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Diel shifts in community composition and feeding of juvenile fishes in the pelagic area of a large shallow lake

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Abstract

Diel cycles of changing ambient illumination have been shown to have strong influence on fish community composition in freshwater systems, mainly due to diel habitat shifts of fish between sheltered and more exposed, but profitable sites. Low information is available, however, from diel patterns of fish community composition and feeding in the central areas of large shallow lakes where lake depth and diameter may hamper diel migrations. We studied whether there are diel differences in species abundance and shifts in feeding modes of the juvenile pelagic fish species over an 8 months sampling period in a shallow lake. The strong decline of perch numbers towards the night suggests low nocturnal activity for this species. In contrast, the nearly constant numbers of roach over the full diel cycle points to pronounced activity under changing light intensities. Increased ruffe numbers at night reflect the good adaptation of this species to feed efficiently at low light intensities. Niche segregation of fish species along the diet axis was low. There was low evidence that diel shifts in the fish community composition were attributed to diel horizontal migrations of species into or out of the pelagic zone. Because availability of preferred zooplanktonic prey was high, differential diel activity patterns of species reflect their genetically fixed, albeit varying adaptations to feed under low-light conditions, instead of being an active avoidance to reduce competition.

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Introduction

Diel cycles of changing ambient illumination have been shown to influence species-specific feeding activities and fish community composition in several aquatic ecosystems. A clear replacement pattern between

diurnally active species and their nocturnal counterparts in almost all functional groups was described in particular from tropical and temperate coral reefs (Ebeling & Bray, 1976; Hobson & Chess, 1978; Bohl, 1980; Helfman, 1993).

The diel pattern is less pronounced in temperate freshwater systems. The distinction between either diurnal or nocturnal activity is less clearly expressed for many freshwater fish, and thus there are no complete replacement sets of species which cover all trophic guilds from herbivores to piscivores (Helfman, 1981, 1993). However, distinct differences in fish community

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composition and abundance has been found in freshwater lakes and rivers as a consequence of diel migrations of fish between safe resting sites and more profitable, but often also more risky feeding sites (Werner, Gilliam, Hall, & Mittelbach, 1983; Gliwicz & Jachner, 1992). Since individual predation risk declines with increasing fish size, diel horizontal migrations have often been described for juvenile fish. As an example, young cyprinids and percids migrate between the main channel during dark periods and the shallow lentic habitats in rivers or adjacent floodplain lakes during daytime (Garner, Clough, Griffiths, Deans, & Ibbotson, 1998; Baras & Nindaba, 1999; Borchering, Bauerfeld, Hintzen, & Neumann, 2002).

Similarly, young fish perform diel horizontal migrations between littoral areas covered with complex structures and the adjacent open water habitats in shallow, non-turbid lakes (Jacobsen & Berg, 1998; Okun & Mehner, 2005). Diel vertical migrations of coregonids were found in deep lakes where the fish stay mainly in deep, cold layers during the day and ascend into warmer layers with higher zooplankton densities during the night (Rudstam & Magnuson, 1985; Hamrin 1986). All these studies have in common that the diel habitat shifts of fish were explained by a trade-off between an increased use of sheltered sites at daylight to reduce feeding risk from day-active predators, and the opportunity to feed in the more exposed but also more profitable habitats during twilight periods and at night (compare Gliwicz & Jachner, 1992; Hölker, Haertel, Steiner, & Mehner, 2002).

No information is available, however, from diel patterns of fish community composition and feeding in the central areas of shallow temperate lakes. Whereas the majority of the bottom of shallow lakes can be covered by submerge macrophytes thus allowing for short-range diel horizontal migrations of fish between

inside and outside the macrophyte beds (Jacobsen & Berg, 1998), higher plants cannot settle and grow under the low-light conditions at the bottom in the deepest region of those lakes. Thus, the pelagic area of shallow lakes does not offer structured hiding places and is rather homogeneous for young fish with respect to food availability and predation risk. The low lake depth may not allow for effective vertical migrations into deep and dark water layers. In addition, if the lake has a large surface area and diameter, even diel horizontal migrations between littoral and pelagic areas may be hampered.

Therefore, we studied whether there are at all diel differences in the juvenile fish community in the pelagic area of a large shallow lake. We focused on changes in species abundance and shifts in feeding modes of the dominant species along the day–night cycle over an 8 months sampling period. The patterns found are discussed with respect to species-specific adaptations of feeding to changing illumination strength, and to the resulting patterns of niche segregation between potentially competing fish species.

Study site

Lake Müggelsee is a shallow eutrophic, polymictic lake in Berlin, Germany. Surface area is 7.3 km², mean water depth is 4.9 m (Fig. 1). Despite a decline of nutrient loads since 1990, the lake is still eutrophic (Köhler, Behrendt, & Hoeg, 2000). Up to the 1960s, extensive zones of the lake bottom were covered with submerged vegetation, but as a result of an increased turbidity, they disappeared almost completely. From the 1990s on, macrophytes were observed again, but with currently less than 2% coverage of lake area (Körner,

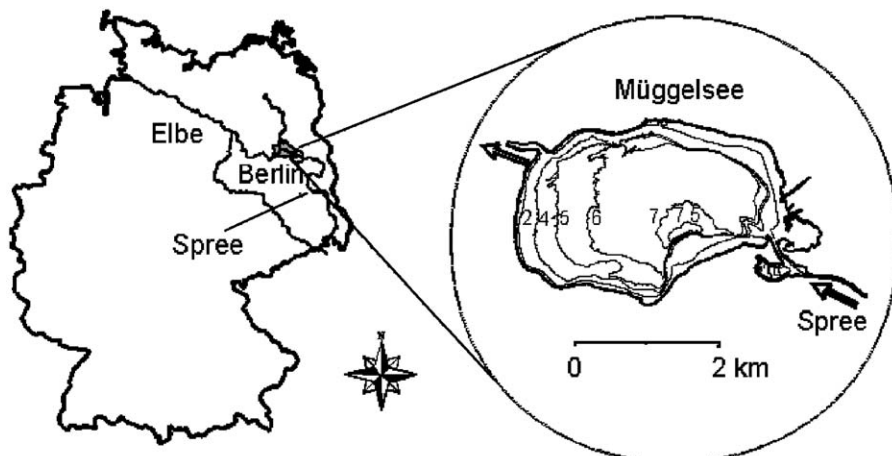


Fig. 1. Lake Müggelsee and its location in Germany.

2001). In contrast, emergent vegetation (*Phragmites* spp.) characterizes the lake shore and forms dense belts.

Material and methods

Zooplankton samples were obtained monthly using a 5-L Friedinger sampler. Volumetrically integrated zooplankton samples were taken weekly at 1-m intervals from the surface to the bottom at five different stations across the lake, accounting for possible inhomogeneities (for details, see Driescher, Behrendt, Schellenberger, & Stellmacher, 1993). Samples were screened through a 50- μm mesh, and fixed with formaldehyde (4% final concentration). Animals were identified and counted under a microscope at 40 \times magnification.

Juvenile fish were sampled in the pelagic area of Müggelsee at both daytime (from 9 a.m.) and during the night (from 11 p.m.) monthly between April and November 2000. Owing to technical problems with the equipment, data from July are missing. Fish were caught by towing a demersal trawl (cod end: mesh size 6 mm, opening width: 6.5 m) over a 500 m distance with an average speed of 1.9 m s^{-1} at three stations in the central area of the lake. The exact orientation of field sites was supported by a GPS. Owing to the low lake depth, approximately the whole water column was sampled during each haul.

After capture, fish were identified to species, counted, measured to nearest mm and weighed to nearest 0.01 g wet mass (wm). Fish abundance (ind ha^{-1}) and biomass (kg wm ha^{-1}) were calculated from each sampling haul (towed distance \times net width = 3250 m^2 = 0.325 ha).

If available, stomach or gut contents of 12 specimens of the dominant species were analysed at each sampling date (day and night) by identifying, counting and measuring prey organisms. The lengths of all prey items were converted into wet masses using length–mass relationships from literature (Mehner, Schultz, & Herbst, 1995). Furthermore, the index of relative importance (IRI %) was calculated for several food categories according to George & Hadley (1979)

$$\text{IRI}(\%) = \frac{Ni + Bi + Fi}{\sum_i (Ni + Bi + Fi)} \times 100,$$

where N is the relative proportion (in numbers), B the relative biomass and F is the frequency of occurrence of prey component i found in the stomach of a fish species. The diet overlap between two fish species x and y was calculated using the similarity index (S) by Schoener (1970), based on the IRI for the n food categories:

$$S = 1 - 0.5 \left(\sum_{i=1}^n |\text{IRI}_{xi} - \text{IRI}_{yi}| \right).$$

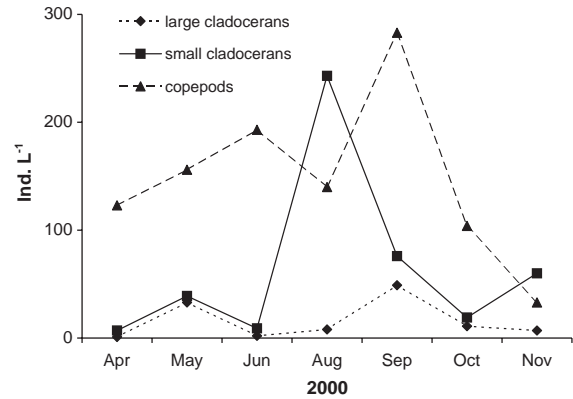


Fig. 2. Abundance (ind L^{-1}) of copepods, small cladocerans and large cladocerans in the pelagic area of Müggelsee from April to November 2000.

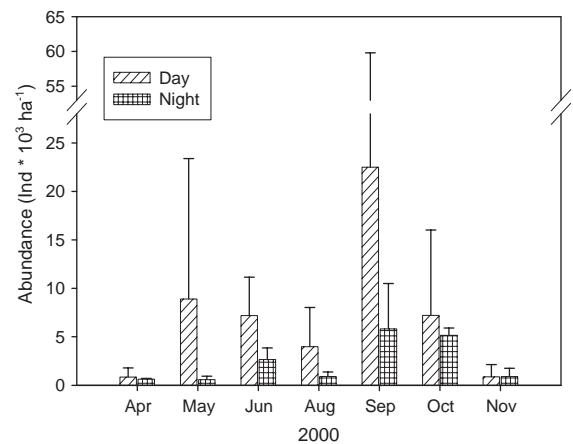


Fig. 3. Total abundance of juvenile fish (ind ha^{-1}) in the pelagic area of Müggelsee from April to November 2000. Values are means \pm SE of three replicate samples each during daytime and at night.

In addition, monthly similarity in fish community composition in the pelagic area between day and night was calculated by the same index, here replacing IRI by the proportion of the several fish species from the total catch in either day or night samples. Because data deviated from parametric assumptions, seasonal and diel differences in fish abundance and biomass were tested with the non-parametric Mann–Whitney U -test and Kruskal–Wallis-test.

Results

Zooplankton was dominated by copepods (mainly cyclopoids) (Fig. 2). Except for November, densities of copepods were always higher than 100 ind L^{-1} . Small cladocerans (mainly *Bosmina* sp.) were found in higher

abundances only in August and September. Large cladocerans (*Daphnia* sp.) had highest densities of 33 or 49 ind L⁻¹ in May and September. Overall, zooplankton density was about four times higher at the maximum in September (408 ind L⁻¹) as compared to the minimum abundance found in November (100 ind L⁻¹).

A total of 66,456 (174.8 kg wm) juvenile fishes, representing five species, was caught during the study period. The catch of perch (*Perca fluviatilis* L.) was substantially higher (70.7% of numbers) than that of all other species (ruffe, *Gymnocephalus cernuus* (L.), 13.4%; roach, *Rutilus rutilus* (L.), 8.4%; smelt, *Osmerus eperlanus* (L.), 5.9%; pikeperch, *Sander lucioperca* (L.), 1.6%). In perch, age-0 individuals were dominant ($\approx 80\%$), whereas in the other species, the proportions of age-0 and -1 fish were comparable.

There were significant differences in the mean diel fish densities over the seasonal course (Kruskal–Wallis-test, $\chi^2 = 18.97$, df = 6, $p = 0.004$) (Fig. 3). Differences were also significant for the biomasses (Kruskal–Wallis-test, $\chi^2 = 20.74$, correct ! df = 6, $p = 0.002$). Average day–night densities and biomasses peaked in September (14161 ind ha⁻¹, 42 kg ha⁻¹) and were lowest in April (728 ind ha⁻¹, 3.6 kg ha⁻¹).

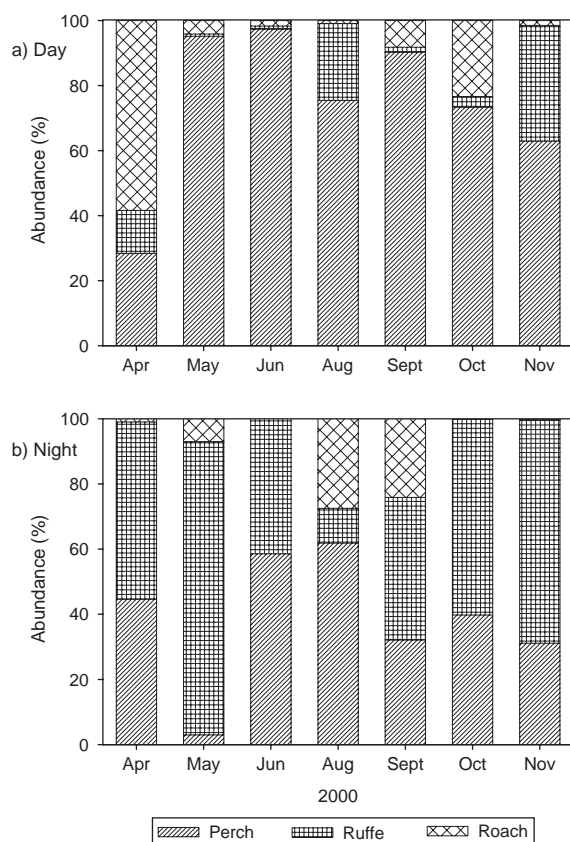


Fig. 4. Relative density proportions (%) of young perch, ruffe and roach in the pelagic area of Müggelsee at day (a) and night (b) from April to November 2000.

During the study, day-time densities of fish found in the pelagic habitat were higher than at night (Fig. 3), although differences were not significant (Mann–Whitney U -Test, $U = 12$, $p = 0.128$). Regarding to the three main species, perch was the dominant one during the day, but its proportion was lower at night (Figs. 4a and b). By contrast, ruffe density increased at night, and species composition shifted from perch to ruffe dominance. The density proportion of roach in the pelagial did not differ between day and night. Day–night differences in density were significant only in ruffe (Mann–Whitney U -test, ruffe: $U = 9$, $p = 0.047$; roach: $U = 12$, $p = 0.11$; perch: $U = 12$, $p = 0.11$). Overall, similarity in species composition in the pelagic area between day and night calculated by the Schoener's index was low with a seasonal average of 0.37 (min 0.11 in April, max 0.65 in August).

Owing to the low numbers of pikeperch and smelt in the catches, no diet analyses were made for these species. In total, the diet of 94 roach, 152 perch and 120 ruffe was inspected. Seasonal changes in the IRI of prey categories were low for all species (Figs. 5a–c). In roach, IRI of zooplanktonic prey categories was substantially higher than that of benthic prey at both day and night (Fig. 5a). Small cladocerans were the most important group, followed by nearly similar proportions of large cladocerans and copepods. Zooplankton also dominated the diet of perch (Fig. 5b) over the diel course, with similar proportions of the three plankton groups. In ruffe, however, IRI of benthic insect larvae was higher than in both other species, partly exceeding 50% (Fig. 5c). Compared to copepods and small cladocerans, large cladocerans were only rarely ingested by the ruffe. Diet overlap between species was on a seasonal average lower at day than at night, and overall lowest between ruffe and roach (Table 1). Diel diet similarity was highest within the species and lower between all species combinations (Table 1).

Discussion

Our study has shown substantial diel differences in density and species composition of the pelagic juvenile fish community in Müggelsee. The total catch of fish decreased by about 68% on average from day to night, and species dominance shifted from perch to ruffe. In contrast, the diet composition of the dominant fish species was highly similar between day and night and along the season. A high diet similarity was even found between the three main species. This indicates that the diel differences in the fish community rather reflect differential species-specific genetic adaptations to the feeding under either daylight or darkness conditions than any behavioural segregation

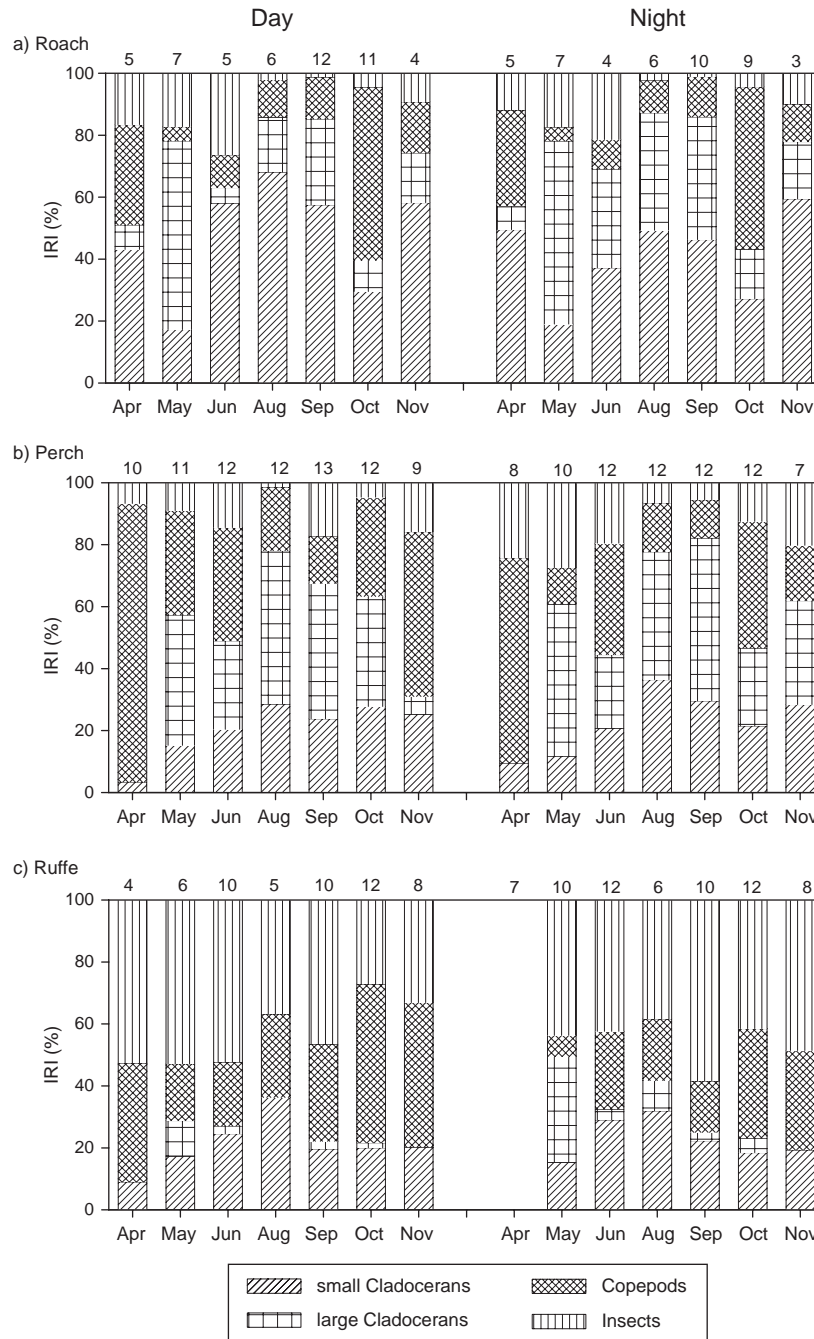


Fig. 5. Index of Relative Importance (%) of small cladocerans, large cladocerans, copepods and insects in the diet of young roach (a), perch (b) and ruffe (c) from Müggelsee during day and at night between April and November 2000. Numbers above bars = numbers of intestines analysed.

along the temporal niche axis to reduce current interspecific competition.

Diel activity patterns are well documented for roach and both percids (Craig, 1977; Rask, 1986; Bergman, 1988; Jamet, Gres, Lair, & Lasserre, 1990). The high numbers of perch found in the pelagic habitat during the day reflect the pronounced activity of this species under daylight conditions (Alabaster & Stott, 1978), which reflects its strong reliance upon visual orientation during

foraging (Mills, Confer, & Kretchmer, 1986; Bergman, 1988; Diehl, 1988). By contrast, the night is known as a low-active period for perch, accompanied by substantial changes in the behaviour of the fish. For example, the break-up of perch shoals into individuals, settling down separately near the lake bottom (Hasler & Villemonte, 1953; Alabaster & Stott, 1978; Emery, 1973) may explain, why the numbers of caught perch in the night trawls decreased such obviously at night. In contrast,

Table 1. Average similarity index (*S*) over the months studied in the pelagial at day and night.

Intraspecific similarity		Interspecific similarity			
Species	Day/night	Species	Day/night	Day	Night
Roach-Roach	0.89	Roach-Perch	0.76	0.58	0.71
Perch-Perch	0.81	Roach-Ruffe	0.62	0.54	0.57
Ruffe-Ruffe	0.83	Perch-Ruffe	0.61	0.57	0.61

Right part of the table: interspecific similarity: species *i* day – species *j* night; species *i* day – species *j* day; species *i* night – species *j* night.
 Left part of the table: intraspecific similarity: species *i* day – species *i* night.

ruffe can orientate in addition by its effective lateral line sensory organs (Disler & Smirnov, 1977). Therefore, uptake of prey is possible under both, daylight and low-light conditions and even in darkness, thus making the benthivorous ruffe to a more nocturnal species (Disler & Smirnov, 1977; Bergman, 1988). In roach, no clear distinction between either diurnal or nocturnal activity phases was found, since catch and also gut fullness of roach was comparable between day and night during all sampling months. In correspondence herewith, additional gill net catches in Müggelsee did not show significant day–night differences in roach numbers (see Okun & Mehner, 2002). This corroborates the high behavioural plasticity of roach resulting from the ability to feed even under changing light intensities (Diehl, 1988; Jamet et al., 1990; Hammer, Temming, & Schubert, 1994).

Our data give no evidence for a strong niche segregation along the diet axis. All three species ingested zooplanktonic prey to a high extent, only weakly corroborating the increased degree of benthivory from roach over perch to ruffe at coexistence (Bergman & Greenberg, 1994). In absence of interspecific competition, a zooplankton-dominated diet is well known for both juvenile roach and perch (Craig, 1978; Jamet et al., 1990; Persson & Greenberg, 1990). In contrast, the bottom-living ruffe was described to be primarily benthivorous (Hansson, 1984; Bergman & Greenberg, 1994), although a high uptake of zooplankton was occasionally found also in other aquatic systems (Hölker & Hammer, 1994; Werner, Mehner, & Schultz, 1996). Bergman and Greenberg (1994) found in experimental enclosures with the three species, that perch responded strongly to declining ruffe densities by increasing the degree of benthivory, while both ruffe and roach showed only modest changes in their diet compositions. No such patterns were found in the pelagic area of Müggelsee. Here, diet composition did not change during the sampling period and between day and night, irrespective of the varying relative proportions of the fish species in the community.

There are two possible explanations. First, the obvious dominance replacement of perch by ruffe from day to night may have prevented intense competition

between both percids such that perch competed only with roach under daylight conditions, and ruffe competed only with roach at night. For the competitively inferior perch an increase in the degree of benthivory can be expected, whereas the diet composition of ruffe and roach should remain unchanged (Persson & Greenberg, 1990; Bergman & Greenberg, 1994). This was clearly not the case in Müggelsee, where the overall amount of benthos in the diet of perch was constantly low. As an alternative explanation and in contrast to the situation in the experiments by Bergman & Greenberg (1994), it can be suggested that the overall availability of zooplankton in the pelagic area of Müggelsee was high enough to ensure that the young fish did not compete for a scarce resource.

Indeed, total abundance of cladocerans and copepods was always higher than 100 ind L⁻¹, whereas annual average fish biomass was about 16 kg ha⁻¹ at daytime. Critical biomasses of juvenile fish which induced drastic density declines in their zooplankton prey were found with 20–50 kg ha⁻¹ (Post & McQueen, 1987; Hülsmann & Mehner, 1997). Accordingly, it is unlikely that the juvenile fish community in the pelagic area of the Müggelsee suppressed the development of the zooplankton, and thus fish growth was probably neither zooplankton-limited. Consequently, the differential diel activity patterns of perch, roach and ruffe seem to reflect their genetically fixed, albeit varying adaptations to feed under low-light conditions, instead of being an active avoidance mechanism to reduce current exploitative competition.

The diel changes in fish abundances may be related to diel horizontal migrations of certain species into or out of the pelagic area of Müggelsee. Predation risk in the pelagic area is mainly induced by adult pikeperch, a species, which is known to be active in crepuscular and dark periods (Craig, 1987). Thus, perch may have profited from leaving the pelagic area at dusk towards safe places in the littoral (compare Emery, 1973; Hanych, Ross, Magnien, & Suggars, 1983; Imbrock, Appenzeller, & Eckmann, 1996). Indeed, Okun & Mehner (2005) found a slight increase of juvenile perch densities in littoral habitats of Müggelsee at night, as compared with the daylight catches. However, the same

advantage of reduced predation risk would hold for roach and ruffe which both did not leave the pelagic area at night. Whereas the ruffe may detect potential predators in the darkness efficiently, this is not clear for roach.

However, it can be discussed whether diel horizontal migrations between littoral and pelagic habitats are profitable for juvenile fish in large shallow lakes. Owing to the low coverage of the littoral by submerged macrophytes in Müggelsee, efficient hiding places for juvenile fish can be found only in the dense reed stands at the shoreline of the lake. By assuming that fish swim with 1.6 body lengths per second (see Hölker et al., 2002) during straight migration, a 6 cm long fish can swim about 10 cm s^{-1} or 350 m h^{-1} at maximum. The half diameter of Müggelsee is more than 1 km, indicating that juvenile fish would never reach the other habitat within the about 1 h long crepuscular periods. In contrast, this is possible for fishes with more than 18 cm length by swimming with the same speed of 1.6 body lengths per second. Therefore, it can be assumed that the diameter of the lake is an important determinant of whether young fish can improve their fitness by migrating horizontally between habitats, which are either safe or profitable. A higher migration intensity can be expected in small lakes where littoral and pelagic are spatially closely coupled and where time and energy to be invested in migrations are relatively low in comparison to the total time and energy budgets of the fish.

Previous studies showed that roach populations rather strongly responded to pikeperch stocking in lakes by stopping their diel horizontal migrations into pelagic areas at night and instead remained in the littoral instead all over the diel cycle (Brabrand & Faafeng, 1993; Hölker et al., 2002). Since roach density in the pelagic area of Müggelsee did not decline during the night, and ruffe density even increased, there is little evidence to assume that the predation risk by pikeperch was high enough to induce diel horizontal migrations of juvenile fish. Instead, the drastic decline in juvenile fish density towards the night was overwhelmingly attributed to a decline in perch density, and it can be assumed that perch rested close to the bottom thus reducing the catching efficiency of the demersal trawl for this species in darkness (Alabaster & Stott, 1978).

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