Long-term zooplankton body size and species changes in a subtropical lake: implications for lake management

K. David Hambright[1]

University of Oklahoma, Norman, and Yigal Allon Kinneret Limnological Laboratory, Israel

With 8 figures and 3 tables

Abstract: Analysis of long-term (1970–2002) zooplankton body sizes in Lake Kinneret, as recorded in an historical zooplankton sample archive, combined with re-analysis of published long-term zooplankton taxonomic abundance data revealed previously undetected patterns in zooplankton biomass and demonstrates a profound long-term impact of planktivorous fish predation intensity driven by fishery harvest practices. During the 1970s, crustacean zooplankton biomass remained relatively constant at a mean (±SD) of 1.50 ± 0.26 g m^{-3}, dropped precipitously in the 1980s reaching 0.57 g m^{-3} by 1993, and rebounded to 1.33 ± 0.19 g m^{-3} in the early 2000s. The 1980s decline reflects decreased cladoceran biomass due to a decline in mean body mass in the three dominant cladoceran genera (*Diaphanosoma, Ceriodaphnia, Bosmina*) and decreased copepod biomass that resulted from a shift in dominance by large *Mesocyclops ogunnus* to small *Thermocyclops dybowskii*. Although crustacean body sizes remained small through the early 2000s, cladoceran and copepod densities increased by ~34 and > 300 %, respectively, after 1994 leading to a dramatic increase in crustacean zooplankton biomass. These patterns indicate an intensification in fish predation throughout the 1980s and 1990s, and although zooplankton biomass rebounded in 1996–2002 to ~80 % of the 1970s levels due to sharp increases in crustacean densities, smaller cladoceran and copepod body sizes suggest that Lake Kinneret zooplankton continue to be strongly influenced by intense fish predation.

Key words: historical sample archive, zooplankton body size, planktivory, Lake Kinneret.

Introduction

Long-term data sets can provide valuable insight into historical trends and other developments in ecosystems (Edmondson 1991, Carpenter 2002, Jackson & Fureder 2006). However, such data sets can prove to be limiting in that the original samples from which the data were generated are often no longer available for new analyses. Archival samples, whether preserved samples in a laboratory or museum (e.g., Davis & Pyenson 2007, Klimov et al. 2007) or samples archived naturally (e.g., in lake sediments Brendonck & De Meester

2003, Mackay 2007) on the other hand can not only provide valuable insight into historical developments, but also can be analyzed or re-analyzed with newer methodologies to provide additional comprehension beyond that possible from the original long-term data set itself. A very powerful tool emerges when analysis of the two types of data sets can be combined (e.g., Freeland et al. 2007).

Since the 1960s, researchers have used multi-annual changes in zooplankton assemblages to infer densities, biomass, or predation intensities of planktivorous and piscivorous fishes in lakes (Brooks &

[1] **Author's address:** Program in Ecology and Evolutionary Biology, Biological Station and Department of Zoology, University of Oklahoma, Norman OK 73019, USA.

E-mail: dhambright@ou.edu

Dodson 1965, Galbraith 1967, Carpenter et al. 1987, Mills et al. 1987). One of the more useful long-term analyses that have been developed is that of using dynamics of zooplankton body sizes in freshwater lakes in the characterization of biomass and production of fishes (Mills & Schiavone 1982). Indeed, changes in zooplankton body morphologies recorded in lake sediments have even been used to infer dynamics in the intensity of predation by predators over periods spanning decades to over a century (e.g., Kerfoot 1981b, Sanford 1993).

For nearly four decades, Lake Kinneret, Israel, has been well studied, including weekly and bi-weekly monitoring of scores of physical, chemical, and biological parameters. The resultant long-term database has contributed to considerable understanding of factors affecting the ecological characteristics of the lake (e.g., Berman et al. 1995, Zohary 2004, Roelke et al. 2007). Particularly useful has been the long-term record of zooplankton in the lake. As early as the mid 1980s, trends in species abundances and biomass in the zooplankton record have been used to advise lake managers, particularly with respect to fisheries management, in which supplemental stocking programs for some species were discontinued due to a decline in zooplankton biomass (Gophen et al. 1983a, Gophen et al. 1983b). More recently, a continued decline in zooplankton biomass into the 1990s (Fig. 1A) (Gophen 2003) was instrumental in supporting decisions by lake managers to instigate a culling program for the dominant planktivorous fish in the lake, bleak *Acanthobrama terraesanctae* (previously *Mirogex terraesanctae*), following the collapse of the bleak fishery by over harvest (Hambright & Shapiro 1997) and a population explosion of small, subcommercial-sized bleak (Walline et al. 2000, Ostrovsky & Walline 2001). Since the culling program began (1994), zooplankton biomass has rebounded, suggesting a reduction in top-down predation pressure on zooplankton and signaling a successful biomanipulation of Lake Kinneret (Gophen 2003).

Here, I present new analyses of zooplankton body sizes from a long-term sample archive of zooplankton from Lake Kinneret. These data, coupled with a reformulation of the long-term zooplankton record (to account for changing zooplankton body sizes), reveal somewhat different patterns in long-term trends than those recorded in the previously published long-term data record. Moreover, this analysis suggests that the bleak culling program has been not only unsuccessful, but has instead likely exacerbated already strong top-down planktivore effects. These data and analyses

highlight the usefulness and power of both long-term data sets and historical sample archives.

Methods

Study site

Lake Kinneret is a warm, monomictic lake located between 32° 42′ to 32° 53′ N, at –209 m altitude in the north of Israel in the Dead Sea Rift Valley (part of the Afro-Syrian Rift Series). The lake has been classified historically as naturally eutrophic (Serruya 1978, Berman et al. 1995), though recent paleolimnological analyses (Hambright et al. 2004, Hambright et al. 2008), suggest that the modern levels of high production have existed only since the mid 20th century. During the first three decades of formal scientific study, Lake Kinneret was considered to be relatively stable with respect to phytoplankton abundances, species composition, and primary production (Berman et al. 1992, Berman et al. 1995, Zohary 2004), although several reports have warned of declining zooplankton biomass and increasing abundances of nanophytoplankton and phosphorus availabilities (Gophen et al. 1990b, Hambright et al. 1994, Hambright et al. 2004). Since the mid 1990s, the Lake Kinneret phytoplankton assemblage has exhibited increasing variation in species composition and biomass (Zohary 2004, Roelke et al. 2007).

The zooplankton assemblage of Lake Kinneret is typical for a subtropical lake with relatively high levels of zooplanktivory, with small cladocerans (*Diaphanosoma brachyurum, Ceriodaphnia reticulata, C. rigauldi, Bosmina longirostris typica, B. l. cornuta*) and copepods (*Mesocyclops ogunnus, Thermocyclops dybowskii*) representing the crustaceans, and numerous rotifers and protists representing the microzooplankton (Gophen 1978b, Hambright et al. 2007). Prior to 1993, Lake Kinneret supported several commercial fisheries. At an annual rate of 1,022 tons between 1970 and 1992, the endemic zooplanktivorous bleak constituted ~60 % of the total commercial harvest. The remaining ~40 % was comprised of two native planktivorous cichlids (*Sarotherodon galileaus* and *Oreochromis aurea*) and three exotic planktivores, silver carp (*Hypothalmichthyes molitrix*) and grey mullets (*Liza remada, Mugil cephalus*) (Ben-Tuvia et al. 1992). In 1993, the bleak fishery collapsed following nearly a decade of increasing harvest pressure on larger individuals in the population (Hambright & Shapiro 1997) leading to an increased population dominated by small subcommercial-sized bleak (Ostrovsky & Walline 2001). Similar tendencies toward over-harvest have been reported for other fish species as well (Ostrovsky 2005).

In 1994, a bleak culling program was initiated, in which 170–940 tons of small, subcommercial-sized bleak, in addition to the 0–642 tons of commercially-harvested bleak, were removed from the lake annually through 2004 (Fig. 1B) in an attempt to shift the bleak population size structure toward larger body sizes, renew the fishery, and allow for higher zooplankton biomass (Ostrovsky & Walline 2001, Gophen 2003). As early as 1996, both the bleak population and fishery began showing signs of recovery. Both the mean size of harvested bleak and the size of the commercial harvest increased steadily between 1996 and 2001. Concurrently, zooplankton biomass increased substantially, averaging ca. 40 g m^{-2} in 1996–2001 (Fig. 1A) and leading to the conclusion that the culling program had successfully achieved the desired effects (Gophen 2003). However,

with respect to the bleak population and fishery, the recovery fell short of expectations and the fishery collapsed again in 2004 as commercial-sized individuals once again became rare in the harvest (Fig. 1; J. Shapiro, Israel Department of Fisheries, pers. comm.). Thus the hypothesized relationship between the bleak culling program and zooplankton biomass warrants further examination.

Hypotheses

Based on Fig. 1A and the assumption that the zooplankton biomass trends resulted from changes in planktivorous fish predation pressure (*sensu* Gophen et al. 1990a), we can use the size-efficiency hypothesis of Brooks & Dodson (1965) to generate two testable hypotheses:

H_1: If the 1970–1994 decline in zooplankton biomass was a result of increased predation pressure from planktivorous fish, we would expect to see a shift in species and size structure of the zooplankton assemblage to smaller forms over that time period.

H_2: If the 1995–2002 recovery in zooplankton biomass was driven by a reduction in planktivory, we would expect to see a shift in species and size structure of the zooplankton assemblage to larger forms after 1994.

Alternatively, Hambright & Shapiro (1997) showed that commercial harvest pressure on bleak increased substantially between 1980 and 1993 due to a gradual increase in mean fish age and size harvested. They hypothesized that the resulting trend of decreasing mean ages and body sizes in the bleak population during that period would have translated into increasing predation pressure on the zooplankton, particularly if the total biomass remained unchanged or increased. Thus:

H_3: If planktivore predation pressure increased during 1980–1994, we would expect to see a decline in mean zooplankton body sizes during this period.

Furthermore, because the culling program essentially continued an excessively high harvest rate on the bleak population (*sensu* Hambright & Shapiro 1997), particularly on the larger individuals (Hambright & Zohary 2001), we would predict that predation pressure on zooplankton remained high and zooplankton body sizes remained small during the culling period. If so, the observed increase in zooplankton biomass between 1995 and 2002 would not be related to fish predation pressure, but to some other factor such as increased zooplankton densities due, perhaps, to increased food availability.

Therefore:

H_4: If the bleak culling program resulted in a continuation of high planktivore predation pressure on zooplankton, we would expect to find alternative factors, such as increased zooplankton densities, to explain the observed increase in zooplankton biomass during 1995–2002.

I tested these hypotheses by 1) analyzing zooplankton body size variation in ethanol-preserved archived zooplankton samples collected during 1970–2002, and 2) combining this new body-size based analysis with existing species records contained in the Kinneret Limnological Laboratory (KLL) database.

Long-term database

Since January 1969, Lake Kinneret waters have been routinely (weekly and biweekly) monitored for variability in basic limnological parameters including general physical attributes, water chemistry, phytoplankton, and zooplankton. Most data collect-

Fig. 1. A. Annual mean zooplankton biomass (g m^{-2}) in Lake Kinneret during 1970–2002, showing the long-term decline during 1970–1994 (solid circles) and recovery during 1995–2002 (open circles) (after Gophen (2003) but based on total zooplankton biomass as recorded for a central monitoring station (A) in the Kinneret Limnological Laboratory database). **B.** Annual harvest (metric tons) of bleak from Lake Kinneret during 1943–2004; solid circles indicate commercial harvest, open circles indicate combined commercial and culling harvest (modified from Hambright & Shapiro (1997) using additional data from the Israel Department of Fisheries, courtesy of J. Shapiro).
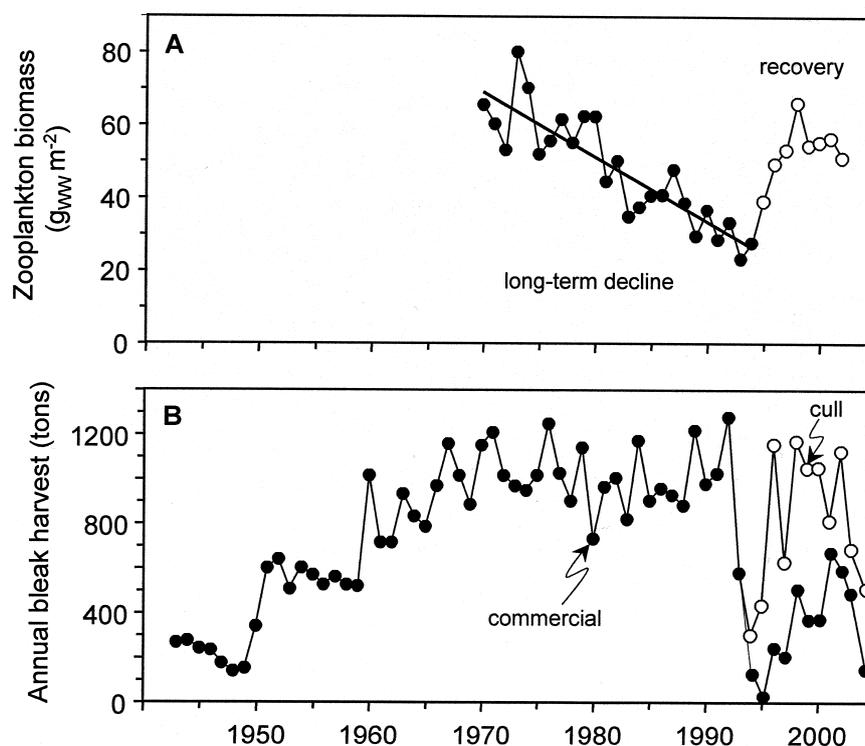
ed as part of the routine monitoring program are stored in the KLL database, from which I obtained either annual or monthly means of taxon-specific zooplankton densities and biomass for this present analysis. Details of the Lake Kinneret monitoring program can be found in Serruya (1978) and references therein and long-term trends in zooplankton biomass have been reported by Gophen (1984, 1992a, 2003). The monitoring program for zooplankton remained unchanged during 1970–2002. Briefly, five stations (one central station, A, and four peripheral stations, D, G, K, and H) were sampled bi-weekly with a 5-L Ruttner bottle as part of the basic routine monitoring program by the Kinneret Limnological Laboratory. A single 0.8- to 1-L depth-integrated (i.e., mixed) sample was produced from 3 to 12 separate 1-L subsamples from multiple-depth Ruttner deployments (e.g., Station A: samples collected at 1, 3, 5, 7, 10, 15, 20, 30, and 40 m, plus, during thermal amixis, additional samples at the depth of the thermocline (z_t), and at $z_t - 1$ m and $z_t + 1$ m). All depth-integrated samples were preserved in 4 % Formalin, enumerated microscopically by species stage (e.g., copepod naupliar and copepodid stages) and size class (e.g., for cladocerans, small and large). Densities were converted to wet weight biomass by multiplying densities of organisms by specific values representing mean biomass estimates for individuals within a given stage or size class for each species. The two dominant cyclopoid species (*Mesocyclops ogunnus* and *Thermocyclops dybowskii*) were differentiated routinely only at copepodid stage VI (i.e., adults). Juvenile copepodid and naupliar stages were enumerated in bulk according to life history stage (naupliar stages I–III and IV–VI, and copepodid stages I, II, III, IV, and V), but were not separated by species. Individual zooplankton biomass values (as wet weight, see Gophen 1973, Gophen & Azoulay 2002, Gophen 2005) were determined either directly using an ultrabalance or indirectly by measuring body lengths and widths of 25–50 individuals per stage or size class and estimating biovolume (converted to wet weight biomass assuming a specific gravity of 1) based on the geometric formula for an ellipsoid. Areal estimates for individual taxa were calculated based on lake (during mixis) or thermocline (during amixis) depth and are reported in the KLL database. For further details on sampling and treatment of zooplankton data for Lake Kinneret, see e.g., Gophen (1984, 1992a, 2003).

Zooplankton archive

In addition to the routine monitoring of zooplankton biomass, a single vertical haul of a 25-cm diameter, 63-μm mesh conical net was taken at the central lake station (A) and its contents along with ~0.5 L of lake water were preserved unanalyzed in 4 % formalin. In 2002, these archived samples were split into two separate archives as follows:

1. The original sample was mixed thoroughly and a 20-mL subsample poured into a glass scintillation vial. All information recorded on the outside of the original container was recorded on archival paper with indelible ink and placed inside the vial. The vial was capped and archived for future analysis of original Lake Kinneret water representative of the time of sampling.
2. The remaining original sample was then poured through a 63-μm mesh nylon filter and the formalin-containing water was discarded (in a hazardous chemical storage facility). All material retained on the filter was washed with de-ionized water, washed into a 20-mL glass vial and resuspended

in a mixture of 70 % ethanol and 1 % glycerine. All information recorded on the outside of the original container was recorded on archival paper with indelible ink and placed inside the vial. The vial was capped and shelved for subsequent analysis.

Samples that could not be restored were discarded. All samples (including both the 20-mL formalin-preserved original sample and the 20-mL ethanol-glycerine-preserved sample) are shelved in an archival cabinet (for environmental stability) in the KLL zoology laboratory.

Zooplankton body size

Samples preserved in ethanol and glycerine were washed in de-ionized water and resuspended in a known volume of de-ionized water, usually 50–100 mL. Small subsamples (typically 1 mL, but dependent on sample density) were extracted and placed into a 3-mL settling chamber. The chamber was filled to capacity with de-ionized water and capped with a cover glass. After 10–15 minutes (sufficient time for settling) the chamber was placed on an inverted microscope and analyzed using an updated version of the plankton analysis software CAPAS (now available as PlanktoMetrix™) in conjunction with computer/video-based high-resolution image analysis (Hambright & Fridman 1994). This procedure was repeated until 26–50 individuals of each taxon (Table 1) were measured. We assumed rotifer body sizes were invariant. For cladocerans we identified individuals to species and measured (nearest 1 μm) total body length (excluding tail spine if present). Multiple *Ceriodaphnia*

Table 1. Taxonomic groups identified and measured and regression coefficients (see Fig. 2) used to estimate body mass.

Taxa/life history stage	Regression coefficients	
	a	b
Cladocerans		
Diaphanosoma brachyurum	109	3.32
Ceriodaphnia reticulata	308	3.28
C. rigauldi	308	3.28
Moina rectirostris[a]	308	3.28
Bosmina longirostris typica	243	2.67
B. l. cornuta	243	2.67
Chydorus sphaericus[a]	243	2.67
Copepods		
Mesocyclops ogunnus	63.6	3.13
Thermocyclops dybowskii	63.6	3.13
cyclopoid nauplii	63.6	3.13
Eudiaptomus dreischi[b]	46.7	2.13
calanoid nauplii[b]	46.7	2.13

[a] *Moina rectirostris* (first recorded in the KLL database in 1986) was present in archive samples throughout 1970–2002; *Chydorus sphaericus* (first recorded in the KLL database in 1983) was present in archive samples beginning in 1981. Combined, *Moina* and *Chydorus* comprised a small fraction (mean ± SD, 2.7 ± 4.7 %) of the total cladoceran biomass during 1981–2002.
[b] *Eudiaptomus dreischi* (recorded in the KLL database between 1986 and 2000, Azoulay 2002), did not contribute substantially to total copepod biomass (mean ± SD, 4.8 ± 8.7 %).
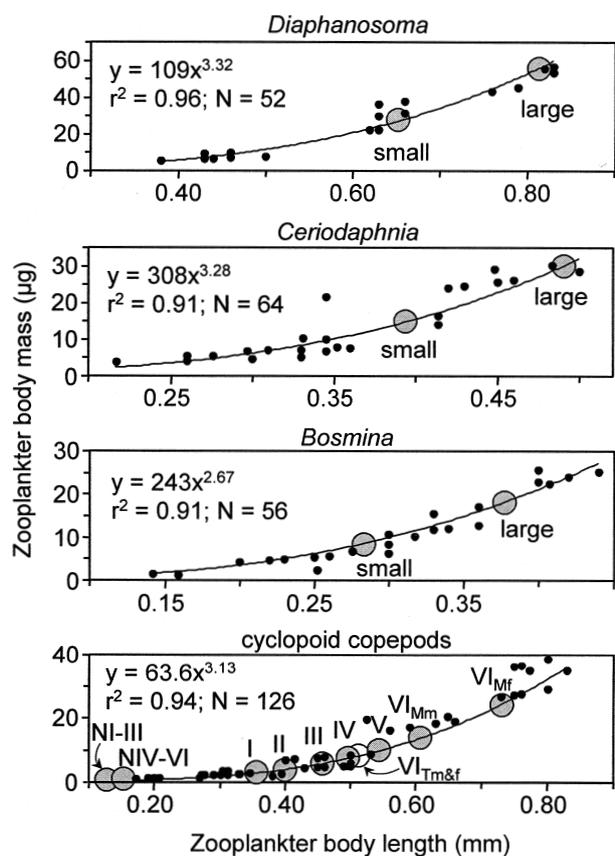
Fig. 2. Length-mass (as wet weight) relationships for major zo-oplankton groups used to estimate mean individual body mass (small points and regression line) and discrete values (large circles) used in qualitative size or stage class estimates of individual body mass for dominant cladoceran and copepod genera (see for example, Gophen et al. 1990a). Cladocerans were categorized as either "small" or "large"; copepods were categorized by life history stages (nauplii I–III and IV–VI; juvenile copepodids I, II, III, IV, V; adult male *Mesocyclops* VI_{Mm}, adult female *Mesocyclops* VI_{Mf}, and adult male and female *Thermocyclops* $VI_{Tm\&f}$).

and *Bosmina* species were measured and analyzed separately, but data are presented here at the generic level for simplicity. For copepods we distinguished between cyclopoid and calanoid nauplii and copepodids (but did not stage nauplii or copepodids) and measured total body length (excluding caudal rami). Subsequent comparisons of measured size distributions (this study) and size distributions derived from original life-history stage-based analyses (as in Gophen 1978a) revealed similar patterns (see text below, and Fig. 2). Therefore the original (higher resolution) life-history stage-based size distributions are used herein. Individual zooplankton body lengths were converted to biomass (as wet weight) based on length-weight regressions (Fig. 2) built into CAPAS. These regressions were generated using biomass values estimated for individual zooplankters indirectly by measuring length and width and calculating the biovolume of an ellipsoid as described above. Following analysis, all material was returned to the 20-mL vial and re-preserved in 70 % ethanol, 1 % glycerine. Due to the time required per

sample analysis, one arbitrarily chosen sample per month (if available) was analyzed, for a total of 408 samples.

To better understand the role of previously observed species shifts (e.g., Gophen 1988) on overall body size changes within the cyclopoid copepod assemblage, animals were collected from the lake in summer-fall 2002 and ten individuals of each naupliar and copepodid stage for both *M. ogunnus* and *T. dybowskii* were identified and measured as detailed above for archive samples.

Recalculation of long-term trends

To estimate mean monthly biomass, mean individual body mass for each cladoceran taxon for each month was calculated and multiplied by the species-specific mean monthly density as recorded in the KLL database for the centrally-located station A (also the station from with the archival samples were taken). Previous analysis of zooplankton biomass in the lake revealed that zooplankton biomass estimated from Station A only (Hambright, unpubl. report) was not statistically different than zooplankton biomass based on five stations in the lake (e.g., Gophen 2003). For months in which there was no sample available for body size measurements or for which a species-specific mean monthly density was unavailable, an average value of the months before and after the missing month were used. No archive samples were available or preserved well enough for analysis of a 21-month period during 1991–1992. To estimate size-specific biomasses for this period, I used an average species-specific mean mass for the closest months before and after the missing month (e.g., the mean mass for a given taxon in May 1991 was estimated as the average of the mean masses for that taxon in May 1990 and May 1993). For cyclopoid copepods, original life history stage-based size distributions and densities (as in Gophen (1988), but from Station A only) were used to calculate mean monthly biomass values. The resulting mean monthly biomass estimates for cladocerans and copepods were then averaged for each year to estimate taxon-specific annual wet weight biomass (g m^{-3}) for the epilimnion of Lake Kinneret.

Results

Although constant biomass values for individual copepod stages provided a relatively good approximation of the size distributions of copepods, the use of only two cladoceran size classes (i.e., small and large) for individual taxa did not capture the true nature of long-term size variation in the cladocerans (Fig. 2), and as a result, tended to overestimate cladoceran biomass relative to biomass estimates based on measured body sizes. As such, the long-term trend in zooplankton biomass in the lake based on measured body sizes (Fig. 3) revealed a different pattern than that reported previously (Fig. 1A). During the 1970s, crustacean zooplankton biomass remained relatively constant at a mean (±SD) of 1.50 ± 0.26 g m^{-3}, dropped precipitously in the 1980s reaching 0.57 g m^{-3} by 1993, and rebounded to 1.33 ± 0.19 g m^{-3} in the early 2000s.

Published reports document a consistent and long-term decline in total zooplankton biomass between 1970 and 1994 (e.g., Gophen 2003). While this new analysis also reveals a significant negative trend in zooplankton biomass between 1970 and 1994, the current analysis shows that the consistent decline in zooplankton
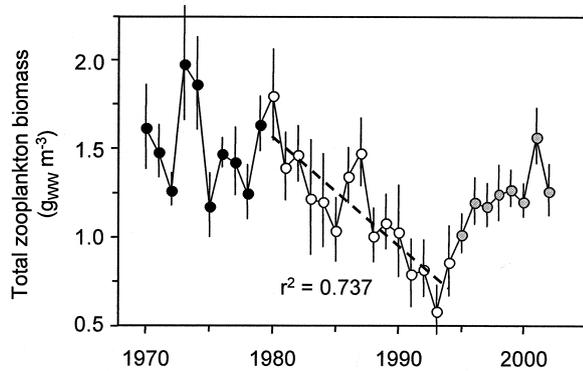
biomass is better described by a negative regression limited to the period 1980–1994 and corresponding to prediction of hypothesis H_3 (Table 2). Both records indicate an increase in zooplankton biomass after 1994, approaching levels (~80 %) of the 1970s during the early 2000s.

The decline in zooplankton biomass was caused by both changes in mean individual body sizes within the cladocera (Figs. 4, 5A) and shifts in species composition within the cyclopoid copepods (i.e., a gradual replacement of the larger-bodied *Mesocyclops* with the smaller-bodied *Thermocyclops* – Table 3, Fig. 5B). These body size and species changes resulted in well-defined declines in cladoceran and copepod biomass (Fig. 6), as well as overall mean crustacean body mass (Fig. 7A). Although many of these changes can be described by significant trends during the period 1970–1994, with the exception of proportion *Mesocyclops*, they are all better described by regressions limited to the period 1980–1994, even though the sample size is considerably smaller (e.g., $N_{1970-1994}$ = 25 versus $N_{1980-1994}$ = 15) (Table 2).

Both previously reported and present records indicate that total zooplankton biomass increased after 1994, while the current record indicates that mean crus-

Fig. 3. Annual mean (±SE) total zooplankton biomass (g m^{-3}) in Lake Kinneret during 1970–2002 based on re-analysis of the long-term record from the Kinneret Limnological Laboratory database in conjunction with analysis of zooplankton body sizes in historical sample archives. Symbols correspond to time periods in *a priori* hypotheses 3 and 4 (see text): 1970–1979, black circles; 1980–1994, open circles; 1995–2002, grey circles.

Table 2. Regression statistics for predictions based on main (H$_1$) and alternative (H$_3$) hypotheses regarding long-term changes in Lake Kinneret zooplankton. H$_1$: Fish predation pressure on zooplankton increased during 1970–1994. H$_3$: Fish predation pressure increased during 1980–1994.

| Prediction	Time period	N	CV	F	P	Hyp. supported
Zooplankton biomass declined	1970–1994	25	0.581	31.8	<0.001	
	1980–1994	15	**0.737**	36.5	<0.001	**H$_3$**
Diaphanosoma body mass declined	1970–1994	23	0.079	2.0	0.174	
	1980–1994	13	**0.496**	12.8	0.003	**H$_3$**
Ceriodaphnia body mass declined	1970–1994	23	0.213	6.2	0.020	
	1980–1994	13	**0.732**	35.5	<0.001	**H$_3$**
Bosmina body mass declined	1970–1994	23	0.401	15.4	<0.001	
	1980–1994	13	**0.885**	100.4	<0.001	**H$_3$**
Cladoceran body mass decreased	1970–1994	25	0.317	10.7	0.003	
	1980–1994	15	**0.910**	131.4	<0.001	**H$_3$**
% Mesocyclops decreased	1970–1994	25	**0.597**	34.1	<0.001	**H$_1$**
	1980–1994	15	0.435	10.0	0.007	
Cladoceran biomass decreased	1970–1994	25	0.311	10.4	0.004	
	1980–1994	15	**0.757**	40.4	<0.001	**H$_3$**
Cyclopoid biomass decreased	1970–1994	25	0.735	63.8	<0.001	
	1980–1994	15	**0.773**	44.3	<0.001	**H$_3$**
Crustacean body mass decreased	1970–1994	25	0.392	14.8	<0.001	
	1980–1994	15	**0.785**	47.6	<0.001	**H$_3$**
Crustacean density decreased	1970–1994	25	0.508	23.8	<0.001	
	1980–1994	15	**0.551**	15.9	0.002	**H$_3$**
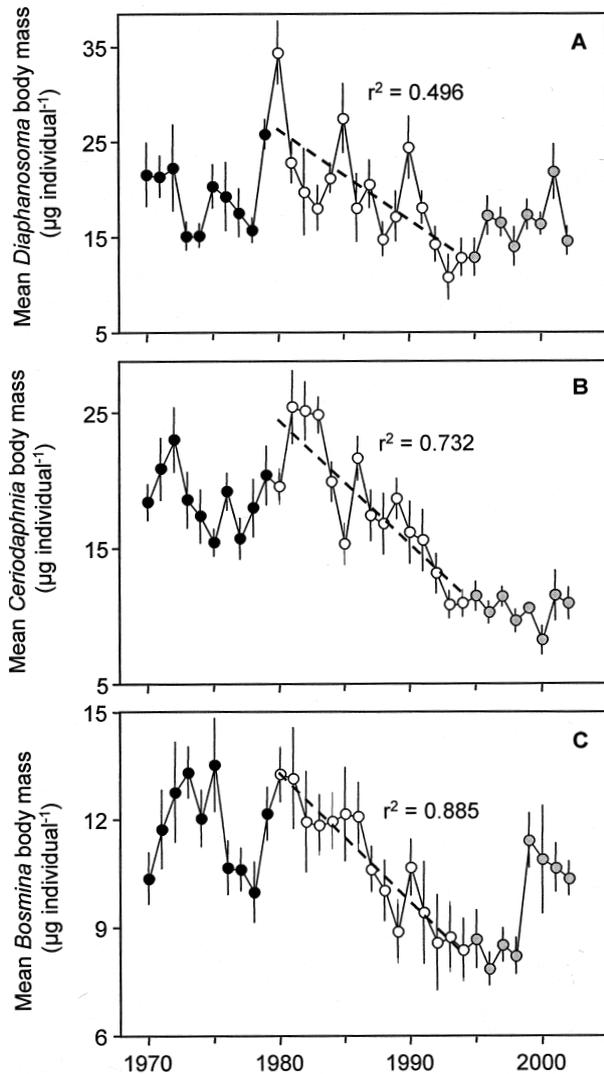
Fig. 4. Annual mean (±SE) body mass (µg per individual) for dominant cladoceran genera, *Diaphanosoma*, *Ceriodaphnia*, and *Bosmina* in Lake Kinneret during 1970–2002. Symbols as in Fig. 3.

Fig. 5. A. Annual mean (±SE) cladoceran body mass (µg per individual) and **B.** annual mean (±SE) proportion of *Mesocyclops*, relative to adult cyclopoid biomass (as a proxy for mean cyclopoid body size – see Table 3), in Lake Kinneret during 1970–2002. Symbols as in Fig. 3.

Fig. 6. Annual mean (±SE) biomass (g m⁻³) of **A.** cladocerans and **B.** cyclopoid copepods in Lake Kinneret during 1970–2002. Symbols as in Fig. 3.

tacean body mass remained relatively small through 2002 (Fig. 7A). Moreover, the current analysis reveals that the increase in total zooplankton biomass was produced by an increase in crustacean densities after 1994 (Fig. 7B). Between 1994 and 2002, cladoceran densities increased by ~34 %, while cyclopoid copepodid densities increased by over 300 %.

Also during 1980–1992, and again during 1994–2002 (note that harvest was negligible in 1993), the mean body length of bleak harvested from the lake increased (Fig. 8A). The 1980–1992 trend was correlated negatively with mean crustacean body mass (Fig. 8B), but no relationship was found between harvested bleak size and mean crustacean body mass
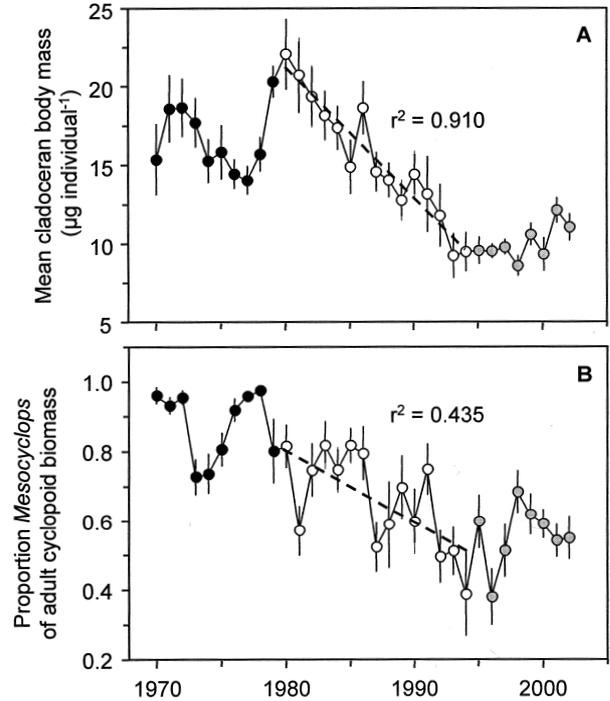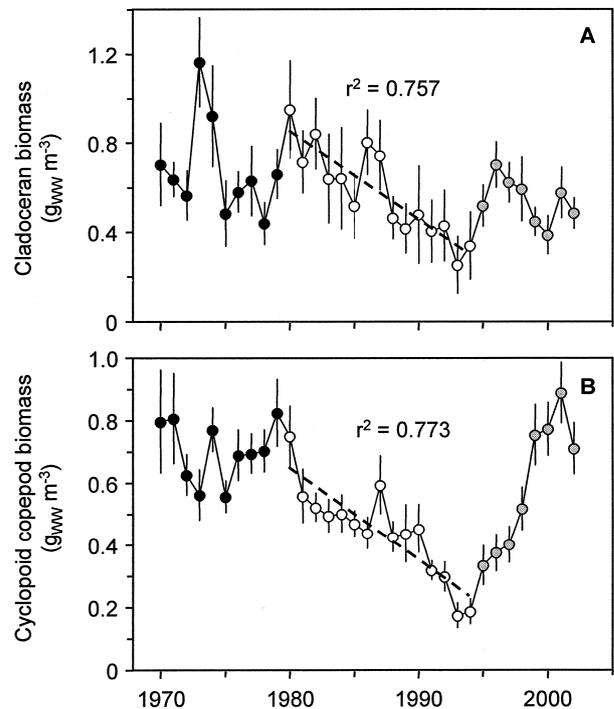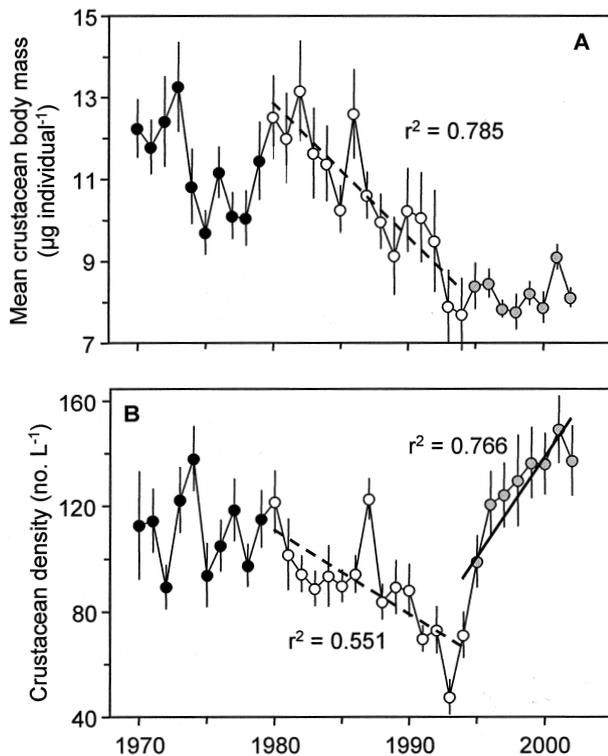
Fig. 7. A. Annual mean (±SE) body mass (µg individual^{-1}) and **B.** density (no. L^{-1}) of crustaceans in Lake Kinneret during 1970–2002. Symbols as in Fig. 3.

during 1994–2002, as mean crustacean body mass remained relatively small throughout this period.

Discussion

The long-term patterns in zooplankton body sizes, species composition, and biomass generated by this reanalysis of the long-term record and sample archive weakly support hypothesis H_1 and fail to support hypothesis H_2. Alternative hypotheses H_3 and H_4 are more strongly supported. Body sizes of the dominant cladocerans and relative abundances of the two cyclopoid copepods were variable in the 1970s, but no consistent trends were apparent that can be attributed to increasing intensity of planktivory. Between 1980 and 1994, however, mean individual body sizes of *Diaphanosoma*, *Ceriodaphnia*, and *Bosmina* consistently declined, and there was a gradual shift in dominance in the copepod assemblage from the larger-bodied *Mesocyclops* to the smaller-bodied *Thermocyclops*. These trends, which led to an overall reduction in mean crustacean body mass, are consistent with expectations of increased size-selective planktivory (*sensu* Brooks &
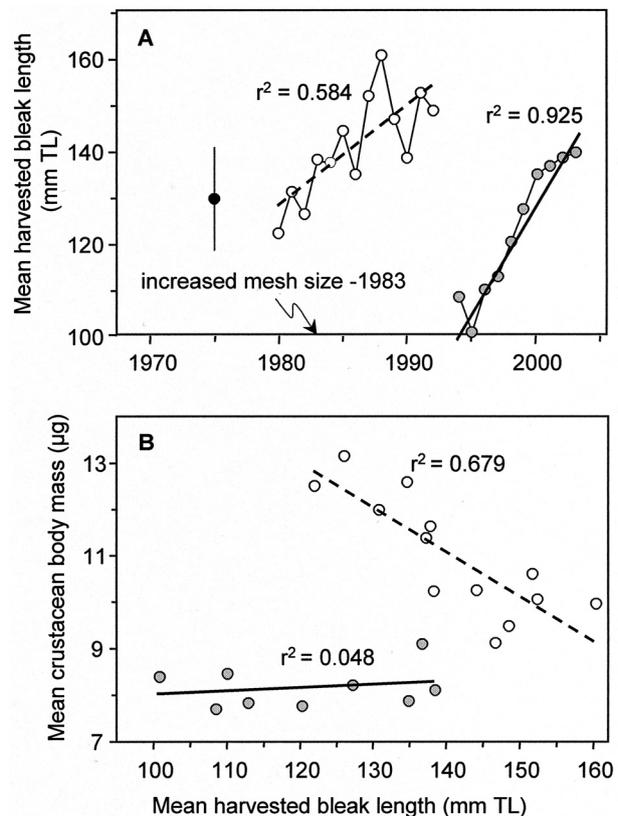

Fig. 8. A. Annual mean (±SE) length (mm total length) of harvested bleak during 1980–2002 (solid circle and bars indicate estimated mean and range of harvested bleak sizes prior to the 1980s – J. Shapiro, Israel Department of Fisheries, pers. comm.; open circles indicate mean sizes harvested during 1980–1992; grey circles indicate mean sizes harvested during 1994–2002) and **B.** mean crustacean body mass (µg individual^{-1}) plotted against mean harvested bleak size in Lake Kinneret during 1980–1992 (open circles) and during 1994–2002 (grey circles). Fisheries data modified from Hambright & Shapiro (1997) and supplemented with data from the Israel Department of Fisheries, courtesy of J. Shapiro.

Dodson 1965) and support hypothesis H_3 – zooplankton biomass appears to have declined in Lake Kinneret during 1980–1994 as a result of increasing predation pressure from size-selective planktivorous fish. Likewise, a lack of an increase in mean crustacean body mass after 1994 supports the alternative hypothesis H_4, rather than the original hypothesis H_2. Thus, the post-1994 increase in zooplankton biomass due to increased crustacean densities does not reflect a reduction in predation pressure by planktivorous fish, but instead suggests that predation intensity remained high and that zooplankton resources may have increased.

It is important to note that these hypotheses were generated from published reports of zooplankton biomass (e.g., Gophen 2003) and from an analysis of the

Table 3. Mean (± 95 % CI) body lengths (µm) for life history stages of *Mesocylops ogunnus* and *Thermocyclops dybowskii* collected from Lake Kinneret during summer–fall 2002. N = 10 for each life-history stage for each species. Note that copepodid stages IV–VI are split according to sex. Mean body lengths of *Mesocyclops* and *Thermocyclops* for all 12 life-history stages and sexes are significantly different across taxon (ANOVA; all p < 0.001).

Life-history stage	*Mesocyclops ogunnus*		*Thermocyclops dybowskii*	
	Body length (µm)	95 % CI	Body length (µm)	95 % CI
nauplius I	120	1.78	102	2.95
nauplius II	144	1.65	132	1.77
nauplius III	167	2.83	154	1.89
nauplius IV	192	1.76	163	1.62
nauplius V	202	1.02	178	4.35
nauplius VI	225	3.28	204	5.97
copepodid I	345	9.85	280	4.58
copepodid II	418	6.99	322	3.37
copepodid III	471	5.35	374	15.7
copepodid IV-male	539	3.99	445	7.93
copepodid V-male	584	6.51	512	3.68
copepodid VI-male	592	12.3	524	8.63
copepodid IV-female	591	5.20	492	3.82
copepodid V-female	646	6.89	590	17.2
copepodid VI-female	769	15.0	620	29.4

dominant fishery (Kinneret bleak) in the lake (Hambright & Shapiro 1997). Clearly there is variability in the patterns and timing of the size and biomass trends reported here that fall beyond the simple explanations inherent in the four hypotheses examined. Nevertheless, the patterns allow these general hypotheses to be tested and the observed variability can be used to identify alternative or more explicit hypotheses for future study. It is also important to note that previous reports of the zooplankton biomass decline were used successfully to elicit fishery management actions aimed at reducing planktivory (Gophen et al. 1983a, Gophen et al. 1983b). Indeed, stocking of the Jordan Saint Peter's fish and exotic silver carp into Lake Kinneret ceased in the mid 1980s due to such efforts (Gophen 2000). Moreover, reports of the severe decline in zooplankton biomass in the early 1990s were highly influential in the government-subsidized culling program to remove subcommercial-sized bleak (Gophen 2003). The differences between these earlier reports and this present analysis lie mostly in the timing of the hypothesized relationships and the hypothesized mechanisms behind these patterns. As such this study does not necessarily refute previously published findings, but rather, refines earlier hypotheses given new insight derived from the analysis of zooplankton body size changes.

Both previous and current analyses indicate a long-term decline in zooplankton biomass. The relative strengths of the temporal patterns documented here support more strongly the hypothesis that the long-term decline was limited to the period 1980–1994. Also, both previous and current analyses suggest an important role for planktivorous fish in the observed patterns. Previous reports (see Gophen 2003) suggest that planktivore predation pressure stemmed from planktivorous fish abundances (e.g., increasing through 1994 and decreasing since). In this current study, the nature of the zooplankton decline, i.e., decreasing crustacean body sizes, also suggests that the mechanism of the decline was increasing size-selective planktivory. However, analyses of long-term fishery harvests (e.g., Hambright & Shapiro 1997), relationships such as those in Fig. 8, and continued small crustacean body sizes post 1994, point more explicitly to an increase in predation pressure (increasing through 1994 and remaining high through 2002) independent of planktivore abundances, but related to reduced planktivore body sizes.

This new analysis of zooplankton body sizes corroborates the conclusions of Hambright & Shapiro (1997) that increased harvest pressure on the bleak population, and particularly the larger-sized individuals, by the commercial bleak fishery which led to a shift in body sizes in the bleak population toward smaller sizes, likely led to increased predation pressure on the zooplankton. This effect is reflected in the negative correlation between mean bleak body size harvested and mean crustacean body mass in the lake during this period (i.e., 1980–1993). General fisheries and metabolic theories can be invoked to explain

the link between harvested fish size and zooplankton size. Numerous examples of the effects of fish overharvest were discussed by Larkin (1977). In general, overharvest can lead to domination of a fish population by smaller and younger individuals, particularly when harvest is targeted at the largest (and oldest) individuals in the population. Such practice can lead to conditions of instability in the population and eventual collapse of the fishery. Indeed, the bleak population in the early and mid 1990s was dominated by small, subcommercial-sized individuals (i.e., < 120 mm TL) and was substantially larger than previously observed (Walline et al. 2000, Ostrovsky & Walline 2001). The subsidized culling program was initiated in 1994 in order to reduce both the absolute and relative abundance of these small individuals (Gophen 2003). However, the culling program was conducted by the commercial fishers using the same purse seine-based techniques normally used during harvest, with the resulting impact of the culling program being concentrated on the larger individuals in the population, and that concentration increasing on larger individuals over the duration of the culling program (see Fig. 8). Thus, absolute abundances may have declined with each harvest, but as occurred in the 1980s, this practice eventually led to a domination of the bleak population by small individuals (J. Shapiro, Israel Department of Fisheries, pers. comm.) and a second collapse of the fishery (see Fig. 1). From metabolic theory (*sensu* Brown et al. 2004) one would predict that predation pressure on the zooplankton would be elevated under such conditions as mass-specific ingestion rates would be predicted to increase exponentially with decreasing fish body size. Even as the bleak population density was reduced by the culling program, the decreasing fish body size in the lake would be expected to yield higher rates of predation. Of course, severe reductions in abundance would eventually lead to reduced planktivory regardless of fish size. However, continued domination of the crustacean zooplankton during the culling period by smaller-bodied zooplankton indicates that although fish abundances may have been declining under the culling program, fish predation pressure remained high. In fact, it appears that predation intensity was so high by the mid 1990s that zooplankton body sizes were already at or near their minimum, thereby negating a possible relationship between harvested fish size and zooplankton size during the culling period.

The possible alternative reasons for the dramatic increase in zooplankton densities after 1994 are not directly addressed by this study, yet some speculation is warranted. Reviews of classic "fish effect" studies (e.g., Hurlbert & Mulla 1981, Drenner & Hambright 2002) lead to the conclusion that top-down (fish) predation effects are more likely to influence zooplankton body sizes and species composition, rather than general zooplankton abundance and biomass (but see Gliwicz 2002). By contrast, overall zooplankton biomass (as affected by the interaction of body sizes and densities) is more likely to be affected by bottom-up factors, such as food availability and quality. Developments in the Lake Kinneret phytoplankton support this hypothesis. Although, routine phytoplankton monitoring indicates that the seasonal phytoplankton assemblages during 1970–1993 were rather stable with respect to species composition and population dynamics (Berman et al. 1995, Zohary 2004), analysis of annual nanophytoplankton biomass in the lake revealed a gradual increase in nanophytoplankton biomass during that period fueled by increasing phosphorus availabilities (Hambright et al. 1994). This conclusion has been corroborated by recent paleolimnological investigations that have revealed a major increase in overall productivity (as indicated by accumulation rates of phytoplankton and bacterial pigments and zooplankton remains) of the lake throughout the 20th century, with a notable shift in the mid 1980s (Hambright et al. 2004, Hambright et al. 2008) concomitant with the period of increased harvest pressure on bleak. Thus, it appears that zooplankton biomass declined during 1980–1994 due to decreasing body sizes under intense top-down pressure from fish predation even though food resources may have been increasing at the time.

Since 1994, the Lake Kinneret phytoplankton assemblages have undergone even more dramatic changes compared with the previous period, with deviations including: the absence of the spring *Peridinium gatunense* blooms in some years and increased variability in the magnitude of the bloom in other years; the intensification of winter blooms of the filamentous diatom *Aulacoseira granulata*; and increased summer phytoplankton biomass with the appearance of new taxa and the appearance and establishment of both toxigenic and nitrogen-fixing cyanobacteria (Zohary 2004, Roelke et al. 2007). Although many of these changes (e.g., increased large, inedible taxa) may not be directly beneficial to zooplankton, it is generally assumed that the overall level of zooplankton resources has increased since 1994 (see for example, Gophen 2003). Thus zooplankton, still under intense top-down predation pressure (as evidenced by continued small body sizes), may have responded to the increased bottom-up production with increased densities leading to the observed increased biomass.

The gradual decline in *Bosmina* body sizes during 1980–1994 is curious given that *Bosmina* is relatively small to begin with and not typically considered an important food item for planktivorous fishes (O'Brien 1987). In Lake Kinneret, however, *Bosmina* is an important, albeit, negatively selected, food source for bleak (Easton & Gophen 2002). Thus, the shift to smaller body sizes is logical given that bleak is a visually-feeding, size-selective planktivore (see Kerfoot 1981b). Interestingly, although body sizes of larger cladocerans and cyclopoid copepods remained small after 1994, indicating continued high predation intensity by fish, there was a dramatic increase in mean *Bosmina* body sizes between 1998 and 1999 that suggests that other factors may also be important in regulating *Bosmina* body sizes. For example, it has been well documented that copepod predation can be an important source of mortality for small cladocerans like *Bosmina* (Kerfoot 1981a). Also, both gut analyses (Gophen 1977) and bioenergetics modeling (Blumenshine & Hambright 2003) have suggested that cyclopoids are responsible for a substantial fraction (40–60 %) of total zooplankton consumption in Lake Kinneret. However, Gophen (1977) found that *Bosmina* were much less important food items than *Diaphanosoma* and *Ceriodaphnia* for adult *Mesocyclops*. Nevertheless, the long-term shift in cyclopoid species (Fig. 5B, see also Gophen 1988) and the dramatic four-fold increase in copepod densities after 1994 could have played a role in the increase in *Bosmina* body sizes in 1998 and 1999.

There are some methodological differences between this present analysis and previous analyses (e.g., Gophen et al. 1990a) that could contribute to differences in the long-term patterns generated, but it appears that these differences are insufficiently large to alter the conclusions reached. For example, in the majority of previous reports of zooplankton biomass in Lake Kinneret, lake-wide biomass estimates were calculated as a weighted composite of five stations and reported as areal (i.e., per m^2) values (e.g., Gophen 2003). There has been debate over the use of areal or volumetric (as presented here) presentations of pelagic data, particularly in cases in which the depth of the mixed layer fluctuates over time (e.g., Carpenter et al. 1999, Nürnberg 1999). Such is the case for Lake Kinneret. Both long-term and seasonal fluctuations in water levels in Lake Kinneret have been shown to affect the depth of the mixed layer during winter-spring mixis (but not during summer-fall amixis, see Hambright et al. 1994). Although such fluctuations have occurred during the time period examined, and preliminary assessment of these fluctuations on the estimation of

zooplankton biomass revealed a tendency for overestimation of zooplankton biomass at times of relatively low water levels (Hambright, unpubl. report), this effect appears to have little impact on the trends reported here. This conclusion is further supported in Gophen's (1992b) detailed assessment of long-term trends in Lake Kinneret zooplankton in which zooplankton biomass is presented both areally and volumetrically revealing the same trends shown here in Fig. 1).

Previous analyses of long-term trends in zooplankton (e.g., Gophen 2003) were based on analyses of individual zooplankton species. However, constant biomass values (albeit two size classes for each species) were used for cladocerans across the long-term record such that fluctuations in body sizes were not fully reflected. In the present analysis of body sizes, I made no differentiation between species within the major cladoceran genera (e.g., *Ceriodaphnia reticulata* and *C. rigaudi* and *Bosmina longirostris typica* and *B. l. cornuta* were grouped as *Ceriodaphnia* and *Bosmina*, respectively). Nevertheless, the length-weight regressions were developed using the same taxonomic resolution and therefore the use of body size within taxonomic groups captured both species and body size variability over time. By contrast, use of ontogenetic stages in the copepods in previous studies (e.g., Gophen 2003) did capture the observed patterns in relative shifts in dominance between *Mesocyclops* and *Thermocyclops*, and even though only stage VI individuals were separated by species, the effect of the species shift on mean cyclopoid body size and total cyclopoid biomass was accurately reflected. However, because stage-specific differences in body size were not accounted for in either previous studies or the present analysis, it is likely that both analyses have underestimated the extent of the long-term decline in cyclopoid copepod biomass during *Mesocyclops-Thermocyclops* shift. Thus the resulting differences between the zooplankton biomass data reported here and data reported previously stem primarily from changes in mean cladoceran body sizes throughout the period examined.

In their analysis of the bleak harvest of the 1980s and the fishery collapse of 1993, Hambright & Shapiro (1997) recommended a reduction in bleak harvest with a relaxation of harvest intensity on larger individuals. This new analysis of zooplankton, especially zooplankton body sizes, supports that earlier recommendation. Although the harvest rate of ~1000 tons was reached by 1970 and was maintained roughly at that rate throughout the next three decades, the harvest of the 1970s was more evenly spread across several size (age) classes of the bleak population and the

bleak population remained relatively stable. However, a gradual intensification of harvest on larger individuals during the 1980s led to a shift in size and age structure of the bleak population in the lake toward smaller and younger fish (Hambright & Shapiro 1997). This present analysis of zooplankton suggests that the same phenomenon occurred again the 1990s and that planktivore predation pressure was once again too high to sustain a relatively large-bodied zooplankton assemblage. Moreover, these data suggest that in order to stabilize the bleak population and encourage development of larger-bodied zooplankton, the harvest of bleak, particularly of larger fish sizes, should be reduced substantially.

Lake Kinneret has undergone dramatic and extensive eutrophication, particularly within the last 50 years, due to a series of hydrological modifications to the lake and its watershed, including impoundment, wetland draining, and extreme water level fluctuations – all contributing factors to increased phosphorus availabilities (Hambright et al. 2004, Hambright et al. 2008). The resulting changes in phytoplankton abundances and composition have likely been exacerbated by top-down effects of more recent fishery harvest practices that led to reduced zooplankton body sizes and hence reduced grazing pressure (with respect to the size range of grazeable phytoplankton). Our understanding of such long-term ecosystem changes has been substantially improved by continual analyses of the long-term data record for Lake Kinneret. Additional analyses of preserved archival zooplankton samples has greatly enhanced that understanding.

Acknowledgments

References

Azoulay, B., 2002: The autecology of the new invader *Eudiaptomus dreischi* in Lake Kinneret. – Ph.D. Dissertation, Hebrew University of Jerusalem, Jerusalem.

Ben-Tuvia, A., Davidoff, E. B., Shapiro, J. & Shefler, D., 1992: Biology and management of Lake Kinneret Fisheries. – Isr. J. Aquacult. **44:** 48–65.

Berman, T., Stone, L., Yacobi, Y. Z., Kaplan, B., Schlichter, M., Nishri, A. & Pollingher, U., 1995: Primary production and phytoplankton in Lake Kinneret: a long-term record (1972–1993). – Limnol. Oceanogr. **40:** 1064–1076.

Berman, T., Yacobi, Y. Z. & Pollingher, U., 1992: Lake Kinneret phytoplankton: stability and variability during twenty years (1970–1989). – Aquat. Sci. **54:** 104–127.

Blumenshine, S. & Hambright, K. D., 2003: Top-down control in Lake Kinneret: a role for invertebrate predation. – Hydrobiologia **491:** 347–356.

Brendonck, L. & De Meester, L., 2003: Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. – Hydrobiologia **491:** 65–84.

Brooks, J. L. & Dodson, S. I., 1965: Predation, body size, and composition of plankton. – Science **150:** 28–35.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B., 2004: Toward a metabolic theory of ecology. – Ecology **85:** 1771–1789.

Carpenter, S. R., 2002: Ecological futures: building an ecology of the long now. – Ecology **83:** 2069–2083.

Carpenter, S. R., Kitchell, J. F., Cole, J. J. & Pace, M. L., 1999: Predicting responses of chlorophyll and primary production to changes in phosphorus, grazing, and dissolved organic carbon (Reply to comment by Nürnberg). – Limnol. Oceanogr. **44:** 1179–1182.

Carpenter, S. R., Kitchell, J. F., Hodgson, J. R., Cochran, P. A., Elser, J. J., Elser, M. M., Lodge, D. M., Kretchmer, D., He, X. & von Ende, C. N., 1987: Regulation of lake primary productivity by food web structure. – Ecology **68:** 1863–1876.

Davis, E. B. & Pyenson, N. D., 2007: Diversity biases in terrestrial mammalian assemblages and quantifying the differences between museum collections and published accounts: A case study from the Miocene of Nevada. – Palaeogeogr. Palaeocl. **250:** 139–149.

Drenner, R. W. & Hambright, K. D., 2002: Piscivores, trophic cascades and lake management. – The Scientific World Journal **2:** 284–307.

Easton, J. & Gophen, M., 2002: Trophic relations between zooplankton and bleaks (*Acanthobrama* spp.) in Lake Kinneret (Israel). – Verh. Internat. Verein. Limnol. **28:** 1258–1261.

Edmondson, W. T., 1991: The uses of ecology: Lake Washington and beyond. – University of Washington Press, Seattle.

Freeland, J. R., Anderson, S., Allen, D. & Looney, D., 2007: Museum samples provide novel insights into the taxonomy and genetic diversity of Irish red grouse. – Conserv. Gen. **8:** 695–703.

Galbraith, M. G., 1967: Size-selective predation on *Daphnia* by rainbow trout and yellow perch. – Trans. Amer. Fish. Soc. **96:** 1–10.

Gliwicz, Z. M., 2002: On the different nature of top-down and bottom-up effects in pelagic food webs. – Freshwat. Biol. **47:** 2296–2312.

Gophen, M., 1973: Zooplankton in Lake Kinneret.– In: Berman, T. (ed.): Lake Kinneret: Data Record. – NCRD, Jerusalem, pp. 61–67.

– 1977: Food and feeding habits of *Mesocyclops leuckarti* (Claus) in Lake Kinneret (Israel). – Freshwat. Biol. **7:** 513–518.

– 1978a: The productivity of *Mesocyclops leuckarti* (Claus) in Lake Kinneret (Israel). – Hydrobiologia **60:** 17–22.

– 1978b: Zooplankton.– In: Serruya, C. (ed.): Lake Kinneret. – Dr. Junk Publishers, The Hague, 297–311

– 1984: The impact of zooplankton status on the management of Lake Kinneret (Israel). – Hydrobiologia **113:** 249–258.

– 1988: Changes of copepod populations in Lake Kinneret during 1969–1985. – Hydrobiologia **167/168:** 375–379.

– 1992a: Long-term changes of plankton communities in Lake Kinneret, Israel. – Asian Fish. Sci. **5:** 291–302.

– 1992b. Zooplankton development in Lake Kinneret during the period 1969–1991, Special Report No. T7/92. – Kinneret Limnological Laboratory, Israel Oceanographic and Limnological Research.

– 2000: Lake Kinneret (Israel) ecosystem: long-term instability or resiliency? – Air Soil Water Poll. **123:** 323–335.

– 2003: Water quality management in Lake Kinneret (Israel): hydrological and food web perspectives. – J. Limnol. **62, Suppl. 1:** 91–101.

– 2005: Seasonal rotifer dynamics in the long-term (1969–2002) record from Lake Kinneret (Israel). – Hydrobiologia **546:** 443–450.

Gophen, M. & Azoulay, B., 2002: The trophic status of zooplankton communities in Lake Kinneret (Israel). – Verh. Internat. Verein. Limnol. **28:** 836–839.

Gophen, M., Drenner, R. W. & Vinyard, G. G., 1983a: Fish introductions into Lake Kinneret – call for concern. – Fish. Manage. **14:** 43–45.

– – – 1983b: Cichlid stocking and the decline of the Galilee Saint Peter's fish (*Sarotherodon galilaeus*) in Lake Kinneret, Israel. – Can. J. Fish. Aquat. Sci. **40:** 983–986.

Gophen, M., Serruya, S. & Spataru, P., 1990a: Zooplankton community changes in Lake Kinneret (Israel) during 1969–1985. – Hydrobiologia **191:** 39–46.

Gophen, M., Serruya, S. & Threlkeld, S., 1990b: Long term patterns in nutrients, phytoplankton and zooplankton of Lake Kinneret and future predictions for ecosystem structure. – Arch. Hydrobiol. **118:** 449–460.

Hambright, K. D., Eckert, W., Leavitt, P. R. & Schelske, C. L., 2004: Effects of historical lake level and land use on sediment and phosphorus accumulation rates in Lake Kinneret. – Environ. Sci. Tech. **38:** 6460–6467.

Hambright, K. D. & Fridman, S., 1994: CAPAS: A computer-assisted plankton analysis system for the Macintosh. – Fisheries **19:** 6–8.

Hambright, K. D., Gophen, M. & Serruya, S., 1994: Influence of long-term climatic changes on the stratification of a subtropical, warm monomictic lake. – Limnol. Oceanogr. **39:** 1233–1242.

Hambright, K. D. & Shapiro, J., 1997: The 1993 collapse of the Lake Kinneret commercial bleak fishery. – Fish Manage. Ecol. **4:** 275–283.

Hambright, K. D. & Zohary, T., 2001: Lake Kinneret dilul program: success or not? – Agamit **151:** 7–9.

Hambright, K. D., Zohary, T., Eckert, W., Schwartz, S. S., Schelske, C. L., Laird, K. R. & Leavitt, P. R., 2008: Exploitation and destabilization of a warm, freshwater ecosystem through engineered hydrological change. – Ecol. Appl., **18:** 1591–1603.

Hambright, K. D., Zohary, T. & Güde, H., 2007: Microzooplankton dominate carbon flow and nutrient cycling in a warm subtropical freshwater lake. – Limnol. Oceanogr. **52:** 1018–1025.

Hurlbert, S. H. & Mulla, M. S., 1981: Impacts of mosquitofish (*Gambusia affinis*) predation on plankton communities. – Hydrobiologia **83:** 125–151.

Jackson, J. K. & Fureder, L., 2006: Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. – Freshwat. Biol. **51:** 591–603.

Kerfoot, W. C., 1981a: A history of predation on *Bosmina*. – Ecology **62:** 216–233.

– 1981b: Long-term replacement cycles in cladoceran communities: a history of predation. – Ecology **62:** 216–233.

Klimov, P. B., O'Connor, B. M. & Knowles, L. L., 2007: Museum specimens and phylogenies elucidate ecology's role in coevolutionary associations between mites and their bee hosts. – Evolution **61:** 1368–1379.

Larkin, P. A., 1977: An epitaph for the concept of maximum sustained yield. – Trans. Amer. Fish. Soc. **106:** 1–11.

Mackay, A. W., 2007: The paleoclimatology of Lake Baikal: A diatom synthesis and prospectus. – Earth-Sci. Rev. **82:** 181–215.

Mills, E. L., Forney, J. L. & Wagner, K. J., 1987: Fish predation and its effect on the Oneida Lake food chain. – In: Kerfoot, W. C. & Sih, A. (eds): Predation: direct and indirect impacts on aquatic communities. – University Press of New England, Hanover.

Mills, E. L. & Schiavone, J. A., 1982: Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivity. – N. Amer. J. Fish. Manage. **2:** 14–17.

Nürnberg, G., 1999: Determining trophic state in experimental lakes. – Limnol. Oceanogr. **44:** 1176–1179.

O'Brien, W. J., 1987: Planktivory by freshwater fish: thrust and parry in the pelagia. – In: Kerfoot, W. C. & Sih, A. (eds): Predation: direct and indirect impacts on aquatic communities. – University Press of New England, Hanover, pp. 3–16.

Ostrovsky, I., 2005: Assessing mortality changes from size-frequency curves. – J. Fish. Biol. **66:** 1624–1632.

Ostrovsky, I. & Walline, P., 2001: Multi-annual changes in the pelagic fish *Acanthobrama terraesanctae* in Lake Kinneret (Israel) in relation to food sources. – Verh. Internat. Verein. Limnol. **27:** 2090–2094.

Roelke, D. L., Zohary, T. & Hambright, K. D., 2007: Alternative states in the phytoplankton of Lake Kinneret, Israel (Sea of Galilee). – Freshwat. Biol. **52:** 399–411.

Sanford, P. R., 1993: *Bosmina longirostris* antennule morphology as an indicator of intensity of planktivory by fishes. – Bull. Mar. Sci. **53:** 216–227.

Serruya, C., (ed.), 1978: Lake Kinneret. – Dr. Junk Publishers, The Hague.

Walline, P. D., Tyler, J. A., Brandt, S. B., Ostrovsky, I. & Jech, J. M., 2000: Lavnun abundance: how changes may affect consumption of Lake Kinneret zooplankton. – Arch. Hydrobiol., Spec. Iss. Adv. Limnol. **55:** 493–511.

Zohary, T., 2004: Changes to the phytoplankton assemblage of Lake Kinneret after decades of a predictable, repetitive pattern. – Freshwat. Biol. **49:** 1355–1371.