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Refuge availability and sequence of predators determine the seasonal succession of crustacean zooplankton in a clay-turbid lake

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Abstract The contribution of predators and abiotic factors to the regulation of the biomass and seasonal succession of crustacean zooplankton was studied in Lake Rehtijärvi (southern Finland). Field data in combination with bioenergetics modeling indicated that invertebrate planktivory by *Chaoborus* depressed cladoceran populations during early summer. In particular, bosminids that generally form the spring biomass peak of cladocerans in stratified temperate lakes did not appear in the samples until July. In July, predation pressure by chaoborids was relaxed due to their emergence period and cladoceran population growth appeared to be limited by predation by planktivorous fish. The effect of fish predation was amplified by reduced refuge availability for cladocerans. The concentration of dissolved oxygen below the epilimnion was depleted, forcing cladocerans to move upward to less turbid and thus more dangerous water layers. The effect of size selective predation by fish resulted in reduced mean size of cladocerans during the period when refuge thickness (thickness of the water layer with oxygen concentration <1 mg l^{-1} and water turbidity >30 NTU) was lowest. The results confirmed that in clay-turbid lakes, invertebrate predators could be the main regulators of herbivorous zooplankton even when cyprinid fish are abundant.

Keywords Zooplankton · Invertebrate predators · Planktivorous fish · Dissolved oxygen · Refuge

Introduction

In a given lake, the seasonal development of zooplankton biomass often follows a certain pattern from year to year (e.g. Gliwicz 1977; Sommer 1989; Lampert and Sommer 1997). Based on data from numerous lakes and ponds, the sequential seasonal events in zooplankton and phytoplankton communities were described in the PEG-model, which was proposed as a standard of comparison for the seasonal succession of planktonic communities in lakes (Sommer et al. 1986). According to the model data, in stratifying eutrophic lakes the highest biomass of cladocerans often occurs in spring, followed by a mid-summer minimum and a moderate increase in autumn. The spring peak of cladocerans usually consists mainly of small species such as bosminids, while larger species increase later (Gliwicz and Pijanowska 1989; Lair and Ayadi 1989).

Studies in the stratifying and eutrophic Lake Hiidenvesi (southern Finland) have demonstrated

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that in a clay-turbid lake, the seasonal development of the cladoceran community may substantially differ from that described in the PEG-model (Liljendahl-Nurminen et al. 2003; Horppila and Liljendahl-Nurminen 2005). In Lake Hiidenvesi, the spring biomass peak of cladocerans is missing and a single biomass peak occurs in late July–early August. It was shown that the spring biomass peak of cladocerans in Lake Hiidenvesi was eliminated by intense predation by chaoborid larvae (*Chaoborus flavicans* (Meigen)) and the biomass peak of cladocerans occurred in late summer due to the emergence period of the larvae (Liljendahl-Nurminen et al. 2002, 2003). The dominating role of chaoborids was unexpected, because in Lake Hiidenvesi the density of planktivorous fish is high and invertebrate predators themselves are preferred food items for fish. Usually it has been assumed that invertebrates can substantially regulate herbivorous zooplankton only if the density of planktivorous fish is very low (Benndorf 1995; Scheffer 1998). It was suggested that the coexistence of chaoborids and fish in Lake Hiidenvesi was facilitated by clay turbidity, which prevented efficient predation by fish (Liljendahl-Nurminen et al. 2003, 2008a, b). High water turbidity greatly reduces the feeding efficiency of visual predators like fish, while invertebrates are mostly tactile predators and thus less affected by turbidity (Vinyard and O'Brien 1976; Eiane et al. 1997). Additionally, compared to fish, chaoborid larvae are very tolerant of low oxygen (e.g. Sæther 1997) and they can occupy the hypolimnion of stratified lakes, where they spend the day and migrate at night into the epilimnion to forage on zooplankton (Borkent 1981; Luecke 1986; Horppila et al. 2000a).

Effective fishing of planktivorous fish is frequently used as a tool to reduce phytoplankton biomass (biomanipulation, food web management) (Mehner et al. 2002). Removal of planktivorous fish is thought to reduce predation pressure on herbivorous zooplankton and enhance their grazing capacity, which should lead to increased water clarity (Shapiro et al. 1975; Mehner et al. 2002). A reduction in the populations of herbivorous zooplankton by invertebrate predators may be avoided by allowing a moderate density of planktivorous fish, which in turn prey upon the invertebrate predators (Benndorf 1995). If high concentrations of inorganic suspendoids facilitate the coexistence of fish and invertebrate predators at high densities, management of clay-turbid lakes by food web management may be problematic because invertebrate predators are usually beyond the control of lake managers (Horppila and Liljendahl-Nurminen 2005). The densities of invertebrate predators in lakes are rarely known and therefore it is unclear, whether invertebrate predators or fish are generally more important in regulating the abundance of zooplankton grazers in turbid lakes.

To clarify the importance of invertebrate predators in clay-turbid conditions, we studied the contribution of invertebrate predators to the regulation of herbivorous zooplankton in Lake Rehtijärvi. Compared with Lake Hiidenvesi, the fish community in Lake Rehtijärvi is substantially different. In Lake Hiidenvesi, the planktivorous fish community was overwhelmingly dominated by smelt (*Osmerus eperlanus* (L.)), whereas in Lake Rehtijärvi cyprinids (e.g. roach *Rutilus rutilus* (L.)) are also abundant (Horppila et al. 2003 and unpublished). Compared with smelt cyprinids, including roach, are less affected by high turbidity and more tolerant to low oxygen concentrations (Stott and Cross 1973; Moeller and Scholz 1991; Horppila et al. 2004; Pekcan-Hekim and Horppila 2007). Thus, the possibilities of chaoborids to control herbivorous zooplankton may depend on the structure of the fish community.

Materials and methods

Lake Rehtijärvi is situated in southern Finland (60°51′ N, 23°30′ E). The surface area of the lake is 0.4 km^2 and maximum and average depths 25 and 9.2 m, respectively. The lake has an elongated shape, with a length from northwest to southeast of 2.0 km and maximum width of 0.3 km. The lake is eutrophic, with total phosphorus concentration varying between 50 and 100 µg l^{-1}, and total nitrogen concentration between 600 and 1,200 µg l^{-1}. Due to high concentration of inorganic suspendoids, water turbidity in the epilimnion usually exceeds 30 NTU and often approaches 100 NTU at near-bottom layers (Horppila and Niemistö 2008). The fish density in the lake is 5,000–10,000 ind. ha^{-1}, and the biomass c. 100 kg ha^{-1}. Abundant fish species include e.g. roach (*Rutilus rutilus* (L.)), perch (*Perca fluviatilis* (L.)) and smelt (*Osmerus eperlanus* L.), (echosounding and experimental trawling, T. Malinen unpublished).

The study was conducted between May and October 2005 at three replicate sampling stations, with water depth at the stations varying from 22 to 24 m. Samples for zooplankton were taken every 2 weeks with a tube sampler ($h = 1$ m, $V = 7.5$ l). Samples were hauled between 10 a.m. and 3 p.m. from each metre and combined into five separate layers (0–4, 4–8, 8–12, 12–20, 20–bottom). Samples were then filtered through a 50 μm net and zooplankton were counted using inverted microscopy. Cladocerans were identified to species and copepods to species or family level. Thirty individuals from each group were measured. Biomass was calculated using length-carbon regressions described by Luokkanen (1995). The datasets were tested for possible temporal autocorrelation with the Durbin–Watson test. For each taxon, the value of the Durbin–Watson statistic was >1.5, suggesting that no significant autocorrelation was present (SAS Institute Inc. 1989) and the between-depth biomass differences in cladocerans, cyclopoids and calanoids were tested with analysis of variance for repeated measurements (ANOVAR). Pairwise comparisons were conducted with Bonferroni *t*-tests.

The density-weighted average depth of cladocerans, cyclopoids, and calanoids from each sampling date was calculated (Wissel and Ramcharan 2003). Production of cladocerans (P) was calculated by the model of Shuter and Ing (1997) recommended by Stockwell and Johannsson (1997): $P/B = 10^{(\alpha+(\beta \times t))}$, where B = biomass (μg C l^{-1}), $\alpha = -1.725$, $\beta = 0.044$, t = water temperature (the average temperature of each sampling layer). The amplitude of the possible diurnal vertical migrations by cladocerans in the clay turbidity level of Lake Rehtijärvi is only few decimeters (Dodson 1990; Horppila et al. 2000a; Alajärvi and Horppila 2004), and their effects on the production estimates could thus be ignored.

The density of chaoborids and the predatory cladoceran *Leptodora kindtii* in the water column were determined at each station by three replicate vertical net hauls from the bottom to the surface (net diameter 50 cm, mesh size 183 μm). Additionally, three replicate bottom samples were taken from each station with an Ekman sampler (area 279 cm^2) and washed through a 500 μm sieve. In the laboratory, *Leptodora* and chaoborid larvae were counted and 30 larvae from each replicate sample were measured to the nearest 0.1 mm from the posterior edge of the eye to the base of the anal fan. The consumption of zooplankton by *Chaoborus flavicans* was estimated by using a bioenergetics model by Cressa and Lewis (1986) and adapted to temperate populations by Yan et al. (1991):

$$C = (R + G)/AE$$

where C = consumption rate; R = respiration rate; G = growth rate; AE = assimilation efficiency.

Assimilation efficiency was set at 0.67 (Swift 1976; Yan et al. 1991; Ramcharan et al. 2001) and the mass-specific respiration (R) was calculated using the equation by Yan et al. (1991):

$$\log(R/M) = -0.11 - 0.33 \log \mathrm{M}$$

where M is predator mass (μg dry mass). Consumption of oxygen was converted to consumption of prey biomass assuming that 1 ml O_2 = 0.536 mg C at a respiratory quotient of 1 (Lampert 1984) and that carbon comprises 47.3% of prey dry mass (Hall and Likens 1981). According to Ramcharan et al. (2001), the temperature correction factor can be excluded from the calculations, because respiration was noticed to be very low for *Chaoborus* as an ambush predator. Growth rate was calculated as the change in the average individual mass of each instar between sampling events. Consumption of zooplankton by population of *C. flavicans* was estimated presuming that all the larvae in water column migrate to the epilimnion (uppermost 8 m) to feed (Horppila et al. 2000a; Liljendahl-Nurminen et al. 2003). Similar to numerous other lakes, in Lake Rehtijärvi *C. flavicans* spend the daytime in the metalimnion and hypolimnion and migrate at night into the epilimnion (confirmed by echosounding, unpublished data). In spring, most larvae in sediment were assumed to still be in diapause and thus their biomass was ignored to avoid the overestimation of consumption (Liljendahl-Nurminen et al. 2003).

The profiles of dissolved oxygen, temperature and water turbidity were measured at each station with a YSI-6600 sonde. Samples for chlorophyll *a* were taken from the top 4 m layer, filtered through Whatman GF/C filters and analysed spectrophotometrically after extraction with ethanol. The refuge thickness for cladocerans (Tessier and Welser 1991) was quantified as the thickness of water column between 1 mg l^{-1} oxygen concentration and 30 NTU turbidity. Cladocerans tend to avoid oxygen concentrations below 1 mg l^{-1} (Wright and Shapiro 1990), whereas turbidity above 30 NTU severely reduces the feeding efficiency of planktivorous fish (Vinyard and O'Brien 1976; Horppila et al. 2004). Seasonal variations in refuge thickness were studied together with the mean size of cladocerans (weighted with the density of each species), which is a good indicator of predation pressure exerted by planktivorous fish (e.g. Soranno et al. 1993). For comparison, we also studied variations in the mean size of cyclopoid copepods that are less vulnerable to fish predation (e.g. Winfield et al. 1983).

To examine the contribution of fish predation to the regulation of planktonic communities, diets of perch and roach in the lake were studied. Fish obtained for diet analysis (242 perch, size range 4.7–16.9 cm; 238 roach, size range 6.0–15.7 cm) were captured by trawling (cod end mesh size 3 mm) on 16 June, 20 July, 15 August and 25 October. The stomach contents of perch were analysed for fullness and volume proportions of different food items (Windell 1971). Since roach lack a distinct stomach, the content of the anterior third of their gut was analysed. The gut contents were estimated for volume proportions of different food items. The proportion of cladocerans and copepods in the diets of fish captured at different times of the summer were compared using analysis of variance (ANOVA, arcsin $\sqrt{x}$-transformed data).

Results

Abiotic conditions

At the beginning of the study (18 May), the water column was weakly stratified, temperature ranging 9–11°C in the epilimnion (0–6 m depth) and 4–5°C in the hypolimnion (Fig. 1). The thermocline was situated at 6–8 m depth. During July, surface water temperature reached 20°C. The thermocline descended 2 m during the summer and was between 7 and 9 m depth in early October. Autumn circulation took place in late October and at the end of the study, vertical temperature difference was only 1°C. The concentration of dissolved oxygen was >5 mg l^{-1} throughout the water column in May but during the stratification period (May–October) oxygen in the hypolimnion was depleted. In July, a steep metalimnetic oxygen minimum was recorded, with oxygen concentration of <1 mg l^{-1} at 5 m depth but reaching 3 mg l^{-1} at deeper layers. In August, oxygen concentration deteriorated in the hypolimnion as well. In the epilimnion, turbidity was c. 40 NTU in May and decreased thereafter until July, when it was 20 NTU (Fig. 1). Towards autumn, turbidity in the epilimnion increased again, approaching 60 NTU in October. During the stratification period, turbidity increased sharply in the metalimnion and exceeded 90 NTU in the hypolimnion (Fig. 1). The concentration of chlorophyll *a* increased steadily from May to July and reached the maximum value of 19 µg l^{-1} on 25 July. In August, chlorophyll *a* decreased to below 15 µg l^{-1}, but peaked again at 18 µg l^{-1}on 14 September due to a cyanobacterial bloom.

Density of predators and prey

The density of *Chaoborus flavicans* larvae reached a maximum of 4,945 ind. m^{-2} on 31 May (Fig. 2). The larval density in the water was 3,276 ind. m^{-2}, the rest of the larvae being in the sediment. Thereafter, the density of larvae decreased to a minimum of 222 ind. m^{-2} on 9 August. At that time, almost all larvae (211 ind. m^{-2}) were in the water column (Fig. 2). On 14 September, larval density again exceeded 2,000 ind. m^{-2}. The density of the predatory cladoceran *Leptodora kindtii* was between 300 and 350 ind. m^{-2} in June and early July. Thereafter, the population declined to below 120 ind. m^{-2} for the rest of the summer (Fig. 2).

For herbivorous crustacean zooplankton, calanoid copepods (mainly *Eudiaptomus gracilis* Sars) were the dominating group in the May and June, with a biomass exceeding 80 µg C l^{-1} at 0–4 m depth and 35 µg C l^{-1} at 4–8 m depth (Fig. 3). Over the course of the summer, the biomass of calanoids at 0–4 m decreased and in July cyclopoids (mainly *Mesocyclops leuckarti* Claus, *Thermocyclops oithonoides* Sars) were the dominating group, with a biomass approaching 100 µg C l^{-1}. At 4–8 m depth, the biomass of calanoids was higher than the biomass of cyclopoids throughout the summer. The biomass of cladocerans was very low in May and June, but increased over the course of the summer and exceeded 40 µg C l^{-1} in the two topmost water layers on 14 September (Fig. 3). For cladocerans, as

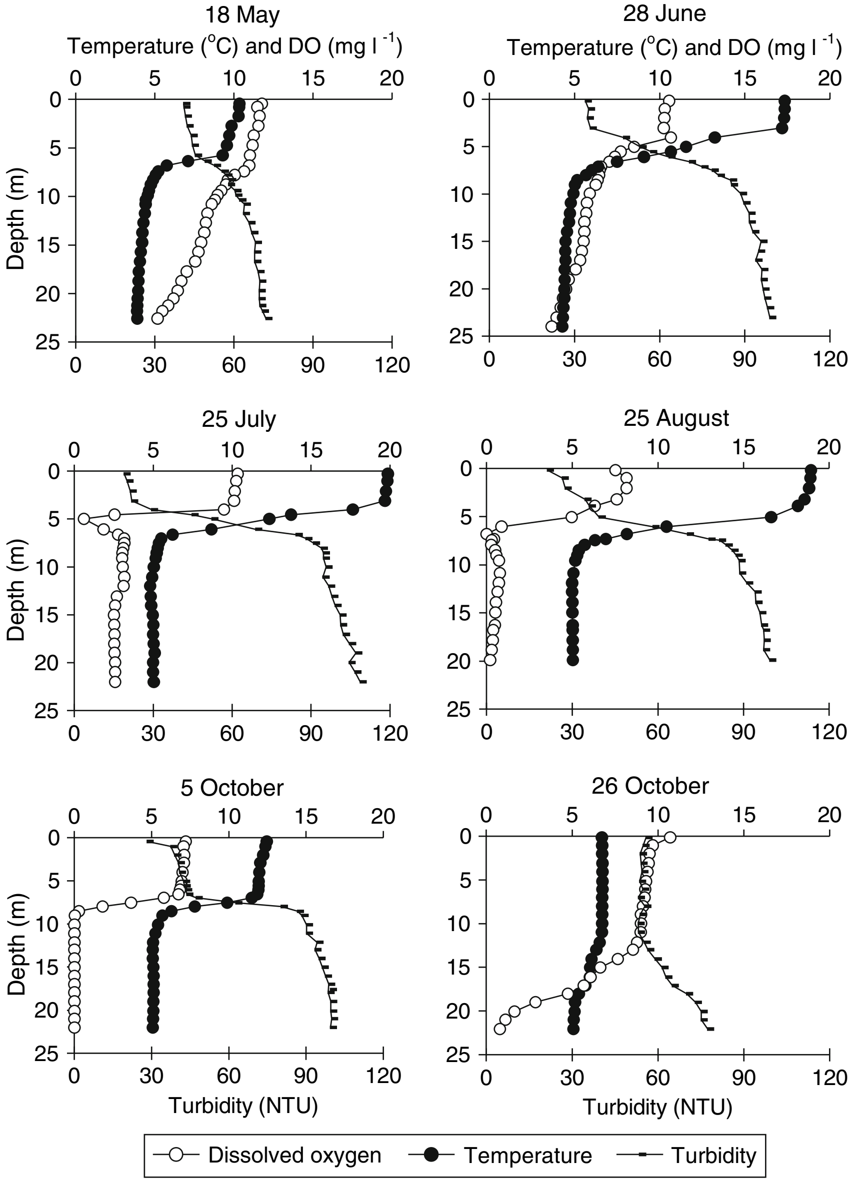
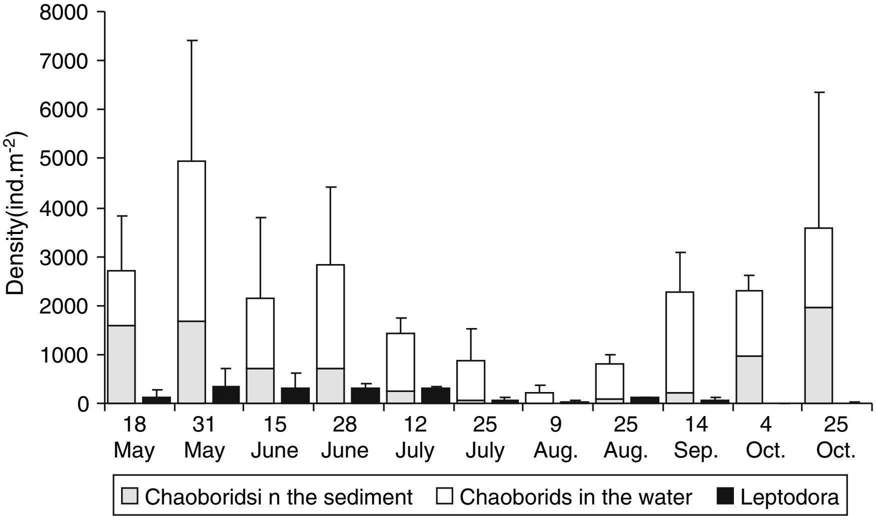


Fig. 1 The vertical profiles of temperature, dissolved oxygen (top *x*-axis) and turbidity (bottom *x*-axis) in Lake Rehtijärvi during the study period

well as in both copepod orders, the biomass at 0–4 and 4–8 m depths was significantly higher than at water layers deeper than 8 m (ANOVAR, $P < 0.001$). The time–depth interaction was highly significant ($P < 0.0001$), indicating that the timing of the biomass development depended on depth.

The cladoceran community was dominated by daphnids (mainly *Daphnia cristata* Sars and *Daphnia cucullata* Sars), which made up >70% of the cladoceran biomass for most of the study period (Fig. 4). Bosminids were virtually absent from the samples in May and June, but appeared (mainly *Bosmina coregoni* O. F. Müller) in July (Fig. 4). Throughout the study, however, the share of bosminids remained <10% of cladoceran biomass. Other observed cladoceran species (e.g. *Diaphanosoma brachyurum* Lieven, *Chydorus sphaericus* O. F. Müller) occurred at low densities. At 0–4 m depth, the clacoderan biomass rose constantly to the peak value of 43 μg C l^{-1} on 14 September. At 4–8 m water layer, cladoceran biomass remained below 5 μg C l^{-1} until late August when it increased steeply

Fig. 2 The density of *Leptodora kindtii* and the density of *Chaobrus flavicans* larvae in the water column and in the sediment. Ninety five percentage confidence limits for chaoborids are for the total density of larvae



and reached 40 μg C l^{-1} on 14 September. At deeper water layers, cladoceran biomass remained below 6 μg C l^{-1} throughout the study.

The average depth of cyclopoid copepods was 2–3 m in May–July and increased thereafter, reaching 6 m in October (Fig. 5). The average depth of calanoids increased from 2.4 m in May to 5.7 m in late June and fluctuated thereafter between 4.5 and 6.5 m. The average depth of cladocerans decreased from 7 m in May to 2.5 m in July. Thereafter, it increased until the end of the study period (Fig. 5).

Production and size of prey versus consumption by predators

The mean size of cladocerans was 0.60 mm in June, but decreased to a minimum of 0.45 mm on 9 August (Fig. 6). In September, the mean size increased again and reached 0.60 mm in October. The fluctuations in the mean size closely followed the seasonal variations in the refuge thickness (Fig. 6). The lowest refuge thickness values (<5 m) were observed in August and September, concomitantly with the lowest cladoceran mean size. The mean size of cyclopoids fluctuated between 0.66 and 0.77 mm and the largest average size was observed in August.

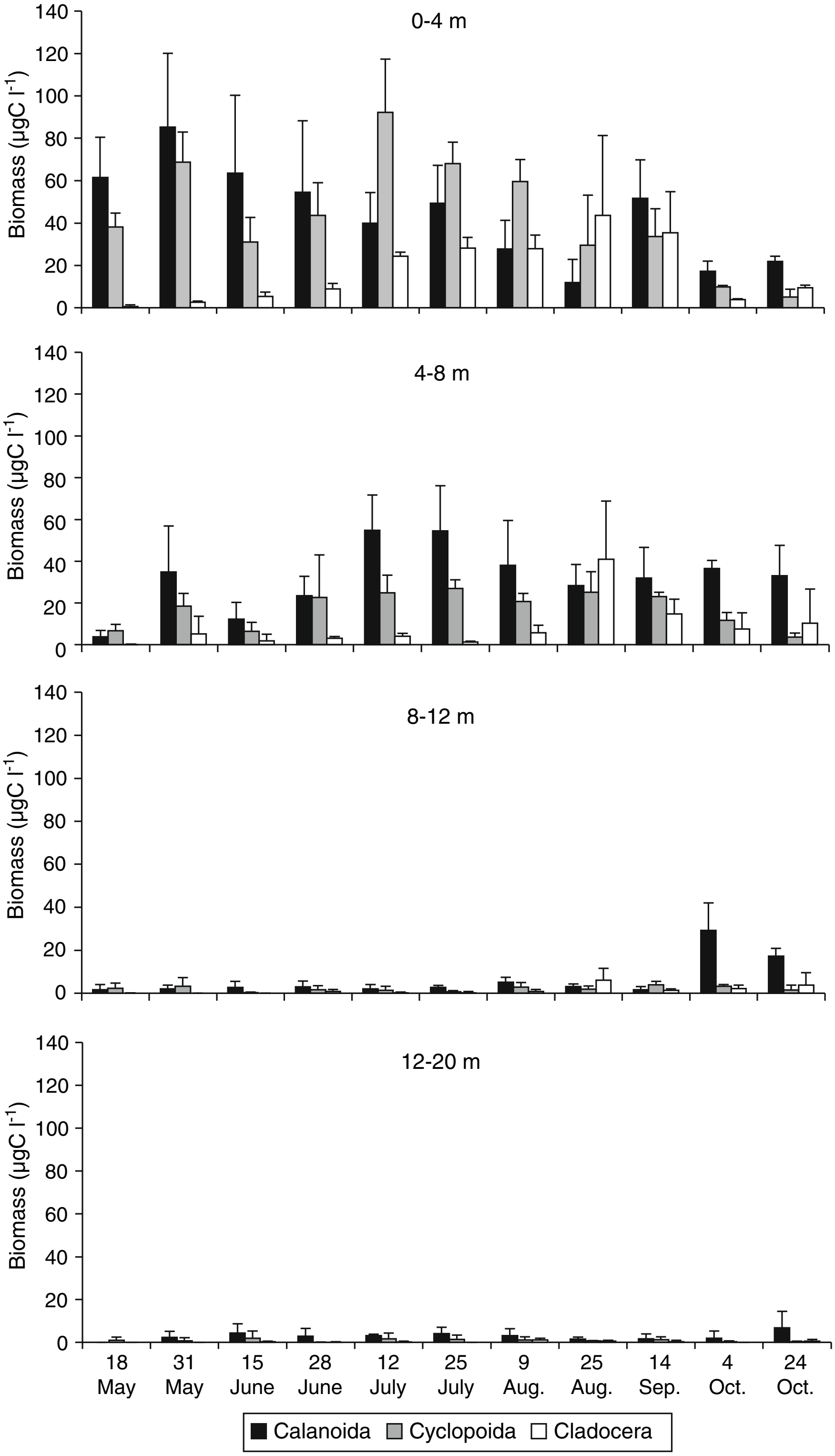
The production rate of cladocerans increased steadily during the summer and reached a maximum value of 3.5 μg C l^{-1} d^{-1} between 25 August and 14 September (Fig. 7). The food consumption rate of chaoborids was 3.1 μg C l^{-1} d^{-1} in May, which clearly exceeded the production of cladocerans (<0.5 μg C l^{-1} d^{-1}). In July, consumption by chaoborids declined to below 1 μg C l^{-1} d^{-1} and further fell to below 0.1 μg C l^{-1} d^{-1} in August (Fig. 7). In September, the rate of food consumption again exceeded 1 μg C l^{-1} d^{-1}.

The diet of roach was diverse in June, including zooplankton predators *Leptodora* (27%), chaoborids (27%), and other zoobenthos (12%). Herbivorous zooplankton made up only 6% of the diet but increased steeply over the course of the summer and constituted 37% of the diet in July and 95% and 85% in August and October, respectively. The increase in the proportion of cladocerans from July to August was significant (ANOVA, $P < 0.05$). The main prey for perch during June and July was *Leptodora*, which made up 56–57% of the stomach contents. The proportion of herbivorous cladocerans in the diet of perch was significantly higher in August and October than in June and July ($P < 0.01$). Copepods were also an important food source, and dominated the diet of perch in August and October. Statistically, the proportion of copepods consumed by perch was significantly lower in August than during the other months ($P < 0.05$).

Discussion

The effect of predation by fish on the early-summer development of pelagic zooplankton is not often very strong, because temperature is low and

Fig. 3 The seasonal development of crustacean zooplankton biomass at different depths (+95% confidence limits) in Lake Rehtijärvi during the summer 2005. The water layer >20 m was excluded from the figure due to very low biomass



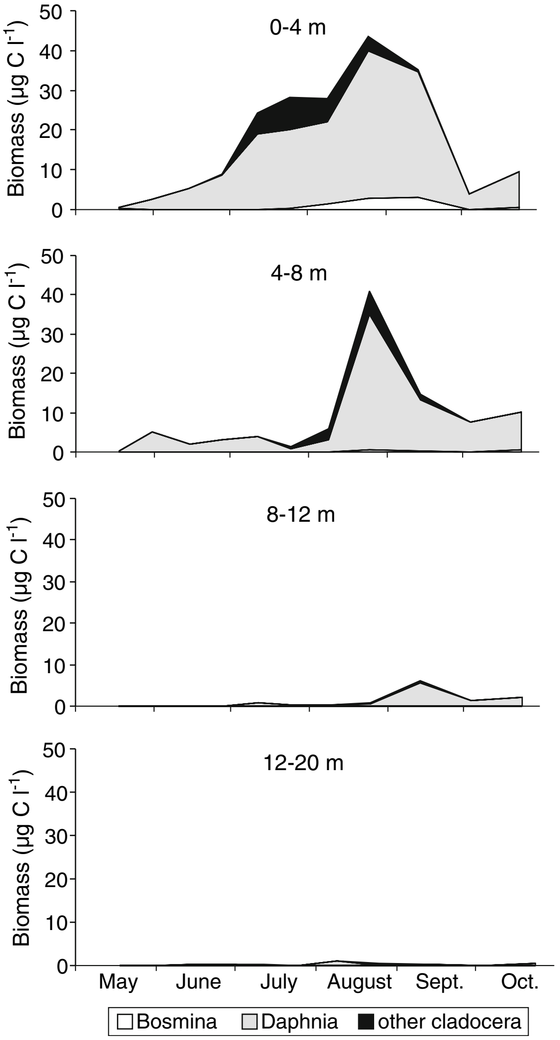


Fig. 4 The seasonal development of cladoceran biomass at different depths in Lake Rehtijärvi during the summer 2005. The water layer >20 m was excluded from the figure due to very low biomass

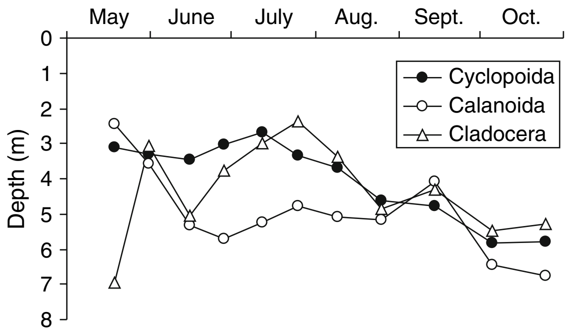


Fig. 5 The seasonal fluctuations in the average depth of cladocerans, cyclopoids and calanoids

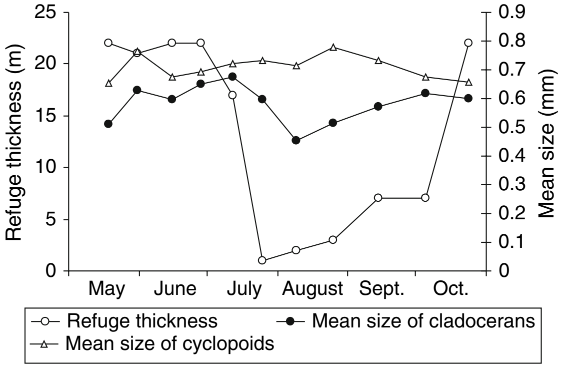


Fig. 6 Seasonal fluctuations in the refuge thickness and mean size of cladocerans and cyclopoids

young-of-the-year fish are just hatching (Gliwicz and Pijanowska 1989). This is one of the reasons for the rapid early summer biomass increase of zooplankton. In Lake Rehtijärvi, the consumption rate by chaoborids eliminated the early summer biomass peak of cladocerans. Therefore, the seasonal succession of cladocerans did not follow the pattern suggested for eutrophic lakes by the PEG-model. The strong effect of chaoborids could also be seen in the species composition of cladocerans. Bosminids were very sparse in early summer, although the spring biomass peak of cladocerans in temperate lakes, including lakes in southern Finland, usually consists mostly of bosminids (Lair and Ayadi 1989; Sammalkorpi et al. 1995). When feeding, *Chaoborus flavicans* usually selectively preys upon cladocerans, especially for bosminids, and high predation pressure by chaoborids in early summer may prevent the formation of the peak (Elser et al. 1987; Liljendahl-Nurminen et al. 2003).

In Lake Rehtijärvi, the predation pressure by planktivorous fish in early summer was probably low compared with the predation pressure exerted by chaoborids. The density of planktivorous fish in Lake Rehtijärvi is considerably lower than in Lake Hiidenvesi, where zooplankton consumption by fish was shown to be of minor importance compared with the consumption rate by *C. flavicans* (Liljendahl-Nurminen et al. 2003). Since consumption rate by chaoborids in the two lakes was similar, planktivorous fish had a minor effect on the early-summer development of herbivorous zooplankton in L. Rehtijärvi. The PEG model suggests that after the spring biomass peak of herbivorous zooplankon, fish predation accelerates the decline of their biomass in midsummer

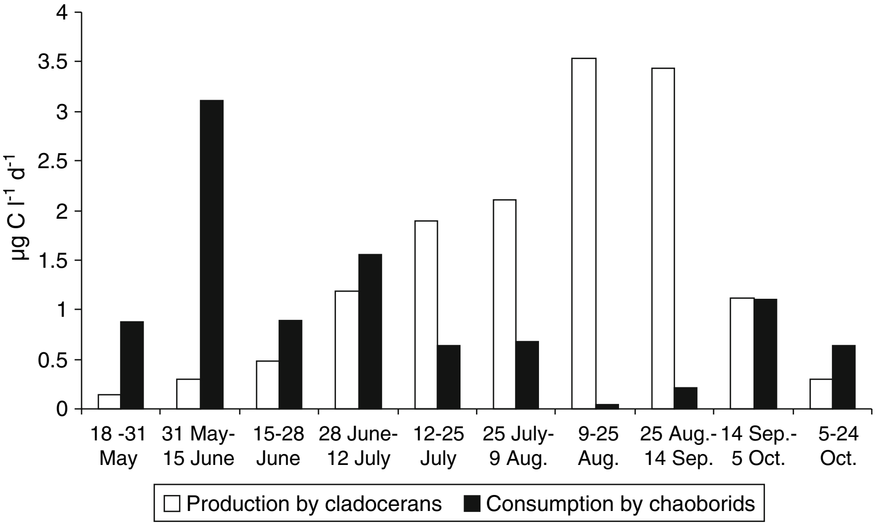


Fig. 7 Production rate of cladocerans and consumption rate by *C. flavicans* instar IV

and causes a shift towards smaller average body size (Sommer et al. 1986). Accordingly, in Lake Rehtijärvi, fish predation probably had a considerable effect on cladocerans in July and August. This is indicated by the increasing share of cladocerans in the diets of fish over the course of the summer and by the timing of the highest cladoceran biomass. The biomass peak of cladocerans did not occur during the biomass minimum of chaoborids, but was delayed to late August–early September. Additionally, the mean size of cladocerans decreased steeply in August when predation by chaoborids was lowest, indicating strong size-selective predation by fish (Post and McQueen 1987; Soranno et al. 1993). Similar size reduction did not occur in cyclopoids, which are less vulnerable to fish predation due to their good escape ability (e.g. Winfield et al. 1983).

The effect of fish predators on cladocerans was amplified by abiotic factors. The availability of refuges from fish predation is an important determinant of zooplankton abundance (e.g. Tessier and Welser 1991). In Lake Rehtijärvi, high water turbidity and low light intensity provide an efficient refuge. Clay-turbidity exceeding 30 NTU combined with very low light intensity greatly reduces the prey capture rate of planktivorous fish (Vinyard and O'Brien 1976; Horppila et al. 2004). In the clay-turbidity level of Lake Rehtijärvi, less than 1% of the surface light is left at 5 m depth (Horppila et al. 2004), the deeper layers being unprofitable for planktivorous fish. It was thus unexpected that the average daytime population depth of cladocerans was <3 m in July, when predation pressure by visually orienteering planktivorous fish was highest due to increasing water temperature and consumption of herbivorous zooplankton by young-of-the-year fish. Additionally, in July, water turbidity in the epilimnion was reduced due to the low discharge from the drainage area. These results suggest that depth distribution of cladocerans in Lake Rehtijärvi was initially regulated by seasonal variations in the vertical profile of dissolved oxygen, a phenomenon reported from other lakes (Wright and Shapiro 1990; Tessiel and Welser 1991). Cladocerans were forced upwards in the water column by the steep oxygen minimum that was formed in the metalimnion in late July. Consequently, cladocerans were more vulnerable to fish predators, and size-selective predation by fish resulted in a decrease in the individual mean size of cladocerans and a subsequent decline in the population biomass development.

The biomass of cladocerans decreased at 4–8 m and 8–12 m layers in late July, when oxygen concentration in the metalimnion deteriorated. The low biomass of cladocerans at 4–8 m depth in July compared with 0–4 m depth could not be attributed to predation since the biomass and consumption rate by chaoborids were low at the time. Likewise, fish were not responsible for the reduced biomass of cladocerans as the oxygen concentration in the metalimnion was too low even for cyprinids. Low fish predation rate at 4–8 m depth was also indicated by the higher biomass of calanoids compared with cyclopoids. With increasing fish planktivory, the abundance of calanoids in relation to cyclopoids usually decreases (e.g. Sarvala et al. 1998).

Copepods were generally found in deeper layers than cladocerans, suggesting that they were less affected by low oxygen than cladocerans, a phenomenon previously reported in other studies (Wissel and Ramcharan 2003, with references). For copepods, perch were more important predators than roach, which selectively prey upon cladocerans when feeding on zooplankton. The dietary differences between roach and perch have been documented in other Finnish lakes and are attributed to the superiority of perch over roach in capturing the fast swimming copepods (Lessmark 1983; Horppila et al. 2000b; Uusitalo et al. 2003). Both fish species switched from large invertebrate predators to herbivorous zooplankton when the availability of the former was reduced. Thus also variations in the availability of alternative, more preferred food items, such as chaoborids and *Leptodora*, affected the predation pressure on herbivorous cladocerans.

The study demonstrated that chaoborids might regulate pelagic zooplankton communities although cyprinid fish are abundant. This can be explained by the combined effects of different refuges. Recently, Liljendahl-Nurminen et al. (2008a, b) showed experimentally that although oxygen and turbidity refuges alone may not significantly reduce the feeding rate of fish, a combination of elevated turbidity and lowered oxygen concentration is an efficient refuge against fish predation. Low oxygen concentration limits the time fish can spend in the metalimnion, while high turbidity lengthens the time fish need for prey detection. Cyprinids are relatively well tolerant of lowered oxygen concentration (e.g. Stott and Cross 1973) and are probably able to make short visits into the metalimnetic depths occupied by chaoborids in Lake Rehtijärvi. However, the water turbidity in the metalimnion is so high and prey detection consequently difficult that such short time visits do not facilitate efficient feeding.

The density of *Leptodora kindtii* seemed to be controlled by predation by fish. In favourable temperatures, *Leptodora* can maintain high population density for several months and the highest densities are often observed in July–August (Sebestyén 1960; Branstrator and Lehman 1991). In Lake Rehtijärvi, the density of *Leptodora* decreased under favourable temperature during a period when it served as the main prey of perch. Due to its large size, *Leptodora* is a preferred prey item for many planktivorous fish species and its population density is often controlled by fish (Herzig 1995; Uusitalo et al. 2003; Alajärvi and Horppila 2004). In clay-turbid lakes, *Leptodora* is vulnerable to fish predation, because it does not migrate vertically to the hypolimnion (Horppila et al. 2000). *Leptodora* may control the biomass of herbivorous cladocerans when its density exceeds 500 ind. m^{-3} (Herzig 1995). The density of *Leptodora* in Lake Rehtijärvi remained clearly below this value, suggesting that *Leptodora* did not effectively contribute to the regulation of zooplankton. However, since the maximum population density of *Leptodora* occurred simultaneously with the spring peak of chaoborids and *Leptodora* preferentially feed on cladocerans (Karabin 1974; Lunte and Luecke 1990), *Leptodora* may have amplified the impact of chaoborids on the spring development of cladocerans. Predatory cyclopoid copepods can affect cladoceran zooplankton, but their effects are minor compared to those of chaoborids (Neill and Peacock 1980). Accordingly, the cladoceran biomass in Lake Rehtijärvi developed independently of cyclopoids.

The biomass of zooplankton is regulated not only by predation but also by food availability, which regulates reproduction rate (Gliwicz 1977; Ghilarov 1985). The zooplankton populations in Lake Rehtijärvi were aggregated into the epilimnion and biomass below 8 m depth was very low. This was expected, since phytoplankton biomass in clay-turbid lakes is restricted to near-surface layers due to weak light penetration. The amplitude of diurnal vertical migrations by zooplankton in turbid-water lakes is also low, usually <1 m in the turbidity level found in Lake Rehtijärvi (Dodson 1990; Horppila et al. 2000a). Although the chlorophyll *a* concentration in Lake Rehtijärvi suggested that food was not the factor limiting the growth of zooplankton biomass, food limitation of zooplankton could be caused by the occurrence of inedible algae. Large-sized cyanobacteria, which increase in abundance together with increasing nutrient concentrations, may interfere with food collection by cladocerans (Gliwicz 1977; Webster and Peters 1978). Nonetheless, in Lake Rehtijärvi, the highest biomass of cladocerans occurred simultaneously with the late-summer cyanobacterial bloom, suggesting that food limitation was not severe. This was supported by the fact that *Bosmina* *coregoni*, which is especially sensitive to the effects of cyanobacteria, showed the highest biomass during the dominance of cyanobacteria. While high concentrations of inorganic suspended matter may also be harmful to some zooplankton, cladocerans being more sensitive than copepods (Hart 1988; Kirk and Gilbert 1990). Direct negative effects of suspended clay on zooplankton in Lake Rehtijärvi were unlikely. The concentration of suspended solids was not on a harmful level (Kirk and Gilbert 1990) and the highest cladoceran biomass coincided with highest water turbidity.

In conclusion, the results demonstrated that in a clay-turbid lake invertebrate predators could be the main regulators of herbivorous zooplankton even when the density planktivorous fish, including cyprinids, is high. Due to the dominating role of invertebrates, the seasonal succession of zooplankton does not follow the predictions of the PEG-model, which could thus be adjusted for clay-turbid conditions. In clay-turbid circumstances, when both visually feeding fish and tactile invertebrate predators are plentiful, refuges for pelagic zooplankton against predation may be unavailable. The seasonal succession of zooplankton is controlled by the combined effects of invertebrate and vertebrate predation and refuge availability, which varies seasonally in relation to the occurrence of different predators. In Lake Rehtijärvi, predation by invertebrates was relaxed in mid summer, but since hypolimnetic refuge from fish predation was concomitantly diminished, the biomass development of cladocerans was delayed. The results also confirm that in deep clay-turbid lakes, food web management may be an ineffective method for water quality improvement, because invertebrate predators can prevent the effects of fish manipulations from affecting the grazing capacity of herbivorous zooplankton.

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