake a pronounced ontogenetic niche-shift from a planktivorous, to a benthivorous and finally a piscivorous life stage if possible (Persson 1988). Roach feed most efficiently on zooplankton under turbid conditions, whereas perch is the superior forager on macroinvertebrates, and in structurally complex habitats (Winfield 1986; Diehl 1988). Omnivores have, however, been shown to profit from the additional macroinvertebrate food sources associated with submerged macrophytes in clear lakes (Diehl 1993; Mittelbach 1988). The enhanced supply of nutritional invertebrate food sources quickens the growth of omnivorous fish, whereas the resulting effect on the ecosystem differs between perch and roach. Faster growing perch become piscivorous earlier and with greater probability, thus a high availability of invertebrates directly promotes piscivory (Diehl 1993; Persson 1986). Alternately, the rapid growth of roach could on the one hand release zooplankton from predation pressure if large individuals preferentially feed on macroinvertebrates, but on the other hand, rapidly growing roach soon reach a size refuge against fish predation which enables them to feed upon zooplankton in the pelagic zone during daytime. Accordingly, the diet and growth of omnivores should be affected by the difference in the abundance of macroinvertebrates between lakes of opposing plant regimes and should further affect the feedback mechanism by which they stabilize any given current stable state of a lake.

Fish biomass and species composition, along with diet and habitat use of omnivorous fish, strongly affect the resilience of the current state of a lake, and consequently are likely to influence the way a shallow lake reacts to the increased inflow of organic carbon from terrestrial catchments. The latter is expected to be one impact of climate change along with elevated atmospheric CO<sub>2</sub> concentrations, and has recently been observed in rivers and lakes throughout Europe and North America (Evans et al. 2005; Evans et al. 2006). Little is known, however, about the pathways of terrestrial carbon to and within food webs of shallow lakes (Grey et al. 2001; Pace et al. 2004; Carpenter et al. 2005). Some studies suggest that the enhanced subsidy of allochthonous carbon alters the availability of food resources (France 1995; Theil-Nielsen & Søndergaard 1999) and therefore the community structure of fish, with consequences for the stability of shallow lakes as explained below.

Terrestrial organic carbon is a spatial subsidy since it enters shallow lakes lacking in major tributaries primarily at the land-water interface (Wetzel 1992). Terrestrial particulate organic carbon has been shown to be trapped by emergent and submerged macrophytes in the littoral zone (Vermaat et al. 2000), where it stimulates the secondary production of macrozoobenthos (France 1995). The dissolved fraction of terrestrial organic carbon might further enhance the food availability of invertebrates by stimulating the epiphytic biofilm production (Wetzel & Søndergaard 1998; Theil-Nielsen & Søndergaard 1999). Consequently, a high inflow of allochthonous carbon might enhance the biomass of littoral invertebrates relative to the biomass of pelagic zooplankton, thus omnivorous fish are thought to preferentially feed upon the more abundant benthic food sources and release zooplankton from predation pressure (Lewin et al. 2004; Okun et al. 2005). Additionally, increased macroinvertebrate food sources were found to enhance the biomass of piscivorous fish (VanderZanden & Vadeboncoeur 2002). Summing up, hypothesized diet shifts of omnivorous fish and enhanced biomass of piscivorous fish could reduce predation pressure on zooplankton and indirectly increase water transparency, effectively stabilizing the clear-water state.

This is one of the hypotheses of the TERRALAC project, which aims to investigate the influence of increased allochthonous carbon fluxes on shallow lake ecosystems. Therefore a turbid, phytoplankton dominated (Kleiner Gollinsee) and a clear, macrophyte dominated (Schulzensee) shallow lake with similar primary production were divided with plastic curtains and one half of each lake was manipulated by the controlled input of allochthonous particulate carbon (maize leaves) in autumn, 2010.

The present study was carried out before dividing and manipulating the two lakes, and investigates their fish community structure, general fish habitat use, and diet and growth of omnivorous fish with a specific focus on the effect on regime stability. Our analyses were designed to answer the following central questions:

We asked (i) whether there is a profound difference in fish community structure between the opposing lakes. We expected a higher proportion of piscivores and a lower proportion of benthivores to the total fish biomass in the clear, richly vegetated lake relative to the turbid lake.

(ii) whether the spatial and temporal dispersal of fish as proxy for habitat use differs between the lakes. We expected temporal habitat preferences to be more distinct in the clear lake, where submerged macrophytes should intensify the contrast between the littoral and the pelagic zone.

(iii) whether there is a difference in the share of benthic macroinvertebrates in the diet of omnivorous fish between the lakes, and whether these differences in diet composition result in differences in growth and the condition of omnivorous fishes between the lakes. We expected omnivores to feed relatively more on benthic macroinvertebrates in the clear lake, and thus to grow more rapidly and to be in a better condition than their conspecifics in the turbid lake, where benthic macroinvertebrates were expected to be less abundant.

## 2 Material and methods

### Site description

Kleiner Gollinsee (53°01'42"N 13°35'18"E) and Schulzensee (53°14'50"N 13°16'28"E) are shallow lakes situated about 100 km away from Berlin in north-east Germany. This region named Uckermark is characterized by wide oak and pine forests interspersed with open heathlands and several hundred lakes, with the absence of any large stream or creek. During a preliminary campaign in 2007, different lakes in this area were investigated to identify two lakes of different macrophyte colonization, but similar primary production. By reason of very similar fundamental characteristics, but opposite stable states, Kleiner Gollinsee and Schulzensee were chosen to be the target lakes for TERRALAC. For a better overview, similarities and differences (highlighted in bold font) are provided in Table 1.

**Table 1.** Descriptive parameters of Kleiner Gollinsee and Schulzensee; <sup>a</sup>annual mean calculated from bi-weekly measures from April to November 2010; <sup>b</sup>plant coverage estimated in June 2010 by investigation from boat, combined with satellite photographs

	Kleiner Gollinsee	Schulzensee
Area	3.4 ha	3.5 ha
Shore line	0.6 km	0.7 km
Mean depth	1.8 m	2.0 m
Max. depth	2.5 m	4.3 m
Secchi-depth <sup>a</sup>	<b>1.4 m</b>	<b>2.0 m</b>
Total phosphorus <sup>a</sup>	42.1 µg l <sup>-1</sup>	32.1 µg l <sup>-1</sup>
Emergent macrophytes <sup>b</sup>	6.6 %	2.1 %
Floating leaf plants <sup>b</sup>	1.8 %	2.1 %
Submerged macrophytes <sup>b</sup>	<b>0 %</b>	<b>27%</b>

The two lakes had no surface inflow and outflow, but were in contact with the ground water. At both lakes, the catchment was dominated by conifer forests, and alder represented the primary bank tree species. Each lake was surrounded by a dense reed belt of *Phragmites australis* and *Typha latifolia*, followed by patches of *Nymphaea alba* and *Nuphar lutea*. In addition to the coverage of emerging and floating leaved macrophytes, which was similar in both lakes, only in Schulzensee *Ceratophyllum submersum* formed dense beds, covering almost one third of the lake during summertime. In 2010, turbidity was consistently higher in Kleiner Gollinsee than in Schulzensee, save for one short period in late May/early June.

## 2.1 General community structure

Fish community structure was estimated by carrying out exactly the same fishing effort at each lake, in early September 2007 as well as in early September 2010. Fish were sampled in the pelagic and littoral zone by gill netting, and additionally in the reed covered part of the littoral zone by electrofishing. Therefore, eight benthic NORDIC multi-mesh gill nets (length 30 m, height 1.5 m; 12 mesh-size panels each being 2.5 m long with 5, 6.25, 8, 10, 12.5, 16, 19.5, 24, 29, 35, 43 and 55 mm; Lundgrens Fiskredskapsfabrik AB, Stockholm, Sweden) were set perpendicular to the shore line, with each net covering pelagic as well as littoral waters. All gill nets were set before dusk and lifted after dawn to ensure fishing during the likely maximum activity periods for all fish species. In the reed covered area, fish were sampled by electrofishing, applying a voltage of about 200-300 V DC (20-30 A electrofishing aggregates EFG 4000, Bretschneider Spezialelektronik, Breitenbrunn, Germany) between anodic handnets (4.5 m long, 40 cm diameter, 6 mm mesh size) and a copper cathode (5 m long). A team of two individuals performed electrofishing from a boat during the daytime. Prior to fishing, we adjusted the electric current to be as low as possible due to the lakes' conductivity, but still yielded positive fish galvanotaxis. We sampled fish by applying 15 dips at each of 6 randomly chosen locations. At each dip, the anode was submerged for a maximum duration of about 15 s, or shorter if fish already displayed positive galvanotaxis. Between the dips we punted the boat approximately 10 m.

For fish caught by gill netting we determined species, number, total length ( $L_T$ , estimated to the nearest mm) and wet weight (estimated to the nearest 0.1 g; research scale BL 12; Sartorius, Göttingen, Germany). For fish caught by electrofishing, only species, number

and  $L_T$  were measured in the field. Wet weight was calculated using length-weight-regressions (derived from specimens caught with gill nets) to avoid additional stress that would have been caused by anesthetizing the fish in order to weigh them correctly.

### Statistical analyses

Number per unit effort (NPUE) and wet weight per unit effort (WPUE) were calculated for each lake in 2007 and 2010 by pooling fishes caught by gill netting with those caught by electrofishing. To characterize community structure, we calculated the proportion of species (Figure 1; Figure 2) as well as feeding guilds (Table 2) of the total NPUE and WPUE respectively. Feeding guilds were defined by main food sources as follows. Perch (*Perca fluviatilis*) were divided into two size groups, as they display an ontogenetic niche shift (Persson, 1986). We defined small perch ( $L_T \leq 15$  cm) feeding mainly on zooplankton and macroinvertebrates and large perch ( $L_T > 15$  cm) being potentially piscivorous. Sunbleak (*Leucaspius delineatus*) and bleak (*Alburnus alburnus*) were defined as planktivores (Granadolorencio & Garcianovo 1986; Boikova 1986; Wanzenbock 1989; Vollestad 1985), pike (*Esox lucius*) and large perch as piscivores (Craig 2008; Persson 1986), bream (*Abramis brama*), white bream (*Blicca bjoerkna*) and tench (*Tinca tinca*) as benthivores (Kennedy & Fitzmaur 1968; Brabrand 1984; Kennedy & Fitzmaur 1970), rudd (*Scardinius erythrophthalmus*) as herbivore (Prejs & Jackowska 1978) and roach (*Rutilus rutilus*), small perch and ruffe (*Gymnocephalus cernua*) were supposed to be omnivorous, feeding mostly on zooplankton and benthic macroinvertebrates (Persson 1986; Diehl 1988; Holker & Thiel 1998).

Size-frequency distribution was estimated for all fish caught by gill netting and electrofishing in September 2007 and September 2010. Therefore,  $L_T$ -intervals were 2 cm wide, excluding the lower endpoint but including the upper endpoint and starting at 0 cm (Figure 3).

## 2.2 Spatial and temporal dispersal

To investigate temporal patterns in inhabitancy of the littoral and the pelagic zone, we conducted exactly the same effort of fishing in each habitat at day as well as at night. Therefore three benthic NORDIC multi-mesh gill nets (as given above) were randomly set and exposed for three hours in the littoral zone (except the reed covered area) and at the same time another three nets were randomly set and left for three hours in the pelagic zone. We avoided fishing during dusk and dawn, because the rapid change of light inten-

sity is well known to be the trigger for horizontal migrations between the habitats (Ringelberg et al. 1967). Consequently all six nets (three in each habitat) which were exposed during the day were lifted two hours before sundown and those for the night were set one hour after sundown. At each lake, this procedure was carried out on three subsequent days in spring (late April to early May), summer (end of June) and autumn (end of September) 2010.

After lifting, nets were immediately put on crushed ice and were brought to the shore, where we determined species, number,  $L_T$  (nearest mm) and wet weight (nearest 0.1 g, research scale BL 12; Sartorius, Göttingen, Germany) of all fish. Fish were separately placed in sealable plastic bags along with an individually labeled piece of waterproof paper, stored in crushed ice for maximum 9 hours, and finally preserved at  $-18^{\circ}\text{C}$  in a deep freezer until laboratory analyses were carried out (see 2.3).

### **Statistical analyses**

We calculated NPUE as the number of all fish caught in each net during a three hours exposure time. Data was not normally distributed within each factor combination (daytime/habitat/season), therefore 12 separate, non-parametric Mann-Whitney-Wilcoxon tests (each comparing NPUE of the nine nets (three nets at three subsequent days) representing a combination of daytime and season in the littoral zone with the NPUE of the nine nets that were simultaneously set in the pelagic zone) were carried out (Table 3). Alpha levels were corrected by dividing through the number of multiple comparisons, thus differences in NPUE between tested groups were significant if

$$p \leq 0.004 = 0.05 / 12.$$

Additionally, we investigated the spatial distribution of the most abundant species at day and at night for each lake and each season. Therefore the total number of specimens caught during the day versus the night for each season was calculated for the two habitats and displayed as stacked columns. This was carried out for roach in Schulzensee and Kleiner Gollinsee (Figure 4) as well as for sunbleak in Kleiner Gollinsee (Figure 5).

### 2.3 Diet, growth and condition of omnivorous fish

In 2010, roach was the only omnivorous species abundant in both lakes. Thus all analyses concerning the diet, growth and condition of omnivorous fish were conducted with roach.

#### Diet

The diet of an animal is affected by the availability of food resources. Accordingly, we estimated the availability of crustacean plankton and benthic macroinvertebrates in both lakes. Further, diet of roach was investigated on the one hand by analyzing gut contents, which represent a snapshot of previously ingested prey and on the other hand by stable isotope analysis of muscle tissue, which integrate over isotope signatures of digested food for some weeks.

#### Resources

The availability of zooplankton and benthic macroinvertebrates was estimated in summer 2010. Therefore at the end of July, zooplankton was sampled in the littoral as well as in the pelagic zone of each lake, utilizing a cylindrical water sampler (volume approx. 7 L). In each habitat, water was taken from the entire water column, collected in a bucket and from the resultant mixed sample, a 10 L subsample was sieved through a net (mesh size 30  $\mu\text{m}$ ). The fraction  $\geq 30 \mu\text{m}$  was fixed in 4% formalin and was sent to Sabine Schmidt-Halewicz from the University of Konstanz, who counted crustaceans and measured their body length.

At the end of June, macrozoobenthos was sampled in the eulittoral zone (0-1 m depth) of Kleiner Gollinsee and Schulzensee. Therefore at two randomly chosen spots per lake, we marked an area of 3  $\text{m}^2$  and visually estimated the proportion of the area covered with sand, reed and wooden debris. Sand habitat was sampled by slightly pushing a Surber sampler into the sandy sediment and then shoveling the sand located within the frame (0.2  $\text{m}^2$ ) into the net. Reed habitat was sampled by cutting reed halms, carefully taking them out of the water with a dip net and then brushing down attached animals with a tooth-brush. Further, reed detritus was sampled by kick netting with hand nets (frame 23 x 23 cm; mesh size 500  $\mu\text{m}$ ). To collect macroinvertebrates from wooden debris, we carefully transferred pieces of wood into a dip net and then emptied the net into a white photo dish, where we broke down the bark and brushed down attached animals with a tooth-brush. All samples were stored in 1 l boxes, filled up with 96% ethanol. At the laboratory, Jürgen Schreiber identified and counted the organisms.

### Statistical analyses

Body length of crustaceans was converted into dry weight according to Dumont et al. 1975 respectively Masundire 1994. Carbon mass was assumed as 50% of dry weight.

To calculate the total macroinvertebrate dry mass of a sample, counts per species were multiplied with mean individual dry weight according to Mährlein 2009 (unpublished data). Then dry weight was converted into carbon mass, according to the proportion of carbon, measured for each invertebrate species in the course of stable isotope analysis. Mean carbon mass density for the eulittoral zone was calculated in respect to the mean area proportions of sand, reed and wooden debris at each lake.

Carbon mass per volume (crustacean zooplankton) respectively carbon mass per area (macroinvertebrates) is given for the habitats of each lake in Table 4.

### Gut content analysis

Gut contents were investigated and classified according to the lake, season, habitat and daytime. To guarantee a full factorial design, we took a subset of 10-20 individuals (sampled as described in 2.2), representing each factor combination and reflecting the size distribution of the sample. After this pre-selection, fish were defrosted, the entire intestinal tract was extracted and transferred to 10 ml glass beakers, and filled with 5% formalin. The preservation enabled a rapid pace of work, and the hardening effect of formalin on the intestinal tracts facilitated further handling. At least one day before working with intestinal tracts, the formalin dilution was replaced by tap water in order to minimize potentially harmful formalin evaporations. However, all the following steps were carried out under a local extraction device. The anterior third of the gut was evaluated for fullness (five categories: 0,  $\frac{1}{4}$ ,  $\frac{1}{2}$ ,  $\frac{3}{4}$ , 1), cut off, and its contents were carefully squeezed onto a glass well, and there evenly dispersed by adding some water. This preparation was inspected through a stereo microscope (Leica Wild MZ8, Leica, Bensheim, Germany) and the volume proportion (equivalent to area proportion at uniform depth) of each prey category observed in the sample was estimated to the nearest 10% (adapted from Windell 1968). We analyzed the gut content of 385 roach and grouped the observed prey items into six categories; namely benthic macroinvertebrates (i.e. trichoptera, gastropods and *Asellus aquaticus*), chironomids, algae & detritus, zooplankton (i.e. *Daphnia sp.*, *Bosmina sp.*, copepods, water mites, ostracods, rotifers and *Leptodora kindtii*), chaoborus and bryozoans. These categories are rather general due to the triturating effect of the roach

pharyngeal teeth, which made it impossible to identify most organisms beyond family or order level.

### **Statistical analyses**

By means of comparability among samples, only fish whose anterior third of the gut was at least half-full, were included in statistical analysis. Items from each category were found in more than 5% of the remaining 226 fish, consequently all six categories were considered in this analysis. A further outlier analysis among individual roach, based on category proportion differences using the Bray-Curtis distance measure was performed using PC-ORD version 4 (McCune & Mefford, 1999; MJM Software Design, Gleneden Beach, OR, USA) and identified four outliers, with an average distance of more than 2.5 standard deviations away from the grand mean distance. Those fish were removed from analysis, so that the final matrix consisted of 222 roach  $\times$  6 categories. The following multivariate analyses were conducted with PRIMER version 6 (Clarke & Gorley, 2006, Plymouth Marine Laboratory, Plymouth, UK). Non-metric multi-dimensional scaling (MDS-plot, Figure 7) and four unique one-way analyses of similarities (one-way ANOSIM) with lake, season, habitat or daytime as grouping variable were performed. Therefore the matrix was reassembled using a Bray-Curtis similarity measure.

ANOSIM is based on the assumption that if the diet compositions of two groups (defined by factors such as lake) are significantly different, the similarities between groups should be lower than the similarities within each group. This is expressed by the R statistic, which ranges from 0 to 1, where  $R = 1$  if all replicates of a group are more similar to each other than to any replicate from another group. For R values between 0 and 1 the following gradation provides orientation:  $R > 0.75$  for well separated groups,  $R > 0.5$  indicates overlapping but clearly different and  $R < 0.25$  for groups that are barely separable at all (Clarke & Gorley 2001). Moreover, ANOSIM is a non-parametric test, thus it does not require distributional assumptions such as multivariate normality and homogeneity of variance.

In addition to the multivariate analysis of gut content composition, we calculated mean proportions of gut contents separately for roach caught in spring, summer and autumn in Kleiner Gollinsee and Schulzensee (Figure 6).

### **Stable isotope analysis**

The proportions of food from different sources, and the trophic position relative to a baseline were calculated for roach by using a two-end-member mixing model (Post 2002).

According to this model, the isotopic baseline for each lake was generated using the stable isotope ratios of nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) of primary consumers from the pelagic as well as from the littoral food web. We used long-lived primary consumers, because they integrate over the temporal and spatial variation of consumed primary producers (Post 2002). The mean trophic fractionation was assumed to be 3.4‰ for nitrogen and 0.0‰ for carbon. Consequently,  $\delta^{15}\text{N}$  was used to calculate the trophic position and  $\delta^{13}\text{C}$  which is generally depleted at the base of the pelagic food web relative to the base of the littoral food web, was used to calculate the proportions of the ultimate food sources.

We sampled roach, their potential prey and long-lived primary consumers at Kleiner Gollinsee and Schulzensee, and analyzed their stable isotope ratios as follows.

Frozen roach, which had been sampled (as outlined in section 2.2) during spring, summer and autumn, were defrosted and a small piece of dorsal muscle tissue was excised. Zooplankton were sampled in June by hauling a zooplankton net (mesh size 200  $\mu\text{m}$ ) vertically through the entire water column. Samples were sieved through a 500  $\mu\text{m}$  mesh to remove larger items (i.e. fry) and were left overnight in clean water to allow gut evacuation. We collected bivalves with hand nets from the sediments in front of the reed belt, from which we dissected a small piece of foot tissue. Macroinvertebrates from the littoral zone were sampled using dip nets (500  $\mu\text{m}$  mesh size). The dip net content was transferred into a white photo dish, from where we picked individuals with tweezers. Macroinvertebrates were left overnight in clean water to allow them to void their guts. We also tried to sample macroinvertebrates from the profundal habitat using an Ekman dredge, but we did not find any macroinvertebrates inhabiting those muddy sediments. All samples were dried in an oven at 60 °C for at least 6 hours, ground to a fine powder using a mortar and pestle, and about 0.6 mg of sample material was weighed into tin cups. Stable isotope analyses were carried out at the Institute for Environmental Research, University of Jyväskylä, Finland, using a FlashEA 1112 elemental analyzer coupled to a Thermo Finnigan DELTA<sup>plus</sup> Advantage mass spectrometer (Thermo Electron Corporation, Waltham, MA, USA). Stable isotope ratios are expressed as parts per thousand (‰) delta values ( $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ ) referred to the international standards for carbon (PeeDee Belemnite) and nitrogen (atmospheric nitrogen) (Peterson & Fry 1987).

### Statistical analyses

To generate the baseline, we decided to use bivalves (*Anodonta anatina* in Kleiner Gollinsee and *Pseudanodonta complanata* in Schulzensee) representing the pelagic food web

and *Asselus aquaticus* respectively for the littoral food web, because they showed the highest discrimination in  $\delta^{13}\text{C}$  values among long-lived primary consumers (Figure 8). We calculated the following, baseline corrected, two-source mixing model (Post 2002).

$$\lambda_{\text{roach}} = \lambda_{\text{B}} + \{\delta^{15}\text{N}_{\text{roach}} - [\delta^{15}\text{N}_{\text{pelagicB}} \times \alpha + \delta^{15}\text{N}_{\text{littoralB}} \times (1 - \alpha)]\} / \Delta_{\text{n}} \quad \text{F1}$$

Where  $\lambda_{\text{roach}}$  is the trophic position of roach,  $\Delta_{\text{n}}$  is the trophic fractionation of nitrogen (3.4‰),  $\lambda_{\text{B}}$  is the trophic position of baseline organisms (2 for primary consumers), and  $\alpha$  is the proportion of nitrogen in roach ultimately derived from the base of the pelagic food web. We assumed a similar flow of nitrogen and carbon through the food web, consequently  $\alpha$  could be estimated using carbon isotopes according to Post 2002 as follows

$$\alpha = (\delta^{13}\text{C}_{\text{roach}} - \delta^{13}\text{C}_{\text{littoralB}}) / (\delta^{13}\text{C}_{\text{pelagicB}} - \delta^{13}\text{C}_{\text{littoralB}}) \quad \text{F2}$$

$\lambda$  and  $\alpha$  were calculated for each fish and mean values for groups defined by season and lake are given in Table 5. Additionally, mean values of isotope signature of roach are displayed in an isotopic biplot together with baseline organisms in Figure 9.

## Growth

Water temperature and food supply are the key factors which affect the somatic growth of fish (Tesch 1968). Seasonal changes of these factors in the temperate zone result in an annual alteration of rapid and slow growth, which is reflected by hard structures i.e. scales, cleithra, opercula, otoliths and spinous soft rays (Tesch 1968). Preliminary tests with roach from Kleiner Gollinsee and Schulzensee had shown that annual marks (annuli) were most distinct on scales, compared to cleithra, opercula and spinous soft rays. Consequently, age and growth analyses were conducted by counting and measuring the distance between annual marks on scales as follows.

Frozen roach, which had been sampled as outlined in section 2.2 were defrosted, and eight scales were taken from each fish by using a pair of tweezers. To avoid bias, we collected scales from the same location (the row above the lateral line, starting vertically below the end of the dorsal fin and going eight scales tailwards) of each fish. Scales were cleaned by rubbing between finger tips and put between two glass slides, then wrapped with adhesive tape. From these preparations the distances between the nucleus (center of the scale) and the end of each annulus (the changeover from narrow to wide spaced rings) as well as the radius of the scale were measured along the same axis (anterior-posterior axis,  $\pm 15^\circ$  due to readability) to the nearest 1  $\mu\text{m}$  by using a measuring microscope (Quick Scope Vision Measuring Machine, Mitutoyo Corporations, Japan). Three of the eight scales prepared of each fish were measured to calculate mean values.

### Statistical analyses

From these mean radii, length-at-age ( $L_t$ ) was back-calculated using the formula

$$L_t = c + r_t \times (L_T - c)/r_T \quad (\text{Fraser 1916; Lee 1920}) \quad \text{F3}$$

where  $r_t$  is the radius of annulus  $t$ ,  $r_T$  is the total scale radius and  $c$  is the intercept with the ordinate from the regression of  $L_T$  on mean  $r_T$  (Kleiner Gollinsee,  $c = 3.26$  cm; Schulzensee,  $c = 2.56$  cm). To compare the growth of roach between the lakes, von Bertalanffy growth curves were fitted to length-at-age-data, applying the method of least squares (Figure 10). The von Bertalanffy equation for organic growth is as follows

$$L_t = L_{\text{inf}}(1 - e^{-K(t-t_0)}) \quad (\text{VonBertalanffy 1957}) \quad \text{F4}$$

where  $L_t$  is the mean total length at age  $t$ ,  $L_{\text{inf}}$  is the asymptotic mean  $L_T$ ,  $K$  is the growth coefficient and  $t_0$  is the age at which the mean  $L_T$  is zero.  $t_0$  is usually a small negative number with low informative content. Thus we did not predefine it to guarantee a better fitting of the curve. Separate two tailed students T-Tests were carried out to test for differences in  $K$  and  $L_{\text{inf}}$  between the lakes.

Additionally, we compared the total length, back-calculated for the first annulus ( $L_1$ , calculated according to F3) of roach which completed their first year of life in 2007, 2008 or 2009, with  $L_T$  of young-of-the-year 2010, measured in September (Figure 11. g-h).

Further we calculated the annual length-increment of roach in its 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup> year of life, passed in 2007, 2008 and 2009. Therefore, we used the back-calculated total length of the annulus  $x$  and  $x-1$  to calculate the length-increment in the  $x$  year of life ( $LI_x$ ) as follows:

$$LI_x = L_x - L_{x-1} \quad \text{F5}$$

For 2010, length-increment of 1+, 2+ and 3+ roach between May 2010 (latest annulus) and September 2010 was calculated as difference between  $L_T$  measured in September 2010 and the back-calculated total length for the latest annulus (according to F3). Annual length-increment in 2007, 2008 and 2009 was compared with length-increment from May to September in 2010 (Figure 11. a-f).

### Condition

The caloric density of roach was used as a proxy for body condition. For calorimetric analysis, frozen roach which had been sampled in June 2010 as given in 2.2, were defrosted, scaled and fins were cut off. Then, each fish was homogenized using an immersion blender and a subsample of about 1 g was freeze-dried (Sublimator 3x4x5, Zirbus Technology, Bad Grund, Germany). The freeze-dried material was ground using a mortar

and pestle and for each fish, three subsamples à 0.1 g were subjected to the calorimeter (PARR 6400 Automatic Calorimeter, PARR Instrument Company, IL, USA).

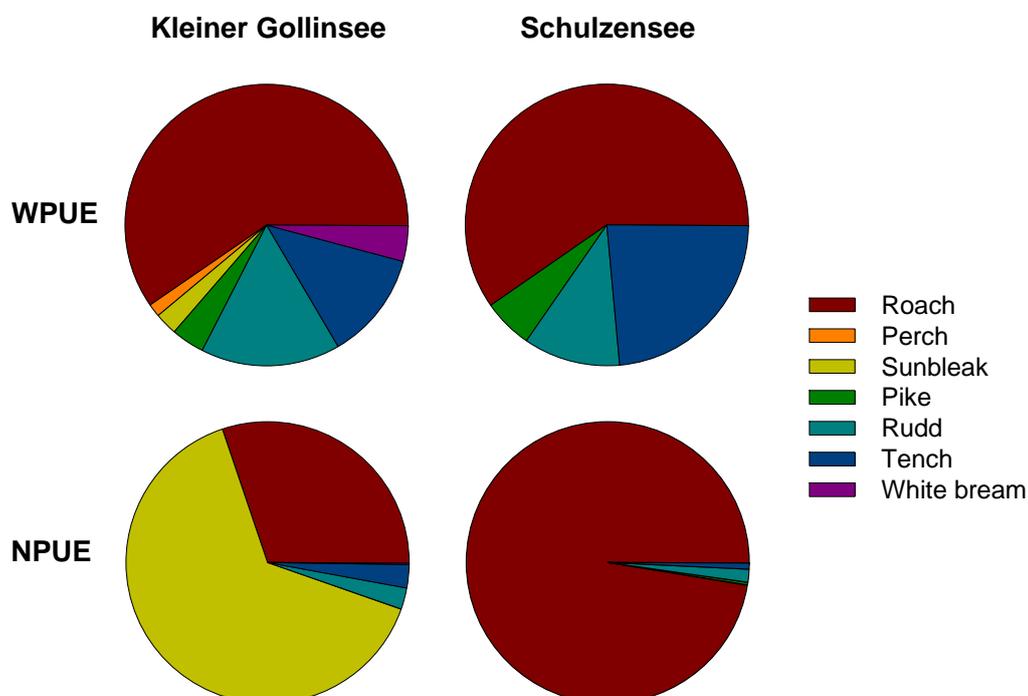
### **Statistical analyses**

Mean caloric density was calculated for each fish. Analysis of covariance (ANCOVA) was carried out with factors lake (Kleiner Gollinsee/Schulzensee) and habitat (littoral zone/pelagic zone) nested within lake as independent variables, mean caloric value as dependent variable and log(wet weight) as covariate, using PASW Statistics 18 (SPSS Inc., 2009, Chicago, IL, USA). Assumptions for normal distribution and homoscedasticity were met. Interaction term of lake and log(wet weight) was not significant (ANCOVA,  $F_{1,40}=0.470$ ;  $P=0.497$ ), therefore only main effects were analyzed.

### 3 Results

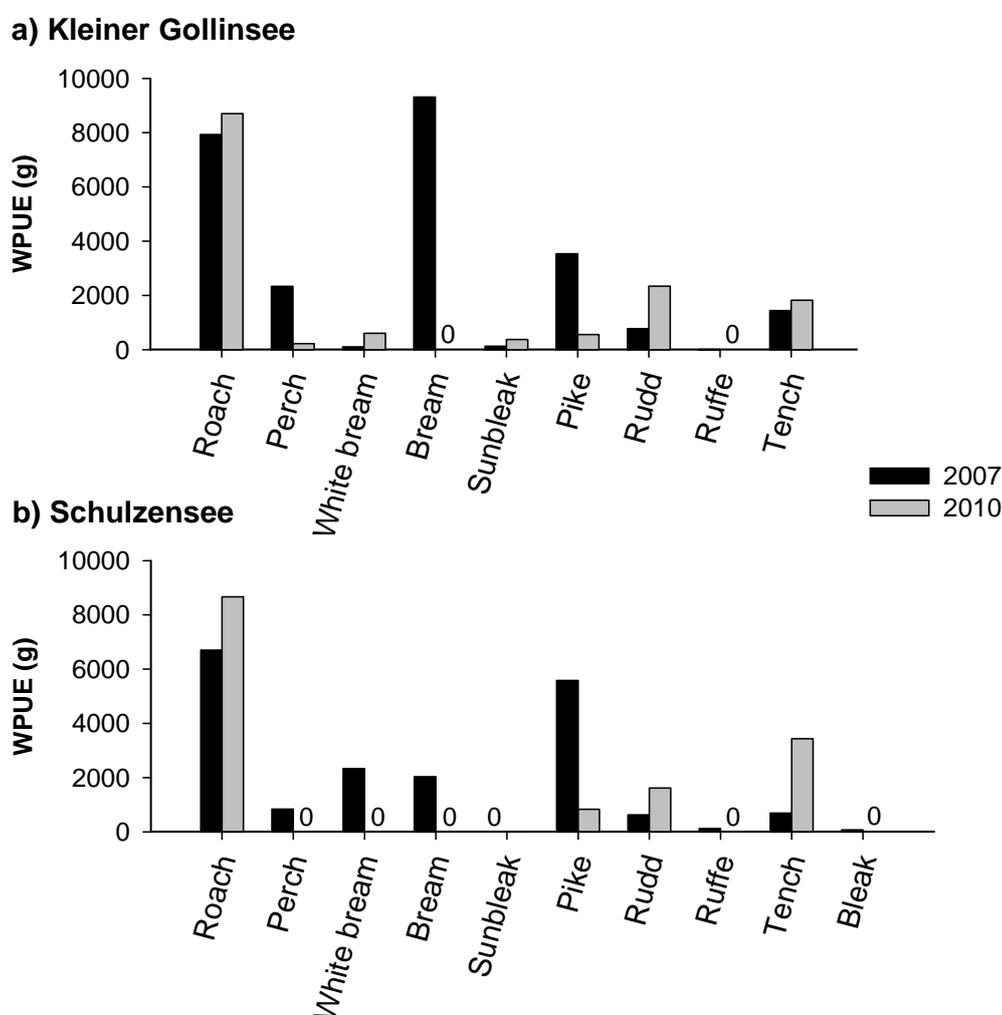
#### 3.1 General community structure

In September 2010, a total of 3203 fish (14.6 kg of fish biomass) were caught at Kleiner Gollinsee and 1331 individuals (14.5 kg) at Schulzensee. Considering WPUE, roach was the dominant species in both lakes, accounting for almost two thirds of total fish biomass, followed by rudd and tench with more than 10% each (see Figure 1). Pike contributed roughly 5% in both lakes, whereas single individuals of white bream and perch were only caught in Kleiner Gollinsee and not in Schulzensee. Sunbleak was highly abundant in Kleiner Gollinsee, where it accounted to 64.4% of NPUE, but only to 2.6% of WPUE due to its small size. In contrast, only few sunbleak were caught in Schulzensee. Abundance data (NPUE) was dominated by young-of-the-year of roach and sunbleak. In Kleiner Gollinsee sunbleak numerically represented 64.4% and roach 30.2% of the catch and in Schulzensee roach dominated NPUE with 97.4%. All other species together contributed with less than 5% to the total NPUE in both lakes.



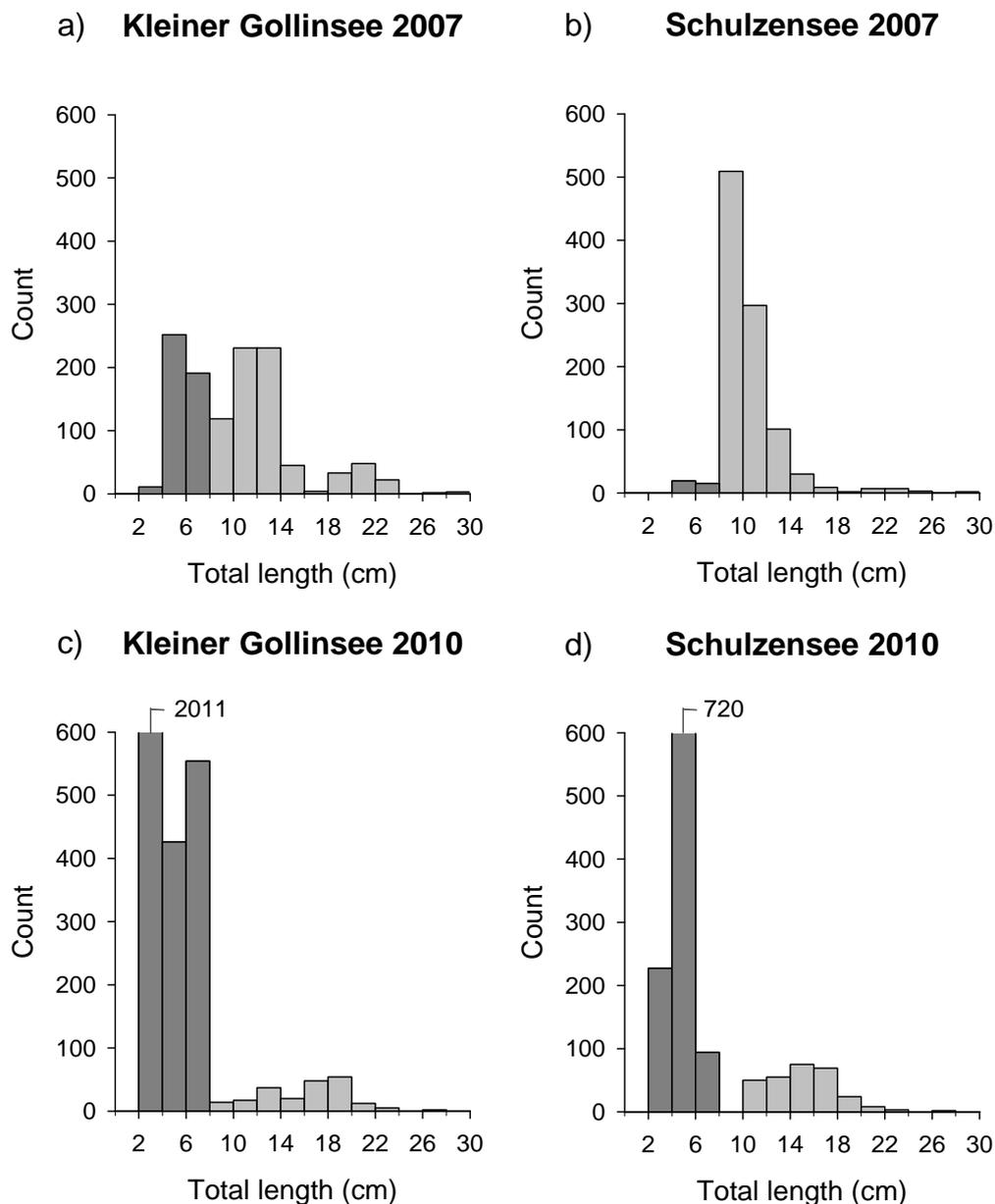
**Figure 1.** Wet weight per unit effort (WPUE) and number per unit effort (NPUE) of Kleiner Gollinsee and Schulzensee analyzed by species. Fish were caught by gill netting and electrofishing in September 2010.

In September 2007, 1200 fish (25.6 kg) were caught in Kleiner Gollinsee and 1012 individuals (19.0 kg) in Schulzensee. Compared with 2010, the WPUE in 2007 was 1.8 times higher at Kleiner Gollinsee and 1.3 times higher at Schulzensee, whereas NPUE was lower at both lakes. Species composition also differed markedly between 2007 and 2010 (see Figure 2). Total number of fish species decreased in both lakes from 9 (2007) to 7 (2010) in Kleiner Gollinsee and from 10 (2007) to 5 (2010) in Schulzensee. Perch and bream held high biomass proportions in 2007 (especially in Kleiner Gollinsee), but were not caught in 2010 (except 2 perch in Kleiner Gollinsee). Pike biomass decreased markedly, whereas the WPUE of roach, rudd and tench increased in both lakes. In Kleiner Gollinsee the WPUE of sunbleak was three times higher in 2010 than it was in 2007.



**Figure 2.** Wet weight per unit effort (WPUE) separated by species for 2007 and 2010. Cases when no specimen was caught are highlighted with 0.

Size-frequency distributions of fish changed markedly in both lakes between 2007 and 2010 (see Figure 3). In September 2007, we generally caught more large individuals ( $L_T \geq 25$  cm) of perch, bream, white bream, pike and tench than in 2010, when large fish were solely represented by tench and pike. In each lake, abundance of young-of-the-year and adult sunbleak (defined as all fish with  $L_T \leq 8$  cm and highlighted in dark grey in Figure 3) was several times higher in 2010 compared to 2007.



**Figure 3.** Size-frequency distribution of fish caught by applying exactly the same effort of fishing in Kleiner Gollinsee and Schulzensee in September 2007 and September 2010. Fish equal or less than 8 cm (young-of-the-year and sunbleak) are highlighted in dark grey. Length intervals are 2 cm wide, exclude the lower and include the upper endpoint and start at 0 cm. Fish larger than 30 cm accounted for less than 1% of each catch and are not displayed. Bars with more than 600 counts are cut off and counts are given above.

The percentage contributions of feeding guilds to the total WPUE of each lake differed markedly between 2007 and 2010 (see Table 2) according to the changes in species biomass composition already mentioned above. In 2007, the proportion of piscivores was double in Schulzensee as in Kleiner Gollinsee, where benthivores dominated the fish community biomass. At the same time, herbivorous and planktivorous fish represented less than 3% and omnivores almost 40% of WPUE in both lakes. In contrast, fish communities of both lakes were almost equally structured in 2010. Biomass of piscivores had declined to a marginal proportion of about 5% in both lakes, whereas the proportion of herbivores rose significantly. The extinction of bream affected benthivory in Kleiner Gollinsee more strongly than in Schulzensee, where benthivores were almost solely represented by tench. The lake-wide proportion of omnivorous fish rose to 60% in both lakes, thus omnivores were by far the dominant guild in 2010.

**Table 2.** Percentage contributions of feeding guilds to total WPUE of Kleiner Gollinsee (G) and Schulzensee (S) in September 2007 and September 2010.

	2007		2010	
	G	S	G	S
Omnivore	39%	37%	60%	60%
Planktivore	0%	0%	3%	0%
Benthivore	42%	27%	17%	24%
Piscivore	15%	33%	5%	6%
Herbivore	3%	3%	16%	11%

### 3.2 Spatial and temporal dispersal

There was no clear pattern in habitat use between the lakes, but a significant difference in NPUE between the littoral and pelagic zone was observed more often at Kleiner Gollinsee than at Schulzensee (Table 3). Significant differences in fish abundance between the habitats were observed exclusively during the day, when abundance of fish was higher in the littoral zone.

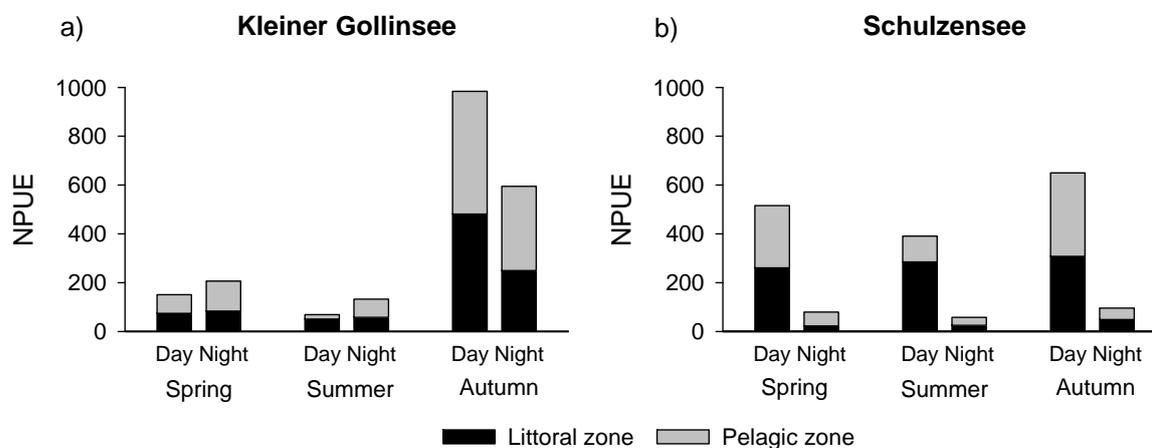
**Table 3.** Results of non-parametric Mann-Whitney-Wilcoxon tests for difference of NPUE (total number of fish caught in one net) between the littoral and the pelagic habitat for each lake and each season in 2010 at day and at night. Alpha levels are corrected by dividing through the number of multiple comparisons, thus differences in NPUE between the tested groups are significant if  $p \leq 0.004$  (highlighted in bold font).

Lake	Season	Daytime	Median(NPUE)		U	p
			Littoral zone	Pelagic zone		
Kleiner Gollinsee	Spring	<b>Day</b>	<b>59</b>	<b>1</b>	<b>7.5</b>	<b>0.003</b>
		Night	18	18	37.0	0.757
	Summer	<b>Day</b>	<b>30</b>	<b>1</b>	<b>2.5</b>	<b>0.001</b>
		Night	25	34	26.0	0.199
	Autumn	Day	79	59	29.0	0.309
		Night	42	30	33.5	0.536
Schulzensee	Spring	Day	28	29	39.0	0.894
		Night	4	4	28.5	0.283
	Summer	<b>Day</b>	<b>35</b>	<b>10</b>	<b>3.0</b>	<b>0.001</b>
		Night	6	2	21.0	0.083
	Autumn	Day	47	29	39.0	0.895
		Night	6	5	32.0	0.451

For roach and sunbleak, as the most abundant species, we separately investigated spatial dispersal during day and night at different seasons.

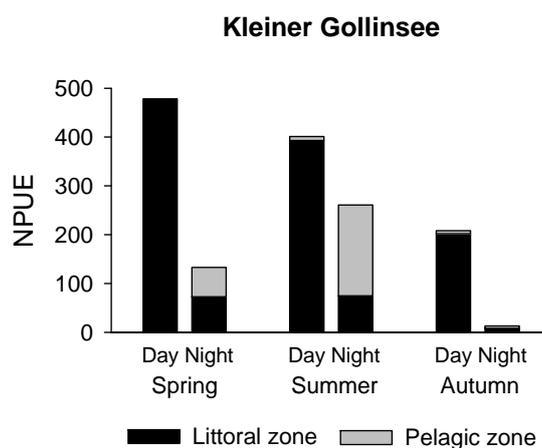
Roach were caught in almost equal amounts in the littoral as well as in the pelagic zone at

day and at night in both lakes (see Figure 4). Only in summer were roach more abundant in the littoral zone of both lakes during the day.



**Figure 4.** Distribution of roach between the habitats at day and at night, displayed as stacked bars of NPUE for each season. NPUE = total number of roach caught in three benthic NORDIC gill nets, which were exposed on three subsequent days for three hours per day.

Sunbleak was highly abundant in Kleiner Gollinsee, but only rarely caught in Schulzensee. Consequently, temporal and spatial dispersal of sunbleak was only analyzed in Kleiner Gollinsee, where at daytime sunbleak were almost exclusively caught in the littoral zone (see Figure 5). At night, sunbleak were dispersed more evenly between the littoral and the pelagic zone.



**Figure 5.** Distribution of sunbleak between the habitats at day and at night, displayed as stacked bars of NPUE for each season. NPUE = total number of sunbleak caught in three benthic NORDIC gill nets, which were exposed on three subsequent days for three hours per day.

### 3.3 Diet, growth and condition of omnivorous fish

#### Diet

##### Resources

In July 2010, crustacean zooplankton density in the littoral and in the pelagic zone, as well as the density of benthic macroinvertebrates in the eulittoral zone was higher in Kleiner Gollinsee (see Table 4). During the day, the crustacean zooplankton density was two times higher in the littoral, than in the pelagic zone of Kleiner Gollinsee, whereas there was no difference in zooplankton density between the habitats in Schulzensee. Macroinvertebrate density of the sublittoral zone of both lakes was not measured in 2010. But qualitative samplings of the unvegetated sublittoral zone of Kleiner Gollinsee showed that the muddy sediments were almost not inhabited by macroinvertebrates. For the vegetated sublittoral zone in Schulzensee we estimated a macroinvertebrate density of  $97 \text{ mgCm}^{-2}$ , according to findings of Mährlein 2009, who quantified the macroinvertebrate density in the sublittoral zone of Schulzensee as 20% of the density of macrozoobenthos in the eulittoral zone.

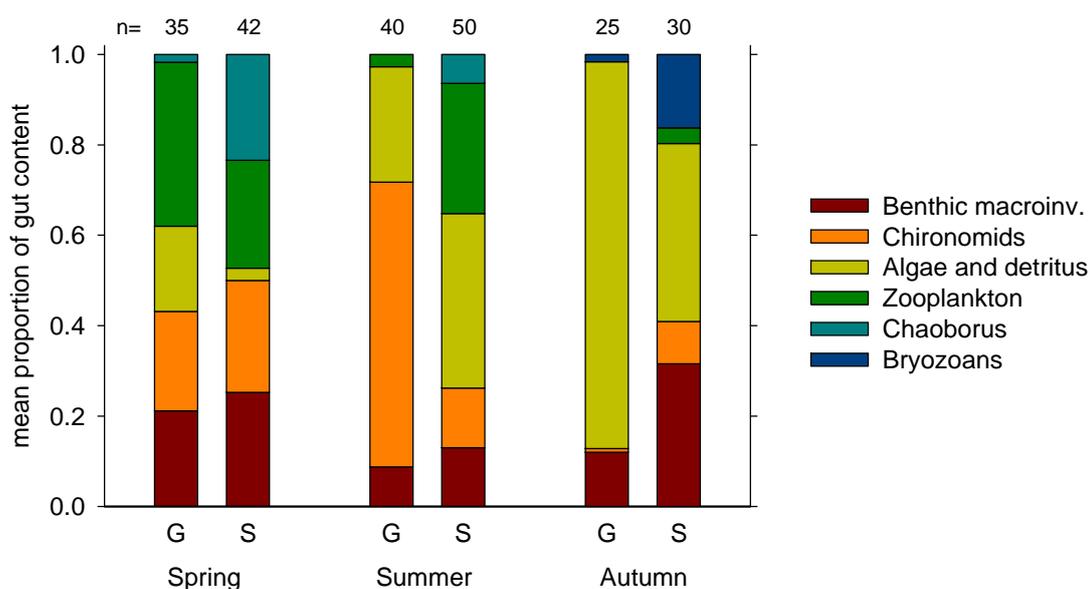
**Table 4.** Carbon mass densities of crustacean zooplankton and macrozoobenthos in different habitats of Kleiner Gollinsee and Schulzensee. Samples were taken at daytime in July 2010. Note the difference in units according to the spatial dispersal of organisms.

		Kleiner Gollinsee	Schulzensee
Crustaceans ( $\text{mgCm}^{-3}$ )	Littoral	127	32
	Pelagic	63	30
Macrozoobenthos ( $\text{mgCm}^{-2}$ )	Eulittoral	604	484

#### Gut content analysis

In spring, summer and autumn 2010, roach of both lakes were feeding on benthic macroinvertebrates, chironomids, zooplankton, algae and detritus. Chaoborus larvae were only consumed during spring and summer and represented higher mean proportions of gut content in Schulzensee compared to Kleiner Gollinsee (see Figure 6). In autumn bryozo-

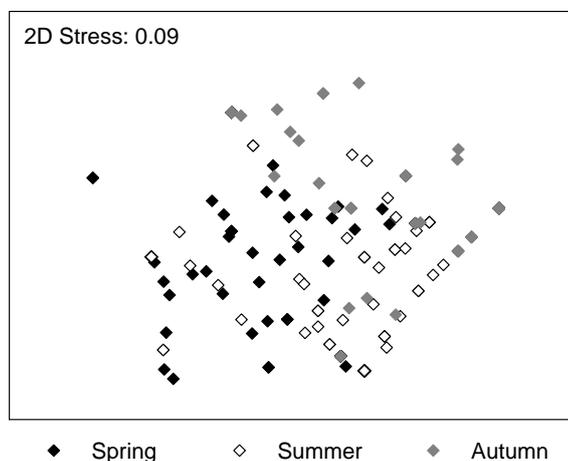
ans asexually produced resting buds (statoblast) which remained in the cystid tubes of the former colony and were consumed by roach, especially in Schulzensee. In Kleiner Gollinsee, zooplankton were an important food source in spring but not in summer and autumn, whereas in Schulzensee zooplankton consisted of roughly 30% of the diet of roach during spring and summer. In both lakes, benthic macroinvertebrates were an important food source of roach throughout the year, whereas at each sampling, their mean contribution to the diet was higher in Schulzensee. Chironomids were frequently found in the guts of roach from Schulzensee. The share of chironomids in the diet varied strongly, however, between seasons in Kleiner Gollinsee, where they represented more than half of the diet in summer, but were not ingested in autumn. The mean proportion of algae and detritus in the diet of roach increased from spring to autumn in both lakes. Especially in Kleiner Gollinsee, this non-animal food source contributed to more than 80% to the diet of the roach sampled in autumn.



**Figure 6.** Mean volume proportions of diet components observed in the guts of roach, which were caught in Kleiner Gollinsee (G) and Schulzensee (S) at spring, summer and autumn. Numbers above bars: sample size.

We observed high differences in the composition of ingested prey between individuals caught in the same net. Accordingly, diet composition did not clearly differ between groups divided by factor lake (ANOSIM: R-statistic = 0.041,  $p = 0.002$ ), season (ANOSIM: R-statistic = 0.163,  $p = 0.001$ ) or habitat (ANOSIM: R-statistic = 0.020,  $p = 0.013$ ). Furthermore, the low separation between the samples, labeled by season in the

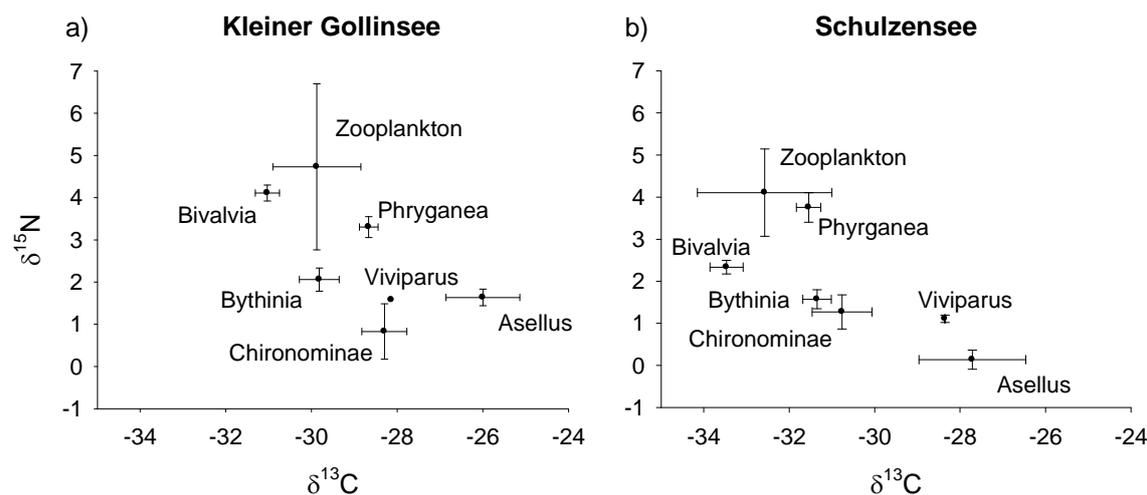
MDS-plot (Figure 7) displays that seasonal differences in the diet compositions of roach were much smaller than differences of gut content composition between individuals caught at the same season.



**Figure 7.** Non-metric multi-dimensional scaling of individual gut content composition of roach labeled by season. Fish were caught in Kleiner Gollinsee and Schulzensee.

### Stable isotope analysis

$\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of invertebrates of corresponding groups differed between the lakes, but their relative position in the isotopic biplot was similar (see Figure 8).

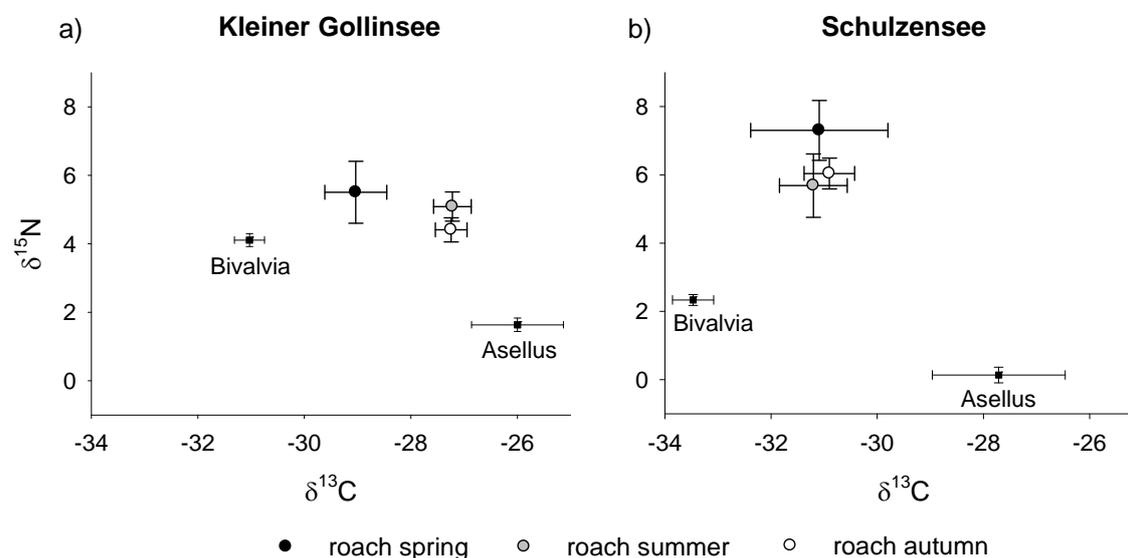


**Figure 8.** Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values ( $\pm$  SD) of different consumers from Kleiner Gollinsee and Schulzensee. All samples were taken in summer and zooplankton was additionally sampled in spring.

At each lake, bivalvia displayed the most negative mean  $\delta^{13}\text{C}$  and *Asellus aquaticus* displayed the most positive mean  $\delta^{13}\text{C}$ . To set the isotopic baseline of the mixing model,

consequently bivalves were chosen to represent primary consumers of the pelagic food web and *Asellus aquaticus*, respectively for the littoral food web. The  $\delta^{13}\text{C}$  values measured for other invertebrates were in between the  $\delta^{13}\text{C}$  values of these baseline organisms. Considering the isotopic biplot, zooplankton was in close proximity to the pelagic base (bivalvia), whereas  $\delta^{13}\text{C}$  values of trichoptera (*Phyrganea sp.*) and chironomids were almost centered between the food web bases. Stable isotope signatures of gastropods differed between species according to their feeding behavior (*Bythinia sp.* = filterfeeder and scraper; *Viviparus sp.* = scraper).  $\delta^{15}\text{N}$  values were generally higher in consumers of the pelagic food web.

The proportion of carbon ultimately derived from the pelagic food web was constantly around 50% in muscle tissue of roach from Schulzensee (see Table 5). Whereas in Kleiner Gollinsee in spring, roach obtained 50% of their carbon from the pelagic zone, but obtained 90% of their carbon from the littoral food web during summer and autumn. The seasonal shift towards more positive (littoral)  $\delta^{13}\text{C}$  values of roach in Kleiner Gollinsee is further displayed in Figure 9, which also shows the constant relative position of roach to bivalvia and asellus in Schulzensee.



**Figure 9.** Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values ( $\pm$  SD) of primary consumers of the pelagic food web (Bivalvia) and the littoral food web (Asellus) and roach caught in spring, summer and autumn at Kleiner Gollinsee and Schulzensee. Bivalvia and asellus were sampled during summer.

**Table 5.** Mean trophic position ( $\lambda$ ) and mean proportion of food from the pelagic food web ( $\alpha$ ) of roach in Kleiner Gollinsee (G) and Schulzensee (S) at different seasons.  $\alpha$  and  $\lambda$  were calculated with a two-end-member mixing model according to Post 2002.

	Spring		Summer		Autumn	
	G	S	G	S	G	S
$\lambda$	2.8	3.7	3.0	3.2	2.76	3.30
SD( $\lambda$ )	0.21	0.18	0.16	0.28	0.10	0.12
$\alpha$	0.53	0.52	0.10	0.54	0.11	0.48
SD( $\alpha$ )	0.14	0.26	0.08	0.13	0.07	0.10

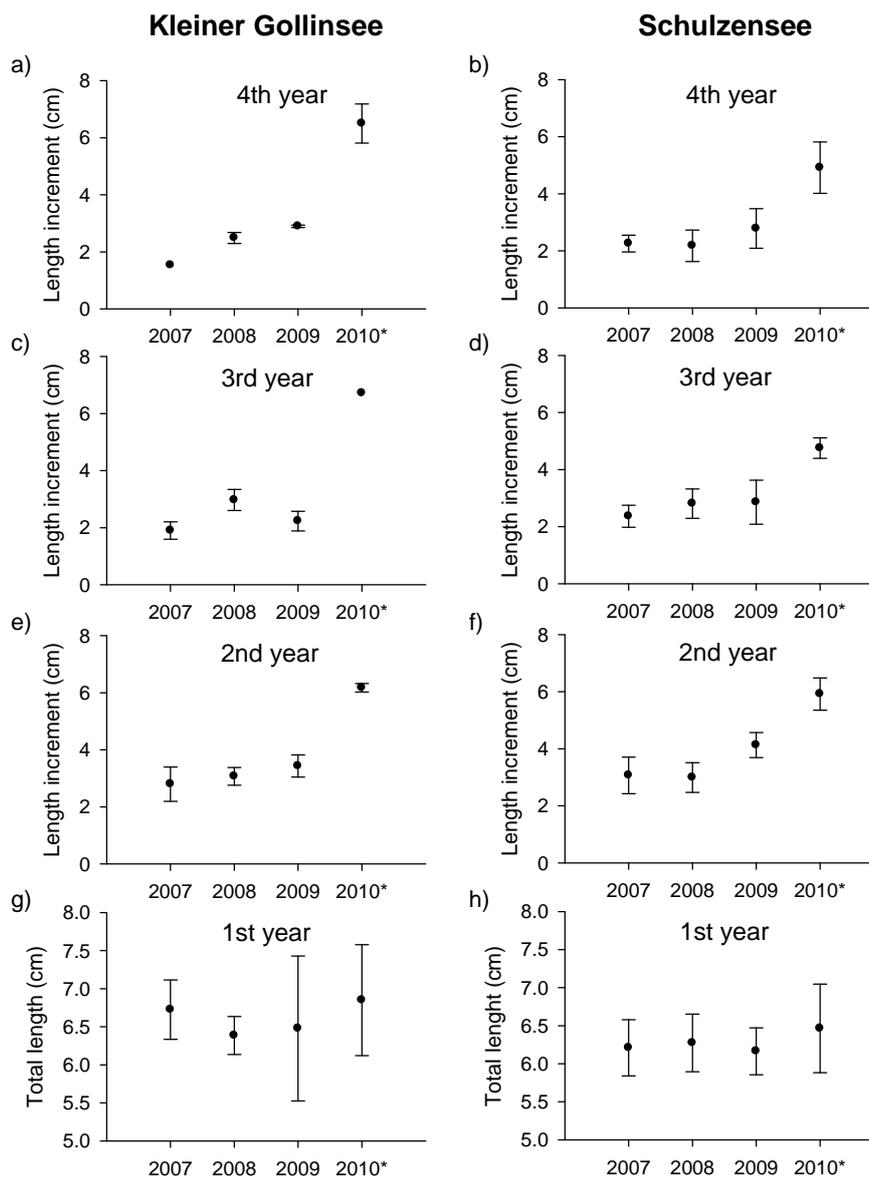
## Growth

We analyzed the scales of 195 roach from Kleiner Gollinsee and 193 individuals from Schulzensee. In both lakes annuli on scales were laid in May. The parameters of the curves for organic growth (Figure 10), which describe the growth of roach during the period 2003-2009, were significantly different between the lakes. Roach reached significantly higher ( $T_{2,383}=2.458$ ,  $p=0.014$ ) maximum length in Schulzensee ( $L_{inf} = 22.1$  cm), than in Kleiner Gollinsee ( $L_{inf} = 16.6$  cm). But roach grew significantly faster ( $T_{2,383}=2.134$ ,  $p=0.033$ ) during their first years in Kleiner Gollinsee ( $K = 0.41$ ) compared to Schulzensee ( $K = 0.25$ ).



**Figure 10.** Von Bertalanffy growth curves for roach in Schulzensee and Kleiner Gollinsee. Grey lines: 95% confidence bands. Fish were caught in 2010. Age and growth was determined by means of scales.

In both lakes, the growth of roach in 2010 was extraordinary high compared to the growth in previous years (see Figure 11). Mean length increment of 1+, 2+ and 3+ roach during a four month period (May – September) was markedly higher in 2010 than the annual length increment of these age classes in 2007, 2008 or 2009. The mean total length of young-of-the-year roach in September 2010 (after four month of growth) was already as high as the back-calculated total length of one year old roach in 2007, 2008 or 2009.

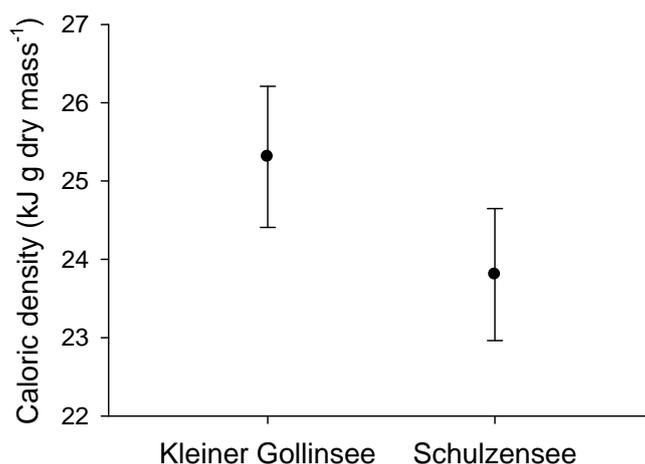


**Figure 11.** a-f: mean back-calculated annual length increment ( $\pm$  SD) of roach during their 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup> year in 2007, 2008 and 2009, and mean length increment ( $\pm$  SD) of 1+, 2+ and 3+ roach \*during four month (May – September) in 2010; g-h: mean back-calculated total length ( $\pm$  SD) at the end of the first year (May to May) of roach hatched in 2007, 2008 and 2009, and mean total length ( $\pm$  SD) of young-of-the-year measured \* after four month in September 2010. Note: sample size was  $\geq 10$  for each data point, only in a), c) and e) sample size was lower and some data points represent single individuals.

Comparing the lakes in 2010, the length increment of 3+ roach during a four month period (May- September, see Figure 11. a-b) was significantly higher ( $T_{2,43}=-5.847$ ,  $p<0.001$ ) in Kleiner Gollinsee (Mean=6.5 cm) than in Schulzensee (Mean=4.9 cm).

### Condition

In total we analysed the caloric density of 40 roach (20 from each lake). The caloric density was significantly higher (ANCOVA:  $F_{1,40}=20.907$ ;  $p<0.001$ ) of roach from Kleiner Gollinsee (Mean=25.3 kJ/g) than of roach from Schulzensee (Mean=23.8 kJ/g) (see Figure 12). There was no significant difference in caloric density between the habitats within each lake (ANCOVA:  $F_{1,40}=0.674$ ;  $p=0.417$ ) and no significant effect of log(weight) (ANCOVA:  $F_{2,40}=1.555$ ;  $p=0.225$ ).



**Figure 12.** Mean caloric density ( $\pm$  SD) of roach caught in Kleiner Gollinsee ( $n=20$ ) and Schulzensee ( $n=20$ ) in June 2010. Values were determined by bomb calorimetry.

## 4 Discussion

Shallow lakes display a strong dichotomy between two opposing stable states which differ in turbidity and abundance of submerged macrophytes and can be described as alternative equilibria (Scheffer et al. 1993). The clear-water, macrophyte-dominated state, as well as the turbid phytoplankton-dominated state, are stabilized by numerous feedback mechanisms between biotic and abiotic components in which fishes are important operational components of each ecosystem. Characteristic differences in species and biomass composition of fish as well as differences in their habitat and resource utilization contribute to the reinforcement of oppositional states, and may further result in a different system response to the increased influx of allochthonous carbon expected with climate change. Omnivorous fish, with their flexible feeding habits including pelagic zooplankton and benthic macroinvertebrates in the littoral zone, are expected to play an especially crucial role in sustaining the clear-water regime under more allochthonous conditions.

In 2010, our investigations revealed few differences in fish communities between the study lakes, although the lakes displayed major differences in turbidity and macrophyte colonization. A strong winter fish kill had equalized the fish communities and further affected the feeding and growth conditions of surviving fishes in each lake.

### 4.1 General community structure

In 2007, the biomass composition of fishes displayed characteristic differences between the turbid and the clear lake, which were consistent with findings of several authors in similar lakes (Persson 1991; Lammens 1989; Meijer et al. 1995). Accordingly, the fish community of Kleiner Gollinsee could be considered typical for a turbid lake and the fish community of Schulzensee as typical of a clear, vegetated lake. In 2010, after the winter fish kill, there were no differences in fish community structure between the lakes, whereas both lakes had lost regime-characteristic components.

In 2007, Kleiner Gollinsee was dominated by bream, which are known to stabilize the turbid state by resuspending sediment particles and nutrients (Meijer et al. 1990; Breukelaar et al. 1994). Furthermore, total fish biomass as well as the number of young-of-the-year fish and thus the potential predation pressure on zooplankton was higher in Kleiner Gollinsee, where lake-wide predation by piscivores was low. At Schulzensee, the high

proportion of piscivores (two times greater than in Kleiner Gollinsee) had a negative effect on the overall fish biomass and abundance of planktivorous fry, thus probably stabilizing the clear state by reducing predation pressure on zooplankton. Fishes of the planktivorous and herbivorous guild contributed similarly little to the total fish biomass, whereas omnivorous fish represented almost 40% of total fish biomass in both lakes. Surprisingly, roach were the dominant omnivores in the turbid as well as in the clear lake, whereas we had expected a dominance of perch in the clear, vegetated lake, due to its high foraging efficiency in structured habitats (Diehl 1988; Persson 1994). However, a dominance of roach was also found in four of five mesotrophic lakes of the same region, studied by Radke & Eckmann in 2001, who together with Haertel et al. (2002) found that perch were comparatively more affected by piscivorous fish predation than roach, which might explain the dominance of roach under mesotrophic conditions.

The strong winter between 2009 and 2010 significantly altered these communities. A long-lasting ice coverage, and additionally a snow layer which prevented photosynthetic oxygen production under the ice, had likely led to a severe oxygen depletion for fish. The resulting fish kill was first observed after the ice had melted from the lakes and hundreds of dead fish, especially large individuals, had drifted ashore. Due to the different oxygen requirements among fish species and the fact that large individuals suffer more from oxygen depletion than their smaller specimens, the hypoxia had an equalizing effect on the former different fish communities of the lakes. Bream, perch and ruffe died out and pike was only represented by few small specimens in both lakes. Accordingly in September 2010, total fish biomass was significantly lower in both lakes, but still higher in Kleiner Gollinsee. On the one hand, predation pressure on zooplankton might have been lowered by the decline in total fish biomass, but on the other hand this effect was countered by extremely high abundance of cyprinid fry as a consequence of the strong cutback of piscivorous fish in both lakes. In Kleiner Gollinsee, planktivory was additionally altered by sunbleak, which doubled their population compared to 2007. The proportion of omnivorous fish and thus their potential influence on the current regime increased in both lakes, but in 2010 omnivorous fish were solely represented by roach. The equalization of fish communities by the fish kill had different consequences for the stability of the current state of each lake. In Kleiner Gollinsee, the turbid state was probably strengthened by the reduction of piscivorous fish and the accordant increase of small planktivorous fish like fry and sunbleak. On the other hand, turbidity caused by the resuspension of sediment particles and nutrients probably decreased according to the strong decline of benthivorous

fish. Consequently, the turbid state of Kleiner Gollinsee might have been less affected, as oppositional effects may have outweighed each other, whereas the clear state of Schulzensee was strongly destabilized by the strong decline of piscivores and the resulting increase of planktivorous and omnivorous fish.

## 4.2 Spatial and temporal dispersal

Habitat use is a trade-off between resource utilization and predator avoidance (Gauthier & Boisclair 1997). Both predation pressure and food availability in a certain habitat vary during the day, as piscivorous fish alter their activity level and prey organisms potentially migrate between different habitats. Furthermore, the structure provided by submerged macrophytes influences the interaction between fish and their prey, as well as the interaction between piscivorous fish and prey fish. Accordingly, we expected differences in spatial and temporal dispersal of fish to be more pronounced in the clear lake, where submerged macrophytes intensify the contrast between the pelagic and the littoral habitat and predation by piscivorous fish is generally assumed to be more intense.

There was, however, no clear pattern of temporal and spatial dispersal of fish in either lake. Significant differences in the dispersal of fish between the littoral and the pelagic zone were solely observed during the day, when fish densities were higher in the littoral zone. At night, fish were evenly dispersed in both lakes. Surprisingly, an accumulation of fish in the littoral zone was more often observed at Kleiner Gollinsee than at Schulzensee. However, the dispersal of fish in general is a rough measure, thus we separately analyzed the spatial and temporal dispersal of the most abundant species, which were roach and sunbleak in Kleiner Gollinsee, and roach in Schulzensee. Sunbleak displayed a strong temporal pattern in habitat use, whereas they exclusively inhabited the littoral zone during the day, but were caught in equal amounts in the pelagic as well as in the littoral zone at night. Predation pressure is unlikely to have caused the migration behavior of sunbleak, as the biomass of the piscivorous guild was extremely low and consisted only of pike, which are known to cause an opposing habitat use of prey fish by foraging in the littoral zone during the day. Accordingly, food availability must have driven the migration of sunbleak and in fact, the density of crustacean zooplankton was two times higher in the littoral zone than in the pelagic zone of Kleiner Gollinsee during the day (Table 4). Such an accumulation of zooplankton in the littoral zone during the day has been interpreted as a predator avoidance strategy for crustaceans, which use the structurally rich habitat as a daytime refuge, and often migrate into the pelagic zone to feed on phytoplankton during

the night (DeMeester et al. 1993; DeStasio 1993; Lauridsen & Buenk 1996). We do not have data of zooplankton dispersal at night, but it is likely that crustacean zooplankton moved into the pelagic zone and sunbleak followed their migration at night. In Schulzensee, where the abundance of sunbleak was low, zooplankton densities did not differ between the pelagic and the littoral zone during the day. This indicates that predation by sunbleak was the main reason for an accumulation of crustacean zooplankton in the littoral zone of Kleiner Gollinsee during the day. In contrast, roach did not display such a general preference for a habitat, neither by day nor by night, even if in summer more roach were caught in the littoral zone during the day. The equal dispersal of roach between the habitats corresponds with the findings of the gut content analyses, which indicate a high flexibility in habitat and resource use among individual roach, as individuals caught in the same net either fed on zooplankton or on benthic resources.

In short, we did not observe a clear difference in general fish inhabitation of the littoral respectively the pelagic zone between the lakes. The structure represented by floating leaved plants and reeds was obviously sufficient to influence the temporal and spatial dispersal of crustaceans and sunbleak in Kleiner Gollinsee, but there was no additional effect on the dispersal of fish by submerged macrophytes in Schulzensee. However, the situation in 2010 was special, because the biomass of piscivores was equally low in both lakes, thus predation pressure which is known to be an important factor for habitat use did not affect the spatial and temporal dispersal of fish.

### **4.3 Diet, growth and condition of omnivorous fish**

Omnivorous fish feed on zooplankton as well as on macrozoobenthos (VanderZanden & Vadeboncoeur 2002; Jones & Waldron 2003). Their foraging behavior respective to their diet is influenced by several factors such as resource availability, predator abundance, and competition (Persson 1983; Persson 1988; Persson & Greenberg 1990). While this situation is complex, several authors have shown that the share of macroinvertebrates in the diet of omnivores and the individual growth of omnivores is positively correlated with the abundance of macroinvertebrates (Diehl 1993; Mittelbach 1988), which again is generally higher in vegetated habitats (Gilinsky 1984; Diehl 1988; Hargeby et al. 1994). Accordingly, we expected omnivorous fish to feed relatively more on benthic macroinvertebrates and consequently display faster growth and better body condition in Schulzensee, than their conspecifics in Kleiner Gollinsee.

In the year after the fish kill, the omnivorous guild consisted only of roach, thus our analyses of the diet, growth and condition of omnivores were restricted to roach. Furthermore, the fish kill strongly affected the feeding and growth conditions of omnivorous fish in both lakes, thus we observed a high contrast in growth of omnivores between 2010 compared to previous years, while the results of the diet analyses support the uniqueness of the lake conditions in 2010. In 2010 there was no general difference in the share of macroinvertebrates in the diet of roach between the lakes, yet we observed seasonal changes in the diet composition. In contrast to our expectations, zooplankton and macroinvertebrate densities as well as body conditions of roach were higher in the slightly more eutrophic, turbid lake. In 2010 the growth of roach was extraordinarily high in both lakes, whereas back-calculations revealed significant differences in the growth of roach between the lakes in previous years.

### **Diet**

On the one hand, multivariate analysis of gut content composition did not reveal significant differences between roach grouped by lake or season, since the variability of gut content composition between individuals of each group was high due to selective feeding on different resources. On the other hand, the results from stable isotope analyses indicate significant seasonal differences between the lakes, which can be explained when considering the mean proportion of gut content of roach calculated for each lake and each season. According to the mean proportion of gut content (Figure 6) in Kleiner Gollinsee, the share of zooplankton in the diet of roach was high in spring, but negligibly low during the rest of the year. This is a typical pattern of planktivory in adult roach, which successfully exploit the high densities of zooplankton in spring but switch to benthic food sources when zooplankton densities are reduced by planktivorous fry (Crowder 1985). In Schulzensee, however, zooplankton still represented about one third of the diet in summer, which might be explained by the hampering effect of submerged macrophytes on the interaction between roach and crustaceans, as well as by the lower predation pressure on zooplankton due to a lower total fish biomass. Benthic macroinvertebrates such as trichoptera and gastropods contributed to 10-30% of the mean roach diet in both lakes. Chironomids also accounted for 10-20% of the mean gut content of roach in Schulzensee, whereas in Kleiner Gollinsee chironomids were the major food source during the summer, but were rarely found in the guts of roach sampled in the autumn. The share of algae and detritus in the diet of roach increased over the year in both lakes, but was always

higher in Kleiner Gollinsee, where non-animal resources represented more than 80% of the diet of roach in autumn. This seasonal shift in the mean composition of gut contents correspond with the shift of  $\delta^{13}\text{C}$  values of roach from Kleiner Gollinsee and the resultant decline in  $\alpha$  (mean proportion of food ultimately derived from the pelagic food web) according to the mixing model (Table 5). In Schulzensee, mean  $\delta^{13}\text{C}$  values and mean  $\alpha$  of roach did not change during the year and indicate that almost 50% of the food was constantly derived from the pelagic food web. The pelagic signature in roach tissue corresponds with the high share of zooplankton and chaoborus in their diet during spring and summer, whereas in autumn, high quantities of benthic bryozoan colonies were ingested, thus keeping the pelagic signature at high levels, even when the share of zooplankton in the diet was low.

Summing up, in Schulzensee almost half of the diet constantly consisted of pelagic resources, whereas the mean diet composition of roach in Kleiner Gollinsee changed strongly between the seasons, with the share of littoral resources such as chironomids, algae and detritus being highest during the summer and autumn. The mean contribution of benthic macroinvertebrates (except chironomids) to the diet of roach was consistently higher in Schulzensee, but in general, the proportion of benthic macroinvertebrates of the diet of roach was low. Alternative non-animal resources such as algae and detritus, which are of poor quality but can be considered an almost unlimited resource (Persson 1983), played an important role in the diet of roach.

### **Growth and condition**

In both lakes, the growth of roach during 2010 was highly affected by the fish kill. Most likely, the decline in total fish biomass and the loss of strong competitors such as perch reduced the interspecific competition for food, and thus resulted in the extraordinarily rapid growth of surviving roach. Additionally, the strong decline of piscivorous fish probably released roach from behavioral constraints such as restricted habitat use or reduction of activity level, and thus further promoted their growth. Such a strong increase in growth is typical during the year after a fish kill, and has been observed by several authors (Rask et al. 1996; Ruuhijärvi et al. 2010). Comparing the lakes, length increment of 3+ roach during summer 2010 (May – September), as well as the caloric density (as a proxy for body condition, measured in June 2010), were significantly higher in Kleiner Gollinsee. This is likely due to the higher densities of prey organisms found in the different habitats (Table 4) during the summer of 2010, which is probably a result of the slightly more eu-

trophic conditions in Kleiner Gollinsee. The situation in 2010 was unique, however, and growth in the years before the fish kill, when annual length increment of roach was constantly lower (Figure 11), followed different patterns in each lake. According to the growth curves (Figure 10), older roach reached significantly higher maximum lengths in Schulzensee, which may indicate a higher availability of large prey items such as trichoptera and gastropoda, which especially support the growth of large individuals (Hellawell 1972). Whereas juvenile growth was low, it was significantly higher in Kleiner Gollinsee, and might be explained by higher densities of zooplankton, which are the main food source of juvenile roach (Hartley 1947). Unfortunately, we do not have any comparative data of resource densities in the lakes before the fish kill and thus cannot relate the observed differences in the growth of roach with potential differences in food availability. Considering the results of diet and growth analyses in 2010, there is no evidence that feeding on macroinvertebrates promoted the growth of roach.

#### **4.4 Initial situation and conclusions for the TERRALAC project**

The TERRALAC project studies the effect of the increased influx of organic carbon from terrestrial catchments on food webs of shallow lakes of opposing regimes. The studies are carried out at the clear-water, macrophyte-dominated Schulzensee and the turbid phytoplankton dominated Kleiner Gollinsee. In autumn 2010, after the final sampling for the present study, the lakes were divided with plastic curtains and maize leaves were added to one half of each lake to simulate a high inflow of particulate allochthonous carbon. One major hypothesis to be tested during the coming years is whether the stability of a clear lake is increased by the high subsidy of terrestrial organic carbon. Therefore, the following assumed mechanisms must be tested. Allochthonous carbon is thought to stimulate the secondary production of benthic macroinvertebrates in the littoral zone more strongly than the production of pelagic zooplankton. The resulting increase of macroinvertebrate biomass relative to the biomass of pelagic zooplankton might further release zooplankton from predation pressure if omnivorous fish change their feeding behavior and preferentially feed upon the more abundant and larger benthic invertebrates. Additionally, an increase of benthic macroinvertebrates might enhance the biomass of piscivorous fish, which profit from macroinvertebrate food during some ontogenetic stages as well as from the increase of omnivorous prey fish. Finally, diet shifts of omnivorous fish and the high biomass of piscivorous fish will indirectly result in higher grazing losses of phytoplankton and increased water transparency. These mechanisms will be tested, but the outcome

of the experiment also depends on the initial structure of the fish community, especially the proportions of omnivorous and piscivorous fish.

The fish community of Schulzensee was radically restructured by the fish kill in the winter of 2009/10. The former typically high proportion of piscivorous fish declined to a marginal 5% of total fish biomass, and the population of perch disappeared completely. The latter affects future omnivory as well as future piscivory since perch linked and contributed to both feeding guilds due to their ontogenetic niche shift (Persson 1986). On the one hand, the relative proportion of omnivorous fish and thus their potential influence on the resilience of the clear state increased by the fish kill, but on the other hand, the importance of benthic macroinvertebrates as a resource for omnivorous fish might have decreased with the loss of perch, which is the more efficient benthic feeder compared to roach (Persson & Greenberg 1990; Diehl 1988). Furthermore, roach depend less strongly on macroinvertebrate resources than perch, because roach can also feed on algae and detritus (see 3.3 Diet; Persson 1983), whereas perch is restricted to animal food sources (Persson 1986). The direct effect of increased invertebrate resources on the stock of piscivorous fish might be hampered by the loss of perch. Growth of perch is strongly correlated with the availability of invertebrate food, thus a high supply of invertebrates promote an early shift to piscivory (Persson 1986). Whereas pike only feed on macroinvertebrates during a relatively short phase in early life, the growth of adult pike strongly depends on the availability of prey fish and is not further supported by additional macroinvertebrate food (Soupir et al. 2000; Venturelli & Tonn 2006).

In conclusion, the initial situation to test the hypothesis whether the higher influx of allochthonous carbon increases the resilience of the clear-water state was strongly affected by the winter fish kill. The present fish community in Schulzensee, with its extremely low proportion of piscivores, does not represent a typical fish community of a clear, vegetated lake (Persson 1991), which is assumed in the suggested scenario. Additionally, due to the loss of perch, the present system lacks a very important operational component linking invertebrate resources to piscivory.

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## Erklärung

Hiermit versichere ich eidesstattlich, dass ich die vorliegende Diplomarbeit selber geschrieben habe und sie – abgesehen von der Beratung durch meine akademischen Lehrer – nach Inhalt und Form meine eigene Arbeit ist. Ich habe keine anderen als die angegebenen Hilfsmittel und Quellen verwendet. Ich und meine Betreuer sind damit einverstanden, dass diese Diplomarbeit nach Abschluss des Verfahrens öffentlich zugänglich gemacht wird.

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Ort, Datum

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Unterschrift