



A metalimnetic oxygen minimum indirectly contributing to the low biomass of cladocerans in Lake Hiidenvesi – a diurnal study on the refuge effect

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Abstract

The diurnal vertical migrations of smelt (*Osmerus eperlanus*), larvae of phantom midge (*Chaoborus flavicans*) and cladoceran zooplankton in eutrophic Lake Hiidenvesi were studied in order to clarify the factors behind the low zooplankton biomass. In the study area, an oxygen minimum occurred in the metalimnion in the 10–15 m depth. No diurnal fluctuations in the position of the minimum were observed. Cladocerans inhabited the epilimnion throughout the study period and their vertical movements were restricted to above the thermocline and above the oxygen minimum. *C. flavicans* conducted a diurnal migration. During the day, the majority of the population inhabited the 12–15 m depth just in the oxygen minimum, while during darkness they were found in the uppermost 8 m. Smelts started ascending towards the water surface before sunset and reached the uppermost 3 m around 23:00. During daytime, the majority of smelts inhabited the depth of 7–9 m, where the water temperature was unfavourably high for them (18 °C). Smelts thus probably avoided the steep oxygen gradient in the metalimnion, whereas *Chaoborus* used the oxygen minimum as a refuge against predation. Those smelts that were found in the same water layers as *Chaoborus* used the larvae as their main prey. The metalimnetic oxygen minimum thus seemed to favour the coexistence of vertebrate and invertebrate predators, leading to a depression of cladoceran zooplankton.

Introduction

Cladoceran assemblages are regulated by both vertebrate and invertebrate predators. In order to diminish the predation pressure, cladocerans may conduct both horizontal and vertical migrations between refuges and feeding areas (Stich & Lampert, 1981; Dini & Carpenter, 1988; Ringelberg et al., 1991; Lampert, 1993). In pelagic zones of lakes, where physical refuges such as macrophyte beds (e.g. Timms & Moss, 1984) are not available, low light intensities or low concentrations of dissolved oxygen may work as refuges against predators (Shapiro, 1990). Thus, cladoceran zooplankton tend to inhabit deeper waters during daylight and migrate upwards at night. Reversed migrations have also been detected in a number of studies (e.g. Calaban & Mackarewicz, 1982), and

have usually been connected to predation pressure by invertebrate predators (Lampert, 1993). Since invertebrate predators, as well as many fish species, also show migration patterns, the interactions within the pelagic communities are complex and may cause unexpected results, e.g. when eutrophicated lakes are being restored through reduction of planktivorous fish (Benndorf, 1995; Wissel & Benndorf, 1998).

Cladocerans can tolerate lower oxygen concentrations than fish and may use oxygen gradients as refuges against predation (Zaret, 1975; Shapiro, 1990). According to Hanazato (1992), however, hypolimnetic low-oxygen layers may favour the coexistence of vertebrate and invertebrate predators, leading to a depression of zooplankton communities. Especially larvae of phantom midge (*Chaoborus*), which are known as voracious predators on small cladocer-

ans and copepods (Fedorenko, 1975; Vanni, 1988; Lair, 1990) are very tolerant to low oxygen concentrations (Luecke, 1986). Since chaoborids themselves are favourable food items for fish (Parma, 1971; Eie & Borgström, 1981), they perform massive vertical migrations ascending near the surface after sunset and descending to deeper waters or to benthic habitat during the day (Malueg & Hasler, 1966; Parma, 1971).

In the pelagic zone of Lake Hiidenvesi (southwestern Finland), the biomass of cladocerans remains below $50 \mu\text{g C l}^{-1}$ throughout the summer (Tallberg et al., 1999) being low compared with other eutrophic lakes in the area (Luokkanen, 1995; Sarvala et al., 1998). The seasonal development of the cladoceran biomass is also exceptional. The spring peak is missing and the highest biomass takes place in July–August (Tallberg et al., 1999). Both planktivorous smelt (*Osmerus eperlanus* (L.)) and larvae of *Chaoborus flavicans* (Meigen) exist in high densities in the water column, explaining the scarcity of cladocerans. *Mysis relicta* Loven also inhabits the lake, but its density remains below 1 ind. m^{-3} (unpublished). The cladoceran biomass inversely follows the seasonal fluctuations of the *C. flavicans* density (unpublished), highlighting the importance of predation in regulating the cladoceran community. The mechanisms facilitating the existence of both vertebrate and invertebrate predators in high quantities are not known. In summer, before the emergence of *C. flavicans*, the hypolimnetic oxygen concentration stays above 4 mg l^{-1} (Tallberg et al., 1999) and does not considerably restrict the downward migrations of fish (Wright & Shapiro, 1990). A hypolimnetic oxygen refuge for *Chaoborus* against the predation pressure by fish (Hanazato, 1992; Irvine et al., 1997) thus does not exist. However, a metalimnetic oxygen minimum occurs in the lake during the summer stratification period (Tallberg et al., 1999). The effects of metalimnetic oxygen minima on the movements of fish and invertebrate animals have only rarely been examined (Schram & Marzolf, 1994; Aku et al., 1997). In the present study, the diurnal changes in the oxygen profile and in the vertical distribution of cladocerans, *C. flavicans* and smelts were examined to clarify, whether the metalimnetic oxygen minimum contributes to the coexistence of smelt and *C. flavicans* and thus to the low biomass of cladocerans in L. Hiidenvesi. Data on the diet composition of smelts are also presented. The mechanisms behind the metalimnetic oxygen minimum are discussed.

Study area

Lake Hiidenvesi is situated in southwestern Finland. The total area of the lake is 30.3 km^2 . The lake is made up of several separate basins with different morphology and water quality. The Kiihkelyksenselkä basin, where the present study was conducted, has an area of 9.7 km^2 , the mean and maximum depths being 11.2 m and 33 m, respectively. The total phosphorus concentration in the epilimnion during the open water season is on average $50 \mu\text{g l}^{-1}$. Due to suspended inorganic material and frequent phytoplankton blooms, Secchi depth rarely exceeds 120 cm. During the summer stratification period, the oxygen profile is negatively heterograde, an oxygen minimum occurring in the thermocline. The biomass of cladocerans in the area is below $50 \mu\text{g C l}^{-1}$ and the assemblage is dominated by small-sized species. The average size of the most abundant daphnid (*Daphnia cristata* Sars) remains below 0.6 mm (Tallberg et al., 1999). Planktivorous smelt (*Osmerus eperlanus* (L.)) is the dominant fish species in the area (T. Malinen, unpublished). Several cyprinid species, including bleak (*Alburnus alburnus* (L.)) and roach (*Rutilus rutilus* (L.)), as well as percids, perch (*Perca fluviatilis* L.) and pikeperch (*Stizostedion lucioperca* (L.)) are also common (Vinni et al., 2000).

Material and methods

The study was carried out on 21 July–22 July 1998 in the deepest part of the Kiihkelyksenselkä basin (water depth 30 m). Samples for chemical analysis, phytoplankton and zooplankton were taken at 14:00, 21:30, 01:00, 05:00 and again at 14:00. The sampling times were planned according to sunset (22:15) and sunrise (4:40). Samples for cladocerans were hauled with a tube sampler (length 1 m, volume 7.5 l) from each metre down to 28 m. Samples from 4 m layers were combined, filtered through a $50 \mu\text{m}$ plankton net and preserved with formaldehyde. Samples for phytoplankton species composition were taken from the three uppermost 4 m layers and preserved with acid Lugol's solution. Oxygen and temperature profiles were measured with a YSI oxygen meter and light intensity at different water layers with a LI-COR quantum meter. The value of the vertical light attenuation coefficient was calculated with the equation

$$E = \ln(I_0/I_z)/Z$$

(e.g. Scheffer, 1998), where I_z and I_0 are the intensities of light at depth Z (5 m) and just below the water surface. Water samples for dissolved phosphorus were taken at each sampling occasion from each of the 4 m layers, and samples for total phosphorus and chlorophyll *a* at the last sampling occasion.

In the laboratory, phytoplankton was counted using the inverted microscope technique introduced by Utermöhl (1958). A minimum of 10 cells from each of the dominant species were measured and the cell numbers were converted to biomass using stereometric equations (Edler, 1979). Cladocerans were enumerated using inverted microscopy and identified to species level. When available, 30 individuals from each species were measured.

The distributions of fish and *Chaoborus* were studied by echosounding in a fixed transect near the sampling station at water sampling times, and additionally, from 22:00 to 02:00 at intervals of half an hour. Echosoundings were conducted with a SIMRAD EY-500-echosounder that was equipped with a split-beam transducer 120-7F (operating frequency 120 kHz and beam opening angle 7° at -3 dB level). The transducer was mounted to a towed body, which was lowered to a depth of 0.6 m. Pulse duration was set to 0.3 ms and ping interval to minimum value. The echosounding equipment was calibrated by a standard copper sphere (target strength -40.4 dB). The data was analysed with EP 500-software with the time-varied gain $20 \log R$ and with an integration threshold of -80 dB. For each transect the echo integral values ($s_a \text{ m}^{-2}$) were computed in 20 cm layers. Because of the very high *Chaoborus* densities and the presence of small fish it was impossible to separate the echo integrals from *Chaoborus* and from fish by thresholding. Even the method developed by Eckmann (1998) failed to allocate the reflected echo energy to *Chaoborus* and fish. However, because the presence of fish as well as *Chaoborus* can be seen from the frequency distribution of integral values in a small volume of water (T. Malinen, unpublished), it was possible to divide integral concentrations into three classes: those containing mainly fish, mainly *Chaoborus*, and those containing fish and *Chaoborus* in comparable biomasses. Due to the difficulties in separating the echo integral from *Chaoborus* and from fish, *Chaoborus* density was estimated by vertical hauls (3 replicates) with a $180 \mu\text{m}$ plankton net (diameter 30 cm) at each sampling occasion.

Smelts for stomach content analysis were captured with a pelagic trawl (cod-end 3 mm) on 24 July

(12:00–18:00) with 7 hauls. The fish were weighed to the nearest g and measured to the nearest mm (total length). The stomach contents of the smelts were estimated with a volumetric points method (Windell, 1971). The analysed smelts were divided into two groups according to the depth of the trawl in the haul: 5–10 m ($n = 40$, size range 60–90 mm) and >10 m ($n = 127$, size range 70–210 mm). The former group was used to determine the daytime diet of smelt in the epilimnion and metalimnion whereas the latter one is a pure sample from the hypolimnion.

Results

At 0–8 m depth, the water temperature was mainly between 17 and 18 °C (Figure 1). The thermocline was at 8–10 m depth, water temperature being 11–12 °C at 12 m depth, thereafter decreasing steadily. The concentration of dissolved oxygen in the epilimnion was $8\text{--}9 \text{ mg l}^{-1}$ with the exception of the last sampling occasion (9.6 mg l^{-1}) (Figure 1). The oxygen concentrations at night (1:00 and 5:00) were slightly lower than those measured during the day. Just below the thermocline, at 10–15 m depth, a metalimnetic oxygen minimum occurred, the concentration at 12 m depth falling to 4.5 mg l^{-1} . At 15–25 m depth, the oxygen concentration was $5\text{--}6 \text{ mg l}^{-1}$. The light extinguished in the upper part of the epilimnion. Even during the brightest daylight, below 2 m less than 5% and below 10 m less than 1% of the surface irradiance remained (Figure 1).

The concentration of soluble reactive phosphorus remained below $5 \mu\text{g l}^{-1}$ in the epilimnion throughout the study period. The concentration increased steeply towards the deeper layers, being $20\text{--}25 \mu\text{g l}^{-1}$ below 25 m depth. There were no differences between the sampling occasions. The concentration of total phosphorus was $30 \mu\text{g l}^{-1}$ at the surface, decreased slightly in the thermocline and increased thereafter towards the deeper layers, exceeding $55 \mu\text{g l}^{-1}$ at 25 m depth.

The chlorophyll *a* concentration was $12 \mu\text{g l}^{-1}$ in the surface layer, $6 \mu\text{g l}^{-1}$ at 6 m depth and below $3 \mu\text{g l}^{-1}$ in the deeper water. Phytoplankton biomass in the surface layer fluctuated between 1.5 and 3.5 mg l^{-1} , except on the last sampling occasion, when it rose to 10 mg l^{-1} (Figure 1). Below 8 m depth, the biomass was below 1 mg l^{-1} . Phytoplankton was heavily dominated by cyanophytes (*Aphanizomenon flos-aquae* (Linné) Ralfs), with diatoms (mainly *Rhizosolenia longiseta* Zacharias and *Aulacoseira italica* (Ehren-

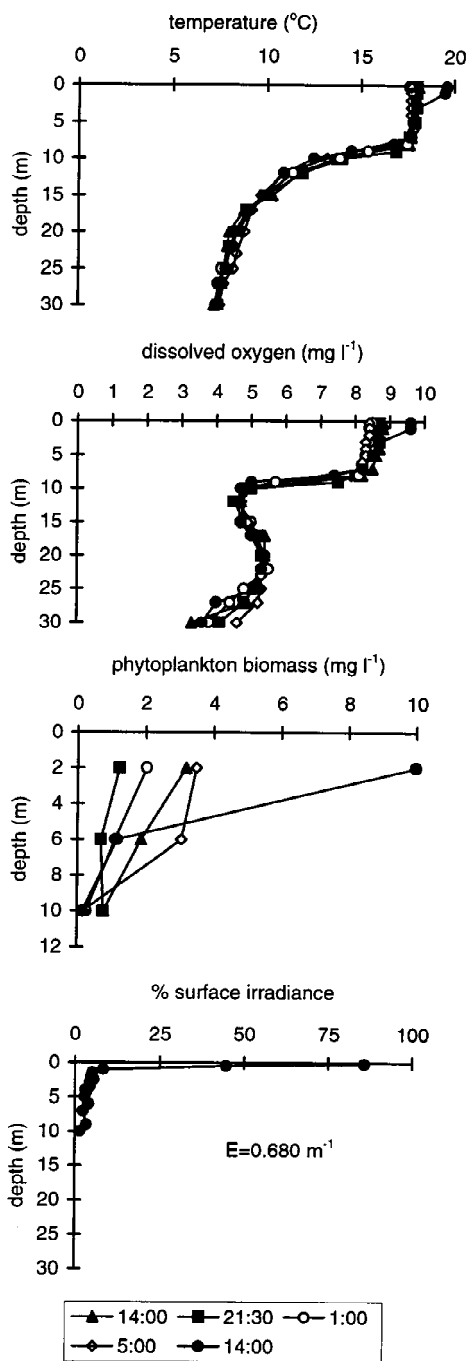


Figure 1. The vertical profiles of temperature, dissolved oxygen, phytoplankton biomass and light intensity (plus the light attenuation coefficient) during the study period.

berg) Simonsen) the second most abundant group. The initiation of an *A. flos-aquae*-bloom could be traced in the ascending pattern of the cyanophyte biomass. The cyanophyte biomass increased from 1.5 (21:30) to 10 mg l⁻¹ (14:00) in the surface layer. Below 8 m, cyanophytes almost disappeared after sunset, and in the intermediate layer the biomass peak (at 3.1 mg l⁻¹) occurred at sunrise.

The density of cladoceran zooplankton was low. Only the two most abundant species *Daphnia cristata* and *Bosmina coregoni* O.F. Müller occurred in densities higher than 10 ind. l⁻¹. The densities of *Daphnia cucullata* Sars, *Daphnia hyalina* Leydig, *Limnospira frontosa* Sars, *Diaphanosoma brachyurum* Lieven, *Leptodora kindtii* Focke and *Chydorus sphaericus* O. F. Müller remained below 5 ind. l⁻¹ throughout the study period. The cladocerans were concentrated in the upper layers of the water column; over 90% of all individuals inhabited the 0–12 m depth throughout the study period (Figure 2). With few exceptions, over 75% of the cladocerans were found in the epilimnion (0–8 m). Cladocerans were small-sized. *Daphnia hyalina* (1.0 mm), *Limnospira frontosa* (1.2 mm) and *Leptodora kindtii* (1.4 mm) were the only species exceeding 1 mm in average length. The average lengths of *Daphnia cucullata* and *Daphnia cristata* were 0.6 mm.

Most cladoceran species showed no clear diurnal migration patterns (Figure 2). The results suggested, however, that *Daphnia cucullata* migrated bimodally between the two uppermost water layers (Figure 2). At the time of sunset and sunrise, the largest part of the population inhabited the 4–8 m layer, while during daylight and at the darkest night the majority of the population was found in the 0–4 m layer (Figure 2).

According to the net hauls the density (\pm 95% conf. limits) of *Chaoborus* larvae in the water column was 1425 ± 255 ind m⁻². The echosounding revealed a clear migration of *Chaoborus* (Figure 3). During the day, the majority of *Chaoborus* inhabited the depth of 10–15 m. Some *Chaoborus* started their migration upwards already before sunset. At 21:31, two layers with high *Chaoborus* density could be detected: one at the depth of 8–10 m and another at 10–15 m. The latter group started ascending around sunset. At first, the ascent was slow but after the sunset the migration speed increased. Some *Chaoborus* stopped their migration at the depth of 7–10 m at midnight, whereas others continued towards the water surface. By 1:15 most of these upper-migrating *Chaoborus* reached the 'blind zone' of the echosounder. At sunrise (4:29),

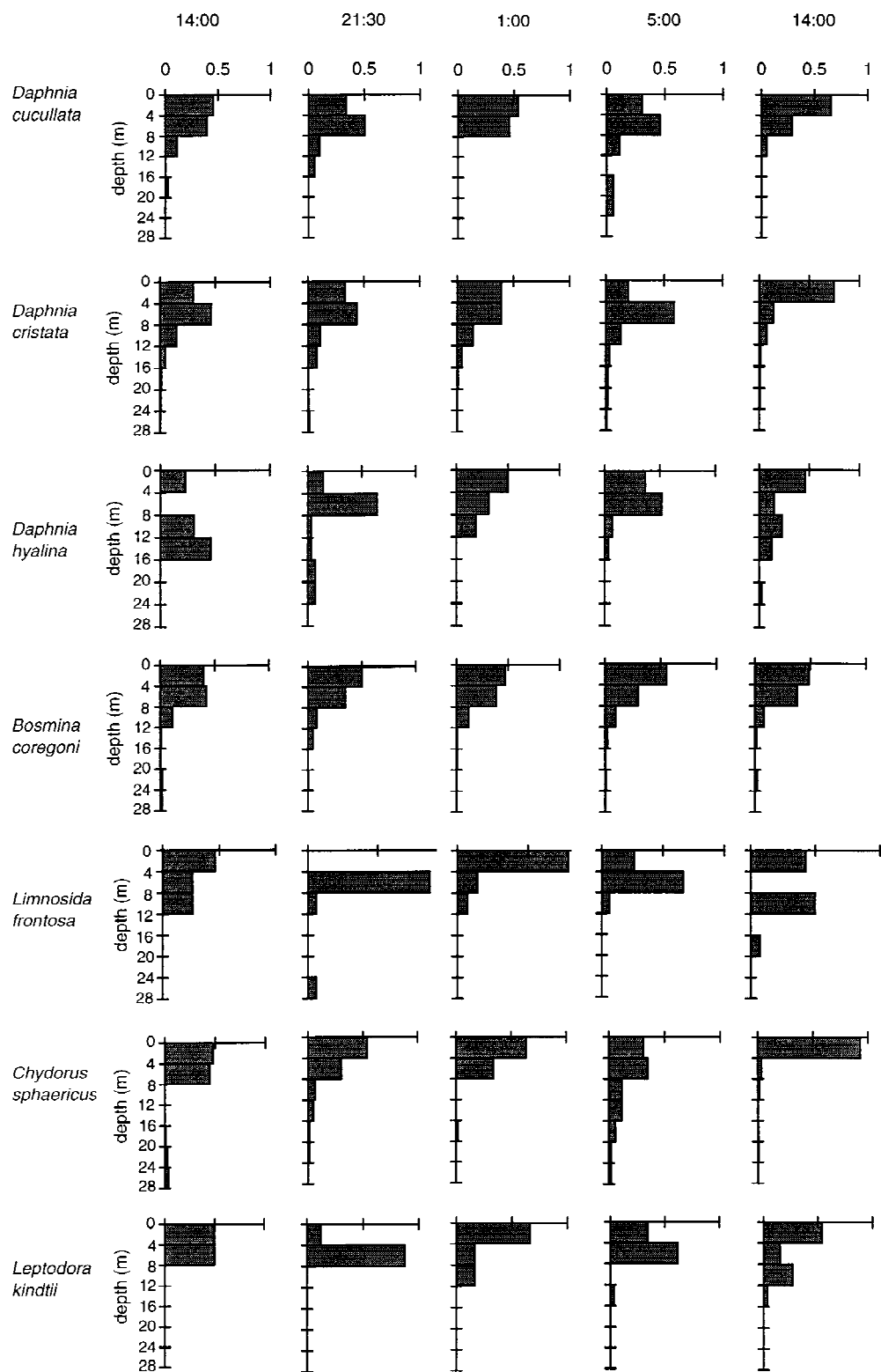


Figure 2. The vertical distribution (proportion of total population abundance) of different cladoceran species during the study period.

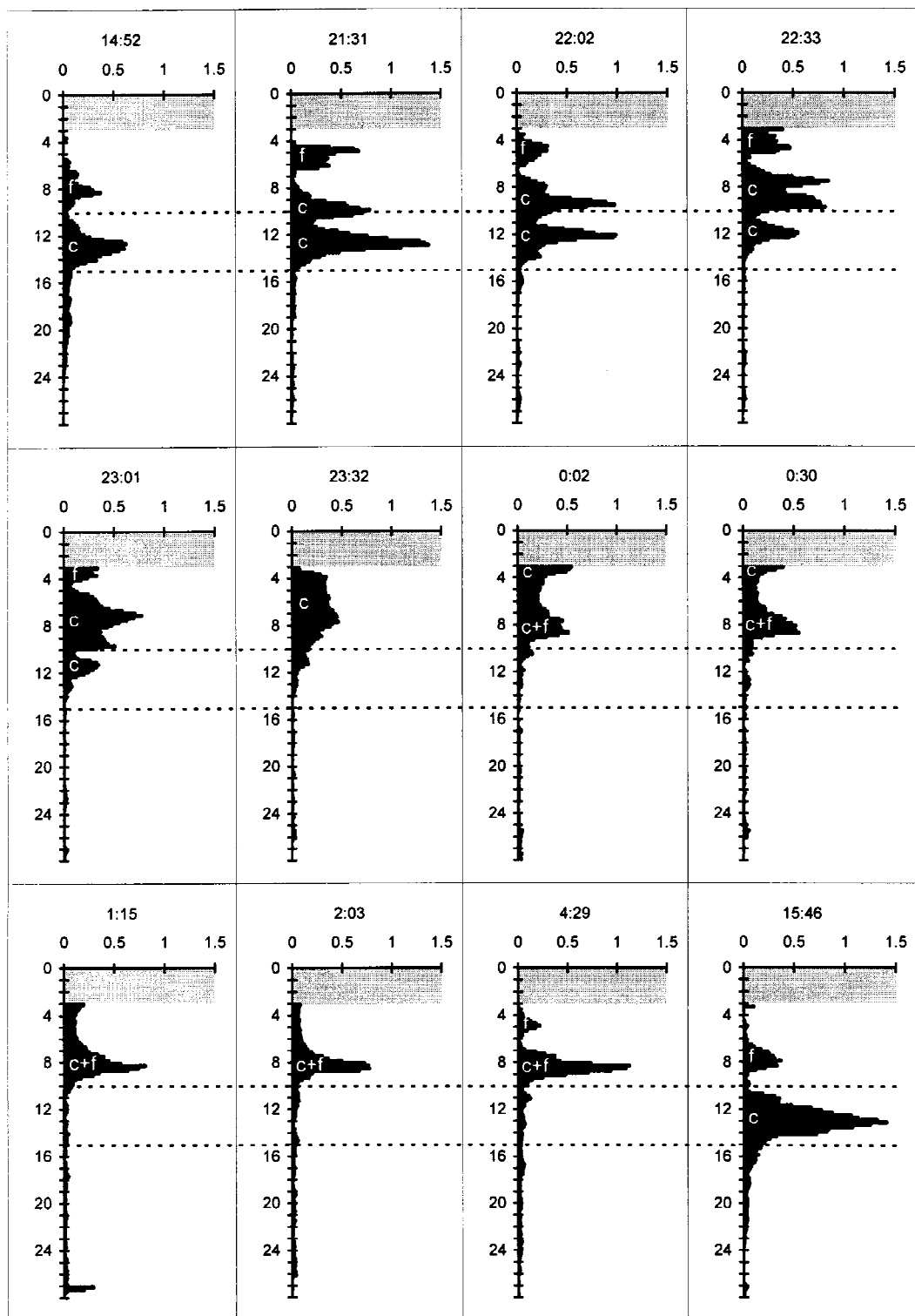


Figure 3. The vertical distribution of echo integral ($s_a m^{-2}$) during the study period. The 'blind zone' of the echosounder near the water surface is indicated by a grey layer, 'f' refers to fish and 'c' to *Chaoborus*, respectively. The position of the metalimnetic oxygen minimum is marked with dotted horizontal lines.

the descent had not yet started but by afternoon most *Chaoborus* had reached the same depth as during the previous day.

The majority of smelts inhabited the depth of 7–9 m during daytime (Figure 3). They started ascending towards the water surface before sunset and reached the 'blind zone' around 23:00. By afternoon, most smelts again inhabited the same depth as during the previous day.

The diet composition of smelt depended clearly on the sampling depth. In smelt captured from the upper 10 m layer, cladocerans dominated the diets with 72% volume percentage, while in deeper hauls *Chaoborus* made up over 70% of the stomach contents. In zooplanktonic diets, *Daphnia*, *Bosmina* and *Leptodora* were the most important groups (Figure 4).

Discussion

The explanations for the occurrence of metalimnetic oxygen minima include decomposition of settling material in the denser water of the metalimnion (Birge & Juday, 1911; Thienemann, 1928), methane oxidation (Ohle, 1958), respiration by zooplankton (Minder, 1923; Shapiro, 1960) and oxygen uptake by the sediment (Alsterberg, 1927). In L. Hiidenvesi, the last three hypotheses could be easily rejected. Methane bubbles reaching the metalimnion would have been detected by the echosounder. Most likely, however, methane would have been oxidized already in the oxygenated hypolimnion. Nor did respiration by *Chaoborus* cause the minimum, since the vertical position of the oxygen minimum did not change in spite of the massive diurnal migration by *Chaoborus*, while the finding by Alsterberg (1927) holds only in lakes with gentle slopes (Wetzel, 1983). The densities of copepods were not explored in the present study, but in the summer of 1997, when a clear metalimnetic oxygen minimum took place, no aggregation of copepods in the metalimnion was observed (Tallberg et al., 1999). Thus the decreased concentration of dissolved oxygen was likely connected to the slow sinking rate of decomposable material in the metalimnion. The relatively low content of organic matter in the sediment also suggests that decomposition of sinking material in the water column is intensive.

The results demonstrated that the great majority of cladocerans inhabited the epilimnion throughout the study period and their vertical movements were restricted above the thermocline and thus above the

oxygen minimum. The oxygen concentration in the metalimnion was not low enough to form an unpenetrable barrier for cladocerans (Prepas & Rigler, 1978). Taleb et al. (1993) found that cladocerans migrated diurnally into hypolimnetic low-oxygen layers to avoid predation by *Chaoborus*. In their lake, however, *Chaoborus* burrowed into the sediment during the day. Since in L. Hiidenvesi *Chaoborus* stopped their downwards migration at 12–15 m depth, crossing the thermocline did not benefit cladocerans due to the predation pressure by *Chaoborus* in the deeper layers. Limnetic larvae of *C. flavicans* have been observed to feed throughout the day (Parma, 1971). Avoidance of steep temperature gradients may also explain the aggregation of cladoceran assemblages in the epilimnion (Calaban & Mackarewicz, 1982). Due to the low transparency of the water, most of the algal biomass was restricted to the few upper metres, which may also partly explain the scarcity of cladocerans below the thermocline.

Bimodal migration patterns in zooplankton assemblages have been reported. In such cases, however, cladocerans have been found to sink during darkest night due to reduced activity (McNaught & Hasler, 1964). Interestingly, the present study suggested that in L. Hiidenvesi *D. cucullata* descended during dusk and dawn, being higher in the water column during daylight and the darkest night. A more detailed exploration of the migration pattern by cladocerans was not possible since the samples were analysed in 4 m layers. The amplitude of migrations by cladocerans decreases with decreasing body size and water clarity and may be less than 1 m in turbid waters (McNaught & Hasler, 1964; Dodson, 1990).

The migration pattern by *C. flavicans* was similar to those found in numerous other studies (Malueg & Hasler, 1966; Parma, 1971; Sardella & Carter, 1983): a rapid ascent to the surface during darkness and a return to deeper layers around sunrise. Such behaviour was most likely connected with predation risk. Those smelts that inhabited the same water layer with *Chaoborus* used the larvae as their main food resource (Figure 4). The larvae did not, however, dive to near-bottom layers or to the sediment, but the majority of the population stayed in the 11–13 m depth, which is a common phenomenon in turbid waters (Parma, 1971).

In many lakes, smelts spend the hours of daylight near the bottom and migrate to the surface during night (e.g. Heist & Swenson, 1983). Vertical migrations by smelts are regulated by light for prey detection and by water temperature (Hakkari, 1978; Heist & Swenson,

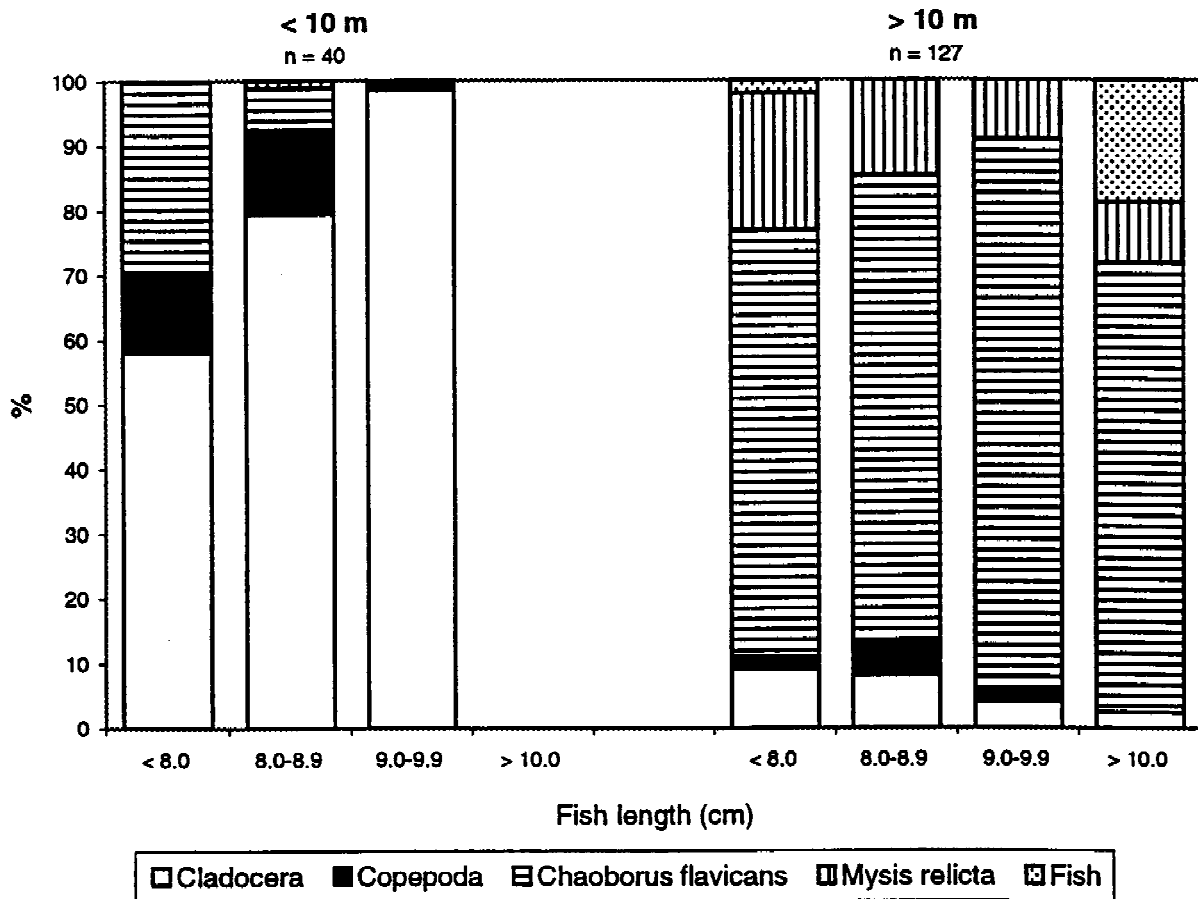


Figure 4. The diet composition (volume percentages) of smelts captured in the Kiihkelyksenselkä basin from 5 to 10 m and 10 to 20 m depths in July 1998.

1983; Burczynski et al., 1987; Nellbring, 1989), but the threat of piscivore predation has also been suggested to induce migration (Gliwicz & Jachner, 1992). The nocturnal upward migrations by rainbow smelts may be restricted by water temperatures in the epilimnion (Heist & Swenson, 1983; Burczynski et al., 1987). In Europe, smelts may migrate diurnally from 20 to 30 m depth to the surface and across temperature gradients of more than 10 °C, but spend the daylight hours in temperatures below 10 °C (Dembinski, 1971). Generally, smelts seem to avoid temperatures above 14–15 °C (Nellbring, 1989, with references). In Lake Hiidenvesi, the nocturnal upward migration by smelts was probably regulated by light and/or prey availability. In the 0–5 m layer, the zooplankton biomass is considerably higher than in deeper layers (Tallberg et al., 1999). It was, however, very unexpected that during the day the majority of smelts stayed in the epilimnion where the water temperature was 18 °C.

Light for prey detection alone is not a likely explanation for such behaviour, since at 8 m depth, where the majority of smelts stayed during daytime, light was practically extinct. The most obvious explanation for the unexpected behaviour of smelts is thus the avoidance of the oxygen minimum in the metalimnion. It can be argued that the heterogeneity of the oxygen profile was not important, but that the steeply decreasing oxygen concentration in the metalimnion was enough to restrict the downward migration by smelts. However, the majority of the *C. flavicans* population stopped their downward migration just in the oxygen minimum, suggesting that they used the minimum as a refuge. The oxygen concentration in that layer was not low enough to form an absolute boundary for fish, but most likely restricted the time fish were willing to spend in that stratum (Wright & Shapiro, 1980). Smelts have been observed to prefer zones where

oxygen concentration is above 5 mg l⁻¹ (Moeller & Scholz, 1991).

According to the present dataset, it seems that in L. Hiidenvesi the metalimnetic oxygen minimum restricts the vertical downward movements of smelts. Since the migrations of *C. flavicans* are not affected, smelt and invertebrate predators are able to coexist in high quantities, which results in low biomass of cladocerans.

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References

- Alsterberg, G., 1927. Die Sauerstoffschichtung der Seen. Bot. Notiser 1927: 255–274.
- Aku, P. M. K., L. G. Rudstam & W. M. Tonn, 1997. Impact of hypolimnetic oxygenation on the vertical distribution of cisco (*Coregonus artedii*) in Amisk Lake, Alberta. Can. J. Fish. Aquat. Sci. 54: 2182–2195.
- Benndorf, J., 1995. Possibilities and limits for controlling eutrophication by biomanipulation. Int. Rev. ges. Hydrobiol. 80: 519–534.
- Birge, E. A. & C. Juday, 1911. The inland lakes of Wisconsin. The dissolved gases of the water and their ecological significance. Wisc. Geol. Nat. Hist. Surv. Bull. 22: 1–1259.
- Burczynski, J. J., P. H. Michaletz & G. M. Marrone, 1987. Hydroacoustic assessment of the abundance and distribution of rainbow smelt in Lake Oahe. N. Am. J. Fish. Mgmt 7: 106–116.
- Calaban, M. J. & J. C. Makarewicz, 1982. The effect of temperature and density on the amplitude of vertical migration of *Daphnia magna*. Limnol. Oceanogr. 27: 262–271.
- Dembinski, W., 1971. Vertical distribution of vendace *Coregonus albula* L. and many other fish species in some Polish lakes. J. Fish Biol. 3: 341–357.
- Dini, M. L. & S. R. Carpenter, 1988. Variability in *Daphnia* behavior following fish community manipulations. J. Plankton Res. 10: 621–635.
- Dodson, S., 1990. Predicting diel vertical migration of zooplankton. Limnol. Oceanogr. 35: 1195–1200.
- Eckmann, R., 1998. Allocation of echo integrator output to small larval insect (*Chaoborus* sp.) and medium-sized (juvenile fish) targets. Fish. Res. 35: 107–113.
- Edler, L., 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Baltic Mar. Biol. Publ. 5: 138.
- Eie, J. A. & R. Borgström, 1981. Distribution and food of roach (*Rutilus rutilus* (L.)) and perch (*Perca fluviatilis* L.) in the eutrophic lake Årungen, Norway. Verh. int. Ver. Limnol. 21: 1257–1263.
- Fedorenko, A. Y., 1975. Instar and species-specific diets in two species of *Chaoborus*. Limnol. Oceanogr. 20: 238–249.
- Gliwicz, Z. M. & A. Jachner, 1992. Diel migrations of juvenile fish: a ghost of predation, past or present. Arch. Hydrobiol. 124: 385–410.
- Hakkari, L., 1978. On the productivity and ecology of zooplankton and its role as food for fish in some lakes in Central Finland. Biol. Res. Rep. Univ. Jyväskylä 4: 1–87.
- Hanazato, T., 1992. Direct and indirect effects of low oxygen layers on lake zooplankton communities. Ergebn. Limnol. 35: 87–98.
- Heist, B. G. & W. A. Swenson, 1983. Distribution and abundance of rainbow smelt in western Lake Superior as determined from acoustic sampling. J. Great Lakes Res. 9: 343–353.
- Irvine, K., 1997. Food selectivity and diel vertical distribution *Chaoborus edulis* (Diptera, Chaoboridae) in Lake Malawi. Freshwat. Biol. 37: 605–620.
- Lair, N., 1990. Effects of invertebrate predation on the seasonal succession of a zooplankton community: a 2-year study in Lake Aydat, France. Hydrobiologia 198: 1–12.
- Lampert, W., 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. Arch. Hydrobiol. Beih. Ergebn. Limnol. 39: 79–88.
- Luecke, C., 1986. A change in the pattern of vertical migration of *Chaoborus flavicans* after the introduction of trout. J. Plankton Res. 8: 649–657.
- Luokkanen, E., 1995. Vesikirppuyhteisön lajisto, biomassa ja tuotanto Vesijärven Enonselällä. Helsingin yliopiston Lahden tutkimus- ja koulutuskeskuksen raportteja ja selvityksiä 25. 1–53 (in Finnish with English summary).
- Malueg, K. W. & A. D. Hasler, 1966. Echo sounder studies on diel vertical movements of *Chaoborus* larvae in Wisconsin (U.S.A.) lakes. Verh. int. Ver. Limnol. 16: 1697–1708.
- McNaught, D. & A. D. Hasler, 1964. Rate of movement of populations of *Daphnia* in relation to changes in light intensity. J. Fish. Res. Bd Canada 21: 291–318.
- Minder, L., 1923. Studien über den Sauerstoffgehalt des Zurichsees. Arch. Hydrobiol. (suppl.) 3: 107–155.
- Moeller, H. & U. Scholz, 1991. Avoidance of oxygen-poor zones by fish in the Elbe River. J. Appl. Ichthyol. 7: 176–182.
- Nellbring, S., 1989. The ecology of smelts (genus *Osmerus*): a literature review. Nordic J. Freshwat. Res. 65: 116–145.
- Ohle, W., 1958. Die Stoffwechselfeldynamic der Seen in Abhängigkeit von der Gasausscheidung ihre Schlammes. Vom Wasser 25: 127–149.
- Parma, S., 1971. *Chaoborus flavicans* (Meigen) (Diptera, Chaoboridae). An autecological study. Doctoral Dissertation, University of Groningen.
- Prepas, E. & F. H. Rigler, 1978. The enigma of *Daphnia* death rates. Limnol. Oceanogr. 23: 970–988.
- Ringelberg, J., B. J. G. Flik, D. Lindenaar & K. Royackes, 1991. Diel vertical migrations of *Daphnia hyalina* (sensu lato) in lake Maarsseveen: Part I. Aspects of seasonal and daily timing. Arch. Hydrobiol. 121: 129–145.
- Sardella, L. C. & J. C. H. Carter, 1983. Factors contributing to co-existence of *Chaoborus flavicans* and *C. punctipennis* in a small meromictic lake. Hydrobiologia 107: 155–164.
- Sarvala, J., H. Helminen, V. Saarikari, S. Salonen & K. Vuorio, 1998. Relations between planktivorous fish abundance, zooplankton and phytoplankton in three lakes of differing productivity. Hydrobiologia 363: 81–95.
- Scheffer, M., 1998. Ecology of shallow lakes. Chapman & Hall. London: 357 pp.
- Schram, M. D. & G. R. Marzolf, 1994. Metalimnetic oxygen depletion: Organic carbon flux and crustacean zooplankton distribution in a quarry embayment. Trans. Am. Microsc. Soc. 113: 105–116.

- Shapiro, J., 1960. The cause of a metalimnetic minimum of dissolved oxygen. *Limnol. Oceanogr.* 5: 216–227.
- Shapiro, J., 1990. Biomanipulation: the next phase making it stable. *Hydrobiologia* 200/201 (Dev. Hydrobiol. 61): 13–27.
- Stenson, J. A. E., 1990. Creating conditions for changes in prey community structure by *Chaoborus* spp. in a lake in Sweden. *Hydrobiologia* 198 (Dev. Hydrobiol. 60): 205–214.
- Stich, H. B. & W. Lampert, 1981. Predator evasion as an explanation of diurnal vertical migration. *Nature* 293: 396–398.
- Taleb, H., N. Lair, P. Reyes-Marchant & J.-L. Jamet, 1993. Observations on vertical migrations of zooplankton at four different stations of a small, eutrophic temperate zone lake, in relation to their predators. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 39: 199–216.
- Tallberg, P., J. Horppila, A. Väisänen & L. Nurminen, 1999. Seasonal succession of phytoplankton and zooplankton along a trophic gradient in a eutrophic lake – implications for food web management. *Hydrobiologia* 412: 81–94.
- Thienemann, A., 1928. Der Sauerstoff im eutrophen und oligotrophen See. Ein Betrag zur Seetypenlehre. *Die Binnengewässer*, Band IV: 1–175.
- Timms, R. M. & B. Moss, 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish in a shallow wetland ecosystem. *Limnol. Oceanogr.* 29: 472–486.
- Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton Methodik. *Mitt. Int. Ver. Limnol.* 9: 1–38.
- Vanni, M.J., 1988. Freshwater zooplankton community structure: introduction of large invertebrate predators and large herbivores to a small-species community. *Can. J. Fish. aquat. Sci.* 45: 1758–1770.
- Vinni, M., J. Horppila, M. Olin, J. Ruuhijärvi & K. Nyberg, 2000. The food, growth and abundance of five co-existing cyprinids in lake basins of different morphometry and water quality. *Aquat. Ecol.* (submitted).
- Wetzel, R., 1983. *Limnology*. 2nd edn. Saunders College Publishing, Philadelphia, PA: 767 pp.
- Windell, J. T., 1971. Food analysis and rate of digestion. In Ricker, W. E. (ed.), *Methods for Assessment of Fish Production in Fresh Waters*. IPB Handbook 3. Blackwell, Oxford: 215–226.
- Wissel, B. & J. Benndorf, 1998. Contrasting effects of the invertebrate predator *Chaoborus obscuripes* and planktivorous fish on plankton communities of a long term biomanipulation experiment. *Arch. Hydrobiol.* 143: 129–146.
- Wright, D. & J. Shapiro, 1990. Refuge availability: a key to understanding the summer disappearance of *Daphnia*. *Freshwat. Biol.* 24: 43–62.
- Zaret, T., 1975. Strategies for existence of zooplankton prey in homogeneous environments. *Verh. int. Ver. Limnol.* 19: 1484–1489.