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Benthic and planktonic primary production along a nutrient gradient in Green Bay, Lake Michigan, USA

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Abstract: Primary production in lakes occurs in both planktonic (water column) and benthic (bottom) habitats. How whole-lake primary production is distributed between these 2 habitats—referred to as *autotrophic structure*—is a key ecosystem property. Empirical research examining the balance between benthic and planktonic primary production in lakes is scarce, and how autotrophic structure changes across depth, nutrient, water clarity, and biological invasion gradients is unclear. Therefore, we are ill equipped to anticipate ecosystem-level responses to environmental change. We assessed the magnitude of offshore planktonic, nearshore planktonic, and nearshore benthic gross primary production (GPP) along a gradient of nutrients, water clarity, and *Cladophora* biomass in Green Bay, Lake Michigan, USA, during summer 2010, 2011, and 2012. Benthic and planktonic GPP varied strongly along the trophic gradient. Planktonic GPP increased with nutrients status, whereas benthic GPP decreased. From shore to 10 m depth, autotrophic structure shifted from planktonic dominance near the mouth of the Fox River (95% planktonic) to a mix of benthic and planktonic GPP 35 km from the mouth of the Fox (~40% benthic). The steep bathymetry at more-distant sites reduced the relative importance of benthic GPP at the whole-ecosystem level. Our work highlights the dual-pathway (i.e., benthic and planktonic) nature of lentic food webs from the perspective of GPP, and shows how both trophic status and bathymetry affect autotrophic structure.

Key words: benthic primary production, planktonic primary production, autotrophic structure, dreissenids, *Cladophora*, eutrophication, nutrients, Lake Michigan, Green Bay, Laurentian Great Lakes

Researchers studying lakes have emphasized measurement of planktonic primary production and processes (Vadeboncoeur et al. 2002) with particular emphasis on planktonic primary production in studies of eutrophication (Carpenter et al. 1998, Correll 1998). However, recognition is growing that substantial primary production occurs in both planktonic and benthic habitats. How whole-lake primary production (planktonic + benthic) is distributed between these 2 habitats is a poorly understood, but fundamental ecosystem property referred to as the *autotrophic structure* (Higgins et al., in press). Little understanding exists of how primary production is partitioned between these habitats, how partitioning varies along environmental gradients, and the effects of environmental change on autotrophic structure.

Benthic primary production can be a significant contributor to littoral zone, and sometimes to whole-lake, primary production (Vadeboncoeur et al. 2001, 2008, DeNicola et al. 2003, van de Bogert et al. 2007, Sadro et al. 2011). Even in lakes where benthic habitats are a minor contributor to whole-lake primary production, top predators generally assimilate C fixed by both benthic and planktonic autotrophs (Vander Zanden and Vadeboncoeur 2002, Vander Zanden et al. 2011), often leading to a disproportionately high importance of benthic primary production as a source of energy for higher trophic levels relative to its contribution to whole-lake primary production (Vander Zanden et al. 2006).

Nearshore benthic habitats in Lake Erie and Lake Ontario are primary production hotspots, with areal rates of benthic primary production equal to or exceeding planktonic primary production down to depths of 12 m (DeNicola et al. 2003, Davies and Hecky 2005, Malkin et al. 2010). These high rates of primary production are associated with mats of the filamentous green macroalga *Cladophora glomerata*, which are a widespread problem throughout coastal areas of the lower Laurentian Great Lakes (DeNicola et al. 2003, Davies and Hecky 2005, Malkin et al. 2010). In these ecosystems, the growth and biomass accrual

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of *Cladophora* is controlled primarily by the availability of hard substratum (e.g., rocky lake bottom) for attachment of filaments, water clarity, and the supply of bioavailable P (Higgins et al. 2008). *Cladophora* blooms were a common problem in the Great Lakes from the 1950s through the early 1980s, but successful implementation of strict P-abatement programs as part of the Canada–USA Great Lakes Water Quality agreement reduced total P (TP) loading and concentrations to levels that significantly reduced growth rates and biomass (Higgins et al. 2008). The resurgence of widespread *Cladophora* blooms in the Great Lakes has been attributed to the arrival of the nonnative zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena rostriformis bugensis*) (Hecky et al. 2004, Auer et al. 2010). Dreissenids have a well described set of effects on lakes: reduced phytoplankton biomass and primary production, increased light penetration, increased bioavailability of P at the sediment–water interface, and increased biomass and primary production of benthic primary producers (Lowe and Pillsbury 1995, Hecky et al. 2004, Higgins et al. 2008, Higgins and Vander Zanden 2010).

Some investigators have measured the balance between benthic and planktonic primary production in lakes (Malkin et al. 2010, Sadro et al. 2011), but most investigators have not considered how autotrophic structure varies along key ecological gradients, such as nutrient status and water clarity. In the coming decades, nutrient-abatement efforts paired with global environmental change will alter nutrient regimes, shift temperature and precipitation patterns, and bring new species invasions (Carpenter et al. 2011). Our limited understanding of lake autotrophic structure leaves researchers and resource managers ill equipped to anticipate how lake ecosystems will respond to such changes.

Green Bay, Lake Michigan, USA, presents a unique opportunity to study how autotrophic structure varies across key gradients (e.g., nutrient levels and water clarity) within a single ecosystem. Large inputs of nutrients and sediment from the Fox River lead to nutrient-enriched and turbid waters within inner Green Bay. However, trophic status decreases and water clarity increases with distance from the Fox River. Differences in basin morphology, which can influence the available habitat for benthic autotrophs, also occur with increasing distance from the Fox River. Water depths are shallow near the mouth of the Fox River but give way to deeper water and steep slopes in middle and outer Green Bay. We assessed how autotrophic structure varies along these gradients in a large lake basin during the summer stratification period.

METHODS

Study sites

We measured benthic and planktonic gross primary production (GPP) at 4 transects along Green Bay's nutrient gradient. GPP transects were 1.2, 12.8, 22.4, and 34.8 km from the mouth of the Fox River (transects 1, 2, 3, and 4, respectively; Fig. 1) at locations selected to span the full trophic gradient of Green Bay. At each transect, we used chamber incubations to estimate nearshore benthic GPP (GPP_B) and free-water gas dynamics to estimate nearshore planktonic GPP (GPP_{NP}) and offshore planktonic GPP (GPP_{OP}). At transect 1, benthic substrate consisted almost entirely of mud and sand. Transect 2 had a mixture of sand, gravel, and small rocks. Substrate at transects 3 and 4 was composed almost entirely of medium to large rocks.

Water chemistry

We measured total P (TP), soluble reactive P (SRP), total N (TN), chlorophyll *a* (chl *a*), total suspended solids (TSS), and the light attenuation coefficient (K_d) at 5 offshore locations along the trophic gradient every 2 wk during June–August 2010 and 2011 (14–25 sampling events/transect). We transported water samples to the laboratory on ice where samples were frozen (SRP, TSS, chl *a*) or treated with a weak solution of HCL (TP, TN). Samples were processed by the US Geological Survey (USGS)-certified water-chemistry laboratory at University of Wisconsin-Madison within 3 wk of field collection. We estimated K_d from vertical light profiles, taken

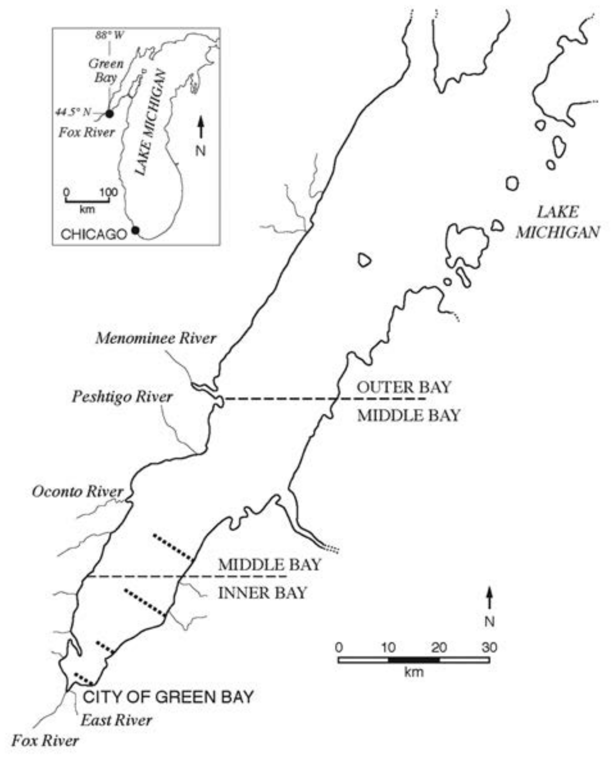

Figure 1. Map of Green Bay, Lake Michigan, USA. Dashed lines represent transects 1 to 4.

at 1-m depth intervals with a LI-COR 250A underwater light meter with a flat-plate (LI-192) sensor (LI-COR, Lincoln, Nebraska).

Cladophora biomass

We estimated *Cladophora* % cover at 1-m depth once a month from late May to late August (with the exception of transect 1, which lacked *Cladophora*) with a 0.33-m^2 quadrat at 10 locations at each transect. We estimated *Cladophora* biomass from an empirical relationship between *Cladophora* % cover and biomass (sensu Higgins et al. 2005) developed by direct comparison of these variables measured at a subset of locations and dates. We estimated *Cladophora* % cover visually within each quadrat, harvested *Cladophora* filaments by hand, and transferred them to a mesh bag. We blotted *Cladophora* filaments with a paper towel and weighed them to estimate wet mass (WM; g). We dried filaments overnight at 60°C and reweighed them to estimate dry mass (DM; g). The relationship between % cover and WM was linear: biomass = 0.88 (% cover) (CV = 0.22), with no significant difference in the multiplier among categories (5, 10, and 100%) of % cover. We converted estimated WM to DM with our empirically derived equation: ln(DM) = 0.86ln(WM) – 1.37 ($r^2 = 0.88$, $p < 0.0001$, $F = 653.9$, $n = 85$, df = 86), and expressed values as g/m^2. We averaged estimates of DM/m^2 for each transect and used them in subsequent calculations (see GPP_B estimates below).

Planktonic primary production

We estimated GPP_{OP} and GPP_{NP} from June to August 2010, 2011, and 2012 from diurnal fluctuations of O_2 and estimates of air–water gas exchange. At each transect, we deployed a YSI multiparameter sonde (model 6600 V2-4; Yellow Springs Instruments, Yellow Springs, Ohio) at 1.5-m depth in the middle of the Bay (OP) and ~1 km from shore (NP). We measured dissolved O_2 (DO) and temperature every 15 min. We used the bookkeeping method to estimate GPP from free-water DO (Odum 1956)

$$\mathrm{GPP} = \mathrm{NEP} + \mathrm{R} + \mathrm{D} \qquad \text{(Eq. 1)}$$

where NEP = net ecosystem production, R = ecosystem respiration, and D = rate of diffusion between lake and atmosphere (see Table 1 for symbol definitions) (Odum 1956). GPP estimates can be converted from O_2 to C units by multiplying by 0.375 and can be converted from C to O_2 units by multiplying by 2.667.

We calculated instantaneous rates of volumetric NEP (NEP_t) over 15-min intervals with the equations outlined by Staehr et al. (2010) so that

$$\mathrm{NEP}_t = \Delta \mathrm{O}_2 - \mathrm{D}_t \qquad \text{(Eq. 2)}$$

Table 1. Definition of symbols used in the model.

Symbol	Definition	Units
Y	Dissolved O_2 concentration at time t	μM
ΔO_2	Difference in dissolved O_2 concentration between time t and time t +1	μM
t	Time	Day fraction
T	Temperature	°C
NEP_t	Instantaneous rate of net ecosystem production	g C $m^{-2}d^{-1}$
GPP	Daily volumetric rate of gross primary production	g C $m^{-2}d^{-1}$
R	Daily volumetric rate of respiration	g C $m^{-2}d^{-1}$
D_t	Instantaneous rate of diffusion between lake and atmosphere	g C $m^{-2}d^{-1}$
z	Depth of integration at location x	m
k	Coefficient of gas exchange	m/h
k_{600}	Coefficient of gas exchange with a Schmidt number = 600	m/h
O_{2sat}	O_2 saturation as a function of temperature	mg/L
Sc	Schmidt coefficient	Dimensionless
U_{10}	Wind speed 10 m above the ground	m/s

$$\mathrm{D}_t = k(\mathrm{Y}_t - \mathrm{O}_{2\mathrm{sat}})/z \qquad \text{(Eq. 3)}$$

where t = time interval, k is the coefficient of gas exchange between the water surface and the atmosphere, z = depth of integration, Y_t = DO concentration at time t, and O_{2sat} was derived using the equation of Weiss (1970) and corrected for barometric pressure using the methods in USGS memoranda 81.11 and 81.15 (USGS 1981a, b).

$$k = k_{600}(\mathrm{Sc}/600)^{-1/2} \qquad \text{(Eq. 4)}$$

where

$$\mathrm{Sc} = 0.0476\mathrm{T}^2 + 3.7818\mathrm{T}^2 - 120.1\mathrm{T} + 1800.6 \qquad \text{(Eq. 5)}$$

(Wanninkhof 1992) and

$$k_{600} = (2.07 + 0.215\mathrm{U}_{10}{}^{1.7})/100 \qquad \text{(Eq. 6)}$$

(Cole and Caraco 1998) where T = temperature and U_{10} = wind speed 10 m above the ground. We obtained wind data from the National Oceanic and Atmospheric Administration's (NOAA) National Data Buoy Center for a location (lat 45°5′45″N, long 87°35′24″W) near Marinette, Wisconsin (www.ndbc.noaa.gov/station_page.php?station=mnmm4). We summed NEP_t obtained from each 15-min time step to obtain daily estimates of NEP (g C m^{-3} d^{-1}). We estimated daytime R from the average nocturnal R for the evenings before and after each daytime period. We calculated daily GPP (g C m^{-3} d^{-1}) by summing daily NEP and daily R. We converted volumetric rates to areal rates (g C m^{-2} d^{-1}) by multiplying volumetric rates by the depth of the mixed layer or the water depth (if mixed layer > water depth). Where water depth was shallower than the mixed layer depth, we corrected planktonic GPP for the benthic signal by adding the depth-specific benthic net primary production (NPP; see following section). For each transect, we calculated the average GPP_{OP} and GPP_{NP}. As noted elsewhere (e.g., Staehr et al. 2010), our approach is based on the assumption that daytime and nocturnal R are equivalent. If daytime R exceeds nocturnal R, our estimates of NEP will be unaffected, but estimates of GPP will be elevated.

GPP_B

We did benthic chamber incubations 3 to 4 times at each transect. At transects 2, 3, and 4, we collected rocks with attached *Cladophora* from 1-m depth and placed them in 2-L clear Plexiglas® chambers. We incubated a total of 6 chambers across a range of light levels (created by screening material, and including ≥1 completely opaque chamber) for 45 to 90 min under natural sunlight at ambient lake temperature. We measured ambient and within-chamber photosynthetically active radiation (PAR) with a Li-Cor 250A light meter every 30 min and temperature and DO inside each chamber with a YSI ProODO probe inserted through a sampling port every 15 min. Before the first DO and temperature readings, we placed all chambers in the dark with the top gasket removed for 5 min. Water in the chambers was mixed gently via the natural movement of the surrounding water and by a mixing paddle built into the chambers.

Benthic substrata at transect 1 consisted of sand and mud and lacked *Cladophora*. We collected sediment cores with ~1-L (5.5-cm diameter) clear Plexiglas chambers and measured temperature and DO in situ. We sealed the cores on both ends and incubated them with the method described above. We agitated cores gently by hand every 15 min rather than with a paddle. At the end of the incubation, we measured temperature and DO in each chamber and compared them to initial conditions measured in situ.

We estimated NPP in each chamber from the net change in DO during the incubation, corrected for chamber volume. We converted values from O_2 to C units by multiplying by 0.375 (photosynthetic quotient of 1; Davies and Hecky 2005). At transects 2, 3, and 4, we normalized C fixation to *Cladophora* DM in each chamber, after collecting, drying (37.7°C, 24 h), and weighing collected material.

We calculated GPP_B with data obtained from the incubations. We set light intensity at the onset of photosaturation (I_K) to 300 µmol photons m^{-2} s^{-1}, which is near the middle of I_K values reported in a literature review of *Cladophora* (Higgins et al. 2008). We calculated the maximum rate of GPP_B (BP_{max}) as the average GPP_B in chambers receiving >300 µmol photons m^{-2} s^{-1}. We used this approach because it yielded more robust estimates of BP_{max} than did dynamically fitting incubation data to saturation-tangent functions used to fit photosynthetic–irradiation (PI) curves to incubation data. We modeled daily GPP_B at each transect by inserting average BP_{max} into the equation

$$GPP_B = BP_{max}\tanh\left[I_0 e^{\frac{-K_d[\text{depth}]}{I_K}}\right] \qquad \text{(Eq. 7)}$$

(Vadeboncoeur et al. 2008) where K_d is the average light attenuation coefficient at that transect, depth is 1 m, and surface light (I_0) was modeled as a sine function and estimated at 15-min intervals with the equations by Fee (1990). We summed rates of GPP_B corresponding to each modeled solar-irradiance value to estimate daily GPP_B (g C m^{-2} d^{-1}). To scale biomass-specific GPP_B up to areal GPP_B at transects 2, 3, and 4, we multiplied biomass-specific GPP_B by average *Cladophora* DM/m^2 at 1 m depth for each transect.

Data manipulation

We used estimates of benthic and planktonic GPP to model areal (g C m^{-2} d^{-1}) GPP–depth curves from the 0 to 10-m depths at each transect. We modeled GPP_B every 0.5 m with average BP_{max} from each transect and the equations used to estimate GPP_B (see previous section; Fee 1990, Vadeboncoeur et al. 2008). We estimated areal planktonic GPP at each 0.5-m depth by integrating the average daily volumetric GPP_{OP} (g C m^{-2} d^{-1}) at that transect to depth. At each depth, we summed benthic and planktonic GPP to estimate depth-specific total GPP (benthic + planktonic). We calculated the benthic fraction (B_f) of total GPP as $B_f = GPP_B$/total GPP.

To evaluate how GPP_B, planktonic GPP, and their relative importance (autotrophic structure) varied along the trophic gradient, we integrated the area under benthic and planktonic GPP–depth curves. This produced an overall picture of the contributions of benthic and planktonic production to total primary production at each transect, but did not incorporate among-site differences in bathymetry. We call this approach the GPP–depth integration method, which is based on the approach of Higgins et al. (2012).

We expanded upon the GPP–depth integration method by incorporating transect-specific bathymetric data. We obtained bathymetric data from a NOAA nautical map of Green Bay (OceanGrafix chart 14910; www.mdnautical

.com). We determined depth every 100 m from shore to the middle of Green Bay along each transect. We estimated total transect GPP_B, planktonic GPP (g C/d), and B_f by summing along the transect with the same approach as the GPP–depth integration method, but with the real bathymetric data. We did all modeling and statistical analyses in R (version 2.15.0; R Project for Statistical Computing, Vienna, Austria).

RESULTS

Nutrients, water clarity, and *Cladophora*

Nutrients, chl *a*, TSS, and K_d were highest at transect 1 and decreased sharply with distance from the Fox River (Fig. 2A–F). Mean *Cladophora* biomass varied significantly among sites (ANOVA, $F = 24.49$, df = 1, $p \leq 0.0001$). *Cladophora* was absent at transect 1 and averaged 52.1 to 73.6 g DM/m^2 at transects 2 to 4 (Table 2).

Planktonic and benthic GPP measurements and depth trends

Volumetric GPP_{OP} decreased from 4.7 to 0.4 g C m^{-3} d^{-1} from transect 1 to 4 (ANOVA, $F = 165.84$, df = 1, $p < 0.0001$; Table 2). Areal GPP_{OP} decreased from 11.6 g C m^{-2} d^{-1} to 3.3 g C m^{-2} d^{-1} from transect 1 to 4 (ANOVA, $F = 96.327$, $p < 0.0001$, df = 1; Table 2). Volumetric GPP_{NP} ranged from 0.5 and 1 g C m^{-3} d^{-1} and did not vary with location (ANOVA, $F = 0.021$, df = 1, $p = 0.8857$). Areal GPP_{NP} varied among transects (ANOVA, $F = 5.927$, df = 1, $p = 0.0153$) and had the highest rates at transects 2 and 3 (Table 2). BP_{max} was ~4× higher at transect 1 (soft sediment) than transect 2 (hard substrate). BP_{max} was highest at transects 3 and 4 (Table 2).

For each transect, we used our empirical GPP measurements to model how areal benthic and planktonic GPP varied with depth (Fig. 3A–C). GPP_B was highest in shallow water and decreased with depth (Fig. 3A). GPP_B at depths <1 m were almost 4× higher at transect 1 than transect 2, and declined to 0 g C m^{-2} d^{-1} by 2 m at both transects. Transects 3 and 4 had higher GPP_B at shallow depths and declined to 0 g C m^{-2} d^{-1} at 6 m for transect 3, and 8 m for transect 4. In contrast, planktonic GPP increased linearly with depth, with the highest rates at transect 1 and lowest rates at transects 3 and 4 (Fig. 3B). B_f declined rapidly as a function depth at transects 1 and 2, and extended to greater depths at transects 3 and 4 (Fig. 3C).

Benthic and planktonic contributions to total transect GPP

We used 2 methods to estimate benthic and planktonic contribution to total GPP (g C/d) at the 4 transects. In the 1st method, GPP–depth integration, the areas under the benthic and planktonic GPP–depth curves (Fig. 3A, B) were compared. We plotted these estimates of benthic and planktonic GPP (g C/d) against potential trophic drivers (Fig. 4A–H). Planktonic GPP increased linearly with trophic variables, whereas GPP_B values suggested a threshold response between transects 2 and 3. B_f was low at transects 1 and 2 (0.04 and 0.02, respectively) but increased substantially at transects 3 and 4 (0.3 and 0.38 respectively). Planktonic GPP was highest at transect 1 and lowest at transect 4 (Table 2, Fig. 5A). In the 2nd method, local bathymetry was incorporated to estimate benthic and planktonic contribution to total transect GPP for each transect. With this method, the benthic contribution to total transect GPP was highest at transect 1 (0.10) and lower at transects 2, 3, and 4 (0.02, 0.05, and 0.04, respectively; Table 2, Fig. 5B).

The 2 methods produced different estimates of benthic and planktonic contribution to total transect GPP (Fig. 5A, B). The GPP–depth integration method showed decreasing total GPP and increasing B_f (to a maximum near 0.4) with distance from the Fox River. However, the method based on transect-specific bathymetry showed little change in total GPP among transects, with a maximum B_f of 0.1 (transect 1) and a minimum of 0.02 (transect 2).

DISCUSSION

Studies of lake primary production, and particularly research on eutrophication, have traditionally been focused on the dynamics and consequences of primary production in the pelagic zone of lakes (Carpenter et al. 1998, Correll 1998). However, a broader view of lake ecology and eutrophication would consider both benthic and planktonic autotrophs. Such an approach is of particular relevance for the Laurentian Great Lakes and other systems impacted by nutrient enrichment and dreissenid mussels. Our study highlights the broader implications of eutrophication for autotrophic structure in the Laurentian Great Lakes. Though we consider autotrophic structure along a spatial trophic gradient, our approach and findings are applicable to other situations where changes in nutrient status occur either across space or through time.

Benthic and planktonic GPP as a function of depth

GPP_B changed with depth at all transects but the rate of change depended on nutrient status. GPP_B declined rapidly with depth at the 2 most eutrophic transects (1 and 2), and continued to much greater depths (6–8 m) at the least eutrophic transects (3 and 4). We attribute the large variation in maximum depth of GPP_B to differences in light attenuation between transects in inner Green Bay (1 and 2) and those in middle/outer Green Bay (3 and 4).

GPP_B at depths <2 m at transects with *Cladophora* were among the highest reported for *Cladophora* and

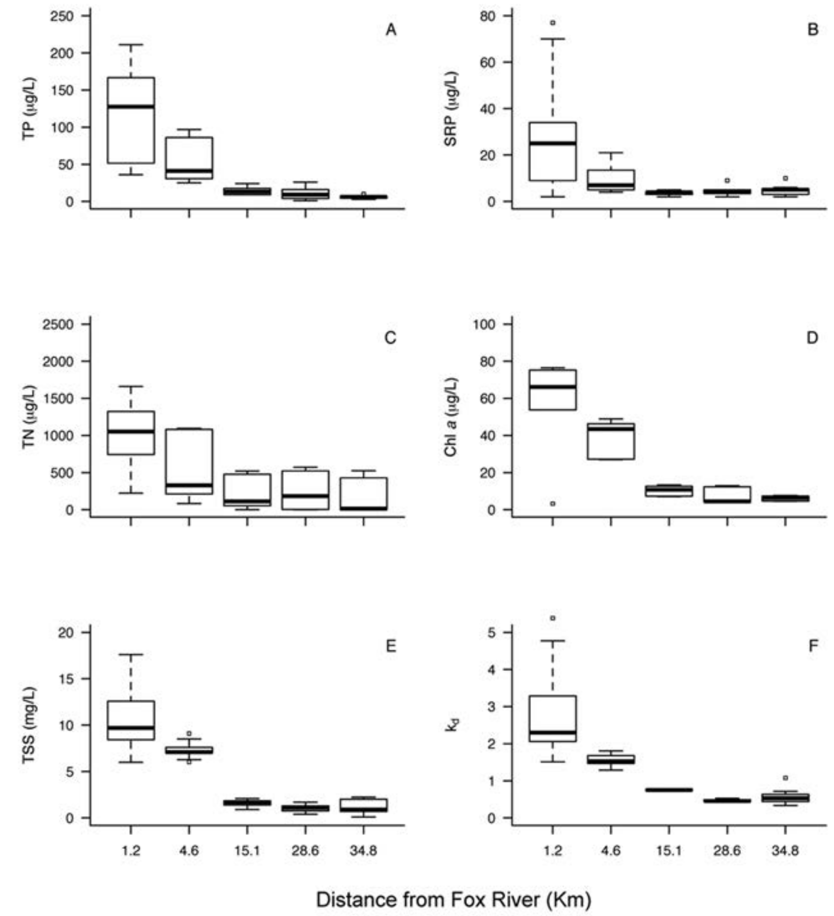

Figure 2. Mean total P (TP) (A), soluble reactive P (SRP) (B), total N (TN) (C), chlorophyll *a* (chl *a*) (D), total suspended solids (TSS) (E), and light attenuation coefficient (K_d) (F) at 5 locations along the trophic gradient in Green Bay, Lake Michigan, USA. All data were collected during 2010 and 2011 at offshore planktonic (OP) locations. Water-quality sampling sites do not correspond with gross primary production (GPP) transects except at distances 1.2 km (transect 1) and 34.8 km (transect 4).

were similar to primary production rates in highly productive tropical coral reefs (Carpenter 1985, Gattuso et al. 1998). Below 2 m at transects 3 and 4, our estimates of GPP_B were comparable to previous estimates of GPP_B in *Cladophora* mats in the Great Lakes. Malkin et al. (2010) reported rates of GPP_B between 0.8 and 1.6 g C m^{-2} d^{-1} in Lake Ontario, and Davies and Hecky (2005) reported GPP_B rates of 0.9 g C m^{-2} d^{-1} in Lake Erie *Cladophora* mats. Average *Cladophora* biomass (~60–80 g DM/m^2) at transects 3 and 4 were similar to, but slightly lower than reports for Lakes Erie and Ontario, whereas our maximum biomass estimates were similar to previous reports (Higgins et al. 2005, 2008). Our estimates of BP_{max} at transects with *Cladophora* (transects 2, 3, and 4 had mean BP_{max} of 2.1 mg C m^{-2} d^{-1}) agree well with reported values for other locations in the Great Lakes (BP_{max} ranging from 1–4 mg C m^{-2} d^{-1} reported by Malkin et al. (2010).

Autotrophic structure and environmental variables

Trophic status played a role in structuring the relative contribution of benthic and planktonic primary production along the trophic gradient in Green Bay. As nutrient concentration decreased, total planktonic primary production decreased whereas total GPP_B increased (GPP–depth integration method). Planktonic GPP was more responsive to nutrient status than GPP_B. This result is not surprising given that phytoplankton are generally nutrient limited (Hecky et al. 1993). In contrast, benthic algae tend to be light rather than nutrient limited (Vadeboncoeur et al. 2001), and this limitation explains the more muted response of benthic algae to water-column nutrient status.

Nutrients were correlated with changes in benthic and planktonic GPP, but bathymetry strongly influenced patterns of GPP. We anticipated that oligotrophic sites (i.e., transect 4) would have the largest B_f to total GPP because

Table 2. Planktonic and benthic primary production characteristics along the trophic gradient. Planktonic (plank) gross primary production (GPP) rates are mean (±1 SD), whereas benthic (benth) GPP is reported as the mean production rate for each individual transect. *Cladophora* biomass at each transect is shown as mean (±1 SD). Maximum benthic production (BP_{max}) is the average BP_{max} rate (mg C m^{-2} h^{-1}) at each transect. All estimates of planktonic and benthic production using M1 and M2 are in units of g C/d. B_f = the benthic fraction of total GPP using either M1 or M2.

Site	Offshore GPP plank (g C m^{-3} d^{-1})	Offshore GPP plank (g C m^{-2} d^{-1})	Nearshore GPP plank (g C m^{-3} d^{-1})	Nearshore GPP plank (g C m^{-2} d^{-1})	*Cladophora* biomass (g/m^2)	BPmax	M1 total GPP plank	M1 total GPP benth	M1 *Bf*	M2 total GPP plank	M2 total GPP benth	M2 *Bf*
1	4.7 ± 2.2	11.6 ± 5.6	0.6 ± 2.1	1.5 ± 5.1	0	161.4	107.1	4.6	0.04	144.3	15.7	0.10
2	1.1 ± 0.6	6.4 ± 4.0	1.0 ± 1.6	4.4 ± 6.7	52.1 ± 41.6	43.1	85.6	1.7	0.02	148.5	2.9	0.02
3	0.6 ± 0.5	5.0 ± 3.8	0.8 ± 0.8	4.8 ± 4.7	73.6 ± 38.4	281.2	40	17.1	0.30	174.7	8.2	0.05
4	0.4 ± 0.3	3.3 ± 2.0	0.5 ± 0.9	2.6 ± 4.5	69.4 ± 27.5	238.7	38.6	23.2	0.38	160.4	6.8	0.04

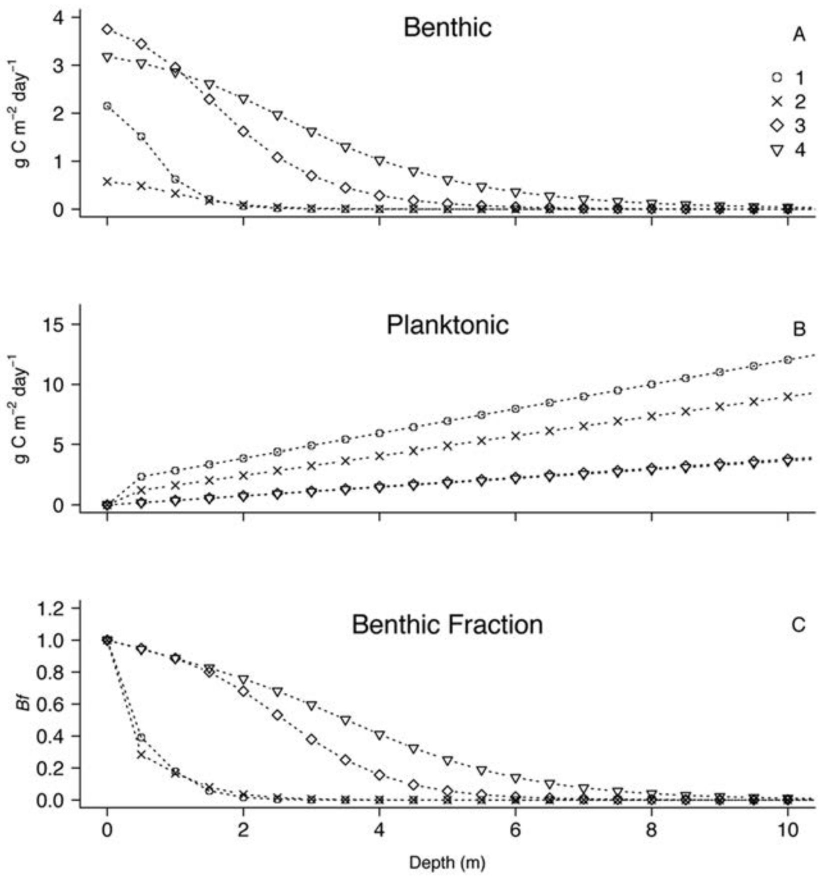

Figure 3. Benthic gross primary production (GPP_B) (A), planktonic GPP (B), and the benthic fraction of total GPP (B_f) (C) as a function of depth at transects 1 to 4. GPP_B was derived from chamber estimates, whereas planktonic GPP was derived from free water O_2 dynamics and adjusted for the benthic signal.

of increased water clarity, but we found the opposite to be true. The most eutrophic location (transect 1), had the greatest benthic contribution ($B_f = 0.1$). Thus, despite high areal rates of GPP_B at shallow depths at transect 3 and 4, the steep bathymetry restricted GPP_B to a narrow strip of the littoral zone. Meanwhile, the high water clarity at these sites (Fig. 2F) allowed planktonic primary production to extend to greater depths. Our results indicate that trophic status may be an important factor in determining the relative importance of benthic and planktonic primary production at fine spatial scales, but bathymetry can be a driving factor at the ecosystem level in large lakes. Considering that much of Lake Michigan has even higher ratios of planktonic volume to littoral surface area than transects 3 and 4, benthic habitats are likely to be important contributors only in nearshore areas, whereas planktonic primary production is the dominant contributor of fixed energy and nutrients at the ecosystem scale.

In addition to nutrient status and bathymetry, biological invasion also has the potential to shape autotrophic structure. Establishment of dreissenid mussels in the Great Lakes has sharply reduced phytoplankton biomass and light attenuation (Brezonik et al. 2005, Binding et al. 2007) and redirected nutrients to nearshore benthic habitats (Hecky et al. 2004) to yield increased GPP_B (Higgins et al. 2008, Auer et al. 2010). These changes have led to increased reliance on benthic resources in Great Lake food webs (Sierszen et al. 2006, Rennie et al. 2009) despite the dominance of planktonic primary production at the whole-lake level. GPP_B may not be a significant contributor to total ecosystem primary production, but on an areal basis, rates of GPP_B are equivalent to those occurring in coral reefs (Carpenter 1985, Gattuso et al. 1998). This narrow band of extremely high productivity may explain why these shallow littoral areas are also hotspots of biodiversity in large lakes across the globe (Vadeboncoeur et al. 2011). Furthermore, Great Lake food webs may rely disproportionately on benthic-derived C and could be sensitive to changes in rates of GPP_B in nearshore and littoral habitats. For these reasons, changes in GPP_B consequent to eutrophication, dreissenid mussels,

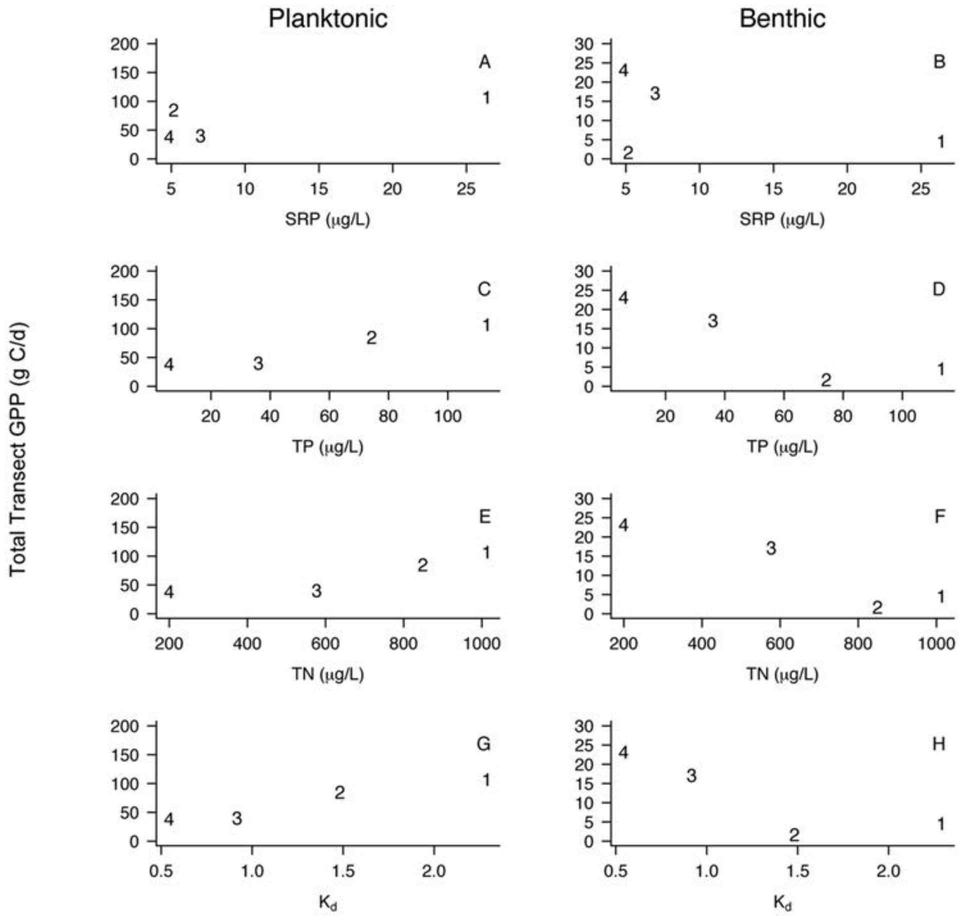

Figure 4. Total daily transect planktonic (A, C, E, G) and benthic (B, D, F, H) gross primary production (GPP) as a function of soluble reactive P (SRP) (A, B), total P (TP) (C, D), total N (TN) (E, F), and the light attenuation coefficient (K_d) (G, H). Both benthic and planktonic total transect GPP were calculated as the area under the GPP vs depth curves from the depth–integration method (Fig. 3A–C). Data points are indicated by transect numbers (1–4).

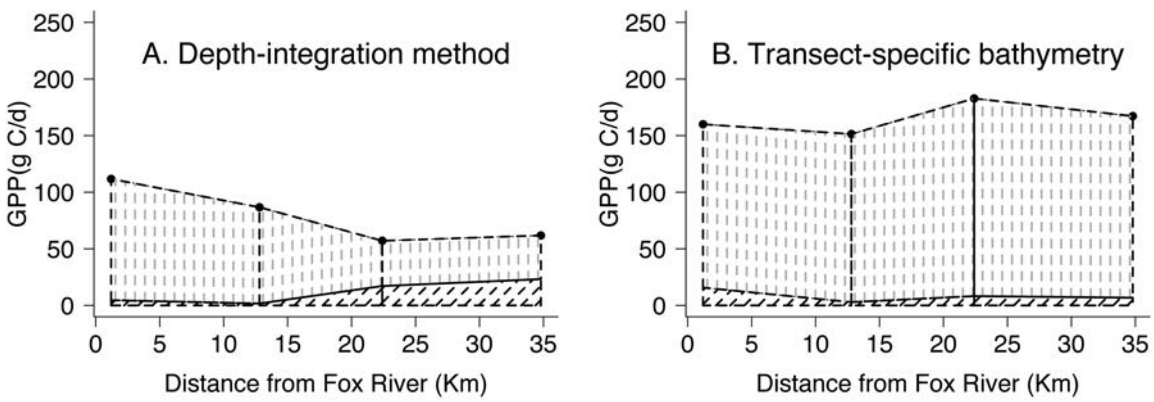

Figure 5. Total gross primary production (GPP) and benthic contribution to total GPP calculated by the depth–integration method (A) and using transect-specific bathymetry (B) as a function of distance from the Fox River. Points represent total daily GPP in each transect, vertical grey lines indicate planktonic contribution to total GPP, and black diagonal lines indicate benthic contribution to total GPP.

and other drivers could have a large influence on lake food webs and biodiversity without substantially affecting total lake primary production.

Benthic and planktonic primary production in Green Bay: past trends and future scenarios

The cumulative effects of eutrophication and biological invasions have undoubtedly influenced rates of both planktonic and benthic primary production over the past 25 y. TP entering Green Bay via the Fox River increased from a mean of ~100 μg/L in 1986 to a peak of nearly 210 μg/L between 2001–2004 before dropping to current levels near 150 μg/L (Green Bay Metropolitan Sewage District; http://www.newwater.us). This increase in P load corresponded to increases in areal planktonic primary production from 2.5 g C m^{-2} d^{-1} in 1986 (Auer and Canale 1986) to 3.7 g C m^{-2} d^{-1} in 1990 (Millard and Sager 1994). Volumetric rates of planktonic production also increased during that time period from 3.0 g C m^{-3} d^{-1} in 1986 to near 6 g C m^{-3} d^{-1} in 1990.

Current TP concentrations in inner Green Bay are similar to levels in 1990, and our estimates of volumetric planktonic production are comparable to those reported in the early 1990s (Millard and Sager 1994). At more distant locations from the Fox River (e.g., our transect 4) TP declined from ~80 μg/L in 1986 to ~5 μg/L in 2010–2011, presumably as a result of filtration by dreissenid mussels. Though TP in middle Green Bay has declined, planktonic primary production appears to have increased since 1990. Part of this discrepancy is a result of differences in methods used to calculate planktonic GPP. However, although dreissenids reduced phytoplankton biomass in the Great Lakes through grazing, they also may have increased phytoplankton-specific growth rates (Heath et al. 1995). Dreissenid-induced increases in water clarity in the Great Lakes (Budd et al. 2001, Binding et al. 2007) may have offset reductions in phytoplankton biomass, resulting in increased biomass-specific rates of planktonic primary production and higher rates of volumetric and areal GPP (Millard and Sager 1994).

At present, nutrient abatement offers the best opportunity to control nuisance growth of both benthic and planktonic algae in Green Bay. However, reductions in suspended sediment and nutrient loading from the Fox River could increase phytoplankton primary production near transect 1 because of increased light. In contrast, P reduction may do little to reduce nuisance *Cladophora* at transects 3 and 4, where dreissenid density is high and water-column TP and light attenuation are currently at levels indicative of an oligotrophic state.

CONCLUSION

On an areal basis, the benthic contribution to total primary B_f in Green Bay was high in shallow water and declined with depth, but how the benthic contribution changed with depth varied strongly along the trophic gradient. GPP_B made relatively minor contributions to total primary production at the transect or whole-lake level in Green Bay (and presumably other Great Lakes) during summer stratification because of steep bathymetry and large ecosystem size. However, on an areal basis, the narrow band of high GPP_B is probably important for maintenance of biodiversity hotspots in the littoral zones of large lakes (Vadeboncoeur et al. 2011). Furthermore, GPP_B contributes a disproportionately large amount of fixed energy and nutrients to higher trophic levels in food webs of large lakes invaded by dreissenid mussels (Rennie et al. 2013). Thus, food webs in large lakes may be sensitive to changes in GPP_B. The relative contributions of benthic and planktonic habitats to total primary production (autotrophic structure) at an individual location or the ecosystem level is a fundamental ecosystem attribute that is poorly explored but demands future research.

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