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Grass carp do not consume the nuisance benthic cyanobacterium, *Lyngbya wollei*

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ABSTRACT

Grass carp, *Ctenopharyngodon idella*, (Cuvier and Valenciennes, 1844) are an effective biological control for many aquatic plants, especially submersed macrophytes and macrophytic algae. Despite limited data, grass carp are sometimes promoted as a tool for controlling filamentous algae, including some cyanobacteria, in small impoundments. One important cyanobacterium, *Lyngbya wollei* (Farlow ex Gomont) comb. nov., is a nuisance species in North America that forms benthic mats and surface scums and can produce multiple intracellular toxins and off-flavor compounds. Current management of *Lyngbya* calls for approaches similar to those for other nuisance algae, including chemical control using herbicides and biological control using grass carp when herbicides are not practical. Although agency biologists and private consultants recommend stocking grass carp to control filamentous algae, no conclusive empirical data show that grass carp consume *Lyngbya*. We conducted mesocosm experiments where different densities of grass carp of varying sizes were fed diets either containing a macrophyte, variable watermilfoil (*Myriophyllum heterophyllum* Michx.) and/or *Lyngbya*. In general, grass carp did not consume *Lyngbya* when offered by itself or with milfoil, regardless of carp density or size. To test one mechanism mediating the lack of *Lyngbya* consumption by grass carp (i.e., chemical ecology), a feeding experiment where ground *Lyngbya* was fed to grass carp in agar pellets suggests that the secondary chemistry of *Lyngbya* prevents grass carp consumption. Although anecdotal observation suggests that high rates of grass carp stocking appear to control *Lyngbya,* the results of this study suggest that the mechanism of control is not direct consumption (e.g., physical disruption of the benthic mats).

Key words: cyanobacteria, *Ctenopharyngodon idella,* HAB, harmful algal bloom, management.

INTRODUCTION

Since their introduction into the United States in 1963 for aquatic plant management (Courtenay et al. 1984), grass carp [*Ctenopharyngodon idella* (Cuvier and Valenciennes, 1844)] have been well-studied for their feeding preferences and ability to control aquatic weeds (Pine et al. 1989, Hanlon et al. 2000, Dibble and Kovalenko 2009). Grass carp, especially small individuals (< 4 kg), can consume two to three times their body weight of plant material per day (Masser 2002, Wright and Reeves 2004) and have been shown to effectively control submerged and floating macrophytes under certain conditions (Stoot and Orr 1970, Osborne and Sassic 1981, Hanlon et al. 2000, Piplova 2006). However, despite limited data and disagreement in the literature, grass carp are promoted for controlling filamentous algae, including benthic cyanobacteria, as part of an integrated weed management plan, especially in the southeastern United States, (Zolcynski and Smith 1980, Shireman et al. 1985, Shelton and Murphy 1989, Masser 2002, Wright and Reeves 2004, Bayne 2005, Madsen et al. 2012).

Lyngbya wollei (Farlow ex Gomont) comb. nov. (hereafter *Lyngbya*) is a benthic, filamentous cyanobacterium that is native to Asia, Africa, and Australia. *Lyngbya is* aesthetically displeasing, often forming dense surface mats, and is potentially harmful to other organisms because of the potential for some strains to produce intracellular dermatotoxins, hepatotoxins, and neurotoxins (Carmichael et al. 1997, Burns 2004). It also produces musty off-flavor compounds, including methylisoborneol (MIB) and geosmin, which can taint drinking water and aquaculture-raised fishes (Schrader and Blevins 1993). *Lyngbya* is tolerant of reduced light (Speziale et al. 1988, 1991) and can form dense mats on lake bottoms in nutrient-enriched habitats. Mats can become displaced and float to the water surface where they effectively shade other autotrophs (Paerl and Huisman 2009). Moreover, in the southeastern United States, *Lyngbya* is a perennial species that can grow throughout the year, allowing it to create massive standing crops that exceed those of other nuisance filamentous algae (Speziale et al. 1991).

Due to the nuisance and potential negative economic impacts caused by this taxon, recreational fisheries and water resource managers are interested in controlling *Lyngbya*. Grass carp have been promoted as an effective biological control of *Lyngbya* as part of an integrated pest management plan (Zolczynski and Smith 1980, Shelton and Murphy 1989, Masser 2002, Wright and Reeves 2004), yet limited data indicate that grass carp control filamentous algae, including *Lyngbya* (Zolczynski and Smith 1980). Although high grass carp stocking rates (62 to 125 grass carp ha^{-1}) are often suggested for controlling filamentous algal blooms, including *Lyngbya* blooms (Wright and Reeves 2004), we are unaware of any replicated studies documenting that grass carp consume *Lyngbya*. In fact, one study reported that grass carp might not control *Lyngbya* because

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it is not a preferred diet item (Dyck 1994). Failure to fully understand the interaction between grass carp and *Lyngbya* could lead to conditions that favor the establishment and proliferation of *Lyngbya*. Stocking grass carp could stimulate the growth of *Lyngbya* by reducing or eliminating competitors (e.g., macrophytes and filamentous algae and cyanobacteria) for light and nutrients. This effect has been observed in some systems where grass carp were stocked and macrophytes and algae that were less preferred by the grass carp actually increased in abundance as other species were reduced (Fowler and Robson 1978, Van Dyke et al. 1984).

The primary objectives of our study were to determine the effect of grass carp size, density, and food options on direct consumption of *Lyngbya*. Secondarily, we were interested in determining if morphological defenses of *Lyngbya* deterred grass carp consumption. Plant defenses against consumers are diverse and can include structures (e.g., thorns, sheaths), size, and secondary metabolites (Ehrlich and Raven 1964, Gomez and Zamora 2002). To address these questions, we conducted a series of laboratory feeding experiments.

MATERIALS AND METHODS

Study site

All experiments were conducted in the wet lab facility at the E. W. Shell Fisheries Station at Auburn University, Auburn, AL. A recirculating tank system without a biofilter was used for all experiments. All experiments using whole plant material were conducted in aerated 150-L tanks ($n = 18$) that were partially filled (95 to 112 L) with dechlorinated water and covered with window screen prior to holding grass carp. The experiment using pelleted plant material was conducted in aerated 25-L mesocosms ($n = 16$) partially filled (13 L) with dechlorinated water and covered with window screen.

Study organisms

Prior to each experiment, triploid grass carp were seined from one of three holding ponds where they were segregated by size and placed in a large sump tank attached to the recirculating tank system or directly in experimental tanks. Fish were fasted for 2 to 3 d prior to the start of each experiment to increase hunger and increase feeding rate. Grass carp used to replace those that died in the experiments were maintained in the sump tank.

To examine direct consumption of *Lyngbya,* the filamentous cyanobacterium was collected from a pond at the E. W. Shell Fisheries Station and returned to the laboratory to remove large debris, including larval and adult insects, snails, leaches, worms, sticks, and leaves. Given the structural complexity of *Lyngbya* in the field, smaller items, including other minor components of the algal community, were not removed. Thus, *Lyngbya* used for our experiments was not a pure culture but instead a "*Lyngbya* complex" consistent with material found in nature. *Lyngbya* accounted for $\approx 95\%$ of the biomass provided to grass carp.

Watermilfoil (*Myriophyllum heterophyllum* Michx., hereafter called milfoil) is a native aquatic plant in Alabama (USDA, NRCS 2010) that grass carp were shown to consume in preliminary experiments (data not shown) and served as a control. Milfoil was collected from Okhussee Thloko, a public fishing pond in Tuskegee, AL, and returned to the laboratory for cleaning prior to being used in feeding experiments.

Grass carp feeding assays

The overall study design included five experiments to explore factors influencing grass carp consumption of *Lyngbya*. Experiment 1 determined if, given a choice of another palatable plant species, grass carp consume *Lyngbya*. Hereafter this is referred to as the *Choice experiment*. Experiment 2 examined basic consumption rates of *Lyngbya* in the absence of other palatable species (*No-choice experiment*). Experiment 3 compared grass carp density effects on *Lyngbya* consumption (*Density experiment*). Experiment 4 examined the influence of grass carp size on *Lyngbya* consumption (*Size experiment*). Finally, Experiment 5 examined if *Lyngbya* deterred grazing by use of chemical compounds (*Chemical deterrence experiment*).

Choice experiment. Five small (range = 7 to 12 cm total length [TL]) grass carp were added to each of nine tanks where they were fasted for 2 d before being simultaneously offered two different diets, including milfoil (10 g wet weight, $\sim$ 0.75 g dry weight) and *Lyngbya* (5 g wet weight, $\sim$ 1.5 g dry weight), that were attached to 7.6 cm by 7.6 cm plastic mats secured to the bottom of each tank. Both plants were also added to nine control tanks that lacked fish to measure autogenic changes in plant mass during the experiment. Dataloggers were used to measure temperature from all enclosures during the feeding trial (water temperature = 27 C). Four additional samples of each diet were collected at the start of the experiment to estimate plant wet-to-dry weight conversion factors. Plant dry weights were estimated by drying samples for 24 h at 50 C. Remaining plant material was collected from each tank after 24 h and dried. Percent change in plant dry weight was estimated for each plant species in each tank with the following equation: $100 \times [((T_f / (T_i \times \text{correction factor})) - 1]$ where T_i and T_f were the initial and final weights for the treatment diet (modified from Stachowicz and Hay 1996). The correction factor was calculated as the average ratio of the final to initial plant weights.

No-choice experiment. Five small (range = 7 to 12 cm TL) fish were added to each of 10 tanks where they were fasted for 2 d before being separately offered one of two different diets, including milfoil (21.4 g wet weight, $\sim$ 1.5 g dry weight) or *Lyngbya* (5 g wet weight, $\sim$ 1.5 g dry weight), that were attached to plastic mats secured to the bottom of each tank. Dataloggers collected temperature data from all enclosures during the feeding trial (water temperature = 23 C). Each plant also was added separately to four control tanks lacking fish to measure autogenic changes in plant mass during the experiment. Four additional samples of each diet were collected at the start of the experiment to calculate plant wet-to-dry weight conversion factors. Plant material in the

tanks was collected after 24 h and dried as previously described to estimate change in dry weight of plant material in the experimental tanks.

In order to confirm that grass carp response was not a function of the fish being satiated, after the *Lyngbya* was removed from tanks with fish in the no-choice experiment, milfoil (21.4 g wet weight) was added to each tank. All remaining plant material was removed after another 24 h and dried to calculate percent weight change over time.

Density experiment. A third experiment was conducted to determine if fish density influenced preference for *Lyngbya* or milfoil. In response to a disease outbreak prior to the start of this experiment, experimental fish were quarantined in a separate tank system and treated for 1 wk prior to use with formalin (100 ppm every day added to flow-through system and a 15 min static 200 ppm treatment every third day) to remove any external parasites. Small grass carp (range = 7 to 12 cm TL) were added to each of 12 tanks (six tanks with five fish, and six tanks with 10 fish) where they were fasted for 3 d before being separately offered either milfoil (21.4 g wet weight) or *Lyngbya* (5 g wet weight) attached to plastic mats secured to the bottom of each tank. Thus, a total of three replicates per density treatment containing fish were used. Each plant species was also added to three fishless control tanks to measure autogenic changes in plant mass during the experiment. Dataloggers collected temperature data from all enclosures during the feeding trial (water temperature = 22 C). After 24 h, two fish were found to have escaped their tanks and were replaced with similar-sized fish. After an additional 24 h (48 h total), all plant material was collected and processed as described above for earlier experiments to calculate wet and dry weights. Initial dry weights were estimated from a wet-to-dry weight regression created for milfoil or *Lyngbya* from preliminary experiments.

Size experiment. A fourth experiment was conducted to determine if fish size influenced their preference for *Lyngbya* or milfoil. Eight small (range = 7 to 12 cm TL), four medium (range = 14 to 19 cm TL), or two large (range = 21 to 24 cm TL) fish were added to one of 12 tanks (four tanks per fish size treatment). Fish were given no food for 2 d before being offered *Lyngbya* (5 g wet weight) attached to a plastic mat secured to the bottom of each tank. Dataloggers collected temperature data from all enclosures during the feeding trial (water temperature = 25 C). Four additional samples of *Lyngbya* were collected to estimate a wet-to-dry weight conversion factor for the start of the experiment. Plant material in the tanks was collected after 24 h and dried as above to estimate the change in dry weight of plant material in the tanks.

After the *Lyngbya* was removed from treatment tanks, milfoil (20 g wet weight) was added and carp were allowed to feed for 24 h before any remaining plant material was removed and dried to determine if grass carp avoidance of *Lyngbya* could be attributed to fish satiation. Prior to replacing *Lyngbya* with milfoil, four dead fish in separate tanks were replaced with appropriately sized replacement fish. Relative change in dry weight in plant material was estimated as above for the grass carp density experiment.

Chemical deterrence experiment. To determine if the structure or chemical constituents of *Lyngbya* deter grass carp consumption, *Lyngbya* was freeze-dried, ground into a fine powder, and then incorporated into agar-based pellets (15% sodium alginate). To promote grass carp consumption of pellets, feed used to maintain the fish was crushed and added to all agar pellets (accounting for 28% of each pellet by dry mass). Thus, all pellets contained 15% sodium alginate and 28% fish feed. To include a palatable control plant to the agar pellets as a replacement for *Lyngbya* biomass, iceberg lettuce was processed in the same manner as *Lyngbya* and incorporated in agar pellets. Four pellet diets were included in this experiment: 1) 57% lettuce, 0% *Lyngbya* (control); 2) 40% lettuce, 17% *Lyngbya*; 3) 19% lettuce, 38% *Lyngbya*; and 4) 0% lettuce, 57% *Lyngbya*. All percentages are of the total dry mass of the pellets. Each pellet type (total wet weight fed to fish = 0.3 g) was offered separately to three small (range = 7 to 12 cm TL) grass carp that were fasted for 7 d to maximize potential consumption. There were four replicates per treatment with fish and two replicates of each treatment in mesocosms without fish to account for changes in pellet mass not due to fish. After 30 min, pellets were removed and final wet weights were recorded. Percent change in pellet weight was calculated as described before for percent change in plant mass.

Statistical analysis

Analysis of variance (ANOVA) with Tukey's pairwise comparisons was used to assess differences among treatment means. One-way Student's *t*-tests determined if treatment means were equal to 0. For two experiments (*No-choice* and *Size*) where milfoil was offered to the same fish previously exposed to *Lyngbya*, a paired *t*-test was used to compare treatment means for plant weight change of control (milfoil) and experimental (*Lyngbya*) diets. All values were considered significant at $\alpha < 0.05$.

RESULTS AND DISCUSSION

In all of the various feeding experiments conducted, grass carp did not consume *Lyngbya*, despite experiments that manipulated available whole plant diets, fish density, fish size, or percent composition of ground *Lyngbya* in pellet diets. When given a choice between milfoil and *Lyngbya* (*Choice experiment*) grass carp consumed significantly more milfoil than *Lyngbya* (Figure 1; ANOVA, $F_{1,16} = 676$, $P < 0.001$). Grass carp reduced milfoil biomass by > 80% whereas grass carp had no effect on *Lyngbya* biomass (*t*-test mean = 0, $T_8 = 0.47$, $P = 0.65$). In the *No-choice experiment*, grass carp consumed > 75% milfoil biomass but did not consume *Lyngbya* when either was offered separately (Figure 2; *t*-test mean = 0, $T_8 = 1.46$, $P = 0.22$). Again, there was a large ecological difference in the amount consumed by grass carp when comparing consumption of both diets (ANOVA, $F_{1,8} = 232$, $P < 0.001$). To determine if fish were not consuming *Lyngbya* due to a factor other than diet preference (e.g., satiation or disease), we replaced *Lyngbya* with milfoil and found that fish that previously avoided *Lyngbya* consumed a similar amount of milfoil compared to

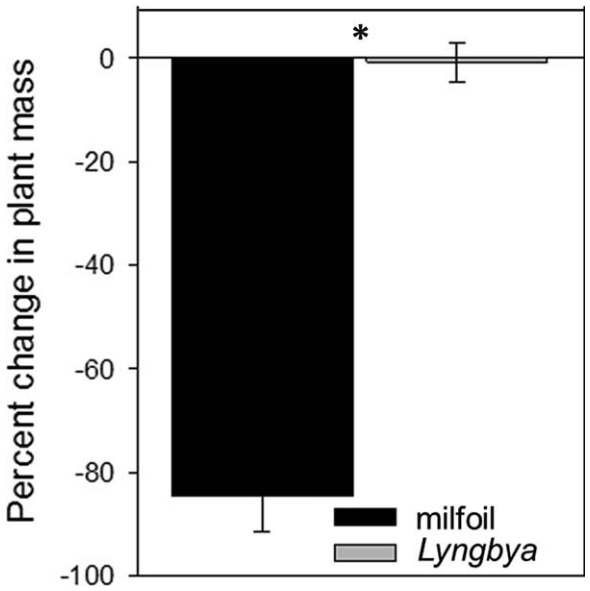

Figure 1. Effect of paired diet choice on grass carp consumption of milfoil and *Lyngbya*. Error bars represent 95% confidence intervals. * indicates significance of ANOVA at $\alpha = 0.05$.

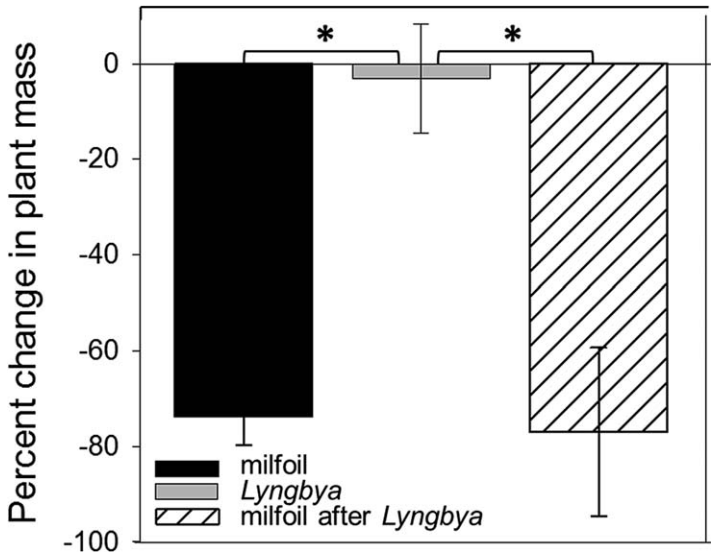

Figure 2. Effect of plant type (milfoil or *Lyngbya*) on grass carp consumption. Milfoil or *Lyngbya* when offered separately (no choice). Hashed bar indicates milfoil offered to same fish previously fed *Lyngbya*. Error bars represent 95% confidence intervals. The left bracket indicates the results of an ANOVA, and the right bracket shows the results of the paired *t*-test (H_o = means are equal for same fish fed *Lyngbya* and then offered only milfoil). * indicates significance at $\alpha = 0.05$.

fish initially offered this edible plant (Figure 2; ANOVA, $F_{1,9} = 0.18$, $P = 0.69$). The same fish that were initially offered and avoided *Lyngbya* consumed > 75% of the control diet that replaced *Lyngbya* (Figure 2; *t*-test mean = 0, $T_4 = 12$, $P < 0.001$) indicating that these fish would have eaten if offered a palatable choice but actively avoided *Lyngbya*. Three fish died during this experiment; however, we did not observe any effects of these deaths on the feeding behavior of other fish in the affected tanks.

The number of grass carp (*Density experiment*; 5 or 10 fish) positively affected the amount of plant consumed (Figure 3; ANOVA, $F_{1,8} = 7$, $P = 0.03$) as did the food type offered (Figure 3; ANOVA, $F_{1,8} = 107$, $P < 0.001$). A significant interaction existed between food type by fish density (Figure 3; ANOVA, $F_{1,8} = 13$, $P = 0.01$). Grass carp density had a large negative effect on milfoil but no effect on *Lyngbya* (Figure 3). As expected, the high fish density treatment resulted in higher consumption of milfoil (Figure 3; ANOVA, $F_{1,5} = 14$, $P = 0.02$), whereas fish at both densities avoided *Lyngbya* (*t*-test mean = 0; five fish treatment: $T_5 = 0.70$, $P = 0.56$; ten fish treatment: $T_5 = -0.40$, $P = 0.73$)

Fish size also had no significant impact on amount of *Lyngbya* consumed (*Size experiment* Figure 4; ANOVA, $F_{2,9} = 0.74$, $P = 0.50$; *t*-test mean = 0; small fish: $T_3 = 0.04$, $P = 0.97$; medium fish: $T_3 = -1.55$, $P = 0.22$; large fish: $T_3 = 0.63$, $P = 0.57$). As in the *No-choice experiment*, fish offered milfoil after being offered *Lyngbya* generally consumed milfoil (Figure 4; paired *t*-test; $T_{11} = 5$, $P < 0.001$). The lone exception to this pattern was the large fish treatment (*t*-test mean = 0; $T_3 = -1.69$, $P = 0.19$), which could have resulted from high variation attributable to mortality in this treatment. When one fish died, the remaining grass carp in the tank might have been more stressed due to isolation or other conditions in that tank.

Fish avoided agar pellets made from fish feed and lettuce containing *Lyngbya* (*Chemical deterrence experiment*; Figure 5; ANOVA, $F_{3,12} = 156$, $P < 0.001$). In the pair-wise comparisons, grass carp avoided pellets containing ≥ 17% (by dry mass) *Lyngbya*, whereas they readily consumed pellets lacking the cyanobacterium (Figure 5; *t*-test mean = 0; $T_3 = -48.48$, $P < 0.001$).

Grass carp have been studied extensively for their preference and ability to consume multiple types of aquatic macrophytes (e.g., 166 publications cited in review by Dibble and Kovalenko 2009). Some studies have documented that grass carp consume filamentous green algae (*Cladophora* sp. and *Pithophora* sp.), as well as charophytes (*Chara* sp. and *Nitella* sp.), especially after preferred macrophytes are eliminated, but that grass carp avoid consuming some species entirely (Avault 1965, Lembi et al. 1978, Lewis 1978, Pine et al. 1989, Colle and Shireman 1994). For example, past studies suggest that the chlorophyte, *Spirogyra*, is avoided because the texture of the alga makes it difficult to ingest (Prowse 1971). There is mixed evidence that grass carp will consume different species of filamentous algae, and only one unreplicated study documented that grass carp control *Lyngbya* in the field (Zolczynski and Smith 1980). In that study, grass carp stocked at a rate of 74 fish ha^{-1} over 4 yr and a partial draining of the lake showed 100% control of *Lyngbya*. However, this study did not document consumption of *Lyngbya* by grass carp. Because this study was uncontrolled, conducted in a single pond, and confounded by other management actions, it is unclear what factors mediated the loss of *Lyngbya* from this system (Zolczynski and Smith 1980).

Water quality managers and pond owners currently need an effective control agent for the spread of nuisance

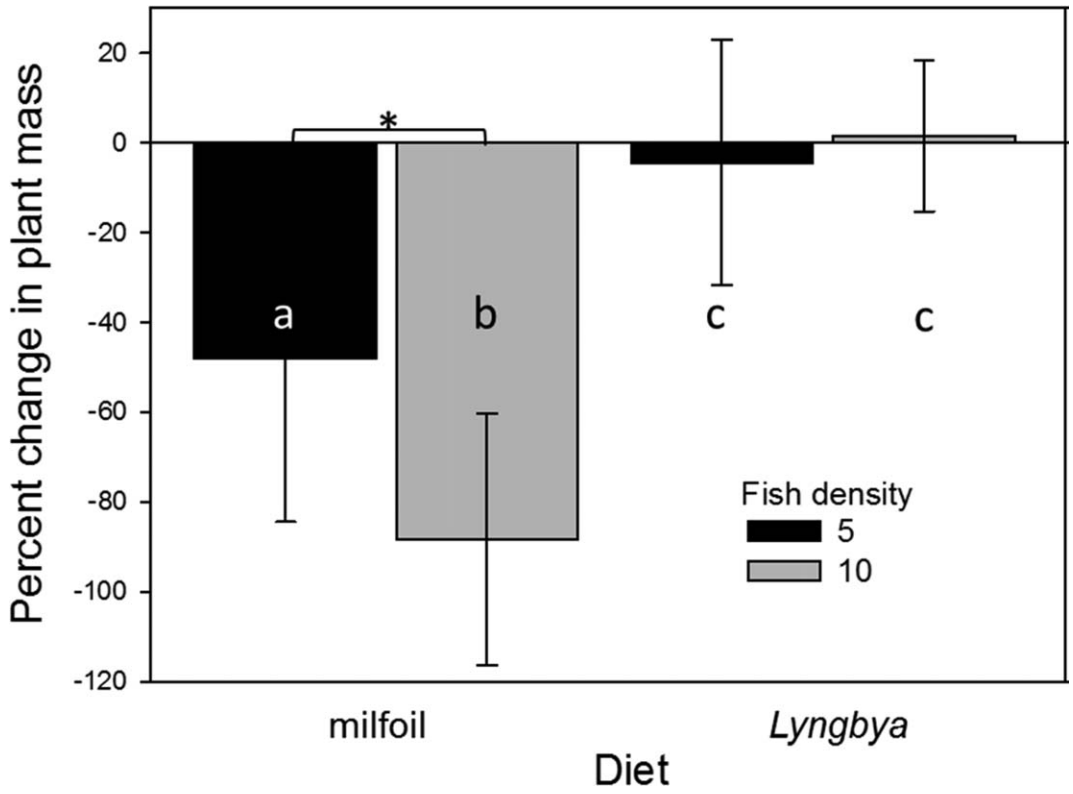

Figure 3. Effect of grass carp density (5 [black bars] or 10 [gray bars] fish) on consumption of milfoil or *Lyngbya*. Error bars represent 95% confidence intervals. * indicates significance of a paired *t*-test at $\alpha = 0.05$. Letters indicate grouping based on Tukey's multiple comparison test ($\alpha = 0.05$).

Lyngbya. The basic management strategy for nuisance aquatic vegetation (including filamentous algae) is prevention first, followed by control using physical, biological, and chemical methods (Shelton and Murphy 1989). Given that herbicide applications are not practical for some water bodies (e.g., drinking water reservoirs), it is important to evaluate the role of biological control agents, such as grass carp, for controlling nuisance filamentous (Shireman and Smith 1983). Grass carp are an exotic species and might not be a viable option for aquatic weed control in many places. However, in the southeastern United States, grass carp are routinely used for aquatic weed control. For this reason, and because grass carp are promoted by consultants, managers, and public agencies as one tool to control filamentous algae, it is critical to rigorously determine if grass carp directly consume *Lyngbya* (Wright and Reeves 2004).

Past studies have shown that temperature has a large impact on grass carp consumption. For example, when water temperatures reach above 16 C, grass carp feed more intensely and less selectively (Stroganov 1963). Because all of our experiments were conducted when the water temperature was > 22 C, we would expect grass carp to be less selective and more likely to consume a wide range of offered diets, including less-preferred species. Also, because fish were given no food for 2 to 3 d prior to each experiment, our results should be considered conservative regarding grass carp feeding preferences. Results from several mesocosm experiments indicate that grass carp generally avoided *Lyngbya* while they actively consumed a palatable but not highly preferred macrophyte species (milfoil). When given no choice and only offered *Lyngbya*, grass carp did not consume the filamentous cyanobacterium.

Small grass carp (e.g., 10 to 13 cm TL) are generally more effective at controlling nuisance aquatic vegetation than larger grass carp because they have higher energy demands (per unit body mass) and feeding rates (Osborne and Sassic 1981, Masser 2002, Piplova 2006). Although some studies suggest that smaller grass carp (i.e., 3 to 9 cm TL) are more likely to consume filamentous algae, including periphyton (Osborne and Sassic 1981, Watkins et al. 1981, Wright and Reeves 2004), fingerling grass carp begin eating macrophytes when they reach 5 cm TL (Sobolev 1970). However, such small carp are subject to fish and bird predation until they are at least > 20 cm TL. Our experiments generally focused on small grass carp, but large stocker size grass carp were also tested in one experiment and results were similar across carp sizes. These consistent findings are likely a result of all grass carp used in this study to be considered as juveniles.

Lyngbya grows in coarse mats similar to *Pithophora* sp. and should be readily available for the carp to bite and ingest (Prowse 1971). However structural traits of aquatic macrophytes and algae have been shown to be effective deterrents of grazers (Hay et al. 1994, Taylor et al. 2003). In one study, the polysaccharide sheath of *Lyngbya* was shown to prevent amphipod herbivory (Camacho and Thacker 2006). Results from the experiments where *Lyngbya* was ground and incorporated into agar pellets demonstrated that unpalat-

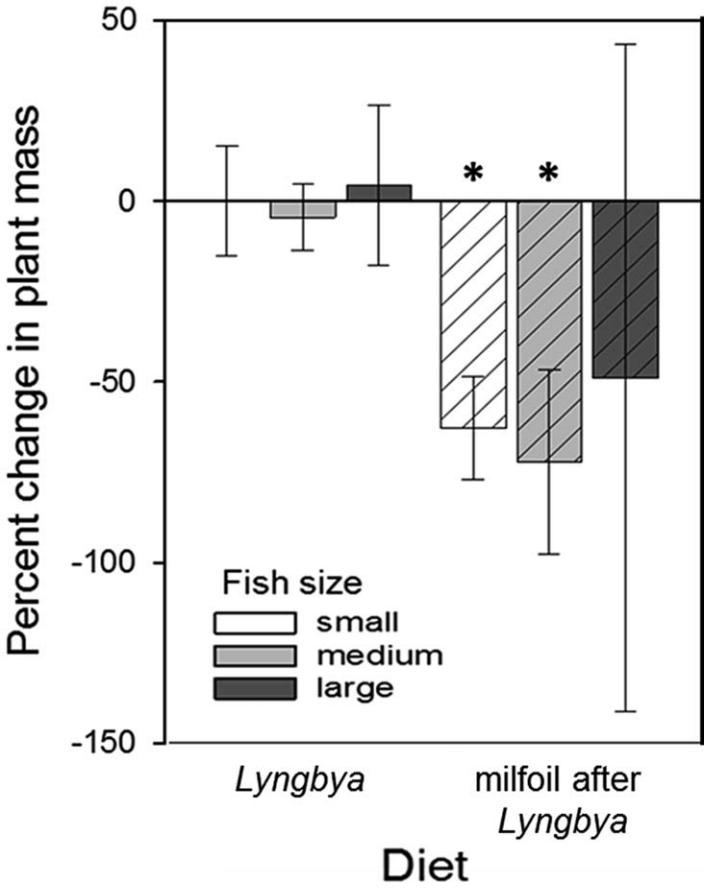

Figure 4. Effect of grass carp size (small [7 to 12cm total length or TL, white bars]; medium [14 to 19cm TL, light gray bars]; or large (21 to 24cm TL, dark gray bars]) on plant consumption. Error bars represent 95% confidence intervals. Hashed bar indicates milfoil offered to same fish earlier fed *Lyngbya*. * indicates significance of a paired *t*-test (H_o = means are equal for same fish fed *Lyngbya* and then offered only milfoil) for each treatment at $\alpha = 0.05$.

able chemical components mediate grass carp avoidance of *Lyngbya*. Grass carp are known to avoid feeding on macrophytes that produce toxins (Murphy et al. 2002), and *Lyngbya* has been shown to produce saxitoxin in response to amphipod herbivory (Thacker et al. 2005). However, further experiments are needed to determine which secondary metabolites actively deter grass carp consumption of *Lyngbya*.

Pond managers have anecdotal evidence documenting declines in *Lyngbya* after stocking grass carp into ponds as part of an integrated pest management plan. We demonstrate that grass carp do not consume *Lyngbya* in an experimental setting. However, we do not contend that grass carp are unable to control *Lyngbya* through other mechanisms, such as disrupting mats. It is possible that grass carp indirectly consume some *Lyngbya* while attempting to consume organisms living within the *Lyngbya* mat. If carp are tearing apart *Lyngbya* mats and causing them to float to the surface of the pond and senesce, they might have significant effects on the abundance of the cyanobacterium in the pond. If toxic secondary metabolites mediate the interaction between grass carp and *Lyngbya*, carp might effectively

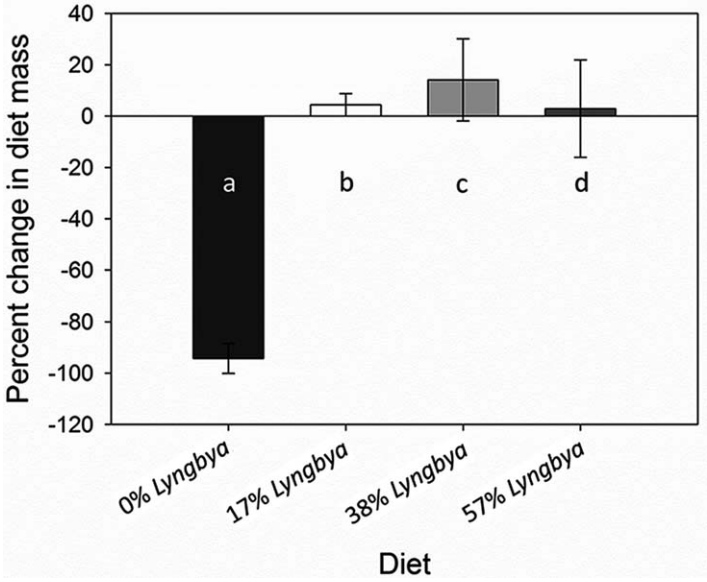

Figure 5. Effect of *Lyngbya* (% dry weight) in pellets on grass carp consumption. Error bars represent 95% confidence intervals. Letters indicate grouping based on Tukey's multiple comparison test ($\alpha = 0.05$).

control *Lyngbya* that do not produce high levels of secondary metabolites due to variation in physiology, season, and population structure. Clearly, understanding the potential for grass carp to effectively control this nuisance cyanobacterium will require a better understanding of the biology and ecology of both species. Carefully controlled field experiments will be needed to validate anecdotal observations describing the effectiveness of high grass carp stocking densities related to the control of *Lyngbya* through consumptive or nonconsumption mechanisms in nature.

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