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Iron fertilization and the *Trichodesmium* response on the West Florida shelf

Jason M. Lenes[1], *Brian P. Darrow, Christopher Cattrall, Cynthia A. Heil, Michael Callahan, Gabriel A. Vargo, and Robert H. Byrne*
College of Marine Science, University of South Florida, 140 Seventh Avenue South, St. Petersburg, Florida 33701

Joseph M. Prospero
Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149

David E. Bates
Department of Physics, University of Miami, 1320 Campo Sano Drive, Coral Gables, Florida 33146

Kent A. Fanning
College of Marine Science, University of South Florida, 140 Seventh Avenue South, St. Petersburg, Florida 33701

John J. Walsh
College of Marine Science, University of South Florida, 140 Seventh Avenue South, St. Petersburg, Florida 33701; Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149

Abstract

Prior laboratory studies of *Trichodesmium* have shown a high iron requirement that is consistent with the biochemical demand for iron in the enzyme nitrogenase. Summer delivery of iron, in the form of Saharan dust, may provide an explanation for *Trichodesmium* blooms observed in offshore waters of the West Florida shelf over the last 50 yr. During ecology and oceanography of harmful algal blooms (ECOHAB) field studies, background iron levels (0.1–0.5 nmol kg^{-1}) were found at the surface during periods of minimal dust delivery (May 2000 and October 1999). In contrast, total dissolved iron concentrations on the order of $\sim$16 nmol kg^{-1} were measured at the West Florida shelf-break after a July 1999 Saharan dust event that was identified by advanced very high resolution radiometer (AVHRR) imagery, ground-based radiometers, air mass analysis, and aerosol samples (dust and non–sea-salt nitrate) collected throughout South Florida. The *Trichodesmium* response following this July dust event was a 100-fold increase over background biomass, reaching a surface stock of $\sim$20 colonies L^{-1}. Surface dissolved concentrations of both inorganic and organic phosphorus decreased below detectable limits during this bloom. Dissolved organic nitrogen concentrations associated with the bloom (15–20 μM) were 3–4-fold greater than background and much larger than ambient NO_3^- concentrations ($<$0.5 μmol kg^{-1}). If all dissolved organic nitrogen (DON) is converted to urea and ammonium, this organic nitrogen could have supported the red tide of $>$20 μg chl L^{-1} of the toxic dinoflagellate, *Gymnodinium breve,* found along the West Florida coast during October 1999.

Iron availability has been characterized as an important controlling factor in the primary production and nutrient cycles of oceanic ecosystems (Martin and Fitzwater 1988; Barber and Chavez 1991). Laboratory studies indicate that iron plays a critical role in nitrogen fixation by the cyanobacterium *Trichodesmium spp.* (Rueter 1988; Rueter et al. 1990; Paerl et al. 1994). In this context, blooms of *Trichodesmium erythraeum* have been observed within 75 km of the west coast of Florida for more than 50 yr (King 1950), where ambient nitrate concentrations within 5 km of the coast are less than 0.50 μmol kg^{-1} (Steidinger et al. 1998). Accurate depictions of fluctuations in surface iron concentrations in response to Saharan dust deposition and cyanobacterial uptake has not been explored within this 100–150-km wide, oligotrophic shelf ecosystem (Fig. 1).

Duce (1986) and Martin and Gordon (1988) indicated that a majority of phytoplankton Fe-requirements might be supplied by atmospheric deposition. Direct uptake of particulate iron is of negligible significance in most phytoplankton (Rich and Morel 1990), whereupon iron bioavailability to

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[1] Corresponding author (lenes@seas.marine.usf.edu).

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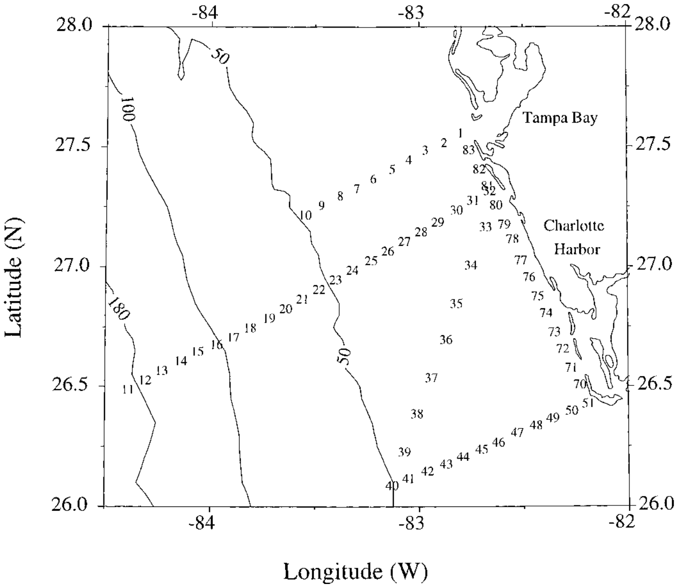

Fig. 1. ECOHAB cruise track of monthly surveys on the central West Florida shelf, between Tampa Bay and Charlotte Harbor.

algal assemblages is controlled by dissolved iron species. In contrast to this generalization for phytoplankton, Rueter et al. (1990, 1992) suggested that *Trichodesmium* may take up both dissolved and particulate iron associated with dust.

Saharan dust in vast quantities is swept into air streams over West Africa during the dry summer months and is transported thousands of kilometers across the Atlantic Ocean to the Caribbean and eastern United States (Schütz et al. 1981). Desert dust often contains iron oxides. Recent investigations (Carder et al. 1991; Young et al. 1991) suggest that aerosols may be an important source of iron to phytoplankton in several oligotrophic oceanic regions. Indeed, aeolian input is believed to be responsible for 30–96% of the dissolved iron in the photic zone of the Sargasso Sea and 16–76% in the central North Pacific gyre (Duce 1986).

Concentrations of Fe(II) are generally much lower in seawater than in freshwater (Miller et al. 1995) due to rapid Fe(II) oxidation rates (Millero and Sotolongo 1989) and Fe(III)-oxide solubility limitations (Byrne and Kester 1976). At ambient seawater pH, maximum Fe(II) concentrations range from 4 to 8% of total iron concentrations (Miller et al. 1995). The low solubility and high reactivity of ferric iron, plus the obligate role of iron in metabolic processes, limits dissolved iron concentrations to nanomolar levels (Waterbury et al. 1997). On the West Florida shelf, summer iron stocks should be controlled by two dominant factors: (1) Local riverine inputs (Kim and Martin 1974; U.S.G.S. 1976–1981) and (2) far-field aerosol dust (Carder et al. 1991; Prospero 1999). This input iron will be depleted by biological uptake, particulate scavenging, sediment deposition, and physical export.

Previous assessments of iron inputs to the West Florida shelf have not included direct measurements of iron concentrations. Instead, estimates of iron inputs have been based on time series dust records at Fort Myers and Miami, dust composition, and relative wet (75%) and dry (25%) mineral deposition rates (Walsh and Steidinger in press). With a combined wet and dry deposition rate of $\sim$1.25 g m^{-2} yr^{-1} (Prospero et al. 1987; Landing et al. 1995) and a $\sim$3.5% mass fraction of iron in mineral aerosols (Duce et al. 1991; Zhu et al. 1997), about 80% of the estimated annual loading (0.6 mM Fe m^{-2}) may be deposited in 1 month on the West Florida shelf.

The large (2.2×10^{-3}) Fe/N ratio for the diazotroph *T. erythraeum* (Rueter et al. 1992) compared, for example, to less than 2×10^{-4} for diatoms and flagellates (Sunda and Huntsman 1995) is a reflection of the high iron levels required for optimal nitrogenase enzyme activity. Diazotrophs are a source of ammonium during population growth (Prufert-Bebout et al. 1993) and, as well, after bloom collapse (Devassy et al. 1978). Since 50–100% of the dissolved organic nitrogen (DON) excreted by *Trichodesmium* is amino acids (Capone et al. 1994; Glibert and Bronk 1994), diazotrophs are capable of eliminating or mitigating nitrogen limitation for other components of the phytoplankton community and the microbial loop. Thus we postulated that large pools of released DON might accumulate in the water column during periods of Fe availability on the outer shelf.

Nitrogen half-saturation constants, k_N, for the toxic dinoflagellate *Gymnodinium breve* range from $\sim$130 μmol kg^{-1} for amino acids (Baden and Mende 1979) to $\sim$1.1 μmol kg^{-1} for urea and $\sim$0.5 μmol kg^{-1} for ammonium, nitrite, and nitrate (Steidinger et al. 1998). The high k_N values for amino acids indicate (Fukami et al. 1991; Gentien 1998) that when amino acids are available, *G. breve* depends upon bacterial transformation of amino acids into urea and ammonium for fueling subsequent red tides. Alternatively, during periods of iron-limited growth and reduced nitrogen fixation, the ammonium released by some *Trichodesmium* populations might be directly used by *G. breve* (Prufert-Bebout et al. 1993). As an example, elevated inorganic nutrients (NH_4, PO_4) and organic nutrients (DON) associated with short-term (i.e., 7–10 d) *Trichodesmium* blooms in the Great Barrier Reef lagoon have been shown to significantly influence phytoplankton and zooplankton community dynamics (O'Neil et al. pers. comm.).

In this work, we examine changes of *Trichodesmium* abundances, dissolved iron stocks, PO_4 and DON/DOP concentrations across the West Florida shelf in relation to observations of air mass optical properties at St. Petersburg and Dry Tortugas, and atmospheric dust and non–sea-salt nitrate at Miami. The transport of Saharan dust to southern Florida was monitored through the use of AVHRR imagery. The arrival of dust at the West Florida shelf is described in terms of increases in the concentration of dissolved iron, diazotrophs, and labile organic nitrogen, with associated depletion of PO_4 and DOP. The proposed causal relationship of Walsh and Steidinger (in press), that *Trichodesmium* provides a nitrogen source for *G. breve,* investigated in this work will allow future research into the impact of cyanobacterial nitrogen fixation on food chain nutrient supply and thus prediction of red tides along the West Florida coast.

Methods

Iron sampling and analysis—Sampling for total dissolved iron (Fe_T) in the surface ocean was conducted aboard the R/

V *Suncoaster* and R/V *Bellows* in August of 1998, during monthly cruises from June to October 1999, and in May 2000. As part of the ECOHAB Florida project, 44 stations were sampled as far offshore as the 180-m isobath (Fig. 1).

The sampling device consisted of a 150-ml Teflon bottle fitted with a specialized cap that allowed water to enter from the side of the cap while air exits through the top.

The Teflon bottle was placed snugly inside a Delrin bottle, with a special cap that allowed for water and air flow in the same manner as the Teflon cap. The bottle was cast ahead of the ship with a fishing rod as the ship headed into the wind at 1 knot. The bottles typically filled with seawater in 30–45 s from the top 2 m of the water column. All samples were analyzed within 10 min after collection.

Seawater samples were analyzed for total dissolved iron, without filtration, using spectrophotometric procedures similar to those of Waterbury et al. (1997). Four hundred microliters of 0.01 M hydroxylamine hydrochloride were added to 100 ml of the seawater sample to reduce Fe(III) to Fe(II). Next, 200 μl of 0.01 M ferrozine (Sigma) reagent was added to 50 ml of this solution and the solution was introduced to the 10-m waveguide using a peristaltic pump. The concentration of iron in the solution was determined from the absorbance of the Fe(II)-ferrozine complex at 562 nm. The absorbance baseline for these measurements was obtained using the seawater sample combined with hydroxylamine hydrochloride without added ferrozine. The 10-m pathlength liquid core waveguide (LCW) used in this work produced a detection limit for total iron on the order of 0.1 nmol kg^{-1}.

The spectrophotometric system was calibrated using an iron stock solution prepared from ferrous ammonium sulfate in 0.01 M HCl. Calibration curves showing absorbance plotted against iron concentration ($[\text{Fe}_T]$) consistently conformed to Beer's law ($A = \epsilon \times [\text{Fe}_T] \times l$), where ϵ is the molar absorptivity of the iron ferrozine complex and l is pathlength. The molar absorptivity (ϵ) obtained in these calibrations was essentially identical to that obtained using a 1-cm pathlength and a conventional spectrophotometer.

Atmospheric optical properties—Aerosol optical depth (τ_a) is a measure of atmospheric turbidity. Clean maritime atmospheres possess optical depths from a reference wavelength at 500 nm [$\tau_a(500)$] of approximately 0.15, whereas this value for Saharan dust over the tropical North Atlantic is often between 0.3 and 0.5 (Reddy et al. 1990; Korotaev et al. 1993). Aerosol optical depth is commonly related to wavelength by $\tau(\lambda) \propto \lambda^{-\eta}$, where η is the Angstrom exponent (Angstrom 1964). Air mass origin may be characterized by this exponent. Small aerosols (e.g., maritime or tropospheric) display a strong spectral nature with Angstrom exponents between 1 and 2 (Hoppel et al. 1990; Reddy et al. 1990). Larger dust aerosols (e.g., Saharan) evince a more nonspectral behavior, with Angstrom values less than 0.8 and often less than 0.5 (Tanré et al. 1988; Reddy et al. 1990).

Measurement of aerosol optical depth was taken by two different instruments. The CIMEL (CIMEL Électronique) sun and sky radiometer retrieves aerosol optical depth in eight spectral bands. This instrument comprises a federation of ground-based remote sensing stations (AERONET) dedicated to assessing global aerosol optical properties (Holben et al. 1998). We obtained the daily optical depths from a CIMEL operating in the Dry Tortugas (http://www.aeronet.gsfc.nasa.gov:8080/). From these data we calculated the daily Angstrom exponent using a least-squares fit of optical depth versus wavelength between 400 and 870 nm. The Dry Tortugas (24.63°N, 82.89°W) are free of anthropogenic influence yet often experience the same air masses as Miami and St. Petersburg. The Microtops, a five-channel hand-held sunphotometer, measured aerosol optical depth in St. Petersburg to establish the presence of Saharan dust over the offshore oceanic sampling sites. These local measurements, combined with air mass back trajectory calculations from hybrid single particle Lagrangian integrated trajectory (HYSPLIT) and CIMEL optical depths in the Dry Tortugas, afford a complete air mass classification (Smirnov et al. 1995) capable of distinguishing Saharan dust from aerosols of continental origin. The HYSPLIT model is supplied by the Air Resources Laboratory of the National Oceanic and Atmospheric Administration (NOAA) (http://www.arl.noaa.gov/ready). Trajectories of 90-h duration were calculated at 1800 UTC (universal time coordinates) for heights of 500, 1,000, and 3,000 m above sea level.

Aerosol sampling of atmospheric dust and nitrate—Daily aerosol samples were obtained by drawing ~1,500 m^3 of air through Whatman filters located ~30 m above ground on an island approximately 4 km east of mainland Miami (Prospero 1999). The filters were extracted with deionized water and the extracts were then analyzed for major soluble inorganic ions. Non–sea-salt (NSS) nitrate was determined by suppressed ion chromatography (Savoie et al. 1989). The filter residue, obtained by ashing filters over 14 h at 500°C in a muffle furnace (less the ashed blank), was considered mineral dust. To compensate for the loss of soluble and volatile soil minerals, an adjustment factor of 1.3 (Prospero 1999) was applied to these dust data.

Trichodesmium counts—During monthly ECOHAB surveys, the concentration of *Trichodesmium* in surface water at selected stations was determined (within 3 h of collection) over a 72-h period by direct microscopic count. Surface water containing *Trichodesmium* was collected with 8-liter Nisken bottles, drained into a 10-liter Nalgene carboy, and pumped through a 49-mm Whatman GF/F filter at ~70 ml min^{-1}. Filters were placed cell side up in a petri dish and both single trichomes and colonies (''puffs'' and ''tufts'') of *Trichodesmium* were counted with a Meiji Model EMZ-TR dissecting microscope. Colony size and single trichomes were noted.

Dissolved organic matter—Nitrogen and phosphorus samples were collected from Nisken bottles and filtered through precombusted (2 h at 450°C) Whatman GF/F filters. Total dissolved nitrogen (TDN) concentrations were determined using the persulfate oxidation method of Solórzano and Sharp (1980*a*). Inorganic nitrogen values were determined using methods recommended by Gordon et al. (1993). DON was then determined as the difference between the inorganic nitrogen and TDN estimates.

Total dissolved phosphorus (TDP) measurements were

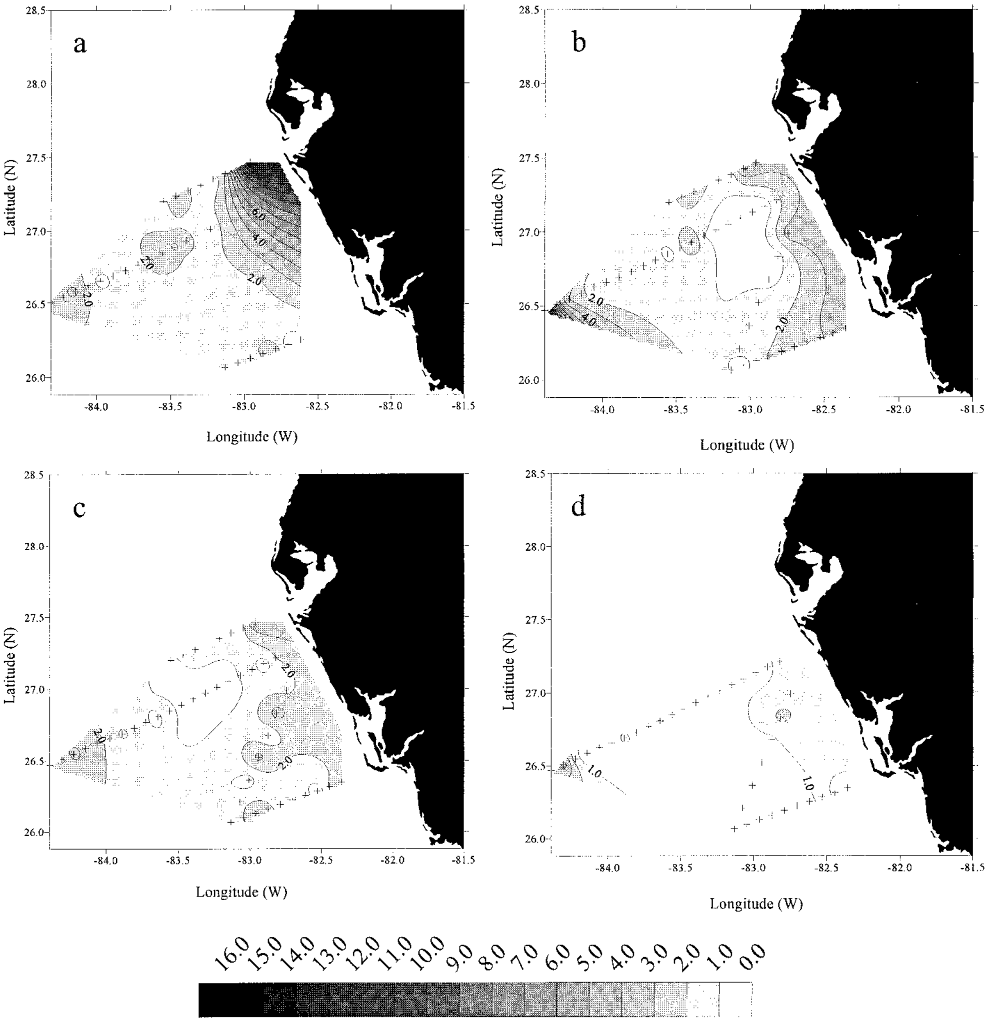

Fig. 2. The 1999 surface distributions of dissolved iron (nmol Fe kg^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

made by using the high temperature–hydrolysis technique of Solórzano and Sharp (1980*b*). Inorganic phosphorus values were again determined using methods recommended by Gordon et al. (1993). Dissolved organic phosphorus (DOP) was then determined as the difference between the inorganic phosphate and TDP estimates.

Sampling of surface salinity—Surface salinities along the 1999 ECOHAB cruise tracks (Fig. 1) were measured with a Falmouth Scientific microCTD-model MBP sensor. Measurements were averaged over 30 s intervals over the 3-d cruise track. During August 1998 only CTD data were available, whereupon discrete surface observations from individual stations were obtained.

Results

Dissolved iron levels—Total dissolved iron concentrations measured on the 5–7 July 1999 cruise (Fig. 2b), following the Saharan event of Fig. 3, reached ~16.0 nmol kg^{-1} at Sta. 11. In contrast, the iron found off the West Florida shelf during the October 1999 cruise, in the absence of Saharan dust input, represents mean background levels <0.1 nmol kg^{-1} at Stations 11–22 (Table 1) between the 50- and 200-m isobaths (Fig. 1). The same background concentrations of Fe were found in May 2000. Similar results were also obtained from the August 1998 cruise, with a mean of 0.2 nmol kg^{-1} at these offshore stations. High iron content of the West Florida river systems (~3,000 nmol kg^{-1} within the Peace River at Arcadia, Florida) led to elevated iron concentrations (1–2 nmol kg^{-1}) at the 10-m isobath in October 1999, May 2000, and August 1998.

Four Saharan dust events were observed in Miami during June–July 1999 (16–17 June, 26 June–4 July, 8–13 July, 19–21 July) with a mean interval of 6.3 d (Fig. 4a). The observed surface iron stocks at stations remote from riverine supplies (Stations 11–22) were averaged to yield a July mean of 3.0 nmol kg^{-1} (Table 1). Dissolved iron concentrations exhibited a cross-shelf minimum (Fig. 2b) of <0.1 nmol kg^{-1} at salinities greater than 36.0 (above the 20–50-m isobaths). This iron minimum at a salinity >36 lies between the offshore salinity minimum (~34.5) and low local river-

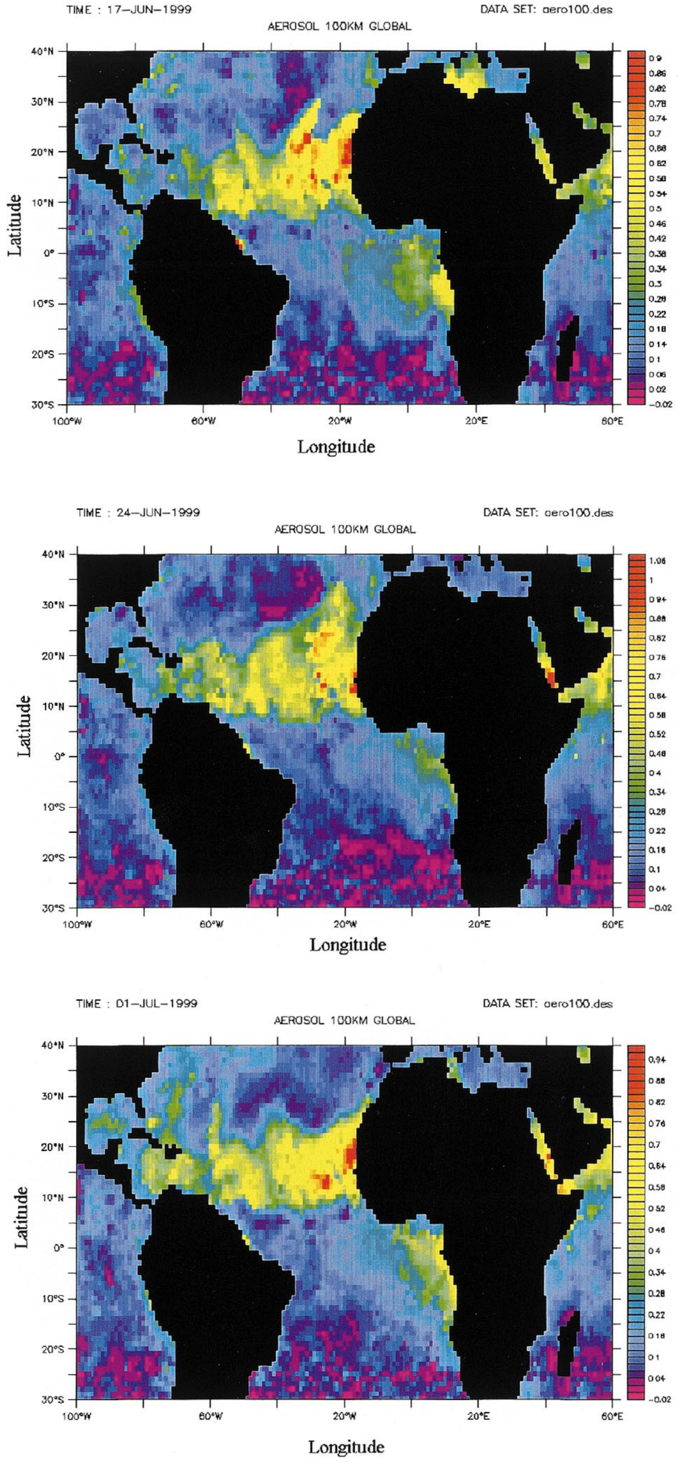

Fig. 3. AVHRR imagery of the 1999 aerosol optical thickness of the atmosphere, adjacent the Sahara Desert and above the Gulf of Mexico, during (a) 17 June, (b) 24 June, and (c) 1 July—from the Satellite Active Archive at PMEL (Pacific Marine Environmental Laboratory).

influenced salinities (~32.0) where iron concentrations were >3.0 nmol kg^{-1}. The mean 3.0 nmol kg^{-1} per event iron influx, as measured in July 1999, would lead to a cumulative 1-month input of ~12.0 nmol kg^{-1} within the 5-m surface mixed layer (Walsh and Steidinger in press).

The 6–8 August 1999 cruise occurred during a large Saharan dust event observed at both Miami (Fig. 4a) and Dry Tortugas (Table 1). Owing to an anticyclonic trajectory in the Gulf of Mexico similar to that shown in Fig. 5, this dust took a few days longer to arrive at St. Petersburg (Fig. 4b). Thus, offshore iron concentrations at the time of shipboard sampling (mean $[Fe_T] \sim 1.5$ nmol kg^{-1} at Stations 11–22) were lower than iron concentrations in July ($[Fe_T] \sim 3.1$ nmol kg^{-1}). By September 1999, Saharan dust supply gives way to continental sources, further reducing dissolved iron concentrations (Fig. 2d) from earlier months. A mean of 1.1 nmol kg^{-1} was found during 7–9 September following a continental dust event (Fig. 5).

In contrast, at the beginning of the dust season (5–8 June 1999), the dissolved iron at these stations was 2.0 nmol kg^{-1} (Fig. 2a). Nearshore concentrations exhibited a 14 nmol Fe kg^{-1} maximum, presumably representing a mixing event during the rough seas encountered. The lower salinity plume (~35.5) originating at the mouth of Tampa Bay extended farther offshore in June (Fig. 6a) than July (Fig. 6b). The linear regression between offshore dissolved iron concentration (June–October 1999) and the mean dust collected at Miami each month during all events (>10 $\mu g\ m^{-3}$) had a coefficient of determination (r^2) of 0.92.

Diazotroph populations—Background populations of *Trichodesmium* on the outer shelf during October 1999 were 0.1–0.2 colonies L^{-1}. During the ECOHAB survey of 5–8 June 1999 (Fig. 7a) populations were tenfold greater than these background levels. *Trichodesmium* abundance on the West Florida shelf during July 1999 exhibited a second tenfold increment after a Saharan dust event, reaching ~20.0 colonies L^{-1} at Sta. 16 above the 100-m isobath (Fig. 7b).

The local maximum of *Trichodesmium* stocks on the outer shelf in June corresponded to the iron minimum (Fig. 2a). Similarly, the July iron minimum of 1.3 nmol kg^{-1} between Stations 15 and 22 (Fig. 2b) also corresponded to the location of maximal *Trichodesmium* abundance. This implies removal of dissolved iron from the surface waters as the summer *Trichodesmium* populations grow on the West Florida shelf. A similar relation between dissolved iron and *Trichodesmium* was also observed across the Great Barrier Reef (Jones et al. 1986).

Likewise, a high *Trichodesmium* affinity for inorganic phosphorus (Karl et al. 1992) led to a July depletion of phosphorus stocks from the midshelf areas. Whereas June concentrations were ~0.50 μmol DOP kg^{-1} and ~0.30 μmol PO_4 kg^{-1} (Figs. 8a and 9a), after the July *Trichodesmium* population increase, P stocks within the bloom decreased to nearly undetectable levels for both organic and inorganic phosphorus (Figs. 8b and 9b). A high alkaline phosphatase activity (Yentsch et al. 1972) would provide rapid use of organic phosphorus within the population during periods of growth.

At Sta. 16 the surface stock decrease of *Trichodesmium*

Table 1. The dates of ECOHAB cruise in relation to (1) duration of the Saharan and Continental aerosol events (dates) and (2) backward trajectories of air masses from St. Petersburg, (3) mean weight ratios of atmospheric nitrate/dust concentrations (μg m^{-3}) sampled at Miami, (4) mean Angstrom exponents from the Dry Tortugas CIMEL, (5) total Tampa rainfall (cm), (6) mean aerosol optical thickness, $\tau_{\mathrm{aer}}(500)$, above St. Petersburg, and (7) mean dissolved iron (nmol kg^{-1}) within surface waters of the West Florida shelf at Stations 11–22, between the 50 m and 200 m isobaths.

ECOHAB cruise	Dust event	Air mass trajectory	Miami NO_3/dust	Dry Tortugas exponent	Tampa rainfall	St. Petersburg $\tau_{\mathrm{aer}}(500)$	W. Florida iron
1–3 May 2000	none	—	—	—	0.0	—	0.2
5–8 Jun 1999	—	—	0.49	—	0.3	0.19	2.0
	16–17 Jun	SE	0.08	0.60	3.8	—	—
	26 Jun–4 Jul	SE	0.07	0.27	5.9	—	—
5–7 Jul 1999	—	—	0.18	0.57	0.8	0.19	3.1
	8–13 Jul	SE	0.05	0.27	1.3	0.24	—
	19–21 Jul	SE	0.05	0.29	0.0	0.15	—
	28–31 Jul	NW	0.30	—	0.0	0.48	—
6–8 Aug 1999	7–11 Aug	SE	0.09	0.44	2.7	0.18	1.5
	27–30 Aug	NW	0.19	1.64	0.0	0.28	—
	3–6 Sep	NW	0.50	1.80	1.3	0.33	—
7–9 Sep 1999	—	—	0.24	1.10	0.8	—	1.1
5–7 Oct 1999	none	—	—	0.16	—	—	<0.1
6–10 Aug 1998	none	—	0.36	—	7.3	—	0.2

between July and August (Fig. 7c) mirrored the decrease in mean iron concentrations (Table 1). Although the local diazotroph maximum was still associated with iron minima (Fig. 2c), other limiting factors may also have been operative. By September 1999, despite levels of dissolved iron (Fig. 7d) at the half-saturation value of ~1.1 nmol kg^{-1} (Table 1), the offshore *Trichodesmium* abundance is minimal, with only ~0.5 colonies L^{-1} found at Sta. 16 (Fig. 8d). In contrast, a maximum concentration of 8.5 colonies L^{-1} was then located just off the mouth of Charlotte Harbor, where surface inorganic phosphorus was ~0.20 μmol PO_4 kg^{-1} and DOP was nearly undetectable (Fig. 9d and 8d).

Despite abundant iron (>2 nmol kg^{-1}) and phosphorus stocks within these nearshore waters, by 5–7 October 1999 the diazotroph population had been reduced to 0.5 colonies L^{-1} off Charlotte Harbor when a red tide of $>2 \times 10^6$ cells L^{-1} (i.e., >20 μg chl L^{-1}) was found. With an estimated saturation light intensity of ~300 μE m^{-2} s^{-1} for *Trichodesmium* (Carpenter and Roenneberg 1995), compared to a noon PAR of ~1,500 μE m^{-2} s^{-1} at the surface of the West Florida shelf (Penta pers. comm.), these diazotrophs must balance their iron nutrition needs (atmospherically derived) against the costs of near surface photoinhibition. In the absence of sufficient colored dissolved organic matter (CDOM) sunscreen (Keiber et al. 1990), termination of surface diazotroph blooms in both offshore and nearshore waters of the West Florida shelf may result from cumulative photolytic losses, since grazing losses seem to be minimal (O'Neil et al. 1996).

Dissolved organic nitrogen—Dissolved organic nitrogen released within surface waters by *Trichodesmium* populations provides a source of new nitrogen. The mean DON concentration across the West Florida shelf was ~4 μmol kg^{-1} in September 1998, following the occurrence of minimal iron concentrations during August (Fig. 10b). These 1998 DON concentrations are similar to midshelf values of ~5 μmol kg^{-1} in September 1999 (Fig. 11d). In contrast, larger DON values (~20 μmol kg^{-1}) were found in June 1999, just beyond the 100-m isobath, whereas nearshore values remained ~5 μmol kg^{-1} (Fig. 11a). These observations are consistent with a threefold increment of DON (5 μmol kg^{-1} to 14 μmol kg^{-1}) observed off Hawaii after a *Trichodesmium* bloom (Karl et al. 1992).

Although the *Trichodesmium* abundance increased by an order of magnitude from June to July (Fig. 7b), DON stocks declined from 20 to 14 μmol kg^{-1} (Fig. 11b). This may reflect uptake of labile amino acids (C/N ~ 4.3) released by the diazotrophs (Capone et al. 1994). In contrast, nearshore concentrations of DON composed, presumably, of more refractory (C/N > 20) riverine carbohydrates (Gardner et al. 1996) increased to ~22 μmol kg^{-1} during July. This coastal influx of DON was associated with low salinities off Charlotte Harbor (Fig. 6b) after a July rain event preceding the cruise by a few days (Fig. 12).

The concentrations of nearshore DON in August (Fig. 11c) and September (Fig. 11d) continued to be associated with low salinity plumes from Tampa Bay and Charlotte Harbor (Fig. 6c,d). The regression between dissolved organic nitrogen and salinity along the 10-m isobath during the June–October 1999 ECOHAB cruises (Fig. 1) produced an r^2 of 0.95, indicating that DON was a conservative property. In contrast, the DON versus salinity relationship at stations between the 50- and 100-m isobaths, with an r^2 of only 0.29, is consistent with less refractory offshore pools of DON. Although the Mississippi River influence on salinity (Del Castillo et al. pers. comm.) increased on the outer shelf (Fig. 6c,d), the concentration of apparently labile DON offshore (Figs. 11c,d) was significantly reduced (~8 μmol kg^{-1} in August and ~5 μmol kg^{-1} in September). Within offshore waters, DON uptake presumably continued for at least a month while, as indicated by the absence of surface populations of *Trichodesmium* (Fig. 7d), nitrogen fixation had ceased.

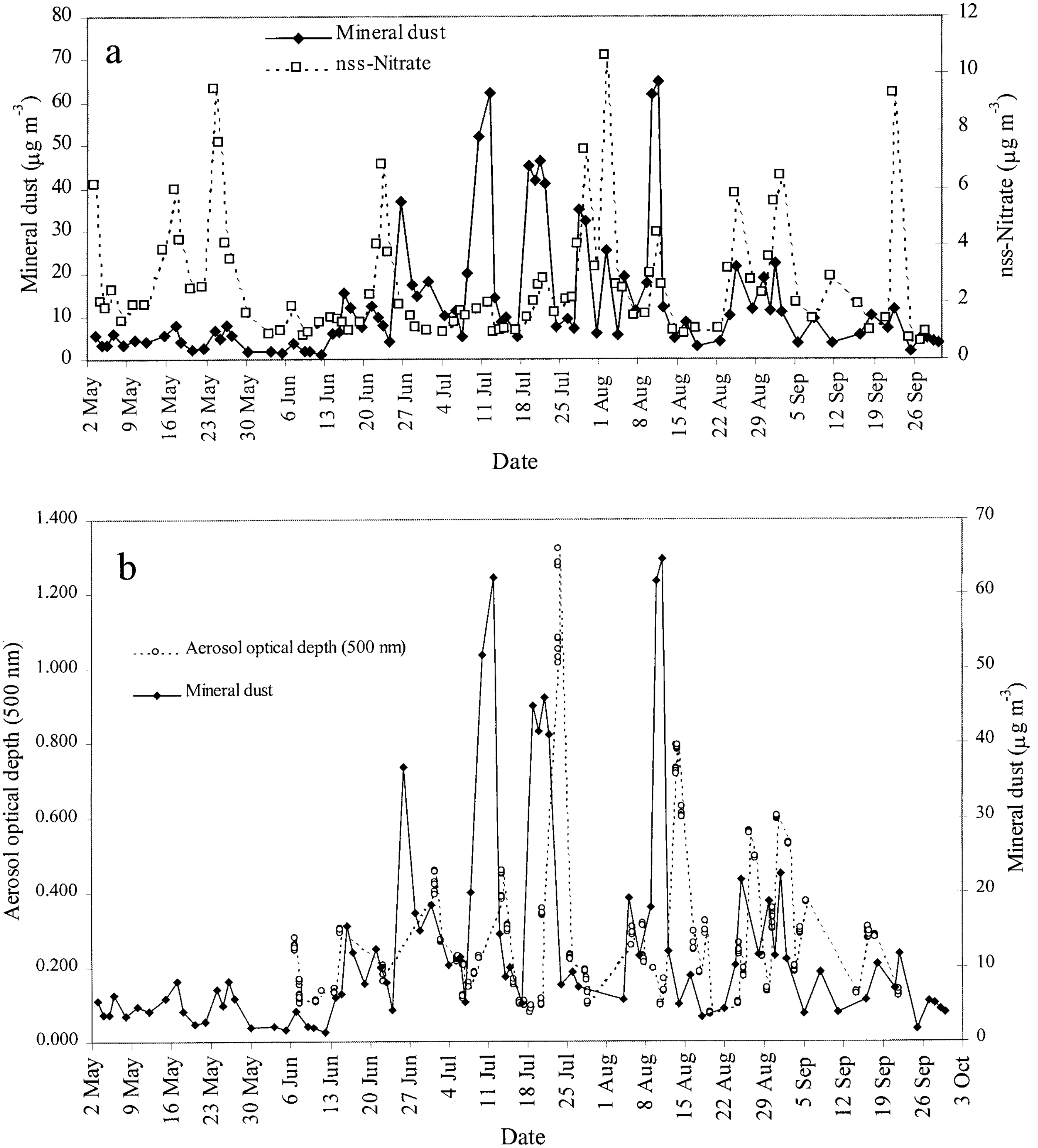

Fig. 4. Daily observations of mineral dust (μg m^{-3}) of the atmosphere above Miami during May–September 1999 in relation to (a) non-sea-salt nitrate (μg m^{-3}) of air 30 m above ground at Miami, and (b) aerosol optical thickness at 500 nm, $\tau_{\mathrm{aer}}(500)$, above St. Petersburg.

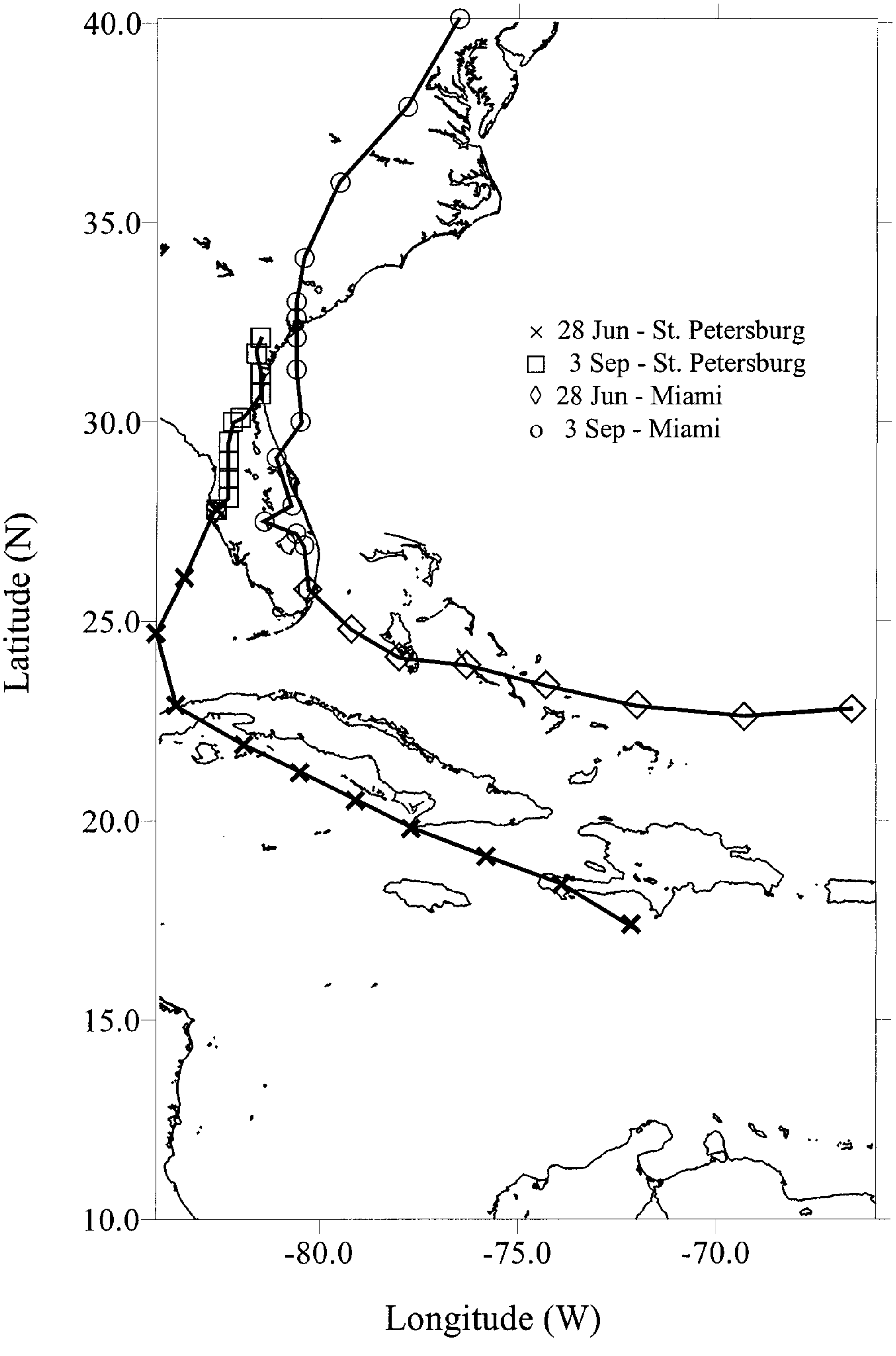

Fig. 5. The daily backward trajectories, computed with HYSPLIT, representative of air mass flow at 500, 1,000, and 3,000 m above ground/sea level over a 90-h period ending at 1800 h on 28 June 1999 and on 3 September 1999 from St. Petersburg and Miami.

Saharan dust episodes—The history of the first major Saharan dust event of 1999 was traced with AVHRR imagery. Figure 3a indicates the beginning of a Saharan dust pulse on 17 June 1999, with the highest optical thickness, i.e., highest concentration of dust, found directly off the African coast. As the winds transported the dust across the Atlantic, a large fraction settled, thereby reducing the amount that eventually reached the West Florida shelf. In Fig. 3b, troughs of higher

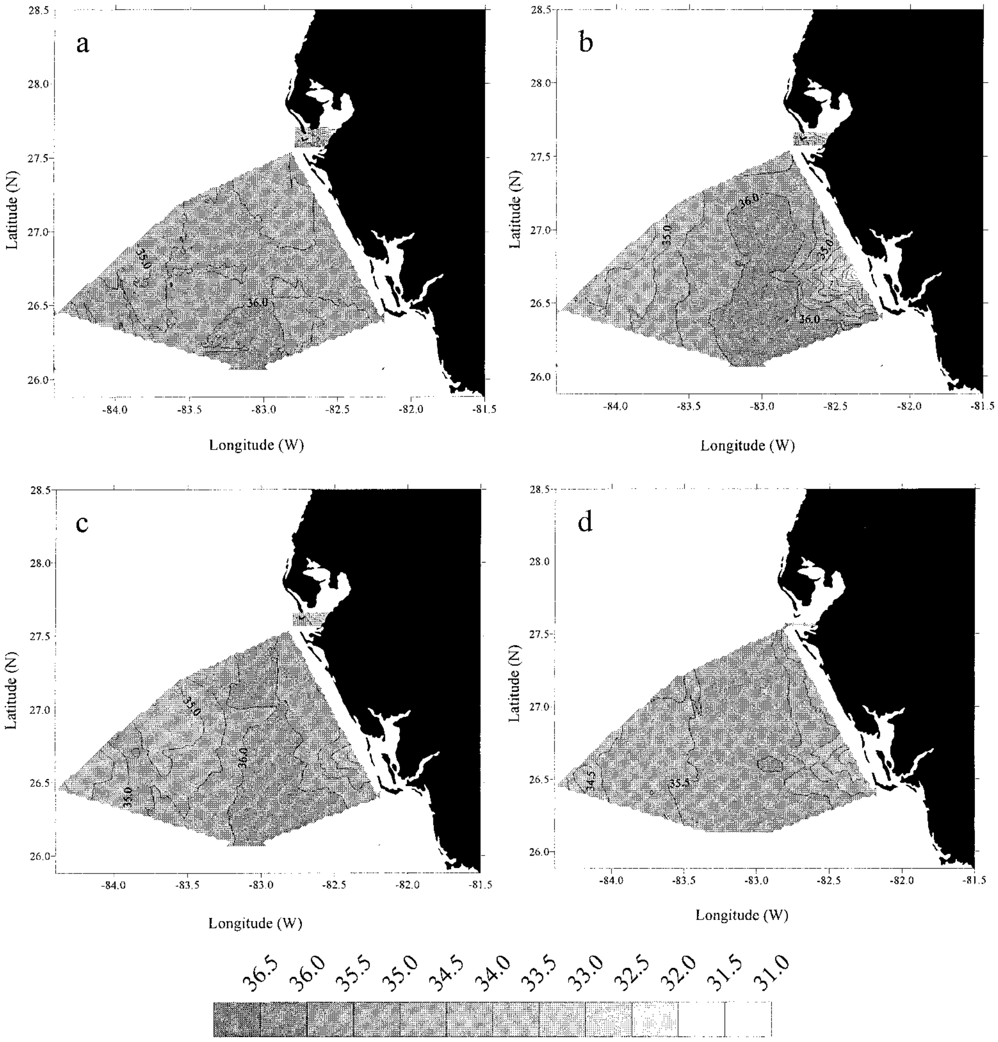

Fig. 6. The 1999 surface distributions of salinity across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

optical thickness are observed on 24 June above the equatorial Atlantic Ocean, reflecting waves of dust supplied to Barbados. A week later (Fig. 3c) the dust front was west of Miami in the Gulf of Mexico.

The winds at Miami are southerly or southeasterly (Fig. 5) during episodes of high optical thickness. This is also seen in back trajectories from St. Petersburg on 28 June for air masses at a height of 1,000 m (Fig. 5). Mean summer wind speeds are 3–5 m s^{-1}, and the path for a southeast wind from Miami to St. Petersburg is such that direct air mass transit (~400 km) between the two locations should take between 20 and 32 h. However, the prevailing wind patterns at St. Petersburg are variable (Henry et al. 1994). Saharan dust can then arrive via westerly or northwesterly winds after turning sharply from its original course over south Florida (Fig. 5). Such a track will increase the distance that must be covered by an air mass, leading to a more usual transit time of ~60 h.

The aerosol sampling system at ~30 m above the ground in Miami caught 37 and 18 μg m^{-3} of mineral dust (Fig. 4) during successive 27 June and 1 July 1999 rainfall events. The atmospheric nitrate concentrations were minimal. A mean 0.07 nitrate/dust weight ratio (Table 1) reflects little contribution from continental aerosols. The CIMEL spectral radiometer at Dry Tortugas in the southern West Florida shelf confirmed that the mean Angstrom exponents of aerosols during this southeast wind event were typical ($\eta = 0.27$) of pure Saharan dust (Tanré et al. 1988; Dubovik et al. 2000). The mean $\tau_a(500)$ value, seen by CIMEL over 26 June–1 July, was 0.26.

Microtops II estimates of $\tau_a(500)$ above St. Petersburg were not available in late June, but an optical depth of 0.42 at 500 nm was found on 1 July (Fig. 4b). During seven other dust events, a daily $\tau_a(500) > 0.30$ was also found, when dust concentrations were >10 μg m^{-3} at Miami. Of these eight large June–September dust events, the three during 28–31 July, 27–30 August, and 3–6 September were of continental rather than Saharan origin (Table 1). For example, the NSS-nitrate/dust ratio was ≤0.50, air mass trajectories were from the north (Fig. 5), and the mean Angstrom exponent

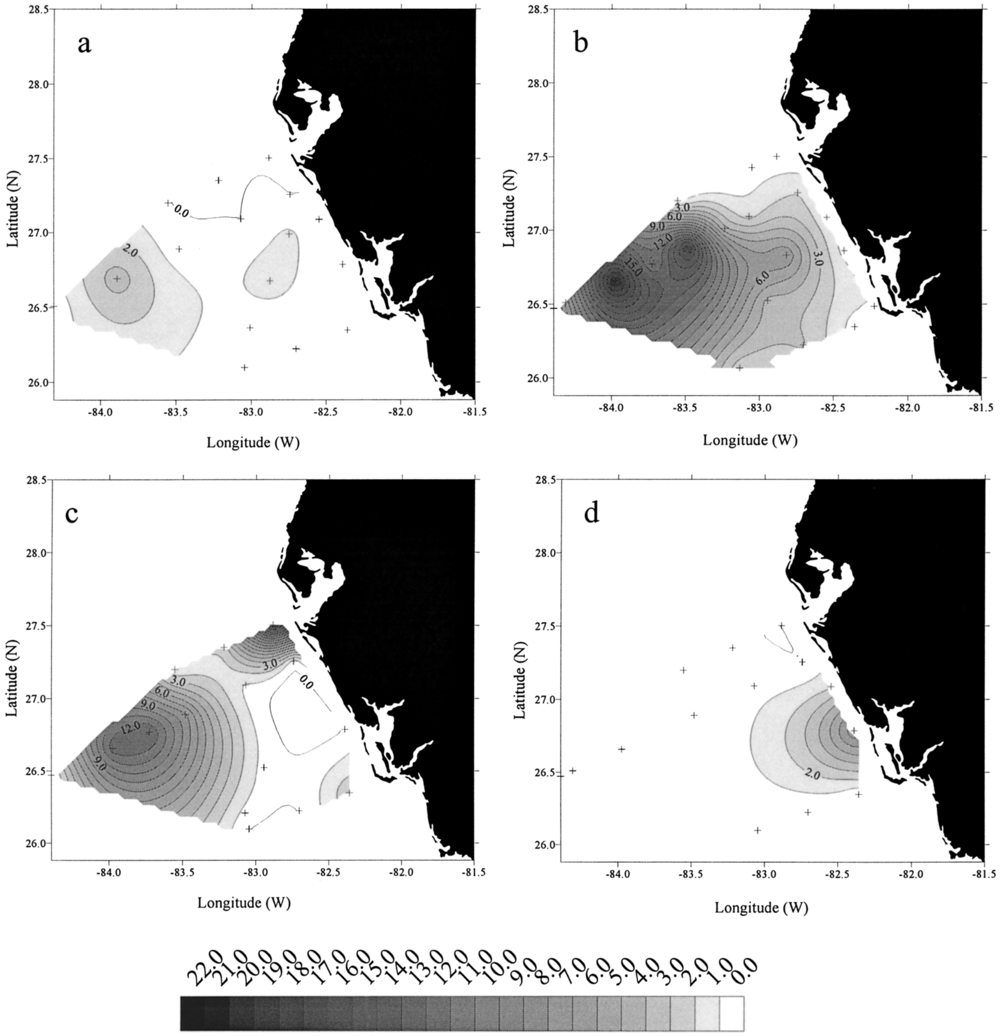

Fig. 7. The 1999 surface distributions of *Trichodesmium* populations (colonies L^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

was 1.80 during 3–6 September. By matching the peaks in the mineral dust concentration at Miami and the aerosol optical depth at St. Petersburg during the Saharan events, a 60 h transit time with an r^2 of 0.98 over seven data bins was calculated.

Continental dust episodes—NSS-nitrate/dust ratios can help discriminate source regions. Low ratios indicate mineral dust of Saharan origin, whereas high ratios are often associated with polluted air masses (Prospero 1999). The dust collected at Miami decreases and non–sea-salt nitrate increases during the latter half of August and early September (Fig. 4a). By 27–30 August, winds at Dry Tortugas were from the northwest with a mean Angstrom exponent equal to 1.64 (Table 1). Concurrently, the mineral dust at Miami was only 12 μg m^{-3}, with a NSS-nitrate/dust ratio of 0.19. Increased NSS-SO_4 concentrations, closely related to NSS-NO_3 concentrations, have been associated with trajectories traced back to the Gulf of Mexico and then north into the central United States (Prospero et al. 2001). It will be shown that less dissolved iron was found on the West Florida shelf after these periods of continental dust supply.

Salinity fields—Although the outflow of the Apalachicola River is larger than the sum of all other Florida rivers between Capes San Blas and Romano (Nordlie 1990) (peak discharge of ~1,300 m^3 s^{-1} in February–April; Gilbes et al. 1996), this freshwater signal does not influence the summer salinity regime of the ECOHAB study site (Fig. 1). Furthermore, the smaller Peace River influx to Charlotte Harbor (~65 m^3 s^{-1}; McPherson et al. 1990) during the local mid-June to September summer rains (Fig. 12), was observed only as surface nearshore, low salinity plumes. Salinities of 32–34 at the 10-m isobath were observed during July–September 1999 (Fig. 6b,c,d), compared to 35.5 in June 1999 (Fig. 6a). The freshwater efflux from Tampa Bay was smaller, with local minima of 34.5–35.0 at the 10-m isobath during July–September.

Along the break and outer shelf of the central West Florida shelf, low salinity surface lenses between 34 and 35 were

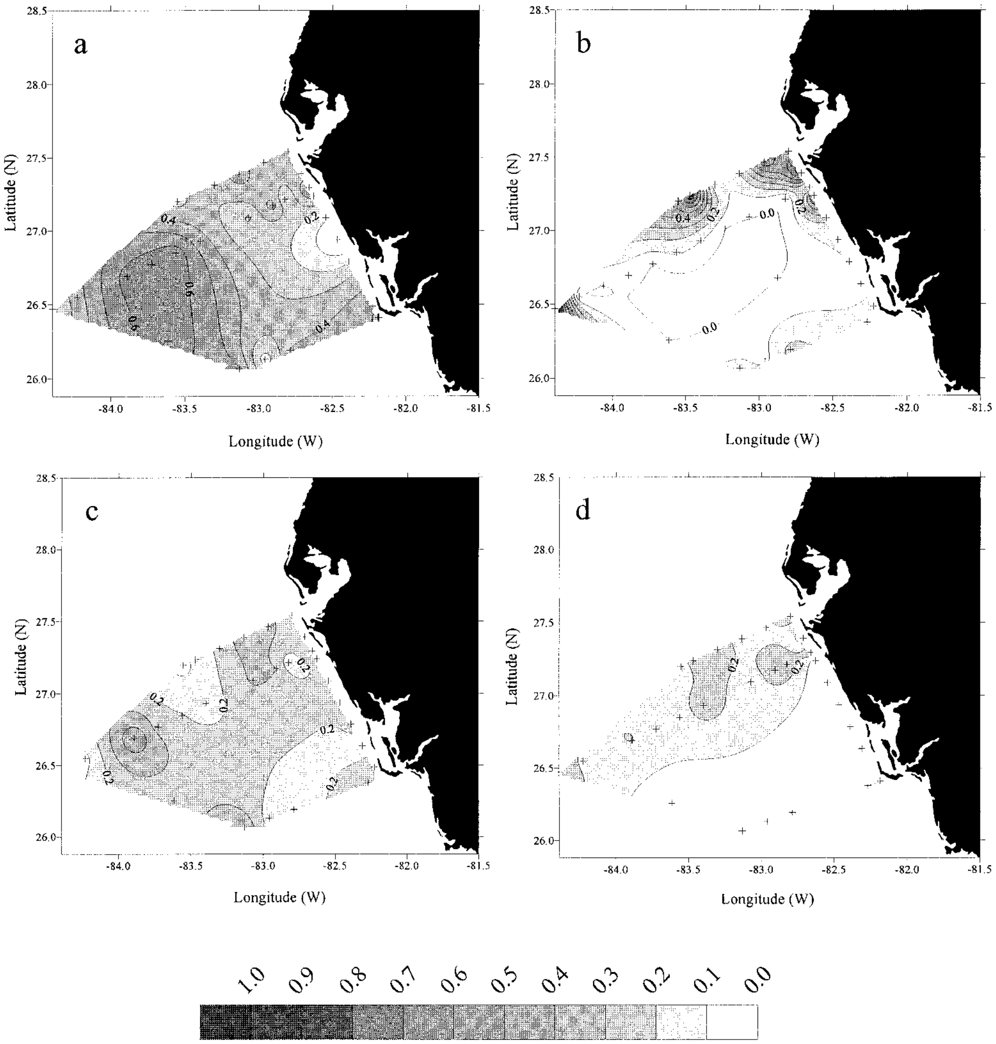

Fig. 8. The 1999 surface distributions of dissolved organic phosphorus (μmol DOP kg^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

found above the 50–100-m isobaths during August 1999 (Fig. 6c), with an attributed Mississippi River origin (e.g., Gilbes et al. 1996). Furthermore, during August 1998, the low salinity water on the outer shelf was associated with high amounts of colored dissolved organic matter of Mississippi origin (Del Castillo et al. pers. comm.). Since terrestrial runoff is a source of iron, with ~3,000 nmol kg^{-1} found in the Peace River (U.S.G.S. 1976–1981), these local and far-field freshwater influxes are potentially dominant sources of dissolved iron on portions of the West Florida shelf.

Interannual variation—Two types of iron input conditions are encountered on the West Florida shelf in relation to local rainfall and Saharan dust caught at Miami. Variations in [Fe_T] between a low dust/low rain summer (1998) and high dust/high rain summer (1999) demonstrate the impact of Saharan dust input. During August 1998, for example, the total monthly rainfall at Tampa Airport was 16.6 cm and the cumulative dust caught at Miami was 90.3 μg m^{-3}, compared to 21.2 cm and 144.5 μg m^{-3} in August 1999. The mean dissolved iron stocks on the outer West Florida shelf were 0.2 nmol kg^{-1} (Table 1) during August 1998 (Fig. 10b) and 1.5 nmol kg^{-1} in August 1999 (Fig. 2c), which reflects smaller dust loading (Fig. 10c) and less wet deposition (Fig. 12) in 1998.

Since the August 1999 salinities within this region were no lower than 34.5 (Fig. 6c), compared to 31.0 during August 1998 (Fig. 10a), the Mississippi River can be eliminated as a major iron source to the West Florida shelf. Furthermore, when dust loading and wet deposition were low, as during August 1998, observed iron stocks were also low, and only a small *Gymnodinium breve* concentration (~5 × 10^4 cells L^{-1}) was found during November 1998 within 10 km of the coast. Subsequent to a tenfold iron stock increase due to greater aeolian supplies (August 1999), a large red tide of >5 × 10^6 cells L^{-1} occurred (October 1999). Correlation of dust arrival, total iron concentrations, diazotroph abundance, DON accumulation, and PO_4/DOP use provide clues into the interdynamics of this complex shelf ecosystem. In the absence of intrusions of particle-rich water of

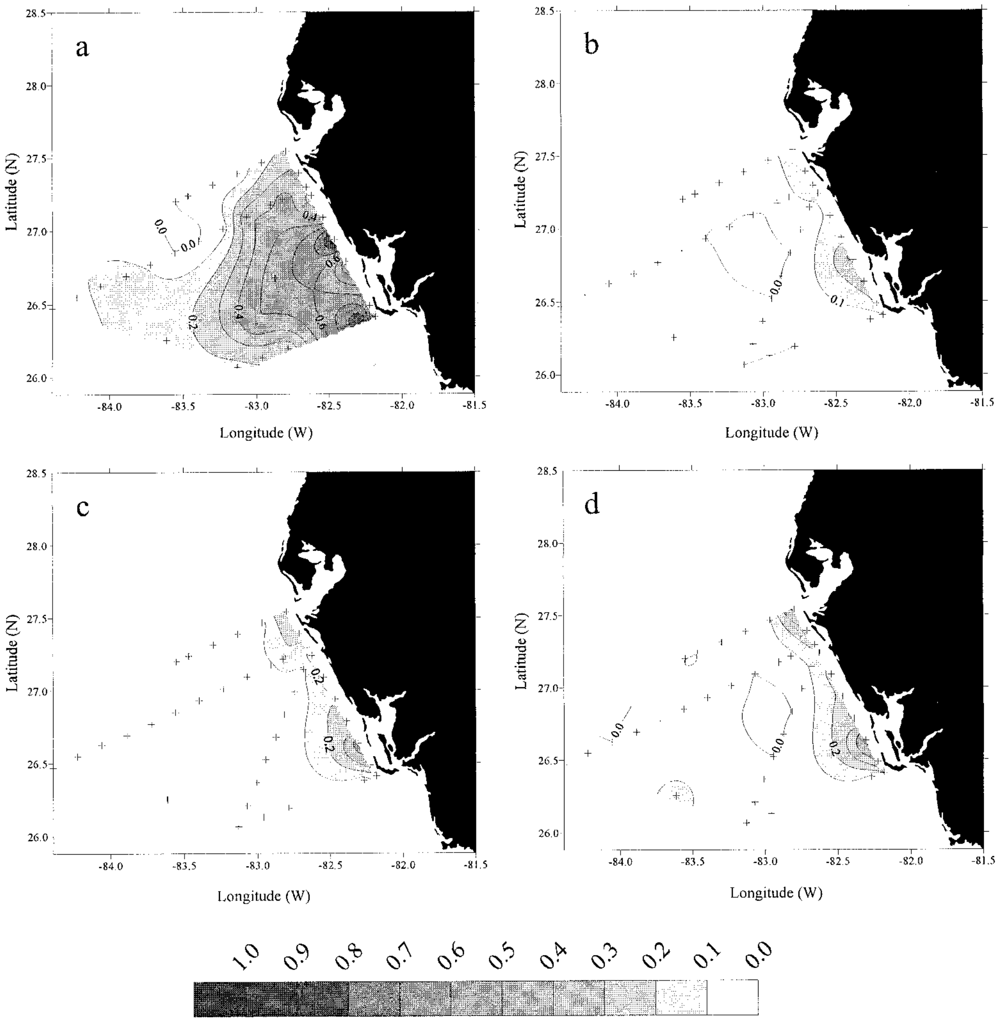

Fig. 9. The 1999 surface distributions of inorganic phosphorus (μmol PO_4 kg^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

the Loop Current (Haddad and Carder 1979), the shelf system depends upon aeolian sources of iron-mediated nitrogen supply.

Discussion

Daily aerosol sampling carried out previously in Fort Myers on the southwest coast of Florida and in Miami on the East coast (Prospero et al. 2001) showed maximal dust input over the summer months (June–August). If one has $\tau_a(500)$ as an independent assessment the aerosol type, the Miami dust data can be used as a proxy for dust loading to the West Florida shelf. One approach for verification of Saharan events is the use of atmospheric non–sea-salt nitrate as an index of local pollutants at Miami, with a nitrate/dust weight ratio criterion of ≤ 0.1 for dust events. Both air mass trajectories and the Angstrom exponent of mineral dust can provide additional source corroboration.

The optical depths measured by the CIMEL sunphotometer in the Dry Tortugas mirrored those of the Microtops with little time lag in July and the first half of August, but these time series became asynchronous afterward. Late summer in the Gulf of Mexico usually marks changing meteorological conditions—sluggish winds, a northward shift in the prevailing wind patterns, and a sharply increased frequency of tropical disturbances. All of these features decrease the consistency of the prevailing wind patterns (Henry et al. 1994). At Dry Tortugas, fluctuating Angstrom exponents then suggest an infrequent presence of dust and inconsistent delivery of iron to the ocean.

At only monthly sampling intervals, the persistence of aeolian derived iron in surface waters of the West Florida shelf cannot be directly observed. Sampling frequency at any particular station was limited due to the large size of the ECOHAB area. However, during iron fertilization experiments in the equatorial Pacific, Martin et al. (1994) measured a similar (6.2 nmol kg^{-1}) dissolved iron concentration within the core of their patch 4 h after surface fertilization. Owing to convective mixing of the water column, concentrations dropped rapidly to 3.6 nmol kg^{-1} after the first day, at which point concentrations decreased ~15% per day over 6–7 d.

Rainfall during 1–4 July 1999 (4.1 cm at the Tampa Air-

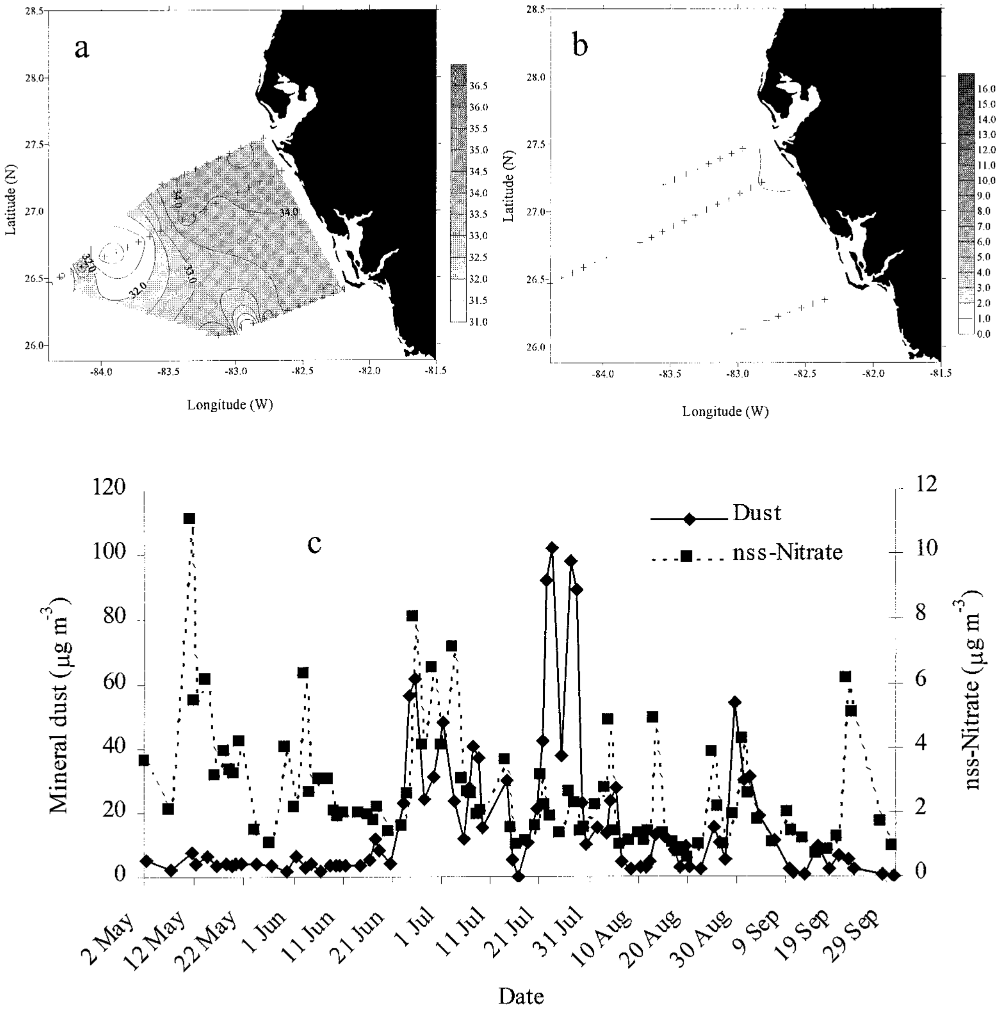

Fig. 10. The surface distributions of (a) salinity and (b) dissolved iron (nmol Fe kg^{-1}) across the West Florida shelf during 6–10 August 1998 in relation to (c) mineral dust ($\mu g\ m^{-3}$) and non-sea-salt nitrate ($\mu g\ m^{-3}$) of air sampled daily 30 m above ground at Miami during May–September 1998.

port) provided local washout of Saharan dust. During a similar precipitation event on 6 August 1999 (Fig. 12), an iron concentration of 52.4 nmol kg^{-1} was observed in rainwater at Sta. 3. Mixed throughout the 5-m surface mixed layer in July 1999, such an influx would produce a concentration near 10.5 nmol kg^{-1}, as was observed in offshore waters. A cumulative iron fertilization of ~12 nmol kg^{-1} within the surface mixed layers of the outer West Florida shelf can be estimated from the four Saharan dust events during 16 June–21 July 1999. If we assume a further loading of ~3 nmol kg^{-1} from the last (28–31 July 1999) Saharan event, and ~1 nmol kg^{-1} from each of the three continental events (Table 1), the estimated 1999 summer aeolian influx to the surface mixed layer of the West Florida shelf is 18 nmol kg^{-1}.

Most *Trichodesmium* colonies on the West Florida shelf had a small number of trichomes (filaments), also found when populations were sampled discretely with bottles off Barbados (Borstad 1978). Assuming a colony size of 3×10^3 cells (Borstad 1978), instead of 3×10^4 cells for large colonies collected with nets (Carpenter 1983), and a cellular chlorophyll content of 1.2×10^{-6} μg $cell^{-1}$ (Borstad 1982), a range of 3–20 colonies L^{-1} in July (Fig. 7b) yields a pigment biomass of 0.01–0.07 μg chl L^{-1}. With an observed mean total chlorophyll stock of 0.14 μg chl L^{-1}, the diazotrophs would constitute 7–50% of the phytoplankton community biomass. Letelier and Karl (1996) found that *Trichodesmium* populations off Hawaii constituted a similar range (10–40%) of their total observed biomass of 0.12 μg chl L^{-1}.

Our measured concentrations of *Trichodesmium* may underestimate the actual stocks, since our surface sampling did not account for vertical migration or for the presence of subsurface peak abundances. Indeed, off Barbados during the Saharan dust season of July–October 1974, 20 of 23 stations exhibited subsurface diazotroph maxima (Borstad 1978). *Trichodesmium* concentrations at 16.3 m were 3.2 times larger than the surface populations, with significant abundance to a depth of 50 m. The ability to migrate (Villareal and Carpenter 1990) at a mean velocity of 2 m h^{-1} (Kromkamp and Walsby 1992) allows *Trichodesmium* to move over a 50-m water column within 1 d.

For a population with a C/chl weight ratio of 220 (Car-

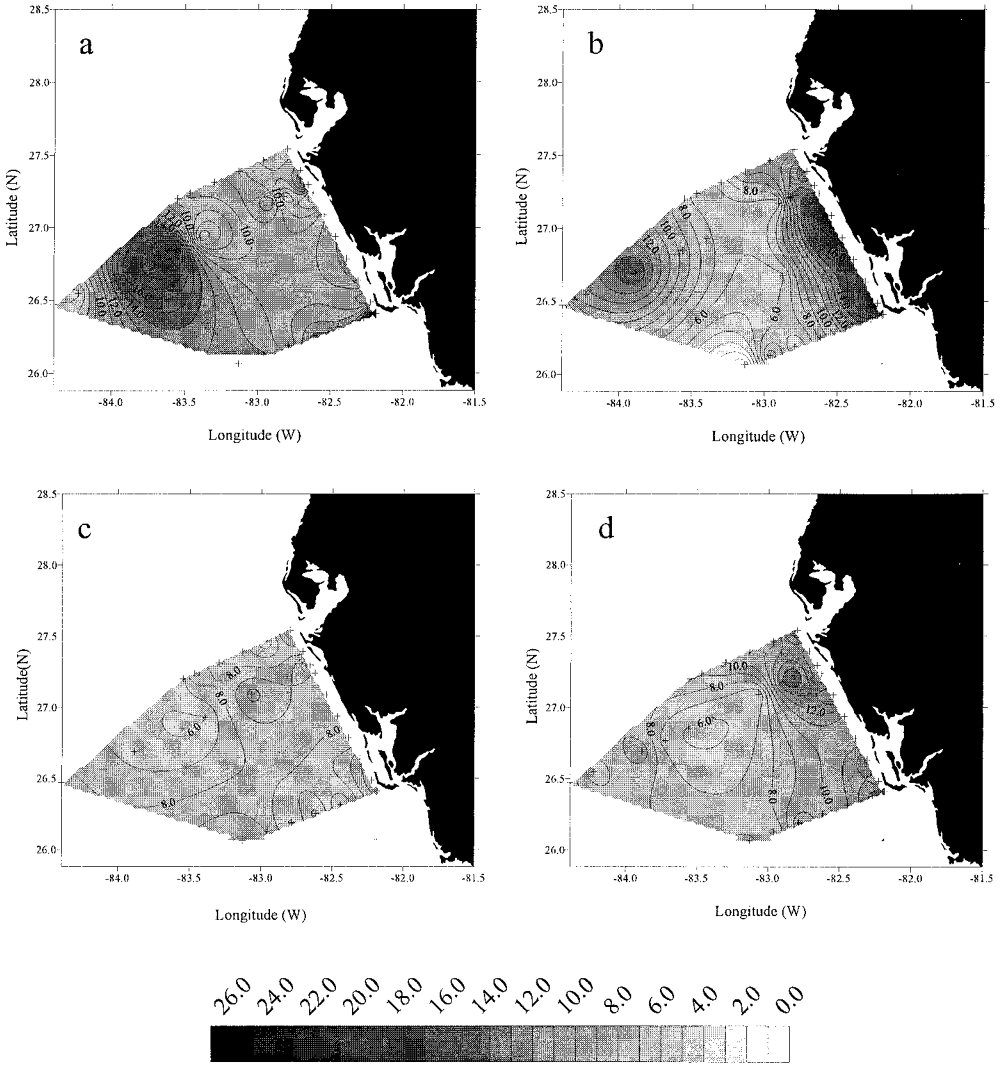

Fig. 11. The 1999 surface distributions of dissolved organic nitrogen (μmol DON kg^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

penter 1983), a molar C/N ratio of 6.1 (McCarthy and Carpenter 1979), and a molar N/Fe ratio of 465 (Rueter et al. 1992), a surface stock of 0.07 μg chl L^{-1} of *Trichodesmium* represents a minimal iron demand of ~0.45 nmol Fe kg^{-1}. Since these diazotrophs can excrete up to ~50% of their fixed nitrogen in the form of DON (Glibert and Bronk 1994), a total iron demand of ~0.9 nmol Fe kg^{-1} might be required for a 0.42 μmol kg^{-1} increment of both forms of organic nitrogen (DON + PON). The measured July depletion of iron at Stations 15–22 was indeed 1.7 nmol Fe kg^{-1}, compared to the mean (3.1 nmol kg^{-1}) found at all of Stations 11–22 across the outer shelf (Table 1), fueling both surface and possibly larger subsurface populations.

With a molar N/P ratio of 16 for *Trichodesmium* (Walsh 1996), the combined 0.42 μmol kg^{-1} production of PON + DON (calculated from Sta. 16 on July 1999) would require a phosphorus supply of ~0.03 μmol P kg^{-1}. Indeed, a mean surface concentration of 0.02 μmol PO$_4$ kg^{-1} was still present at Stations 11–22 in July 1999 (Fig. 9b), i.e., after phosphate depletion. In June 1999, the phosphate stock was instead a mean of 0.08 μmol PO$_4$ kg^{-1} (Fig. 9a).

Since diazotrophs exhibit both alkaline phosphatase activity (Yentsch et al. 1972) and a high affinity for phosphomonoesters (McCarthy and Carpenter 1979), continued phosphorus demands during subsequent dust events could be met, as well, by the observed surface organic stocks of ~0.22 μmol DOP kg^{-1} (Fig. 8) on the outer shelf. Therefore the absence of DOP could indicate a growing population.

Using an N/P ratio of 16 for *Trichodesmium* colonies and a 50% excretion/fixation ratio for nitrogen, a mean diazotroph biomass of 1.4 μg chl L^{-1} and 4.2 μmol DON kg^{-1} would be produced over ~90 d of cumulative iron supply within the surface waters. Following bacterial degradation of the released DON and photolysis of the intact *Trichodesmium* colonies, a new total nitrogen supply of 8.4 μmol kg^{-1} might thus be derived from nitrogen fixation and might have been available to *G. breve* during summer of 1999. A PON/chl ratio of 0.4 for these shade-adapted dinoflagellates

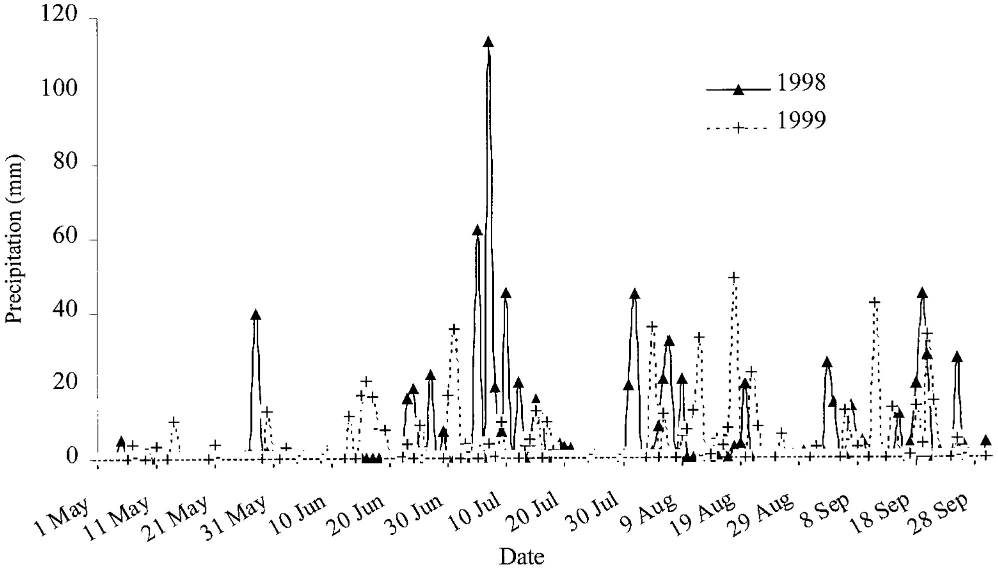

Fig. 12. The daily rainfall (mm day^{-1}) at Tampa International Airport during June–August 1998 and 1999.

(Walsh and Steidinger in press) then suggests a cumulative red tide of 21 μg chl L^{-1}, as was actually observed in coastal waters off West Florida during October 1999.

An associated phosphorus demand of 0.52 μmol kg^{-1} over the 90 d could be partially met by residual phosphorus stocks of ~0.20 μmol PO$_4$ kg^{-1} and ~0.13 μmol DOP kg^{-1} that are always present within 2–4 km of the Florida coast once the *T. erythraeum* and *G. breve* blooms (Steidinger et al. 1998) are near shore. Indeed, during October 1986, 0.3 μmol PO$_4$ kg^{-1} were left behind by ~10 μg chl L^{-1} of *T. erythraeum* and ~20 μg chl L^{-1} of *G. breve* above the 20-m isobath (Walsh and Steidinger in press). Furthermore, the ~0.42 μmol PO$_4$ kg^{-1} phosphate at a depth of 75 m during July 1999 at Sta. 16 could provide a significant phosphorus source for migrating *Trichodesmium* (Karl et al. 1992) in offshore waters.

Conclusion

During summer months, Saharan dust is carried across the Atlantic by prevailing winds, which fertilize the ocean with iron. In oligotrophic basin and shelf ecosystems of the Gulf of Mexico, this iron frequently removes a nutrient limitation for many species of phytoplankton, including the diazotroph *T. erythraeum* and, subsequently, the nitrogen-starved toxic dinoflagellate *G. breve* within phosphorus-replete coastal waters (Walsh and Steidinger in press). The 1999 time series of optical thickness data at St. Petersburg and Dry Tortugas are consistent with observations of aerosol dust at Miami and AVHRR imagery and demonstrate the efficacy of satellite-borne estimates of dust/iron inputs. Future ecological models of multiple plankton groups initialized with satellite observations will allow a more quantitative examination of the causal relationships posed by these ECOHAB cruise results.

Implication of *Trichodesmium* in the nutrient dynamics of *G. breve* red tides is not a new idea: "The physiology, metabolism, and tactic responses of *G. breve* . . . must be understood and the source . . . of nutrients determined before it is possible to suggest a solution or remedy. . . . red tide organisms might be able to utilize atmospheric nitrogen as some of the blue-green algae are capable of doing" (Lasker and Smith 1954). We do present, however, new observations on the mechanisms by which these processes may occur, thus providing constraints on future numerical models of red tide forecasts. The role of *Trichodesmium* on the West Florida shelf is not only to influence the competitive success of red tide organisms, but to also have a major impact on the nitrogen and phosphorus cycles during summer months.

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