A LIFE LESS ORDINARY
Foraging behaviour and predator avoidance in young-of-the-year perch

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Ulrike König
aus Papenburg

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Berichterstatter:	PD. Dr. Jost Borcherding
	Prof. Dr. Hartmut Arndt

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"Das Ziel der Wissenschaft ist es immer gewesen, die Komplexität der Welt auf simple Regeln zu reduzieren."

Benoît Mandelbrot

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INTRODUCTION

Although generalists can have flexible foraging patterns benefiting from a wide range of food resources, they were found less efficient foragers compared to individuals that are selective and specialize in one prey type not suffering from, for example, time delays due to switching between prey types (Werner et al. 1981; Bernays & Funk 1999; Dukas & Kamil 2001). Diets of individuals within a population are seldom a mere sample of all prey types available, but show that most fish can be highly selective, thus selecting another foraging strategy than generalists (Kaiser & Hughes 1993). The rate at which the forager encounters a given food or prey type, the energetic value of which and the predator avoidance strategies are most important aspects influencing individual feeding strategies (Stephens & Krebs 1986; Bolnick et al. 2003). The reason for diet variation and specialisation has been studied thoroughly and let to the development of the optimal diet theory (ODT; Schoener 1968; Werner & Hall 1974; Pulliam 1974; Svanbäck & Bolnick 2005). ODT suggests that an individual selects a foraging strategy to maximise its energetic income, which depends on energetic content, encounter rates, the individual’s efficiency in detecting, capturing, handling and last digesting of prey types available. An individual’s efficiency in detecting, capturing, handling and digesting of prey types can determine the diet because individuals’ abilities differ (Wilson et al. 1993; Svanbäck & Bolnick 2005). Therefore, the individual is bound to drop the prey type with less energetic value than its energetic return of the individual’s capture success. Abilities can be determined by coincidence, for example by the time of individual hatching of fish. Borcherding et al. (in prep.) found the timing to have crucial influence on population structure, as only the largest perch of the young-of-the year (YOY) age cohort were able to prey on energetically profitable fish larvae while the smaller siblings got stuck in competition on zooplankton, leading to enlarged differences in growth and specialisation processes within the YOY age cohort of perch. However, consumption efficiency of a given prey has been observed to depend on other prey types (Persson 1985). When mixed prey was offered, intake rates of profitable and less profitable prey types were similar. European perch, *Perca fluviatilis*, appeared to be unable to use different feeding techniques at the same time with maximum efficiency (Persson 1985). Quite similarly Warburton & Thomson (2006) found impaired foraging efficiency of silver perch (*Bidyanus bidyanus*), when foragers were faced with mixed prey and maximized foraging efficiency on patches of a single prey type.

Besides ODT, learning is known to contribute to prey selection processes by improving prey cognition, attack mode and handling efficiency of the individual, consequently affecting foraging behaviour (Godin 1978; Hughes 1979; Croy & Hughes 1991a; b; Hughes et al. 1992). So learning can alter the ratio of gains to costs related with foraging on previously consumed prey (Reiriz et al. 1998). Previous studies showed that learned foraging skills have a strong influence on the profitability of prey, especially when prey items are of high energetically profitability but hard to catch (Kaiser & Hughes 1993; Hughes & Croy 1993). An acquired search image can improve the ability to detect preferred prey and lessen the detection rate of alternative targets (Langley 1996; Reiriz et al. 1998). Beeck (2000) conducted experiments in which European perch trained on fish larvae (bream, *Abramis brama*) and untrained perch were offered daphnids (*Daphnia pulicaria*) and bream larvae. Untrained perch switched from bream to daphnids with increasing daphnid densities (number of daphnids per litre ≥ 5) in accordance with the assumptions of ODT. Conversely, experienced perch once trained on fish remained piscivorous at *Daphnia* densities of up to 100 individuals per litre. The experience of perch feeding on fish larvae seems to have modified the ratio of gains for these in the study. Perch that were experienced in feeding on prey fish larvae were also superior in capturing these to inexperienced fish.

Foraging behaviour is not only influenced by ODT and learning but also depends strongly on predation threat the forager is exposed to. In most ecosystems predation is a major structuring force. Foragers can be affected either directly (by being preyed upon) or indirectly (Nilsson 2001; Hölker et al. 2007). These effects can have strong impacts on prey populations and decisions by individual predators and prey can have cascading effects on population and community dynamics (e.g. continuing from fish to zooplankton to nutrient level of the ecosystem, Mills et al. 1987a; Benndorf 1990; Carpenter et al. 1994; Mehner et al. 2005a; b). The availability of profitable food strongly influences the growth capacities of juveniles. Byström et al. (2004) have shown that the trade-off between foraging gain and predation risk is more likely for individuals large enough to be resource limited but still small enough to be vulnerable to predation. Thus, individual survival is increased with high growth rates in early life stages (Wilbur 1988; Post et al. 1999. Size-dependent influences on the trade-off between feeding and hiding were shown by Magnhagen & Borcherding (2008) for two populations of European perch. The degree of boldness to forage for food in the presence of a predator changed between the YOY and the 1+ age class in response to the experience of recent predation risk (Magnhagen & Borcherding 2008). However, changes in degree of boldness of behaviour can be altered also within one size class. Most studies have so far focused on different age classes when examining the influence of body size on foraging behaviour in the trade-off to predator avoidance. As described by Beeck et al. (2002), the YOY perch can split into a bimodal size distribution, with the small size perch being mainly zooplanktivorous while the larger perch fed to a certain amount on prey fish. The larger size cohort is still vulnerable to predation (Lundvall et al. 1999) and can be nearly exclusively the prey of older perch (Beeck 2003; Persson et al. 2003). In short-term laboratory experiments, Borcherding (2006) demonstrated that two size classes of YOY perch behaved differently regarding the trade-off between food and shelter under the threat of predation. The larger size class increased the utilisation of the open water area when prey fish were available there more than the smaller size class did. Individuals may reduce activity levels or increase their use of less risky habitats to reduce predation risk (Werner et al. 1983; Werner & Gilliam 1984; Persson & Eklöv 1995). So, if the uptake of food resources in a specific habitat is linked to a certain habitat-specific predation risk, a trade-off exists between foraging and predator avoidance that may severely affect behaviour and activity levels.

When preferred prey resources are shared by more than one species, one predator may be the better competitor and deplete this food resource (interspecific competition, equal results can be found for intraspecific competition e.g. in large cohorts). This has an indirect effect on the other specimen having to open up alternative food resources which may include foraging on inferior prey or in suboptimal habitats. For example, European perch are known to forage most successfully in open water. But especially smaller fish tend to avoid open water habitats and switch to habitats with complex structures and areas of submerged vegetation to seek shelter and intensify foraging on more profitable food (Borcherding 2006). This habitat shift can be due to competition (e.g., with roach, *Rutilus rutilus* L.) or to predation risk. Therefore, juvenile fish species need habitats with high structural complexity as feeding grounds as well as a refuge against predators (Savino & Stein 1989; Diehl 1993; Hargeby et al. 1994; Lauridsen & Buenk 1996; Burks et al. 2002). Increased structures in the littoral area create more microhabitat types (enlarging total niche space) allowing the coexistence of competitors and persistence of predators and their prey (Crowley 1978; Crowder & Cooper 1982; Chick & Mcivor 1994). Vegetation not only enhances structural diversity in water bodies but reduces the development of phytoplankton, thus stabilizing water conditions by reducing dissolved nutrients and limiting re-suspension of fine sediments (Scheffer 1999; Donabaum et al. 1999; Dokulil & Teubner 2003). In current flood plains many gravel pit lakes have emerged during the last decades due to the exploitation of gravel and sand, but these non-natural water bodies often differ immensely from natural lakes and most importantly often lack structural diversity in the littoral area (Berndt 1991; LAWA 1998). They might turn out to be alternative biotopes within flood plains with strong anthropogenic influence as their dimensions often outbalance that of naturally existing inshore waters such as oxbow lakes (DGL 1995a; Neumann et al. 1996; Scharbert & Greven 2002). Artificial floating islands provide critical riparian edge habitat, comprising new land mass for use by all kinds of organisms and provide wave mitigation and erosion control (BioHaven® floating islands; Tanner & Headley 2006; Steward 2007; Stewart et al. 2008; Tanner & Headley 2008; www.floatingislandinternational.com, www.aldenlab.com/index.cfm/News?NID=160) and have been successfully applied in ecosystem management and environmental protection. The roots of artificial floating islands grow down below the island matrix to create a very large surface area not only for nutrient uptake but also as additional habitat. Artificial floating islands have been used throughout the world as a means of aggregating fish (Welcomme 2002; Nakamura & Mueller 2008). In India floating islands have existed for centuries. Formed through dense growth of aquatic weeds and grasses they are spread throughout lakes and used as natural fish aggregating devices (locally called 'Phums, Suresh 2009).

This study should first lay open the effect of additional vegetated areas in poorly structured, anthropogenic influenced water bodies by means of planted artificial floating islands. It was hypothesised that the structured root cavities should increasingly be colonized by a rich macroinvertebrate fauna. An increased abundance of macrozoobenthos and the additional space provide shelter for the juvenile fish community. The strongly structured root cavities should lead to an increased utilisation of the plant islands by fish. Thus, our second hypothesis was that the abundance of juvenile fish in the area of the plant islands should increase above abundances at the natural shoreline of the gravel pit lake.. Consequently, this study should allow a first estimation how far such planted islands may contribute to conventionally restored and improve not restored shore lines in the recultivation of gravel pit lakes which extended littoral areas.

In the second part of this study, the relationship between prey availability and predator avoidance for two size classes of the YOY cohort of perch was further analysed in mesocosm experiments. In contrast to short-term laboratory experiments (Borcherding 2006), the YOY perch here had time to adapt to experimental conditions and to gain experience on the experimental factors. Instead of shelter formed by submerse vegetation the mesocosms were separated in three compartments, with two of them excluding the predator. Thus, the behavioural adaptations as well as changes in activity level of the two size classes of YOY perch should depend only on the effects of the two factorial components of this trade-off situation, the presence and absence of the predator and availability of small fish offered as food. It was hypothesised (1) that perch independent of size reduce residence time in the presence of a predator, and (2) that large perch will show different behaviour compared to the smaller members of the YOY cohort when prey fish are offered.

To address the question in what way foraging strategies can be influenced by experience and to gain better understanding on the behavioural consequences of food selection, YOY perch in the third part of the study were trained on two different food resources (zooplankton and cyprinid fish larvae) for 6 weeks. Each group developed different morphotypes (Heermann et al. 2007; Heynen 2007; Langkau 2008). A fixed concentration of zooplankton with different levels of fish was offered the different groups of perch. Additionally, instead of fish a novel food resource, the mysid *Limnomysis benedenii*, was offered. The hypotheses of the study were 1) that perch will prefer the food resource they were trained on over alternatives and feed on it according to its density and 2) when the preferred food resource is depleted perch start foraging on the less preferred food resource.

To conduct studies concerning the ecology of fish population it is essential to get fish samples which truly reflect the population structure. In the fourth part of the study, various fishing techniques were applied in field studies to obtain information on the population structure such as gillnetting and electrofishing. The capture success of the methods depends mainly on the activity of individuals, their abundance and the habitat in which each method is applied. In cases of bimodality, where two size cohorts display different behaviour in foraging, activity and habitat choice distinct differences in length-frequency distribution of perch sampled by different methods were expected. In shallow experimental ponds the capture success of multi-mesh gillnetting and electrofishing was examined. To gather further information on the sampling of juvenile perch in large water bodies of greater depth, three gravel pit lakes were studied. Additionally, in the deep gravel pit lakes bongo-net fishing was used in spring to monitor perch larvae in the pelagic zone after hatching. The three methods were compared and recommendations how to improve fish stock assessment were given.

Furthermore, studies concerning the ecology of fish population often require a variety of measurements such as length and weight, which are often used in modelling, monitoring and to describe basic biological relationships (Hoyle et al. 2000; Jennings et al. 2001; Morison et al. 2003). Also a variety of other examinations such as stomach content analyses to establish fish diet are important for ecological studies of fish communities. Commonly it is not possible to conduct these analyses in the field, either because it is impossible to take the instruments needed into the field or simply because there is not enough time to measure the length and weight of all individuals caught. Therefore in the last part of this study, fish were preserved for later analyses in the laboratory. Common preservatives are freezing, alcohol and formalin and are known to affect size and weight of individuals preserved. Not only density of the preservative but also original length of fish influences the strength of changes: small fish are affected stronger than larger specimen (Fowler & Smith 1983; Treasurer 1992; Fey 1999). The latter gives some evidence that morphological characteristics are also affected by different preservation techniques (Sagnes 1997). During the last years new morphometric analyses (based on landmarks, Bookstein 1991) became increasingly important in ecological studies in fish (Hjelm et al. 2001; Svanbäck & Eklöv 2004; Olsson & Eklöv 2005; Svanbäck & Eklöv 2006; Heermann et al. 2007), however, differences between preservation techniques and related shape changes have not been considered until now. In order to estimate what preservation technique would be the best for ecological studies, in which the results of a variety of analyses are of interest, YOY perch were preserved with three techniques (freezing, ethanol, and formalin) and length, weight and shape changes over a period of eight weeks were examined. In addition, a short experiment should give first cues how these preservation techniques may affect stomach analyses in fish. The effect of preservation technique on length, weight, body shape and condition of stomach content of juvenile perch was quantified and a recommendation on which preservative should be used when studying a variety of ecological aspects in a multi-disciplinary approach was given.

References

Beeck, P. (2000). Die frühe Piscivorie von 0+ Flußbarschen (*Perca fluviatilis*) – Ein ungewöhnliches Räuber-Beute System mit weitreichenden Konsequenzen für die Fischartengemeinschaft eines eutrophen Baggersees. Diplomarbeit. Universität zu Köln.

Beeck, P. (2003). The early piscivory of European perch (*Perca fluviatilis*): A neglected phenomenon with notable consequences for the population structure and fish community in lake ecosystems. PhD Thesis. Universität zu Köln.

Beeck, P., Tauber, S., Kiel, S. & Borcherding, J. (2002). 0+ perch predation on 0+ bream: a case study on a eutrophic gravel pit lake. *Freshwater Biology* **47,** 2359-2369.

Benndorf, J. (1990). Conditions for effective biomanipulation; conclusions derived from whole-lake experiments in Europe. *Hydrobiologia* **200/201,** 187-203.

Bernays, E. A. & Funk, D. J. (1999). Specialists make faster decisions than generalists: experiments with aphids. *Proceedings of the Royal Society of London Series B-Biological Sciences* **266,** 151-156.

Berndt, J. (1991). Ökologische Aspekte bei der Gestaltung und Nutzung von Baggerseen in der Aue. *Natur und Landschaft* **66,** 160-163.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161,** 1-28.

Bookstein, F. L. (1991). *Morphometric tools for landmark data: geometry and biology.* Cambridge: Cambridge University Press.

Borcherding, J. (2006). Prey or predator: piscivorous 0+ perch (*Perca fluviatilis*) in the trade-off between food and shelter. *Environmental Biology of Fishes* **77,** 87-96.

Borcherding, J., Beeck, P., DeAngelis, D. L. & Scharf, W. (2009). Phenology affects size-dependent life history strategies that cause divergence in population structure. *Ecology* **submitted**.

Burks, R. L., Lodge, D. M., Jeppesen, E. & Lauridsen, T. L. (2002). Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater Biology* **47,** 343-365.

Byström, P., Andersson, J., Persson, L. & De Roos, A. M. (2004). Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young arctic char. *Oikos* **104,** 109-121.

Carpenter, S. R., Munozdelrio, A., Newman, S., Rasmussen, P. W. & Johnson, B. M. (1994). Interactions of anglers and walleyes in escanaba lake, wisconsin. *Ecological Applications* **4,** 822-832.

Chick, J. H. & Mcivor, C. C. (1994). Patterns in the Abundance and Composition of Fishes Among Beds of Different Macrophytes - Viewing A Littoral-Zone As A Landscape. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 2873-2882.

Crowder, L. B. & Cooper, W. E. (1982). Habitat Structural Complexity and the Interaction Between Bluegills and Their Prey. *Ecology* **63,** 1802-1813.

Crowley, P. H. (1978). Effective Size and Persistence of Ecosystems. *Oecologia* **35,** 185-195.

Croy, M. I. & Hughes, R. N. (1991a). The Influence of Hunger on Feeding-Behavior and on the Acquisition of Learned Foraging Skills by the 15-Spined Stickleback, *Spinachia spinachia* l. *Animal Behaviour* **41,** 161-170.

Croy, M. I. & Hughes, R. N. (1991b). The Role of Learning and Memory in the Feeding-Behavior of the 15-Spined Stickleback, Spinachia-Spinachia l. *Animal Behaviour* **41,** 149-159.

DGL (1995). Examination, Inspection and Evaluation of Gravel Pit Lakes; Recommendations and decision support of the German Society of Limnology e.V.(DGL) concerning planning, nature conservation and water quality.

Diehl, S. (1993). Effects of habitat structure on resource availability, diet and growth of benthivorous perch, perca-fluviatilis. *Oikos* **67,** 403-414.

Dokulil, M. T. & Teubner, K. (2003). Eutrophication and restoration of shallow lakes - the concept of stable equilibria revisited. *Hydrobiologia* **506,** 29-35.

Donabaum, K., Schagerl, M. & Dokulil, M. T. (1999). Integrated management to restore macrophyte domination. *Hydrobiologia* **396,** 87-97.

Dukas, R. & Kamil, A. C. (2001). Limited attention: the constraint underlying search image. *Behavioral Ecology* **12,** 192-199.

Fey, D. P. (1999). Effects of preservation technique on the length of larval fish: methods of correcting estimates and their implication for studying growth rates. *Archive of Fishery and Marine Research* **47,** 17-29.

Fowler, G. M. & Smith, S. J. (1983). Length Changes in Silver Hake (Merluccius-Bilinearis) Larvae - Effects of Formalin, Ethanol, and Freezing. *Canadian Journal of Fisheries and Aquatic Sciences* **40,** 866-870.

Godin, J. J. (1978). Behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha* Wahlbaum) towards novel prey: influence of ontogeny and experience. *Environmental Biology of Fishes* **3,** 261-266.

Hargeby, A., Andersson, G., Blindow, I. & Johansson, S. (1994). Trophic web structure in a shallow eutrophic lake during a dominance shift from phytoplankton to submerged macrophytes. *Hydrobiologia* **280,** 83-90.

Heermann, L., Beeck, P. & Borcherding, J. (2007). Two size classes of 0+ perch: is phenotypic plasticity based on food resources? *Journal of Fish Biology* **70,** 1365-1377.

Heynen, M. (2007). Phenotypic plasticity in juvenile perch (*Perca fluviatilis* L.): Does nutrition influence morphology and behaviour? Diplomarbeit. Universität zu Köln.

Hjelm, J., Svanbäck, R., Byström, P., Persson, L. & Wahlström, E. (2001). Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. *Oikos* **95,** 311-323.

Hölker, F., Dörner, H., Schulze, T., Haertel-Borer, S. S., Peacor, S. D. & Mehner, T. (2007). Species-specific responses of planktivorous fish to the introduction of a new piscivore: implications for prey fitness. *Freshwater Biology* **52,** 1793-1806.

Hoyle, S. D., Queensland.Dept.of Primary Industries. & Fisheries Research and Development Corporation (Australia) (2000). *Integrated fish stock assessment and monitoring program*. Deception Bay, Qld.: Southern Fisheries Centre, Dept. of Primary Industries.

Hughes, R. N. (1979). Optimal Diets Under the Energy Maximization Premise - Effects of Recognition Time and Learning. *American Naturalist* **113,** 209-221.

Hughes, R. N. & Croy, M. I. (1993). An Experimental-Analysis of Frequency-Dependent Predation (Switching) in the 15-Spined Stickleback, Spinachia-Spinachia. *Journal of Animal Ecology* **62,** 341-352.

Hughes, R. N., Kaiser, M. J., Mackney, P. A. & Warburton, K. (1992). Optimizing Foraging Behavior Through Learning. *Journal of Fish Biology* **41,** 77-91.

Jennings, S., Kaiser, M. & Reynolds, J. D. (2001). *Marine Fisheries Ecology*. Oxford: Blackwell Publishing.

Kaiser, M. J. & Hughes, R. N. (1993). Factors Affecting the Behavioral Mechanisms of Diet Selection in Fishes. *Marine Behaviour and Physiology* **23,** 105-118.

Langkau, M. (2008). Piscivore versus planktivore: How does morphological change influence ecological performance?

Langley, C. M. (1996). Search images: Selective attention to specific visual features of prey. *Journal of Experimental Psychology-Animal Behavior Processes* **22,** 152-163.

Lauridsen, T. L. & Buenk, I. (1996). Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. *Archiv fur Hydrobiologie* **137,** 161-176.

LAWA (1998). *Gewässerbewertung - stehende Gewässer: Vorläufige Richtlinie für eine Erstbewertung von natürlich entstandenen Seen nach trophischen Kriterien.* Kulturbuch-Verlag, Berlin.

Lundvall, D., Svanbäck, R., Persson, L. & Byström, P. (1999). Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 1285-1292.

Magnhagen, C. & Borcherding, J. (2008). Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness? *Animal Behaviour* **75,** 509-517.

Mehner, T., Holker, F. & Kasprzak, P. (2005a). Spatial and temporal heterogeneity of trophic variables in a deep lake as reflected by repeated singular samplings. *Oikos* **108,** 401-409.

Mehner, T., Ihlau, J., Dörner, H. & Hölker, F. (2005b). Can feeding of fish on terrestrial insects subsidize the nutrient pool of lakes? *Limnology and Oceanography* **50,** 2022-2031.

Mills, E. L., Forney, J. L. & Wagner, K. J. (1987). Fish predation and its cascading effect on the Oneida Lake food chain. In *Predation: direct and indirect impacts on aquatic communities* (Kerfoot, W. C. & Sih, A., eds.), pp. 118-131. Hanover, N.H. (USA): University Press of New England

Morison, A. K., Brown, I. W. & Jones, G. K. (2003). Post mortem shrinkage of four species of temperate and tropical marine fishes, without freezing or preservation. *Journal of Fish Biology* **62,** 1435-1449.

Nakamura, K. & Mueller, G. (2008). Review of the performance of the artificial floating island as a restoration tool for aquatic environments. World Environmental and Water Resources Congress.

Neumann, D., Staas, S., Molls, F., Seidenberg-Busse, C., Petermeier, A. & Rutschke, J. (1996). The significance of man-made lentic waters for the ecology of the Lower River Rhine, especially for the recruitment of potamal fish. *Archiv für Hydrobiologie Supplementband* **113,** 267-278.

Nilsson, P. A. (2001). Predator behaviour and prey density: evaluating density-dependent intraspecific interactions on predator functional responses. *Journal of Animal Ecology* **70,** 14-19.

Olsson, J. & Eklöv, P. (2005). Habitat structure, feeding mode and morphological reversibility: factors influencing phenotypic plasticity in perch. *Evolutionary Ecology Research* **7,** 1109-1123.

Persson, L. (1985). Optimal foraging - the difficulty of exploiting different feeding strategies simultaneously. *Oecologia* **67,** 338-341.

Persson, L., De Roos, A. M., Claessen, D., Byström, P., Lövgren, J., Sjögren, S., Svanbäck, R., Wahlström, E. & Westman, E. (2003). Gigantic cannibals driving a whole-lake trophic cascade. *Procedings of the National Academy of Sciences, USA* **100,** 4035-4039.

Persson, L. & Eklöv, P. (1995). Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* **76,** 70-81.

Post, J. R., Parkinson, E. A. & Johnston, N. T. (1999). Density-dependent processes in structured fish populations: Interaction strengths in whole-lake experiments. *Ecological Monographs* **69,** 155-175.

Pulliam, H. R. (1974). Theory of Optimal Diets. *American Naturalist* **108,** 59-74.

Reiriz, L., Nicieza, A. G. & Brana, F. (1998). Prey selection by experienced and naive juvenile Atlantic salmon. *Journal of Fish Biology* **53,** 100-114.

Sagnes, P. (1997). Potential artefacts in morphometric analyses of fish: Effects of formalin preservation on 0+ grayling. *Journal of Fish Biology* **50,** 910-914.

Savino, J. F. & Stein, R. A. (1989). Behavior of Fish Predators and Their Prey - Habitat Choice Between Open Water and Dense Vegetation. *Environmental Biology of Fishes* **24,** 287-293.

Scharbert, A. & Greven, H. (2002). Umgestaltete Abgrabungsseen: Auengewässer der Zukunft? Reconstructed gravel pit lakes: floodplain lakes of the future? *Verh.Ges.Ichthyol.* **3,** 131-187.

Scheffer, M. (1999). The effect of aquatic vegetation on turbidity; how important are the filter feeders? *Hydrobiologia* **408/409,** 307-316.

Schoener, T. W. (1968). The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49,** 704-726.

Stephens, D. W. & Krebs, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.

Steward, F. (2007). Biomimetic floating islands that maximize plant and microbial synergistic relationships to revitalize degraded fisheries, wildlife habitats, and human water resources. Final Report to Montana Board of Research and Commercialization Technology (MBRCT).

Stewart, F. M., Mulholland, T., Cunningham, A. B., Kania, B. G. & Osterlund, M. T. (2008). Floating islands as an alternative to constructed wetlands for treatment of excess nutrients from agricultural and municipal wastes-results of laboratory-scale tests. *Land Contamination & Reclamation* **16,** 25-33.

Suresh, V. R. (2009). Floating Islands: a Unique Fish Aggregating Method. *NAGA* **23,** 11-13.

Svanbäck, R. & Bolnick, D. I. (2005). Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research* **7,** 993-1012.

Svanbäck, R. & Eklöv, P. (2004). Morphology in perch affects habitat specific feeding efficiency. *Functional Ecology* **18,** 503-510.

Svanbäck, R. & Eklöv, P. (2006). Genetic variation and phenotypic plasticity: causes of morphological and dietary variation in Eurasian perch. *Evolutionary Ecology Research* **8,** 27-49.

Tanner, C. C. & Headley, T. (2006). Application of Floating Wetlands for Enhanced Stormwater Treatment: A Review. 324. Auckland Regional Council. National Institute of Water and Atmospheric research (NIWA) Client Report: HAM2006-123.

Tanner, C. C. & Headley, T. (2008). Floating treatment wetlands - an innovative solution to enhance removal of fine particulates, copper and zinc. *NZWWA - water & wastes in New Zealand*.

Treasurer, J. W. (1992). Length and weight changes in 0+ perch, *Perca fluviatilis* L. following fixation in formalin. *Journal of Fish Biology* **41,** 1033-1036.

Warburton, K. & Thomson, C. (2006). Costs of learning: the dynamics of mixed-prey exploitation by silver perch, *Bidyanus bidyanus* (Mitchell, 1838). *Animal Behaviour* **71,** 361-370.

Welcomme, R. L. (2002). An evaluation of tropical brush and vegetation park fisheries. *Fisheries Management and Ecology* **9,** 175-188.

Werner, E. E. & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15,** 393-425.

Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64,** 1540-1548.

Werner, E. E. & Hall, D. J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). *Ecology* **55,** 1042-1052.

Werner, E. E., Mittelbach, G. G. & Hall, D. J. (1981). The Role of Foraging Profitability and Experience in Habitat Use by the Bluegill Sunfish. *Ecology* **62,** 116-125.

Wilbur, H. M. (1988). Interactions between growing predators and growing prey. In *Size structured populations* (Ebenman, B. & Persson, L., eds.), pp. 157-172. Berlin, Heidelberg: Springer-Verlag

Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. (1993). Shy-bold continuum in Pumpkinseed Sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology* **107,** 250-260.

CHAPTER I

Can floating textile plant carriers represent alternative habitats for the fish community in gravel pit lakes which lack structural diversity in the littoral area?

König, Ulrike[1]; Werneke, Ulrich[2] ; Mählmann, Jens[3] & Borcherding, Jost[1]

1 University of Cologne, Zoological Institute, General Ecology and Limnology, Ecological Research Station Grietherbusch, 46459 Rees-Grietherbusch
2 Naturschutzzentrum Kreis Kleve e.V., Niederstr. 3, 46459 Rees-Bienen
3 Sächsisches Textilforschungsinstitut e.V. (STFI), Annaberger Str. 240, 09125 Chemnitz

Abstract

In current flood plains many gravel pit lakes have emerged during the last decades. As their dimensions often outbalance that of naturally existing waters such as oxbow lakes, they may turn out to be alternative biotopes. However, artificial water bodies differ from natural lakes; they often lack a distinct littoral zone. Because diverse littoral zones are essential for spawning and recruitment of fishes, such structural diversity is essential in the recultivation of gravel pit lakes. At steep banks that lack structural diversity, planted floatable textile mats may be an alternative to establish littoral elements to minimise structural deficiencies. The objective of this study was to analyse the functionality of such plant islands for the invertebrate fauna and the juvenile fish community. The rhizosphere underneath the plant carriers provided living space for a rich invertebrate fauna. The utilisation of this food resource and the additional shelter for the juvenile fish community under the plant islands depended on the relative position of the mats to the shoreline, and the development of macrophytes in the natural littoral. Overall, the fish community used the new habitat underneath the plant islands less than expected.

Introduction

Loss of natural inshore waters of flood plains leads to a pronounced decrease in biodiversity of riverine landscapes (Copp 1990; Ward 1998; Amoros & Bornette 2002). In current flood plains many gravel pit lakes have emerged during the last decades due to the exploitation of gravel and sand. As their dimensions often outbalance that of naturally existing inshore waters such as oxbow lakes, they may turn out to be alternative biotopes within flood plains with strong anthropogenic influence (DGL 1995b; Neumann et al. 1996; Scharbert & Greven 2002). However, artificial water bodies regularly differ immensely from natural lakes: often they carry a low amount of nutrients as they are fed by ground water supply, are much deeper due to the industry's interest in economic dredging and therefore have an unfavourable area to volume ratio and most important often lack a distinct littoral zone (Berndt 1991; LAWA 1998). However, littoral structures are essential for spawning and recruitment of fishes (Thorpe 1977; Zeug & Winemiller 2008). Both juvenile fish and macrozoobenthos species need habitats with high structural complexity as feeding grounds as well as a refuge against predators (Savino & Stein 1989; Diehl 1993; Hargeby et al. 1994; Lauridsen & Buenk 1996; Burks et al. 2002). Increased structures in the littoral area create more microhabitat types (enlarging total niche space) allowing the coexistence of competitors and persistence of predators and their prey (Crowley 1978; Crowder & Cooper 1982; Chick & Mcivor 1994). Consequently, prey density and diversity is positively correlated with structural complexity (Gerking 1957; Stein 1977; O'Connor 1991; Wright & Flecker 2004; Schneider & Winemiller 2008).

Technical textiles and artificial floating islands have been successfully applied in ecosystem management and environmental protection (e.g. restoration of Salford quay, England: pers.comm. Heather Webb APEM Ltd. and other projects: http://floatingislandinternational.com). Technical textiles have been installed (1) to relieve the sewage water system by roof top vegetation, (2) greening of facades in enhancing the residence time of rain water, (3) have been applied successfully as substrates for organisms used for waste water treatment (Mählmann et al. 2001), (4) are used for restoration of water bodies (e.g. as substrates for organisms for water treatment such as biological filters by means of mussels (Kusserow & Uhlmann 1998) and (5) as plant carriers for greening of open pit water bodies (Mählmann et al. 2002; Mählmann & Arnold 2002; Mählmann et al. 2004). Vegetation not only enhances structural diversity in water bodies but reduces the development of phytoplankton, thus, stabilizing water conditions (reducing dissolved nutrients, limiting re-suspension of fine sediments Scheffer 1999; Donabaum et al. 1999; Dokulil & Teubner 2003). Further, vegetated artificial floating islands have been applied successfully in the removal of pollutants such as nitrates, phosphates, ammonia and heavy metals from water bodies. They provide critical riparian edge habitat, comprising new land mass for use by all kinds of organisms as well as stabilising and protect embankments, sequester carbon dioxide and other greenhouse gases from the atmosphere and provide wave mitigation and erosion control (BioHaven® floating islands Tanner & Headley 2006; Steward 2007; Stewart et al. 2008; Tanner & Headley 2008. For further information and application of artificial islands visit http://www.floatingislandinternational.com, http://www.aldenlab.com). The roots of artificial floating islands grow down below the island matrix to create a very large surface area not only for nutrient uptake but also as additional habitat. Therefore, they may be an appropriate tool for restoration of gravel pit lakes by means of plant islands, as aquatic plants play an important role in structuring water bodies (Scheffer et al. 1993).

Artificial floating islands have been used throughout the world as a means of aggregating fish (Welcomme 2002; Nakamura & Mueller 2008). In India floating islands have existed for centuries. Formed through dense growth of aquatic weeds and grasses they are spread throughout lakes and used as natural fish aggregating devices (locally called 'Phums, Suresh 2009). Until now, no investigations exist that evaluated the functionality of the floating plant islands used in this study regarding the macrozoobenthos and fish community. Therefore, the objective was to examine if floatable textile plant carriers can be an adequate way to establish littoral elements, thus, minimising structural deficiencies of artificial gravel pit lakes and creating a near-natural alternative habitat especially for juvenile fish. We expected the rhizosphere to develop into a diverse habitat with differently structured roots within the first year. With increasing complexity of the root cavities we hypothesised first that the new habitat should increasingly be colonized by a rich macroinvertebrate fauna. An increased abundance of macrozoobenthos and the additional space provide shelter for the juvenile fish community. The strongly structured root cavities should lead to an increased utilisation of the plant islands by fish. Thus, our second hypothesis was that the abundance of juvenile fish in the area of the plant islands should increase above abundances at the natural shoreline of the gravel pit lake. Consequently, our study should allow a first estimation how far such planted islands may contribute to conventionally restored and improve not restored shore lines in the recultivation of gravel pit lakes that lack extended littoral areas.

Material & Methods

In June 2005, textile plant islands were installed at two gravel pit lakes in the Lower Rhine Region, North Rhine Westphalia, Germany: Lake Reeser Meer and Lake Ginderich. Both sites were strongly dominated by piscivorous fish. At Lake Reeser Meer catch consisted of 80% perch (*Perca fluviatilis*) and a smaller percentage of Cyprinids (12% *Alburnus alburnus*, 8% *Rutilus rutilus*) while pike (*Esox lucius*) and pikeperch (*Sander lucioperca*) were caught sporadically. Both lakes were quite similar except an increased turbidity at Lake Ginderich. Therefore, the results presented here are tied up only referring to Lake Reeser Meer and its most abundant fish species perch.

Study site

Lake Reeser Meer is owned and dredged by Niederrheinische Sand- und Kiesbaggerei (NKSB). The lake is recently dredged and in parts still dug today thus currently the area is about 1.18 km^2. In 2004 / 2005 the western lakeshore has been recultivated conventionally by means of gravel banks with sandy sections and vegetated areas (mainly willows) creating a narrow littoral zone of 1 - 2 m width and 0.2 -0.5 m depth. The bank has a steepness of 1:1 to 1:3. Mean water temperature during May to October in the littoral zone was 19 ± 2.9 °C between 2005 and 2007.

Textile plant islands

Floatable textile mats have been produced by the Sächsisches Textilforschungsinstitut (STFI) using a two needle bar warp knitting machine (type GWM1200, Jakob Müller Frick/CH) with extremely coarse knitting tools (gauge 72 mm). The knitted structure was manufactured by using PE film tapes (width 18 mm) in an open pillar stitch lapping. The ground yarns were reinforced by h*igh strength* polypropylene (PP) yarns of 220 tex. Only the loop forming threads at the left and the right selvedges of the knitted structure were reinforced by using a 3200 tex PP-yarn. Coated PE-foam-yarn with a diameter of about 25 mm to archive the required buoyant force was inserted as a weft insertion in every 3rd course using the front weft carrier of the described machine. The weft carrier in the back was used to insert the UV stabilized olive-green PE film (width 340 mm) to allow implementation of macrophytes.

The textile grid-like structure allows macrophytes to be implanted while the roots grow down into the water body. In 2005, regional plants, such as slender tufted-sedge (*Carex gracilis*), soft rush (*Juncus effusus)*, reed canary grass (*Phalaris arundinacea*), purple-loosestrife (*Lythrum salicaria*), water forget-me-not (*Myosotis palustris*), marsh marigold (Caltha palustris) and brooklime (*Veronica beccabunga*) were placed into the textile structure of the floating textile islands (10 – 12 plants per m^2) to provide various roots creating a diverse habitat below the textile mats. To protect the vegetation from extensive feeding due to geese and ducks, which are highly abundant in the Lower Rhine Region, a safety fence was added after planting the textile mats (Secugrid 60/60 Q6, Fa. Naue GmbH & Co KG, Adorf, Vogtland Germany). In spring 2006, the textile mats were restocked with kingcup, slender tufted-sedge, yellow iris, soft rush, purple-loosestrife, water forget-me-not and brooklime as a lot of the plants formerly implanted did not survive the winter.

Five plant islands of 24 m^2 each were fitted in line 20 - 30 m in distance parallel to the western shoreline. The water depth below the plant islands was 9 – 10 m in 2005/6. In 2007, the islands were moved towards the shore decreasing the distance to 5 – 10 m with 4 – 5 m water depth to the ground (Tab. 1). Vegetation density was estimated of area covered by plants per island (vegetation coverage [%]). Root coverage (%) below each island was determined through at least six randomly distributed square frames (area of 0.16 m^2) in which number of roots and density were assessed by scuba diving.

Zooplankton

Zooplankton was sampled via vertical haul (mesh size 250 µm, 25 cm diameter). The vertical haul was dropped to 1.5 m then slowly pulled up three times at each plant island and five times in the conventionally recultivated area (control). Samples were preserved in 96 % ethanol, counted and at least 15 individuals of each species were measured by use of a binocular. The abundant zooplankton organisms were grouped into categories.

Macrozoobenthos

To sample the macrozoobenthos community at the control area and underneath the floating plant mats a new method was established. In accordance to the suction sampler (Mörtl 2003) an underwater suction apparatus was developed (Fig. 1). A water pump creates low pressure in a filter box which continues through a flexible hose up to a water strainer (25 x 25 cm base dimension). The filter box contains a conical bag with a mesh size of 500µm and 1500 cm^2 internal surface. Macrozoobenthos is sucked into the filter box where it is collected in the conical bag by placing the water strainer either on the bottom of the mat or on the surface of the control area. Five samples were taken at the control site and underneath the textile mats within the roots during spring, summer and autumn. The apparatus was build to stay either on the shore or inside the boat so the diver only has to take the hose with the water strainer to the sampling site.

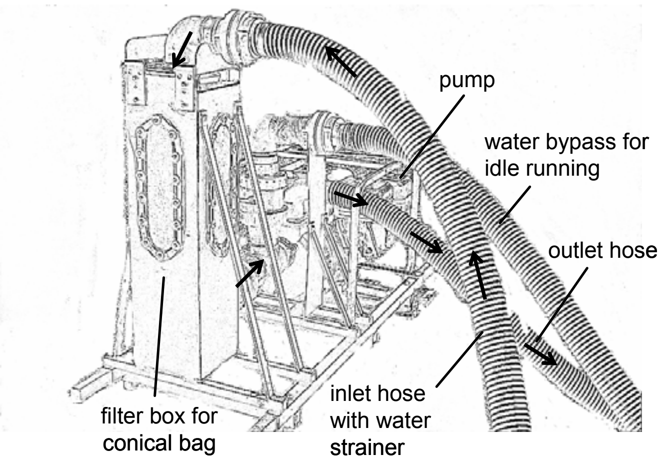

Figure 1: Macrozoobenthos sampler. The underwater suction aperatus aperatus stays on the shore or inside the boat. The diver only carries the hose with the water strainer. Macrozoobenthos is sucked into the filter box by the inlet water hose, collected in a conical bag and the water is then released through the outlet hose. A third hose keeps the pump running between samplings. Arrows indicate water flow.

All individuals were preserved in 80 % ethanol, counted and determined to species level if possible. In this study, we will focus on the main macrozoobenthos organisms that were detected in stomach content analyses. These were grouped into the following categories: mayfly larvae (Ephemeroptera), mysids (Mysidacea), amphipods, caddis fly larvae and dragon- and damselfly larvae (Trichoptera, Odonata). Amphipods were further divided into Gammaridae (mainly *Gammarus pulex* and *Gammarus roesili*) and a ponto-caspian invasive species belonging to the family of Corophiidae, *Chelicorophium curvispinum*. In addition, the abundance of the zebra mussel, *Dreissena polymorpha*, was analysed representing sessile, epilithic organisms (Borcherding & Sturm 2002).

Fish community

In 2005, five times from July until October and at least once a month from May to September in 2006 and 2007, four to five gill nets were exposed in the control area as well as on the sides of the islands facing the shoreline. The nets were set for five hours during midday (11:00 – 16:00) in 2005 and 2006. To analyse the occurrence of perch in the littoral area and the plant islands in the course of the day, gillnets were set for 10 hours during daytime (9:00 – 19:00) and for 14 hours at night (19:00 – 9:00) in 2007.

Fishes caught were preserved in 4 % formaldehyde solution. All were measured to the nearest 1 mm (total length) and, if available, at least 20 randomly chosen individuals of each catch (control and either floating plant mat) were weighed to the nearest 0.01 gram (wet mass) and used for stomach content analysis. Stomach contents were identified to species or genus for the important prey organisms and at least 15 randomly chosen prey of each category were measured to the nearest 0.01 mm, if available. Biomasses were calculated using length-weight regressions of Bottrell et al. (1976) and Mehner et al. (1995). In addition to stomach content analyses we calculated the index of stomach fullness (Hyslop 1980) expressed as ISF (%) = 100 (bprey / bmpred) with bprey = reconstructed biomass of prey in the stomach; bmpred = wet body mass of predator.

Data treatment and statistical analysis

To acquire comparability between gillnet catches, the nominal catches were converted in standardised catches (CPUE = catch per unit effort): CPUE = $(C_n \cdot A_s/A_n) / t$
with C_n = nominal catch, A_s = area of standard net [$219.3 m^2$], A_n = area of used net [m^2], t = fishing time [h]. Due to high standard variation the CPUE was log+1 transformed. Statistical analyses were performed to compare the occurrence of zooplankton, macrozoobenthos and young-of-the-year (YOY) perch using a general linear model (GLM), with place and year as between-subject factors and months as within-comparisons. (SPSS 16).

Results

In 2005, the vegetation covered in average 15 % of the plant island and the roots underneath developed a degree of cover of 21 % (Tab. 1). Both, vegetation on the plant islands as well as density of root structure further increased in 2006. In 2007, the vegetation coverage was reduced to a similar value found in 2005. Nevertheless, root density underneath the textile plant carriers further increased creating a diverse habitat.

Table 1: Basic parameters of the floating textile plant carriers at Lake Reeser Meer.

Year	Shore distance [m]	Water depth [m]	Vegetation coverage [%]	Root coverage [%]
2005	20 - 30	9	15	21
2006	25 - 35	9 - 10	35	35
2007	5 - 10	5	16	40

Zooplankton and macrozoobenthos

Zooplankton consisted mainly of daphnids and copepods. Although seasonal changes in the zooplankton diversity and abundance occurred, no significant differences could be found between the conventionally recultivated littoral area and textile plant islands (neither for time nor interaction of time and place).

Main categories of macrozoobenthos were mayfly larvae (Ephemeroptera), mysids (Mysidacea), caddis fly larvae (Trichoptera), dragon- and damselfly larvae (Odonata), Gammaridae (mainly *Gammarus pulex* and *Gammarus roesili*) and *Chelicorophium curvispinum*. We found significant differences between abundance of most categories at the conventionally recultivated shoreline and underneath the vegetated islands within the root cavities. The abundance of mayfly larvae, as well as mysids (mainly *Limnomysis benedenii*), were much lower at plant islands than at control sites (Ephemeroptera: ANOVA df = 1, F = 13.924, p = 0.002; Mysidacea: ANOVA n.s.; Fig. 2b, c). Although the overall results for mysids were not significant due to high standard variation, the interaction term of place and year revealed the significantly higher abundance of mysids at the natural littoral area (ANOVA df =1, F = 4.01, p = 0.06). In contrast, Amphipods (Gammaridae, *C. curvispinum*), caddis fly larvae (Trichoptera) and dragon- and damselfly larvae (Odonata) were less abundant in the littoral area (*C. curvispinum*: ANOVA df = 1, F = 20.284, p < 0.0001; Trichoptera: ANOVA df = 1, F = 7.397, p = 0.015; Odonata: ANOVA df = 1, F = 51.486, p < 0.0001). Abundances of *C. curvispinum*, caddis fly larvae and dragonfly/ damselfly larvae did not only differ between littoral area and plant islands. Analyses show that abundances at the plant islands vary significantly over the years (*C. curvispinum* ANOVA df = 2, F = 8.788, p = 0.001; trichoptera: ANOVA df = 2, F = 5.274, p = 0.01; odonata: ANOVA df = 2, F = 3.860, p = 0.032; Fig 2d, f, e, g). Pair-wise comparison revealed that abundance of caddis fly larvae, *C. curvispinum* and dragonfly/damselfly larvae strongly increased from 2006 to 2007 (Trichoptera p = 0.018, *C. curvispinum* p = 0.002, Odonata p = 0.036). The same trend occurred for Gammaridae, but as the abundance already showed a strong increase from 2005 to 2006 and as standard variation was high, this was not significant.

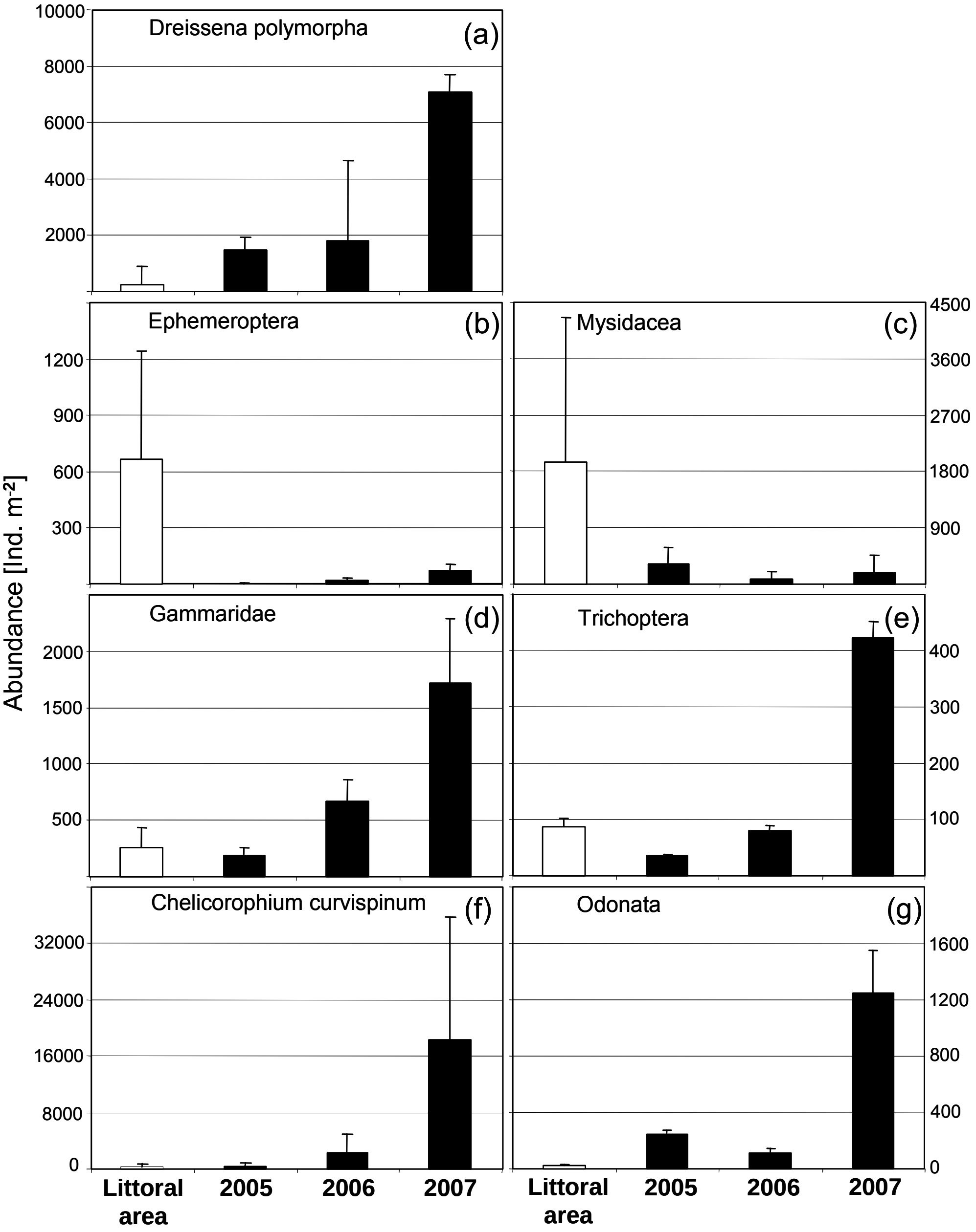

Figure 2: Main macrozoobenthos groups found on control areas at the conventionally recultivated littoral area (white, mean of 2005 and 2006) and associated with rooted plant islands (black) from 2005 till 2007. Note the differences of scaling between groups.

Fish community

The abundance of perch caught differed significantly between years (ANOVA: df = 2, F = 20.609, $p < 0.001$). In 2005, most perch were caught with an average CPUE of 56 ± 12 individuals. Catches were profoundly reduced in 2006 but increased again in 2007 (from approximately 20 ± 8 to 31 ± 10). Over all years, there were no significant differences between littoral areas and plant islands. However, differences between the littoral area and plant islands within each year differed significantly (Fig. 3; ANOVA (interaction place x year): df = 2, F = 5.667, $p < 0.004$).In 2005, significantly more perch were caught at the plant islands, whereas in 2006 nearly all individuals were caught only in the littoral area. In 2007, the overall catch in the littoral area and plant islands was more or less equal. The statistical analysis revealed differences of the perches' usage of both sites, expressed by the significant interaction term of daytime and place (Fig. 4; ANOVA: df = 1, F = 7.617, p = 0.006). Compared to the

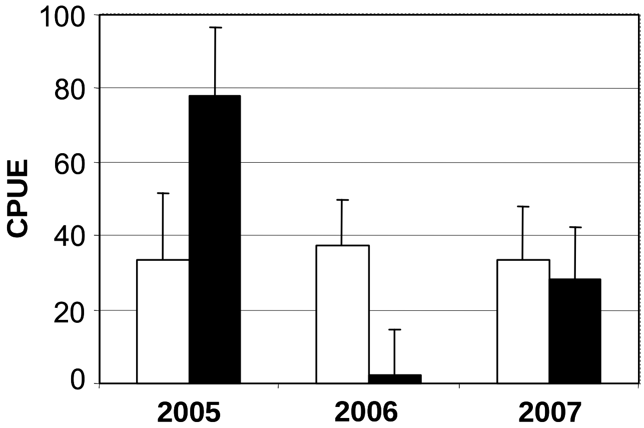

Figure 3: Mean catch-per-unit-effort (CPUE) for YOY perch from 2005 till 2007 separated into control sites (littoral area = white) and plant islands (black).

littoral area, only half the amount of perch was caught at the plant islands at night, while during daytime abundance of perch was significantly higher there than in the littoral area.

Stomach content analyses of perch revealed no differences between plant islands and catches from the commonly recultivated littoral area, both in 2005 and 2006. At least 80% of the content consisted of zooplankton biomass, mainly daphnids and copepods. In contrast, differences in stomach content of perch between littoral areas and plant islands were found in 2007. Perch used less zooplankton and mainly fed on macrozoobenthos, such as amphipods and mysids at the plant islands from June till August (Fig. 5). This difference was also observed at night but less pronounced.

Generally perch consumed more amphipods than mysids, but the amount of mysids eaten during the day was lower than at night. The index of stomach fullness (ISF) was not significantly different between the littoral area and root cavities at the plant islands, but slightly increased during the day compared with values for the night samples (ANOVA: df = 1 F = 9.155, p = 0.004). In general, the SFI decreased from June till September at both sites.

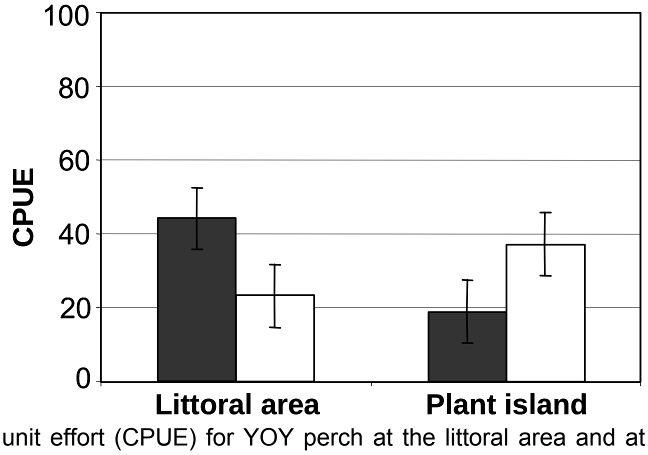

Figure 4: Mean catch per unit effort (CPUE) for YOY perch at the littoral area and at the plant islands at night (grey) and during the day (white) in 2007.

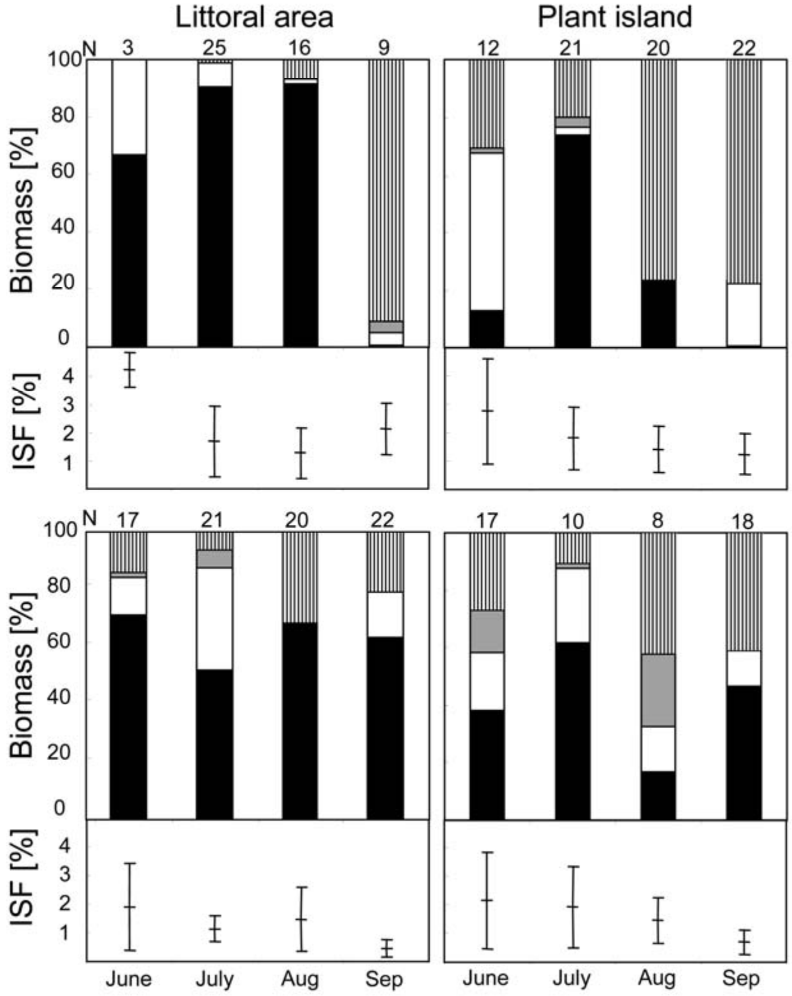

Figure 5: Main groups found in the stomach content analyses (% biomass, bars) and index of stomach fullness (% ± SD, horizontal lines and whiskers) of YOY perch from June until September in 2007 during daytime (above) and at night (below). Black: plankton; white: mysids; grey: macrozoobenthos with main abundance in the littoral area and vertical lines: macrozoobenthos with main abundance at the plant islands. N = number of perch analysed.

Discussion

The rhizosphere below the plant islands was hypothesised to provide living space for a rich invertebrate fauna that might be used as an additional food resource by the fish community. From 2005 till 2007, the root cavities developed into a diverse and complex habitat with overall increased macrozoobenthos abundance, especially when the islands were near the shoreline being connected to natural stocks of macrophytes in the littoral zone. A selective effect was observed for most macrozoobenthos groups, driven either by (1) substrate-bound macrozoobenthos preferring the natural littoral, (2) the advantage of mobile species that are capable of quickly habituating new niches (e.g. invasive species like *Dikerogammarus villosus*, *Chelicorophium curvispinum*, *Dreissena polymorpha*, Ricciardi & Rasmussen 1998; Ricciardi 2003) or (3) the favouring of native species like juvenile damselfly larvae. This led to changes of dominant species and lower biodiversity at the plant islands. Nevertheless, the locally increased abundance of the invertebrate fauna at the plant islands, which coincided with our first hypothesis, resulted in increased food resources for the fish community.

In 2005, significantly more perch were caught at the plant islands indicating that perch preferred the plant islands to the littoral areas during summer, according to our second hypothesis. Conventional restoration by means of gravel banks with sandy sections and vegetated areas of the western lakeshore were finished at the end of 2004/beginning of 2005. The plant islands were installed in June 2005. YOY perch in that area of the lake probably searched for any structures available for refuge, as they also took shelter below landings, boats and pontoons (personal observation; Fausch 1993 usage of overhead cover, Helfman 1981 utilisation of shade). Also, especially juvenile fish are known to associate with floating objects not necessarily consisting of vegetation and being of anthropogenic origin (Riera et al. 1999; Castro et al. 1999; Welcomme 2002). In 2005, growth of roots underneath the plant islands and their colonization with macrozoobenthos had just started but were not well established. In contrast to 2005, preference of the underside of the plant islands by the juvenile fish did not continue in 2006. The fish even seemed to avoid the plant islands and were much more abundant at the shore. As the main reasons for this unexpected result we assume: (1) The newly established vegetation on the conventionally restored banks and especially (2) a distinctly increased water level that resulted in the availability of vast shallow zones of the shoreline. Here flooded terrestrial macrophytes offered areas of high structural diversity. This increase in water level also resulted in a greater distance of the plant islands from the shoreline. Subsequently the connection of natural habitat and the islands' root cavities was further decreased. Large schools of YOY fish were observed in this newly flooded areas (personal observation, not quantified), probably using the shallowness to be more secure from predators. Later in the year 2006, perch used the natural habitat near the shore, where extensive stocks of macrophytes (mainly stonewort *Chara contraria*, western waterweed *Elodea nuttallii*, pondweed *Potamogeton spp.*, fan-leaved water-crowfoot *Ranunculus circinatus*) had developed in water depth from 1 - 2 m downwards (personal observation, not further quantified). To reach the islands' root cavities and use this refuge area more extensively, juveniles would have had to leave the vegetation, exposing them to predators in the pelagic area (Bean & Winfield 1995; Jacobsen & Perrow 1998).

The loss of connectivity between vegetated banks and the plant islands was assumed to be the essential factor for the usage of the rhizosphere by juvenile fish that encouraged us to reposition the plant islands in 2007. Shore distance was reduced from more than 20 m in 2006 to 5-10 m, bisecting water depth below the plant islands. The submerged vegetation of the banks was then positioned almost directly below the plant islands, restoring connectivity between shoreline and the islands' below side. Although the overall perch abundance at the plant islands increased in 2007 compared to lowest values of 2006, it did not reach the level of 2005 and also did not exceeded abundances in the littoral area. However, during the day significantly more perch used the plant islands while during night more perch were caught in the littoral area. Jacobsen & Berg (1998) outlined that piscivorous predators affected habitat use by YOY perch in the morning, midday and evening, but not at night, probably depending on the diel hunting activity of visually oriented predators like perch and pike (Jacobsen et al. 2002; Skov et al. 2007). The diel usage of the habitats is also reflected in the usage of the food resources, as perch that were caught at the plant islands during daytime also increased their feeding on macrozoobenthos species with high abundances at the plant islands (e.g. Amphipoda, Okun & Mehner 2005). In contrast, during the night no clear differences in food selection between perch from both habitats existed and a more diverse food usage was found. Thus, the root cavities of the plant islands not only provided shelter against predators, but also offered food resources that were used by the YOY perch during the day.

CONCLUSION

The results of our study give some evidence that the textile plant islands are suitable as a new tool of restoration only to a limited extent when the main focus is on the fish community. Although other studies have shown artificial floating islands to improve “wildlife habitat” for a range of animals not only including fish but also birds (Hancock 2000; Steward 2007), the results in our study were not as indicative. If the textile plant islands are densely vegetated and connectivity between shoreline and the islands' root cavities is provided (i.e. low distance to the shoreline or low water level below the islands), they can enhance structural heterogeneity and food supply for juvenile fish in gravel pit lakes. We have shown that textile plant islands contribute to the recruitment of YOY fish by offering an increased abundance of macrozoobenthos, which can improve the fishes' diet, and providing additional shelter from predatory specimen, as structural complexity of the habitat often reduces predatory efficiency by reducing prey capture rates (Crowder & Cooper 1982).

However, investigations at another gravel pit lake at the Lower Rhine, the Diersforter Waldsee (Beeck & Borcherding 2001; Beeck & Scharbert 2005; Heermann et al. 2008 unpublished reports) revealed that at well restored shallow littoral zones with complex structured banks up to 60 times as many juvenile fish may be found than at not restored shorelines or simple gravel banks. Therefore, the textile plant islands should never replace restoration of natural banks creating complex structured littoral zones with shallow water areas to meet the needs of a variety of fishes (Copp 1997, DGL1995, p.89).

But by all means they can be a good measure to further improve the natural habitat as they can help improve water quality (Tanner & Headley 2006; Tanner & Headley 2008), enhance the habitat for a range of species such as birds as well as fish (Steward 2007), and can be used for bank stabilisation and erosion control. At sites with large water level fluctuations such as reservoirs, dams and lakes that are strongly influenced by flooding, they may provide stable vegetation and help to initiate habitat regeneration when the plant islands' vegetation is dense and permanently established. Artificial floating islands can also be applied to improve old insufficiently restored water bodies, in fish farming and aquaculture to improve artificial ponds structurally.

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References

Amoros, C. & Bornette, G. (2002). Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* **47,** 761-776.

Bean, C. W. & Winfield, I. J. (1995). Habitat use and activity patterns of roach (*Rutilus rutilus* (L.)), rudd (*Scardinius erythrophthalmus (*L.)), perch (*Perca fluviatilis* (L.)) and pike (*Esox lucius* (L.)) in laboratory: the role of predation threat and structural complexity. *Ecology of Freshwater Fish* **4,** 37-46.

Beeck, P. & Borcherding, J. (2001). Untersuchung zum Fischbestand des Diersforter Waldsees unter besonderer Berücksichtigung der rekultivierten Bereiche. Nörvenich.

Beeck, P. & Scharbert, A. (2005). Fischereiliche Untersuchung der Nassabgrabung Diersforter Waldsee und Brüggenhofsee unter besonderer Berücksichtigung der Rekultivierungsmaßnahme. Nörvenich, unpublished.

Berndt, J. (1991). Ökologische Aspekte bei der Gestaltung und Nutzung von Baggerseen in der Aue. *Natur und Landschaft* **66,** 160-163.

Borcherding, J. & Sturm, W. (2002). The seasonal succession of macroinvertebrates, in particular the zebra mussel (Dreissena polymorpha), in the River Rhine and two neighbouring gravel-pit lakes monitored using artificial substrates. *International Review of Hydrobiology* **87,** 165-181.

Bottrell, H. H., Duncan, A., Gliwicz, Z. M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. & Weglenska, T. (1976). A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* **24,** 419-456.

Burks, R. L., Lodge, D. M., Jeppesen, E. & Lauridsen, T. L. (2002). Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater Biology* **47,** 343-365.

Castro, J. J., Santiago, J. A. & Hernández-Garciá, V. (1999). Fish associated with fish aggregation devices off the Canary Islands (Central-East Atlantic). *SCIENTIA MARINA* **63,** 191-198.

Chick, J. H. & Mcivor, C. C. (1994). Patterns in the Abundance and Composition of Fishes Among Beds of Different Macrophytes - Viewing A Littoral-Zone As A Landscape. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 2873-2882.

Copp, G. H. (1990). Effect of regulation on 0+ fish recruitment in the Great Ouse, a lowland river. *Regulated rivers: Research & Management* **5,** 251-263.

Copp, G. H. (1997). Microhabitat use of fish larvae and 0+ juveniles in a highly regulated section of the river Great Ouse. *Regulated rivers: Research & Management* **13,** 267-276.

Crowder, L. B. & Cooper, W. E. (1982). Habitat Structural Complexity and the Interaction Between Bluegills and Their Prey. *Ecology* **63,** 1802-1813.

Crowley, P. H. (1978). Effective Size and Persistence of Ecosystems. *Oecologia* **35,** 185-195.

DGL (1995). Untersuchung, Überwachung und Bewertung von Baggerseen. Empfehlungen und Entscheidungshilfen der Deutschen Gesellschaft für Limnologie e.V. für Planung, Naturschutz und Gewässergüte (Examination, Inspection and Evaluation of Gravel Pit Lakes; Recommendations and decision support of the German Society of Limnology e.V.(DGL) concerning planning, nature conservation and water qaulity). Eigenverlag der DGL, Krefeld 1998.

Diehl, S. (1993). Effects of habitat structure on resource availability, diet and growth of benthivorous perch, perca-fluviatilis. *Oikos* **67,** 403-414.

Dokulil, M. T. & Teubner, K. (2003). Eutrophication and restoration of shallow lakes - the concept of stable equilibria revisited. *Hydrobiologia* **506,** 29-35.

Donabaum, K., Schagerl, M. & Dokulil, M. T. (1999). Integrated management to restore macrophyte domination. *Hydrobiologia* **396,** 87-97.

Fausch, K. D. (1993). Experimental-Analysis of Microhabitat Selection by Juvenile Steelhead (Oncorhynchus-Mykiss) and Coho Salmon (Oncorhyncus-Kisutch) in A British-Columbia Stream. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 1198-1207.

Gerking, S. D. (1957). A Method of Sampling the Littoral Macrofauna and Its Application. *Ecology* **38,** 219-226.

Hancock, M. (2000). Artificial floating islands for nesting Black-throated Divers Gavia arctica in Scotland: construction, use and effect on breeding success. *Bird Study* **47,** 165-175.

Hargeby, A., Andersson, G., Blindow, I. & Johansson, S. (1994). Trophic web structure in a shallow eutrophic lake during a dominance shift from phytoplankton to submerged macrophytes. *Hydrobiologia* **280,** 83-90.

Heermann, L., König, U. & Borcherding, J. (2008). Fischereiliche Untersuchung des Diersforter Waldsee und des Brüggenhofsee unter Berücksichtigung der Rekultivierungsmaßnahme. unpublished.

Helfman, G. S. (1981). The Advantage to Fishes of Hovering in Shade. *Copeia* 392-400.

Hyslop, E. J. (1980). Stomach content analysis - a review of methods and their application. *Journal of Fish Biology* **17,** 411-429.

Jacobsen, L. & Berg, S. (1998). Diel variation in habitat use by planktivores in field enclosure experiments: the effect of submerged macrophytes and predation. *Journal of Fish Biology* **53,** 1207-1219.

Jacobsen, L., Berg, S., Broberg, M., Jepsen, N. & Skov, C. (2002). Activity and food choice of piscivorous perch (Perca fluviatilis) in a eutrophic shallow lake: a radio-telemetry study. *Freshwater Biology* **47,** 2370-2379.

Jacobsen, L. & Perrow, M. R. (1998). Predation risk from piscivorous fish influencing the diel use of macrophytes by planktivorous fish in experimental ponds. *Ecology of Freshwater Fish* **7,** 78-86.

Kusserow, R. & Uhlmann, D. (1998). Technology of a Dreissena-Filter to remove Suspended Matter from the Effluents of Waste Water Treatment Plants. Proceedings Eighth International Zebra Mussel and Aquatic Nuisance Species Conference , 229-240.

Lauridsen, T. L. & Buenk, I. (1996). Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. *Archiv fur Hydrobiologie* **137,** 161-176.

LAWA (1998). *Gewässerbewertung - stehende Gewässer: Vorläufige Richtlinie für eine Erstbewertung von natürlich entstandenen Seen nach trophischen Kriterien.* Kulturbuch-Verlag, Berlin.

Mählmann, J. & Arnold, R. (2002). Schwimmende Pflanzeninseln. *grünForum LA* **10,** 29-30.

Mählmann, J., Arnold, R. & Fuchs, H. (2002). Technische Textilien für den Einsatz in der angewandten Limnologie. Tagungsband der Deutschen Gesellschaft für Limnologie (DGL) .

Mählmann, J., Arnold, R. & Fuchs, H. (2004). Schwimmende textile Pflanzeninseln zur Biotopneubildung - Teil 1: Konstruktion und Handhabung. *grünForum.LA* **1,** 35-37.

Mählmann, J., Zscheile, H., Arnold, R. & Bartl, A.-M. (2001). Textile structures with very large surfaces for wastewater treatment. *Technical Textiles* **44,** 138.

Mehner, T., Schultz, H. & Herbst, R. (1995). Interaction of zooplankton dynamics and diet of 0+ perch (*Perca fluviatilis* L.) in the top-down manipulated Bautzen reservoir (Saxony, Germany) during summer. *Limnologica* **25,** 1-9.

Mörtl, M. (2003). Biotic interactions in the infralittoral of Lake Constance.

Nakamura, K. & Mueller, G. (2008). Review of the performance of the artificial floating island as a restoration tool for aquatic environments. World Environmental and Water Resources Congress Ahupua'a.

Neumann, D., Staas, S., Molls, F., Seidenberg-Busse, C., Petermeier, A. & Rutschke, J. (1996). The significance of man-made lentic waters for the ecology of the Lower River Rhine, especially for the recruitment of potamal fish. *Archiv für Hydrobiologie Supplementband* **113,** 267-278.

O'Connor, N. A. (1991). The effect of habitat compexity on the macroinvertebrates coclnising wood substrates in a lowland stream. *Oecologia* **85,** 504-512.

Okun, N. & Mehner, T. (2005). Distribution and feeding of juvenile fish on invertebrates in littoral reed (Phragmites) stands. *Ecology of Freshwater Fish* **14,** 139-149.

Ricciardi, A. (2003). Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. *Freshwater Biology* **48,** 972-981.

Ricciardi, A. & Rasmussen, J. B. (1998). Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 1759-1765.

Riera, F., Grau, A., Grau, A. M., Pastor, E., Quetglas, A. & Pou, S. (1999). Ichthyofauna associated with drifting floating objectsin the Balearic Islands (western Mediterranean)*. *SCIENTIA MARINA* **63 ,** 229-235.

Savino, J. F. & Stein, R. A. (1989). Behavior of Fish Predators and Their Prey - Habitat Choice Between Open Water and Dense Vegetation. *Environmental Biology of Fishes* **24,** 287-293.

Scharbert, A. & Greven, H. (2002). Umgestaltete Abgrabungsseen: Auengewässer der Zukunft? Reconstructed gravel pit lakes: floodplain lakes of the future? *Verh.Ges.Ichthyol.* **3,** 131-187.

Scheffer, M. (1999). The effect of aquatic vegetation on turbidity; how important are the filter feeders? *Hydrobiologia* **408/409,** 307-316.

Scheffer, M., Hosper, S. H., Meijer, M.-L., Moss, B. & Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* **8,** 275-279.

Schneider, K. N. & Winemiller, K. O. (2008). Structural complexity of woody debris patches influences fish and macroinvertebrate species richness in a temperate floodplain-river system. *Hydrobiologia* **610,** 235-244.

Skov, C., Nilsson, P. A., Jacobsen, L. & Brönmark, C. (2007). Habitat-choice interactions between pike predators and perch prey depend on water transparency. *Journal of Fish Biology* **70,** 298-302.

Stein, R. A. (1977). Selective Predation, Optimal Foraging, and Predator-Prey Interaction Between Fish and Crayfish. *Ecology* **58,** 1237-1253.

Steward, F. (2007). Biomimetic floating islands that maximize plant and microbial synergistic relationships to revitalize degraded fisheries, wildlife habitats, and human water resources. . Final Report to Montana Board of Research and Commercialization Technology (MBRCT).

Stewart, F. M., Mulholland, T., Cunningham, A. B., Kania, B. G. & Osterlund, M. T. (2008). Floating islands as an alternative to constructed wetlands for treatment of excess nutrients from agricultural and municipal wastes-results of laboratory-scale tests. *Land Contamination & Reclamation* **16,** 25-33.

Suresh, V. R. (2009). Floating Islands: a Unique Fish Aggregating Method. *NAGA* **23,** 11-13.

Tanner, C. C. & Headley, T. (2006). Application of Floating Wetlands for Enhanced Stormwater Treatment: A Review. 324. Auckland Regional Council. National Institute of Water and Atmospheric research (NIWA) Client Report: HAM2006-123.

Tanner, C. C. & Headley, T. (2008). Floating treatment wetlands - an innovative solution to enhance removal of fine particulates, copper and zinc. *NZWWA - water & wastes in New Zealand*.

Thorpe, J. E. (1977). Synopsis of biological data on perch, *Perca fluviatilis* Linnaeus, 1758, and *Perca flavescens* Mitchill, 1814. *FAO Fisheries Synopsis* **113,** 1-138.

Ward, J. V. (1998). Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* **83,** 269-278.

Welcomme, R. L. (2002). An evaluation of tropical brush and vegetation park fisheries. *Fisheries Management and Ecology* **9,** 175-188.

Wright, J. P. & Flecker, A. S. (2004). Deforesting the riverscape: the effects of wood on fish diversity in a Venezuelan piedmont stream. *Biological Conservation* **120,** 439-447.

Zeug, S. C. & Winemiller, K. O. (2008). Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. *River Research and Applications* **24,** 90-102.

CHAPTER II

Size dependent foraging-predation risk trade-off in young-of-the-year perch

U. König[1], P. Fischer[2], P. Klahold[3] and J. Borcherding[1]

1. University of Cologne, Zoological Institute, General Ecology and Limnology, Research Station Grietherbusch, 46459 Rees-Grietherbusch, Germany
2. Alfred Wegener Institute, Kurpromenade, D-27498 Helgoland (Building A-213)
3. Limnological Institute, University of Konstanz, Universitaetsstr. 10, D-78457 Konstanz, Germany

Abstract

With respect to the trade-off between food and shelter under the threat of predation, previously performed short-term laboratory experiments resulted in different behaviour of two size classes of young-of-the-year (YOY) perch *Perca fluviatilis*. Using a passive integrated transponder system, we studied individual variation of behaviour of these two size classes of YOY perch in mesocosm experiments, where the fish were able to increase their potential food intake by entering a compartment in which small cyprinids were provided as prey fishes, but where also a predator (pike) was present. When no prey fish but only the predator was in the food compartment, the residence time of both size classes of perch was significantly reduced in this compartment. When prey fish were present, the large YOY perch significantly increased the activity level in the test tank while the small size class perch did not. Furthermore, activity periods of small perch shifted to daylight under the threat of predation while large perch were more active during the twilight periods. These results provide evidence that small and large size YOY perch differ in behaviour under the threat of predation when prey fish are available, they thus adjusted the trade-off between foraging and predator avoidance in dependence to size.

Introduction

Most organisms undergo tremendous changes in size over their ontogeny and high growth rates in early life stages have been suggested to increase individual survival (Wilbur 1988; Post et al. 1999). Variation in growth is closely connected to individual responses to habitat specific resource levels and predation risk (Byström et al. 2004). Individuals may reduce activity levels or increase their use of less risky habitats to reduce predation risk (Werner et al. 1983; Werner & Gilliam 1984; Persson & Eklöv 1995). If the uptake of food resources in a specific habitat is linked to a certain habitat-specific predation risk, a trade-off exists between foraging and predator avoidance that may severely affect behaviour and activity levels. This choice depends on individual body size as the capacity to capture and to process larger food organisms increases with size (Persson et al. 1998; Persson et al. 2004), while predation risk is known to be a decreasing function of body size (Werner & Gilliam 1984; Persson et al. 2004). When size-dependent components are further enhanced by learning processes and experience (Kelley et al. 2003; Laland et al. 2003; Kelley & Magurran 2003), small-scale size differences between individuals may have pronounced effects on this trade-off situation.

In fish, successful foraging on large and energetically valuable organism is gape size limited (Hartmann 1983). If fish are vulnerable to predation due to their size, a trade-off between foraging and predator avoidance can be expected. Such size-dependent influences on the trade-off between feeding and hiding was shown by Magnhagen & Borcherding (2008) for two populations of perch (*Perca fluviatilis*). The degree of boldness to forage for food in the presence of a predator changed between the YOY and the 1+ age class in response to the experience of recent predation risk, thus on a longer time scale (Magnhagen & Borcherding 2008) . However, changes in degree of boldness of behaviour can be altered also within one size class.

Most studies have so far focused on different age classes when examining the influence of body size on foraging behaviour in the trade-off to predator avoidance. As described by Beeck et al. (2002), the young-of-the-year (YOY) perch can split into a bimodal size distribution, with the small size perch being mainly zooplanktivorous while the larger perch fed to a certain amount on prey fish. The larger size cohort is still vulnerable to predation (Lundvall et al. 1999) and can be nearly exclusively the prey of older perch (Beeck 2003; Persson et al. 2003). In short-term laboratory experiments, Borcherding (2006) demonstrated that the two size classes of YOY perch behaved differently regarding the trade-off between food and shelter under the threat of predation. The larger size class increased the utilisation of the open water area when prey fish were available there more than did the smaller size class.

Based on these findings, we studied the presence of a predator and availability of prey fish for two size classes of YOY perch in mesocosm experiments. In contrast to the above described short-term laboratory experiments (Borcherding 2006), the YOY perch here had much more time to adapt to the conditions and to gain experience on the experimental factors. Instead of shelter formed by submerse vegetation, the mesocosms were separated in three compartments, with two of them excluding the predator. Thus, the behavioural adaptations as well as changes in activity level of the two size classes of YOY perch should depend only on the effects of the two factorial components of this trade-off situation, the presence and absence of the predator and availability of small fish offered as food. We hypothesised (1) that perch independent of size reduce residence time in the presence of a predator, and (2) that large perch will show different behaviour compared to the smaller members of the YOY cohort when prey fish are offered.

Material & Methods

Two size classes of young of the year perch, (total length: 64.8 mm ± 3.5 SD and 93.8 mm ± 6.0 SD) were collected by beach seining mainly for the smaller individuals and by electro fishing to obtain larger conspecifics during the first week of August 2005 at the lower Rhine. They were held in aquaria (18°C) under natural light regime (14h light : 10h dark) at the Ecological Research Station in Rees-Grietherbusch. We marked 100 individuals of each size class with passive integrated transponders (PIT-tags, TROVAN®, 12 * 2 mm, glass encapsulated). Tagging was conducted as recommended by Prentice et al. (1990). The perch were not fed for 48 hs prior to the tagging and then were anesthetized with chlorobutanol (1,1,1-trichloro-2-methyl-2-propanol.). The tag was injected into the body cavity by a standard PIT-tagging syringe with a 12-gauage hypodermic needle. Each tag and needle were sterilised with 96% alcohol and thoroughly dried prior to injection. Injection was performed at a low angle just above the anal fin. Then penetration depth of the injection needle was manually adjusted to a minimum so that the tag was implanted just beneath the body wall. The puncture wound almost immediately closed when the needle was removed and was additionally treated with tissue glue to keep external trauma as low as possible. All animals were tagged at least three weeks prior to the experiments to make sure the wounds were fully healed and that no tagging-induced changes in behaviour occurred (Prentice et al. 1990; Fischer et al. 2001). Perch were fed zooplankton collected at a local gravel pit lake (mainly *Daphnia spp*. and *Chaoborus spp*.) and then continually trained to feed on frozen red chironomid larvae. In the beginning of September they were transported to the Limnological Institute of the University of Constance where we conducted the experiments. Perch were not specially trained to feed on bream larvae but were tested to feed on collected bream before the experimental period commenced.

Young of the year bream were caught from an artificial pond where they had been hatched for other studies. They were caught by beach seine and held in aquaria with 12:12 light cycle one week prior to the experiments. Bream were fed frozen chironomids once a day prior to the experiments but not during the experimental period.

Experimental Design

We carried out a total of four experiments (two experiments with small and two with large YOY perch) from 7 September 2005 to 5 October 2005. Each experiment lasted for 12 days with a pause of five to six days between the experiments. Each experiment we divided into four subsequent experimental periods: only perch, perch with predator, perch with predator and prey fish, again perch with predator. The second experiment started after the first period of experiment one was finished, the third after the first period of the second experiment was finished and the last experiment started after the first period of the third experiment. This time schedule allowed us to use the same predator for all experiments to avoid a bias due to different motivation of two predators to prey upon perch.

All experiments were carried out in two mesocosms (5 * 1 m base dimension, water depth 0.9 m). Both mesocosms were equally divided in three compartments by net dividers. In each divider we installed two passing tunnels (diameter 65 mm, Fig.1) both equipped with circular PIT-antennas to detect the time and direction of movements of the fish between the compartments continuously.

Hereby, the exact time each individual perch spent in either three compartments was calculated. The PIT system has previously been applied successfully in various behavioural studies, making detailed studies on diel activity and behavioural patterns possible (Brännäs et al. 1994; Burns et al. 1997; Lucas et al. 1999; Gibbons & Andrews 2004). The system was run as flow through system with a water inlet in the central compartment and one water outlet at the end of each lateral mesocosm. For all experiments filtered (300 µm filter size) lake water was pumped directly into the mesocosms. Data loggers were placed in the lateral compartments to monitor the water temperature continuously. Water temperature was 13.6 ± 1.5°C in mesocosm 1 and 14.1 ± 1.4°C in mesocosm 2 during the experimental time. To reduce habitat-specific effects on the recorded behaviour, we provided no structures in any of the three compartments. As the mesocosms were situated outside, the light regime naturally varied between 13 h light during the beginning and gradually declined towards 11.5 h at the end of the experiments.

To set-up the experiment, we randomly selected 25 perch (first large than small) from a pool of 100 fish each. All selected fish were measured (total length), their PIT-ID was identified with a portable detector and they were introduced into the central compartment of a mesocosm.

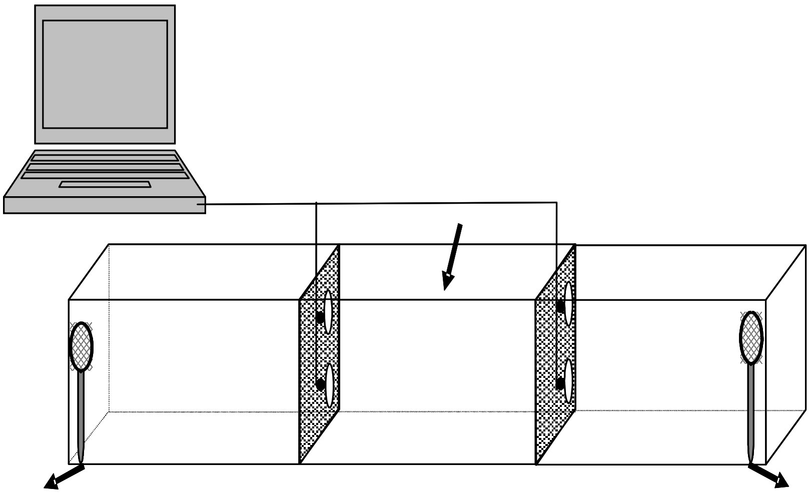

Figure 1: Experimental set-up of the mesocosms separated into three compartments by nets with two passing tunnels each: Arrows = water inlet and outlets; black circles = PIT antennas connected to the computer unit.

To get a definite start value on perch distribution in the mesocosm and also as a control for the PIT-registration system, the passing tunnels among the three compartments were closed between 1200 hours and 1230 hours and we counted the fish in each compartment. This procedure was repeated every day during the experiment and fish were fed during this time with red chironomid larvae (1 % of the fishes' weight, depending on number of fish for each compartment) to maintain an identical nourishment and level of appetite throughout the duration of the experiment.

After the introduction, perch were acclimated to the mesocosm for 24h to learn to change through the passing tunnels. At day two the experiment started and all movements of the perch were registered over the dial cycle: this phase is subsequently referred to as the first experimental period. At day six, we introduced the pike to the central compartment. The pike had a total length of 350 mm and could therefore not pass the tunnels. However, the size was certainly large enough to prey on both size classes of perch used in the experiment (e.g. Magnhagen & Heibo 2001). This phase (regarded as the second experimental period) lasted for another two days. At day eight of the experiment, we started the third experimental period by additionally introducing YOY prey fish (bream, *Abramis brama,* total length: 24.4 mm ± 2.3 SD, thus available as prey for both size classes of perch, Persson et al. 2004 and also tested prior to the experiments) to the central compartment. To prevent predation on the prey fish by the pike but nevertheless to provide an olfactory and visible attractor for the perch, the prey fish were placed in a perspex tube (diameter 25 cm, length 60 cm) with the bottom and top closed by gauze net (mesh size 250 µm). Young of the year bream were not stressed in the perspex tube when no perch was present. However, they showed predator avoidance when perch were in close proximity to the perspex tube. This phase also lasted for another two days. At day 10 of the experiment, we removed the bream larvae from the central compartment and only the predator and the perch remained in the mesocosms for another two days (experimental period four). The experiment was terminated on the 12th day in the morning by removing and counting all remaining perch and the predator from the mesocosms. We then drained, cleaned, refilled the mesocosms and started the next experiment the following day. Each perch were examined only once and the perch not used in the experiments as well as the bream and the pike were released right after the experiments at their original sites. Perch used in this study were preserved for further analyses (morphometric analyses) not shown in this present study.

Analyses

The date and the time of all compartment changes of all fish were automatically logged together with the respective PIT-tunnel number. Based on these data, we could determine in which compartment each fish stayed at any time during the experiment as well as the transition frequency among the three compartments of one mesocosm.

Basic data processing (calculating the whereabouts of each fish in the mesocosms over 24 hours) we carried out by means of the SAS System for Windows V8 (SAS/IML, 1985; SAS/STAT, 1988). We calculated residence time of each of the 25 fish in any of the three compartments as percentage of the duration of the four phases of the day (dawn, day, dusk and night), which were calculated using the astronomical calendar (*http://www.calsky.com/cs.cgi/Calendar?*) for each day of the experiment. Although we expected behaviour, i.e. activity and therefore the number of compartment changes per time, to vary between twilight, day and night periods, analysis of average residence time of a fish per visit in either three compartments per phase of the day revealed no differences among the four phases of the day. Consequently, mean values were calculated for a 24h period. Furthermore, the perch did not show any significant preference of one of the two outer compartments. Therefore, we summed up the residence times in these two “no food – no predator” compartments and compared to the central “treatment-compartment”.

Day one and day 13 of the experiments we removed from the calculations so were individuals that were captured by the pike or were in the wrong compartment compared to the computer registrations when the experiment was finished. This ensured that fish for which the PIT-system failed to detect the compartment changes correctly were eliminated from the analysis. As a measure of activity, we calculated the transition frequency per h and individual for each period as well as for the 24h period.

Statistics

We conducted identical experiments with large and small perch in two identical mesocosms. Changes in residence time of perch in either of the (two) compartments “no food – no predation” and “treatment” due to the introduction of the predator or the prey fish were analysed by a Likelihood-Ratio Chi^2-Test (Nagl 1992).

For analysing the changes in transition frequency, we used a MANOVA Repeated Measurement Design to test for effects of the two different mesocosms, the two perch sizes and the four experimental periods (one to four) as well as its interactions. In this analysis, we used time (in terms of day two to 12 of the experiment) as repeated (within) factor and tested the effects of time (days of the experiment) on each of the above named discrete factors (mesocosm, fish size and experimental period).

Ethical Note

The aim of the study was to examine the effect of perceived predation risk on the behaviour of the perch, which was done by introducing a piscivorous pike (*Esox lucius* L.) into the central compartment of the mesocosm. In order to minimize stress, experimental perch had the opportunity to learn (before the pike’s introduction) to use the other compartments where the pike could not follow. Two weeks before the experiments the pike was caught in Lake Constance by a local fisherman with a fyke net. It was held in an extra chamber (1 x 2 m) of the artificial pond at natural light conditions (13:11). In order to justify a “real” predation risk by the pike, its experience with the experimental prey was enhanced by feeding small perch (four to six) prior to and in between the experiments. Perch not eaten by the pike were removed after 30 minutes. The pike was observed to feed on perch to ensure that it could be predatory on perch throughout the experiments.

Results

Residence Time

During the first experimental period, in which only perch were in the mesocosm, perch of both size classes significantly preferred the middle compartment and did not spread equally in the three compartments (Fig. 2, LRχ^2-statistic: n = 10, df = 1; mesocosm 1/large perch: $\chi^2 = 6.27$, $p < 0.05$; mesocosm 2/large perch: $\chi^2 = 6.27$, $p < 0.05$; mesocosm 1/small perch: $\chi^2 = 2.79$, $p < 0.1$; mesocosm 2/small perch: $\chi^2 = 15.74$, $p < 0.001$). Small differences during this experimental period may be attributed to a further habituation to the mesocosm.

During the second experimental period, when we introduced the predator, the residence time of the large perch in the middle compartment significantly decreased. This avoidance behaviour we observed independently in both replicate experiments (Fig. 2a, 2c - LRχ^2-statistic: n = 4, df = 1; mesocosm 1/large perch: $\chi^2 = 9.71$, $p < 0.01$; mesocosm 2/large perch: $\chi^2 = 15.87$, $p < 0.01$). The introduction of the predator to the small perch provoked a very similar avoidance response of the perch towards the outer (non-predator) compartments (mesocosm 2: Fig. 2d - $\chi^2 = 8.82$, $p < 0.01$) even though this was not statistically significant in mesocosm 1 (Fig. 2b -$\chi^2 = 1.66$, $p > 0.5$.).

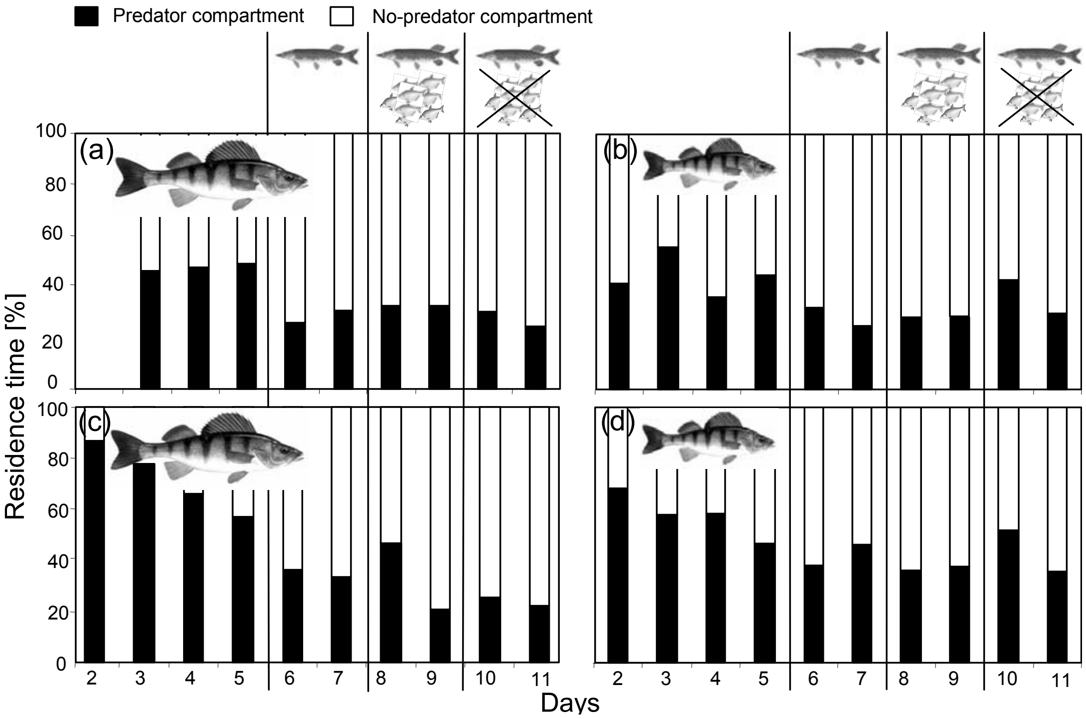

Figure 2. Residence time [%] of large (a, c) and small (b, d) perch during four different experimental periods: first only perch, second with perch and predator, third with perch, predator and prey, fourth with perch and predator. Top: mesocosm 1, bottom: mesocosm 2.
grey = predator compartment, white = no-predator compartments.

The additional introduction of prey fish to the middle compartment did not result in a significant return of neither the large nor the small perch towards the middle compartment in any experiment (LRχ^2-statistic: n = 4, df = 1; mesocosm 1/large perch: $\chi^2 = 0.14$, n.s; mesocosm 2/large perch: $\chi^2 =$

0.34, n.s.; mesocosm 1/small perch: χ^2 = 1.36, n.s.; mesocosm 2/small perch: χ^2 = 1.46, n.s.). Also, the removal of the prey fish on day 10 of the experiment had no overall significant effect on the behaviour of the perch (LRχ^2-statistic: n = 4, df = 1; mesocosm 1/large perch: χ^2 = 0.15, n.s; mesocosm 1/small perch: χ^2 = 0.02, n.s.; mesocosm 2/small perch: χ^2 = 0.13, n.s.).

Transition Frequency

The transition frequency increased with time during the first phase of the experiment (Fig. 3). With the introduction of the pike, different behavioural responses were observed in the two size classes. While the larger perch slightly decreased activity with the introduction of the pike (Fig. 3a, MANOVA-RM: F1, 24= 3.46, n.s. and Fig. 3c- MANOVA-RM: F1, 24 = 8.13, p = 0.01), the small perch of mesocosm 2 did not show any significant response (Fig. 3d). In contrast, the small perch of mesocosm 1 significantly increased their activity from an average of 0.97 to 1.86 compartment changes per hour (Fig. 3b- MANOVA-RM: F1, 24 = 12.31, p = 0.01).

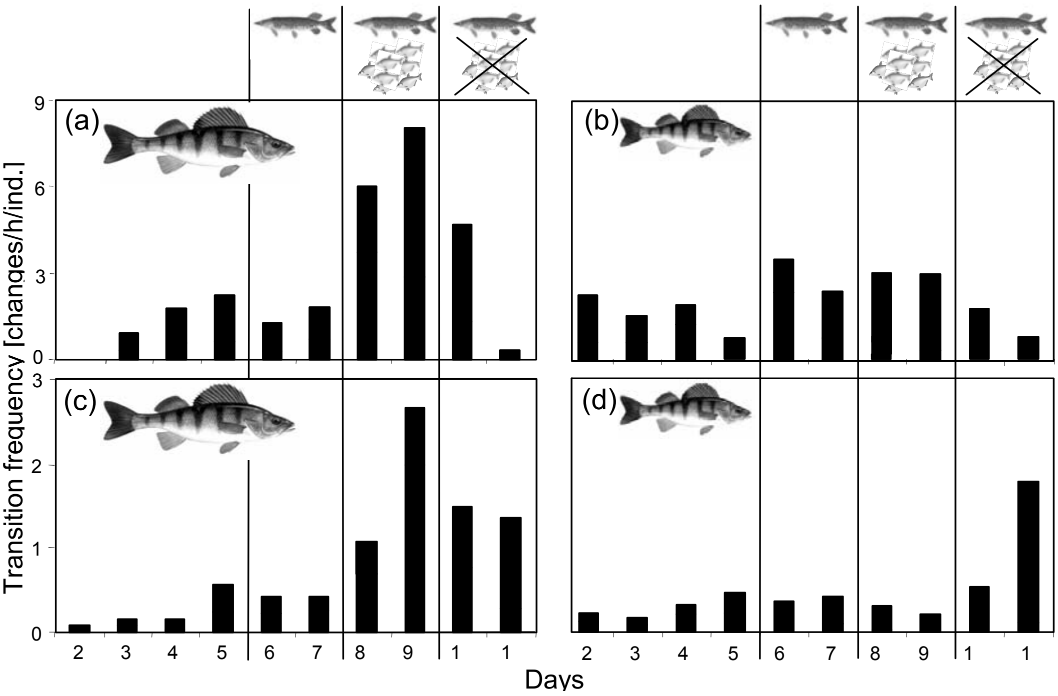

Figure 3. Transition frequency [changes h/ind.] of large (a, c) and small (b, d) perch in the two mesocosms during different experimental periods: first only perch, second with perch and predator, third with perch, predator and prey, fourth with perch and predator. Top: mesocosm 1, bottom: mesocosm 2.

When we introduced the prey fish, the transition frequency of the large perch significantly increased (Fig. 3a- MANOVA-RM: F1, 24 = 9.21, p = 0.0001 and Fig. 3c- MANOVA-RM: F1, 24 = 11.53, p = 0.01), and rapidly decreased as the prey fish were removed again (Fig. 3a - MANOVA-RM: F1, 24 = 32.34, p = 0.0001). In contrast, no such changes in transition frequency were observed in the small sized perch with introduction and removal of the prey fish (Fig. 3b, d).

Diel Activity

We also analysed transition frequency separately for the different phases of the day. For this, each 24h period was divided into dawn, day, dusk and night and the respective transition frequencies were calculated as percentage of the total observed transitions among compartments over 24 hours for this day. Because transitions among compartments hardly occurred during night (less then 1%), we only analysed day and twilight in detail.

During the experimental period with only perch in the mesocosm, we observed up to 60 % of total changes between the compartments during the day period for both size classes (Fig. 4). When the predator was introduced, the larger perch significantly increased their twilight activity (Fig. 4a- MANOVA-RM: F1, 24 = 21.13, p = 0.0001) and increased it even more when prey fish were added to the system (Fig. 4c- MANOVA-RM: F1, 24 = 9.81, p = 0.005). When we removed the prey fish in the last experimental period, the twilight activity significantly decreased for the large size perch (Fig. 4a- MANOVA-RM: F1, 24 = 36.2, p = 0.0001). In contrast, the small size class of perch steadily reduced their twilight activity when the predator was introduced and later when the prey fish were introduced and removed (Fig. 4), though the single step-by-step observations did not reveal to be significant.

During the course of the experiment, no large sized perch was captured by the pike, while in both replicate experiments with small sized perch, a few fish were caught by the pike (Fig.4, number of perch).

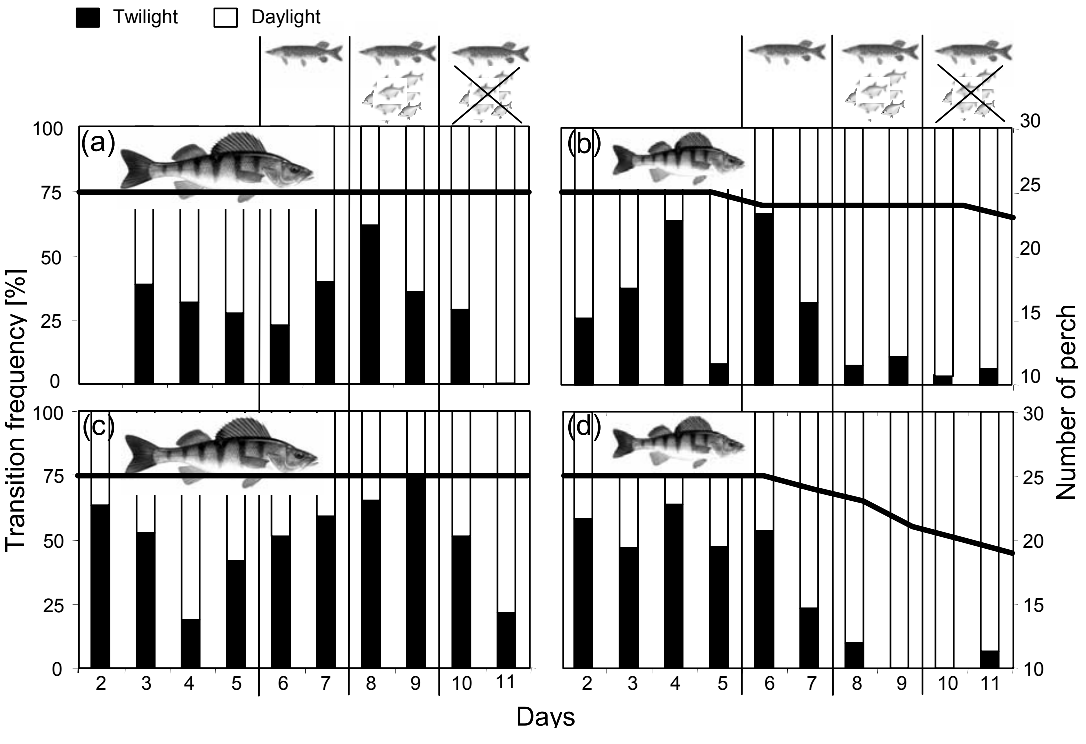

Fig.4. Activity level [%] during day (white) and twilight (black) based on the transition frequency of large (a, c) and small perch (b, d) in the two mesocosms during different experimental periods: first only perch, second with perch and predator, third with perch, predator and prey, fourth with perch and predator. Top: mesocosm 1, bottom: mesocosm 2. The black line gives the number of perch during the experiments (right Y-axis).

Discussion

The results of the analyses of residence time reflect the predator avoidance behaviour for both size classes. With the introduction of a predator, perch shifted from the predator compartment to the outer compartments where the predator could not follow. A similar shift to safer habitats under the threat of predation in perch was observed in a variety of previous studies (e.g. Persson 1991; Christensen & Persson 1993; Eklöv & Persson 1995; Snickars et al. 2004). Furthermore, we observed no significant difference in time spent in the predator compartment between the large and the small perch, thus no size-dependent differences were observed considering the effect of predation only. (1997) obtained similar results, as the presence of a predator significantly reduced the proportion of time spent in a feeding patch by all perch, independent of body size. Likewise, Borcherding (2006) could not find any overall differences between small and large YOY perch. However, when additional prey fish were offered in these experiments, large perch were more courageous in using open water habitats for foraging than smaller perch of the same age class did (Borcherding 2006). Studies on fishes have demonstrated that individuals differ in degrees of boldness and that this can influence an animal’s reactions to a variety of situations. In humans this phenomenon is known as the ‘shy bold continuum’ and is thought to be the fundamental axis of behavioural variation (Wilson et al. 1993). Individual variation in boldness may affect how animals avoid predators or determine how much risk is accepted in foraging for food. For example, Magnhagen (2006) found that perch had a cautious foraging behaviour in populations with a high predation pressure during juvenile stages, while bold perch were observed in a lake with low predation on small fish. So, although the degree of boldness must not prevail in every behavioural pattern, the large perch might just be bolder in their foraging behaviour than smaller ones of the same age. However, size related increase of residence time in the predator compartment was not observed in our experiments after prey fish were introduced to the large perch. This indicates that an increase in residence time in the immediate vicinity of a predator is not necessarily an overall valid proxy to distinguish behavioural differences between the two size classes of YOY perch. However, boldness in individuals has been shown to positively correlate also with activity (Huntingford et al. 1990; Utne et al. 1997; Ward et al. 2004). Sneddon (2003) classified bold fish as not only spending more time in an open water area but also exhibiting a higher level of activity. This is in close correlation to our results in which the level of activity by means of transition frequency between compartments significantly increased in the large perch but not in the small ones. This clearly shows that the large perch were more courageous swimming into the predator compartment even though the total time spent there (residence time) did not increase in parallel. The increase in activity level in the large perch thus indicates a certain degree of boldness on the behaviour of the large perch, possibly increasing the chance of capturing a prey fish in the middle compartment while simultaneous trying to reduce the predation risk by shortening the individual visits of this more dangerous habitat. This complex trade-off between increasing individual activity and reduction of the duration of an individual visit in the predator’s habitat levelled off when the prey fish were removed again from the predator compartment. Then the large perch became less active again, reaching a similar level as during the first experimental period without predator and prey fish.

In contrast, the small size class of perch did not show such an increase in activity as response to the introduction of the prey fish, although (1) the prey fish were of appropriate size (Persson et al. 2004) and (2) the small perch always tried to attack the prey fish when entering the predator/food fish compartment (personal observations). Johnsson (1993) showed a similar behaviour in small rainbow trout which, in contrast to larger trout, also did not take more risk during foraging when a food stimulus was provided and furthermore, Lundvall et al. (1999) could demonstrate that predation pressure is lower on larger perch than on small perch. The latter observation we could verify also in this study as only a few small perch were captured by the pike, even though the pike used as predator in our experiment was able to catch both size classes. Probably, the signal of successful predation of the pike on a few small perch was more important for the smaller size class to adjust the trade-off between foraging and predator avoidance, than for the larger ones that were not captured by the pike and tried to use the possibility to catch energetically valuable food.

Besides residence time and overall activity, we were able to analyse also transition frequency separately for the different periods of day. Fish, especially perch, are known to become nocturnal or forage at twilight to avoid threat of predation (Helfman 1993). However, Pettersson et al. (2001) found for Crucian carp that their typically nocturnal behaviour shifted to an aperiodic diel pattern under the risk of predation. In the present study, a shift in diel activity became apparent for large and small perch. As was expected, the large perch increased their level of activity especially at twilight when a predator was present and even more when additional prey fish were introduced, although their overall residence time in the predator’s compartment did not significantly increase. This clearly supports the above argumentation that the large size class in perch reacted to the presence of a predator by a trade-off between an increased number of visits in a potentially dangerous habitat and a decrease in the duration of stay of a single visit. This behaviour, however, is specifically pronounced during the twilight phase when the risk of being preyed upon is high but also the chance to be successful as predator itself. The fact that in our experiments no large perch was preyed upon at all might validate this assumption in the here performed experiments. Overall, the large YOY perch in the mesocosm study did not only have less fear of the pike, but were bolder than the small YOY perch when facing a profitable food resource, thus acting as predators themselves (Borcherding 2006).

For the small perch, however the level of activity during twilight constantly decreased with the introduction of pike. This is quite unique as a similar shift in behaviour has not been observed in other behavioural studies yet. With respect to a regularly increased feeding activity of juvenile fish at twilight (Pitcher & Turner 1986), it must be assumed that the small and more vulnerable perches’ shift to daytime activity might be an alternative way to avoid the threat of predation. This size-related trade-off within an age class has up till now not been observed and might have an important impact on the development of the YOY age cohort. Fraser et al. (2004) showed that guppies, which did not have the opportunity to feed at night time, not only grew less but also exhibited reduced daytime courtship. Although the reduction of encounter probability should be less energetically demanding than an escape manoeuvre (Fuiman & Magurran 1994), avoiding risky habitats (or in this case risky time scales) can be costly in the long run. By changing their main activity to daytime, less food will be available for the smaller perch because zooplankton, as the main food resource of YOY perch (Persson & Greenberg 1990), avoid the surface and littoral areas during day (Bohl 1980). Small perch that already are at a disadvantage compared to the larger size class (higher vulnerability to predation, lowered ability to prey on larger food organism) are further ousted because of their more costly mode of predator avoidance. Consequently, the observed decrease in twilight activity of the small YOY perch compared to their larger conspecifics is assumed to further increase the effects of the “juvenile bottleneck” (competition with roach and 1+perch, Persson & Greenberg 1990), and, thus may further enhance survival and recruitment of the larger individuals within an age cohort (Beeck et al. 2002; Borcherding et al. 2007).

Acknowledgements

The experiments conducted in the present study comply with the current laws of Germany.

References

Beeck, P. (2003). The early piscivory of European perch (*Perca fluviatilis*): A neglected phenomenon with notable consequences for the population structure and fish community in lake ecosystems. PhD Thesis. Universität zu Köln.

Beeck, P., Tauber, S., Kiel, S. & Borcherding, J. (2002). 0+ perch predation on 0+ bream: a case study on a eutrophic gravel pit lake. *Freshwater Biology* **47,** 2359-2369.

Bohl, E. (1980). Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia* **44,** 368-375.

Borcherding, J. (2006). Prey or predator: piscivorous 0+ perch (*Perca fluviatilis*) in the trade-off between food and shelter. *Environmental Biology of Fishes* **77,** 87-96.

Borcherding, J., Hermasch, B. & Murawski, P. (2007). Field observations and laboratory experiments on growth and lipid content of young-of-the-year perch. *Ecology of Freshwater Fish* **16,** 198-209.

Brännäs, E., Lundqvist, H., Prentice, E., Schmitz, M., Brännäs, K. & Wiklund, B. S. (1994). Use of the Passive Integrated Transponder (Pit) in A Fish Identification and Monitoring-System for Fish Behavioral-Studies. *Transactions of the American Fisheries Society* **123,** 395-401.

Burns, M. D., Fraser, N. H. C. & Metcalfe, N. B. (1997). An automated system for monitoring fish activity patterns. *Transactions of the American Fisheries Society* **126,** 1036-1040.

Byström, P., Andersson, J., Persson, L. & De Roos, A. M. (2004). Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young arctic char. *Oikos* **104,** 109-121.

Fischer, P., Kautz, H., Weber, H. & Obergfell, W. (2001). The use of passive integrated transponder systems (PIT) triggered by infrared-gates for behavioural studies in nocturnal, bottom-dwelling fish species. *Journal of Fish Biology* **58,** 295-298.

Fraser, D. F., Gilliam, J. F., Akkara, J. T., Albanese, B. W. & Snider, S. B. (2004). Night feeding by guppies under predator release: effects on growth and daytime courtship. *Ecology* **85,** 312-319.

Fuiman, L. A. & Magurran, A. E. (1994). Development of predator defences in fishes. *Reviews in Fish Biology & Fisheries* **4,** 145-183.

Gibbons, J. W. & Andrews, K. M. (2004). PIT tagging: Simple technology at its best. *Bioscience* **54,** 447-454.

Hartmann, J. (1983). Two feeding strategies of young fish. *Archiv für Hydrobiologie* **96,** 496-509.

Helfman, G. S. (1993). Fish behaviour by day, night and twilight. In *Behaviour of teleost fishes* (Pitcher, T. J., ed.), pp. 479-512. London: Chapman & Hall

Huntingford, F. A., Metclafe, N. B., Thorpe, J. E., Graham, W. D. & Adams, C. E. (1990). Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology* **36,** 877-881.

Johnsson, J. I. (1993). Big and brave:size selection affects foraging under risk of predation in juvenile rainbow trout, *Oncorhynchus mykiss*. *Animal Behaviour* **45,** 1219-1225.

Kelley, J. L., Evans, J. P., Ramnarine, I. W. & Magurran, A. E. (2003). Back to school: can antipredator behaviour in guppies be enhanced through social learning? *Animal Behaviour* **65,** 655-662.

Kelley, J. L. & Magurran, A. E. (2003). Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries* **4,** 216-226.

Laland, K. N., Brown, C. & Krause, J. (2003). Learning in fishes: from three-second memory to culture. *Fish and Fisheries* **4,** 199-202.

Lucas, M. C., Mercer, T., Armstrong, J. D., McGinty, S. & Rycroft, P. (1999). Use of a flat-bed passive integrated transponder antenna array to study the migration and behaviour of lowland river fishes at a fish pass. *Fisheries Research* **44,** 183-191.

Lundvall, D., Svanbäck, R., Persson, L. & Byström, P. (1999). Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 1285-1292.

Magnhagen, C. (2006). Risk-taking behaviour in foraging young-of-the-year perch varies with population size structure. *Oecologia* **147,** 734-743.

Magnhagen, C. & Borcherding, J. (2008). Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness? *Animal Behaviour* **75,** 509-517.

Magnhagen, C. & Heibo, E. (2001). Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. *Functional Ecology* **15,** 754-762.

Nagl, W. (1992). Statistische Datenanalyse mit SAS. In *Studienbuecher zur quantitativen und qualitativen Wirtschafts- und Sozialforschung* p. 413. Campus Verlag

Persson, L., Claessen, D., De Roos, A. M., Byström, P., Sjögren, S., Svanbäck, R., Wahlström, E. & Westman, E. (2004). Cannibalism in a size-structured population: Energy extraction and control. *Ecological Monographs* **74,** 135-157.

Persson, L., De Roos, A. M., Claessen, D., Byström, P., Lövgren, J., Sjögren, S., Svanbäck, R., Wahlström, E. & Westman, E. (2003). Gigantic cannibals driving a whole-lake trophic cascade. *Procedings of the National Academy of Sciences, USA* **100,** 4035-4039.

Persson, L. & Eklöv, P. (1995). Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* **76,** 70-81.

Persson, L. & Greenberg, L. A. (1990). Interspecific and intraspecific size class competition affecting resource use and growth of perch, *Perca fluviatilis*. *Oikos* **59,** 97-106.

Persson, L., Leonardsson, K., Roos, A. M. d., Gyllenberg, M. & Christensen, B. (1998). Ontogenetic Scaling of Foraging Rates and the Dynamics of a Size-Structured Consumer-Resource Model. *Theoretical Population Biology* **54,** 270-293.

Pettersson, L. B., Andersson, K. & Nilsson, K. (2001). The diel activity of crucian carp, Carassius carassius, in relation to chemical cues from predators. *Environmental Biology of Fishes* **61,** 341-345.

Pitcher, T. J. & Turner, J. R. (1986). Danger at dawn: experimental support for the twilight hypothesis in schoaling minnows. *Journal of Fish Biology* **29,** 59-70.

Post, J. R., Parkinson, E. A. & Johnston, N. T. (1999). Density-dependent processes in structured fish populations: Interaction strengths in whole-lake experiments. *Ecological Monographs* **69,** 155-175.

Prentice, E. F., Flagg, T. A., McCutcheon, C. S., Brastow, D. F. & Cross, D. C. (1990). Equiqment, Methods, and an Automated Data-Entry Station for PIT Tagging. *American Fisheries Society Symposium* **7,** 335-340.

Sneddon, L. U. (2003). The bold and the shy: individual differences in rainbow trout. *Journal of Fish Biology* **62,** 971-975.

Snickars, M., Sandström, A. & Mattila, J. (2004). Antipredator behaviour of 0+ year *Perca fluviatilis*: effect of vegetation density and turbidity. *Journal of Fish Biology* **65,** 1604-1613.

Utne, A. C. W., Brännäs, E. & Magnhagen, C. (1997). Individual responses to predation risk and food density in perch (Perca fluviatilis L.). *Canadian Journal of Zoology* **75,** 2027-2035.

Ward, A. J. W., Thomas, P., Hart, P. J. B. & Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (Gasterosteus aculeatus). *Behavioral Ecology and Sociobiology* **55,** 561-568.

Werner, E. E. & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15,** 393-425.

Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64,** 1540-1548.

Wilbur, H. M. (1988). Interactions between growing predators and growing prey. In *Size structured populations* (Ebenman, B. & Persson, L., eds.), pp. 157-172. Berlin, Heidelberg: Springer-Verlag

Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. (1993). Shy-bold continuum in Pumpkinseed Sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology* **107,** 250-260.

CHAPTER III

What matters? The effect of food conditioning and novel prey on prey selection of young-of-the-year perch.

König, Ulrike & Borcherding, Jost

University of Cologne, Zoological Institute, General Ecology and Limnology, Ecological Research Station Grietherbusch, 46459 Rees-Grietherbusch

Abstract

Optimal diet theory suggests that a selected foraging strategy should maximise energetic income. Therefore, a prey type with less energetic value than its energetic return of the capture success is bound to be dropped. However, learning might improve prey cognition and handling efficiency and can alter the ratio of gains to costs. To gain better understanding on how experience affects on behavioural consequences of food selection, young-of-the-year perch were trained on two different food resources. These trained perch and untrained specimen from the field were offered a fixed concentration of zooplankton, together with three different levels of fish (energetically equivalent, half and double the zooplankton value). Additionally, mysids instead of fish were offered as a novel food resource that was positively selected only at high energetic values. Although fish was the preferred prey for all groups of perch, only trained perch (piscivorous and planktivorous) positively selected fish at all energetic values offered. Not only experience in food resources, but also predation pressure, experienced only by the field perch prior to the experiments, was suggested to influence perch's behaviour. Juvenile perch exhibit a complex mode of behaviour with regards to feeding behaviour allowing them to change strategies when necessary.

Introduction

Generalists can have flexible foraging patterns (Marschall et al. 1989) and benefit from a wide range of food resources. Yet**,** Persson (1985) showed that consumption efficiency of a given prey is not independent of other prey types. When mixed prey was offered, intake rates of profitable and less profitable prey types were similar. Perch (*Perca fluviatilis*) appeared to be unable to use different feeding techniques at the same time with maximum efficiency (Persson 1985). Quite similarly, Warburton & Thomson (2006) found impaired foraging efficiency of silver perch (*Bidyanus bidyanus*) when foragers were faced with mixed prey and maximized foraging efficiency on patches of a single prey type. It has been shown that generalists are less efficient foragers compared to individuals that are selective and specialize in one prey type not suffering from, for example, time delays due to switching between prey types (Werner et al. 1981; Bernays & Funk 1999; Dukas & Kamil 2001). The rate at which the forager encounters a given food or prey type, the energetic value of which and the predator avoidance strategies are most important aspects influencing individual feeding strategies (Stephens & Krebs 1986; Bolnick et al. 2003). The diets of individuals within a population are seldom a mere sample of all prey types available but show that most fish can be highly selective (Kaiser & Hughes 1993). The reason for diet variation and specialisation has been studied thoroughly and let to the development of the optimal diet theory (Schoener 1968; Werner & Hall 1974; Pulliam 1974; Svanbäck & Bolnick 2005).

Optimal diet theory (ODT) suggests an individual to select a foraging strategy to maximise its energetic income, which depends on energetic content, encounter rates, the individual's efficiency in detecting, capturing, handling and lastly digesting of prey types available. An individual's efficiency in these constrains can determine the diet because individuals have different abilities (Wilson et al. 1993; Svanbäck & Bolnick 2005). Therefore, the individual is bound to drop the prey type with less energetic value than its energetic return of the individual's capture success. Abilities can be determined by coincidence, for example by the time of individual hatching of fish. Borcherding et al. (in prep.) found this timing to have crucial influence on population structure, as only the largest perch of the young-of-the-year (YOY) age cohort were able to prey on energetically profitable fish larvae while the smaller siblings got stuck in competition on zooplankton, leading to enlarged differences in growth and specialisation processes within the YOY age cohort of perch.

Another important parameter that affects an individual's diet breadth is its experience. Learning improves prey cognition, attack mode and handling efficiency of the individual (Godin 1978; Hughes 1979; Croy & Hughes 1991a; Croy & Hughes 1991b; Hughes et al. 1992) and therefore alters the ratio of gains to costs related with foraging on previously consumed prey (Reiriz et al. 1998). Previous studies showed that learned foraging skills have a strong influence on the profitability of prey, especially when prey items are of high energetically profitability but hard to catch (Kaiser & Hughes 1993; Hughes & Croy 1993). An acquired search image can improve the ability to detect preferred prey and lessen the detection rate of alternative targets (Langley 1996; Reiriz et al. 1998). Beeck (2000) conducted experiments in which perch trained on fish larvae (bream, *Abramis brama*) and untrained field perch were offered daphnids (*Daphnia pulicaria*) and bream larvae. Field perch switched from bream to daphnids with increasing daphnid densities (no preying on fish when 5 or more daphnids per litre were available) in accordance with the assumptions of ODT. Conversely, experienced perch once trained on fish remained piscivorous at *Daphnia* densities of up to 100 individuals per litre (Beeck 2000). The experience of perch feeding on fish larvae seems to have modified the ratio of gains for these in this study. Perch that were experienced in feeding on prey fish larvae were also superior in capturing fish to inexperienced fish.

To address the question in what way foraging strategies can be influenced by experience and to gain better understanding on the behavioural consequences of food selection, YOY perch were fed with two different food resources (zooplankton and cyprinid fish larvae) for 6 weeks. Each group developed different morphotypes (Heermann et al. 2007; Heynen 2007; Langkau 2008). The prey selectivity of perch with different previous training was investigated, when offered different proportions of zooplankton and fish. Additionally, instead of fish a novel food resource, the mysid *Limnomysis benedenii*, was offered. The hypotheses of the study were 1) that perch will prefer the food resource they were trained on over alternatives and feed on it according to its density, and 2) when the preferred food resource is depleted perch start foraging on the less preferred food resource.

Material & Methods

Field Samples

Young-of-the-year perch, (total length 41 mm ± 2.8 mm standard deviation, SD) were collected by beach seining during the first half of June 2007 at Lake Speldrop in the floodplain of the River Rhine (51°469510 N; 6°229420 E, Beeck et al. 2002). Lake Speldrop is a eutrophic gravel pit lake of 7 ha in size and a maximum depth of 16 m. Most of the banks are steep (>60°) and consist mainly of sand and gravel. Submerged vegetation is almost absent.

Training

To produce perch, which are trained on one specific food resource (fish or zooplankton), the collected perch were randomly transferred to four experimental containers (circular fish tanks of 2 x 1.1 and 2 x 1.8 m^3) under natural light regime at the Ecological Research Station in Rees-Grietherbusch. Perch were stocked according to tank size with 25 individuals in smaller tanks and 37 in the larger ones resulting in 62 perch trained on either food resource. To reduce habitat-specific effects on growth and behaviour, no structures were provided. Therefore, both food resources were easily accessible and growth differences that might influence the perches behaviour kept to a minimum. Perch were allowed to acclimatise for one day and then the perch in two of the tanks were fed daily with cyprinid fish larvae for six weeks (bream and white bream, 13.8 mm ± 4.4 SD at beginning of the experiment; 19.3 mm ± 6.3 SD at the end of the experiment). In the other tanks, perch were fed with zooplankton (mainly *Daphnia* spp. and copepods). The energy content of prey added to the containers were equal irrespective of prey type (calculations based on energy ratio of 1 to 3.37, Cummins & Wuycheck 1971; Dumont et al. 1975; Borcherding et al. 2007). Piscivorous perch were fed with a quantity of 15 % of their total body mass and planktivorous perch according to the equalized energy level with 51 % of their total body mass over 54 days. Three weeks prior to the experiments perch were transferred to aquaria (20 ± 1°C) under natural light regime (14h light: 10h dark). Because juvenile perch are known to be stressed and show unnatural behaviour when held individually (Magnhagen & Staffan 2003) they were held in groups of four in the laboratory. Three perch of each group were marked with Alcian blue dye on their caudal fin (one dot either ventrally, dorsally or marked both ventrally and dorsally) to make sure each individual perch could be identified during the experiments while being held in small schools. Before being handled, the fish were always anaesthetized with tricaine methanesulphonate (MS 222). Trained perch were still fed the same food resources and the ratio was kept equal to before. At the same time we collected field perch from Lake Speldrop by beach seine. They were not specially trained and were mainly planktivorous. Field perch were fed plankton consisting not only of daphnids and copepods but also a small amount of Chaoborus larvae. They were handled exactly like trained perch.

Behaviour Observations

Experiments were conducted in a 54L aquarium (60 * 30 * 30 cm) at a constant water temperature of 20 ± 1°C. The light regime was approximately 1000 lx above water surface with a light period of 14 h. Trials were carried out during daytime and were conducted on an individual level. As single perch are known to show stressed behaviour under experimental conditions, and juvenile perch are naturally found in shoals (Magnhagen & Staffan 2003), the three additional perch were functioning as buddies but did not participate in the experiment. Thus, they were introduced to a chamber (1/4th of the aquarium), which was separated by a perforated Perspex pane (25 holes per square decimetre, 5 mm diameter) to ensure visual and olfactory contact between buddies and experimental perch throughout the experiment. The remaining part of the aquarium was further divided by an opaque pane into a food compartment (half the aquarium) and an acclimation area (the remaining quarter between food and buddy compartment, Fig.1). A few minutes before the experiment started prey organisms were introduced to the food compartment, and then the experimental perch was introduced to the middle compartment. After 5 minutes acclimation the dividing pane was pulled up to allow the perch to forage and the experiment started. After the foraging period of 10 minutes, the removed pane was re-introduced and the experiment terminated. This was done without visual contact of the perch to the observer. All perch independent of their training were introduced to the set up previously to the actual experiments, to minimize handling induced behaviour (Milinski 1997).

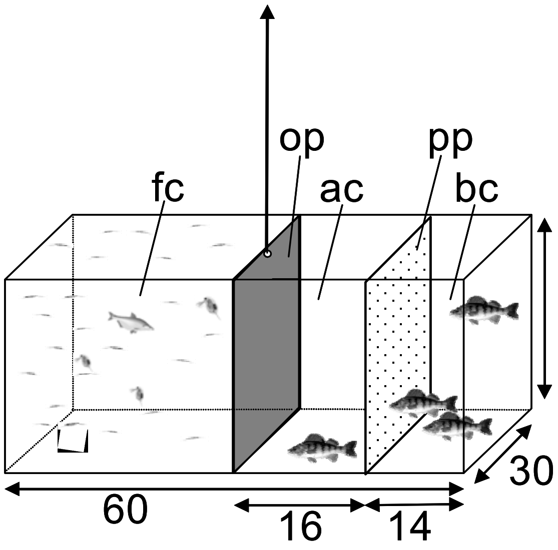

Figure 1: Experimental set-up of the 54l aquarium. Ac = acclimation area, bc = buddy compartment, fc = food compartment, op = removable opaque dividing pane, pp = perforated Perspex pane. Measurements given are in cm.

Perch with different experience (trained planktivorous perch, trained piscivorous perch and untrained perch from Lake Speldrop; referred to as field perch) were tested in the same way. Ten replicates of fish from each of the three training regimes were performed (Tab. 1). In optimal foraging theory profitability is defined as energy per unit handling time. Therefore, the density of high ranked prey determines if lower ranked prey will be included in the diet (Townsend & Winfield 1985; Stephens & Krebs 1986). This is why each perch was offered a fixed concentration of zooplankton (low ranked prey) with three different levels (half, equal and double the energetic value of zooplankton available) of alternative food resource (high ranked prey) in a repeated measurement design (Tab. 1). The energetic value of daphnids was calculated according to the maximum consumption rate of YOY perch with 8 daphnids per litre (Beeck 2000). Thus, a total of 240 daphnids were offered in the experimental arena along with the alternative prey for each experiment. As alternative food resource cyprinid fish larvae were offered, which were known prey to the piscivorous perch. To create the three different levels (half, equal and double the energetic value of zooplankton available) one, two and four cyprinid fish larvae were introduced into the food chamber. In a second series of experiments, a novel food resource for all groups of perch was offered as alternative prey. Now, ten replicates of fish from each of the three training regimes were offered mysids (*Limnomysis benedenii*) in groups of 6, 12 and 24 individuals to create the different levels of higher ranked prey. Energetic value of mysids was calculated according to Borcherding et al. (2006). Perch and food levels were randomly chosen and each perch only participated in experiments once a day. Experimental fish were not fed prior to trials. The buddies were fed with zooplankton at the end of the day.

Table 1: Number of individual perch used in the experiments on different food resources (1 fish, 6 mysids = half the energetic value of 240 daphnids; 2 fish, 12 mysids = equal energetic value of alternative prey and daphnids; 4 fish, 24 mysid = double the energetic value of 240 daphnids). In total 60 perch were examined and 180 experiments conducted. Ten perch of each group were individually offered 240 daphnids with one of the three different concentrations of fish or mysid prey. The next day measurements were repeated with the same perch and another concentration of alternative prey and so on. The same perch were used for all three concentrations within one food resource (fish or mysids), but different perch were examined between the two alternative food resources.

	240 daphnids									
	Fish					Mysids				
	1		2		4	6		12		24
Field perch	10	→	10	→	10	10	→	10	→	10
Planktivores	10	→	10	→	10	10	→	10	→	10
Piscivores	10	→	10	→	10	10	→	10	→	10

Morphometric and Statistical Analyses

To analyze morphological differences between the groups of perch, individuals were placed on a piece of Styrofoam with a cavity to avoid deformation and photographed with a digital camera next to a ruler. Eighteen landmarks as well as the ruler endpoints were digitized with the tpsDigit and tpsUtility software (available at: http://life.bio.sunysb.edu/morph/) and the x-y co-ordinates were recorded. Data was further analysed with the Integrated Morphometrics Package (IMP) (http://www3.canisius.edu/~sheets/morphsoft.html). Procrustes superimposition (Rohlf & Slice 1990) was performed with all specimens with the IMP software programme CoordGen6. The shape differences between groups were analysed with a canonical variates analysis (CVA) using the software CVAGen6. Partial warp scores were computed and overall shape difference was analysed with a MANCOVA by combining the partial warp scores and the uniform components with cohort as the grouping variable and LCS as the covariate (Zelditch et al. 2000). The tests of significance of the canonical variate axes are all based on Wilk's λ value at a $p < 0.05$ level of significance. CVAGen6 was also used to depict the deformation as vectors on landmarks. Further information on the morphometric analyses can be obtained from Heermann et al. (2007).

The behaviour of perch was monitored by video as well as a computer program (perchmon, Magnhagen & Borcherding 2008) which records one behavioural unit per second. During the experiment the observer types in the behaviour by code number. We distinguished the following different behavioural modes: inactivity, activity (swimming), feeding (including hunting) as well as the number of eaten prey. We then calculated energy uptake, activity and efficiency as absorbed energy of alternative prey relative to the level of activity. The condition factor was calculated according to the formula by Fulton (Bagenal & Tesch 1978): $K= 105 * W / TL -3$, with W = wet weight [g] and TL = total length [mm]. To test if the condition factor differed between groups of perch we conducted an ANOVA with training as between-subject factor.

Furthermore, we determined the food selection index based on Ivlev‘s electivity index E (Jacobs 1974) for the alternative food resource. The selectivity index is independent of relative abundance of compared food types and reflects directly differential capture rates (mA, mB): Relative difference $D = (mA-mB) / (mA+mB)$.

The chosen variables were used in a general linear model (GLM), with training and alternative food resources as between-subject factors and density of the alternative food as within-subject comparisons (SPSS 15).

Results

Table 2: Total length, weight and condition factor for YOY perch in June before training (start) and for the three types of perch at the time of the experiments (field, trained piscivorous, trained planktivorous perch)

Perch	Length [mm]	Weight [mg]	Condition factor
Start	41 ± 3	0.7 ± 0.2	1.01 ± 0.02
Field	75 ± 6	3.8 ± 1.1	0.90 ± 0.08
Planktivorous	82 ± 4	5.0 ± 0.8	0.92 ± 0.06
Piscivorous	101 ± 7	10.8 ± 2.6	1.04 ± 0.09

Morphometric analysis

The condition factor exhibits significant differences between the groups (ANOVA, df = 2, F = 20.645, $p < 0.0001$). Piscivorous perch had a higher condition factor than trained planktivorous and field perch (Tab. 2). The canonical variate analysis of trained (piscivorous and planktivorous) perch and field perch found two significant CVA axes (Axis 1(x): $\lambda = 0.0087$, $\chi^2 = 196.6844$ df = 64; p = 1.9984e-015, eigenvalue = 23.0168; Axis 2(y): $\lambda = 0.2100$, $\chi^2 = 64.7662$, df = 31, p = 0.000356811, eigenvalue = 3.7618). The first canonical variate axis discriminated field perch and trained planktivorous perch from trained piscivorous perch, while the second axis discriminated field perch and trained piscivorous perch from trained planktivorous perch. Piscivorous and planktivorous perch raised in the tanks developed a smaller head region and were deeper bodied than the field perch from Lake Speldrop (Fig. 2a, b). Planktivorous perch had in comparison to field perch a longer and slightly thinner tail region, while the vectors on landmarks indicate a shorter and thicker tail region for piscivorous perch. Further, piscivorous perch developed a smaller head region, they were deeper bodied than planktivorous perch (Fig. 2c). Another important difference is the position of the pectoral fins as well as the end of the operculum. Both were situated more ventrally for the trained perch in comparison to field perch (Fig. 2a, b), but for piscivorous compared to planktivorous perch they were shifted upwards and forward with the rest of the head region (Fig. 2c).

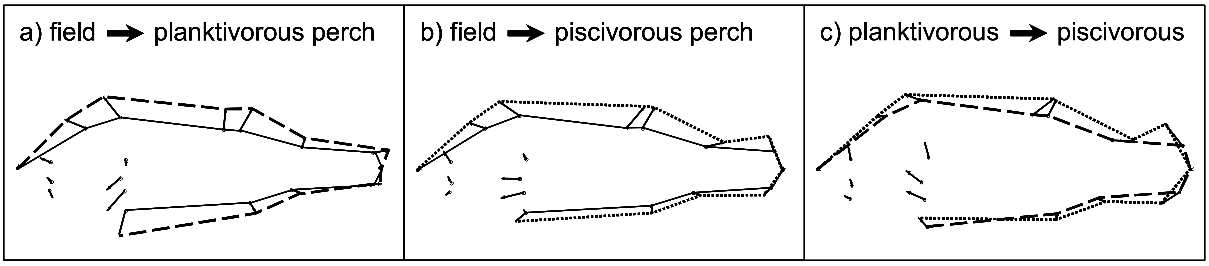

Figure 2: Shape difference correlated with the first canonical variate axis of (a) field and planktivorous perch, (b) field and piscivorous perch, and (c) planktivorous and piscivorous perch. The shape changes were obtained by regressing the shape on the CVA scores, depicted as growth vectors starting from the field or planktivorous to the planktivorous or piscivorous perch), respectively. Field perch = solid line, planktivorous perch = dashed line, piscivorous perch = dotted line

Behavioural observations

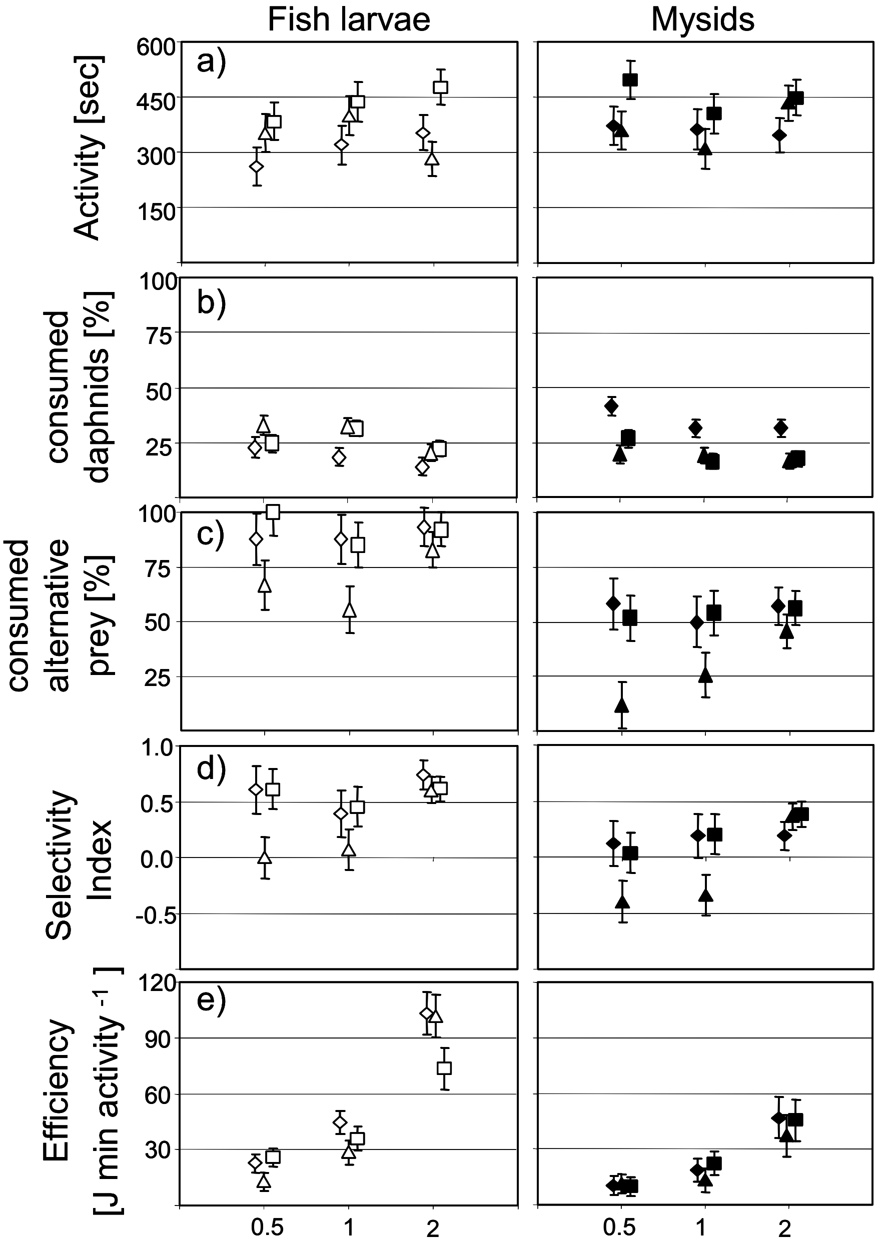

Figure 3: Mean values (± standard error) of (a) activity [sec], (b and c) consumed prey in relation to prey availability [%], (d) selectivity index on the alternative prey, and (e) efficiency [J min activity^{-1}] of trained piscivorous (diamond), trained planktivorous (square) and field (triangle) perch. Left = treatments with fish larvae as alternative prey to daphnids, right = treatments with mysids as alternative prey offered. X-Axis: 0.5 = alternative prey offered has half the energetic value of daphnids, 1 = equal energetic values of daphnids and alternative prey, 2 = alternative prey offered has double the energetic value of daphnids.

Activity and overall food density

Planktivorous perch were most active and piscivorous perch had the same activity as field perch (post hoc comparison: p = 0.027; Fig. 3a, Tab. 3). Activity of perch did not differ between fish and mysid trials. Food density in terms of overall energy content had a significant effect (Tab. 3) on food uptake for all examined perch, the more food was offered, the more was consumed. Significant values were found for total energetic value and alternative food resource, revealing that fish was always the preferred food resource. The factor training was not significant (Fig. 3, Tab. 3). In none of the treatments had the density of alternative prey any effect on daphnids consumed during the trial period (Fig. 3b) or on consumed alternative prey (Fig. 3c). However, consumed alternative prey perch increased with increasing mysid density for field perch (Fig. 3c).

Food selection

Food selection depended on the energetic value of the alternative prey offered and on the perches' training (Fig. 3d, Tab. 3). A significant difference in selectivity was observed between trained planktivorous perch and field perch (post hoc comparison: p = 0.005). Trained perch always positively selected fish while field perch only selected fish at the highest energetic value offered. When mysids were offered all groups of perch showed positive selection only at higher energetic values. Perch from Lake Speldrop even seemed to avoid mysids at low densities as the food selection index was negative for these values. No significant difference in selectivity was observed between planktivorous and piscivorous perch. Piscivorous perch also always selected fish and only positively selected mysids at high energetic values.

Feeding efficiency

Considering the feeding efficiency, the energetic value offered had a significant effect on all groups (Fig. 3e; Tab. 3). The factor training was not significant between the different groups of perch. Although results for fish showed higher levels of efficiency, the same tendency was found for mysids (post hoc comparison p < 0.001). Piscivorous perch were not more efficient than planktivorous and field perch. However, slightly increased values for efficiency of piscivorous perch may hint at an increased ability to catch prey fish. Therefore, when the number of daphnids eaten was further compared we found a significant difference (Fig. 4).

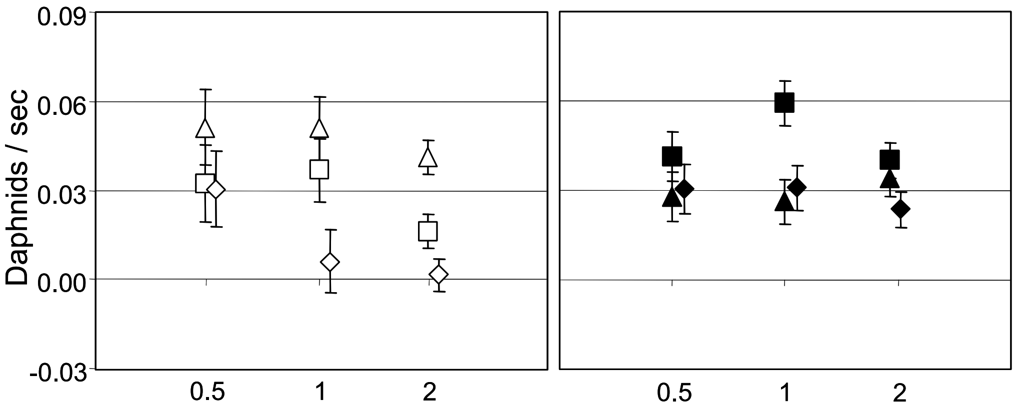

Figure 4: Mean number of daphnids consumed [± standard error] before (white) and after (black) the first fish larvae was successfully captured. Diamond = trained piscivorous perch, square = trained planktivorous perch, triangle = field perch. X-Axis: 0.5 = alternative prey offered has half the energetic value of daphnids, 1 = equal energetic values of daphnids and alternative prey, 2 = alternative prey offered has double the energetic value of daphnids.

Number of daphnids eaten until the first fish was caught depended on the density of alternative prey and on the training of perch (Tab. 3). Though density of alternative prey did not correlate with daphnids eaten after the first fish was captured, the amount of daphnids eaten during this period depended on the training (Tab. 3). Piscivorous perch foraged to the same extent on daphnids as both the planktivorous and the field groups when only one prey fish was available. They rapidly decreased their consumption of daphnids when fish of equal or more energetic value than that of daphnids available were offered. A less pronounced decrease of daphnid consumption occurred for trained planktivorous and field perch only at the highest energetic value of fish larvae. During the period after the first fish was eaten, piscivorous perch fed on the same amount of daphnids regardless of the amount of fish available, which was similar to the amount they fed on before the first fish was consumed at low fish density (Fig. 4). Field perch fed on less daphnids after the first fish was successfully caught than before and trained planktivorous perch slightly increased their consumption of daphnids.

Table 3: Results of generalized linear model (GLM) testing overall differences of training and alternative food resource in respect to activity, total energy uptake, food selection, feeding efficiency and daphnids consumed before and after1st fish was caught (only for trials with fish as alternative food). Training (field = untrained perch, pla = trained planktivorous perch; pis = piscivorous perch) and alternative prey (fish or mysids) were tested as between-subject factors, and density of alternative prey were tested as within-subject variables (energetic value: 1 = half, 2 = equal, 3 = double the energetic value of daphnids offered simultaneously). Differences (P < 0.05) between separate groups were tested with Bonferroni post hoc comparison of means.

		Overall effects			Bonferroni post hoc
		df, df_{err}	F	P	
Activity	Training	2, 54	4.144	0.021	pla > pis, field
	Alternative prey	1, 54	0.891	0.349	
	Training * alternative prey	2, 54	0.096	0.909	
	Within-subject	1, 54	0.66	0.42	
Total energy uptake	Training	2, 54	2.34	0.106	
	Alternative prey	1, 54	12.513	0.001	fish > mysid
	Training * alternative prey	2, 54	0.862	0.428	
	Within-subject	1, 54	210.232	< 0.001	3 > 2 > 1
Food selection	Training	2, 47	6.809	0.003	pla, pis > field
	Alternative prey	1, 47	18.662	< 0.001	fish > mysid
	Training * alternative prey	2, 47	0.055	0.946	
	Within-subject	1, 47	11.655	0.001	3 > 1, 2
Feeding efficiency	Training	2, 54	1.396	0.256	
	Alternative prey	1, 54	51.172	< 0.001	fish > mysid
	Training * alternative prey	2, 54	0.966	0.387	
	Within-subject	1, 54	132.734	< 0.001	3 > 2 > 1
Daphnids before fish	Training	2, 27	10.043	0.001	field > pis, pla
	Within-subject	1, 27	5.076	0.033	
Daphnids after fish	Training	2, 27	5.535	0.010	pla > pis, field
	Within-subject	1, 27	0.012	0.913	

Discussion

Trained perch always positively selected fish while field perch only selected fish at the highest energetic value of alternative prey offered. When a novel food resource was offered both trained and field perch showed selection of this prey only at high energetic values, and field perch even seemed to avoid mysids at low densities. Piscivorous perch and field perch showed the same level of activity, which was significantly reduced compared to trained planktivorous perch. This reduced activity, however, is probably of different origin. While piscivorous perch had a higher condition factor, and therefore did not need to be as active as planktivorous perch (Borcherding & Magnhagen 2008), field perch may have been more cautious foragers. Predation pressure on field perch was high in Lake Speldrop in August (König & Heynen, unpublished data), while trained perch did not experience threat of predation more than two months prior to the experiments. Magnhagen (2006) found that perch had a cautious foraging behaviour in populations with a high predation pressure during juvenile stages, while bold perch were observed in a lake with low predation on small fish. This can have a great impact on the fish's behaviour as has recently been shown (Magnhagen 2006; Magnhagen & Borcherding 2008). The field perches' cautious foraging behaviour is reflected in the lower selectivity of the alternative prey types, both of which need more foraging skills to feed on than feeding on zooplankton and therefore are more risky under natural conditions. These field perch showed a trade-off in favour of safety due to prior experienced threat of predation, but when profitability of the harder acquired prey was high, a threshold was reached and the trade-off changed in favour of foraging. This supports the theory that experience has a strong influence on the profitability of prey, especially when prey items are of high profitability but hard to catch (Kaiser & Hughes 1993; Hughes & Croy 1993).

Although piscivorous perch were no more effective in catching prey fish than planktivorous and field perch, they showed slightly higher values for efficiency. Nevertheless, density of prey fish and treatment of perch had a significant effect on daphnids eaten until the first fish is consumed. Piscivorous perch foraged to a smaller extent on plankton when fish were available compared to planktivorous and field perch. Langkau (2008) found that piscivorous perch were also superior in feeding on plankton. In these experiments, however, only one prey type was offered at the time (Langkau 2008). As foraging efficiency of perch can be reduced in the presence of multiple prey types (Persson 1985; Warburton & Thomson 2006) this might explain why we did not find the same results although the perch were from the same stock.

Generalists may be unable to perform several strategies compared to specialists and may thus be less successful than experienced individuals (Bolnick et al. 2003). This mechanism can contribute to the differences between trained (experienced) and field (more generalized) perch in our study. The fact that all animals tested fed on zooplankton even though the piscivorous perch had only encountered zooplankton at an early developmental phase suggests that perch inhabit inherent prey cognition, which is in accordance with several other studies(Stradmeyer & Thorpe 1987a; Mills et al. 1987b; Stradmeyer & Thorpe 1987b; Olla et al. 1992). Mills et al. (1987) tried to condition yellow perch (*Perca flavescens*) on certain ratios of two kinds of zooplankton (feeding these for 15 days prior to trials) and discovered that the prey consumed by the perch did not fit into this "trained" ratio. In accordance with optimal diet theory we would have expected piscivorous perch to positively select fish at all offered densities as they were experienced in handling fish. In optimal foraging theory profitability is defined as energy per unit handling time. Therefore, the density of high ranked prey should determine if lower ranked prey will be included in the diet (Townsend & Winfield 1985; Stephens & Krebs 1986). Planktivorous specimens were expected to only select fish, when it was of the same energetic value as plankton or exceeded it. However, the experiments revealed that fish was always the preferred food resource independent on the perches' previous feeding mode. As the fish larvae offered were relatively small and did not show strong escape responses probably due to the lower swimming ability of juvenile fish, fish proved to be the most profitable food although plankton densities were high. Field perch were clearly planktivorous when caught (König & Heynen unpubl. data) and had the same condition factor as the trained planktivorous perch. We thus assumed them to behave more similar to the latter than to the trained piscivorous perch. But this was clearly not the case. For example, the food selection index for field perch was half the value of trained planktivorous perch when the energetic value of alternative prey was low, while for trained planktivorous perch it equalled that of trained piscivorous perch. In addition, field perch more resembled piscivorous perch regarding activity. Field perch had developed an intermediate type in morphology when compared with both trained types, which may indicate a different life history to trained planktivorous perch (Heermann et al. 2007). Throughout their early life stage they have had the possibility to feed on other food resources than zooplankton and experienced predation threat, which can not only influence the perches morphology (Webb 1984; Ehlinger 1989; Ehlinger 1990; Svanbäck & Eklöv 2003; Andersson et al. 2005; Olsson et al. 2007) but also the responses during the experiments.

The aim of this study was to investigate whether YOY perch prefer the trained food resource over alternatives or if they use actual available food resources independent on their training. Foraging strategies can be influenced by prior feeding experience. We found that trained piscivorous perch had the tendency to prey more effectively on fish and consume less daphnids before the first fish was caught during the experiments. But the effect of training was not as pronounced as expected. On the other hand the abundance of alternative prey availability had a significant effect: if a certain threshold was exceeded (more than equal energetic value of alternative prey to that of daphnids), alternative prey was positively selected. Though piscivorous perch fed on less daphnids than both planktivorous types during fish trials, they tended to feed on more daphnids during trials when mysids (novel food and hard to catch) were offered. This shows that although experience can be favourable it does not have a limiting effect.

In addition, we found some hints that predation threat, as only experienced by the field perch prior to the experiments, influenced the foraging behaviour. Field perch depended to a greater extent on the abundance of alternative prey, which was especially obvious in number of consumed mysids and their selectivity regarding the alternative prey types, fish and mysids. This should be due to their learned trade-off between predator avoidance and risk taking in feeding behaviour. The higher density of alternative prey, the more the trade-off switches from staying save and feeding on easily caught daphnids to feeding on harder to get but more profitable prey. Consequently we can conclude that YOY perch exhibit a complex mode of behaviour with regards to feeding behaviour, allowing them to change strategies when necessary. Not only experience in food resources but other types of experience, for example of predation pressure, might have a strong influence on their foraging behaviour.

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The experiments conducted in the present study comply with the current laws of Germany.

References

Andersson, J., Byström, P., Persson, L. & De Roos, A. M. (2005). Plastic resource polymorphism: effects of resource availability on Arctic char (*Salvelinus alpinus*) morphology. *Biological Journal of the Linnean Society* **85,** 341-351.

Bagenal, T. B. & Tesch, F. W. (1978). Age and growth. In *Methods for assessment of fish production in fresh waters* (Bagenal, T. B., ed.), pp. 101-136. Oxford, London, Edinburgh, Melbourne: Blackwell Scientific Pub.

Beeck, P. (2000). Die frühe Piscivorie von 0+ Flußbarschen (*Perca fluviatilis*) – Ein ungewöhnliches Räuber-Beute System mit weitreichenden Konsequenzen für die Fischartengemeinschaft eines eutrophen Baggersees. Diplomarbeit. Universität zu Köln.

Beeck, P., Tauber, S., Kiel, S. & Borcherding, J. (2002). 0+ perch predation on 0+ bream: a case study on a eutrophic gravel pit lake. *Freshwater Biology* **47,** 2359-2369.

Bernays, E. A. & Funk, D. J. (1999). Specialists make faster decisions than generalists: experiments with aphids. *Proceedings of the Royal Society of London Series B-Biological Sciences* **266,** 151-156.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161,** 1-28.

Borcherding, J., Hermasch, B. & Murawski, P. (2007). Field observations and laboratory experiments on growth and lipid content of young-of-the-year perch. *Ecology of Freshwater Fish* **16,** 198-209.

Borcherding, J. & Magnhagen, C. (2008). Food abundance affects both morphology and behaviour of juvenile perch. *Ecology of Freshwater Fish* **17,** 207-218.

Borcherding, J., Murawski, S. & Arndt, H. (2006). Population ecology, vertical migration and feeding of the Ponto-Caspian invader Hemimysis anomala in a gravel-pit lake connected to the River Rhine. *Freshwater Biology* **51,** 2376-2387.

Croy, M. I. & Hughes, R. N. (1991a). The Influence of Hunger on Feeding-Behavior and on the Acquisition of Learned Foraging Skills by the 15-Spined Stickleback, *Spinachia spinachia* l. *Animal Behaviour* **41,** 161-170.

Croy, M. I. & Hughes, R. N. (1991b). The Role of Learning and Memory in the Feeding-Behavior of the 15-Spined Stickleback, Spinachia-Spinachia l. *Animal Behaviour* **41,** 149-159.

Cummins, K. W. & Wuycheck, J. C. (1971). Caloric equivalents for investigations in ecological energetics. *Mitteilungen der internationalen Vereinigung für theoretische und angewandte Limnologie* **18,** 1-158.

Dukas, R. & Kamil, A. C. (2001). Limited attention: the constraint underlying search image. *Behavioral Ecology* **12,** 192-199.

Dumont, H. J., Van de Velde, I. & Dumont, S. (1975). The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos in continetal waters. *Oecologia* **19,** 75-97.

Ehlinger, J. T. (1989). Learning and individual variation in bluegill foraging: habitat-specific techniques. *Animal Behaviour* **38,** 643-658.

Ehlinger, T. J. (1990). Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. *Ecology* **71,** 886-896.

Godin, J. J. (1978). Behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha* Wahlbaum) towards novel prey: influence of ontogeny and experience. *Environmental Biology of Fishes* **3,** 261-266.

Heermann, L., Beeck, P. & Borcherding, J. (2007). Two size classes of 0+ perch: is phenotypic plasticity based on food resources? *Journal of Fish Biology* **70,** 1365-1377.

Heynen, M. (2007). Phenotypic plasticity in juvenile perch (*Perca fluviatilis* L.): Does nutrition influence morphology and behaviour? Diplomarbeit. Universität zu Köln.

Hughes, R. N. (1979). Optimal Diets Under the Energy Maximization Premise - Effects of Recognition Time and Learning. *American Naturalist* **113,** 209-221.

Hughes, R. N. & Croy, M. I. (1993). An Experimental-Analysis of Frequency-Dependent Predation (Switching) in the 15-Spined Stickleback, Spinachia-Spinachia. *Journal of Animal Ecology* **62,** 341-352.

Hughes, R. N., Kaiser, M. J., Mackney, P. A. & Warburton, K. (1992). Optimizing Foraging Behavior Through Learning. *Journal of Fish Biology* **41,** 77-91.

Jacobs, J. (1974). Quantitative measurements of food selection. *Oecologia* **14,** 413-417.

Kaiser, M. J. & Hughes, R. N. (1993). Factors Affecting the Behavioral Mechanisms of Diet Selection in Fishes. *Marine Behaviour and Physiology* **23,** 105-118.

Langkau, M. (2008). Piscivore versus planktivore: How does morphological change influence ecological performance?

Langley, C. M. (1996). Search images: Selective attention to specific visual features of prey. *Journal of Experimental Psychology-Animal Behavior Processes* **22,** 152-163.

Magnhagen, C. (2006). Risk-taking behaviour in foraging young-of-the-year perch varies with population size structure. *Oecologia* **147,** 734-743.

Magnhagen, C. & Borcherding, J. (2008). Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness? *Animal Behaviour* **75,** 509-517.

Magnhagen, C. & Staffan, F. (2003). Social learning in young-of-the-year perch encountering a novel food type. *Journal of Fish Biology* **63,** 824-829.

Marschall, E. A., Chesson, P. L. & Stein, R. A. (1989). Foraging in A Patchy Environment - Prey-Encounter Rate and Residence Time Distributions. *Animal Behaviour* **37,** 444-454.

Milinski, M. (1997). How to avoid seven deadly sins in the study of behavior. *Advances in the study of behavior* **26,** 159-180.

Mills, E. L., Widzowski, D. V. & Jones, S. R. (1987). Food Conditioning and Prey Selection by Young Yellow Perch (*Perca flavescens*). *Canadian Journal of Fisheries and Aquatic Sciences* **44,** 549-555.

Olla, B. L., Davis, M. W. & Ryer, C. H. (1992). Foraging and Predator Avoidance in Hatchery-Reared Pacific Salmon - Achievement of Behavioral Potential. *Importance of Feeding Behavior for the Efficient Culture of Salmonid Fishes* **2,** 5-12.

Olsson, J., Svanbäck, R. & Eklöv, P. (2007). Effects of resource level and habitat type on behavioral and morphological plasticity in Eurasian perch. *Oecologia* **152,** 48-56.

Persson, L. (1985). Optimal foraging - the difficulty of exploiting different feeding strategies simultaneously. *Oecologia* **67,** 338-341.

Pulliam, H. R. (1974). Theory of Optimal Diets. *American Naturalist* **108,** 59-74.

Reiriz, L., Nicieza, A. G. & Brana, F. (1998). Prey selection by experienced and naive juvenile Atlantic salmon. *Journal of Fish Biology* **53,** 100-114.

Rohlf, F. J. & Slice, D. (1990). Extensions of the procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* **39,** 40-59.

Schoener, T. W. (1968). The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49,** 704-726.

Stephens, D. W. & Krebs, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.

Stradmeyer, L. & Thorpe, J. E. (1987a). Feeding behaviour of wild Atlantic salmon, *Salmo salar* L., parr in mid- to late summer in a Scotish river.

Stradmeyer, L. & Thorpe, J. E. (1987b). The responses of hatchery-reared Atlantic salmon, *Salmo salar* L., parr to pelleted and wild prey. *Aquaculture and Fisheries Management* **18,** 51-61.

Svanbäck, R. & Bolnick, D. I. (2005). Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research* **7,** 993-1012.

Svanbäck, R. & Eklöv, P. (2003). Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos* **102,** 273-284.

Townsend, C. R. & Winfield, I. J. (1985). The application of optimal foraging theory to feeding behaviour in fish. In *eds. Fish energetics: New Perspectives* (Tytler, P. & Calow, P., eds.), pp. 67-98. London: Croom Helm

Warburton, K. & Thomson, C. (2006). Costs of learning: the dynamics of mixed-prey exploitation by silver perch, *Bidyanus bidyanus* (Mitchell, 1838). *Animal Behaviour* **71,** 361-370.

Webb, P. W. (1984). Form and Function in Fish Swimming. *Scientific American* **251,** 72-82.

Werner, E. E. & Hall, D. J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). *Ecology* **55,** 1042-1052.

Werner, E. E., Mittelbach, G. G. & Hall, D. J. (1981). The Role of Foraging Profitability and Experience in Habitat Use by the Bluegill Sunfish. *Ecology* **62,** 116-125.

Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. (1993). Shy-bold continuum in Pumpkinseed Sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology* **107,** 250-260.

Zelditch, M. L., Sheets, H. D. & Fink, W. L. (2000). Spatiotemporal reorganization of growth rates in the evolution of ontogeny. *Evolution* **54,** 1363-1371.

CHAPTER IV

Development of abundance and size structure of young-of-the-year perch populations using three methods

Scharf, Werner; Heermann, Lisa; König, Ulrike & Borcherding, Jost

University of Cologne, Zoological Institute, General Ecology and Limnology, Ecological Research Station Grietherbusch, 46459 Rees-Grietherbusch

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W.R. Scharf, L. Heermann, U. König, J. Borcherding*

Zoological Institute of the University of Cologne, Department of General Ecology & Limnology, Ecological Field Station Grietherbusch, D-50923 Köln, Germany

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ABSTRACT

The reliable assessment of fish populations, which can vary in their spatial and demographic structure, assumes that the results are independent of the assessment method used. To test this assumption for the size structure of the young-of-the-year (YOY) age cohort of perch, three gravel pit lakes and four shallow ponds were monitored using three sampling methods from May to October. While bongo nets were used for early juveniles in the pelagic zone, electrofishing and multi-mesh gillnets were used later in the year when perch had moved to the littoral zone. Since bigger perch (post-larvae) switch from the pelagic to the littoral zone during ontogenesis, bongo net catches during June in the pelagic area of the lakes sampled only the smaller perch, while simultaneous electrofishing in the littoral zone caught bigger perch. Later in the season in the littoral zone, smaller perch were caught only by electrofishing and the bigger ones with gillnets. Monthly samples caught by electrofishing and gillnets in the experimental ponds from June to September showed even larger differences between the sizes of perch. Because the size distribution of the YOY perch cohort in the ponds had broadened considerably, there was sometimes no overlap in the length–frequency distributions between the two methods used, clearly demonstrating that using a single method is not sufficient for drawing a complete picture of the population size structure. This was verified by the removal of fish from the experimental ponds in October. Our results give clear evidence (and thus confirm previous studies) that using one method alone would result in an incomplete picture of the development of the size structure of the YOY perch population, due to the facts that (1) not all perch switch simultaneously between different habitats during ontogenesis and (2) that swimming performance, habitat-specific occurrence and activity change with size, thus affecting the method-specific catchability. Consequently, at least two appropriate methods must be used in an overlapping/parallel sampling design in order to draw a reliable picture of the development of the YOY perch population in any given body of water.

1. Introduction

Fish sampling programs and devices must provide accurate measurements of both changes in abundance and variations in the size structure of the population in order to obtain key parameters like density, growth or mortality rates. Furthermore, survey design must provide adequate spatial and temporal resolution (Pepin and Shears, 1997) to enable field samples to reveal habitat-related ecological processes. Proper understanding of the processes that influence population dynamics of fishes in temperate waters is based on extensive knowledge of recruitment from the juvenile to the adult stage (Persson and Greenberg, 1990; Post and McQueen, 1994). Differential food uptake in terms of quality and quantity affects not only the size of juvenile fishes (Byström and Garcia-Berthou, 1999; Borcherding et al., 2000; Beeck et al., 2002; Persson et al., 2004) but also their morphology (Svanbäck and Eklöv, 2002; Eklöv and Svanbäck, 2006; Olsson et al., 2006; Heermann et al., 2007), their behaviour in the trade-off between foraging and predation risk (Borcherding, 2006; Olsson et al., 2007; Borcherding and Magnhagen, 2008; Magnhagen and Borcherding, 2008) and the energy reserves that can be used up during periods of food shortage in winter (Griffiths and Kirkwood, 1995; Borcherding et al., 2007). Thus, knowledge of the ecological processes in juvenile fishes during the period from hatching in spring until the first winter is essential in order to understand recruitment into the adult stage.

Besides methodological constraints on the accurate sampling of larval and juvenile fish, the assessment of development may be further complicated when ontogenetic habitat shifts occur. After hatching, Eurasian perch (*Perca fluviatilis*) move to the pelagic zone

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* Corresponding author. Tel.: +49 2851 8575.
E-mail address: Jost.Borcherding@Uni-Koeln.de (J. Borcherding).

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and remain there for 1–2 months before they return to the littoral zone (Wang and Eckmann, 1994). This habitat shift may be associated with a size-related ontogenetic shift in their diet (Persson and Greenberg, 1990). Early piscivory in juvenile perch leads to a bimodal length–frequency distribution (LFD) after the first summer (cf. Beeck et al., 2002). To study this, Urbatzka et al. (2008) conducted experiments in shallow experimental ponds to quantify food uptake and related growth of young-of-the-year (YOY) perch. Because the ponds were not only shallow but also contained extended areas of submerged vegetation, the authors used electrofishing, which was expected to be the best method for that habitat (Cowx, 1989). During the sampling period from June until the end of August, only perch smaller than 60 mm in total length (TL) were caught in the ponds, and the calculated growth rates were low in comparison to samples from gravel pit lakes of the same geographical region (cf. Borcherding et al., 2007; Urbatzka et al., 2008). However, after draining the ponds at the end of the experiment and extracting all the perch, the LFD revealed that about 10% of the approximately 45,000 YOY perch ha^{-1} were larger than 100 mm TL; the largest were 175 mm TL (Urbatzka et al., 2008). This example raises the question as to why all these larger perch were never caught in the experimental ponds during the summer season, although an appropriate and generally accepted method was used.

In our study we repeated the experiments of Urbatzka et al. (2008) in the ponds. In addition to electrofishing, however, we also applied multi-mesh gillnets (Appelberg, 2000) which were especially adapted to the small (0.4–0.7 ha) and shallow ponds and to the size of juvenile perch. We expected to find extreme differences in the LFD of perch sampled using the two methods in a parallel sampling design. To be able to give more general recommendations for the sampling of YOY perch in larger and deeper waters as well, we additionally investigated three different gravel pit lakes using both methods. With respect to the development of the perch larvae in the pelagic zone after hatching, we used bongo net fishing in spring as a third standard method (Pepin and Shears, 1997; Wanzenböck et al., 1997; Tischler et al., 2000). In addition to the methodological comparison with overlapping electrofishing in the littoral zone, the results should help determine whether the offshore period of perch is time-restricted (Wang and Eckmann, 1994) or whether it depends on a critical size in relation to developmental stage (Urho, 1996).

2. Materials and methods

2.1. Study sites

The YOY perch populations of three gravel pit lakes situated by the Lower River Rhine were sampled (Borcherding et al., 2007). The first lake, Lake Speldrop, is situated near Rees (51°46′50″N, 6°22′42″E; Germany). Excavation here stopped in the 1960s without any following reconstruction of the biotope. This eutrophic lake has a surface area of about 7 ha and a maximum depth of about 16 m. The depth depends on the groundwater level, which in turn depends on the water level of the River Rhine. With the exception of some small littoral areas of moderate incline, the banks are steep (inclination of about 30–45°) and mainly covered with gravel, bricks and other construction debris. Sedimented sludge is completely absent and submerged macrophytes are not established. Phanerophytes grow along almost the entire shoreline, protecting the lake from wind so that there is usually a stable summer stagnation with an anoxic hypolimnion starting at a depth of about 5–6 m.

The second site, the mesotrophic Lake Reeser Meer, was partly reconstructed during the early 1990s. It is also situated near Rees (51°45′N, 6°28′E; Germany). Its surface area is about 28.5 ha; the maximum depth is about 17 m, depending on the groundwater level. Due to reconstruction, the littoral zone is not as homogeneous as in Lake Speldrop. Some of the gentle slopes are covered with sedimented sludge, others are covered with gravel. Where aquatic plants are present, a submerged macrophyte (*Elodea* sp.) is prominent, covering the entire littoral zone in some areas. Due to the absence of phanerophytes, especially along the northwestern shore line, the lake is not as well protected from the wind as Lake Speldrop. Both waters lie outside the normal floodplain of the River Rhine, in contrast to the third investigated water, Lake Pfeiffer.

Lake Pfeiffer is located near Xanten (51°38′16″N, 6°29′02″E; Germany) and is situated in the floodplain of the River Rhine. Consequently, during periods of high water it is temporarily connected with the Rhine via an oxbow. The lake is mesotrophic and more shallow than the other two lakes discussed above. Its maximum depth is about 5 m, depending on the water level of the River Rhine, and its surface area is about 7 ha. The shoreline is surrounded by phanerophytes, and the littoral zone is similar to that of Lake Speldrop; so most banks are steep, except one with a moderate inclination, and sedimented sludge is almost completely absent. The littoral zone of Lake Pfeiffer is normally covered with *Elodea* sp. down to a depth of approximately 3 m, but in 2006 these macrophytes were found only in small, irregularly spread patches. In contrast to the other lakes, the presence of woody debris greatly increases the structural diversity of the littoral zone.

In addition to sampling the gravel pit lakes, YOY perch populations were monitored in four ponds with areas of 0.4–0.7 ha and maximum depths of 2 m (mean depths of about 1 m, Urbatzka et al., 2008). The ponds are situated near Lohmar (50°49′33″N, 7°12′59″E; Germany). These ponds are fed by a small stream, are situated in a line and are connected by overflows. They are oligo to mesotrophic. The ponds were completely drained in late winter. Ponds 3 and 4 were later restocked with calculated ratios of mature perch and bream *Abramis brama* (not further considered in this study), and ponds 1 and 2 restocked solely with mature perch. When the parental fish had spawned, they were removed from the ponds by gillnetting to guarantee undisturbed development of the offspring. The ponds were partially to completely covered by submerged vegetation e.g. *Potamogeton* sp. or *Chara* sp., and therefore the structural diversity of these waters can be characterized as relatively complex.

2.2. Fish sampling

2.2.1. Bongo net sampling

Immediately after hatching, larval perch undertake a clear habitat shift into the pelagic zone where they stay until the early fingerling stages (Wang and Eckmann, 1994). Using bongo nets, we caught the perch from larval to early fingerling stages weekly in the pelagic zone of the lakes (cf. Pepin and Shears, 1997; Wanzenböck et al., 1997). Sampling was always performed after sunset (Wang and Eckmann, 1994; Guillard et al., 2006). In the experimental ponds, however, no bongo net trawling was possible because the ponds are too shallow and large areas are covered with submerged vegetation.

We used two parallel bongo nets fixed to an aluminum boat (4 m length) with a 3.7 kW outboard motor (Fig. 1). The mouth of each net was 0.5 m in diameter, stabilized by a stainless steel frame. The main cylinders of the net had dark entrances and were 1.8 m long, followed by 0.5 m long cones (Fig. 1). The mesh size was adapted to the developmental stage of the fish, with three different mesh sizes being used: 0.75 mm by 1.5 mm, to 1.5 mm square, and at least 3 mm square. The towing speed ranged from 3.8 km h^{-1} for the smallest mesh size to 6.9 km h^{-1} for the net with biggest mesh size. The push net was fixed on a steel frame which could be lowered down

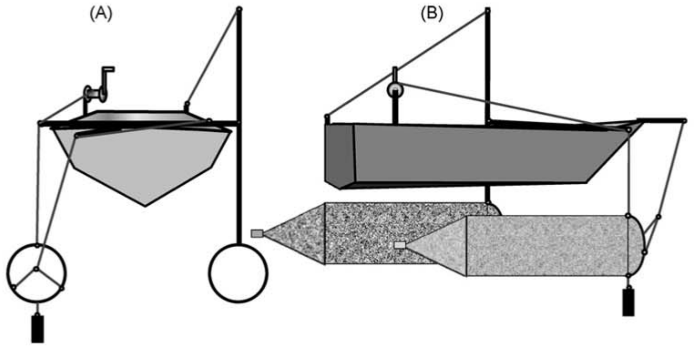

Fig. 1. Schematic diagram of the boat and the bongo net construction: front view (A) and right side view (B).

to 1.5 m. The other net was a trawl which was connected by rope to a hoist. An iron weight of 32 kg was fixed on the distal side of the net frame. The weight held the bongo net vertical during towing. Additionally, the net was braced by two 0.5 mm diameter stainless steel wires fixed on the lower third of the net's frame. These wires were 0.5 m long and ran together to a small polyamide rope which was fixed to a frame on the front of the boat. The trawl net was used down to a depth of 4 m. At top speed, the net with the biggest mesh size was usable down to 2 m. The amount of filtered water was estimated with a flow meter (Hydrobios, Kiel, Germany). On every sampling date, four surveys were performed with both type of nets, resulting in a total of eight samples taken in different depths (3× 0.5–1 m, 2× 1–1.5 m, 1 × 1.5–2 m, 1 × 2.5–3 m, and 1 × 3.5–4 m). To standardize the number of perch caught during the season, irrespective of the sampling depth (not considered in this study), the catch per unit effort for this method ($CPUE_B$) was calculated as follows: first the mean density was calculated for three depth classes (<1, 1.5–3, and >3 m, including zero samples) and then averaged as individuals per m^3 for one date and location. All caught fish were immediately fixed in 4% formaldehyde solution.

2.2.2. Electrofishing

The larval fish in the ponds were sampled monthly by electrofishing (EFGI 4000 J. Brettschneider, Germany), with point abundance sampling (PAS) by boat (modified after Persat and Copp, 1989; Beeck et al., 2002). A 10-cm diameter ring anode was used initially and this was changed later to a 12.5-cm diameter one (when the perch were larger). Fish were collected at 50 randomly chosen points per pond, covering all kind of habitats (littoral zones, but also in the middle of the pond). In the gravel pit lakes, perch return to the littoral zone after their pelagic phase. During that period we started to investigate the littoral zone by electrofishing with the aforementioned fishing gear and the 12.5 mm ring anode in the afternoon until evening hours. We approached the littoral zone from the pelagic zone as silently as possible and collected fish at an average of 85 randomly chosen points. Because of the steep gradient of the lake banks, the sampling area was always very close to the bank in order to observe shallow areas up to 1.5 m maximum depth of. Starting in late May, electrofishing in the lakes was performed weekly until mid-June, and afterwards every 2 weeks. All perch were immediately ice-cooled and later deep-frozen. The catch per unit effort of the PAS ($CPUE_E$) is the mean number of perch caught per point (including zero samples).

2.2.3. Gillnet fishing

We used two types of sinking polyamide monofilament multi-mesh gillnets (Appelberg, 2000). For the younger stages of perch the nets had mesh sizes 6, 8, 10, and 12 mm and for the older stages we used, in addition, multi-mesh gillnets with 15 and 20 mm mesh size. Six of the nets with smaller mesh sizes and at least two of those with larger mesh sizes were used on each sampling date. Each net was 6 m long and 1.5 m high. Each of the mesh panels of the smaller sizes were 2.25 m^2, whereas the bigger ones were 4.5 m^2 per panel. The nets were set in the evening for between 1.5 and 2.5 h, depending on the expected density of perch. Applying this method provides some advantages over a gang of different single-mesh nets which are normally used: firstly, the multi-mesh panels are much smaller than commonly available single-mesh nets, reducing the number of captured fish drastically when applied at high perch densities as in our waters; secondly, using more nets with all the mesh sizes allows the coverage of all different habitats in the littoral zone with the complete set of mesh sizes, and thirdly, identical nets set in parallel can be additionally used to calculate a mean CPUE and its variation, and this irrespective of the mesh-size selectivity (cf. Appelberg et al., 1995), which otherwise has to be taken into account.

In the gravel pit lakes, bi-weekly gillnet fishing started in mid-June when perch switched to the littoral zone. In the experimental ponds, gillnet fishing was always conducted simultaneously with electrofishing but at different places to avoid the possibility of electrofishing scaring fish into the nets. All perch were preserved in 4% formaldehyde solution. To allow the comparison of perch caught during the season, the catch per unit effort ($CPUE_N$) was formulated as follows:

$$\text{gillnet fishing}: \mathrm{CPUE_N} = \frac{(A_s/A_n)C_n}{t}$$

with A_s = area of standard net (219.3 m^2), A_n = area of the net used (m^2), C_n = nominal catch, and t = exposure time (h).

2.2.4. Fish removal from the experimental ponds

All ponds were completely drained at the end of the pond experiments in mid-October. All fish were caught in a metal-sieve chamber at the outlet. The fish biomass per pond was weighed and four sub-samples with a total number of about 1060–2480 perch per pond were measured. Finally, the total number of individuals per pond was calculated.

2.2.5. Statistics

Although no direct comparison of the different CPUEs is possible, and thus no overall absolute abundance of perch can be given, the seasonal changes in the relative densities can be estimated with the sampling method-specific CPUEs. In addition, the overlap of the different methods is a first step in understanding the

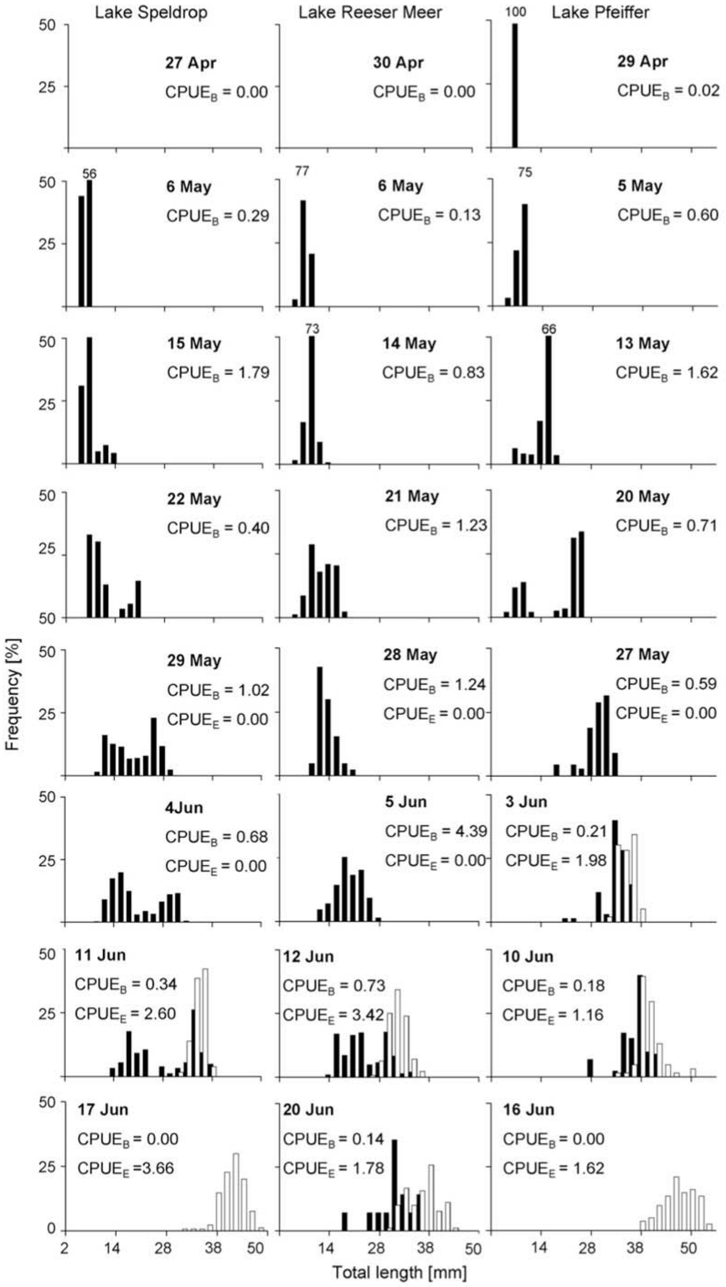

Fig. 2. Length–frequency distribution and CPUE of YOY perch in the gravel pit lakes caught on different sampling dates in spring 2006 using bongo net fishing (black columns, CPUE$_B$) and electrofishing (white columns, CPUE$_E$).

quantitative differences between them. Irrespective of these failures in the overall estimation of quantitative densities, the total length of all sampled fish was measured to the nearest 1 mm, and all length data were used to produce LFDs separately for each method, which were compared with ANOVAs using SPSS (Ver. 14.0.1, SPSS Inc.). In all cases the length data were used as the dependent variable, while date, method and lake were the independent variables.

Table 1
Three-way ANOVA testing the effect of the three gravel pit lakes, sampling date and fishing method (bongo net versus electrofishing) on the mean TL of perch in the gravel pit lakes for all dates on which the two methods caught perch at the same time (see Fig. 2)

	df, df_{err}	F	P
Lake	2, 2335	368.3	<0.0001
Date	2, 2335	89.9	<0.0001
Method	1, 2335	137.2	<0.0001
Lake × Date	0		
Lake × Method	2, 2335	18.1	<0.0001
Date × Method	2, 2335	0.54	0.586
Lake × Date × Method	0		

3. Results

Hatching of perch in the gravel pit lakes started around the end of April. Perch fry in the shallowest Lake Pfeiffer were found 1 week earlier than in the other investigated lakes. After hatching, the perch fry in the lakes were caught by bongo net trawling. The density of the perch fry increased continuously during the first 3 weeks (Fig. 2). In the middle of May, perch fry density in Lake Speldrop peaked at 1.8 ind. m^{-3}, before stabilizing at a somewhat lower level by the end of May. In Lake Pfeiffer the variation in abundance was similar in sequence and range to that of Lake Speldrop, while in Lake Reeser Meer the steady increase lasted until the beginning of June (4.4 ind. m^{-3}). The results of bongo netting revealed that some perch hatched 2–3 weeks later than their siblings (Fig. 2).

We started the PAS surveys in the littoral zone of the gravel pit lakes in late May; early enough to rule out any larval perch abundance there. At the return of the post-larvae to the littoral zone, the individuals were between ca. 30 and 40 mm TL, whereas the smaller individuals (which stayed in pelagic zone) had TLs of between 14 and 22 mm (Fig. 2). The numbers of fish in the bongo net catches decreased rapidly from the beginning of June onwards, this fishing method was therefore stopped after the third week of June. For all parallel catches of bongo and electrofishing, the statistical analysis revealed significant size differences depending on the method, explaining about 4% of the total variance (Table 1). The perch caught by electrofishing in the littoral zone were always larger than those caught with the bongo nets in the pelagic areas (Fig. 3).

From mid-June onwards we started gillnet fishing in the littoral zone; the three methods thus overlapped for each lake. First, perch were caught with the 6 mm mesh size from about 40 mm onwards (Fig. 4). With increasing size of the fish, first the $CPUE_N$ revealed an increasing trend while, later on, catches oscillated more or less without recognizable trends in the three gravel pit lakes. For the first samples from mid-June onwards, the mean sizes of the perch caught with either electrofishing or gillnets did not differ considerably (Fig. 5). In the following period, however, the accordance of the LFDs of both methods decreased (significant interaction term Date × Method, ANOVA, df = 6, 1558, $F = 36.4$, $p < 0.0001$), especially in Lake Speldrop where the biggest YOY perch were caught with gillnets only and the smallest ones (50 mm in October) only with PAS (Fig. 4).

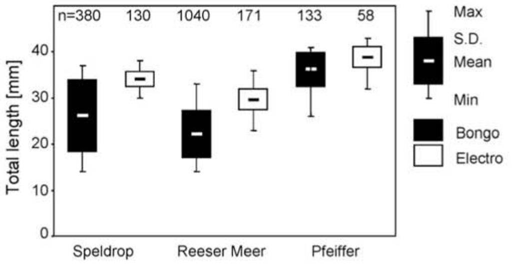

Fig. 3. Box-plot of perch sizes from the three gravel pit lakes caught using bongo nets (black) and electrofishing (white) around 11 June 2006, n = number of perch.

Table 2
Two-way ANOVAs testing the effect of sampling date and fishing method (electrofishing versus gillnets) on the mean TL of perch in the gravel pit lakes for all dates on which the two methods were used at the same time and the $CPUE_E$ was >0.5 (cf. Fig. 4)

Lake Speldrop ($r^2 = 0.744$)	df, df_{err}	F	P
Date	6, 1558	298.7	<0.0001
Method	1, 1558	282.7	<0.0001
Date × Method	6, 1558	36.4	<0.0001
Lake Reeser Meer ($r^2 = 0.603$)			
Date	4, 1100	270.8	<0.0001
Method	1, 1100	164.3	<0.0001
Date × Method	3, 1100	5.79	0.001
Lake Pfeiffer ($r^2 = 0.800$)			
Date	2, 462	309.1	<0.0001
Method	1, 462	82.2	<0.0001
Date × Method	2, 462	7.66	0.001

In contrast to Lake Speldrop, in Lake Reeser Meer there was a relatively good accordance observable between these two methods, although, as also found in Lake Speldrop, the biggest individuals were caught by the gillnets and not by PAS. In Lake Pfeiffer, the $CPUE_E$ showed a remarkable and early decrease by the beginning of July and persisted at a low level (Fig. 4). This corresponded with observations that YOY perch were no longer visible in the shallow areas of the lake's littoral zone. This was in clear contrast to both the other lakes. Overall the statistical analysis revealed significant differences in the sizes of the perch caught with electrofishing and gillnets. For each lake, around 7% of the total variability of the sizes could be explained by the methods used (all $p < 0.0001$; Table 2), and the perch caught with gillnets were always larger than those sampled with electrofishing (Fig. 5).

The hatching period of perch in the experimental ponds started in the beginning of May, similar to that in the gravel pit lakes, but in the ponds the period lasted only about 1 week, i.e. less time than in the lakes. After the hatching of perch we used only the PAS method in parallel with gillnets to study the development of the juvenile perch. In the last third of June, gillnets caught some bigger individuals of the YOY perch, which did not occur in the electrofishing samples (Fig. 6). The $CPUE_E$ results for the ponds had similar ranges to those for the gravel pit lakes. Gillnet catches were, however, about 20 times lower in the ponds. At this time, the resulting LFDs of both methods partly overlapped but still the biggest individuals were almost exclusively taken by gillnets whereas the smallest ones were only caught by the PAS (Fig. 6). Until the end of August, gillnet fishing in ponds 1 and 4 gave similar results for the smaller-sized perch compared with the catches by electrofishing; electrofishing was thus stopped at this time. In contrast, the smallest perch in ponds 2 and 3 were only caught by electrofishing and not by gillnets; both methods were thus used until the end of the sampling period. Again the statistical analysis revealed a significant effect of the fishing method, explaining lower percentages for ponds 1 (2%) and 4 (10%), but quite a high percentage for ponds 2 (30%) and even 59% for pond 3. As for the gravel pit lakes, the perch caught by gillnet were always larger than those caught by electrofishing (Fig. 7 and Table 3).

To compare the results of our two fishing methods in the experimental ponds with the relative abundance of sizes within the LFDs, we emptied the ponds completely and sampled all fish. In accordance with the range of sizes caught on the last sampling date in

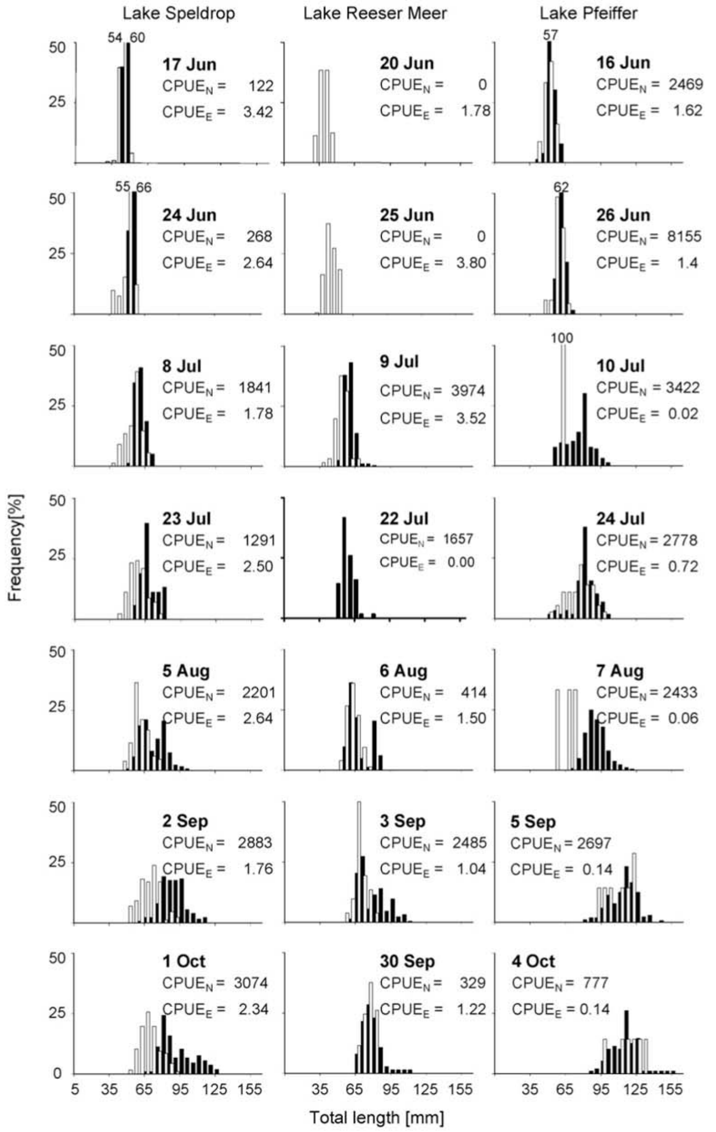

Fig. 4. Length–frequency distribution and CPUE of YOY perch in the gravel pit lakes caught on different sampling dates in summer 2006 using electrofishing (white columns, CPUE$_E$) and gillnets (black columns, CPUE$_N$).

September, the size ranges of perch at the time of removal were quite similar. However, the shape of the corresponding LFDs was completely different (Fig. 6); the abundance of the small perch was much higher than expected from the final catches in September (cf. Fig. 6 and Table 4).

In order to describe a more general trend for the observed difference between electrofishing and gillnets that includes the three different gravel pit lakes as well as the shallow experimental ponds, a regression of these differences on the independent variable 'fish size' was computed. This independent variable was chosen because increasing differences over the course of the season became obvious, especially for the gravel pit lakes (cf. Fig. 5). Because the number of perch caught usually varied greatly between the two methods, we had to use the median of the TL as the independent variable. Although there was a significant relationship between the median TL and the observed difference between samples from electrofishing and gillnets for the samples from the gravel pit lakes ($R^2 = 0.628$, $p < 0.01$, $n = 17$), there was no overall significant relationship for all values including the ponds (Fig. 8A). However, using the absolute size range of all captured perch as an independent variable reveals a highly significant correlation with the observed difference between the samples from electrofishing and gillnets

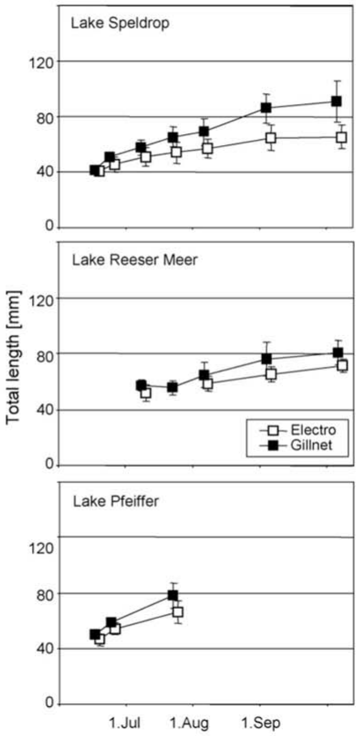

Fig. 5. Mean TL ± S.D. of perch caught in the gravel pit lakes using electrofishing (white) and gillnets (black) for all samples in 2006, when the CPUE$_E$ was >0.5.

(Fig. 8B). Thus, the more the LFD of a perch population widened, the larger was the difference between the two sampling methods.

4. Discussion

4.1. Bongo net sampling and electrofishing

In the first part of the study, bongo net sampling was the only applicable method for catching larval perch in the lakes. Especially in waters with an extended pelagic area such as the gravel pit lakes, this is the most practical method for following the development of perch fry after hatching. When using push or trawl nets, several factors which influence catch efficiency must be taken into account. To reduce the forewarning of larval fish by the noise of the vessel itself or its propeller (Ona and Godo, 1990), we attached the fishing gear to the front third of the boat. Visibility, e.g. with respect to light intensity or transparency, can reduce catch efficiency, as fishes with visual perception are better able to avoid an approaching net (Glass and Wardle, 1989). Therefore, our bongo nets had a dark entrance and always the bongo net sampling was done after sunset (Wang and Eckmann, 1994; Guillard et al., 2006). Thus, we reduced the expected catch variability during the day that might depend on visibility and on ontogenetic-determined behaviour, such as diurnal horizontal or vertical migration of perch larvae (e.g. Cech et al., 2005; Scharf, unpublished results). Juza and Kubecka (2007) recommend a 3 m × 3 m trawl for quantitative night sampling of the fry community. Nevertheless, net openings between 40 and 80 cm revealed no significant difference in the density of captured post-larval fish, whereas smaller nets were less efficient (Mooij, 1996). Although it can be assumed that bigger openings are more effective, both net size and mesh size strongly affect another important factor: the towing speed (Mous et al., 2002). When using mesh sizes of between 0.75 and 3 mm, the achieved speed of 3.8–6.9 km h^{-1} was adequate to compensate for the escape speed of perch larvae larger than 40 mm TL (Pepin and Shears, 1997). Overall we can assume that the catch efficiency of the bongo net sampling was quite good for the ontogenetic stages of perch in the pelagic area of the gravel pit

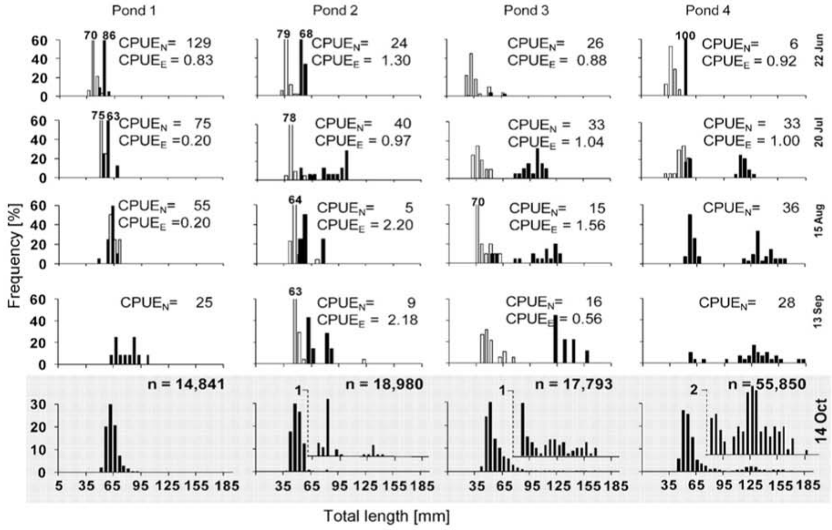

Fig. 6. Length–frequency distribution and CPUE of YOY perch in the experimental ponds caught on different sampling dates in summer 2006 using electrofishing (white columns, CPUE$_E$) and gillnets (black columns, CPUE$_N$). In addition, the total number of perch and the LFD (grey shaded) of each pond from the fish extraction in mid-October are given. Here the frequency of the perch >85 mm TL is shown with higher resolution on the *Y*-axis.

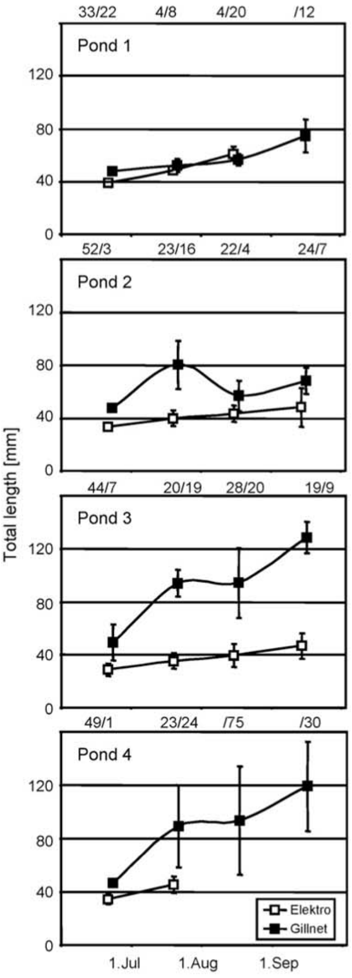

Fig. 7. Mean TL ± S.D. of perch caught in the experimental ponds using electrofishing (white) and gillnets (black) for all parallel samples in 2006. The number of perch is given above each panel (electrofishing/gillnets).

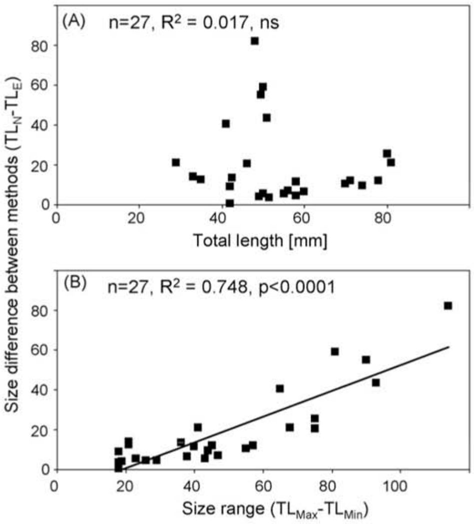

Fig. 8. The absolute difference between the mean TL of all perch from the gillnet catches (TL_N) and the catches by electrofishing (TL_E) according to the median perch size of both sampling methods (A), and the absolute size range of all sampled perch (B) for all parallel catches in 2006.

lakes, which is confirmed by our estimated densities of up to 100-fold more than other European waters (cf. Wanzenböck et al., 1997; Cech et al., 2005, 2007; Guillard et al., 2006; Juza and Kubecka, 2007).

The successive LFDs of our bongo net samples clearly show the addition of smaller perch larvae to the existing cohort. The addition of these smaller larvae on successive sampling dates can be considered as providing a reliable estimate of the length of the hatching period, which was in the range of 2–3 weeks in the gravel pit lakes. Spawning and hatching of perch is temperature dependent, and the spawning period can last between 1 and more than 9 weeks (Thorpe, 1977; Sandström et al., 1997; Gillet and Dubois, 2007). In particular, the length of the spawning period is important for the assessment of the YOY age cohort of perch (Huss et al., 2007) because related differences in size of early and late hatching larvae may be the basis for size-specific development within the YOY cohort, e.g. due to food abundance, competition for food, predation and other seasonal processes that are size dependent (e.g., Brabrand, 1995; Mehner et al., 1998a,b; Byström and Garcia-Berthou, 1999; Beeck et al., 2002; Graeb et al., 2004).

There is an ongoing discussion as to whether the offshore period of perch is time-restricted (Wang and Eckmann, 1994) or whether it depends on a critical size in relation to developmental stage (Urho, 1996). Our results support the latter hypothesis, as there were no major size differences in the post-larval perch between the three lakes on arrival in the littoral zone, but the duration of the pelagic period was found to vary in consecutive years (Beeck, Borcherding, Scharf, unpublished results). In the littoral zone, where bongo net sampling is restricted, perch were caught first with electrofishing. Consequently, we assumed that the observed significant size difference between bongo netting and electrofishing was partly related to

Table 3
Two-way ANOVAs testing the effect of sampling date and fishing method (electrofishing versus gillnets) on the mean TL of perch in the experimental ponds for all dates on which the two methods were used at the same time and the $CPUE_E$ was >0.5 (cf. Fig. 6)

Pond 1 ($r^2 = 0.840$)	df, df_{err}	F	P
Date	2, 85	118.6	<0.0001
Method	1, 85	8.00	0.006
Date × Method	2, 85	22.7	<0.0001
Pond 2 ($r^2 = 0.708$)			
Date	3, 143	13.7	<0.0001
Method	1, 143	91.6	<0.0001
Date × Method	3, 143	11.0	<0.0001
Pond 3 ($r^2 = 0.874$)			
Date	3, 158	68.3	<0.0001
Method	1, 158	640.3	<0.0001
Date × Method	3, 158	27.4	<0.0001
Pond 4 ($r^2 = 0.680$)			
Date	1, 93	10.4	0.002
Method	1, 93	11.5	0.001
Date × Method	1, 93	3.49	0.065

Table 4
Results of the fish removal from the experimental ponds in mid-October

Pond	All perch (ind. ha^{-1})	Perch < 100 mm TL	Perch > 100 mm TL		TL$_{max}$ (mm)
		Individuals (%)	n	Individuals (%)	
1	37,100	100.0	0	0.0	90
2	47,500	99.8	38	0.2	137
3	29,700	98.3	302	1.7	165
4	79,800	97.4	1452	2.6	182

habitat-specific occurrence of the juvenile perch. However, it could also be that a part of the perch population stayed in the pelagic zone but was not caught because of the size-specific escape capability when fishing with bongo nets (cf. Post et al., 1997; Tischler et al., 2000; Cech et al., 2005; Juza and Kubecka, 2007). In such a case, other methods should be applied to test for larger perch in the pelagic zone, either using hydroacoustics in combination with pelagic gillnets (e.g. Imbrock et al., 1996; Schmidt et al., 2005) or by purse seining (Radke et al., 1997; Tischler et al., 2000).

4.2. Electrofishing and gillnet catches

While bongo net sampling or other trawling methods as well as hydroacoustics or purse seining are most efficient for the pelagic zone, electrofishing is more appropriate in the littoral zone (Cowx, 1989). Here, the depth limitation of electrofishing due to the restricted range of the electric field is of minor importance (Copp and Garner, 1995). For the efficiency of capture by electrofishing, two contrasting size-related processes are important: (1) the mobility of juvenile fish increases as they develop and enhance their escape probability from the effective field and (2) the susceptibility of fish to electricity increases with increasing body size (Copp and Garner, 1995). However, Copp and Garner (1995) indicated that size selectivity is of limited importance in the capture of YOY freshwater fish when using PAS with stealth in the littoral zone, as used in our studies.

Limits in the efficiency of gillnets are also size-specific, because the lowest mesh size of 6 mm allows no catches of fish smaller than about 40 mm TL (Appelberg, 2000). To use gillnets for sampling smaller sizes of fish as well, standardization attempts with respect to the Water Framework Directive of the European Union now recommend 5 mm as the minimum mesh size (Prchalova et al., 2009). Nevertheless, above a TL of 50 mm all sizes of perch can be caught with gillnets as used in this study. We started gillnet fishing when we expected perch larger than 40 mm TL at our study sites. In June, when using electrofishing and gillnets simultaneously in the gravel pit lakes, there were only small size differences in the fish between the samples from the two methods. Over the course of the sampling period, however, a significant difference became obvious, as gillnet catches always contained the largest YOY perch compared with those from the parallel electrofishing. This trend increased during the season throughout all the investigated lakes but showed the strongest effect in Lake Speldrop. Comparable trends were also found for the experimental ponds that contained no larger perch (pond 1) or only a very small number (pond 2), as revealed by the fish removal at the end of the experimental period. However, for the ponds 3 and 4, in which more than 1% of the YOY perch were larger than 100 mm TL in October, extreme differences in the mean size of fish in the samples from electrofishing or gillnets were found. The search for a more general trend in the size differences of fish between the two methods revealed, for the gravel pit lakes, a significant positive correlation with increasing size of the YOY perch populations. However, for both the gravel pit lakes and the experimental ponds, the absolute size range of all catches was clearly the better predictor of differences in the mean size of fish in electrofishing and gillnet catches.

In the gravel pit lakes of our investigation, CPUE$_E$ values increased with the successive habitat shift of the juvenile perch to the littoral zone. While the efficiency of electrofishing is primarily less dependent on the activity of the individuals, gillnets can only catch fish that are active during the fishing period and at the fishing locality where the nets are set. Thus, missing sizes of a fish population in gillnet catches cannot solely be seen in the light of efficiency of the nets, but must be interpreted more with respect to the activity patterns and habitat-specific occurrence of the target individuals.

In Lake Speldrop, the smallest perch were always caught by electrofishing in the shallow areas of the littoral zone (depth <50 cm), but not in the somewhat deeper parts of the littoral zone, where gillnets were set only a few metres away. Although the YOY perch were big enough ($\geq$50 mm in October) to be trapped in the gillnets, they were never caught with this method. In Lake Pfeiffer, the CPUE$_E$ decreased sharply in the beginning of July. Here all juvenile perch (which were significantly larger than in Lake Speldrop) avoided the shallow areas, although the littoral zone has a similar morphology to that of Lake Speldrop and although there is a higher degree of structural diversity due to woody debris and submerged vegetation. These results for the gravel pit lakes give clear evidence that size-specific occurrence of the perch caused the observed size differences between electrofishing and gillnet catches. The reason for this differential occurrence in the different habitats may be related to size-specific patterns of foraging, competition or predation (Eklöv and Diehl, 1994; Beeck et al., 2002; Olsson and Eklöv, 2005; Borcherding, 2006; Eklöv and Svanbäck, 2006; Koenig et al., 2006; Borcherding et al., 2007; Olsson et al., 2007; Magnhagen and Borcherding, 2008). In lakes with more shallow but unstructured littoral zones, beach seining is also a very effective method for estimating densities of fish up to sizes of about 100 mm TL (e.g., Staas, 1996; Jurajda et al., 1997). However, this method could not be used either in the gravel pit lakes with their steep banks or in the ponds with their dense submerged vegetation.

The only type of habitat in the experimental ponds is shallow water with large amounts of submerged vegetation and thus a high degree of structural complexity. Here the differences between the LFDs from electrofishing and gillnet sampling must be due to reasons other than those for the gravel pit lakes. In particular, the differences in the LFDs of the ponds 3 and 4 at the final sampling date in September (as compared with the actual populations in the ponds, as revealed by the fish removal in October) verify that the small-sized perch were clearly underrepresented in all samples. This is in accordance with the magnitude of variation in CPUE$_E$ values in the ponds that were of a similar range as seen in the lakes, whereas the CPUE$_N$ values were around 20-fold lower than in the lakes. In contrast to the habitat-specific occurrence patterns in the lakes, this gives clear evidence that the small perch in the experimental ponds were obviously not active, thus being caught in lower numbers in the gillnets. In contrast to the gillnet samples, PAS is relatively independent of the swimming performance of the fish (not to be confused with the escape ability) and consequently this method is also suitable for resting or slow-swimming fish that are not trapped by gillnets. We know (1) from stomach analyses that large-sized YOY perch prey on their small-sized siblings in the ponds (Urbatzka et al., 2008, Heermann and Borcherding, unpublished results), and that (2) small-sized YOY perch are more timid than their larger siblings when foraging for food under the risk of predation (Borcherding, 2006; Koenig et al., 2006). Consequently, we assume reduced swimming activity of the small-sized perch in the experimental ponds due to high predation pressure by their cannibalistic siblings, for which no risk from predatory fish exists.

5. Conclusions

In order to monitor the development of a YOY perch population over their first summer, e.g. to study size-related influences of food abundance, competition or predation (Persson et al., 2004), it is absolutely necessary to find and to follow all size classes on all sampling dates (cf. Beeck et al., 2002). Important aspects of the life-cycle may otherwise be missed or may lead to misinterpretations, as suggested by Urbatzka et al. (2008). Observed differences between the bongo net catches and electrofishing, and between electrofishing and gillnet samples in the gravel pit lakes, were assumed to depend partly on the different occurrence of different size classes of perch at the sampling locations, due either to time differences in the size-specific habitat shift or to small-scale differences where perch stay in the littoral zone. However, the observed differences between electrofishing and gillnet samples in the shallow experimental ponds presumably depend on differences in the activity level of small and large YOY perch, possibly forced by differential predation risk (Magnhagen, 2006; Heermann and Borcherding, unpublished results). While confirming preliminary studies (Wanzenböck et al., 1997; Tischler et al., 2000), our results offer additional evidence that at least two of the three methods used in this study should be applied in an overlapping and parallel sampling design, in order to be sure of obtaining all relevant data on the development of the size structure of the YOY perch population of interest. To extend knowledge of the habitat-specific occurrence of perch after they arrive in the littoral zone, additional sampling of the pelagic zone should be carried out using more efficient methods such as purse seining or hydroacoustics. Furthermore, the sampling design must be extended when differences in the vertical distribution are expected (cf. Cech et al., 2005). Especially when unknown perch populations are studied, an extended and well-designed sampling programme is absolutely necessary to obtain reliable results on certain aspects of the life-cycle.

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References

Appelberg, M., 2000. Swedish standard methods for sampling freshwater fish with multi-mesh gillnets. Fiskeriverket Inform. 1, 3–27.

Appelberg, M., Berger, H.M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J., Rask, M., 1995. Development and intercalibration of methods in nordic freshwater fish monitoring. Water Air Soil Pollut. 85, 401–406.

Beeck, P., Tauber, S., Kiel, S., Borcherding, J., 2002. 0+ perch predation on 0+ bream: a case study on a eutrophic gravel pit lake. Freshwater Biol. 47, 2359–2369.

Borcherding, J., 2006. Prey or predator: piscivorous 0+ perch (*Perca fluviatilis*) in the trade-off between food and shelter. Environ. Biol. Fish. 77, 87–96.

Borcherding, J., Hermasch, B., Murawski, P., 2007. Field observations and laboratory experiments on growth and lipid content of young-of-the-year perch. Ecol. Freshwater Fish 16, 198–209.

Borcherding, J., Magnhagen, C., 2008. Food abundance affects both morphology and behaviour of juvenile perch. Ecol. Freshwater Fish 17, 207–218.

Borcherding, J., Maw, S.K., Tauber, S., 2000. Growth of 0+ perch (*Perca fluviatilis*) predating on 0+ bream (*Abramis brama*). Ecol. Freshwater Fish 9, 236–241.

Brabrand, A., 1995. Intra-cohort cannibalism among larval stages of perch (*Perca fluviatilis*). Ecol. Freshwater Fish 4, 70–76.

Byström, P., Garcia-Berthou, E., 1999. Density dependent growth and size specific competitive interactions in young fish. Oikos 86, 217–232.

Cech, M., Kratochvil, M., Kubecka, J., Drastik, V., Matena, J., 2005. Diel vertical migrations of bathypelagic perch fry. J. Fish Biol. 66, 685–702.

Cech, M., Kubecka, J., Frouzova, J., Drastik, V., Kratochvil, M., Matena, J., Hejzlar, J., 2007. Distribution of the bathypelagic perch fry layer along the longitudinal profile of two large canyon-shaped reservoirs. J. Fish Biol. 70, 141–154.

Copp, G.H., Garner, P., 1995. Evaluating the microhabitat use of freshwater fish larvae and juveniles with point abundance sampling by electrofishing. Folia Zool. 44, 145–158.

Cowx, I., 1989. Developments in Electrofishing. Fishing New Books, Oxford.

Eklöv, P., Diehl, S., 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. Oecologia 98, 344–353.

Eklöv, P., Svanbäck, R., 2006. Predation risk influences adaptive morphological variation in fish populations. Am. Nat. 167, 440–452.

Gillet, C., Dubois, J.P., 2007. Effect of water temperature and size of females on the timing of spawning of perch *Perca fluviatilis* L. in Lake Geneva from 1984 to 2003. J. Fish Biol. 70, 1001–1014.

Glass, C.W., Wardle, C.S., 1989. Comparison of the reactions of fish to a trawl gear, at high and low light intensities. Fish. Res., 249–266.

Graeb, B.D.S., Dettmers, J.M., Wahl, D.H., Caceres, C.E., 2004. Fish size and prey availability affect growth, survival, prey selection, and foraging behavior of larval yellow perch. Trans. Am. Fish. Soc. 133, 504–514.

Griffiths, D., Kirkwood, R.C., 1995. Seasonal variation in growth, mortality and fat stores of roach and perch in lough Neagh, Northern Ireland. J. Fish Biol. 47, 537–554.

Guillard, J., Perga, M.E., Colon, M., Angeli, N., 2006. Hydroacoustic assessment of young-of-year perch, *Perca fluviatilis*, population dynamics in an oligotrophic lake (Lake Annecy, France). Fish. Manag. Ecol. 13, 319–327.

Heermann, L., Beeck, P., Borcherding, J., 2007. Two size classes of 0+ perch: is phenotypic plasticity based on food resources? J. Fish Biol. 70, 1365–1377.

Huss, M., Persson, L., Bystrom, P., 2007. The origin and development of individual size variation in early pelagic stages of fish. Oecologia 153, 57–67.

Imbrock, F., Appenzeller, A., Eckmann, R., 1996. Diel and seasonal distribution of perch in Lake Constance: a hydroacustic study and in situ observations. J. Fish Biol. 49, 1–13.

Jurajda, P., Reichard, M., Hohausova, E., 1997. A survey of inshore 0+ juvenile fish community in the Nove Mlyny lowland reservoir, Czech republic. Folia Zool. 46, 279–285.

Juza, T., Kubecka, J., 2007. The efficiency of three fry trawls for sampling the freshwater pelagic fry community. Fish. Res. 85, 285–290.

Koenig, U., Klahold, P., Fischer, P., Borcherding, J., 2006. Bold and shy: mesocosm experiments on the trade-off between feeding and predator avoidance of two size classes of 0+ perch. J. Fish Biol. 69 (Suppl. C), 255.

Magnhagen, C., 2006. Risk-taking behaviour in foraging young-of-the-year perch varies with population size structure. Oecologia 147, 734–743.

Magnhagen, C., Borcherding, J., 2008. Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness? Anim. Behav. 75, 509–517.

Mehner, T., Bauer, D., Schultz, H., 1998a. Early omnivory in age-0 perch (*Perca fluviatilis*)—a key for the understanding long-term manipulated food webs? Verh. Int. Verein. Limnol. 26, 2287–2289.

Mehner, T., Plewa, M., Hülsmann, S., Worischka, S., 1998b. Gape-size dependent feeding of age-0 perch (*Perca fluviatilis*) and age-0 zander (*Stizostedion lucioperca*) on *Daphnia galeata*. Arch. Hydrobiol. 142, 191–207.

Mooij, W.M., 1996. Variation in abundance and survival of fish larvae in shallow eutrophic lake Tjeukemeer. Environ. Biol. Fish. 46, 265–279.

Mous, P.J., Van Densen, W.L.T., Machiels, M.A.M., 2002. The effect of smaller mesh sizes on catching larger fish with trawls. Fish. Res. 54, 171–179.

Olsson, J., Eklöv, P., 2005. Habitat structure, feeding mode and morphological reversibility: factors influencing phenotypic plasticity in perch. Evol. Ecol. Res. 7, 1109–1123.

Olsson, J., Svanbäck, R., Eklöv, P., 2006. Growth rate constrain morphological divergence when driven by competition. Oikos 115, 15–22.

Olsson, J., Svanbäck, R., Eklöv, P., 2007. Effects of resource level and habitat type on behavioral and morphological plasticity in Eurasian perch. Oecologia 152, 48–56.

Ona, E., Godo, O.R., 1990. Fish reaction to trawling noise: the significance for trawl sampling. Rapp. P. -v. Reun. Cons. Int. Explor. Mer. 189, 159–166.

Pepin, P., Shears, T.H., 1997. Variability and capture efficiency of bongo and Tucker trawl samplers in the collection of ichthyoplankton and other macrozooplankton. Can. J. Fish. Aquat. Sci. 54, 765–773.

Persat, H., Copp, G.H., 1989. Electrofishing and point abundance sampling for the ichthyology of large rivers. In: Cowx, I. (Ed.), Developments in Electrofishing. Fishing New Books, Oxford, pp. 203–215.

Persson, L., Claessen, D., De Roos, A.M., Byström, P., Sjörgren, S., Svanbäck, R., Wahlström, E., Westman, E., 2004. Cannibalism in a size-structured population: energy extraction and control. Ecol. Monogr. 74, 135–157.

Persson, L., Greenberg, L.A., 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)–roach (*Rutilus rutilus*) interaction. Ecology 71, 44–56.

Post, J.R., Johannes, M.R.S., McQueen, D.J., 1997. Evidence of density-dependent cohort splitting in age-0 yellow perch (*Perca flavescens*): potential behavioural mechanisms and population-level consequences. Can. J. Fish. Aquat. Sci. 54, 867–875.

Post, J.R., McQueen, D.J., 1994. Variability in first-year growth of yellow perch (*Perca flavescens*)—predictions from a simple model, observations, and an experiment. Can. J. Fish. Aquat. Sci. 51, 2501–2512.

Prchalová, M., Kubečka, J., Říha, M., Mrkvička, T., Vašek, M., Jůza, T., Kratochvíl, M., Peterka, J., Draštík, V., Křížek, J., 2009. Size selectivity of standardized multimesh gillnets in sampling coarse European species. Fish. Res. 96, 51–57.

Radke, R.J., Helms, C., Eckmann, R., 1997. Möglichkeiten der Nutzung kleiner Ringwaden zur Bearbeitung fischökologischer Fragestellungen. Fischer. Teichwirt 4, 150–152.

Sandström, O., Abrahamsson, I., Andersson, J., Vetemaa, M., 1997. Temperature effects on spawning and egg development in Eurasian perch. J. Fish Biol. 51, 1015–1024.

Schmidt, M.B., Gassner, H., Meyer, E.I., 2005. Distribution and biomass of an underfished vendace, *Coregonus albula*, population in a mesotrophic German reservoir. Fish. Manag. Ecol. 12, 169–175.

Staas, S., 1996. The occurrence of larval and juvenile 0+ fish in the Lower River Rhine. Arch. Hydrobiol. 113 (Suppl), 325–332.

Svanbäck, R., Eklöv, P., 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. Oecologia 131, 61–70.

Thorpe, J.E., 1977. Synopsis of biological data on perch, *Perca fluviatilis* Linnaeus, 1758, and *Perca flavescens* Mitchill, 1814. FAO Fish. Synopsis 113, 1–138.

Tischler, G., Gassner, H., Wanzenböck, J., 2000. Sampling characteristics of two methods for capturing age-0 fish in pelagic lake habitats. J. Fish Biol. 57, 1474–1487.

Urbatzka, R., Beeck, P., Van der Velde, G., Borcherding, J., 2008. Alternative use of food resources causes intra-cohort variation in the size distribution of young-of-the-year perch (*Perca fluviatilis*). Ecol. Freshwater Fish. 17, 475–480.

Urho, L., 1996. Habitat shifts of perch larvae as survival strategy. Ann. Zool. Fennici 33, 329–340.

Wang, N., Eckmann, R., 1994. Distribution of perch (*Perca fluviatilis* L.) during their 1st year of life in Lake Constance. Hydrobiologia 277, 135–143.

Wanzenböck, J., Matena, J., Kubecka, J., 1997. Comparison of two methods to quantify pelagic early life stages of fish. Arch. Hydrobiol. Spec. Issues Adv. Limnol. 49, 117–124.

CHAPTER V

How to preserve? Preservation techniques and their consequences for morphometric analysis in fish

König, Ulrike & Borcherding, Jost

University of Cologne, Zoological Institute, General Ecology and Limnology, Ecological Research Station Grietherbusch, 46459 Rees-Grietherbusch, Germany

Abstract

For studies in fish ecology it is important to preserve and store caught fish as it is often not possible to analyse individuals in the field. This not only includes length and weight measurements, but also a variety of other analyses such as stomach content analyses, stable isotopes or otolith analysis. In this study, juvenile perch were measured and frozen at -20°C, preserved in 70% ethanol or 4% formalin and remeasured after 24h, 3 days, 7 days and then on a weekly basis for eight weeks. Ethanol strongly decreased length and weight of preserved perch. Formalin preservation also led to comparable length reduction but increased the weight of preserved perch. In contrast, frozen perch showed less shrinkage and only moderate weight loss. In the morphometric analysis also freezing clearly revealed the lowest shape differences compared to fresh fish, and in contrast to ethanol and formalin. Hence, we would recommend freezing as the most preferable preservation method, especially in multi-disciplinary studies on fish ecology.

Introduction

Studies concerning the ecology of fish population often require a variety of measurements such as length and weight. Fish length is frequently used in modelling, monitoring and to describe basic biological relationships (Hoyle et al. 2000; Jennings et al. 2001; Morison et al. 2003). Also a variety of other examinations such as stomach content analyses to establish fish diet, stable isotopes to determine trophic status or otolith analysis for age determination is important for ecological studies of fish communities. Regularly it is not possible to conduct these analyses in the field, either because it is impossible to take the instruments needed into the field or simply because there is not enough time, for example, to measure the length and weight of all individuals caught. Therefore, fish are preserved for later analyses in the laboratory. The most common preservatives are freezing, alcohol and formalin and they are known to affect the size and weight of individuals preserved. Correction factors have been suggested to estimate body length before preservation (Annelida: Costa-Paiva et al. 2007, fish: Fey & Hare 2005; Buchheister & Wilson 2005; Neave et al. 2006). Not only density of the preservative but also original length of fish influences the strength of changes: small fish are affected stronger than larger specimen (Fowler & Smith 1983; Treasurer 1992; Fey 1999). The latter gives some evidence that morphological characteristics are also affected by different preservation techniques (Sagnes 1997). During the last years new morphometric analyses (based on landmarks, Bookstein 1991) became increasingly important in ecological studies in fish (Hjelm et al. 2001; Svanbäck & Eklöv 2004; Olsson & Eklöv 2005; Svanbäck & Eklöv 2006; Heermann et al. 2007), however, differences between preservation techniques and related shape changes have not been considered until now.

Formalin has been used traditionally and is known to provide excellent results, especially when stomach content analyses are conducted. It has become a standard method for fixation and preservation and has made many studies comparable among each other. It is supposed to reduce morphological distortion and quickly permeates the tissue, but also bears considerable health risks (e.g., Black A.R. & Dodson S.I. 2003). As an alternative preservative alcohol has been recommended by Black A.R. & Dodson S.I. (2003), at least for daphnids. It is less hazardous and has good preservation characteristics. It is easy to store without disposal complications and low costs. Ethanol-stored tissues can be used for analyses that formalin-stored ones can not such as genetic (Sambrook et al. 1989) and otolith analyses (Kristoffersen & Salvanes 1998). On the other hand, for several examinations organisms should be stored frozen (e.g., stable isotopes, RNA-DNA ratio used to measure fish growth).

In order to estimate what preservation technique would be the best for ecological studies, in which the results of a variety of analyses are of interest, we preserved young-of-the-year (YOY) perch (*Perca fluviatilis*) with three techniques (freezing, ethanol, and formalin) and analysed length, weight and shape changes over a period of eight weeks. In addition, a short experiment should give first cues how these preservation techniques may affect stomach analyses in fish. The objectives of this study were 1) to quantify the effect of preservation technique on length, weight, body shape and condition of stomach content of juvenile perch and 2) to give a recommendation on which preservative should be used when studying a variety of ecological aspects in a multi-disciplinary approach.

Methods

Young-of-the-year (YOY) perch were sampled at experimental ponds with areas from 0.4 to 0.7 ha and maximum depths of 2 m (mean depths of about 1 m, Urbatzka et al. 2008). The ponds are situated near Lohmar (50°49’33’’N, 7°12’59’’E; Germany) and were completely drained for the removal of fish for another study in October 2007. Randomly chosen perch (66.5 ± 10.2 mm) were collected from sub-samples of these ponds and transported to the laboratory of the Ecological Research Station in Rees-Grietherbusch. They were randomly distributed in aquaria and held at 16°C under natural light regime (10h light: 14h dark) for two weeks. Perch were not fed 24h prior to measurements and the following preservation to diminish variation due to stomach content rather than preservation method. Before being preserved, fish were anaesthetized to minimize handling stress which may cause shrinkage in fish (Fowler & Smith 1983). They were dead at the time of initial measurements of length, weight and body shape. After being blotted dry with paper towels (Parker 1963), each fish was weighed (± 0.001 g) and measured (± 0.01 mm total length) immediately and individually preserved in vials. Fish were randomly chosen and 20 individuals each were used for formalin (4%) and ethanol (70% anhydrous ethyl alcohol) preservation. For ice preservation, 200 fresh individuals were measured and only 20 individuals of this group were defrosted and remeasured at a time to avoid handling effects due to reoccurring freezing and thawing. Ice perch were placed flat and straight in a freezer bag and individually frozen at -20°C. Frozen fish were thawed at room temperature and individuals from all preservation methods were blotted with paper towels prior to measurements. To investigate the effect of each preservation method on perch length and weight, fish were remeasured and reweighed after 24h, three days, one week and then weekly up to 8 weeks, as we did not expect to find much ongoing change (Treasurer 1992). Each fish was identified and retraceable by placing a label including a number and the preservation technique inside the vials and freezer bags. In addition, we also analysed the condition of stomach contents of an additional group of perch (52.4 ± 3.9 mm). The perch were fed a fixed amount of mysids, *Limnomysis benedenii*, three hours prior to formalin, ethanol and ice preservation, as three hours sampling intervals are thought to provide reliable estimates in stomach content analyses (Beeck 2003; Finstad 2005).

Changes in length and weight were expressed in terms of percentage. This term is described as ‘gain’ representing shrinkage when values are negative and enlargement when values are positive: Gain [%] = $[(L_t-L_0)/L_0]*100$; with L_0 = initial length and L_t = length at time t.

The same calculation was repeated for weight measurements. The relationship between initial and preserved measurements was calculated using a logarithmic regression:

$L_0 = a + b * \ln(x)$ (Treasurer 1992; Paradis et al. 2007).

To analyze morphological differences between the groups of perch (fresh perch and perch after eight weeks of preservation either with freezing, ethanol or formalin), individuals were placed on a piece of Styrofoam which contains a hollow space to avoid deformation. They were photographed with a digital camera next to a ruler. By tpsDigit and tpsUtility software (available at: http://life.bio.sunysb.edu/morph/) eighteen landmarks on the perch as well as ruler endpoints were digitized and the x-y co-ordinates were recorded. Data was further analysed with the Integrated Morphometrics Package (IMP) (http://www3.canisius.edu/~sheets/morphsoft.html). By means of the

IMP software programme CoordGen6 procrustes superimposition was performed with all specimens (cf. Rohlf & Slice 1990). The shape change of groups was analysed with a canonical variates analysis (CVA) using the software CVAGen6. Partial warp scores were computed and overall shape change was analysed with a MANCOVA by combining the partial warp scores and the uniform components with cohort as the grouping variable and LCS as the covariate (Zelditch et al. 2000). The tests of significance of the canonical variate axes are all based on Wilk's λ value at a $p < 0.05$ level of significance. Further information on the morphometric analyses can be obtained from Heermann et al. (2007).

Results

Significant differences were found in length changes for YOY perch preserved either in ice, 70% ethanol or 4% formalin (Fig. 1). For the parameter length, perch preserved frozen at -20°C did not follow a regression formula but generally showed a slightly lower size of about 2 %, independent of preservation duration (Fig. 1, Tab. 1).

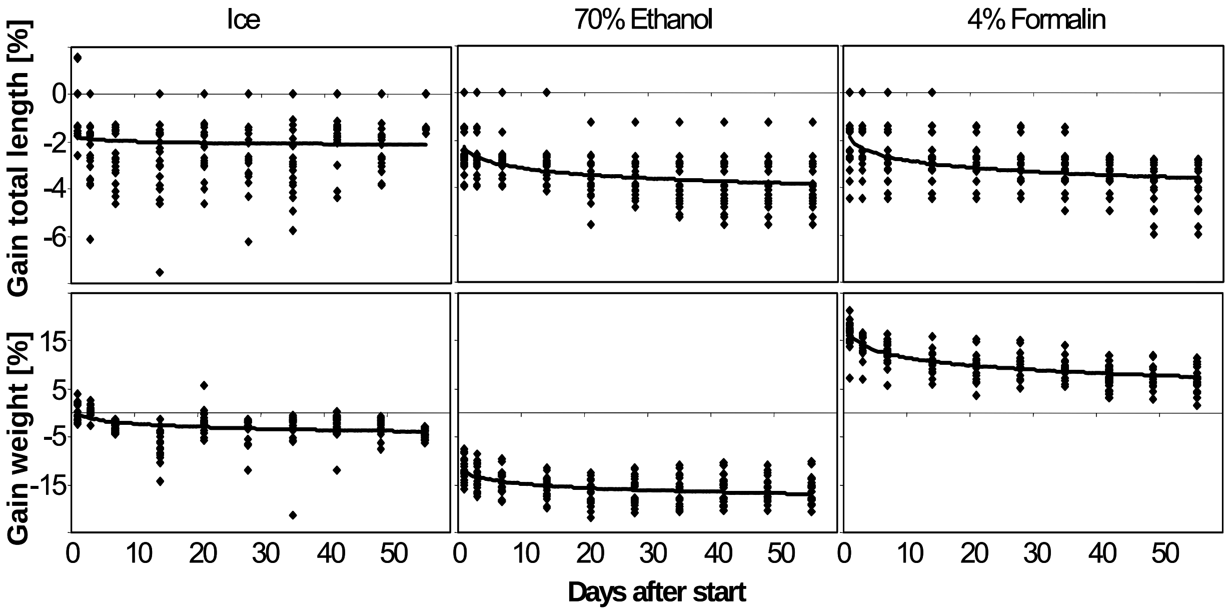


Figure 1: Length and weight changes of YOY perch in relation to the duration of the preservation described as gain total length [%] (upper panel) and gain weight [%] (lower panel) in comparison to the unpreserved start group. Preservation technique: ice (left), 70% ethanol (middle) and 4% formalin (right).

When perch were preserved either in 70% ethanol or 4% formalin, length shrinkage of about 3% were observed after 10 days that increased slightly up to about 3.5 % after 60 days (Fig. 2). In contrast, weight differences were much higher and clearly changed with preservation technique and time. The difference between fresh weight and weight of preserved perch was lowest for frozen fish (2.3 % after 10 days) and only increased slightly with the duration of the preservation (Fig. 1 and 2). Fish preserved in 70% ethanol lost approximately ten times more weight than frozen fish resulting in a

Table 1: Parameters (a, b) of the logarithmic regression equation for conversion of preserved lengths and weights to fresh values for three preservatives. n = number of perch analysed.

Preservation technique		n	a	b	r	p
Ice	L_t [mm]	199	-1.805	-0.077	0.066	n.s.
	Weight [g]	199	-0.149	-0.923	0.382	$p < 0.001$
70% Ethanol	L_t [mm]	200	-2.290	-0.387	0.462	$p < 0.001$
	Weight [g]	200	-11.990	-1.216	0.492	$p < 0.001$
4% Formalin	L_t [mm]	200	-1.877	-0.426	0.483	$p < 0.001$
	Weight [g]	200	16.732	-2.278	0.757	$p < 0.001$

weight decrease of almost 15% (after 10 days) to17 % (after 60 days) compared to fresh weight. In contrast, preservation with 4% formalin caused a distinct increase in weight (about 11 % after 10 days) that decreased in relation to the preservation duration (Fig. 1 and 2).

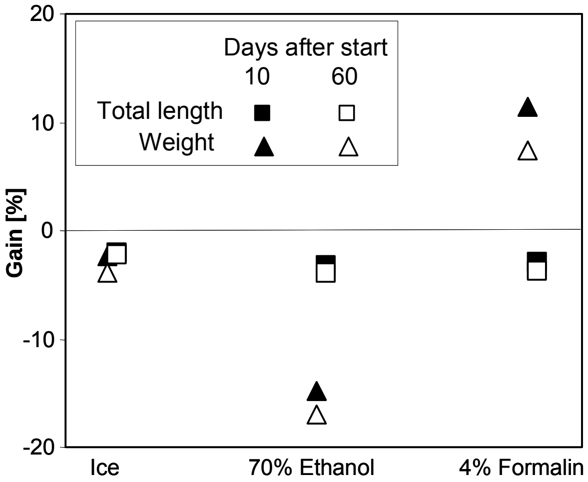


Figure 2: Changes of length (squares) and weight (triangles) after 10 days (black) and after 60 days (white) of preservation in ice, 70% ethanol and 4% formalin.

Morphometric analyses between the body shape of fresh perch and that of preserved perch offered three significant axes; the first two of them are given in the CVA plot in figure 3. The first axis clearly distinguished fresh and frozen perch from perch preserved in ethanol and formalin (CVA MANOVA: $\lambda = 0.0217$, $\chi^2 = 386.92$, df = 96, $p < 0.001$; eigenvalue 5.59). The second axis separated perch preserved in ethanol from all other perch and the third axis separated frozen perch from the rest (CVA MANOVA: Axis 2 $\lambda = 0.1430$, $\chi^2 = 196.46$, df = 62, $p < 0.001$, eigenvalue 2.13 and Axis 3 $\lambda = 0.4468$, $\chi^2 = 81.38$, df = 30, $p < 0.001$, eigenvalue 1.24). In order to quantify morphometric changes due to the different preservation techniques we analysed the differences between individual fresh and preserved perch separately for each technique. Results support the CVA plot revealing that fresh perch and frozen perch are most similar in body shape possessing an eigenvalue of 8.6 and a much lower p-value than we received for ethanol and formalin (Tab. 2).

Table 2: Results from CVA Manova between scores of fresh perch and eight weeks after preservation

Preservation	λ	χ^2	df	p	eigenvalue
Ice	0.104	49.758	32	$p = 0.023$	8.599
4% Formalin	0.010	102.130	32	$p < 0.001$	102.779
70% Ethanol	0.008	106.386	32	$p < 0.001$	124.928

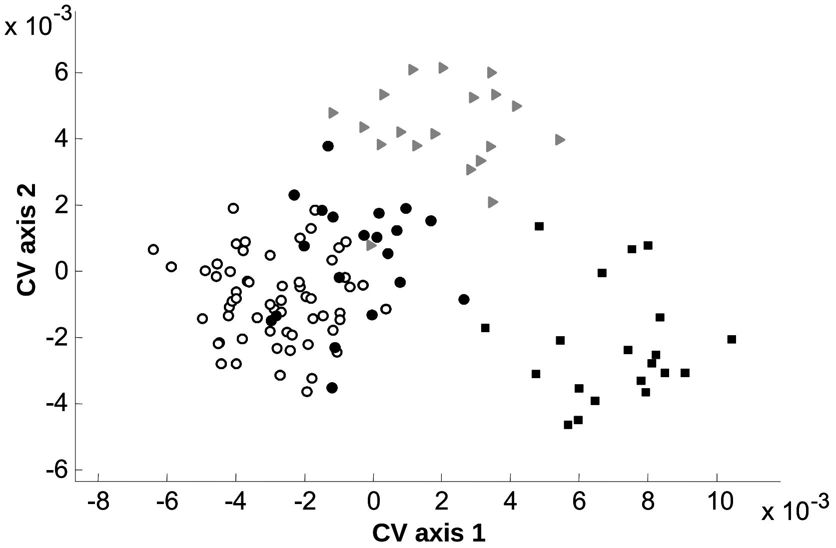
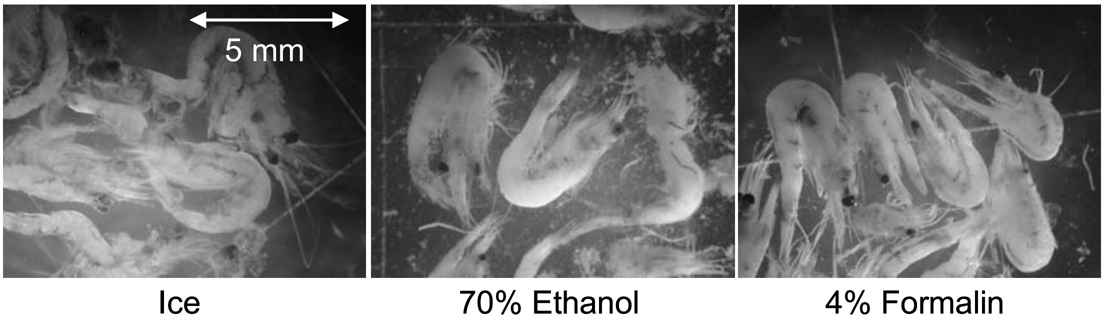


Figure 3: Morphometric analyses of perch after eight weeks preservation. Canonical variate scores of perch unpreserved (empty circles, n=60) and the three preservation techniques (filled symbols, each n=20), depicted along the first and the second canonical variate axis. Circles (black) = freezing, triangles = 70% ethanol, squares = 4% formalin

Stomach content analyses revealed that formalin displayed the best preservation results (Fig. 4). Mysids were well preserved without any noticeable signs of the digestion process. Also, preservation of frozen perches' stomach content was fairly good. The mysids were lighter in colour with little disintegration visible. Only preservation of stomach content of perch in 70% ethanol showed strong signs of degradation. Here we detected mysids with missing head or tail regions and some amorphous tissue due to the digestion processes.



Ice
70% Ethanol
4% Formalin

Figure 4: Pictures of stomach content (mysids *Limnomysis benedenii*) of YOY perch preserved with ice, 70% ethanol and 4% formalin.

Discussion

Independent on the preservation technique, most important changes due to the preservation occurred during the first days, which was reflected through the logarithmic regression and has been found in other studies as well (Fowler & Smith 1983; Fisher et al. 1998; Fey 1999). Ethanol preserved individuals showed more shrinkage than perch preserved with formalin which has been known to take place for a variety of fish species (Fowler & Smith 1983; Fox 1996; Fisher et al. 1998; Moku et al. 2004; Neave et al. 2006; Paradis et al. 2007 for silver hake (*Merluccius bilinearis*), herring (*Clupea harengus*), yellow perch (*Perca flavescens*), myctophid fish, lampreys and yellow perch respectively). Other studies, e.g. by Fey (1999) and Hjörleifsson & Kleinmacphee (1992, flounder *Pleuronectes americanus*) found opposite results. Conflicting results in the literature might result from different handling as this can already lead to shrinkage (Fox 1996). We limited non-preservative changes as fish were held in aquaria for two weeks after catch and were anaesthetised prior to experiments to reduce handling induced stress.

We observed ethanol to cause a decrease in weight while formalin increased weight in YOY perch (Billy 1982; Buchheister & Wilson 2005). Freezing resulted in a general shrinkage of about 2 % and only moderate weight loss. Florin & Lingman (2008) found a similar range of shrinkage: freezing of adult flounder (*Platichthys flesus* L.) and turbot (*Psetta maxima* L.) resulted in a 2.1% and 1.9% decrease after 25 days. The same magnitude of changes was discovered in other studies (Ajah & Nunoo 2003; Buchheister & Wilson 2005). As well as for ethanol and formalin opposite results have been recorded by Engel (1974) and Johnston & Mathias (1993), which found a stronger decrease by freezing than preservation in formalin. Nevertheless, our results give clear evidence that freezing exhibited the smallest deviation from the unpreserved fish for all preservatives examined, as well as for changes in size as for weight.

Likewise, morphometric analyses revealed frozen perch to be much more similar with fresh perch than perch preserved in ethanol and formalin. Comparisons to other studies are difficult, as morphometric changes with landmark analysis have not been examined for the three preservatives before. Only Sagnes (1997) has made an attempt of examining the effect of formalin on overall body measurements in grayling (*Thymallus thymallus*), rather than length and weight changes alone. Although the author quoted that a 4% formalin solution usually caused decreases in various body lengths and fin areas and increases in various body widths, the picture becomes more complicated when the size of the juveniles and differences between two populations were taken into account (Sagnes 1997). And of course there was no comparison between the effects of different preservation techniques. The earliest studies on fish morphology using landmark data were made on museum material (e.g. Zelditch & Fink 1995) that is regularly preserved in formalin (Black A.R. & Dodson S.I. 2003), however, details concerning this aspect are often missing. This is also due to some more recent ecological studies in fish (e.g. Svanbäck & Eklöv 2006), but regularly the analysis is based either on frozen (Hjelm et al. 2001) or fresh fish (Olsson & Eklöv 2005). Sometimes different preservation methods were used within one study (e.g. Heermann et al. 2007). As long as no direct morphometric comparisons between differentially preserved fish are performed within one study, usage of different preservation techniques may be unproblematic. However, our results clearly indicate that morphological deviations between differentially preserved groups may be as large to overrun differences that are interpreted in the light of ecological adaptations.

One of the objectives of this study was to give a recommendation on which preservative should be used when studying population dynamics in fish. Of course, the choice of the preservation method is determined by the study objective. However, many studies focus on multiple objectives, thus, usage of different methods can be recommended (Kruse & Dalley 1990). In accordance with Ajah & Nunoo (2003) our results have revealed frozen perch to be the best choice as a preservative, and this for different purposes. Not only length and weight differences between fresh and preserved specimen were lowest compared with ethanol and formalin, but also morphometric shape changes. Although the pictures of the stomach contents of perch have clearly shown the superiority of formalin in this respect, the results for frozen fish were still reasonably good. Formalin displays very good preservation characteristics, however, health concerns for formaldehyde exposure have already let to prohibition of formalin usage in several countries. Inhalation of formaldehyde vapours can not completely be avoided when working with formalin preserved organisms and is highly irritating to the upper respiratory tract and eyes. It is also a severe skin irritant and sensitizer and can even result in numbness and hardening of the skin. This makes it difficult to use in the field and usage of special clothing such as rubber gloves is necessary. Even allergic responses to very low concentrations have been reported (Black A.R. & Dodson S.I. 2003). Long term effects include cancer and mutation and can occur through permanent exposure to even undetectable fumes (OSHA 2001).

Ethanol is suitable for some analyses that formalin can not be used for but has also revealed to cause the strongest length and weight changes. And it provided the poorest results in stomach content analyses. Further, ethanol can evaporate from screw cap sample bottles and snap cap vials. Also, zooplankton has been shown to become brittle. Thus it may not be suitable for long term storage (Black A.R. & Dodson S.I. 2003).

Freezing can be used for all important analyses such as stomach content, condition factor, otoliths and stable isotopes. Therefore, it should be introduced as a standard preservation technique. Handling in the field is easy, it is cheap and freezing does not bear any health risks. Specimen should be kept as flat as possible and avoid air contact when freezing to reduce damage, body shrinkage and weight loss due to desiccation (Paradis et al. 2007). Only for RNA-DNA related analyses specimen should be preserved and stored with dry ice (-80°C) as for such analyses nucleic acid denaturation has to be avoided (Weber et al. 2003).

Acknowledgements

The experiments conducted in the present study comply with the current laws of Germany.

References

Ajah, P. O. & Nunoo, F. K. E. (2003). The effects of four preservation methods on length, weight and condition factor of the clupeid *Sardinella aurita* Val. 1847. *Journal of Applied Ichthyology* **19,** 391-393.

Beeck, P. (2003). The early piscivory of European perch (*Perca fluviatilis*): A neglected phenomenon with notable consequences for the population structure and fish community in lake ecosystems. PhD Thesis. Universität zu Köln.

Billy, A. J. (1982). The Effects of Formalin and Isopropyl-Alcohol on Length and Weight Measurements of Sarotherodon-Mossambicus Trewavas. *Journal of Fish Biology* **21,** 107-112.

Black A.R. & Dodson S.I. (2003). Ethanol: a better preservation technique for *Daphnia*. *Limnology and Oceanography: Methods* **1,** 45-50.

Bookstein, F. L. (1991). *Morphometric tools for landmark data: geometry and biology.* Cambridge: Cambridge University Press.

Buchheister, A. & Wilson, M. T. (2005). Shrinkage correction and length conversion equations for *Theragra chalcogramma*, *Mallotus villosus* and *Thaleichthys pacificus*. *Journal of Fish Biology* **67,** 541-548.

Costa-Paiva, E. M., Paiva, P. C. & Klautau, M. (2007). Anaesthetization and fixation effects on the morphology of sabellid polychaetes (Annelida : Polychaeta : Sabellidae). *Journal of the Marine Biological Association of the United Kingdom* **87,** 1127-1132.

Engel, S. (1974). Effects of Formalin and Freezing on Length, Weight and Condition Factor of Cisco and Yellow Perch. *Transactions of the American Fisheries Society* **103,** 136-138.

Fey, D. P. (1999). Effects of preservation technique on the length of larval fish: methods of correcting estimates and their implication for studying growth rates. *Archive of Fishery and Marine Research* **47,** 17-29.

Fey, D. P. & Hare, J. A. (2005). Length correction for larval and early-juvenile Atlantic menhaden (*Brevoortia tyrannus*) after preservation in alcohol. *Fishery Bulletin* **103,** 725-727.

Finstad, A. G. (2005). Effect of sampling interval and temperature on the accuracy of food consumption estimates from stomach contents. *Journal of Fish Biology* **66,** 33-44.

Fisher, J. S., Andersson, M. R. & WILLIS, D. W. (1998). Total Length Reduction in Preserved Yellow Perch Larvae. *North American Journal of Fisheries Management* **18,** 739-742.

Florin, A. B. & Lingman, A. (2008). Shrinkage of flounder *Platichthys flesus* (L.) and turbot *Psetta maxima* (L.) following freezing. *Journal of Fish Biology* **72,** 731-736.

Fowler, G. M. & Smith, S. J. (1983). Length Changes in Silver Hake (Merluccius-Bilinearis) Larvae - Effects of Formalin, Ethanol, and Freezing. *Canadian Journal of Fisheries and Aquatic Sciences* **40,** 866-870.

Fox, C. J. (1996). Length changes in herring (*Clupea harengus*) larvae: Effects of capture and storage in formaldehyde and alcohol. *Journal of Plankton Research* **18,** 483-493.

Heermann, L., Beeck, P. & Borcherding, J. (2007). Two size classes of 0+ perch: is phenotypic plasticity based on food resources? *Journal of Fish Biology* **70,** 1365-1377.

Hjelm, J., Svanbäck, R., Byström, P., Persson, L. & Wahlström, E. (2001). Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. *Oikos* **95,** 311-323.

Hjörleifsson, E. & Kleinmacphee, G. (1992). Estimation of Live Standard Length of Winter Flounder Pleuronectes-Americanus Larvae from Formalin-Preserved, Ethanol-Preserved and Frozen Specimens. *Marine Ecology-Progress Series* **82,** 13-19.

Hoyle, S. D., Queensland.Dept.of Primary Industries. & Fisheries Research and Development Corporation (Australia) (2000). *Integrated fish stock assessment and monitoring program*. Deception Bay, Qld.: Southern Fisheries Centre, Dept. of Primary Industries.

Jennings, S., Kaiser, M. & Reynolds, J. D. (2001). *Marine Fisheries Ecology*. Oxford: Blackwell Publishing.

Johnston, T. A. & Mathias, J. A. (1993). Length reduction and dry weight loss in frozen and formalin-preserved larval walleye, *Stizostedion vitreum* (Mitchill). *Aquaculture and Fisheries Management* **24,** 365-371.

Kristoffersen, J. B. & Salvanes, A. G. V. (1998). Effects of formaldehyde and ethanol preservation on body and otoliths of *Maurolicus muelleri* and *Benthosema glaciale*. *Sarsia* **83,** 95-102.

Kruse, G. H. & Dalley, E. L. (1990). Length Changes in Capelin, Mallotus-Villosus (Müller), Larvae Due to Preservation in Formalin and Anhydrous Alcohol. *Journal of Fish Biology* **36,** 619-621.

Moku, M., Mori, K. & Watanabe, Y. (2004). Shrinkage in the body length of myctophid fish (Diaphus slender-type spp.) larvae with various preservatives. *Copeia* 647-651.

Morison, A. K., Brown, I. W. & Jones, G. K. (2003). Post mortem shrinkage of four species of temperate and tropical marine fishes, without freezing or preservation. *Journal of Fish Biology* **62,** 1435-1449.

Neave, F. B., Mandrak, N. E., Docker, M. F. & Noakes, D. L. (2006). Effects of preservation on pigmentation and length measurements in larval lampreys. *Journal of Fish Biology* **68,** 991-1001.

Olsson, J. & Eklöv, P. (2005). Habitat structure, feeding mode and morphological reversibility: factors influencing phenotypic plasticity in perch. *Evolutionary Ecology Research* **7,** 1109-1123.

OSHA . Regulations (Standards - 29 CFR) Substance technical guidelines for formalin - 1910.1048 App A. 2001.
Ref Type: Report

Paradis, Y., Brodeur, P., Mingelbier, M. & Magnan, P. (2007). Length and weight reduction in larval and juvenile yellow perch preserved with dry ice, formalin, and ethanol. *North American Journal of Fisheries Management* **27,** 1004-1009.

Parker, R. R. (1963). Effects of Formalin on length and weight of fishes. *J.Fish.Res.Bd.Can.* **20,** 1441-1455.

Rohlf, F. J. & Slice, D. (1990). Extensions of the procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* **39,** 40-59.

Sagnes, P. (1997). Potential artefacts in morphometric analyses of fish: Effects of formalin preservation on 0+ grayling. *Journal of Fish Biology* **50,** 910-914.

Sambrook, J., Fritsch, E. E. & Maniatis, T. (1989). *Molecular cloning: a laboratory manual.* Cold Spring Harbor Laboratory.

Svanbäck, R. & Eklöv, P. (2004). Morphology in perch affects habitat specific feeding efficiency. *Functional Ecology* **18,** 503-510.

Svanbäck, R. & Eklöv, P. (2006). Genetic variation and phenotypic plasticity: causes of morphological and dietary variation in Eurasian perch. *Evolutionary Ecology Research* **8,** 27-49.

Treasurer, J. W. (1992). Length and weight changes in 0+ perch, *Perca fluviatilis* L. following fixation in formalin. *Journal of Fish Biology* **41,** 1033-1036.

Urbatzka, R., Beeck, P., Van der Velde, G. & Borcherding, J. (2008). Alternative use of food resources causes intra-cohort variation in the size distribution of young-of-the-year perch (*Perca fluviatilis*). *Ecology of Freshwater Fish* **doi: 10.1111/j.1600-0633.2008.00300.x**.

Weber, L. P., Higgins, P. S., Carlson, R. I. & Janz, D. M. (2003). Development and validation of methods for measuring multiple biochemical indices of condition in juvenile fishes. *Journal of Fish Biology* **63,** 637-658.

Zelditch, M. L. & Fink, W. L. (1995). Allometry and Developmental Integration of Body Growth in A Piranha, Pygocentrus-Nattereri (Teleostei, Ostariophysi). *Journal of Morphology* **223,** 341-355.

Zelditch, M. L., Sheets, H. D. & Fink, W. L. (2000). Spatiotemporal reorganization of growth rates in the evolution of ontogeny. *Evolution* **54,** 1363-1371

ABSTRACT

Foraging behaviour has been examined in various studies. Foraging patterns can be flexible for generalists, which benefit from a wide range of food resources. Foraging is influenced by a variety of factors such as consumption efficiency, optimal diet theory, learning and experience, size-related habitat usage and predation threat. Optimal diet theory suggests that a selected foraging strategy should maximise energetic income. Therefore, a prey type with less energetic value than its energetic return of the capture success is bound to be dropped. Learning improves prey cognition and handling efficiency of the individual and can alter the ratio of gains to costs related with foraging on previously consumed prey. If the uptake of food resources in a specific habitat is linked to a certain habitat-specific predation risk, a trade-off exists between foraging and predator avoidance that may severely affect behaviour and activity levels. The trade-off between foraging gain and predation risk is more likely for individuals large enough to be resource limited but still small enough to be vulnerable to predation. Smaller fish tend to avoid open water habitats and switch to habitats with complex structures and areas of submerged vegetation to seek shelter and intensify foraging on more profitable food.

Juvenile fish need habitats with high structural complexity as feeding grounds as well as a refuge against predators. In current flood plains many gravel pit lakes have emerged during the last decades due to the exploitation of gravel and sand, which may turn out to be alternative biotopes as their dimensions often outbalance that of naturally existing inshore waters such as oxbow lakes. Non-natural water bodies often differ immensely from natural lakes and most important repeatedly lack structural diversity in the littoral area. At steep banks lacking structural diversity, planted floatable textile mats may be thus an alternative to establish littoral elements to minimise structural deficiencies. The objective of this study was to analyse the functionality of such plant islands for the invertebrate fauna and the juvenile fish community. The rhizosphere underneath the plant carriers provided living space for a rich invertebrate fauna. The root cavities developed into a diverse and complex habitat with overall increased macrozoobenthos abundance, especially when the islands were near the shoreline being connected to natural stocks of macrophytes in the littoral zone. Usage of the plant islands differed between day and night. More fish were found at the plant island during the day than at restored littoral area, while at night the opposite distribution was observed. In summary, the locally increased abundance of macrozoobenthos improved the fishes' diet, and provided additional shelter from predatory specimen, as structural complexity of the habitat often reduces predatory efficiency by reducing prey capture rates. This study showed that artificial plant islands can enhance structural heterogeneity and food supply, therefore being beneficial for recruitment of juvenile fish in gravel pit lakes, when densely vegetated and connectivity between shoreline and the islands' root cavities is provided.

As the foraging behaviour and predator avoidance is dependent on size, two size classes of YOY perch were analysed in mesocosm experiments, using a passive integrated transponder system. The fish were able to increase their potential food intake by entering a compartment in which small cyprinids were provided as prey fishes, but where also a predator (pike) was present. When no prey fish but only the predator was in the food compartment, the residence time of both size classes of perch was significantly reduced in this compartment. When prey fish were present, the large YOY perch significantly increased the activity level in the test tank while the small size class perch did not.

Furthermore, activity periods of small perch shifted to daylight under the threat of predation while large perch were more active during the twilight periods. These results provide evidence that small and large size YOY perch differ in behaviour under the threat of predation when prey fish are available, they thus adjusted the trade-off between foraging and predator avoidance in dependence to size.

To gain better understanding on the effect experience has on the behavioural consequences of food selection YOY perch were trained on different food resources. These trained perch and untrained specimen from the field were offered a fixed concentration of zooplankton with different levels of fish (energetically equivalent, half and double the zooplankton value). Additionally, instead of fish a novel food resource, *Limnomysis benedenii*, was offered that was selected only at high energetic values. Although fish was the preferred prey for all groups of YOY perch, only trained perch (piscivorous and planktivorous) positively selected fish at all energetic values offered. Not only experience in food resources, but also predation pressure, experienced only by the field perch prior to the experiments, influenced perch behaviour. YOY perch exhibit a complex mode of behaviour with regards to feeding behaviour allowing them to change strategies when necessary.

To conduct studies concerning the ecology of fish population it is essential to get fish samples which truly reflect the population structure. Various fishing techniques were applied in field studies to obtain information on the population structure such as gillnetting and electrofishing. The capture success of the methods depends mainly on the activity of individuals, their abundance and the habitat in which each method is applied. In cases of bimodality where two size cohorts display different behaviour in foraging, activity and habitat choice distinct differences in length-frequency distribution of perch sampled by different methods were expected. In shallow experimental ponds the capture success of multi-mesh gillnetting and electrofishing was examined. To gather further information on the sampling of juvenile perch in large water bodies of greater depth, three gravel pit lakes were studied. Additionally, in the deep gravel pit lakes bongo-net fishing was used in spring to monitor perch larvae in the pelagic zone after hatching. The three methods were compared and recommendations how to improve fish stock assessment were given. It is then important to preserve and store caught fish as it is often not possible to analyse individuals in the field. This not only includes length and weight measurements but also a variety of other analyses, most commonly stomach content analyses. In this study, juvenile perch were measured and frozen at -20°C, preserved in 70% ethanol or 4% formalin and remeasured after 24h, 3 days, 7 days and then on a weekly basis for eight weeks. Ethanol strongly decreased length and weight of preserved perch. Formalin preservation also led to comparable length reduction but increased the weight of preserved perch. In contrast, frozen perch showed less shrinkage and only moderate weight loss. In the morphometric analysis also freezing clearly revealed the lowest shape differences compared to fresh fish. Hence, freezing is recommended as the most preferable preservation method, especially in multi-disciplinary studies on fish ecology.

KURZZUSAMMENFASSUNG

Das Verhalten von Organismen bei der Nahrungssuche ist bereits in vielen Studien untersucht worden. Bei Generalisten, die von einer großen Nahrungsauswahl profitieren, gestaltet sich die Nahrungssuche flexibel. Dabei beeinflussen verschiedene Faktoren die Nahrungssuche. Zum Beispiel wird die Nahrungsselektion nicht nur durch Lernprozesse beim Jagen und Fressen bestimmter Beute moduliert, sondern auch durch größenabhängige Habitatwahl und Fraßdruck gesteuert.

Nach der optimal diet theory (ODT) soll eine vom Individuum gewählte Strategie der Nahrungssuche seinen energetischen Gewinn maximieren. Infolgedessen müssten Beutetypen mit negativer Energiebilanz nicht oder in sehr geringem Ausmaß im Nahrungsspektrum vorhanden sein. Eine negative Energiebilanz entsteht dann, wenn der Energiegehalt einer Beute nicht die Kosten deckt, die dem Räuber durch Fang, Ingestion und Verdauung der Beute entstanden sind. Lerneffekte können das Erkennen und die Effizienz im Umgang mit der Beute zusätzlich verbessern und somit das Kosten-Nutzen Verhältnis von einer zuvor genutzten Nahrungsquelle positiv beeinflussen. Tritt eine Kopplung von habitatspezifischen Nahrungsressourcen mit habitatspezifischen Prädationsdruck auf den Räuber auf, entsteht eine Trade-off Situation zwischen Nahrungssuche und Prädationsvermeidung, die das Verhalten und die Aktivität der Organismen stark beeinflusst. Ein solcher Trade-off kommt vor allem bei Individuen zum tragen, die groß genug sind, um Ressourcen-limitiert zu sein und gleichzeitig noch klein genug, um unter starkem Prädationsdruck zu stehen. Zum Beispiel, wechseln kleine Fische vom Pelagial zu komplexen Habitaten des Litorals mit Flächen submerser Vegetation. In diesen finden sie nicht nur Schutz vor Prädation, sondern auch profitablere Nahrungsquellen. In den meisten Ökosystemen ist der Fraßdruck einer der Faktoren, die sich entscheidend direkt oder indirekt auf die Beute auswirken. Dies kann große Folgen für die Beutepopulation haben. Beispielsweise kann über den Fraßdruck der Fische das Zooplanktonvorkommen und darüber wiederum sogar der Nährstoffgehalt eines Gewässers beeinflusst werden. So können sich Entscheidungen von einzelnen Räubern und Beutetieren auf Populationsebene und auf Ebene der Lebensgemeinschaften fortpflanzen.

In dieser Studie wurde deshalb die Nahrungssuche im Zusammenhang mit Räubervermeidungsstrategien bei juvenilen Flussbarschen, *Perca fluviatilis*, untersucht. Jungfische sind auf einen komplex strukturierten Lebensraum angewiesen, in dem zum einen eine ausreichende Nahrungsgrundlage geboten ist und der zum anderen als Zufluchtsort vor Prädatoren dient. In heutigen Flussauen sind in den letzten Jahrzehnten durch Abgrabungen von Kies viele Baggerseen entstanden. Ihre Ausdehnung übertrifft häufig die noch vorhandenen, natürlichen Seitengewässer. Sie könnten wertvolle Ersatzlebensräume in den anthropogen überformten Auen darstellen, unterscheiden sich strukturell aber stark von den natürlichen Gewässern: sie sind tiefer, haben ein ungünstigeres Verhältnis von Fläche zu Volumen und meistens ein gering ausgeprägtes Litoral. An den meist sehr steil angelegten Ufern könnten künstliche Pflanzeninseln zusätzliche Strukturen schaffen. Diese künstlichen Uferstrukturen könnten die Defizite der Abgrabungsgewässer verringern und als Ersatzlebensräume in den neuen Gewässern dienen. Ein Ziel dieser Studie war es, die Funktionalität der künstlichen Pflanzeninseln im Hinblick auf das Makrozoobenthos und die Fischartengemeinschaft zu beurteilen. Der Wurzelbereich unter den künstlichen Pflanzeninseln entwickelte sich zu einem diversen Lebensraum mit reichhaltiger Evertebratenfauna. Dies war besonders ausgeprägt, wenn die Pflanzeninseln nah am Ufer installiert und gut an die im Litoral natürlich vorkommenden Makrophyten angebunden waren. Die Nutzung der Unterseiten der Pflanzeninseln variierte im Tagesverlauf. Sie wurden am Tag stärker als die untersuchten herkömmlich rekultivierten Uferbereiche frequentiert. In der Nacht waren die Tiere verstärkt im Litoral vorzufinden. Zum einen hat die lokal erhöhte Abundanz des Makrozoobenthos zu einer Verbesserung der Nahrungsqualität der Jungfische geführt. Zum anderen wurde gezeigt, dass die Wurzelräume einen komplex strukturierten Lebensraum darstellen, weshalb er am Tag als zusätzliche Schutzstrukturen aufgesucht wird. Künstliche Pflanzeninseln können somit die Strukturvielfalt und das Nahrungsangebot in einem Gewässer lokal erhöhen. Zusammenfassend lässt sich festhalten, dass sich die Pflanzeninseln bei guter Anbindung an das natürliche Litoral und gut entwickeltem Wurzelraum positiv auf den Rekrutierungserfolg von Jungfischen auswirken können.

Die Aufnahme von Nahrungsressourcen in einem bestimmten Habitat ist verbunden mit einem Standort-spezifischen Fraßrisiko. Somit muss ein Kompromiss zwischen Nahrungsaufnahme und Räubervermeidung eingegangen werden, der das Verhalten und die Aktivität des betroffenen Individuums stark beeinflussen kann. Dieser Trade-off wurde in Mesokosmosexperimenten mit zwei Größenklassen von juvenilen Flussbarschen weitergehend untersucht. Die Barsche konnten ihre potentielle Nahrungsaufnahme erhöhen, indem sie ein Kompartiment aufsuchten, in welchem zu bestimmten Zeitperioden Cyprenidenlarven als Beutefische angeboten wurden. Zeitgleich war immer ein Räuber (Hecht, *Esox lucius*) anwesend. Die Barsche waren zuvor mit „Passive Integrated Transponders“ (PIT-tags) markiert worden, so dass ihre Aktivität und ihr Aufenthaltsort zu jeder Zeit individuell nachverfolgt werden konnte. Wenn sich nur der Räuber ohne die Beutefische in dem Kompartiment befand, war dort die Aufenthaltszeit beider Größenklassen signifikant geringer. Waren gleichzeitig Beutefische verfügbar, erhöhten die großen juvenilen Barsche ihre Aktivität im Testbecken, während die kleine Größenklasse dies nicht tat. Des Weiteren verlagerte sich bei Anwesenheit des Räubers der Zeitraum, in dem die kleinen Barsche aktiv waren, in den Tag hinein. Die großen Barsche wurden im Gegensatz dazu stärker dämmerungsaktiv. Diese Ergebnisse zeigen deutlich, dass sich beide Größenklassen unterschiedlich verhalten, wenn Beutefische vorhanden sind und gleichzeitig ein Prädationsrisiko besteht. Der Trade-off von Futtersuche und Räubervermeidung verändert sich folglich in Abhängigkeit von der Größe der Barsche.

Um genauer zu verstehen, welchen Effekt Erfahrung auf das Verhalten bei der Nahrungsselektion hat, wurden junge Flussbarsche auf unterschiedliche Nahrungsquellen konditioniert. Diesen trainierten Barschen und gleich alten untrainierten Barschen aus dem Freiland wurde in Laborexperimenten eine fest definierte Menge Zooplankton (hauptsächlich *Daphnia* spp.) mit verschiedenen Dichten von Beutefischen angeboten (mit der Hälfte der Energie der angebotenen Menge an Daphnien; energetisch gleich oder mit der doppelten Menge Energie). In weiteren Experimenten wurde statt der Beutefische ein für alle Barsche neuer Beuteorganismus, die Schwebgarnele (*Limnomysis benedenii*) angeboten. Diese zuvor unbekannte aber profitable Nahrungsquelle wurde nur dann positiv selektiert, wenn sie in hoher Dichte verfügbar war. Beutefische wurden zwar von allen Barschen unabhängig von der Vorbehandlung bevorzug gefressen, aber bei geringen Dichten und somit geringem Energiegewinn nur von den trainierten Barschen positiv selektiert. Die Studie konnte zeigen, dass nicht nur die Erfahrungswerte bei der Auswahl einer Nahrungsquelle eine wichtige Rolle für das Verhalten der Barsche spielen, sondern auch der

Prädationsdruck. Für die Barsche aus dem Freiland war der Prädationsdruck im Monat vor den Experimenten besonders stark, während die trainierten Barsche keinem Prädationsdruck ausgesetzt waren. Barsche zeigen im Gegensatz zur herkömmlichen Meinung komplexe und flexible Verhaltensweisen im Hinblick auf die Futtersuche, welche es ihnen erlauben sich auf ihre Umgebung einzustellen und ihre Nahrungsstrategien den Umständen entsprechend zu verändern.

Um die Ökologie von Fischpopulationen untersuchen zu können, sind repräsentative Fischfänge essentiell. Verschiedene Fangtechniken (Stellnetze, Elektrobefischung) werden in Feldstudien eingesetzt, um Informationen über die Populationsstruktur zu erlangen. Der Fangerfolg der Methoden hängt hauptsächlich ab von der Aktivität der Individuen, ihrer Abundanz und dem Habitat, in welchem die jeweilige Methode angewendet wird. Wenn Bimodalität in einer Population auftritt, in der zwei Größenklassen unterschiedliches Verhalten bei der Futtersuche, in der Aktivität und der Habitatwahl zeigen, werden mit unterschiedlichen Fangmethoden höchstwahrscheinlich auch Unterschiede in der Längenhäufigkeitsverteilung der gefangenen Tiere auftreten. Diese Studie untersucht in flachen Experimentalteichen den Fangerfolg von Multimaschennetzen und Elektrobefischung. Um weitere Informationen über die Probennahme juveniler Barsche in tiefen Gewässern zu erhalten, wurden zusätzlich drei Baggerseen erforscht. Hier wurde neben den Stellnetzen und der Elektrobefischung eine weitere Methode getestet: mit einem Bongonetzes wurde im Frühjahr die Entwicklung der Barschlarven im Pelagial mitverfolgt. Der Vergleich der drei Methoden hat gezeigt, dass eine Methode allein nicht genügt, um ein repräsentatives Bild der Fischartengemeinschaft zu erhalten. Daher wird empfohlen, mindestens zwei Methoden anzuwenden, um die Abschätzung von Fischbeständen zu verbessern.

Es ist in fischökologischen Studien meist nicht möglich die Fänge direkt zu analysieren, deshalb müssen gefangene Individuen konserviert und aufbewahrt können. Das beinhaltet nicht nur Längen- und Gewichtsmessungen, sondern auch verschiedene andere Untersuchungen, wie zum Beispiel Magenanalysen. In dieser Studie wurden deshalb juvenile Barsche vermessen und auf drei verschieden Arten konserviert: Einfrieren bei -20°C, Konservierung in 70% Ethanol und in 4% Formol. Die Barsche wurden nach 24 Stunden, drei Tagen, einer Woche und dann wöchentlich über einen Zeitraum von 60 Tagen gemessen. Barsche, die in Ethanol konserviert waren zeigten eine starke Abnahme in Länge und Gewicht. Formol führte ebenfalls zu einer Längenabnahme, während das Gewicht der Barsche jedoch anstieg. Im Gegensatz dazu kam es bei den eingefrorenen Tieren zu der geringsten Längenabnahme und nur zu mäßiger Gewichtsabnahme. In der Morphometrie zeigte sich ebenfalls, dass die eingefrorenen Tiere die wenigsten Veränderungen im Vergleich mit den frischen Barschen aufwiesen. Deshalb sollte Einfrieren vor allem bei multidisziplinären Untersuchungen in der Fischökologie als bevorzugte Konservierungsmethode angewendet werden.

ERKLÄRUNG

Köln, den 03.06.09

Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit - einschließlich Abbildungen und Tabellen - die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzellfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie - abgesehen von den auf der folgenden Seite angegebenen Teilpublikationen - noch nicht veröffentlicht worden ist sowie, dass ich solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen dieser Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von PD Dr. habil Jost Borcherding betreut worden.

TEILPUBLIKATIONEN

Scharf, W., Heermann, L., König, U. and Borcherding, J. 2009. Development of abundance and size structure of young-of-the-year perch populations using three methods. *Fisheries Research* 96: 77–87