Chapter 13
Metazoan Zooplankton

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Abstract The Lake Kinneret metazoan zooplankton has been monitored since 1969 and currently includes the enumeration of 31 species of cyclopoids, cladocerans, and rotifers in samples collected fortnightly at five stations from around the lake. The zooplankton community has exhibited notable interannual and long-term variation since the start of the monitoring program that have included a decline in community size from the 1970s and 1980s to an extended period of low abundance and biomass in the 1990s followed by an increase during the first decade of the millennium. Along with the increase in abundances since the late 1990s, there has been an increase in interannual variation, which may be related to the unstable phytoplankton population and/or to the large changes in lake level. The introduction of an additional sampling protocol since 2003 has highlighted the highly vertically aggregated nature of some of the rotifer species often found in very high densities near the thermocline. Seasonally, the lowest densities are found during the summer and the highest during the winter–spring. There is no indication of vertical migration by zooplankton in the lake. The zooplankton are patchily distributed and repeated sampling indicates that abundance estimates collected over a period of a year could vary by a factor 2–3 just due to fine-scale patchiness. Zooplankton in the lake play an important role as key nutrient recyclers with microzooplankton accounting for $>85\%$ of the daily mineralization of P and N in the lake.

Keywords Grazing · Herbivorous · Predatory · Vertical migration · Nutrient recycling

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13.1   Taxonomic Background

The Lake Kinneret metazoan zooplankton (zooplankton hereafter) species can be divided taxonomically into three major groups: two orders representing the subphylum Crustacea (Copepoda, Cladocera) and the class Monogonata representing the phylum Rotifera. The copepods have been represented in the past by up to 6 species (Gophen and Azoulay 2002), the cladocerans by 8 species, and the number of rotifer species has been reported to range between 10 and 35 (Gophen 2005). Currently, 2 cyclopid species, 8 cladoceran species, and 21 rotifer species are routinely collected as part of the ongoing lake monitoring program (Chap. 32). Zooplankton can also be separated according to two basic functional groups: predators (adult copepods, some rotifers) and grazers. The grazers can be further divided into macro-grazers (cladocerans and juvenile copepods) and micro-grazers (mostly rotifers and copepod nauplii). Note that protozoan zooplankton, i.e., ciliates and flagellates, are excluded from the microzooplankton in this chapter due to a lack of long-term information. Nevertheless, ciliates and flagellates are covered elsewhere (Chap. 14).

Table 13.1 lists the species routinely monitored and their groupings according to functional group.

Sampling The ongoing monitoring of zooplankton in the lake is based on two sampling approaches. The first approach, termed "mix sampling," has undergone only minor changes since the initiation of the monitoring program in 1969 to date, i.e., more than 42 years of a near-consistent sampling protocol, while the second, "profile sampling," was started in 2003. The mix sampling is conducted at five fixed pelagic stations (A, D, G, H, K, see locations in Fig. 32.1, Chap. 32). At each station, 1 L of water is collected using a 5-L Rodhe sampler from each of up to 12 depths, the water samples from the different depths are mixed in a bucket from which 0.8 L is extracted and preserved. Until 2003, all samples were treated, fixed, and preserved in formaldehyde. Since then, however, samples collected are stored on board in sodium bicarbonate-citric acid, transferred at the laboratory to formaldehyde, for fixing, for 24–48 h, and then transferred to 70 % ethanol + 1 % glycerin for preserving.

The mix sampling provides a good overall picture of the zooplankton assemblage but suffers from two main shortcomings. The first is the lack of information on the vertical distribution of the organisms and, the second, is the relative large error associated with species that are either rare or highly aggregated at a certain depth. The small volume of water sampled and analyzed increases the probability of error associated with abundance estimates of rarer species. In order to address these shortcomings, the profile sampling protocol was initiated in 2003 (Hambright and Gal 2004). According to the profile sampling protocol, samples are collected from up to nine depths during the non-stratified periods (1, 3, 5, 7, 10, 15, 20, 25, 33 m). During the stratified periods, samples are collected down to the thermocline with additional samples being collected at 1 m above, within, and 1 m below the thermocline, as with the mix sampling. Moreover, these samples are collected using a 10-L sampler, in which the entire 10 L are filtered through a 63-μm-mesh net, thus reduc-

Table 13.1 List of zooplankton categories (species and life stages or relative size) monitored routinely as part of the Kinneret monitoring program, and associated functional group: predatory (P), and grazers which are separated into macrozooplankton grazers (Ma) and microzooplankton grazers (Mi). Also provided is a list of the mean lengths (and SD) of copepod and cladoceran species based on measurements conducted since 2007 using the Planktometrix software. (Hambright 2008)

Species-developmental stage	Taxonomic grouping	Functional group	Mean length (μm)	SD	Sample size
Cyclops sp. NI–NVI	Copepoda	Mi	145.8	38.6	123,914
Mesocyclops ogunnus CI	Copepoda	Ma	272.1	29.0	8,013
Mesocyclops ogunnus CII	Copepoda	Ma	316.1	17.2	6,108
Mesocyclops ogunnus CIII	Copepoda	Ma	366.8	25.2	9,147
Mesocyclops ogunnus CIV	Copepoda	Ma	447.6	33.7	9,395
Mesocyclops ogunnus CV-male	Copepoda	P	475.3	34.6	667
Mesocyclops ogunnus CV-female	Copepoda	P	565.0	52.0	6,304
Mesocyclops ogunnus CVI-male	Copepoda	P	545.0	48.7	4,547
Mesocyclops ogunnus CVI-female	Copepoda	P	723.9	78.5	2,762
Mesocyclops ogunnus CVI-female with eggs	Copepoda	P	752.8	96.9	321
Thermocyclops dybowski CI	Copepoda	Ma	268.5	26.6	6,694
Thermocyclops dybowski CII	Copepoda	Ma	313.8	17.0	4,057
Thermocyclops dybowski CIII	Copepoda	Ma	364.9	23.5	7,564
Thermocyclops dybowski CIV	Copepoda	Ma	434.2	32.7	6,809
Thermocyclops dybowski CV-male	Copepoda	P	447.2	29.1	2,623
Thermocyclops dybowski CV-female	Copepoda	P	494.2	42.7	2,284
Thermocyclops dybowski CVI-male	Copepoda	P	498.4	34.5	4,591
Thermocyclops dybowski CVI-female	Copepoda	P	571.2	46.8	4,308
Thermocyclops dybowski CVI-female with eggs	Copepoda	P	567.6	40.6	851
Diaphanosoma brachyurum-small	Cladocera	Ma	331.7	58.9	1,593
Diaphanosoma brachyurum-large	Cladocera	Ma	602.3	135.6	5,585
Bosmina longirostris typica-small	Cladocera	Ma	251.5	28.7	5,007
Bosmina longirostris typica-large	Cladocera	Ma	338.3	40.0	3,642
Bosmina longirostris cornuta-small	Cladocera	Ma	262.7	29.8	369

Table 13.1 (continued)

Species-developmental stage	Taxonomic grouping	Functional group	Mean length (μm)	SD	Sample size
Bosmina longirostris cornuta-large	Cladocera	Ma	350.8	38.5	2,662
Ceriodaphnia reticulata-small	Cladocera	Ma	260.3	34.2	5,130
Ceriodaphnia reticulata-large	Cladocera	Ma	373.4	57.3	8,216
Ceriodaphnia rigaudi-small	Cladocera	Ma	253.4	26.1	1,296
Ceriodaphnia rigaudi-large	Cladocera	Ma	386.9	62.4	3,578
Ceriodaphnia pulchella-large	Cladocera	Ma	145.0	239.6	3
Chydorus sphaericus-small	Cladocera	Ma	219.8	18.0	538
Chydorus sphaericus-large	Cladocera	Ma	293.0	36.3	996
Moina rectirostris-small	Cladocera	Ma	339.1	45.7	191
Moina rectirostris-large	Cladocera	Ma	536.7	99.5	656
Asplanchna brightwelli	Rotifera	P	–	–	–
Asplanchna priodonta	Rotifera	P	–	–	–
Synchaeta oblong	Rotifera	Mi	–	–	–
Synchaeta pectinata	Rotifera	Mi	–	–	–
Polyarthra remata	Rotifera	Mi	–	–	–
Hexarthra sp	Rotifera	Mi	–	–	–
Brachionus sp1	Rotifera	Mi	–	–	–
Trichocerca stylata	Rotifera	Mi	–	–	–
Collotheca sp.	Rotifera	Mi	–	–	–
Anuraeopsis fissa	Rotifera	Mi	–	–	–

NI–NVI represent nauplii stages 1–6 and CI–CVI represent copepodid stages 1–6

P predatory, *Ma* macrozooplankton grazers, *Mi* microzooplankton grazers, *SD* standard deviation

ing the error associated with rarer species. Species-specific densities typically range from tens and up to hundreds of individuals per liter. Furthermore, most, or even the entire sample is counted, reducing error even further, especially for the rare species in the sample. Nevertheless, species occurring at densities of 1–2 individuals per 10 L or less are likely to be underrepresented, resulting in a bias in our description of the species assemblage but having no effect on zooplankton biomass estimates.

Zooplankton enumeration and biomass estimation on both "mix" and "profile" samples are conducted as described by Gophen (2005) and by Gal and Anderson (2010). Since the start of the profile sampling in 2003, only station A mix samples have been analyzed routinely. Zooplankton biomass is estimated based on the application of species-specific conversion factors to wet weight (Gophen 1978; Gophen 2005).
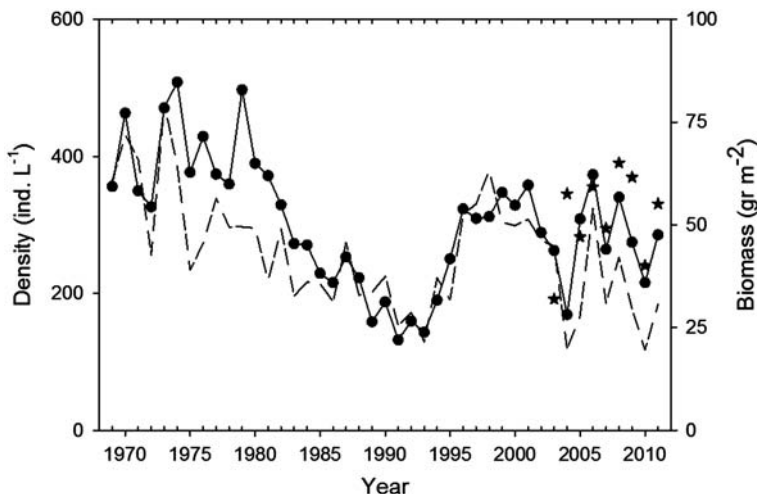
Fig. 13.1 Long-term record of annual mean total zooplankton biomass (*dashed line*) and density based on mix (*black circles, solid line,* 1969–2011) and profile (*stars,* 2003–2011) sampling from station A

13.2 Temporal Dynamics: Interannual Patterns

The Lake Kinneret zooplankton have exhibited large interannual variation since 1969 (Gophen 2003; Hambright 2008; Gal and Anderson 2010), and the total zooplankton density can be divided into three distinct periods (Fig. 13.1). Total densities were stable through to 1980 with mean annual values ranging between 326 and 508 ind. L^{-1} and a multiannual mean of 408 ind. L^{-1}. Between 1980 and 1993, there was a marked decrease in zooplankton density in the lake reaching a minimum of 132 ind. L^{-1} in 1991. Since 1996, however, the zooplankton have maintained a relatively moderate mean density (295 ind. L^{-1}) with a high degree of variability with $>2\times$ difference between the minimum (2004) and maximum (2006) mean annual values. The wet weight biomass dynamics largely mirrors the changes in abundances except for the period 1975–1982, during which the biomass did not demonstrate a period of elevated values. As the biomass is not directly measured as part of the monitoring program but rather estimated via constant species-specific conversion factors, we predominantly use abundance in the remainder of this chapter. Further information on the relative changes in biomass and density during 1970–2002 can be found in Hambright (2008).

The long-term dynamics in the zooplankton density was accompanied by changes to the relative contribution of the various groups (Fig. 13.2). Copepod contribution to the total zooplankton abundance declined from a mean value of 61 % (1969–1979) to 55 % during 1980–1999 and has maintained a similar level over the past 6 years (2006–2011). During 2001–2003, copepod contribution was at the highest level since 1969 (71–74 % of total abundance); however, these values were
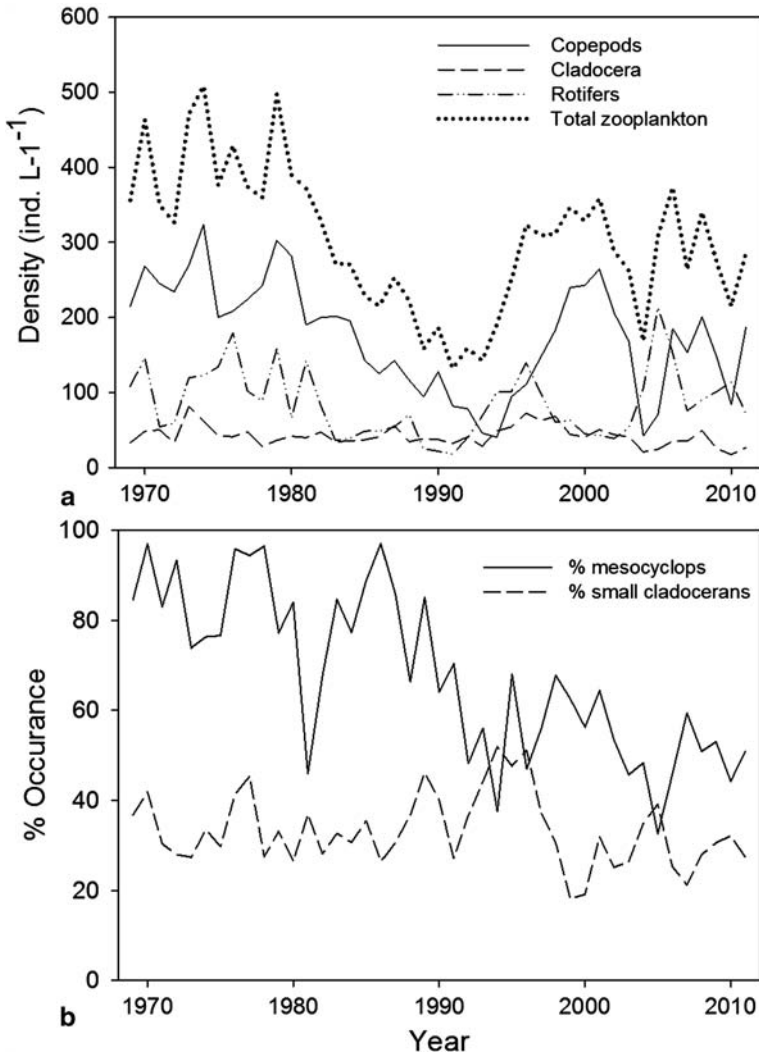
Fig. 13.2 a The annual mean contribution of the three taxonomic groups to total zooplankton density for the period 1969–2011 based on the mix sampling. **b** The annual mean proportion of adult *M. ogunnus* of the total copepod adult density (*solid line*) and of small cladoceran species to total cladocerans (*dashed line*)

followed by the lowest ever (23–25 %) during 2004–2005. These values followed a regime shift that occurred in the copepod population resulting in a significant change to the population characteristics (Gal and Anderson 2010). According to Gal and Anderson (2010), using tools taken from the world of statistics and econometrics, the copepod population shifted, with high probability, to a different regime in 1993 indicated by the major decline in predatory zooplankton in the lake. This observation is in line with additional reports of changes that occurred to the ecosystem

during that period. For example, Roelke et al. (2007) reported the phytoplankton changes in the lake during the mid-1990s as a shift to an alternate state and Zohary (2004) described the large shift away from a very stable and predictable phytoplankton succession pattern to one characterized by large variations in composition and biomass.

Long-term changes in zooplankton species composition, biomass, and other parameters have often been linked to changes in fish predation pressure on the zooplankton (Brooks and Dodson 1965; Carpenter et al. 1987; Galbraith Jr 1967). Body size has frequently been used as an indicator of changes in predation pressure (Mills et al. 1987) and it is therefore insightful to examine long-term changes in density or biomass in the context of composition and body size. And indeed, the decrease in zooplankton abundance and biomass from 1980 to 1993 has been linked to intensified fish predation pressure which led to a decrease in the relative contribution of the larger species and the overall biomass (Hambright 2008). During the period 1980–1999, the copepod contribution to the total zooplankton biomass declined to a mean of 29 % from a mean of 35 % (1969–1975), but has increased since 2006 and averaged 45 % over the past 6 years (2006–2011).

Gophen (1978) reported that during 1969–1975, 90 % of the total copepod biomass consisted of *Mesocyclops ogunnus,* the large body size species. It is therefore interesting to note the consistent decrease in contribution of *M. ogunnus* adults to the total adult cyclopoid population, while the contribution of the smaller species, *Thermocyclops dybowski* increased (Fig. 13.2b, see also, Hambright 2008). The decline of the contribution of the large species was evident even during the period of moderate levels of abundance of zooplankton between 1996 and 2001 reaching a mean value below 50 % in recent years (2006–2011). The lowest value was found in 2005 during which copepods contributed on average only 33 % of the total zooplankton density.

The decrease in copepod contribution to the total zooplankton density has been linked to an extreme increase in the bleak (*Mirogrex terraesanctae*) population resulting in excessive predation pressure on the predatory and herbivorous zooplankton (Gal and Anderson 2010; Ostrovsky and Walline 2000; Zohary and Ostrovsky 2011). Alternatively, Hambright (2008) argues that overharvest of the bleak population resulted in a decrease in mean bleak body sizes (see Hambright and Shapiro 1997), which through allometric scaling of body size and metabolism, resulted in an increase in predation pressure on zooplankton. While both hypotheses have support in the form of indirect evidence, they remain untested and confounded by possible roles of resource availability and competition. Nevertheless, there is little evidence pointing to changes in the resources as a possible explanation for the changes in the zooplankton community. While large changes to the phytoplankton community in the lake have occurred since the mid-1990s (Chap. 10.1), a large portion of the phytoplankton biomass in the lake remain inedible for herbivorous zooplankton (Zohary 2004; Hambright et al. 2007).

The relative annual contribution of small species to the total cladoceran assemblage also changed over time with a marked shift in the interannual variation prior to, and following, 1995 (Fig. 13.2b, see also Hambright 2008). Through to 1995,

the relative mean (standard deviation, SD) contribution of the small cladoceran *Bosmina longirostris* was 35 % (22 %) with a coefficient of variation (CV) of 63 %. Following a large increase during 1994–1996, the contribution of this species decreased to a lower mean level of 31 % but with larger variations and a resulting CV of 78 %. The larger variation since the mid-1990s was also reflected in the total cladoceran abundance (Fig. 13.2a). Peak annual mean cladoceran abundance occurred in 1996 (72.5 ind. L^{-1}) declining to minimum values in 2004 (20.9 ind. L^{-1}) and 2010 (17.3 ind. L^{-1}). Mean annual rotifer contribution to the total zooplankton biomass, for the period 1969–2011, was 9 %, up from the previously reported 7 % (Gophen 1978), though the mean annual values ranged between 2 and 23 %, with peak values occurring during periods of low adult copepod density (Fig. 13.3).

The observed temporal pattern reflected in the profile-based sampling coincides with the trend observed in the mix sampling (Fig. 13.1). Throughout the 9 years of profile sampling, with the exception of only 1 year (2004), there is an overlap in the trends seen in the two sampling protocols. However, in most cases, the profile sampling provides higher estimates of zooplankton density than mix sample-based estimates. This is expected, in part, due to the improved representation of species that tend to congregate at confined depths like rotifers (see below) and rare species. Indeed there is a consistent difference between the two methods which tends to relate to species composition and distribution. Therefore, on dates during which there are large congregations of certain species such as the rotifer *Anuraeopsis fissa* that occurs along the thermocline in extreme densities (thousands per liter) during the fall, there will be large differences between the two methods. In addition, the sampling of a larger volume of water (10 L at each depth vs. 1 L for all depths) reduces some of the effect of variability in the water column (see Sect. 13.4).

Separation of the zooplankton into functional groups can provide additional insight into the assemblage from a food-web perspective. The predatory zooplankton, composed of the adult stages of the two cyclopoid species in the lake, have varied between 8 and 38 ind. L^{-1} with a mean annual value of 21 ind. L^{-1} (Fig. 13.3a). The herbivores, comprised of the cladoceran species and copepodid stages of the cyclopoids, varied in density between 31 and 117 ind. L^{-1} while the mean annual density was 78 ind. L^{-1}. The microzooplankton, consisting of the majority of the rotifers along with the naupliar stages of the cyclopoids, exhibited large variation with densities ranging between 56 and 365 ind. L^{-1}, with a mean annual density over the 43 years, of 190 ind. L^{-1}. Part of the large variation in abundances can be linked to the dramatic decline in predatory zooplankton and the shift from a stable *Peridinium*-dominated phytoplankton community to an unstable cyanobacteria-abundant community that occurred during the mid-1990s (see Chap. 10.1, Gal and Anderson 2010; Zohary 2004) which may have affected some of the foodweb interactions. For example, from 1969 through to the mid-1990s, there was a positive correlation ($r=0.53$) between the copepods and rotifer densities, but from the mid-1990s through to 2011 the correlation was negative ($r=-0.67$, Fig. 13.2). The negative correlation suggests predator–prey interactions between the copepods and rotifers. This may be an outcome of the decreasing contribution of the relatively large adult *M. ogunnus* to the total adult cyclopoid assemblage.
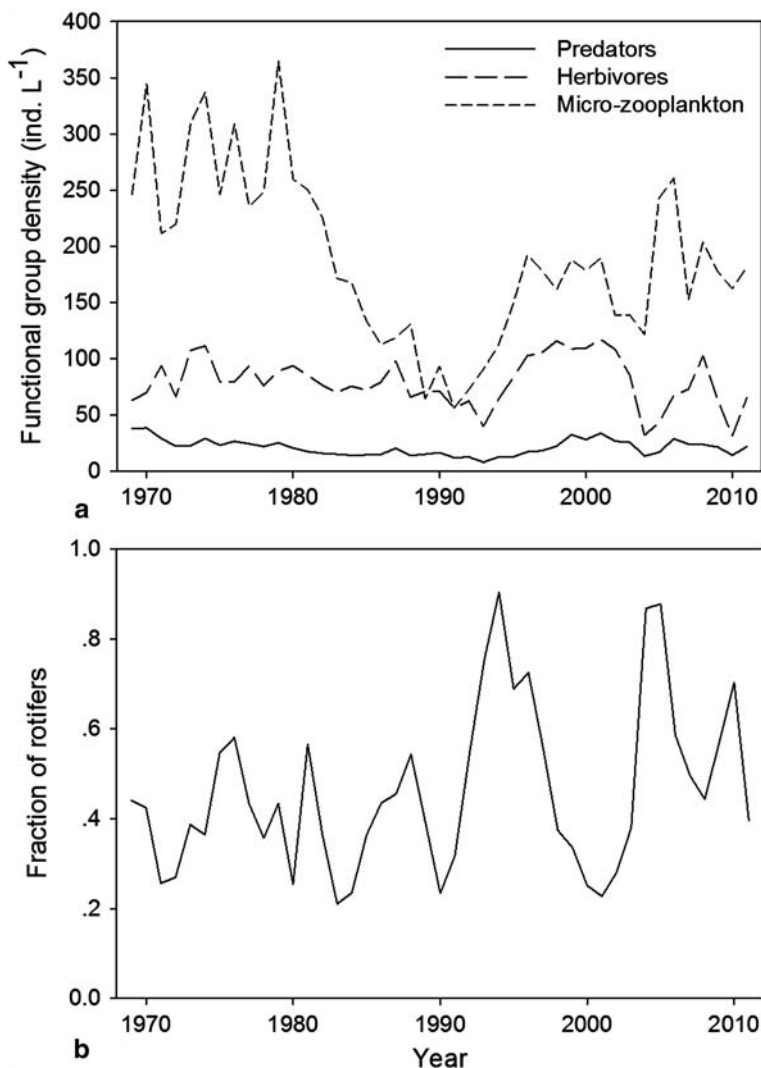
Fig. 13.3 The annual mean contribution of the three functional groups for the period 1969–2011 based on the mix sampling (**a**) and the annual mean relative portion of rotifers of the total micro-zooplankton (rotifers + nauplii) group (**b**)

13.3 Temporal Dynamics: Seasonal Patterns

There are seasonal differences in the distribution of the three taxonomic groups of zooplankton in the lake. Gophen (1978) reported that there was little seasonal variation in the copepod biomass but that cladoceran and rotifer biomass peaked during the winter–spring and was lowest during the summer. Gophen (2005) further

reported that rotifer biomass was typically at its highest during spring (April–May) and was lowest between July and December, with intermediate values in the winter (January–March). The results of the profile sampling conducted between 2003 and 2011 indicate a large degree of variation across the various months for all three groups. While the variation hinders detection of any statistically significant seasonal patterns, it is possible to visually identify a number of trends emerging from the data (Fig. 13.4). The copepod abundance reflected trends of higher values during the winter–spring decreasing toward the summer and intermediate values during the fall. Indeed, during the first half of the year (January–June) the copepod abundance was significantly higher than in the second half of the year ($p < 0.05$, $n = 53$, Mann–Whitney U test). The summer months were also characterized by larger variability than the other months. The cladocerans exhibited a smaller degree of variability with a similar trend, and though not as predominant, of lower values during the summer. The rotifers also exhibited large variations, but there was a clear trend of significantly ($p < 0.001$, $n = 53$, Mann–Whitney U test) higher abundances during January–June with the lowest values occurring during August–November.

13.4 Temporal Dynamics: Fine-Scale Patterns

One of the main characteristic traits of zooplankton communities is their patchy distribution over a wide range of spatial scales (Haury et al. 1978; Pinel-Alloul et al. 1988). Patchy distributions greatly affect the required sampling resources and as a consequence will have implications on the results and conclusions. Only limited information on the patchy distribution of zooplankton in the lake has been reported. Pinel-Alloul et al. (2004) reported variability ranging between 16 and 63 % between triplicates of samples collected at a number of depths on one occasion. Kalikhman et al. (1992) detailed spatial relationships between fish, zooplankton, and abiotic conditions, on a single date, and linked the variability in zooplankton spatial distribution to fish predation pressure. They showed high zooplankton biomass at the center and southeast part of the lake and low biomass in the western and northern parts.

In order to provide additional information on the fine-scale patchiness in the zooplankton distribution in the lake, we conducted a "patchiness study" in which we collected a series of repeated samples over 9 months (Gal and Easton, unpublished data). The sampling included five replicate samples of 10 L collected, from a depth of 5 m at station A, 11 times over a period from March to December 2004. The replicates were collected within minutes of each other between 9:00–10:00 on the day of sampling. Samples were collected using the protocol for "profile" sampling (see above). In the laboratory, the entire sample was counted when possible. Subsampling was used when samples included large quantities of phytoplankton. Samples were enumerated under a dissecting scope and organisms were grouped into four gross taxonomic categories: nauplii, copepods, cladocerans, and rotifers.

Results of the analysis indicate the existence of a large variation in zooplankton density estimates between the replicate samples. There was no relation between
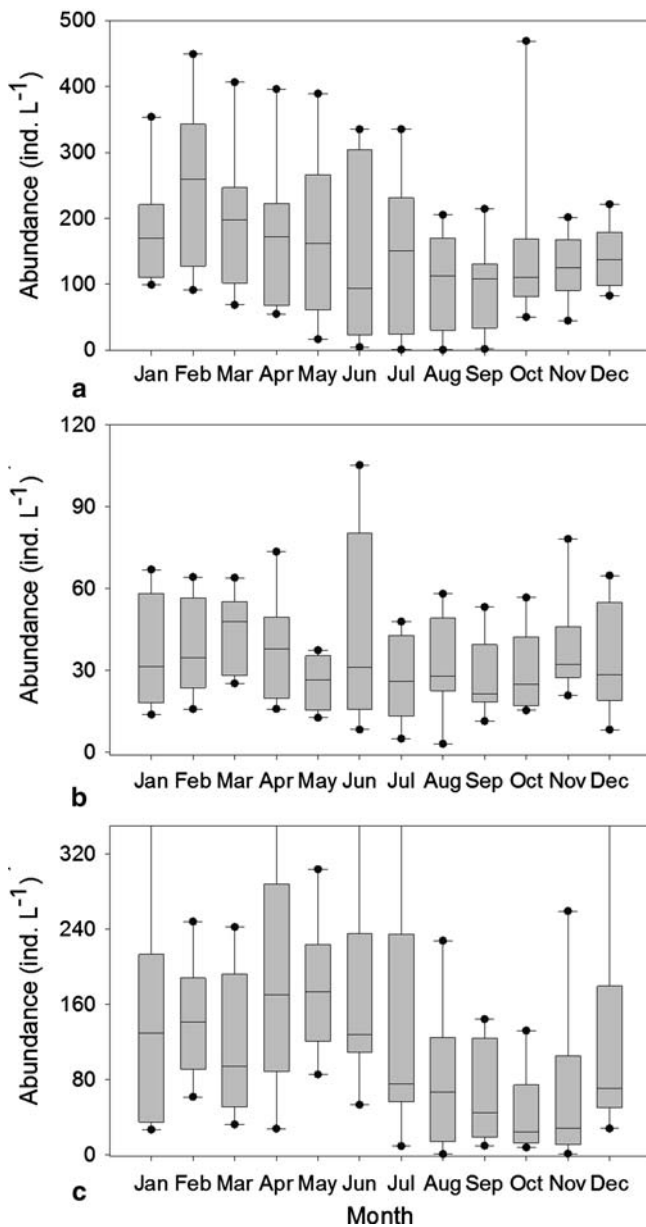
Fig. 13.4 Box plot presentation of monthly abundances of copepods (**a**), cladocerans (**b**), and rotifers (**c**) over a 9-year period (2003–2011) based on profile sampling

the number of individuals counted and the variability. For example, the differences between the standard deviations for samples collected on March 30 and December 21 were small, while the average density on March 30 was lower by nearly an order of magnitude than the density on December 21. For densities of each separate taxonomic group (copepods, cladocera, and rotifers), and the total zooplankton density, we examined the differences between replicates, on a given date, by calculating the coefficient of variation (CV, Fig. 13.5) and also the ratio between the highest and lowest densities over the five replicates. Finally, for each group, we determined the range of ratios (highest to lowest densities per date) found over the entire year (Table 13.2) thus providing a range of error associated with the density estimates. The rotifers, and then cladocerans, displayed the largest differences between the minimum and maximum density over the five replicates. The mean variation over all samples ranged between 1.9 (total zooplankton density) and 3.3 (rotifers) suggesting that abundance estimates collected over a period of a year could vary by a factor of 2–3 just due to fine-scale patchiness. CV values were relatively high for all groups but especially for rotifers, where the values approached 80 on two occasions and values of approximately 40 (37–45) on six additional sampling dates. The calculated CV values did not differ greatly, however, among the other groups.

The relatively large variation in density estimates, especially for rotifers, between samples collected over a short period of time highlight the difficulty in accurately estimating zooplankton abundance for a given date based on a single sample. As a consequence, conclusions should not be drawn based on a single date or limited number of sampling dates. The fine-scale variation also limits our ability to fully understand the interactions between zooplankton and phytoplankton at fine scales. Given the fine-scale variability, trends over extended periods of time should be examined in order to study changes to zooplankton in the lake and efforts should be made to introduce replicate sampling thereby increasing certainty in the estimated abundances.

13.5   Spatial Dynamics: Vertical Patterns

To date, only a limited number of studies have reported on the vertical distribution of zooplankton in the lake and have focused on either one specific date (Easton and Gophen 2003; Pinel-Alloul et al. 2004) or a limited number of seasonal cycles (Gophen 1978). While these studies have provided information on the vertical distribution, they have at times missed significant characteristics that may result in a bias against species with high densities at specific depths. The samples collected since 2003, as part of the profile sampling, generally reinforce the seasonal and taxonomic specific distributions previously reported (Gophen 1978). Nevertheless, results of the profile sampling, conducted since 2003 (Fig. 13.6), provided additional information, supporting the continued need for the profile sampling protocol.
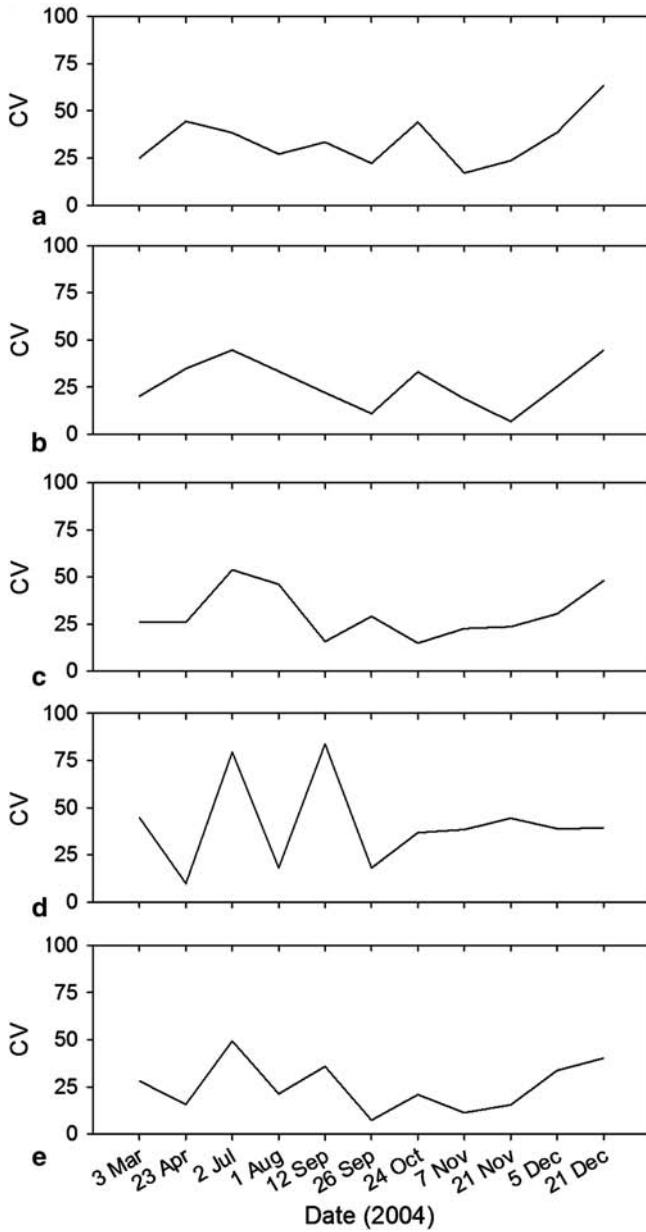
Fig. 13.5 The calculated CV values for each sampling date in 2004 for **a** Nauplii, **b** copepods, **c** cladocerans, **d** rotifers, and e total zooplankton. (Data based on the patchiness study)

Table 13.2 The minimum and maximum values of the *ratio* between the highest and lowest density estimates for a given sampling date, per group, over the entire sampling period and the range of CV values found over the course of the year. (Data collected as part of the patchiness study conducted March–December 2004; see text)

Group	Minimum	Maximum	Min–Max CV
Nauplii	1.4	4.1	17.1–63.5
Copepods	1.2	4.3	6.8–44.7
Cladocerans	1.4	5.7	14.9–53.8
Rotifers	1.2	12.8	9.8–83.8
Total density	1.2	4.1	7.3–49.4

CV coefficient of variation

There were seasonal differences in the vertical distribution of zooplankton in the lake with noticeable variation in the densities, especially in the rotifer distribution. During the winter–early spring, prior to the onset of stratification, the zooplankton were distributed relatively homogenously over the water column with the exception of the top 1 m which exhibited lower densities and a deep peak in rotifers found at the top of the thermocline in 2006. With the onset of stratification in the spring, however, we found larger portions of the assemblage concentrated at approximately 5-m depth (cladocera and Rotifera) with a slightly deeper peak in the copepod distribution which coincided with the lower boundary of the thermocline in 2005. The shallow rotifer peak resulted, at times, in large densities as found, for example, in April 2011 when the rotifer *Keratella cochlearis* densities ranged between 1,602 and 2,200 ind. L^{-1} at depths of 3–7 m. During the summer, the zooplankton were confined to the layer delimited by the metalimnion, with peak rotifer densities occurring, during both in 2005 and 2006, in proximity to the mid-upper metalimnion, typically at 15 m, often reaching large densities ($>1,000$ ind. L^{-1}). Peak values of 1,400 and 1,800 ind. L^{-1} were found, for example, on June 16 and 30, 2008, respectively, and 1,500 ind. L^{-1} on July 19, 2009. Copepods and cladocerans also exhibited a peak distribution in the metalimnion in 2005 but not in 2006 during which they exhibited shallower peaks. Indeed, Pinel-Alloul et al. (2004) similarly reported peak densities at 5 and 15 m during the summer. During the fall, with the deepening of the thermocline, but prior to overturn, we typically found a relatively homogenous distribution of copepods and cladocerans from the surface down to the thermocline. The rotifers, however, were usually found congregating near the lower boundary of the thermocline. To date, the highest rotifer density recorded was found during this period with the species *Anuraeopsis fissa* reaching a density of 7,131 ind. L^{-1} on Dec. 24, 2005 in the thermocline (depth of 24 m).

Diel vertical migration which often characterizes zooplankton in lakes with high fish predation pressure and large-bodied zooplankton has been studied, to a limited degree, in Lake Kinneret. The result, however, has been somewhat contradictory, though it is clear that no major vertical migration takes place in the lake. Gophen (1978) mentioned vertical migration and later Gophen (1979) reported that the vertical migration was predominantly by copepods and cladocerans. He linked the migration to light conditions and *Peridinium* densities with most of the migration
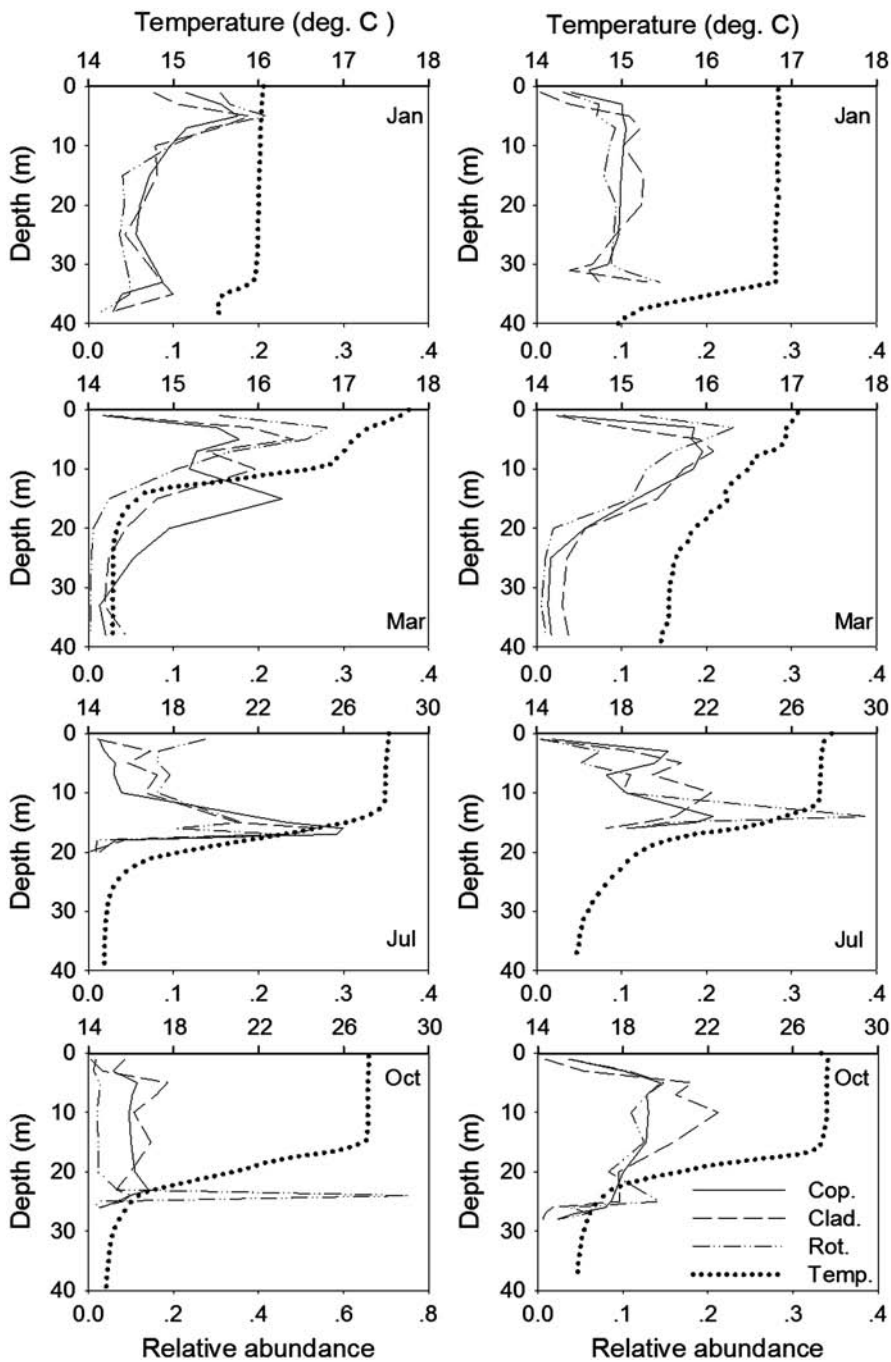
Fig. 13.6 Monthly mean relative vertical distribution (shown as fraction of group-specific density) of the three taxonomic groups, and temperature profiles, for four dates during 2005 (*left panels*) and 2006 (*right panels*) representing the distinct seasons. (Data based on profile sampling)

occurring during sunrise and sunset. More recently, Easton and Gophen (2003) reported that only limited vertical movement was observed during a 24-h study. The vertical movement exhibited by the cyclopoids, according to their observations, mimicked seiche movement. Thus, it is likely that the observed change in vertical placement is not an active form of vertical migration, but rather a passive form of movement with the water.

13.6   Grazing and Nutrient Mineralization

Crustacean zooplankton are considered not only as the main link between primary producers and upper trophic levels but also as important sources of mineralized nutrients for producers (Sterner and Elser 2002). A number of modeling studies of the Lake Kinneret ecosystem support the role of zooplankton as nutrient recyclers in the ecosystem. Based on the model they constructed of the carbon flows in the Lake Kinneret ecosystem, Stone et al. (1993) calculated that microbial grazers provided 40 and 46% of herbivore zooplankton and copepod carbon requirements, respectively, during the spring and 36% of the copepod demand during the summer. Furthermore, some 45% of total bacterial production was consumed by zooplankton in the summer. In a separate model of the carbon flow in the lake, Hart et al. (2000) showed that more than 40% of the carbon fixed by phytoplankton is grazed by zooplankton of which cladocerans accounted for 63% of the herbivory. Microzooplankton and cladocerans proved to be the main bacteria grazers while copepods were the main microzooplankton consumers. These links result in an efficient pathway and increased utilization of bacterial productions bypassing the protozoan portion of the microbial loop. Hambright et al. (2007) experimentally tested this model and showed that mass-specific carbon ingestion rates by microzooplankton (there defined as all grazers passing through 150-μm mesh, and consisting of rotifers, nauplii, ciliates, and flagellates) were 20 times higher than ingestion rates of crustaceans, with most carbon ingested by microzooplankton in the form of bacteria. Nevertheless, microzooplankton ingestion rates on pico- and nanophytoplankton were substantially higher than crustacean ingestion rates, and more phytoplankton taxa were grazed by microzooplankton. Even when correcting for differing biomass between the two grazer groups, microzooplankton grazing inflicted up to ten times higher mortalities on both phytoplankton and bacteria than did crustaceans.

Zooplankton grazing is translated not only into carbon flow through the system but also into remineralization of nitrogen and phosphorous into biological available forms. Bruce et al. (2006), in their application of the ecosystem model DYRESM-CAEDYM, estimated that, during 1997–1998, zooplankton remineralization provided 3–46% and 5–55% of the P and N uptake by phytoplankton, respectively. Furthermore, they calculated that zooplankton excretion provided approximately 60% of the total nutrient fluxes in the photic zone of the lake during stratification. The role of nutrient recycling by zooplankton has also been experimentally documented

(Hambright et al. 2007). Hambright et al. (2007) measured crustacean mineralization rates of 0.04 and 0.36 µg µgC$_{zoop}$$^{-1}$ day^{-1} of P and N, respectively, while microzooplankton rates were 2.8 µgP µgC$_{zoop}$$^{-1}$ day^{-1} and 20 µgN µgC$_{zoop}$$^{-1}$ day^{-1}. According to their results, the Lake Kinneret microzooplankton, with mineralization rates 55–70 times higher than crustacean rates, accounted for >85% of the daily mineralization of P and N in the lake, with turnover rates of 0.36 and 1.1 days, respectively.

13.7   Summary

We have characterized the Lake Kinneret zooplankton on a number of temporal and spatial scales and have reported on the seasonal patterns along with a strikingly patchy distribution observed in the various zooplankton taxonomic groups. The zooplankton in the lake has exhibited interannual variation in abundance and biomass over the past four decades along with changes in the relative contributions of the various taxonomic groups and the larger species. Some of the changes coincided with the shifts observed in the lake ecosystem, especially since the mid-1990s, such as the changes in phytoplankton succession in the lake including the increasing dominance of cyanobacteria species and unpredictable occurrence of *Peridinium*. While the underlying processes leading to those changes are yet to be fully uncovered, the impact of abiotic changes, namely changes to lake level, on the ecosystem, in general, and on the zooplankton, in particular, have been hypothesized. Indeed, recently, a data-driven modeling study linked between the rate of change in lake level and zooplankton abundance in the lake (Gal et al. 2013). The changes have also affected the interactions between the various zooplankton taxonomic groups. This was most obvious in the relationship between the copepods and rotifers with a clear negative correlation between their abundances since the mid-1990s (Fig. 13.2). It remains unclear whether the zooplankton community is stabilizing following decades of change or if it will continue to fluctuate in reaction to the ongoing changes to the biotic and abiotic components of the ecosystem. The changes to the zooplankton community in the lake have wide implications due to their role as nutrient recyclers. Given the large differences in excretion rates between crustacean zooplankton and microzooplankton, major declines or increases in either of these groups will change the amount of nutrients available to primary producers in the lake. This in turn could potentially influence the phytoplankton assemblage in the lake.

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