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Increased Benthic Algal Primary Production in Response to the Invasive Zebra Mussel (*Dreissena polymorpha*) in a Productive Ecosystem, Oneida Lake, New York

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Abstract

Increased water clarity associated with zebra mussel (*Dreissena polymorpha*) populations may favor benthic algal primary production in freshwater systems previously dominated by pelagic phytoplankton production. While zebra mussel-mediated water clarity effects on benthic primary production have been implicated in published reports, few production estimates are available. This study estimates benthic primary production in Oneida Lake, NY before and after zebra mussel invasion (1992), using measured photosynthetic parameters (P^B_{max}, α^B and β) from sampled benthic algal communities. In the summers of 2003 and 2004, primary production was measured as O_2 evolution from algal communities on hard (cobble) and soft (sediment) substrate from several depths. We also backcast estimates of benthic primary production from measurements of light penetration since 1975. Estimates of whole-lake epipelic and epilithic algal primary production showed a significant (4%) increase and exhibited significantly less interannual variability subsequent to the establishment of zebra mussels. We applied our model to two lakes of differing trophic status; the model significantly overestimated benthic primary production in a hypereutrophic lake, but there was no significant difference between the actual and predicted primary production values in the oligotrophic lake. The hypereutrophic lake had higher zebra mussel densities than Oneida (224 vs. 41 per sample respectively). Though total community respiration (measured in total darkness) was factored into our model predictions of production, our model may need modification when heterotrophic respiration is a large portion of total community metabolism.

Key words: *Dreissena*; ecosystem engineering; nonindigenous species; Oneida Lake; periphyton; primary production.

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Our understanding of the importance of trophic linkages between pelagic and benthic habitats in freshwater lakes has increased over the past two decades (Hansson 1990; Hecky and Hesslein 1995; Blumenshine et al. 1997; Vadeboncouer et al. 2001). Current evidence indicates that, given sufficient nutrient and light availability to the benthos, benthic primary production can greatly contribute to whole-lake primary production (Hecky and Hesslein 1995; Vadeboncouer et al. 2002; Vadeboncouer et al. 2003). In a literature review for the past 30 years of freshwater lake primary production research, Vadeboncouer et al. calculated annual primary production averages from 29 lakes worldwide, finding 69 g C/m^2 per year for phytoplankton, compared with 58 g C/m^2 per year for benthic algae (2002). Anthropogenic influences such as eutrophication and its converse, oligotrophication, as well as invasive species can modify benthic-pelagic pathways and cause ecosystem-wide alterations in water clarity and nutrients that can affect benthic primary production (Ludyanskiy et al. 1993; Strayer et al. 1999; Vadeboncouer et al. 2001). Therefore, it is important to better understand how temporally dynamic factors such as light and

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nutrients affect benthic primary production, especially as these environmental controls may shift due to anthropogenically-driven changes such as species introductions.

The number of studies that focus on benthic primary production is small compared with those that focus on phytoplankton primary production (Vadeboncoeur and Lodge 2000; Vadeboncouer et al. 2002; Vadeboncouer et al. 2003). Consequently the paucity of studies of benthic primary production represents a significant knowledge gap in our understanding of how freshwater lakes function (Hansson 1990; Hecky and Hesslein 1995; Blumenshine et al. 1997; Vadeboncouer et al. 2001). The majority of research on primary production in lakes has traditionally focused on phytoplankton, including investigations of the dynamic behavior of photosynthesis-irradiance (P/I) curves (Fee 1969; Jassby and Platt 1976; Macedo et al. 1998), methods of measurement (Lewis and Smith 1983; Marra et al. 1985), length of incubations (Macedo et al. 1998), effects of nutrients (Schindler 1974) and light (Graham et al. 1982; Falkowski and LaRoche 1991). In addition, many benthic studies either use few samples, or don't report the number of replicates used to estimate photosynthetic parameter values for benthic primary production (Jones 1984; Brandini et al. 2001; Nozaki 2001; Vadeboncouer et al. 2003). Consequently, there is a need for a more systematic assessment of spatial and temporal variation of benthic primary production within the context of changing environmental conditions in lakes.

Light is the primary factor limiting benthic primary production in nutrient-adequate systems (Wetzel 2001); therefore, any system-wide increase in light availability has the potential to increase benthic primary production and biomass (Lassen et al. 1997). The zebra mussel (*Dreissena polymorpha*), a benthic grazer of phytoplankton, has invaded many inland freshwater bodies in North America since 1986, and has almost universally led to increased water clarity in the invaded systems (Hebert et al. 1991; Caraco et al. 1997; Idrisi et al. 2001; Vanderploeg et al. 2002). The potentially positive response of benthic primary production to such a widespread increase in light availability could be significant in systems previously dominated by pelagic primary production (Strayer et al. 1999).

The zebra mussel and con-generic quagga mussel (*D. bugensis*) are often considered ecosystem engineers that change both the physical and chemical structure of an ecosystem (Karatayev et al. 2002; Vanderploeg et al. 2002). Increased water clarity, due to zebra mussel invasion or changes in nutrient concentration, has enhanced benthic primary production in some systems by enlarging the bottom area that is exposed to sufficient irradiance to support primary producers (Lowe and Pillsbury 1995; Blumenshine et al. 1997; Lassen et al. 1997; Pillsbury and Lowe 1999; Vadeboncoeur and Lodge 2000). In pelagic-dominated systems, increased benthic primary production could alter food web structure and energy allocation by shifting food sources from pelgaic microbes, invertebrates, and vertebrate predators, to benthic sources (Lowe and Pillsbury 1995; MacIsaac 1996; Strayer et al. 1999; Idrisi et al. 2001). One of the first steps toward understanding possible ecosystem-wide effects of the zebra mussel is to examine effects on the primary producers, thereby predicting possible shifts in energy transfer to higher trophic levels.

Benthic primary production estimates exist for very few freshwater lakes and many of the studies that have assessed the effect of *Dreissena* on benthic production have, by necessity, relied on a few pre-introduction measurements to establish background levels of the parameter measured (Lowe and Pillsbury 1995, benthic primary production; Fahnenstiel et al. 1995, phytoplankton production; Mayer et al. 2002, macrophyte depth). Such studies are unable to evaluate the potentially confounding effects of inter-annual variability or long-term trends in unrelated variables such as climate that are only detectable with larger time series (Magnuson et al. 2000). Therefore we have taken a hybrid approach to examining the effect of zebra mussel introduction on benthic primary productivity in which we combine new measurements of benthic primary production across a range of light levels (2003–2004) with long-term light data to backcast estimated production levels before, during and after zebra mussel invasion and assess inter-annual variation.

Our study system was Oneida Lake, NY, USA, a mesotrophic temperate lake with a long history (30 years) of limnological data spanning the years before and after zebra mussel establishment in 1992. This lake is generally well mixed thermally during the open water season and nutrients rarely become limiting, with only brief periods of N-limitation in late summer (Idrisi et al. 2001). To quantify the potential temporal and spatial changes in benthic primary production that can occur with the invasion of the zebra mussel, the following objectives were addressed: (i) estimate whole-lake summer epipelic and epilithic primary production and within-system variability; (ii) develop a light-based benthic primary production model for sediment and rock habitats to assess water clarity induced effects of the zebra mussel; and (iii) apply the light-based model from Oneida Lake to two lakes of different trophic status. No long-term benthic primary production estimates exist for Oneida Lake, therefore, our approach was to combine two years of new laboratory measurements of benthic primary production, taken throughout the growing season and across a range of substrate types and depths, with existing long-term data on light penetration in order to estimate long-term change in benthic primary production.

Results

Oneida Lake field observations

Seasonal trends of photosynthetically active radiation (PAR) to the benthos increased through June, and decreased from mid-July through August in association with the arrival of macrophyte stands and phytoplankton blooms each summer. Mean monthly light attenuation coefficients (k) for June through August of 2003 were $k = 0.51$, 0.58, 0.86, and for 2004 were $k = 0.63$, 0.66, 0.71, respectively. Mean PAR measured just above the water surface around midday ranged from 100 μmol/m^2 per s on cloudy/rainy days to 2 100 μmol/m^2 per s on sunny days. In early July, preceding the increase in phytoplankton biomass, there was an increase in macrophyte colonization at all sample sites except Taft Bay, where there was no soft substrate. In both 2003 and 2004, zebra mussels were abundant on cobble but were not observed on sediment. At some sites the colonies of mussels were dense, creating mounds formed of living and dead mussel shells and sediment deposition from pseudofeces (Karatayev et al. 2002). Algal communities were also different between hard and soft substrate. Most shallow cobble was covered in *Cladophora spp.*, while sediment communities had more diatoms, with a higher (chl-*c*) than cobble communities.

Oneida Lake photosynthetic parameters

Photosynthesis-irradiance curves were fit to the oxygen evolution data using all 171 samples from both 2003 and 2004. One-way ANOVAs were used to determine significant differences in photosynthetic parameters between study sites in order to determine which samples could be included to build the whole-lake primary production model. Photosynthetic parameters P^B_{max}, α^B, and β between sites were compared using a one-way ANOVA. There was no significant difference in photosynthetic parameters between sites, for algae on cobble (P^B_{max} ($P < 0.12$), α^B ($P < 0.11$), β ($P < 0.23$)) or sediment (P^B_{max} ($P < 0.31$), α^B ($P < 0.89$), β (($P < 0.84$))), thus parameters from all sites were pooled to create the primary production model.

Using one-way ANOVAs, differences were found between algal photosynthetic parameters and month or substrate. However, there were no significant differences between algae on sediment and cobble for P^B_{max} and α^B when all months and both years were combined, but β (photoinhibition) was significantly greater in algae on cobble than on sediment ($P < 0.01$). Mean photosynthetic parameter values varied significantly between months in cobble algae (Table 1) and increased throughout the summer, with P^B_{max} and α^B significantly higher ($P < 0.03$; $P < 0.002$) in August than in June or July, showing the trend of an increase in primary production throughout the summer. Photoinhibition (β) was significantly higher ($P < 0.01$) in June than in July or August, thereby greatest at the beginning of the summer when light penetration was greatest. Parameters for sediment algae showed no significant difference between months (Figure 1A–C). Maximum rates of production of algal communities on sediment and cobble occurred during different months. Mean primary production (mg C/m^2 per d) on both shallow (0–2 m) and deep (2–7 m) sediment was highest in July (Table 2), while mean primary production on both shallow and deep cobble was highest in August (Table 2).

Looking at differences with depth for sediment samples, P^B_{max} was significantly highest from 0–25 cm and gradually decreased as depth increased. There were no other significant differences in parameters with depth in either sediment or cobble algae. In sediment algae α^B generally increased and β decreased, with depth. On cobble algae P^B_{max} increased between 0–25 cm and 25–50 cm and then decreased, whereas α^B remained low until an increase after 100 cm, and β had its highest values in communities at 0–25 cm and 50–100 cm (data not shown).

Pre- and post-zebra mussel trends

In order to examine the trend in whole-lake (sediment and rock habitats) summer production before and after zebra mussels,

Table 1. Mean photosynthetic parameters for each depth/substrate category

	Average parameter			Average parameter		
	Values: Cobble (mg O_2 mg/chl-*a* per h)			Values: Sediment (mg O_2 mg/chl-*a* per h)		
Jun (0–25)	11.55	0.04	0.000 5	12.91	0.04	0.000 3
Jul (0–25)	6.21	0.05	0.000 9	15.26	0.09	0.000 2
Aug (0–25)	9.63	0.11	0.000 3	16.46	0.08	0.000 3
Jun (25–50)	6.27	0.23	0.000 6	4.88	0.03	−0.000 2
Jul (25–50)	8.05	0.03	0.000 2	8.95	0.03	0.000 3
Aug (25–50)	24.24	0.11	0.000 1	17.10	0.09	−0.000 1
Jun (50–100)	12.25	0.06	0.000 9	7.40	0.04	−0.000 2
Jul (50–100)	7.04	0.04	0.000 8	11.23	0.16	−0.000 1
Aug (50–100)	49.94	0.33	0.000 3	12.57	0.03	0.000 8
Jun (>100)	3.00	0.06	0.000 4	3.31	0.06	0.000 0
Jul (>100)	7.73	0.06	−0.000 3			
Aug (>100)	20.55	1.07	0.000 0	7.52	0.04	−0.000 1

Cobble and sediment communities each have four depth ranges, 0–25 cm, 25–50 cm, 50–100 cm, >100 cm (Rg 1, Rg 2, Rg 3, Rg 4). Each of the eight categories has a mean value for each of the three photosynthetic parameters (P^B_{max}, α^B, β) in mg O_2 mg/chl-*a* per h.

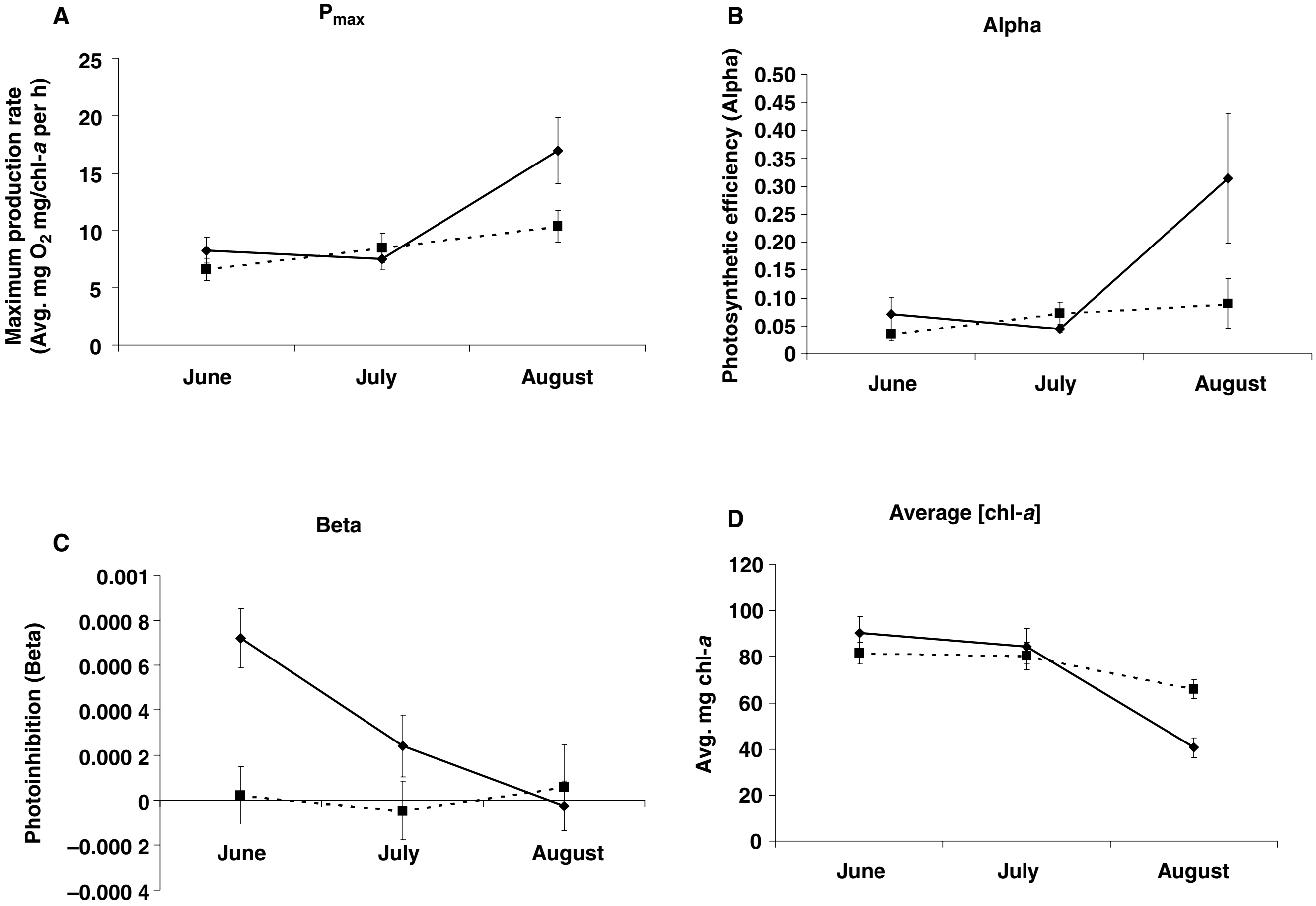

Figure 1. Mean photosynthetic parameters and chl-*a* for each month.

(A) Mean P^{B}_{max} (mg O_2 mg/chl-*a* per h) greater on cobble in August ($P < 0.027$).

(B) Mean α^{B} greater on cobble in August ($P < 0.002$).

(C) Mean β greater on cobble in June ($P < 0.011$).

(D) Mean chl-*a*/m^2 lesser on cobble in August ($P < 0.000\ 04$).

Values are means for all depth communities within each month and are separated by cobble (solid line with circles) and sediment (dashed line with squares) communities. Significant differences (indicated by asterisks) between months were found using one-ways ANOVAs. Standard error bars shown are for all samples within a month. Note different scales on y-axes.

mean monthly primary production model estimates (June–August) were calculated for the summer of each year (1975–2004). Back-casted whole-lake summer epipelic and epilithic primary production ranged from a low of 47 800 in 1985 to a high of 51 600 kg C/d in 1996 (Figure 2A). There was more total primary production on sediment than cobble, due to the large area covered by sediment in Oneida. Estimated sediment algae primary production ranged from 37 900 in 1985 to 40 500 kg C/d in 1996 (Figure 2B), and cobble totals ranged from 9 890 in 1975 to 11 000 kg C/d in 1993 (Figure 2C).

Inter-annual variation in benthic algal primary production showed a significant decrease after zebra mussel establishment (Figure 2A; *t*-test for independent samples with separate variance estimates, $P = 0.04$). This trend follows the significant decrease in inter-annual variability of mean summer light attenuation after zebra mussel introduction in 1992 (*t*-test for independent samples with separate variance estimates, $P = 0.000\ 1$). In addition, the highest rates of primary production (mg C/m per d) were found in shallow sediment in July, which is also the month that showed the most significant decrease in inter-annual variability of light attenuation.

Model estimates of primary production (mg C/m^2 per d) differed before and after zebra mussel introduction depending on month and depth (Table 2; *t*-tests for independent samples). Mean primary production on sediment (Table 2) in shallow samples (0–2 m) in June and July ($P = 0.001$, $P = 0.000\ 2$),

Table 2. Benthic mg C/m^2 per d before and after zebra mussel introduction on sediment and cobble

ID	Pre-mean	Post-mean	*t*-value	d.f.	*P*
Cobble					
JunShal	1 687	1 707	−3.86	28	0.000 6
JulShal	3 387	3 424	−4.20	28	0.000 2
AugShal	3 053	3 068	−1.82	28	0.079 1
JulDeep	260	274	−4.09	28	0.000 3
AugDeep	258	265	−1.66	28	0.107 2
Sediment					
JunShal	1 978	1 957	3.85	28	0.000 6
JulShal	1 346	1 337	4.26	28	0.000 2
AugShal	2 867	2 857	2.72	28	0.010 9
JunDeep	272	270	3.74	28	0.000 8
JulDeep	557	616	−4.08	28	0.000 3
AugDeep	628	637	−1.96	28	0.058 8

Values are means for shallow (0–2 m) and deep (2–7.5 m) algae on sediment and cobble. Significant values shown in bold. “Pre” designates the years 1975–1991, and “Post” the years 1992–2004. **Cobble:** Benthic algal communities on shallow cobble showed significantly greater gross primary production (GPP) during pre-zebra mussel years for June–August, whereas communities on hard deep substrate showed significantly greater GPP during pre-zebra mussel years for June, and during post-zebra mussel years for July. As with deep sediment, there was no significant difference found for deep cobble in August. **Sediment:** Benthic algal communities on shallow sediment showed greater mg C/m^2 per d during post-zebra mussel years for June and July, but no significant difference for August, whereas communities on deep sediment showed greater GPP during post-zebra mussel years for July but not August. Greatest inter-annual variation was in deep sediment during August.

and deep samples (2.0–7.5 m) in July ($P = 0.000\ 3$) were significantly greater after zebra mussel introduction. In contrast, estimates of primary production on cobble (Table 2) were significantly higher in the years before zebra mussel introduction for shallower samples in June, July, and August ($P = 0.001$, $P = 0.000\ 2$, $P = 0.01$) and deep samples in June ($P = 0.001$), while deep post-zebra mussel samples in July had significantly higher production values ($P = 0.000\ 3$). Algae on shallow cobble appear to show an effect of increased photoinhibition, thereby lowering their contribution to whole-lake production in the post-zebra mussel time period. There were no significant differences in mean primary production before and after zebra mussels for August values on deep sediments or shallow and deep cobble. When comparing mean whole-lake epipelic and epilithic primary production (kg C/d) for June–August 1975–2004 Oneida Lake the years before (17), and after (13) zebra mussel introduction, epipelic and epilithic primary production (kg C/d) significantly increased by 4% (Two-tailed *T*-test; $P = 0.001$) to 51 000 kg C/d once zebra mussels were established (Figure 3).

Model validation

We cross-validated our model by predicting the measured production values of the 20% of samples excluded from the model. When the predicted mg O$_2$ mg/chl-*a* per h for all combined depth ranges and substrate types were compared with the actual data using a two-tailed *t*-test, there was no significant difference ($P = 0.91$). Actual and predicted values from individual depth ranges varied slightly in either the positive or negative, but there were no significant differences between predicted and actual production rates for the whole lake estimate.

In order to examine the model’s ability to predict primary production for specific depth/substrate categories, the prediction error for each depth/substrate category was calculated as the difference between estimated and actual production values (mg O$_2$ mg/chl-*a* per h) and divided by the mean actual values, giving the coefficient of variation (CV) for the model predictions. Mean CV varied dramatically between depth/substrate categories, with a low value of 7% for the shallowest sediment algae in August, and a high value of 922% for cobble algae from 25–50 cm in August, reflecting the large natural variability in photosynthetic parameters among different communities.

Application to other lakes

In order to test the applicability of the light-based model to lakes with different trophic status, cobble algal communities were sampled in July and August 2004 from two lakes representing both ends of a trophic continuum, Onondaga Lake (hypereutrophic) and Skaneateles Lake (oligotrophic). The algal communities used to develop the model in Oneida Lake are acclimated to mesotrophic conditions, with mean summer levels of NO$_3^-$ at 184 μg/L and of total phosphorus (TP) at 27 μg/L over the past 30 year (CBFS long-term dataset). Benthic algal communities in Oneida and Onondaga were dominated by filamentous *Cladophora spp*. in August, whereas algal communities in Skaneateles were dominated by diatoms. Light attenuation varied between the three lakes; therefore the model parameters for Onondaga and Skaneateles were assigned based on light attenuation and not depth.

As in the model validation for Oneida Lake, the predicted model values for the Onondaga and Skaneateles samples were compared with their actual laboratory measured values (mg O$_2$ mg/chl-*a* per m^2) with a *t*-test for independent samples. The model significantly overestimated actual benthic primary production in Onondaga samples ($P \leq 0.000\ 1$), but there was no significant difference ($P = 0.95$) between the actual and predicted primary production values for Skaneateles. In addition, photosynthesis-irradiance curves were fit to the actual production values from Onondaga and Skaneateles and the mean parameters compared with those from the Oneida model. Predicted model parameter estimates were less than actual values from Onondaga (Table 3), and were greater than actual

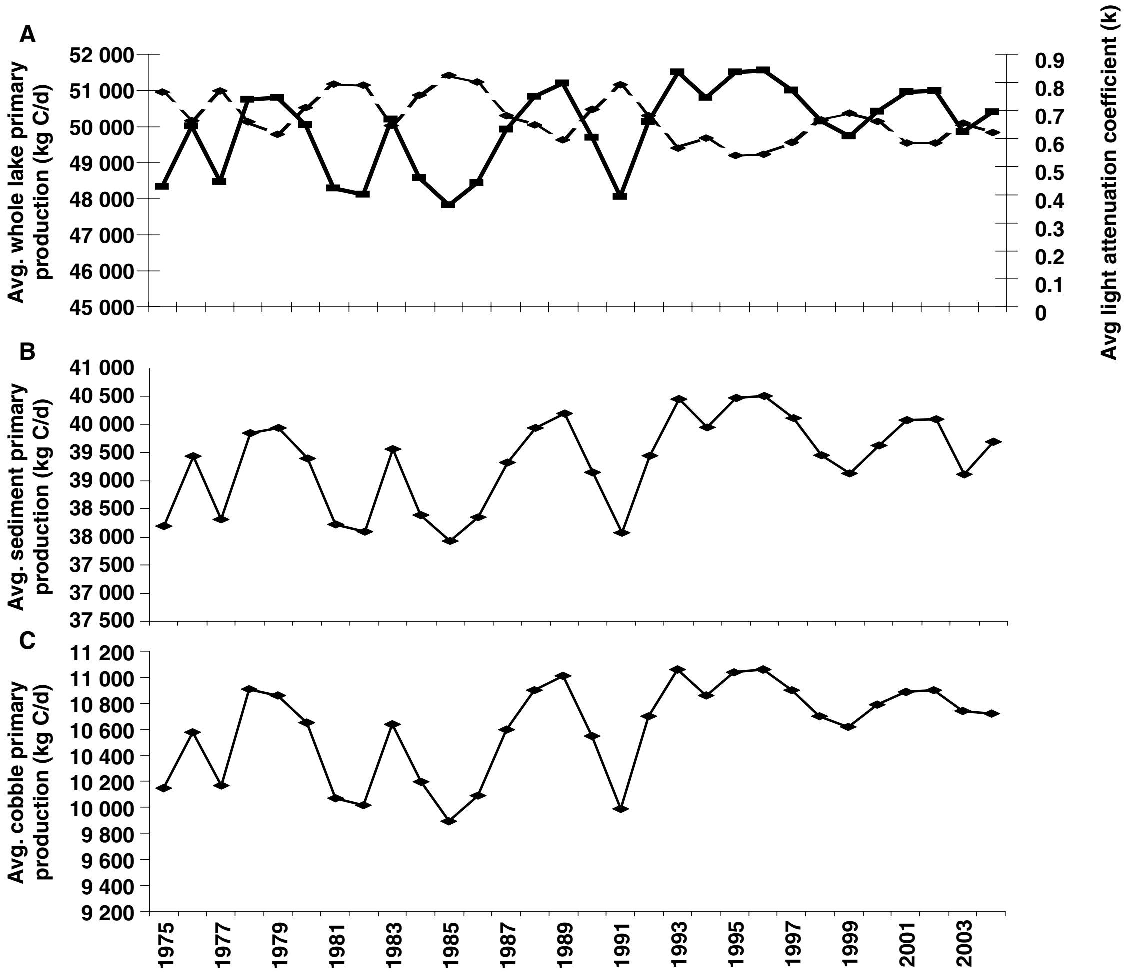

Figure 2. Mean whole-lake epipelic and epilithic summer gross primary production (GPP) from 1975–2004.

(A) When both substrates are combined (solid line) the driving effect of zebra mussel introduction on benthic primary production is a decrease in inter-annual variation and an increase in production. Interannual variability significantly decreased for mean annual light attenuation coefficient (dashed line) after 1992 ($P = 0.000\ 1$). For algal primary production on sediment **(B)** and cobble **(C)**, interannual variation decreases and mean production increases after zebra mussel introduction in 1992.

Primary production rates in kg C/d calculated from a mean of all 3 months for every year. Interannual patterns are different between cobble and sediment, and production values are greater for sediment algae than for cobble algae.

July Skaneateles values, but less than the August values (Table 3). Therefore the model did predict overall production for Skaneateles, but did not successfully predict individual photosynthetic parameters in either the hypereutrophic or the oligotrophic lake. There was a striking difference between the mean number of zebra mussels present on sampled rocks from Oneida (41) versus Onondaga (224) raising the question of whether high zebra mussel respiration in Onondaga Lake may interfere with the application of our model to this system. However, the comparison to this hyper-eutrophic system is nonetheless valuable as the lakes are similar in other respects, for example, location and climate.

Chl-*a*, *b*, *c*

In this study chl-*a* was used as an index of algal biomass. One-way ANOVAs were used to find differences in [chl-*a*] among months and depths in Oneida Lake. Mean chl-*a* on cobble was significantly higher in June and July than in August (Figure 1D, $P < 4.2\mathrm{E}^{-5}$). On sediment there were no significant differences between mean chl-*a* for each month, although the means for June and July were slightly higher than those in August (Figure 1D).

There were no significant differences between mean chl-*a* values for algae from different depth ranges on cobble

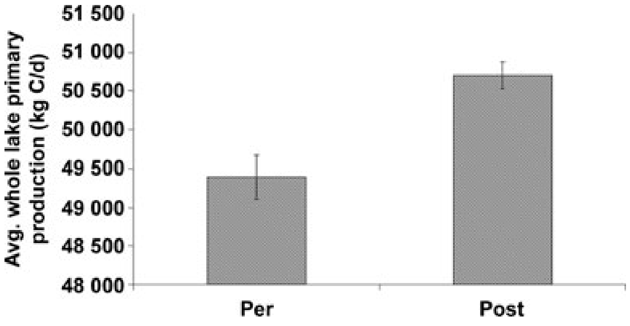

Figure 3. Mean summer epipelic and epilithic gross primary production (GPP) before and after zebra mussels.

Primary production values (kg C/d) are means of June–August during the 17 years before (1975–1991), and 13 years after (1992–2004) zebra mussel introduction. Bars shown are the standard error for the number of years. Benthic GPP post-zebra mussel is significantly greater than pre-zebra mussel in Oneida Lake (two-tailed *t*-test, $P = 0.001$). Standard error is greater among the years before zebra mussel introduction.

Table 3. Mean actual photosynthetic parameters for Onondaga and Skaneateles lakes for July and August compared with predicted parameters from the Oneida model

	Jul	JulModel	Aug	AugModel
Onondaga parameters vs. model predictions				
P_{max}	2.04	7.73	7.72	20.55
α	0.21	0.06	0.08	1.07
β	0.000 0	−0.000 3	0.000 1	0.000 0
Skaneateles parameters vs. model predictions				
P_{max}	16.20	8.05	7.87	24.20
α	0.09	0.03	0.33	0.11
β	0.000 3	0.000 2	−0.000 3	0.000 1

P^{B}_{max} (mgO$_2$ mg/chl-*a* per h), α^{B}, and β for July and August in Onondaga and Skaneateles cobble are means for eight and ten samples, respectively. Onondaga values are over-predicted in both months; Skaneateles values are under-predicted in July and over-predicted in August.

(Figure 4A). The only significant differences in chl-*a* with depth range for algal communities on sediment were in August. Chl-*a* in mg/m^2 was significantly higher from 50–100 cm than from $>$100 cm in August (Tukey's honestly significant differences (HSD) Test, $P < 0.008$). Therefore, in general, variance in mean chl-*a* (mg/m^2) differed more between months (June = 1 599, July = 3 407, August = 845) than depth ranges (0–25 cm = 3 939, 25–50 cm = 1 726, 50–100 cm = 1 694, $>$100 cm = 2 245).

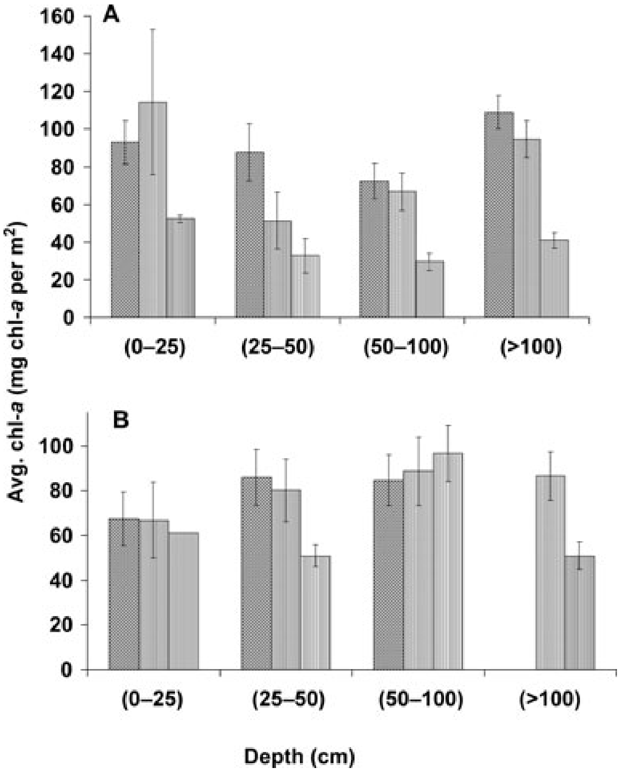

Figure 4. Mean chl-*a*/m^2 per month versus depth range.

(A) There were no significant differences in mean chl-*a* between depth ranges for hard substrate, though August values as a whole were significantly lower than the other two months (one-way ANOVA, $P < 0.000\,04$). **(B)** On sediment there were no significant differences between mean chl-*a* at different depth ranges in June or July. Values from 50–100 cm were significantly higher than those from $>$100 cm in August (Tukey's honestly significant difference (HSD) Test, $P < 0.008$).

Chl-*a* means for each month (June, diagonal stripes; July, dots; August, vertical stripes) separated by substrate.

To get some idea of benthic algal biomass and chlorophyll composition the distribution of chlorophylls b and c with depth and month were examined (Figure 5A,B). Benthic algal community structure has likely changed during the three-decade time period, because algae with different types of pigments will benefit from changing light levels (Wetzel 2001), however, historical data on benthic algal community structure is lacking in the Oneida Lake system. There was a difference between chl-*b* and *c* concentration in algae on different substrates, with significantly greater (chl-*b*) on cobble than sediment ($P < 0.000\,2$), and greater (though not significant) (chl-*c*) on sediment than on cobble. Similar to the trend of chl-*a*, chl-*b* and chl-*c* (mg/m^2) were significantly lower in August than June or July ($P < 0.001$ chl-*b*, $P < 0.000\,4$ chl-*c*) on both substrates. Chl-*b* and *c* varied between depths, but with no clear relationship to the depth gradient. When algae from different substrates were separated, there were no significant differences for chl-*b* and *c* with depth from sediment communities ($P < 0.32$, $P < 0.25$), but there were for cobble communities, making them more highly

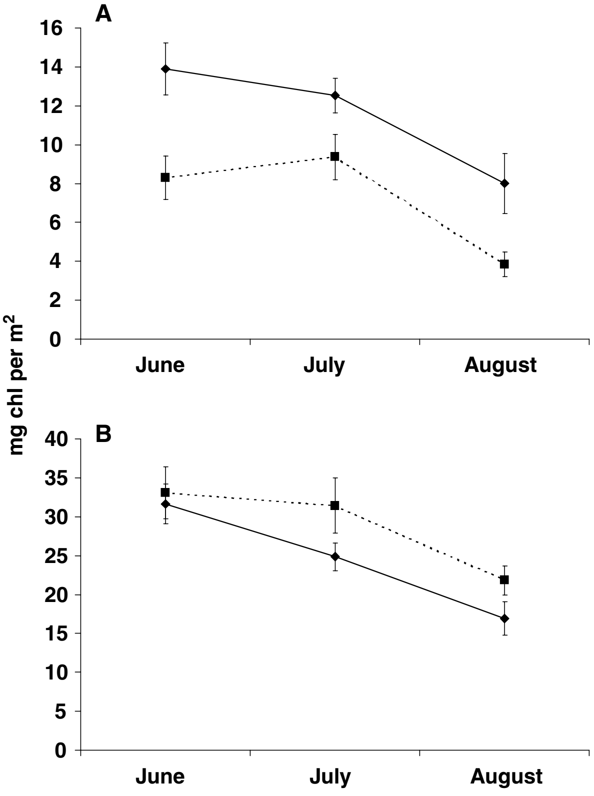

Figure 5. Mean chl-*b* and c for each month in mg/m^2.

Chl-*b* and c were significantly greater in June than in August in algae on cobble (solid line) than on sediment (dashed line) ($P < 0.027$ chl-*b*, 0.002 chl-*c*). There was also significantly less chl-*b* in algal communities in August than in June or July ($P < 0.017$, 0.005), and no significant differences between months in chl-*c* ($P < 0.057$).

variable in chl-*b* and chl-*c* with depth ($P < 0.001$, $P < 0.008$). Whereas these patterns in chlorophyllous pigments do not directly measure species composition, they demonstrate spatial variation in algal biomass, and algal communities that respond uniquely to different wavelengths of light.

Discussion

There is a striking lack of benthic algal primary production studies in freshwater published reports, perhaps leading to a biased perception that benthic production is not important in whole lake energy balance (Vadeboncouer et al. 2002; Vadeboncouer et al. 2003). Although pelagic production has been shown to dominate some freshwater systems, there are others that receive a substantial percentage of whole-lake primary production from benthic algae and macrophytes (Hecky and Hesslein 1995; Lassen et al. 1997), therefore, it is critical to understand the relative importance of the contribution of different primary producers and how these food sources are transferred to upper trophic levels. Further, a paucity of historical measurements of benthic production makes it difficult to evaluate responses of this important ecosystem parameter to environmental change.

In light of the recent widespread invasion of the zebra mussel and its associated increase in water clarity in freshwater systems, the relative contribution of benthic algal primary production to whole-lake primary production has increased relative to pelagic primary production. Our study of the response of epipelic and epilithic algal photosynthesis to zebra mussel introduction shows that a small but significant net increase in benthic production at the whole-lake scale does occur, and individual depth and substrate communities differ in the direction of their response.

Photosynthetic parameters

Mean monthly values of algal P^B_{max} on cobble (7.5–16.9 mg O_2 mg/chl-*a* per h) and sediment (6.6–10.4 mg O_2 mg/chl-*a* per h) fell into the range of previously reported benthic algal primary production values (Blanchard and Montagna 1992; Hecky and Hesslein 1995; Wetzel 2001; Vadeboncouer et al. 2002; Vadeboncouer et al. 2003). Mean P^B_{max} and α^B values from all samples were not significantly different between cobble or sediment algae, but a much larger area of the bottom in Oneida Lake within the photic zone is covered in sediment, making those algal communities greater contributors to whole-lake benthic algal primary production.

Maximum photosynthetic rates and photosynthetic efficiency were exhibited in August (Figure 4A,B), whereas mean chl-*a* showed an opposite trend on cobble, with significantly lower biomass in August (Figure 1D). Highest light attenuation also occurred in August from late summer phytoplankton blooms, and it follows that the observed increase in benthic primary production on cobble was due to a higher efficiency of the photosynthetic apparatus, rather than an increase in biomass. A significant incidence of photoinhibition ($\beta = 0.001$) occurred during the month of June (Figure 1C), when there are correspondingly high midday light levels and no phytoplankton shading. This is surprising because algae should be adapted to high light in June when the spring clear water phase consistently allows for great light penetration. However, it is possible that as the algal community on coble develops filamentous forms such as *Cladophora* spp. provide self-shading, which can reduce photoinhibition (Pillsbury and Lowe 1999). In June, when the filamentous canopy is not very tall, sensitive under-story taxa may respond negatively to high light. In contrast to patterns in cobble algal production, sediment algal communities had their highest maximum photosynthetic rates in July. Senescing macrophyte communities are present on soft sediment in August, contributing to lower light levels on that substrate, and therefore less primary production for the algal communities than in July.

Pre- and post- zebra mussel differences

Light is often considered the limiting factor to benthic photosynthetic rate in lakes. However, algae can respond negatively to high light levels (photoinhibition) and our estimates of benthic primary production in Oneida Lake clearly demonstrate that algae in shallow cobble areas are likely to show reduced production after zebra mussel introduction due to photoinhibition (Figure 1C). For example, algal communities on shallow cobble had significantly higher production before zebra mussels, despite an increase in surface area provided by the mussel shells themselves, whereas algae on shallow sediment had significantly higher production after zebra mussels. In contrast to what we saw in shallow areas, mean primary production values for deep samples in July were significantly greater after zebra mussel introduction on both substrates. This result is similar to that seen in Saginaw Bay when productivity rates measured at 5.5 m increased shortly after zebra mussel colonization (Lowe and Pillsbury 1995). With the onset of phytoplankton blooms in July–August, it is clear that zebra mussel filtering has enabled benthic photosynthesis to continue at higher rates later into the summer than may have previously occurred. Algal communities with varied nutrient availability and light environments had different responses to the overall increase in light penetration after zebra mussel introduction, but there was a net increase in epipelic and epilithic algal primary production at the whole-lake scale.

We estimate that whole-lake summer epipelic and epilithic primary production has significantly increased by 4% relative to the pre-zebra mussel period (Figure 3). This number is smaller than we expected and reflects the fact that our model predicts both increases and losses in primary production due to photoinhibition, which was not considered in previous studies (Lowe and Pillsbury 1995). The 4% increase may be of more local ecological importance in some areas of the lake than in others, based on the particular algal community present. The lack of past community structure data for benthic algae in Oneida Lake made it necessary to assume that algal community photosynthetic parameters have remained the same since 1975. Though benthic algal community structure has likely changed in Oneida Lake since 1975, *Cladophora* has likely contributed to benthic algal production throughout the period (Holeck et al. 1998). However, we have included measurements of photosynthetic parameters from communities spanning the range of depths and substrates in the lake, and therefore likely have represented a broad range of conditions in our productivity-irradiance relationship.

Idrisi et al. (2001) found no significant difference in aerial phytoplankton primary production before and after zebra mussels because a significant decrease in algal biomass was offset by an increase in both maximum photosynthetic rate and photosynthetic efficiency. It is probable that benthic algal photosynthetic maximum and efficiency likewise increased after 1992, as changes in both light and nutrient availability affect algal biomass and photosynthetic efficiency (α) per unit chlorophyll (Idrisi et al. 2001). Therefore, whole-lake benthic algal photosynthesis has probably increased more than our predicted 4% because our model did not include an increase in maximum photosynthetic rate and efficiency, thereby underestimating the increase estimated using constant measured parameters.

An unexpected and interesting finding was that trends of primary production on cobble, sediment, and both combined, have significantly less inter-annual variation after zebra mussel establishment (Figure 2A–C, $P = 0.04$). The trend was similar on both hard and soft substrate even though nutrient sources available to algal communities of these substrates differ, as does the interplay between nutrient and light benefits associated with zebra mussels. While algal communities on soft substrates have the advantage of access to sediment nutrients (Vadeboncoeur and Lodge 2000), communities on hard substrates may also benefit from the nutrient deposits collected in groups of zebra mussels. Past research on Oneida Lake has shown that light attenuation (k) has decreased significantly since zebra mussel invasion (Mayer et al. 2000, 2002; Idrisi et al. 2001), but monthly means have not been previously examined. When mean summer monthly k values were compared between June, July, and August, it was found that inter-annual variation of light attenuation in all three summer months (especially July) significantly decreased after zebra mussel establishment (Figure 2A). Whole-lake benthic production studies by Hakanson and Boulion (2004) have also found light availability to be a key factor, with the ratio of depth/Secchi depth at each site describing 75% of variability in benthic primary production between all 42 sampling sites in nine lakes. Considering how decreased inter-annual variation in light attenuation in Oneida Lake has directly affected patterns in inter-annual benthic algal photosynthesis, benthic primary production could be providing a more reliable food source for primary consumers since 1992.

Our light-driven model of benthic primary productivity, developed in a eutrophic lake, showed that light availability to the benthos is a driving influence on primary production, and provided good predictions of benthic primary productivity in an oligotrophic lake (Skaneateles). The Oneida model significantly overestimated benthic primary production in Onondaga Lake, even though Onondaga is more nutrient rich. The high density of small zebra mussels in Onondaga Lake may have contributed to the model's lack of predictive ability, even though total darkness respiration measurements that included total community (autotrophic and heterotrophic) respiration were factored into our model of gross primary production (GPP). Some of the cobble from Onondaga had negative net rates of photosynthesis because the respiration rate of the invertebrate communities (mostly zebra mussels) was high, creating a very high noise to signal ratio. Further, the presence of zebra mussel clusters may elevate the level of microbial activity (Lohner et al. 2007) thereby further enhancing heterotrophic respiration. The benthic communities from Oneida and Onondaga were both from cobble (inorganic substrate), and likely received a majority of their nutrients from the water column, but benthic algae in Onondaga have the potential advantage of higher nutrient levels surrounding the zebra mussel clusters that cover the cobble (Kahlert and Pettersson 2002), even though production may be lowered by the high levels of pollutants found in this lake.

In our study, the main goal of creating a primary production model based on light was to elucidate changes in annual summer benthic primary production after a system-wide disturbance by zebra mussel establishment. Our model suggests that whole-lake benthic algal primary production has indeed increased as predicted, but we are also able to suggest that photoinhibition caused by increased light levels may decrease primary production in some shallow algal communities. To our knowledge past studies have not found photoinhibition to be common in benthic algae, though few studies have specifically examined benthic photosynthetic responses to zebra mussel introduction and its associated dramatic increase in water clarity.

Based on the findings of this study and others (Strayer et al. 1999; Idrisi et al. 2001) it is obvious that the intense grazing activity of zebra mussels can indeed have system-wide effects on primary production. Considering the emerging patterns in altered benthic and pelagic community structures and food web links in recently invaded systems as well as those reported earlier in invaded European lakes (Karatayev et al. 2002), it is essential that researchers continue to examine the long-term direct and indirect effects of zebra mussels on the under-studied benthic regions of freshwater systems. Changes in benthic community structure and energy allocation due to zebra mussels' preferential colonization of hard substrates, negative effects on native mussels, and positive effects on smaller benthic invertebrate nutrient sources and habitat heterogeneity, will all contribute to altered food web links between pelagic and benthic regions. The full extent to which *Dreissena* will alter primary production and energy allocation to upper trophic levels is yet unknown. In Oneida Lake, the effect of zebra mussels on water clarity is known to be significant (Idrisi et al. 2001), making the zebra mussel-mediated increase in light availability to benthic primary producers a first step toward predicting long-term community and ecosystem structure effects.

Materials and Methods

Study site

Oneida Lake is a 207 km^2 shallow, mesotrophic lake northeast of Syracuse, NY. It has a maximum depth of 16 m and mean depth of 6.8 m (Idrisi et al. 2001), and is generally thermally well-mixed during the ice-free season. Phosphorus inputs from the surrounding watershed have dramatically decreased since 1988, and inter-annual water column TP fluctuations have decreased during this period as well. Zebra mussels were first identified in 1991 and by 1992 were firmly established, with maximum numbers of nearly 44 000 individuals/m^2; by 1993 mean density had dropped to under 20 000 ind./m^2, and biomass has remained relatively constant since then (Figure 6). Since the establishment of zebra mussels in Oneida Lake, phytoplankton biomass has significantly decreased, Secchi disk depth has significantly increased, and there has been an increase in clear-water days (Idrisi et al. 2001). Recent data have also shown the area of bottom receiving at least 1% of surface light has significantly increased from 90 km^2 to 111 km^2 since the establishment of zebra mussels (Zhu et al. 2006).

Field methods

Algae-covered cobble and sediment were collected from three transects, extending from 0.0–6.5 m in depth, along the southern shore of Oneida Lake in 2003 and 2004, with an additional site on the northern shore in 2004 (Figure 7). Samples were collected at random from each transect at least once per month from June to August with the aim of sampling a wide variety of benthic algal communities each month. Samples were collected between 09.00 and 13.00 hours, when incident light, and visibility, were at maximum. The number of samples collected each day varied with weather and time constraints, with at least five samples collected. Water temperature and depth were recorded at each sampling site using a 6 600 Yellow Springs Instruments (YSI) water probe and data-logger (Yellow Springs, OH, USA). A quantum spherical light sensor (Biospherical Inc. QSP 2 100, San Diego, CA, USA) was used to measure PAR levels above the water surface, just under the water surface and at the sample depth at each sampling site along a transect. A spherical sensor may overestimate the light available to benthic algae, as it measures down- and up-welling light; however, the spherical sensor was used so that our light measurements would be comparable to those in the Oneida Lake long-term dataset, which were used for backcasting purposes (see Primary production model, backcasting and validation section of Materials and Methods).

Cobble and/or sediment samples were taken at each sampling site and stored in fresh lake water in coolers. Cobble was collected using either snorkel or scuba with minimal disturbance to the algal film on the exposed cobble surface. Deep cobble was not collected in June due to the frequency of rainstorms. Shallow sediment cores were also collected by hand using 20 cm long, 17.6 diameter clear plexiglass tubes, pressed vertically into the sediment. Deeper cores were sampled using a gravity corer or collected by scuba divers. The top 8–10 cm of sediment was

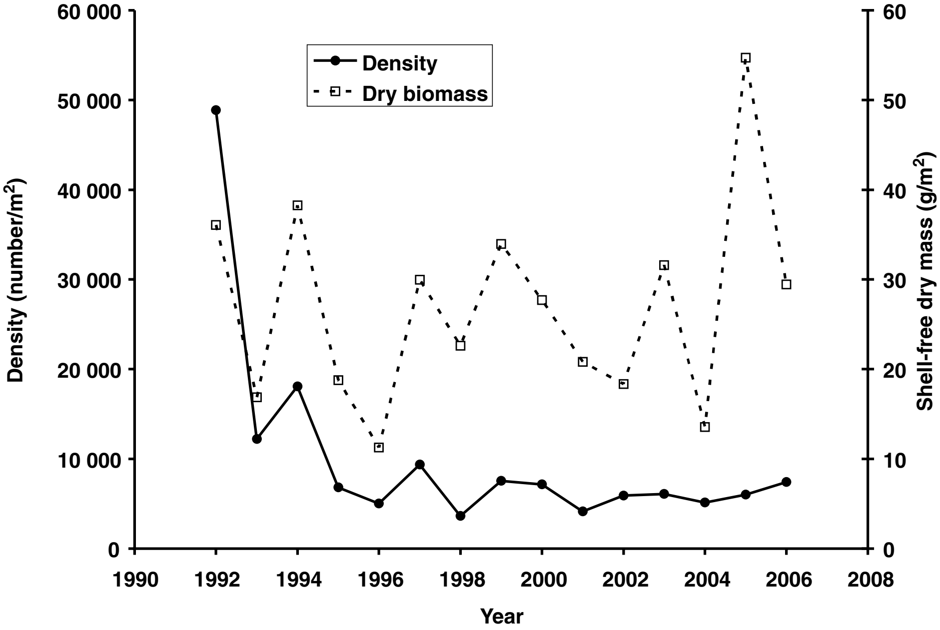

Figure 6. Annual estimates of lake-wide zebra mussel density (number/m^2) and dry biomass (grams/m^2) across all substrate types.

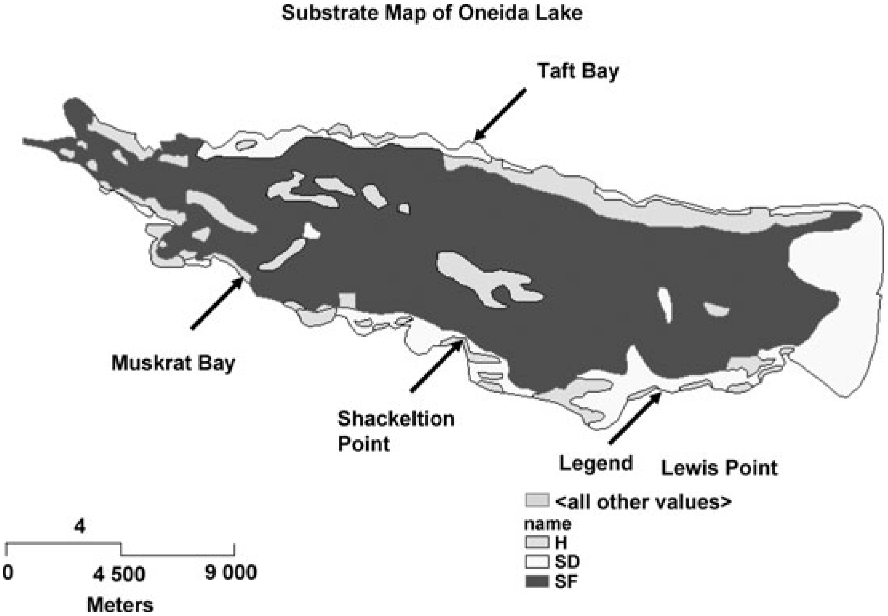

Figure 7. Schematic of Oneida Lake, New York showing substrate type and area coverage.

White areas indicate sandy substrate (SD), light gray areas are hard substrate (HD), and dark gray areas are soft substrate (SF), mostly organic mud. Arrows indicate the sites used for benthic algal sampling in 2003 and 2004.

extruded from the cores into shorter photosynthesis chambers of the same circumference. All cores were placed in coolers containing fresh lake water before being transported back to the lab.

Photosynthesis chambers

All samples (still in their coolers) were placed in a temperature/light-regulated environmental chamber in the laboratory on the day of collection. Environmental settings were adjusted for each set of samples to match current midday lake temperature (°C), with a decrease in night-time temperature and a 12:12 photoperiod that mimicked the conditions of the lake overnight.

Photosynthetic measurements were made the morning following sample collection. Cobble samples (still containing any attached zebra mussels) were placed in individual transparent (30 cm diameter) clear plexiglass cylinders (photosynthesis chambers), and the lids were sealed with a layer of petroleum jelly to prevent air leaks. Sediment samples were kept in the chambers in which they were collected. Fluorescent and incandescent light banks produced an incident water surface light intensity of approximately 1 000 μmol/m^2 per s. Eight different light levels (0–1 000 μmol/m^2 per s) were created using two to 14 layers of neutral density shade cloth. PAR was measured within the environmental chamber throughout the study with a spherical light sensor to ensure that the highest light intensity did not change more than 30 μmol/m^2 per s.

Photosynthetic rate was measured as the change in dissolved oxygen (mg O_2/L), using YSI 5 300A biological oxygen probes that fit snugly into the photosynthesis chamber lids. Oxygen measurements were taken for approximately 2 h in total darkness (respiration), at full light (1 000 μmol/m^2 per s) and at seven decreasing light levels (410, 200, 145, 100, 85, 70, 60 μmol/m^2 per s). Preliminary trials suggested that the order of light intensities (increasing or decreasing) did not affect the production-irradiance relationship. Further, measuring primary production across decreasing light intensities prevented the need for time allotment for the photosynthetic apparatus to adjust to increasing PAR. In general, measuring production-irradiance relationships can be done in either decreasing or increasing order depending on taxon-specific responses (Walker 1987). We used a short incubation period (1–3 h) consistent with previous photosynthesis studies (Blanchard and Montagna 1992; Macedo et al. 1998; Vadeboncoeur and Lodge 2000). Oxygen (O_2) evolution or consumption rates were calculated by the difference between readings at 2-min intervals and the means were taken for each light level.

During measurement of photosynthesis, all samples were kept at constant temperature within water baths. Sample water temperature was recorded after incubation and varied $\leq$ 1 °C. Water within each photosynthesis chamber was also continuously stirred, either from below by stir bar (cobble) or from above with upright stir sticks (sediment), in order to keep O_2 concentrations near the probes from depleting. In order to isolate O_2 evolution of the benthic samples from the small amount produced by phytoplankton in their surrounding lake water, we periodically measured O_2 evolution from fresh lake water alone, in order to subtract a standard amount of phytoplankton photosynthesis from our incubation chamber readings. A mean phytoplankton primary production rate was calculated for each month and subtracted from the whole-chamber measurements in order to examine benthic primary production rates exclusively.

Chlorophyll

Chlorophyll concentrations were assayed from algal material on both the sediment and cobble surfaces. On cobble a 6.25 cm^2 area of the exposed surface was scraped, brushed and rinsed to remove all algae. Cobble surface area was estimated in 2003 by tracing cobble onto graph paper, whereas it was estimated in 2004 by covering only algae-covered surface with aluminum foil and weighing the foil to determine area in cm^2 (Lowe and Pillsbury 1995). For sediment cores, the first 2 cm of sediment (Vadeboncoeur and Lodge 1998) were retained from each sample. All samples were frozen prior to analysis.

Chlorophyll samples were filtered using GF/F glass fiber Whatman filters (Springfield Mill, UK). Chlorophyll was extracted in 10 mL dimethyl sulfoxide (DMSO) at 60 °C for 2 h (adapted from Speziale et al. 1984), then centrifuged. Absorbances for chl-*a* (2003, 2004) and chl-*b*, and *c* (2004) absorbance were read on a Beckman spectrophotometer (Model DU 640C, Fullerton, CA, USA). Chl-*a* (2003 and 2004) and chl-*b* and *c* (2004 only) were estimated according to Strickland and Parsons (1965).

Photosynthetic parameters

Oxygen evolution rates (mg O_2 mg/chl-*a* per h) for all 171 cobble and sediment samples were standardized to [chl-*a*]. Biomass per unit area of different algal communities varied substantially, so standardization to chl-*a,* as an index for biomass, (rather than area) was a more representative measure of primary production in different communities. Respiration rates measured in total darkness were assumed to be constant for the incubation period (Bott et al. 1997; Macedo et al. 1998), and were added back into production rates to yield estimates of GPP. The data (mg O_2 mg/chl-*a* per h) were fit to the photosynthesis equation of Jassby and Platt (1976) modified with a photoinhibition parameter (see Litchman et al. 2003). This equation was used to find the photosynthetic parameters and create the primary production model. The equation is based on the hyperbolic tangent function and includes parameters for photosynthetic efficiency (α^B), maximum production rate (P^B_{max}), and photoinhibition (β), with (I) representing incident light; $P = P^B_{max} \tanh(\alpha^B I / P^B_{max})(1/(1 + \beta I))$.

Production estimation

For each field season (2003 and 2004), all benthic samples were divided into four depth ranges (0–25 cm, 25–50 cm, 50–100 cm, and >100 cm) and two substrate categories (soft and hard), for a total of eight categories of algal communities (Table 1). Actual photosynthetic measurements for the fourth depth range included values primarily close to 1 m, but also including some up to 2 m. Our intent here was to get a representative sample of algal communities at different depths (and therefore different light environments) for between-year primary production comparisons. The three photosynthetic parameters (P_{max}, α^B, β) from all samples were used to calculate the mean in each algal category, resulting in eight sets of mean parameters. As explained below, these parameters were then used with light data to estimate whole-lake epipelic and epilithic algal primary production for summers 1975–2004.

Cobble and sediment samples were separated in the production estimates because algal species composition has been found to be more similar on the same substrate due to similar nutrient sources (Stevenson et al. 1985; Vadeboncouer et al. 2001). Light attenuation data from the Cornell Biological Field Station long-term dataset June–August 2003 and 2004 (taken with a spherical LiCor sensor) were used to obtain mean light attenuation coefficients for June, and July, while weekly values were calculated for August, because light attenuation varied significantly between weeks in August in 2003 and 2004 (one-way ANOVA, $P < 0.005$). Two assumptions of the model were: (i) mean monthly/weekly (August) light attenuation coefficients sufficiently described the summer light environment in Oneida Lake; and (ii) the production–light relationship is similar before and after zebra mussel introduction, though benthic algal community composition may have changed over time. While photosynthetic parameters of individual algal communities may change with alterations in taxonomic composition and other environmental conditions, our measurements of production were taken in two separate years, and from a variety of depths and microhabitats and therefore likely represent a substantial portion of the range of possible production–light relationships. Further, since the changes in water clarity and hence light intensity that occurred after *Dreissena* introduction was large and significant (Mayer et al. 2000; Idrisi et al. 2001; Mayer et al. 2002) it is likely that the effect of increased light is large relative to possible variability in the production–light relationships that is not captured by our sampling.

Mean attenuation coefficients were used to adjust surface PAR values to the light environments of each depth/substrate category for each month. Surface PAR values were estimated in half-hour intervals based on latitude, longitude, and mean cloud conditions using Fitsolar, which is part of a computer package developed by Fee (1998). The three parameters (α^B, P^B_{max}, β) estimated for all of the samples were used to calculate the mean in eight algal categories in June, July, and August (Blanchard and Montagna 1992) and combined with the Fitsolar light values. This information was used to estimate benthic algal photosynthesis in a manner similar to Fee's (1998) approach to measuring whole lake phytoplankton photosynthesis.

Whole-lake production values were converted from mg O_2 to mg C using a photosynthetic quotient of 1.2 (Macedo et al. 1998). Daily production estimates for each depth/substrate category were subsequently multiplied by the area of the lake that contains each particular depth range and substrate (i.e., shallow cobble). As the available bathymetric map of Oneida did not have as fine a resolution as was used in our sampling methods, photosynthetic parameters from the shallowest depth ranges (0–100 cm) were combined to predict mean production on all areas 0–1 m deep in the lake. Likewise, parameters for all areas $>$100 cm for each substrate were used to predict production on all areas 1.0–7.5 m deep in the lake. Although the fine scale resolution of our sampling is lost by this approach, the fact that we systematically sampled different depths in both the $<$1 m and $>$1 m ranges ensured that we represented the range of production-irradiance relationships found in these depth zones. 7.5 m was selected as an average photosynthetic cut-off point in the lake, where midday bottom light levels were from 40–50 μmol/m^2 per s (compensation point) during the summer. At depths greater than 7.5 m we assumed there was no net primary production. Similar compensation points were found in Graham et al. (1982) for *Cladophora* communities. Due to the lack of deep cobble data in June but available data for July, the relationship between June and July data on sediment was used to estimate primary production for deep June cobble samples.

Primary production model, backcasting and validation

Secchi data from 1975–2002 were converted to attenuation coefficients using the relationship between Secchi disk depth and light attenuation for the period 1993–2000, $\log_{10}\text{Secchi} = -0.5203 \times \log_{10}k + 0.0487$ ($R^2 = 0.64$). Mean attenuation was calculated for June, July, and August. For each year these mean monthly attenuation coefficients and the Fitsolar-generated incident light data were used to calculate light availability to the benthos for the eight categories of algal communities. Production estimates were calculated for each summer, as described earlier, using the mean photosynthetic parameters calculated from 80% of the 2003 and 2004 combined data. Twenty percent of the data were withheld for model validation.

In order to validate the model's predictions, the technique of cross-validation was used (Snee 1977; Zhang 1997). In cross-validation all data from the years sampled are combined, with a large percentage used to make the model, and a small percentage used to test the model (Snee 1977; Zhang 1997). The mean photosynthetic parameters calculated from 80% (randomly selected) of the combined 2003 and 2004 samples were used to make the production model, and then used to predict the actual mg O_2 mg/chl-*a* per h readings that were measured in the lab for the remaining 20% of the 2003 and 2004 samples. Differences between expected and observed production values were used as a measure of prediction error, to calculate the mean coefficient of variation for the model's prediction of each depth/substrate category. In addition, the entire set of predicted and observed production values for all depth/substrate categories were compared with a *t*-test to look for an overall significant difference between predicted and actual production values for the whole-lake estimate. Whole-lake production estimates presented in this paper are based on the final production model and are based on all depth/substrate data.

Light model in other systems

The light model developed for Oneida Lake was also used to predict benthic primary production in a hypereutrophic (Onondaga) and an oligotrophic (Skaneateles) lake, and then compared to measured samples in order to determine if the light-based Oneida Lake model could be applied to lakes of different trophic status. Benthic algal samples on cobble (4–5 per month) were collected from Onondaga and Skaneateles in July and August of 2004 in the manner previously described. Onondaga Lake is a hypereutrophic, light-limited lake, whereas Skaneateles Lake is a naturally clear oligotrophic lake. Both Onondaga and Skaneateles lakes have established populations of zebra mussels.

Statistical analysis

All analyses were completed in Statsoft *Statistica* (1998), including ANOVAs, t-tests, curve-fitting, and variance estimates for model validation. All analyses were considered significant at $P < 0.5$.

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