

Seasonal and interannual particle export in an African rift valley lake: A 5-yr record from Lake Malawi, southern East Africa

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Abstract

A time-sequencing sediment trap was deployed at 300–350 m in Lake Malawi, East Africa, from 1987 to 1992 to measure particulate export to the deep, anoxic hypolimnion in the northern and central lake regions. The monthly settling particulate samples provide a data set of seasonal and interannual export fluxes of organic carbon, biogenic opal, calcium carbonate, and lithogenic material. Maximum total particle fluxes ($\sim 50\text{--}400\text{ mg m}^{-2}\text{ d}^{-1}$) occurred primarily during the dry, windy season (April through October) when algal productivity is high because of wind-induced upwelling of nutrient-enriched metalimnion and hypolimnion waters. Peak-flux particulates contained an abundance of *Aulacoseira* and *Stephanodiscus* diatom valves and chains. The total particle mass flux during the wet, austral summer months (November through March) was consistently one to three orders of magnitude less than that measured during the dry months and consisted of mineral shards, terrestrial plant debris, and scattered diatom tests. The 5-yr trap data provide support for the claim that the light–dark lamination couplets, abundant in northern and central lake cores, reflect seasonal delivery to the sediments of diatom-rich particulates during the windy months and diatom-poor material during the wet season. However, interannual and spatial variability in upwelling and productivity patterns, as well as El Niño–Southern Oscillation (ENSO)-related rainfall and drought cycles, appears to exert a strong influence over the magnitude and geochemical composition of particle export to the deep hypolimnion of Lake Malawi.

Lake Malawi, located between 9°S and 15°S, is at the southern end of the western arm of the East African rift system. As the fifth largest lake in the world by volume, with maximum depths of >700 m and an overall length of 570 km, it represents a substantial lacustrine sedimentary reservoir containing up to 25 Ma yr of continuous sedimentation history (Johnson et al. 2002). The lake is meromictic, with substantial physical mixing occurring primarily in the upper 100–250 m during the windy winter period of minimal stratification. Below approximately 220 m, the lake waters are permanently anoxic, nutrient rich, and isothermal at about 22.7°C (Beauchamp 1953; Eccles 1974). Permanent stratification and the oxic–anoxic boundary are maintained by moderately small chemical and thermal gradients in the metalimnion (105–220 m) between the 0- to 105-m epilimnion and deep (>220 m) hypolimnion (Hutchinson 1957; Wüest et al. 1996; Vollmer et al. 2002). Recent studies of density stratification and ventilation in Lake Malawi have shown that the temperature gradient has a stronger effect on the density structure than the salinity gradient (Wüest et al. 1996; Vollmer et al. 2002). Total dissolved nutrient flux into the surface mixed layer is thus highly dependent on seasonal

wind-mixing events and the overall exchange rates between the epi-, meta-, and hypolimnion (Hamblin et al. 1999; Bootsma et al. in press). Turbulent mixing across the pycnocline, coupled with seasonal deep-water intrusions of evaporative cooled surface waters in the southern part of the lake, produces volume exchange times of $\sim 3\text{--}4$ yr between the epilimnion and metalimnion and $\sim 5\text{--}14$ yr between the metalimnion and hypolimnion (Gonfiantini et al. 1979; Vollmer et al. 2002).

The monsoon-type climate of Malawi is controlled by the interannual latitudinal movements of the Inter-Tropical Convergence Zone (ITCZ). As a consequence of its geographic location at the southern limit of the ITCZ, Lake Malawi experiences one well-defined rainy season per year (Beadle 1981). This is in contrast to the large rift lakes farther north, such as Tanganyika and Victoria, which generally experience two wet seasons annually (Beadle 1981). November to March represents the summer rainy season in Malawi when the winds are generally weak and northerly, the river runoff is high, and the ITCZ is located at its most southerly position over East Africa at 12–13°S. Because of its location near the equator, the northern end of the lake may occasionally experience a longer rainy season than the southern reaches of the lake, with rains persisting into April and May (Beadle 1981; Bootsma et al. 2003; Hecky et al. 2003). During the annual monsoon rains, the lake receives approximately 60% of its annual water input via rainfall to the lake surface, with inflow from 13 rivers accounting for the remaining 40% (Hecky et al. 2003). Surface evaporation is responsible for the majority (80%) of annual water output from the lake, with minimal outflow occurring through one outlet, the Shire River in the south (Beauchamp 1953; Eccles 1974). The windy winter season begins in about April when the ITCZ moves toward the equator and strong southerly winds become dominant (Eccles 1962, 1974). Persistent southerly

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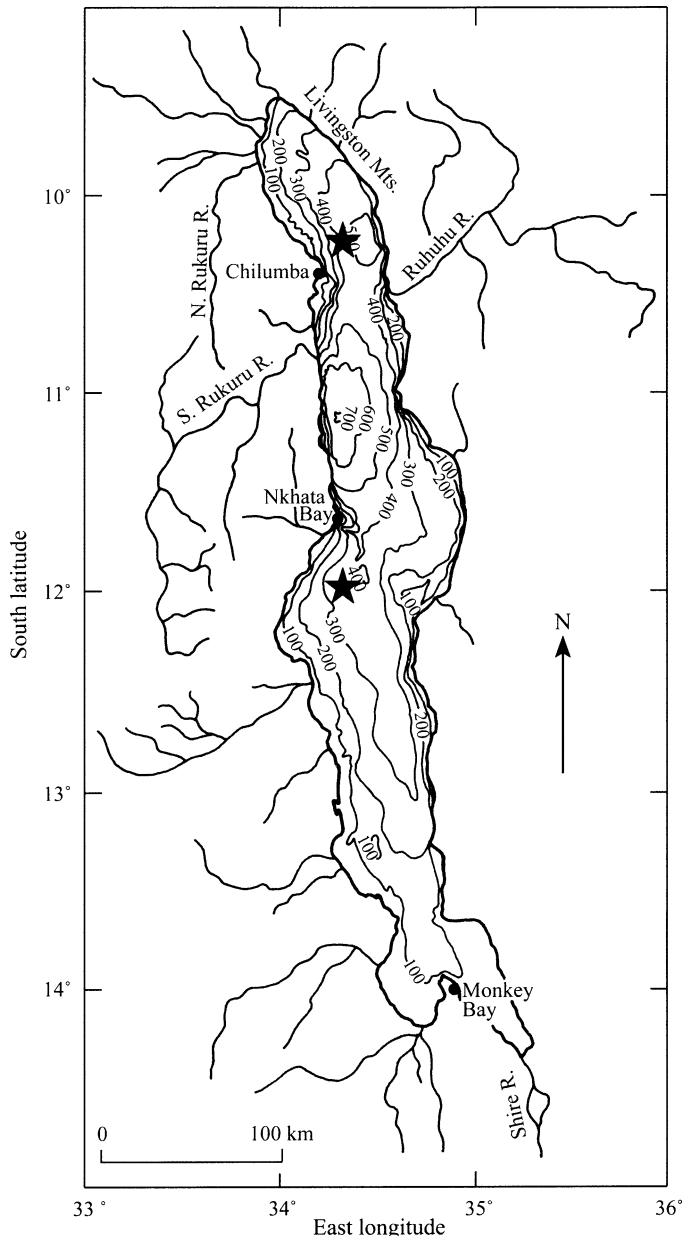


Fig. 1. Geographic setting of Lake Malawi in south-central East Africa. Contoured lake bathymetry in meters. Stars denote sediment trap mooring locations: northern lake site = 1987–1991 deployment; central lake site = 1991–1992 deployment.

winds that can last until early October produce a deepening of the thermocline, with strong physical mixing focused in the upper 220 m of the lake (Eccles 1974; Degnbol and Mapila 1982). Localized upwelling of deep, nutrient-rich waters frequently occurs during periods of maximum wind stress between May and September (Eccles 1974; Hecky et al. 1996). The biological impact of the seasonal transport of nutrients to the surface during the windy season promotes diatom blooms, resulting in maximum levels of primary production of $\geq 1.0 \text{ g C m}^{-2} \text{ d}^{-1}$ compared to significantly lower rainy-season values of $0.2\text{--}0.5 \text{ g C m}^{-2} \text{ d}^{-1}$ (Talling 1969; Degnbol and Mapila 1982; Hecky and Kling 1987; Bootsma

1993). Annual planktonic carbon production is estimated to range from 180 to 360 g m^{-2} by Wüest et al. (1996) on the basis of vertical diffusivity and chemical gradients in the lake.

Pronounced north-to-south gradients exist on Lake Malawi in terms of annual rainfall, river discharge, ventilation, and phytoplankton productivity. Rainfall and river discharge is significantly greater in the north, as reflected by the high lake-wide levels of water-column turbidity recorded off the Ruhuhu River Delta (Fig. 1) and the abundance of silt and sand in the northern lake basins (Eccles 1974; Johnson and Davis 1989; Pilskaln and Johnson 1991; Halfman and Scholz 1993; Hecky et al. 2003). Upwelling, cold, deep-water formation and possibly internal wave propagation appear to be focused in the shallower southern reaches of the lake, although localized, divergent upwelling zones occur throughout the lake (Eccles 1974; Hecky et al. 1996; Hamblin et al. 1999; Vollmer et al. 2002). Phytoplankton production, biomass, and deposition, as well as fisheries yield, are all enhanced in the southern lake region when compared to the north (Eccles 1962; Hecky and Kling 1987; Owen 1989; Owen and Crossley 1992; Bootsma 1993).

The sedimentary record recovered in Lake Malawi cores from bottom depths below approximately 220 m consists of thick sequences of finely laminated diatom ooze and diatom-rich clays, nonlaminated diatom mud, and silty clay turbidity flow deposits or homogenites (Johnson and Davis 1989; Pilskaln and Johnson 1991; Barry et al. 2002). The laminated sequences, deposited under an anoxic sedimentation regime and representing a major sedimentary facies in the lake, consist of light–dark couplets or annual varves of approximately 1-mm thickness that have accumulated in the lake basin during the past $\sim 11,000$ yr at a rate of $\sim 0.7\text{--}1.5 \text{ mm yr}^{-1}$ (Pilskaln and Johnson 1991; Barry et al. 2002). The varved sediments are particularly prevalent in cores from the northern half of the lake, whereas nonlaminated diatom mud deposits are widespread in the relatively shallower southern lake region (Johnson and Davis 1989; Pilskaln and Johnson 1991). During extended periods of geologic time, anoxic deposition provides for the preservation of long sediment records of seasonal-to-annual paleoflux events represented by laminated sequences. Such sediments hold great potential for providing high-resolution geochronologies and records of paleoclimatic change (Johnson et al. 2002).

In an effort to refine our interpretation of the seasonal paleoflux events preserved as sedimentary varves in Lake Malawi, a sediment trap program was initiated in 1987 in the deep northern basin (Pilskaln and Johnson 1991). The objective of the trap program was to obtain, over a multiyear period, a time series of settling particulate material within the anoxic hypolimnion in order to better define the seasonal flux events associated with the formation of the underlying varved sediment record, to assess the inter- and intra-annual significance of algal blooms on the benthic delivery of organic carbon and biogenic silica, and to examine the relationship of interannual variations in the geochemical particulate fluxes to regional climate fluctuations.

Methods

The sediment trap deployed in this study was a large-aperture, cone-shaped trap with a baffled surface collection area of 0.5 m² (MK VI Time-Series Trap, McLane; Honjo and Doherty 1988). Monthly settling particulate samples were collected in a rotating carousel of prepoisoned (4% formalin solution, buffered with combusted Na-borate to pH 7.9–8.0) sample bottles whose collection and closure positions underneath the trap cone were controlled by an electronic microprocessor and stepping motor system (Honjo and Doherty 1988). The sites for the 1987–1991 northern Lake Malawi mooring deployments (10°14'S, 34°21'E) and the 1991–1992 central lake deployment (12°03'S, 34°23'E) are shown in Fig. 1. The trap sampling depth was 350 m at the northern site (~100 m above the bottom) and 300 m (90 m off the bottom) for the 1991–1992 central lake deployment. The site change for the final year of the trap time series was necessitated by complications arising from crew and vessel availability for working at the northern end of the lake in 1991–1992. At the northern site, dissolved oxygen concentrations have been shown to decrease rapidly below 20 m, with an anoxic water column present below ~170 m (Vollmer et al. 2002). The central lake trap site is characterized by a slightly deeper anoxic hypolimnion boundary at 240 m (Vollmer et al. 2002). The subsurface mooring was anchored to the bottom by railroad wheels. An acoustic release placed above the anchor and a set of glass floatation spheres above the trap allowed a surface recovery of the mooring. Turn-around (e.g., recovery, sample retrieval, redeployment) of the trap mooring occurred annually, using three different Malawi vessels during the course of the project. Vessel repairs and logistics created gaps in the time series of 3 weeks in May 1988 and 1 month between late January and late February 1991 when the mooring redeployment could not occur immediately following the recovery.

Upon their return to the laboratory, all trap samples were gently sieved through a 1-mm Nitex sieve, split into quantitative aliquots with a multihead precision splitter, and examined microscopically (Pilskaln et al. 1996). Particulate organic carbon and nitrogen (POC and PON) content of the particulate material was determined on decalcified samples using a Perkin-Elmer CHN analyzer when there was an adequate mass of organic matter available. Inorganic carbon was measured by coulometry (Coulometric Carbon Analyzer) after closed-system acidification with phosphoric acid and CaCO₃ content was calculated from the evolved CO₂. Biogenic opaline silica (bioSiO₂) analyses of the trap samples were completed using a modified version of the sodium carbonate leach method of Mortlock and Froelich (1989), and lithogenic content of the trap material was calculated by subtracting the biogenic opal value from the total noncombustible fraction of the sample (Pilskaln et al. 1996). All trap samples were chemically analyzed within approximately 6 months after being transported to the laboratory immediately following sample recovery in the field. Particulate subsamples were examined with a stereomicroscope and a scanning electron microscope to document particle components.

Results

Sediment trap timer malfunctions resulted in the collection of 3 months (vs. 1 month) of settling particulate material in a few of the trap cups: 1989–1990 cup 6 and 1990–1991 cups 7–9 (Table 1). A seasonal particulate export pattern was observed in which the maximum total mass flux (TMF) and peaks in the geochemical component fluxes occurred primarily during the windy winter season, with minimum values occurring in the rainy summer months (Table 1; Figs. 2, 3). Peak TMF values ranging from ~50 to 480 mg m⁻² d⁻¹ were obtained between April and early November, with minimum TMF values ≤1.0 mg m⁻² d⁻¹ observed between late November and March (Fig. 2). Mass-flux peaks in 1987 and 1988 of 100–200 mg m⁻² d⁻¹ occurred near the end of the windy winter season (April through October), whereas the 1989 peak, which represented the largest measured mass export value of 484 mg m⁻² d⁻¹, occurred in the late rainy/early windy season (Fig. 2). In 1990–1992, lower mass fluxes overall were observed at the northern site (1990 deployment) and at the central site (1991–1992 deployment; Table 1; Fig. 2). Several moderately small TMF peaks ranging from 40 to 50 mg m⁻² d⁻¹ occurred in 1990–1992 during the windy winter months, and one peak of 65 mg m⁻² d⁻¹ was observed in the 1990 rainy summer season (Fig. 2). Greater than 97% (dry weight) of the collected particulate material was <1 mm, with an insignificant contribution to the flux by larger particles in the form of fish fecal pellets and insect and zooplankton carapaces. Zooplankton swimmers identified in the >1-mm and <1-mm sieve fractions of the trap material were removed and not included as components of the mass flux.

The major geochemical mass fluxes were provided by POC, bioSiO₂, CaCO₃, and lithogenic particles (Table 1; Fig. 2). These component fluxes followed the same seasonal pattern as the TMF throughout most of the time series (Figs. 2, 3). However, the fluxes of carbonate and lithogenic material remained flat, displaying no export peaks, in 1991 (Fig. 3). PON fluxes were extremely low, representing an average of only 0.7% of the TMF compared to ≥9% for the other components (Table 1). Particulate nitrogen was frequently undetectable by the CHN analyzer if the organic nitrogen content of the sample was <0.5% (Table 1). The low PON content of the sinking particulates was expected, as organic nitrogen is remineralized more quickly relative to organic carbon with very rapid regeneration occurring in anoxic waters (Karl and Knauer 1991; Hassett et al. 1997).

The collected particulates were dominated by lithogenics, representing an average of 43% (dry weight) of the settling particulate material collected between 1987 and 1992. Lithogenic fluxes ranged from <1.0 mg m⁻² d⁻¹ during the generally low export/summer season to >100 mg m⁻² d⁻¹ during the winter months (Fig. 3). The high lithogenic content of the samples, present primarily as clay minerals, was not surprising considering the evidence for the frequent occurrence of turbidity flows along the lake basin and the fact that substantial suspended particle loads enter the northern half of the lake via a number of large rivers (Johnson and Davis 1989; Pilskaln and Johnson 1991; Halfman and Scholz 1993;

Hecky et al. 2003). Biogenic opal in the form of diatom tests was of secondary importance, representing 15–60% (dry weight) of the time-series samples. Fluxes of bio-SiO_2 were as high as 30–90 $\text{mg m}^{-2} \text{d}^{-1}$ during seasonal maxima and dropped to barely detectable amounts in samples collected during the rainy season of certain years (Fig. 3).

POC content of the sinking particles ranged widely from a low of 5% to a high of 28% (dry weight), with an average value of 9%, although there were a significant number of samples collected primarily during the low flux/rainy season for which neither POC nor PON content could be measured (see Table 1). Organic C:N molar ratios ranged from 9.4 to 14.2 with an average value of 10.6 (Table 1). The high C:N ratios reflect the degraded nature of the organic material in the hypolimnion-collected particulates and are indicative of nitrogen deficiency in the phytoplankton (Hecky et al. 1996). $\text{C}_{\text{org}}:\text{bio-Si}$ molar ratios were high, with an average value of 2.0 (Table 1). For comparison, similar molar ratios of 0.2–0.6 are reported for settling particulates collected in marine systems such as the Southern Ocean polar frontal region, where globally significant accumulations of biogenic silica occur (Honjo et al. 2000). The elevated $\text{C}_{\text{org}}:\text{bio-Si}$ ratios in Lake Malawi sinking particulates reflect a high diatom silica remineralization rate occurring in the lake waters that contributes substantially to the elevated levels of soluble-reactive silica in the meta- and hypolimnion (Hamblin et al. 1999; Bootsma et al. 2003).

CaCO_3 was present in small amounts in the trap samples as ostracode shell fragments and authigenic micrite, representing an average of 3% of the settling particulate material. The presence of biogenic and authigenic calcite in Lake Malawi has been reported in shallow-water sediment cores, along with the suggestion that authigenic calcite may precipitate within the supersaturated surface lake waters that occur during low lake-level stands or during periods of high productivity (Owen 1989; Ricketts and Johnson 1996). However, the high dissolved CO_2 content of the hypolimnion makes the deep lake waters highly corrosive to carbonate minerals with very little surviving dissolution to become incorporated into modern, deep basin sediments (Ricketts and Johnson 1996).

During the time series, POC and opal fluxes were the most tightly coupled of all four major geochemical components ($r^2 = 0.85$, Fig. 4). Carbonate and lithogenic fluxes displayed weaker relationships to the seasonal POC export, with r^2 values of 0.41 and 0.64, respectively (Fig. 4). This could indicate additional transport mechanisms to the deep hypolimnion of CaCO_3 and clay mineral matter, in addition to their incorporation into sinking organic and opal-rich particulates produced in the water column via physical or biological aggregation processes. Additional mechanisms for the delivery of CaCO_3 and clay material to the trap are the sinking of individual ostracode shells as well as lateral processes, such as localized turbid sediment flows originating upslope (Barry et al. 2002). The lithogenic flux actually showed a stronger association with opal export ($r^2 = 0.80$) than with POC (Fig. 4). A possible explanation for this association is the lateral transport to the basin of diatom-rich mud resuspended from shallow basin slopes located above the oxic–anoxic interface. Such a mechanism would provide

an additional input of opal and lithogenics to the trap but possibly not organic carbon.

Particulate samples collected during the windy winter season flux maxima were overwhelmingly dominated by abundant aggregates and single chains or valves of the pelagic diatoms *Aulacoseira* sp. and *Stephanodiscus* sp. (Figs. 5, 6A). Also observed were occasional tests of *Surirella* sp., a large diatom that is commonly found in near-shore sediments but that has been frequently reported from plankton samples (Talling 1969; Owen 1989; Haberyan 1990; Patterson and Kachinjika 1995; Fig. 5A). The highest abundances of diatoms and diatom flocs were observed in the samples collected during the peak mass particulate fluxes of 1987 through 1989 (Figs. 2, 3). Small zooplankton fecal pellets were periodically numerous, although they were easily disaggregated. The lack of highly fragmented or broken diatom valves and the abundance of aggregated, intact chains in the trap samples, particularly during the peak-flux periods (Fig. 5), suggest that zooplankton grazing played a relatively minor role in the delivery of phytoplankton material to the trap. Valves of *Stephanodiscus* were frequently more numerous relative to those of *Aulacoseira* in the trap samples collected early in the 1987 and 1988 dry, windy seasons before the major peak in particle flux was observed (Fig. 5C). The smaller-volume rainy summer-season samples were notably devoid of diatom aggregates, with a relatively low abundance of diatom tests. Rainy-season particulates were characterized by the presence of mineral shards, black terrestrial plant debris, amorphous organic matter, and clay particles (Fig. 6C). Phytoliths that enter the lake via surface runoff and that could potentially provide an input of particulate biogenic silica to the trap (Bootsma et al. 2003) were not an obvious component of the collected samples.

Discussion

Seasonal export pattern and mechanisms—Although limited in terms of spatial coverage, the data presented in this study represent, to our knowledge, the only continuous, multiyear record of seasonal particle export in the deep, hypolimnion waters of an African rift lake at this time. Annual maxima and minima in the delivery of planktonic diatom silica and POC to the hypolimnion of Lake Malawi, as documented by the export time series, appear to be coupled to seasonal variations in wind-mixing events and the injection of nutrients into the epilimnion. Previously reported data on the seasonal variation in $\delta^{15}\text{N}$ values obtained from a subset of the trap samples as a proxy for upwelling and phytoplankton isotopic fractionation activity (François et al. 1996) provide independent confirmation that peak export events are associated with nutrient injection into the epilimnion.

Windy winter-season export peaks consist predominantly of a mix of *Aulacoseira* and *Stephanodiscus*, indicating that the monthly sediment trap sampling scheme was too coarse to document the established variability in the relative abundance of these two diatom genera as a function of changing environmental variables of light, nutrient availability, and wind-mixing regime (Lund 1954; Kilham et al. 1986; Hecky and Kling 1987; Kilham 1990). According to these studies,

Table 1. Lake Malawi particle fluxes: Jun 87–Jan 91 northern lake site (10°14'N, 34°21'E) and Feb 91–Mar 92 central lake site (12°03'N, 34°23'E). 1987–1990 PON fluxes published in error in François et al. (1996). Correct values given below. Trap sample $\delta^{15}\text{N}$ values from François et al. (1996).*

Event No.	Collection dates	Total mass flux (mg m ⁻² d ⁻¹)	POC flux (mg m ⁻² d ⁻¹)	PON flux (mg m ⁻² d ⁻¹)	SiO ₂ flux (mg m ⁻² d ⁻¹)	CaCO ₃ flux (mg m ⁻² d ⁻¹)	Lithogenic flux (mg m ⁻² d ⁻¹)	Molar C:N	Molar C _{org} :Si _{bio}	$\delta^{15}\text{N}$ (‰)
1	04 Jun 87–04 Jul 87	12.31	1.27	0.12	1.84	0.58	6.80	12.3	3.4	+0.9
2	05 Jul 87–04 Aug 87	7.77	0.98	0.11	1.39	0.40	3.72	10.4	3.5	+2.1
3	05 Aug 87–04 Sep 87	10.75	1.13	0.11	3.57	0.56	4.02	12.0	1.6	+2.5
4	05 Sep 87–04 Oct 87	39.50	3.39	0.28	17.66	1.44	13.80	14.1	1.0	-0.9
5	05 Oct 87–04 Nov 87	95.61	4.50	0.55	30.41	1.62	49.29	9.6	1.0	+0.2
6	05 Nov 87–04 Dec 87	0.29	n/a	n/a	0.06	<0.01	0.21	n/a	n/a	n/a
7	05 Dec 87–04 Jan 88	0.05	n/a	n/a	n/a	<0.01	<0.01	n/a	n/a	n/a
8	05 Jan 88–04 Feb 88	0.08	n/a	n/a	<0.01	<0.01	0.02	n/a	n/a	n/a
9	05 Feb 88–04 Mar 88	0.08	n/a	n/a	0.01	<0.01	0.01	n/a	n/a	n/a
10	05 Mar 88–04 Apr 88	0.12	n/a	n/a	0.01	<0.01	0.01	n/a	n/a	n/a
11	05 Apr 88–04 May 88	0.19	n/a	n/a	0.03	<0.01	0.07	n/a	n/a	n/a
1	26 May 88–26 Jun 88	12.05	1.21	0.10	1.51	0.53	6.91	14.2	4.0	+1.3
2	27 Jun 88–26 Jul 88	9.19	1.26	0.12	1.40	0.54	4.30	12.3	4.5	+1.7
3	27 Jul 88–26 Aug 88	30.66	2.17	0.27	5.44	1.04	18.71	9.4	2.0	-0.9
4	27 Aug 88–26 Sep 88	217.28	10.74	1.30	33.64	6.10	151.90	9.6	1.6	-1.8
5	27 Sep 88–26 Oct 88	0.55	0.06	*	0.20	0.05	0.15	*	1.6	*
6	27 Oct 88–26 Nov 88	0.50	0.05	*	0.17	0.07	0.17	*	1.5	*
7	27 Nov 88–26 Dec 88	0.14	n/a	n/a	0.01	<0.01	0.03	n/a	n/a	n/a
8	27 Dec 88–26 Jan 89	0.19	n/a	n/a	0.03	<0.01	0.04	n/a	n/a	n/a
9	27 Jan 89–26 Feb 89	0.16	n/a	n/a	0.01	<0.01	0.05	n/a	n/a	n/a
10	27 Feb 89–26 Mar 89	4.13	0.19	*	1.78	0.17	1.50	*	0.5	*
11	27 Mar 89–11 Apr 89	483.96	23.20	2.56	94.73	15.03	307.86	10.6	1.2	-2.4
1	12 Apr 89–12 May 89	254.55	13.26	1.44	33.85	7.39	165.96	10.7	2.0	+0.1
2	13 May 89–12 Jun 89	28.16	1.31	0.16	5.69	0.91	17.39	9.5	1.2	-0.2
3	13 Jun 89–12 Jul 89	31.88	1.58	0.17	6.07	0.83	19.67	10.8	1.3	+0.7
4	13 Jul 89–12 Aug 89	0.10	n/a	n/a	n/a	0.01	0.05	n/a	n/a	n/a
5	13 Aug 89–12 Sep 89	0.09	n/a	n/a	n/a	<0.01	0.04	n/a	n/a	n/a
6	13 Oct 89–26 Jan 90	36.13	1.57	*	7.35	1.14	22.49	*	1.1	*
1	27 Jan 90–27 Feb 90	65.29	4.17	0.50	9.42	2.37	39.10	9.7	2.2	+0.8
2	28 Feb 90–27 Mar 90	21.96	1.32	0.16	3.04	0.71	13.45	9.6	2.2	+1.2
3	28 Mar 90–27 Apr 90	6.02	0.44	0.05	0.63	0.06	3.89	10.2	3.5	+1.2
4	28 Apr 90–27 May 90	48.61	2.27	0.25	6.78	0.63	32.82	10.6	1.7	+0.9
5	28 May 90–27 Jun 90	3.30	0.24	0.03	0.53	0.10	1.93	9.4	2.3	+1.1
6	28 Jun 90–27 Jul 90	1.43	0.14	*	n/a	0.04	n/a	*	*	*
7	28 Jul 90–27 Sep 90	44.04	2.90	0.32	12.95	0.44	22.61	10.6	1.1	+1.2
8	28 Sep 90–27 Nov 90	33.37	1.78	0.22	8.09	0.56	18.55	9.5	1.1	+0.8
9	28 Nov 90–25 Jan 91	30.75	1.67	*	7.89	0.51	16.22	*	1.1	*

n/a, sample mass too small for analysis; *, undetectable nitrogen; n/m, $\delta^{15}\text{N}$ not measured.

Table 1. Continued.

Event No.	Collection dates	Total mass flux (mg m ⁻² d ⁻¹)	POC flux (mg m ⁻² d ⁻¹)	PON flux (mg m ⁻² d ⁻¹)	SiO ₂ flux (mg m ⁻² d ⁻¹)	CaCO ₃ flux (mg m ⁻² d ⁻¹)	Lithogenic flux (mg m ⁻² d ⁻¹)	Molar C:N	Molar C _{org} :Si _{bio}	δ ¹⁵ N (‰)
1	25 Feb 91–25 May 91	4.90	1.42	*	1.24	0.14	0.57	*	5.8	*
2	26 Mar 91–25 Apr 91	3.24	0.72	*	0.83	0.31	0.55	*	4.3	*
3	26 Apr 91–25 May 91	3.21	0.47	*	0.95	0.30	n/a	*	2.5	*
4	26 May 91–25 Jun 91	3.83	0.46	*	1.32	0.25	0.50	*	1.7	*
5	26 Jun 91–25 Jul 91	44.00	3.68	0.43	30.11	0.04	5.38	10.0	0.6	n/m
6	26 Jul 91–25 Aug 91	43.96	3.73	0.45	35.02	<0.01	0.30	9.6	0.5	n/m
7	26 Aug 91–25 Sep 91	0.02	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
8	26 Sep 91–25 Oct 91	0.40	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
9	26 Oct 91–25 Nov 91	0.10	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
10	26 Nov 91–25 Dec 91	0.08	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
11	26 Dec 91–25 Jan 92	0.06	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
12	26 Jan 92–25 Feb 92	0.02	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
13	26 Feb 92–10 Mar 92	0.09	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

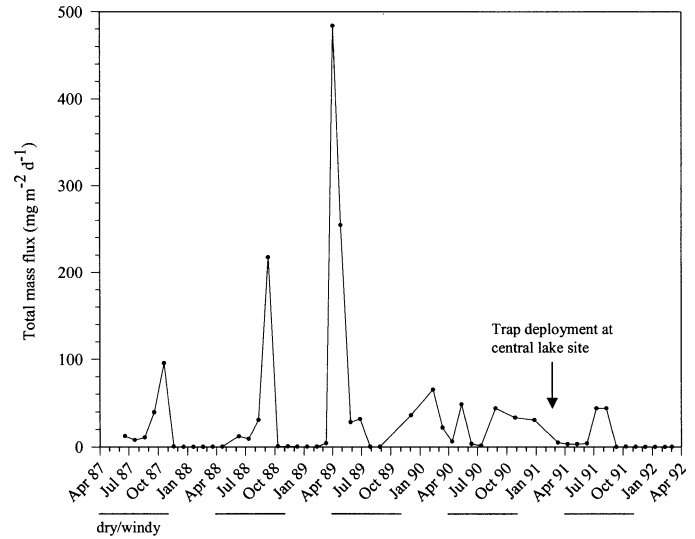


Fig. 2. Time series of the total mass flux (TMF) of particulate material in mg m⁻² d⁻¹, 1987–1992. Horizontal bars under the time series represent the duration of the annual dry, windy season (approximately April through October). The arrow indicates the date (25 February 1991) when the trap deployment site was moved from the northern lake basin to the central lake location.

Aulacoseira sp. requires elevated Si:P ratios and high levels of turbulent wind mixing and can tolerate lower light levels than *Stephanodiscus* sp. Thus, the presence of *Aulacoseira* sp. in the water column as well as in sediment cores has been associated with conditions of minimal stratification and a deep mixed layer, whereas the presence of *Stephanodiscus* sp. is indicative of increased stratification and lower Si:P ratios (Owen and Crossley 1992; Gasse et al. 2002). However, the collection of *Stephanodiscus*-rich/*Aulacoseira*-poor particulate samples during the months preceding the mass-flux peaks in 1987 and 1988 does reflect the findings of Kilham et al. (1986) from several African rift lakes. Elevated water-column abundances of *Stephanodiscus* have often been observed to precede winter *Aulacoseira* blooms, and *Stephanodiscus* may become the dominant diatom genera following *Aulacoseira* blooms near the end of the mixing season (Kilham et al. 1986).

The mixed assemblage of *Aulacoseira* and *Stephanodiscus* in the particulate material collected during the peak export events may also reflect different particle aggregation and settling dynamics between the different diatom genera. *Aulacoseira* blooms would be expected during the height of the wind-mixing season when dissolved silica concentrations are greatest. During the bloom growth phase, the diatom produces thick-walled valves in long filaments shown to exhibit very high settling velocities relative to other freshwater planktonic diatoms (Lund 1954; Kilham 1990). The decline in silica concentrations resulting from *Aulacoseira* growth, coupled with the decrease in turbulent mixing as the windy/high-productivity season diminishes, promotes mass settling of long, dense *Aulacoseira* filaments out of the epilimnion (Lund 1954; Kilham 1990). Planktonic diatoms are known (primarily from the marine literature) to produce substantial amounts of polysaccharide material during bloom senes-

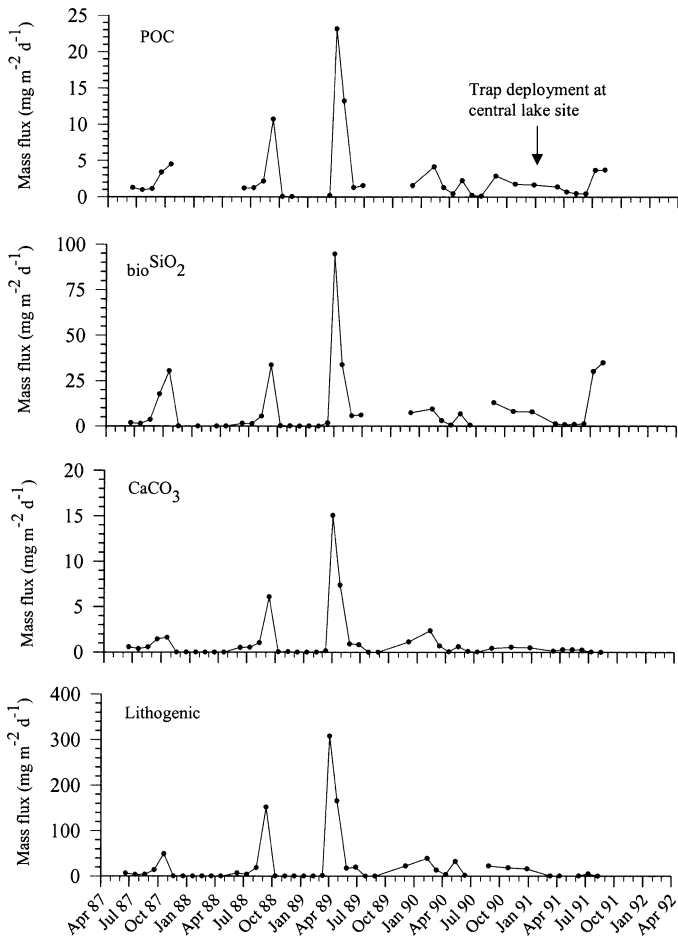


Fig. 3. Time-series mass fluxes of the major geochemical components in $\text{mg m}^{-2} \text{d}^{-1}$. The arrow indicates the date (25 February 1991) when the trap deployment site was moved from the northern lake basin to the central lake location.

cence that are frequently associated with nutrient depletion (Allredge et al. 1993). This leads to the formation of large, sticky aggregates that sink rapidly out of the surface waters and passively scavenge smaller suspended or sinking particles (McCave 1984; Allredge and Gotschalk 1989). Lake Malawi peak opal and POC export events represented by a mixed-diatom assemblage most likely result from the aggregation of long, heavy *Aulacoseira* filaments that scavenge the relatively lighter *Stephanodiscus* cells as the algal flocs sink out of the epilimnion following a reduction in silica levels and wind mixing.

The extremely low particle fluxes measured during a majority of the rainy summer seasons on Lake Malawi from 1987 to 1992 indicate minimal input of planktonic biogenic material to the hypolimnion during these months. Even though the dissolved and particulate nutrient influx to the lake via river discharge is elevated at this time, we observed a minimal response of the offshore phytoplankton community, as reflected by the production of sinking particulate biogenic material (Bootsma 1993; Bootsma et al. 2003; Hecky et al. 2003). Approximately 25% of the annual silica input to the epilimnion of Lake Malawi is from rivers,

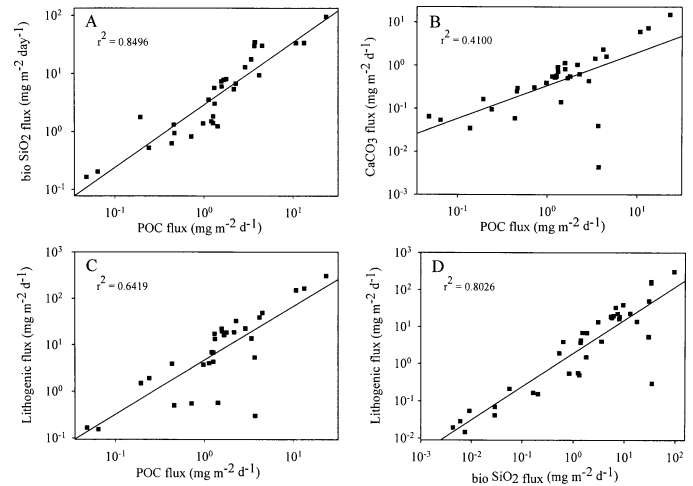


Fig. 4. Regressions of various geochemical mass fluxes during the complete time series: (A) POC versus bioSiO_2 , (B) POC versus CaCO_3 , (C) POC versus lithogenics, and (D) bioSiO_2 versus lithogenics.

whereas 75% is provided by vertical exchange with silica-rich deep waters, although this varies regionally to some extent (Vollmer et al. 2002; Bootsma et al. 2003; Hecky et al. 2003). Additionally, a greater amount of the total silica transferred annually to the epilimnion via upwelling, compared to river-input silica, is soluble-reactive silica and thus immediately available for diatom uptake (Hamblin et al. 1999; Bootsma et al. 2003). The trap time-series results provide general support for the scenario presented in previously published ventilation and nutrient dynamics studies demonstrating that wind-induced, vertical mixing of nutrients into the epilimnion, versus river input, exerts a dominant influence over the annual production and mass export of particulate biogenic silica and organic carbon.

The presence of occasional terrestrial plant debris collected in the traps during the rainy season indicates at least some contribution to the settling particulate material from river discharge. At the same time, the trap data did not show any large increase in lithogenic content or resultant fluxes during the rainy season when a greater suspended clay particle input to the lake might be expected. Suspended particle profiles completed off some of the largest river deltas in the lake show highly elevated turbidity levels above the bottom, but these extend out only to a maximum distance of 10 km from the river mouths, with no near-bottom turbid layers observed in water depths ≥ 200 m (Halfman and Scholz 1993). The time-series trap locations in the present study (all at depths > 200 m) were located ≥ 50 km offshore from major river deltas. Thus, the trap deployments may have been too far offshore to collect material from laterally advected, dense particle plumes originating from the rivers or at sufficient depths above the bottom to sample near-bottom, muddy turbidity flows hypothesized by Barry et al. (2002). Sediment traps, however, are not designed to collect suspended material—they are designed to collect the larger, heavier, and rarer sinking particle aggregates that are responsible for the mass delivery of particles to the underlying sediments (Honjo and Doherty 1988). The presence of significant amounts

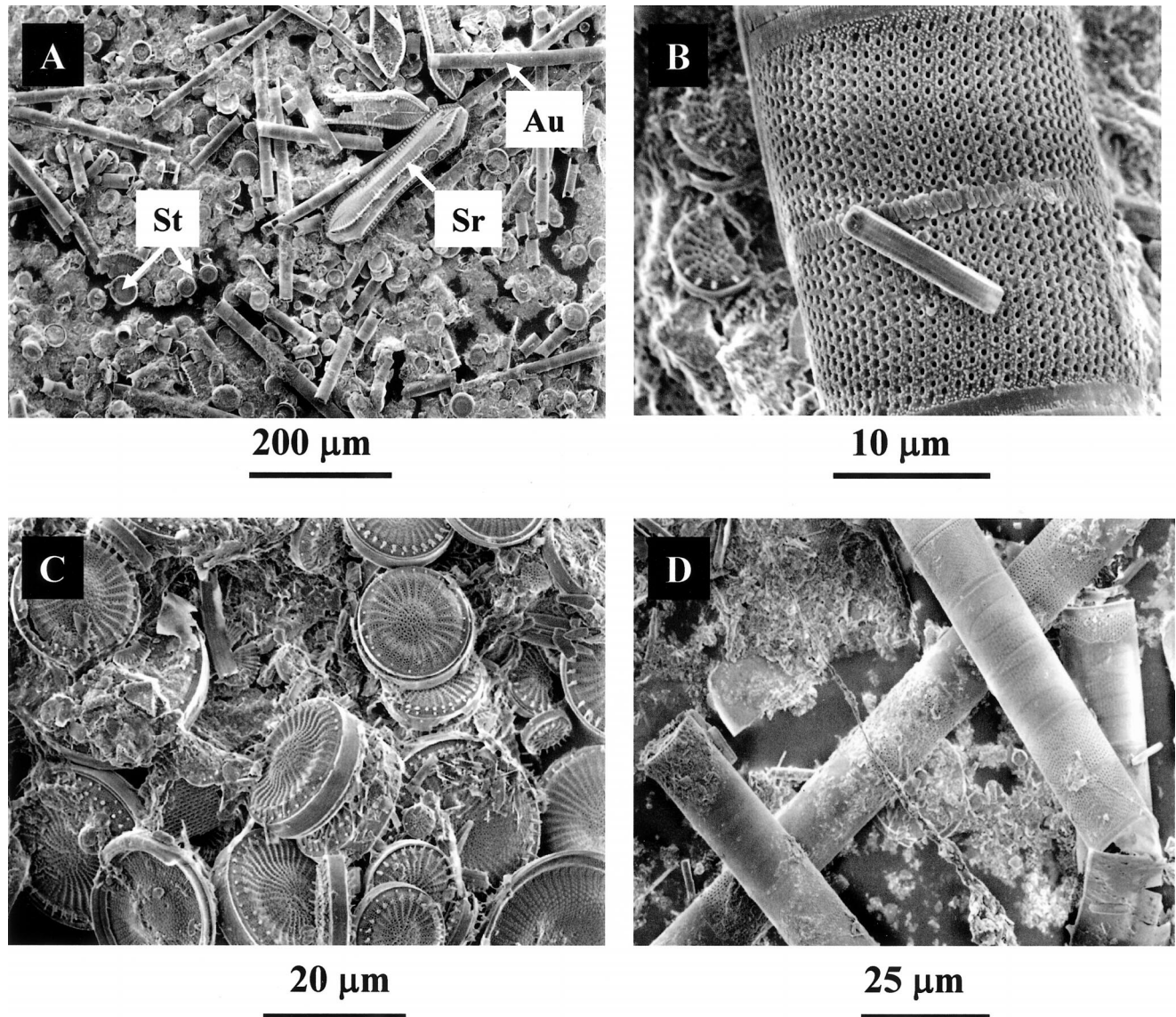


Fig. 5. Scanning electron micrograph images of sediment trap material collected during 1987–1989 peak periods in particulate mass flux. (A) Particulate sample from August 1998 to September 1988 TMF maxima showing a mixture of *Aulacoseira* filaments (Au) and *Stephanodiscus* valves (St) with smaller amounts of the large, box-shaped *Surirella* (Sr). (B) High-magnification view of valve surfaces in an *Aulacoseira* chain. (C) *Stephanodiscus*-rich trap material collected from August 1987 through September 1987 preceding the October 1987 through November 1987 flux peak. (D) *Aulacoseira* chains from the March 1989 through April 1989 peak-flux event.

of fine lithogenic material in the offshore trap samples, particularly concentrated in samples collected during peak export periods, indicates that suspended lithogenic particles in the water column were most likely passively scavenged from the water column by large, fast-settling algal aggregates that sank into the trap. This process of lithogenic particle scavenging by sinking particulate organic matter has been documented a number of times in the marine environment and has been inferred in lakes (Hay et al. 1990; Asper et al. 1992; Dymond et al. 1996; Pilskaln et al. 1996).

Interannual variability in fluxes and climate effects—Interannual variability at any one point on the lake in ventilation and upwelling dynamics (i.e., strength and position of

upwelling fronts), nutrient levels, phytoplankton production, river discharge, and duration of the wind-mixing season (Bootsma 1993; Vollmer et al. 2002; Bootsma et al. 2003; Hecky et al. 2003) will lead to widely varying particle export fluxes from year to year. Significant differences observed in the magnitude and exact timing of the particle export maxima measured in northern Lake Malawi from 1987 through 1991 provide support for the interannual variability in the biophysical and chemical parameters that drive particle formation and sinking flux. Of particular note is the large 1989 particle export peak that occurred at the very beginning of the windy winter season, compared to the 1987 and 1988 peaks occurring near the end of the wind-mixing period. The year-to-year difference in the timing of these events suggests

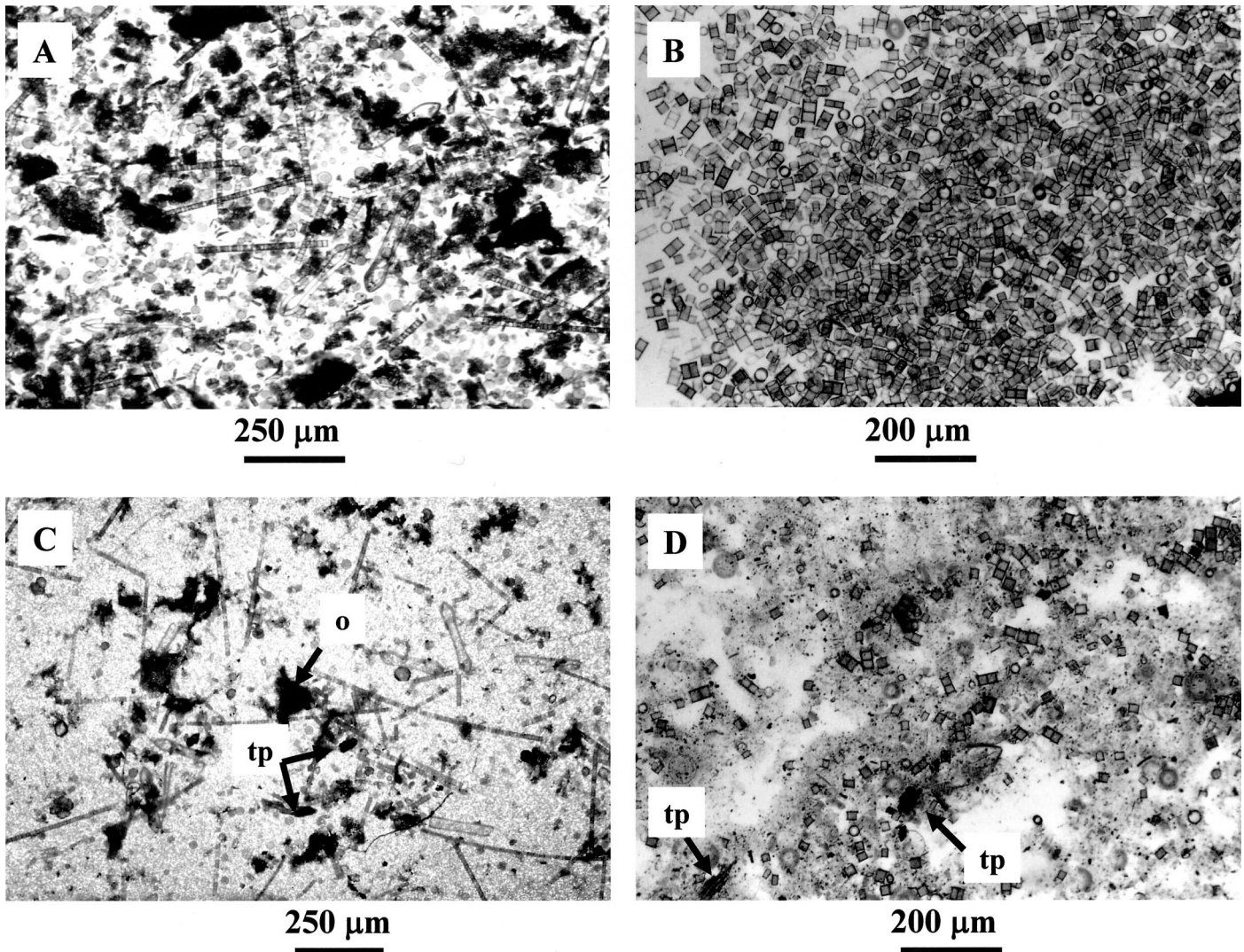


Fig. 6. Microscopic smear slides of trap samples compared to sedimentary varve components. (A) Trap particulate material full of diatoms and dark organic matter from the peak-flux period in August 1988 through September 1988 compared to (B) *Aulacoseira*-dominated light laminae from northern basin piston core. (C) Trap material collected between December 1988 and January 1989 in the rainy summer season showing scattered chains of *Aulacoseira*, a few *Surirella* and *Stephanodiscus* valves, and some terrestrial plant matter (tp) and amorphous organic debris (o). (D) Smear slide of dark laminae components consisting of abundant clay particles, scattered *Aulacoseira* valves, some *Stephanodiscus*, and a few black, carbonized terrestrial plant particles (tp).

that the relatively simple scenario of large diatom blooms being driven by wind mixing and associated nutrient injection into the surface waters is complicated or modified by additional parameters such as extended rainy seasons, variations in the nutrient loads of river inflow, and changes in phytoplankton community composition. If the first 2 yr of the trap data are focused on, it might be concluded that the primary mechanism of particle delivery in the northern lake is via the formation of senescent diatom aggregates near the end of the wind-mixing season when nutrient levels are declining. However, the occurrence of an extremely large 1989 mass-flux peak at the end of the rainy season and very early in the windy season indicates that other factors are contributing to the bloom generation and the formation of diatom-rich, sinking particles. Interannual variability in the timing of the major, bloom-related export peaks responsible for the

formation of the seasonal white laminae is also suggested from $\delta^{15}\text{N}$ analyses of several diatom-rich laminae from northern lake cores obtained near the sediment trap site (Pilskaln and Johnson 1991; François et al. 1996). The nitrogen isotopic data indicate that, in some years, the white laminae are composed of material produced at the beginning of the wind-mixing/upwelling season, whereas diatom-rich laminae deposited in other years represent a longer-term, integrated bloom signal (François et al. 1996). Similarly, interannual (and spatial) differences between the north and central lake regions in upwelling strength, epilimnion nutrient concentrations, and productivity levels could account for the relatively lower annual export fluxes measured at the 1991–1992 central lake site when compared to the 1987–1991 north basin trap site. Because it is not possible to cross-correlate cores throughout Lake Malawi on the basis of lamination patterns

and lithogenic changes, it may be that the relative importance of various mechanisms of particle delivery to the sediment varies substantially north to south (Pilska and Johnson 1991).

Over longer timescales, the determination of whether or not interannual particle flux and particle delivery to the sediments display a relationship to patterns of regional climate variability reproducible over multiple decades is of keen interest to paleolimnologists and those attempting to forecast the lake's response to climate change.

Long-term rainfall patterns in Malawi are placed within a south-central Africa group that also includes Mozambique, Namibia, Zambia, Zimbabwe, and Madagascar (Gommes and Petrassi 1996). Malawi rainfall patterns and their relationship to the quasi-global El Niño-Southern Oscillation (ENSO) cycles are similar to those of southern Africa and are uncorrelated with those of East Africa (i.e., Tanzania, Kenya, and Uganda) and the Horn of Africa region just to the north of Malawi, where the majority of the large rift lakes are located (Gommes and Petrassi 1996; Nicholson 1996; Gommes and Bakun 1998; Fig. 1). Generally, warm ENSO phases are associated with the occurrence of El Niño, the anomalous warming of sea-surface temperatures across the equatorial zone of the central and eastern Pacific Ocean coupled to a significant weakening or disruption of the east-west trade winds. Occurring less frequently are cold ENSO phases, identified by unusually cold sea-surface temperature periods commonly referred to as La Niña events (Philander 1989). A 1973–1993 record of sub-Saharan rainfall and drought variability indicates that the south-central region has displayed a highly persistent structure. The probability of the occurrence of extremely wet and dry years versus average years is about equal (Gommes and Petrassi 1996). One rainfall period per year occurs in the south-central region, and warm ENSO phases are typically dry years, with cold ENSO events being wet (Gommes and Bakun 1998; Fig. 7). This is in marked contrast to the patterns reported for East Africa, where much of the region exhibits a bimodal annual rainfall pattern, the long-term rainfall pattern displays a slight downward trend, and warm phases of ENSO are wet (Gommes and Petrassi 1996; Nicholson 1996; Gommes and Bakun 1998).

Figure 7 illustrates that 1987 through part of 1988 was a dry, warm ENSO phase for Malawi. Mid-1988–1990 represented a period with above-normal rainfall levels and a transition from weak, warm ENSO conditions to a 1989 cold ENSO year, followed by a return to warm ENSO conditions in 1990. From mid-1990 until 1995, the south-central Africa region experienced a long warm phase of ENSO accompanied by extremely low rainfall levels (Fig. 7). The largest TMF measured in the time series occurred between late March and mid-May 1989, during a very wet, cold ENSO phase (Figs. 2, 7). An unusually long rainy season in 1988–1989 resulted in substantial flooding in Malawi, and the country also experienced one of the most significant earthquakes on a worldwide basis in early 1989 (OFDA/CRED International Disaster Database, www.cred.be/emdat/profiles/natural/malawi).

Several explanations are possible for the mechanism behind the apparent stimulation of diatom production and the

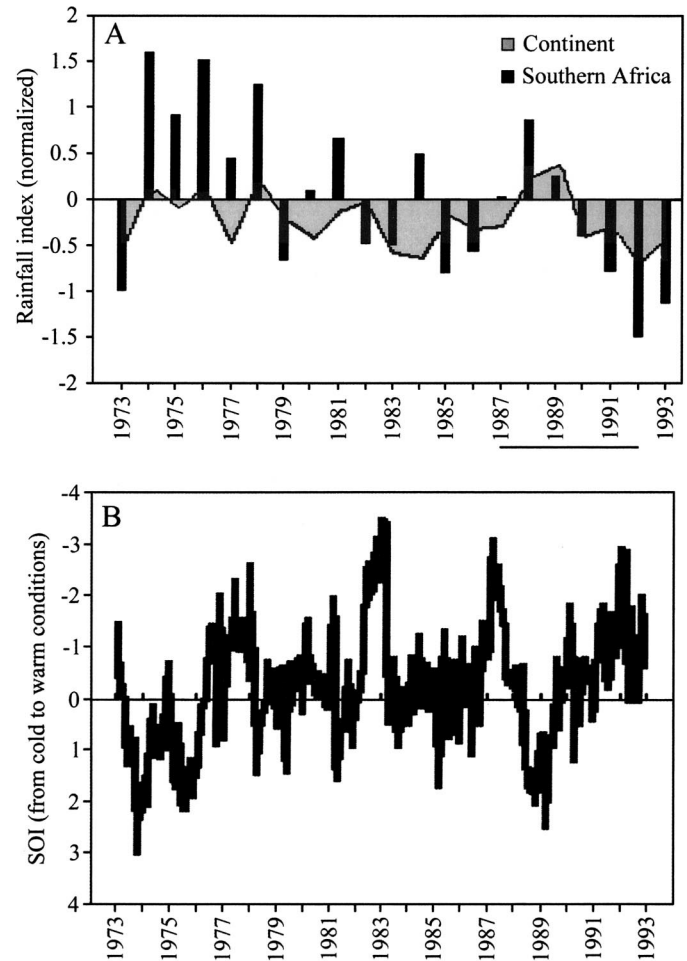


Fig. 7. (A) Rainfall index (normalized) for southern Africa compared to the continent as a whole, 1973–1993 (from Gommes and Petrassi 1996). Malawi's rainfall patterns follow those of southern and south-central Africa (Gommes and Petrassi 1996). Note above-normal rainfall in late 1988–1990 and below-normal rainfall in 1990–1993. (B) Recent variations in the Southern Oscillation Index (SOI) (from Gommes and Bakun 1998). Negative values represent warm sea-surface-phase ENSO years, and positive values correspond to cold sea-surface-phase ENSO years. Horizontal bars beneath the years delineate the duration of the 1987–1992 sediment trap time series.

resultant massive export of opal and POC measured by the sediment trap from March 1989 to May 1989. Although Bootsma and Hecky (1999) noted that, in rare cases, tectonic activity might trigger upwelling in the lake, no strong evidence exists to indicate that the significant 1989 seismic event promoted a large-scale mixing of what would have been a highly stratified water column at the end of the 1988–1989 summer rainy season. A more likely hypothesis is that large increases in river discharge provided direct nutrient input to the northern lake region and triggered an algal bloom. Volumetrically, the rivers flowing into the northern lake basin account for a greater percentage of the total river input over time compared to the southern drainages (Hecky et al. 2003). Additionally, northern rivers exhibit higher total nitrogen : total phosphorus ratios than do southern rivers, and

the concentration of soluble-reactive silica in river inflow has been shown to respond proportionally to runoff (Hecky et al. 2003). Therefore, at least in the northern basin of Lake Malawi, river inputs may affect nutrient dynamics over short timescales (Hecky et al. 2003). An extended rainy season, flooding, and high-volume runoff of the northern basin rivers in 1989 may have provided a direct, allochthonous nutrient input to the epilimnion, thus stimulating diatom growth and biogenic particle production.

A second possible mechanism that could have led to vertical mixing and nutrient injection into the epilimnion is that enhanced river discharge resulting from the substantial rains destabilized stratified lake conditions in the northern end of the lake at the end of the rainy season. Several studies have suggested the possibility that deep intrusions of cold river water in the north where river input is high lead to the sporadic upwelling of bioavailable nutrients from deeper waters (Bootsma and Hecky 1999; Vollmer et al. 2002). Diatom populations responding rapidly to a short, intense nutrient input with a massive bloom would result in large pulses of sinking particulate material early in the year such as that measured by the 1989 trap.

The lack of a significant difference in the lithogenic mass fraction of the trap material collected during the 1989 TMF peak event (65%) compared to the previous years' peaks (70% for 1988 and 52% for 1987) suggests that direct, allochthonous nutrient input to the epilimnion via river inflow was not the primary force behind the inferred bloom and resultant particle export peak in 1989. Alternatively, the scenario of sporadic, deep-water upwelling is supported by the results of an examination of stable nitrogen isotope fractionation in Lake Malawi in which elevated nutrient levels in the northern lake region were inferred from $\delta^{15}\text{N}$ data obtained from a subset of the 1987–1989 time-series trap samples (François et al. 1996). When sufficient surface nitrate is available, phytoplankton preferentially utilize the lighter ^{14}N isotope rather than the heavier ^{15}N isotope during nitrate uptake (Altabet 1996). This results in the algal biomass and sinking particles produced at the beginning of a bloom being isotopically light or depleted in ^{15}N (i.e., $\delta^{15}\text{N}$ of $<0\text{‰}$ as a function of NO_3^- utilization) compared to those of the sinking, algal-rich particulate material produced near the end of a bloom when the surface nitrate supply has been depleted (Altabet 1996; François et al. 1996). Isotopic mass balance considerations require that the $\delta^{15}\text{N}$ of sinking particulates be equal to that of the nitrate supplied. Therefore, it is expected that as stratification increases and the supply of upwelled "new" nitrate decreases, the available nitrate will become heavier, as dictated by Rayleigh fractionation kinetics, and the $\delta^{15}\text{N}$ of the sinking particulate material will increase to values $>0\text{‰}$ (Altabet 1996). That each of the major export peaks in 1987 and 1988 was accompanied by significant, 3–4‰ decreases in the $\delta^{15}\text{N}$ of the sinking particulate material to values of -0.9‰ to -2.4‰ (Table 1) indicates that deep, vertical mixing events provided an ample supply of lighter $^{14}\text{NO}_3^-$, resulting in ^{15}N -depleted, algal-rich particulates collected by the trap (François et al. 1996). The highly depleted $\delta^{15}\text{N}$ value of -2.4‰ for the trap material collected during the March–April peak in TMF is a strong signal of nitrate supply to the epilimnion from underlying waters oc-

curing at the end of the rainy season and quite early in the dry/windy season (Table 1).

From 1990 to the end of the time series, there were several dry-season export peaks of moderate size recorded by the trap at the northern site (1990) and at the central site (1991–1992), but no large export events were observed that were of similar magnitude to those of the preceding years (Table 1; Fig. 2). Bootsma (1993) noted that primary productivity levels in 1990–1991 in the lake were quite low compared to average values reported for earlier years. It is possible that the smaller 1990–1992 seasonal peaks in biogenic material delivery (when compared to those of 1987–1989) reflect a trend of decreasing diatom production in the lake. In particular, the relatively low 1990 total mass, biogenic silica, and POC fluxes coincident with isotopically heavy, particulate $\delta^{15}\text{N}$ values (Table 1) suggest a minimal supply of deep, upwelled nitrate, a slow, continuous utilization of euphotic NO_3^- by the phytoplankton, and a low, sustained level of primary production (François et al. 1996). An examination of the regional climate patterns during the early 1990s shows a warm ENSO phase from 1990/1991 to 1995 that was accompanied by severe drought conditions in Malawi (OFDA/CRED International Disaster Database; Fig. 7). Reduced river inflow during long drought periods, possibly accompanied by changes in wind forcing along the lake, could result in a reduction in nutrient recharge of the hypo- and metalimnion (Hecky et al. 2003), thus affecting lake productivity, particle export, and sedimentation rates in the deep basins. Speculation about the effects of persistent droughts on large, subtropical lake ecosystems, and especially on fish production, has important implications for understanding how global climate-warming trends will affect large populations that are economically dependent on the lake.

In the only other sediment trap study to date in Lake Malawi spanning >1 yr, cylinder-style traps were deployed in which single samples were collected during consecutive 3- to 4-month deployment periods between mid-May 1997 and January 1999 (Bootsma and Hecky 1999; Bootsma et al. 2003). The traps were placed at several depths in the upper 200 m at two shallow stations in the southern (200-m bottom depth) and northern (244-m bottom depth) lake regions. Similar to the results presented here, the 1997–1999 trap study showed a pattern of elevated biogenic silica export occurring in the north between May and September during the windy winter season (Bootsma and Hecky 1999; Bootsma et al. 2003). Longer-term, 100-m fluxes measured at the southern site showed a somewhat different pattern, with peak biogenic silica exports observed in the late windy/early rainy season (September through January; Bootsma and Hecky 1999; Bootsma et al. 2003). Interestingly, the Bootsma trap study reported fluxes of particulate biogenic silica and nitrogen in the upper 200 m that were several-fold to an order of magnitude greater than the fluxes measured in the present study conducted in the deep hypolimnion. Local sediment resuspension caused by the breaking of internal waves on the shallow bottom and lateral advection of resuspended sediment from upslope areas are likely explanations for the elevated fluxes found in the Bootsma et al. studies. This is strongly supported by the authors' documentation of increasing particle mass flux with depth for traps located on the

same mooring and the high amount of lithogenic material collected in the traps (Bootsma and Hecky 1999; Bootsma et al. 2003). Additional factors strongly affecting particulate biogenic fluxes that should be considered when comparing our 1987–1992 trap study results to those of the 1997–1999 Bootsma et al. study are the interannual and spatial variability in algal production, the effects of variable trap design on particle collection efficiency, the collection of monthly versus 3- to 4-month samples, and the remineralization of particulate nutrients occurring between the metalimnion and hypolimnion (Gardner 1979; Buesseler et al. 1994; Bootsma et al. 2003).

Relationship of modern time-series export to sedimentary paleoflux record—Pilskaln and Johnson (1991) first described the Lake Malawi laminated sediment sequences as annual varves consisting of light–dark couplets. Their findings have been substantiated by additional geochronology, paleoecology, and geochemical studies of the lake cores (Barry et al. 2002; Gasse et al. 2002; Johnson et al. 2002). Preliminary observations from the first 2 yr of the time-series trap study were noted in the Pilskaln and Johnson (1991) study in which seasonal, diatom-rich samples obtained during the 1987 and 1988 windy winter months provided a modern mechanism to explain the *Aulacoseira*-dominated light laminae in the underlying sediment record. Complete results of the northern Lake Malawi particle export time series, as well as those of the stable isotope study of the collected particulates and seasonal varves (François et al. 1996), generally support the interpretation of the sub-mm light laminae as representing the paleoflux deposition of diatom-rich particulates produced during the high-productivity/wind-mixing season on the lake. In northern and central lake cores accounting for up to 24,000 yr of deposition, thick packets of the light–dark laminae couplets can be cross-correlated within particular regions of the lake where they represent a primary stratigraphic unit (Johnson and Davis 1989; Pilskaln and Johnson 1991; Owen and Crossley 1992; Barry et al. 2002). This indicates that the seasonal delivery to the sediments of diatom-rich particle matter has been a persistent mode of sedimentation in Lake Malawi throughout the Holocene, despite major fluctuations in lake level (Barry et al. 2002). Assuming a relationship between seasonal total particle mass flux and lamination thickness under anoxic depositional regimes (Anderson and Dean 1988; Hay 1988), the time-series trap data suggest, however, that significant interannual variability in the timing and magnitude of diatom-rich export events gives rise to years in which the resulting white laminae are relatively thin or possibly absent.

Compositional comparison of the modern particle export samples to the underlying sediment record documents a substantial bias toward the sediment preservation of the thick-walled valves of *Aulacoseira* versus other prominent diatoms present in sinking particulates (Fig. 6A,B). Analyses of cores collected throughout the lake show a dominance of *Aulacoseira* in the laminated sections as well as in the nonlaminated diatom mud deposits (Owen 1989; Pilskaln and Johnson 1991; Gasse et al. 2002). The same biasing issue was also noted in Haberyan (1990) and was based on a diatom species analysis of sinking particulate material and under-

lying surface sediments collected from a near-shore area in southern Lake Malawi.

Although no valve counts were completed on the trap samples, *Stephanodiscus* sp. was extremely common (Fig. 5) and was occasionally more numerous than *Aulacoseira* sp., as was noted in the material collected early in the 1987 and 1988 windy winter seasons (Fig. 5C). This may reflect an overall recent trend of decreasing abundance of *Aulacoseira* in the lake, as has been noted elsewhere (Bootsma 1993; Patterson and Kachinjika 1995). However, the present time series is not long enough or of sufficient spatial coverage to fully assess the issue of lake-wide fluctuations in phytoplankton assemblages. Nevertheless, changes in diatom community structure, as well as the settling and preservation bias, have important implications for paleolimnology studies of Lake Malawi. Core analyses often use the *Aulacoseira*:*Stephanodiscus* ratio and weight percentage of biogenic silica as important indicators of enhanced or decreased upwelling intensity, degree of stratification, and changes in lake level (Barry et al. 2002; Gasse et al. 2002). Selective dissolution and grazing of diatoms and trace element requirements for growth, as well as factors that affect sinking rate and thus delivery to the sediments (e.g., variation between species in buoyancy, resting cell formation, aggregation rates), all complicate the use of modern diatom assemblages in interpreting the paleoecology of fossil assemblages. Therefore, we must continue to rely on additional proxies of paleovariations in lake-mixing dynamics and lake level, in combination with the diatom record, to offer the most accurate reconstruction of lake paleoecology (Brown et al. 2000; Johnson et al. 2002).

The formation of the dark laminae in the Lake Malawi varve couplets, in which diatoms are significantly less abundant and terrigenous plant debris is more prevalent than in the light laminae, has been attributed to deposition during the rainy season (Pilskaln and Johnson 1991; Barry et al. 2002). Microscopic examinations of the windy-season/peak-flux samples and the rainy-season/low-flux samples when compared to smear slides of the light and dark laminae do show basic compositional similarities (Fig. 6). The light laminae and peak export particulates are both rich in diatom valves, especially those of *Aulacoseira* sp. (Fig. 6A,B), whereas relatively few diatoms, occasional terrestrial plant debris, and abundant fine lithogenic particles characterize the dark laminae and the very low-flux/rainy-season trap material (Fig. 6C,D). The rainy-season particle mass fluxes are very small—two to three orders of magnitude smaller than the dry-season fluxes. This makes it problematic to explain the deposition of dark laminae, which are of similar thickness to the light laminae, based solely on particle sinking from the overlying column (Barry et al. 2002). However, the generation of near-bottom, sediment-laden flows off the major river deltas during the rainy season could transport near-shore and terrigenous particles out to the deep, anoxic lake regions and thus provide material for incorporation into the dark laminae (Johnson and Davis 1989; Pilskaln and Johnson 1991; Halfman and Scholz 1993). Clearly, a better understanding of the modern relationship between the spatio-temporal variability in lateral particle input to the lake and deposition dynamics is needed before we can determine the

quantitative significance of such particle sources to the sedimentation regime of the lake basin.

Time-series analysis of varve thickness in laminated sequences from northern Lake Malawi suggests ENSO-scale periodicities that are closely associated with rainfall anomalies in the region (Johnson 1996; Nicholson 1996). The results of the time-series particle flux study indicate that, during the years examined, the highest annual mass export of biogenic silica and particulate organic matter to the deep northern lake basin was observed during a wet, cold ENSO phase. Only one such cold period was covered by the trap time series, and thus, it would be of interest to determine whether the findings presented here merely reflect interannual variations in production, upwelling dynamics, etc., or whether the variability in magnitude and pattern of particle export is repeatable over longer timescales related to global climate cycles. This determination becomes particularly important in light of the demonstrated relationship between Lake Malawi sedimentary varve thickness and ENSO cycles. What we now require is a quantitative model of the relationship between particle supply and deposition as a function of ENSO-scale drought and rainfall cycles, which will strengthen our ability to predict the long-term effects of climate variability on such large lake ecosystems.

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