Nutrient limitation of benthic algae in Lake Baikal, Russia

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Abstract: Lake Baikal, one of the world's largest and most biologically diverse lakes, has recently begun to experience uncharacteristic nuisance blooms of filamentous benthic algae. To contribute to understanding the causes of these blooms, we deployed nutrient-diffusing substrata (NDS) at 10 sites varying in shoreline land use in the southwestern portion of the lake. Our objectives were to assess the nature of nutrient limitation of benthic algae in Lake Baikal, the relationship between land use and limitation status, and the effect of enrichment on algal community composition. Algal biomass measured as chlorophyll *a* (Chl *a*) responded strongly to nutrient enrichment and showed serial limitation by N and P at all sites. Chl *a* levels were ~2 and 4× higher on N- and N+P-amended NDS, respectively, than on unenriched controls. Periphyton biomass varied significantly among sites, but differences in periphyton biomass and nutrient limitation status were not related to shoreline land use. The taxonomic composition of periphyton varied significantly among landuse categories, nutrient treatments, and sites. The filamentous green alga *Stigeoclonium tenue*, which has been associated with recently observed nuisance blooms in Lake Baikal, tended to be most abundant on N- and N+P-amended NDS. The results of our study demonstrate strong nutrient limitation of the periphyton in Lake Baikal and highlight the potential value of improved nutrient controls for addressing benthic algal blooms in the lake.

Key words: periphyton, eutrophication, nutrient limitation, Lake Baikal, benthic algae, nutrient diffusing substrata

Eutrophication, caused by excessive inputs of P and N, is a threat to freshwater ecosystems worldwide (Smith et al. 1999, Jenny et al. 2016). A common symptom of eutrophication in rivers and lakes is benthic algal blooms, which can cause undesirable changes to ecosystem function and services, including loss of biodiversity, hypoxia, and degradation of water quality (Smith et al. 1999, Jenny et al. 2016). In lakes, benthic algae can proliferate at nuisance levels in the nearshore even in the absence of noticeable eutrophic conditions offshore. For example, severe blooms of *Cladophora glomerata* are common in Lakes Ontario and Michigan, whereas nutrient and phytoplankton levels in the offshore indicate oligotrophy (Hecky et al. 2004, Higgins et al. 2008, Bootsma et al. 2015). Localized benthic algal blooms have been observed in deep oligotrophic lakes of the Pacific Northwest (Rosenberger et al. 2008, Hampton et al. 2011) and in oligotrophic Lake Ohrid (Schneider et al. 2014). Some authors have suggested that in lakes, benthic algal blooms may be an early-warning indicator of eutrophication, appearing before noticeable increases of nutrient and phytoplankton concentrations in the pelagic zone (Lambert et al. 2008, Rosenberger et al. 2008, Hampton et al. 2011).

Mitigating the effects of eutrophication requires understating the nature of nutrient limitation in the system (e.g., which nutrient is limiting) and the relationship between environmental conditions (e.g., land use) and algal production (Smith et al. 1999, Dodds et al. 2002, Bootsma et al. 2015). Much work has been done to understand nutrient limitation and its correlates for phytoplankton in lakes and for benthic algae in streams (Pringle 1990, Guildford and Hecky 2000, Francoeur 2001, Dodds et al. 2002, Harpole et al. 2011, Price and Carrick 2014), but less is known about nutrient limitation of lake benthic algae. Studies of periphyton nutrient limitation in large lakes and of spatial patterns in algal

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nutrient status in relation to land use are especially scarce (but see Carrick and Lowe 1988, Kahlert et al. 2002, Houben 2008, Rosenberger et al. 2008).

Recently, uncharacteristic blooms of green filamentous benthic algae (*Spirogyra* spp., *Stigeoclonium tenue*, and *Ulothrix* spp.) have been observed in the nearshore of Russia's oligotrophic Lake Baikal (Kravtsova et al. 2014, Timoshkin et al. 2014, Volkova et al. 2018). Lake Baikal is the deepest, most voluminous, oldest, and most biologically diverse lake in the world (Kozhov 1963, Timoshkin 1995, Moore et al. 2009). The littoral zone of Lake Baikal supports benthic communities characterized by unusually high endemic diversity and includes hundreds of species of benthic algae, sponges, crustaceans, gastropods, worms, insects, and fish (Kozhov 1963, Timoshkin 1995). Benthic algal blooms were first recorded in 2008 in the town of Listvyanka, a major tourist destination on Baikal's western shore, but since then have been observed in many other locations along developed and undeveloped shorelines (Kravtsova et al. 2014, Timoshkin et al. 2014, 2016, Volkova et al. 2018). How these blooms affect the unique littoral benthos of Lake Baikal is still uncertain, but recent studies suggest strong negative consequences for fish, sponges, and other macroinvertebrates in areas affected by the blooms (Khanaev et al. 2016, Timoshkin et al. 2016, N. A. Rozhkova, Limnological Institute, SB RAS, Irkutsk).

Evidence points to nutrient inputs from leaky septic systems and severely outdated sewage treatment facilities as the cause of these emerging blooms, but significant disagreement exists about the causes and spatial extent of these blooms in Russia (e.g., Denikina et al. 2016, Grachev 2017, Timoshkin et al. 2018). The severity of the problem and confusion over its causes highlight the importance of understanding the ecology of these blooms, their spatial extent, and relationship to shoreline land use. To achieve some of these objectives, we deployed nutrient-diffusing substrata (NDS) experiments at 10 sites in the nearshore of Lake Baikal, across a landuse gradient. We tested 3 specific hypotheses: 1) The periphyton in Lake Baikal will be colimited by N and P because of the relatively low N : P ratio in Lake Baikal water (average molar ratio = 23; O'Donnell et al. 2017). 2) Nutrient limitation will be less severe along developed than undeveloped shorelines because of higher nutrient availability associated with human habitation. 3) Benthic algal communities will differ between developed and undeveloped shorelines and with nutrient enrichment treatment.

METHODS

Study site

We worked along a ~20-km portion of the southwestern shoreline of Lake Baikal. We chose this study area because it includes undeveloped stretches of shoreline as well as some of the more densely populated parts of the lake's shore. We deployed NDS blocks at 10 nearshore sites (Table 1, Fig. 1A–C). Sites 1–4 were in Listvyanka, a town with a permanent population of ~2000 residents and major tourist destination on the lake (~300,000 visitors in 2014); sites 5–8 were along relatively undeveloped portions of the shoreline (forested, with a hiking trail running along the shore); and sites 9 and 10 were in Bol'shie Koty, a medium-sized village (~150 permanent residents) that experiences moderate tourist traffic in summer and has a handful of hotels and a biological field station (best available estimate of annual tourist traffic is between 5000 and 15,000 visitors). Most households and hotels in Listvyanka and Bol'shie Koty rely on unsealed (infiltration-based) septic systems that leach nutrients and contribute to localized bacterial pollution of

Table 1. Characteristics of sites at which nutrient-diffusing substrates (NDS) were deployed. * indicates site with detailed algal taxonomic analysis. NH_4^+ concentrations were measured only during NDS deployment in August. PO_4^{3-} and $NO_3^- + NO_2^-$ concentrations were measured during deployment and retrieval, and the average of both measurements is reported. CFU = colony forming unit.

Site	Coordinates (lat, long)	Shoreline land use	NDS depth (m)	PO_4^{3-} (μg/L)	NO_3^- + NO_2^- (mg/L)	NH_4^+ (mg/L)	Enterococci (CFU/100 mL)	*Escherichia coli* (CFU/100 mL)
1	51°50.841, 104°52.252	Developed (town)	3.2	6	0.06	0.02	6	26
2*	51°50.997, 104°52.092	Developed (town)	3	5	0.05	0.02	2	813
3	51°52.083, 104°49.770	Developed (town)	3	5	0.05	0.02	0	288
4	51°50.711, 104°52.500	Developed (town)	2.5	6	0.06	0.10	1	8
5	51°50.784, 104°54.008	Undeveloped (forested)	2.8	6	0.06	0.02	2	0
6*	51°51.522, 104°56.306	Undeveloped (forested)	2.8	7	0.06	0.03	0	161
7	51°53.292, 105°02.316	Undeveloped (forested)	2.8	11	0.10	0.02	0	0
8*	51°54.142, 105°06.220	Undeveloped (forested)	3	7	0.07	0.27	0	0
9*	51°54.154, 105°04.125	Developed (village)	3	6	0.05	0.02	252	1000
10	51°53.966, 105°03.849	Developed (village)	3	6	0.05	0.01	0	0

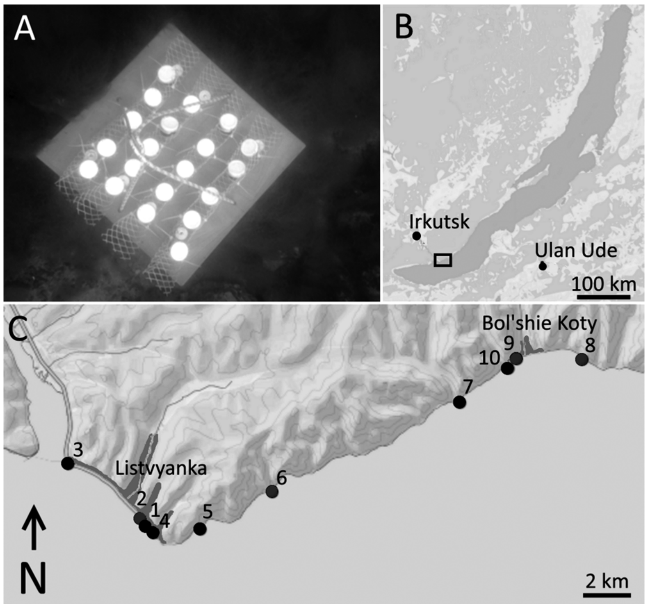

Figure 1. A.—Nutrient-diffusing substrate (NDS) tile deployed in Lake Baikal. B.—Map of Lake Baikal showing location of NDS experiment deployment (black square). C.—Map of experiment deployment area. Numbers represent station names, and 2, 6, 8, and 9 were stations where taxonomic analysis was performed on benthic algae.

the ground- and stream water (Kravtsova et al. 2014, Timoshkin et al. 2018).

NDS construction and deployment

NDS treatment blocks consisted of a concrete tile (50 × 50 cm) to which plastic NDS cups were attached. We attached cups with zip-ties and electrical tape to plastic netting, which we fastened to the concrete block with metal screws and washers so that NDS cups would face upward (Fig. 1A). To construct NDS cups, we filled 30-mL polypropylene jars brim-full with a solution of high-purity Noble agar (A5431; Sigma–Aldrich, St Louis, Missouri) and different combinations of nutrients. Control cups received only a 2% agar solution, whereas P-, N-, and N+P-amended (hereafter +P, +N, and +NP, respectively) cups were filled with a 2% agar solution with 0.5 M KH_2PO_4, 0.5 M NH_4Cl, or both, respectively (Tank et al. 2006). Each NDS cup was capped with a ~1.6-mm thick, 38-mm diameter, porous plastic (10-μm pore size) disk cut to size from a larger sheet (GenPore, Reading, Pennsylvania). The porous plastic disks served as the nutrient diffusion and periphyton growth surface. The porous plastic is made from low-reactivity, ultra-high-molecular-weight polyethylene and is designed to provide consistent filtration and diffusion of fluids. Plastic disks were soaked in deionized water for 24 h before use to preleach water-soluble materials that may have been left after the manufacturing process. Polyethylene is frequently used as a standardized periphyton growth surface (e.g., Bécares et al. 2008), and we used it here in the same way (rather than as an imitation of a natural inorganic substrate). We reasoned that periphyton abundance and community composition might differ between natural substrata and the plastic disks, but the disks would enable comparisons of biomass and community response among sites and nutrient treatments. The porous plastic was held in place by the jar lid into which a 35-mm hole was cut (Fig. S1). We attached 20 NDS cups to each tile (5 replicates each for control, +P, +N, +NP treatments).

We deployed 1 NDS treatment block at each site on 14 August 2015 and retrieved them 32 to 33 d later on 15–16 September. During NDS deployment and retrieval, we collected water samples ~0.5 m above the lake bottom and analyzed them for PO_4^{3-} and $NO_3^-+NO_2^-$ concentrations. We measured NH_4^+ concentrations only for the deployment date. We also collected samples for microbiological characterization of the near-bottom water at the time of deployment. We did not measure water clarity, but it was consistently high during deployment and retrieval. Tiles at all sites were visible from the surface at their deployment depths of ~3 m.

Sample processing and analyses

Immediately after retrieval, we detached NDS cups from the concrete tiles and photographed them. We removed the porous plastic disks from NDS cups and bisected them with scissors along the midline into 2 equal halves. We further cut 1 half into 2 quarters. We used 1 half of each plastic disk for chlorophyll (Chl *a*) extraction and 1 quarter of each disk for taxonomic analysis. We attempted to use the remaining quarter to measure algal dry mass, but the precision of the balance available to us at the field station was too low to do so. We wrapped the half disk to be used for Chl *a* analysis in aluminum foil and froze it. Algae for taxonomic analysis were scraped off the ¼ disk with a scalpel into a vial and preserved with Lugol's solution at a concentration sufficient to turn the liquid light brown.

For Chl *a* analysis, we thawed the ½ disks in the dark, removed the algae by scraping, and manually ground the disks and algae in porcelain mortars with 90% acetone containing 1% $MgCO_3$. We allowed disks and algae to soak in the acetone for 30 min in the dark, poured the acetone into a centrifuge tube, and repeated the extraction process once more with fresh acetone. We combined both portions of the acetone for analysis, centrifuging the extract for 20 min at 4000 to 5000*g* before analysis. We measured Chl *a* concentrations spectrophotometrically at 630, 647, 664, and 750 nm, accordingly to commonly used protocols. We report nonphaeopigment-corrected (Stich and Brinker 2005) Chl *a* concentrations as μg Chl a/cm^2 of disk surface area.

Because of time and cost limitations, taxonomic analysis of algae was performed on samples from 4 of the 10 sites

(Fig. 1C): sites 2 and 9 near settlements, and sites 6 and 8 along relatively undeveloped coastlines. Small cells (volume $< 1000\ \mu m^3$) were double-counted in a 0.1-mL Nageotte chamber using a Peraval light microscope (Carl–Zeiss, Oberkochen, Germany) under 720 to 1200× magnification. We counted large cells (volume $> 1000\ \mu m^3$) in the whole sample under 400 to 1000× magnification with the aid of CX 21 (Olympus, Tokyo, Japan) light microscopes. We estimated algal biovolume based on cell volume measurements and count data. We estimated cell volume based on average cell dimension measurements and geometric shapes corresponding most closely to those of algal cells (e.g., a cylinder for filamentous algae). Algae were identified using keys by Gleser et al. (1988), Tsarenko (1990), and Izhboldina (2007). We expressed cell numbers and biovolumes per cm^2 of disk surface area. Chl *a* and taxonomic data are accessible online through the Environmental Data Initiative (Ozersky et al. 2018).

For P and N chemical analysis, we filtered water samples through 0.45-μm membrane filters. We measured PO_4^{3-} spectrophotometrically using the ammonium molybdate method (Wetzel and Likens 2000), NO_3^- by high-performance liquid chromatography (HPLC; Baram et al. 1999), and NO_2^- and NH_4^+ spectrophotometrically with the Griess (pink azo dye) and indophenol blue methods, respectively (Wetzel and Likens 2000). We quantified thermotolerant *Escherichia coli* by filtration and sample concentration using selective HiCrome agar (No. M1571; Himedia, Mumbai, India). We quantified fecal enterococci by membrane filtration and sample concentration with Slanetz and Bartley medium (No. M 612, Himedia) and bile esculine azide agar (No. M493, Himedia). We identified bacterial colonies according to Gerhardt et al. (1981) and Holt et al. (1994).

Statistical methods

We conducted all statistical analyses in the R statistical computing environment (version 3.2.5; R Project for Statistical Computing, Vienna, Austria). We used mixed-effects analysis of variance (ANOVA) models in the *lme4* package (Bates et al. 2015) to examine the effects of nutrient treatment (control, +P, +N, +NP) and shoreline landuse category (developed, undeveloped) on benthic algal development. Nutrient treatment and land use were fixed factors and site identity was a random factor nested within landuse category. We fitted 3 models: 1) with Chl *a* (across all 10 sites), 2) cell abundance and 3) cell biovolume (across the 4 sites for which detailed taxonomic analysis was performed) as the response variables. Quantile plots revealed that all response data were log-normally distributed, so data were log(x)-transformed prior to analysis. We used the *lmerTest* package to generate *F*- and *p*-values and denominator degrees of freedom for the mixed-effects models based on the Satterthwaite approximation (Kuznetsova et al. 2017) and the *RLRsim* package (Scheipl et al. 2008) to assess whether the variance added by the random factor (site) was significantly different from 0. The *lsmeans* package (Lenth 2016) was used to perform post hoc Tukey tests.

We used nonmetric multidimensional scaling (NMDS) on Bray–Curtis dissimilarities of $\sqrt[4]{x}$-transformed cell counts and biovolumes (Clarke and Warwick 2001) to visualize differences in algal taxonomic composition among treatments, landuse categories, and sites. We used blocked permutational analysis of variance (PERMANOVA; Anderson 2001) to assess whether taxonomic composition of benthic algal communities (in terms of abundance and biovolume) varied with land use, nutrient treatment, and their interaction. Land use and nutrient treatment were parameterized as fixed factors and site was used as a blocking (random) variable. Species abundance was $\sqrt[4]{x}$-transformed prior to analysis to help satisfy the assumption of equality of multivariate dispersion and to reduce influence of most abundant species. Species biovolumes were not transformed because transformation increased multivariate dispersion. However, the overall results for both analyses were qualitatively the same regardless of whether data were transformed. We used similarity of percentages (SIMPER; Clarke and Warwick 2001) analysis on $\sqrt[4]{x}$-transformed densities and biovolumes to identify the taxa that contributed most to community dissimilarity between landuse categories and among treatments within each site for which taxonomic analysis was performed. We did not include rare taxa (those appearing in <10% of samples) and those known to be mainly planktonic (e.g., *Asterionella* sp.) in multivariate analyses. The *vegan* package was used for all multivariate analyses (Oksanen et al. 2013).

RESULTS

Periphyton biomass

Benthic Chl *a* ranged from 0.36 to 12.4 $\mu g/cm^2$, averaging 2.67 $\mu g/cm^2$ across all replicates (Fig. 2A). Abundance of algae on NDS disks ranged much more widely than Chl *a*, from 3020 to 1,392,000 cells/cm^2, averaging 174,400 cells/cm^2 (Fig. 2B). Algal biovolume was less variable than cell densities but more variable than Chl *a*, ranging from 0.052 to 3.97 mm^3/cm^2, with an average of 0.49 mm^3/cm^2 (Fig. 2C). Chl *a*, algal cell densities, and biovolumes varied significantly among nutrient treatments, but not landuse categories (Fig. 2A–C; Table 2). No significant landuse × treatment interaction was detected for any algal biomass variable. This result suggests consistent effects of nutrient enrichment along developed and undeveloped shorelines (Table 2). Chl *a* and cell densities differed among sites (both $p < 0.001$), but biovolumes did not ($p = 0.12$). Tukey post hoc tests showed significant differences in Chl *a* levels between all treatment pairs, with lowest Chl *a* levels on +P substrata (0.83 ± 0.44 [SD] $\mu g/cm^2$) and highest on +NP substrata (5.75 ± 2.33 $\mu g/cm^2$). For cell densities, significant ($p < 0.05$) differences were only seen for contrasts

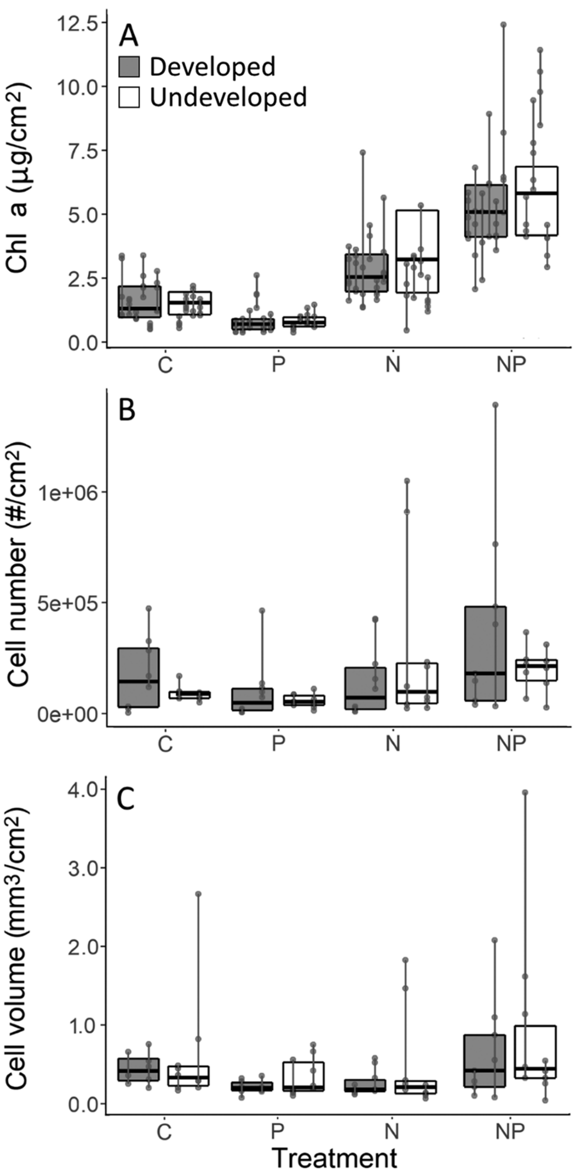

Figure 2. Box-and-whisker plots for chlorophyll *a* (Chl *a*) concentrations (A), total cell densities (B), and algal biovolumes (C) in different nutrient-diffusing substrate treatments at sites along developed and undeveloped shorelines. Lines in boxes are medians, box ends are quartiles, and points represent individual observations. Points connected by vertical lines show site-specific values, arranged by ascending site number from left to right within each box.

between control vs +NP and +P vs +NP treatments. Contrasts between +N vs +P and +N vs +NP had associated *p*-values of 0.051 and 0.07, respectively. Cell biovolume did not differ significantly among treatments at the $\alpha = 0.05$ level, but +P vs +NP and +N vs +NP contrasts had *p*-values of 0.057 and 0.082, respectively. At the 4 sites where Chl *a*, cell density, and cell biovolume were measured on the same NDS cups, the 3 indicators of algal abundance were significantly but weakly correlated (Fig. S2).

Periphyton communities

PERMANOVA showed significant differences in algal community composition (as cell densities) between landuse categories ($F_{1,69} = 40.2$, $p \leq 0.005$) and treatments ($F_{3,69} = 5.00$, $p \leq 0.005$) with a significant interaction between the 2 ($F_{3,\ 69} = 3.42$, $p \leq 0.005$). Community composition expressed as biovolume also differed between landuse categories ($F_{1,69} = 5.20$, $p \leq 0.005$) and among treatments ($F_{3,69} = 2.26$, $p \leq 0.005$), but with no significant interaction between them ($F_{3,69} = 1.28$, $p = 0.055$). NMDS plots agreed with the results of PERMANOVA and showed differences in community composition between landuse categories, among treatments, and among sites (Fig. 3A, B). Differences among sites and landuse categories appeared to be larger and more consistent for cell-density than cell-biovolume data. Based on cell densities, algal communities appeared to be more similar between control and +P treatments and +N and +NP treatments than other combinations (Fig. 3A). These differences were not as pronounced for the biovolume data (Fig. 3B). A few taxa contributed strongly to dissimilarities among landuse categories and treatments in terms of cell densities and biovolumes (SIMPER; Fig. 4A, B, Table S1). The most abundant groups (*S. tenue*, *Tetrasporopsis* spp., *Monoraphidium* spp., *Oedogonium* sp., *Ulothrix* spp., and *Spirogyra* spp.) were most important. Differences among treatments were site-specific, with different groups contributing to dissimilarities among treatments (see also the NMDS plot; Fig. 3A, B).

DISCUSSION

Periphyton biomass

Benthic Chl *a* levels varied among sites, but a consistent, nonadditive pattern of benthic Chl *a* response to nutrient amendment was observed across all 10 sites. P addition alone

Table 2. Results of mixed-effect analysis of variance (ANOVA) tests on effects of nutrient treatment, land use, and their interaction on chlorophyll *a* (Chl *a*), cell number, and cell biovolumes on nutrient-diffusing substrates (NDS). *F*-values, *p*-values, and denominator degrees of freedom are based on the Satterthwaite approximation.

Variable	Factor	df	*F*	*p*
Chl *a* (μg/cm^2)	Treatment	3,177	285.3	<0.0001
	Land use	1,9.9	0.013	0.912
	Interaction	3,177	2.57	0.056
Cell density (no./cm^2)	Treatment	3,73	8.82	<0.0001
	Land use	1,4	0.073	0.80
	Interaction	3,73	0.531	0.66
Cell biovolume (mm^3/cm^2)	Treatment	3,73.1	3.54	<0.0001
	Land use	1,4	0.95	0.39
	Interaction	3,73.1	0.14	0.94

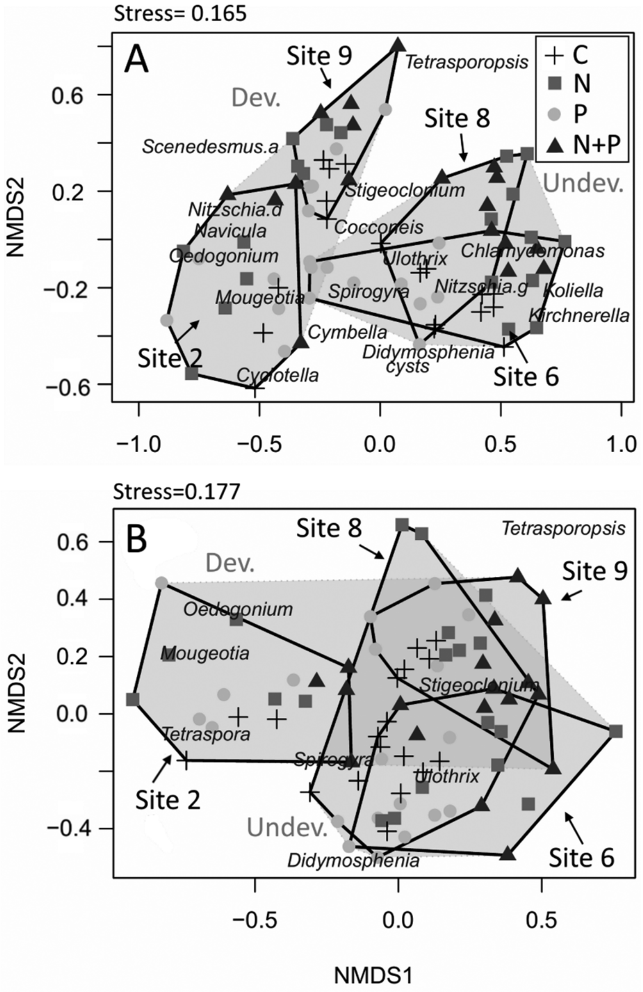

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination plots of benthic algal communities at 4 sites, showing differences by land use, site, and nutrient treatment for cell densities (A) and cell biovolumes (B). Plots are based on Bray–Curtis dissimilarities of $\sqrt[4]{x}$-transformed densities and biovolumes. Dev. = developed, Undev. = undeveloped shoreline land use.

suppressed Chl *a* levels, whereas +N alone and +NP addition increased Chl *a* roughly 2 and 4× relative to controls, respectively. These results support our 1st hypothesis and suggest that benthic algal communities in the study area are serially limited by N and then P. Serial limitation (sensu Harpole et al. 2011) or some other form of colimitation of periphyton and phytoplankton by P and N is a common finding across many studies (Carrick and Lowe 1988, Francoeur 2001, Harpole et al. 2011), including in work on Lake Baikal phytoplankton (Goldman et al. 1996, O'Donnell et al. 2017). The negative response of Chl *a*, cell densities, and, in many replicates, biovolume to P addition alone is interesting. Negative biomass responses to single-nutrient additions have been observed in other studies of periphyton and phytoplankton (reviewed by Francoeur 2001, Harpole et al. 2011). We propose that in southwestern Baikal benthic algae were generally P-replete, such that P addition alone, at the high levels delivered by NDS, was toxic to periphyton (Harpole et al. 2011), but the addition of N, the 1st limiting nutrient, increased biomass resulting in additional demand for P and the nonadditive biomass increase in +NP-amended treatments.

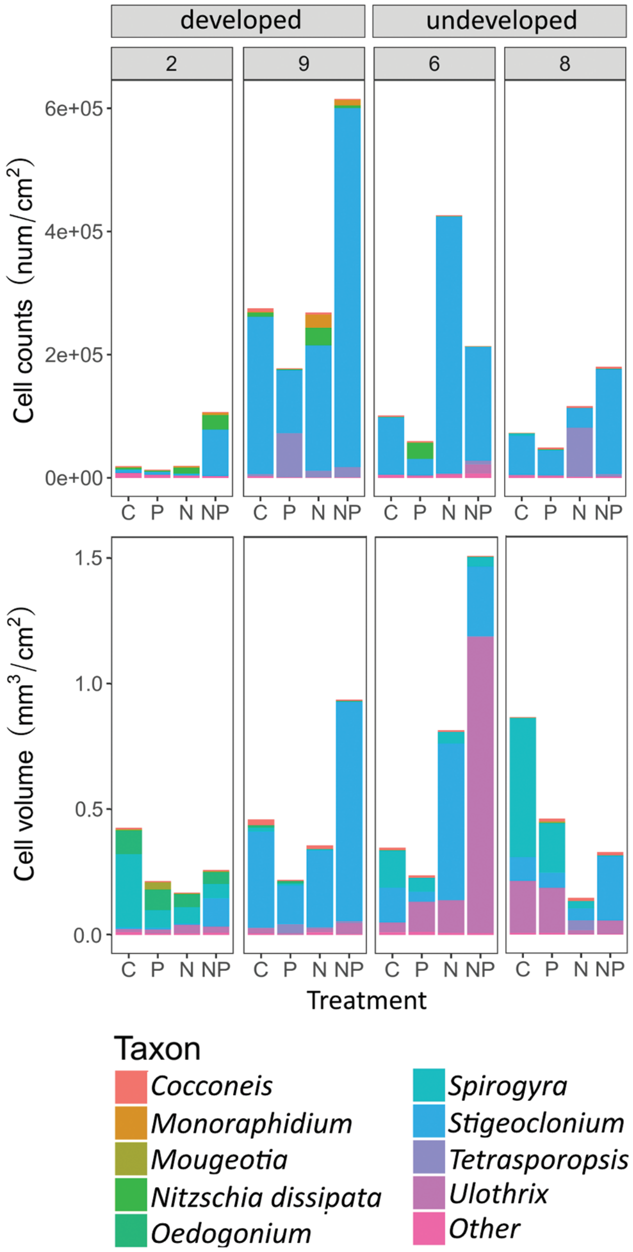

Figure 4. Average abundance (A) and cell volumes (B) of main algal groups on different nutrient-diffusing substrate treatments at 4 sites (2 developed, 2 undeveloped).

We expected that algae would be more abundant and less nutrient limited at developed than undeveloped shoreline sites because of localized nutrient enrichment. Contrary to this hypothesis, we found no significant differences in algal biomass on control substrata or in the magnitude of response to enrichment between sites along developed and undeveloped shorelines. Landuse and nutrient-loading differences affect between-system variation in biomass and nutrient limitation of benthic algae in lakes and rivers (e.g., Dodds et al. 2002, Vadeboncoeur and Steinman 2002, DeNicola et al. 2006, Lambert et al. 2008, Scanlan et al. 2015). However, less is known about variation in lake benthic algal biomass and response to enrichment across landuse gradients within a single system. Conflicting results are seen from the Laurentian Great Lakes (Bootsma et al. 2015) and from other systems where localized responses of periphyton to land use have been studied explicitly. Results of some studies done in the Laurentian Great Lakes have shown that *Cladophora* biomass and nutrient limitation status were localized around nutrient point sources and urban areas (Auer et al. 1982, Higgins et al. 2008, Houben 2008, Althouse et al. 2014). Rosenberger et al. (2008), working in deep, oligotrophic lakes in Washington and Idaho also saw differences in algal biomass and community composition between developed and undeveloped shoreline sites, and Schneider et al. (2014) observed high *Cladophora* biomass near river inflows and villages in Lake Ohrid. In contrast, some large-scale survey studies from the Great Lakes showed no relationship between land use, nutrient loads, and *Cladophora* biomass (Depew et al. 2011, Shuchman et al. 2013, Howell 2017).

Depew et al. (2011) attributed some of the lack of difference in *Cladophora* biomass among developed and undeveloped shorelines to mixing of near- and offshore waters along exposed shorelines in large lakes, and other investigators (e.g., Howell et al. 2012) showed that nearshore nutrient concentrations in large lakes are highly variable in space and time. As in the Laurentian Great Lakes, the nearshore environment in Lake Baikal is physically dynamic, with long-shore and nearshore–offshore transport of water and solutes (Troitskaya et al. 2015), which may explain why no large differences in Chl *a* levels and responses to enrichment were observed between our developed and undeveloped sites. The lack of consistent differences in nutrient concentrations and fecal indicator bacteria numbers between developed and undeveloped sites supports the idea of dilution and transport of materials along the shore. This finding implies that the effects of localized nutrient inputs may be manifested along large areas in the nearshore zone. Localized responses of benthic algae to enrichment also might occur on smaller spatial scales than captured in our study, e.g., directly near stream mouths or areas of high-nutrient groundwater discharge (Timoshkin et al. 2018). Untangling the effects of land use and other factors on lake periphyton is complicated by the very high spatial variability in biomass and nutrient status of lake benthic algae (Kahlert et al. 2002, Houben 2008), and intensive sampling, targeting wide spatial scales, is needed to better resolve the relationship between land use, nutrients, and periphyton blooms in Lake Baikal and other systems.

Benthic algal abundance and cell biovolume were measured for only a subset of sites (2 along developed shorelines and 2 along undeveloped areas) and provided a less consistent picture of nutrient limitation than benthic Chl *a* levels. Some of this inconsistency may be explained by the greater power to detect between-treatment differences with the greater replication of our Chl *a* data (10 vs 4 sites) and the added variability inherent in analyzing subsamples (as would be the case for counting and estimating cell volumes). Different measures of benthic algal biomass often are only moderately correlated and have their own individual limitations (Baulch et al. 2009). Nonetheless, the 3 metrics of biomass were in general agreement in our study. All provided support for N and P colimitation and indicated greater variability among sites than between landuse categories.

Periphyton communities

Algal community composition in terms of cell abundances and biovolume differed significantly among sites and treatments. The filamentous green alga *S. tenue* was numerically dominant across all sites, and differences in its abundance explained the largest portion of multivariate distances among communities at different sites and on different NDS treatments. *Stigeoclonium tenue* tended to be most abundant on +N or +NP substrata at all sites, which is consistent with its status as an indicator of eutrophic conditions in field surveys (including in Lake Baikal), NDS studies, and laboratory experiments (McLean and Benson-Evans 1974, de Vries et al. 1985, Fairchild et al. 1985, Carrick and Lowe 1988, Kravtsova et al. 2014). Variation in average cell biovolume among sites and treatments was mainly a result of differences in *Spirogyra*, *Oedogonium* sp., *Ulothrix* spp., and *S. tenue*. *Ulothrix* was most common at undeveloped sites, whereas *Oedogonium* was found only at the most developed site. *Spirogyra*, which is often considered an indicator genus of nutrient enrichment (O'Neal and Lembi 1988, Schneider and Lindstrøm 2011) and is among the main contributors to benthic blooms in Lake Baikal (Timoshkin et al. 2016), was most abundant on control substrata at all 4 sites. This somewhat counterintuitive finding may be because the levels, ratios, or form of nutrients (organic vs inorganic) supplied in our NDS experiments selected against *Spirogyra* or because our level of taxonomic resolution for *Spirogyra* (identified only to genus) prevented us from detecting species-specific responses to the nutrient amendments, which if strongly contrasting, might explain the weak response at the genus level.

Algal community composition differed among landuse categories, sites, and treatments at the site level, with more distinct differences for cell densities than biovolumes. Differences in cell densities appeared to be larger among sites than among treatments, with the 2 undeveloped sites (6 and 8) having the most similar community composition. At 3 of 4 sites, community composition was most similar on +NP and +N substrata, suggesting generally similar community responses to fertilization by +N and +NP in our study area. Despite some similarities in response to enrichment, community composition was different among sites, across treatments, and for each specific treatment. Rosenberger et al. (2008) observed differences in periphyton community composition between developed and undeveloped sites in oligotrophic lakes. We also saw statistically significant differences in community composition between the 2 developed and 2 undeveloped sites, but much of this difference appears to be the result of high variation between individual sites rather than presence of similar communities at developed and undeveloped sites (Fig. 3A, B). High spatial heterogeneity in benthic algal biomass and community composition is a common finding in stream and lake studies (Kahlert et al. 2002, Pei et al. 2010, Tornés and Sabater 2010, Atkinson and Cooper 2016), and our study lacks the power to discriminate fully the reasons for the observed variation.

Our results are based on an NDS experiment, an approach known to suffer from several limitations. The materials from which NDS are constructed and the forms and ratios in which nutrients are added can affect results of NDS studies (Fairchild et al. 1985, Pringle 1990, Capps et al. 2011). Our results also could be partially confounded by differences in water clarity among sites. Thus, the lack of difference in Chl *a* concentrations on control substrata at sites along developed and undeveloped shorelines could be caused by suppression of periphyton growth by lower light levels at the developed sites, despite higher nutrient availability. We think that differences in light penetration were not a major factor in our study because of the uniformly high water clarity at the study sites. Overall, it seems unlikely that our finding of consistent and strong N and P co-limitation along the southwestern shore of Lake Baikal is strongly biased by the above-mentioned caveats.

Conclusions

The enormous volume of Lake Baikal and the relatively low population density in its watershed has led some to claim that the lake is immune to eutrophication (e.g., Grachev 2002). The emergence and recurrence of benthic algal blooms in Lake Baikal over the past decade clearly shows that this assumption is false. Given their position at the land–water interface, benthic algae can intercept even low-level nutrient inputs from the land (Hampton et al. 2011) and build up nuisance levels of biomass in the absence of eutrophication symptoms in the pelagic zone (Hecky et al. 2004, Rosenberger et al. 2008). The littoral eutrophication and benthic algal blooms in Baikal are having negative effects on the littoral ecosystem of this unique lake (Khanaev et al. 2016, Timoshkin et al. 2016, 2018), which has been designated a United Nations Educational, Scientific and Cultural Organisation (UNESCO) world heritage site in part because of its high biodiversity. Our study shows that benthic algae in Lake Baikal are strongly nutrient limited. This suggests that nutrient load reductions, through improved sewage treatment, better regulations of septic systems, and banning of P-containing detergents have a strong potential to alleviate the problem of benthic algal bloom in Lake Baikal, as they have in other systems (Parker and Maberly 2000, Higgins et al. 2008).

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