# Effects of hydrographic and climatic forcing on diatom production and export in the tropical southeastern Indian Ocean

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ABSTRACT: We examined a 32 mo continuous record of the flux of diatoms, silicoflagellates and bulk components collected between November 2000 and July 2003 at the pelagic mooring site Java Mooring (JAM), off southern Java in the tropical southeastern Indian Ocean. Temporal variations in the flux mainly reflected the dynamics of monsoon-driven seasonality of oceanographic and atmospheric conditions. Highest diatom fluxes coincided with the SE monsoon season during La Niña in September 2001, with the NW monsoon season in February/March 2003 and with the early SE monsoon season in 2003. Enhanced fluxes of diatoms, opal and organic carbon toward the end of the NW monsoon season are related to riverine nutrient inputs and the subsequent development of diatom-dominated phytoplankton blooms. During the SE monsoon season, the entrainment of nutrients from the subsurface into surface waters, due to upwelling, enhanced flux. A highly diverse diatom community characterized the fluxes throughout the sampling period. Several pelagic, warm-water species of the genus *Nitzschia*, accompanied by *Thalassionema nitzschioides* var. *parva* and *T. nitzschioides* var. *inflata*, dominated during periods of strong stratification, high sea surface temperature and low surface water productivity. The simultaneous occurrence of the pelagic *Azpeitia tabularis*, *Fragilariopsis doliolus* and *Planktoniella sol* and the coastal planktonic diatoms *Actinocyclus curvatulus* and *Thalassiosira oestrupii* var. *venrickae* reveals the intermingling of water masses of moderate-to-low nutrient content. Coastal upwelling diatoms *Thalassionema nitzschioides* var. *nitzschioides* and resting spores of *Chaetoceros* spp. occur most abundantly during the NW monsoon season. The diatom assemblage at the JAM site responded, with slight changes, to El Niño/Southern Oscillation occurrence. The co-occurrence of diatom species with different ecological affinities mirrors the fact that the JAM site was located in a region with large hydrographic variability over short time intervals.

KEY WORDS: Diatoms · Particle fluxes · Monsoon · Upwelling · Indian Ocean · Indonesian Archipelago

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## INTRODUCTION

The SE Indian Ocean off southern Java is a key area along the return branch of the global conveyor belt (Gordon 2005). It is well known that small changes in the sea surface temperature (SST) in this area can result in significant changes of precipitation patterns across the Indo-Pacific region (Neale & Slingo 2003), the thermocline structure in the southern Atlantic (Hirst & Godfrey 1993) and the global heat exchange (Gordon et al. 1992). The variability pattern in surface primary productivity, chlorophyll *a* concentration, SST, water mass circulation and the position of the Intertropical Convergence Zone (ITCZ) in the SE

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Indian Ocean are strongly monsoonal (Gordon 2005, Qu et al. 2005, Susanto et al. 2006).

The island of Java has a unique position in the western Indonesian Archipelago and experiences a strong response to monsoon seasonality. The seasonal swing of the SST is accentuated by Ekman upwelling: during the SE monsoon, southeasterly winds from Australia generate upwelling along the Java and Sumatra coasts (Gordon 2005). During the NW monsoon, NW winds produce weaker biological responses. Interannual variability in the upwelling intensity is present, probably as a consequence of annual variations in atmosphere–ocean teleconnections (Susanto et al. 2001). The intensity and seasonality of the monsoonal winds, and their complex interplay with climate phenomena such as the El Niño/Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD), may therefore be influenced by sea–air exchange processes and the inter-ocean throughflow within the Indonesian seas (Saji et al. 1999, Webster et al. 1999, Susanto et al. 2001).

Information on the temporal dynamics of diatom production is still scarce for the entire Indian Ocean. Based on net samples collected during the Indian Ocean Expedition of the RV 'Meteor', Simonsen (1974) took an inventory of all diatom species encountered within an extensive working area along the NE African coast, the Persian Gulf, the Gulf of Oman and the western coast of India, and included remarks on the distribution and ecology of these species. Koning et al. (2001) studied the diatom composition of settling particles collected in sediment traps off Somalia, NW Indian Ocean. In this area, diatoms represented >90% of the total siliceous microorganisms. A distinct succession of seasonal diatom species of 'pre-upwellers', 'upwellers' and 'oceanic species' occurred off Somalia (Koning et al. 2001). Less is known, however, about the seasonal dynamics of diatom populations and the contribution of diatoms to primary production and opal fluxes in the tropical SE Indian Ocean.

Materials collected by sediment trap allow the characterization of the seasonal and interannual variability of bulk and microorganism fluxes. In particular, assessment of the temporal occurrence of planktonic organisms helps in the calibration of species-specific ecological tolerances, as well as in the species potential for paleoceanographic reconstructions in a particular study area. In the present study, we examined a 32 mo continuous record of bulk component, diatom and silicoflagellate fluxes collected at the pelagic JAM site deployed off southern Java at approximately 8° 16′ S, 108° 09′ E between November 2000 and July 2003. A central objective of our work was to determine the effect of seasonal and inter-annual variability of hydrography, winds and nutrient availability on the production and export of diatoms and silicoflagellates. We demonstrated that variations in the qualitative composition of the diatom community mainly follow monsoonal-driven changes in the oceanographic and climatic conditions of the western tropical Indian Ocean. Our observations on the present-day distribution of diatoms off southern Java will help in the interpretation of diatoms as indicators of past environmental changes: mainly those involving variations in upwelling intensity and productivity.

## Oceanographic setting

The monsoonal circulation and the seasonal migration of the ITCZ drive the seasonal dynamics of its climate and hydrography off southern Java. During the austral summer (boreal winter), a southerly position of the ITCZ and the seasonal occurrence of the NW monsoon lead to an accumulation of large amounts of moisture gathered by crossing SE Asian and Indonesian seas and resulting in heavy rains in Sumatra and Java (Gordon 2005). During the austral winter (boreal summer), the SE monsoon originates in the high-pressure belt of the southern hemisphere and is relatively dry and cool when it reaches Indonesia (Gordon 2005). The SE monsoon gains moisture from the Indonesian and SE Asian seas and meets the ITCZ in a northerly position, leading to heavy precipitation on the SE Asian mainland. The SE winds also foster coastal upwelling south of Java, which is associated with lower SSTs and higher chlorophyll *a* concentrations (Gordon 2005, Susanto et al. 2006).

Ocean currents in the SE Indian Ocean move according to the wind regime. During the NW monsoon season, the South Java Current, derived from the Equatorial Counter Current (Fig. 1), moves towards the southeast to meet the Leeuwin Current, a narrow strip of warm, saline waters that originates in the eastern part of the Indonesian Archipelago (Tomczak & Godfrey 1994). The South Java Current and the Leeuwin Current combine to form the South Equatorial Current, which moves westward at ~15° S (Fig. 1). In the SE monsoon season, the South Java Current takes an opposite direction, flowing northwestward and feeding the South Equatorial Current, thus reducing its contribution to the Leeuwin Current. Advection of fresher Java Sea waters through the Sunda Strait and run-off from Sumatra and Java are responsible for the low-salinity 'tongue' in the South Java Current (Qu et al. 2005). The thick barrier layer off Sumatra that prevents cold thermocline water from entering the mixed layer explains why the SST depression off Sumatra is small compared to other eastern boundary upwelling areas (Qu et al. 2005).
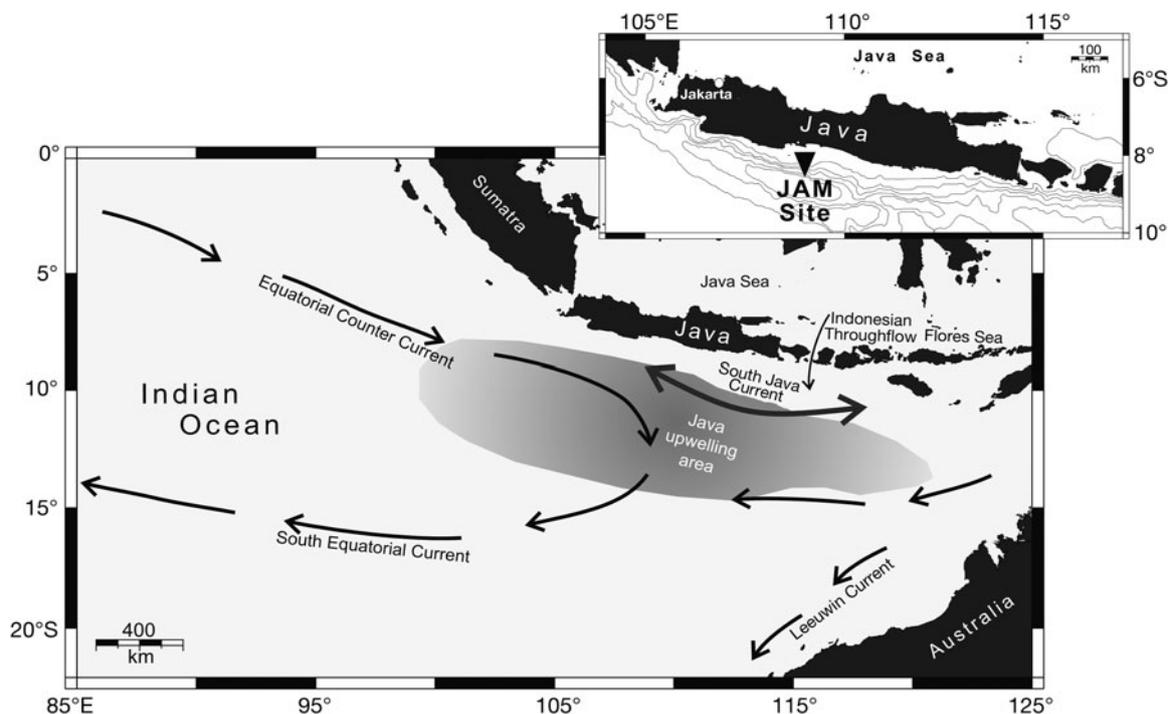
Fig. 1. Schematic map of the study area showing the principal surface currents (black arrows; after Gordon & Fine 1996). The gray shading (darker shades indicate greater intensity) represents the upwelling area off Java and Sumatra. The insert depicts the location of the mooring site JAM off southern Java in the SE tropical Indian Ocean

The Indonesian Throughflow, the only present-day, low-latitude oceanic connection between the major ocean basins, enters the Indian Ocean as a response to the higher steric height in the Pacific Ocean (Gordon 2005). The Java upwelling system is counterbalanced by increases in the Indonesian Throughflow and, consequently, except for brief periods, fails to bring subsurface nutrients to the surface (Godfrey 1996). In addition, the Indonesian Throughflow flows through the Lombok Strait, also neutralizing a significant SST depression off Java during the upwelling season.

## MATERIALS AND METHODS

**JAM mooring site.** A time-series sediment trap MARK VII was deployed at a water depth of approximately 2200 m at the JAM site (08°16.4'S, 108°08.96'E; Fig. 1) between November 2000 and July 2003 (Rixen et al. 2006). During the sampling period, 55 samples were taken, with a time resolution varying between 12 and 22 d. Details on sampling intervals and daily fluxes are presented in Table 1.

**Chemical analyses of bulk biogenic particles.** We followed the methods previously detailed in Rixen et al. (2006). Total carbon and organic carbon were determined using a Carlo Erba Nitrogen Analyzer 1500. Calcium carbonate results were derived from the dif-

ference between total and organic carbon. Opal concentration was determined photometrically after extraction of silicon with a sodium carbonate solution (Mortlock & Froelich 1989).

**Siliceous phytoplankton analysis.** For the present study either 1/16 or 1/64 splits of the original samples were used. Samples were rinsed with distilled water and prepared according to the methodology described by Romero et al. (1999, 2000). Diatom and silicoflagellate analyses were carried out on permanent slides of acid-cleaned material (Mountex mounting medium). Qualitative and quantitative analyses were done at 1000× magnification using a Zeiss-Axioscope with phase-contrast illumination. Several traverses across the slide were examined, depending on abundance (between 400 and 750 valves slide$^{-1}$ were counted). Each diatom was identified to the lowest taxonomic level possible. Silicoflagellates were only identified at group level. Counting of 2 replicate slides indicated that the analytical error for the diatom and silicoflagellate flux estimates was ≤15%. The resulting counts yielded the abundance of individual diatom taxa as well as daily fluxes of diatom valves and silicoflagellate skeletons m$^{-2}$ d$^{-1}$ calculated according to Sancetta & Calvert (1988), as follows:

$$F = \frac{(N) \times (A/a) \times (V) \times (\text{Split})}{(\text{days}) \times (D)}$$

Table 1. Daily flux of total particles, opal, calcium carbonate, organic carbon, lithogenics, diatoms and silicoflagellates at the JAM mooring site (29°12′S, 13°07′E) off southern Java in the tropical SE Indian Ocean from November 2001 to July 2003

| Days since start of trap experiment | Collection period started | Total particles (mg m$^{-2}$ d$^{-1}$) | Opal (mg m$^{-2}$ d$^{-1}$) | Calcium carbonate (mg m$^{-2}$ d$^{-1}$) | Organic carbon (mg m$^{-2}$ d$^{-1}$) | Lithogenics (mg m$^{-2}$ d$^{-1}$) | Diatoms (valves m$^{-2}$ d$^{-1}$) | Silicoflagellates (skeletons m$^{-2}$ d$^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| 11 | 11 Nov 2000 | 195.87 | 26.89 | 21.17 | 8.19 | 133.03 | 1 652 105 | 115 937 |
| 27 | 29 Nov 2000 | 271.96 | 36.79 | 20.91 | 9.86 | 196.52 | 2 246 835 | 221 443 |
| 45 | 12 Dec 2000 | 403.55 | 56.29 | 28.93 | 12.14 | 296.45 | 2 409 638 | 148 897 |
| 63 | 4 Jan 2001 | 239.81 | 34.01 | 30.33 | 11.51 | 159.04 | 1 273 344 | 145 830 |
| 81 | 22 Jan 2001 | 91.93 | 14.76 | 14.17 | 3.96 | 55.86 | 536 237 | 41 103 |
| 99 | 9 Feb 2001 | 233.86 | 27.17 | 15.22 | 7.76 | 177.50 | 1 549 342 | 83 000 |
| 117 | 27 Feb 2001 | 723.58 | 88.28 | 34.44 | 22.57 | 560.34 | 4 393 928 | 474 307 |
| 135 | 17 Mar 2001 | 385.85 | 49.77 | 25.74 | 12.23 | 284.49 | 2 338 904 | 126 075 |
| 153 | 4 Apr 2001 | 234.91 | 24.59 | 13.86 | 13.49 | 172.16 | 999 120 | 44 265 |
| 171 | 22 Apr 2001 | 153.53 | 21.32 | 17.10 | 6.77 | 102.93 | 2 024 796 | 90 702 |
| 189 | 10 May 2001 | 200.85 | 39.08 | 40.71 | 10.20 | 102.71 | 3 153 720 | 156 500 |
| 207 | 28 May 2001 | 139.62 | 25.55 | 30.03 | 7.42 | 70.67 | 2 187 563 | 75 088 |
| 225 | 15 Jun 2001 | 150.38 | 19.55 | 10.54 | 6.42 | 108.74 | 1 367 424 | 3 952 |
| 243 | 3 Jul 2001 | 402.55 | 55.59 | 103.29 | 14.85 | 216.89 | 4 393 052 | 203 933 |
| 261 | 21 Jul 2001 | 105.3 | 14.98 | 21.74 | 5.30 | 59.04 | 886 919 | 52 172 |
| 279 | 8 Aug 2001 | 387.16 | 51.41 | 59.74 | 15.86 | 247.39 | 6 014 477 | 230 566 |
| 297 | 26 Aug 2001 | 446.85 | 71.32 | 55.50 | 14.65 | 293.62 | 6 513 561 | 577 051 |
| 315 | 13 Sep 2001 | 613.78 | 138.77 | 46.89 | 33.34 | 368.08 | 12 035 347 | 244 047 |
| 333 | 1 Oct 2001 | 306.12 | 67.62 | 56.45 | 11.90 | 160.65 | 5 434 764 | 237 154 |
| 351 | 19 Oct 2001 | 161.39 | 29.84 | 18.91 | 6.65 | 100.66 | 2 442 802 | 97 526 |
| 369 | 6 Nov 2001 | 135.7 | 25.04 | 28.55 | 5.95 | 71.39 | 1 656 770 | 93 168 |
| 416 | 22 Dec 2001 | 239.36 | 34.66 | 13.17 | 10.15 | 173.26 | 748 155 | 74 697 |
| 432 | 7 Jan 2002 | 321.73 | 45.27 | 25.17 | 9.17 | 234.80 | 3 272 333 | 544 203 |
| 448 | 23 Jan 2002 | 349.11 | 49.68 | 22.70 | 9.64 | 259.39 | 2 320 994 | 312 134 |
| 464 | 8 Feb 2002 | 288.60 | 51.66 | 25.34 | 9.26 | 194.93 | 4 802 170 | 426 860 |
| 480 | 24 Feb 2002 | 236.22 | 40.87 | 23.80 | 8.07 | 157.03 | 682 943 | 48 019 |
| 497 | 12 Mar 2002 | 350.88 | 55.37 | 51.83 | 12.42 | 221.32 | 2 286 472 | 374 150 |
| 512 | 28 Mar 2002 | 402.58 | 68.80 | 41.25 | 12.83 | 269.43 | 3 429 174 | 347 490 |
| 528 | 13 Apr 2002 | 243.00 | 60.53 | 29.04 | 10.09 | 135.27 | 2 486 062 | 201 573 |
| 544 | 29 Apr 2002 | 192.71 | 38.94 | 28.94 | 7.12 | 112.01 | 2 341 837 | 148 282 |
| 560 | 15 May 2002 | 167.11 | 33.54 | 18.66 | 7.34 | 101.72 | 1 653 925 | 208 074 |
| 576 | 31 May 2002 | 118.28 | 22.43 | 11.17 | 4.80 | 76.02 | 2 070 936 | 143 398 |
| 592 | 16 Jun 2002 | 201.26 | 32.36 | 17.40 | 6.78 | 139.29 | 1 792 782 | 161 848 |
| 608 | 2 Jul 2002 | 304.36 | 49.15 | 45.17 | 10.42 | 191.28 | 2 479 768 | 173 410 |
| 624 | 18 Jul 2002 | 264.50 | 45.04 | 31.76 | 9.30 | 170.96 | 3 261 474 | 226 769 |
| 640 | 3 Aug 2002 | 306.40 | 54.69 | 41.70 | 10.99 | 190.23 | 3 169 133 | 104 037 |
| 656 | 19 Aug 2002 | 734.80 | 129.99 | 75.68 | 33.72 | 468.43 | 4 232 528 | 46 687 |
| 672 | 4 Sep 2002 | 511.80 | 98.78 | 84.33 | 19.55 | 293.50 | 5 992 877 | 18 675 |
| 688 | 20 Sep 2002 | 379.78 | 98.29 | 67.37 | 18.92 | 180.07 | 1 999 999 | 57 803 |
| 704 | 6 Oct 2002 | 304.87 | 98.59 | 49.88 | 14.57 | 130.16 | 2 296 984 | 60 693 |
| 720 | 22 Oct 2002 | 507.26 | 155.27 | 92.90 | 27.98 | 208.72 | 2 129 768 | 102 264 |
| 736 | 7 Nov 2002 | 470.84 | 117.71 | 61.89 | 19.06 | 256.94 | 5 577 935 | 32 679 |
| 746 | 11 Nov 2002 | 210.84 | 59.51 | 26.72 | 5.14 | 115.36 | 1 636 512 | 119 430 |
| 773 | 12 Dec 2002 | 473.99 | 104.01 | 47.96 | 13.32 | 298.05 | 3 766 556 | 423 783 |
| 790 | 31 Dec 2002 | 513.11 | 117.04 | 52.98 | 12.78 | 320.07 | 2 798 760 | 156 940 |
| 807 | 17 Jan 2003 | 338.05 | 82.65 | 47.94 | 9.68 | 190.02 | 3 659 082 | 269 144 |
| 824 | 2 Feb 2003 | 464.85 | 127.75 | 47.37 | 13.59 | 265.28 | 5 028 358 | 170 867 |
| 841 | 20 Feb 2003 | 495.37 | 130.54 | 46.65 | 14.82 | 291.51 | 8 407 019 | 402 546 |
| 858 | 9 Mar 2003 | 1041.49 | 214.84 | 92.54 | 26.08 | 687.17 | 6 477 865 | 395 870 |
| 875 | 26 Mar 2003 | 441.91 | 93.62 | 38.43 | 12.02 | 288.22 | 5 147 309 | 370 552 |
| 897 | 17 Apr 2003 | 682.89 | 178.42 | 46.87 | 20.22 | 421.20 | 6 234 577 | 222 331 |
| 909 | 29 Apr 2003 | 703.28 | 158.94 | 41.48 | 15.98 | 474.09 | 4 305 853 | 175 749 |
| 926 | 16 May 2003 | 297.90 | 68.64 | 30.44 | 10.19 | 180.47 | 3 871 182 | 319 111 |
| 943 | 2 Jun 2003 | 367.65 | 82.19 | 28.53 | 8.90 | 240.91 | 3 649 829 | 313 867 |
| 960 | 19 Jun 2003 | 696.42 | 294.26 | 61.32 | 26.14 | 293.79 | 6 687 361 | 267 829 |
| 977 | 6 Jul 2003 | 577.48 | 226.46 | 60.33 | 19.09 | 256.34 | 9 821 817 | 261 566 |

where ($N$) is the number of specimens (valves), in an area ($a$), as a fraction of the total area of a Petri dish ($A$) and the dilution volume ($V$) in milliliters. This value is multiplied by the sample split (Split), representing the fraction of total material in the trap, and then divided by the number of days (days) of deployment and the trap collection area ($D$).

**Principal components analysis.** To investigate the-covariability between the different diatom populations, as observed in a preliminary analysis of the temporal distribution of species, a principal component analysis (PCA) was carried out by means of SPSS, Version 15.0.1 (http://support.spss.com/Products Ext/SPSS/Patches/SPSSforWindows/). The extraction of principal components amounts to a variance maximizing (varimax) rotation of the original variable space. The criterion for the rotation is to maximize the variance (variability) of the 'new' variable (factor), while minimizing the variance around the new variable. Out of approximately 150 diatom species recognized in 55 sediment trap samples, the PCA covered the 22 most abundant diatom species. The average relative contribution of each of these 22 diatoms exceeds 1% for the entire sampling period. The diatom dataset from the JAM sediment trap results in 5 factors (diatom Groups 1 to 5) that account for ca. 76% of the original variance.

## RESULTS

### Total particle flux

Total particle flux peaked in every NW and SE monsoon season, except for the NW monsoon season in 2002 (Table 1, Fig. 2). Major peaks (>600 mg m$^{-2}$ d$^{-1}$) occurred in early March 2001, September/October 2001, August/September 2002 and February/March 2003. The magnitude of maxima differed from year to year. Total particle flux was mainly composed of lithogenics, the contribution of which varied strongly on a seasonal basis (Fig. 2). Opal (biogenic silica) was the main component of the bulk biogenic flux. The highest opal maxima (>150 mg m$^{-2}$ d$^{-1}$) occurred in September/October 2001, August/September and October/November 2002, and February/March and June 2003. The flux of organic carbon was generally enhanced at the end of the NW and during the SE monsoon seasons. Calcium carbonate

had 3 main maxima: 2 during SE monsoon seasons (2001 and 2002) and 1 during the 2003 NW monsoon season.

### Seasonal and interannual variations in diatom fluxes

The diatom flux ranged from $5.4 \times 10^5$ to $1.2 \times 10^7$ valves m$^{-2}$ d$^{-1}$ between November 2000 and July 2003 (Table 1, Fig. 3). Highest diatom maxima (>$8.4 \times 10^6$ valves m$^{-2}$ d$^{-1}$) occurred mostly during the monsoon seasons in September 2001, February/March 2003 and June/July 2003. Secondary peaks in diatom flux ($4.4 \times 10^6$ to $6.2 \times 10^6$ valves m$^{-2}$ d$^{-1}$) occurred in February/March 2001, early February 2002, early September 2002, early November 2002, February/March 2003 and late June 2003. Fluxes of silicoflagellates followed a similar temporal pattern to that exhibited by diatoms, except during the 2002 SE monsoon season (Table 1, Fig. 3).
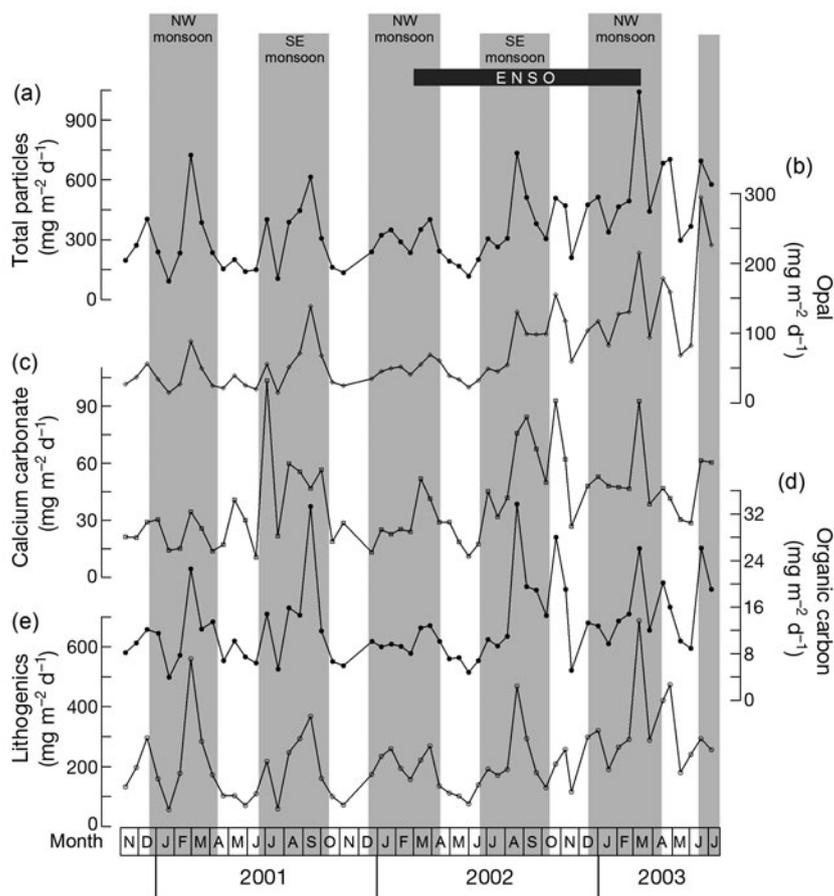


Fig. 2. Temporal changes in the flux of (a) total particles, (b) opal, (c) calcium carbonate, (d) organic carbon and (e) lithogenics (mg m$^{-2}$ d$^{-1}$) at the mooring site JAM off southern Java in the tropical SE Indian Ocean from November 2000 through to July 2003 (see also Table 1). Grey shading highlights the NW and SE upwelling seasons. ENSO: El Niño/Southern Oscillation
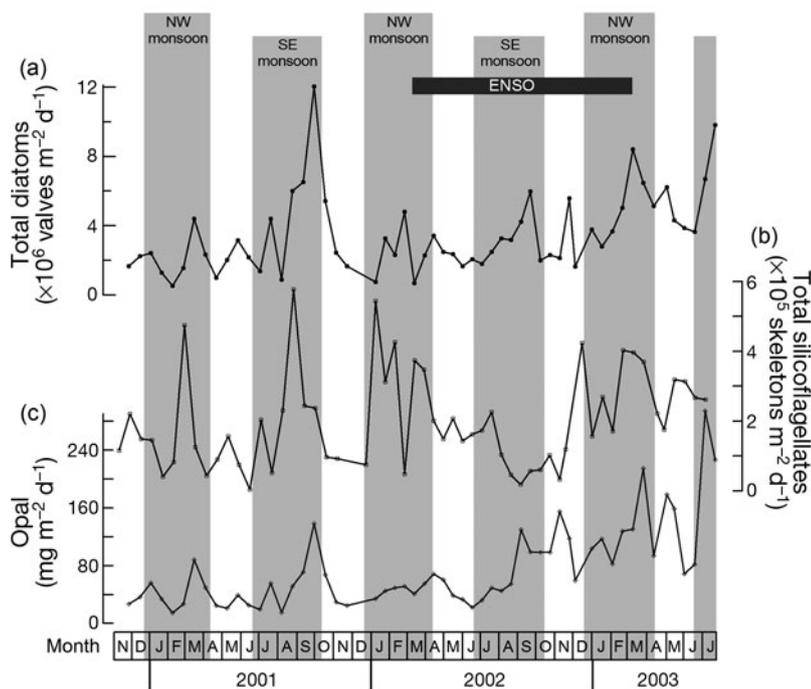
Fig. 3. Temporal changes in the flux of (a) total diatoms (valves m$^{-2}$ d$^{-1}$), (b) total silicoflagellates (skeletons m$^{-2}$ d$^{-1}$) and (c) opal (mg m$^{-2}$ d$^{-1}$) at the mooring site JAM off southern Java in the tropical SE Indian Ocean from November 2000 through July 2003 (see also Table 1). Grey shading highlights the NW and SE upwelling seasons. ENSO: El Niño/Southern Oscillation

## Temporal variations in the abundance of diatom species

The opal fraction at the JAM site comprised 165 marine and 13 freshwater diatoms, silicoflagellates, radiolarians, phytoliths and the dinoflagellate *Actiniscus pentasterias*. The complete list of diatom species is given in Appendix 1. In terms of the numbers of individuals, diatoms dominated the opal fraction throughout the year: their flux was always 1 to 4 orders of magnitude higher than that of the other siliceous organisms encountered. Fig. 3 depicts the temporal variations in the fluxes of diatoms and silicoflagellates.

The most important contributors to the diatom flux were the pelagic species *Nitzschia bicapitata* (average relative contribution for the entire sampling period = 15.0%), *Thalassionema nitzschioides* var. *parva* (8.5%), *N. interruptestriata* (4.4%), *Thalassionema bacillare* (3.0%), *Thalassiosira subtilis* (2.3%), *Rhizosolenia bergonii* (2.0%), *Planktoniella sol* (1.9%), *Fragilariopsis doliolus* (1.9%), *Thalassiosira oestrupii* var. *oestrupii* (1.3%), *N. sicula* (1.2%), *Thalassiosira lineata* (1.2%), *Thalassionema nitzschioides* var. *inflata* (1.2%), *Rhizosolenia setigera* (1.1%) and *Azpeitia tab-*

*ularis* (1.0%). Several neritic diatoms contributed seasonally to the flux: *Thalassionema nitzschioides* var. *nitzschioides* (9.7%), resting spores of *Chaetoceros* spp. (6.6%), *Actinocyclus curvatulus* (5.9%), *Thalassiosira oestrupii* var. *venrickae* (4.6%) and *Cyclotella litoralis* (1.0%).

Due to the high diversity of the diatom assemblage at the JAM site and in order to summarize the ecological information delivered by the main diatom contributors, we applied PCA to the relative abundance (%) of 22 diatom species. The first 5 components explained 76% of the total variance (Tables 2 & 3). Group 1 (~31% of the total variance) comprised the oligotrophic, open-ocean, warm-water diatoms *Nitzschia bicapitata*, *N. interruptestriata* and *N. sicula*, with minor contributions by *Thalassionema nitzschioides* var. *inflata* and *T. nitzschioides* var. *parva*. The highest relative contribution of Group 1 occurred during May/July 2001 and May/July 2002 (Fig. 4). Group 2, which explained ~17% of the variance, comprised *Azpeitia tabularis*, *Fragilariopsis doliolus*, *Planktoniella sol*, *Rhizosolenia bergonii*, *Thalassionema frauenfeldii*, *Thalassiosira oestrupii* var. *oestrupii* and *Thalassiosira subtilis*, pelagic species thriving in oligotrophic-to-mesotrophic waters of low-to-intermediate latitude oceans and the coastal *Cyclotella litoralis*. The relative contribution of Group 2 decreased steadily from the beginning of the sampling period until August/September 2002, peaked during October/November 2002 and decreased thereafter (Fig. 4). Group 3 comprised a mixture of coastal components, such as spores of an unidentified *Chaetoceros* species and *Thalassionema nitzschioides* var. *nitzschioides*, accompanied by pelagic *Thalassionema bacillare* and *R. setigera*, and explained 11.5% of the total variance. Group 3 peaked mainly during the NW monsoon season (Fig. 4). The coastal diatoms *Actinocyclus curvatulus* and *Thalassiosira oestrupii* var. *venrickae* were the main components of Group 4, with minor contributions from the pelagic *Thalassiosira lineata*. The temporal occurrence of Group 4 resembled that of Group 2. Group 5 mainly represents a coastal upwelling-related signal comprised of 2 resting spores of *Chaetoceros* spp. (*C. affinis* and *C. compresus*) (7.5% of the total variance). Group 5 showed maxima during the late SE monsoon season in 2001 and 2002, and in the early NW monsoon season in 2003.

Table 2. Varimax loadings matrix (rotation: varimax normalized). Factor scores for analysis of 55 sediment trap samples using 22 diatom taxa with average abundances ≥1.0% of the total diatom assemblage at the JAM site between November 2000 and July 2003. **Bold** print indicates the dominant species or group of species within each factor (loadings > 0.700). For the relative contribution of each factor (group) see Fig. 4. RS: resting spore

| Diatom species | Group 1 | Group 2 | Group 3 | Group 4 | Group 5 |
|---|---|---|---|---|---|
| *Actinocyclus curvatulus* | 0.061 | 0.422 | −0.311 | **0.516** | −0.449 |
| *Azpeitia tabularis* | 0.168 | **0.675** | 0.144 | 0.007 | 0.202 |
| *Chaetoceros affinis* RS | −0.303 | 0.263 | −0.188 | −0.425 | **0.501** |
| *Chaetoceros compresus* RS | 0.166 | −0.140 | −0.409 | 0.263 | **0.456** |
| *Chaetoceros* sp. RS | −0.190 | 0.163 | **0.504** | −0.108 | 0.029 |
| *Cyclotella litoralis* | 0.096 | **0.599** | 0.023 | −0.001 | 0.245 |
| *Fragilariopsis doliolus* | 0.138 | **0.577** | −0.118 | 0.477 | 0.060 |
| *Nitzschia bicapitata* | **0.376** | −0.584 | −0.580 | −0.064 | −0.066 |
| *Nitzschia interruptestriata* | **0.614** | 0.483 | −0.0765 | 0.397 | −0.087 |
| *Nitzschia sicula* | **0.516** | 0.132 | −0.206 | −0.164 | −0.125 |
| *Planktoniella sol* | −0.083 | **0.502** | 0.134 | 0.163 | 0.253 |
| *Rhizosolenia bergonii* | −0.654 | 0.477 | −0.143 | 0.164 | −0.160 |
| *Rhizosolenia setigera* | 0.169 | −0.108 | **0.817** | −0.063 | −0.261 |
| *Thalassionema bacillare* | −0.188 | −0.603 | **0.483** | −0.254 | 0.263 |
| *Thalassionema frauenfeldii* | 0.166 | **0.535** | −0.465 | 0.260 | 0.252 |
| *Thalassionema nitzschioides* var. *nitzschioides* | 0.086 | −0.237 | **0.674** | −0.094 | 0.385 |
| *Thalassionema nitzschioides* var. *inflata* | **0.546** | 0.033 | 0.118 | 0.406 | −0.264 |
| *Thalassionema nitzschioides* var. *parva* | **0.630** | 0.416 | −0.078 | 0.155 | 0.210 |
| *Thalassiosira lineata* | −0.030 | −0.596 | −0.341 | **0.161** | 0.111 |
| *Thalassiosira oestrupii* var. *oestrupii* | −0.598 | **0.340** | −0.080 | 0.273 | 0.066 |
| *Thalassiosira oestrupii* var. *venrickae* | 0.065 | −0.363 | 0.081 | **0.533** | 0.314 |
| *Thalassiosira subtilis* | 0.263 | **0.519** | 0.140 | −0.274 | −0.428 |

## DISCUSSION

Variations in the magnitude of fluxes at the JAM site mirrored the temporal variability of hydrographic and atmospheric conditions off southern Java in the SE tropical Indian Ocean. Good correlations between diatoms and organic carbon (r = 0.68, n = 55) and diatoms and opal (r = 0.69, n = 55) show that the seasonal cycle of diatom production and export was strongly coupled with the monsoon's seasonality. The dependence of diatom production on nutrient availability is clearly shown by the monsoon-driven seasonality of fluxes: almost 70% of the total annual diatom flux was intercepted during the NW and SE monsoon seasons at the JAM site (Fig. 5). Enhanced fluxes of diatoms, opal and organic carbon towards the end of the NW monsoon seasons were related to the riverine nutrient input and the subsequent development of a diatom-dominated phytoplankton bloom. During the SE monsoon season, the entrainment of nutrients from the subsurface into surface waters due to upwelling was found to enhance flux.

### SE monsoon

The highest diatom, opal and organic carbon fluxes recorded between June and August reveal the greatest seasonal effect on the productivity of surface waters along the southern coast of Java in response to the SE monsoon upwelling season (Moore et al. 2003). The bi-weekly averaged flux rate of organic carbon and the siliceous fraction (opal, diatoms and silicoflagellates) shows double peaks, one at the beginning and one at the end of the upwelling SE monsoon season (Fig. 5). Maxima of bi-weekly averaged fluxes early in the SE monsoon upwelling season were probably due to the shallowing out of the mixed layer and the associated input of nutrients from subsurface waters as a consequence of the increasing wind stress (Qu et al. 2005). The second peak at the end of the SE monsoon season is related to the bloom of diatoms due to the occurrence of upwelling off southern Java.

During our trap experiment, the weak La Niña conditions turned into weak ENSO conditions in early 2002, as indicated by the Southern Oscillation Index falling from 2 to −1.5 (Fig. 4). It has been proposed that

Table 3. Total variance explained by the first 5 factors of the principal component analysis (see Table 2)

| Factor | Variance (%) | Accumulated variance |
|---|---|---|
| 1 | 30.76 | 30.76 |
| 2 | 17.34 | 48.10 |
| 3 | 11.47 | 59.57 |
| 4 | 8.93 | 68.50 |
| 5 | 7.54 | 76.04 |

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ENSO suppresses the build up of the buoyant low-salinity layer during the NW monsoon, due to its impact on precipitation rates over Indonesia (Rixen et al. 2006). Since this layer caps off the nutrient-enriched subsurface waters and has to be removed in order to allow nutrients to upwell, a thinner, low-salinity layer is responsible for the increase in the mean SE monsoon fluxes under ENSO conditions (Rixen et al. 2006). Although our sediment trap record did not fully cover

the entire upwelling period during the 2003 SE monsoon season, maxima of diatom, opal and organic carbon recorded by late June 2003, 1 mo earlier than in the 2001 and 2002 cycles, points to the vigorous onset of the upwelling season in 2003. Additional evidence for the occurrence of more intense upwelling in June/July 2003 was given by the strong decrease in SST, exceeding the lowest values recorded in previous years (Fig. 4).

Seasonal differences in the magnitude of opal and diatom maxima can be seen for the JAM site. Although the opal fluxes during the 2003 SE monsoon increased after the preceding moderate ENSO conditions, the diatom flux was higher during the SE monsoon in 2001 than in 2003 (Fig. 3). The composition of the diatom assemblage, as well as the degree of silicification and size of the valves, might have contributed to the different magnitudes of the opal and diatom maxima. While diatoms attributed to PCA Groups 2, 3 and 5 were the main contributors to the SE monsoon peak in 2001, a much more diverse assemblage occurred during the 2003 SE monsoon (Fig. 6).

Temporal changes in the species composition of the diatom community at the JAM site off Java were related to the seasonal dynamics of the main hydrographic and atmospheric conditions in the tropical SE Indian Ocean. The occurrence of resting spores of *Chaetoceros* spp. (Group 5), typical of high-productivity, coastal upwelling regimes of low-to-intermediate latitudes in the world's oceans (Romero et al. 2001, 2002, 2009), revealed high nutrient input during the upwelling periods associated with the SE monsoon. After the dominant La Niña conditions in 2001, a stronger riverine discharge followed during the SE upwelling season 2001 off southern Java. Since the contribution of *Chaetoceros* spp. resting spores increased during the late SE upwelling season in 2001 (Fig. 6), we speculate that the moderate flux of opal during the later phase of the SE monsoon in 2001 was a consequence of less-silicified valves produced in surface waters.

**Intermonsoon**

The transition months between monsoon seasons, April/May and October/November, showed the lowest wind speed and



Fig. 4. Temporal changes in the relative contribution of 5 diatom groups (%) at the mooring site JAM off southern Java in the SE tropical Indian Ocean from November 2000 through July 2003 (see Table 2 for qualitative composition of diatom groups). The Southern Oscillation Index from the NOAA Climate Prediction Center (www.cpc.ncep.noaa.gov/data/indices) and the sea surface temperature (SST, °C) are also shown. Grey shading highlights the NW and SE upwelling seasons. ENSO: El Niño/Southern Oscillation

wind stress off southern Java (Susanto et al. 2006). The weakening of the wind system was coupled with the uninterrupted rise in SST (Fig. 4), the reduction in the vertical mixing and the decrease of the nutrient content in the upper water column (Susanto et al. 2001).

The diatom assemblage quickly responded to the changing atmospheric and oceanographic conditions during the intermonsoon periods off southern Java (Fig. 6). The dominance of diatom Group 1 during intermonsoons mirrored the highly stratified, nutrient-depleted surface waters and low primary productivity (chlorophyll $a$ < 0.2 mg C m$^{-3}$ h$^{-1}$; Qu et al. 2005, Susanto et al. 2006). It is well known that small *Nitzschia bicapitata* and *N. interruptestriata*, main contributors to Group 1, are common components of the open-ocean, nutrient-poor waters of tropical and subtropical areas of the world's oceans during periods of productivity collapse, following the shutdown of nutrient entrainment and the onset of stratification (Romero et al. 1999, 2000). Similarly, Koning et al. (2001) associated high numbers of *N. bicapitata* off Somalia with the retreating monsoonal upwelling in the western Indian Ocean.

## NW monsoon

Weakened river discharge under ENSO conditions was assumed to cause the flux decrease by late 2002 during NW monsoons off southern Java (Rixen et al. 2006). This interpretation was supported by the enhanced flux of organic carbon under La Niña conditions (NW monsoon in 2000/2001), yet slightly reduced organic carbon flux during the early 2002 ENSO (NW monsoon in 2001/2002). Our longer time-series data, however, show highest opal and organic carbon fluxes during the 2002/2003 NW monsoon, following a moderate ENSO event (Fig. 4). The impact of river discharge on export fluxes off Java and Sumatra might play an important role in the spatial variation of collected fluxes. In areas where the terrestrial nutrients are not consumed and exported from the euphotic zone, the biological production is generally enhanced, while enhanced stratification in the upper water column reduces the input of nutrients into subsurface waters (Ittekkot et al. 1991). Accordingly, we have interpreted that the occurrence of high fluxes during the NW monsoon in 2002/2003 was mainly caused by the input of nutrients from subsurface waters, due to the ENSO-driven, weakened freshwater discharges, which led to stronger vertical mixing. Our assumption was supported by the increased flux of lithogenics (Fig. 2), considered to be indicative of both stronger riverine input (Hendiarti et al. 2004) and increased availability of nutrients in surface waters off southern Java (Rixen et al. 2006 and references therein).

Further support for our interpretation is given by the diatom community thriving at the JAM site. Diatoms of Group 3, mainly *Thalassionema nitzschioides* var. *nitzschioides*, represented nutrient-enriched coastal conditions associated with the occurrence of the NW monsoon season off southern Java (Fig. 6). The presence of *T. nitzschioides* var. *nitzschioides* indicated
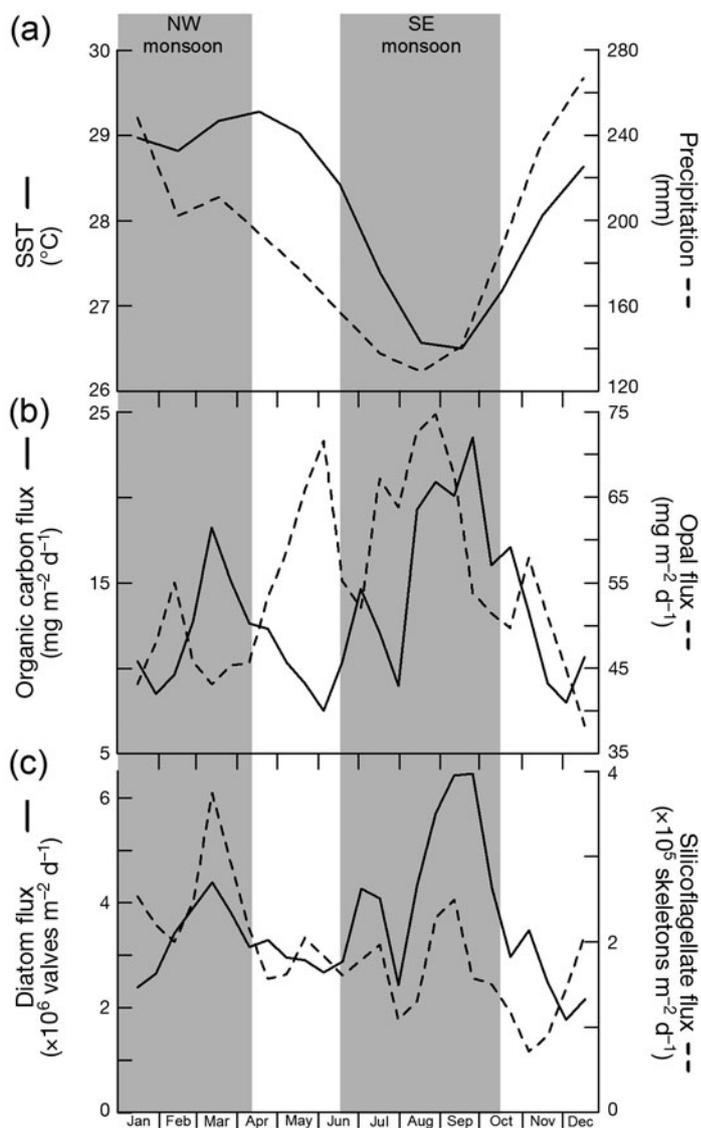


Fig. 5. (a) Monthly mean SST selected for the JAM site and the Indonesian continental precipitation rates derived from the German Weather Service. The global and 1 × 1° gridded SST and the precipitation rates were averaged for the areas 108 to 109° E and 8 to 9° S, as well as for 95 to 135° E and 10° S to 7° N. (b) Bi-weekly organic carbon and opal fluxes and (c) bi-weekly diatom and silicoflagellate fluxes averaged for the sampling period between November 2000 and July 2003 at the JAM site off southern Java. Bi-weekly values were calculated by lineally interpolating daily fluxes on a 14 d basis for the entire JAM trap experiment. Grey shading indicates the NW and SE monsoon periods
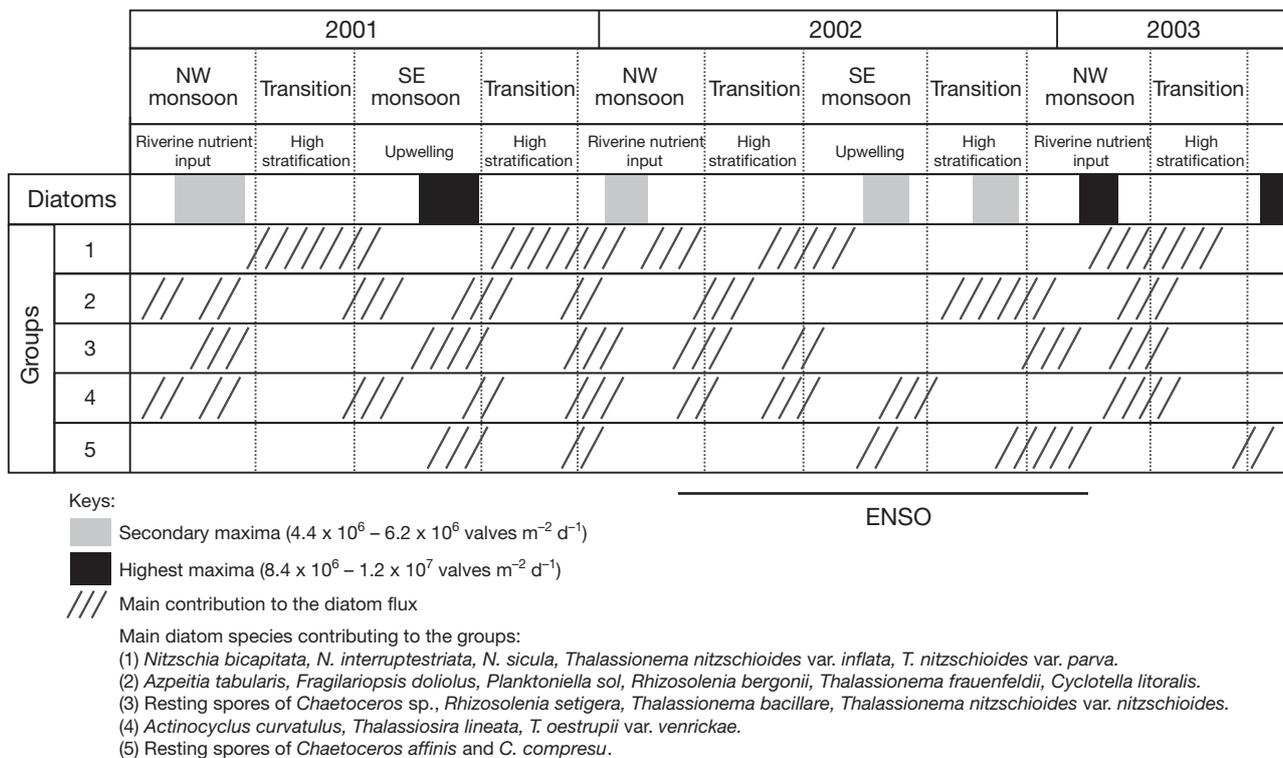
Fig. 6. Schematic of the temporal distribution of monsoon seasons and transition periods of diatom maxima and diatom species or groups of species at the pelagic JAM site in the tropical SE Indian Ocean between November 2000 and July 2003. Black shading: highest diatom maxima; grey shading: moderate diatom maxima; diagonal lines: periods of higher contribution for each diatom group. ENSO: El Niño/Southern Oscillation

increased nutrient supply from subsurface waters, in combination with some freshwater fluvial input (Romero et al. 2002). Similarly, Koning et al. (2001) observed that *T. nitzschioides* dominated the diatom assemblage during periods of more intense upwelling and low SST off Somalia.

A comparison of available diatom fluxes for the tropical Indian Ocean shows some differences on an annual basis. Although this comparison was mainly based on different sampling periods (2001 to 2003, eastern basin, [present study], vs. 1992 to 1993, western basin [Koning et al. 2001]), the total yearly diatom fluxes in open-ocean areas off southern Java and in the Somali Basin were on the same order of magnitude ($10^9$ valves m$^{-2}$ d$^{-1}$), while diatom fluxes measured over the Somalian slope were 1 order of magnitude higher (Koning et al. 2001). This difference might reflect (1) higher values of primary production of the surface waters (Antoine et al. 1996) and silicate content in the subsurface waters off Somalia (Ragueneau et al. 2000), or (2) year-to-year differences due to different sampling periods.

During the moderate 2002/2003 ENSO, the qualitative composition of the diatom assemblage revealed only moderate changes off southern Java. Probably as

a response to ENSO occurrence and the associated intensification of the upwelling, the contribution of diatom Group 5 increased by the late SE monsoon season in 2002 (Fig. 6). Immediately following this, an enhanced contribution of Group 2 diatoms in the SE to NW monsoon transition reflected similar hydrographic conditions to those already described for diatom Group 1: waters of low-to-moderate nutrient content and diatoms occurring most abundantly when stratification is high. The low relative contribution of diatom Group 1 points to more productive surface waters under the preceding La Niña conditions than during transition periods.

The response to ENSO events shown by the trapped diatom assemblage differed among various regions of the world's oceans. Although total diatom fluxes in the subarctic Pacific Ocean decreased significantly in response to the 1982/1983 ENSO, the composition of the diatom flora revealed only minor changes (Takahashi 1987). Similarly, the upwelling-associated resting spores of *Chaetoceros* spp. dominated the diatom community in coastal waters off northern Chile under both ENSO and La Niña conditions (Romero et al. 2001). On the contrary, significant changes in the qualitative composition of the diatom community in other

low-latitude coastal systems were related to the occurrence of ENSO. An increase in the relative contribution of eastern tropical Pacific diatoms and the simultaneous decrease of coastal-upwelling diatoms in the Santa Barbara Basin in 1997/1998 were associated with warm-water incursions into the near-shore area off California and decreased upwelling intensity due to the occurrence of ENSO (Lange et al. 1997). In the Cariaco Basin off Venezuela, the composition of the diatom assemblage showed a major shift during the boreal winter following the strong 1997/1998 ENSO: the highly diverse diatom assemblage during ENSO years comprised a mixture of pelagic and coastal planktonic diatoms, while only coastal diatoms dominated during La Niña years in the same region (Romero et al. 2009). However, a comprehensive understanding of the ENSO-driven forcing on the interannual variability of diatom fluxes in the tropical Indian Ocean requires further investigation, which should be complemented by longer term data sets to establish more clearly its role in the development of the diatom community response and the cascade to the rest of the food web.

## CONCLUSIONS

A central objective of our work was to determine whether and when the production and export of particulates, diatoms and silicoflagellates off southern Java occurs. To answer this question we followed the year-round flux of particulates and the quantitative and qualitative changes of the trapped diatom assemblage for ca. 2.5 yr. Our main observations are summarized as follows:

(1) Fluxes of diatoms, opal and organic carbon were highest during the NW and SE monsoon seasons off southern Java. During the SE monsoon season, the flux dynamics were driven by the occurrence of upwelling, whereas riverine nutrient input seems to be the main mechanism behind the increase of fluxes during the NW monsoon season.

(2) The occurrence of ENSO has a moderate effect on the production and export of diatoms. The ENSO-induced reduction of riverine nutrient discharge increased the fluxes during both monsoon seasons by weakening the stratification in the upper water column.

(3) Diatoms were the most important contributors to opal production and export measured off southern Java. The highly diverse diatom community at the JAM site was a mixture of representatives from pelagic conditions (mainly *Nitzschia bicapitata*, *N. interruptestriata* and *N. sicula*), high productivity, coastal upwelling (resting spores of *Chaetoceros* spp., *Thalassionema*

*nitzschioides* var. *nitzschioides* and *Cyclotella litoralis*) and coastal planktonic diatoms (*Actinocyclus curvatulus* and *Thalassiosira oestrupii* var. *venrickae*). The dominance of pelagic, tropical/subtropical diatoms with secondary contributions by upwelling-associated and coastal planktonic diatoms reflected the influence of both offshore and coastal waters, with considerable hydrographic variability over short time intervals.

(4) A moderate shift in the composition of the diatom community occurred during the 2002/2003 ENSO event off southern Java. Probably as a response to ENSO occurrence and the associated intensification of upwelling, the contribution of coastal upwelling diatoms increased by late 2002.

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**Appendix 1.** The list presents all the species, varieties or forms of diatoms (Bacillariophyceae) found in JAM sediment trap samples from November 2000 through to July 2003. Each species is followed by the author's name and year of description. In a few cases we were unable to identify the taxon to the species level. If this taxon was found repeatedly the generic name was used, followed by the abbreviation 'sp.'. RS: resting spore

| |
|---|
| *Actinocyclus curvatulus* Janisch, 1874 |
| *A. elongatus* Grunow, 1881 |
| *A. octonarius* Ehrenberg, 1838 |
| *A. subtilis* (Gregory) Ralfs, 1861 |
| *Actinoptychus senarius* (Ehrenberg) Ehrenberg, 1838 |
| *A. vulgaris* Schuman, 1867 |
| *Adoneis pacifica* G. W. Andrews & P. Rivera, 1987 |
| *Alveus marinus* (Grunow) Kaczmarska & G. Fryxell, 1996 |
| *Amphora decussata* Grunow, 1877 |
| *Amphora* sp. |
| *Asterolampra marylandica* Ehrenberg, 1844 |
| *Asteromphalus arachne* Brébisson, 1857 |
| *A. cleveanus* Grunow, 1874 |
| *A. flabellatus* (Brébisson) Greville, 1859 |
| *A. heptactis* (Brébisson) Ralfs, 1861 |
| *A. sarcophagus* Wallich, 1860 |
| *A shadboltianus* (Greville) Ralfs, 1860 |
| *Azpeitia africana* (Janisch *ex* Schmidt) G. Fryxell & T. P. Watkins, 1986 |
| *A. barronii* G. Fryxell & T. P. Watkins, 1986 |
| *A. neocrenulata* (Van Landingham) G. Fryxell & T. P. Watkins, 1986 |
| *A. nodulifera* (A. Schmidt) G. Fryxell & T. P. Watkins, 1986 |
| *A. tabularis* (Grunow) G. Fryxell & T. P. Watkins, 1986 |
| *Bacteriastrum elongatum* Cleve, 1897 |
| *B. furcatum* Shadbolt, 1854 |
| *Biddulphia alternans* (J. W. Bailey) Van Heurck, 1885 |
| *Campylodiscus clypeus* (Ehrenberg) Kützing, 1844 |
| *Campyloneis* sp. |
| *Catenula pelagica* Mereschkowsky, 1903 |
| *Chaetoceros affinis* Lauder, 1864 |
| *C. bacteriastroides* Karsten, 1907 |
| *C. concavicornis* Manguin, 1917 |
| *C. decipiens* Cleve, 1873 |
| *C. dydimus* Ehrenberg, 1845 |
| *C. lorenzianus* Grunow, 1863 |
| *C. messanensis* Castracane, 1875 |
| *C. pseudocurvisetus* Manguin, 1910 |
| *C. radicans* Schuett, 1895 |
| *C. affinis* Lauder, 1864 RS |

Appendix 1 (continued)

*C. cinctus* Gran, 1897 RS
*C. compressus* Lauder, 1864 RS
*C. constrictus* Gran, 1867 RS
*C. coronatus* Gran, 1897 RS
*C. debilis* Cleve RS
*C. diadema* (Ehrenberg) Gran, 1897 RS
*C. dydimus* Ehrenberg, 1845 RS
*C. pseudocurvisetus* Manguin, 1910 RS
*C. radicans* Schütt, 1895 RS
*C. vanheurckii* Gran, 1900 RS
*Chaetoceros* spp. RS
*Cocconeis dirupta* Gregory, 1857
*C. disculus* (Schumann) Cleve, 1895
*C. pelta* Schmidt, 1864
*C. pseudomarginata* Gregory, 1857
*C. stauroneiformis* (Rabenhorst) Okuno, 1957
*Corethron criophilum* Castracane, 1886
*Coscinodiscus argus* Ehrenberg, 1839
*C. centralis* Ehrenberg, 1839
*C. concinnus* Wm. Smith, 1856
*C. reniformis* Castracane, 1886
*Cyclotella litoralis* Lange & Syvertsen, 1989
*Cymatopleura solea* (Brébisson & Godey) Wm. Smith, 1851
*Delphineis karstenii* (Boden) Fryxell, 1978
*D. surirella* (Ehrenberg) Andrews, 1981
*Detonula pumila* (Castracane) Gran, 1900
*Diplomenora* sp.
*Diploneis bombus* Ehrenberg, 1844
*D. didyma* (Ehrenberg) Cleve, 1880
*D. papula* var. *constricta* Hustedt, 1927
*Ditylum brightwellii* (West) Grunow, 1880
*Entomoneis alata* (Ehrenberg) Kützing, 1884
*Fallacia nyella* (Hustedt *ex* Simonsen) D. G. Mann, 1990
*Fragilariopsis doliolus* (Wallich) Medlin & Sims, 1996
*Gosleriella tropica* Schütt, 1892
*Grammatophora marina* (Lyngbye) Kützing, 1884
*Guinardia cylindrus* (Cleve) Hasle, 1996
*Haslea gigantea* (Hustedt) Simonsen, 1974
*H. hyalinissima* Simonsen, 1974
*Hemiaulus hauckii* Grunow, 1880
*H. membranaceus* Cleve, 1873
*Hemidiscus cuneiformis* Wallich, 1860
*Hyalodiscus stelliger* J. W. Bailey, 1854
*Leptocylindrus mediterraneus* (H. Peragallo) Hasle, 1975
*Licmophora* sp.
*Lioloma elongatum* (Grunow) Hasle, 1996
*Mastogloia* sp.
*Navicula distans* Wm. Smith, 1853
*Navicula* sp.
*Neodelphineis indica* (F. J. R. Taylor) Hasle, 1993
*Nitzschia bicapitata* Cleve, 1901
*N. braarudii* Hasle, 1960
*N. capuluspalae* Simonsen, 1974
*N. dietrichii* Simonsen, 1974
*N. interruptestriata* (Heiden) Simonsen, 1974
*N. kolaczekii* Grunow, 1867
*N. longicollum* Halse, 1960
*N. sicula* (Castracane) Hustedt, 1958
*N. sicula* aff. *N.* cf. *sicula*
*Nitzschia* spp.
*Odontella aurita* (Lyngbie) Agardh, 1832
*O. longicruris* (Greville) Hoban, 1983
*O. mobiliensis* Bailey, 1845

*Opephora* sp.
*Paralia sulcata* (Ehrenberg) Cleve, 1873
*Planktoniella sol* (Wallich) Schütt, 1860
*Pleurosigma directum* Grunow, 1880
*P. planktonicum* Simonsen, 1974
*Porosira denticulata* Simonsen, 1974
*Proboscia alata* (Brightwell) Sundström, 1986
*P. alata* f. *indica* (Peragallo) Sundström, 1986
*Psammodiscus nitidus* (Gregory) Round & D. G. Mann, 1980
*Psammodyction panduriformis* (Gregor) D. G. Mann, 1990
*Pseudo-nitzschia inflatula* var. *capitata* Simonsen, 1974
*P. pungens* (Grunow ex Cleve) Hasle, 1965
*P. pungiformis* (Hasle) Hasle, 1971
*P. subfraudulenta* Hasle, 1965
*Pseudosolenia calvar-avis* (Schultze) Sundström, 1986
*Pseudotriceratium punctatum* (Wallich) Simonsen, 1974
*Rhizosolenia acicularis* Sundström, 1986
*R. acuminata* (H. Peragallo) H. Peragallo, 1892
*R. bergonii* H. Peragallo, 1892
*R. borealis* Sundström, 1986
*R. imbricata* Brightwell, 1858
*R. robusta* Norman, 1861
*R. setigera* Brightwell, 1858
*R. styliformis* Brightwell, 1858
*Roperia tesselata* (Roper) Grunow, 1880
*Skeletonema costatum* (Greville) Cleve, 1873
*Surirella* sp.
*Tabullaria* sp.
*Thalassionema bacillare* (Heiden) Kolbe, 1955
*Thalassionema* aff. *T.* cf. *bacillare* 1
*Thalassionema* aff. *T.* cf. *bacillare* 2
*T. frauenfeldii* (Grunow) Hallegraeff, 1986
*T. nitzschioides* var. *nitzschioides* (Grunow) Van Heurck, 1880
*T. nitzschioides* var. *capitulata* (Castracane) Moreno-Ruiz, 1996
*T. nitzschioides* var. *inflata* Kolbe, 1928
*T. nitzschiodes* var. *parva* (Heiden) Moreno-Ruiz, 1996
*T. pseudonitzschioides* (Schuette & Schrader) Hasle, 1996
*Thalassiora angulata* (Gregory) Hasle, 1978
*T. bioculata* (Grunow) Ostenfeld, 1908
*T. conferta* Hasle, 1977
*T. delicatula* Ostenfeld, 1908
*T. diporocyclus* Hasle, 1972
*T. eccentrica* (Ehrenberg) Cleve, 1904
*T. elsayedii* G. Fryxell, 1975
*T. endoseriata* Hasle & G. Fryxell, 1977
*T. ferelineata* Hasle & G. Fryxell, 1977
*T. leptopus* (Grunow) Hasle & G. Fryxell, 1977
*T. lineata* Josué, 1968
*T. nanolineata* (Mann) G. Fryxell & Hasle, 1977
*T. oestrupii* var. *oestrupii* (Ostenfeld) Hasle, 1972
*T. oestrupii* var. *venrickae* G. Fryxell & Hasle, 1972
*T. partheneia* Schrader, 1972
*T. plicata* (Grunow) Schrader, 1974
*T. poroseriata* (Ramsfjell) Hasle, 1972
*T. punctigera* (Castracane) Hasle, 1983
*T. sacketii* f. *sacketii* G. Fryxell, 1977
*T. sacketii* f. *plana* G. Fryxell, 1977
*T. subtilis* (Ostenfeld) Gran, 1900
*T. symmetrica* G. Fryxell & Hasle, 1972
*Thalassiosira* sp.

Appendix 1 (continued)

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|---|---|
| *Thalassiothrix spathulata* Hasle, 1999 | *Epithemia* sp. |
| *Toxarium* sp. | *Eunotia* sp. |
| *Trachyneis aspera* Cleve, 1894 | *Gomphonema* sp. |
| *Trigonium* sp. | *Hantzschia amphyoxis* (Ehrenberg) Grunow, 1880 |
| Freshwater diatoms | *Luticola mutica* (Kütz.) D. G. Mann, 1990 |
| *Achnanthes delicatula* (Kützing) Grunow, 1880 | *Navicula cryptotenella* Lange-Bertalot, 1985 |
| *Aulacoseira granulata* (Ehrenberg) Ralfs *in* Pritchard, 1861 | *Pinnularia* sp. |
| *Cyclotella meneghiniana* Kützing, 1884 | *Rhopalodia* sp. |
| *Cymbella* sp. | *Sellaphora pupula* Kützing, 1844 |