Interacting in the dark: a study of the diel vertical migrations of pelagic plankton and fish in Lake Ladoga

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The diel vertical distribution of nutrients, phytoplankton, zooplankton and fish were studied simultaneously at two pelagial stations in Lake Ladoga in August 1995. At one site (Valaam) cryptophyceans dominated in phytoplankton, while at the other (Konevits) diatoms were more common. In Valaam the algae were distributed unevenly, mainly in the surface layers, while in Konevits the algae were distributed evenly throughout the entire 0–20 m layer. In Valaam a clear diel migration pattern was observed by most of studied zooplankton taxa, while in Konevits only large *Cyclops* and *Limnocalanus* migrated. The peak total density of pelagic fish was more than twice as high in Konevits as in Valaam, while the zooplankton density was three times lower in Konevits than in Valaam. In Valaam the clear surface maximum of cryptophyceans probably affected the migration pattern of most species of herbivorous zooplankton. In Konevits the lower temperature in the metalimnion, where the daytime zooplankton maximum occurred, and evenly distributed food resources may have limited zooplankton migration, despite the existing predation pressure.

Introduction

Migration patterns influence the population and community ecology of zooplankton, the trophic dynamics of aquatic food webs, and vertical transport in the water column (Williamson *et al.* 1996). Photoresponses of zooplankton appear to be the central regulatory behaviour in diel vertical migration (Haney 1993). Underwater distribution of light provides the primary orientation cues, and



light determines the zone of visual predation and sets limits on the region of phototrophic production of food (Ringelberg 1980, Bayly 1986, Haney 1993). According to Lampert (1993), diel vertical migration (DVM) can be viewed from three aspects: (1) proximate causes or controlling factors such as the effect of light stimulus on timing of DVM; (2) ultimate causes such as reductions in predation and competition, and (3) consequences for the ecosystem, for example, possible indirect effects of DVM on compartments other than migrating populations.

Individual behaviour of algae and zooplankton cannot be measured in the field. Thus, DVM is a population phenomenon; the population average moves, but individual animals may have quite different behaviours, including no movements (Dawidowicz and Loose 1992a, Larsson and Dodson 1993, Loose and Dawidowicz 1994).

In Lake Lagoda the daytime vertical distributions of plankton and fish have been studied since the early 20th century (Andronikova 1996). HowFig. 1. Study sites of diel vertical migration in Lake Ladoga in 1995.

ever, the pelagial zone of Lake Ladoga has some peculiarities, for example, the cladoceran maximum is located in the 10-20 m depth layer, which differs from Lake Saimaa (SE Finland) where the summertime maximum is at the surface (Rahkola et al. 1994, Andronikova 1996). In Lake Ladoga the different communities are usually separated from each other vertically: phytoplankton occurs mainly at the surface, while in most cases the zooplankton maxima are located in the metalimnion (5–20 m) (Andronikova 1996), where phytoplankton is scarce; and most of the fish are found at depths below 20 m, where zooplankton is rare. In Lake Ladoga the diel dynamics of plankton distribution had not been recorded before 1993, when the first studies of zooplankton migrations were made.

As part of the joint Russian-Finnish evaluation of human impact on Lake Ladoga, in the Valaam and Konevits regions we observed the diel vertical distributions of nutrients, phytoplankton, zooplankton and fish simultaneously.

Study areas

Lake Ladoga is a large (area 17 891 km², volume 837 km²) open and deep lake with a mean depth of 47 m and a maximun depth of 230 m (Sorokin *et al.* 1996). In August 1995, we studied two regions: one near Valaam (total depth 47 m, $61^{\circ}29'54''N$, $31^{\circ}01'60''E$) and another near Konevits (total depth 56 m, $60^{\circ}55'48''N$, $30^{\circ}39'42''E$). On 1 August 1995 the sun rose at 5:00 and set at 22:00. During the study period the weather was sunny and calm; the mean air temperature measured at Lappeenranta airport (SE Finland) was +18–21 °C and the wind velocities were 1–2 m s⁻¹. Both the Valaam and the Konevits stations are situated in the open and deep northern part of Lake Ladoga (Fig. 1).

The Konevits and Valaam sampling stations differed from each other. Secchi depth of the water was slightly greater at Konevits (3.2 m) than in Valaam (2.9 m). The epilimnion was slightly deeper in Valaam than in Konevits in August 1995. In Valaam the epilimnion was much thicker in August 1993 than in 1995 (Fig. 2). The study sites were initially chosen because of different dominant fish species: near Konevits the commercial fish catch consists mainly of vendace (*Coregonus albula* L.) while Valaam is considered to be whitefish (*C. lavaretus* L.) and smelt (*Osmerus eperlanus* (L.)) area.

Methods

Three replicates of water and plankton samples were collected with a plankton pump from the depths of 0–5, 5–10, 10–15 and 15–20 m. The collective sample (70 l) from each depth was pumped into a large container and mixed. The water and phytoplankton samples were removed from the container and the rest of the water was washed through a zooplankton net (mesh size 48 μ m). Furthermore, zooplankton samples below 20 m were taken with a 120 μ m mesh Juday plankton net (mouth diameter 0.25 m, total length 1.20 m).

At both sites, zooplankton was sampled at seven depth intervals: 0–20 m was sampled in 5 m layers, and on both sites the water column below 20 m was divided into three equal layers: these



Fig. 2. Daytime thermal stratification in Valaam in August 1993 and 1995 and in Konevits in August 1995.

were 9 m each in Valaam (20–29, 29–38 and 38– 47 m) and 12 m each in Konevits (20–32, 32–44 and 44–56 m). Three replicate samples were collected every six hours for 24 hours on 1–2 August in Konevits and 3–4 August in Valaam during the 1995 expedition. In August 1993 the zooplankton samples were taken with a Juday plankton net every 4 hours at depths of: 0–3 m, 3–8 m, 8–13 m, 13–18 m, 18–23 m, 23–28 m, 28–38 m, 38–48 m and 48–57 m.

Phytoplankton samples were identified and counted using an inverted microscope; for zooplankton counting both inverted and stereo microscopes were used. The detailed counting procedure was described by Holopainen *et al.* (1996) and Karjalainen *et al.* (1996). The analyses of water quality variables (chlorophyll *a*, N_{tot}, NO₂+NO₃-N, P_{tot}, PO₄-P, pH, colour and total and particulate organic carbon (TOC, POC)) were made using the methods of National Board of Waters and the Environment (1981). Primary production was measured *in situ* using the ¹⁴C method (Steemann Nielsen 1952, Niemi *et al.* 1983). Temperature and transparency values were measured in the field during the expedition.

To study the diel vertical movements of fish, random samples were collected at both sampling stations. The acoustic data were collected with a Simrad EY-M echosounder. The equipment and the method used for counting fish are described in more detail by Lindem (1983), Bayona (1984), Jurvelius (1991) and Jurvelius and Sammalkorpi (1995). The transducer was towed at a depth of 1 m (Jurvelius et al. 1984). The speed of the small motor boat used for towing in these round-theclock surveys was ca 2 m s⁻¹. The calm weather was excellent for the study. In Konevits the data were collected at 00:30, 1:00, 2:00, 7:00, 11:00, 21:00, 22:00, 23:00 and 24:00, and in the Valaam area acoustic data were gathered at 1:00, 2:00, 4:00, 8:00, 12:00, 15:00, 18:00, 21:00, 22:00, 23:00 and 24:00. The duration of each survey was ca. 10 minutes.

Fish density was counted in 5 m depth layers. Only in cases of low density was a thicker layer used to obtain enough single fish echoes (> 100) for each density estimate. The total areal density (fish ha^{-1}) was estimated by adding together the densities from corresponding depth layers. The fish species identification was done with five surface and two midwater trawlings in Konevits. In Valaam region trawling was prohibited.

Phyto- and zooplankton abundances were compared in two different ways. First, the sampling stations were compared so that the three replicated plankton samples in Konevits and Valaam were compared by the Wilcoxon matchedpairs test. Second, temporal changes in the vertical migration pattern were observed so that the depth layer where the maximum density of plankton population occurred was tested at each time interval by Kruskal-Wallis one-way analysis of variance.

The vertical distribution pattern of fish density at same time and at the same depth layer were compared between stations by Wilcoxon matchedpairs test. From the samples collected at night (24:00, 1:00, 2:00), the relative size distributions of fish were compared by the Kolmogorov-Smirnov test.

Results

Water quality

In the surface water (0-5 m) the mean total phosphorus and phosphate phosphorus contents of the water were higher at Valaam ($26 \mu g l^{-1}$ and $5 \mu g l^{-1}$, respectively) than at Konevits ($P_{tot} = 16 \ \mu g \ l^{-1}$, PO_4 -P = 3 µg l⁻¹). No significant differences were found in the total nitrogen concentrations of the two stations, but the concentrations of dissolved nitrogen (NO₂+NO₃-N) were somewhat smaller at Valaam. The daytime concentration of POC was lower than the nighttime concentration at both stations. In Valaam the mean POC concentration was 0.9 mg l⁻¹ at midnight, with maxima of 1.1 mg l^{-1} observed at 0–5 and 10–15 m, and 0.6 mg l^{-1} at noon. In Konevits the values were lower, 0.8 mg l^{-1} at midnight and only 0.3 mg l^{-1} at noon. Primary production of phytoplankton was higher in Valaam (626 mg m⁻² d⁻¹) than in Konevits (526 mg m⁻²d⁻¹). In the surface water (0–2 m) the chlorophyll a concentration was twice as high in Valaam (16.5 mg m^{-3}) than in Konevits (6.8 mg m^{-3}) .

Phytoplankton

Species composition and biomass in Konevits and Valaam

The total phytoplankton biomass (0-20 m) was almost the same at the Konevits (16.8 g m^{-2}) and Valaam sampling stations (14.2 g m^{-2}) . However, in the surface layers (0-5 m) the biomass in Valaam (1.7 g m^{-3}) was twice as high as in Konevits (0.9 g m^{-3}) .

In Valaam, cryptophyceans (*Cryptomonas* spp., *Rhodomonas lacustris* Pascher & Ruttner and *Katablepharis ovalis* Skuja) dominated (77% of total density and 52% of biomass) in the 0–20 m depth layer; while in Konevits diatoms (*Asterionella formosa* Hassall, *Aulacoseira* spp., *Diatoma*



Fig. 3. Vertical distribution of phytoplankton abundance at midnight and noon in Konevits and Valaam in August 1995.

tenuis (Lyngb.) Ag.) were more common both in density (66%) and biomass (56%, Fig. 3). In Valaam, diatoms formed only 2% of the density.

In Valaam on the surface (0-5 m) the densities of cryptophyceans were three times as high and the biomass nearly twice as high as the values in Konevits. Comparing all depths (0-20 m)at both sampling stations, the difference in the numbers of cryptophyceans was statistically significant (p = 0.001), but no difference (p = 0.08) in biomass was detected. Some vertical differences in species composition were also found between the two sampling stations. In Valaam the biomass of dinophyceans (*Gymnodinium fuscum* (Ehrenberg) Stein) was higher in deeper water than at the surface. On the other hand, in Konevits below a depth of 5 m diatoms dominated in the phytoplankton biomass (p < 0.001).

Diel vertical distribution patterns of phytoplankton

In Valaam the biomass of phytoplankton was concentrated mainly in the surface waters and decreased gradually with depth during the whole study period; on the contrary, in Konevits the diel vertical differences were small due to the even distribution of diatoms. In Valaam the motile flag-



Fig. 4. Diel vertical distribution patterns of *Cryptomonas* sp. (500–2 000 μ m³) and *Katablepharis ovalis* and *Rhodomonas lacustris* (both < 500 μ m³) in Valaam in August 1995.

ellated cryptophyceans formed the main part of the phytoplankton density and clear differences were found in their diel vertical distribution (Fig. 4). In the 5–10 m depth layer the density of cryptophyceans (*Cryptomonas* sp. 500–2 000 μ m³) increased from 36 000 cells 1⁻¹ in the evening (18: 00) to 140 000 cells 1⁻¹ at midnight and decreased

again early in the morning (6:00) to 38 000 cells l⁻¹; statistically significant at p < 0.05. Numbers of small sized cryptophyceans (*Rhodomonas lacustris* and *Katablepharis ovalis*; both < 500 µm³) increased prominently in the 5–10 m depth during the dark period (Fig. 4); temporal changes were statistically significant (p < 0.05) also at other depths, except for 0–5 m.

Zooplankton

Differences between stations

In 1995 the mean crustacean zooplankton density (m⁻²) during the sampling period was 3.2 times higher in Valaam than in Konevits. At midday in Valaam the density of cladocerans was 175 000 animals m^{-2} and that of copepods was 1 054 000 animals m⁻², in Konevits there were 20 000 cladocerans m⁻² and 84 000 copepods m⁻². The density of Bosmina, Daphnia, Limnocalanus and small cyclopoid species differed significantly (p <0.001) between stations when tested by the Wilcoxon matched-pairs test. The densities of Eudiaptomus, Eurytemora, Cyclops did not differ. For example, the densities of small cyclopoids (Mesocyclops leuckarti and Thermocyclops oithonoides), which formed most of the crustacean zooplankton abundance, were 4-10 times higher and the density of the dominant cladoceran (Bosmina) 2-7 times higher in Valaam. Only the

large Cyclops was more abundant in Konevits.

Diel vertical migration

In Konevits, statistically significant diel changes in the vertical distribution pattern were observed only in large copepods: *Cyclops* (p < 0.01) and *Limnocalanus* (p < 0.05). In Valaam, of all the taxa studied, the depth of the maximum occurrence differed between sampling times within the study period for all major taxa (p < 0.05) except for the small cyclopoids (*Mesocyclops leuckarti* and *Thermocyclops oithonoides*) and *Bosmina longispina*.

The diel migration of the calanoid copepod Limnocalanus macrurus was very pronounced (Fig. 5). In 1995 it extended from the lower metalimnion to hypolimnion in the range 8-50 m in Konevits and 11-27 m in Valaam (Table 1). In Konevits, Bosmina remained mainly in the uppermost 10 m during the study period, while in Valaam the maximum density was detected between 10 and 20 m during daylight and the animals moved to the surface layers during the hours of darkness (Fig. 5). Only small vertical displacements of Eudiaptomus and small cyclopoids were apparent, and these occurred within about a 10 m layer (Fig. 5). These displacements were not regular, however, and did not fit the typical migration pattern. Except for Limnocalanus, zooplankters migrated less in Konevits than in Valaam (Table 1).

At the Valaam sampling station the migration amplitude of the common zooplankton species was much larger in 1993 than in 1995 (Table 1). In particular, the cladocerans *Bosmina* (12 m) and *Daphnia* (8 m) and the large copepods *Limnocalanus* (26 m) and *Cyclops* (20 m) migrated more in 1993.

Table 1. Displacement of the level of maximal densities of the main zooplankton taxa during their diel vertical migrations in Valaam in 1993 and 1995 and in Konevits in 1995 (– = no migration detected).

Species	Valaam 1993	Valaam 1995	Konevits 1995	
Bosmina longispina	4–16 m	7–14 m	3–6 m	metalimnion
Daphnia spp.	5–13 m	5–9 m	_	metalimnion
Cyclops lacustris	9–29 m	6–14 m	3–8 m	meta- and upper hypolimnion
Eudiaptomus spp.	_	3–6 m	_	epilimnion
Eurytemora lacustris	8–15 m	4–9 m	_	epi- and upper metalimnion
Limnocalanus macrurus	10–36 m	11–27 m	8–50 m	lower meta- and hypolimnion

12:00

12:00

12:00



Fig. 5 (above and on the right). Diel vertical distribution of seven dominant zooplankton taxa in Konevits (left columns) and Valaam (right columns) in August 1995.

Fish

After midnight the echograms indicated that fish density was more than twice as high in Konevits as in Valaam at 2–40 m layer (Fig. 6). Fish were more abundant in Konevits (p = 0.04) than in Valaam during the whole dark period: 22:00, 23:00, 24:00, 1:00 and 2:00. However, during the whole 24-hour study period the fish density did not differ between stations (p = 0.07). Daytime absence of fish from the surface water was noted at both stations. No fish were observed above 10 m between 7:00–23:00 in Konevits and between 8:00–15:00 in Valaam. The relative size distribution of fish (based on acoustic data) was com-





pared only at 24:00, 1:00 and 2:00. because at these times the densities differed most between the stations. The size distributions of fish in different layers and at the two stations differed from each other at midnight (KS = 0.11, p < 0.01), at 1:00 (KS = 0.22, p < 0.001) and at 2:00 (KS = 0.26, p < 0.001). The fish were larger in Valaam than in Konevits.

Fish spent most of the day at depths below 20 m. In the surface layer (2-20 m) the majority of

Valaam

Eudiaptomus

10 15

20

29

38

47

small cyclopoids

fepth (m)



Fig. 6. Total fish density in the 2–40 m depth layer in Valaam and Konevits regions (fish ha⁻¹) in August 1995.

fish appeared for a few hours after midnight (Fig. 7). At both stations the vertical distribution was fairly similar. In Konevits the fish started to ascend at about sunset (21:00) and the second migration appeared just after midnight. Contrary to the situation in Valaam, in Konevits the DVM of fish was bimodal. In Valaam, migration started at dusk; and the majority of the fish remained in the surface layers (2–20 m) throughout the night. In Konevits, the diel pattern of vertical distribution of fish appeared to be typical of smelt while in Valaam this distribution was more typical of vendace. Simultaneous trawl catches indicate that in Konevits the midnight surface maximum is formed by smelt.

Discussion

Research on the subject of diel vertical migration has developed along two distinct lines: a mortality-avoidance hypothesis, and a metabolic and demographic advantage hypothesis. Several metabolic and demographic costs are associated with the DVM of zooplankton (Lampert 1989, Dawidowicz and Loose 1992a, 1992b, Loose and Dawidowicz 1994). According to Lampert (1989), these costs can be divided into three components: reduced quantity and quality of food in deep water, decreased metabolic rate through a vertical temperature gradient down to a cold hypolimnion, and higher energy demands due to enhanced swimming of vertically migrating animals.

In recent years strong support has been provided for the mortality-avoidance hypothesis. According to Lampert (1993), this hypothesis explains the timing of DVM: the more visible zooplankton are the strongest migrators, and fish abundance affects migration amplitude. Our results were only for one diurnal series for both stations, so it is very difficult to draw conclusions on predation pressure. The peak total density of pelagic fish was more than twice as high in Konevits as in Valaam, while the zooplankton density was 3.2 times lower in Konevits than in Valaam. During the dark period, fish abundance - and presumably also predation pressure - was much higher in Konevits. In Valaam at midnight *Bosmina* ascended to the surface, and during the day it remained in the darkness below 10 m. In Konevits Bosmina did not migrate to avoid predation even though it was obviously endangered by fish predators: during the dark period the fish density was high and Bosmina was the main item in the vendace diet at that time (Pechnikov et al. 1997). Furthermore, in Konevits the higher fish density apparently decreased the zooplankton density, especially the density of cladocerans compared to Valaam. Limnocalanus, nevertheless, had a very pronounced migration amplitude (42 m) at Konevits station compared to Valaam station (16 m). According to Pechnikov et al. (1997), Limnocalanus is an important food item in the diet of vendace in autumn. The diet of smelt was not studied; according to literature its diet consists of large food items like mysids, Leptodora kindti, Bythotrephes longimanus and Heterocope appendiculata, but smelt do not feed on cladocera (e.g. *Bosmina*) to the same extent as do vendace (Nilsson 1979, Enderlein 1981, Garnås 1983).

In our study we tried to estimate the costs of zooplankton migration by observing the algal distribution and temperature gradient. The vertical distribution of algae differed at the two stations: in Valaam the algae were distributed unevenly with most on the surface layers, while in Konevits the algae were distributed evenly throughout the entire 0–20 m layer. In Valaam the flagellate cryptophyceans, which are considered to be the most suitable food for zooplankton, dominated,



Fig. 7. Diel vertical distribution of fish in Konevits and Valaam in August 1995.

which was typical to open pelagial area of Lake Ladoga (Holopainen et al. 1996, Holopainen and Letanskaya 1998). In Valaam the clear surface maximum of cryptophyceans probably affected the migration pattern of most species of herbivorous zooplankton. Most of the zooplankton taxa could benefit from the maximum abundance of algae in the upper layers. In Konevits the number of cryptophyceans was three times lower than in Valaam. In the literature the vertical distribution of algae has shown to have a positive influence on DVM of zooplankton (Pijanowska and Dawidowicz 1987, Dini and Carpenter 1992). Johansen and Jakobsen (1987) demonstrated that the DVM of zooplankton occurred at high concentrations of food, but not at low, which was also the case (e.g. Bosmina) in Valaam but not in Konevits. This underlines the cost involved in leaving the food-rich upper layers.

Kerfoot (1985), however, pointed out that the effect of low temperature in deeper layers cannot be overcome by higher algal densities. The retardation of Daphnia growth due to migrating downward to low temperature contributes to the disadvantages of DVM much more than the reduction in food does (Dawidowicz and Loose 1992a, Loose and Dawidowicz 1994). In 1995 the temperature of the metalimnion was +1.5-2 °C higher in Valaam than in Konevits, and in Valaam the temperature was +8 °C higher in 1993 than in 1995 (Fig. 2). According to Timo Huttula (pers. comm.), the difference between the thermocline in Konevits and Valaam in 1995 may be due to internal wave action. In Valaam the migration amplitude of the dominant zooplankton species reached much deeper in 1993 than in 1995. In Konevits the combined effect of low temperature and lower and evenly distributed densities of edible algal increased the costs of zooplankton migration.

In Lake Ladoga the daytime vertical distributions patterns of plankton are well-known (Rahkola *et al.* 1994, Andronikova 1996, Andronikova and Avinsky 1997, Holopainen and Letanskaya 1998). Besides plankton we have in this study also observed the diel vertical migration of fish. Although our results of migration are based on single diurnal series obtained at two stations, information on diel migrations will help us to understand different relationships and community functions better.

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