

An Experimental Study of the Plankton Community Impacts of Two Omnivorous Filter-Feeding Cichlids, *Tilapia galilaea* and *Tilapia aurea*

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We conducted laboratory selective grazing experiments and outdoor mesocosm experiments assessing impacts of two cichlids, *Tilapia galilaea* and *Tilapia aurea*, on plankton from Lake Kinneret, Israel. Laboratory feeding rates of both fish increased for larger particles, reaching maximum values for zooplankton and *Peridinium cinctum*. *Tilapia galilaea* had higher feeding rates on *Peridinium elpatiewsky* and on intermediate-sized nanoplankton. Outdoor mesocosm experiments examining fish impacts on plankton community structure included two 21-d spring and summer experiments of replicated 2 × 2 factorial design (*T. galilaea* × *T. aurea*). Both fish suppressed crustaceans and rotifers. In the spring, fish also suppressed chlorophyll concentration and the dominant phytoplankton *P. cinctum*. In the summer, when nanoplankton dominated the phytoplankton and the smaller *P. elpatiewsky* was the most abundant dinoflagellate, only *T. galilaea* suppressed *Peridinium* spp., while presence of *T. aurea* was associated with increased chlorophyll concentration. Overall, *T. galilaea* suppressed more and enhanced fewer nanoplankton taxa than did *T. aurea*. Production of each fish species was lowest when both species were together, suggesting potential competition for plankton resources.

Les auteurs ont réalisé des essais de broutage sélectif en laboratoire et des essais extérieurs en mésocosme dans le but d'évaluer les incidences de deux cichlidés, *Tilapia galilaea* et *Tilapia aurea*, sur le plancton du lac Kinneret (Israël). Les taux d'alimentation en laboratoire des deux poissons augmentaient avec la grosseur des particules pour atteindre des valeurs maximales avec le zooplancton et *Peridinium cinctum*. Les *Tilapia galilaea* présentaient des taux d'alimentation plus élevés pour *Peridinium elpatiewsky* et le nanoplancton de taille intermédiaire. Les essais extérieurs en mésocosme ayant pour but de déterminer les effets des poissons sur la structure de la communauté planctonique comprenaient deux expériences de 21 d, réalisées au printemps et en été, d'une conception par réplique factorielle 2 × 2 (*T. galilaea* × *T. aurea*). Les deux poissons ont supprimé les crustacés et les rotifères. Au printemps, les poissons avaient aussi pour effet de supprimer la chlorophylle et l'organisme phytoplanctonique dominant *P. cinctum*. Au cours de l'été, lorsque le nanoplancton dominait le phytoplancton et que *P. elpatiewsky*, plus petit, était le dinoflagellé le plus abondant, seul *T. galilaea* faisait disparaître les espèces de *Peridinium* tandis que la présence de *T. aurea* correspondait à une augmentation de la concentration de chlorophylle. De façon générale, *T. galilaea* supprimait un plus grand nombre de taxons de nanoplancton et en favorisait un nombre plus restreint que ne le faisait *T. aurea*. La production de chacune des espèces de poisson était la moins élevée lorsque les deux espèces étaient présentes ensemble, ce qui porte à croire à une compétition possible pour les ressources planctoniques.

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In Lake Kinneret, Israel, declines in the catch of the Galilee Saint Peter's fish (*Tilapia galilaea* = *Sarotherodon galilaeus*) relative to that of the previously rare blue tilapia (*Tilapia aurea*) were associated with stocking of blue tilapia (Gophen et al. 1983). Based on evidence derived from diet studies and laboratory experiments, we hypothesized that competition between these fish species could have contributed to the reduced catch of *T. galilaea*. Both species are primarily planktivorous, feeding on zooplankton and phytoplankton (Spataru 1976; Spataru and Zorn 1978; Gophen 1980). *Tilapia galilaea* and *T. aurea* larger than 62 and 76 mm standard length (SL), respectively, feed on plankton as pump filter-feeders using rapid non-directed suction to draw water and food particles into the buccal cavity (Gophen et al. 1983). Smaller fish may filter-feed but also visually locate and attack individual food items. In laboratory feeding experiments, *T. galilaea* and *T. aurea* had similar feeding selectivities for zooplankton (Gophen et al. 1983) but their selectivities for phytoplankton have not been compared.

In this study, we conducted two sets of experiments to assess the impacts of the two cichlid species on plankton from Lake Kinneret, Israel. The first group of laboratory experiments examined selective plankton grazing by the fish, and a second set of outdoor mesocosm experiments examined fish impacts on plankton community structure.

Materials and Methods

Prior to the selective grazing experiments, fish were collected from the lake or acquired from kibbutz Mevo Hama fish rearing ponds and acclimated at the Yigal Allon Kinneret Limnological Laboratory for 1 mo in 60-L plastic tubs continually supplied with water and plankton pumped from the lake. In the selective grazing experiments, fish feeding rates on lake plankton were measured by monitoring declines of phytoplankton and zooplankton densities in the 60-L plastic tubs containing five to eight feeding *T. galilaea* or *T. aurea* (121–142 mm SL). At the beginning of each experiment, the tubs were cleaned and nearshore water containing plankton was pumped into the tubs. To ensure that adequate plankton densities and a full zooplankton species complement were present in each experiment, we supplemented plankton in the tubs with zooplankton collected from the lake with a 63- μ m-mesh net. This resulted in initial zooplankton concentrations ranging from 278 to 3780 organisms/L. Plankton were kept in suspension by aeration, movements of the fish, and stirring every 10 min. Feeding trials were conducted at $28.8 \pm 0.1^\circ\text{C}$ under combined fluorescent and natural sunlight. After completion of each grazing experiment, fish were transferred to clean tubs with a continual flow of lake water and plankton for 24–48 h.

During each experiment, duplicate water samples were collected from tubs initially and after 60 min of feeding. This was accomplished by stirring each tub and then quickly lowering a 6-cm-diameter Plexiglas tube onto a randomly placed rubber stopper on the tub bottom (Drenner et al. 1982). Zooplankton were removed from one sample with a 63- μ m-mesh sieve and preserved in 5% formalin. Phytoplankton in 125 mL of unfiltered water from the second sample were preserved by addition of 1% Lugol's solution. Zooplankton and phytoplankton were counted with a dissecting microscope and inverted compound microscope, respectively. Phytoplankton taxa included in the analyses were those that occurred at densities ≥ 75 organisms/mL and that were present in at least two of the five feeding

trials conducted for each fish species. We corrected for particle loss due to zooplankton feeding by monitoring the loss of phytoplankton and zooplankton from fishless control tubs. Feeding rate constant (k) was calculated as

$$k = (D_1 - D_2)/G$$

where G is grams of fish per litre and D_1 and D_2 are instantaneous particle loss rates in tubs with and without fish, respectively, calculated as

$$D = -\ln(P_i/P_f)/T$$

where P_i and P_f are initial and final plankton densities (organisms per millilitre) and T is the experiment duration (hours) (Dodson 1975).

The mesocosm experiments examined the impacts of both fish species on lake plankton in a linear array of eight cylindrical 5-m³ black plastic tanks (1.9 m in diameter). Because the Lake Kinneret phytoplankton community alternates between *Peridinium* dominance in winter and spring and nanoplankton dominance during the summer and fall (Pollinger and Berman 1978), we conducted experiments during spring and summer. Experiments of 3 wk duration began 24 March and 5 August 1985.

Experiments were of 2×2 factorial design (presence or absence of *T. galilaea* \times presence or absence of *T. aurea*), allowing us to examine main and interaction effects of the fish species. Two replicates of each treatment combination (no fish, *T. galilaea*, *T. aurea*, and *T. galilaea* + *T. aurea*) were assigned to tanks using a randomized block design. Blocks consisted of tanks 1–4 and tanks 5–8.

Prior to the mesocosm experiments, fish were collected from the lake or acquired from kibbutz Mevo Hama fish rearing ponds and acclimated at the Yigal Allon Kinneret Limnological Laboratory for at least 4 d in outdoor holding tanks prior to each experiment. Holding tanks continually received water and plankton pumped from the lake. Before stocking and after experiments, fish were individually weighed and measured. The spring and summer experiments utilized, respectively, 6 or 5 per tank of each fish species in single species treatments, and 12 or 10 fish, in the treatment combination having both *T. galilaea* and *T. aurea*. Average fish biomass for each species group added to the tanks was 620.5 g (range 606.4–637.5 g, mean SL = 140 mm) in the spring experiment and 610.1 g (range 601.1–615.9 g, mean SL = 151 mm) in the summer experiment. No fish mortality occurred during the experiments.

Double biomass was used in tanks containing both fish species and was necessary to hold the impact of each fish species constant within the context of the factorial design. Also, the equivalent density and biomass of each fish species in the presence or absence of each other holds intraspecific competition constant while allowing interspecific competition to vary (Werner and Hall 1977, but see Maiorana 1977). Although the biomass levels used in our experiments may exceed those likely to be observed for these species in Lake Kinneret, they were selected for these experiments to allow assessment of community responses during relatively short-term experiments while minimizing container effects. We feel that the community responses seen are qualitatively similar to impacts expected from fish in the lake although they may differ in magnitude.

Tanks were filled at the beginning of each experiment with water pumped from approximately 30 m offshore at a depth of 1.5 m. In the first experiment, no water was added to the tanks after initial filling. Because additional experiments (not presented here) indicated that continuous addition of lake water reduced diel fluctuations of dissolved oxygen, the tank system

was modified before the second experiment to provide continuous addition of approximately 1 L lake water/min to each tank. Previous experiments indicated that temperatures in the tanks differed by less than 4° from values measured in a nearby cove of the lake.

After filling the tanks, we supplemented zooplankton in them with plankton collected 1–2 km offshore. Sixteen 10-m vertical hauls using a 300- μm -mesh, 44-cm-diameter conical plankton net were pooled and equal portions of the composite added to each tank. This assured the presence of limnetic forms in all tanks.

Tanks were mixed for 2 h daily by an air-lift mixer system. Air from a blower was injected 1 m below the water surface into 5-cm-diameter open plastic pipes suspended from floats in each tank. Mixers moved a water volume equivalent to tank volume in approximately 1 h, destratifying and aerating the tanks. Because *Peridinium* divide primarily at night and are sensitive to agitation during this period (Pollinger and Serruya 1976), we operated mixers only during the day.

Tanks were sampled initially and twice weekly for 3 wk. Mean tank water temperatures ranged from 17 to 22°C and from 28 to 32°C during the spring and summer experiments, respectively. On each sampling date, a single composite water sample was produced for each tank by mixing five replicate samples collected with a 2.5-m-long, 1.5-cm-diameter plastic pipe lowered to within 10 cm of the tank bottom. Aliquots were taken for analysis of chlorophyll, water chemistry, and phytoplankton. For each sample, we made triplicate fluorometric chlorophyll determinations on 90% acetone extracts of material retained by a glass fiber filter (0.8–1.0 μm pore size) (APHA 1981). Fluorimeter readings were calibrated by comparison with spectrophotometric chlorophyll determinations (Strickland and Parsons 1972; D. Wynne, Yigal Allon Kinneret Limnological Laboratory, P.O. Box 345, Tiberias, Israel, pers. comm.).

Water chemistry analyses were performed for the spring experiment by the Mekorot Watershed Unit, Kinneret Limnological Laboratory, using standard methods (APHA 1981; Nydhal 1978; Solorzano 1969). Parameters examined included total phosphorus, total dissolved phosphorus, soluble reactive phosphorus, total Kjeldahl nitrogen, ammonia, nitrite, and nitrate.

Phytoplankton were preserved by adding 1% Lugol's iodine solution and settled overnight before counting with an inverted microscope. Dinoflagellate densities for each tank were determined by counting all cells in a 1-mL subsample, while densities of other algal taxa were determined by counting 20% of the material settled from 10-mL samples.

Zooplankton samples were collected from each tank at the conclusion of the mixing period with single vertical hauls of a 63- μm -mesh, 16-cm-diameter net. At least 200 organisms or one third the total sample volume from each tank was counted using a dissecting microscope.

Data from the community response experiments were analyzed using a multivariate profile analysis of repeated measures (Wilkinson 1984; Winer 1971). This procedure sums data across sampling dates into a univariate test to detect treatment effects (Wilkinson 1984). Statistical significance was inferred at the $P < 0.1$ level.

Results

In the selective grazing experiments, feeding rates of *T. galilaea* increased with particle size, leveling when particles

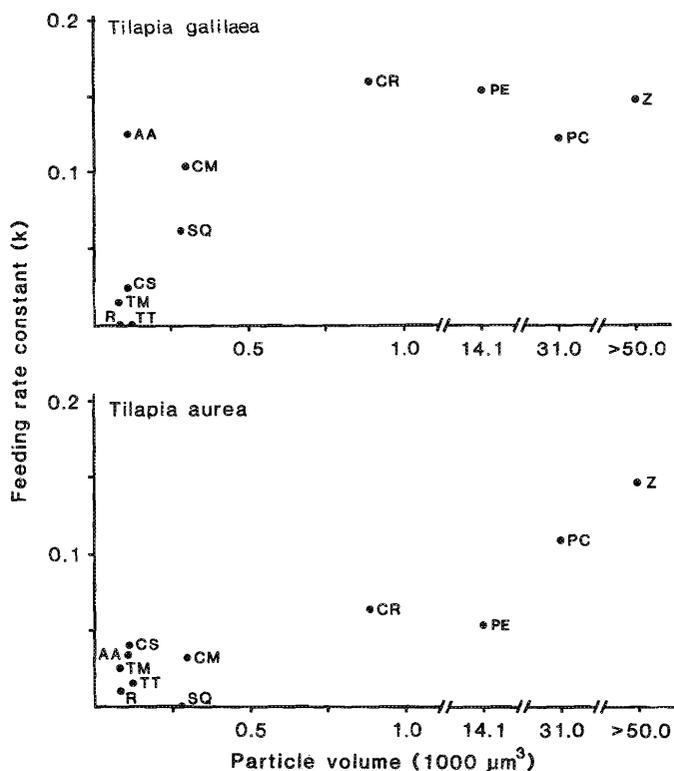


FIG. 1. Feeding rate constants (k) of *Tilapia galilaea* and *Tilapia aurea* (litres per gram of fish per hour) for zooplankton (Z), *Peridinium cinctum* (PC), *Peridinium elpatiewsky* (PE), *Cryptomonas reflexa* (CR), *Scenedesmus quadricauda* (SQ), small *Cyclotella* sp. (CS), *Tetraedron minimum* (TM), *Tetraedron trigonum* (TT), and *Rhodomonas minuta v. nannoplan* (R).

exceeded 500 μm^3 (Fig. 1). *Tilapia galilaea* had maximum feeding rates on zooplankton, *Peridinium cinctum*, and some intermediate-sized nanoplankton. Feeding rates of *T. aurea* also increased with particle size, with highest feeding rates on *P. cinctum* and zooplankton. *Tilapia aurea* had lower feeding rates than *T. galilaea* on *Peridinium elpatiewsky* and intermediate-sized nanoplankton. Neither fish efficiently grazed the smallest nanoplankton.

In the spring mesocosm experiment, presence of *T. galilaea* was associated with reduced densities of *Ceriodaphnia* spp., adult *Mesocyclops* sp., copepodids, copepod nauplii (Fig. 2), *Peridinium* spp., and *Cyclotella* spp. (Fig. 3) and total phosphorus concentration (Table 1) and chlorophyll concentration (Fig. 3). Presence of *T. galilaea* was also associated with increased densities of *Acronema augustum*, *Tetraedron* spp., and *Chrysochromulina* spp. (Fig. 3) and increased concentration of dissolved inorganic nitrogen (Table 1). Presence of *T. aurea* was associated with reduction in densities of *Ceriodaphnia* spp., *Bosmina* spp., adult *Mesocyclops* sp., copepodids, copepod nauplii, *Keratella* spp. (Fig. 2), and *Peridinium* spp. and chlorophyll concentration (Fig. 3). Increased nanoplankton densities associated with *T. aurea* include those of *Coelastrum microporum*, *Cyclotella* spp., *Golenkenia radiata*, *A. augustum*, *Rhodomonas minuta v. nannoplan*, *Tetraedron* spp., and *Chrysochromulina* spp. (Fig. 3). Because nanoplankton species accounted for only a small fraction of the total algal biomass in this experiment, their enhancement in the presence of either fish species did not offset reductions in chlorophyll concentration due to *Peridinium* suppression.

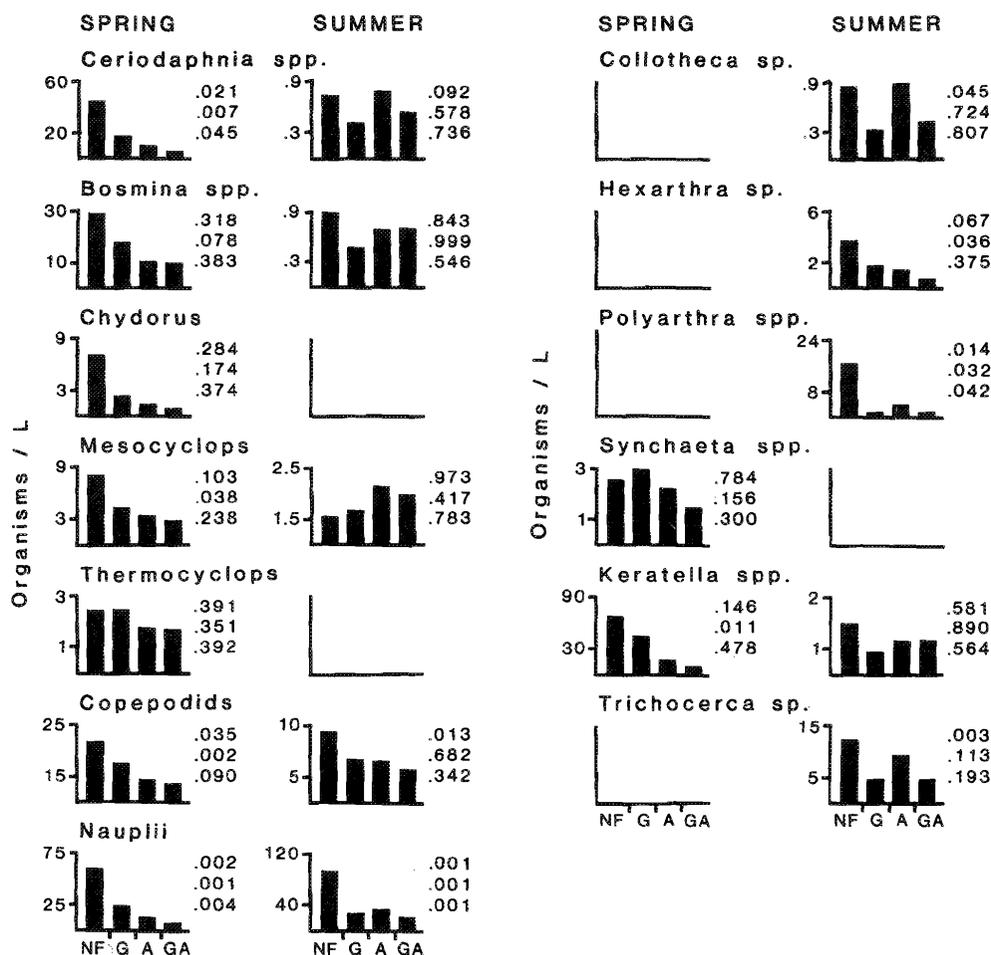


FIG. 2. Mean numbers of zooplankton in no fish (NF), *Tilapia galilaea* (G), *Tilapia aurea* (A), and *T. galilaea* + *T. aurea* (GA) treatment combinations for the spring and summer experiments. Probability values for *T. galilaea* (upper) and *T. aurea* (middle) main effects and interactions (lower) are given to the right of each histogram. Evaluation of *T. galilaea* or *T. aurea* main effects from this figure and Fig. 3 can be achieved by comparing the mean values for treatments containing the species (G and GA for *T. galilaea*, A and GA for *T. aurea*) with those from which it is absent (NF and A for *T. galilaea*, NF and G for *T. aurea*).

TABLE 1. Mean values of water chemistry parameters (mg/L) in replicate tanks during the spring experiment. Treatments were no fish (NF), *T. galilaea* (G), *T. aurea* (A), and *T. galilaea* + *T. aurea* (GA). Probability values for *T. galilaea* (Tg) and *T. aurea* (Ta) main effects and interactions (Tg × Ta) are given.

	Treatment combinations				Probability values		
	NF	G	A	GA	Tg	Ta	Tg × Ta
Phosphorus							
Total dissolved	0.013	0.016	0.017	0.013	0.919	0.663	0.028
Orthophosphate	0.006	0.007	0.008	0.008	0.542	0.514	0.571
Total	0.063	0.053	0.048	0.042	0.022	0.005	0.538
Nitrogen							
Nitrite	0.012	0.017	0.017	0.020	0.004	0.004	0.237
Nitrate	0.124	0.210	0.228	0.250	0.019	0.007	0.083
Ammonia	0.023	0.128	0.127	0.297	0.001	0.001	0.072
Total	1.094	1.089	0.954	1.059	0.194	0.057	0.162

In the summer experiment, presence of *T. galilaea* was associated with reduced densities of *Ceriodaphnia* spp., copepodids, copepod nauplii, *Collotheca* spp., *Hexarthra* sp., *Polyarthra* spp., *Trichocerca* spp. (Fig. 2), *Peridinium* spp.,

Chroococcus turgidus, *G. radiata*, *Chodatella citrififormis*, and *A. augustum* and increased densities of *R. minuta* v. *nannoplana* (Fig. 3). Presence of *T. aurea* was associated with reduced densities of copepod nauplii, *Hexarthra* sp., *Polyarthra*

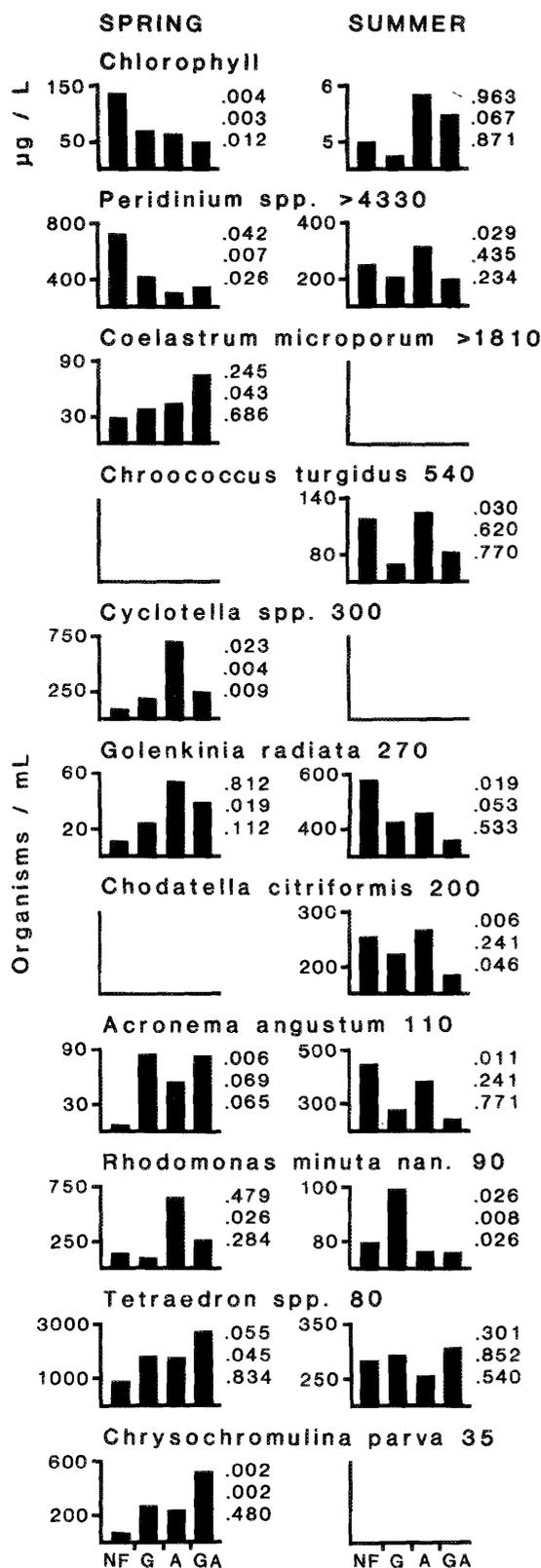


FIG. 3. Mean chlorophyll concentration ($\mu\text{g/L}$) and mean phytoplankton densities in no fish (NF), *Tilapia galilaea* (G), *Tilapia aurea* (A), and *T. galilaea* + *T. aurea* (GA) treatment combinations for the spring and summer experiments. Phytoplankton volume (μm^3) is given to the right of each genus name. Probability values for *T. galilaea* (upper) and *T. aurea* (middle) main effects and interactions (lower) are given to the right of each histogram.

spp. (Fig. 2), *G. radiata*, and *R. minuta* v. *nannoplan* and increased chlorophyll concentration (Fig. 3). Total chlorophyll concentrations were much lower during the summer experiment than during the spring.

Significant interaction effects were observed infrequently in our data, suggesting that in most cases the effects of the two fish species were independent and additive. Interactions between main effects for zooplankton were observed for two groups (nauplii and copepodids) in the spring experiment (Fig. 2) and three (*Ceriodaphnia* sp., nauplii, and *Polyarthra* sp.) in the summer (Fig. 2). Phytoplankton taxa showed two significant interactions (*C. turgidus* and *P. cinctum*) in the spring experiment (Fig. 3) and two significant interactions (*C. citriformis* and *R. minuta* v. *nannoplan*) in the summer experiment (Fig. 3). Potential mechanisms for producing interaction effects in tank experiments may include behavioral interactions between fishes, or between fish and zooplankton, or nonlinear biomass effects on specific parameters.

In the spring experiment, fish biomass increased in all tanks. When alone, biomass of *T. galilaea* and *T. aurea* increased by 9.9 and 4.0% ($t = 3.497$, $P = 0.002$), respectively. In the treatment combinations with both fish, biomass increased and by 3.3% for *T. galilaea* and by 0.7% for *T. aureus* ($t = 3.174$, $P = 0.005$). Both species exhibited significantly reduced growth rates in the presence of the other species ($t = 3.830$, $P = 0.001$ for *T. galilaea* and $t = 3.636$, $P = 0.002$ for *T. aurea*).

During the summer experiment, fish biomass declined in all treatments. When alone, biomass of *T. galilaea* declined by 5.6%, while that of *T. aurea* decreased by 9.2% ($t = 2.084$, $P = 0.054$). *Tilapia galilaea* biomass decreased by 14.3% and *T. aureus* biomass by 5.3% ($t = 4.317$, $P = 0.001$) in the treatment with both fish. Both fish species had significantly greater weight loss in the presence of the other species ($t = 4.094$, $P = 0.002$ for *T. galilaea* and $t = 2.3265$, $P = 0.036$ for *T. aurea*).

Discussion

In the mesocosm experiments, *T. galilaea* and *T. aurea* had similar effects on zooplankton, suppressing several crustacean and rotifer taxa while enhancing none. Both fish suppressed *Peridinium* in the spring when *P. cinctum* ($31\,000\ \mu\text{m}^3/\text{cell}$) was the dominant dinoflagellate species. In the summer, when the smaller dinoflagellate *P. elpatiewsky* ($14\,000\ \mu\text{m}^3/\text{cell}$) was the most abundant large algal species, only *T. galilaea* suppressed *Peridinium* sp. Overall, *T. galilaea* suppressed more and enhanced fewer nanoplankton taxa than did *T. aurea*. These results are consistent with feeding trials which showed that both fish had maximum feeding rates on zooplankton and *P. cinctum*, but *T. galilaea* had higher feeding rates than *T. aurea* on *P. elpatiewsky* and on intermediate-sized nanoplankton. Other studies (Drenner et al. 1984a, 1984b, 1986, 1987) have shown direct suppression of zooplankton and phytoplankton by omnivorous filter-feeding fish and have suggested that such fish may indirectly enhance phytoplankton through their effects on nutrients and zooplankton predation. Small nanoplankton species that are inefficiently grazed by these fish might be especially sensitive to such enhancement.

Our data from the spring experiment indicate that the fish can significantly increase the dissolved nitrogen fraction in the tanks, chiefly through increases in ammonia and nitrate, without having significant impacts on the total nitrogen present. A

reversal of these effects was observed with phosphorus. Tanks containing fish had significantly reduced total phosphorus concentrations without significant effects on the dissolved fractions. We suspect that the increase in dissolved nitrogen compounds reflects the metabolic release of ammonia by the fish. The decrease in phosphorus probably results from loss through sedimentation of fecal pellets which are tightly bound and sink rapidly to the bottom of the tanks. Other experiments (not presented here) indicate that fish substantially increased sedimentation rates through feces production.

The direct and indirect effects of these two cichlids on phytoplankton have potentially important implications for water quality of Lake Kinneret (Serruya et al. 1980) which annually provides 35% of Israel's freshwater. *Peridinium* accounts for over 80% of the annual algal biomass in Lake Kinneret (Serruya et al. 1979). Because *T. galilaea* has been considered the most important consumer of *Peridinium*, Serruya et al. (1980) suggested that *Peridinium* abundance and levels of suspended and dissolved organic materials might be suppressed by increasing the density of *T. galilaea* in the lake. In the mesocosm experiments reported here, *T. galilaea* suppressed total chlorophyll levels when *Peridinium* was abundant in the spring, but did not significantly affect chlorophyll levels in the summer experiment when *Peridinium* densities and algal biomass were much lower. While it is possible that the use of the continuous inflow in the summer experiment contributed to these seasonal differences, other experiments (not reported here) showed that *T. galilaea* continues to suppress algal abundance when *Peridinium* is dominant and the tanks are receiving continuous inflow.

Because it has been suggested that *T. galilaea* utilizes *Peridinium* more intensively than *T. aurea* in the lake, Gophen et al. (1983) expressed concern that displacement of *T. galilaea* by *T. aurea* could alter algal population dynamics and result in increased algal abundance and reduced water quality in the lake. While we find few differences between the fish in their ability to consume *P. cinctum*, differences in grazing efficiency on intermediate- and small-sized phytoplankton could be important, especially during the nanoplankton period.

Although *T. aurea* did show somewhat greater reductions in *Peridinium* and chlorophyll in the spring experiment, *T. galilaea* grew significantly more. During the summer experiment, both fish species lost weight, and *T. aurea* lost significantly more than did *T. galilaea*. Although several factors may have contributed to these results, they could reflect a higher food conversion efficiency for *T. galilaea* as suggested by Spataru (1976).

Despite the difference in algal grazing efficiencies of the two cichlids, they exhibit a high degree of overlap in resource utilization, particularly for zooplankton and *P. cinctum*. Although our experiments permitted only limited behavioral flexibility and may thus have increased apparent niche overlap (Werner and Hall 1976), the data support the conclusions of Gophen et al. (1983) that stocking of *T. aurea* could divert resources from *T. galilaea* in Lake Kinneret.

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