



## Top-down control in pelagic systems: a role for invertebrate predation

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### Abstract

Limnologists have long recognized the importance of predation in freshwater communities. The majority of study of predator effects has involved vertebrate predators, with emphasis on planktivorous fish. Documented effects of planktivorous fish have been so dramatic that manipulations of their populations are seen by many as potential tools in lake management. However, the success of such manipulations is often less than desired due to the ubiquitous complexity of food webs and the pervasiveness of compensatory responses to food web manipulation. Recently, enormous effort has been applied to the Lake Kinneret pelagic food web in effort to reduced the abundance of the planktivorous Kinneret bleak *Acanthobrama terraesanctae* and thereby increase the biomass of herbivorous zooplankton in the hopes of increasing water clarity. We compared potential predation pressure on Lake Kinneret herbivorous zooplankton by bleak and the other major zooplankton predators in the lake, the cyclopoid copepods *Mesocyclops ogunnus* and *Thermocyclops dybowskii*. We found that, despite having much lower biomass, cyclopoid copepods accounted for a greater portion of the predation mortality on herbivorous zooplankton than bleak. Our results suggest that reductions in predation pressure by bleak will not yield subsequent increases in herbivorous zooplankton biomass. Rather, reductions in bleak predation pressure may allow for increases in cyclopoid copepod abundance and thereby a net increase in predation pressure on herbivorous zooplankton.

### Introduction

Since the 1960s, and typically credited to publications such as Hairston et al. (1960) and Paine (1966), ecologists have recognized that observed community dynamics are often dominated by effects of predation. Of course, the actual importance that predation plays in any given community is dependent on many aspects of the particular community. This is especially true for lakes, in which the extreme variability in the roles of piscivory in different lakes fueled the ‘top

down–bottom up’ dichotomy (Carpenter et al., 1985; McQueen et al., 1989; DeMelo et al., 1992). It is now widely held that most of this variability emanates from the intricacies of the particular community under study (Drenner & Hambright, in prep.). For example, increases in predation (e.g., by predator supplementation) can result in compensatory shifts in relative abundances of herbivore species differing with respect to vulnerability to predation thus damping any cascade of predator effects to the primary producers. The literature is replete with such examples (see Smith, 1967;

Hambright, 1994; Benndorf et al., 2000; Ramcharan et al., 2001a). Likewise the presence of intraguild predators (Polis et al., 1989; Mylius et al., 2001) can lessen the transfer of effects of a particular predator through a food chain (Benndorf et al., 2000; Ramcharan et al., 2001a). Thus the complexity of a given community, whether it can be viewed as a simple linear food chain or a food web, will influence the relative strengths of predator effects (Hairston & Hairston, 1993; Polis & Strong, 1996).

The pelagic community of Lake Kinneret (Sea of Galilee), Israel has long been considered a classic case that can be described in terms of, not one, but two simple linear food chains: a non-grazed net-phytoplankton to decomposer chain and the more typical nanophytoplankton to herbivorous zooplankton to planktivorous fish food chain (piscivores are absent) (e.g., Serruya et al., 1980). During spring, the phytoplankton of the lake are typically dominated (as much as 95% of the standing biomass) by a population of the large, thecate dinoflagellate *Peridinium gatunense*. Because *Peridinium* are not grazed substantially by any metazoan herbivore, the majority of *Peridinium* carbon is considered to pass directly to decomposers (Viner, 1998; Zohary et al., 1998; Hambright et al., 2002). During the remainder of the year, phytoplankton are dominated by small, nanoplanktonic species that are consumed by herbivorous cladoceran and copepod zooplankton which are then fed upon by planktivorous fish (Gophen, 1984). Research during the past decade has provided clear evidence that the *Peridinium*-based food chain is not so simple, in that it is now considered that *Peridinium* serves as the base of a very complex microbial-loop dominated food web (Zohary et al., 1998, 2000a,b; Hart et al., 2000). Likewise, recent food-web models incorporating microbial loop components (Walline et al., 1993; Hart et al., 2000) have also suggested that the nanoplankton-based trophic system is equally complex. Interestingly, these models also predict that planktivorous fish may serve as minor predators on herbivorous zooplankton, with the majority of top down regulation on the herbivorous zooplankton by way of predatory cyclopoid copepods.

Here we examine this prediction further and present results from a guild-specific analysis of predation pressure on herbivorous zooplankton that corroborates model predictions and suggest that top-down forces from planktivorous fish in Lake Kinneret may be dampened by the compensatory response of intraguild predators.

### The study system: Lake Kinneret

Lake Kinneret is a relatively large (168 km<sup>2</sup>), warm monomictic, subtropical freshwater lake in northern Israel. Physical, chemical and biological characteristics of the lake have been extensively detailed for more than three decades (see Serruya, 1978; Berman et al., 2000). Because the lake serves as the primary surface reservoir for Israel's domestic water consumption, water quality in the lake is of extreme importance (Berman, 1972; Hambright et al., 2000) and is thus reflected in most management activities. One such management activity is centered on the long-standing paradigm that the lake's good water quality can be preserved by the maintenance of high zooplankton biomass through the artificial reduction in standing stocks of planktivorous fish (Gophen, 1995). Gophen (1984) and Gophen et al. (1990a,b) documented, a gradual, but substantial decline in zooplankton biomass of Lake Kinneret since the 1970s. They attributed this decline to increasing predation pressure from zooplanktivorous fish resulting from excessive fish stocks. As a result, calls were made for increasing commercial fishing pressure on the dominant planktivore, the Kinneret bleak (*Acanthobrama terraesanctae* [= *Mirogrex terraesanctae*) (e.g., Gophen, 1995). There was little response from the commercial fishery because harvest rates (tons per annum) were limited by demand from an already saturated market (J. Shapiro, Isr. Dept. Fish., Tiberias, pers. comm.). Nevertheless, harvest pressure did increase during the late 1980s and early 1990s as a result of an unrelated increased fishing effort on larger size classes in the Kinneret bleak population (Hambright & Shapiro, 1997). This increased selectivity on larger individuals in the harvest resulted in reduced mean body size and age in the population. Eventually the bleak fishery collapsed altogether in 1993/94 as the population became devoid of individuals of commercially harvestable sizes (Hambright & Shapiro, 1997) yet bleak population density had increased more than 2-fold (Ostrovsky & Walline, 2001). Following the collapse, a government subsidy was advocated to allow for continued harvest of the Kinneret bleak population, albeit on very small, non-marketable fish (Walline et al., 2000). This program began in 1995 and has continued through 7 years to no avail – the population remains large and dominated by sub-commercial sizes (J. Shapiro, pers. comm.).

Regardless of the efficacy of the subsidy program on effecting the fish population, our study was instigated by an even more basic question: If lake managers

wish to affect herbivorous zooplankton biomass in Lake Kinneret, is manipulation of the bleak population an appropriate strategy?

## Methods

We compared predation pressure on Lake Kinneret herbivorous zooplankton by the two major groups of known zooplankton predators in the lake, the planktivorous cyprinid fish, Kinneret bleak, and the adult and stage V copepodids of the cyclopoid copepods, *Mesocyclops ogunnus* (formerly *M. leuckarti*) and *Thermocyclops dybowskii*. In keeping with the current long-standing view of herbivory in Lake Kinneret (e.g., Serruya et al., 1980), we defined 'herbivorous zooplankton' as all members of the Cladocera (mostly *Ceriodaphnia* spp., *Bosmina* spp., *Diaphanosoma* sp., *Moina* sp., and *Chydorus* sp.) and juvenile copepodid stages of *M. ogunnus* and *T. dybowskii*. The micro-grazers (protists, rotifers and copepod nauplii) were excluded from our analyses.

In general, potential predation pressure was estimated for both predators using temperature-dependent, mass-specific ingestion rates, diet composition, and monthly standing stock (cycloids) or growth and standing stock (bleak) estimates for predator populations. For all analyses we used the epilimnetic monthly mean temperatures for 1989–1999 from the Lake Kinneret database (Kinneret Limnological Laboratory, 2001).

### Invertebrate predation: cycloids

Though somewhat omnivorous, we considered all stage V copepodids and adult of *M. ogunnus* and *T. dybowskii* as predatory (Gophen, 1977). We characterized invertebrate predator biomass using 1989–1999 monthly biomass estimates from the Lake Kinneret database (Kinneret Limnological Laboratory, 2001) (Fig. 1A). Areal biomass (calculated as the product of volumetric biomass and epilimnion thickness on each sampling date) and rate values for cycloids were multiplied by the lake area (170 km<sup>2</sup>) to produce lake-wide standing stocks or rates (i.e., mass or mass day<sup>-1</sup>). Monthly temperature-dependent specific ingestion rates for invertebrate predators based on data for adult female *M. ogunnus* from Gophen (1976), were expressed by the quadratic equation:

$$\text{Ingestion (g}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}) = -0.008T^2 + 0.454T - 4.65, \quad (1)$$

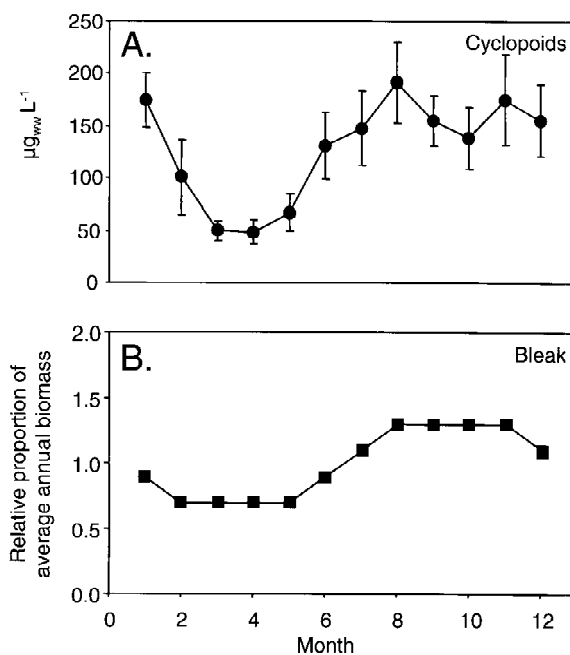


Figure 1. (A) Mean ( $\pm$  SE) monthly biomass ( $\mu\text{g}_{\text{ww}}\text{L}^{-1}$ ) of stage V and adult cycloids copepods in Lake Kinneret during 1989–1999. Monthly means were calculated from biweekly, depth-integrated samples from three pelagic (>25 m) stations (Kinneret Limnological Laboratory, 2001). (B) Index of monthly adjustment to bleak biomass. Monthly and seasonal variation around annual biomass estimates are influenced by several factors such as spawning (–) during Nov–Jan, and year-round fishing pressure (–) that peaks Nov–Mar when >70% of harvest occurs, and hatching, recruitment and growth (+) during spring and summer.

where  $T$  is the mean epilimnion temperature in °C (Fig. 2). Although these estimates are based on *Artemia* nauplii as the sole source of food, recent laboratory experiments using natural Lake Kinneret zooplankton assemblages (KDH, unpublished) corroborated the absolute ingestion rates derived from Equation (1) and found that herbivorous zooplankton (cladocerans + juvenile cycloids) constituted  $84 \pm 2\%$  of cyclopoid diets. Micro-grazers accounted for the remainder.

### Vertebrate predation: planktivorous fish

Unlike crustaceans, most fishes exhibit indeterminate growth and allometrically related energy demands which require an additional input of age, size structure, and growth in order to estimate prey demand. We used a fish bioenergetics model (Hanson et al., 1997) which incorporates temperature with fish mass and growth to estimate a daily energy ration and thus prey demand.

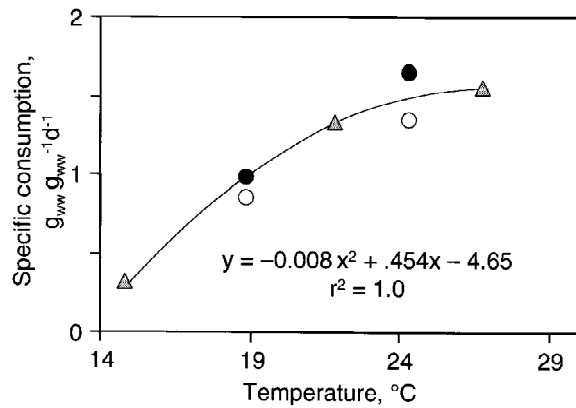


Figure 2. Temperature-specific consumption rates of cyclopoid copepods in Lake Kinneret. Triangles and fitted curve indicate results from Gophen (1976) for adult female *M. ogunnus* feeding on *Artemia* nauplii; circles are ingestion rates of natural copepod assemblages estimated by density-dependent mortality rates of large herbivorous zooplankton (open circles) and total herbivorous zooplankton (closed circles) (KDH, unpublished). Micro-zooplankton (= protists, rotifers and copepod nauplii and calculated as the difference in consumption between total and large herbivores) accounted for a mean of 16% of copepod consumption in these two experiments.

Observed bleak growth rates were inputs to the model. The model output was an estimate of the amount of energy needed to manifest the observed growth primarily based on water temperature, fish body size, and predator and prey energy densities. Coefficients for these relationships in the model are taken from prior studies (Cummins & Wuycheck, 1971; He, 1986). We followed Walline et al. (2000) in setting optimal ( $T_{opt} = 27^\circ\text{C}$ ) and maximum ( $T_{max} = 30^\circ\text{C}$ ) temperatures for Lake Kinneret bleak consumption.

Bleak production and prey demand estimates were based on published age structure (Davidoff, 1982) and von Bertalanffy growth coefficients (Ostrovsky & Walline, 1999). The resulting growth trajectories are similar to those generated in other studies on Lake Kinneret bleak (Steinitz, 1959; Davidoff, 1986). Although these age structure and growth variables are not contemporaneous, we sought to generally characterize a bleak population prior to the collapse of the bleak fishery. The total annual growth and the resulting energy demand was modeled separately for three bleak cohorts (Age I–III inclusive) to account for allometric variation in growth rates and prey demand.

In order to estimate lake-wide predation pressure we estimated an annual mean bleak biomass of 2700 t (Walline et al., 1991; Hambright & Shapiro, 1997; Ostrovsky & Walline, 1999). We used a mean annual

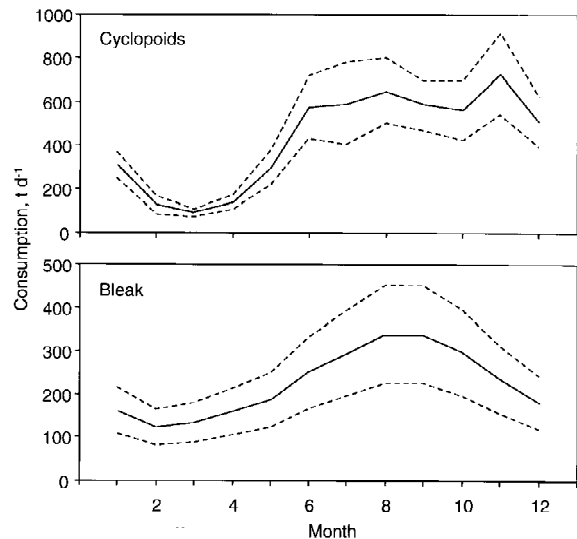


Figure 3. Mean annual pattern of consumption rates (tons day<sup>-1</sup>) of bleak and cyclopoid copepods on Lake Kinneret herbivorous zooplankton  $\pm$  error. Error terms are S.E. of monthly biomass estimates for cyclopoids, and  $\pm$  33% of monthly biomass estimates for bleak.

biomass value near the high end of the available range of estimates to avoid underestimating bleak predation pressure. Monthly estimates of bleak biomass are not available as they are for zooplankton. We therefore devised a monthly index of this seasonal variation (up to 30%) based on mechanisms most likely to influence bleak biomass such as fishing, spawning, recruitment, and growth (Fig. 1B). Although no data are available for earlier time periods, a recent report (Walline & Kallikman, 2000) indicated a similar pattern in seasonal dynamics of bleak biomass in 1998–99.

Experiments on the feeding rate and diet of bleak on zooplankton prey (KDH, unpublished) demonstrated that 88% of the prey consumed by bleak was herbivorous zooplankton; the remainder being predatory cyclopoids. This result is supported by other studies finding the predominance of herbivorous pelagic zooplankton in bleak diets (Gophen & Scharf, 1981; Gophen & Threlkeld, 1989; Easton & Gophen, in press). Thus, the predation pressure by bleak on herbivorous zooplankton is estimated as the product of the total ration estimated from the bioenergetics model  $\times$  0.88.

## Results

Our analyses suggest that invertebrate predators exert most (66%) of the predation pressure on herbivorous

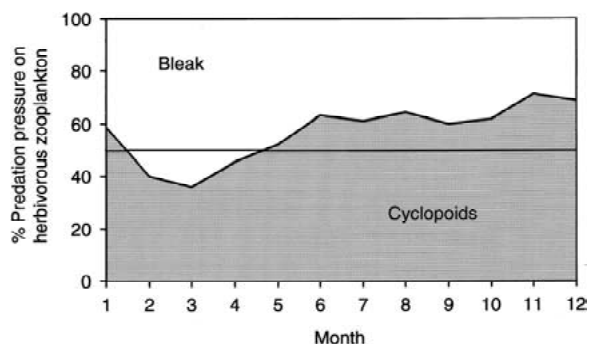


Figure 4. Mean annual pattern of proportional consumption of Lake Kinneret herbivorous zooplankton by bleak and cyclopoid copepods. Cyclopoids average 66% of the annual consumption between these two predators. The horizontal line delineates equal proportions between predators.

zooplankton in Lake Kinneret, with higher proportions in June–December (Figs 3 and 4). The predation pressure of vertebrate and invertebrate predators varies seasonally but in similar ways on an annual cycle. Predation pressure for both predators is largely dictated by water temperature and predator biomass which are both relatively low in late winter and early spring compared to late summer. During late winter and early spring bleak inflict a slight majority of the predation mortality on herbivorous zooplankton (Fig. 4). However, this season also corresponds to the nadir of both bleak and cyclopoid predation pressure (Fig. 3), and thus relatively low predation pressure and potential for limitation of herbivore biomass.

Cyclopoids consume greater quantities of herbivorous zooplankton than bleak despite nearly an order of magnitude less biomass in the lake. Monthly mean predatory cyclopoid biomass ranged from 204 to 782 t. For this comparison, we estimated bleak biomass to range between 1890 and 3510 t, to account for seasonal variation due to fishing, spawning, recruitment, and growth, though fishing mortality is likely underestimated by our approach. As expected, mass specific consumption rates on herbivorous zooplankton by cyclopoids (mean =  $921 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ; range 242–1284  $\text{mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ) versus bleak (mean =  $74 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ; range = 42–122  $\text{mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ) was an order of magnitude higher. Consequently, the effects of a reduction in bleak biomass (whether stochastic or managed) on herbivorous zooplankton prey may be mitigated by just ca. one-tenth of an increase in biomass of stage V and adult copepodids (Fig. 5).

In contrast to cyclopoids, bleak biomass dynamics are poorly understood. Predation pressure by bleak

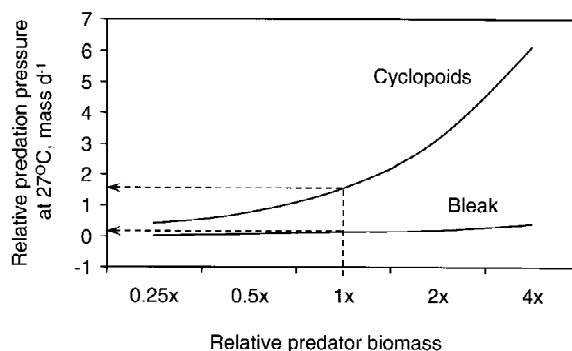


Figure 5. Relationship between consumption rates ( $\text{g day}^{-1}$ ) and standardized relative biomass for vertebrate and invertebrate predators as defined in this study. The slope of the relationship is the mass-specific consumption rate on herbivorous zooplankton for each predator at  $27^\circ\text{C}$ , the temperature of maximum consumption rates for both predators (bleak =  $0.105 \text{ g}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ; age-class weighted average, and cyclopoids =  $1.28 \text{ g}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ). Thus attempting to reduce bleak biomass (e.g., via management) as a mechanism for lower bleak prey demand may be easily confounded by proportionally smaller changes in cyclopoid biomass.

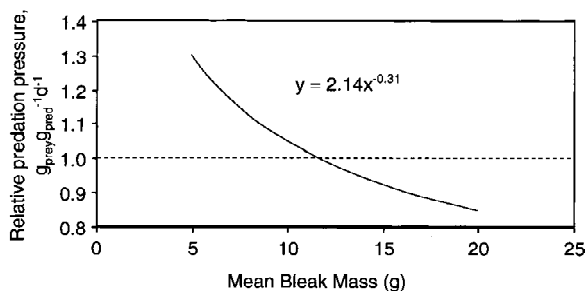


Figure 6. Relationship between mean bleak size and relative total predation pressure ( $\text{g}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ). Relative predation pressure is standardized to the mean bleak size used in our analysis (11.55 g). Given a constant biomass, this relationship demonstrates the greater influence of change in mean predator size relative to total biomass as presented in Figure 5. In contrast to crustaceans, this relationship is relevant for fishes which have indeterminate growth and relatively constant diets over a body-size gradient.

can also vary independently of biomass via changes in population size structure (Fig. 6). This is especially relevant given the recent dramatic changes in the size structure of the bleak population (Hambricht & Shapiro, 1997; Ostrovsky & Walline, 2001). For example, from 1990 to 1992 >95% of individuals in the bleak catch were >125 mmTL, versus an average of 10% during 1995–1999 (J. Shapiro, pers. comm.). This abrupt shift was preceded (1982–1992) by harvests comprised of increasingly larger individuals (Hambricht & Shapiro, 1997). The resultant shift to a smaller size distribution in the unharvested portion

of the population would be expected to increase mass-specific predation rates on herbivorous zooplankton by bleak (Fig. 6).

## Discussion

We found that invertebrate predators account for a greater portion of the predation mortality on herbivorous zooplankton than zooplanktivorous fish. Thus, the consumer trophic structure and prey demand in the Lake Kinneret food web suggest that alternating control of trophic levels through the linear food chain <planktivorous fish – herbivorous zooplankton – phytoplankton> is unlikely. Compared to bleak, the vertebrate predator, invertebrates accounted for a greater proportion of predation pressure on herbivorous zooplankton, despite a much lower biomass. A second related factor is that relative variation in invertebrate biomass will have much greater impact on herbivorous zooplankton predation mortality than changes in vertebrate biomass (Fig. 5). This contrast is driven by differences in mass-specific predation rates between small invertebrate and relatively larger vertebrate predators. Predation rate is therefore a better estimator of predation pressure than predator biomass (Blumenshine et al., 2000), especially when predators vary greatly in size. Ultimately, predation rate should be expressed in terms relative to prey dynamics, e.g., mortality rate, in order to better weigh predation pressure.

### Sources of bias in predation rate estimates

Our estimates of predation for the two predators in Lake Kinneret contain various forms of bias that must be explored further in order to determine the true nature of predation pressure on herbivorous zooplankton in Lake Kinneret. For example, invertebrate predators differ from gape-limited fish in that only smaller prey such as rotifers are consumed whole (Papinska, 1985; Hansen & Santer, 1995), whereas larger prey may be consumed only partially. Maier (1990) found that the 'ingestion efficiency' (ingestion rate/mortality rate) for *Mesocyclops leukarti* feeding on the cladoceran *Moina brachiata* was much lower (0.50) compared to that when feeding on the rotifer *Asplanchna* sp. (0.88). Partial consumption can therefore result in underestimating prey mortality based on predator energy demand. Thus, considering this mode of feeding and our operating definition of herbi-

vorous zooplankton prey (see Methods), consumption rate derived from experiments using *Artemia* nauplii is a conservative estimator of prey mortality inflicted by invertebrate predators and consequently our estimates of total predation pressure on the herbivorous zooplankton may be low. Because these consumption rates were corroborated by experiments using natural plankton assemblages (see Fig. 2) in which consumption was estimated from prey mortality, we conclude that this bias is minimal.

A second form of bias is introduced through omnivory in cyclopoids. Although we assume that all stage V and adult cyclopoids in Lake Kinneret are carnivorous, they clearly can consume large algae and other particles when herbivorous zooplankton may be low in abundance (Gophen, 1977). Thus our estimates may be inflated somewhat even though we adjusted consumption rates downward by 16% to account for ingestion of micro-zooplankton (ciliated and flagellated protists, rotifers and copepod nauplii). However, any omnivory bias is likely countered by the fact that we did not include stage IV cyclopoid copepodids in our analysis. Stage IV copepodids, which account for an additional 34% of copepod biomass, compared with stage V and adults, are also carnivorous as Gophen (1977) found *Ceriodaphnia* to be common items in their guts. Thus, actual consumption could also be 34% higher if stage IV copepodids were included. Overall, however, we feel that cyclopoid predation pressure on herbivorous zooplankton shown in Figure 3 provides a reasonably conservative estimate.

There are also uncertainties with regards to fish predation estimates. Fish biomass is often the largest source of error in estimating fish prey demand (Schnute & Richards, 2001). Lake Kinneret fishery stocks have not been as well documented as fishery catches. We use the few available sources of bleak biomass estimates from both fisheries and research acoustic data. Bleak biomass estimates range from ca. 1687 to 3000 t for the past decade (Walline et al., 1991, 1993, 2000; Hambright & Shapiro, 1997; Ostrovsky & Walline, 1999). Based on these data, the absolute and relative predation pressure of bleak on herbivorous zooplankton is likely overestimated as we used a relatively high estimate of mean annual bleak biomass (2700 t).

Our approach to estimating total bleak consumption with a bioenergetics model originates with estimating the energy demands on a mass-specific basis times the estimated population biomass. Our estimated mean of bleak mass-specific total energy demand

( $95 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ) was 2.5 times that found by Gophen & Threlkeld (1989) ( $38 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$ ). Our estimate is derived from bioenergetics model calculations of the amount of energy needed to produce the observed amount of bleak production in Lake Kinneret. Our resulting estimate of mean daily gross growth efficiency ( $K_1$ , based on mass) is 26%, very close to the general value (28%) for carnivorous fishes (Schroeder, 1981). The estimated low feeding rate in Gophen & Threlkeld (1989) may have been affected by experimental artifacts. The  $38 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$  is the result of bleak feeding on zooplankton in 65-l glass aquaria. Recent research focusing on the explicit effects of experimental enclosure size on planktivore growth and feeding has found that planktivore (*Anchoa mitchelii*) feeding rates in  $1\text{-m}^3$  enclosures were 60% of feeding rates in  $10\text{-m}^3$  enclosures (Mowitt, 1999; Heath & Houde, 2001). *Anchoa mitchelii* growth rates (and thus feeding rates) in the larger enclosures were well within the range observed in the natural system. In fact, applying the bleak ration, mass, and water temperature used in Gophen & Threlkeld (1989) as inputs to the bioenergetics model we used (Hanson et al., 1997) produces a very low proportion of maximum consumption ( $P = 0.27$  or 27%) and an unsustainable growth rate of  $-1\% \text{ day}^{-1}$ . Without actual bleak growth data from Gophen & Threlkeld (1989), cross-validation between their experiment and our approach is impossible. If our modeling approach does overestimate feeding rate, the actual proportion of predation pressure on herbivorous zooplankton by bleak would be even lower than our estimate of 34%.

An alternative bioenergetics approach is to estimate the *potential* predation of bleak on zooplankton, based on fish allometry and water temperature data alone while omitting any basis for actual energy demand. In contrast, we ask the question of how much prey must be consumed to realize an observed amount of bleak production. Walline et al. (2000) used this first approach (potential predation) in assessing the potential for bleak to regulate zooplankton biomass in Lake Kinneret. This approach produces quite different rations than those from the 65-l aquarium experiments of Gophen & Threlkeld (1989). The potential consumption approach of Walline et al. (2000) produced a ration range of  $151\text{--}184 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$  based on April and June 1998 bleak population size structure and water temperature. These high estimates coupled with an estimate of zooplankton production (Walline et al., 1993) led to the conclusion that re-

ductions in bleak biomass (e.g., through management actions) could indeed lead to reduced predation mortality on zooplankton. However, this linear food chain assumption and its utility for management is limited to two ways. First, in that predators rarely realize their maximum potential ration, and secondly in estimating a trophic level impact as represented by a single population from the guild of predators on herbivorous zooplankton. Walline et al. (2000) ultimately suggest that an analysis on the actual consumption of zooplankton by planktivorous fish and predatory invertebrates would be of considerable benefit to Lake Kinneret food web management.

#### *Other estimates of predatory mortality on herbivores*

Though an early carbon-flow model developed for the lake in the 1970s (Serruya et al., 1980) reflects the importance of fish in plankton abundances and production, later models that have allowed for increased food web complexity (including invertebrate predation and the microbial loop) (Walline et al., 1993; Hart et al., 2000) suggest that the earlier model of fish effects may be over-rated. A mass-balanced carbon flow model by Hart et al. (2000) estimated that bleak predation accounts for 31–53% (mean = 42%) of the predation on herbivorous zooplankton, with the higher proportions occurring in spring as in our analysis. Walline et al. (1993) estimated that bleak account for just 20% of the predation mortality on herbivorous zooplankton with the remainder due to cyclopoids. However, this relatively low estimate may be the consequence of a relatively high cyclopoid biomass and an underestimate of bleak ration used in their analysis. The cyclopoid biomass ( $3.2 \text{ g m}^{-2}$ ) used in their model was slightly higher than what we found in the Lake Kinneret database for 1989–1999 (mean =  $2.8 \text{ g m}^{-2}$ ). Walline et al. (1993) estimate a mean annual bleak biomass of 3000 t, but use the relatively low bleak ration of  $38 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$  produced by Gophen & Threlkeld (1989). Based on bioenergetics analysis, a ration of only  $38 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$  would amount to negative growth. Adjusting this estimate of bleak ration to our estimated biomass and ration on herbivorous zooplankton of  $74 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}$  results in bleak accounting for  $20\% \times (2700 \text{ t}/3000 \text{ t})(74 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1} / 38 \text{ mg}_{\text{prey}} \text{ g}_{\text{pred}}^{-1} \text{ day}^{-1}) = 35\%$  of the predation mortality on herbivorous zooplankton, extremely close to our estimate of 34%.

### *Invertebrate predation in pelagic food webs*

Although the Lake Kinneret pelagic food web is unconventional in the absence of piscivores and the relatively small organisms (cyclopoids) constituting the invertebrate predator guild, there are many examples of results similar to ours, in which the predation pressure on zooplankton by invertebrate predators may exceed that of planktivorous fish. Indeed, this is theoretically necessary in order for an intraguild predator to survive (Polis et al., 1989). In other pelagic food webs, invertebrate predators have been shown to functionally replace or have stronger effects on prey than planktivorous fish when the fish are removed (e.g., through biomanipulation or harvest). For example, *Chaoborus* predation rates may exceed production of their zooplankton prey (Saunders & Lewis, 1988; Yan et al., 1991; Ramcharan et al., 2001a). The responses of *Chaoborus* spp. was such that total consumption of zooplankton was either unchanged or higher when planktivorous fish were reduced (Ramcharan et al., 2001b). *Leptodora* have the ability to greatly reduce zooplankton biomass in the absence of planktivorous fishes (Braband et al., 1986; Benndorf, 1995). *Bythotrephes cederstroemi* energy demands in Lake Michigan have been estimated to equal or exceed herbivorous cladoceran production (Lehman & Caceres, 1993; Yurista & Schulz, 1995). These and other examples demonstrate the functional redundancy among species within pelagic feeding guilds. In fact, this redundancy and the compensatory trade-offs in exerting predation pressure upon zooplankton by invertebrates and fish suggest that managing one species as a trophic level is likely ineffectual (Drenner & Hambright, in prep.). Interactions between trophic levels become increasingly diffuse when predator and prey are comprised of several taxa, with no focal predator or prey species (Holt & Lawton, 1994).

### *Specific Implications and conclusions*

The implications of our findings and those of other studies that predatory copepods account for the majority of predation on herbivorous zooplankton suggest that attempts to increase herbivore grazing pressure on phytoplankton through removal of zooplanktivorous fish will likely be diluted and ineffective. Moreover, if consumption by fish represents a substantial source of predatory copepod mortality, a reduction of fish could even have the opposite effect intended if copepods responded positively to the reduction in fish

biomass. Independent of our analysis, whether bleak can regulate herbivorous zooplankton biomass in Lake Kinneret is equivocal. Some studies strongly implicate bleak in a controlling role (Gophen & Pollinger, 1985; Ostrovsky & Walline, 2000), while modeling efforts tend to suggest otherwise (Walline et al., 1993; Hart et al., 2000). Even if bleak account for most of the predation mortality on herbivores in the spring, this is a period of low predation rates on herbivores (Fig. 3 this study, Hart et al., 2000) and herbivores are unlikely to control spring phytoplankton biomass or production which is dominated by largely inedible net-phytoplankton (*Peridinium gatunense*) (Zohary et al., 1998). Two of the main points in our study suggest that management of predation pressure on herbivorous zooplankton through attempted reductions in bleak biomass are likely to be ineffective. First, predation pressure on herbivorous zooplankton by cyclopoids exceeds that of bleak by a 2:1 ratio based on mean daily averages. Second, the mass-specific predation rates by cyclopoids versus bleak are such that small, stochastic changes in cyclopoid biomass are much more likely to affect predation pressure on herbivorous zooplankton than attempts to maintain low biomasses of a relatively fast-growing fish.

Recent experiments and analyses (e.g., Zohary et al., 1998; Hart et al., 2000; Hambright et al., 2002) of the Lake Kinneret pelagic food web suggest complex interactions with implications for the basis for secondary production. Specifically, recent works implicate the micrograzer guild as the primary link between primary production and upper trophic levels (see Hart et al., 2000). Since bleak draw little energy from micrograzers compared to cyclopoids, the expectation is that, in the pelagic food web of Lake Kinneret, cyclopoids are much more important than fish in potential cascading effects to phytoplankton.

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