Science of the Total Environment 622–623 (2018) 49–56

Contents lists available at ScienceDirect

Science of the Total Environment

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

Mussels can both outweigh and interact with the effects of terrestrial to freshwater resource subsidies on littoral benthic communities

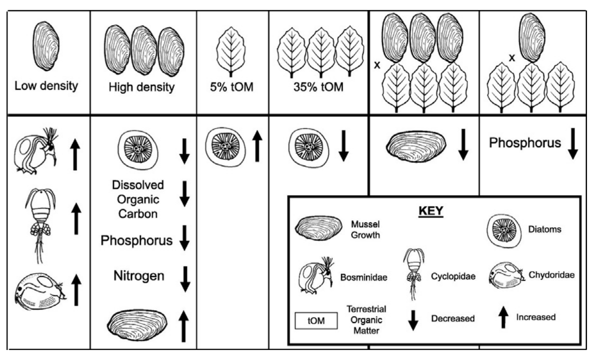
Bethany R. Smith [a,b,*], David C. Aldridge [b], Andrew J. Tanentzap [a]

[a] Ecosystems and Global Change Group, Department of Plant Sciences, University of Cambridge, CB2 3EA Cambridge, UK
[b] Aquatic Ecology Group, Department of Zoology, David Attenborough Building, University of Cambridge, CB2 3QY Cambridge, UK

HIGHLIGHTS

- Zooplankton densities tripled at low mussel densities.
- Phosphorus, nitrogen, DOC and diatoms decreased at high mussel densities.
- Higher sediment tOM reduced benthic diatom concentrations regardless of mussels.
- High tOM inputs in dense lake mussel beds reduce mussel growth and phosphorus supply.
- Top-down control by dominant species may mask bottom-up effects of resource subsidies.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 22 May 2017
Received in revised form 30 October 2017
Accepted 27 November 2017
Available online xxxx

Editor: Daniel Wunderlin

Keywords:
Dominant species
Elliptio complanata
Freshwater
Resource subsidy
tOM

ABSTRACT

Litterfall is an important resource subsidy for lake ecosystems that primarily accumulates in littoral zones. Bivalves are abundant within littoral zones and may modify the effects of terrestrial resource subsidies through trophic interactions and engineering their surrounding habitat. Leaf inputs to lakes and freshwater mussel abundances are changing throughout the boreal ecoregion so we set out to investigate how the co-occurring benthic community might respond.

We set up an in situ mesocosm experiment in Ramsey Lake, Sudbury, ON, Canada. Mesocosms contained sediments of either 5% or 35% terrestrial organic matter (tOM), into which we placed mussels (*Elliptio complanata*) at differing densities (0, 0.4 and 2 mussels m^{-2}, with a sham mussel treatment at 0.4 mussels m^{-2}). Over one month we recorded the sediment chemistry (dissolved organic carbon, nitrogen and phosphorus), littoral organisms (benthic algae and zooplankton) and mussel growth.

At high mussel densities we recorded a 90%, 80%, 45% and 40% reduction in phosphorus, dissolved organic carbon, nitrogen and benthic diatoms, respectively, whereas at low mussel densities we observed a 3-fold increase in zooplankton. We discuss that these results were caused by a combination of bioturbation and trophic interactions. Benthic diatom concentrations were also reduced by 20% in sediments of 35% tOM, likely due to shading and competition with bacteria.

Mussel growth increased at high mussel densities but was offset at high tOM, likely due to the organic matter interfering with filter feeding.

Our results suggest that mussels can alter the geochemical composition of sediments and abundances of associated littoral organisms, in some cases regardless of tOM quantity. Therefore, the dominant top-down control

* Corresponding author at: Department of Life Sciences, Silwood Park Campus, Imperial College London, Ascot, Berkshire SL5 7PY, UK.
E-mail address: b.smith17@imperial.ac.uk (B.R. Smith).

https://doi.org/10.1016/j.scitotenv.2017.11.318

exerted by freshwater mussels may outweigh bottom-up effects of tOM additions. Generally, our study reveals the importance of considering dominant species when studying the effects of cross-ecosystem resource fluxes.

1. Introduction

Resource subsidies are flows of biologically fixed energy and nutrients from one ecosystem to another (Richardson et al., 2010). One such subsidy, terrestrial organic matter (tOM), provides an important link between aquatic and terrestrial ecosystems and can account for up to almost 85% of the biomass of organisms at all trophic levels in different lake ecosystems (Jansson et al., 2007; Tanentzap et al., 2017a). The quantity of tOM exported into receiving waters therefore has great potential to influence whole-lake functioning (e.g. Pace et al., 2004; Karlsson et al., 2015; Tanentzap et al., 2017b).

tOM should influence benthic littoral zones more than pelagic zones because it tends to accumulate nearer to shore. For example, France and Peters (1995) found that all airborne leaf litter input into northwestern Ontario lakes was deposited within the first 11 m of shoreline. However, most studies of tOM inputs into lake ecosystems have generalised across the pelagic zone (e.g. Pace et al., 2004; Karlsson et al., 2015). These studies may therefore underestimate the importance of tOM for whole-lake functioning because the benthic littoral zone can account for >80% of lake primary productivity (Vadeboncoeur et al., 2003), and support diverse biological communities (Walseng et al., 2003). Inputs of tOM are also changing across northern watersheds, because of factors including climate warming and recovery from historical pollution (Monteith et al., 2007), so there is a need to better predict how these changes might impact nearshore communities.

In many freshwater systems, the response of nearshore biota to tOM inputs can be governed by mussels (Bivalvia: Unionoida). Mussels have strong effects on communities and ecosystems, consistent with dominant species (after Power et al., 1996), because they make up >90% of the benthic biomass in some aquatic systems (Negus, 1966; Strayer et al., 1999). The effects of mussels include those of ecosystem engineers that are capable of modifying the physical state of their habitat, thus affecting community composition and structure (Vaughn et al., 2008). Indeed, higher densities of freshwater mussels have been found to be associated with higher macroinvertebrate richness in both lotic and lentic systems (Aldridge et al., 2007; Chowdhury et al., 2016). Infaunal mussel species engineer their surrounding environment by movement and burrowing that causes bioturbation of sediment, and releases nutrients such as nitrogen and phosphorus (Vaughn and Hakenkamp, 2001). Mussels also contribute to sediment composition through the biodeposition of faeces and pseudofaeces (i.e. material that is ejected without ingestion) (Strayer et al., 1999; Vaughn and Hakenkamp, 2001). In addition to these engineering effects, mussels can also have important trophic interactions with other organisms by removing large quantities of algae, zooplankton and dissolved organic carbon (DOC) from the water column and sediments by filtration and deposit-feeding (Nichols et al., 2005; Vaughn et al., 2008). The physical presence of mussel shells also creates habitat for epizoic organisms and provides refuge for benthic fauna (Vaughn and Hakenkamp, 2001).

Here, we aimed to test how changes in mussel densities at different concentrations of tOM altered the chemistry and biota of littoral sediments. Although other studies have investigated how changes in mussel abundances (e.g. MacIsaac, 1996; Francoeur et al., 2002; Ozersky et al., 2012) and tOM (e.g. Pope et al., 1999; Karlsson et al., 2015; Kelly et al., 2014; Fey et al., 2015) independently influence the structure and composition of littoral food webs, little is known about how the two may act in conjunction, particularly in sediments where tOM accumulates. Our approach was to carry out a factorial mesocosm experiment with two different tOM quantities and two different densities of the infaunal freshwater mussel, *Elliptio complanata*. We used *E. complanata* as it has the potential to influence many different ecosystems due to its widespread distribution across North America (Strayer et al., 1981). Additionally, *E. complanata* has been found to peak in density at 0.5 m from the shore (Cyr, 2008), making them particularly likely to influence the effects of tOM in nearshore environments.

We predicted that there would be more resources available to support mussels at higher tOM concentrations (Vaughn et al., 2008) and, therefore, mussel activity and the resulting ecosystem engineering (e.g. bioturbation, biodeposition), feeding interactions, and habitat provision would be enhanced. We expected that the effects of this resource enhancement would be the greatest in conjunction with higher mussel densities because ecological processes undertaken by mussels often scale linearly with biomass (Welker and Walz, 1998; Strayer et al., 1999; Vaughn et al., 2004). We expected to find particularly strong responses from the co-occurring benthic community, so we recorded how the benthic algae, zooplankton and mussels themselves responded to the differing treatments. As mussels can also alter the geochemical composition of the sediments in which they live (Vaughn and Hakenkamp, 2001), we also recorded how the sediment chemistry (dissolved organic carbon, nitrogen and phosphorus) changed.

2. Materials and methods

2.1. Study site

We conducted our experiment in Ramsey Lake in Sudbury, Ontario, Canada (46.47°N 80.95°W; area = 792.2 ha; mean depth = 8.4 m). The 10-year average for spring phosphorus concentrations of 12.89 $\mu g\ L^{-1}$ and Secchi depth reading of 4.8 m indicate that Ramsey Lake is weakly oligotrophic. At our field site the pH of the water averaged 6.53, which is within the hospitable range for *E. complanata* in the Sudbury district (Mackie and Flippance, 1983).

2.2. Experimental design

Our experiment consisted of two tOM quantities (5% and 35% dry-mass basis) in sediment and four mussel treatments: high density (2 mussels m^{-2}); low density (0.4 mussels m^{-2}); 'sham' mussels at the low density; and a mussel-free control. The treatments were informed from surveys carried out in nearby lakes, where mussel densities ranged from 0 to 23 individuals m^{-2} (Cyr, 2008), and had a geometric mean of 2 individuals m^{-2} (Griffiths and Cyr, 2006). Sham mussels were empty shells filled with sand and sealed with adhesive, following Spooner and Vaughn (2006), and were included to tease apart responses to the physical presence of shells versus the biological activity of mussels. We chose the low density treatment for the sham mussel procedural control in order to limit destructive sampling of mussels. Each tOM by mussel treatment combination was replicated five times for a total of 40 mesocosms, which were evenly distributed on either side of a sampling dock.

We constructed mesocosms from free-draining 17.5 L high-density polyethylene (HDPE) containers (surface area: 0.19 m^2, depth: 0.13 m) after Tanentzap et al. (2017b). These mesocosms successfully mirror both the absolute concentrations and temporal dynamics of biogeochemical parameters in natural lake sediments with similar organic matter composition to the treatments (Tanentzap et al., 2017b). Briefly, each mesocosm was filled with either 5% or 35% organic matter consisting of a representative mixture of oven-dried deciduous (primarily *Acer rubrum*, *Betula papyrifera*, *Populus tremuloides*, *Quercus* spp.) and coniferous (*Pinus* spp.) leaf litter collected from the surrounding area