

## Seasonal and ontogenetic variation in diel vertical migration of *Chaoborus flavicans* and its effect on depth-selection behavior of other zooplankton

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### Abstract

We analyzed diel vertical migration (DVM) of zooplankton in June, July, and September in Lake Kärnsjön, Sweden. In this lake, the density of the invertebrate predator *Chaoborus flavicans* was high, and they performed normal DVM. However, the migration pattern of *Chaoborus* differed between its four larval instars. Larger instars were found at greater mean depths during the day than were the smaller instars. In both June and July, very few observations of the fourth instar were made at a depth of 1 m during the night. Hence, in June, when only the fourth instar was present, the upper 1-m layer was a *Chaoborus*-free refuge for other zooplankton during the night. This was not the case in July, when the smaller instars (1–3) hunt at that depth, or in September, when instar four was present there. Crustacean zooplankton showed great flexibility in their DVM behavior. In September, both *Bosmina* and small *Daphnia* tended to perform reverse DVM (i.e., they resided closer to the surface during the day). However, no migration was observed in July. In June, most species performed normal DVM by crowding in the *Chaoborus*-free stratum close to the surface during the night. Both this pattern of normal DVM of zooplankton in June and the reverse DVM in September indicate that invertebrate predation has a strong effect on the zooplankton community in this fish-rich lake, showing that ontogenetic changes in migration pattern of an invertebrate predator may influence the seasonal variation in the depth-selection behavior of other zooplankton.

Predation is considered to be one of the most important factors governing patterns in zooplankton communities (Zaret 1980). Although, in natural systems, two or more predators are usually active at the same time, most experimental and field studies of predation have focused on one predator only. Prey may benefit from the presence of multiple predators if these interfere with each other. Alternatively, a behavioral defense of prey to one predator may increase their exposure to other predators (Fiksen et al. 2005). These interactions may result in a predation effect that cannot be predicted by simply summing the effects of the different predators, an effect called “emergent effects of multiple predators” (Sih et al. 1998).

Small zooplankton in the pelagic zone of a lake face the risk of predation from both planktivorous fish and invertebrate predators. The risk of attack by visual predators such as planktivorous fish increases with the ambient light level and prey characteristics affecting visibility, such as body size, pigmentation, and mobility pattern (De Meester et al. 1999). Invertebrate predators, on the other hand, usually detect their prey by means of

mechanoreceptors (Horridge and Boulton 1967; Strickler 1975). Unlike fish, they are not limited by light conditions or prey visibility. Instead, invertebrate predators are limited by their ability to grasp and handle prey, and the large size and unwieldy shape of prey make this more difficult (Dodson 1974). To avoid these predators, zooplankton have evolved several defenses, such as morphological and behavioral traits, as well as shifts in life history (Tollrian and Dodson 1999). Since one of the costs of many of these defenses involves an increased risk of predation by the other predator category (Tollrian 1995), morphology and behavior must be adjusted to the prevailing threat. However, the populations of the various predators can change rapidly, and, consequently, this fluctuating environment, in combination with strong selection, has led to the evolution of plastic responses in both morphology (Tollrian and Dodson 1999) and behavior (Neill 1990; De Meester et al. 1999).

Diel vertical migration (DVM) is a prime example of a predator avoidance behavior, and it is widespread in freshwater and marine zooplankton populations (see reviews by Hays 2003; Pearre 2003). Normal DVM is when zooplankton use deep water as a dark daytime refuge and migrate to surface waters during the night. This behavior has been shown to be induced by the smell (kairomones) of planktivorous fish (Dawidowicz et al. 1990; Tjossem 1990; Dawidowicz and Loose 1992). The ultimate reason for this behavior is that zooplankton would be exposed to visually hunting fish if they stayed close to the surface during day and would suffer from cold water and low food availability if they resided at greater depth during both night and day. This nocturnal migration is the most common pattern. However, reversed DVM, i.e., populations that reside deeper during the night than during the day, has also been reported (Neill 1990; Ohman 1990).

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### Acknowledgments

Fredrik Palm, Hans Lord, Jan Herrmann, Patrik Stenroth, and two anonymous referees provided helpful comments on earlier drafts of the manuscript. We also thank Åsa Lagergren for valuable help with the field sampling. The study was financially supported by FORMAS (The Swedish research council for environment, agricultural sciences and spatial planning) grants to J. A. E. Stenson.

The traditional view is that invertebrate predators play a significant role only in lakes with very low densities of planktivorous fish (Scheffer 1998). However, this traditional generalization has recently been questioned. In a Finnish lake with smelt (*Osmerus operlanus*), Liljendahl-Nurminen et al. (2003) showed that larvae of the phantom midge *Chaoborus flavicans* may have greater effect than fish on the zooplankton community. In lakes with fish, invertebrate predators usually show distinct normal DVM behaviors (Teraguchi and Northcote 1966; Neill 1990; Chang and Hanazato 2004). This means that for smaller zooplankton, an additional cost of normal DVM behavior is increased spatial overlap with these invertebrate predators. If the small zooplankton instead would perform reverse migration, they would decrease their spatial overlap with the invertebrates, but this would be at the cost of increased exposure to planktivorous fish. The DVM behavior can thus be seen as a trade-off between two different predatory threats where the most adaptive DVM behavior for a small zooplankton individual is influenced by the current density of invertebrate predators (and their DVM behavior) and planktivorous fish. Study of DVM may thus yield information concerning how zooplankton themselves rank the threat from fish and invertebrate predators (Ohman 1990). However, this trade-off may also be modified by other factors such as water transparency, food availability, and their own size, which affects both visibility to fish and the chance to escape invertebrates (Pearre 2003).

*Chaoborus flavicans* has four larval instars. The first and second instars develop rapidly in a few weeks, whereas the third and fourth instars are of longer duration. They pass the winter in their fourth instar, and pupation and emergence can occur from May to October. Both Teraguchi and Northcote (1966) and Gliwicz et al. (2000) have shown that depth-selection behavior between the four larval instars differs. Only the two largest instars show a clear DVM pattern, and the daytime residence depth increases with ontogenetic development. Most studies on the effect of *Chaoborus* predation have focused on the most long-lasting fourth instar, but Swift (1992) has shown that the second instar of the somewhat bigger *Chaoborus cristallinus* strikes successfully at prey of up to 0.8 mm in length, or 0.3 mm in width, and the third instar takes prey of up to 1 mm in length or 0.45 mm in width. Accordingly, both the second and third instars of *Chaoborus flavicans* should also be potential predators on small cladocerans as well as small copepods.

The aim of the present study was to analyze the seasonal dynamics and diel vertical migration of *Chaoborus flavicans* larvae and other zooplankton in Lake Kärnsjön, a deep mesotrophic lake with a rich fish community. We predict that if the population of *Chaoborus flavicans* has a significant effect on the zooplankton community, the predominant migration behavior of other zooplankton should vary with the seasonal population dynamics of *Chaoborus*. We also predict that the strongest responses in this respect should be found in species that are most vulnerable to *Chaoborus* predation. Three sampling periods, June, July, and September, were chosen to include the seasonal variation in the presence of the four *Chaoborus flavicans* instars.

## Methods

**Study site**—Lake Kärnsjön is a mesotrophic lake situated in the southwest of Sweden. The lake has a mean depth of 16 m, a maximum depth of 48 m, and a surface area of 7.16 km<sup>2</sup>. Secchi depth is usually low, especially after rainfall, due to inflow of clay particles from the soils in the drainage basin. The fish community is mainly composed of planktivorous roach (*Rutilus rutilus* L.), bleak (*Alburnus alburnus* L.), smelt (*Osmerus eperlanus* L.), and piscivorous pike (*Esox lucius* L.), pike-perch (*Sander lucioperca* L.), and perch (*Perca fluviatilis* L.) (Fiskenämnden 1988).

**Sampling**—All zooplankton samples were taken at the same sampling station (58°31'997"N, 11°39'774"E) where the depth was 25 m. Zooplankton were sampled in daytime (13:00–14:00 h) and at night (24:00–01:00 h) in 23 September 2004 and in four days of June (08, 10, 14, and 16), four days of July (12, 14, 19, and 21), and 28 September 2005 with a Schindler-Patalas trap (30 liter, 100 µm). Duplicate samples (in 2004, three replicates) were collected at ten different depths (1, 3, 5, 7, 10, 13, 16, 19, 21, and 24.5 m) and preserved with Lugol's solution.

Secchi depth and profiles of water temperature and concentration of dissolved oxygen were measured from the surface to the bottom with a Multiline F/Set-3 oxygen meter at 1-m intervals and were taken each sampling day.

**Laboratory**—All samples were counted visually for *Chaoborus flavicans* larvae. The four larval instars were identified by measuring the length of the larvae. The first instar larvae varied in length from 1.5 to 3.0 mm, the second varied from 3.1 to 5.5 mm, the third varied from 5.6 to 10 mm, and the fourth varied from 11.0 mm upward.

The cladocerans and copepods in all samples taken in September, and in one of the two replicates taken in June and July, were counted in an inverted microscope with 32× and 80× magnification. Cladocerans were identified to species level except *Ceriodaphnia* and *Daphnia*, which were identified to genus. *Daphnia* was also divided into juveniles and adults, except the samples taken in 2004, from the presence of eggs or empty brood pouches. Copepods were classed either as nauplii or as belonging to the families cyclopoida and calanoida, except the large predacious calanoids, *Limnocalanus macrurus* and *Hetercope appendiculata*, which were identified to species level. Samples with very high numbers of *Daphnia* spp., cyclopoid copepods, and *Diaphanosoma brachyurum* were counted from subsamples. Due to very high numbers, nauplii densities were only estimated for 14 June and 14 July, and these estimates were made from subsamples.

**Data analyses**—Daytime and nighttime weighted mean depths (WMD) were calculated for each taxon and *Chaoborus* instar using a modified variant of the model developed by Worthington (1931),

$$\text{WMD} = \frac{\sum (d_i n_i)}{\sum (n_i)}$$

where  $d_i$  is the depth stratum sampled,  $n_i$  is the number of

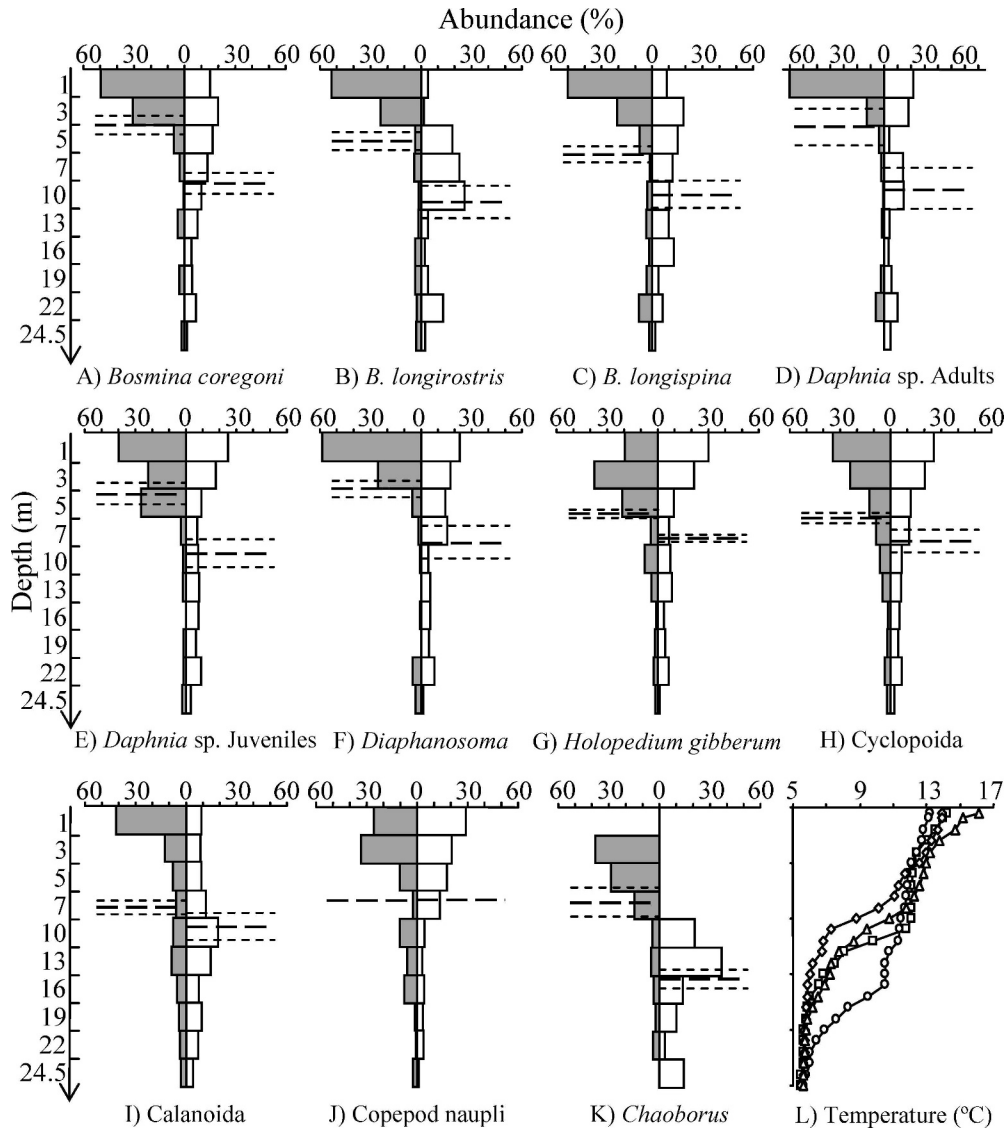


Fig. 1. (A–L) Vertical distribution of *Chaoborus* and crustacean zooplankton during night (gray bars) and day (open bars) in Lake Kärnsjön, June 2005, showing the means of relative abundances (%) of the four sampling occasions. The horizontal lines represent the mean weighted mean depths (thick dotted lines)  $\pm$  standard error (thin dotted lines). Panel L shows vertical temperature profiles.

organisms caught in  $d_i$ , and  $l_i$  is the number of meters represented by the  $i^{\text{th}}$  sample. The  $l_i$  values were included because sampling intervals were not equal over the whole range. The value of  $l_i$  was calculated as the number of meters from half the distance to the sample above (or surface) to half the distance to the sample below (or bottom). Seasonal differences among June, July, and September in DVM behavior were analyzed with the Kruskal–Wallis nonparametric test, and the differences between day and night WMD for each date were used as response variables.

Results

*Secchi depth and profiles of temperature and oxygen*—Secchi depths varied from 1.1 to 1.3 m in June, from 1.3 to

1.6 m in July, and in September it was 0.83 m in 2004 and 1.63 m in 2005. The vertical profiles of temperature are shown in Figs. 1, 2, and 3. Even though the lake was stratified on all dates, the oxygen concentration was over  $5 \text{ mg O}_2 \text{ L}^{-1}$  at all depths and on all dates, which means that all depths were available to fish.

*Chaoborus flavicans*—On the first two sampling occasions in June, only the fourth larval instar of *Chaoborus flavicans* was found in the lake. At the two later dates in June, pupae also appeared, and the total number of *Chaoborus* larvae increased. In July, all four larval instars and pupae were found, although fourth-instar larvae and pupae became less common, indicating that some animals had emerged. In September, all individuals were in their

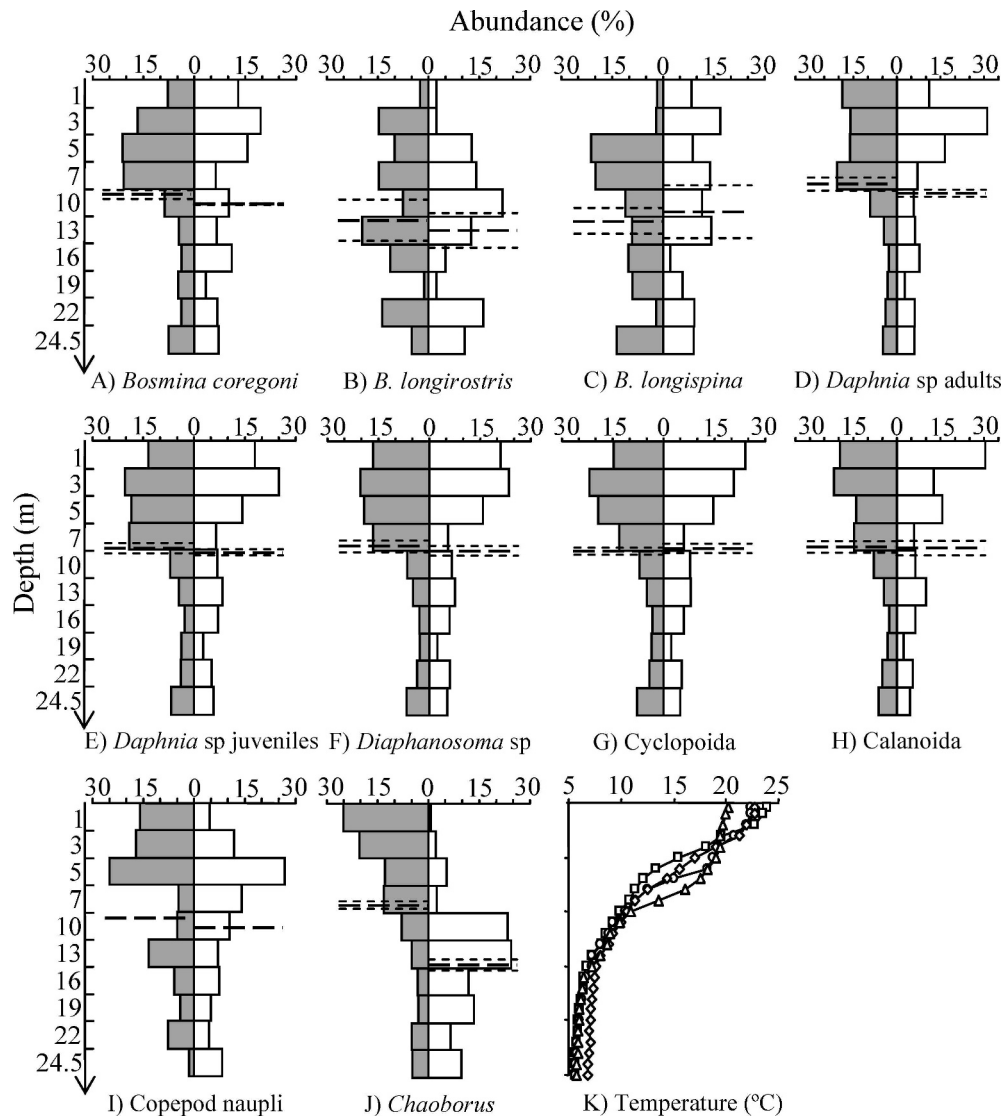


Fig. 2. (A–K) Vertical distribution of *Chaoborus* and crustacean zooplankton during night (gray bars) and day (open bars) in July 2005, showing the means of relative abundance (%) of the four sampling occasions. The horizontal lines represent the mean weighted mean depths (thick dotted lines)  $\pm$  standard error (thin dotted lines). Panel K shows vertical temperature profiles.

fourth instar. The seasonal variation in mean population density of the number of individuals found in the water column shows that the density of the fourth instar was clearly higher during the night than during the day, indicating that part of the population stayed in the sediment during the day (Table 1).

All larval instars, except the first, showed normal diel vertical migration behavior, staying at depths below 7 m during the day and concentrating in the upper part of the vertical profile during the night (Fig. 4). The weighted mean depth varied between the four larval instars. In July, when all four instars were present, the daytime WMD clearly increased with instar size (Fig. 5). In addition, the minimum depths at which the four different instars were found during the day differed: the first instar was first found at 1 m, the second at 3 m, the third at 7 m, and the fourth at 10 m. At night, there were only small differences

in mean depth between any of the larval instars. However, there was a clear difference in the occurrence at the 1-m level. At that depth, a total of two individuals of the fourth instar only were found in July and no individuals were found in June, whereas both instar two and instar three had their highest density at this level. Moreover, in September, the fourth instar migrated all the way up to the surface during the night. This means that in June, the 1-m level at night served as a *Chaoborus*-free refuge, but this was not the case in July and September.

*Other invertebrate predators*—The most abundant invertebrate predator was the calanoid copepod *Limnocalanus macrurus*, which was strongly concentrated at the deepest and coolest region both day and night, and was most abundant in September 2005 with  $>1$  individuals  $L^{-1}$  at 24.5-m depth (Fig. 4). *Leptodora kindtii* only occurred in

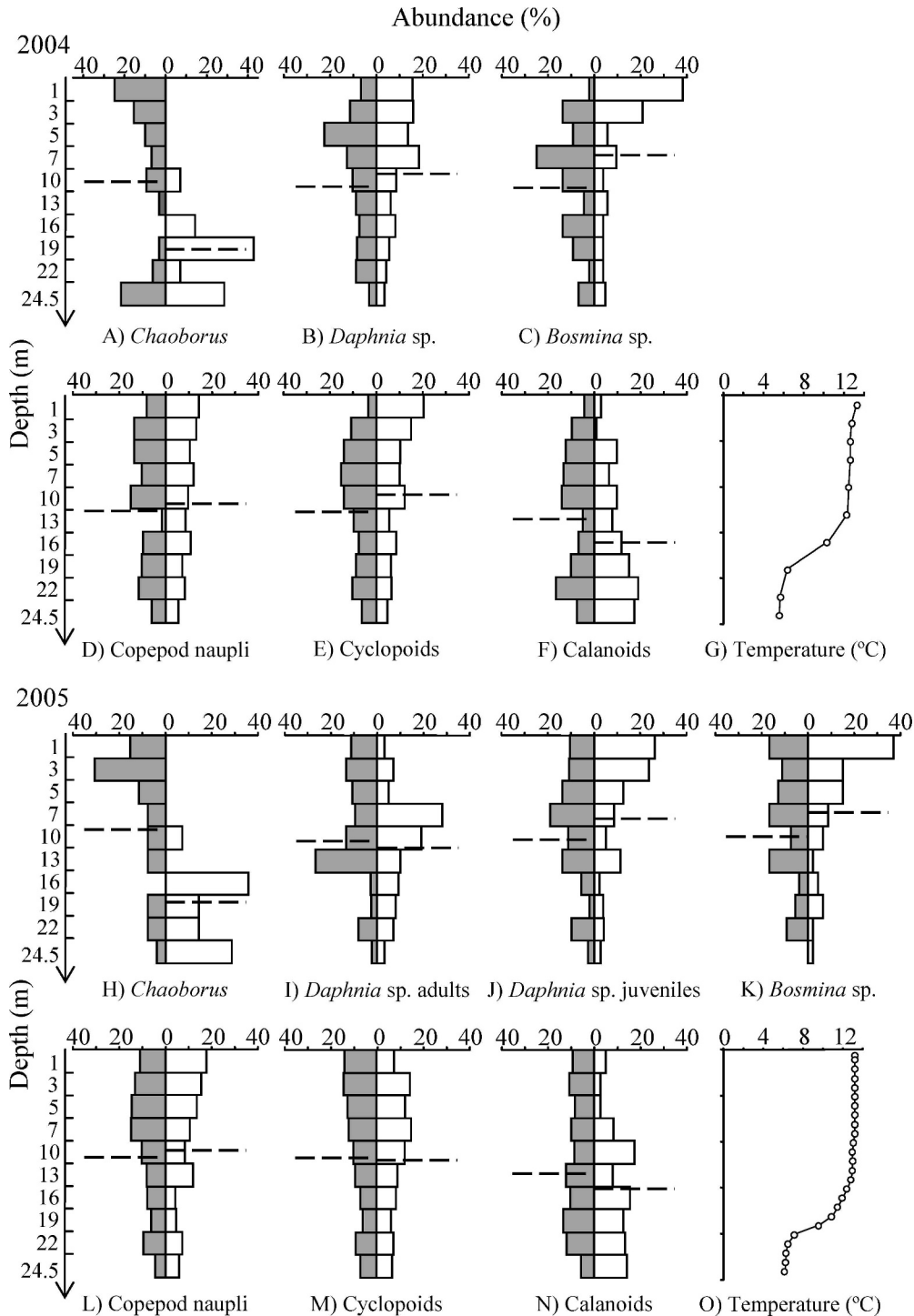


Fig. 3. (A–F and H–N) Relative abundance (%) of the vertical distribution of *Chaoborus* and crustacean zooplankton during night (gray bars) and day (open bars) in September. The dotted lines represent the weighted mean depths, and panel G illustrates the vertical temperature profile.

June and July and showed no DVM in June but a quite clear pattern in July, when it also occurred in its highest densities (>0.15 ind. L<sup>-1</sup>). In addition, the copepods *Hetercope appendiculata* and *Cyclops strenus*, the cladoceran *Polyphemus pediculus*, and the shrimp *Mysis relicta* appeared, but always in very low densities.

*The crustacean zooplankton community*—The herbivorous crustacean zooplankton taxa found in Lake Kärnsjön during the study period included *Bosmina* (*Eubosmina*) *coregoni*, *Bosmina longirostris*, *Bosmina* (*Eubosmina*) *longispina*, *Ceriodaphnia* sp., *Daphnia cristata*, *Daphnia cucullata*, *Diaphanosoma brachyurum*, *Holopedium gibberum*,

Table 1. The mean density (No. L<sup>-1</sup>) of the four instars of *Chaoborus flavicans* in Lake Kärnsjön at day and night in June, July, and September. In June and September, only individuals of the fourth instar were found in the samples.

Period	Jun	Jul	Jul	Jul	Jul	Sep 2004	Sep 2005
Instar	IV	I	II	III	IV	IV	IV
Day	0.019	0.043	0.073	0.062	0.013	0.023	0.023
Night	0.135	0.043	0.129	0.096	0.022	0.054	0.043

*Limnospida frontosa*, copepod nauplii, cyclopoid copepods, and calanoid copepods.

In summer, the crustacean zooplankton population in Lake Kärnsjön was highly dominated by cyclopoid copepods and copepod nauplii, both in June (mean numbers of 6.0 and 18.0 ind. L<sup>-1</sup>, respectively) and in July (22.0 and 59.1 ind. L<sup>-1</sup>, respectively). The most numerous cladoceran in June was *Holopedium gibberum*, which had a mean number of 1.5 ind. L<sup>-1</sup>, but in July, it substantially decreased, and instead juvenile *Daphnia* became the most numerous cladoceran, with a mean number of 8.6 ind. L<sup>-1</sup>. In September, the copepods also dominated with high densities of cyclopoids (4.78 ind. L<sup>-1</sup> in 2004 and 2.49 ind. L<sup>-1</sup> in 2005), calanoids (0.47 ind. L<sup>-1</sup> and 1.9 ind. L<sup>-1</sup>), and nauplii (3.02 ind. L<sup>-1</sup> and 2.17 ind. L<sup>-1</sup>). Both the number of species and population densities of cladocerans were lower in September; the highest mean densities of *Daphnia* were 0.46 ind. L<sup>-1</sup> and 1.07 ind. L<sup>-1</sup>, and densities of *Bosmina* were 0.080 ind. L<sup>-1</sup> and 0.083 ind. L<sup>-1</sup>. We restricted the analyses of vertical distributions to the most common taxa, and in September, all *Bosmina* species were pooled.

All taxa, except copepod nauplii larvae, showed a clear normal diel vertical migration behavior in June (Fig. 1), whereas in July, there were no vertical migration patterns for any of the taxa (Fig. 2). The picture was more mixed in September: *Bosmina* (both years), *Daphnia* (2004), juvenile *Daphnia* (2005), and cyclopoid copepods (2004) showed a tendency of reverse migration, whereas calanoids (both years) showed normal DVM. In the other taxa, only small differences in vertical distribution patterns and weighted mean depths occurred between day and night (Fig. 3). The seasonal differences were significant for *Bosmina* ( $p = 0.043$ ) and *Daphnia* ( $p = 0.030$ ), and the tendency was the same for cyclopoid ( $p = 0.102$ ) and calanoid ( $p = 0.063$ ) copepods.

At 1-m depth at night (where no *Chaoborus* were found in June, but plenty in July and September), the relative abundance of all taxa was much higher in June than in July and September (Fig. 6).

## Discussion

*Depth-selection behavior of Chaoborus flavicans*—As expected, the *Chaoborus flavicans* larvae in Lake Kärnsjön perform a distinct normal diel vertical migration, indicating avoidance behavior toward fish. Our results also support earlier studies that have shown differences in depth distribution (Voss and Mumm 1999) and migration patterns (Teraguchi and Northcote 1966; Gliwicz et al. 2000) among the four larval instars of *Chaoborus flavicans*. This ontogenetic change in migration behavior can probably be explained by changes in predation pressure

on the four larval instars. Since fish are visual predators, the larger the zooplankton, the smaller the amount of light needed for the fish to detect them (Dodson 1974), which may explain the differences in weighted mean depths between the four larval instars during the day in July. The larger instars have both a greater mean depth and a greater minimum depth during the day than the smaller and less visible instars.

The mean depths during the night differed little between the four larval instars. However, the fourth instar was practically never observed at a depth of 1 m during the night, not in June nor in July, whereas the other three instars were more or less abundant at this depth in July. Teraguchi and Northcote (1966) found that very few instar four larvae were present at light intensities above 100 lux, and our result suggests that the threshold of light intensity that triggers downward swimming differs between the ontogenetic stages and that this threshold affects the minimum depth where the different instars are to be found both during night and day. The avoidance of the uppermost strata by instar four during the night in June and July, but not in September, may be a consequence of differences in light intensity. At this high latitude, summer nights are lighter than nights in September and are probably light enough for the large fourth instar larvae to become vulnerable to fish predation at 1-m depth.

We found no indication of DVM for the smallest instar; this is in agreement with other studies (Teraguchi and Northcote 1966; Gliwicz et al. 2000). This may be due to the small size of the first instar, which makes it less exposed to visual predators, and at the same time, an additional cost of normal DVM may be cannibalism from larger conspecifics, which migrate normally. However, contrary to earlier studies (Teraguchi and Northcote 1966; Gliwicz et al. 2000), we found normal DVM behavior already in the second instar, which may indicate a relatively high predation pressure from fish in Lake Kärnsjön compared to lakes in the other studies.

*Chaoborus flavicans* has been shown to induce reversed DVM in copepods at densities from 0.3 to 0.7 ind. L<sup>-1</sup> (Neill 1992). Furthermore, Liljendahl-Nurminen et al. (2003) showed that *Chaoborus flavicans*, at densities from 0.2 to 0.3 ind. L<sup>-1</sup>, probably was the factor behind unconventional seasonal dynamics of cladocerans in Lake Hiidenvesi. Despite high densities of fish and the lack of an oxygen-free refuge, the population density of *Chaoborus* in Kärnsjön is high, or similar to other lakes studied. Therefore, we expect that the *Chaoborus* population also has an effect on the zooplankton community in Lake Kärnsjön. The highest *Chaoborus* density in Lake Kärnsjön (0.32 ind. L<sup>-1</sup>) was recorded at night on 14 June. Lower

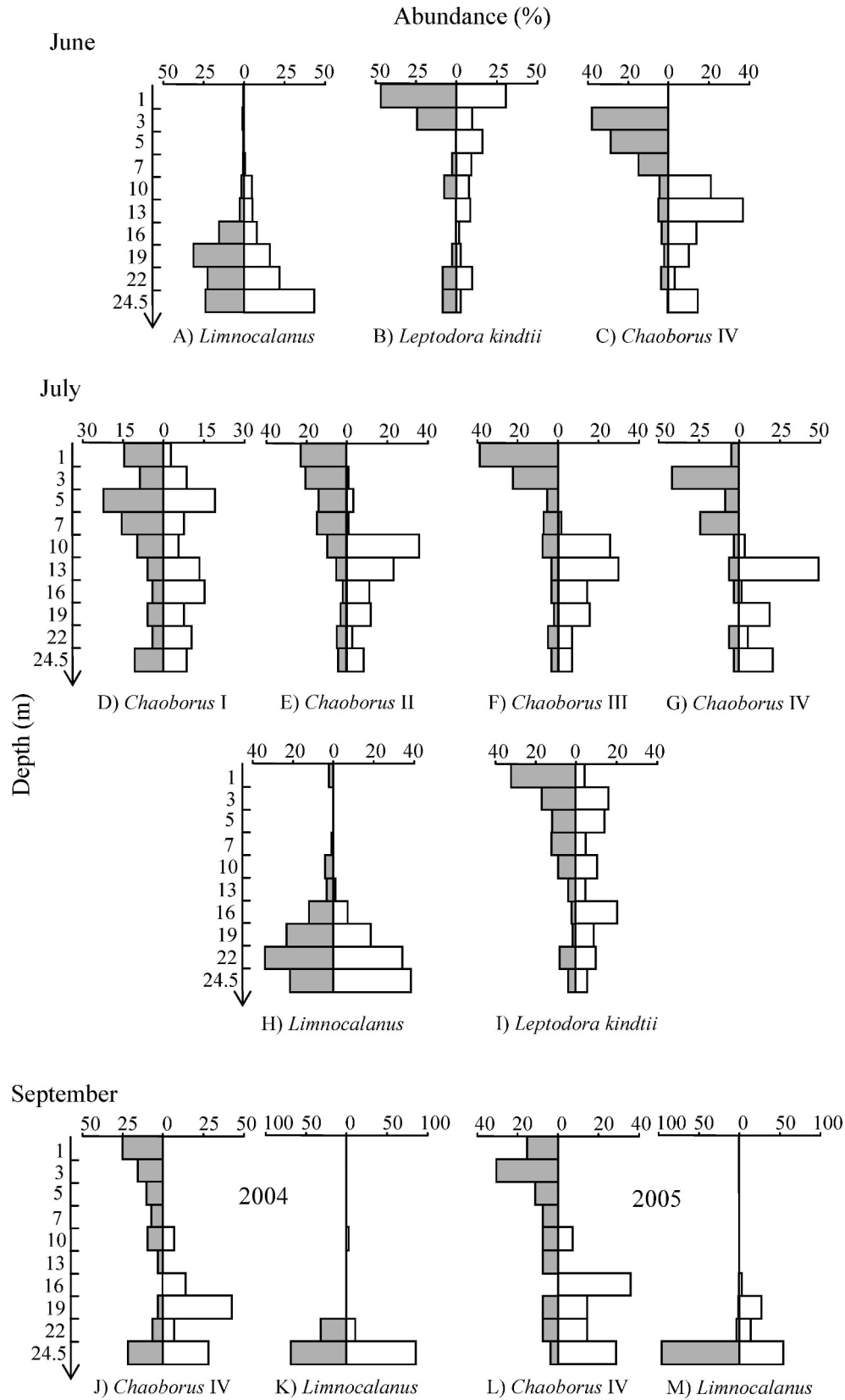


Fig. 4. (A–M) Mean relative abundance (%) of invertebrate predators at night (gray bars) and day (open bars) at different depths in June (mean of four dates), July (mean of four dates), and September (one date in 2004 and one date in 2005).

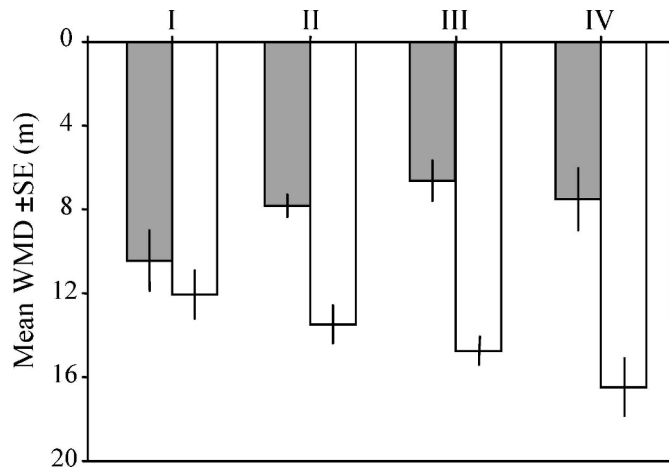


Fig. 5. Weighted mean depths of the four larval instars of *Chaoborus flavicans* during night (gray bars) and day (open bars) in July.

densities on other nights probably reflect that, in both early and late in the season, many individuals may remain in the sediment during both day and night, a pattern previously found by Gliwicz et al. (2000). Furthermore, in early June, the most intensive predation from young of the year fish occurs, and this may explain the low densities of free-swimming *Chaoborus* during the first two dates in June.

*Depth-selection behavior of crustacean zooplankton*—Many taxa in Lake Kärnsjön showed pronounced changes in their migratory behavior among months. The general pattern was a dominance of normal DVM in June, no migration in July, and reverse DVM in September. This change in migratory behavior may indicate that the relative importance of invertebrate and vertebrate predators varies throughout the season. Normal DVM would be favored when fish are most important (Dawidowicz and Loose 1992), and reverse DVM would be favored if normally migrating invertebrates dominate (Neill 1990, 1992). In a marine environment, Ohman (1990) showed that zooplankton switched their migration behavior, from normal to reverse, when the relative threat from fish and invertebrates changed. Accordingly, the normal DVM in Lake Kärnsjön in June could indicate that zooplankton primarily try to escape planktivorous fish, whereas the reverse DVM in September indicates that invertebrates are the most important predator at this time of the year. However, one important difference compared to earlier studies is that the uppermost layer in June acts as a *Chaoborus*-free refuge, whereas, in July, smaller, less light sensitive instars hunt at that range. In September, when nights are darker, high numbers of the fourth instar of *Chaoborus* are found even at a depth of 1 m during the night. Interestingly, it appears that this refuge is utilized to a high extent by other zooplankton in June, when as much as 40–70% of the crustaceans are concentrated there during the night (Fig. 6). In contrast, in both July and September, the patterns were the opposite: almost a fourth of the total population of the *Chaoborus* larvae was found at 1-m depth

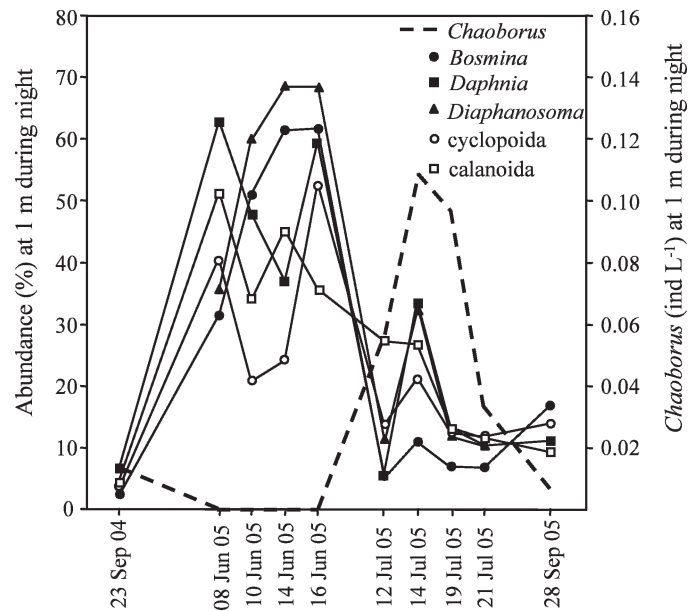


Fig. 6. Abundances (%) of zooplankton and *Chaoborus* (ind. L<sup>-1</sup>) at 1-m depth during the night from ten dates in June, July, and September.

during the night, whereas densities of crustacean zooplankton were much lower at that depth than in June. The differences in population densities at the 1-m level alone explain why the DVM, as indicated by the WMD values, is normal in June. An alternative explanation to why zooplankton stay near the surface during the night in June could be optimization of growth in the warmer surface water. However, the mean difference in temperature between 1 and 3 m was only 0.85°C in June compared to 1.88°C in July.

Although both population density and size distribution of the *Chaoborus* population were very similar in June and September, the migration patterns of most zooplankton are very different. This indicates that zooplankton react to the same *Chaoborus* kairomone signal in totally different (but in both cases adaptive) ways. One possible mechanism for this is a behavioral response in zooplankton to gradients in local *Chaoborus* density. Kleiven et al. (1996) found that *Daphnia pulex* could seek out parts of a chamber with lower kairomone concentration, and our results indicate that such a response can be involved in adaptive depth-selection behavior. However, experimental studies are needed to evaluate how this may work.

In lakes, reverse DVM is a rare phenomenon (Hutchinson 1967), and most examples are from lakes with no, or low densities of fish (e.g., Neill 1990). However, a tendency for reverse DVM for small *Daphnia* has been found in a shallow turbid lake with high densities of the invertebrate predator *Leptodora kindtii* and fish (Alajärvi and Horppila 2004). The same tendency in Lake Kärnsjön points to a situation where at least *Bosmina*, small *Daphnia*, and at times cyclopoid copepods rank the predation threat from invertebrates higher than that from fish. In addition, the very pronounced crowding at the surface layer in June

suggests this. If fish were the most important predator on zooplankton in Lake Kärnsjön, the crustaceans would instead linger closer to the surface during the night in September than in June, since the predation from planktivorous fish, including young of the year, is usually most intensive in June. Furthermore, the avoidance of the 1-m level shown by *Chaoborus* also indicates a severe risk of fish predation here. Therefore, the 1-m level should probably be avoided, not only by fourth instar *Chaoborus* but also by crustacean zooplankton in June, if fish were the most important predator.

The finding of the most marked shifts in DVM pattern in *Bosmina* and *Daphnia* is in agreement with our predictions, since earlier studies have reported high selectivity by *Chaoborus* for these taxa (Liljendahl-Nurminen et al. 2003). On the other hand, *Holopedium* deviates from the pattern of crowding in the uppermost strata during the night in June (Fig. 1G), but it is also well known that the gelatinous capsule of this cladoceran is an efficient defense against *Chaoborus* predation (Stenson 1987).

In summary, our results indicate that zooplankton may vary their depth-selection behavior in a way that seems adaptive as to minimize the predation from *Chaoborus* rather than that from fish. This result supports the finding by Liljendahl-Nurminen et al. (2003) that *Chaoborus* may have a greater effect on the zooplankton community than planktivorous fish, even in lakes with dense fish populations. In addition, for small zooplankton, the lack of a normal DVM pattern in July and September and the crowding at 1-m depth during the nights in June suggest an “emergent effect” of fish and *Chaoborus*, where avoidance of *Chaoborus* results in increased exposure to planktivorous fish.

## References

- ALAJÄRVI, E., AND J. HORPPILA. 2004. Diel variations in the vertical distribution of crustacean zooplankton and food selection by planktivorous fish in a shallow turbid lake. *Internat. Rev. Hydrobiol.* **89**: 238–249.
- CHANG, K.-H., AND T. HANAZATO. 2004. Diel vertical migrations of invertebrate predators (*Leptodora kindtii*, *Thermocyclops taihokuensis* and *Mesocyclops* sp.) in a shallow, eutrophic lake. *Hydrobiologia* **528**: 249–259.
- DAWIDOWICZ, P., AND C. J. LOOSE. 1992. Metabolic costs during predator-induced diel vertical migration of *Daphnia*. *Limnol. Oceanogr.* **37**: 1589–1595.
- , J. PIJANOWSKA, AND K. CIECHOMSKI. 1990. Vertical migration of *Chaoborus* larvae is induced by the presence of fish. *Limnol. Oceanogr.* **35**: 1631–1637.
- DE MEESTER, L., P. DAWIDOWICZ, E. VAN GOOL, AND C. J. LOOSE. 1999. Ecology and evolution of predator-induced behaviour of zooplankton: Depth selection behaviour and diel vertical migration, p. 160–176. *In* R. Tollrian and C. D. Harvell [eds.], *The ecology and evolution of inducible defences*. Princeton Univ. Press.
- DODSON, S. I. 1974. Zooplankton competition and predation: An experimental test of the size-efficiency hypothesis. *Ecology* **55**: 611–613.
- FIKSEN, O., S. ELIASSEN, AND J. TITELMAN. 2005. Multiple predators in the pelagic: Modelling behavioral cascades. *J. Anim. Ecol.* **74**: 423–429.
- FISKENÄMNDEN I O LÄN. 1988. Standardized net-fishing surveys in Munkedal municipality summer and autumn 1988. Munkedal municipality. [In Swedish.]
- GLIWICZ, Z. M., A. BIERNACKA, J. PIJANOWSKA, AND R. KORSACK. 2000. Ontogenetic shifts in the migratory behavior of *Chaoborus flavicans* Meigen: Field and experimental evidence. *Arch. Hydrobiol.* **149**: 193–212.
- HANAZATO, T., AND M. YASUNO. 1989. Zooplankton community structure driven by vertebrate and invertebrate predators. *Oecologia* **81**: 450–458.
- HAYS, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migration. *Hydrobiologia* **503**: 163–170.
- HORRIDGE, G. A., AND P. S. BOULTON. 1967. Prey detection by chaetognaths via vibration sense. *Proc. R. Soc. London Ser. B.* **168**: 413–419.
- HUTCHINSON, G. E. 1967. The vertical migration and horizontal distribution of the zooplankton, p. 725–809. *In* G. E. Hutchinson [ed.], *A treatise on limnology: Volume II. Introduction to the lake biology and the limnoplankton*. John Wiley & Sons.
- KLEIVEN, O. T., P. LARSSON, AND A. HOBAEK. 1996. Direct distributional response in *Daphnia pulex* to a predator kairomone. *J. Plankt. Res.* **18**: 1341–1348.
- LILJENDAHL-NURMINEN, A., J. HORPPILA, T. MALINEN, P. ELORANTA, M. VINNI, E. ALAJÄRVI, AND S. VALTONEN. 2003. The supremacy of invertebrate predators over fish—factors behind the unconventional seasonal dynamics of cladocerans in Lake Hiidenvesi. *Arch. Hydrobiol.* **158**: 75–94.
- MOORE, M. V. 1988. Differential use of food resources by the instars of *Chaoborus punctipennis*. *Freshw. Biol.* **19**: 249–268.
- NEILL, W. E. 1990. Induced vertical migration in copepods as a defense against invertebrate predation. *Nature* **345**: 524–526.
- . 1992. Population variation in the ontogeny of predator-induced vertical migration of copepods. *Nature* **356**: 54–57.
- OHMAN, M. D. 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.* **60**: 257–281.
- PEARRE, S., JR. 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: History, evidence and consequences. *Biol. Rev.* **78**: 1–79.
- SCHOFFER, M. 1998. *Ecology of shallow lakes*. Chapman and Hall.
- SIH, A., G. ENGLUND, AND D. WOOSTER. 1998. Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.* **13**: 350–355.
- STENSON, J. A. E. 1987. Variation in capsule size of *Holopedium gibberum* (Zaddach): A response to invertebrate predation. *Ecology* **68**: 928–934.
- STRICKLER, J. R. 1975. Intra- and interspecific information flow among planktonic copepods: Receptors. *Int. Ver. Theor. Angew. Limnol. Verh.* **19**: 2951–2958.
- SWIFT, M. C. 1992. Prey capture by the four instars of *Chaoborus crystallinus*. *Limnol. Oceanogr.* **37**: 14–24.
- TERAGUCHI, M., AND T. G. NORTHCOTE. 1966. Vertical distribution and migration of *Chaoborus flavicans* larvae in Corbett Lake, British Columbia. *Limnol. Oceanogr.* **11**: 164–176.
- TJOSSEM, S. F. 1990. Effects of fish chemical cues on vertical migration behaviour of *Chaoborus*. *Limnol. Oceanogr.* **37**: 1456–1468.
- TOLLRIAN, R. 1995. Predator-induced morphological defenses: Costs, life history shifts, and maternal effects in *Daphnia pulex*. *Ecology* **76**: 1691–1705.

- , AND S. I. DODSON. 1999. Inducible defences in Cladocera: Constraints, costs and multipredator environments, p. 177–202. *In* R. Tollrian and C. D. Harvell [eds.], *The ecology and evolution of inducible defences*. Princeton Univ. Press.
- VOSS, S., AND H. MUMM. 1999. Where to stay by night and day: Size-specific and seasonal differences in horizontal and vertical distribution of *Chaoborus flavicans* larvae. *Freshw. Biol.* **42**: 201–213.
- WORTHINGTON, E. B. 1931. Vertical movements of freshwater macroplankton. *Int. Rev. Gesam. Hydrobiol.* **25**: 394–436.
- ZARET, T. 1980. *Predation and freshwater communities*. Yale Univ. Press.

*Received: 26 January 2007*  
*Accepted: 23 September 2007*  
*Amended: 4 December 2007*