Limnologica 62 (2017) 5–18

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

Effects of fish and macrophytes on phytoplankton and zooplankton community structure in a subtropical freshwater reservoir

Darren J. Akhurst[a,b], Graham B. Jones[a,c], Malcolm Clark[a,c,*], Amanda Reichelt-Brushett[a]

[a] *School of Environment, Science, and Engineering, Southern Cross University, Lismore, NSW 2480, Australia*
[b] *North American Geochemical, LLC, PO Box 587, Walterboro, SC 29488, USA*
[c] *Marine Ecology Research Centre, Southern Cross University, Lismore, NSW 2480, Australia*

ARTICLE INFO

Article history:
Received 23 October 2015
Received in revised form 11 August 2016
Accepted 8 September 2016
Available online 29 October 2016

Keywords:
Bio-manipulation
Cyanobacteria
Macrophytes
Nutrients
Trophic cascade

ABSTRACT

Excessive macrophyte biomass and cyanobacterial blooms associated with eutrophication and possibly exotic fish frequently compromise freshwater systems. In this study, 20 large (~3.2 m^3), replicated enclosures were used to investigate the effects of piscivorous Australian bass (*Macquaria novemaculeata*), planktivorous gambusia (*Gambusia holbrooki* (Girard)), benthivorous carp (*Cyprinus carpio*), and macrophyte removal on water quality, as well as trophic interactions within the enclosures. Fish effects on reservoir water quality were carp > gambusia **>** bass. *Cryptomonads* spp. (54,083 cells/mL) and *Anabaena* spp. (47,983 cells/mL) increased significantly (63 and 23 fold, respectively) in carp enclosures, possibly because of physiological adaptation to low light, high turbidity, total phosphorus concentrations (TP) and low TN: TP ratios (N-limitation); a consequence of carp benthic grazing. Carp and gambusia caused an unconventional shift from smaller to medium sized zooplankton (e.g. *Boeckella* sp., *Bosmina meridionalis*), possibly a result of copepod nauplius grazing. In the subtropical system studied, fish-induced nutrient recycling appears more important to the outcome of bio-manipulation than grazing impacts. Macrophyte harvesting unexpectedly decreased phytoplankton biomass linked to declines in Euglenophyta and diatoms (*Asterionella* spp.). Cyanophyta (*Oscillatoriales* spp./*Anabaena* spp.) increased in response to macrophyte harvesting and was consistent with findings on European lakes that Cyanophyta abundance tends to be higher in the absence of macrophytes. Results indicate exotic fish removal, nutrient loading control and macrophyte conservation is important in these aquatic systems to maintain high water quality.

1. Introduction

Shallow freshwater reservoirs and lakes in agricultural and urban environments are prone to nutrient enrichment, which often causes prolific growth of aquatic macrophytes and/or intense blooms of potentially noxious cyanobacteria, resulting in eutrophication, a recurrent feature for many rivers, reservoirs and lakes (Webster et al., 2001). Both responses compromise the aesthetic, recreational, conservation and resource values of these systems, however the connections between these are complex (Mehner et al., 2002). Further complexity generally exists from the presence of planktivorous and benthivorous fish that may potentially exert strong “top-down” grazing and/or “bottom-up” nutrient effects on aquatic systems (Drenner and Hambright, 1999; Benndorf et al., 2002). Accordingly, management of freshwater lakes and reservoirs is notoriously difficult and confounded by a lack of studies that examine the interactions of these four phenomena.

The inhibitory role of macrophytes on phytoplankton biomass has been well documented, leading to the theory of “alternate stable states” (Scheffer, 1998; Scheffer et al., 2001). Central to this theory is the proposition that macrophyte communities maintain themselves and resist vegetation shifts because of self-stabilising mechanisms (e.g. shading out phytoplankton; Scheffer et al., 2001; Morris et al., 2003). In contrast, macrophyte loss or removal has been shown to facilitate a long-lasting switch to algal, particularly cyanobacteria dominance (Scheffer, 1998; Scheffer et al., 2001). These changes are strongly linked to specialisation within cyanobacteria to monopolise available light and nutrient resources that are critical to primary productivity in aquatic systems (Rabalais, 2002; Schindler et al., 2008; Gillor et al., 2010). Kosten et al. (2011) suggests that climate effects on the competitive balance between macrophytes and phytoplankton may also be critically important but not straightforward. Phytoplankton responses to nutrient enrichment, macrophyte abundance and/or

---

* Corresponding author at: School of Environment, Science, and Engineering, Southern Cross University, Lismore, NSW 2480, Australia.
E-mail address: malcolm.clark@scu.edu.au (M. Clark).

http://dx.doi.org/10.1016/j.limno.2016.09.009
0075-9511/

fish-induced impacts often results in unpredictable phytoplankton assemblages in tropical and subtropical systems (e.g. Kruk et al., 2009; Iglesias et al., 2011; Kosten et al., 2011) compared to better understood temperate Northern Hemisphere lakes (e.g. Søndergaard and Moss, 1998; Jeppesen et al., 2007).

Attempts to control nuisance phytoplankton traditionally focus on 'bottom-up' nutrient limitation (Schindler, 1977; Hecky and Kilham, 1988; Schindler et al., 2008). An alternative technique is a 'bio-manipulation' approach that first uses food web restructuring to increase consumption of nuisance phytoplankton by herbivorous zooplankton (top-down; Benndorf et al., 2002) and secondly reduces nutrients associated with benthivorous fish (bottom-up; Mehner et al., 2002). This approach to controlling nuisance phytoplankton has been documented extensively in temperate European lakes and has resulted in lower total phosphorus (TP), decreased chlorophyll *a* (Chl- *a*), reduced phytoplankton biomass and higher Secchi depth readings (e.g. Van de Bund and Van Donk, 2002; Jeppesen et al., 2007). However, in subtropical/tropical systems, large-bodied organisms (i.e. Daphnidae), the most efficient zooplankton grazers, typically have a limited abundance (Hunt and Matveev, 2005; Iglesias et al., 2011). Commonly the herbivorous grazing niche is made up of smaller calanoid copepods and rotifers (Jeppesen et al., 2007; Iglesias et al., 2011), most likely because of high predation by fish (Mehner et al., 2002; Jeppesen et al., 2005). Consequently, the classic 'top-down' control of phytoplankton by large zooplankton observed in temperate systems is not clearly evident (Jeppesen et al., 2007; Iglesias et al., 2011).

It has long been proposed that bottom-up effects of nutrients on the structure of pelagic food webs remain effective even in strongly top-down manipulated systems (e.g. McQueen and Mills, 1986; Mehner et al., 2002; Hunt and Matveev, 2005). For example, benthivorous fish, such as common carp, stir up substratum and thus increase sediment re-suspension, water turbidity and internal nutrient loading (Webster et al., 2001; Matsuzaki et al., 2007; Roozen et al., 2007). In addition, benthivorous fish grazing may exert strong bottom-up effects on water quality by directly destroying or uprooting macrophytes (Matsuzaki et al., 2007). Consequently, it has been suggested that the removal of benthivorous fish determines the outcome of bio-manipulation in shallow systems more strongly than removal of planktivorous fish (e.g. gambusia; Drenner and Hambright, 1999; Mehner et al., 2002).

Previously, we examined using enclosures the effects of plant harvesting and 3 fish species; introduced benthivorous juvenile carp (*Cyprinus carpio*), planktivorous mosquitofish (*Gambusia holbrooki* (Girard)) and native piscivorous Australian bass (*Macquaria novemaculeata*), on water quality in a subtropical freshwater reservoir (Akhurst et al., 2012). Phytoplankton responses were reported only in terms of Chl- *a,* and no information was presented on shifts across phytoplankton groups. In this paper, data collected from Akhurst et al. (2012), was first examined to quantify the importance of fish-induced bottom-up nutrient enrichment in regulating phytoplankton and zooplankton community structure in a subtropical reservoir. Second, we tested whether top-down fish predation reduced zooplankton abundance and grazing pressure on phytoplankton (Shapiro et al., 1975). Finally, we tested whether plant harvesting increased the abundance of cyanobacteria (Scheffer, 1998; Morris et al., 2006). Findings were considered in relation to those typical of shallow temperate European freshwater lakes.

2. Materials and methods

2.1. Site description

Emigrant Creek Dam (ECD; −28°45′58″S; 153°31′7″E) is a freshwater reservoir located on the Far North Coast of New South Wales, Australia (Fig. 1). The reservoir has a surface area of approximately 0.5 km^2, maximum depth of 9.5 m and a storage capacity of 820,000 m^3. During summer the water column undergoes regular polymixis, with thermal stratification occurring in the littoral zone during the day and mixing occurring at night. Surface water temperatures at midday are typically ~27 °C, with a temperature differential of ~4 °C over the upper 0.85 m of the water column. The reservoir supports a very depauperate fish faunal community by comparison to surrounding waterways and only 5 fish taxa have been observed: native *Hypseleotris galii* (firetailed gudgeon), *Philypnodon grandiceps* (Flatheaded gudgeon), *Macquaria novemaculeata* (Australian bass), and exotic *Gambusia holbrooki* (gambusia), and *Cyprinus carpio* (carp). As a consequence of the impoundment, the native piscivorous fish (e.g. bass), which require natural flooding or downstream migration to breed (Hunt and Matveev, 2005), cannot successfully reproduce. Approximately 25% of the reservoir area is covered by the exotic noxious submerged macrophyte *Cabomba caroliniana* (fanwort). In addition large masses of the free-floating noxious weed *Salvinia molesta* (salvinia) are also episodically present. Further details of the study site are in Akhurst et al. (2012).

2.2. Experimental design

Twenty large, replicated cylindrical enclosures, 2m-diameter and 1.5 m deep, constructed from 2 mm polyethylene coated steel sheeting were randomly positioned in the northern section of the reservoir at a depth of ~1 m (Fig. 1). In order to leach any possible contaminants, enclosures were first 'aged' by submersion in a distant part of the reservoir for 10 days prior to installation. Enclosures were pushed ~10 cm into the reservoir sediment, contained ~3.2 m^3 of water, were open to the sediment and had ~45 cm above water freeboard. Bird netting was placed over enclosures to prevent bird predation, but also gave a 5% shading effect.

Four replicate enclosures were allocated randomly to each of the 5 treatments (1) no fish + macrophytes (NF + M; 2) no fish + no macrophytes (NF + NM; 3) carp + no macrophytes; (4) gambusia + no macrophytes; and (5) Australian bass + no macrophytes. In all cases the effects of fish additions were compared with NF + NM enclosures. Enclosure effects were measured using 4 open-water sites, compared with NF + M enclosures. Open-water sites were located in the immediate area surrounding enclosures (Fig. 1). Macrophyte effects were measured by comparisons between harvested (NF + NM) and un-harvested enclosures (NF + M).

Macrophytes were harvested (cut at the sediment-water interface) from all enclosures, with the exception of 10% *Cabomba caroliniana* (surface area). Once macrophytes were removed, enclosures were temporally lifted from the sediment (4 h) to re-equilibrate them with open-water sites and were allowed to settle for a further 5 days prior to observations: full details are given in Akhurst et al. (2012). Enclosures were randomly stocked with 600 ± 23.3 g (mean ± 1 SE) of carp, gambusia, and Australian bass (total fish biomass = 1875 kg/ha). This density is consistent with previous experimental fish manipulations (*C. carpio*, 350–6000 kg/ha; King et al., 1997; Angeler et al., 2003).

2.3. Sampling

2.3.1. Nutrients and physico-chemical parameters

Triplicate 50 mL water sample were collected from each enclosure every 6 days over a 5-week period at water depths of 5, 20, 40, 60 and 80 cm intervals to the sediment-water interface using a 12 V submersible pump. Total and soluble nutrient (TN, TP, soluble reactive phosphorus SRP, nitrate NO3-N, and ammonium NH4-N) and trace element (TFe, TMn, total dissolved iron TDFe and total dissolved manganese TDMn) concentrations were determined