Limnol. Oceanogr., 51(3), 2006, 1514–1523

Top-down and bottom-up controls on periphyton biomass and productivity in Lake Tanganyika

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Abstract

We studied the effects of nutrient availability and grazers on periphyton in the littoral zone of Lake Tanganyika. Using a combination of dissolved nutrient ratios, nutrient diffusing substrates, and benthic productivity responses to nutrient supplementation, we evaluated whether nitrogen (N) or phosphorus (P) limited periphyton productivity near Kigoma, Tanzania, during the dry seasons of 2001 and 2002. The relative effects of grazers and nutrients on periphyton were quantified by manipulating grazer access to nutrient diffusing substrates. We found very low ambient concentrations of inorganic N and soluble reactive P, but generally higher concentrations of dissolved organic nutrients. Nutrient diffusing substrates indicated a shift from P limitation in 2001 to co-limitation by N and P in 2002, probably as a consequence of unusual coastal upwelling in 2002. Productivity responses of natural epilithic algae to nutrient supplementation also indicated N–P co-limitation in 2002. However, fish and other large grazers had much stronger effects on periphyton than nutrients. Grazers strongly suppressed periphyton biomass, but had weaker negative effects on area-specific gross primary productivity as a result of large increases in biomass-specific gross primary productivity. We conclude that littoral nutrient availability influenced periphyton productivity, but that top-down control predominated.

Understanding the general conditions favoring top-down and bottom-up control of algal biomass and productivity is a central goal of limnology. Theoretically, low nutrient concentrations could constrain algal growth to the point that the effects of grazers are negligible, or, conversely, intense grazing could overwhelm algal responses to nutrients. In reality, both nutrients and grazers usually have important effects on the productivity of phytoplankton (Brett and Goldman 1997) and periphyton (Steinman 1996; Hillebrand 2002; Liess and Hillebrand 2004). However, this conclusion is based on research in the temperate zone, and there have been few direct comparisons of nutrient and grazer effects in tropical freshwaters.

Meromictic tropical lakes offer a particularly interesting test case because they combine low nutrient availability with intense grazing pressure from a diverse assemblage of animals. In contrast to the annual turnover events that mix most temperate lakes completely, the waters of meromictic lakes are locked in an ''endless summer'' of warm temperatures and stable thermal stratification (Kilham and Kilham 1990). Their stratification facilitates loss of particulate nutrients through sedimentation, as well as chemical transformations across a sharp reduction–oxidation gradient in the metalimnion. These processes result in nutrient scarcity in the epilimnion and accumulation of nutrients in the hypolimnion, and seasonal upwelling of hypolimnetic nutrients is required to balance epilimnetic nutrient budgets over annual time scales (Hecky et al. 1991, 1996). Despite the chronic dearth of nutrients in the surface waters, high primary productivity is maintained by rapid nutrient recycling in the water column.

Benthic grazers are both diverse and abundant in meromictic tropical lakes. This guild includes fishes and macrocrustaceans, along with the grazing insects and mollusks common in temperate lakes. Though species richness of benthic invertebrates shows no latitudinal pattern (Lewis 1996), algae-eating fishes are far more diverse in the tropics (Wootton and Oemke 1992). Experiments in tropical streams demonstrate that grazing fish suppress

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Acknowledgments

We thank G. Kazumbe and C. Solomon for assistance in the field, A. De Wever for identifying *Nitzschia*, F. Vermeylen for statistical assistance, and L. Hedin, M. Brown, R. Howarth, R. Marino, and A. Galford for assistance with chemical analyses. The manuscript was improved by comments from A. Flecker, R. Hecky, C. O'Reilly, T. Thoms, Y. Vadeboncouer, and two anonymous reviewers. The staff of the Tanzanian Fisheries Research Institute offered logistical assistance, and the Tanzanian Committee for Science and Technology granted permission to conduct this project. Funding was provided by the NSF through the Nyanza Project (ATM-9619458), the Cornell IGERT in Biogeochemistry, a dissertation enhancement grant (INT-0321443), and a predoctoral fellowship to P.B.M.

epilithic algal biomass (Power 1990; Flecker et al. 2002) and alter algal responses to nutrients (Flecker et al. 2002).

Though meromictic tropical lakes exhibit an intriguing combination of low nutrient concentrations and high potential grazing rates, the relative strength of bottom-up and top-down control in these systems has been investigated only for phytoplankton (Guildford et al. 2003). Controls on benthic algae may be different than those on phytoplankton (e.g., carbon limitation; Turner et al. 1994). For instance, nutrient availability probably differs between the littoral and pelagic zones because of benthic processes (e.g., epilithic nitrogen fixation; Higgins et al. 2001), exchanges with the terrestrial zone, differences in mixing dynamics (MacIntyre and Melack 1995), isolation from hypolimnetic nutrients, and recycling of nutrients by relatively dense populations of animals (Andre et al. 2003). Similarly, top-down control of benthic algae may be facilitated by the dominance of highly mobile grazers that systematically crop periphyton and actively target patches of high algal biomass.

This article focuses on Lake Tanganyika, the largest meromictic lake in the world (650 × 50 km surface, 1.47 km depth). Its surface waters have low nutrient concentrations that are augmented by biological nitrogen fixation and upwelling of hypolimnetic nutrients (Hecky et al. 1991), with only minor dependence on external loading (Langenberg et al. 2003*a*). Despite the scarcity of nutrients, pelagic phytoplankton in Lake Tanganyika are productive in the upper 50 m of the water column (0.5–2.8 g carbon [C] m^{-2} d^{-1}; Hecky and Fee 1981; Sarvala et al. 1999). Phytoplankton production is closely tied to nutrient upwelling on both seasonal (Hecky and Fee 1981; Hecky and Kling 1981; Langenberg et al. 2003*b*) and multiyear time scales (O'Reilly et al. 2003; Verburg et al. 2003). In the littoral zone, epilithic algae are comparable in productivity to pelagic phytoplankton, ranging from 0.4 to 2.5 g C m^{-2} d^{-1} (Takamura 1988; O'Reilly 2006; Thoms unpubl. data). There is little evidence of light limitation of benthic productivity with depth in the upper 5 m of the littoral zone (Takamura 1988); at our study sites, transparency is high (Secchi depth >12 m) and light attenuation is low (0.20–0.26 m^{-1}).

Though nitrogen (N) limitation of primary productivity is considered most likely in tropical lakes (Hecky and Kilham 1988; Lewis 1996; Talling and Lemoalle 1998), there is no consensus on whether limitation by N or phosphorus (P) prevails in Lake Tanganyika. N limitation has been inferred from low dissolved inorganic N : P (Coulter 1977; Hecky et al. 1991; Edmond et al. 1993) and is indicated by blooms of N-fixing cyanobacteria following upwelling (Hecky and Kling 1981; Salonen et al. 1999; Descy et al. 2005). In contrast, whole-lake nutrient budgets implicate P as the "master element" (Hecky et al. 1996), and dissolved nutrient ratios sometimes indicate P limitation (Chale 2004). Seston stoichiometry reflects moderate N deficiency and extreme P deficiency, and phytoplankton responses to experimental nutrient additions indicate P limitation or co-limitation by N and P (Jarvinen et al. 1999). Taken together, this work indicates that nutrient limitation of primary productivity in Lake Tanganyika varies through space and time, most likely as a function of upwelling (Plisnier 2002; Langenberg et al. 2003*b*). It is also possible that a nutrient other than N and P may limit or co-limit algal growth (e.g., iron; Guildford et al. 2003).

The goals of this study were to quantify littoral nutrient availability and to compare the effects of nutrients and grazers on periphyton. During two consecutive dry seasons, we measured concentrations of inorganic and organic N and P. To test nutrient limitation of periphyton, we used nutrient diffusing substrates (NDSs) and the productivity response of periphyton to nutrient supplementation. Top-down and bottom-up regulation of periphyton accrual and productivity were compared by manipulating grazer access to NDSs. Together these data represent a first assessment of controls on periphyton in Lake Tanganyika.

Methods

Study period and sites—The study was conducted in the rocky littoral zone near Kigoma, Tanzania, during the dry seasons (July–August) of 2001 and 2002. Nutrients were measured at two sites: Maji Menge (4°54′10″S, 29°35′41″W), which is on Bangwe Point to the south of Kigoma and Katabe Bays, and Euphorbia (4°50′57″S, 29°36′32″W), which is north of Kigoma Bay along Kasazi Hill. These sites were selected because their west-facing shorelines do not constrain mixing by waves and because they are not directly affected by human settlements or anthropogenic sedimentation.

Nutrient and grazer manipulations were conducted at a nearby pair of guarded sites, where the risk of vandalism of experiments was lower and the effects of anthropogenic sedimentation could be investigated. The first site was Jakobsen's Beach (4°54′53″S, 29°35′53″E; ~1.3 km south of Maji Menge), a reserve in which shoreline vegetation is protected from clearing and burning. The second site, Hilltop Hotel (4°53′15″S, 29°36′50″E; ~2.7 km north of Maji Menge), has been heavily affected by anthropogenic erosion from the overlooking bluff (McIntyre et al. 2005). Hilltop Hotel was selected for comparison to Jakobsen's Beach in order to test whether sedimentation of iron-rich clays alters nutrient limitation of benthic algae. Dissolved nutrient concentrations at all four study sites are similar during the dry season and are broadly representative of the Kigoma region (McIntyre unpubl. data).

Dissolved nutrients—We monitored littoral nutrient concentrations during the study period to provide context for our experiments. Water samples were collected weekly at Maji Menge and Euphorbia from 06 July to 05 August 2001 and again from 09 July to 05 August 2002. Samples were collected between 09:00 and 12:00 h at a depth of 1 m and a distance of 11 m from the shoreline at each site. They were filtered through prerinsed, serial glass-fiber (Gelman A/E) and membrane (Osmonics PCTE 0.2 μm in 2001, Osmonics Cameo 0.22 μm in 2002) filters into new, well-rinsed bottles. Samples were frozen and transported to Cornell University for analysis by standard colorimetric methods (method and minimum detection limit in parentheses) with an autoanalyzer for NO_3 (cadmium reduction,

0.07 μmol L^{-1} N), total dissolved N (TDN; high-temperature persulfate digestion and cadmium reduction, 0.7 μmol L^{-1} N), soluble reactive phosphorus (SRP; molybdenum blue, 0.02 μmol L^{-1} P), and total dissolved P (TDP; high-temperature persulfate digestion and molybdenum blue, 0.03 μmol L^{-1} P). NH_4 was analyzed from frozen samples in 2001 (phenol-hypochlorite, 0.07 μmol L^{-1} N) and from fresh samples in the field in 2002 (fluorometry following the method of Holmes et al. [1999]; 0.04 μmol L^{-1} N). We estimated dissolved organic N (DON) and dissolved organic P (DOP) as the difference between TDN or TDP and dissolved inorganic N (DIN) or SRP concentrations, respectively. These data were used to calculate molar ratios of DIN : SRP and DON : DOP.

Differences among sites and years in nutrient concentrations (NO_3, DON, SRP, DOP) and ratios (DIN : SRP, DON : DOP) were tested using multivariate analysis of variance (MANOVA) followed by univariate ANOVAs. Sites were considered a random factor. This analysis treated weekly samples as independent replicate observations, which was justified because there were not significant temporal patterns within years and because littoral nutrients are expected to turn over rapidly. When differences were significant, Tukey's HSD method was used to compare every site and year. To test whether dissolved nutrient ratios indicated nutrient limitation, we compared them to benchmark algal N : P ratios representing both optimal growth conditions (molar N : P = 17; Hillebrand and Sommer 1999) and the stoichiometry of natural epilithic algae in Lake Tanganyika in 2004 (mean N : P = 37.5 $\pm$ 1.1 [standard error, SE], n = 48; McIntyre et al. unpubl. data). Comparisons were made using one-sample t-tests with Bonferroni correction (α= 0.003).

Nutrient diffusing substrates—We used NDS experiments to test whether nutrient availability limited periphyton accrual and productivity in 2001 and 2002. This method has been applied successfully in both temperate (e.g., Scrimgeouer and Chambers 1997) and tropical (e.g., Flecker et al. 2002) freshwaters. We used low-profile ceramic pots (diameter, 11.7 cm; depth, 3.4 cm; surface area, 117 cm^2) that were sealed to plastic saucers using aquarium-grade silicon, then filled with a 2% agar gel supplemented with nutrient salts. NDS pots were placed on natural rock substrates and anchored to nearby cobbles.

We compared four nutrient treatments: C (no nutrients added), N (nitrogen added), P (phosphorus added), and NP (nitrogen and phosphorus added). N was added to agar as equal parts NO_3-N ($NaNO_3$) and NH_4-N (NH_4Cl) to achieve a concentration of 1.0 mol N L^{-1} agar. P was added as Na_2HPO_4 to achieve a concentration 0.1 mol P L^{-1} agar. Diffusion rates from NDS pots typically decrease exponentially through time but remain measurable for approximately 1 month (Scrimgeouer and Chambers 1997; Bernhardt and Likens 2004; Hood unpubl. data).

We used a factorial design to compare the effects of nutrient treatments and grazers on periphyton at the relatively pristine Jakobsen's Beach site in 2001. Half of the substrates were protected from large grazers by a plastic cage (1.21-cm^2 square openings) attached to the saucer; the other half were left uncaged, thereby allowing free access by all grazers (signified by a 'G' in the treatment abbreviation). Our other experiments in this system indicate that these cages exclude fishes as well as large snails and crustaceans (McIntyre et al. unpubl. data), and we have observed no evidence of caging artifacts, such as increased sedimentation. Five randomized, complete blocks were established at a depth of 3.5 m, with >5 m between blocks and ~50 cm between substrates within blocks. The experiment lasted 26–27 d.

The 2002 NDS experiment was conducted at both Jakobsen's Beach and Hilltop Hotel. This allowed us to evaluate whether anthropogenic sedimentation at Hilltop Hotel might influence periphyton nutrient limitation. The same four nutrient treatments were tested, and every substrate was protected from grazers by a plastic cage. At each site, six randomized, complete blocks were deployed at 4.0–4.7 m in depth, and the experiment lasted 18–19 d.

At the conclusion of both NDS experiments, periphyton accrual was quantified using chlorophyll *a* (Chl *a*) and ash-free dry mass (AFDM). Periphyton was scrubbed from the top of each substrate and homogenized. Separate subsamples were collected on filters (Gelman A/E) for analysis of Chl *a* and AFDM (combustion at 500°C for 3 h). Chl *a* was extracted in cold, 90% ethanol for 24 h and quantified using a Spectronic 21D spectrophotometer (2001) or Turner Aquafluor fluorometer (2002).

To separate effects on algal productivity from biomass accrual, we measured productivity and respiration of periphyton on each substrate prior to algal sampling. Substrates were incubated within transparent plastic chambers (2.2 liters) of lake water at the same depth at which they had been deployed initially. The dissolved oxygen concentration was measured at the beginning and end of each incubation with a YSI 95 meter. Net primary productivity (NPP) was calculated as oxygenesis during incubation under ambient light conditions for ~20 min. Respiration was measured as oxygen consumption within opaque chambers during ~60-min incubations. Every substrate was used in both light and dark incubations, and gross primary production (GPP) was calculated as NPP in the light plus respiration in the dark. Incubations with empty chambers indicated negligible NPP or respiration by plankton, so all fluxes were interpreted as deriving from substrates. These data allowed direct evaluation of treatment effects on productivity and respiration but were not intended to estimate productivity and respiration of natural periphyton.

The two NDS experiments were analyzed separately because their designs differed. For the 2001 grazer-nutrient experiment, the effects of N, P, the N–P interaction, grazers, and grazer-nutrient interactions on Chl *a*, AFDM, area-specific GPP (AS-GPP), and respiration were tested using MANOVA followed by univariate ANOVAs. A similar MANOVA was used to analyze the 2002 two-site experiment, except that site effects were tested instead of grazer effects. Chl *a* and AFDM data were log transformed to meet statistical assumptions.

To compare the quantitative effects of nutrients and grazers both separately and in combination, we calculated

Table 1. Nitrogen (N) and phosphorus (P) concentrations and molar ratios at Euphorbia and Maji Menge. Mean values and SE (in parentheses) are shown from 4–5 weeks of weekly sampling in 2001 and 5 weeks in 2002. NH_4 was below the minimum detection limit (0.04 μmol L^{-1} N) in 2002 and could not be reliably measured from frozen samples in 2001. Letters indicate statistical groupings from post-hoc comparisons. Ratios in bold type differ significantly from both the idealized (N : P = 17) and observed (N : P = 37.5) stoichiometry of epilithic algae (see text).

Site	Year	*n*	NO_3 (μmol L^{-1} N)	DON (μmol L^{-1} N)	SRP (μmol L^{-1} P)	DOP (μmol L^{-1} P)	DIN : SRP	DON : DOP
Euphorbia	2001	4	0.10 (0.05)	6.52 (0.33)	0.03 (0.00) a	0.07 (0.00) a	**3.6** (1.6) ab	**99.3** (5.3) a
	2002	5	0.04 (0.02)	6.12 (0.41)	0.04 (0.00) a	0.04 (0.00) b	**0.9** (0.5) b	**171.7** (14.7) b
Maji Menge	2001	5	0.14 (0.06)	6.32 (0.41)	0.03 (0.01) a	0.07 (0.01) a	**5.1** (1.3) a	**101.3** (14.3) a
	2002	5	0.08 (0.02)	6.42 (0.36)	0.04 (0.00) a	0.05 (0.01) ab	**2.0** (0.5) ab	**152.8** (17.5) ab

standardized effect sizes for the 2001 NDS experiment following the method of Berlow et al. (1999) and Flecker et al. (2002). This index equals zero when there is no effect and returns symmetric positive or negative values describing proportional differences relative to the control treatment. The effect size of nutrients on algal biomass was calculated as $\log_{10}$ (Chl_P/Chl_C), where P is the treatment with only phosphorus added and no grazers and C is the treatment with no nutrients added and no grazers. The P treatment was chosen to represent the effects of nutrients because only phosphorus was shown to limit algal productivity in 2001. Similarly, the effect of grazers was calculated as $\log_{10}$ (Chl_{CG}/Chl_C), and joint nutrient-grazer effects as $\log_{10}$ (Chl_{PG}/Chl_C). Effects sizes were calculated for each of three response variables: Chl *a* (μg cm^{-2}), AS-GPP (mg O cm^{-2} h^{-1}), and biomass-specific GPP (BS-GPP; mg O μg Chl^{-1} h^{-1}). Independent estimates of effect sizes were calculated for each spatial block of substrates ($n = 5$).

Overnight supplementation experiment—As a means of testing nutrient limitation of natural periphyton, we measured productivity responses to overnight supplementation of dissolved nutrient concentrations at Jakobsen's Beach during July–August 2002. Flat, upward-facing cobbles were collected from a depth of 4 m and incubated at 4 m inside chambers of lake water for ~12 min to measure NPP, as described previously. After this pretreatment incubation, rocks were randomly assigned to one of four treatments: C (no supplementation), N (+64 μmol L^{-1} N, equal contributions from $NaNO_3$-N and NH_4Cl-N), P (+3.8 μmol L^{-1} P as Na_2HPO_4), and NP (+64 μmol L^{-1} N, +3.8 μmol L^{-1} P). Treatments were designed to increase TDN 10-fold and to match an idealized benthic algal N : P of 17 : 1 (Hillebrand and Sommer 1999).

The displacement of each rock was measured, and the appropriate volume of a concentrated nutrient solution (or lake water in treatment C) was injected into each chamber. A preliminary dye study showed that injections were retained within chambers, and that spinning the chamber fully mixed the water inside. Chambers were sealed, spun, and placed on the substrate at 4-m depth under ambient light conditions. After 24 h, chambers were emptied, refilled with fresh lake water, measured for dissolved oxygen and temperature, injected with nutrient solution, spun, and sealed for a posttreatment incubation. Incubations were conducted between 11:00–16:00 h, when photosynthesis at 4 m should not have been strongly light-limited (200–540 μmol quanta m^{-2} s^{-1}). Following the posttreatment incubation, periphyton Chl *a* was quantified as described previously, and the upward-facing surface area of each rock was calculated from a digital photo. Three randomized complete blocks were tested on each of three dates, and incubations were conducted simultaneously within each block. There were no significant differences among treatments in rock surface area (mean = 65.5 ± 2.4 [SE] cm^2; $F_{3,32} = 0.54$, $p = 0.658$), periphyton biomass (mean = 3.0 ± 0.2 μg Chl cm^{-2}; $F_{3,32} = 0.17$, $p = 0.919$), or initial NPP (mean = 0.63 ± 0.03 μg O cm^{-2} min^{-1}; $F_{3,32} = 0.41$, $p = 0.746$).

Treatment effects were calculated as the proportional difference in NPP before (NPP_{pre}) and after (NPP_{post}) nutrient supplementation: $\Delta NPP = (NPP_{post} - NPP_{pre})/NPP_{pre}$. This measure uses repeated observations from the same rock to separate treatment effects from natural variation among rocks. The effects of N, P, the N–P interaction, and block on ΔNPP were tested using ANOVA. Preliminary models indicated that Chl *a* and surface area of rocks had no significant effects, so they were pooled with the error term.

All statistical analyses were conducted using SYSTAT Version 10. Block effects and interaction terms were included in preliminary models but were pooled with the error term when nonsignificant. For simplicity, we present ANOVA results only when their interpretation is justified by a significant MANOVA test.

Results

Dissolved nutrients—Concentrations of DIN and SRP were consistently low at both monitoring sites in 2001 and 2002 (Table 1). In fact, NO_3 and SRP were often near or below the limits of accurate quantification even for instruments tuned for low concentrations. Colorimetric analysis of NH_4 in frozen samples from 2001 indicated concentrations of 0.2–0.4 μmol L^{-1} N, but these data are not shown in Table 1 because we believe they were artifacts of preservation. Fluorometric analysis of hundreds of fresh samples in the field during 2002 and 2004 has indicated that NH_4 concentrations are generally indistinguishable from deionized water (<0.04 μmol L^{-1} N). Organic compounds often accounted for a majority of total dissolved nutrients in the littoral zone, and DON was particularly abundant relative to DIN (Table 1).

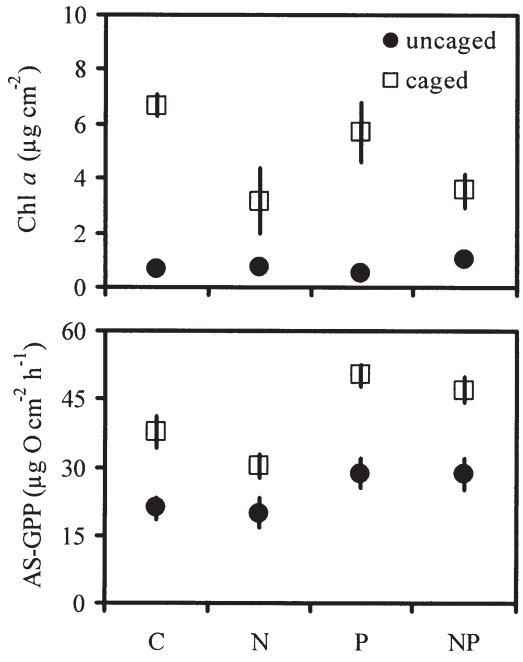

Fig. 1. Effects of nutrients and grazers on algal biomass (Chl *a*) and area-specific gross primary productivity (AS-GPP) on nutrient diffusing substrates in 2001 at Jakobsen's Beach. Substrates were supplemented with no nutrients (C), nitrogen (N), phosphorus (P), or both nitrogen and phosphorus (NP). Caged substrates were protected from large grazers; uncaged substrates were accessible to all grazers. Markers represent means ± SE ($n = 5$).

There were no significant multivariate differences in nutrient concentrations and ratios between sites or site–year interactions; however, years differed significantly (Pillai Trace = 0.67, $F_{6,11} = 3.69$, $p = 0.029$). In 2002, DOP was lower ($F_{1,16} = 20.83$, $p < 0.001$) and SRP was higher ($F_{1,16} = 8.83$, $p = 0.009$) than in 2001. These shifts resulted in lower DIN : SRP ($F_{1,16} = 8.48$, $p = 0.010$) and higher DON : DOP ($F_{1,16} = 18.40$, $p = 0.001$) in 2002 than in 2001. DON was present in excess of DOP relative to optimal (N : P = 17) and observed epilithic algal stoichiometry (N : P = 37.5) at both sites in both years, suggesting P limitation. In contrast, DIN : SRP was significantly lower than these benchmark N : P ratios, suggesting N limitation.

Nutrient diffusing substrates—In 2001, phosphorus had a significant multivariate effect (Pillai Trace = 0.58, $F_{4,26} = 9.02$, $p < 0.001$), reflecting an increase in AS-GPP of P-supplemented substrates ($F_{1,29} = 34.88$, $p < 0.001$) but no change in Chl *a* (Fig. 1), AFDM, or respiration (Table 2). There were no significant effects of nitrogen or nitrogen–phosphorus interaction. Across nutrient treatments, grazers had very strong effects (Pillai Trace = 0.90, $F_{4,26} = 57.63$, $p < 0.001$). Caged pots accrued 3 to 10 times more Chl *a* ($F_{1,29} = 124.34$, $p < 0.001$) and 1.7 to 2.5 times more AFDM ($F_{1,29} = 199.02$, $p < 0.001$) than uncaged pots. AS-GPP and respiration on caged pots were 51–78% ($F_{1,29} = 74.41$, $p < 0.001$) and 17–56% ($F_{1,29} = 17.39$, $p < 0.001$) higher, respectively. There was also a significant interaction between nitrogen and grazing (Pillai Trace = 0.44, $F_{4,26} = 5.16$, $p = 0.003$), because Chl *a* and AFDM on uncaged pots were similar across all nutrient treatments (Fig. 2), whereas caged substrates supplemented with nitrogen had lower Chl *a* ($F_{1,29} = 9.22$, $p = 0.005$) and AFDM ($F_{1,29} = 5.03$, $p = 0.033$) than C and P substrates. Finally, there were differences among blocks of substrates in respiration ($F_{4,29} = 44.94$, $p < 0.001$) and AS-GPP ($F_{4,29} = 2.50$, $p = 0.064$).

Effect size comparisons show that grazers had a stronger influence on algal biomass and productivity than phosphorus in the 2001 NDS experiment (Fig. 2). Grazers reduced Chl *a* by 10 times as much as phosphorus addition, decreased AS-GPP by twice as much as it was increased by

Table 2. Ash-free dry mass (AFDM), biomass-specific gross primary productivity (BS-GPP), and respiration of nutrient diffusing substrates with no added nutrients (C), nitrogen only (N), phosphorus only (P), or both nitrogen and phosphorus (NP). Experiments were conducted at two sites and during 2 yr, and cage refers to the presence (Y) or absence (N) of a plastic cage that prevented large grazers from consuming periphyton. Data are means and SE (in parentheses).

Site	Year	Cage	Treatment	n	AFDM (mg cm^{-2})	BS-GPP (μg O μg Chl^{-1} h^{-1})	Respiration (μg O cm^{-2} h^{-1})
Jakobsen's Beach	2001	Y	C	5	1.31 (0.02)	5.68 (0.50)	6.72 (1.65)
			N	5	0.92 (0.08)	13.38 (2.97)	7.40 (1.44)
			P	5	1.14 (0.11)	10.93 (2.93)	6.97 (1.48)
			NP	5	0.92 (0.06)	16.92 (5.51)	7.17 (1.73)
Jakobsen's Beach	2001	N	C	5	0.56 (0.05)	42.30 (14.52)	5.32 (1.35)
			N	5	0.45 (0.03)	32.75 (5.47)	4.66 (1.58)
			P	5	0.46 (0.02)	57.94 (8.03)	6.40 (1.14)
			NP	5	0.53 (0.05)	35.29 (9.60)	4.99 (1.48)
Jakobsen's Beach	2002	Y	C	6	0.81 (0.10)	10.03 (0.88)	5.58 (0.21)
			N	6	1.05 (0.18)	17.44 (1.27)	4.62 (0.21)
			P	6	0.77 (0.17)	11.41 (1.13)	4.97 (0.25)
			NP	6	1.14 (0.17)	15.11 (1.30)	5.15 (0.13)
Hilltop Hotel	2002	Y	C	6	0.98 (0.12)	8.94 (0.87)	5.50 (0.34)
			N	6	2.25 (0.19)	12.37 (1.11)	4.70 (0.34)
			P	6	1.61 (0.14)	10.66 (0.70)	6.30 (0.41)
			NP	6	1.91 (0.26)	14.39 (1.52)	4.81 (0.35)

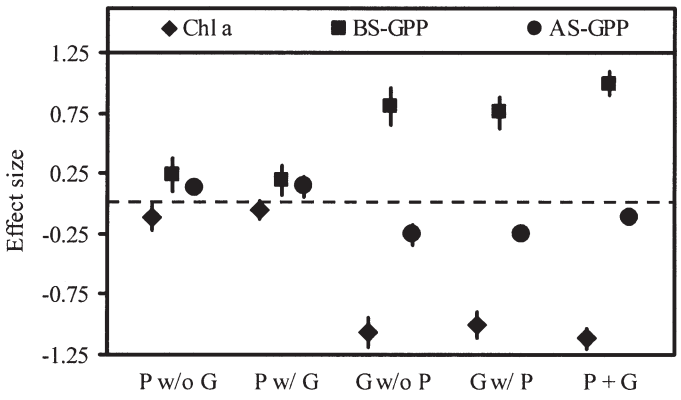

Fig. 2. Effect sizes of phosphorus (P) and large grazers (G) on algal biomass (Chl *a*), biomass-specific gross primary productivity (BS-GPP), and area-specific gross primary productivity (AS-GPP) on nutrient diffusing substrates in 2001 at Jakobsen's Beach. Analyses were conducted for phosphorus in the absence (P w/o G) and presence of grazers (P w/ G), for grazers in the absence (G w/o P) and presence of phosphorus supplementation (G w/ P), and for the combined effects of phosphorus and grazers (P+G). Markers represent means ± SE (n = 5).

phosphorus, and increased BS-GPP by three times as much as phosphorus. As indicated by the lack of a significant grazer–phosphorus interaction in the MANOVA, the joint effects of phosphorus and grazers were comparable to the effects of grazers alone. Moreover, there were no differences between effect sizes of grazers in the presence and absence of added phosphorus or between the effects of phosphorus in the presence and absence of grazers (Fig. 2).

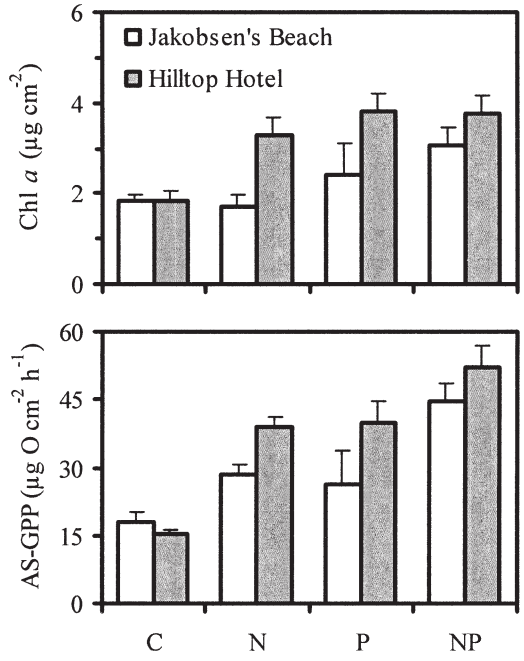

Fig. 3. Effects of nutrients on algal biomass (Chl *a*) and area-specific gross primary production (AS-GPP) on nutrient diffusing substrates in 2002 at Jakobsen's Beach and Hilltop Hotel. All substrates were protected from large grazers by cages. Bars represent means ± SE (n = 6).

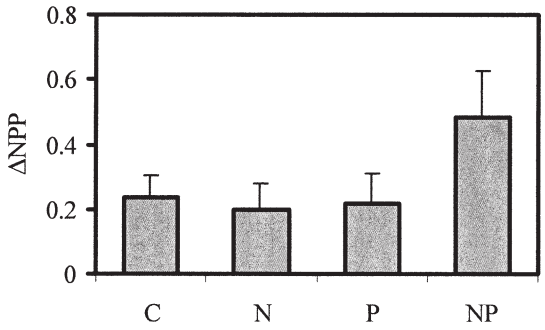

Fig. 4. Change in net primary productivity (NPP) of natural periphyton following overnight supplementation with nutrients in 2002. ΔNPP was calculated as the proportional change in area-specific NPP of the same periphyton before and after incubation for 24 h with addition of no nutrients (C), nitrogen (N), phosphorus (P), or both nitrogen and phosphorus (NP). Bars represent means ± SE (n = 9).

In the 2002 NDS experiment (Fig. 3; Table 2), phosphorus had significant effects (Pillai Trace = 0.60, $F_{4,38}$ = 14.49, $p < 0.001$) by enhancing both Chl *a* ($F_{1,41}$ = 6.03, p = 0.018; Fig. 1) and AS-GPP ($F_{1,41}$ = 29.04, $p < 0.001$). Nitrogen also had significant effects (Pillai Trace = 0.70, $F_{4,38}$ = 22.43, $p < 0.001$), resulting in higher AFDM accrual ($F_{1,41}$ = 12.89, p = 0.001), marginally higher Chl *a* ($F_{1,41}$ = 3.37, p = 0.074), enhanced AS-GPP ($F_{1,41}$ = 30.83, $p < 0.001$), and decreased respiration ($F_{1,41}$ = 12.54, p = 0.001). In addition, the two study sites were significantly different (Pillai Trace = 0.57, $F_{4,38}$ = 12.37, $p < 0.001$). At Hilltop Hotel, more Chl *a* ($F_{1,41}$ = 8.07, p = 0.007) and AFDM ($F_{1,41}$ = 25.82, $p < 0.001$) accumulated on substrates, and AS-GPP was higher ($F_{1,41}$ = 6.22, p = 0.017) than at Jakobsen's Beach (Fig. 3; Table 2). There were no significant interactions between N and P or between nutrients and sites.

Overnight supplementation experiment—Posttreatment NPP (range 0.4–1.3 μg O_2 cm^{-2} min^{-1}) was almost always greater than pretreatment NPP (range 0.2–1.1 μg O_2 cm^{-2} min^{-1}), resulting in mean ΔNPP of 20–48% across treatments (Fig. 4). There were no quantitative or qualitative differences among the C, N, and P treatments. However, the interaction between N and P supplementation was significant because of a doubling of ΔNPP when both nutrients were added ($F_{1,24}$ = 4.42, p = 0.046). There were also significant differences among experimental blocks ($F_{8,24}$ = 5.20, p = 0.001).

Discussion

Littoral nutrient availability—Concentrations of dissolved N and P were low at our littoral study sites in 2001 and 2002 (Table 1). DIN and SRP were particularly scarce, as reported previously from pelagic surface waters (Coulter 1977; Hecky and Kling 1981; Edmond et al. 1993). Inorganic compounds comprised an average of only 1.4% of TDN (range 0–4.6%) and 40.5% of TDP (range 7.6–65.8%), indicating that organic compounds were the major forms of dissolved (<0.22 μm) N and P in the littoral zone.

It is possible that our measurements overestimated dissolved P concentrations as a result of leakage from plankton damaged during filtration (Hudson et al. 2000). This could increase both SRP and DOP estimates but is difficult to assess.

We did not measure particulate N and P, but littoral phytoplankton concentrations observed during this study (0.98 ± 0.06 [SE] μg Chl *a* L^{-1}, $n = 19$) correspond to average particulate nutrient concentrations of 1.63 μmol L^{-1} N (range 0.76–3.23) and 0.09 μmol L^{-1} P (range 0.04–0.17) based on previous measurements of particulate C : N (~9), C : P (~168), and C : Chl *a* (~15) in pelagic surface waters near our study sites (Jarvinen et al. 1999). Comparing these rough estimates of particulate nutrients to measured DON concentrations (Table 1) indicates that DON dominated the water column N pool (mean estimated DON : particulate $N = 4.66$, range 2.06–8.87) and that DOP was a substantial proportion of total water column P (mean estimated DOP : particulate P = 0.73, range 0.19–1.44).

The relative abundance of dissolved organic N and P indicates that access to organic nutrients by either direct assimilation or following mineralization might be a critical control on littoral productivity in Lake Tanganyika. By combining published data on seston stoichiometry (C : N : P ~ 168 : 19 : 1; Jarvinen et al. 1999) and biomass-specific phytoplankton productivity (0.18–0.27 μmol C μg Chl a^{-1} h^{-1}; Sarvala et al. 1999) with our measurements of littoral phytoplankton biomass during this study (mean = 0.98 μg Chl *a* L^{-1}), we estimate average nutrient demand by littoral phytoplankton as 0.02–0.03 μmol N L^{-1} h^{-1} and 0.001–0.002 μmol P L^{-1} h^{-1}. Thus, phytoplankton production would consume an average of 29–44% of usual DIN concentrations and 3–5% of SRP per hour (Table 1). Though crude, these calculations show that mineralization or direct uptake of organic N and P is probably vital for supporting the nutrient demands of littoral phytoplankton, microbes, and periphyton (see also Caraco et al. 1992). There is growing recognition that rapid recycling of organic nutrients is important in temperate lakes (Hudson et al. 2000; Mitchell and Baldwin 2005), and our calculations support the hypothesis that nutrient recycling is critical in meromictic tropical lakes in order to sustain high productivity despite low inorganic nutrient concentrations (Kilham and Kilham 1990).

The stability of organic nutrient concentrations within each monitoring period indicates that the supply and transformation of DON were roughly in equilibrium (Table 1). Sources of DON include leakage by living phytoplankton and microbes (Bronk et al. 1994), lysis and leaching from dead cells, and excretion by consumers (e.g., fishes; Andre et al. 2003). Both phytoplankton and microbes are able to directly assimilate certain forms of DON and DOP (e.g., Bjorkman and Karl 2003; Glibert et al. 2004). In addition, photolysis and other processes can convert DON and DOP into more available forms (e.g., Vahatalo et al. 2003). Photochemical reactions might be especially important in oligotrophic tropical lakes as a result of their combination of strong, year-round solar radiation and low concentrations of ultraviolet-absorbing solids and dissolved compounds.

Nutrient limitation of periphyton productivity—The combination of dissolved nutrient ratios, nutrient diffusing substrates, and the overnight supplementation experiment offered insight into nutrient limitation of periphyton at our study sites. Littoral DIN : SRP consistently indicated N limitation (mean N : P < 6), whereas DON : DOP indicated P limitation (mean N : P > 90) during both years. These ratios must be interpreted cautiously in the absence of direct measurements of nutrient uptake and mineralization rates because they are sensitive to small differences in concentrations and may not reflect actual nutrient availability to periphyton (Turner et al. 1994). Indeed, the calculations presented earlier indicate that mineralization of dissolved or particulate organic nutrients must be important in meeting the daily nutrient demands of phytoplankton, microbes, and periphyton. The N : P of these regenerated nutrients will depend on the sources and processes involved. For instance, the large size and high N : P of dissolved organic pools could enforce P limitation if mineralization or direct uptake of organic nutrients is substantial.

The NDS experiments provided evidence of periphyton nutrient limitation in both 2001 and 2002. Among the variables measured, algal productivity responded most strongly to nutrients. P addition significantly increased AS-GPP, but N had no effect in 2001 (Fig. 1), whereas both N and P had significant, additive effects on AS-GPP in 2002 (Fig. 3). The accrual of Chl *a* and AFDM on substrates was also significantly enhanced by both N and P in 2002 (Fig. 3; Table 2). These patterns indicate that P alone limited periphyton productivity in 2001, but N and P were co-limiting in 2002. Comparing biomass and productivity responses to nutrients at Jakobsen's Beach and Hilltop Hotel in 2002 provided no indication that anthropogenic sedimentation affects nutrient limitation (Fig. 3; Table 2).

The suppression of algal accrual by N in 2001 was puzzling, and we found the same pattern in both a pilot experiment in 2000 and in subsequent work in 2004 (McIntyre et al. unpubl. data). Bernhardt and Likens (2004) also reported N suppression of algal biomass in a NDS experiment and attributed it to competition for N between microbes and algae. This explanation is unlikely to account for our results, because the effects of N on AFDM and respiration rates paralleled those for Chl *a* (Table 2), indicating similar responses by algae and microbes. We also doubt that levels of N or associated ions (Na, Cl) diffusing from substrates were toxic to periphyton, because N had no detrimental effect on periphyton accrual in 2002 (Fig. 3). In any case, we recognize that the NDS approach has various shortcomings (Brown et al. 2001), but we are aware of no better method of experimentally testing nutrient limitation of periphyton. Measurements of productivity and respiration inside static chambers also suffer from experimental artifacts (Bott et al. 1997), yet they added a valuable dimension to the study by elucidating a productivity response to nutrient addition that was at least partially independent of algal biomass (Figs. 1–3).

The overnight supplementation experiment offered direct evidence that natural epilithic algae were co-limited by N and P in 2002 (Fig. 4). This assay focused upon the effects of short-term increases in nutrient availability on

periphyton productivity. Sudden rises in nutrient concentrations may occur in Lake Tanganyika under at least two conditions: following upwelling or when schools of fishes excrete nutrients in a localized area (e.g., Meyer et al. 1983). Our results indicate that natural periphyton can take advantage of such increases, yielding greater benthic productivity within 1 d. We infer that this response was co-limited by N and P because there was no measurable effect on NPP of adding N or P alone (Fig. 4). Had productivity been limited by one nutrient or the other, ambient availability of the nonlimiting nutrient should have allowed at least a small response to addition of the limiting nutrient alone, as is often observed (Francouer 2001).

Both littoral nutrient concentrations and our experimental results indicated an intriguing increase in the availability of P relative to N in 2002. The identity of limiting nutrients is often treated as a static characteristic of an ecosystem, and documented cases of natural shifts in nutrient limitation usually involve hydrological variation such as upwelling (e.g., Wootton et al. 1996) or stream flow regime (e.g., Francouer et al. 1999). In the pelagic zone of Lake Tanganyika, upwelling due to seasonal wind patterns is associated with increased availability of P (Hecky et al. 1991) and blooms of phytoplankton, including N-fixing cyanobacteria (Hecky and Kling 1981; Langenberg et al. 2003*b*; Descy et al. 2005). These shifts are observed annually at the south end of the lake during May through August and at the north end during October through November, though variation in mixing dynamics between years has been observed (Plisnier 2002; Langenberg et al. 2003*b*). Our study sites, which are nearer to the north end of the lake, are not ordinarily affected by the southern upwelling during our July–August study period.

We interpret the change in littoral nutrient limitation in 2002 to be a product of unusual coastal upwelling. In addition to higher SRP concentrations and lower DIN : SRP (Table 1), we observed littoral phytoplankton blooms lasting 2–3 d on six occasions during July–August 2002. During one of these events, we recorded some of the highest phytoplankton biomasses known from Lake Tanganyika (9.8 ± 0.5 [SE] μg Chl *a* L^{-1}, $n = 2$). Anecdotally, each bloom was accompanied by increased turbidity and the presence of jellyfish (*Limnocnida tanganicae*) and diatom colonies (*Nitzschia* sp.) of >100 μm with polysaccharide secretions. We also noted 0.9°C colder water temperatures at Jakobsen's Beach during NDS incubations in July 2001 than during the same period in 2002, and surface temperatures were lower in the pelagic zone as well during 2001 (McAndrew unpubl. data; Smith unpubl. data).

Dry-season upwelling has not been reported previously in the littoral zone of Lake Tanganyika. In our experience studying littoral ecology in the Kigoma region during July–August of 1998–2005, 2002 was the only year during which numerous, short-lived phytoplankton blooms occurred. Moreover, our results from NDS experiments at Jakobsen's Beach during 2000 and 2004 match those from 2001 (McIntyre et al. unpubl. data), indicating that the N–P co-limitation documented in 2002 was atypical. These observations indicate that upwelling can have important effects on nutrient availability and primary productivity in the littoral zone, potentially affecting the hundreds of endemic animal species found there.

Effects of herbivores—Grazers typically have stronger effects on periphyton biomass than nutrient supplementation (Hillebrand 2002), and this was clearly the case in the 2001 NDS experiment (Figs. 1, 2). Though they were unable to completely eliminate algae from uncaged substrates, grazers reduced periphyton biomass to the point that nutrient effects on Chl *a* and AFDM were undetectable. The same pattern was seen in a pilot NDS experiment in 2000 (McIntyre unpubl. data). Grazers may also have selected for different algal taxa during colonization of the substrates (Steinman 1996; Liess and Hillebrand 2004), but we did not measure periphyton composition.

This is the first experimental evidence that grazers suppress periphyton biomass in a meromictic tropical lake, which is not unexpected given the high diversity of littoral grazers in these lakes. Over 100 species of littoral fishes and invertebrates consume benthic algae in Lake Tanganyika (Coulter 1991). The mesh of our cages (1.21 cm^2) was too large to exclude small-bodied grazers (e.g., larval insects, microcrustaceans, small snails); hence, the observed effects are attributable primarily to larger grazers. Our other experiments comparing the effects of different mesh sizes indicate that fish are the dominant grazers in this system (McIntyre et al. unpubl. data), as is the case in many tropical streams (Power 1990; Flecker et al. 2002). Grazing fishes are also likely to be important in other African rift lakes, each of which has an independently evolved suite of rock-grazing cichlids.

Measurements of algal productivity in the 2001 NDS experiment showed that periphyton remained highly productive despite suppression of algal biomass by consumers. Though the AS-GPP of uncaged substrates was lower than that of caged substrates in every nutrient treatment, the decrease was small in proportion to the reduction in algal biomass (Fig. 2). In fact, BS-GPP of uncaged substrates exceeded that of caged substrates for all nutrient treatments. For instance, the uncaged P and NP treatments achieved comparable AS-GPP to the caged N treatment despite having $>70\%$ lower Chl *a*. Resilience of periphyton BS-GPP to grazing is often observed (Steinman 1996; Hillebrand 2002; Liess and Hillebrand 2004); however, strong reductions in algal biomass are usually associated with comparable decreases in AS-GPP (Liess and Hillebrand 2004). On our artificial substrates, grazers increased BS-GPP enough to partially compensate for reduced algal biomass.

In NDS experiments, nutrients often have stronger effects on algal biomass in the presence of grazers than in caged treatments (Hillebrand 2002). This interaction can yield a lack of discernable effects of the joint nutrient-grazer treatment, despite much larger negative effects of grazers alone than positive effects of nutrients alone (e.g., Flecker et al. 2002). The lack of a significant interaction between phosphorus and grazing shows that supplying limiting nutrients did not compensate for the impact of

grazers on algal biomass or productivity in our 2001 experiment (Fig. 3). Moreover, effect sizes of grazers alone and in combination with phosphorus were equivalent. Conversely, nutrients had similar effect sizes in the presence and absence of grazers, indicating that algal nutrient use efficiency was unaffected by grazers.

The overnight supplementation experiment offered indirect evidence of the effects of grazers on natural periphyton. After 24 h of protection from consumers inside the chambers, areal NPP of natural periphyton communities increased by >20% in the control treatment (Fig. 4). This increase was comparable to that resulting from a 10-fold enhancement of dissolved N and P, indicating that grazers have stronger effects on periphyton productivity than natural variability in nutrient concentrations.

We conclude that benthic grazers strongly suppress the biomass of periphyton at our littoral study sites. Their effects can be categorized as overgrazing because benthic AS-GPP is reduced; however, this reduction is small compared to the loss of algal biomass. This discrepancy is explained by the increase in BS-GPP of grazed periphyton, most likely due to selection for vigorous cells and alleviation of nutrient and light limitation (Steinman 1996). Such compensatory responses of periphyton to grazers are undoubtedly critical for sustaining the diversity and abundance of benthic algivores, and thereby the entire littoral food web, in Lake Tanganyika (Hori et al. 1993).

Though our work was restricted to the Kigoma region and the dry season, some of our conclusions may apply more broadly within the littoral zone of Lake Tanganyika and other meromictic tropical lakes. These lakes remain warm and well-lit year-round, allowing long-lived benthic grazers such as fishes and snails to achieve high densities and diversity. In order to meet their energetic and nutritional needs, given the warm temperatures and low nutrient content of algae, these abundant grazers must consume large amounts of periphyton. Thus, our evidence for top-down control of periphyton biomass and productivity is probably widely applicable in meromictic tropical lakes. In contrast, our results regarding nutrient limitation are probably specific to the region and season of our study as a result of spatial and seasonal variation in upwelling of P (Plisnier 2002; Langenberg et al. 2003*b*). Indeed, we have shown that the nature of dry-season nutrient limitation at a single site can change between years. Nonetheless, our results support the overall conclusion of Hecky et al. (1996) that P availability is the ultimate control of primary productivity in meromictic tropical lakes.

In summary, this study demonstrates that both bottom-up and top-down factors influence epilithic algal productivity in Lake Tanganyika, but top-down control has primacy. Three major aspects of the links between nutrients, algae, and grazers appear particularly promising for future work. First, the scarcity of inorganic nutrients indicates that algae and microbes must draw upon dissolved organic nutrients or other sources. Quantifying rates of inorganic nutrient uptake and mineralization of organic nutrients will provide critical insight into littoral nutrient cycling. Second, the paucity of nutrients and control of periphyton by grazers indicate the potential for strong feedbacks between grazers and epilithic algae through nutrient recycling (e.g., Andre et al. 2003). Finally, periodic upwelling of nutrients could be critical in sustaining high littoral productivity and biodiversity. Determining the frequency of littoral upwelling, and its long-term implications for primary and secondary production, is a crucial research frontier in meromictic tropical lakes.

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Received: 10 July 2005
Accepted: 22 November 2005
Amended: 6 December 2005