

## Variability of chlorophyll *a* and photosynthetic parameters in a nutrient-saturated tropical great lake

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### Abstract

Diurnal measurements of Secchi depth, light attenuation, thermal structure, photosynthetic irradiance (PE) parameters, and chlorophyll *a* (Chl *a*) were performed at weekly intervals in three inshore bays in Lake Victoria, Uganda. The only statistically significant diurnal patterns observed were a decline in PE parameters normalized to Chl *a* and a decline in gross integral phytoplankton production. On a weekly timescale, Chl *a* was positively correlated to changes in the mean water-column temperature ( $T_{WC}$ ) in each bay. Meteorologic data in one of these bays suggest that the synchronous increases and decreases in Chl *a* and  $T_{WC}$  are related to the extent of advective exchange with deeper areas of the lake. Analysis of all data from this study, as well as available historic data, reveals that the optical properties of Lake Victoria covary with the concentration of Chl *a*. On weekly timescales, the PE parameters  $\alpha_B$  and  $P_{BM}$  covary, and both parameters generally decline as Chl *a* increases, a pattern consistent with historic data from Lake Victoria. Empirical relations are developed that relate optical properties and PE parameters to Chl *a*. These relations provide a mathematical representation of the limnologic changes that Lake Victoria has experienced through eutrophication and can be used to predict these parameters over larger spatial and temporal scales and facilitate estimates of whole-lake primary production.

Lake Victoria is the second largest freshwater lake by surface area and supports the largest freshwater commercial fishery in the world (Simonit and Perrings 2005). In the latter half of the twentieth century, increases in subsistence agricultural, deforestation, municipal and industrial effluents, and human encroachment on the shoreline that led to wetland degradation collectively gave rise to historically unprecedented nutrient loadings into the lake (Hecky 1993; Vershuren et al. 2002). The eutrophication of Lake Victoria caused a fourfold and eightfold increase in chlorophyll *a* (Chl *a*) in the offshore and inshore, respectively (Mugidde 1993), and a disproportionate increase in phosphorus loading relative to nonbiologically fixed nitrogen and soluble reactive silica loadings caused a taxonomic shift from green algae and siliceous diatoms to nitrogen-fixing cyanobacteria (Hecky 1993; Kling et al. 2001). The increase

in algal biomass has further altered the physical, chemical, and biological environment of Lake Victoria. Secchi depth measurements declined in the offshore from a range of 5.5 to 8.2 m in the 1920s (Worthington 1930) to a mean value of 2.0 m in the early 1990s (Mugidde 1993), with an associated narrowing of the light-transmission spectra that has devastated the diversity of the endemic cichlid fauna that rely upon visual coloration for sexual selection (Seehausen et al. 1997). Furthermore, increased stability of stratification, together with higher organic sedimentation to the hypolimnion, has significantly augmented the volume of seasonally anoxic water (Hecky et al. 1994) and caused loss of fish habitat and a shift in the benthic invertebrate community toward anoxia-tolerant species (Vershuren et al. 2002). In addition to these ecologic stressors, the introduction of the Nile perch in the 1950s eventually resulted, by the 1980s, in the establishment of the large commercial fishery for perch and the further restructuring of the lake's food web (Kitchell et al. 1997). Lake Victoria's fishery is currently considered over-exploited (Simonit and Perrings 2005). By 1995, a 48% decline in commercial harvesting of fish had occurred from its peak in 1990. A fourfold increase in fishing boats has occurred during the past decade, and fish-processing plants continue to be built (Simonit and Perrings 2005).

The high mean concentrations and large range of Chl *a* and macronutrients observed in modern-day Lake Victoria are unprecedented among the world's large lakes (Hecky 1993; Guildford and Hecky 2000). Mugidde (1993, 2001) concluded that phytoplankton populations in Lake Victoria were usually self-shaded by high-chlorophyll standing crops, with the highest crops in the shallowest portions of the lake. Here, we investigate temporal and

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spatial trends of Chl *a* on weekly and diurnal timescales in three inshore bays in Lake Victoria and examine relations between Chl *a* and the vertical attenuation of photosynthetically active radiation ( $k_{PAR}$ ), Secchi depth, and photosynthetic-irradiance (PE) parameters. Seasonal patterns of Chl *a* in Lake Victoria's offshore have been well defined (Hecky 1993; Mugidde 2001). However, within the inshore, only diurnal patterns of Secchi depth (Wanink and Kashindye 1998), thermal structure (MacIntyre et al. 2002), and nutrients and gases (Ramlal et al. 2001) have been directly addressed to date. PE parameters,  $k_{PAR}$ , and Chl *a* permit computation of phytoplankton production (Fee 1990). Therefore, analysis of how  $k_{PAR}$  and PE parameters vary with Chl *a* provides a framework that can be used with remotely sensed Chl *a* data, given a validated algorithm, to obtain highly resolved phytoplankton production estimates for the whole lake. This analysis is particularly important, as financial logistics severely inhibit the frequency of spatial and temporal data collection in Lake Victoria because of its immense surface area, and an accurate estimate of whole-lake phytoplankton production could be used to estimate the maximum sustainable yield of Lake Victoria's fishery by use of existing empirical models (e.g., Melack 1976; Pauly and Christiansen 1995). Finally, the derivation of Chl *a*-specific empirical relations can further extend the interpretation of both historic and current data sets, as often only one or two of these critical parameters have been measured (e.g., Secchi depth in Worthington [1930], Chl *a* and  $k_{PAR}$  in Talling [1965], and Chl *a* in Hecky [1993]) to understand how changing environmental conditions in Lake Victoria have affected the primary productivity of this great lake and its fishery.

## Materials and methods

This study was undertaken in three inshore bays, all located in northern Lake Victoria; Napoleon Gulf and Inner Murchison Bay were sampled in 2001, and Fielding Bay was sampled in 2002. In each bay, one centrally located station was selected to perform the routine measurements described below, and supplemental CTD profiles, Secchi depth, and light-attenuation profiles were carried out at four ancillary stations in each bay. Table 1 provides the location and bottom depth of all stations, and Fig. 1 depicts the central station in each bay, as well as historic stations referenced in this study. The proximity of Napoleon Gulf and Fielding Bay to the Fisheries Research and Resources Institute (FIRRI) in Jinja and the proximity of Inner Murchison Bay to the National Water and Sewerage Corporation (NWSC) in Kampala allowed samples to be immediately transported to the respective research institute for preservation or analysis, with the exception of measurements of phytoplankton photosynthesis in Inner Murchison Bay, which were transported (~2 hours) to FIRRI for incubation. Napoleon Gulf is not a typical embayment, as it experiences consistently high flow of the Nile River, the lake's outlet that exits from the gulf. To assess diurnal variability, measurements of Chl *a*,  $k_{PAR}$ , Secchi depth, and CTD profiles were repeated at three different times each day in each bay (approximately

Table 1. Location and bottom depth of central and ancillary stations within inshore bays.

Station	Latitude	Longitude	Depth (m)
Inner Murchison Bay	0°15'08"N	32°39'36"E	6.0
Inner Murchison Bay Ancillary 1	0°15'13"N	32°38'58"E	6.5
Inner Murchison Bay Ancillary 2	0°14'49"N	32°38'54"E	8.0
Inner Murchison Bay Ancillary 3	0°14'57"N	32°39'00"E	3.5
Inner Murchison Bay Ancillary 4	0°14'34"N	32°39'50"E	5.5
Fielding Bay Central	0°26'51"N	33°16'28"E	7.5
Fielding Bay Ancillary 1	0°26'44"N	33°16'54"E	9.5
Fielding Bay Ancillary 2	0°26'40"N	33°16'15"E	3.0
Fielding Bay Ancillary 3	0°27'07"N	33°16'03"E	3.0
Fielding Bay Ancillary 4	0°27'29"N	33°16'59"E	5.0
Napoleon Gulf Central	0°24'05"N	33°14'53"E	14.0
Napoleon Gulf Ancillary 1	0°24'12"N	33°14'12"E	12.0
Napoleon Gulf Ancillary 2	0°24'01"N	33°15'28"E	9.0
Napoleon Gulf Ancillary 3	0°24'44"N	33°14'59"E	5.5
Napoleon Gulf Ancillary 4	0°23'47"N	33°14'48"E	4.0

09:00 h, 13:00 h, and 18:00 h), with the exception of days 205, 242, and 323 of the year in Inner Murchison Bay, Napoleon Gulf, and Fielding Bay, respectively, when repeated measurements were not possible. Diurnal measurements of PE parameters were only conducted in Fielding Bay.

Secchi depth was measured with a white, 25-cm diameter Secchi disk as the average depth at which the disk was no longer visible upon lowering and raising it in the water column on the shaded side of the boat. A flat-collector LI-COR quantum sensor (LI-COR Biosciences) was used to determine underwater irradiance in the photosynthetically active spectral range ( $\lambda$  400 to 700 nm). Measurements were taken above and below the air-water interface and every 0.5 m thereafter to a depth of approximately 0.1% surface irradiance. Because of instrument noise above and below the air-water interface, only deeper measurements were used to determine  $k_{PAR}$ . The euphotic depth ( $Z_{eu}$ ) was taken as the depth in the water column at which 0.5% of surface irradiance occurs.

Two separate water samples for Chl *a* and PE parameter analyses were collected from the surface and at the base of  $Z_{eu}$ , as estimated in the field as 3.5 times the Secchi depth to the nearest half meter. This value may be a slight underestimation of  $Z_{eu}$ , as data presented in this paper suggest that  $Z_{eu}$  is four times the Secchi depth. Water from each depth was collected by use of a 4-L Niskin sampler and siphoned into separate 3-L, acid-washed carboys that were filled to overflowing by use of a long tube to minimize aeration. Carboys were transported in the dark to the laboratory, where they were gently shaken to ensure a homogenous sample before allocation of water for each analysis. For Chl *a* analysis, duplicate samples of 200 mL of water were passed through Whatman glass-fiber filters that were then extracted in 20 mL of 95% methanol at 4°C

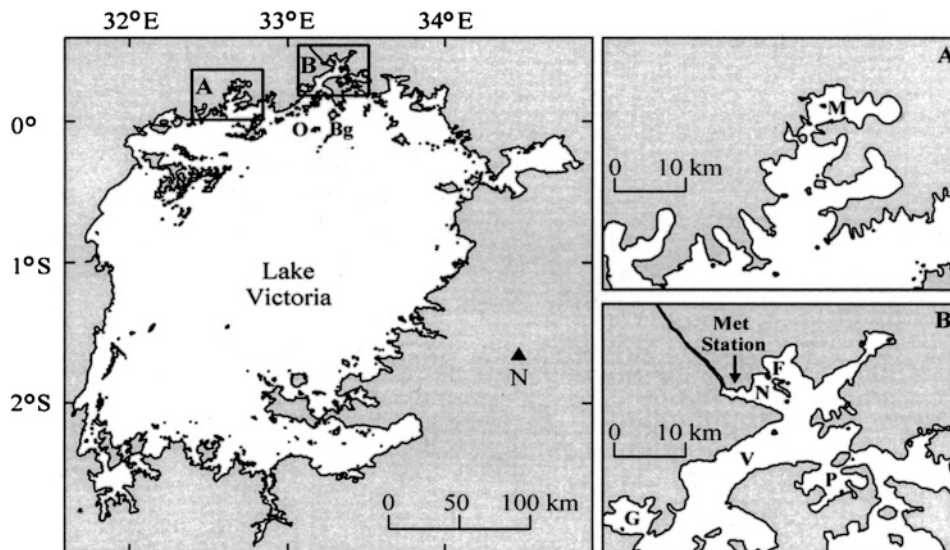


Fig. 1. Map of Lake Victoria shows the sampling location of A, Inner Murchison Bay (M), and sampling locations of B, Napoleon Gulf (N) and Fielding Bay (F), for this study. Also shown are the historic sampling locations Buvumu Channel (V), Pilkington Bay (P), and Bugaia (Bg) from Mugidde (1992) and Grant Bay (G), Kavirondo Gulf (K), and the offshore station (O) from Talling (1965).

for 24 hours. The extract was placed in a Jenway spectrophotometer (Barloworld), and absorbance was measured at wavelengths of 665 and 750 nm. Chl *a* concentration was calculated by application of the method of Talling and Driver (1963). The average relative difference of all duplicate Chl *a* samples was 4.6% ( $n = 106$ ), or  $1.4 \text{ mg m}^{-3}$  for a Chl *a* value of  $30 \text{ mg m}^{-3}$ . The extracted sample was then acidified with  $1 \text{ mol L}^{-1}$  HCl and reread at the same wavelengths to determine the contribution of pheopigments, but the percentage decline in absorbance in every sample was never below the criteria specified by Lorenzen (1967), so no correction for pheopigment contribution was applied.

PE parameters were determined by use of the light-and-dark oxygen method for both surface and  $Z_{\text{eu}}$  water samples. For each sample depth, water from the corresponding carboy was gently delivered into a series of biological oxygen demand (BOD) bottles by placing a tube at the bottom of each bottle and flushing it with approximately three times the bottle volume of the corresponding water sample. For each water sample, 10 BOD bottles were placed in a light-gradient incubator for 2 to 3 hours, 2 BOD bottles were immediately fixed to provide initial dissolved-oxygen concentrations, and 2 BOD bottles were kept in the dark for the length of the incubation to provide an estimate of community respiration. For the oxygen titration, Winkler reagents were prepared according to the technique of Stainton et al. (1977), and a HACH digital titrator (HACH Company [accuracy = 0.00125 mL]) was used to dispense sodium thiosulphate. The average relative percentage difference of all duplicate bottles was 1.12% ( $n = 144$ ). Photosynthetically active radiation (PAR) in the incubator was determined in each bottle position by use of an LI-COR  $4\pi$  quantum sensor, and the volumes of the BOD bottles were

routinely determined as the difference between dry and wet weight after filling with deionized water. Gross photosynthesis (light less dark bottle-oxygen concentrations) versus PAR was statistically fitted to a rectangular hyperbola curve (Jassby and Platt 1976) by application of the computer program PSPARMS (Fee 1990). Briefly, the PE curve has three physiologically meaningful parameters,  $P_M$  is the maximum rate of photosynthesis at saturating light,  $\alpha$  is the slope of the PE curve where photosynthesis is light limited, and  $E_K$  ( $E_K = P_M/\alpha$ ) is the light-saturation parameter of a PE curve (Talling 1957). To facilitate comparison of each variable across a Chl *a* gradient, PE parameters are normalized to Chl *a*, as indicated by the subscript B.

Mean euphotic-zone estimates of PE parameters and Chl *a* ( $\text{Chl}_{Z_{\text{eu}}}$ ) presented in this paper are the average of samples taken from the surface and at the base of the euphotic zone. On average and relative to measurements from the base of the euphotic zone, surface Chl *a* was 8% higher (coefficient of variation [c.v.] 17%), surface  $P_{\text{BM}}$  was 12% lower (c.v. 17%), and surface  $\alpha_B$  was 9% lower (c.v. 22%).

A SBE-19 CTD profiler (Sea-Bird Electronics Inc.) equipped with a WetSTAR fluorometer (WetLABS) collected vertical profiles at each station throughout the day. The conductivity, temperature, and pressure (depth) sensors on the CTD were not altered from the factory calibration, as each sensor is very precise and extremely stable. The CTD sampled at a 2-Hz interval and was lowered at an approximate descent rate of  $0.2 \text{ m s}^{-1}$ , which allowed for measurements of temperature, conductivity, and Chl *a* fluorescence every 0.1 m to the maximum depth of the station. These profiles allow the calculation of average water-column temperature ( $T_{\text{WC}}$ ), and the stability of the water column is calculated as the buoyancy

frequency,  $N = (-g/\rho \cdot d\rho/dz)^{1/2}$ , where  $g$  is gravity and  $\rho$  is density. Only data from early morning profiles (before 09:00 h) are reported, to minimize the influence of the significant diurnal heating that occurred in these inshore bays, as we are interested in persistent and not diurnal structure.

The WetSTAR fluorometer measures *in vivo* Chl *a* fluorescence ( $Chl_F$  [range 0.06–150  $Chl_F$   $mg\ m^{-3}$ , sensitivity  $\geq 0.03\ mg\ m^{-3}$ ]) and is often used to estimate extractable Chl *a* (Lorenzen 1966). However, fluorescence per unit Chl *a*, or fluorescence yield, varies with taxonomic composition (i.e., pigmentation) and physiologic status of the phytoplankton community (Falkowski and Raven 1997). For each profile, extracted Chl *a* taken from the base of the euphotic zone was compared with the  $Chl_F$  at the same depth to derive a calibration factor ( $Chl\ a : Chl_F$ ). This calibration factor was then applied to all other  $Chl_F$  measurements in the profile only below the euphotic zone to derive estimates of extractable Chl *a* at these depths. Combined with the estimate of mean  $Chl_{Zeu}$ , derived Chl *a* measurements beneath the euphotic zone provide an estimate of mean water-column Chl *a* ( $Chl_{WC}$ ) for each profile. This procedure to estimate Chl *a* from  $Chl_F$  assumes that, in any given profile, fluorescence yield ( $Chl\ a : Chl_F$ ) beneath the euphotic zone is static with respect to taxonomic composition and physiologic status. To support this assumption, the calibration factor ( $Chl\ a : Chl_F$ ) has a notably lower average c.v. for diurnal measurements (c.v. = 5%) than on weekly scales (c.v. = 42%), which implies changes in taxonomic composition and physiologic status are small in a given day and, hence, through depth because of frequent mixing to maximum depth in inshore embayments (MacIntyre et al. 2002) relative to longer timescales.

Diel-averaged data in the results section were computed by linear interpolation and static extrapolation between and beyond data points, respectively, following the logic of Fee (1990). Gross integral phytoplankton production (GPP) was calculated by application of an adapted version of Fee's (1990) phytoplankton-production model (<http://biology.uwaterloo.ca/research/uwaeg/web/index.htm>) that allows the input parameters (Chl *a*,  $k_{PAR}$ , and PE parameters) to vary diurnally. To assess how the diurnal variation of the input parameters affect GPP, the model runs that used data only from the morning, noon, or late afternoon, respectively, were compared with model runs in which all parameters were allowed to vary diurnally.

Meteorologic data for the calendar year of 2002 was provided courtesy of the Directorate of Water Development (Uganda) from a meteorologic station (Campbell Scientific) whose location is shown in Fig. 1. At this location, wind speed, wind direction, and air temperature were measured at an approximate height of 3 m above lake level at the Jinja Pier aboard a stationary vessel. Meteorologic data are applied to interpretation of limnologic measurements from Fielding Bay, approximately 6 km east.

Results

Figure 2 depicts the temporal variation of  $Chl_{Zeu}$  and  $Chl_{WC}$ , with points that correspond to daily averages and

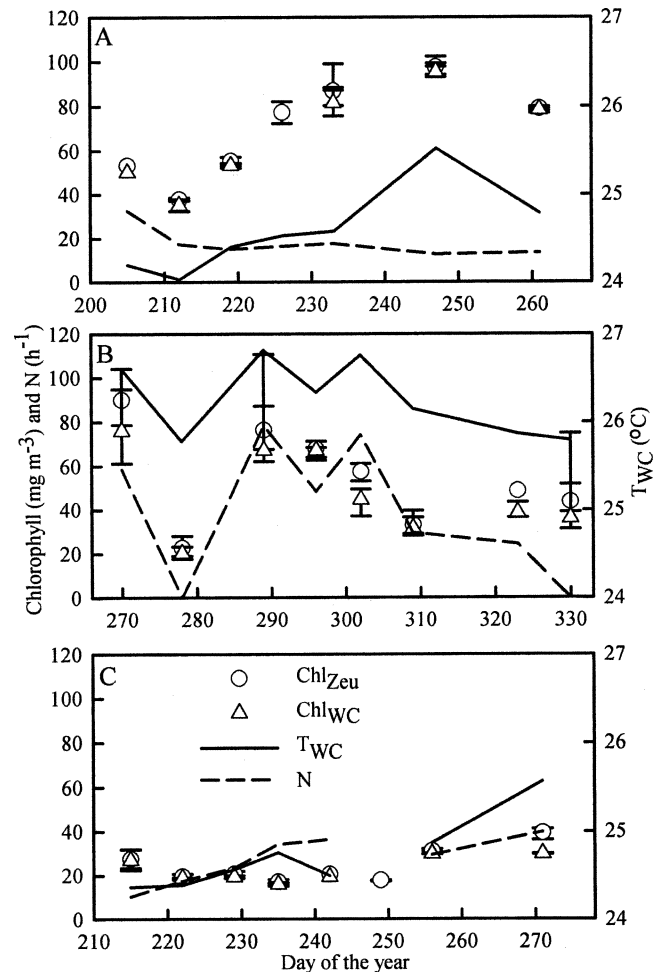


Fig. 2. Temporal variation of  $Chl_{Zeu}$ ,  $Chl_{WC}$ ,  $T_{WC}$ , and  $N$  as measured in the early morning in (A) Inner Murchison Bay, (B) Fielding Bay, and (C) Napoleon Gulf. For  $Chl_{Zeu}$  and  $Chl_{WC}$ , symbols correspond to daily averages, and error bars represent the range of data on that day. Fielding Bay measurements are from 2002. Other bays were measured in 2001.

error bars that encompass the measured diurnal range as well as  $T_{WC}$  and  $N$ , as measured in the early morning in each of the three bays. As summarized in Table 2, weekly variability of  $Chl_{Zeu}$  was approximately 2.5 to 3 times greater than diurnal variability of  $Chl_{Zeu}$  in each bay. On average, shallow Inner Murchison Bay had the highest  $Chl_{Zeu}$ , followed by deeper Fielding Bay, and the lowest  $Chl_{Zeu}$  was in the deepest bay, Napoleon Gulf. The near threefold difference of average  $Chl_{Zeu}$  between Napoleon Gulf and Inner Murchison Bay demonstrates significant spatial variability in these northern bays, as both bays were sampled over the same time period in 2001. In each bay,  $Chl_{Zeu}$  and  $Chl_{WC}$  followed similar temporal patterns and demonstrated that Chl *a* is generally vertically homogenous in these inshore areas, with slightly elevated concentrations in the euphotic zone. The most rapid temporal changes in  $Chl_{WC}$  observed in this study occurred in Fielding Bay. The daily averaged  $Chl_{WC}$  decreased 3.7-fold between days 270 and 278 of the year, followed by a 3.3-fold increase between days 270, 278, and 289.

Table 2. Coefficient of variances (%) of limnologic parameters on different temporal scales in three inshore areas. Mean values of each parameter at each study site over the entire study period are given in parentheses (n.m. = not measured).

	Chl <sub>Z<sub>eu</sub></sub> (mg m <sup>-3</sup> )	k <sub>PAR</sub> (m <sup>-1</sup> )	Secchi depth (m)	P <sub>BM</sub> (mg O <sub>2</sub> mg Chl <sup>-1</sup> h <sup>-1</sup> )	α <sub>B</sub> (mg O <sub>2</sub> mg Chl <sup>-1</sup> mol <sup>-1</sup> m <sup>2</sup> )
Inner Murchison Bay					
Weekly	35.0 (69.5)	21.3 (1.74)	18.6 (0.76)	30.5 (12.1)	43.5 (16.9)
Diurnal	13.5	11.3	10.1	n.m.	n.m.
Spatial	n.m.	10.9	9.6	n.m.	n.m.
Fielding Bay					
Weekly	42.0 (54.9)	16.4 (1.63)	26.1 (0.85)	27.9 (14.7)	50.3 (22.7)
Diurnal	13.5	8.1	12.1	9.0	10.6
Spatial	n.m.	9.3	11.9	n.m.	n.m.
Napoleon Gulf					
Weekly	26.0 (24.2)	15.7 (1.03)	18.4 (1.42)	12.1 (20.4)	24.6 (34.5)
Diurnal	9.6	9.3	10.1	n.m.	n.m.
Spatial	n.m.	13.1	9.7	n.m.	n.m.

a synchronous decrease and increase in T<sub>WC</sub> was also observed. A strong linear correlation was found between T<sub>WC</sub> and Chl<sub>WC</sub> in Fielding Bay ( $r^2 = 0.57$ ,  $p = 0.03$ ,  $n = 8$ ) and Inner Murchison Bay ( $r^2 = 0.87$ ,  $p = 0.006$ ,  $n = 6$ ) but not in Napoleon Gulf ( $r^2 = 0.18$ ,  $p = 0.34$ ,  $n = 7$ ), and N was correlated to Chl<sub>WC</sub> in Fielding Bay ( $r^2 = 0.59$ ,  $p = 0.02$ ,  $n = 8$ ) but not in the other two bays ( $p > 0.5$ ).

Data from a nearby meteorologic station, whose location is shown in Fig. 1, were available during 2002 to investigate potential links between meteorologic parameters with changes in T<sub>WC</sub> and Chl<sub>WC</sub> in Fielding Bay. Time-specific averaged meteorologic data during the 2002 period of observation (days 270 to 330 of the year) demonstrates a diel pattern, shown in Fig. 3A, with maximal air temperature and strong southerly winds that occur around 16:00 h, consistent with an afternoon lake breeze commonly observed around the Lake Victoria basin (Asnani 1993). The prominent mechanisms in Lake Victoria's inshore that induce increases and decreases in T<sub>WC</sub> are solar radiation and latent heat transfer, respectively, where the largest losses of heat correspond with strong nocturnal wind events (MacIntyre et al. 2002). Although solar radiation was not measured at the meteorologic station, the mean air temperature over the 24 hours before each measurement of T<sub>WC</sub> was positively correlated to weekly measurements of T<sub>WC</sub> ( $r^2 = 0.84$ ,  $p > 0.01$ ,  $n = 8$ ) and Chl<sub>WC</sub> ( $r^2 = 0.69$ ,  $p = 0.01$ ,  $n = 8$ ) in Fielding Bay. The diel meteorologic pattern shown in Fig. 3A does not show a consistent nocturnal land breeze, also commonly observed around the Lake Victoria basin (Asnani 1993). However, as shown in Fig. 3B, the maximum nocturnal (19:00 h–06:00 h) wind speed as averaged in a 1-hour time window exceeded 6 m s<sup>-1</sup> on 5 separate days during the 2002 period of observation. Overall, the magnitude of the maximum nocturnal 1-hour wind event before each early morning profile was negatively correlated to both T<sub>WC</sub> ( $r^2 = 0.57$ ,  $p = 0.03$ ,  $n = 8$ ) and Chl<sub>WC</sub> ( $r^2 = 0.65$ ,  $p = 0.02$ ,  $n = 8$ ).

Figure 4 shows the temporal variation of average Z<sub>eu</sub> and Secchi depth in each of the three bays, with points that

correspond to daily averages and error bars that encompass the diurnal range. As summarized in Table 2, with the exception of k<sub>PAR</sub> in Napoleon Gulf, weekly variability of Secchi depth and Z<sub>eu</sub> were approximately two times greater than both diurnal variability and within-bay spatial variability of both parameters in each of the three study areas. On average, both Z<sub>eu</sub> and Secchi depth were

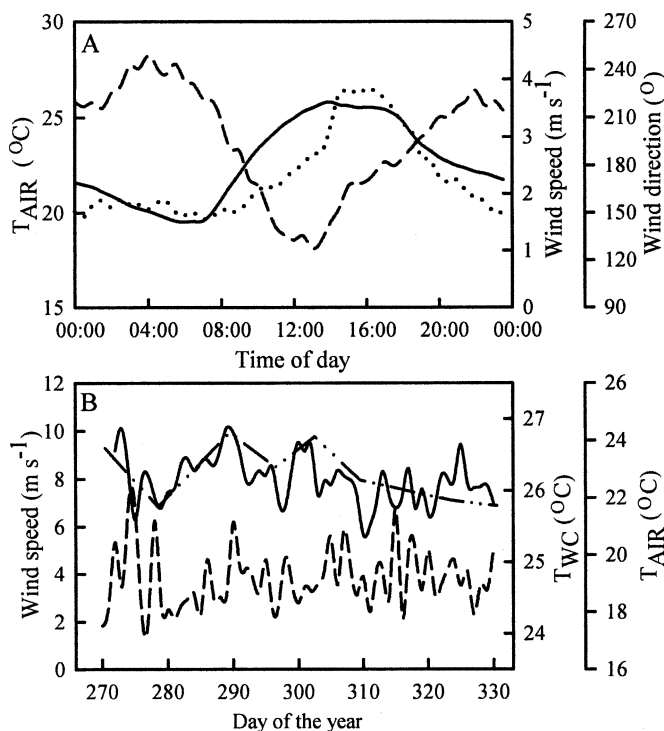


Fig. 3. Meteorologic data from Jinja Pier during 2002 study period (days 270 to 330 of year) shows (A) average diel pattern of T<sub>Air</sub> (solid line), wind speed (dotted line), and wind direction (dashed line) and (B) mean 24-hour T<sub>Air</sub> (solid line), maximum 1-hour nocturnal wind speed (dashed line), and T<sub>WC</sub> (dash-dot line) as measured in nearby Fielding Bay.

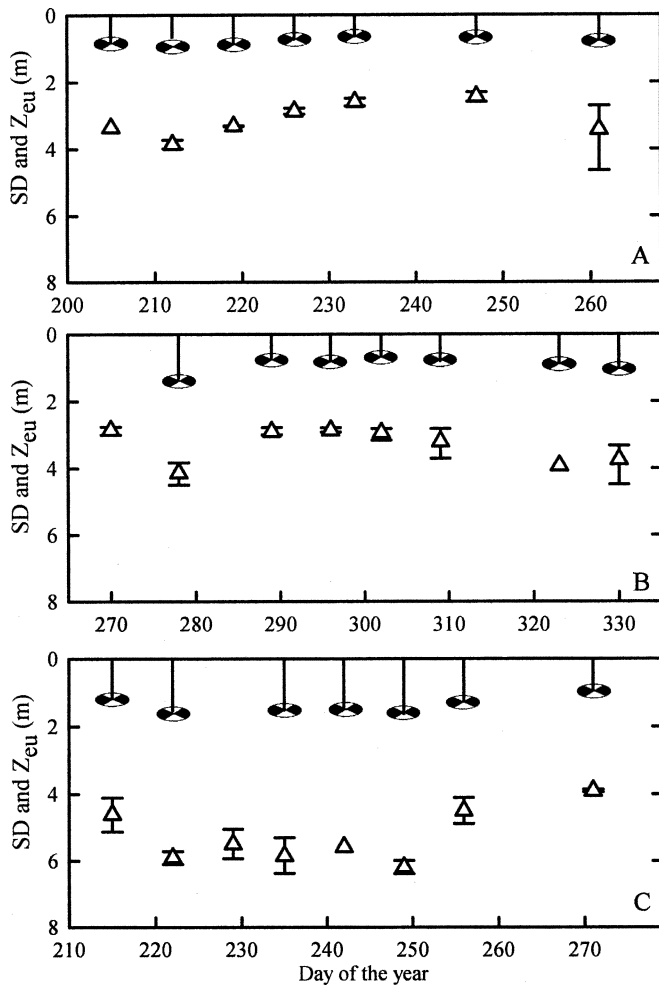


Fig. 4. Temporal variation of  $Z_{eu}$  (open triangles) and Secchi depth (hatched circles) in (A) Inner Murchison Bay, (B) Fielding Bay, and (C) Napoleon Gulf. For  $Z_{eu}$ , symbols correspond to daily averages, and error bars represent the range of data on that day. Fielding Bay measurements are from 2002. Other bays were measured in 2001.

shallowest in Inner Murchison Bay, followed by Fielding Bay, and deepest in Napoleon Gulf. In each bay, Secchi depth and  $Z_{eu}$  exhibited similar temporal patterns, as  $k_{PAR}$  is linearly correlated to the inverse Secchi depth ( $\text{Secchi depth}^{-1} = 0.79 \times k_{PAR} - 0.06, r^2 = 0.90, p < 0.0001, n = 112$ ). Both  $k_{PAR}$  and  $\text{Secchi depth}^{-1}$  were strongly correlated with  $\text{Chl}_{Z_{eu}}$ , as seen in Fig. 5A and 5B, respectively, and both curves became increasingly asymptotic as  $\text{Chl}_{Z_{eu}}$  increased. Because of the covariance between optical properties with Chl *a*, temporal and spatial patterns of  $Z_{eu}$  and Secchi depth are similar to the patterns exhibited by Chl *a* in each bay. Unpublished data (R.E. Hecky, Lake Victoria Ecosystem Project) supplements each relation with more spatially extensive data from several offshore stations that have deeper  $Z_{eu}$  and Secchi depth relative to inshore sites presented here. The historic data of Talling (1965) are also presented in Fig. 5A to assess the historic validity of the  $k_{PAR}$  versus  $\text{Chl}_{Z_{eu}}$  empirical relation. Talling's (1965) attenuation coefficients are

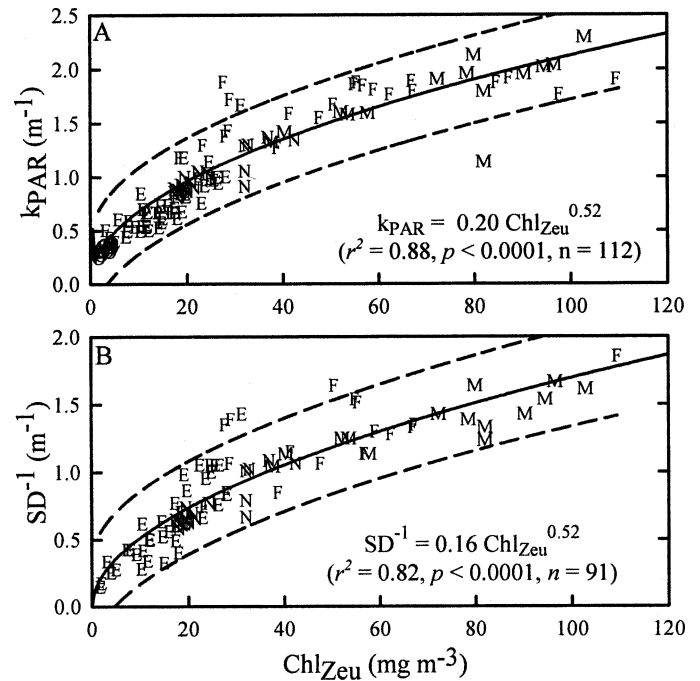


Fig. 5. Regression of  $\text{Chl}_{Z_{eu}}$  versus (A)  $k_{PAR}$  and (B) Secchi depth. The solid line is the regression curve, and dashed lines are 95% prediction intervals of the regression curves. The letter E denotes data from the Lake Victoria Ecosystem Project. All other letters denote sampling locations given in Fig. 1.

wavelength specific ( $k_{\lambda}$ ) and were converted to an estimated  $k_{PAR}$  by application of a series of curves presented in Jerlov (1976) that relate  $k_{\lambda}$  to  $k_{PAR}$ . The empirical curve presented in Fig. 5A was generated by application of  $k_{PAR}$  and  $\text{Chl}_{Z_{eu}}$  from both modern data and Talling's historic data sets. An empirical curve derived by use of only modern data provided an excellent fit to Talling's transformed attenuation data ( $r^2 = 0.91, p < 0.001, n = 15$ ), with a regression equation that was not statistically different from the regression equation in Fig. 5A that includes Talling's data ( $p < 0.05$ ).

Figure 6 depicts the temporal variation of PE parameters in each of the three bays, with points that correspond to daily averages and error bars that encompass the diurnal range for the Fielding Bay data set. As summarized in Table 2, weekly variability of  $\alpha_B$  and  $P_{BM}$  were approximately 4.7 and 3.1 times greater than diurnal variability, respectively, as measured in Fielding Bay. In each bay,  $\alpha_B$  and  $P_{BM}$  exhibited similar temporal patterns, as  $\alpha_B$  was significantly correlated to  $P_{BM}$ , as shown in Fig. 7A, despite a 5.5-fold and 3.5-fold range in each parameter, respectively. In contrast to Chl *a*, on average both  $P_{BM}$  and  $\alpha_B$  were lowest in Inner Murchison Bay, followed by Fielding Bay, and highest in Napoleon Gulf. Accordingly,  $\alpha_B$  and  $P_{BM}$  showed significant correlation to Chl *a* when fitted with equations shown in Fig. 7B and 7C, respectively; in each bay, when Chl *a* was high PE parameters were low, and when Chl *a* was low PE parameters were high. Historic  $P_{BM}$  and Chl *a* data from Lake Victoria were used to

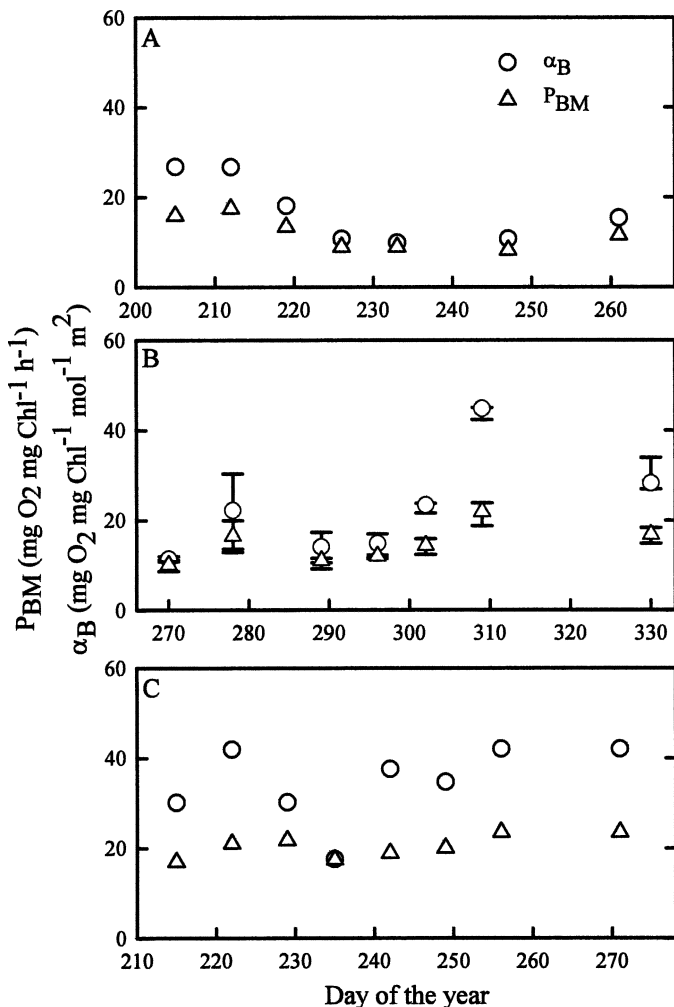


Fig. 6. Temporal variation of  $\alpha_B$  and  $P_{BM}$  in (A) Inner Murchison Bay, (B) Fielding Bay, and (C) Napoleon Gulf. Points correspond to daily averages, and error bars represent the range of data on that day.

validate this relation, as seen in Fig. 7D (Talling 1965; Mugidde 1992). Although increased unexplained variance is present in the historic data sets, a *t*-test of the linearly transformed regression equations of historic and current data sets were not statistically different ( $p < 0.05$ ).

Diurnal variations in PE parameters from samples collected at  $Z_{eu}$ , as well as the diurnally computed GPP, as measured in Fielding Bay, are shown in Fig. 8. Each parameter in Fig. 8 is normalized to its computed daily average, where labels represent day of the year. PE parameters from  $Z_{eu}$ , as well as surface samples (not shown), generally decline through the day, where a two-tailed *t*-test confirms that the differences between the morning and late afternoon population means of each parameter at each depth are statistically significant ( $p < 0.05$ ). On average,  $P_{BM}$  decreased by 11% and 18% and  $\alpha_B$  decreased by 16% and 28% between the morning and late afternoon at the surface and  $Z_{eu}$ , respectively.  $E_K$  generally increases through the day, and the largest average increases of 13% for both surface and  $Z_{eu}$  occur between midday and

late afternoon. However, this pattern is not consistent for each individual day, and two-tailed *t*-tests show that the differences between the morning, midday, and late afternoon population means are not statistically significant ( $p > 0.05$ ). GPP also generally decreases throughout the day, and the average difference between the morning and late afternoon population means of 16% is statistically significant ( $p < 0.05$ ), as calculated by a two-tailed *t*-test. In contrast,  $Chl_{WC}$ ,  $Chl_{Z_{eu}}$ , Secchi depth, and  $k_{PAR}$  (not shown) do not exhibit a statistically significant diurnal pattern; on some days these parameters increased throughout the day and on others they decreased.

## Discussion

*Optical properties covary with Chl a in Lake Victoria*—The strong covariance between  $k_{PAR}$  and Secchi depth<sup>-1</sup> with  $Chl_{Z_{eu}}$  depicted in Fig. 5A,B suggests that the optical properties of Lake Victoria may be considered as “Case I waters” (Morel 1988). However, upon comparison of the empirical relation that describes covariance of  $k_{PAR}$  with  $Chl_{Z_{eu}}$  in Lake Victoria with the same relation within oceanic Case 1 waters ( $k_{PAR} = 0.12 Chl_{Z_{eu}}^{0.43}$  [see eq. 5 in Morel 1988]), the vertical attenuation of irradiance is seen to be approximately twofold higher in Lake Victoria over the range of  $Chl_{Z_{eu}}$  presented in this manuscript, which suggests the presence of additional strong light absorbers in the euphotic zone beyond phytoplankton. Resuspension of optically active, nonliving material through vertical mixing and colored dissolved organics is probable, given the fine unconsolidated organic sediment present at each study site (Silsbe pers. obs.), although the potential contribution of these materials to  $k_{PAR}$  has yet to be quantified in Lake Victoria. The asymptotic nature of the  $Chl_{Z_{eu}}$  versus  $k_{PAR}$  and Secchi-depth curves, termed the “nonlinear biological effect” (Smith and Baker 1978), has been attributed to a decrease in the *Chl a*-specific absorption spectra ( $a^*$ ) of algal cells along an increasing *Chl a* gradient through cellular changes in the package effect and quantity of accessory pigments (Bricaud et al. 1995). The inclusion of the spatially extensive data set of the Lake Victoria Ecosystem Project, as well as the data of Talling (1965), to Fig. 5A demonstrates the validity of the empirical  $Chl_{Z_{eu}}$  versus  $k_{PAR}$  relation spatially and temporally in modern-day Lake Victoria and historically through the eutrophication of Lake Victoria.

Strong correlations of *Chl a* and optical properties allow predictions of one variable from the other. For example, Worthington’s (1930) mean offshore Secchi depth of 7.46 m ( $n = 8$ ), measured in the 1920s, is among the earliest limnologic data recorded for Lake Victoria. From the regression equation of Fig. 5B, a corresponding  $Chl_{Z_{eu}}$  concentration of 2.65 mg m<sup>-3</sup> is estimated for Worthington’s (1930) data set. This 1920s estimate of  $Chl_{Z_{eu}}$  is only slightly less than Talling’s (1965) mean offshore  $Chl_{Z_{eu}}$  concentration of 3.27 mg m<sup>-3</sup> ( $n = 13$ ) and well below the offshore  $Chl_{Z_{eu}}$  concentration of 24.5 mg m<sup>-3</sup> ( $n = 15$ ) reported by Mugidde (1993). Although comparison of these three historic data sets provides insights into the timing of the eutrophication of Lake Victoria, deep vertical mixing

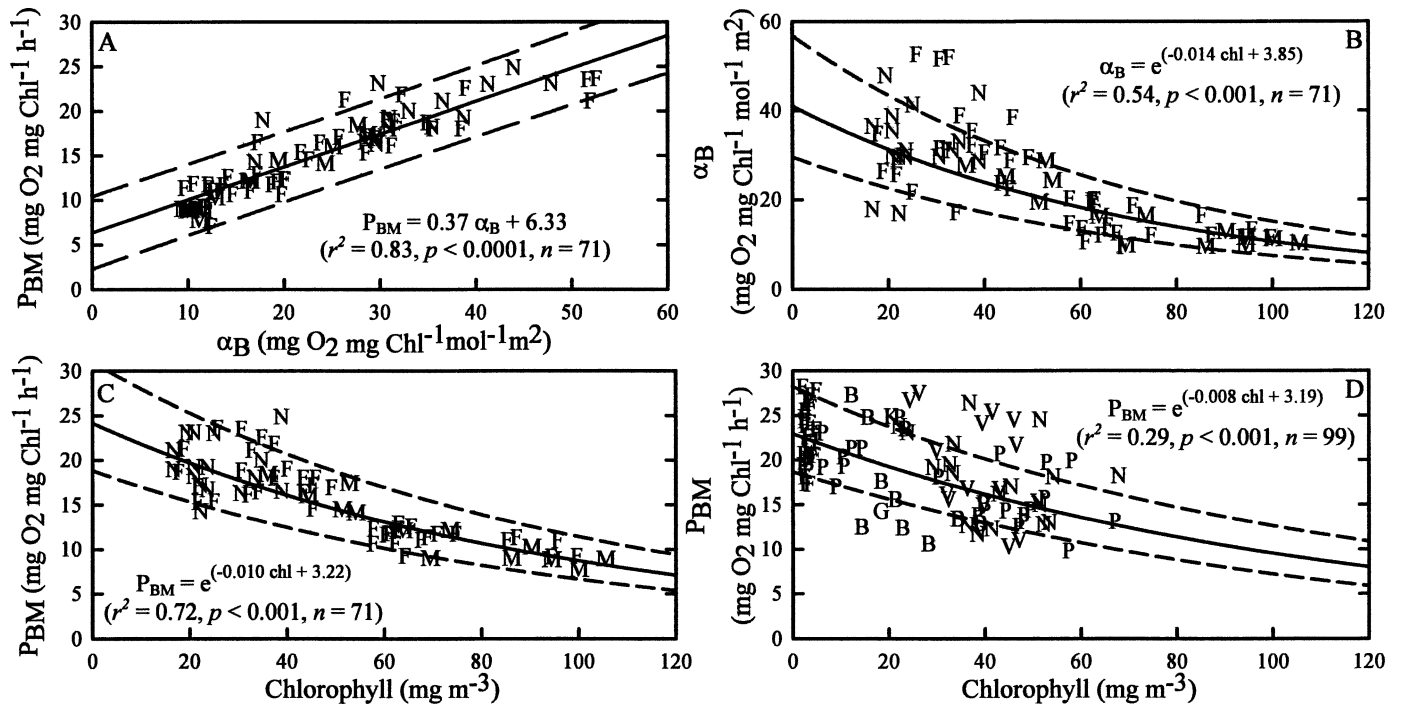


Fig. 7. Regression of (A)  $\alpha_B$  versus  $P_{BM}$  and  $Chl_{zeu}$  versus (B)  $\alpha_B$  and (C)  $P_{BM}$  from this study (M = Inner Murchison Bay, F = Fielding Bay, N = Napoleon Gulf) and (D) historic  $P_{BM}$  from Talling (1965) (O = offshore, G = Grant Bay, K = Kavirondo Gulf) and Mugidge (1992) (N = Napoleon Gulf, P = Pilkington Bay, V = Buvumu Channel). Solid lines are the regression curves, and dashed lines are the 95% prediction intervals of the regression curves.

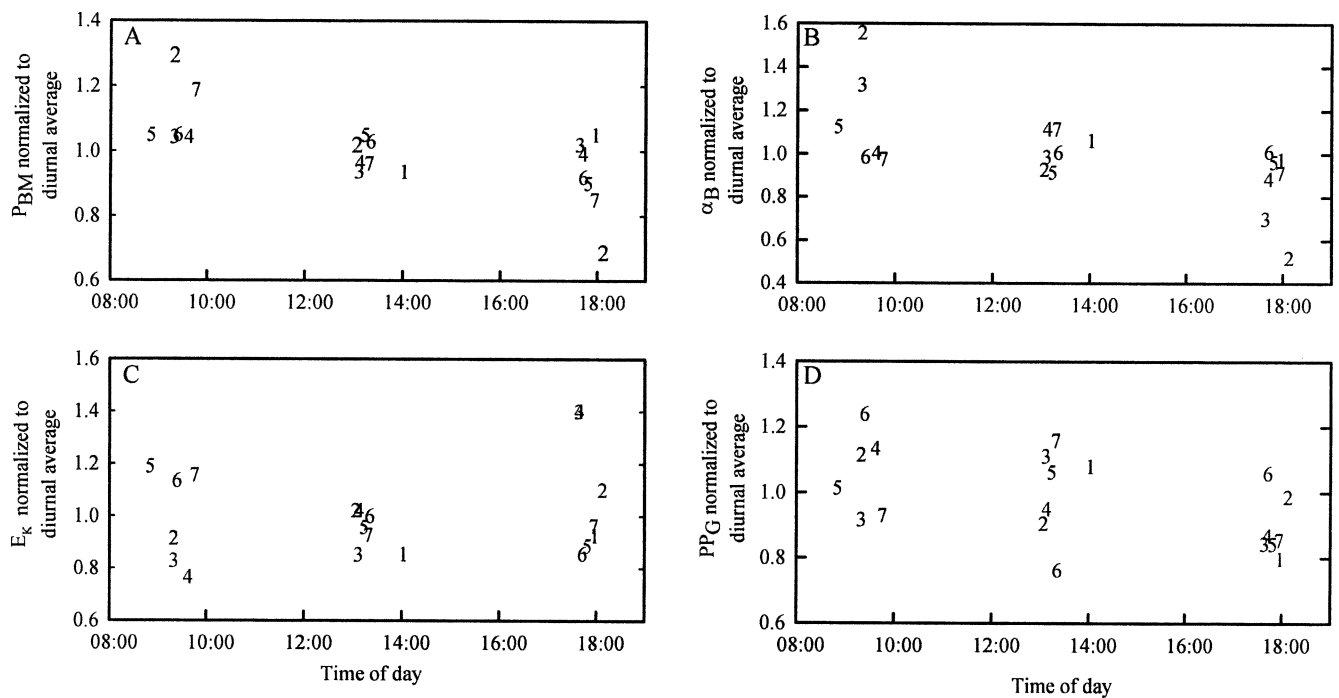


Fig. 8. Time-specific measurements of (A)  $P_{BM}$ , (B)  $\alpha_B$ , (C)  $E_k$ , and (D) GPP normalized to diurnal averages in Fielding Bay. PE parameters are from samples collected at the euphotic depth. Labels correspond to day of the year of measurement (1 is day 270, 2 is day 276, 3 is day 289, 4 is day 296, 5 is day 302, 6 is day 309, and 7 is day 330).



can still maintain low Chl *a* concentrations, as two of the modern-day offshore measurements of Chl *a* (Fig. 5B) acquired through the Lake Victoria Ecosystem Project taken during isothermal conditions are below the 1920s estimate.

*PE parameters are dependent on Chl a in Lake Victoria*— $P_{\text{BM}}$  and  $\alpha_{\text{B}}$  covary, and both parameters generally decline as Chl *a* increases, as shown in Fig. 7. Covariance of PE parameters is commonly observed (Behrenfeld et al. 2004), but this observation is the first explicit instance in which both  $P_{\text{BM}}$  and  $\alpha_{\text{B}}$  are both shown to decrease with increased Chl *a*. A recent examination of physiologic mechanisms that cause PE parameter covariance (Behrenfeld et al. 2004) provides insight as to why  $P_{\text{BM}}$  and  $\alpha_{\text{B}}$  decrease with increased Chl *a* in Lake Victoria. Behrenfeld et al. (2004) identify the ratio of photosystem II:photosystem I (PSII:PSI) as the sole photochemical parameter that links  $P_{\text{BM}}$  and  $\alpha_{\text{B}}$ , but they also propose that growth-dependent changes in reductant demand downstream of the photosynthetic pathways may drive a large degree of PE parameter covariance. As PSII is the site of oxygen evolution, and assuming the quantity of Chl *a* associated with both PSII and PSI is approximately equivalent, a decrease in PSII:PSI, therefore, decreases photosynthetic rates per unit Chl *a* in the sample volume (Falkowski et al. 1981). With respect to growth-dependent changes in reductant demand, Behrenfeld et al. (2004) propose that as nutrient stress increases, photosynthetic reductants become increasingly used for ATP generation through a metabolic pathway that consumes photosynthetically produced  $\text{O}_2$  and, thereby, also decreases photosynthetic rates per unit Chl *a*. In modern-day Lake Victoria, diatoms represent a significant portion of phytoplankton biomass when Chl *a* is low and are increasingly displaced by nitrogen-fixing cyanobacteria as Chl *a* increases (Kling et al. 2001; Mugidde 2001), similar to the historic shift observed through the eutrophication of the lake (Hecky 1993). This transition in community composition is consistent with both arguments brought forth by Behrenfeld et al. (2004) in their explanation of the observed decrease in PE parameters with increased Chl *a*. With respect to the PSII:PSI ratio, it is up to four times higher in diatoms than in cyanobacteria (Berges et al. 1996), such that the shift in community composition toward cyanobacteria with increased Chl *a* will cause a general decrease in the PSII:PSI ratio of the phytoplankton community. With respect to the growth rate-dependent demand for photosynthetic reductants, cyanobacteria have lower growth rates than do diatoms (Kilham and Hecky 1988) and require a high supply of adenosine triphosphate (ATP) to support energetically expensive nitrogen-fixation that becomes an increasingly important nitrogen source as Chl *a* increases (Mugidde 2001).

Behrenfeld et al. (2004) provide a theoretical validation of the trends observed between PE parameters and Chl *a*, and the statistical similarity to the more spatially extensive  $P_{\text{BM}}$  and Chl *a* data of Mugidde (1992) and the historic data of Talling (1965) provide empirical validation. Similar to the relation between Lake Victoria's optical properties

and Chl *a*, the regression equations of Fig. 7 provide a means to estimate PE parameters from Chl *a*. Such an estimate is of particular importance in Lake Victoria, as equipment and the immense surface area of the lake limits the quantity of PE parameter data collection. Figure 7 also provides an empirical model that describes the change in phytoplankton photosynthetic rates during historic eutrophication, where declining photosynthetic rates per unit Chl *a* with increased Chl *a* demonstrates that phytoplankton production has not increased to the same degree as algal Chl *a* biomass.

*Chl a biomass is physically determined in Lake Victoria*—Inner Murchison Bay and Napoleon Gulf were both sampled within the same time period of 2001, and differences between bays are apparent. As summarized in Table 2, on average, the shallower Inner Murchison Bay had euphotic depths 1.7 times less and  $\text{Chl}_{\text{Zeu}}$  concentrations nearly threefold greater relative to the deeper Napoleon Gulf. The average  $\text{Chl}_{\text{Zeu}}$  of 24.2  $\text{mg m}^{-3}$  in Napoleon Gulf presented in Table 2 is slightly lower than the average  $\text{Chl}_{\text{Zeu}}$  of 32.3  $\text{mg m}^{-3}$  presented by Mugidde (1992) for the same station from similar dates ( $n = 5$ ), which provides some evidence that the ongoing eutrophication of Lake Victoria no longer effects algal Chl *a* biomass. In a series of grazing experiments performed on both inshore and offshore waters, Lehman and Branstrator (1993) determined that zooplankton grazing has a negligible effect on Chl *a* and emphasized the role of vertical mixing in the determination of modern-day Chl *a* concentrations. Seasonal changes in thermal stability and mixing depth (Hecky 1993) drive changes in Chl *a* in Lake Victoria's offshore (Mugidde 1992; Kling et al. 2001), as phytoplankton production is light limited and deeper mixing reduces light available for growth (Mugidde 1993). Unlike the offshore, where the maximum potential surface mixed-layer depth of phytoplankton is set by a seasonally transient thermocline (25–65 m [Hecky 1993]), the increased frequency of complete water-column mixing in the inshore emphasizes the importance of a bay's morphometry in defining a finite limit on the surface mixed-layer depth. Provided that nutrients remain in excess or available from nitrogen-fixation into the shallowest depths of the lake (Hecky 1993; Ramlal et al. 2001; Mugidde et al. 2003), the morphometry of inshore areas influence the severity of light limitation that, in turn, affects the quantity of phytoplankton biomass possible before self-shading limits future growth. This hypothesis is not only supported by the differences between Inner Murchison Bay and Napoleon Gulf but also supported by a significant negative correlation ( $r^2 = 0.87$ ,  $p = 0.044$ ,  $n = 4$ ) between station depth with overall averages of  $\text{Chl}_{\text{Zeu}}$  in all three embayments in this study plus the inshore study site of Mugidde (1992 [15 samples from Pilkington Bay with a station depth of 7 m]).

Although station depth influences the mean algal biomass in inshore areas, the large weekly variance of  $\text{Chl}_{\text{Zeu}}$  and  $\text{Chl}_{\text{WC}}$  in inshore areas shown in Table 2 and Fig. 2 emphasizes the dynamic environment in Lake Victoria's inshore. The positive correlation between  $\text{Chl}_{\text{WC}}$

and  $T_{WC}$  on weekly timescales in each bay, as well as  $N$  and  $Chl_{WC}$  in Fielding Bay, suggests hydrodynamic motions influence temporal variance of phytoplankton biomass. Similar to morphometry,  $N$  also influences the vertical mixing of phytoplankton (MacIntyre 1993). However, considering the importance of station depth in influencing phytoplankton biomass and the large diel fluctuations that  $N$  undergoes (MacIntyre et al. 2002), the correlation between  $Chl_{WC}$  and  $N$  in Fielding Bay may be an artifact of an alternate hydrodynamic process. Meteorologic data showed that  $T_{WC}$  and  $Chl_{WC}$  in Fielding Bay was positively correlated with the maximum nocturnal wind speed. Strong overnight winds blew from the north to the south, consistent with observed nocturnal land winds over Lake Victoria (Asnani 1993). A strong northerly nocturnal wind stress over Fielding Bay would not only deepen the surface mixed layer and thereby decrease  $N$  but also, perhaps more importantly, cause water from Fielding Bay to laterally advect south to deeper areas of the lake (i.e., Buvumu Channel in Fig. 1), while causing a return flow at depth (Monismith et al. 1990). Although lateral advection routinely occurs in the inshore, strong nocturnal wind events increase the spatial range of advective exchange to deeper areas of the lake. As deeper areas of Lake Victoria are generally cooler (Silsbe 2004) and, as already shown, are expected to have lower  $Chl\ a$ , hydrologic flushing of Fielding Bay would decrease both  $T_{WC}$  and  $Chl\ a$ . This proposed hydrodynamic process is best supported in Fielding Bay between days 270 and 278 of the year, when  $T_{WC}$  decreased by  $1^{\circ}C$  and both  $Chl_{Zeu}$  and  $Chl_{WC}$  exhibited fourfold decreases after a 3-hour nocturnal wind event with an average northerly wind speed over  $4\ m\ s^{-1}$ . Moreover, in the absence of strong nocturnal wind events between days 278 and 289, both water-column temperature and  $Chl\ a$  increased by  $1^{\circ}C$  and 3.5-fold, respectively, which suggests a decreased exchange with water from deeper areas. Advective exchange between shallow Nyanza Gulf with deeper areas of Lake Victoria has been shown to affect both phytoplankton and nutrient concentrations in the Kenyan side of Lake Victoria (Gikuma-Njuru and Hecky 2005).

*Diurnal variability of PE parameters is not dependant on Chl a in Lake Victoria*—Weekly variance of PE parameters,  $Chl\ a$ , and optical properties in Lake Victoria's inshore bays exceeds diurnal variance. The only statistically significant diurnal patterns observed were the decline in PE parameters normalized to  $Chl\ a$  and GPP through the photoperiod. The light-saturation parameter  $E_k$  increases diurnally on most days, indicative of phytoplankton photoacclimation to high irradiances over the day (Senger and Fleischhacker 1978), but this pattern is not statistically significant within our limited sample size. The decline of PE parameters in Fielding Bay through the day is consistent with several studies that examined diel or diurnal periodicity of PE parameters and showed that  $P_{BM}$  is generally highest in the morning or at midday (Behrenfeld et al. 2004), as well as observed circadian rhythms of growth and cell division in cyanobacteria (Mori et al. 1996). Similar to the overall decline in PE parameters across a  $Chl\ a$  gradient

shown in Fig. 7, the diurnal decreases in PE parameters may reflect ATP-oriented pathways that consume photosynthetically produced  $O_2$  becoming more prevalent in the afternoon (Behrenfeld et al. 2004). The significance of the diurnal decrease in PE parameters is further apparent through the concomitant decline in GPP, especially considering the other parameters that influence GPP ( $Chl\ a$  and  $k_{PAR}$ ) have no such diurnal pattern. The only other diurnal examination of gross photosynthesis in a eutrophic tropical lake occurred in hypereutrophic Lake George (Ganf and Horne 1975), where a similar decrease through the photoperiod was also observed.

The absence of a discernable diurnal pattern for Secchi depth,  $k_{PAR}$ ,  $Chl_{WC}$ , and  $Chl_{Zeu}$  in any of the three inshore areas may be attributed to lateral advection of limnologically distinct water masses within each bay. Contemporaneous euphotic and Secchi-depth measurements at nearby locations around each study site shown in Table 1 demonstrated within-bay spatial patchiness in each study area, and on the basis of the relation presented between  $k_{PAR}$  and Secchi depth with  $Chl_{Zeu}$  presented in Fig. 5, we can reasonably assume a similar small-scale spatial patchiness in  $Chl\ a$ . MacIntyre et al. (2002) documented that complex patterns of mixed-layer deepening and lateral advection are prominent hydrodynamic motions in Lake Victoria's inshore Pilkington Bay. Differential mixing can drive the within-bay spatial variability observed (MacIntyre 1993), and lateral advection of distinct water masses in and out of the sampled stations then complicates the elucidation of diurnal patterns. The proposed link between within-bay spatial variability and diurnal variability is supported by the similar diurnal and spatial coefficients of variance for  $k_{PAR}$  and Secchi depth in each bay, as shown in Table 2.

*Global implications*—In shallow inshore areas of nutrient-rich Lake Victoria, the mean algal biomass is determined by the depth of the bay where hydrodynamic motions cause variance of algal biomass on both spatial and temporal scales. In turn, the quantity of  $Chl\ a$  then influences the optical properties and photosynthetic rates in the water column, as demonstrated through empirical relations shown in Figs. 5 and 7. Similar empirical relations have previously been developed that relate optical properties of a water body to  $Chl\ a$  concentrations (i.e., Morel 1988), but to our knowledge, decreases in PE parameters along an increasing  $Chl\ a$  gradient have not been explicitly shown in any other lake or ocean. Are these relations unique to Lake Victoria? Because Lake Victoria is a tropical lake, the relatively small temperature range minimizes the influence that temperature has on photosynthetic rates (Behrenfeld et al. 2002), whereas the wide range of  $Chl\ a$  in Lake Victoria (Guildford and Hecky 2000) that can be observed in a brief study period allows discernable  $Chl\ a$ -dependent trends to emerge. Morel et al. (1996) presents empirical equations that predict that  $\alpha_B$  decreases with increased  $Chl\ a$ , and a similar decline in  $P_{BM}$  may follow, provided the physiologic factors that cause general linear covariation of PE parameters (Behrenfeld et al. 2004) are consistent with the empirical equations developed by Morel

et al. (1996). In a literature review of lakes with similar Chl *a* ranges that report synchronous Chl *a* and PE-parameter measurements, only two studies were found. A reanalysis of  $P_{BM}$  and Chl *a* data from tropical Lake Awassa (Belay and Wood 1984 [Chl *a* ranges from 20 to 45 mg m<sup>-3</sup>]) shows that a negative-growth model with a regression equation  $P_{BM} = e^{(-0.04Chl_a + 3.56)}$  was statistically significant ( $r^2 = 0.59$ ,  $p = 0.0002$ ,  $n = 18$ ) but not statistically similar to the linearly transformed regression equation of our data set (Student's *t*-test,  $p > 0.05$ ), and Erikson et al. (1998) observed a decline in  $P_{BM}$  with Chl *a* in eutrophic Lake Xolotlan. These studies suggest that relations between the PE parameters and Chl *a* may not be unique to Lake Victoria, but Lake Victoria may be an ideal system to resolve which environmental factors affect photosynthetic rates in a eutrophic environment because it offers a range of optical properties and hydrodynamic environments. The empirical relations presented in this paper can extend historic data sets in which only one parameter was measured or can be applied to lakewide spatial and temporal data sets to facilitate estimates of whole-lake primary production (Silsbe 2004).

When the nonlinear relation between Chl *a* and  $k_{PAR}$  is examined, together with declining PE parameters and increased Chl *a*, in the context of a numerical phytoplankton-production model (Fee 1990), increased Chl *a* through eutrophication does not proportionally increase GPP in Lake Victoria. This finding is of particular relevance to lake stakeholders who must weigh the environmental benefits of improved water quality to be achieved by reduction of nutrient loadings and dependent phytoplankton biomass against the possible reduction of economic benefits of a productive fishery. To resolve these possible conflicts in management objectives, further research that examines the relation between Chl *a* and integral phytoplankton production across a trophic gradient of aquatic ecosystems is necessary to determine the trade-offs between water clarity and nuisance algae as expressed through Chl *a* and integral phytoplankton production.

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