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Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes

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Abstract. While limnological studies have emphasized the importance of grazers on algal biomass and primary production in pelagic habitats, few studies have examined their potential role in altering total ecosystem primary production and its partitioning between pelagic and benthic habitats. We modified an existing ecosystem production model to include biotic feedbacks associated with two groups of large-bodied grazers of phytoplankton (large-bodied zooplankton and dreissenid mussels) and estimated their effects on total ecosystem production (TEP), and the partitioning of TEP between phytoplankton and periphyton (autotrophic structure) across large gradients in lake size and total phosphorus (TP) concentration. Model results indicated that these filter feeders were capable of reducing whole-lake phytoplankton production by 20–70%, and increasing whole-lake benthic production between 0% and 600%. Grazer effects on TEP were constrained by lake size, trophic status, and potential feedbacks between grazing and maximum rates of benthic photosynthesis (BP_{MAX}). In small (mean depth $\bar{Z} < 10$ m) oligotrophic and mesotrophic ($TP < 100$ mg P/m²) lakes, both large-bodied zooplankton and dreissenids were capable of increasing the benthic fraction (Bf) by 10–50% of TEP. Small lakes were also the only systems where TEP had the potential to increase in the presence of large-bodied grazers, but such increases only occurred if grazer-induced changes in water clarity, macrophyte coverage, or nutrient availability stimulated specific growth rates of periphyton. In other scenarios, TEP declined by a maximum of 50%. In very large lakes ($\bar{Z} > 100$ m), Bf was minor (<10%) in the presence or absence of grazers, but increases in littoral habitat and the stimulation of benthic production in these ecosystems could be of ecological relevance because littoral zones in large lakes contain a relatively high proportion of within-lake biodiversity and are important for whole-lake food webs.

Key words: autotrophic structure; benthic-pelagic coupling; community structure; eutrophication; food web; primary production; trophic cascade.

INTRODUCTION

The distribution and abundance of organisms within ecosystems are regulated by both bottom-up and top-down forces (Hairston et al. 1960, Hunter and Price 1992, Power 1992). In lakes, variations in the relative importance of these forces are generally perceived as influencing the productivity, food web structure, and biodiversity within the pelagic zone (e.g., Kitchell and Carpenter 1993, Dodson et al. 2000), not a fundamental restructuring of these attributes between pelagic and benthic-littoral habitats. Although limnological research has emphasized pelagic biota and processes (Vadeboncoeur et al. 2002), a dual energy pathway paradigm is emerging in which higher trophic levels integrate benthic and pelagic food webs (Hecky and Hesslein 1995,

Vander Zanden et al. 2011). Recent studies indicate that benthic-littoral energy pathways support disproportionately high biodiversity relative to pelagic energy pathways (Vadeboncoeur et al. 2011), stabilize food webs (Rooney and McCann 2012), and contribute substantially to the energetic requirements of top trophic levels (Hecky and Hesslein 1995, Vander Zanden et al. 2011). These strong trophic and habitat links to the littoral zone suggest that the distribution of primary production between benthic and pelagic energy pathways has a strong effect on the structure of lake food webs and ecosystem functioning (Vadeboncoeur et al. 2003).

We introduce the term “autotrophic structure” to refer to the partitioning of total ecosystem primary production (TEP) between phytoplankton and benthic primary producers. Lake autotrophic structure is affected by nutrient loading, water clarity, and grazing pressure (Jeppesen et al. 1997, Vadeboncoeur et al. 2008, Genkai-Kato et al. 2012). Increases in nutrient loading (primarily phosphorus) promote phytoplankton growth and biomass and cause reductions in water clarity that

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are detrimental to periphyton and macrophytes (Dillon and Rigler 1974, Scheffer et al. 1993, Vadeboncoeur et al. 2003). In contrast, grazing pressure by large-bodied zooplankton such as *Daphnia* spp. (Mazumder 1994a, b, Mazumder and Havens 1998), and filter-feeding dreissenid mussels (Higgins and Vander Zanden 2010) can suppress phytoplankton biomass and production, and significantly increase water clarity. Since light availability provides a fundamental constraint on photosynthesis, grazer induced improvements in water clarity can result in increased growth rates for periphyton and submerged macrophytes (Jeppesen et al. 1997). Thus, not only do nutrient loading and grazers act in opposite directions to regulate phytoplankton biomass and production, they are also expected to have opposing effects on the autotrophic structure of lakes.

Our goal was to investigate the role of top-down (e.g., grazing) and bottom-up (nutrient availability) forces in modifying the autotrophic base of benthic and planktonic energy pathways in lakes. We examined the ability of two groups of filter feeding herbivores, large-bodied zooplankton (LBZ) and invasive dreissenid mussels, to alter the autotrophic structure and total ecosystem production (TEP) of lakes. To accomplish this, we adapted an existing lake autotrophic structure model (LAS; Vadeboncoeur et al. 2008) that used climatic (e.g., solar insolation), edaphic (e.g., nutrient availability), and morphometric (e.g., lake size and shape) factors to explore the effect of lake morphometry and trophic status on autotrophic structure. We revised the model to include biotic feedbacks associated with large-bodied grazers and investigated the influence of grazers on the autotrophic structure and TEP; bounding our model equations and input variables with information gleaned from observational studies and experiments. Specifically, we test three hypotheses regarding the role of grazers: (1) that reductions in phytoplankton biomass caused by grazers will alter the autotrophic structure of lakes and increase the relative contribution of benthic autotrophs to TEP; (2) that losses in phytoplankton production due to grazing will be offset by increases in benthic production, resulting in no overall change to TEP; and (3) that grazer effects on the autotrophic structure will be diminished as lakes become eutrophic, leading to the erosion of total benthic production and its contribution to TEP. Our overall objective is to provide insights into the conditions where pelagic grazers play an important role in shaping the autotrophic structure and food web structure of lake ecosystems.

METHODS

Model overview

The LAS model (Vadeboncoeur et al. 2008) is a whole-lake primary production model that includes climatic (e.g., solar insolation), edaphic (e.g., nutrient availability), and morphometric (e.g., lake size and shape) factors. The model integrates phytoplankton and periphyton production across 10 cm depth increments,

and a 15-minute time step, over a single 15-hour day. The volume and area (for periphyton productivity) of each depth layer are included in calculations (Table 1). We updated the model in two ways to account for grazer effects on TEP and its partitioning between phytoplankton and periphyton. The first approach (Model 1, the exploratory model) used the LAS model to examine how grazer effects on key response variables such as total ecosystem production (TEP) and benthic contribution to total ecosystem production (BF) varied as a function of lake trophic status and morphometry. The second approach (Model 2, case study) used the same model structure as Model 1, but was configured to allow for the direct input of morphological data (lake size, shape) and ecological response variables (chlorophyll *a* [chl *a*], water clarity) from 25 temperate-zone lakes before and after dreissenid invasion. The advantage of Model 1 is its flexibility to explore the effects of grazers across complete gradients of trophic status, lake size (mean and maximum depth), and lake shape. The advantage of Model 2 is additional realism; many model parameters were provided as model inputs rather than estimated using empirical relationships with other model parameters; natural covariation between these “collected” parameters and natural variation in meteorological conditions, lake shape (DR), and nutrient loading were accounted for.

Similar to other primary production models (e.g., Fee 1990), on which the phytoplankton component of the LAS model was based, the LAS model does not include error terms that were available for some, but not all, parameters. However, the model is based on mechanism, relies on empirical relationships that are well supported in the literature, and we have restricted our interpretation of the model results to evaluating the broad trends in ecosystem responses. Further, model simulations compared reasonably well with phytoplankton production estimates from the literature across wide ranges of trophic status (see Appendix: Table A1, and Vadeboncoeur et al. [2008]), and areal periphyton production was constrained to values representative of those reported in the literature (see *Model 1: exploratory model*). Model simulations were conducted using the statistical software R (version 2.10.0; R Development Core Team 2010). Model parameterization is provided in the Appendix (Table A1).

Model 1: exploratory model

Equations linking the effects of LBZ and dreissenids on phytoplankton biomass (Table 1: Eqs. 10–12) were obtained from meta-analyses reported elsewhere (Mazumder and Havens 1998, Higgins et al. 2011). The effect of grazers on water clarity was captured by an equation linking the light extinction (diffusive attenuation) coefficient (K_d) to chl *a* (Table 1: Eq. 7). Phytoplankton production was calculated using published empirical relationships with morphometry, light, and inorganic nutrients (Table 1: Eqs. 13–15). The

TABLE 1. Equations for the whole-lake primary production model.

Eq. no.	Description	Equation
1	lake surface area (km ²)	$A_0 = 0.285 \times \bar{Z}^{1.303}$
2	maximum depth (m)	$Z_{\text{MAX}} = \frac{\bar{Z}}{\text{DR}}$
3	lake area, A , at depth Z (km ²)	$A_Z = A_0 \left[1 - \left(\frac{Z}{Z_{\text{MAX}}} \right)^\gamma \right]$
4	lake volume, V , above depth Z (km ³)	$V_Z = \frac{\gamma Z}{(\gamma + 1)}$
5	shape factor	$\gamma = \frac{\text{DR}}{(1 - \text{DR})}$
6	thermocline depth	$Z_{\text{therm}} = A_0^{0.185}$
7	diffusive light attenuation coefficient (m ⁻¹)	$K_d = K_b + 0.15(\text{chl } a)$
8	light at depth Z (μmol·m ⁻² ·s ⁻¹)	$I_Z = I_{0t} e^{-K_d Z}$
9	surface irradiance at time t (μmol·m ⁻² ·s ⁻¹)	$I_{0t} = I_{0\text{MAX}} \sin\left(\pi \frac{t}{\text{daylen}}\right)$
10	phytoplankton biomass without large-bodied grazers present (mg chl a /m ³)	$\text{Chl}_{\text{NG}} = 10^{0.97 \log \text{TP} - 0.21}$
11	phytoplankton biomass with large-bodied zooplankton present (mg chl a /m ³)	$\text{Chl}_{\text{LBZ}} = 10^{0.87 \log \text{TP} - 0.60}$
12	phytoplankton biomass with dreissenid mussels present (mg chl a /m ³)	$\text{Chl}_{\text{DM}} = 10^{1.01 \log \text{TP} - 0.66}$
13	phytoplankton maximum photosynthesis (mg C·m ⁻² ·h ⁻¹)	$\text{PP}_{\text{MAX}} = 2.2(\text{chl } a)$
14	daily phytoplankton production at depth Z (mg C/d)	$\text{PP}_Z = \Delta t \sum_{\text{sunrise}}^{\text{sunset}} \text{PP}_{\text{MAX}} \times \tanh\left(\frac{I_Z}{I_k}\right) (V_Z - V_{Z-\Delta Z})$
15	daily whole-lake phytoplankton production (mg C·m ⁻² ·d ⁻¹)	$\text{TPP} = \sum_{Z=0}^Z \frac{\text{PP}_Z}{A_0}$
16	daily periphyton production at depth Z (mg C·m ⁻² ·d ⁻¹)	$\text{BP}_Z = \Delta t \sum_{\text{sunrise}}^{\text{sunset}} \text{BP}_{\text{MAX}} \times \tanh\left(\frac{I_Z}{I_k}\right) (A_{Z-\Delta Z} - A_Z)$
17	daily whole-lake periphyton production at depth Z (mg C·m ⁻² ·d ⁻¹)	$\text{TBP} = \sum_{Z=0}^Z \frac{\text{BP}_Z}{A_0}$

Notes: Literature references for all model equations are provided in Vadeboncoeur et al. (2008), except for Eq. 11 (Mazumder and Havens 1998) and Eq. 12 (Higgins et al. 2011). Variables are mean depth, \bar{Z} ; depth ratio, DR (\bar{Z}/Z_{MAX}); background light attenuation, K_b ; day length, daylen; TP, total phosphorus.

model includes input variables related to morphometry (area, volume, mean depth [\bar{Z}], maximum depth [Z_{MAX}]), and basin shape. Basin shape was characterized by a shape factor, $\gamma = \text{DR}/(1 - \text{DR})$, where DR represents the depth ratio (\bar{Z}/Z_{MAX}) (Carpenter 1983). Most lakes have DR values between 0.3 and 0.7, with higher values representing steep-sided lakes and lower values representing lakes with more gradual slopes (Vadeboncoeur et al. 2008). We used a depth ratio of 0.4 in all model runs because this is the most common value for lakes where $\bar{Z} \geq 5$ m, and production estimates from lakes with depths < 5 m were insensitive to variations in DR (Vadeboncoeur et al. 2008). Since DR was held constant, mean depth and lake surface area were correlated.

Because periphyton can obtain limiting nutrients from the sediments and water column (Hansson 1990, Sandjensen and Borum 1991), robust mechanistic equations linking water-column nutrients to periphyton production were not available. In the absence of such

relationships, we used two values of maximum periphyton photosynthesis (BP_{MAX}): 30 mg C·m⁻²·h⁻¹ and 90 mg C·m⁻²·h⁻¹. Values of 30 mg C·m⁻²·h⁻¹ are common in oligotrophic and mesotrophic lakes that do not have extensive submerged aquatic vegetation (SAV; Liboriusen and Jeppesen 2003, Vadeboncoeur et al. 2003). Values of 90 mg C·m⁻²·h⁻¹ are more common in lakes with high macrophyte coverage that provide increased surface area for attached algae, nutrient enriched systems supporting macroalgal growth (Lowe and Pillsbury 1995, Higgins et al. 2008a), or large tropical lakes (O'Reilly 2006).

The model was modified from Vadeboncoeur et al. (2008) in several ways to account for grazers. First, the effects of grazers on the chl a :TP (total phosphorus) relationship was determined from published empirical relationships (Table 1: Eqs. 10–12) for LBZ (Mazumder 1994a, b, Mazumder and Havens 1998) and dreissenid mussels (Higgins et al. 2011). Further, a positive feedback was included where maximal photosynthetic

rates for phytoplankton were increased by 16% under grazing scenarios (Table 1; also see Heath et al. 1995). All remaining equations in the Vadeboncoeur et al. (2008) model remained unchanged (Table 1), and effects of grazers were assessed across large gradients in TP (3–1000 mg/m³) and mean depth (1–100 m). From these input variables, all other model parameters (e.g., maximum depth, surface area, chl *a*, water clarity, and so on) were calculated (Table 1).

Our model formulation assumed no interaction between BP_{MAX} and the presence or absence of grazers. Increases in BP_{MAX} probably occur if grazer-induced changes in water clarity stimulate macrophyte growth and increase the surface area available for periphyton, or increase the availability of limiting nutrients to periphyton. For this reason, we included two scenarios of potential grazer effects: Scenario A assumed no interaction between grazers and BP_{MAX} (BP_{MAX} held constant at 30 mg·m⁻²·h⁻¹), while Scenario B included a positive interaction between grazers and BP_{MAX} (BP_{MAX} increased from 30 to 90 mg C·m⁻²·h⁻¹). While there are few studies that have directly examined the response of benthic production to variations in planktonic grazers or dreissenid invasions, the studies that do exist generally support Scenario B. Periphyton production increased by approximately three times in response to dreissenid invasion in Lake Huron; the mean pre-dreissenid photosynthetic rate was approximately 31 mg C·m⁻²·h⁻¹ and the mean post dreissenid rates was approximately 90 mg C·m⁻²·h⁻¹ (Fig. 6 in Lowe and Pillsbury [1995]). Similar post-dreissenid photosynthetic rates for benthic algae were also found in Lake Erie, where mean net photosynthetic rates during the June–July growth period ranged from 60 to 226 mg C·m⁻²·h⁻¹ (Davies and Hecky 2005, Higgins et al. 2008a). While little quantitative information is available on the response of BP_{MAX} to LBZ, increases in macrophyte cover that would be expected to increase periphyton biomass and production (Wetzel 1990), are commonly reported (e.g., Jeppesen et al. 1997, Lauridsen et al. 2003).

Model 2: grazer case study

Model 2 was used to estimate the effects of large-bodied grazers on the autotrophic structure and TEP of lakes for a set of 25 north-temperate lakes invaded by dreissenid mussels (Higgins et al. 2011). Model 2 was similar to Model 1, except that equations used to estimate lake-surface area (A_0 , Table 1: Eq. 1), maximum depth (Z_{MAX} , Table 1: Eq. 2), lake shape (γ , Table 1: Eq. 5), K_d (Table 1: Eq. 7), and chl *a* (Table 1: Eqs. 10–12) were removed since these values were provided directly as model inputs.

Model input data were obtained from Table A1 in Higgins et al. (2011) for 25 lakes across North America and Europe before and after dreissenid invasion. Required data on response of TP, chl *a*, and water clarity (e.g., Secchi depth) to dreissenid mussels was

available for at least 3 years pre-invasion and 3 years post-invasion, with a maximum of 10 years during each period (Higgins et al. 2011). Data represented seasonal mean values during the ice-free period (May–October).

Data analysis

The effect of dreissenid mussels on water quality parameters (TP, chl *a*, Secchi depth), primary production of phytoplankton and benthic algae (PPR and BPR, respectively), and total ecosystem production (TEP) were assessed using a meta-analysis technique called the log-response ratio (LR; Gurevitch and Hedges 1999). The LR ($LR = \ln(X_{post}/X_{pre})$) represents a potential change in parameter X (e.g., TEP) in the absence or presence of dreissenid mussels (i.e., between pre-invasion and post-invasion periods). The significance of these changes was assessed using a two-tailed t test on the population of LR values with a 90% confidence interval.

As noted by Vadeboncoeur et al. (2008), the utility of our modeling approach relies on the assumption that the production estimates for phytoplankton and benthic algal components of our model reflect those within natural systems. For benthic algae, maximum areal rates (BP_{MAX} = 30–90 mg C·m⁻²·h⁻¹) were obtained directly from the literature and represent the typical range of values found in situ. For the phytoplankton component, model outputs encompassed the range found in natural systems within each trophic category. However, mean estimates for phytoplankton production within each trophic category tended to occur toward the upper range of reported values (Appendix: Table A2). As such, estimates of the importance of benthic algal production to TEP are likely conservative.

RESULTS

Model 1: exploratory model

Model 1 simulations indicated that the direction and magnitude of grazer effects on TEP and the benthic fraction (Bf) of TEP were strongly influenced by lake size, trophic status, and potential feedbacks on periphyton photosynthesis (i.e., Scenario A vs. B). As the effects of dreissenids and LBZ were similar, only those for one group (LBZ) are shown. The response of dreissenids within Model 1 is provided as supplementary material (Appendix: Fig. A1). Whole-lake phytoplankton production consistently declined (range –20% to –70%) in the presence of large-bodied grazers, however the magnitude of decline was variable and dependent on TP and \bar{Z} (Fig. 1). In general, the largest reductions were found in shallow oligotrophic to mesotrophic systems (TP 3–50 mg/m³). As TP increased beyond 50 mg/m³, herbivores continued to reduce phytoplankton biomass, but reductions in self-shading offset biomass associated declines in phytoplankton production (Fig. 1).

Periphyton production increased in response to grazer induced improvements in water clarity, even in large deep ($\bar{Z} \geq 100$ m) lakes (Fig. 2). The response of Bf to

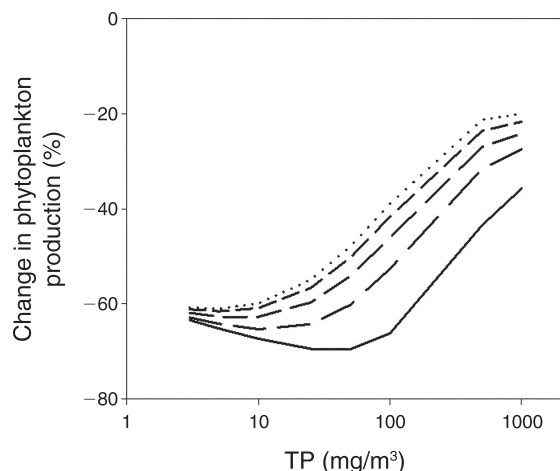


FIG. 1. Effects of large-bodied zooplankton (LBZ) on phytoplankton productivity in relation to lake size and total phosphorus (TP) concentration. Lines represent lakes with different mean depths as follows: 2 m (solid line), 5 m (long dash), 10 m (medium dash), 25 m (short dash), 100 m (dotted). The y-axis represents the change in phytoplankton production from no-LBZ-grazer to LBZ-grazer scenarios.

grazers was dependent on lake size, TP, and feedbacks between grazers and BP_{MAX} (Fig. 3). In shallow lakes ($\bar{Z} \leq 5$ m), the response of Bf to TP was unimodal, with largest changes occurring under mesotrophic to eutrophic conditions. In shallow oligotrophic lakes, the model predicted that Bf was high in the absence and presence of grazers, with grazers having little effect on Bf. In deeper lakes ($\bar{Z} \geq 10$ m), the model predicted that grazer effects on Bf declined with increases in TP due to increases in phytoplankton production and the constraints of lake morphometry on the potential contribution of periphyton to TEP. In the absence of positive feedbacks on periphyton growth (Scenario A), TEP declined in the presence of large-bodied herbivores irrespective of lake size or trophic status (Fig. 3). While periphyton production generally increased due to improved water clarity (Fig. 3), such increases were insufficient to overcome grazer induced losses of phytoplankton production. Nonetheless, the relatively large reduction in phytoplankton production, and smaller increases in benthic production, led to increases in Bf across a large range of lake mean depths and TP (Fig. 3).

Maximal increases in benthic production in response to grazers occurred in very shallow lakes ($\bar{Z} \leq 2$ m) with TP values near 50 mg P/m^3 (Fig. 3). At lower TP values, Bf values in these very shallow lakes were high in the absence of grazers, restricting the potential effects of grazers on both Bf and TEP. As mean depth increased, maximal changes in Bf resulting from grazer effects shifted toward lakes of lower trophic status. Overall, grazer effects on Bf tended to decline with depth and TP. With the exception of deep ($\bar{Z} \geq 100$ m) and highly eutrophic lakes ($TP > 100 \text{ mg P/m}^3$), grazer effects on

Bf were non-negligible (i.e., benthic production increased by at least 10% of TEP). In the presence of grazers, Bf was non-negligible (e.g., $>10\%$ of TEP) in nearly all oligotrophic lakes, with a maximal value of 0.9, and declining with increases in \bar{Z} and TP (Fig. 2).

In Scenario B, where positive feedbacks between herbivores and periphyton photosynthesis were included, herbivore effects on TEP were dependent on both \bar{Z} and TP (Fig. 2). Largest increases of TEP (2–2.5 \times) in response to grazers occurred in shallow ($\bar{Z} \leq 10$ m) oligotrophic ($TP \leq 10 \text{ mg/m}^3$) lakes and values declined with increases in \bar{Z} and TP (Figs. 3, 4). In lakes with $TP > 40 \text{ mg/m}^3$, TEP consistently declined in response to grazer induced declines in phytoplankton production. Herbivore effects on Bf in Scenario B were dependent on both \bar{Z} and TP, and followed a similar pattern to Scenario A. Under this scenario, the maximum grazer effect on Bf was approximately 0.5 (Fig. 3).

Model 2: Case study

Across the 25 natural lakes, dreissenid mussel invasion was associated with significant increases in mean water clarity (+23%), and declines in mean TP (–5%) and phytoplankton biomass (–45%). Our Model 2 simulations predicted that these effects would lead to a significant decline in mean phytoplankton production (–25%) and significant increases in periphyton production (Fig. 5). As with Model 1, the magnitude of effect on periphyton production was dependent on the interaction between grazers and BP_{MAX} . If BP_{MAX} remained constant following dreissenid invasion (Fig. 5, Scenario A), mean benthic algal production was predicted to increase by 11% and mean Bf was predicted to increase by 6% of TEP. If areal rates of benthic photosynthesis increased in response to dreissenids

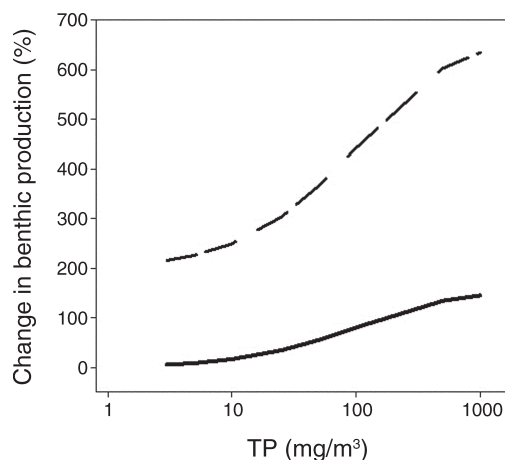


FIG. 2. Effects of large-bodied zooplankton on benthic primary production for a lake with a mean depth of 100 m. Grazer Scenarios A and B (see *Methods*) are represented by a solid line and dashed line respectively. The y-axis represents the change in phytoplankton production from no-LBZ-grazer to LBZ-grazer scenarios.

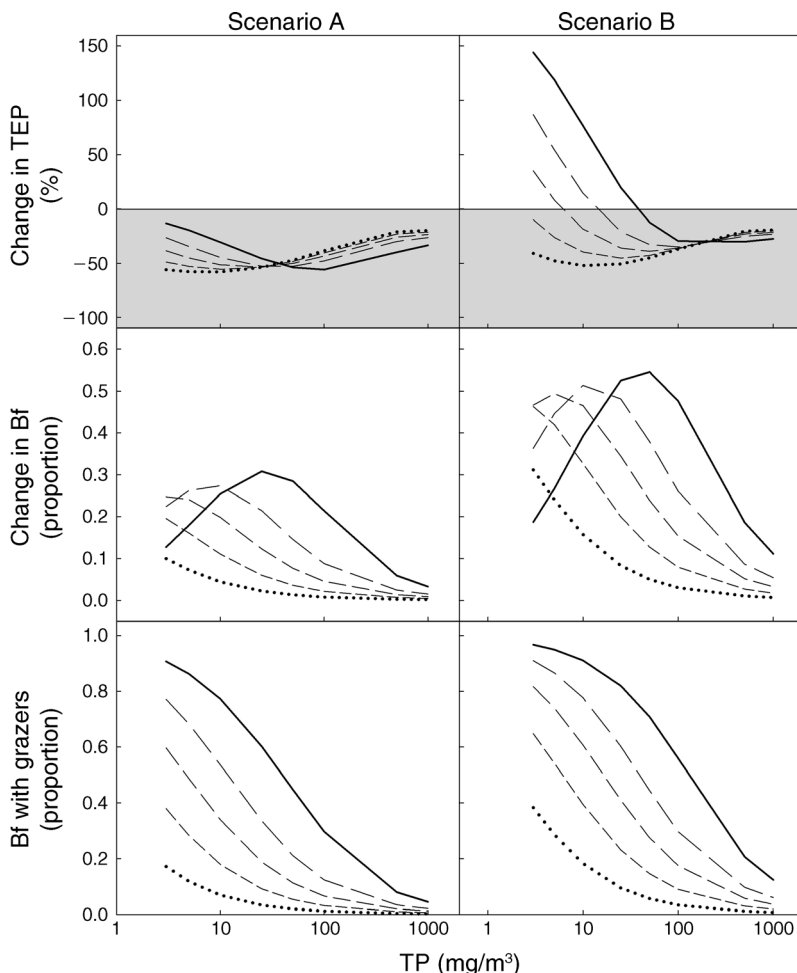


FIG. 3. Effects of large-bodied zooplankton (LBZ) on total ecosystem primary production (TEP) and the benthic fraction (Bf) of TEP. Lines represent lakes with different mean depths as reported in Fig. 1. The shaded portions of upper two panels indicate where LBZ reduce TEP. See *Methods* for descriptions of grazer scenarios A and B.

(Scenario B), total benthic production was estimated to increase by nearly 200% (Fig. 5), and mean Bf increased by 26% of TEP. Under Scenario A, TEP was estimated to decline by 15%, while increases in TEP of 14% were predicted under Scenario B.

DISCUSSION

In our model simulations, large-bodied herbivores reduced total ecosystem production and increased the relative importance of benthic autotrophs to TEP across most lake types (Hypothesis 1). The magnitude of these effects was constrained by both morphometry and nutrient availability, and was also influenced by potential feedbacks between herbivores and periphyton production. In general, the magnitude of herbivore effects on the autotrophic structure declined with increases in lake size. In very large lakes ($\bar{Z} \geq 100$ m), the presence of herbivores had little impact on the autotrophic structure; Bf was a negligible (<10%) proportion of TEP in the absence and presence of

grazers. However, the vast majority (>90%) of the world's lakes are small (<1 km²) and shallow ($\bar{Z} < 10$ m; Wetzel 1990), and in these ecosystems our model simulations indicated that benthic production contribute between 0% and 95% of TEP. Our model predicted that these shallow lakes were the most susceptible to large shifts in the autotrophic structure resulting from large-bodied herbivores; lakes that were dominated by phytoplankton production shifted to dominance by periphyton production when large-bodied herbivores were present. Our results support observations that the coupling of pelagic and benthic habitats can lead to abrupt state transitions between a "turbid-water phytoplankton dominated state" and a "clear-water macrophyte dominated state" (Scheffer et al. 1993, Schindler and Scheuerell 2002). Largest shifts in the autotrophic structure tended to occur in mesotrophic systems where, in the absence of large-bodied herbivores, phytoplankton production contributed a high fraction of TEP (>70%). In these systems, the presence of large-bodied

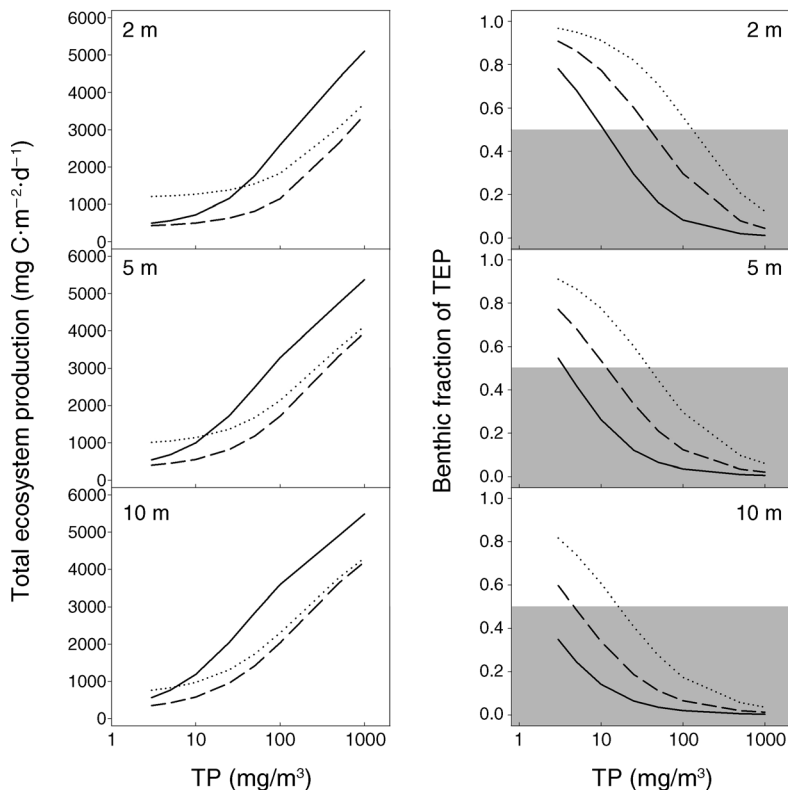


FIG. 4. Effects of large-bodied zooplankton on TEP and Bf in shallow lakes (depth is given on panels). Solid lines represent model simulations in the absence of LBZ, dashed lines represent grazer Scenario A, and dotted lines represent grazer Scenario B (see *Methods*). Shaded sections of panels on right side represent lakes dominated by phytoplankton production, while unshaded sections represent lakes dominated by periphyton production.

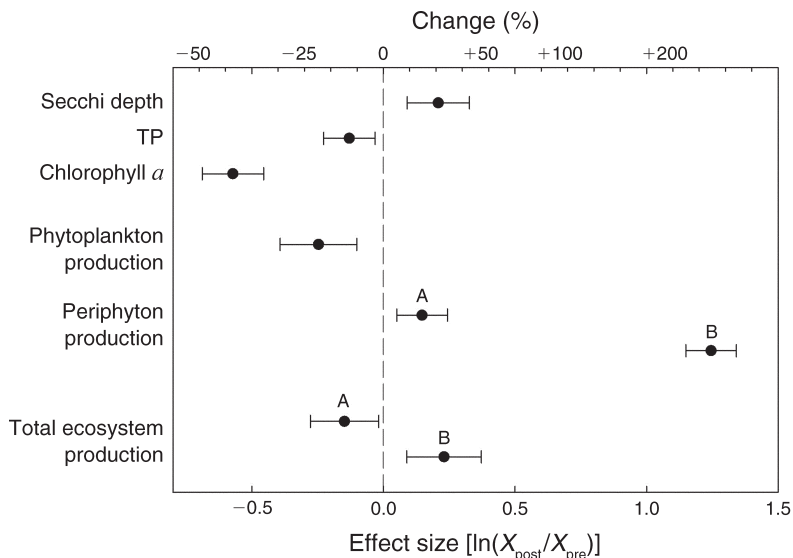


FIG. 5. The effects of dreissenid mussels on water quality parameters and estimates of primary production for 25 lakes across North America and Europe. The effect size is presented as the log response ratio, LR ($LR = \ln(X_{post}/X_{pre})$) represents a potential change in parameter X (e.g., TEP) in the absence or presence of dreissenid mussels (i.e., between pre-invasion and post-invasion periods). See Fig. 2 caption and *Methods* for description of grazer Scenarios A and B. Model outputs for grazer scenarios A and B (see *Methods*) are included for the variables periphyton production and total ecosystem production; other variables were unaffected. Model input data for Secchi depth, total phosphorus (TP), and chlorophyll a is from Higgins et al. (2011).

herbivores typically reduced the contribution of phytoplankton production to TEP to levels below 40%, and in some cases much lower. Biomanipulation studies have indicated that variations in grazer density are capable of inducing regime shifts in shallow lakes, including eutrophied systems (Jeppesen et al. 1990, Moss 1990). In shallow eutrophic ($TP > 50 \text{ mg/m}^3$) lakes our simulations indicated that large-bodied herbivores could induce reasonably large (e.g., $\Delta Bf = 0.2\text{--}0.4$) increases in Bf, however these increases were generally insufficient to induce a regime shift. The discrepancy between our model simulations and in situ studies for shallow eutrophic lakes suggests that either phytoplankton production is over estimated (see *Methods*), or additional factors to grazing (e.g., reductions in internal nutrient loading due to periphyton colonization of sediments, the release of allelopathic chemicals that inhibit phytoplankton growth) may also be important (Jeppesen et al. 1997, Genkai-Kato et al. 2012).

We predicted (Hypothesis 2) that increases in benthic production would offset grazer induced losses to phytoplankton production, with no net change to TEP. However, our model predicted that in most lake types, increases in periphyton production were insufficient to offset herbivore induced reductions in phytoplankton production. Further, the LAS model predicted that shallow lakes ($\bar{Z} \leq 10 \text{ m}$) were the only systems where TEP was likely to increase in the presence of large-bodied herbivores. However, even in these shallow lakes our model indicated that TEP would increase only if herbivores stimulated maximum areal rates of periphyton photosynthesis. Such increases could occur through increases in periphyton biomass or biomass specific photosynthesis in response to reduced resource limitation (e.g., increased nutrient availability) or increased macrophyte coverage and available substratum for the colonization by periphyton. While increases in periphyton growth and biomass accrual have been demonstrated in dreissenid invaded ecosystems (Lowe and Pillsbury 1995, Higgins et al. 2008a), and increases in macrophyte coverage have been described in trophic cascade and biomanipulation experiments (Scheffer et al. 1993, Lauridsen et al. 2003), there remains a large degree of uncertainty in quantifying changes in the BP_{MAX} of periphyton related to filter feeding herbivores. It was for this reason that we chose our two grazer scenarios to encompass the commonly found ranges in periphyton production, and we view the results of these scenarios as benchmarks of potential change rather than absolute values.

Implications of changes in autotrophic structure to food web structure

One of the difficulties in evaluating the relative importance of top-down vs. bottom-up controls of food web structure is the lack of experimental data at ecologically relevant spatial and temporal scales (Power 1992). In addition, the general lack of information on

the response of benthic pathways to trophic cascades, eutrophication, and most ecosystem disruptions in lentic systems has limited the ability to fully evaluate how benthic energy pathways may compensate for disruptions to pelagic energy pathways. The most obvious result of our study was that large-bodied phytoplankton grazers, and factors that control their densities (e.g., trophic cascades, species invasions), can restructure how autotrophic production in lakes is partitioned between pelagic and benthic habitats. Presumably, shifts in the autotrophic structure would have energetic consequences for higher trophic levels (i.e., bottom-up effects) within both benthic and pelagic energy pathways. Such effects have been demonstrated in numerous studies on the establishment of nonnative dreissenid mussels into lake and river ecosystems across North America and Europe. A recent meta-analysis of these studies (Higgins and Vander Zanden 2010) indicated that dreissenid induced reductions in phytoplankton biomass (-47%), and increased macrophyte coverage ($+180\%$) and periphyton biomass ($+170\%$), led to a series of impacts to higher trophic levels. Mean zooplankton biomass declined by 50% and the mean biomass of native zoobenthos increased by 60% (Higgins and Vander Zanden 2010). Case studies have documented shifts in fish behavior, species composition and productivity (Idrisi et al. 2001, Strayer et al. 2004, Rennie et al. 2009, 2013) indicating increased reliance on littoral resources and habitats. Thus, at least in the case of dreissenids, top-down pressure by these phytoplankton grazers induced a series of bottom-up effects in both pelagic and benthic energy pathways, significantly altering the food web structure of invaded ecosystems. The implications of variations in large-bodied zooplankton densities on benthic autotrophs are known to some extent, particularly in small lakes and ponds (e.g., Lauridsen et al. 2003, Jeppesen et al. 2007), but the response of fauna within benthic pathways has not been well studied. If such changes in the food web structure occur, they may also be reflected in either the increased abundance of littoral fishes or the stable isotope signatures of piscivores and benthivores as described for dreissenid invaded systems (Rennie et al. 2009, 2013).

The eutrophication of lakes is already among the leading threats to freshwater ecosystems on a global scale (Carpenter et al. 1998), with forecasts indicating the severity of eutrophication problems will increase dramatically over the next half century due to the rapid expansion of fertilizer use and large-scale conversion of natural ecosystems to agriculture (Tilman 1999, Tilman et al. 2001). The scientific evaluation of eutrophication impacts has generally focused on impacts to pelagic food webs; including harmful phytoplankton blooms, deep-water hypoxia, fish kills and losses in biodiversity and associated ecosystem services (e.g., Carpenter et al. 1998, Dodson et al. 2000). If littoral zones generally support a disproportionately high amount of biodiversity relative

to pelagic energy pathways as has been demonstrated for large lakes (Vadeboncoeur et al. 2011), the erosion of benthic productivity and benthic energy pathways through the process of eutrophication could lead a greater loss of biodiversity and stability than has been recognized from studies focused primarily on pelagic food webs (e.g., Dodson et al. 2000). We hypothesized (Hypothesis 3) that while top-down pressure by grazers could modify bottom-up influences on phytoplankton production, increases in nutrient loading would ultimately lead to the erosion of the autotrophic base of benthic energy pathways. Our results suggest that large-bodied zooplankton and dreissenid mussels can reduce the effects of eutrophication to a limited extent by reducing phytoplankton biomass and promoting benthic productivity, particularly within small shallow lakes. However, the ability of these grazers to maintain benthic energy pathways with increasing TP loading appears to be diminished as lakes transition from mesotrophy to eutrophy.

In our analysis, we have primarily focused on estimating the effects of herbivores on TEP and the autotrophic structure of lakes. However, the effects of herbivores on the absolute changes in primary production of phytoplankton and periphyton are also important. In particular, while the effects of herbivores on Bf in very large lakes was found to be negligible (<10% of TEP), benthic production increased by 0–100% in grazer Scenario A, and 200–600% in grazer Scenario B. While these scenarios serve only as benchmarks, it is clear that the grazer induced increases in benthic production may be substantial in lakes, even very large ones. Regardless of their contribution to TEP, such increases in periphyton production would presumably influence higher trophic levels associated with benthic energy pathways. Increases in the abundance and diversity of benthic fauna in the littoral zone are commonly associated with dreissenid invaded lakes and rivers (Higgins and Vander Zanden 2010), including in large lake ecosystems (Ozersky et al. 2012). There is also a growing body of empirical evidence that benthic energy pathways in large lakes are important for sustaining disproportionately high biodiversity relative to pelagic habitats (Vadeboncoeur et al. 2011). In large lakes, the relative proportion of production occurring between habitat types may be less important than the fact that benthic production is concentrated into relatively small, and largely two-dimensional, surfaces in the littoral zone. Thus, regardless of their relative importance to the autotrophic structure in large lakes, changes in the flow of energy and matter through benthic pathways may have important consequences to higher trophic levels, including the maintenance of high biodiversity.

The LAS model is most relevant to north-temperate zone lakes across North America and Eurasia where LBZ (Gilooley and Dodson 2000) and invasive dreissenid mussels are common. However, the LAS model structure is quite general and could be used to assess how

grazing and potentially other factors (e.g., bioturbation) influence lake autotrophic structure in other types of lakes. We encourage such attempts to revisit the models in Eqs. 10–12 (grazer effects on the chl *a*:TP relationship, Table 1), Eq. 13 (chl *a*:photosynthesis relationship, Table 1), and values of BP_{MAX} to ensure consistency with empirical data at more southern latitudes. Other parameters (e.g., day length, lake size and shape) are easily modified to address regional or local conditions.

Overall, our results indicate that large-bodied herbivores, and factors that control their densities (e.g., trophic cascades, species invasions), can alter total ecosystem productivity and the autotrophic structure of lake ecosystems. In shallow lakes, which dominate the globe, herbivores appear to be capable of dramatically altering the autotrophic structure of lakes; increasing the contribution of benthic autotrophs to TEP. Even in large deep lakes, where effects of herbivores on Bf were negligible, increases in benthic primary production were often large and of potential relevance to littoral zone productivity and biodiversity. Our results imply that, in most cases, grazer influences on the autotrophic structure should be included in conceptual and quantitative models of lake ecosystems.

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SUPPLEMENTAL MATERIAL

Appendix

Table of definitions and input values for model parameters, table comparing model output and estimates from natural ecosystems, and figure of dreissenid model simulations ([Ecological Archives E095-200-A1](#)).