

COMMENT.

FOOD WEB INTERACTIONS AND BIOMANIPULATION IN AUSTRALIAN RESERVOIRS

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Recently, we have been studying the control of phytoplankton biomass in several Australian reservoirs. To manipulate fish communities in order to reduce phytoplankton biomass, one needs a thorough understanding of processes in the plankton-associated food webs. Several models of food web interactions already exist (Shapiro & Wright 1984; Carpenter et al. 1985; McQueen et al. 1986) which focus on the evaluation of zooplankton grazing when the biomass of zooplanktivorous fish is manipulated. More recently, nutrient fluxes within food webs were also taken into account (e.g. Matveev et al. 1994a,b; Gulati 1995). However, in Australia both climate and organisms differ from those in the existing models.

We explored food web interactions of Australian biota at several scales: in laboratory trials, in mesocosms, and by analysing the time-series of plankton and fish biomass in reservoirs. At all scales, grazing by zooplankters was found to have significant effects on phytoplankton at least during some periods of the year. Large grazers, e.g. *Daphnia carinata* and *Boeckella triarticulata*, had higher grazing rates and wider feeding niches than small zooplankters. With clearance rates of 5 ml per animal per hour on lake phytoplankton, eight adult *D. carinata* in 1 litre of water could clear the whole volume in 24 hours, and a sustainable population of *D. carinata* can reach 80 individuals per litre (Matveev et al. 1994a). In two large reservoirs, Lake Hume (surface area 202.5 km², 41 m depth) and Lake Dartmouth (63 km², 170 m depth), *Daphnia* biomass explained more than half of the observed variance in total phytoplankton biovolume (TPB) in the spring and summer of 1994/95. When zooplankton biomass and nutrients were manipulated in enclosures with water from the two lakes, total chlorophyll-a was significantly affected by grazers in 8 out of 12 experiments and by added nutrients in 9 out of 12 of experiments, suggesting similar frequencies of occurrence for bottom-up and top-down effects. The relative importance of the two effects changed seasonally. Increasing cladoceran biomass reduced chlorophyll-a, while increasing the biomass of small copepods could increase chlorophyll-a. Predatory water-mites, *Piona*, had similar stimulating effects on the algae (Matveeva & Matveev 1995). Lake time-series yielded no correlations between total zooplankton biomass and TPB, significant negative correlations between Cladocera and TPB, and positive or no correlations between

Copepoda and TPB in 1994/95. Later in 1995, when acoustic fish-monitoring was performed, Cladocera biomass was again negatively correlated with TPB, while fish biomass was negatively correlated with Cladocera biomass, suggesting trophic-level interactions. In laboratory experiments, adults and juveniles of western carp gudgeon *Hypseleotris klunzingeri* and goldfish *Carassius auratus* all preferred Cladocera to Copepoda. Acoustic biomass of pelagic fish (echointegration above -90 dB) varied seasonally, peaking in both lakes in autumn and having minima in spring. The biomass was positively correlated with TPB in L. Hume and with cyanobacteria biovolume in L. Dartmouth.

In the pelagic zones of seven lakes with varying degrees of trophic status, surveyed in 1995, acoustic fish biomass was highest in eutrophic (Queensland) lakes and lowest in oligotrophic (Snowy Mountains) lakes. In contrast to other continents, where the pelagic zone of reservoirs may remain a "vacant habitat" (Fernando & Holcik 1991), Australian reservoirs contained established populations of fish. The analysis of *in situ* target-strength distributions indicated the predominance of small individuals (<5 cm length) with densities exceeding 100,000 fish per hectare.

In whole-lake experiments in the USA, it was suggested that the mean body length of crustacean grazers was the best index of grazing impact on algae, and was negatively correlated with TPB (Carpenter et al. 1996). Also, it was suggested that the potential for biomanipulation increases with crustacean body length. In world lakes, excluding Australia, the upper limit of crustacean body length was found to be 1.27 mm (Carpenter et al. 1996). In Australian reservoirs, we also found strong negative correlations between mean crustacean body length and TPB; however, the maximal mean length in our reservoirs is much higher - more than 2.0 mm. Thus we suggest that if the crustacean body length hypothesis of Carpenter et al. is applicable to Australia, then the potential for biomanipulation will be higher here than on other continents. The larger mean value for crustacean body length in Australian lakes is due to the presence of the zooplankter *Daphnia carinata*, a species widespread in Australia (Benzie 1988) and occurring perennially in some large lakes (Matveev et al. 1994b), again suggesting a good potential for biomanipulation.

In contrast to the situation found in lakes of the northern hemisphere, the planktivorous fish of Australian reservoirs are relatively small and they may deplete small rather than large zooplankters, so that animals as large as the adults of *D. carinata* may avoid predation. This would result in promotion of *Daphnia*, particularly if fish eliminate its smaller competitors. In our experiments with mosquitofish *Gambusia holbrooki* (Matveev et al. 1994a) and juvenile golden perch *Macquaria ambigua*, large *Daphnia* increased in numbers when fish suppressed smaller *Moina*. In L. Dartmouth, small flathead gudgeon *Philypnodon grandiceps* were found to coexist with *D. carinata* in

the pelagic zone and a positive correlation between crustacean body length and fish acoustic biomass was observed, suggesting the promotion of *Daphnia* by the gudgeons. Interactions of this kind suggest that biomanipulation may involve creating conditions for the protection of some planktivorous fish rather than their eradication. However, the resulting water quality in terms of algal biomass may depend on more than just the relative sizes of planktonic crustaceans. It was suggested that some planktivores stimulate algal growth by excreting nutrients (Matveev *et al.* 1994a). This stimulation may be species-dependent; we found a strong effect for introduced mosquitofish, but no effect for juveniles of native golden perch. The eventual control of phytoplankton will depend on which of the two forces prevail: zooplankton grazing or nutrient supply from fish and other sources. Such complex interactions dictate the necessity of analysing a lake's food web before applying biomanipulation as a management option.

Manipulation of native planktivores for water quality purposes does not contradict the aims of their conservation. Firstly, in some cases, as mentioned, small pelagic fish may need to be maintained at a desired level rather than eradicated. Secondly, in those cases where planktivorous fish must be reduced in numbers, this reduction is not likely to affect adversely the original natural stream population(s) prior to impoundment: the fish to be controlled inhabit a completely artificial habitat - the pelagic zone of man-made reservoirs. According to our estimates, these fish may reach high densities, exceeding 4 individuals per m³. Thirdly, control possibly can be achieved by the addition of native piscivores which may have an even higher conservation value than the planktivores. The aim of biomanipulation should be the establishment and maintenance of a proper ratio of planktivores/piscivores, adequate for water quality requirements. Successful selection of the appropriate ratio for a given reservoir will depend on the extent of our understanding of its food web interactions. For practical application of biomanipulation in management, further development of the food web theory under Australian conditions is needed.

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