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# Effects of deposit-feeding tubificid worms and filter-feeding bivalves on benthic-pelagic coupling: Implications for the restoration of eutrophic shallow lakes

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ABSTRACT

Benthic-pelagic coupling is a key factor in the dynamics of shallow lakes. A 12-week mesocosm experiment tested the hypothesis that deposit-feeding tubificid worms stimulate the growth of pelagic algae while filter-feeding bivalves promote the growth of benthic algae, using the deposit-feeding tubificid *Limnodrilus hoffmeisteri* and the filter-feeding bivalve *Anodonta woodiana*. A tube-microcosm experiment using a $^{32}P$ radiotracer tested for differential effects of tubificids and bivalves on the release of sediment phosphorus (P). In this experiment *A. woodiana* was replaced by *Corbicula fluminea*, a smaller bivalve from the same functional group whose size was more appropriate to the experimental tubes needed for the tracer study. The first experiment recorded greater nutrient concentrations in the overlying water, higher biomass of pelagic algae as measured by chlorophyll *a* (Chl *a*), lower light intensity at the sediment and lower biomass of benthic algae in the worm treatments than in the controls, while nutrients and Chl *a* of pelagic algae were lower and the light intensity and Chl *a* of benthic algae were higher in the bivalve treatments than in the controls. In the second experiment, $^{32}P$ activity in the overlying water was higher in both treatments than in the controls, but highest in the worm treatment indicating that both animals accelerated P release from the sediment, with the biggest effect associated with the presence of worms. Our study demonstrates that worms promote pelagic algal growth by enhancing the release of sediment nutrients, while bivalves, likely through their grazing on pelagic algae increasing available light levels, stimulate benthic algal growth despite enhanced P release from the sediment and thus aid the establishment of clear water states. The rehabilitation of native bivalve populations may therefore enhance the recovery of eutrophic shallow lakes.



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# 1. Introduction

Benthic-pelagic coupling is a key factor in the dynamics of shallow lakes (Hansson, 1988; Threlkeld, 1994). In clear water shallow lakes, benthic algae or macrophytes are the dominant primary producers. Benthic algae reduce the availability of nutrients to the pelagic zone (Carlton and Wetzel, 1988), both directly by taking up nutrients and indirectly by oxidizing surface layer sediments and immobilizing nutrients therein (Hansson, 1990; Wetzel, 2001; Zhang et al., 2013). In turbid eutrophic lakes however, pelagic algae are the dominant primary producers, a situation that tends to be self-enhancing by reducing light penetration to the lake bed and shading benthic algae. The decomposition of algae settling onto dark sediment promotes anoxia at the sediment surface, and thereby increases nutrient release into the overlying water. Thus while benthic algae and pelagic algae interact negatively with one another, in eutrophic shallow lake conditions the balance is shifted in favor of self-reinforcing dominance by pelagic algae (Vadeboncoeur et al., 2003; Liboriussen and Jeppesen, 2003; Genkai-Kato et al., 2012).

Sudden shifts in lake water conditions may occur when environmental thresholds in parameters such as lake depth, nutrient concentration, or trophic structure are crossed (Vadeboncoeur et al., 2008; Genkai-Kato et al., 2012). The balance between clear and turbid states can be affected by benthic animals (Threlkeld, 1994; Covich et al., 1999) such as filter-feeding bivalves and deposit-feeding tubificid worms (Karlson et al., 2007). Tubificid worms are commonly found in eutrophic shallow lakes, where they ingest sediment and release waste at the sediment surface (Gerino et al., 2003; Anschutz et al., 2012), potentially causing the release of nutrients that would otherwise remain buried (Covich et al., 1999). Holdren and Armstrong (1980) reported that tubificid worms had a greater impact on P release than other factors such as redox potential, mixing intensity, temperature and sediment type. Filter-feeding bivalves are common in clear shallow lakes (Gulati et al., 2008; Jeppesen et al., 2012), where they move and forage by plowing through subsurface sediment layers (Jónasson, 1972), displacing nutrients from the sediment to the overlying water. Filter-feeding bivalves may also influence P exchange at the sediment–water interface through defecation and excretion of dissolved P (Meysman et al., 2006). Thus both tubificid worms and bivalves have the potential to increase pelagic algal production and water turbidity through enhanced mobilisation of nutrients (Andersson et al., 1988). While grazing by bivalves may also decrease pelagic algal biomass and detritus (Officer et al., 1982; Vaughn and Hakenkamp, 2001; Byers et al., 2006; Greene et al., 2011) thereby increasing water transparency and boosting benthic algal growth. Grazing may also divert nutrients from overlying water to the sediment (Dame, 1996), which in turn depresses pelagic production. Thus the effects of deposit-feeding tubificid worms and filter-feeding bivalves on benthic-pelagic coupling in shallow lakes constitute an interesting subject of study (Karlson et al., 2007; Alonso-Pérez et al., 2010).

Previous studies have independently examined the functional roles of tubificid worms and bivalves in shallow water bodies (Vaughn and Hakenkamp, 2001; Norling et al., 2007), especially on the biogeochemical cycling of elements between sediments and the overlying water (Andersson et al., 1988; Lohrer et al., 2004; Michaud et al., 2009; Zhang et al., 2010; Anschutz et al., 2012). However few, if any, investigations have compared the effects of the two animal groups. A mesocosm experiment was designed to evaluate the effects of both deposit-feeding tubificid worms (*Limnodrilus hoffmeisteri*) and filter-feeding bivalves (*Anodonta woodiana*) on benthic-pelagic coupling in a shallow lake system. In addition, a microcosm experiment using $^{32}P-PO_4$ as a radioactive tracer was carried out in sediment tubes in order to evaluate the role of tubificid worms and filter-feeding bivalves (*Corbicula fluminea*) on P release. *Corbicula* was selected for its smaller size, which was more appropriate for the diameter of the experimental tubes used in the tracer study. We hypothesized that deposit-feeding worms would enhance pelagic algae growth by accelerating nutrient release from the sediment, while filter-feeding bivalves, through their grazing on pelagic organic particles, would stimulate benthic algae and the establishment of a clear water state. The findings of our study have important implications for management focused on the restoration and maintenance of clear water states in eutrophic shallow lakes around the world (Scheffer et al., 1993; Jeppesen et al., 2012).

# 2. Materials and methods

## 2.1. *Effects of benthic animals on benthic-pelagic coupling*

### 2.1.1. *Experimental mesocosm set-up*

The mesocosm experiments were carried out in 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 collected from a shallow lake in Guangzhou City, air-dried and sieved (mesh size = 0.5 mm) to remove coarse debris. The sediment was homogenized and a 10-cm thick layer was added to each mesocosm. Mesocosms were subsequently filled with lake water (TN = 2.15 mg $L^{-1}$, TP = 0.06 mg $L^{-1}$; soluble reactive P (SRP) was very low) and filtered through a plankton net (mesh size = 0.064 mm). The mesocosms were then exposed to natural sunlight and allowed to equilibrate for two weeks, after which nutrient concentrations in the mesocosms were: TN, 1.99 ± 0.21 mg $L^{-1}$; and TP, 0.14 ± 0.01 mg $L^{-1}$. Water temperature was 27.4 ± 0.2 °C; dissolved oxygen (DO) concentration was 8.36 ± 0.05 mg $L^{-1}$ and pH was 7.3 ± 0.1, chlorophyll *a* concentration (Chl *a*) was 23.7 ± 3.0 μg $L^{-1}$ and the dominant pelagic algae were *Limnothrix* sp. and *Chlamydomonas* sp., while the benthic algae were dominated by *Synedra* sp. and *Limnothrix* sp.

After the equilibration period, an artificial substrate comprising a 2 cm × 2 cm plastic gauze with a mesh size of 2 mm × 2 mm was set close to the sediment surface to enable benthic algae to colonize, and algal biomass to be determined. To each of four mesocosms comprising the bivalve treatment,