



Diel variation in the vertical distribution of fish and plankton in Lake Kinneret: a 24-h study of ecological overlap

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Abstract

Diel vertical migration (DVM) behaviour is a predator avoidance mechanism observed within many zooplankton species in the presence of zooplanktivorous fish. A 24-h survey was carried out in June 1998 to investigate diel variation in the vertical distribution of fish, zooplankton and phytoplankton (chlorophyll) in Lake Kinneret, Israel. Fish revealed diel variation in vertical distribution but had no spatial overlap with zooplankton, and consequently no apparent influence on zooplankton dispersal. Zooplankton revealed some diel variation in distribution being affected by thermocline and oxycline position and movement of the internal the internal seiche wave. Cyclopoid species closely follow the movement of the seiche wave implying that, due to their greater motility, they are following conditions that are suitable to them. The Cladocera species and small rotifers only partly, which may be part of their phototactic behaviour. Physical forces like convection, horizontal and vertical forcing probably have a role in contributing to a homogeneous distribution of the plankton by preventing stratification or interfering with the more motile zooplankton which may be attempting to migrate.

Introduction

Zooplankton are an important link in fresh water aquatic ecosystems, grazing on and controlling small species of phytoplankton (<20 μm), which in turn are the major food source of the zooplanktivorous fish in the upper trophic levels of the system. Selective predation by planktivorous fish is an important factor influencing the composition of zooplankton populations in lakes (Brooks & Dodson, 1965; O'Brien, 1979; Hurlbert & Mulla, 1981; Lazzaro, 1987), and since zooplanktivorous fish are size-selective predators, larger zooplankton taxa and individuals are susceptible to detection, resulting in high mortality rates via fish predation. Consequently Diel Vertical Migration (DVM) in the presence of predatory fish is a commonly adopted spatial avoidance behaviour by larger zooplankton which have been shown to reduce losses to predation by migrating into deeper water during daylight as a refuge. (Duncan et al., 1993; Taleb et

al., 1993). However, zooplankton distribution is also influenced by several other factors; for example, food levels, temperature, oxygen saturation, the presence of fish kairomones (Lampert, 1993), and possibly invertebrate predation, may have an equal or stronger influence on distribution than direct predation by fish. Light intensity appears to be a trigger for directional changes in migration and many zooplankton species are phototactic (Buchanan & Haney, 1980; Haney, 1993; Ringelberg, 1995). The general evidence is that changes in light intensity is the primary factor regulating the vertical distribution of zooplankton and that, predation, temperature, food availability, dissolved oxygen and chemical cues modify the photoresponses of several zooplankton species (Biol Rev Zaret & Suffern, 1976; Stich & Lampert, 1981; Bollens & Frost, 1989; Ringelberg, 1999). Lake Kinneret is a warm monomictic sub-tropical lake in Northern Israel at 209 m below sea level with a surface area of 170 km². This meso-eutrophic lake is generally stratified from

mid-May to November and mixed from December to April. In Lake Kinneret bleak (*Acanthobrama terraesanctae terraesanctae*), which account for 50–65% of the total fish biomass in the lake (Gophen & Landau, 1977), are considered to be 'Particulate' zooplankton feeder (Gophen & Threlkeld, 1989). They were found to exhibit a diel periodicity in foraging activity, feeding mostly in daytime with only low levels of foraging in the dark (Easton & Gophen, 2002 (in press)).

This paper is part of a research project to investigate the occurrence of DVM of zooplankton in Lake Kinneret, and to determine spatial association between zooplankton, phytoplankton and fish (bleak) in order to identify possible factors effecting DVM behaviour. DVM and associated parameters were measured every month for 1 year at mid-day and mid-night and the results indicated only weak vertical migration in the winter (unpublished data). This led us to this part of the study which was designed to look at the distribution and dynamics of fish and plankton migration on a 2-h time scale over 24 h. It was undertaken at early lake stratification (spring–summer), which also enabled us to investigate the importance of a well-determined thermocline (9 °C difference between epilimnion and hypolimnion) and a separate chemocline and oxycline, on the distribution of the biota.

Methods

On 8 June 1998, a 24-h survey, sampling at 2-h intervals was undertaken at station F (Fig. 1), a station 3 km offshore in the north-west of Lake Kinneret where the maximum depth is 23 m. Samples were collected from nine depths: epilimnion: 1, 3, 5, 7, 10 and 15 m metalimnion (two flexible depths between 16 and 18 m, due to the vertical variation of the seiche), and one in the hypolimnion at 20 m which is 3 m above the lake bottom.

Zooplankton samples were taken with a 20-l Schindler Patalas trap, collected and preserved in a formalin solution for a concentration of 1:10. To reduce problems associated with zooplankton patches (Malone & McQueen, 1983; Pinel-Alloul et al., 1988), two samples were taken from each depth increment at stations located 200 m apart. In the laboratory, zooplankton were counted using a computer assisted video analysis system (Hambright & Fridman, 1994).

Identifiable zooplankton included the cladoceran genera *Bosmina* spp., *Ceriodaphnia* spp., *Diaphanosoma* sp., *Moina* sp. and *Chydorus* sp., juvenile and

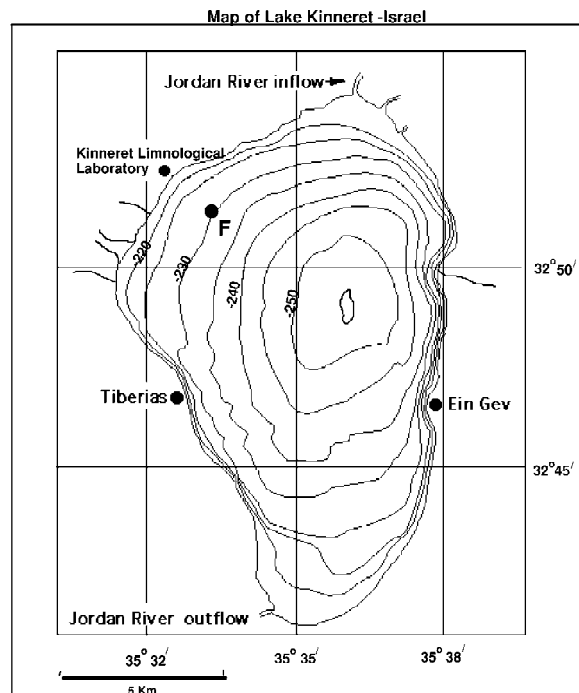


Figure 1. Map of Lake Kinneret showing the position of the survey station (Stn. F).

adult cyclopoid copepods, the calanoid copepod *Eudiatomus* sp., small rotifers (<4.0 μg_{ww} ind⁻¹), e.g., *Keratella*, *Polyarthra* and large rotifers (>4.0 μg_{ww} ind⁻¹) e.g., *Asplanchna* and *Synchaeta*. The very low numbers of *Moina*, *Chydorus* and large rotifers (1–3 ind l⁻¹) found in the samples eventually precluded them from the analysis.

The detection of zooplankton DVM based on a predator-prey theory, requires the ability to distinguish differences between day versus night distributions (visual predation requires light, which would make the greatest changes in vertical migration between day and night). An aid to understanding the patchiness of predator and prey populations, and the outcome of behavioural interactions between predator and prey, has been described by Williamson et al. (1989). We have used their model for predator-prey overlap as a tool for predicting fish predation pressure on zooplankton DVM:

$$o_{ij} = \frac{\sum_{z=1}^m (N_{ij} n_{iz}) m}{\sum_{z=1}^m (N_{jz}) \cdot \sum_{z=1}^m (n_{iz})}$$

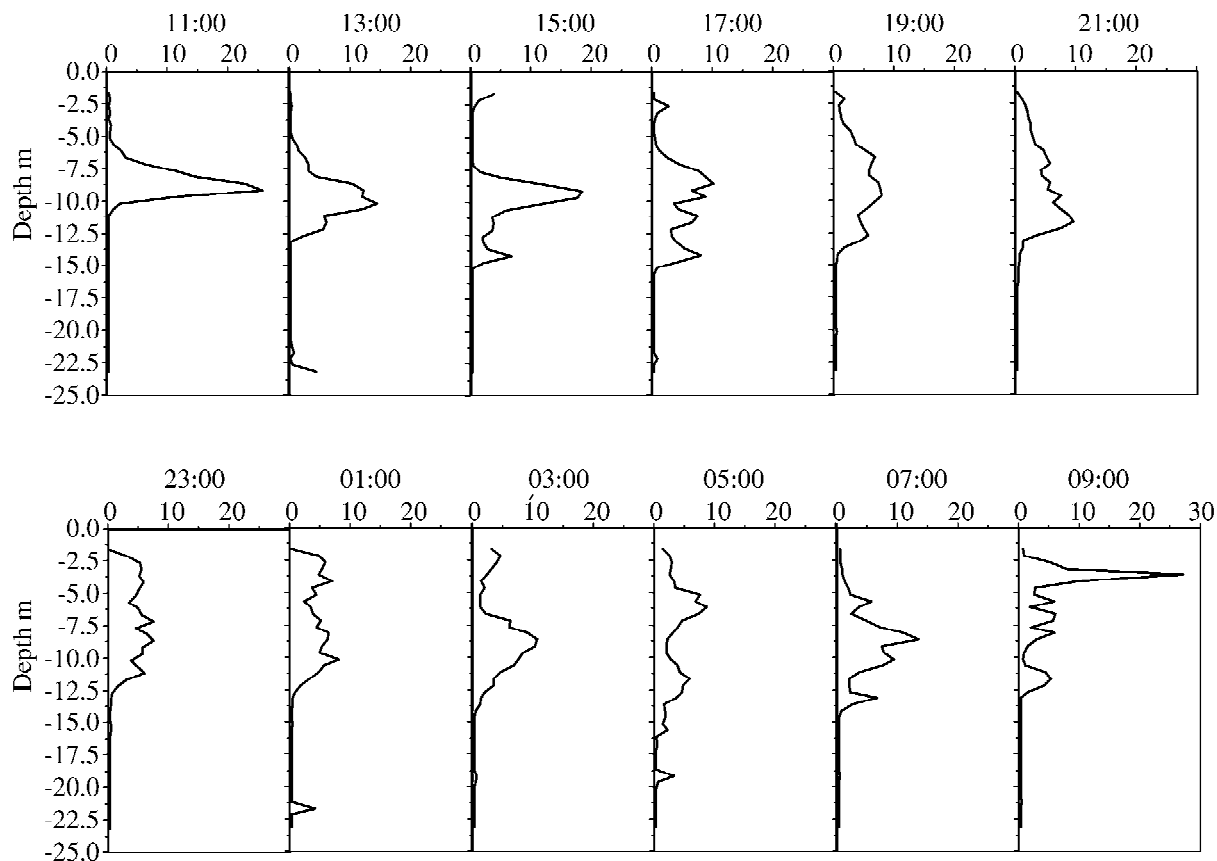


Figure 2. Relative vertical distribution of fish at station F in Lake Kinneret measured in early summer (June 1998) every 2 h over a period of 24 h (11:00–09:00 the next day). Horizontal axis: relative abundance (%); vertical axis: depth in meters.

where z is an individual patch sample, m is the number of patches sampled, and N_j and n_i are population densities for the predator type j and prey type i , respectively.

When either prey or predator populations (or both) are uniformly distributed, o_{ij} is equal to one. Values of less than one represent lower overlap, with a theoretical lower limit of zero. Values greater than one represent greater overlap than would be expected with uniform prey and predator distributions, where the upper limit is determined by the number of patches sampled. In this case the patches are the average depths of the replicate samples combined for a mean day and night value, each depth representing a sample patch. This model examines the changes in the overlap of predator and prey populations for fish (bleak) and zooplankton species on the assumption that they migrate vertically.

Phytoplankton samples were taken with a 5-l Van Dorn bottle in duplicate at each depth parallel to the

zooplankton sampling every 4 h and filtered by size (total phytoplankton and $<20 \mu$, for nanoplankton) for chlorophyll-*a* measurement. The pigment extraction method used is adapted from Standard Methods for the Examination of Water and Wastewater (American Public Health Association, 1992). Light was measured using a Li-Cor quantum light meter and fish abundance (fish ha^{-1}) and distribution were measured using a hydro-acoustic echo sounder SIMRAD EY-M single beam Scientific Echosounder, operating at 70 mHz. Analysis of the data used the Hydro Acoustic Data Analysis System (HADAS) (Walline et al., 1992). Temperature, oxygen concentration, redox potential and specific conductivity were measured simultaneously with a water quality hydroprobe (DataSonde 4 Hydrolab).

The zooplankton was sampled every 2 h and the phytoplankton every 4 h. An acoustic transect for detecting fish was made around the station every 2 h for 15 min. Every 2 h we also measured: light intensity

Table 1. Overlap values of zooplankton and fish for actual and 'reversed' values (described in the text). Effective predator avoidance strategy as a result of DVM would give higher reversed than actual values

Zooplankton	Actual day	Reversed day	Actual night	Reversed night	Total actual	Total reversed
Nauplii	1.22	1.11	1.0	1.17	1.12	1.14
Copepodites (all sp.)	1.31	1.19	1.11	1.25	1.21	1.22
Cyclopoid males (all spp.)	1.54	1.25	1.18	1.42	1.36	1.33
Cyclopoid fem. (all spp.)	1.16	1.07	1.08	1.37	1.12	1.22
<i>Calanoid</i> sp.	0.98	1.14	1.14	1.02	1.06	1.08
<i>Diaphanosoma</i> sp.	1.19	1.19	1.22	1.16	1.20	1.18
<i>Bosmina</i> spp.	1.02	1.05	1.10	1.07	1.06	1.06
<i>Ceriodaphnia</i> spp.	1.11	1.17	1.10	1.03	1.11	1.10
Rotifers – large	1.06	1.07	1.44	1.49	1.25	1.28
Rotifers – small	0.98	1.13	1.09	1.14	1.03	1.14

($\mu\text{m Einsteins m}^{-2}$), temperature ($^{\circ}\text{C}$), oxygen (mg l^{-1}), turbidity (NTU), and redox potential (mV).

Statistical methods

Factorial ANOVA ($\alpha=0.05$) was used to resolve differences between the distribution of zooplankton between day and night. Regression statistics were used to evaluate the effect of temperature, oxygen, turbidity and redox potential on the vertical distribution of zooplankton fish and phytoplankton. P -values above 0.05, and r^2 values below 0.5 were discarded as not being significant. All the analysis were performed using the Macintosh StatView (SAS Institute, Inc.) package.

Results

Fish showed two different distribution patterns (Fig. 2). At daytime (11:00–15:00) the fish swam in schools which tend to be both horizontally and vertically compact and did not appear to move in respect to depth, residing for the most part between 5 and 10 m. Close to darkness at 17:00, the schools started to break up and the fish dispersed both horizontally and vertically. At night (from 17:00 to 07:00) there was a more even distribution between 2.5 and 12.5 m. By 07:00 the fish began to concentrate again into schools and the profile graph showed a peak concentration of fish around 3 m at 09:00. Acoustic transects were taken on a moving boat and only indicate vertical distribution patterns

and not active vertical movement, and therefore show only a temporary representation of fish location.

Nanophytoplankton did not appear to migrate vertically (Fig. 3). However, the larger netphytoplankton (e.g. *Microcystis* spp.) actively concentrated towards the surface at night forming a bimodal dispersion with peaks at 12.5 and 2.5 m. By 07:00 the lower peak at 12.5 m dispersed and the netphytoplankton concentrated closer to the surface.

Regression analysis gave no clear explanation of fish distribution as a function of any of the physical parameters. However, it was seen that fish concentrated mostly in temperatures zones between 20 and 25 $^{\circ}\text{C}$, which is the temperature of the epilimnion at this time of the year. They did not appear to follow particular oxygen concentrations, and they also clearly avoided low redox potential as would be expected.

Regression analysis ($P < 0.05$) was used to analyse relations between turbidity, zooplankton and phytoplankton. The highest turbidity was found in the upper part of the water column and decreased with depth. Zooplankton were insignificantly associated with the turbid layers (r^2 values between 0.01 and 0.03) while only nanoplankton indicated a slightly positive relation (r^2 0.4). Fish appeared to remain mostly in deeper water where turbidity levels are lower. A common feature of the thermocline during the summer stratification in Lake Kinneret is the high turbid layer immediately on top of it. This layer is associated with higher concentrations of bacteria, protozoa, some zooplankton for example rotifers, and suspended particles trapped in the density gradient (Gophen, 1979; Hadas et al., 1998). We did not detect

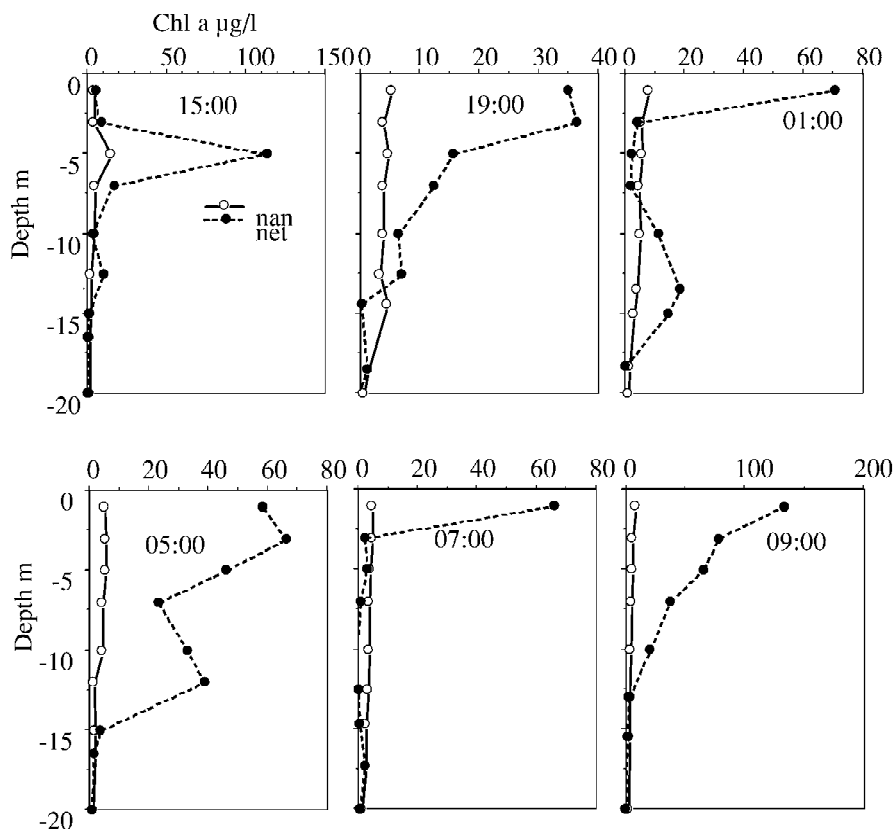


Figure 3. Profile graphs of nanoplankton and net phytoplankton distribution (chlorophyll a concentration $\mu\text{g l}^{-1}$) at 4-h intervals over a period of 24 h (independent variable) in early summer (June 1998), at station F in Lake Kinneret.

this layer in this field study assuming that it was still too early in the summer and prior to its formation.

Oxygen concentration rises fairly consistently from the top of the metalimnion to the surface, but regression analysis failed to show consistent significant relations between zooplankton, phytoplankton and oxygen concentration (in the water column above the oxycline), neither during the day nor night, r^2 values were between 0.001 and 0.4.

Both zooplankton and fish were negatively related with low ORP (r^2 values below 0.1), indicating avoidance of anoxic conditions. There was a fairly constant presence of low numbers of zooplankton of all the species at low ORP (+50 to -50 mV) at 17–20 m. depth. Phytoplankton were found mostly in the photic zone which is too high in the water column to be affected by the chemocline.

Water temperature raises fairly evenly 22–25 °C from the top of the thermocline to the surface. Distribution of zooplankton and phytoplankton were insignificantly related to these thermal changes (r^2 between

0.1 and 0.03). In the colder water (16–22 °C) below the thermocline there were very few zooplankton due to the anoxic conditions.

Relations between the distributions of all the biotic factors can be seen from the correlation matrix (Table 2). The cyclopoid species indicated a significant positive inter-species correlation, and the herbivorous grazer species *Ceriodaphnia*, *Diaphanosoma* and *Bosmina*, significantly correlated between themselves. There were neither correlations with fish for any zooplankton nor between any zooplankton with nanoplankton.

Diel vertical migration

The impact of DVM on overlap between predator and prey populations was estimated by calculating and comparing overlap values (Equation (1)) for each predator–prey pair under two conditions: (1) with the actual observed predator and prey distributions unchanged; and (2) with the day and night distributions

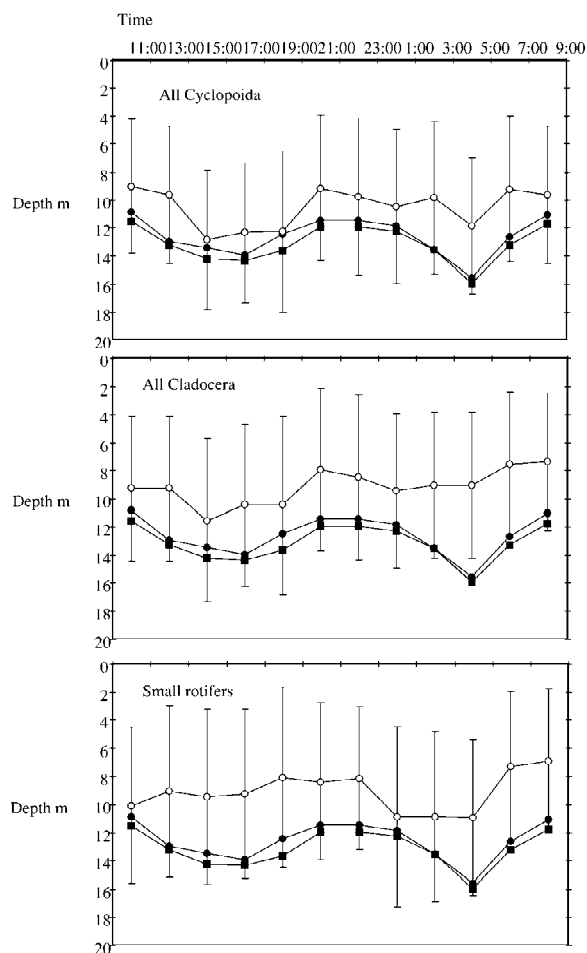


Figure 4. Three graphs showing vertical variability in the depths (dependent variable) of the physical parameters of the thermocline ($^{\circ}\text{C}$, \bullet — (the 21°C isotherm) and dissolved oxygen mg l^{-1} , \blacksquare — (at 1 mg l^{-1}) and the mean depths of the biological variables of all Cyclopoida \circ —, all Cladocera \circ — and small rotifers \circ — (independent variables) over 24 h at station F in early summer (June 1998) in Lake Kinneret.

of the prey reversed so that predator day distributions were paired with night prey distributions and predator night distributions were paired with prey day distributions. If diel vertical migration were an effective predator avoidance strategy that reduced the overlap of the predator and the prey, then the 'reversed' overlap values would be greater than the 'actual' overlap values. In this analysis (Table 1) the 'reverse' overlap values of the totals did not show significantly greater values than the 'actual' total values, indicating that any diel vertical migration did not substantially reduce the overlap or predation risk of any of the

zooplankton prey with the fish (Fig. 4). The maximum increase in the overlap values for reversed vs. actual prey distributions was 0.1 for adult cyclopid females. Zooplankton profiles are given (Fig. 5) to show distribution of the zooplankton at day and night. ANOVA showed no significant differences between the two periods for any of the zooplankton species with P -values all above 0.2.

In Figure 4 the zooplankton can be seen to show vertical movement as a partial response to the deepening and rising movement of the thermocline and oxycline. For Copepoda r^2 values are DO: 0.568 and Temperature: 0.466, for Cladocera 0.2 and 0.3, small rotifers 0.277 and 0.367, respectively. If the times 03:00 and 05:00 are excluded then r^2 values for DO and temperature of both the Cladocera and Copepoda species are between 0.7 and 0.75. The high standard deviations are a result of the large variability of the zooplankton in the epilimnion.

Discussion

This field study was designed to determine the vertical distribution of fish and plankton in Lake Kinneret over a 24-h period in early summer. At the same time it attempts to identify causal factors for distribution in particular the vertical migration of zooplankton. From this study it cannot be concluded that fish predation has an influence on the vertical migration of zooplankton. This is supported by the overlap model results, which showed no overlap or behavioural interactions between fish and zooplankton.

The correlation we would expect to find between herbivorous grazers and their diet nanoplankton was not evident. For the most part nanoplankton were distributed fairly evenly in the epilimnion with slightly higher concentrations in the upper levels, the type of statistical analysis used, (correlation and regression) failed to find associated patterns of distribution of nanoplankton with zooplankton, as the zooplankton were partially distributed in layers and nanoplankton were not. However, the larger species of phytoplankton showed distribution patterns that differ from day to night. Lake Kinneret is a meso-eutrophic lake where phytoplankton production is probably sufficient to provide the majority of the herbivorous zooplankton grazers with enough food resources to enable them to be vertically distributed unrelated to phytoplankton availability. It is evident (both in this and other field studies in this project), that the physical

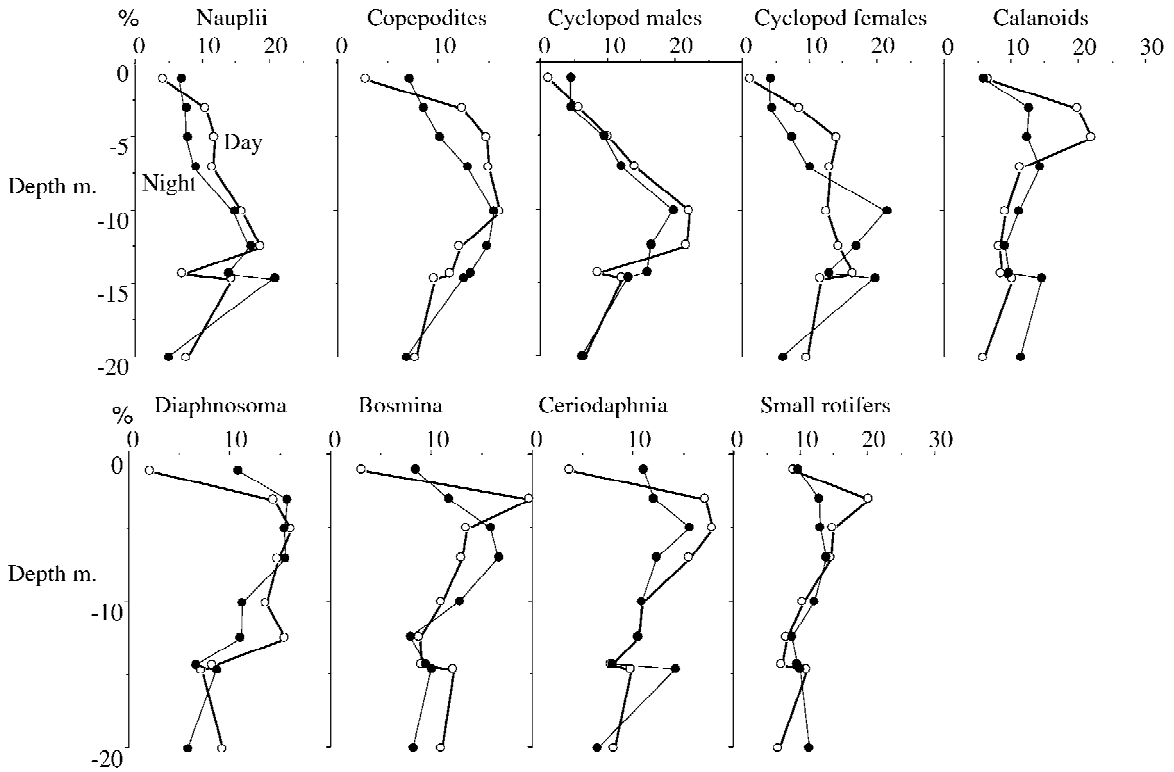


Figure 5. Profile graphs for the distribution of the major zooplankton species in Lake Kinneret. The graphs show relative distribution averaged for day and night periods over 24 h: —○— daylight (07:00–19:00), —●— night (21:00–05:00).

factors which might have a consistent effect on the distribution of the biota within the epilimnion are not temperature, light intensity and oxygen concentration (with the exception of light and phytoplankton: – the larger phytoplankton, >25 μ are concentrated in the upper few meters). However, some of the zooplankton did show periodic vertical movement associated with the 24-h circular motion of the basin scale seiche wave. The epilimnion is for the most part a well-mixed layer that results from wind induced surface turbulence (Antenucci et al., 2000). The thermocline, oxycline and chemocline moved vertically in synchrony with the wind generated basin scale 24-h Kelvin wave (Mode 1 wave), which oscillates the seiche anti-clockwise around the lake on a regular 24-h time scale. This is in response to a strong daily afternoon westerly wind and remains thus for the entire summer season, June–October (Antenucci et al., 2000). At station F the Kelvin wave was shallowest between the hours of 09:00 and 13:00 and would be deepest between 19:00 and 05:00 but for secondary Poincare (Mode 2, wind compression) upward moving wave in-between when the Kelvin wave was at its

deepest at Station F. This secondary wave moved up between 19:00 and 03:00, and partially nullified the deepening of the Kelvin wave at this time (Fig. 4a).

The seiche appears initially to be an artefact in the vertical movement of all the cyclopoid species and partially so for the Cladocera, as in the early hours of the morning the relation to the seiche was weak, suggesting that there may be a behavioural response involved. The cyclopoids are the more motile of the zooplankton species and their synchrony with the thermocline movement implies that they are following conditions that are suitable to them. The Cladocera and the small rotifers were less associated with the seiche movement and maybe responding to phototactic behaviour. It seems that there the importance of physical movement of zooplankton by internal forcing has not been fully understood in lakes where seiching occurs, physical forces like convection, horizontal and vertical forcing, probably have a role in contributing to a homogeneous distribution of the plankton by preventing stratification or interfering with the more motile zooplankton which may be attempting to migrate. Fish were less affected by the seiche movement

and showed variable patterns of distribution between day and night, but the zooplankton can be more easily assumed to be moved (as particles) by the changes in the density (temperature) of the different waves. The more motile zooplankton may also actively avoid (Gophen, 1979) the unsuitable conditions below the seiche by swimming up as the seiche moves up. An annual evaluation of the vertical distribution of zooplankton in the Kinneret (Gophen, 1979), indicated concentrations of zooplankton on the metalimnion, which although were found several times but not always in other surveys, were not evident here. There were no higher turbidity readings in this region nor evidence of concentrations of zooplankton in areas of higher turbidity.

This is a single field study at a particular season and the results found cannot necessarily be extrapolated in the long-term biological events and processes of the lake. The physical structure of the Lake is not uniform throughout the year, nor are temperature and nutrient composition (Serruya et al., 1980). Nevertheless these results do support the results of an annual study of DVM by Easton (PhD. thesis, unpublished), where an annual investigation showed very weak and inconsistent DVM of zooplankton. This field study has pointed to some of the physical and ecological forces which shape the processes between the trophic layers in this lake in early summer, for example fish at this time did not appear to feed on zooplankton in the Kinneret to the point where zooplankton manifest DVM behaviour. A slight DVM of cladocerans and copepods were documented in 1968–1973 (Gophen, 1979). It is possible that the long-term change (Gophen, 1985, 1992) that indicates a shift from larger to smaller body size within species of zooplankton in the Kinneret, may be a reason for the disappearance of predator associated DVM behaviour.

Diel vertical migration of zooplankton is a field of study that has been researched at length and most of these reasons for DVM together with indications of vertical movement were looked for in this survey. Our conclusion is that some of the zooplankton are attempting to move vertically to achieve suitable conditions, but are being interfered with by the internal waves.

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