Can filter-feeding fishes improve water quality in lakes?

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Summary

1.   In this paper we examine the potential of a cichlid fish species (*Sarotherodon galilaeus*) to both maintain positive growth rates through filter-feeding on phytoplankton and improve water quality in Lake Kinneret through suppression of dinoflagellate (*Peridinium gatunense*) blooms.

2.   Seasonal plankton consumption by *S. galilaeus* from Lake Kinneret was examined experimentally by monitoring changes in plankton assemblages during 24 h in 5-m^3 mesocosms containing varying densities of fish. Taxon-specific grazing rates ranged from 0 to 17 mg g_{fish} day^{-1}, with mean total consumption of 1.6% fish body weight per day. During the spring bloom of *P. gatunense*, *S. galilaeus* consumed mostly (94%) netphytoplankton ($\geq$20 μm). The remaining 6% consisted mostly of nanophytoplankton (<20 μm). During the summer and fall, net- and nanophytoplankton accounted for 54 and 42%, respectively, of the diet of *S. galilaeus*. Zooplankton and flagellated and ciliated protozoans made up the remaining 4%.

3.   Simulations using a fish bioenergetics model indicated that consumption rates (*C*) were near maximum in spring (90% C_{max}), while consumption was reduced in summer-fall (59% C_{max}). *Sarotherodon galilaeus* obtains sufficient energy through filter-feeding year-round, although most growth ($\geq$60%) occurs during the spring *P. gatunense* bloom.

4.   Despite efficient feeding on *P. gatunense* and nanophytoplankton by *S. galilaeus*, estimates of instantaneous plankton mortality caused by ingestion were two orders of magnitude lower than maximum potential plankton growth rates. Thus the potential for the *S. galilaeus* population in Lake Kinneret to positively affect water quality through algal suppression is low.

Keywords: bacteria, bioenergetics, Cichlidae, consumer-gradient, filter-feeding, mesocosm, *Peridinium*, phytoplankton, planktivore, protozoa, *Sarotherodon*, zooplankton

Introduction

Planktivorous fish and their ecological roles in freshwater ecosystems have been extensively studied during the past 50 years (Hurlbert & Mulla, 1981; Lazzaro, 1987; O'Brien, 1987; Northcote, 1988; Mehner & Thiel, 1999). Most planktivorous fishes can be broadly categorised as 'particulate' or 'visual' feeding predators that visually orient and consume individual prey items and therefore actively select and ingest the most easily seen prey, typically large-bodied or darkly pigmented zooplankton (O'Brien, 1979; Lazzaro, 1987). Relatively little research has focused on filter-feeding planktivores. These fish either swim with mouth agape and operc.ulars flared, passively forcing water into the mouth and over the gill rakers (tow-net filter feeders) or actively pump water across their gill rakers using a series of rapid non-visually directed

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suctions (pump filter feeders). Hence, filter feeding planktivores tend to passively select and ingest zooplankton with poor escape abilities (Drenner, Strickler & O'Brien, 1978). Unlike particulate feeders, whose diets consist nearly completely of herbivorous and carnivorous zooplankton, filter feeders tend to be more omnivorous with phytoplankton and detritus as major dietary components (Durbin, 1979; Drenner *et al.*, 1987a).

Feeding rate in pump filter feeders is dependent on suction volume (i.e. fish size), pumping rate and plankton density (Drenner *et al.*, 1982). Thus small juvenile filter feeders often feed as obligate particulate feeders because their buccal volumes are not large enough to make filter feeding energetically worthwhile (Yowell & Vinyard, 1993). In obligate filter feeding taxa, intermediate-sized individuals will employ both feeding modes, before switching permanently to filter feeding at larger sizes. Some taxa continue to feed facultatively as filter feeders throughout life, as filter feeding alone may provide insufficient energy input for sustained growth (Dempster, Baird & Beveridge, 1995).

Sarotherodon galilaeus (syn *Tilapia galilaea* Artedi) is a filter-feeding planktivorous cichlid, whose range extends throughout north Africa and the Middle East (Fryer & Iles, 1972; Trewavas, 1973). Like other filter-feeding fishes, *S. galilaeus* consumes both phytoplankton and zooplankton. Small [<20 mm standard length (SL)] *S. galilaeus* consume zooplankton as obligate particulate feeders, switching to filter feeding obligately at sizes greater than 62 mm SL (Drenner *et al.*, 1982). Stomach analyses have revealed that the large thecate dinoflagellate *Peridinium gatunense* Nygaard often constitutes the majority of *S. galilaeus* diets in Lake Kinneret, Israel (Spataru, 1976; Spataru & Zorn, 1976). In laboratory experiments, *S. galilaeus* exhibited high feeding efficiencies for all planktonic components, ranging from large zooplankton to small (10 μm) nanophytoplankton (Drenner *et al.*, 1982, 1987a; Vinyard *et al.*, 1988). Mesocosm experiments revealed that *S. galilaeus* feeding can suppress *P. gatunense* growth, although nanophytoplankton biomass was enhanced by indirect suppression of zooplankton and enhancement of nutrient availabilities (Drenner *et al.*, 1987a). Little information exists pertaining to assimilation efficiency and growth of *S. galilaeus* feeding on *P. gatunense* and other algae, although stable carbon isotope analyses suggest that the majority of *S. galilaeus* body carbon is derived from *P. gatunense* (Zohary *et al.*, 1994). Because *P. gatunense* typically predominates the standing biomass of Lake Kinneret phytoplankton and thus contributes negatively to water quality, *S. galilaeus* are considered beneficial to maintaining good water quality in the lake (Serruya *et al.*, 1979; Serruya, Gophen & Pollingher, 1980).

Sarotherodon galilaeus is also an important component of the Lake Kinneret's commercial fishery (Ben-Tuvia, 1978). Although *S. galilaeus* harvest amounts to <20% of the commercial yield on an annual basis, it is the most valuable species in the lake, and therefore constitutes ~50% of the total income derived from the Lake Kinneret fisheries (Ben-Tuvia *et al.*, 1992). Because of the perceived dual role of this fish in both water quality and commercial fisheries, the *S. galilaeus* population is supplemented by annual stocking of pond-raised fingerlings (Gophen, 1985a, 1995).

Here we examine plankton consumption by *S. galilaeus*, with the primary goal of estimating potential lake-wide plankton mortalities caused by this fish and thus re-evaluate the role of *S. galilaeus* in the management of Lake Kinneret water quality.

Methods

Mesocosm experiments

We estimated taxon-specific clearance and grazing rates for *S. galilaeus* using a modification of the consumer-gradient design (see Lehman, 1980; Epp, 1996) that allows the separation of negative grazing effects on plankton assemblages from the positive effects of nutrient remineralisation from the fish that can occur within experimental containers. Experiments were conducted in nine large (5 m³) outdoor mesocosms filled with water pumped from the lake (1–2 m depth, ~10 m offshore). Zooplankton (especially large-bodied forms) were typically under-represented in the pumped water compared with lake densities. Therefore, zooplankton in the tanks were supplemented by adding zooplankton collected with horizontal tows of a conical plankton net (225 μm mesh) between 5 and 10 m depth (~2 km offshore). Three mesocosms were stocked with ca. 50 g m⁻³ fish, three with ca. 150 g m⁻³ fish and three remained without any fish (Table 1). These densities of fish were chosen as a compromise between using enough fish to

Table 1 Numbers, biomass and sizes (standard length, SL) of fish used in each experiment. Note that three separate experiments were conducted in summer

Experiment	Number of fish per mesocosm	Total biomass (g m^{-3})	Mean (±SE) length (cm SL)
Spring	0	0	–
	6	49 ± 5	107 ± 6
	12	155 ± 28	124 ± 2
Summer-I	0	0	–
	4	46 ± 2	123 ± 2
	12	138 ± 2	124 ± 2
Summer-II	0	0	–
	5	52 ± 5	122 ± 3
	13–17	181 ± 36	123 ± 3
Summer-III	0	0	–
	4–5	67 ± 11	132 ± 4
	16	206 ± 19	127 ± 2

produce detectable effects within 1 day and keeping fish densities low enough to prevent drastic food depletion (see Drenner *et al.*, 1987b). Prior to being used in experiments, all fish were acclimated for several weeks to months in outdoor holding tanks with constant flowing lake water. In order to saturate algal uptake rates for ammonia and phosphate, such that the potential for confounding indirect enhancement of phytoplankton and bacteria by fish excretion of these nutrients was minimal, initial concentrations of dissolved inorganic nutrients were increased by additions of standard solutions of Na_2HPO_4 and NH_4Cl equivalent to 2.0 μM PO_4–P and 15.0 μM NH_3–N. All mesocosms were mixed 4–6 times daily and before sampling by lifting a Secchi disk from bottom to surface 3–4 times each tank. Additionally, mesocosms were mixed with an airlift mixer system (Drenner, Threlkeld & McCracken, 1986) during daylight hours in the spring of *S. galilaeus* experiment (see below).

Mesocosms were sampled at 0 and 24 h to determine initial and final biomasses of zooplankton, chlorophyll *a*, ciliated- and flagellated-protozoans and bacteria. Zooplankton were collected with single vertical hauls of a conical plankton net (63 μm mesh, 18 cm diameter), towed from bottom to top of each mesocosm, preserved in 4% sucrose–formalin (Haney & Hall, 1973) and counted under a dissecting microscope. Biomass was calculated from mean individual zooplankter wet weights (Gophen, 1973). All other parameters were sampled from a composite whole-water sample made from five deployments of a 2-m,

depth-integrating tube sampler (deNoyelles & O'Brien, 1978). Chlorophyll *a* concentrations were determined fluorometrically on whole and filtered (20 μm) water following acetone extraction (Holm-Hansen *et al.*, 1965), thus allowing for estimation of net- (≥20 μm) and nano- (<20 μm) phytoplankton fractions. Net- and nanochlorophyll concentrations were converted to wet weight biomass assuming a chlorophyll content of 0.28 and 0.45%, respectively (Berman, 1978; U. Pollingher, personal communication). Protozoan and bacterial abundances were determined from 0.3% filtered (0.2 μm) formaldehyde-preserved samples after 4′,6-diamidino-2-phenylindole (DAPI) staining and counting using epifluorescence microscopy (Hadas & Berman, 1998). Protozoan biomass was estimated from geometrical-shape determined biovolume and a specific gravity of 1 g cm^{-3}. Bacterial biomass was estimated from numbers (10^6 mL^{-1}), assuming an individual biovolume of 0.04 μm^3, as determined by image analysis of DAPI-stained bacterial samples from similar experiments (Hambright, unpublished data).

Four experiments were conducted in 1992 and 1993 (one during the *P. gatunense* bloom period, April 1993; and three during the nanoplankton period, August and September 1992, and October 1993). Daily water temperatures in mesocosms ranged from 21 to 24 °C in spring experiment and from 22 to 30 °C in summer-fall experiments.

Grazing rates on various planktonic taxa (cladocerans, copepods, copepod nauplii, rotifers, net- and nanophytoplankton, ciliated- and flagellated-protozoans, and bacteria) were determined from the changes in biomass of each taxon over the 24-h experimental period. Clearance rates (CR, L fish^{-1} day^{-1}) were quantified by the negative slope of a linear regression of *r* (the net intrinsic rate of change) for each taxon (*A*) on fish biomass, in which r_A was calculated as

$$r_A = \ln(A_t/A_0)/\Delta t, \tag{1}$$

where A_t and A_0 are initial and final biomass of the particular taxon; $t = 1$ day.

Because nutrients were added at the beginning of the experiment, phytoplankton and bacteria growth was typically enhanced (i.e. $r > 0$ without grazers). However, the slope of the regression indicates fish-dependent (grazing-predation) effects. A negative slope indicates consumption; a slope of 0 indicates that a taxon was not consumed.

Grazing rates, GR (mg g_{fish}^{-1} day^{-1}), were calculated as the product of the mean biomass of a given taxon ($A°$) during the 24-h period, calculated as

$$A° = (A_t - A_0)/(r_A \times \Delta t), \quad (2)$$

and the taxon-specific CR, as GR = $A° \times$ CR.

Bioenergetics

A bioenergetics model [Bioenergetics Version 3.0 (Hanson *et al.*, 1997)] was used to generate common parameters between mesocosms and Lake Kinneret of *S. galilaeus* consumption and growth. Specific daily growth rates (g g_{fish}^{-1} day^{-1}) were simulated based on feeding rates determined in spring and summer mesocosm experiments and general physiological parameters for *Sarotherodon* spp. (Nitithamyong, 1988 – cited in Hanson *et al.*, 1997). Consumption (mg g_{fish}^{-1} day^{-1}), mean fish mass ($g_{fish,WW}$), water temperature and proportions of various prey in *S. galilaeus* diets were taken directly from experimental results. Diet components were defined as nanophytoplankton, netphytoplankton and zooplankton. Protozoan and rotiferan zooplankton were excluded as they constituted a minor portion of *S. galilaeus* diets in mesocosm experiments (see Results). Energy densities (cal g_{WW}^{-1}) of diet categories were generated from taxon-specific values in the literature (Table 2) and proportioned into the three diet categories defined above. *Peridinium gatunense* energy density was calculated as the sum of its proximate composition and specific energy densities of lipid, protein and carbohydrate (Brody, 1945; Berman, 1978; Wynne *et al.*, 1982).

Growth rates of *S. galilaeus* in Lake Kinneret were estimated by von Bertalanffy growth coefficients generated from *S. galilaeus* size distributions from commercial catches during 1998 and 1999 (J. Shapiro, unpublished data). Growth rates were generated independently for each year because 1998 and 1999 were characterised, respectively, by high and low spring *P. gatunense* abundances (T. Zohary, personal communication). Using the von Bertalanffy growth curve for each year, we extracted one year of growth of *S. galilaeus* starting the year as Age 1 individuals (30–50 g) in order to match the size of *S. galilaeus* used in mesocosm experiments (Table 1). Water temperatures were taken from epilimnetic monthly means from the Lake Kinneret database (Kinneret

Table 2 Plankton energy densities applied to *S. galilaeus* growth simulations

Diet category Taxon	Energy density (cal g_{WW}^{-1})	Source
Nanophytoplankton*		
Cyanobacteria	514	Ling (1966), Reynolds (1984)
Bacillariophyceae	574	Ling (1966), Reynolds (1984)
Chlorophyta	658	Ling (1966), Reynolds (1984)
Cryptophyta	625	Ling (1966), Reynolds (1984)
Netphytoplankton		
Peridinium spp.	2370	Brody (1945)†, Berman (1978, p. 269)‡, Wynne *et al.* (1982)§
Zooplankton		
Cladocera, Copepoda	600	Cummins & Wuycheck (1971)

*Nanophytoplankton energy density in simulations based on relative proportions of nanoplankton taxa in Lake Kinneret.
†Energy density of carbohydrates, proteins, lipids.
‡DW : WW ≈ 0.4.
§Proportion of carbohydrates, proteins, lipids, ash.

Limnological Laboratory, 2001). Proportions of diet categories (as defined above) were generated as the product of the monthly mean relative epilimnetic biomass of nano-, net- and zooplankton (Kinneret Limnological Laboratory, 2001) and the clearance rates of *S. galilaeus* generated by the mesocosm experiments (see Results). This procedure to estimate diets of *S. galilaeus* is likely more precise than direct examination of stomach contents given the problems and biases associated with estimating diets from alimentary tract contents, especially in herbivorous fishes (Dempster *et al.*, 1995). Estimates of lake plankton energy densities were as described above for results of mesocosm simulations. Energetic costs of reproduction were not included in the growth simulations since *S. galilaeus* are immature during this phase of their life cycle (Ben-Tuvia, 1959).

Plankton dynamics in Lake Kinneret within the past 6–7 years have been atypical and unpredictable compared with the previous 2–3 decades (Serruya, 1978; Berman, Pollingher & Zohary, 1998) and observed fish sizes and growth differed among years (see Results). Using fish (Landau, 1979) and plankton data (Kinneret Limnological Laboratory, 2001) from the 1970s, a period of relative ecological stability (see

Hambright, Parparov & Berman, 2000), we ran additional simulations, once using all data and once in which total plankton biomass was unchanged but *P. gatunense* was eliminated as a food source, in order to better understand the role of *P. gatunense* in the energy balance of *S. galilaeus*.

Results

Mesocosm experiments

Sarotherodon galilaeus consumed all planktonic taxa examined except bacteria (Fig. 1). Clearance rates ranged from 2.3 L g_{fish} day^{-1} for nanoplankton to 6.4 L g_{fish} day^{-1} for large rotifers, with a mean of 4.8 ± 0.8 L g_{fish} day^{-1} for all taxa consumed. Taxon-specific grazing rates by *S. galilaeus* were dependent on the relative composition of the plankton assemblage. During the spring of *P. gatunense* season, *S. galilaeus* consumed 18.4 mg g_{fish} day^{-1}. Netphytoplankton (mostly *P. gatunense*) constituted 95% of the diet in spring with the remaining 5% consisting of nanophytoplankton, protozoans and zooplankton. However, during the summer and fall nanophyto-
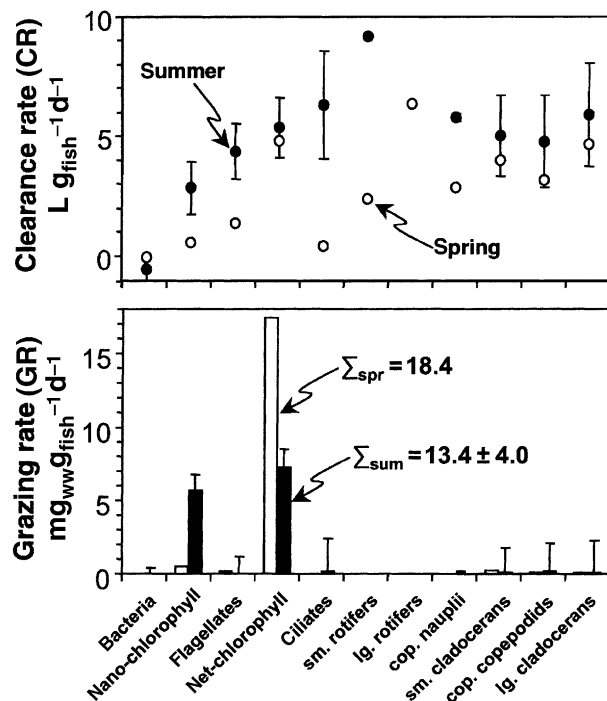

Fig. 1 Clearance rates (CR) and grazing rates (GR) of *S. galilaeus* for Lake Kinneret plankton determined from 1-day mesocosm experiments.

plankton period, in which *S. galilaeus* consumed 13.4 ± 4.0 mg g_{fish} day^{-1}, the contribution by netphytoplankton was reduced to 54%, nanophytoplankton constituted 42% and as in spring, protozoans and zooplankton constituted the remaining 4%.

Bioenergetics

The two independent sources for data input to the bioenergetics model verified both the model and the generalised *Sarotherodon* spp. data as applicable to Lake Kinneret's *S. galilaeus* (Table 3). Mesocosm-derived consumption rates provided reasonable estimates of annual fish growth. Likewise, the bioenergetics model using actual fish growth based on commercial fishery harvests and von Bertalanffy coefficients estimated realistic daily specific consumption rates.

Model simulations of *S. galilaeus* taxon-specific grazing rates in Lake Kinneret highlight the seasonal changes in lake plankton composition and the consequences for *S. galilaeus* growth (Fig. 2). The seasonal fluctuation in plankton composition largely dictated simulated *S. galilaeus* specific growth rates. Daily specific growth rates were highest during spring blooms of energy-dense *P. gatunense*, but were near zero when *P. gatunense* was a minor fraction of the plankton relative to nanophytoplankton and zooplankton. In fact, most of the annual net growth occurred during the spring (April–June 1998: 60%; 1999: 64%).

The maximum daily specific consumption rates occurred from mid-May to mid-June of each year

Table 3 Cross validation of *Sarotherodon galilaeus* consumption and growth rates from mesocosm experiments and bioenergetics modelling. Empirical data indicate the range of daily consumption values for the four mesocosm experiments or the range of annual growth values determined from the commercial fishery for three periods (1998, 1999, 1970–79). Simulation results indicate ranges of daily values for both growth and consumption. Note that when empirically derived consumption results served as model input, growth was the simulation output and vice versa

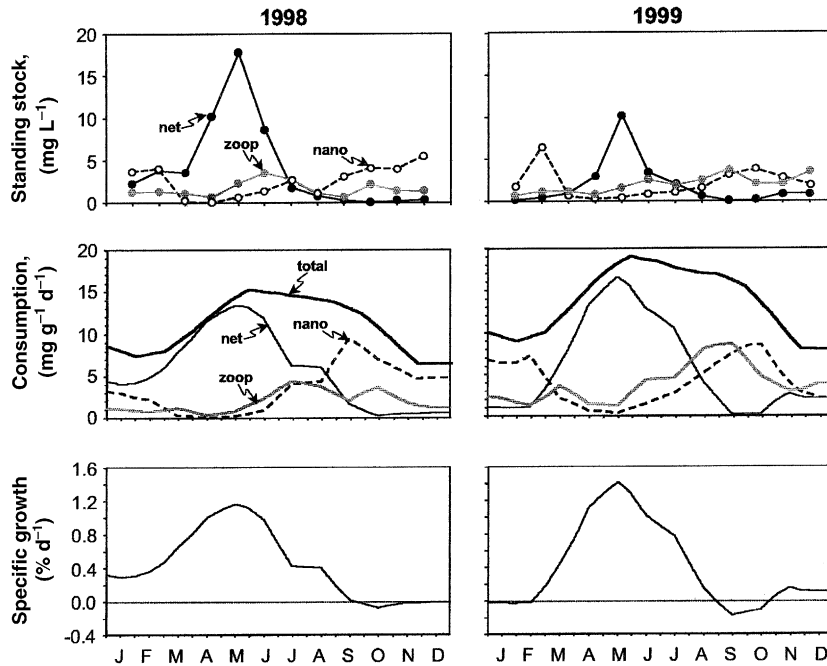|	Consumption (mg g_{fish}^{-1} day^{-1})	Growth (mg g_{fish}^{-1} day^{-1})
Empirical results	6.6–18.4	3.3–4.2
Bioenergetic simulations		
1998	6.9–15.8	−0.6–11.5
1999	8.5–19.9	−1.4–14.2
1970	7.5–17.1	0.3–10.0

Fig. 2 Results of bioenergetics simulations for *S. galilaeus* during 1998 (a normal *Peridinium* year) and (1999) (a low *Peridinium* year). The top panels show available plankton assemblages in Lake Kinneret during each year (monthly means) as model input; the middle panels show simulated total and taxon-specific daily consumption; the bottom panels show simulated mass-specific growth (as % per day).

(Fig. 2), with the exception of the 1970s no-*P. gatunense* scenario, when consumption rates plateaued from June to August. Although mean daily specific growth rates of *S. galilaeus* were similar (0.42 and 0.40%) between years of high (1998) and low (1999) *P. gatunense* blooms, annual mean specific clearance rates were almost 2× higher in 1999 versus 1998 (1.9 L g_{fish} day^{-1} versus 1.0 L g_{fish} day^{-1}) (Table 4). Thus, individuals had to process a greater volume of water because of both the lower overall plankton biomass in 1999 versus 1998 (5.9 mg L^{-1} versus 8.2 mg L^{-1}), and the lower relative proportion of

P. gatunense (30% versus 40%) as total epilimnetic plankton biomass.

Simulations based on the 1970s data revealed that 1999 was basically a normal year with respect to *S. galilaeus* growth and plankton consumption (Table 4). The only difference being that mean plankton biomass in the lake in the 1970s was 43% of the mean biomass in 1999. Thus *S. galilaeus* clearance rates would necessarily have been higher in the 1970s. Removal of *P. gatunense* from the *S. galilaeus* diet (Table 4, far right column) revealed the importance of this taxon to the *S. galilaeus* population in the lake. Simulated annual

Table 4 Mean consumption and growth parameters from *S. galilaeus* bioenergetic simulations. C_{max} is the maximum daily consumption based on fish size, water temperature and the energy densities of predator and prey. The two right-hand columns show results from simulations based on fish and plankton data from the 1970s, one using all data and one in which total plankton biomass was unchanged but *P. gatunense* was eliminated as a source of food (i.e. nanoplankton and zooplankton were the only available food sources included)

	1998	1999	1970–79	1970–79 (No *P. gatunense*)
Initial fish size (g)	50	30	65	65
Fish size after 1 year (g)	232	128	230	73
Grazing rate (mg g_{fish}^{-1} day^{-1})	11.6	13.6	12.5	20.9
Mean ration (proportion of C_{max})	0.73	0.73	0.55	1.0*
Mean growth rate (mg g_{fish}^{-1} day^{-1})	4.2	4.0	3.3	0.7
Mean plankton biomass (mg L^{-1})	8.2	5.9	3.5	3.5
Mean *Peridinium* abundance (% of total plankton)	40	30	39	0
Mean clearance rate (CR) (L g_{fish}^{-1} day^{-1})	1.0	1.9	2.9	4.9

*For this simulation, mean ration was set to C_{max} (i.e. $P = 1$).

growth was reduced to near zero and fish were required to process 2–4 times the amount of water (CR = 4.9 L g_{fish} day^{-1}) compared with 1998 and 1999 (CR = 0.9 and 1.9 L g_{fish} day^{-1}) in order to acquire near-maintenance rations in the absence of *P. gatunense*.

Discussion

As a filter-feeder, *S. galilaeus* can consume large (>20 μm) phytoplankton equally well as they consume zooplankton (Drenner *et al.*, 1987a; Vinyard *et al.*, 1988). Because phytoplankton always dominated the biomass of available plankton in the experiments, phytoplankton constituted the majority of *S. galilaeus* diets. Drenner *et al.* (1987a) demonstrated that *S. galilaeus* feeding rates varied with phytoplankton size, dropping from maximal values as size decreased below 10 μm. Our mesocosm experiment results are consistent with these findings; clearance rates for bacteria were 0 and those for nanophytoplankton were always lower (by ∼50%) than clearance rates for other components. Nevertheless, and as has been documented in diet composition studies (Spataru, 1976; Spataru & Zorn, 1976), nanophytoplankton were a major source of food (42%) for *S. galilaeus* during the summer experiments. We suspect that the low clearance rates for nanophytoplankton in our experiments were due to lack of feeding on the smaller members (e.g. picophytoplankton) of the nanophytoplankton (see Drenner *et al.*, 1987a). Because picophytoplankton typically account for only a fraction of the total nanophytoplankton biomass in the lake (T. Zohary, personal communication), in subsequent bioenergetics simulations, nanophytoplankton were considered consumable by *S. galilaeus* at rates proportional to their abundance in the plankton.

In contrast to phytoplankton, zooplankton typically constituted <2% of *S. galilaeus* diets in both spring and summer experiments. However, this is an artefact of the mesocosms, as zooplankton were under represented in the mesocosms relative to phytoplankton despite supplementing zooplankton in mesocosms (cf. grazing rates on zooplankton in mesocosms and in bioenergetics simulations). Bioenergetics simulations using actual lake plankton data indicated that zooplankton could account for up to ∼50% of *S. galilaeus* diets in the summer when netphytoplankton are rare. During the 1970s when zooplankton constituted a greater proportion of total plankton biomass (42%), our simulations revealed that zooplankton may have accounted for up to 73% of *S. galilaeus* diets. Nevertheless, in mesocosms, efficient grazing on zooplankton yielded high instantaneous mortality rates (0.25–0.47 day^{-1}) for zooplankton, thus supporting earlier contentions (e.g. Drenner *et al.*, 1982; Gophen, 1995) that *S. galilaeus* feeding may be an important factor affecting zooplankton population dynamics in the lake. However, fish densities in our mesocosms were very high (mean = 8.3×10^{-2} g L^{-1}) compared with lake densities (1.3–3.0×10^{-4} g L^{-1}; Landau, 1979). Extrapolation of measured clearance rates to lake densities of *S. galilaeus* yields zooplankton mortality rates not exceeding 0.005 day^{-1}, suggesting, in contrast to earlier conclusions, that *S. galilaeus* plays very little role, if any, in zooplankton population dynamics.

Using laboratory experiments with juvenile cichlids (*Oreochromis* spp.), Dempster *et al.* (1995) concluded that filter feeding provided insufficient food for sustained growth and therefore that additional and alternative food sources were required. Obviously, alternative food sources are used by facultative filter feeders. However, we see little evidence to conclude that filter-feeding in general would be energetically unprofitable for obligate filter-feeding taxa. Instead, we suggest that several factors, including the use of mono-specific algal cultures that may not contain the necessary compliment of essential nutrients (Hart & Santer, 1994) and small-sized fish that may not have yet switched to filter feeding because of its prohibitive costs at small sizes (Durbin, 1979; Lazzaro, 1987; Yowell & Vinyard, 1993), acting either independently or in conjunction, produced a low growth bias in the results of the experiments analysed by Dempster *et al.* (1995). Also as pointed out by Dempster *et al.* (1995), particle size can be important in determining food quality. The one case of positive growth in their study was observed with *O. niloticus* feeding on relatively large algal particles (*Microcystis* and *Anabaena* spp.). In Lake Kinneret, large *P. gatunense* are clearly growth stimulating in *S. galilaeus*, although periods of negative growth occurred during late summer-early fall for both 1998 and 1999 simulations, probably because of high water temperatures (approaching 30 °C) plus relatively low plankton biomass (including the lack of *P. gatunense*), compared with spring. Hence, filter feeding, in general, can provide adequate energy for

fish growth, but may not be advantageous in unproductive warm systems.

Present-day management of Lake Kinneret includes the supplemental stocking of *S. galilaeus* in an attempt to use biological means to improve water quality (e.g. see Serruya *et al.*, 1979; Gophen, 1985b; Berman, 1998). However, an early carbon mass balance model for the lake suggested that *S. galilaeus* control of *P. gatunense* was very unlikely (Serruya *et al.*, 1980). *Peridinium gatunense* daily net growth, *k*, in Lake Kinneret can be described as:

$$k = \mu - s - d - g,$$

where μ = the maximum potential growth rate, s = sedimentation losses, d = death and g = grazing losses (Reynolds, 1984). Typically, during the growth phase of the *P. gatunense* bloom, $k = 0.05–0.1$ (i.e. the population doubles in 1–2 weeks) (Pollingher & Serruya, 1978). A recent study of losses of *P. gatunense* during the bloom period have revealed that $s \sim 0.02$ and $d \sim 0.001$, thus giving a μ of $\sim 0.07–0.12$ (Viner, 1998; Zohary *et al.*, 1998). Here clearance rates of up to 1.9 L g_{fish} day^{-1} were estimated for 1999 (similar to 1.5 L g_{fish} day^{-1} calculated from Drenner *et al.*, [1]1987a)) and a *S. galilaeus* population of 700 t (a high estimate according to Landau, 1979) would result in *P. gatunense* mortality rates (g) of 0.0003–0.0005 (i.e. ≤0.8% of μ). Even considering higher summer clearance rates (CR = 5 L g_{fish} day^{-1}) and as much as 1000 t of *S. galilaeus*, g would not exceed 0.002 or 3% of μ. Thus we conclude that although *P. gatunense* may constitute up to 80% of their body carbon (Zohary *et al.*, 1994), *S. galilaeus* should not exert any controlling force on *P. gatunense* in Lake Kinneret. Only if the *S. galilaeus* population were increased by 10–100-fold would g approach the same order of magnitude as μ and thus the potential to negatively affect *P. gatunense* growth.

With respect to fisheries, however, enhancement of the *S. galilaeus* population could increase the transfer efficiency of the high-energy *P. gatunense* into fish tissue and thus into harvest, especially if harvest were concentrated in late summer or early fall when growth may be expected to be negative. Moreover, at least in terms of food availability, more *S. galilaeus* could be supported in the lake. However, we do not advocate enhancing the *S. galilaeus* population at this point, because secondary and indirect effects of *S. galilaeus* consumption on *P. gatunense* could yield reduced water quality. Previous laboratory experiments (e.g. Drenner *et al.*, 1987a) and our 1-day mesocosm experiments revealed that *S. galilaeus* can efficiently consume nanophytoplankton (although less efficiently than *P. gatunense*). However, in their 7-day mesocosm experiments, Drenner *et al.* (1987a) found that nanophytoplankton biomass was greatly enhanced by *S. galilaeus*, by either nutrient excretion, zooplankton suppression or both. Thus enhancing the *S. galilaeus* stock in Lake Kinneret would likely result in a shift of phytoplankton biomass from *P. gatunense* to nanophytoplankton. Water treatment costs for removing *P. gatunense* (slight chlorination and sedimentation) are much lower than for nanophytoplankton (flocculation and/or filtration). Thus a shift in phytoplankton biomass from *P. gatunense* to nanophytoplankton would mean lower water quality and higher water treatment costs.

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