Interactions between a phytoplanktivorous fish, *Oreochromis aureus*, and two unialgal forage populations

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Synopsis

Juvenile blue tilapia, *Oreochromis aureus*, consume both the motile green alga, *Chlamydomonas* sp., and the filamentous blue-green alga, *Anabaena* sp. Results from a grazing experiment showed little difference between the densities of grazed and ungrazed populations of *Chlamydomonas*, but did show a decrease in density and growth rate in the grazed *Anabaena* population relative to an ungrazed population. Tilapia ingesting *Chlamydomonas* lost weight, similar to the weight loss of unfed control fish. However, fish fed *Anabaena* gained weight. This study provides further evidence that blue tilapia grazing may structure phytoplankton communities directly, and their grazing could shift phytoplankton communities from dominance by large blue-green algae towards dominance by green algae.

Introduction

Herbivorous fishes can structure macroalgal communities in both marine (e.g. Ogden & Lobel 1978, Hixon & Brostoff 1983) and freshwater communities (Power & Matthews 1983). Freshwater phytoplankton communities can be structured directly through grazing by zooplankton (e.g. Porter 1977) or indirectly through zooplanktivorous fish (e.g. Brooks & Dodson 1965, Lynch & Shapiro 1981, Elliott et al. 1983). The ability of a phytoplanktivorous fish to directly structure natural phytoplankton communities has been suggested (Drenner et al. 1984, McDonald 1985a, 1985b), but is yet undocumented.

The blue tilapia, *Oreochromis aureus* (Steindachner), becomes a filter feeder at standard lengths (SL) >29 mm (Gophen et al. 1983), ingesting large phytoplankton (Drenner et al. 1984, McDonald 1985a, 1985b) and zooplankton (Drenner et al. 1984). Thus, blue tilapia can potentially structure phytoplankton communities directly and indirectly. Blue tilapia grazing on *Ankistrodesmus falcatus* (Corda) grow, and enhance population growth of the grazed alga over ungrazed alga (McDonald 1985b). Thus blue tilapia may be able to structure algal communities in unexpected ways, which has important implications for their use in algae control (e.g. Stanley & Jones 1976, Germany & Noble 1977) and aquaculture (e.g. Bowen 1980, Stickney & Winfree 1983).

In this study, I examined the effect of blue tilapia grazing on two unialgal populations, *Chlamydomonas* sp. (a motile, unicellular, green alga) and *Anabaena* sp. (a filamentous blue-green alga). These species are commonly abundant, but morphologically and ecologically distinct and differ from the previously tested *A. falcatus* (McDonald 1985b). The growth of fish when feeding on *Chlamydomonas* and on *Anabaena* was also determined.

Methods

I determined the population dynamics of ungrazed and grazed Chlamydomonas (6-15 µm diameter) and of ungrazed and grazed Anabaena (cell dimmensions: $6 \times 3 \mu m$) in 401 aquaria. Four blue tilapia (SL 59-84 mm) per aquarium provided the grazing pressure. I measured fish growth in the grazing treatments and compared this to unfed fish acting as controls. Four replicate aquaria of each treatment (grazed and ungrazed populations of each algal species, and the unfed fish treatment) were arranged in a randomized complete block design. All algal treatment aquaria contained 161 of medium (fishmeal-soil with a nutrient supplement of 31 g KNO₃ + 2 g KPO₄ in 100 ml distilled water at 1:100 v/v with medium, McDonald 1984). To each of these aquaria I added 41 of xenic algal culture. To reduce contamination of the Anabaena cultures, I added sea salt for a total salinity of approximately 5‰. Also, to reduce possible contamination of unfed control fish aquaria by algae, they were kept in dechlorinated tap water, but otherwise treated similarly to grazing fishes.

After algal innoculation, I allowed the algae to grow for 24 h before introduction of fish into the appropriate aquaria. Fish were fin-clipped for individual identification (Rinne 1976) and then weighed wet and measured prior to their introduction. After introduction, I made direct hemocytometer algal counts on samples from all aquaria. I counted at least 400 cells sample⁻¹ to provide a $\pm 10\%$ accuracy at the 95% confidence level (Guillard 1973). Anabaena filaments were broken by placing the sample in a high speed blender for 45 sec before counting. Subsequent counts were made every other day for 15 days. At the end of 13 days, all fish were wet weighed and the control fish aquaria were discontinued, ending the fish growth experiment. However, after weighing, the grazing fish were returned to their aquaria until the end of the algal growth experiment.

Growth of fish on *Anabaena* had to be determined in a subsequent experiment due to extensive reductions in *Anabaena* density early in the initial experiment (see Results). In this subsequent experiment, I terminated each replicate aquarium seperately (at day 5, 7, 11, and 13), when the algal density became $\leq 1/3$ of the initial density. Because of the different growing periods of the fish in the treatments, I based treatment growth comparisons on mean daily fish weight change rather than total weight change. I used analysis of variance to determine treatment effects on fish weight change. A priori comparisons of weight change in grazing fish to those of unfed controls were made using least significant difference (LSD, Steel & Torrie 1980).

Direct statistical analysis of ungrazed and grazed algal densities was not attempted due to the lack of independence in successive algal population estimates. However, by regressing the natural log transformed algal density against time, I obtained population growth rates (regression coefficients) for grazed and ungrazed algal populations over the course of the experiment. I considered growth rate differences between grazed and ungrazed populations to be indicative of a fish grazing effect (see McDonald 1985b). Growth rate comparisons were made by t-test for homogeneity of these regression coefficients (Steel & Torrie 1980).

At the end of the algal growth experiment, gut contents and fecal samples from randomly selected fish were examined microscopically. The condition of the algae in the gut and in the feces was noted.

Results

The density of grazed *Chlamydomonas* was always lower than the ungrazed density (Fig. 1). The growth equation for the ungrazed *Chlamydomonas* was:

Density = $e^{0.089(Day)+3.33} \times 10^4$ cells ml⁻¹ (r² = 0.55)

and the growth equation for the grazed *Chlamy- domonas* was:

Density = $e^{0.068(Day)+2.91} \times 10^4$ cells ml⁻¹ (r² = 0.26).

Grazed and ungrazed growth rates were not significantly different ($t_{60} = 0.797$, p>0.47).

The grazed density of *Anabaena* was always lower than the ungrazed density (Fig. 2). The ungrazed *Anabaena* growth equation was:

Density = $e^{0.13(Day)+4.47} \times 10^4$ cells ml^{-1} ($r^2 = 0.55$).



Fig. 1. Grazed and ungrazed *Chlamydomonas* sp. densities through time. The density value for each date is the mean $(\pm 1 \text{ SE})$ of four replicates. Growth rates of grazed and ungrazed populations did not differ significantly (p>0.47).

The grazed Anabaena growth equation was:

Density = $e^{-0.096(Day)+4.28} \times 10^4$ cells ml⁻¹ (r² = 0.38).

The grazed and ungrazed *Anabaena* populations growth rates were significantly different ($t_{60} = 7.34$, p<0.001).



Fig. 2. Grazed and ungrazed *Anabaena* sp. densities through time. The density value for each date is the mean $(\pm 1 \text{ SE})$ of four replicates. Growth rate of ungrazed populations was significantly higher than for grazed populations (p<0.001).

Table 1. Mean blue tilapia weight changes during the experimental period in each treatment. Daily mean weight change was computed to allow comparison of treatments of varying lengths. Significant treatment effects ($F_{6,2} = 5.25$, p<0.05) on blue tilapia weight change were found with analysis of variance. This allowed predetermined LSD comparisons between the weight change of algae fed fish and unfed controls (significant difference at the p<0.05 level denoted by *).

Treatment	Time (day)	N	Standard length $(\bar{x} \pm 1SE)$ (mm)	Initial weight (x ± 1SE) (g)	Weight change (x ± 1SE) (g)	Daily weight change $(\tilde{x} \pm 1SE) (g d^{-1})$
Anabaena fed	5	4	70 ± 2	13.3 ± 0.8	0.3 ± 0.4	
	7	4	72 ± 4	12.9 ± 2.6	0.2 ± 0.2	
	11	4	69 ± 2	12.0 ± 0.8	-0.2 ± 0.2	
	13	4	71 ± 4	10.0 ± 0.6	0.2 ± 0.6	$0.02 \pm 0.05^{*}$
Chlamydomonas fed	13	4	67 ± 2	10.2 ± 1.0	-0.8 ± 0.2	
	13	4	66 ± 2	9.6 ± 0.9	-0.1 ± 0.6	
	13	4	72 ± 5	13.3 ± 2.4	0.1 ± 0.3	
	13	4	73 ± 5	13.2 ± 2.3	-2.0 ± 0.5	-0.06 ± 0.04
Unfed controls	13	4	63 ± 2	8.1 ± 0.9	-0.4 ± 0.1	
	13	4	68 ± 2	10.6 ± 1.1	-0.9 ± 0.1	
	13	4	64 ± 1	8.3 ± 0.4	-0.5 ± 0.1	
	13	4	70±4	11.8 ± 2.4	-0.8 ± 0.2	-0.05 ± 0.01
					$LSD_{0.05} = 0.06$	

Blue tilapia sacrificed at the end of the experiment had intact and broken algal cells in their stomachs and intestines. Some intact algal cells were also found in the fish feces. Blue tilapia were ingesting both algae, but only those grazing on *Anabaena* grew (Table 1). Differences in daily weight change due to fish feeding treatments were significant ($F_{6,2} = 5.25$, p<0.05). Blue tilapia fed *Chlamydomonas* had a weight loss ($\bar{x} = -0.06$ g d⁻¹, N = 16) that was not significantly different from the weight loss of unfed control fish ($\tilde{x} = -0.05$ g d⁻¹, N = 16, LSD_{0.05} = 0.06). However, blue tilapia fed *Anabaena* had a significant weight gain ($\bar{x} = 0.02$ g d⁻¹, N = 16, LSD_{0.05} = 0.06) as compared to the unfed controls.

Discussion

Zooplankton grazing results in density increases in certain sheathed green algae (Porter 1975, 1976), in density decreases in most other green algae, or in no effect on blue-green alga densities (Porter 1977). Grazing zooplankton can affect phytoplankton population dynamics directly through consumption or indirectly through regeneration of limiting nutrients (Sterner 1986). In laboratory experiments, blue tilapia affect phytoplankton populations similarly, and through similar mechanisms. Density of grazed Chlamydomonas populations were somewhat reduced relative to the ungrazed populations (Fig. 1), but the difference in growth rates of grazed and ungrazed populations were not significant. The grazed Anabaena density was substantially lower than the ungrazed density (Fig. 2), and the population growth rate decreased significantly with grazing. This suggests that at least the Anabaena populations could be reduced due to grazing by blue tilapia. Grazing by blue tilapia greatly enhanced density and significantly increased the growth rate of a large (cell dimensions: $45 \times 3 \,\mu$ m), unicellular green alga, Ankistrodesmus falcatus. presumably through nutrient regeneration (McDonald 1985b). However, morphology of specific algal groups affects grazing by blue tilapia differently than zooplankton. Unlike zooplankton, blue tilapia reduce the density of a

blue-green alga, have a relatively little effect on a small, unsheathed green alga (this study), and enhance a large, unsheathed green alga (McDonald 1985b).

The blue tilapia diet in natural systems is made up primarily of phytoplankton and zooplankton (Gophen et al. 1983), but they grow when feeding exclusively on A. falcatus (McDonald 1985b). In the present study they were found to grow when feeding on a filamentous blue-green alga Anabaena $(\bar{x} = 0.02 \text{ g d}^{-1})$, but only at approximately 50% of their growth rate when fed A. falcatus (McDonald 1985b). Blue tilapia were unable to grow or maintain themselves ($\bar{x} = -0.06 \text{ g d}^{-1}$) on another green alga, Chlamydomonas. Growth rates of blue tilapia fed A. falcatus and Anabaena were similar to blue tilapia fed artificial diets with <29% fish meal protein (Davis & Stickney 1978). However, blue tilapia feeding on natural available plankton in a fertilized fish pond were found to grow approximately 7 g d^{-1} (calculated from Armbrester 1971). Thus certain algal forage can provide an adequate diet for growth in these fish, but the inclusion of zooplankton in the diet may enhance the fish's growth rate.

Observed growth differences of blue tilapia grazing on different green algae may be due to the ability of the fish to filter the algae, rather than the quality of the algae as a food. McDonald (1985a) found that blue tilapia grazing on unialgal populations of Chlamydomonas and A. falcatus incorporate similar percentages of ingested algal carbon into fish tissue, suggesting that the quality of these green algae are similar with respect to blue tilapia growth needs. However, the blue tilapia ingested only 21% of the Chlamydomonas cells available, relative to 89% of the available A. falcatus cells (McDonald 1985a). Drenner et al. (1984) have shown that blue tilapia's filtration efficiency diminishes when particle sizes are below $25 \,\mu$ m. Thus, only the larger size Chlamydomonas cells in this experiment may have been available to the fish. If this was the case, the observed depression in the grazed Chlamydomonas population density may be due to the removal of large cells, and their removal likely would not greatly affect the population growth rate.

The observed approximate 50% decrease in growth of blue tilapia grazing on the blue-green alga, Anabaena, relative to growth on the green alga, A. falcatus (McDonald 1985b), may also be due to the ability of the fish to filter the algae. Blue tilapia do filter Anabaena flos-aquae less efficiently than A. falcatus $(3.6 \times 10^7 \text{ cells h}^{-1} \text{ versus } 1.9 \times 10^8$ cells h⁻¹, calculated from McDonald 1985a). But, based on this, blue tilapia should grow only 20% as well on Anabaena as on A. falcatus. However, blue tilapia incorporate twice as much ingested A. flosaquae carbon into growth as A. falcatus carbon (McDonald 1985a). Thus, the fish growth when feeding on A. flos-aquae should be about 40% of that when feeding on A. falcatus. This suggests that both the filterability and the quality of the algal food can play a role in determining blue tilapia growth.

Grazing blue tilapia differentially affect certain unialgal populations. Zooplankton have been found to produce similar changes in algal populations (Porter 1977) through similar mechanisms (Sterner 1986), but contrast with the blue tilapia in having opposite effects on specific groups of algae. The results of the current and previous experiments (McDonald 1985a, 1985b), suggest that blue tilapia could structure a phytoplankton community away from dominance by filamentous blue-green algae and towards green algal dominance. However, an understanding of the blue tilapia's direct and indirect effects on natural phytoplankton communities remains to be determined.

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