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Primary Research Paper

Seasonal dynamics of periphyton in a large tropical lake

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Abstract

Tropical aquatic systems are generally assumed to have little seasonality in productivity patterns. However, this study indicated that there was substantial seasonal variation in epilithic productivity and biomass in tropical Lake Tanganyika, due primarily to seasonal patterns in lake hydrodynamics that influence nutrient availability. Although they support much of the lake's biological diversity, epilithic algae made a minor contribution to the total energy budget in Lake Tanganyika. A comparison among large, oligotrophic lakes revealed no significant latitudinal trends in periphyton productivity or biomass. However, Lake Tanganyika has relatively low benthic algal biomass and is therefore more efficient at photosynthesis than the temperate lakes. The influence of wave action and consumer density and diversity may be important in moderating productivity of the epilithic community.

Introduction

Studies of primary productivity in aquatic systems often concentrate on phytoplankton communities and ignore possible contributions from periphyton. Although the area of surface substrate in the littoral zone is usually small compared to the volume of the pelagic, benthic productivity rates are frequently higher than rates among the plankton (Vadeboncoeur et al., 2001). Although they are subject to light limitation by phytoplankton, periphyton may have an advantage over phytoplankton since they may have access to additional nutrients in sedimentary material (Hansson, 1988). In oligotrophic lakes, where nutrient concentrations in the water column are low and the photic zone is relatively deep, periphyton productivity may be an important contributor to fixed carbon in the lake (Loeb et al., 1983; Hawes & Smith, 1994; Hecky & Hesslein, 1995; Vander Zanden & Vadeboncoeur, 2002). Periphyton also provide a niche for exploitation, increasing biodiversity and promoting speciation through competition and specialization (Bootsma et al., 1996). The littoral zone often serves as the spawning grounds for pelagic fish species and provides habitat during the larval or juvenile stage of their life cycle. Energy transfers within this zone can have an important impact on whole-lake processes (MacIntyre & Melack, 1995; Schindler et al., 1996).

Similar to most lakes, very little is known about periphyton and their contribution to the energy budget in Lake Tanganyika, East Africa. Lake Tanganyika is a large (mean width 50 km; length 650 km; mean and maximum depths 570 and 1470 m), oligotrophic, and permanently stratified lake. The clarity of the water allows for light penetration up to 30 m, creating a relatively deep littoral area and a large habitat available for colonization by periphyton. A preliminary study at the lake's northern end suggested that periphyton contribute substantially to littoral zone productivity and play an important role in the littoral food web (Takamura, 1988). The littoral zone of Lake Tanganyika contains one of the world's most diverse freshwater faunas, and the herbivore diversity has been attributed in part to food partitioning of this periphyton resource (Bootsma et al., 1996).

Although the lake is located just south of the equator, there may be strong spatial and temporal patterns in productivity driven by seasonal hydrodynamic changes. During the dry-windy season from May to September, strong southerly winds tilt the permanent thermocline and cause upwelling of the deeper nutrient-rich waters at the south end of the lake. Increased nutrient availability from these upwelling events produces seasonal phytoplankton blooms that can dramatically reduce water clarity (Plisnier et al., 1999). These changes impact upper trophic levels at the southern end of the lake and are reflected as seasonal patterns in community dynamics among pelagic fish species (Phiri & Shirakihara, 1999). Seasonal fluctuations in periphyton productivity may influence the littoral food web, generating a larger scale seasonal pattern in this tropical system.

This study examined seasonal variation in benthic algal dynamics at the southern end of Lake Tanganyika. Since large-scale upwelling events occur primarily in the south, these periphyton should have greater productivity and higher biomass during the dry-windy season. The greater nutrient availability from these upwellings would lead to higher average annual productivity rates than those previously measured for benthic algal communities in the north of the lake. Since light intensity is high in the tropics, there should be photo-inhibition of epilithic productivity at shallow depths. This study focused on epilithic algae because much of the lake shoreline is rocky, and it is these rocky areas that support the greatest biological diversity.

Methods and materials

Study site

While upwelling may increase productivity in the dry-windy season, increased allochthonous nutrient inputs during the rainy season may also increase productivity, possibly obscuring any autochthonous seasonal signal. To minimize terrestrial influences, the study site was located at the base of a cliff on the northern side of Mbita Island, Mpulungu, Zambia. This location ensured that the site had maximum exposure to the lake and that changes in nutrient concentration would to be due to upwelling events rather than increased terrestrial inputs during the wet season. The substrate ranged in size from small pebbles to boulders with a steep slope to 16 m after which it became a level coarse-grained sand surface. Since traditional local beliefs prohibit habitation of the island, human impacts are low and fishing at this location is minimal.

Measurements

Epilithic net productivity and respiration were measured *in situ* using oxygen change in clear and opaque chambers. Carbon fixation and respiration were calculated from the oxygen changes assuming a photosynthetic quotient of one. The chambers were constructed by J. S. Microproducts (East St. Paul, Manitoba, Canada) and covered a surface area of 0.01 m^2 with a volume of 0.8 l. Chambers were held to the rock surface by a lead sock placed over a neoprene skirt adhered to the bottom of the chambers. In order to allow for acclimation, opaque chambers were placed at least 30 min before sampling began. The water in each chamber was stirred with an interior manual paddle before samples were taken through a serum stopper using a needle and 50 ml syringe. Measurements were made along a transect at depths of 1, 2, 3, 5, and 10 m during both the wet (March) and dry-windy (July) season, and additionally at 16 m during the dry-windy season. Over a period of two weeks during each season, measurements were made almost daily at each depth with one to four replications each morning.

To avoid the development of an extensive boundary layer and oxygen supersaturation, incubations were done for as short a time as possible, ranging from 4 min at 1 m to 40 min at 16 m. In deeper water, productivity rates are slower since there is less available light; thus a longer time period was required to ensure sufficiently different initial and final oxygen concentrations. Since water temperatures in Lake Tanganyika are high (ca. 25–28 °C), ambient oxygen concentration is near 100%

saturation, and even with the short incubation times it was difficult to avoid supersaturation and bubble formation in the chambers. The temperature inside the chambers increased by up to 2 °C during the shallow water incubations, making supersaturation inevitable under the high productivity conditions associated with these depths. The loss of dissolved oxygen to bubble formation suggests that the results are likely to underestimate actual epilithic productivity, providing a conservative test for the hypothesis of increased productivity during the dry-windy season.

Dissolved oxygen concentrations were determined using Winkler titration (Stainton et al., 1977). Dissolved oxygen was immediately precipitated as a manganese oxide in the syringes using $MnSO_4$ and alkaline iodide to stabilize the oxygen concentrations. The samples then were stored with ice until return to the laboratory where the titrations were completed. This method allowed for more accurate measurements and greater precision than completing the titrations in the field.

Chlorophyll *a* content was used as measure of algal biomass. Algal scrapings were taken from the rock inside each chamber using a brush-syringe scraper constructed by J. S. Microproducts. Scrapings covered an area of 10.1 cm^2 and were taken in triplicate from each chamber. Samples were filtered through Whatman GF/C filters and extracted overnight in 90% methanol before being centrifuged and analyzed for chlorophyll. Pheophytins and turbidity (measured by absorbance at 750 nm) were accounted for when calculating chlorophyll *a* concentrations. Biomass-specific net productivity (BSNP) was calculated by dividing the net productivity measured in a chamber by the algal biomass in that chamber.

To calculate annual lake-wide epilithic productivity, I used the model developed by Loeb et al. (1983). Since light declines logarithmically with water depth, I used regression analysis of the log transformed net productivity data to establish a relationship between productivity and depth for the wet and dry season. The equations for each season were integrated using calculus to calculate net productivity to a depth of 16 m for each meter of shoreline. This value was used to determine epilithic productivity for the total distance of rocky shoreline in the lake.

For statistical purposes, productivity, respiration, and chlorophyll were log-normalized. Relationships between seasons and across depths were analyzed using a two-way ANOVA. Interaction terms were always included in the analyses. Statistical analyses were performed using JMP (SAS). Three net productivity data points (245, 385, and 2.0 mg C m^{-2} h^{-1}) and one chlorophyll datum (0.2 mg m^{-2}) were identified statistically as outliers and excluded from subsequent analyses.

Results

Productivity and respiration

There were evident seasonal differences in net productivity and respiration of epilithic algae at Mbita Island (Fig. 1). In the dry-windy season, net productivity was significantly higher ($p < 0.001$; $F = 52$) and decreased significantly with depth ($p < 0.001$; $F = 118$; $n = 151$, $r^2 = 0.52$). Respiration was also significantly higher during the dry-windy season ($p < 0.005$; $F = 8$) and decreased with depth ($p < 0.001$; $F = 18$; $n = 119$, $r^2 = 0.17$). Productivity and respiration at 16 m during the dry-windy season averaged 21 ± 3 and 11 ± 2 mg C m^{-2} h^{-1} respectively.

In both seasons, net productivity was related to depth. In the wet season, productivity was described using the equation ln prod (mg C m^{-2} h^{-1}) = 4.2–0.15 * depth (m) (standard error $(SE)_{intercept} = 0.1$, $SE_{slope} = 0.02$, $r^2 = 0.34$, $p < 0.001$) and in the dry season the regression equation was ln prod = 5.1–0.15 * depth (m) ($SE_{intercept} = 0.1$, $SE_{slope} = 0.01$, $r^2 = 0.73$, $p < 0.001$).

Lake-wide epilithic productivity

Integrating epilithic productivity using the logarithmic regression models to a depth of 16 m with 12 h of productivity each day for each season produces a value of 425 g C m^{-1} shoreline for the wet season and 900 g C m^{-1} for the dry-windy season with a total annual value of 1325 g C m^{-1}. This is a conservative value, as the actual three-dimensional productive rock surface area is undoubtedly greater than the two-dimensional approximation used here. The lakeshore is

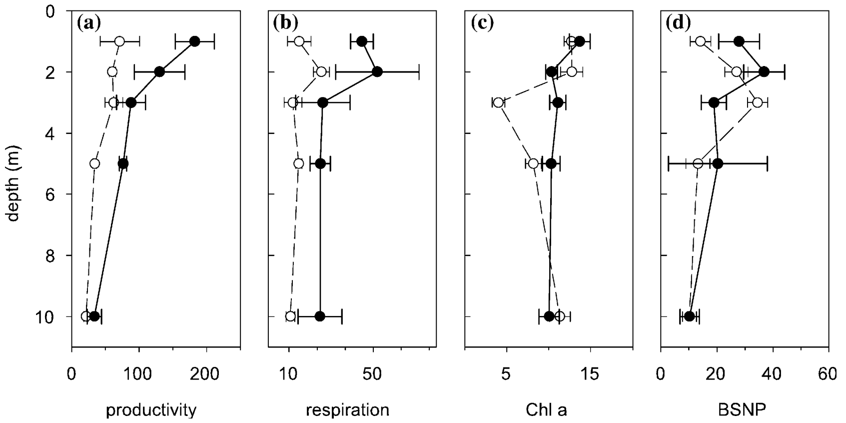

Figure 1. Epilthic (a) net productivity (mg C m^{-2} h^{-1}), (b) respiration (mg C m^{-2} h^{-1}), (c) chlorophyll (mg Chl *a* m^{-2}), and (d) biomass specific net productivity (BSNP, mg C mg Chl a^{-1} h^{-1}) for epilithic algae during the dry-windy and wet seasons. Solid lines and circles represent the dry-windy season, dashed lines and open circles represent the wet season; error bars represent one standard error.

1830 km, approximately 43% of which is rocky substrate (Coenen, 1993); thus annual epilithic productivity would be 2.28×10^6 kg C.

Biomass

Algal pigments showed minor differences in community biomass between the two seasons (Fig. 1). Chlorophyll was not significantly different between seasons ($p < 0.2$; $F = 1.6$). Chlorophyll concentrations at 16 m were 26 ± 3 mg m^{-2}. Biomass specific net productivity increased with depth until 3 m in the wet season but only increased until 2 m in the dry-windy season; after these peaks, BSNP declined with depth (Fig. 1). The difference in BSNP between seasons and across depths was not significant.

Discussion

Epilithic algae are strongly affected by seasonal variations in hydrodynamics at the south end of Lake Tanganyika. Increases in productivity during the dry-windy season suggest that the upwelling of nutrient-rich hypolimnetic waters has a considerable influence on periphyton dynamics. Nutrient concentrations increase in the south end of the lake during the dry-windy season, with reactive phosphorus concentrations increasing from 10 to 20 μg l^{-1} P and nitrate increasing from around 60 to 100 μg l^{-1} N (Plisnier et al., 1999). Phytoplankton blooms during this season have been attributed to this increased nutrient availability and can reduce Secchi depths by 10 m (Plisnier et al., 1999). This decline in light availability does not appear to reduce periphyton productivity over the depths in this study, suggesting that nutrients remain the primary factor limiting algal growth throughout the year in these shallower waters. The regression models suggest that the greatest depth at which productivity occurs is between 33 and 40 m. Secchi depth averages 11.9 m (range 7–20.5 m) annually at the southern end of the lake (Plisnier et al., 1999), which implies that there is 1% incident light (generally considered the minimum amount of light required for aquatic photosynthesis) at an average depth of 35.7 m, which agrees well with the model's predictions.

There is some evidence for photo-inhibition of algal productivity at shallow depths. As has generally been reported for periphyton (Hill, 1996), there does not appear to be photo-inhibition of productivity (per unit area) at shallow depths. However, the initial increase in BSNP with depth suggests that high light intensity may influence algal dynamics at the community level. Algal biomass is relatively greater in the upper few meters, and increasing cell density adversely influences productivity per cell (1987). The effect of light may not be apparent per unit area because photo-inhibition may occur only in the upper layers of the algal mat with compensation through greater productivity from the more protected underlayer of algae within the mat (Boston & Hill, 1991). A similar result was noted in Lake Taupo, New Zealand, where Hawes & Smith (1994) proposed that the reduced BSNP in the upper meter may be caused by photo-inhibition at the community level. In Lake Tanganyika, BSNP increases until 3 m in the wet season but only to 2 m in the dry-windy season. This is consistent with deeper light penetration during nutrient-poor, clear water of the wet season, and suggests that photo-inhibition does influence community productivity at high light intensities.

Primary productivity in Lake Tanganyika

The values for epilithic net productivity in the south of the lake are about 50% higher than those found in the study done on the northwest shoreline. Takamura (1988) found average values of 43–52.4 mg C m^{-2} h^{-1} for epilithic algae at depths of 1.5 and 4.5 m in the dry-windy season, whereas this study found productivity rates of 77.06–79.01 mg C m^{-2} h^{-1} for similar depths. This difference is consistent with the hydrodynamics of the lake basin. Seasonal upwellings are not as extensive in the north (Coulter & Spigel, 1991), and thus it might be expected that average net productivity values are lower. This provides further evidence for the importance of upwelling events and vertical mixing as a source of nutrients for primary producers in Lake Tanganyika.

Although epilithic productivity per unit area in Lake Tanganyika is much greater than that of phytoplankton, epilithic algae make a minimal contribution to the lake's total energy budget. Pelagic productivity ranges from 1.06 g C m^{-2} day^{-1} in the wet season to 2.49 g C m^{-2} day^{-1} during the dry-windy season with an average annual production of 647 g C m^{-2} (Sarvala et al., 1999). With a surface area of 32,600 km^2, annual phytoplankton productivity is approximately 2.11×10^{10} kg C. This is several magnitudes greater than the annual epilithic contribution of 2.28×10^6 kg C. Thus, epilithic productivity makes a minor contribution to the total energy budget of Lake Tanganyika.

This study did not include measurements of epipelic productivity, but since epipelic productivity is generally lower than epilithic productivity it is unlikely to have a large impact. Average epipelic productivity measured on the northeast shoreline ranged from 11.7 mg C m^{-2} h^{-1} at 2 m to 20.0 mg C m^{-2} h^{-1} at 10 m (O'Reilly, 1998). Since wave action and sediment resuspension create less stable conditions in shallower water, more suitable conditions for epipelic algae would only exist below wave base, which is around 5 m for Lake Tanganyika. Therefore, productivity might increase until depths below wave base, and the relationship between depth and productivity may not be logarithmic for epipelic algae. Approximately 31% of the shoreline has been classified as sandy shoreline (Coenen, 1993), and the calculated contribution of epipelic algae to the total annual energy budget was 3.01×10^5 kg C. This is an order of magnitude less than that of epilithic algae and five orders of magnitude less than that of phytoplankton.

Although the total contribution of epilithic productivity to the energy budget of the lake is small, the high productivity rates in the littoral zone support a diverse range of fauna. Seasonal patterns in the pelagic fish species dynamics at the south end of the lake have been documented, and spawning and the juvenile stage of some of these fish species occurs in the littoral zone. Additionally, rock-dwelling cichlid species probably breed continuously with peaks of activity that may be correlated to resource availability (P. Reinthal, University of Arizona, pers. com). At the south end of Lake Tanganyika, it seems possible that these spawning pulses may occur in conjunction with seasonal patterns of periphyton productivity, particularly among the herbivorous species. Therefore, understanding temporal patterns of epilithic primary productivity in the littoral zone may provide insights to community dynamics of the upper trophic levels in Lake Tanganyika.

Comparison with other lakes

Epilithic productivity in Lake Tanganyika does not differ greatly from that of other large oligotrophic lakes (Fig. 2). Algal growth rates are similar to those in Lake Thingvallavatn, Iceland and Georgian Bay, Lake Huron and higher than that of ultra-oligotrophic Lake Tahoe and Crater Lake (Loeb et al., 1983; Duthie & Jones, 1990; St. Jonsson, 1992). The values for Lake Malawi is

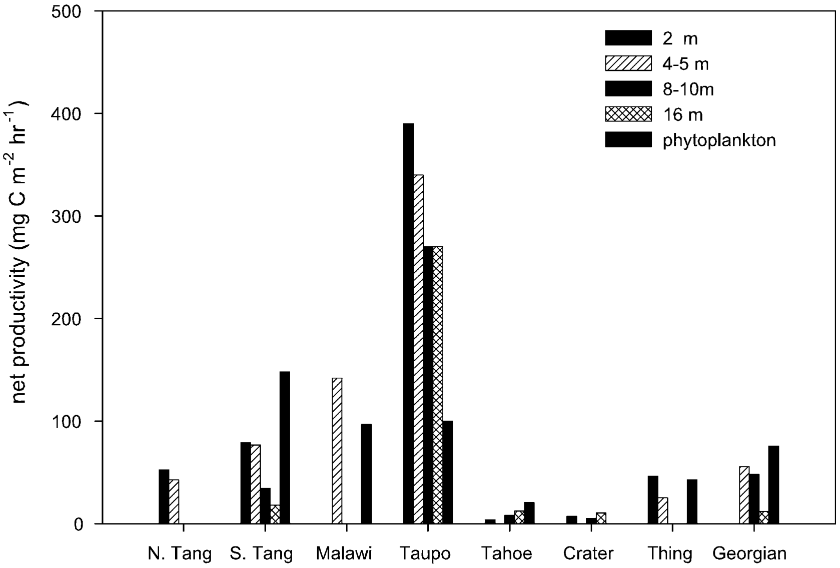

Figure 2. A comparison of epilithic net productivity among large, oligotrophic lakes. Data for southern Lake Tanganyika (S. Tang.) are from this study. Sources (with abbreviations used in the figure) for the other data are as follows: North Tanganyika (N. Tang.) (Takamura, 1988); Lake Malawi (Bootsma, 1993); Lake Tahoe and Crater Lake, North America, (Loeb et al., 1983); Lake Taupo, New Zealand (Hawes & Smith, 1994); Lake Thingvallavatn (Thing.), Iceland, (St. Jonsson, 1992); Georgian Bay, Lake Huron, North America, (Duthie & Jones, 1990).

based on only one datum (Bootsma, 1993), and subsequent work may find that epilithic productivity is similar to that of Lake Tanganyika. However, since algal biomass is low, Lake Tanganyika does have a BSNP that is 2–6 times that of the other lakes, with the only exceptions being Lake Malawi (with few data) and Georgian Bay where BSNP is similar (Fig. 3). Although Lake Taupo has extremely high algal growth rates, it also has unusually high algal biomass (160–500 mg Chl m^{-2}) and thus low BSNP (Hawes & Smith, 1994). In general, these values are substantially higher than those found for periphyton productivity in other north temperate lakes (Vadeboncoeur et al., 2003).

There do not appear to be any latitudinal patterns to epilithic productivity among these lakes. This is surprising, since the higher temperatures and greater available light found in the tropics generally stimulate primary productivity (Lewis, 1987), and these lakes do show a general trend of increasing phytoplankton productivity with decreasing latitude [data from (Goldman, 1988; Duthie & Jones, 1990; Jonasson et al., 1992; Hawes & Smith, 1994; Patterson & Kachinjika, 1995)]. Although it did vary slightly among these lakes, nutrient concentration did not correlate with epilithic productivity. This suggests that neither ambient irradiance nor open-water nutrient concentrations are the primary factors influencing benthic algal dynamics. However, the temperature variation associated with latitudinal change may be important. Higher temperatures increase microbial activity, which would lead to more rapid nutrient cycling within the algal mat. This may be a considerable source of nutrients for periphyton and a reason for the higher BSNP found in Lake Tanganyika.

The role of latitudinal factors on epilithic productivity may be secondary compared to those that have a direct impact on attached algae, such as wave action. Wave action has been invoked as a loss mechanism to explain lower algal biomass in some lakes, particularly at shallow depths (Duthie & Jones, 1990). Waves also play the additional role of reducing the boundary layer and increasing access to nutrients. With a wave base of at least 5 m, water movement could have substantial control over periphyton nutrient access in Lake Tanganyika. Although intermittent storm activity during the wet season periodically deepens the wave base, the persistent

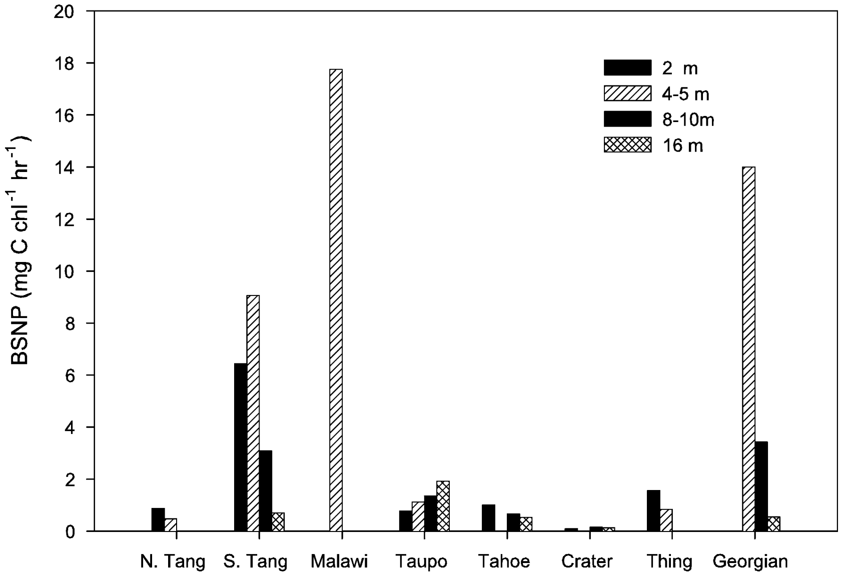

Figure 3. A comparison of epilithic BSNP among large, oligotrophic lakes. Data for southern Lake Tanganyika (S. Tang.) are from this study. Sources for epilithic chlorophyll are as follows: Lake Malawi (Higgins et al., 2003); Lake Tahoe and Crater Lake, North America, (Loeb et al., 1983); Lake Taupo, New Zealand (Hawes & Smith, 1994); Lake Thingvallavatn (Thing.), Iceland, (St. Jonsson, 1992); Georgian Bay, Lake Huron, North America, (Duthie & Jones, 1990).

winds during the dry-windy season likely lead to a constant, deeper wave base. The resulting reduction in the boundary layer may be important in maintaining good access to dissolved inorganic carbon and nutrients and in keeping the rock surface free of sediment. Wave activity has also been invoked as an influential factor in Georgian Bay, which also has high BSNP (Duthie & Jones, 1990).

Consumer density and diversity have also been implicated in the regulation of primary productivity. Grazing decreases the boundary layer, eliminates detritus and dead algal cells, and increases nutrient availability. In addition to other primary consumers, the study site had at least 6 snail species at relatively high densities (28 snails m^{-2}, SE = 1.4, n = 109) and up to 10 species of cichlid grazers (Hori et al., 1995). This consumer species richness may be one of the reasons for the low algal biomass in Lake Tanganyika (Naeem et al., 2000). Moderate densities of grazers may increase nutrient availability (Lombardo & Cooke, 2002) and enhance carbon uptake efficiency (Munoz et al., 2000). Grazers have been found to influence productivity in Lake Tahoe and have been implicated in maintaining nutrient availability for epilithic algae in Lakes Tahoe (Flint & Goldman, 1975), Thingvallavatn (St. Jonsson, 1992) and Malawi (Andre et al., 2003). A combination of wave action and consumer impact leading to low algal biomass and high BSNP rates would be consistent with the low BSNP in Lake Taupo, where there is low wave action, low herbivore density, and exceptionally high algal biomass (Hawes & Smith, 1994).

Although seasonality is more commonly perceived as belonging to temperate zones, this study documents significant temporal variability in epilithic productivity in tropical Lake Tanganyika. Increased upwelling during the dry-windy season led to increases in periphyton biomass and productivity. Although epilithic algal productivity (per unit area) is similar to that in other large oligotrophic lakes, algal biomass is relatively lower and thus photosynthesis appears to be more efficient compared to other lakes. Wave action and grazer impact may be important factors influencing the periphyton community in Lake Tanganyika, where the wave base is relatively deep and the primary consumer level consists of a high diversity and density of species.

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