Upwelling couples chemical and biological dynamics across the littoral and pelagic zones of Lake Tanganyika, East Africa

J. R. Corman,[a,b,1,*] P. B. McIntyre,[a,b,2] B. Kuboja,[b] W. Mbemba,[b] D. Fink,[c] C. W. Wheeler,[b] C. Gans,[b] E. Michel,[b,d] and A. S. Flecker[a]

[a] Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York
[b] Nyanza Project, Department of Geosciences, University of Arizona, Tucson, Arizona
[c] Cornell Laboratory of Ornithology and Department of Statistical Science, Cornell University, Ithaca, New York
[d] Department of Zoology, The Natural History Museum, London, United Kingdom

Abstract

We studied the effects of upwelling on nutrient and phytoplankton dynamics in the pelagic and littoral zones of Lake Tanganyika near Kigoma, Tanzania. During the dry season of 2004, a rise in the thermocline and sudden drop in surface water temperatures indicated a substantial upwelling event. Increases in concentrations of nitrate, soluble reactive phosphorus, and silica in the surface waters occurred simultaneously after the temperature drop. Within days, chlorophyll *a* concentrations increased and remained elevated, while inorganic nutrient concentrations returned to preupwelling levels and organic nutrient concentrations peaked. We observed parallel temporal patterns of water temperature, nutrient concentrations, and phytoplankton chlorophyll in both the pelagic and the littoral zones, demonstrating that upwelling strongly affects the nearshore ecosystem as well as the pelagic zone. Concurrent records from 12 littoral sites indicated spatial variation in the timing, magnitude, and biological response to upwelling. There was no discernable latitudinal pattern in the timing of upwelling, suggesting that mixing did not result from a progressive wave. Our monitoring, as well as other multiyear studies, suggests that dry-season upwelling occurs during most years in northern Lake Tanganyika. The observed sensitivity of littoral nutrients and phytoplankton to upwelling suggests that reductions in upwelling due to global climate change could strongly affect the dynamics of the spectacular nearshore ecosystem of Lake Tanganyika, as has been proposed for the pelagic zone.

Upwelling provides a critical source of nutrients to the photic zone of many lakes and marine ecosystems. Although most limnological studies focus on the pelagic, littoral, or benthic zones separately (Vadeboncoeur et al. 2002), hydrodynamic processes such as upwelling can influence ecosystems across multiple zones simultaneously. In lakes, increases in pelagic productivity following upwelling of hypolimnetic nutrients are well known (Hecky et al. 1996), but few studies have assessed the magnitude and ecological significance of upwelling in the littoral zone (MacIntyre and Melack 1995; MacIntyre and Jellison 2001). Upwelling could provide a substantial source of internal nutrient loading to nearshore areas as well as synchronizing temporal productivity patterns in the pelagic and littoral zones. In this article, we use a high-resolution record of an upwelling event in Lake Tanganyika to study the coupling of physical, chemical, and biological dynamics across the pelagic and littoral zones.

Upwelling plays a particularly important role in ecosystem dynamics of meromictic tropical lakes, where seasonal mixing is incomplete. These lakes are locked in an "endless summer" in which sedimentation of particulate

nutrients depletes epilimnetic nutrient pools with only occasional replenishment through partial mixing of the water column (Kilham and Kilham 1990). The lack of complete mixing results in nutrient scarcity within the epilimnion and sustained anoxia in the nutrient-rich hypolimnion. In these lakes, internal recycling is thought to be critical for supporting high primary productivity despite low ambient nutrient concentrations (Kilham and Kilham 1990). Biological processes, such as remineralization of nutrients by microbes and animals, may help to minimize sedimentary losses (Andre et al. 2003). Hydrological processes, such as upwelling of hypolimnetic nutrients, also provide a vital source of nutrients to the surface waters (Hecky et al. 1996).

Lake Tanganyika lies in the East African Rift Valley (Fig. 1) and is the largest meromictic lake on Earth, holding approximately 18% of the world's liquid freshwater (Wetzel 2001). Its temperature varies by only 4°C across a depth range of up to 1470 m (Coulter and Spigel 1991), and a difference of < 2°C at the thermocline (50–100-m depth) is sufficient to maintain stable stratification. Predictable seasonal wind patterns over the 650 × 50-km surface of Lake Tanganyika lead to partial mixing of the water column in certain areas and during particular months. During the 4-month dry season (May–September), prevailing southeast winds cause the thermocline to tilt as epilimnetic waters are displaced northward. At the southern end of the lake, the nutrient-rich hypolimnion may rise all the way to the water surface; prolonged mixing occurs

* Corresponding author: jrcorman@asu.edu

Present addresses:
[1] School of Life Sciences, Arizona State University, Tempe, Arizona
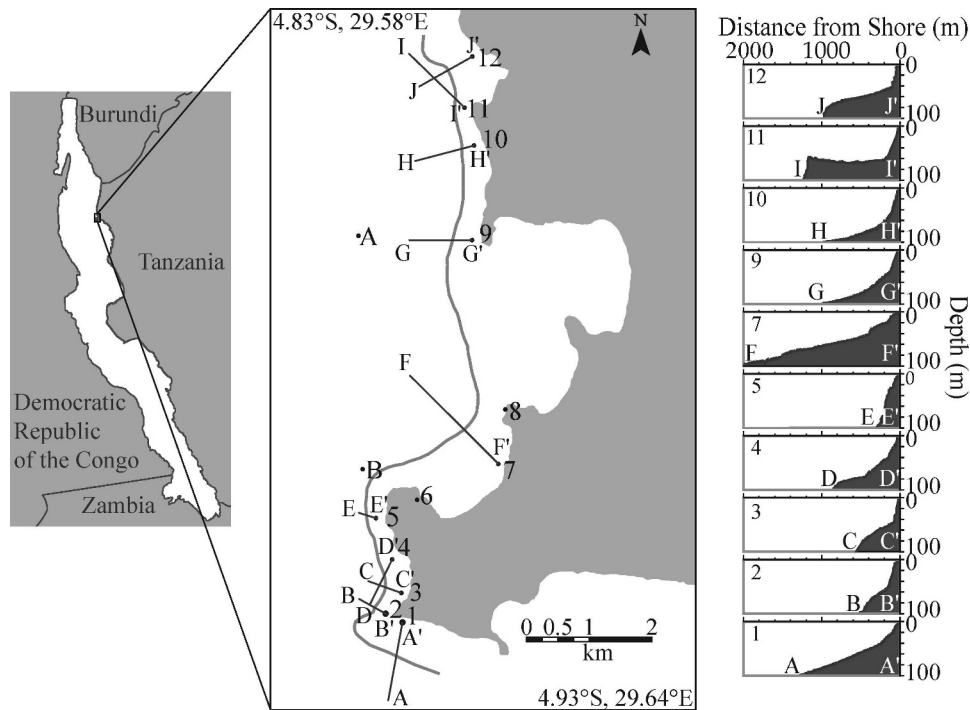[2] School of Natural Resources and Environment, University of Michigan, Ann Arbor, Michigan

Fig. 1. Location and bathymetric detail of study area of Lake Tanganyika near Kigoma, Tanzania. Littoral site locations (1–12) and pelagic site locations (A, B) are indicated in the middle panel. The contour line in the middle panel indicates the location of the 60-m contour, and straight transect lines mark the shortest travel distance from the 60-m contour to each littoral site. Bathymetric profiles are shown in the right panel.

during this "primary upwelling" (Coulter and Spigel 1991). In the northern basin, the thermocline persists but is pushed 60–70 m deeper (Plisnier et al. 1999). As the winds decline at the onset of the wet season, the longitudinal tilting pattern is reversed, causing a "secondary upwelling" in the north (Coulter and Spigel 1991; Plisnier and Coenen 2001). As the thermocline depth equilibrates, an internal wave begins with an amplitude of 30–40 m. The wave persists for 6 to 7 months, becoming a standing wave that persists throughout the year but gradually decreases in amplitude (Coulter and Spigel 1991; Plisnier et al. 1999). In addition, recent hydrodynamic models suggest Kelvin waves occur in Lake Tanganyika and could produce mixing and upwelling on a local scale (Naithani and Deleersnijder 2004).

The upwelling of nutrients is a critical control on pelagic productivity in Lake Tanganyika because external nutrient inputs can account for only 7–14% of annual primary productivity (Langenberg et al. 2003a). Epilimnetic phytoplankton biomass is generally low (< 1.0 μg chlorophyll a L^{-1}; Descy et al. 2005) but increases dramatically follow upwelling of nutrient-rich hypolimnetic water (1.96 μg chlorophyll a L^{-1}; Descy et al. 2005). Nitrogen-stable isotope data show that this additional phytoplankton growth is fueled by rapid uptake of nutrients from upwelling (O'Reilly et al. 2002). Thus, elevated phytoplankton biomass is generally associated with primary and secondary upwelling in the southern and northern ends of

the lake, respectively (Hecky et al. 1996; Plisnier and Coenen 2001; Bergamino et al. 2007). During the rest of the year, Plisnier and Coenen (2001) suggest that internal waves create localized pulses of primary productivity every 28–33 d and may also generate periodic fluctuations in secondary production. The periodicity of these waves is also noted by Coulter and Spigel (1991) to be between 25 and 30 d, while Huttula (1997) determined it to be from 23.4 days during the dry season to 34.8 d during the wet season. These monthly upwellings are thought to weaken through time, yielding a dampened pattern of coupled fluctuations in physical, chemical, and biological dynamics (Plisnier and Coenen 2001).

Although upwelling in the pelagic zone of Lake Tanganyika is well documented, its occurrence and consequences in the littoral zone have received relatively little attention in this or most other lakes. Nearshore chemistry and hydrodynamics are known to be influenced on a local scale by river inflows in Lake Tanganyika (Cocquyt et al. 1991; Vandelannoote et al. 1996), but results from other lakes suggest that vertical and horizontal water movement associated with upwelling could have more widespread effects on the littoral zone (MacIntyre and Melack 1995). Indeed, turbulent mixing along benthic substrates can enhance the effects of upwelling along shorelines compared to open waters (MacIntyre et al. 1999). The varying slope of Lake Tanganyika's deep, narrow basin (Tiercelin and Mondeguer 1991) provides an

Table 1.   Coordinates and bathymetric description (distance to 60-m contour, corresponding to the depth of the thermocline) of 12 littoral (1–12) and two pelagic (A and B) sites. The horizontal distance from shoreline to 60-m contour is not applicable (NA) for pelagic sites.

Site ID	Latitude ($4°S$)	Longitude ($29°E$)	Horizontal distance from shoreline to 60-m contour (m)
1	55.067′	35.911′	535
2	54.982′	35.766′	201
3	54.804′	35.901′	273
4	54.516′	35.822′	190
5	54.161′	35.682′	195
6	54.003′	36.037′	680
7	53.694′	36.735′	898
8	53.277′	36.795′	655
9	51.769′	36.509′	301
10	50.956′	36.526′	182
11	50.630′	36.445′	172
12	50.191′	36.512′	446
A	51.714′	35.547′	NA
B	53.714′	35.581′	NA

opportunity to assess bathymetric influence on water movements to the littoral zone during upwelling.

The objectives of this study were to evaluate the effects of upwelling in the pelagic and littoral zones of Lake Tanganyika and to quantify spatial variation in upwelling along the shoreline. We use time series of temperature, nutrient concentrations, and phytoplankton biomass in the pelagic and littoral zones of Lake Tanganyika to compare the occurrence and consequences of upwelling between zones. Within the littoral zone, we use concurrent data from 12 sites to assess spatial variability in upwelling and to address controls on the magnitude and origin of nearshore upwelling. Specifically, we hypothesized that sites with steep bathymetry experience more intense upwelling because substrate-associated turbulence occurs nearer to shore and upwelled nutrients are diluted into a relatively smaller volume of littoral water. We also use temperature records from our north–south array of littoral sites to assess whether the observed upwelling event was attributable to a progressive wave (e.g., secondary upwelling, Kelvin waves) or a standing wave. A progressive wave would produce sequential thermal anomalies along the coastline, whereas a standing wave would generate simultaneous and sustained upwelling across a large region. By characterizing upwelling dynamics at a relatively fine spatial and temporal scale, our overarching goal was to gain insight into the role of upwelling in littoral ecosystem functioning in Lake Tanganyika.

Methods

We focused on two pelagic and 12 littoral sites in Lake Tanganyika's northern basin, near Kigoma, Tanzania (Fig. 1). All sites were identified using GPS (Table 1). Pelagic sites were several kilometers offshore; littoral sites

flanked Kigoma Bay and were separated by $\sim$ 1-km shoreline distance (Fig. 1). At each littoral site, we used a Raytheon V8010 echosounder to generate depth profiles to a depth of 100 m ($\geq$ 3 transects per site); bathymetric contours were mapped using interpolation (Fig. 1).

We monitored water temperature (a semiconservative tracer of hydrodynamics), nutrient concentrations, and phytoplankton biomass (as chlorophyll *a* [Chl *a*]) at each site over a 28-d period (19 July–14 August 2004). At pelagic sites, we collected water samples every 3–4 d at 1-, 10-, 20-, 30-, 40-, 60-, 80-, and 100-m depths using a Niskin bottle. Pelagic water temperature (0.01°C resolution) and dissolved oxygen concentrations were recorded from 0 to 120 m using a Seabird 19 sonde. The thermocline and oxycline were designated as the points of maximum change in the temperature and oxygen profiles, respectively. At littoral sites, we collected water samples every 2–3 d at a distance of 10 m from shore and 1-m depth using a horizontal Van Dorn bottle. Littoral water temperatures (0.125°C resolution) were recorded every 15 min using iButton 1921H loggers placed on the substrate at 5-m depth from 22 July to 12 August. All sites were sampled the same day between 08:00 and 12:00 h. Logistical constraints required cessation of pelagic water sampling on 05 August (though temperature and oxygen profiling continued through 14 August) and of littoral water sampling between 08 and 13 August.

Water samples were kept on ice in the dark until processing ($<$ 4 h). Phytoplankton were filtered (Gelman A/E) from 2.0 liters of water and analyzed for Chl *a* by fluorometry, following extraction for 24 h in cold, buffered 90% ethanol. For chemical analyses, samples were filtered (Gelman A/E) and analyzed at the field laboratory for the following nutrients (methods and our detection limits in parentheses): silica (Si; molybdate complex; 1.78 μmol Si L^{-1}), soluble reactive phosphorus (SRP; molybdenum blue; 0.02 μmol P L^{-1}), and ammonium (NH_4; fluorometry following Holmes et al. 1999; 0.04 μmol N L^{-1}). Si and SRP samples were analyzed using a Thermo Spectronic Genesys 20; NH_4 samples were analyzed using a Turner Aquafluor fluorometer. Additionally, we filtered (Osmotics Cameo, 0.22-μm pore size) and froze samples from all littoral sampling dates and two pelagic sampling dates. These were transported to Cornell University for analysis of nitrate and nitrite (NO_3, hereafter "nitrate"; cadmium reduction; 0.07 μmol N L^{-1}), total dissolved phosphorus (TDP; high-temperature persulfate digestion and molybdenum blue; 0.03 μmol P L^{-1}), and total dissolved nitrogen (TDN; high-temperature persulfate digestion and cadmium reduction; 0.7 μmol N L^{-1}) using an autoanalyzer (American Public Health Association et al. 1995). A subset of frozen samples was also analyzed for SRP and Si to confirm field results. Dissolved organic N (DON) was calculated as TDN minus inorganic N ($NH_4 + NO_3$); dissolved organic P (DOP) was calculated as TDP minus SRP.

Statistics—Before evaluating littoral temperature records, iButton loggers were cross-calibrated to standardize results among loggers. The logger from Site 10 failed during

the study period, and its data were lost. Temperature records were compared among 11 littoral sites using a penalized regression spline model fitted with smooth, nonparametric components for both intra- and interday trends (Wood 2000). This approach allowed us to separate longer interday fluctuations in temperature from daily heating and cooling cycles. The resulting model explained 83% of the total variation in temperature based on site identity, time of day, and date. Temperature modeling was performed in R (Ihaka and Gentleman 1996) using the mgcv routine (Wood 2000).

Standardized temperature time series were used to quantify the following upwelling characteristics at each littoral site: onset (defined as the time of initial inflection point), magnitude (defined as the temperature difference between initial and second inflection points), and duration (defined as the time between onset and return to preupwelling temperatures).

To evaluate spatiotemporal variation in concentrations of nutrients and Chl *a* in the pelagic zone, we used mixed models with a repeated-measures structure. We tested for differences among sites (random factor), depths (fixed factor), dates (fixed, repeated factor), and depth–date interactions. The significance of site effects was assessed using a likelihood ratio test. A similar model structure was applied to littoral data to assess differences in nutrients and Chl *a* among sites (random) and dates (fixed, repeated). Finally, we examined whether the pelagic and littoral zones exhibited comparable concentrations and dynamics of nutrients and Chl *a* in surface waters (1-m depth) on the seven dates when both were sampled. Differences among zones (fixed), dates (fixed, repeated), sites nested within zones (random), and zone–date interactions were tested. These models were implemented using Proc Mixed in SAS 9.1. We used Tukey's honestly significant differences tests for post hoc comparisons, or, when interactions were significant, we used slice analysis to evaluate the effect of each factor while controlling for the other.

We also assessed potential explanations for variation among littoral sites in upwelling characteristics (onset, magnitude, duration) and the ensuing chemical and biological dynamics. First, we used multiple regression to test whether variation in each upwelling characteristic was related to site bathymetry or relative position along the north–south axis of the lake. Bathymetric differences were described using the minimum lateral distance between the shore and 60-m-depth contour of our bathymetric map, reflecting roughly how far hypolimnetic nutrients must travel to reach our littoral sampling locations during upwelling. Latitudinal position was defined as the distance along the lake axis from the northernmost site and used to evaluate whether upwelling occurred sequentially in a northward or southward direction. Second, to examine the association between upwelling and nutrient dynamics, we used multivariate multiple regression to test whether upwelling magnitude, bathymetry, or site position predicts increases in SRP, NO_3, Si, DOP, and DON relative to background concentrations. Finally, the relationship between nutrient increases and phytoplankton biomass increases was tested using multiple regression.
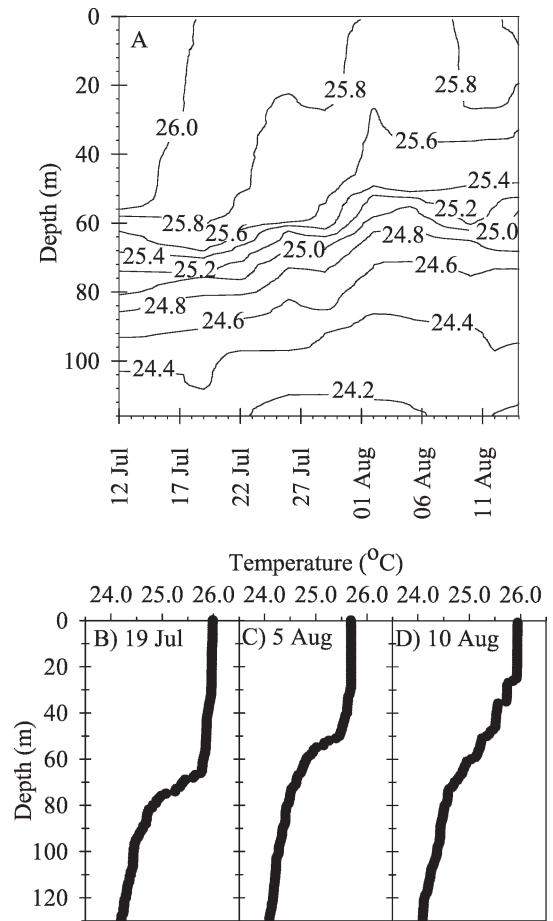

Fig. 2. Temporal change in pelagic temperature profiles. (A) Contour graph represents temperatures from 0 to 100 m at site A from 12 July through 14 August 2004; profiles illustrate temperature patterns observed on (B) 19 July before upwelling, (C) 05 August immediately after upwelling, and (D) 10 August 2004 as mixing weakened thermal stratification.

Results

Hydrodynamics—There was clear evidence of an upwelling event during our monitoring period. During mid-July, pelagic temperatures showed a range of $1.71^\circ C$ in the upper 100 m, decreasing to $1.56^\circ C$ by 22 July and to $1.49^\circ C$ by 02 August (Fig. 2). Similarly, the thermocline was at ~ 70 m on 19 July (Fig. 2A,B), rose to nearly 60 m by 22 July, and reached 50–55 m by 02 August (Fig. 2A). Surface water temperatures (0–5 m) dropped $0.30^\circ C \pm 0.01$ (SD) between 19 July and 05 August (Fig. 2C). The thermocline weakened by 02 August and remained weak through 10 August (Fig. 2D). Both pelagic sites showed the same temporal and depth patterns of water temperatures.

Littoral temperature data indicated an upwelling event coincident with that in the pelagic zone. Water temperatures at littoral sites were relatively stable until the end of July (Fig. 3). By 01 August, temperatures began to drop sharply (Fig. 3). Average daily littoral temperatures were $25.82^\circ C$ before the event and decreased by $0.34^\circ C \pm 0.04$ (SD) by 04 August (Fig. 3). This decrease was less than diel
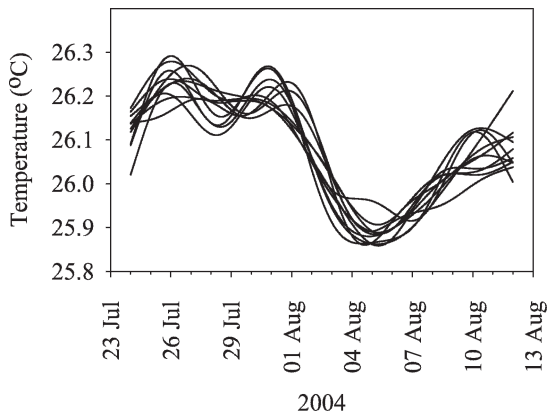
Fig. 3. Water temperatures at 11 littoral monitoring sites from 24 July to 11 August 2004, illustrating spatial variation in the onset, magnitude, and duration of thermal anomalies. Across all sites, temperatures began to drop around 28–31 July. Each line indicates a different site; diel fluctuations have been removed, and time series have been smoothed.

fluctuations (0.49°C ± 0.11 [SD]) but was clearly distinguishable even in the raw temperature record. The magnitude of temperature changes was significantly related to latitudinal position; temperature drops declined with distance from the northernmost site (*t*-test, $t = -3.01$, df $= 8$, $p = 0.017$). The largest decrease was at site 9 (0.41°C) and the smallest at site 2 (0.29°C). Although onset times varied among sites by 74.0 h, there was no significant latitudinal (north-to-south or south-to-north) pattern in upwelling onset. Lower temperatures lasted for an average of 142.6 ± 34.1 h (SD; Fig. 3) before temperatures returned to preupwelling levels. The duration of upwelling increased significantly with distance from the northernmost site (*t*-test, $t = 2.867$, df $= 8$, $p = 0.021$). There was no statistical evidence that littoral bathymetry affected the onset, duration, or magnitude of the temperature anomaly from upwelling.

Chemistry—In the pelagic zone, depth profiles of oxygen and nutrients exhibited a pattern similar to temperature (Figs. 2A, 4A,B). On 19 July, the oxycline was at 70 m and began rising by 26 July, reaching 40 m by 05 August and then descending after 05 August (data not shown). The chemoclines for SRP and Si showed the same pattern, rising steadily through 02 August and descending after 05 August (Fig. 4A,B). The two pelagic sites showed statistically similar patterns of nutrient chemistry across depths and dates. There were highly significant main effects of both depth and date; however, depth–date interactions complicated interpretation of SRP ($F_{31,32} = 2.34$, $p = 0.010$) and Si ($F_{38,40} = 2.03$, $p = 0.015$) dynamics. Slice analyses showed that concentrations varied significantly among dates only in samples collected at ≥ 40 m (depth $=$ 1–30 m, $p \geq 0.101$; depth $=$ 40–100 m, $p \leq 0.014$), but increased concentration of Si and P with depth was highly significant across all dates ($p < 0.001$ in all comparisons). Pelagic nitrate data were available only for 05 and 14 August, but they also showed a general increase with depth
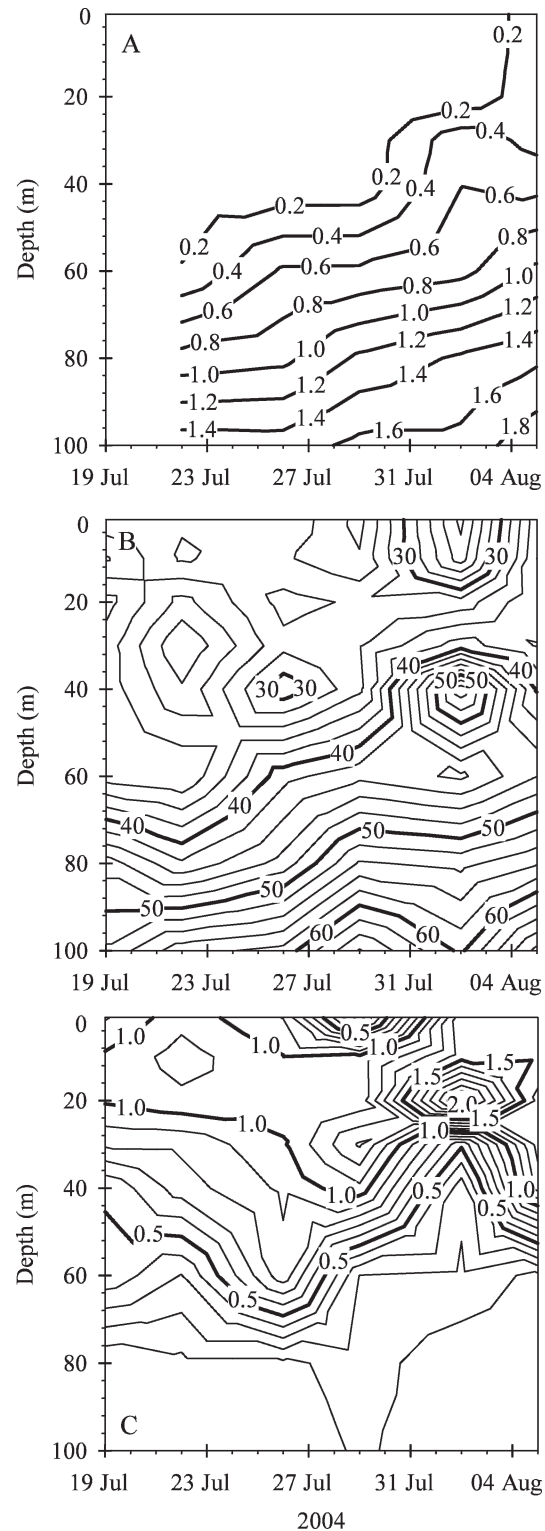

Fig. 4. Contour graphs from 19 July through 05 August 2004 at pelagic site A of (A) soluble reactive phosphorus (SRP, μmol P L^{-1}), (B) silica (Si, μmol Si L^{-1}), and (C) chlorophyll *a* (Chl *a*, μg Chl *a* L^{-1}) concentrations. SRP and Si concentrations increase in the epilimnion through 02 August, with a coincident increase in Chl *a* concentration on 02 and 05 August. The blank space in (A) represents missing data for 19 July.

Table 2. Percent change in concentrations of soluble reactive phosphorus (SRP), silica (Si), nitrate (NO_3), chlorophyll *a* (Chl *a*), dissolved organic nitrogen (DON), and dissolved organic phosphorus (DOP) from baseline concentrations to upwelling concentrations at each littoral site (1–12).

Site ID	SRP (%)	Si (%)	NO3 (%)	Chl *a* (%)	DON (%)	DOP (%)
1	−11	7	−23	−18	60	12
2	61	3	307	130	66	331
3	248	9	438	192	37	276
4	125	16	737	155	−10	220
5	405	20	2384	188	36	259
6	199	14	1775	101	32	402
7	239	10	1599	129	15	474
8	67	2	281	151	37	331
9	202	8	441	166	35	259
10	245	13	215	130	62	309
11	220	12	913	71	48	264
12	164	12	711	167	18	−53

as well as 58% higher mean concentrations in the upper 40 m on 05 August (1.81 μmol NO_3-N L^{-1} ± 0.48 [SD]) than 14 August (1.14 μmol NO_3-N L^{-1} ± 1.60 [SD]; data not shown).

Littoral nutrient concentrations varied significantly through time (SRP: $F_{9,98} = 30.48$, $p < 0.001$; Si: $F_{9,98} = 16.22$, $p < 0.001$; NO_3: $F_{9,99} = 9.96$, $p < 0.001$) in accordance with temperature shifts. Concentrations of SRP, NO_3, and Si were significantly higher on 05 August than any other date (all $p \leq 0.016$), then returned to preupwelling conditions (defined as the average between 19 and 31 July, hereafter "baseline") by 07 August and dropped marginally lower by 14 August. There were also differences in SRP concentrations among littoral sites ($\chi^2 = 4.79$, df = 1, $p = 0.029$), though no pairwise comparisons were significant.

Upwelling produced the largest increases in SRP, Si, and NO_3 at site 5 (405%, 20%, and 2384%, respectively) and the smallest changes at site 1 (−11%, 7%, and −23%) and site 8 (67%, 2%, and 281%; Table 2). Both upwelling magnitude and littoral bathymetry had significant multivariate effects on nutrient dynamics ($F_{5,3} = 18.79$, $p = 0.019$, and $F_{5,3} = 11.07$, $p = 0.038$, respectively). Oddly, both NO_3 and DON changes were negatively related to the magnitude of upwelling ($F_{1,7} = 7.70$, $p = 0.027$, and $F_{1,7} = 4.22$, $p = 0.079$, respectively). NO_3 and SRP dynamics also were influenced by littoral bathymetry ($F_{1,7} = 14.97$, $p = 0.006$, and $F_{1,7} = 3.86$, $p = 0.090$, respectively); sites with the steepest bathymetry received the greatest nutrient inputs. Neither site characteristics (latitudinal position and bathymetry) nor upwelling characteristics (onset, magnitude, or duration) predicted spatial variation in Si or DOP dynamics.

There were no overall differences in surface nutrient concentrations between the pelagic and littoral zones, but there were significant differences among sampling dates for SRP ($F_{5,69} = 41.27$, $p < 0.001$) and Si ($F_{6,70} = 12.70$, $p < 0.001$). Significant zone–date interactions arose for SRP ($F_{5,69} = 4.62$, $p = 0.001$) and Si ($F_{6,70} = 4.63$, $p < 0.001$) because of lower littoral concentrations of SRP on 05 August ($p < 0.001$) and of Si on 29 July ($p = 0.012$), 02 August ($p < 0.001$), and 05 August ($p = 0.056$; Figs. 4, 5). Pelagic surface SRP concentrations more than tripled from baseline to 05 August (reaching 0.28 μmol P L^{-1} ± 0.01 [SD]), while littoral SRP increased 180% (reaching 0.17 μmol P L^{-1} ± 0.07). Similarly, surface silica concentrations increased nearly 20% in the pelagic (reaching 37.03 μmol Si L^{-1} ± 0.56) but only 11% in the littoral (reaching 34.46 μmol Si L^{-1} ± 1.42). Temporal changes in surface concentrations of SRP and Si accord well with the pelagic depth gradient at the beginning of the study period, when SRP was 0.2–0.4 μmol P L^{-1} and Si was 34–38 μmol Si L^{-1} at 60-m depth (Fig. 4). In addition, littoral NO_3 increased by 815% (reaching 0.55 μmol N L^{-1} ± 0.48; Fig. 5). By 14 August, Si and SRP concentrations in both the pelagic and littoral zones had returned to baseline levels (Fig. 5A). NH_4 levels were uniformly low (generally below detection limit: < 0.04 μmol N L^{-1}) at all pelagic and littoral sites throughout the study period.

Dissolved organic nutrients showed different temporal dynamics from inorganic nutrients. In the pelagic zone, DON (measured only on 05 and 14 August) increased slightly with depth and constituted ~ 80% of TDN. DOP (measured only on 05 and 14 August) was always < 0.05 μmol L^{-1}, contributing less than 15% to TDP. In the littoral zone, average DON and DOP concentrations were stable before the upwelling, then rose dramatically on 07 August (DON: $F_{9,99} = 9.23$, $p < 0.001$; DOP: $F_{9,97} = 35.23$, $p < 0.001$) and remained elevated through 14 August (Fig. 5). Proportional postupwelling increases were 36% for DON and 257% for DOP. Mean TDN:TDP ratio across all sites dropped from 53.9 ± 12.8 (SD) on 29 July to 25.7 ± 9.3 (SD) on 05 August. DON constituted 97% of TDN, and DOP constituted 18–80% of littoral TDP.

Phytoplankton biomass—In the pelagic zone, phytoplankton biomass (as Chl *a*) varied significantly with depth ($F_{7,8} = 51.52$, $p < 0.001$; Fig. 4C). It was consistently highest at 10–20 m, averaging 1.21 μg L^{-1} Chl *a* ± 0.37 (SD). There were also significant differences among
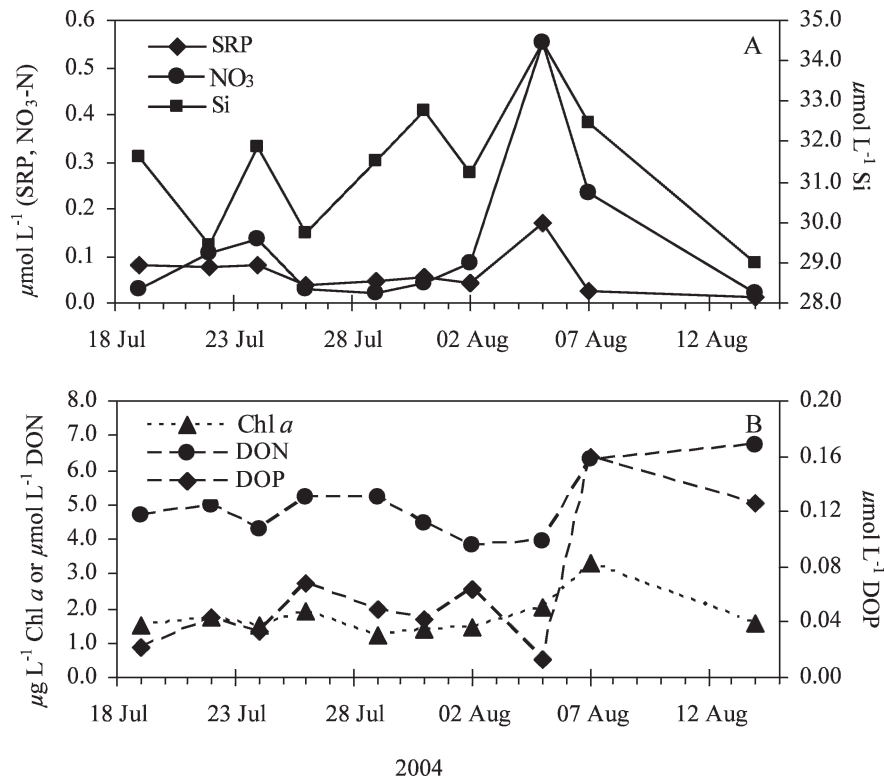
Fig. 5.   Mean concentrations of (A) dissolved inorganic nutrients (soluble reactive phosphorus, nitrate, and silica) and (B) chlorophyll *a* and dissolved organic nutrients (organic nitrogen and organic phosphorus) across littoral sites from 18 July through 14 August. Soluble reactive phosphorus (SRP), nitrate (NO_3), and silica (Si) increase on 05 August, followed by an increase in chlorophyll *a* (Chl *a*), dissolved organic nitrogen (DON), and dissolved organic phosphorus (DOP) on 07 August. Note that (A) Si and (B) DOP are plotted on the secondary axis.

sampling dates ($F_{6,40} = 6.77$, $p < 0.001$); peak values were observed across all depths on 02 and 05 August, reaching 2.15 ± 0.02 (SD) and 1.49 ± 0.07 (SD) μg Chl *a* L^{-1}, respectively (Fig. 4C). However, depth–date interactions were also significant ($F_{38,40} = 3.51$, $p < 0.001$) because Chl *a* differed significantly among dates only at depths ≤ 40 m ($p < 0.047$). At 60 m and below, phytoplankton biomass was consistently < 0.87 μg Chl *a* L^{-1}. There were no differences in Chl *a* between pelagic sites.

In the littoral zone, surface phytoplankton Chl *a* varied significantly among sampling dates ($F_{9,98} = 13.32$, $p < 0.001$; Fig. 5). Mean values peaked on 07 August (3.33 μg L^{-1} ± 0.66 [SD]) and were significantly higher than all previous (1.52 μg L^{-1} ± 0.40 [SD]) and subsequent (1.58 μg L^{-1} ± 0.36 [SD]) dates ($p < 0.001$). Although nutrients and Chl *a* were not measured between 07 and 14 August, our daily field observations indicated that phytoplankton biomass remained elevated until 13 August.

Littoral Chl *a* also varied significantly among sites ($\chi^2 = 13.32$, df $= 1$, $p = 0.005$). Site 1 had the highest phytoplankton biomass, while all other sites were similar. Following upwelling, the greatest change in Chl *a* from baseline to 07 August was observed at site 3 (192% increase) and the smallest at site 1 (18% decrease). The increase in Chl *a* associated with upwelling conditions was not significantly correlated with changes in nutrient concentrations.

Discussion

There was clear evidence of contemporaneous upwelling in the pelagic and littoral zones. Although the overall character of the event was similar to previous reports of upwelling in the pelagic zone (Coulter and Spigel 1991; Plisnier et al. 1999; Langenberg et al. 2003*b*), our higher temporal resolution and joint pelagic–littoral sampling offer new insights into upwelling dynamics in Lake Tanganyika. There was a steady rise in the thermocline for at least 11 d prior to the upwelling (Fig. 2) but no decrease in littoral water temperatures during this period. Upwelling affected surface temperatures on 01 August, after which we observed cooler surface waters for approximately 1 week in both the pelagic and the littoral zones (Figs. 2, 3). Pelagic temperature, oxygen, and nutrient data all indicate that the rising thermocline remained highly stable, preventing vertical mixing (Rimmer et al. 2005). Only after the thermocline was closest to the surface did thermal stratification weaken considerably (Fig. 2).

In the pelagic zone, the temperature of surface waters on 05 August corresponded to temperature observed at approximately 60 m on 12 July, suggesting the mixing or displacement of surface water extending to at least 60 m. Similarly, the average temperature drop in the littoral zone (0.34 ± 0.04°C [SD]) indicated the equivalent of complete flushing with water from approximately 66 m. Although rough, these calculations underscore the great depth across which upwelling produces mixing in Lake Tanganyika. Moreover, large thermal anomalies were observed along the shoreline even within large bays with relatively shallow bathymetry (sites 1, 6, 7, and 8; Fig. 1). Together with the long duration of influence of the thermal anomaly, this set of observations indicates upwelling of a large volume of water from a substantial depth.

There are several potential mechanisms that could be responsible for this upwelling event, including an internal standing wave derived from the 2003 seiche (Coulter and Spigel 1991; Plisnier et al. 1999), new secondary upwelling following early cessation of the southerly winds, or a progressive Kelvin wave (Naithani and Deleersnijder 2004). Neither the Kelvin wave nor the secondary upwelling hypothesis matches the available data. A Kelvin wave is an internal progressive wave that propagates clockwise around the perimeter of the lake with peak amplitudes at the shore. Although hydrodynamic models indicate the potential for Kelvin waves in Lake Tanganyika (Naithani and Deleersnijder 2004) and suggest a potential role in littoral upwelling (Naithani et al. 2007), the slow rise of the thermocline and lack of a directional pattern in the onset of upwelling along the ~ 9-km distance between our sites argue against a Kelvin wave. Similarly, secondary upwelling and associated progressive internal waves are unlikely explanations. In addition to the lack of a directional pattern of onset, the event occurred in early August, which is at least 1 month before new secondary upwelling is typically observed in the northern basin (Coulter and Spigel 1991; Plisnier et al. 1999; Langenberg et al. 2003*b*), although observations of smaller scale upwellings in this region have occurred during the same time period as our study (Huttula 1997). No major changes in the wind or air temperature were observed at a shoreline weather station in Kigoma during June–August, as would be expected prior to either large-scale secondary upwelling or upwelling driven by local weather anomalies.

Taken together, the temporal and spatial patterns of upwelling that we documented in July–August 2004 are most compatible with an internal standing wave derived from seiching during 2003. Following cessation of southerly winds in September or October, seiching gives rise to secondary upwelling in the northern basin that propagates southward as the thermocline depth begins to equilibrate (Coulter and Spigel 1991; Plisnier et al. 1999). The initial internal progressive wave is transformed into a standing wave that produces upwelling events up to 7 months after secondary upwelling (Coulter and Spigel 1991; Plisnier et al. 1999). The persistence of such internal waves throughout the year is demonstrated by pelagic temperature data (Huttula 1997).

The steady rise of the thermocline over nearly 2 weeks also matches the observed periodicity of internal waves in Lake Tanganyika (Coulter and Spigel 1991; Plisnier et al. 1999). However, the strength of upwelling, both in terms of its duration of influence and in terms of the magnitude of chemical and biological effects, exceeded that expected from a standing wave that has been dampened continuously since the initial secondary upwelling the previous year (Plisnier and Coenen 2001). It is also worth noting that we observed a sudden, single-day drop in lake level of ~ 10 cm along the Kigoma shoreline on 26 July 2004, as might be expected from a surface seiche. Thus, we consider internal standing waves to be the most likely source of dry-season upwelling in northern Lake Tanganyika, but a definitive resolution awaits further investigation. Its origins notwithstanding, upwelling in the central and northern basins of Lake Tanganyika during July–August of the dry season does not fit the traditional model of seasonal upwelling dynamics in Lake Tanganyika (Coulter and Spigel 1991; Plisnier et al. 1999). However, a recent analysis of remote sensing imagery in Lake Tanganyika (Bergamino et al. 2007) shows clear evidence of a secondary peak in pelagic phytoplankton occurring in August in the central basin of most years between 1998 and 2004. Moreover, Descy et al. (2005) found deeper mixed layers and secondary peaks of phytoplankton Chl *a* in the pelagic zone near Kigoma during June–August 2002 and 2003. In our daily fieldwork in the littoral zone of this region during July–August 1998–2007, we rarely observed littoral phytoplankton blooms before 2002, and the observed blooms generally lasted only a few days. However, we inferred that repeated, short-lived phytoplankton blooms in 2002 were associated with an influx of P from upwelling (McIntyre et al. 2006), and herein we have provided strong thermal, chemical, and biological evidence of upwelling in 2004. During the 2004 event, our field team observed anomalously cold water, phytoplankton blooms, and the presence of jellyfish in the littoral zone for at least 10 d. Our continued monitoring of littoral water temperatures during July–August 2005–2007 revealed thermal anomalies like that in 2004 during 2006 and 2007 but not 2005 (P. B. McIntyre unpubl.). Together, these independent lines of evidence suggest that dry-season upwelling is a regular occurrence and must be incorporated into conceptual models of the hydrodynamics of Lake Tanganyika. Further field data, particularly that which might trace the extent of mixing, and satellite imagery will undoubtedly offer insight into the spatial and temporal extent of dry-season upwelling and the consequent productivity response.

Upwelling in the littoral zone—Upwelling produced a larger drop in surface temperature in the littoral zone than in the pelagic zone (0.34°C vs. 0.30°C), most likely because of enhanced turbulent mixing caused by friction along the substrate (MacIntyre and Jellison 2001). However, this difference could be a by-product of the disparity in temporal resolution between our continuous littoral temperature record and the twice-weekly depth profiles in the pelagic. In contrast to the temperature shift, increases in concentrations of SRP and Si in the littoral zone were lower

than in the pelagic zone (0.11 vs. 0.23 μmol P L^{-1}; 3.27 vs. 5.86 μmol Si L^{-1}). Lower observed shifts in littoral nutrient concentrations could arise from more rapid uptake of upwelled nutrients, both because of higher littoral phytoplankton biomass under baseline conditions (Fig. 5) and because of nutrient uptake by periphyton (McIntyre et al. 2006).

There was substantial variation among littoral sites in the magnitude and effects of upwelling. Few studies have examined upwelling dynamics in the littoral zone of lakes (MacIntyre and Melack 1995; Megard et al. 1997), but our results suggest that internal loading can vary widely even among nearby sites. Similar spatial differences in upwelling have substantial effects on ecosystem productivity along continental margins in marine ecosystems (Menge et al. 1997). We had expected to find a predictable cascade of relationships among littoral bathymetry, upwelling characteristics (onset, magnitude, duration), increases in nutrient concentrations, and the phytoplankton biomass response across sites. However, few of these relationships were supported. Sites with steeper bathymetry did show greater influx of NO$_3$ and SRP, but bathymetry was not related to Si or organic nutrient dynamics. The inverse relationship between changes in temperature and dissolved N (NO$_3$ and DON) associated with upwelling were also unexpected. Correlations between bathymetry and nutrient increases should not have been obscured by anthropogenic loading or other local factors because we focused on increased above-background levels. However, the lack of response of Chl *a* concentrations to nutrient increases could reflect the displacement of epilimnetic plankton during upwelling of hypolimnetic waters with low Chl *a*. Resolving the causes of the intriguing spatial variation in littoral upwelling will require further work, and assessing the interannual repeatability of these upwelling patterns is a critical first step in resolving both their causes and the long-term significance for littoral ecology.

Effects of upwelling on nutrients and phytoplankton—As the thermocline peaked and its stability weakened, hypolimnetic waters were mixed upward into the epilimnion. As expected, this upwelling increased epilimnetic SRP and Si levels in the pelagic and littoral zones. In contrast to previous suggestions that the hypolimnion acts as a sink for N in Lake Tanganyika (Hecky et al. 1996), we also observed significant increases in NO$_3$ and TDN following upwelling (O'Reilly et al. 2002). Although our monitoring was more frequent than previous studies on Lake Tanganyika, the rapid nutrient dynamics evident in our data (Figs. 4, 5) underscore the possibility that maximum concentrations following upwelling could have been higher than we recorded. Indeed, the lack of a significant correlation across littoral sites between increases in phytoplankton Chl *a* and NO$_3$ or SRP concentrations suggests that algal or microbial nutrient uptake mediated observed nutrient concentrations.

There is a chronic scarcity of nutrients in the surface waters of Lake Tanganyika (Hecky et al. 1991; Edmond et al. 1993), and both periphyton (McIntyre et al. 2006) and phytoplankton (Järvinen et al. 1999; De Wever et al. 2008)

respond significantly to experimental increases in nutrient availability. Our work confirms that upwelled nutrients fuel large, rapid increases in planktonic biomass in the pelagic and littoral zones. Pelagic phytoplankton biomass (Chl *a*) was highest on the same date as peak nutrient concentrations (Fig. 4). In the littoral zone, which was sampled more frequently than the pelagic, we captured the expected delay in phytoplankton growth following the influx of nutrients (Plisnier et al. 1999) and dilution of phytoplankton stocks. In both zones, elevated phytoplankton biomass was sustained for at least a week despite a rapid decrease in nutrient concentrations following the initial bloom. This suggests that copepods and other consumers are unable to suppress phytoplankton biomass as strongly as benthic grazers limit periphyton biomass (McIntyre et al. 2006).

In addition to the classic sequence of decreased water temperature, increased nutrient availability, and heightened phytoplankton productivity associated with upwelling, our littoral monitoring revealed a pulse of DON and DOP following the phytoplankton bloom. Unlike SRP, Si, and NO$_3$, organic nutrients were unlikely to be supplied entirely by upwelling. The increase in these compounds following upwelling presumably represents exudates or lysis products from phytoplankton and microbes (Bronk et al. 1994; Ward and Bronk 2001).

The conversion of upwelled NO$_3$ and SRP into DON and DOP may be an important mechanism of epilimnetic nutrient retention. Unlike particulate nutrients, which sink through the water column, or dissolved inorganic nutrients, which are rapidly utilized, dissolved organic compounds could remain in surface waters for relatively long periods. Indeed, DOP and particularly DON typically make up a large proportion of dissolved nutrient pools in the littoral zone of Lake Tanganyika (Fig. 5; McIntyre et al. 2006). Thus, the production of organic nutrients following upwelling may create a long-lasting nutrient source to microbes and phytoplankton in the epilimnion (Cotner and Wetzel 1992; Vähätalo et al. 2003; Gilbert et al. 2004). Interestingly, the ratio of inorganic N : P associated with upwelling in the littoral zone was far lower than the ratio of dissolved organic N : P after upwelling (4.29 vs. 20.16). This could reflect N fixation in response to upwelling (Hecky and Kling 1981; Järvinen et al. 1999) and subsequent leakage of this new N into the DON pool (Bronk et al. 1994; Hecky et al. 1996).

Our records of successive changes in water temperature, nutrient concentrations, and phytoplankton biomass in the littoral and pelagic zones provide the first clear evidence that upwelling has similar effects both offshore and inshore in Lake Tanganyika. This sort of linkage between pelagic and littoral dynamics rarely has been demonstrated in lakes (MacIntyre and Melack 1995), and it has important implications for nearshore ecosystem processes. Studies of primary productivity (Takamura 1988; O'Reilly 2006) and food webs (Hori et al. 1993) generally regard the littoral zone of Lake Tanganyika as a closed system fueled by benthic productivity. However, the transfer of nutrients from the hypolimnion to the epilimnion and littoral zone via upwelling events highlights the importance of large-

scale processes that link the dynamics of pelagic and littoral zones. The duration of the temperature drop recorded in the littoral zone and the corresponding burst in phytoplankton throughout the region suggest that upwelling is a significant driver of productivity in the littoral zone as well as the pelagic zone.

There is growing concern that global warming may suppress upwelling in Lake Tanganyika (O'Reilly et al. 2003; Verburg and Hecky 2003) and other tropical lakes (Vollmer et al. 2005) causing decreases in pelagic productivity (although see Sarvala et al. 2006). Given the strong effects that upwelling had in the littoral zone, strengthening of the thermal stratification in the lake could have significant effects on the influx of nutrients into the epilimnion and energy flow into the littoral food webs.

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