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A short-term study of vertical and horizontal distribution of zooplankton during thermal stratification in Lake Kinneret, Israel*

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Abstract

This study documents for the first time both vertical and horizontal distribution patterns of the zooplankton community in Lake Kinneret during the period of thermal stratification. The zooplankton distribution patterns were explored in relation to abiotic (temperature, oxygen) and biotic (picocyanobacteria, ciliates, flagellates, phytoplankton, fish) environmental gradients. Sampling was carried out on 6–7 July 1992 at five stations and six depths from nearshore to offshore. Zooplankton abundance and biomass varied from 5 to 267 ind. l^{-1} (mean: 95 ind. l^{-1}), and from 0.1 to 65 d.w. mg m^{-3} (mean: 24 d.w. mg m^{-3}). Zooplankton taxonomic groups (Rotifera, Cladocera, Cyclopoida, Calanoida) and size classes (micro-, meso- and macrozooplankton) showed peaks of maximal density and biomass in the epilimnetic and metalimnetic strata (5 and 14 m). Depth, accounting for 31–39% of total spatial variation, reflected the vertical distribution of zooplankton in relation to temperature and oxygen declines, and the higher concentration of food resources (protists and phytoplankton) in the epilimnion and metalimnion. Onshore–offshore distance, accounting for 17–22% of the total spatial variance, reflected different distribution patterns shown among zooplankton groups and size classes. The macrozooplankton (Copepoda, Cladocera) was more abundant offshore, whereas microzooplankton (Rotifera and nauplii) predominated nearshore. These horizontal distribution patterns were related to small increases in temperature and phytoplankton biomass, and higher concentrations of fish in the littoral zone. Although limited to a short temporal scale, our study indicated that zooplankton spatial distribution in Lake Kinneret during the period of thermal stratification was related to physicochemical, food and predation factors, manifested differently along the vertical and nearshore–offshore gradients.

Introduction

Despite the importance of spatial heterogeneity to the ecology of zooplankton (Pinel-Alloul, 1995; Beaver & Havens, 1996; Megard et al., 1997; Folt & Burns, 1999), few studies have examined horizontal distribution of zooplankton in relation to environmental gradients in warm monomictic large lakes. Most of the studies were conducted in temperate or alpine dimictic lakes in North America (Johannsson et al., 1991; Patalas & Salki, 1992; Bürgi et al., 1993; Stockwell & Sprules, 1995) and Europe (Holopainen et al., 1993; Viljanen & Karjalainen, 1993; Masson & Pinel-Alloul, 1998; Pinel-Alloul et al., 1999; Masson et al.,

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2001). Lake Kinneret is especially suited for studies of spatial distribution of zooplankton because it does not contain large predator fish, and thus it shows tight interactions between crustacean zooplankton and planktivorous fish (Kalikhman et al., 1992; Walline et al., 1993, 2000). Furthermore, the seasonal dynamics of the planktonic food web typically shows a winter–spring dinoflagellate bloom followed by a nanoplankton-dominated summer assemblage, leading to different interactions between the zooplankton grazers and the microbial loop community (Malinsky-Rushansky et al., 1995; Zohary et al., 1998). However, the spatial distribution of the zooplankton in Lake Kinneret has yet received little attention. Gophen (1979) described the vertical distribution and diurnal migration of zooplankton in the pelagic zone of the lake. Recently, Kamenir et al. (1998) also described the size structure of planktonic communities in Lake Kinneret. Whole-lake horizontal distribution of zooplankton and fish during winter was also studied with respect to phytoplankton, temperature and oxygen gradients (Kalikhman et al., 1992; Yacobi et al., 1993). However, these studies considered neither the vertical axis of the lake, nor the microbial communities that might play an important role in the pelagic food web in this lake (Stone et al., 1993).

This study documents for the first time the vertical and horizontal distribution of zooplankton groups and size classes in Lake Kinneret, during the period of thermal stratification and nanoplankton dominance. Although carried out on a short temporal scale of 2 days on 6–7 July 1992, this research provides new insights about how zooplankton is distributed at different depths along the nearshore–offshore transect with respect to physico-chemical gradients, phytoplankton groups and size classes, microbial communities, and fish distribution. The study focuses on the spatial distribution of both taxonomic groups (Rotifera, Cladocera, Cyclopoida, Calanoida) and size classes (Micro-: <200 μm; Meso-: 200–500 μm; Macro-: >500 μm). Given the dominant role of the zooplankton in the transfer of energy to fish in this planktivory-dominated lake (Gophen et al., 1988; Landau et al., 1988; Landau, 1991; Walline et al., 2000) and its potential trophic linkages with the microbial components (Stone et al., 1993), it is important to clearly understand and resolve how the interaction between abiotic and biotic factors may translate into spatial patterns of zooplankton distribution, and how it varies among zooplankton groups or size classes.

Methods

Study site

Lake Kinneret (32° 45–53′ N and 35° 30–38′ E) is located in northern Israel at 210 m below sea level (Fig. 1A). Its surface area is 168 km^2 and that of the watershed basin is 2730 km^2. Mean and maximum depths are 25 and 43 m, respectively (Serruya, 1978). This warm monomictic large lake is generally stratified from mid-May to November and mixed from December to March. The sampling survey was undertaken in the western part of the lake on 6–7 July 1992 mornings (9–12 h) (Fig. 1A). The year of our survey was the coldest of the century (minimum winter water temperature: 12.3 °C) and one of the wettest years on record. It was characterized by the highest whole lake total inflow volume (>1500×10^6 m^3) and nutrient loadings (P: 186 t; N: 4668 t) (Zohary et al., 1998). Samples were collected at discrete depths at 5-m intervals from 1 to 30 m in one pelagic (P1), two sublittoral (SL1, SL2) and two littoral (L1, L2) stations on an offshore to nearshore transect (Fig. 1B). Temperature and oxygen depth profiles were recorded with a YSI thermistor. Light attenuation was estimated with a Lamba LiCor 185 quantum meter and Secchi depth was recorded at each station. Water pH and conductivity were also measured.

Water sampling and microbial community

Water samples (three replicates) were collected with a Rodhe-Aberg 5L sampler, and transferred to the laboratory in dark glass bottles for determination of the microbial communities. For determination of picocyanobacteria, 20ml subsamples were fixed with 1.4 ml of 0.2 μm filtered 5% buffered formaldehyde (final concentration 0.6%) and stored at 4 °C until counting. Subsamples (20 ml) for ciliates were preserved with a solution of glutaraldehyde–paraformaldehyde at a final concentration of 1%. Aliquots of the preserved

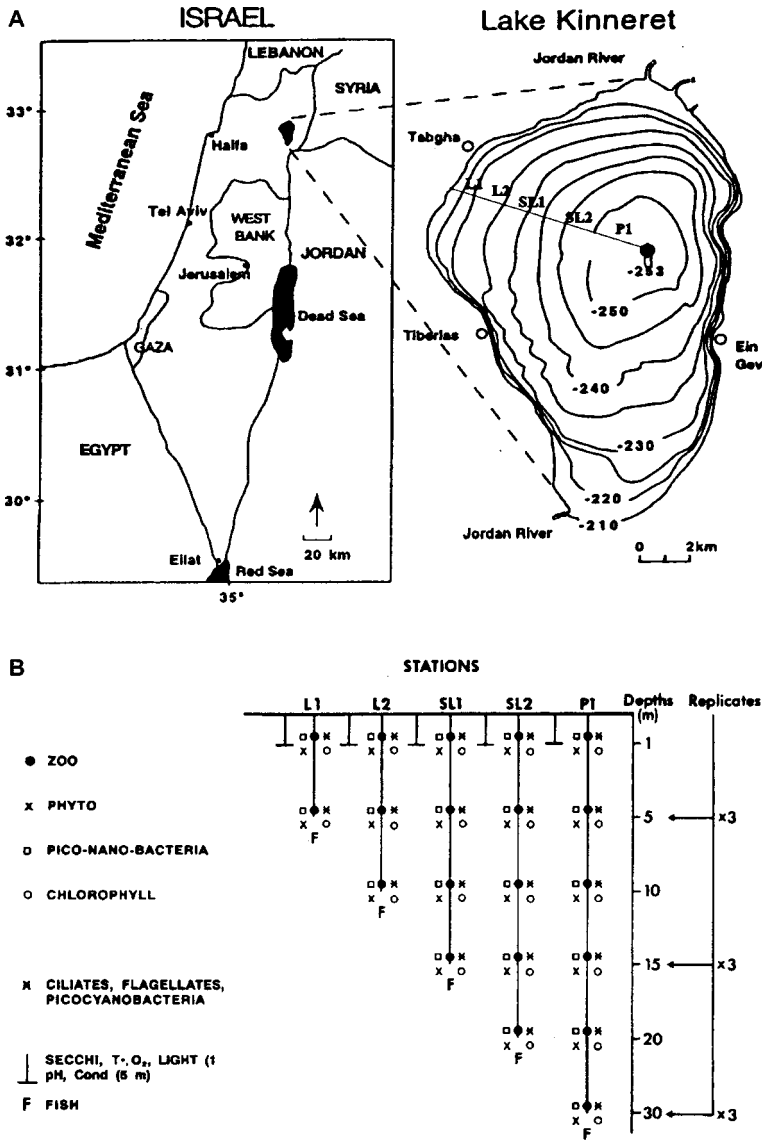

Figure 1. Location and bathymetric map for Lake Kinneret, showing the location of the inshore–offshore transect (modified from Zahory et al., 1998). Isodepths are in meters below sea level.

water subsamples of picocyanobacteria (5 ml) and ciliates (10–15 ml) were filtered through 0.2 μm and 0.8 μm 25 mm Nuclepore™ membranes filters, respectively, under low vacuum (<3 mmHg). Water subsamples (10 ml) for heterotrophic and mixotrophic flagellates were fixed with a solution of nickel chloride (80%) and neutralized glutaraldehyde (25%) at final concentrations of 1.5% and 0.5%, respectively. Flagellates were stained for at least 10 min with 0.2% proflavine solution at a final concentration of 5×10^{-4}% in subsamples, and filtered through 3 μm black polycarbonate Nuclepore™ filters. Microscopic enumeration of nanoflagellates, ciliates and picocyanobacteria were made using methods described by Malinsky-Rushansky et al. (1995) and Hadas & Berman (1998).

Phytoplankton

Phytoplankton samples (100 ml), collected as above, were preserved in 1% acid Lugol solution,

and species were counted and sized with an inverted microscope (Utermöhl, 1958). Wet weight biomass was calculated from calibrated volumetric measurement of each algal species (Pollingher, 1978). The abundance (cells 10^3 ml^{-1}) and the biomass (μg 10^3 ml^{-1}) of taxonomic groups (Cyanophytes, Cryptophytes, Diatoms, Euglenophytes, Pyrrophytes, Chlorophytes and Xanthophytes) and size classes (Pico: <2 μm; Nano: 2–20 μm; Micro: >20 μm) were estimated. Chlorophyll *a* biomass was measured by fluorometry after filtration on GF/F filters and extraction by 90% acetone (Holm-Hansen et al., 1965). The contribution of each size class to total chlorophyll biomass was determined by filtering lake water through 3 μm PoreticsJ polycarbonate membrane filters (Pico) or a net of 20-μm mesh size (Pico-plus Nano-) before filtration on GF/F filters. Chlorophyll *a* in nano- and microphytoplankton size classes was estimated by difference.

Zooplankton

Zooplankton (triplicate samples) were collected with a Rodhe-Aberg 5L sampler. Triplicates were then pooled and filtered on a plankton net of 63 μm mesh size. Zooplankton was anaesthetized with carbonated water and preserved in 4% buffered formaldehyde. At station P1, triplicate samples of 15 l were also collected at three depths (epilimnion: 5 m; metalimnion: 14 m; hypolimnion: 28 m) to evaluate zooplankton sampling variance. In the laboratory, zooplankton was concentrated in 20-ml scintillation vials and fixed with glycerol ethanol 70%. Zooplankton species were sorted, sized and counted on 5–10 ml subsamples. We estimated the abundances of species and taxonomic groups (Cladocera, Cyclopoida, Calanoida, Rotifera, Nauplii) and size classes (Micro: <200 μm; Meso: 200–500 μm; Macro: >500 μm). Zooplankton abundance was expressed as ind. l^{-1}, and converted to dry-weight biomass (d.w. mg m^{-3}) by measuring individual length and using length–dry weight relationships for crustaceans or geometric formula for rotifers (Gophen, 1978).

Fish echosounding

As an additional environmental variable, fish abundance was estimated from an echosounding survey concomitant with the synoptic zooplankton sampling program. Fish abundance was determined by 10–15 min acoustic survey tracks made parallel to the shore at each station using a Simrad equipment (70 kHz EY-M Scientific Echosounder) (Walline et al., 1992). Vessel speed during acoustic transects was 4.5–5.0 knots. The first 3 m of the echograms were discarded because of surface interference (e.g. waves). Because computer recording was not made *in situ*, fish abundance at each depth and station was qualitatively estimated by counting targets on the echograms over the distance between two stations, and ranking the counts in ascending order of abundance classes from 0 to 5. Because we did not operate the hydroacoustic data recording, we could not determine the size of the fish from target strength signals.

Statistical analysis

First, correlation analysis (*r* Spearman) was used to detect collinearity among environmental variables, and the strongest interactions between environmental and zooplankton variables (Sokal & Roff, 1995). Based on these correlations, we retained 12–13 factors (temperature, oxygen, picocyanobacteria, ciliates, heteroflagellates, mixoflagellates, total chlorophyll *a*, all phytoplankton variables) as the most representative of the environmental heterogeneity to be included in principal component analysis (PCA). Four PCA analyses were done on the correlation matrices based on zooplankton abundance or biomass data, and considering either taxonomic or size classes of the phytoplankton and zooplankton. All the analyses were performed using SYSTAT 5.0 (Wilkinson, 1992) and the 'R package' of Legendre & Vaudor (1991).

Results and discussion

Abiotic and biotic environmental gradients

Lake Kinneret was well stratified at offshore stations (P1, SL2), and well mixed throughout the water column at nearshore stations (SL1, L2, L1) (Fig. 2). The highest variations in abiotic factors was observed on the vertical axis of the lake in the offshore stations. In contrast, horizontal varia-

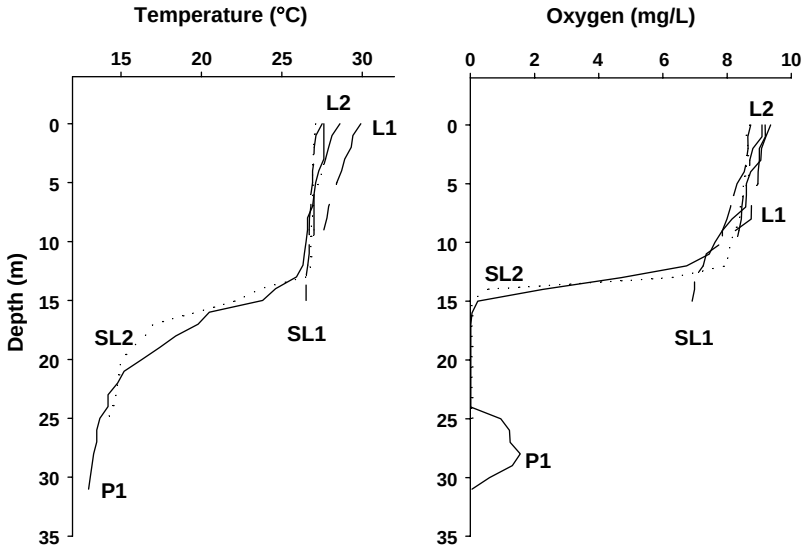

Figure 2. Vertical profiles of water temperature and oxygen concentrations at the different stations along the nearshore–offshore transect.

tions in temperature and oxygen concentrations in the epilimnion from nearshore to offshore was weak (27.1–29.9 °C, and 8.7–9.35 mg l^{-1}, respectively). Secchi depth varied from 3.5–3.7 m offshore to 2.5–3.3 m nearshore, and the euphotic depth was of 5–6 m at all stations. Water pH varied from 7.6 to 8.7; the higher values being found at 5–10 m and the lowest in the hypolimnion (20–28 m). Water conductivity ranged from 947 to 1060 μS cm^{-1}, and increased in the anoxic hypolimnion.

Overall, wide variations in phytoplankton density and biomass were evident over the vertical profiles and the horizontal transect (Table 1); maximum density occurred in the epilimnion, at 5 m (Fig. 3). Phytoplankton size structure was characterized by a dominance of nanoplanktonic algae (81%), as observed during the summer stratification period in Lake Kinneret (Pollinger & Berman, 1977, 1982; Berman et al., 1992). Picoplanktonic algae accounted for 18% of total phytoplankton abundance, whereas microplanktonic algae represented less than 1% in numbers. The most important phytoplankton groups numerically were the Cyanophytes (55%), Chlorophytes (25%) and Diatoms (14%), whereas the Dinophytes, included in the microphytoplankton, were sparse in numbers but comprised most of the biomass (83%) due to their large size (Table 1).

Chlorophyll *a* biomass varied greatly over vertical and horizontal nearshore–offshore distances (Table 1), with micro- and nano-size fractions accounting for most of the total Chlorophyll *a* (67 and 29%, respectively). The highest biomass of Chlorophyll *a* was found between 5 and 14 m, with maximum values at 14 m (Fig. 3). This peak was explained by a high concentration of Chlorophyll *a* in the micro-size fraction (48 mg m^{-3}) and the highest abundance of the dinoflagellate *Peridinium gatunense* (334 cells ml^{-1}) (data not shown).

Picocyanobacteria density and biomass varied widely, especially with depth (Table 1, Fig. 3). Peak abundances were observed in the epilimnion (1–10 m); densities decreased in the metalimnion (14 m), and were low in the hypolimnion (20 m) as reported over the summer season by Malinsky-Rushansky et al. (1995).

Relatively to phytoplankton, ciliates were low in numbers (Table 1), and were most abundant in the epilimnion (Fig. 3). Heterotrophic flagellates were three times more abundant than the mixotrophic flagellates (Table 1), but were distributed relatively evenly throughout the water column above the thermocline, whereas mixotrophic flagellates increased vertically to a peak abundance at 10 m in the epilimnion before declining again (Fig. 3). Similar ranges in ciliate and nanoflagellate

Table 1. Total variations in biomass of chlorophyll *a*, and abundance of microbial components, and phytoplankton groups and size classes in Lake Kinneret on 6–7 July 1992

Biotic Factors	Abundance		Biomass	
	Mean ± SD	Ranges	Mean ± SD	Ranges
Chlorophyll *a* total (mg m^{-3})			11.1 ± 10.9	1.3–50.7
Micro: >20 μm (mg m^{-3})			7.4 ± 10.6	0.1–48.2
Nano: 2–20 μm (mg m^{-3})			3.3 ± 2.2	0.2–11.2
Pico: <3 μm (mg m^{-3})			0.2 ± 0.1	0.02–0.38
Picocyanobacteria (cells × 10^3 ml^{-1} or $\mu g \times 10^3$ ml^{-1})	154 ± 81	2.9–220	647 ± 338	12–1047
Ciliates*	3.8 ± 3.6	0–13	20 ± 23	0–45
Heteroflagellates*	82 ± 77	0–257	1.2 ± 1.3	0–4.4
Mixoflagellates*	25 ± 30	0–110	0.4 ± 0.6	0–2.3
Phytoplankton (cells × 10^3 ml^{-1} or $\mu g \times 10^3$ ml^{-1})	10.5 ± 8.6	0.9–41.7	10.8 ± 8.5	0.9–33.1
Composition				
Cyanophytes	5.8 ± 7.7	0.03–35	0.2 ± 0.5	0–2.2
Cryptophytes	0.4 ± 0.2	0.1–1.1	0.14 ± 0.1	0.04–0.4
Diatoms	1.5 ± 0.7	0.1–2.7	0.36 ± 0.26	0.02–0.84
Dinophytes	0.1 ± 0.08	0.02–0.25	8.9 ± 8.0	0.5–31.4
Chlorophytes	2.6 ± 1.3	0.5–4.9	1.1 ± 0.6	0.1–2.6
Size classes				
Micro: >20 μm	0.1 ± 0.08	0.03–0.3	8.9 ± 8.1	0.5–31.4
Nano: 2–20 μm	8.5 ± 7.8	0.7–37.4	1.9 ± 0.9	0.3–4.4
Pico: <3 μm	1.8 ± 1.3	0.05–4.1	0.002 ± 0.004	0.001–0.016

*Cells ml^{-1} or μg ml^{-1}.

numbers were reported by Hadas & Berman (1998), who also observed maximum abundances of ciliates in the epilimnion.

Fish distribution was typical for daytime with a contagious distribution of fish in shoals in the epilimnion and metalimnion (Fig. 4). At night, the shoals break down and the fish redistribute more evenly (J. Easton, pers. comm). Offshore, between station P1 and SL2, the echogram showed a few small schools in the epilimnion, and a few large fish sitting in the metalimnion or at the bottom (Fig. 4). The prevalence of fish above 15 m is attributable to the fact that Lake Kinneret is typically anoxic below the thermocline (Walline et al., 2000). Between stations SL2 and SL1, the number of shoals of fish at the thermocline depth increased. Nearshore (between stations L1 and L2) echograms showed much larger concentrations of fish shoals close to the surface. The nearshore distribution is typical of that of Kinneret fingerling sardine (*Acanthobrama terraesanctae*, previously *Mirogrex terraesanctae*) which are almost exclusively zooplanktivorous (Landau et al., 1988; Gophen & Threlkeld, 1989; Walline et al., 2000). In general, echograms indicated an increase in fish abundance from offshore to nearshore stations. They also suggest that fish favour oxygenated waters as deep as possible, except in the nearshore shallow water where the fish were very close to the surface and in large numbers. Using the same equipment, and estimating the fish numbers with HADAS, a

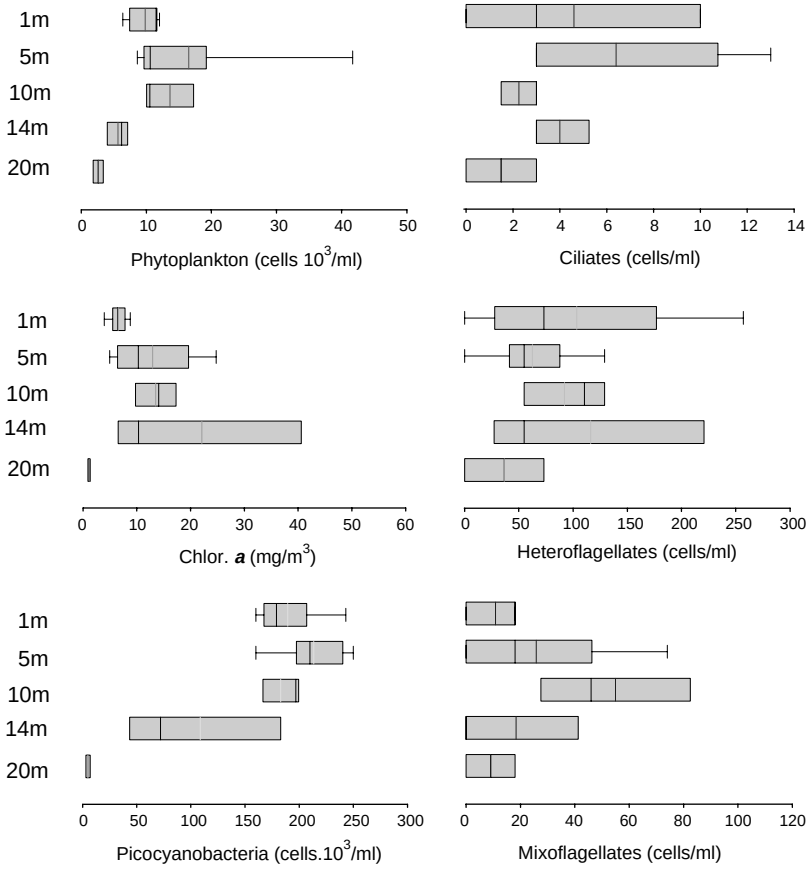

Figure 3. Variations in biotic environmental factors (Box-plots: median and quartiles): density of total phytoplankton (cells 10^3 ml^{-1}), chorophyll *a* biomass (mg m^{-3}), densities of picocyanobacteria (cells 10^3 ml^{-1}), ciliates (cells ml^{-1}), heterotrophic flagellates (cells ml^{-1}), and mixotrophic flagellates (cells ml^{-1}).

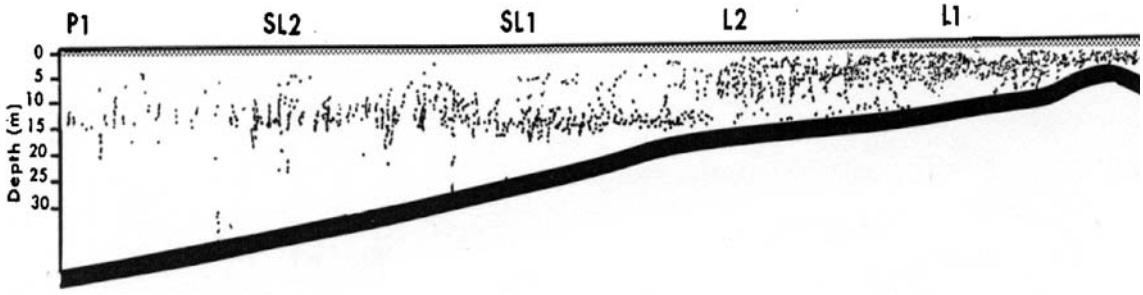

Figure 4. Fish echograms at each station along the nearshore–offshore transect.

newly developed echo-counting computer analysis system, Walline et al. (1992, 2000) estimated that fish stocks of the Kinneret sardine (*Acanthobrama terraesanctae*) varied from 61 to 218 million from 1988 to 1990, and that the population is composed of two cohorts of large (>12 cm) and small (<12 mm) fish. Over the whole lake, previous acoustic surveys conducted at night during December 1990 and February–March 1991 (Kalikman et al., 1992; Yacobi et al., 1993) also indicated highest fish densities in the western part of the lake and nearshore.

Table 2. Total variations of zooplankton groups and size classes in Lake Kinneret on 6–7 July 1992

Zooplankton	Abundance		Biomass	
	Mean ± SD (Nb l^{-1})	Ranges (Nb l^{-1})	Mean ± SD (d.w. mg m^{-3})	Ranges (d.w. mg m^{-3})
Composition				
Total	94.8 ± 74.1	4.8–266.6	24.4 ± 22.3	0.1–65.1
Rotifera	22.7 ± 22.6	0.6–53.7	0.4 ± 0.3	0.01–1.0
Cladocera	25.5 ± 23.4	0.1–82.7	13.2 ± 12.1	0.06–39.4
Calanoida	0.2 ± 0.3	0–1.2	0.5 ± 0.8	0–3.0
Cyclopoida	26.3 ± 25.8	0.7–88.6	10.1 ± 10.4	0.02–34.6
Nauplii	20.1 ± 20.4	0.5–93.0	0.3 ± 0.2	0.01–0.8
Size classes				
Macro: >500 μm	14.3 ± 14.5	0–49.0	6.7 ± 7.6	0–28.2
Meso: 200–500 μm	42.6 ± 41.4	0.3–148.5	17.3 ± 16.4	0.1–57.8
Micro: <200 μm	42.4 ± 35.4	1.3–111.8	0.4 ± 0.3	0.03–0.89

Zooplankton community and distribution patterns

Along the horizontal transect, total abundance and biomass of zooplankton (at all depths) varied from 5 to 267 ind. l^{-1}, and 0.1 to 65 d.w. mg m^{-3}, respectively. The corresponding mean density and biomass was 95 ind. l^{-1} and 24 d.w. mg m^{-3} (Table 2). Variation between zooplankton triplicate samples ranged from 16 to 63%. Cyclopoids (including nauplii) were numerically dominant (49%), followed by cladocerans (27%) and rotifers (24%), whereas calanoids were of minor importance (0.25%). Consequently, small size fractions (micro-and meso-zooplankton) were the most frequent (42% for each size fraction), while macrozooplankton only accounted for 14% of zooplankton density. Cladocerans (54%) and copepod cyclopoids (41%) were co-dominant in terms of biomass, and the small zooplankton (rotifers, nauplii) and the calanoids were of minor importance (1–2% of total biomass). Consequently, the meso- (71%) and macrozooplankton (27%) comprised most of the biomass. Rotifera comprised 16 species, with *Conochilus* sp., *Keratella valga*, *K. cochlearis*, *Asplanchna priodonta* and *Polyarthra* sp. as the most abundant species. Cladocera included three species: *Bosmina longirostris*, *Ceriodaphnia* sp., and *Diaphanosoma brachyurum*, the bosmid accounting for 50% of total cladoceran numbers. *Eudiaptomus vulgaris* was the unique calanoid species encountered in few numbers. Among the cyclopoids, *Mesocyclops ogunnus* and *Thermocyclops dybowskii* were found in similar abundances. In general, zooplankton composition, size structure and abundance observed in this survey are similar to those reported in earlier studies (Berman et al., 1972; Gophen, 1978, 1979, 1988; Gophen et al., 1990).

The vertical and horizontal distribution of zooplankton groups and size fractions, in terms of density is presented in Figure 5. The patterns in terms of biomass were very similar, and are thus not presented. In terms both of taxonomic groups and size fractions, zooplankton were concentrated between 5 and 15 m in the epilimnetic and metalimnetic water layers. Few zooplankters were observed near the surface (1 m) or in the hypolimnion (below 20 m). Gophen (1978, 1979) also found zooplankters restricted to the epilimnetic and metalimnetic layers during summer stratification. However, in this study we observed two vertically distinct peaks at site P1: an upper peak at 5–7 m, especially for the cladocerans, and a deeper peak at 14 m for the nauplii and cyclopoid copepods. Zooplankton groups and size classes also showed different horizontal distributions along the nearshore–offshore gradient. Cladocerans and cyclopoids represented respectively by the macro- and meso-zooplankton, were more abundant offshore in the pelagic (P1) and sublittoral (SL2–SL1) stations. In contrast, rotifers, included in the microzooplankton, were more evenly spread

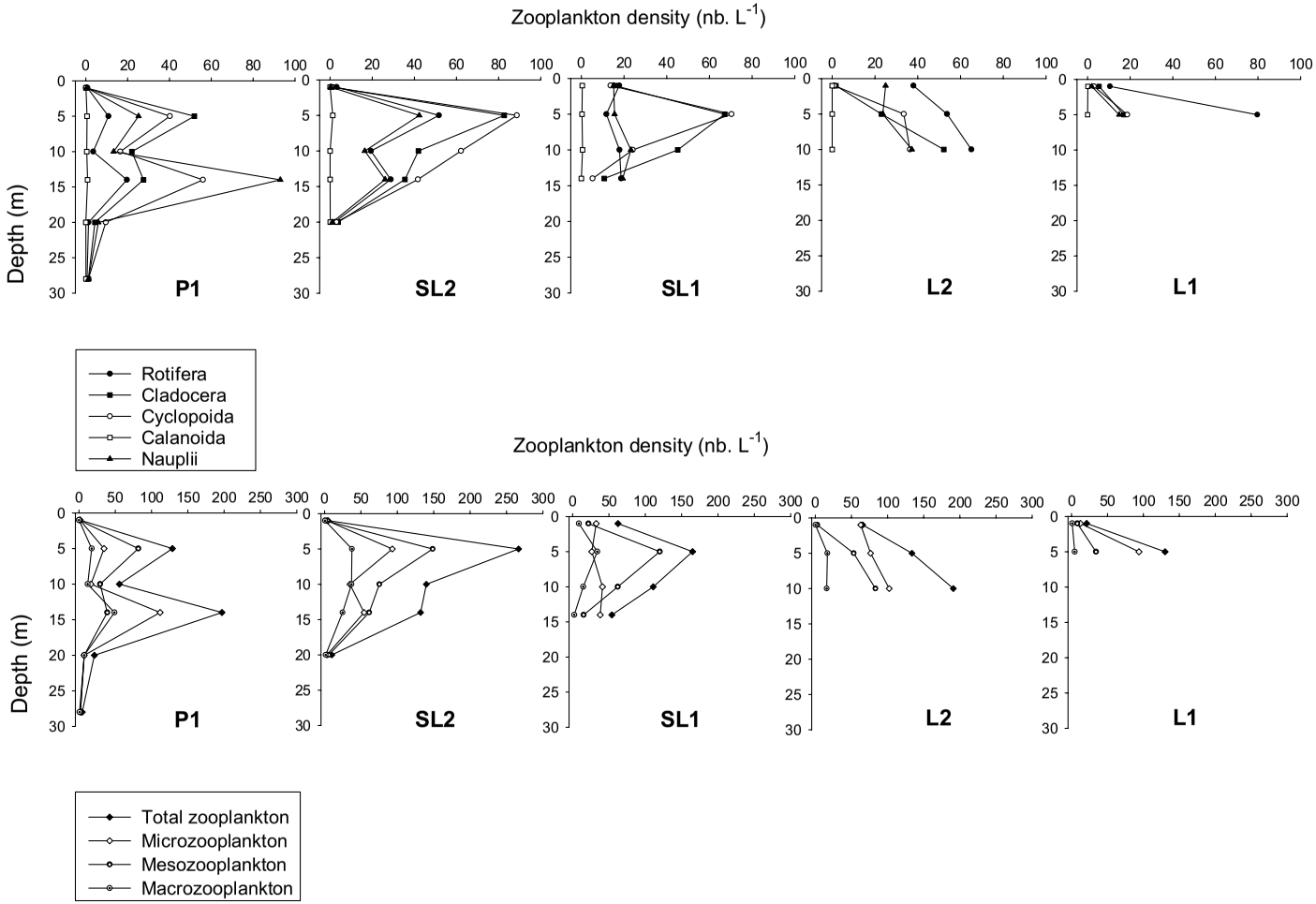

Figure 5. Depth and horizontal variations in the density of zooplankton taxonomic groups (Rotifera, Cladocera, Cyclopoida, Calanoida, Nauplii) (upper graph), and total zooplankton and size classes (macro: >500 μm, meso: 200–500 μm, micro: <200 μm) (lower graph).

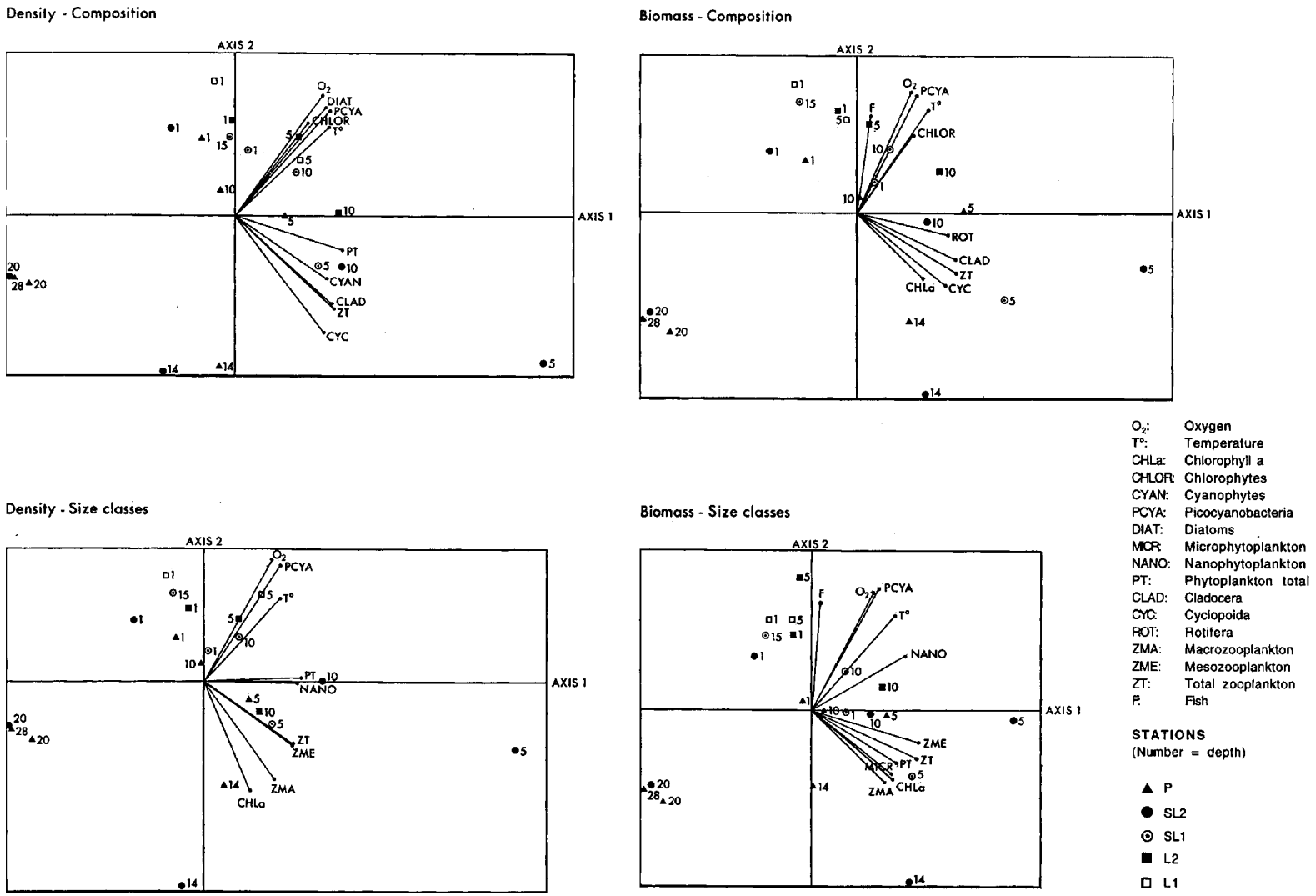

Figure 6. PCA ordinations of environmental variables and sampling stations, based on the density or biomass of zooplankton taxonomic groups (Rotifera, Cladocera, Cyclopoida, Calanoida), and size classes (macro: >500 μm, meso: 200–500 μm, micro: <200 μm). Arrows indicate vectors of environmental descriptors. The angles between vectors correspond to the strength of the correlation between the environmental variables. Axis 1 and Axis 2 are the first two principal components of the PCA ordination, representing the main environmental gradients. Numbers and symbols indicate the station and the depth of sampling.

throughout the horizontal transect, with generally higher numbers nearshore at the littoral stations L1 and L2 (Fig. 5). In general, the vertical and horizontal distribution of zooplankton described in this study is consistent with previously observed patterns. Over the whole-lake spatial scale (20×12 km), zooplankton abundance also increased along the west–east transverse gradient (Kalikham et al., 1992). The rotifer distribution pattern may be due to the fact that small rotifers are less vulnerable than crustaceans to predation by the Kinneret sardine which was very abundant near the western shoreline of the lake (Landau et al., 1988; Gophen & Threlkeld, 1989). In contrary, the meso- and macrozooplankton predominant in the pelagic and sublittoral stations, are dominant prey of the Kinneret sardine, which comprised more than 80% of fish numbers. Walline et al. (2000) showed that the potential consumption of zooplankton by this fish is greater during June. Their model simulations calculated potential consumption of zooplankton at 384 tons d^{-1}, representing 53% of the daily production of zooplankton.

Relationships between environmental factors and zooplankton distribution

In all PCA ordinations, a similar characteristic pattern of trajectories for the environmental and zooplankton variables and the positions of the stations was defined. Two main environmental gradients were detected along the two first PCA axes: (1) the vertical gradient along the axis 1, and (2) the horizontal nearshore–offshore gradient along the axis 2 (Fig. 6). Since the first axis explained one-third (32–39%) of the total variance in environmental and zooplankton variables, vertical environmental gradients had the greater influence on the distribution pattern of zooplankton during summer stratification. Most of the zooplankton variables (Rotifera, Cladocera, Cyclopoida, meso and macro-size fractions), Chlorophyll *a* biomass, and some phytoplankton variables (mainly the Cyanophytes, and the micro- and nano-phytoplankton) have positive loadings on PCA axis 1. This axis represents a decreasing gradient with depth in food resources that is associated with the decrease in zooplankton abundance and biomass. Indeed, the extreme position of the 5-m depth at station SL2 in the lower right quadrants is typical of the epilimnetic peak in Chlorophyll *a* biomass, rotifer density, and Cladocera and Cyclopoida biomass. In contrast, hypolimnetic stations (20– and 28-m depths) with low Chlorophyll *a* biomass, phytoplankton and zooplankton abundance, were positioned at the extremes in the lower left quadrant. The stations in the surface layer (1 m), with low zooplankton and Chlorophyll *a* biomass, had negative loadings on the first axis, but were positioned on the upper left quadrant because of higher temperature and oxygen concentration. The PCA axis 2 explained 17–22% of the total variance in environmental and zooplankton variables. Axis 2 represents the horizontal gradient. It discriminated the littoral stations L1 and L2, with slightly higher temperature and oxygen concentrations, higher density or/and biomass of picocyanobacteria, chlorophytes and diatoms, from the sublittoral (SL1 and SL2) and pelagic (P1) stations. At the extreme negative end of axis 2, we found the metalimnetic depth (14 m) of the offshore stations (P1 and SL2), richer in zooplankton, but cooler and less oxygenated. When considering PCA ordinations based on biomass data, fish abundance was also an important factor positively related to the offshore–nearshore environmental gradient (PCA axis 2). However, fish abundance showed only weak negative correlation with macrozooplankton biomass (r Spearman $= -0.164$). No significant relationships were found between protozoan and zooplankton variables. However, higher abundance of ciliates was associated with higher Chlorophyll *a* biomass, and higher zooplankton biomass (data not shown).

Our short-term survey indicated that vertical and horizontal distribution of zooplankton during summer stratification in Lake Kinneret is primarily influenced by the physicochemical stratification in the pelagic zone. Secondly, horizontal gradients in abiotic factors (higher temperature and oxygen concentration in the littoral zone), food resources (picocyanobacteria, chlorophytes, diatoms) and planktivores (fish abundance) discriminated the nearshore and offshore stations. However, zooplankton variables and environmental variables related to the nearshore–offshore gradient (axis 2) were only weakly correlated, as shown by their orthogonal trajectories in the PCA ordinations. In previous multidisciplinary surveys of plankton and

fish horizontal distribution conducted over the whole-lake scale, similar and divergent relationships were found between zooplankton and environmental gradients. During a first survey conducted at night in December 1990, zooplankton density was positively related to temperature gradients, and concentrated in the littoral zone in the eastern and south-eastern parts of the lake. Copepod density was higher in the western part of the lake and negatively related to fish density (Kalikham et al., 1992). However, during the second survey carried out in February–March 1991 at lower temperature (14–15 °C), the horizontal distribution of zooplankton was governed by physical conditions and not by fish planktivory (Yacobi et al., 1993). The lack of strong linkages between macrozooplankton and fish distribution in our study might also be explained by the qualitative estimation of fish abundances. Based on fish echograms and macrozooplankton horizontal patterns of distribution, it seemed that the fish distribution pattern was effectively inverse to that of the macrozooplankton. Comparisons between spatial surveys at different scales are difficult. Sampling procedures may also account for certain observed discrepancies. In our small-scale survey, we collected zooplankton at 5 m depth intervals throughout the water column at daytime whereas in the large-scale surveys, zooplankton was collected at night only at 2 m depth, were they should have their peaks of abundance. Moreover, Yacobi et al. (1993) emphasized the principle that relationships between pelagic organisms and controlling environmental variables are not spatially continuous and temporally stable, but will change with sampling scale, along seasons, and with meteorological conditions. Our study emphasized also the importance of paying attention to zooplankton functional categories based on size to evaluate the relationships between abiotic and biotic environmental gradients and the zooplankton spatial distribution over depth and from nearshore to offshore zones. Our study suggests that the relative effect of abiotic and biotic factors may vary with scale of observation (i.e. vertical or horizontal scales), and also with the functional zooplankton group considered (size classes and related taxonomic groups). It may also be relevant to recognize that vertical (Diel Vertical Migration) and horizontal dispersion patterns can be very dynamic, with the extent of dynamic change influenced by size on life history stage (Hart, 1978; Hart & Allanson, 1976).

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