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

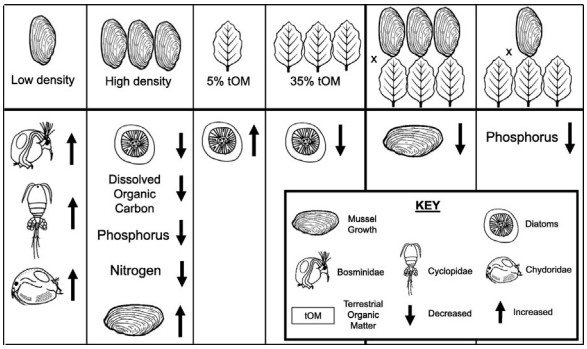
Bethany R. Smith [a,b,*], David C. Aldridge [b], Andrew J. Tanentzap [a]

[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 1 December 2017

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 μg 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

and mixed at a 2:1 dry-mass ratio, respectively. Litterfall was pre-sorted into <1 and 1–10 mm size fractions at a 3:7 ratio to mimic natural sediments (Tanentzap et al., 2017b). Inorganic materials consisting of clay (<0.063 mm), sand (0.063–1 mm) and gravel (>1 mm) were also mixed in a 2:5:3 ratio, respectively, again based on surveys of natural sediments (Tanentzap et al., 2017b). The final sediment mixture was filled to a height of 0.08 m in each mesocosm and underlain by 7 kg of ~2mm-diameter crushed granitic rock.

Once constructed, we attached a 1 mm × 1 mm nylon screen to each mesocosm to prevent disturbance of the sediments and ensure standardised shading. To stimulate decomposition, all mesocosms underwent a 14-day soaking period with water from Ramsey Lake before deployment at depths of between 0.45 ± 0.05 m on 27 July 2015. HDPE lids were secured to each mesocosm to prevent loss of sediment whilst the mesocosms were lowered into the lake and were removed one week later.

We collected individuals of *Elliptio complanata* from near Restoule, Ontario (46.03°N, 79.72°W). Individuals were allowed to acclimatise in a flow-through aquarium for 5 days prior to deployment. The aquarium was supplied with Ramsey Lake water and an identical inorganic substrate as in the mesocosms. During acclimatisation, all mussels were gently scrubbed to remove any biota on the shells and we measured shell length (the maximum posterior-anterior distance) to the nearest 0.1 mm. Individuals with lengths <61 mm and >90 mm were removed leaving 140 mussels of approximately the same size (mean ± standard error: 78.1 ± 0.7 mm), which were randomly assigned to the different treatments. On the 10 August 2015, mussels were placed upright in their designated mesocosms. In the process, the 1 mm × 1 mm screening was replaced with a 1 cm × 1 cm plastic mesh to protect the mussels against predation whilst allowing free movement of smaller organisms. Sampling from the mesocosms began on the 17 August and lasted until the 7 September.

2.3. Field sampling

2.3.1. Sediment chemistry

Pore-water was sampled on a weekly basis from immediately beneath the sediment surface in three of the five treatment replicates using a permanently-installed 3 mL syringe placed horizontally along the sediment surface (n = 24). Samples were immediately filtered through a 0.45 μm glass fibre filter and acidified for DOC measurements taken within 30 days on a Shimadzu TOC500A total organic carbon analyser (Shimadzu Scientific Instruments, Kyoto, Japan). We included method blanks (acidified MilliQ® water) and certified reference material standards every 30 samples to ensure no instrument drift occurred. At the conclusion of the experiment (7 September), total nitrogen and phosphorus were determined colorimetrically (Hach Methods 10,208 and 10,209/10210, respectively) on the treatment triplicates of 0.45 μm filtered water using a Hach DR3900 Benchtop VIS spectrophotometer (HACH Company, Loveland, CO, USA). We did not expect empty shells to affect the nutrient dynamics, therefore the sham mussel treatments were not analysed for nitrogen and phosphorus.

2.3.2. Benthic algae

We measured benthic algae on three separate occasions over two weeks for all mesocosms (n = 40). Recordings were taken using a chlorophyll fluorometer (bbeMoldaenke, Kiel-Kronshagen, Germany) to estimate the areal concentrations (μg chlorophyll *a* cm^{-2}) of diatoms (fluorescence excitation at 470 nm), green algae (Chlorophyceae) (525 nm) and cyanobacteria (Cyanophyceae) (610 nm). Biomass estimated with this approach has been validated with traditional methods, such as chlorophyll extraction and physical counts of algal cells (Kahlert and McKie, 2014; Harris and Graham, 2015), and is entirely appropriate for resolving thin biofilms (<2 mm) (Echenique-Subiabre et al., 2016), such as those in our study. Each mesocosm was sampled 5 times on a sampling date (in each corner and the centre) and then readings for each taxon were averaged to gain a mesocosm-wide estimate. Preliminary data analysis revealed that concentration of cyanobacteria and green algae were negligible (mean ± SE: 0.001 ± 0.000 and 0.025 ± 0.008 μg chlorophyll *a* cm^{-2}, respectively), so all analyses focussed on the diatoms.

2.3.3. Invertebrates

We collected zooplankton for all mesocosms in the final week of the experiment (n = 40). Animals were captured using a 500 mL vertical funnel trap deployed overnight at a 5 cm height above the surface sediment following Tanentzap et al. (2017b). Samples were then filtered through an 80 μm sieve and preserved in 70% ethanol following Black & Dodson (2003). Cladocerans were enumerated to family and copepods were enumerated to order (Cyclopoida, Calanoida and Harpacticoida) after Witty (2004).

At the end of the experiment, all mussels were removed and re-measured for shell length.

2.4. Statistical analysis

We tested whether chemical and biological responses varied across the tOM and mussel treatments. First, we first tested whether each of DOC and benthic algae differed across the treatments using linear mixed effects models to account for repeated measurements from each mesocosm. Nitrogen and phosphorus were recorded only once so a linear model was fitted to each. Responses that were not normally distributed were log-transformed (DOC and phosphorus). Second, we tested if zooplankton abundances varied across the different treatments by separately fitting linear models with negative binomial error structures to counts of each of the dominant families: Bosminidae, Chydoridae and Cyclopidae. We used negative binomial errors because the count data were overdispersed (Ver Hoef and Boveng, 2007). Finally, for mussel growth, we fitted a linear mixed effects model to the absolute change in length of each individual, again to account for repeated measurements of the same mesocosm.

All models were initially fitted fully saturated with tOM treatment, mussel treatment, the nuisance factor of the side of our sampling dock, and date where applicable, as well as the interaction between tOM treatment and mussel density. The model for mussel growth also included the initial shell length as a covariate. The interaction term was removed if it was non-significant and we interpreted the main effects. We report effect sizes and 95% confidence intervals (CIs) for the treatments as compared to our experimental controls of no mussels (or low mussel density for mussel growth) and 5% tOM and reject null hypotheses if the 95% CIs do not overlap zero. All analyses were conducted in R version 3.2.3. All means are quoted with ± standard errors.

3. Results

3.1. Sediment chemistry

Both DOC and total nitrogen responded individually to the treatments with no interactive effects. The quantity of DOC in the sediment pore-water decreased significantly from 33.3 mg L^{-1} in the controls to 7.4 mg L^{-1} (95% CI for difference: −36.5 to −23.4 mg L^{-1}) and 14.1 mg L^{-1} (95% CI for difference: −32.2 to −7.1 mg L^{-1}) in the high and sham mussel treatments, respectively (Fig. 1a). The average quantity of DOC in the low density treatments was 21.0 mg L^{-1}, which was not significantly different from the control (95% CI for difference: −27.8–9.9 mg L^{-1}). The quantities of DOC did not differ significantly between the high and low tOM treatments (95% CI for difference: −24.0–3.72 mg L^{-1}; Fig. 1b). Similarly, nitrogen decreased from 0.99 ± 0.19 mg L^{-1} in the controls to 0.55 ± 0.09 mg L^{-1} in the high density mussel treatments (95% CI for difference: −0.88–<0.01 mg L^{-1}; Fig. 1c), and showed no response to tOM (95% CI for difference overlapping zero; Fig. 1d).

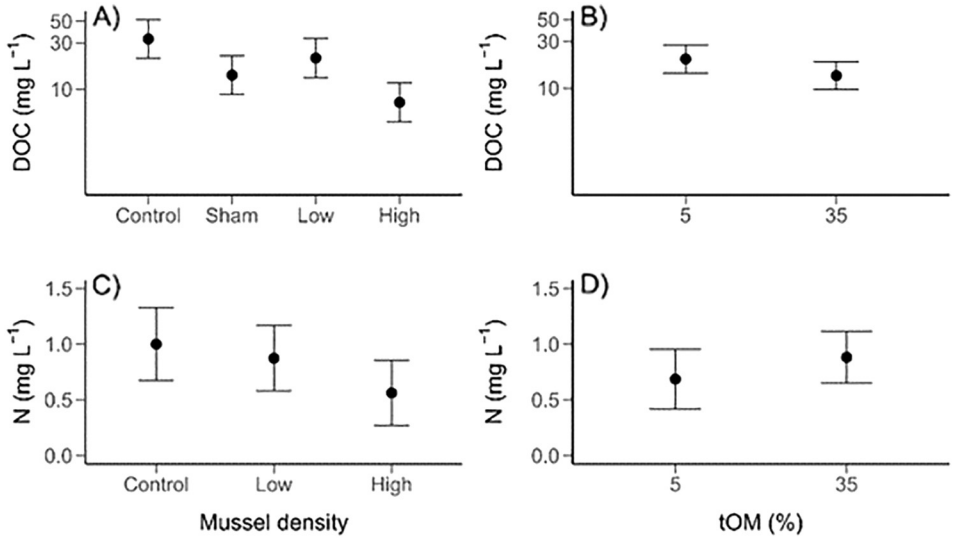


Fig. 1. Means and associated 95% confidence intervals for DOC (A and B) and total nitrogen (C and D) concentrations in response to mussel and tOM treatments separately. The interaction term between mussels and tOM was non-significant and dropped from these models. DOC values are averaged across all sampling dates, whilst nitrogen (N) was measured once at the end of the experiment.

Phosphorus concentrations depended on both mussel density and tOM concentration (Fig. 2). There was a ten-fold decrease in phosphorus concentrations from the controls (mean concentration: 0.22 ± 0.08 mg L^{-1}) to the high density mussel treatments (mean concentration: 0.02 ± 0.01 mg L^{-1}; 95% CI for difference: −0.34 to −0.29 mg L^{-1}). However, the low mussel density treatments only had lower phosphorus concentrations than the control in the high but not low tOM treatments, i.e. mussel × tOM interaction (Fig. 2). Mean phosphorus concentrations in the low mussel treatments at low and high tOM quantity were 0.21 ± 0.01 mg L^{-1} and 0.11 ± 0.05 mg L^{-1} (95% CI for difference: −0.33 to −0.14 mg L^{-1}), respectively.

3.2. Benthic algae

Diatoms differed with both tOM content and mussel density (Fig. 3a,b). We found that there were significantly less diatoms at 35% tOM content (mean concentration: 0.35 ± 0.02 μg chlorophyll *a* cm^{-2}) in comparison to 5% tOM (mean concentration: 0.44 ± 0.02 μg chlorophyll *a* cm^{-2}; 95% CI for difference: −0.14 to −0.04 μg chlorophyll *a* cm^{-2}). There were also fewer diatoms in the high density mussel treatment (mean concentration: 0.25 ± 0.03 μg chlorophyll *a* cm^{-2}) as compared with the control (mean concentration: 0.43 ± 0.02 μg chlorophyll *a* cm^{-2}; 95% CI for difference: −0.24 to −0.10 μg chlorophyll *a* cm^{-2}). The controls did not differ from either the low density (mean concentration: 0.40 ± 0.03 μg chlorophyll *a* cm^{-2}; 95% CI for difference: −0.10–0.04 μg chlorophyll *a* cm^{-2}) or sham (mean concentration: 0.48 ± 0.03 μg chlorophyll *a* cm^{-2}; 95% CI for difference: −0.02–0.12 μg chlorophyll *a* cm^{-2}) mussel treatments. Across time there were no differences in diatom abundance as all 95% CIs overlapped zero for the effects of different sample dates.

3.3. Zooplankton

A total of 10 zooplankton families (7 Cladocera and 3 Copepoda) were identified in the samples along with both cycolopoid and calanoid nauplii. Of the zooplankton, the most abundant families were Bosminidae, Chydoridae and Cyclopidae, accounting for 90.2%, 2.5% and 5.2% of all counts, respectively. Bosminidae dominated the samples with a mean number of individuals across all the mesocosms of 3600 ± 704 individuals L^{-1} (range: 96–18,850 individuals L^{-1}), compared to a mean of 206 ± 36 individuals L^{-1} Cyclopidae (range: 0–900 individuals L^{-1}) and 100 ± 16 individuals L^{-1} Chydoridae (range: 16–584 individuals L^{-1}).

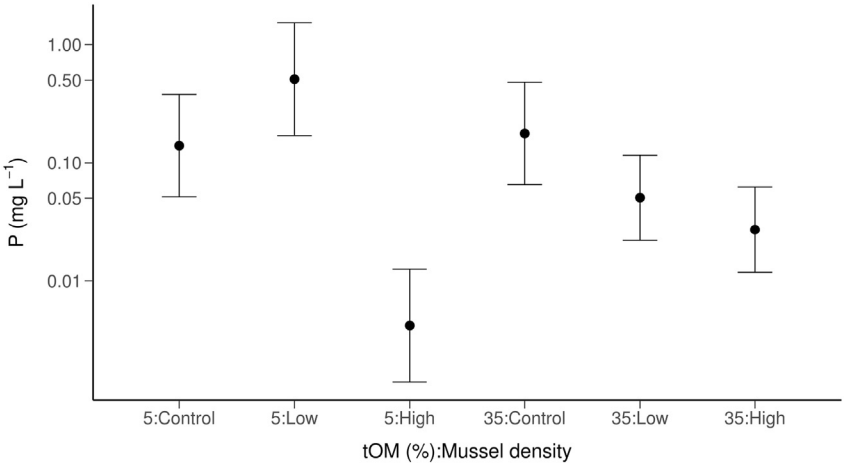


Fig. 2. Means and associated 95% confidence intervals for the response of total phosphorus (P) to the tOM × mussel density treatments. P was measured once at the end of the experiment.

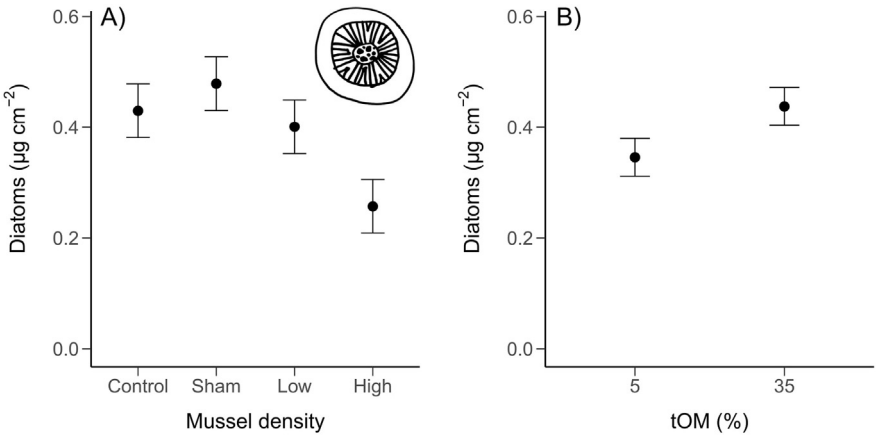


Fig. 3. Means and associated 95% confidence intervals for the benthic diatoms sampled during the experiment. Points are averaged across all three sampling dates. A) Diatom response to the mussel treatments. B) Diatom responses to the tOM treatments. The interaction term between mussels and tOM was non-significant and thus dropped from these models.

On average, the Bosminidae more than tripled in the sham and low density mussel treatments relative to the control from a mean density of 1543 ± 514 individuals L^{-1} to 4594 ± 1519 and 4144 ± 1753 individuals L^{-1}, respectively (95% CI for differences: 226–2051 individuals L^{-1}; 95% CI for difference: 157–1713 individuals L^{-1}, respectively; Fig. 4a). Although there was an increase in Bosminidae at high mussel densities to a mean of 4122 ± 1518 individuals L^{-1}, the difference relative to the controls was smaller (95% CI for difference: 62–1315 individuals L^{-1}). Cyclopidae differed from Bosminidae in their distribution with a significant increase from 117 ± 30 individuals L^{-1} in the controls to 302 ± 76 individuals L^{-1} in the low density treatments (95% CI for difference: 35–480 individuals L^{-1}; Fig. 4c). Chydoridae followed a similar pattern to the Cyclopidae, increasing from 69 ± 11 individuals L^{-1} in the controls to 163 ± 55 individuals L^{-1} in the low density treatment (95% CI for difference: 16–201 individuals L^{-1}; Fig. 4e). None of the major groups (Bosminidae, Chydoridae or Cyclopidae) responded to the tOM treatments (95% CI for difference: −61–429; −6–67 and −42–32 individuals L^{-1}, respectively; Fig. 4b,d,f).

3.4. Mussel growth

We found that mussels living at higher densities grew larger than those living at lower densities (95% CI for difference: 0.12–0.93 mm; Fig. 5). On average, mussels living at the lower densities showed little growth, with a change in length of 0.07 ± 0.16 mm, whereas those in the lower tOM content mesocosms showed a greater increase in length with a change of 0.13 ± 0.07 mm. However, the greater growth in the high density treatments was offset at higher tOM concentrations, resulting in the mean change in shell length changing from 0.33 ±

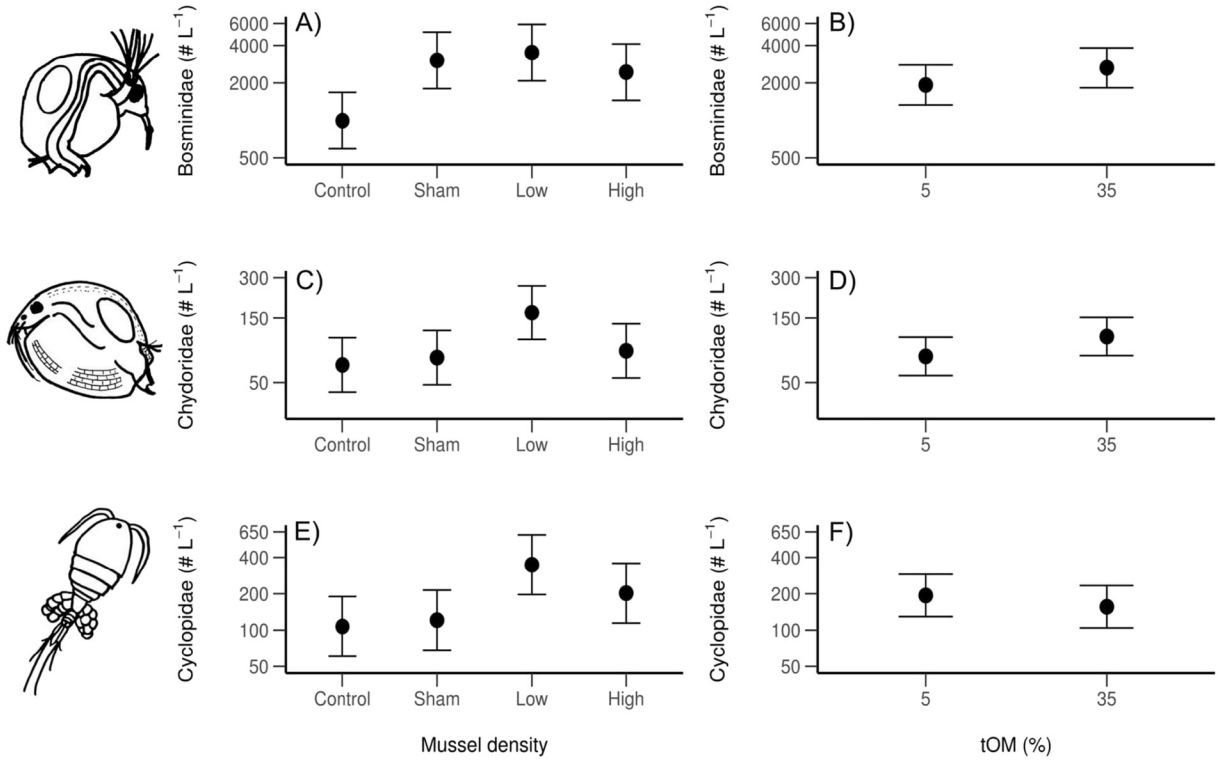


Fig. 4. Means and associated 95% confidence intervals for the dominant zooplankton families in response to both varying mussel densities and concentrations of terrestrial organic matter (tOM). The interaction term between mussels and tOM was non-significant and thus dropped from these models. Zooplankton families included Bosminidae (A and B), Chydoridae (C and D) and Cyclopidae (E and F).

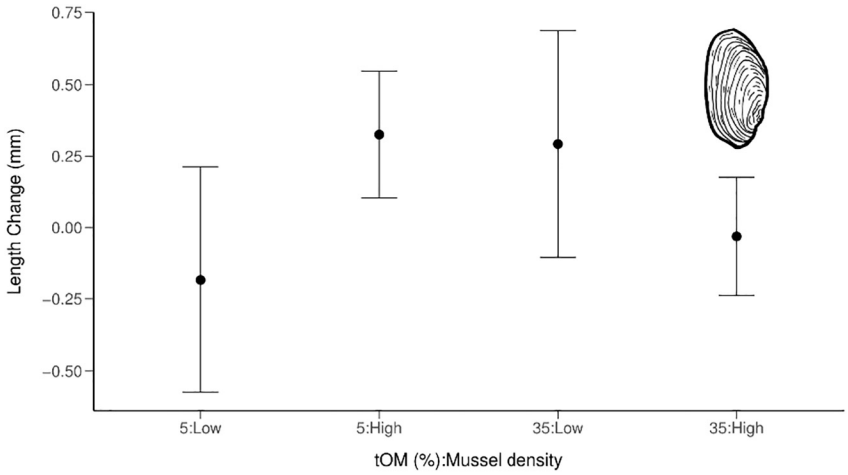


Fig. 5. Means and associated 95% confidence intervals for the change in mussel shell length during the course of our 40 day experiment in response to the tOM × mussel density treatments.

0.11 mm at low tOM to −0.04 ± 0.08 mm in the high tOM treatment (95% CI for the difference: −1.43 to −0.28 mm; Fig. 5). As expected, the amount of growth slowed in larger mussels (95% CI for effect of initial size: −0.05 to −0.02 mm mm^{-1}).

4. Discussion

Here, we found that the widespread mussel *Elliptio complanata* influenced sediment chemistry and co-occurring benthic communities over the relatively short timescale of our study, regardless of tOM quantity in most cases. Interactions between mussel density and tOM concentration were observed for some response variables with mussel growth and phosphorus concentrations decreasing at high and low mussel density, respectively, when in conjunction with high tOM. The tOM treatment on its own only altered diatom abundances.

4.1. Sediment chemistry

Bioturbation may explain the decrease in DOC, total phosphorus and total nitrogen that we observed at high mussel densities. By increasing the aerobic respiration rates of sedimentary microorganisms by up to 250% (Mermillod-Blondin, 2011), bioturbation can result in key nutrients being taken up at greater rates in the high mussel density mesocosms. The physical mixing of the sediments during mussel bioturbation can also increase the flux of phosphorus from the sediments to the water column (Chakrabarty and Das, 2007; Chen et al., 2016). For nitrogen, its decrease at higher mussel densities could also be due to denitrification, which can be enhanced by bivalve biodeposition (Newell et al., 2002). Although the decrease in nitrogen between the controls and the high mussel density was weak, a stronger result may have been detected with repeated measures.

Another explanation for the decrease in DOC at high mussel densities is that it may have been directly consumed by the mussels. For example, Roditi et al. (2000) reported that DOC in natural waters could contribute up to 50% of the carbon intake of zebra mussels (*Dreissena polymorpha*). Bosminidae may similarly have been responsible for the decrease in DOC in the sham mussel treatments, as their numbers tripled and their biomass has also been shown to be supported by terrestrially derived DOC (Tanentzap et al., 2017a).

In addition, we found that the phosphorus concentrations decreased at low mussel densities in the high but not the low tOM treatments. One explanation is that the high tOM treatment may have promoted benthic bacterial production (Ask et al., 2009), resulting in a drawdown of phosphorus. The effect of mussels on phosphorus may therefore be context-dependent, depending upon the density of mussels and the environmental conditions.

4.2. Benthic algae

Diatoms may decline in abundance at high mussel densities because they can form part of the diet of mussels (Allen, 1914; Holland, 1993; Tang et al., 2014). Freshwater mussels access benthic food items through cilia-generated water currents that pull material in through the anterior portion of the shell while the foot is extended (Nichols et al., 2005). In a field experiment in a Michigan headwater stream, Raikow and Hamilton (2001) showed that the diet of *Elliptio dilatata* comprised 80% deposited and 20% suspended organic material, including algae. By extension, it is plausible that the decrease in benthic diatoms at high mussel densities in our study may be a result of deposit feeding by *E. complanata*.

A reduction in phosphorus, nitrogen and DOC at high mussel densities may also explain the lower abundances of diatoms in these treatments as resources for growth may have been limited. Furthermore, the decrease in nutrients at high mussel densities may have enabled bacteria, which have higher affinities for phosphorus and nitrogen (Currie and Kalff, 1984; Vadstein, 2000), to outcompete and restrict algal growth. Bacteria may be especially competitive at higher tOM concentrations, where they are less dependent upon algae-generated carbon (Rier and Stevenson, 2002). In addition, Smith et al. (1995) hypothesise that bacterial ectoenzymes used to degrade organic matter can inhibit diatom aggregation by reducing diatom mucus stickiness.

Finally, higher tOM treatments may have affected the diatoms in a more direct way too. More suspended material above the sediments at higher tOM could have shaded the benthos and reduced diatom standing crop (Stevenson et al., 1991; Cottingham and Narayan, 2013). Both high mussel densities and tOM therefore have the potential to reduce an important food source for higher trophic levels, which if sustained over time could alter broader food web dynamics.

4.3. Zooplankton

The difference in response to our treatments by the different zooplankton families may have resulted from different aspects of the mussels' engineering capabilities and biological activity. The similar increase in Bosminidae at both the sham and low density mussel treatments suggests that these cladocerans benefited from the habitat and refuge provided by shell structure (Spooner and Vaughn, 2006). Refuge may have been especially important as predators such as young-of-the-year yellow perch (*Perca flavescens*) occurred in our study site (Brown et al., 2009). Although we observed a significant increase in Bosminidae in the high mussel density treatments, it was not as pronounced as in the sham and low density treatments. This could be due to mussels

filtering Bosminidae out of the water column (Shevtsova et al., 1986; Vaughn et al., 2008), or greater turbidity from bioturbation that reduced the feeding efficiency of Bosminidae themselves (Arruda et al., 1983).

Unlike the Bosminidae, Cyclopidae and Chydoridae were more abundant only at low mussel densities, showing no response to the sham mussel treatments. This finding suggests that both Cyclopidae and Chydoridae responded to the biological activity of mussels and not the habitat provided by their shells. Whilst Bosminidae are primarily filter feeders, Cyclopidae and Chydoridae are primarily littoral benthic species, feeding through a combination of filtering small particles from the water and scraping detritus and diatoms off surfaces (Wetzel, 2001). The benefit conveyed by mussels was therefore likely that of an indirect food web response. Spooner and Vaughn (2006) found a similar result, whereby grazing zooplankton increased in abundance in the presence of living mussels that fertilised surrounding algal growth. Additionally the decline in diatoms at high mussel densities could therefore have reduced food for these organisms and led to lower colonization of the higher mussel density mesocosms in comparison to the low mussel density mesocosms.

We found no effects of tOM on zooplankton abundance despite previous studies having reported a vast array of responses (e.g. Cottingham and Narayan, 2013; Fey et al., 2015). For example, studies manipulating leaf additions to lakes have shown that zooplankton respond to changes in tOM, with Copepoda being less sensitive than Cladocera (Cottingham and Narayan, 2013; Fey et al., 2015). However, these studies did not include a dominant species. Mussels have been shown to greatly influence zooplankton communities and abundances (Higgins and Vander Zanden, 2010) and we hypothesise that the dominant top-down control exerted by freshwater mussels outweighs any bottom-up effects of tOM additions on the zooplankton, as has been demonstrated previously with zebra mussels (*Dreissena polymorpha*) (Sinclair and Arnott, 2015).

4.4. Mussel growth

The result that the mussels in our experiment grew larger under higher densities at 5% tOM seems counterintuitive as higher density implies lower per capita food intake and mussels would have had less tOM as a potential food source (Hakenkamp and Palmer, 1999). However, the combined filtering effect of many mussels may draw down relatively more resources from the water column than at lower density, preventing local resource depletion and enhancing food consumption, particularly in shallower waters (DiDonato and Stiven, 2001). Greater growth at 5% tOM may also have arisen because higher tOM concentrations can interfere with feeding mechanisms rather than the 5% tOM treatments conferring a direct benefit. For example, Kat (1982) found that *Elliptio complanata* had significantly lower growth rates in muddy substrates than in a sand, gravel and clay mix due to the suspension of fine sediments above the muddy substrates, which clogged their gill filaments and reduced feeding efficiencies. The higher tOM treatments would have mirrored these muddy substrates with more suspended material and small leaf particles available to interfere with the mussels' feeding. In addition, higher tOM mesocosms could have produced anoxic conditions, which have been shown to decrease the survival rate of juvenile *E. complanata* (Sparks and Strayer, 1998) and increase stress levels (Cyr et al., 2012).

Our results also have relevance for freshwater mussel conservation because we found that higher tOM interfered with mussel growth at high mussel densities. Native freshwater mussels are experiencing substantial population declines in North America with nearly 70% of species threatened (Lydeard et al., 2004). Increases in tOM, as observed across the northern hemisphere (Monteith et al., 2007), may therefore pose an additional problem for freshwater mussel populations. Moreover, increases in tOM may alter the relative importance of within-lake versus terrestrial resources in aquatic food webs by interfering with mussel growth and reducing the rates of ecological processes undertaken by mussels (Strayer et al., 1999; Vaughn et al., 2004).

4.5. Conclusions

We found that the freshwater mussel *Elliptio complanata* substantially altered the geochemical composition of sediments and abundances of associated littoral organisms (benthic algae and zooplankton) in our mesocosms, often regardless of tOM quantity. Therefore, our results show how a dominant lake species may influence the surrounding benthos through ecosystem engineering, trophic interactions and habitat provision, much more strongly than the bottom-up effects of tOM additions that are widely reported (Pace et al., 2004; Cottingham and Narayan, 2013; Tanentzap et al., 2014; Karlsson et al., 2015). Although our study was conducted over a relatively short period, it was during a time in which interactions between the surrounding benthos and terrestrial inputs to lakes are generally the greatest – late summer to early autumn leaf senescence (Berggren et al., 2015; Tanentzap et al., 2017a). The interactions between mussels and tOM may however differ seasonally and we encourage future studies to explore longer term interactions. We also found how some of the effects of mussels, such as on phosphorus concentrations and mussel growth, are context-dependent and interact with tOM additions. Nonetheless, our finding that *Elliptio complanata* can impact the surrounding benthos in just one month highlights the strength of the interactions we observed and reveals the importance of considering dominant species when studying the effects of cross-ecosystem resource fluxes.

Acknowledgements

We thank two anonymous reviewers for improving the manuscript and everyone at the Vale Living with Lakes Centre, Sudbury, Ontario who supported our project, in particular Erik Szkokan-Emilson, John Gunn, Lynne Witty and Chloé Orland (funding: John Ray Trust Memorial Fund to B.R.S. and NERC Standard Grant NE/L006561/1 to A.J.T).

References

Aldridge, D.C., Fayle, T.M., Jackson, N., 2007. Freshwater mussel abundance predicts biodiversity in UK lowland rivers. Aquat. Conserv. Mar. Freshwat. Ecosyst. 17, 259–266.
Allen, W.R., 1914. The food and feeding habits of freshwater mussels. Biol. Bull. 27 (3), 127–146.
Arruda, J.A., Marzolf, G.R., Faulk, R.T., 1983. The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. Ecology 1225–1235.
Ask, J., Karlsson, J., Persson, L., Ask, P., Byström, P., Jansson, M., 2009. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. Ecology 90 (7), 1923–1932.
Berggren, M., Bergström, A.-K., Karlsson, J., 2015. Intraspecific autochthonous and allochthonous resource use by zooplankton in a humic lake during the transitions between winter, summer and fall. PLoS One 10, e0120575.
Black, A.R., Dodson, S.I., 2003. Ethanol: a better preservation technique for *Daphnia*. Limnology and Oceanography-Methods 1, 45.
Brown, T.G., Runciman, B., Bradford, M.J., Pollard, S., 2009. A biological synopsis of yellow perch *Perca flavescens*. Fisheries and Oceans Canada, Nanaimo.
Chakrabarty, D., Das, S.K., 2007. Bioturbation-induced phosphorous release from an insoluble phosphate source. Biosystems 90 (2), 309–313.
Chen, M., Ding, S., Liu, L., Xu, D., Gong, M., Tang, H., Zhang, C., 2016. Kinetics of phosphorus release from sediments and its relationship with iron speciation influenced by the mussel (*Corbicula fluminea*) bioturbation. Sci. Total Environ. 542, 833–840.
Chowdhury, G.W., Zieritz, A., Aldridge, D.C., 2016. Ecosystem engineering by mussels supports biodiversity and water clarity in a heavily polluted lake in Dhaka, Bangladesh. Freshwater Sci. 38, 188–199.
Cottingham, K.L., Narayan, L., 2013. Subsidy quantity and recipient community structure mediate plankton responses to autumn leaf drop. Ecosphere 4 (7), 1–18.
Currie, D.J., Kalff, J., 1984. A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. Limnol. Oceanogr. 29 (2), 298–310.
Cyr, H., 2008. Physical forces constrain the depth distribution of the abundant native mussel *Elliptio complanata* in lakes. Freshw. Biol. 53 (12), 2414–2425.
Cyr, H., Storisteanu, D.M., Ridgway, M.S., 2012. Sediment accumulation predicts the distribution of a unionid mussel (*Elliptio complanata*) in nearshore areas of a Canadian shield lake. Freshw. Biol. 57 (10), 2125–2140.
DiDonato, G.T., Stiven, A.E., 2001. Experimental studies of interactions between two unionids, *Elliptio waccamawensis* and *Leptodea ochracea*: variation in negative and positive effects. J. Freshw. Ecol. 16 (2), 303–316.
Echenique-Subiabre, I., Dalle, C., Duval, C., Heath, M.W., Couté, A., Wood, S.A., Humbert, J.F., Quiblier, C., 2016. Application of a spectrofluorimetric tool (bbe BenthoTorch) for monitoring potentially toxic benthic cyanobacteria in rivers. Water Res. 101, 341–350.

Fey, S.B., Mertens, A.N., Cottingham, K.L., 2015. Autumn leaf subsidies influence spring dynamics of freshwater plankton communities. Oecologia 178 (3), 875–885.
France, R., Peters, R., 1995. Predictive model of the effects on lake metabolism of decreased airborne litterfall through riparian deforestation. Conserv. Biol. 9 (6), 1578–1586.
Francoeur, S.N., Pinowska, A., Clason, T.A., Makosky, S., Lowe, R.L., 2002. Unionid bivalve influence on benthic algal community composition in a Michigan Lake. J. Freshw. Ecol. 17 (4), 489–500.
Griffiths, N.A., Cyr, H., 2006. Are there hot spots for *Elliptio complanata* in the shallow littoral zone of a large Canadian shield lake? Can. J. Fish. Aquat. Sci. 63 (9), 2137–2147.
Hakenkamp, C.C., Palmer, M.A., 1999. Introduced bivalves in freshwater ecosystems: the impact of *Corbicula* on organic matter dynamics in a sandy stream. Oecologia 119 (3), 445–451.
Harris, T.D., Graham, J.L., 2015. Preliminary evaluation of an in vivo fluorometer to quantify algal periphyton biomass and community composition. Lake and Reservoir Management 31 (2), 127–133.
Higgins, S.N., Vander Zanden, M.J., 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. 80 (2), 179–196.
Holland, R.E., 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, western Lake Erie since the establishment of the zebra mussel. J. Great Lakes Res. 19 (3), 617–624.
Jansson, M., Persson, L., De Roos, A.M., Jones, R.I., Tranvik, L.J., 2007. Terrestrial carbon and intraspecific size-variation shape lake ecosystems. Trends Ecol. Evol. 22 (6), 316–322.
Kahlert, M., McKie, B.G., 2014. Comparing new and conventional methods to estimate benthic algal biomass and composition in freshwaters. Environ. Sci.: Processes Impacts 16 (11), 2627–2634.
Karlsson, J., Bergström, A.K., Byström, P., Gudasz, C., Rodríguez, P., Hein, C., 2015. Terrestrial organic matter input suppresses biomass production in lake ecosystems. Ecology 96 (11), 2870–2876.
Kat, P.W., 1982. Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia: Unionidae). Malacol. Rev. 15, 119–127.
Kelly, P.T., Solomon, C.T., Weidel, B.C., Jones, S.E., 2014. Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. Ecology 95 (5), 1236–1242.
Lydeard, C., Cowie, R.H., Ponder, W.F., Bogan, A.E., Bouchet, P., Clark, S.A., Cummings, K.S., Frest, T.J., Gargominy, O., Herbert, D.G., Hershler, R., 2004. The global decline of nonmarine mollusks. Bioscience 54 (4), 321–330.
MacIsaac, H.J., 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. Am. Zool. 36 (3), 287–299.
Mackie, G.L., Flippance, L.A., 1983. Intra-and interspecific variations in calcium content of freshwater mollusca in relation to calcium content of the water. J. Molluscan Stud. 49 (3), 204–212.
Mermillod-Blondin, F., 2011. The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. J. N. Am. Benthol. Soc. 30 (3), 770–778.
Monteith, D.T., Stoddard, J.L., Evans, C.D., de Wit, H.A., Forsius, M., Høgåsen, T., Wilander, A., Skjelkvåle, B.L., Jeffries, D.S., Vuorenmaa, J., Keller, B., 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450 (7169), 537–540.
Negus, C.L., 1966. A quantitative study of growth and production of unionid mussels in the River Thames at Reading. J. Anim. Ecol. 513–532.
Newell, R.I., Cornwell, J.C., Owens, M.S., 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. Limnol. Oceanogr. 47 (5), 1367–1379.
Nichols, S.J., Silverman, H., Dietz, T.H., Lynn, J.W., Garling, D.L., 2005. Pathways of food uptake in native (Unionidae) and introduced (Corbiculidae and Dreissenidae) freshwater bivalves. J. Great Lakes Res. 31 (1), 87–96.
Ozersky, T., Evans, D.O., Barton, D.R., 2012. Invasive mussels alter the littoral food web of a large lake: stable isotopes reveal drastic shifts in sources and flow of energy. PLoS One 7 (12), 51249.
Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Van de Bogert, M.C., Bade, D.L., Kritzberg, E.S., Bastviken, D., 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427 (6971), 240–243.
Pope, R.J., Gordon, M.A., Kaushik, N.K., 1999. Leaf litter colonization by invertebrates in the littoral zone of a small oligotrophic lake. Hydrobiologia 392 (2), 99–112.
Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. Bioscience 46 (8), 609–620.
Raikow, D.F., Hamilton, S.K., 2001. Bivalve diets in a midwestern US stream: a stable isotope enrichment study. Limnol. Oceanogr. 46 (3), 514–522.
Richardson, J.S., Zhang, Y., Marczak, B.L., 2010. Resource subsidies across the land–freshwater interface and responses in recipient communities. River Res. Appl. 26 (1), 55–66.
Rier, S.T., Stevenson, J.R., 2002. Effects of light, dissolved organic carbon, and inorganic nutrients [2pt] on the relationship between algae and heterotrophic bacteria in stream periphyton. Hydrobiologia 489 (1–3), 179–184.
Roditi, H.A., Fisher, N.S., Sañudo-Wilhelmy, S.A., 2000. Uptake of dissolved organic carbon and trace elements by zebra mussels. Nature 407 (6800), 78–80.
Shevtsova, L.V., Zhdanova, G.A., Movchan, V.A., Primak, A.B., 1986. Experimental interrelationship between Dreissena and planktonic invertebrates. Hydrobiol. J. 22 (6), 36–39.
Sinclair, J.S., Arnott, S.E., 2015. Effects of an invasive consumer on zooplankton communities are unaltered by nutrient inputs. Freshw. Biol. 60 (1), 161–173.
Smith, D.C., Steward, G.F., Long, R.A., Azam, F., 1995. Bacterial mediation of carbon fluxes during a diatom bloom in a mesocosm. Deep-Sea Res. II Top. Stud. Oceanogr. 42 (1), 75–97.
Sparks, B.L., Strayer, D.L., 1998. Effects of low dissolved oxygen on juvenile *Elliptio complanata* (Bivalvia: Unionidae). J. N. Am. Benthol. Soc. 17 (1), 129–134.
Spooner, D.E., Vaughn, C.C., 2006. Context-dependent effects of freshwater mussels on stream benthic communities. Freshw. Biol. 51 (6), 1016–1024.
Stevenson, R.J., Peterson, C.G., Kirschtel, D.B., King, C.C., Tuchman, N.C., 1991. Density-dependent growth, ecological strategies, and effects of nutrients and shading on benthic diatom succession in streams. J. Phycol. 27 (1), 59–69.
Strayer, D.L., Cole, J.J., Likens, G.E., Buso, D.C., 1981. Biomass and annual production of the freshwater mussel *Elliptio complanata* in an oligotrophic softwater lake. Freshw. Biol. 11 (5), 435–440.
Strayer, D.L., Caraco, N.F., Cole, J.J., Findlay, S., Pace, M.L., 1999. Transformation of freshwater ecosystems by bivalves. Bioscience 49 (1), 19–27.
Tanentzap, A.J., Szkokan-Emilson, E.J., Kielstra, B.W., Arts, M.T., Yan, N.D., Gunn, J.M., 2014. Forests fuel fish growth in freshwater deltas. Nat. Commun. 5, 4077.
Tanentzap, A.J., Kielstra, B.W., Wilkinson, G.M., Berggren, M., Craig, N., del Giorgio, P.A., Grey, J., Gunn, J.M., Jones, S.E., Karlsson, J., Solomon, C.T., 2017a. Terrestrial support of lake food webs: synthesis reveals controls over cross-ecosystem resource use. Sci. Adv. 3 (3), 1601765.
Tanentzap, A.J., Szkokan-Emilson, E.J., Desjardins, C.M., Orland, C., Yakimovich, K., Dirszowsky, R., Mykytczuk, N., Basiliko, N., Gunn, J., 2017b. Bridging between litterbags and whole-ecosystem experiments: a new approach for studying lake sediments. J. Limnol. 76:431–437. https://doi.org/10.4081/jlimnol.2017.1588.
Tang, H., Vanderploeg, H.A., Johengen, T.H., Liebig, J.R., 2014. Quagga mussel (*Dreissena rostriformis bugensis*) selective feeding of phytoplankton in Saginaw Bay. J. Great Lakes Res. 40, 83–94.
Vadeboncoeur, Y., Jeppesen, E., Zanden, M., Schierup, H.H., Christoffersen, K., Lodge, D.M., 2003. From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. 48 (4), 408–1418.
Vadstein, O., 2000. Heterotrophic, Planktonic Bacteria and Cycling of Phosphorus. Advances in Microbial EcologySpringer US, pp. 115–167.
Vaughn, C.C., Hakenkamp, C.C., 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshw. Biol. 46 (11), 1431–1446.
Vaughn, C.C., Gido, K.B., Spooner, D.E., 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: species roles and effects of abundance. Hydrobiologia 527 (1), 35–47.
Vaughn, C.C., Nichols, S.J., Spooner, D.E., 2008. Community and foodweb ecology of freshwater mussels. J. N. Am. Benthol. Soc. 27 (2), 409–423.
Ver Hoef, J.M., Boveng, P.L., 2007. Quasi-poisson vs. negative binomial regression: how should we model overdispersed count data? Ecology 88 (11), 2766–2772.
Walseng, B., Yan, N.D., Schartau, A.K., 2003. Littoral microcrustacean (Cladocera and Copepoda) indicators of acidification in Canadian shield lakes. Ambio 32 (3), 208–213.
Welker, M., Walz, N., 1998. Can mussels control the plankton in rivers? A planktological approach applying a Lagrangian sampling strategy. Limnol. Oceanogr. 43 (5), 753–762.
Wetzel, R.G., 2001. Limnology: Lake and River Ecosystems. 3rd edn. Gulf Professional Publishing, Houston.
Witty, L., 2004. Practical Guide to Identifying Freshwater Crustacean Zooplankton. Ontario Ministry of the Environment, Sudbury.