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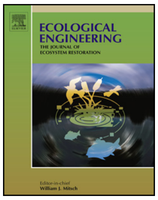

Effects of benthic-feeding common carp and filter-feeding silver carp on benthic-pelagic coupling: Implications for shallow lake management

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ABSTRACT

Benthic–pelagic coupling is a key factor in the dynamics of shallow lakes. A 12-week mesocosm experiment was set up to test the hypotheses that benthic-feeding common carp (*Cyprinus carpio*) reduce the growth of benthic algae and promote eutrophication and that filter-feeding silver carp (*Hypophthalmichthys molitrix*) stimulate benthic algae growth and promote the establishment of a clear-water state. Compared to the controls, the common carp treatment had higher concentrations of total nitrogen (TN) and total phosphorus (TP) in the water column, higher biomass of pelagic algae (measured as chlorophyll *a*), higher total suspended solids (TSS) concentrations, lower light intensity, and lower biomass of benthic algae at the sediment surface. Silver carp did not change the chlorophyll *a* of pelagic algae relative to the controls, but they did decrease the biomass of benthic algae and increase TP and TSS. A microcosm experiment using ^{32}P radiotracer was conducted to examine effects of the two carp species on the release of sediment phosphorus (P). The P release to the water column was higher with common carp present than without common carp. This was not the case in the silver carp experiments. Our findings show that both common carp and silver carp deteriorate water quality by increasing TP and TSS concentrations and decreasing the biomass of benthic algae at the sediment surface. Common carp had a larger negative effect on water quality than silver carp, perhaps because only common carp enhanced P release from the sediment. The implications for lake management are that removal of both common carp and silver carp from shallow lakes may enhance the growth of benthic algae and help promote the establishment of a clear-water state.

1. Introduction

Benthic–pelagic coupling refers to the reciprocal dependence of processes in sediments and in the water column (Marcus and Boero, 1998; Soetaert et al., 2000; Schindler and Scheuerell, 2002).

Like submerged macrophytes, benthic algae may contribute to maintaining shallow lakes in a clear-water state (Genkai-Kato et al., 2012). Benthic algae are capable of decreasing the availability of nutrients to pelagic algae in the water column (Carlton and Wetzel, 1988; Dodds, 2003) by consuming nutrients for growth and, indirectly, by oxidizing the top sediment layer, thereby immobilizing nutrients, most notably phosphorus (P), in the sediment (Hansson, 1990; Wetzel, 2001). In addition, benthic algae release extracellular material that acts as glue to stabilize the sediment surface and reduce sediment and nutrient resuspension (Tolhurst et al., 2008; Lubarsky et al., 2010). Thus, benthic algae can substantially reduce the growth of pelagic algae and contribute to maintaining

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clear-water conditions (Genkai-Kato et al., 2012), i.e. low pelagic algal biomass and/or low levels of total suspended solids (TSS). Benthic algae may dominate whole-lake primary productivity in clear shallow lakes unless macrophytes are abundant (Vadeboncoeur et al., 2002), whereas pelagic algae are the main contributor to primary productivity in shallow eutrophic lakes (Timms and Moss, 1984; Liboriussen and Jeppesen, 2003; Vadeboncoeur et al., 2003). At high pelagic algae biomass, in contrast, light may become a limiting factor for benthic algae production, resulting in poor algal growth (Hansson, 1988, 1992; Gjerløv and Richardson, 2010). Loss of benthic algae further promotes growth of pelagic algae due to reduced competition for nutrients and enhanced nutrient release from the sediment (Zhang et al., 2013), leading to high pelagic algal biomass and high TSS. These feedback mechanisms may facilitate a shift from clear to turbid water states in shallow lakes (Søndergaard et al., 2003; Zhang et al., 2014).

Fish may also affect the balance between the clear and turbid water states. Being mobile, fish participate in both benthic and pelagic food webs, thereby effectively linking benthic and pelagic habitats (Schindler and Scheuerell, 2002; Wagner et al., 2012). In China and elsewhere various benthic and filter-feeding carp species are stocked in lakes in order to improve fisheries or, in a few cases, silver carp have been stocked in an attempt to restore eutrophic lakes (Xie, 1996). The effect on the lake ecosystems of the various carp species may differ, not least between benthic-feeding species, such as the common carp (*Cyprinus carpio*) and the filter-feeding silver carp (*Hypophthalmichthys molitrix*). The bottom-dwelling common carp feed mainly on benthos by sucking up sediments from which they select edible items (García-Berthou, 2001). Such feeding behavior can cause sediment resuspension and potentially release of nutrients sequestered in the sediment (Rahman et al., 2008). Silver carp mostly inhabit the upper water layer, although in shallow lakes this species also increases the release of sediment-bound nutrients to the water column through their foraging activity and food processing (Persson, 1997; Schindler and Eby, 1997). Both species release nutrients through excretion. Thus, both common and silver carp possess the potential to increase pelagic algal production and water turbidity through enhanced mobilization of nutrients (Persson, 1997). However, the net effect of silver carp is not clear from past research and several authors consider silver carp to be useful in maintaining good water quality in lakes (Radke and Kahl, 2002; Attayde et al., 2010). This is because filtering by silver carp may decrease the pelagic algal biomass and detritus, thereby increasing water transparency. Other authors have questioned the positive effect of silver carp as they also feed on zooplankton and are not efficient at filtering smaller algae (Jeppesen et al., 2012; Zhao et al., 2013). Although an extensive literature is available on the effects of fish on lake food webs and ecosystem processes (Hambright et al., 2002; Milstein et al., 2006; Rahman et al., 2008), more work is needed to clarify the role of fish, and in particular silver carp, on benthic-pelagic coupling.

We conducted a mesocosm experiment to evaluate the effects of benthic-feeding common carp and filter-feeding silver carp on benthic-pelagic coupling in shallow lakes. In addition, a microcosm experiment using ^{32}P-PO$_4$ as a tracer was undertaken to evaluate the role of common and silver carp on sediment P release. We hypothesized that benthic-feeding common carp will increase eutrophication by accelerating the release of P from the sediment, which will increase the biomass of pelagic algae and TSS and reduce the growth of benthic algae. In contrast, we hypothesized that filter-feeding silver carp will promote the establishment of a clear-water state in shallow lakes by grazing on pelagic organic particles and stimulating benthic algae growth, although disturbance of the sediment and predation on zooplankton may potentially counteract the positive effect on water clarity.

2. Materials and methods

2.1. Effects of fish on the benthic-pelagic coupling

2.1.1. Experimental mesocosm setup

The mesocosm experiments were carried out in 12 circular plastic tanks (upper diameter = 54 cm, bottom diameter = 40 cm, height = 60 cm) containing sediment and water. Sediment (total nitrogen (TN) = 1.13 mg g^{-1}; total phosphorus (TP) = 0.56 mg g^{-1}) was obtained from Ming Lake, a eutrophic shallow water body in Guangzhou City (Zhang et al., 2014). The sediment was air dried, powdered, and sieved through a stainless sieve (mesh size, 0.5 mm) to remove coarse debris and clumps. The homogenized sediment was added as a ~10 cm thick layer to each mesocosm. These were then filled with water (TN = 1.67 mg L^{-1}, TP = 0.04 mg L^{-1}) collected from the lake and filtered through a plankton net (mesh size = 0.064 mm). The mesocosms were then exposed to natural sunlight and equilibrated for two weeks. Thereafter, nutrient concentrations in the mesocosms were 1.58 mg L^{-1} for TN and 0.06 mg L^{-1} for TP.

After the equilibration period, a petri dish (diameter 5 cm) filled entirely with the homogenized sediment was inserted into the sediment in each of the mesocosms. The sediment surfaces inside and outside the petri dish were kept at the same level to allow benthic algal colonization and determination of algal biomass. One common carp (10.8 ± 0.3 cm, 14.4 ± 0.3 g) was added to each of four mesocosms and one silver carp (10.7 ± 0.3 cm, 11.8 ± 0.8 g) was added to each of another four mesocosms. The biomass of common carp (63.1 ± 1.3 gm^{-2}) and silver carp (51.7 ± 3.3 gm^{-2}) used in our mesocosm experiment are within the range of biomass observed in shallow lakes – biomass densities as high as 150 g m^{-2} have been reported (Xie, 1999; Lu et al., 2002). The remaining four mesocosms held no fish and served as controls. The fish were maintained in 100-L tanks for two weeks prior to their introduction to the mesocosms. Two silver carp died during the experiment and were replaced with living specimens. Nitrogen (N) in the form of KNO$_3$ and phosphorus as NaH$_2$PO$_4$ were added weekly to each mesocosm at rates of 1.5 mgN L^{-1} wk^{-1} and 0.1 mgP L^{-1} wk^{-1}, respectively. Rain water (TN = 1.95 mg L^{-1}, TP = 0.02 mg L^{-1}) was added to the mesocosms, when needed, to maintain a constant water level during the experiment. The experiment ran from April to July 2014, and the mesocosms were exposed to natural sunlight for its entire duration.

2.1.2. Sampling and analysis

Nutrients, TSS and pelagic algae: Water samples (1 L) were collected every two weeks from each mesocosm prior to the addition of nutrients for analysis of TSS, pelagic algal chlorophyll *a*, TN, and TP. TP and TN levels were determined after persulfate digestion (APHA, 1998). Chlorophyll *a* was determined spectrophotometrically after ethanol extraction at room temperature according to Jespersen and Christoffersen (1987). TSS was determined as matter retained on GF/C filters after drying at 105 °C for 24 h.

Benthic algae: The petri dish with benthic algae was removed every two weeks from each mesocosm after pelagic algae sampling and replaced by another petri dish filled with the homogenized sediment. Benthic algae were collected by scraping the surface of the sediment in the petri dish using a razor blade (Barbour et al., 1999). Benthic algal biomass (chlorophyll *a*) was measured by spectrophotometry as described for pelagic algae. Algae growing on the wall of the tanks were brushed after benthic algae were sampled. Prior to the sampling of benthic algae, light intensity at the sediment surface was measured between 0900 and 1200 h using an underwater irradiance meter (ZDS-10W).