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John J. Walsh
University of South Florida, jwalsh@marine.usf.edu

K. A. Steidinger

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Saharan dust and Florida red tides: The cyanophyte connection

John J. Walsh
College of Marine Science, University of South Florida, St. Petersburg, Florida

Karen A. Steidinger
Florida Marine Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, Florida

Abstract. Prediction of the consequences of harmful algal blooms for humans and other vertebrates is constrained by an inadequate understanding of the factors that promote their initiation. A simple exponential growth model of net production is used for analysis of four time series at different sampling intervals over ~40 years of red tide strandings, associated fish kills, and concomitant dust loadings on the West Florida shelf. At least large summer blooms of a toxic dinoflagellate *Gymnodinium breve* appear to be primed regularly by an aeolian supply of nutrients. Wet deposition of Saharan mineral aerosols may alleviate iron limitation of diazotrophic cyanophytes, which in turn fuel the nitrogen economy of red tides in the eastern Gulf of Mexico. Vagaries of the wind-induced circulation and of selective grazing pressure on phytoplankton competitors within phosphorus replete coastal waters then determine each year the residence times for exposure of *G. breve*–mediated neurotoxins to fish, manatees, and humans along the southeastern United States.

1. Introduction

Both the origin of and the nitrogen supply for red tides in the eastern Gulf of Mexico have remained obscure despite a long history of bloom events first recorded in 1542 by A. N. Cabeza de Vaca. Over the past century the seasonal duration of red tides each year off west Florida has varied from none to 12 months [*Steidinger et al.*, 1998], with >80% of the blooms apparently occurring in late summer-fall. Their causative agent was not identified until 1947 [*Davis*, 1948] as the dinoflagellate *Gymnodinium breve*, which produces brevetoxins.

Blooms of *G. breve* originate ~20–75 km offshore [*Steidinger and Haddad*, 1981; *Tester and Steidinger*, 1997] of central Florida at depths of ~15–40 m (Figure 1), yielding surface stocks of as much as 30–60 μg chl L^{-1} [*Carder and Steward*, 1985]. These red tides force closure of shellfish beds and regularly drive tourists from Florida beaches, with occasional impact as far away as North Carolina, where an economic loss of $25 million occurred in 1987 [*Tester and Fowler*, 1990]. At population levels of $>1 \times 10^5$ cells L^{-1}, or a biomass of >1 μg chl L^{-1}, compared to background abundances of $\leq 1 \times 10^3$ cells L^{-1} in the offshore Gulf of Mexico [*Geesey and Tester*, 1993], discolorations, fish and manatee kills, neurotoxic shellfish poisoning, and respiratory irritation of humans ensue within nearshore waters.

While physical aggregation mechanisms at tidal fronts may lead to local blooms of dinoflagellates in the English Channel [*Holligan et al.*, 1983; *Tett*, 1987] and North Sea [*Wyatt and Saborido-Rey*, 1993; *Joint et al.*, 1997], on Georges Bank [*Franks and Chen*, 1996; *Anderson*, 1997], and within the Bay of Fundy [*Balch*, 1981; *White*, 1987], as well as in the Seto Inland Sea [*Kishi and Ikeda*, 1986; *Yanagi et al.*, 1995], their accumulation is still the result of growth from nutrient supplies of the aphotic zone in these temperate ecosystems [*Longhurst*, 1998].

In contrast, 10% of surface photosynthetically active radiation (PAR) can be found at a depth of ~30 m on the oligotrophic subtropical West Florida shelf. Thus the chlorophyll stocks within the upper 0.5 cm of sediment are usually twofold to fourfold those of the overlying water column (G. Vargo, personal communication, 2000), as is also found on the Georgia shelf [*Nelson et al.*, 1999]. Pelagic biomass is then <0.5 μg chl L^{-1}.

Even a modest fall bloom of *G. breve* (Figure 2a), amounting to ~10 μg chl L^{-1} within the upper 5–10 m, or 50–100 mg chl m^{-2}, and a particulate organic nitrogen (PON)/chl (μmol/μg) ratio of 0.4 for shade-adapted populations [*Shanley and Vargo*, 1993], with a C/chl ratio of 30, suggests that at least 20–40 mmol N m^{-2} of dissolved new nitrogen are required to yield such dinoflagellate stocks on the West Florida shelf. Here, however, the nitrate stocks above the 40 m isobath (Figure 2c) are generally <0.25 μmol NO_3 kg^{-1}, i.e., <10 mmol NO_3 m^{-2}, except during episodic intrusions of the Loop Current [*Haddad and Carder*, 1979; *Paluskiewicz et al.*, 1983] denoted by higher salinities (Figure 2b). Recent high-sensitivity fluorometric methods [*Masserini and Fanning*, 2000] suggest that the background nitrate stocks on the West Florida shelf are actually <0.01 μmol NO_3 kg^{-1}.

At such low background levels, local anthropogenic nutrient supplies, i.e., deposition of NO_x in Florida coastal waters [*Paerl*, 1997], may now modulate the present yield of today's phytoplankton populations. However, at only ~37% of the estuarine supply, they are not yet a major factor unless industrial releases were also large in 1542 and somehow missed by de Vaca! Indeed, we shall find that there was no difference in the intensity and duration of red tides between 1957 and 1992. Furthermore, during 1947 a large Florida red tide was found [*Gunther et al.*, 1948], when eutrophication presumably had little impact on the Gulf of Mexico [*Walsh et al.*, 1981].

Moreover, the supply of nitrate from either northern Florida

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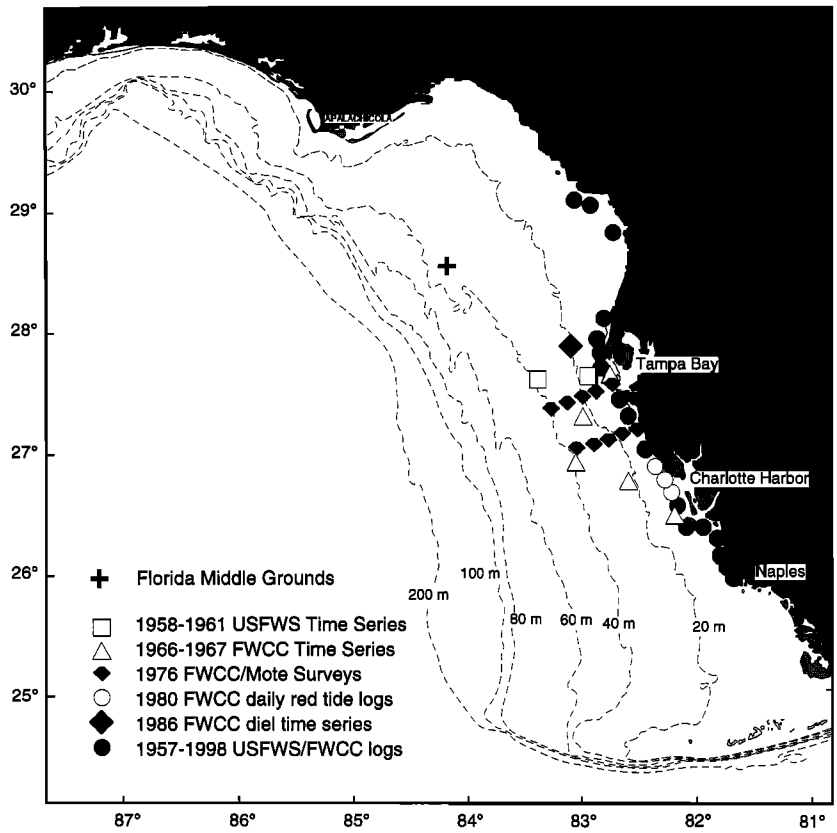

Figure 1. The location of 1969–1970 zooplankton time series (plus) on the 30 m isobath of the Florida Middle Ground in relation to 1958–1961 nutrient time series on the 15 and 40 m isobaths (open squares), to 1966–1967 plankton time series on the ~5, 25, and 40 m isobaths (open triangles), to 1976 plankton time series between the 5 and 40 m isobaths (solid pentagons), to 1986 nutrient and red tide time series on the 20 m isobath (solid diamond), and to 1957–1998 red tide time series on the 5–10 m isobaths (open and solid circles) of the West Florida shelf.

rivers or the Loop Current instead yields both pelagic diatoms in the water column and benthic ones within the upper 0.5 cm of sediment [*Khromov*, 1969; *Saunders and Glenn*, 1969; G. Vargo, personal communication, 2000], not dinoflagellates, as also found on the Louisiana [*Dortch and Whitledge*, 1992; *Nelson and Dortch*, 1996] and Georgia [*Nelson et al.*, 1999] shelves. This is hardly a surprise since the former can grow ~10 times faster than *G. breve* and most dinoflagellates have a half-saturation k_{NO_3} of ~7.2 μmol NO_3 kg^{-1} compared to one of ~1.3 μmol NO_3 kg^{-1} for diatoms [*Smayda*, 1997]. Thus the oxidized forms of inorganic anthropogenic nitrogen deposited within Tampa and Sarasota Bays [*Paerl*, 1997] may also be consumed by diatoms rather than by dinoflagellates.

Although considered an oceanic resident of tropical seas, the diazotroph *Trichodesmium erythraeum* appears to play an important role in the nitrogen economy of toxic red tides of *G. breve* within coastal waters of the southeastern United States. Off the west coast of Florida, *T. erythraeum* is the dominant species of these colonial nitrogen fixers, while *Trichodesmium thiebautii* tends to be the most abundant form off the east coast. At very high levels of discoloration seen by aircraft above the West Florida shelf the surface stocks of these cyanophytes amount to >200 μg chl L^{-1}, as found off St. Petersburg Beach during May 2000 (C. Heil, personal communication, 2000).

The 1947 red tide [*Gunther et al.*, 1948] and the paucity of nitrate led to the early hypothesis that [*Lasker and Smith*, 1954, p. 175] "*G. breve* ... red tide organisms might be able to utilize atmospheric nitrogen as some of the blue-green algae are capable of doing." We, instead, pose a direct link between population increments of *T. erythraeum* and *G. breve*, as previously suggested [*Chew*, 1955; *Steidinger*, 1973; *Taylor and Pollingher*, 1987], but with Saharan dust now identified as the trigger mechanism for initiation of at least large red tides.

At individual stations of our fixed sampling grids, maximal diazotroph populations during any one prior cruise to the West Florida shelf, were instead ~5–10 μg chl L^{-1}, such that the above tenfold higher amount in May 2000 might have been induced by physical concentration, for example, Langmuir cells and internal waves, effecting small-scale patchiness [*Franks*, 1997]. These nitrogen fixers are also found in the South Atlantic Bight, where *Trichodesmium* spp. impact the plankton dynamics of both the Georgia [*Dunstan and Hosford*, 1977] and North Carolina [*Guo and Tester*, 1994] shelves. Here seasonal maxima of *Trichodesmium* spp. occur in July, when the Georgia shelf populations of ~4.0 μg chl L^{-1} are 100-fold those of the Gulf Stream. These cyanophytes are also associated with red tides of *G. breve* in North Carolina waters [*West et al.*, 1996].

Diazotrophs, such as *T. erythraeum* found regularly off West Florida beaches [*King*, 1950], require iron to form the enzyme nitrogenase for fixation of N_2 and show increased rates in response to Fe additions [*Rueter*, 1988; *Rueter et al.*, 1990; *Paerl*

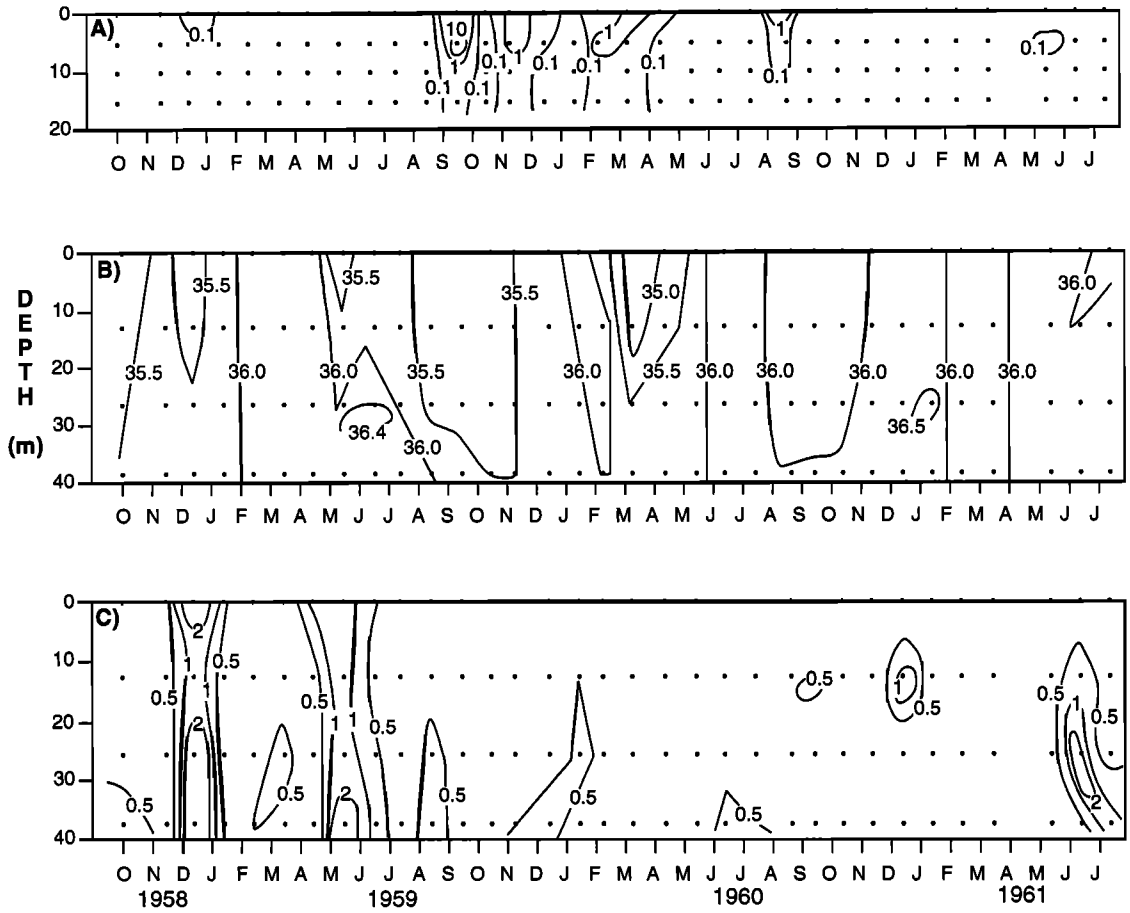

Figure 2. Time series of (a) red tides of *Gymnodinium breve* (10^5 cells L^{-1}) on the 15 m isobath and of (b) salinity and (c) nitrate (μmol L^{-1}) on the 40 m isobath of the West Florida shelf during 1958–1961.

et al., 1994]. During summer the worldwide historical reports of the subtropical oceanic distributions of *Trichodesmium* spp. [*Carpenter*, 1983] indeed suggests that their relatively high but nonbloom [*Capone and Carpenter*, 1982] abundances of $>10^2$ trichomes L^{-1} ($\sim 10^4$ cells L^{-1} or 0.01 μg chl L^{-1}) within the upper 5 m parallel the >100 mg m^{-2} yr^{-1} isopleth of annual Fe deposition in the different oceans [*Duce and Tindale*, 1991], downstream of the adjacent desert source areas [*Sokolik and Toon*, 1996].

Within the lee of Barbados, however, their seasonal maxima amount to only 0.3 μg chl L^{-1} [*Steven and Glombitza*, 1972; *Borstad*, 1982] when Saharan dust is high [*Prospero and Nees*, 1986] but where $\sim$0.05 μmol PO_4 kg^{-1} prevail over the upper 25 m of the water column [*Steven et al.*, 1970], typical of P-limited offshore regions [*Codispoti*, 1989; *Tyrell*, 1999]. In contrast, the molar ratios of dissolved inorganic nitrogen (NO_3 + NH_4 + NO_2) and phosphate in the Peace River, entering Charlotte Harbor [*Fraser and Wilcox*, 1981; *McPherson et al.*, 1990], and in the Alafia River, entering Tampa Bay, are instead usually <2. They both drain the phosphate-rich Hawthorne formation of central west Florida [*Dragovich et al.*, 1968], such that at least $\sim$0.20 μmol PO_4 kg^{-1}, as well as $\sim$0.20 μmol dissolved organic phosphorus (DOP) kg^{-1} [*Lenes et al.*, 2001], are always found within 2–4 km of the Florida coast [*Dragovitch et al.*, 1961, 1963; *Vargo and Shanley*, 1985].

At times, surface stocks of $\sim$0.40 μmol P kg^{-1} of both PO_4 and DOP are also found above the 40 m isobath at midshelf, prior to iron-stimulated blooms of *Trichodesmium*; afterward, these inorganic and organic forms of phosphorus are undetectable [*Lenes et al.*, 2001]. When the coastal populations of these cyanophytes are neither Fe- nor P-limited [*Karl et al.*, 1992], are not grazed by most copepods [*Roman*, 1978; *O'Neil et al.*, 1996], and remain at their optimal temperatures of 25°–30°C [*Carpenter and Romans*, 1991], they would exhibit maximal growth, yielding observed biomasses of at least tenfold greater amounts on the West Florida and Georgia shelves than off Barbados.

Subsequent excretion of dissolved organic nitrogen (DON) by *Trichodesmium*, at a rate of $\sim$50% of their nitrogen fixation [*Glibert and Bronk*, 1994], is consistent with a $\sim$50% respiration loss of carbon during gross photosynthesis [*Carpenter and Roenneberg*, 1995]. This DON could then serve as the initial nitrogen source in offshore breeding waters for the subsequent noxious red tides found later at the coast. During 1999 we found increments of DON after population increases of *Trichodesmium* on the West Florida shelf [*Lenes et al.*, 2001] (also found off Hawaii [*Karl et al.*, 1992] and on the Great Barrier Reef (C. Heil, personal communication, 2000)).

Like other dinoflagellates [*Pomeroy et al.*, 1956; *Carlsson and Graneli*, 1993], *G. breve* can also utilize ammonium, vitamins, amino acids, and urea at varying rates [*Wilson*, 1966; *Baden and Mende*, 1979; *Shimizu and Wrensford*, 1993; *Steidinger et al.*, 1998]. Some of the DON utilized by *G. breve* may be of estuarine or sea bed origin, as well as from pelagic diazotrophs.

Since *G. breve* blooms originate offshore away from nearshore supplies of both iron and DON [*Ingle and Martin*, 1971; *Kim and Martin*, 1974], however, we consider here the food chain impact of nitrogen fixation from an aeolian Fe supply, described by *Darwin* [1839, pp. 5–6]: "I collected a little packet of this brown-colored fine dust... From the direction of the wind whenever it has fallen, ... we may be sure that it all comes from Africa... It has often fallen on ships... even more than a thousand miles from the coast of Africa and at points sixteen hundred miles distant in a north and south direction."

In this paper, we explore the causal chain of conditional probabilities that must all occur to permit land fall of large red tides on west Florida beaches: Saharan dust; rainfall; iron-stimulated *Trichodesmium*; DON release; selective grazing on faster growing dinoflagellate competitors; initiation of *G. breve* red tide; onshore currents; P replete regime for bloom formation. We examine ~40 years of plankton data on the West Florida shelf and of concurrent dust observations at Fort Myers, Miami, and Barbados to test this hypothesis.

For example, background levels of 0.1–0.5 nmol Fe kg^{-1} were measured [*Lenes et al.*, 2001] with a fiber-optic spectrometer in surface waters of the outer West Florida shelf during an August 1998 Ecology and Oceanography of Harmful Algal Blooms (ECOHAB) Florida cruise in the absence of major cyanophyte or dinoflagellate blooms that summer and fall (Figure 3). In contrast, after documentation of large aerosol optical thickness events by advanced very high resolution radiometer (AVHRR) imagery (see http://www.nrlmry.navy.mil/aerosol/) and local radiometric data in St. Petersburg, as well as by direct observations of wet deposition of Saharan dust on June 27, 1999, at Miami, surface values of 16.0 nmol Fe kg^{-1} were found at the edge of the shelf, above the 175 m isobath, on July 6, 1999.

At the same time a tenfold incremental increase of *Trichodesmium* colonies occurred in this region over those found on the preceding ECOHAB survey of June 5–8, 1999, depleting both PO_4 and DOP concentrations to <0.01 μmol P kg^{-1}. During October 1999, after prior landward movement of the diazotroph stocks and, presumably, red tide inocula during August–September, large *G. breve* populations of $>5 \times 10^6$ cells L^{-1} were then found nearshore on the 5–10 m isobaths, between Tampa Bay and Charlotte Harbor (Figure 1). Were these one-of-a-kind phenomena during 1999 and 2000 or different realizations of the usual sequence of events defining the plankton succession leading to large red tides on the West Florida shelf? Small red tides may be another matter, primed perhaps by the vagaries of decomposition of sea grass and terrestrial plant debris.

2. Methods

2.1. Dust Time Series

The length of dust time series at Fort Myers on the southwest coast of Florida is not as extensive [*Prospero*, 1999a] as those at either Barbados (1965–2000) or Miami (1974–2000), but concurrent dust data during 1995–1996 [*Prospero et al.*, 2001] suggest that the seasonal cycle of a summer maximum of Saharan aerosols, reflecting northward movement of the prevailing winds [*Swap et al.*, 1996], is the same at ~26°30′N, 82°W, ~26°N, 80°W, and ~13°N, 60°W. The mean annual stock of mineral aerosols above both Miami and Fort Myers is about 40% of that at Barbados [*Prospero*, 1999b], yielding a combined dry (25%) and wet (75%) deposition rate [*Prospero et al.*, 1987] of ~1.25 g m^{-2} yr^{-1}. Most of this influx at Miami occurred in summer months of the rainy season during 1982 and 1983; note that there were large red tides along the West Florida coast in both years (Figure 3). We thus examine rainfall and wind data from Tampa, Sarasota, Venice, and Fort Myers records during 1976–1996.

With an iron composition of 3.5% of mineral aerosols [*Duce et al.*, 1991; *Zhu et al.*, 1997] an influx of ~80% of the annual loading, i.e., 0.6 mmol Fe m^{-2}, may occur during just 1 month at Miami, as well as above the West Florida shelf. The impacts of Saharan dust can be found both throughout Florida in soils [*Landing et al.*, 1995] and (by satellite) above the eastern Gulf of Mexico [*Carder et al.*, 1991; *Lenes et al.*, 2001], where arrival of Saharan aerosols during June–August may stimulate iron-starved cyanophyte blooms on the oligotrophic West Florida shelf followed by red tides of *G. breve*.

For example, at estimated dissolution rates of ~10% for iron aerosols [*Moore et al.*, 1984; *Zhuang et al.*, 1990] a dissolved iron stock of ~12 nmol Fe kg^{-1} might then have been supplied cumulatively from such 1982–1983 dust events within a 5 m surface mixed layer over 1 month. Recall that we observed similar amounts at a few stations in July 1999 [*Lenes et al.*, 2001]. A simple linear regression of offshore iron stocks in the West Florida shelf during ECOHAB cruises and monthly total dust at Miami, of all events with mineral aerosol concentrations of >10 μg m^{-3}, yields an r^2 of 0.92 over June–October 1999.

The molar particulate N/Fe ratio for *Trichodesmium* is only 465 [*Rueter et al.*, 1992], compared to ~5000 [*Martin et al.*, 1989; *Brand*, 1991] for nitrate-using diatoms [*Timmermans et al.*, 1994] and ~16000 [*deBaar et al.*, 1990] for smaller, ammonium-using flagellates [*Sunda and Huntsman*, 1997]. On the basis of an inverse relation of molar N/Fe ratios and half-saturation constants for Fe uptake, with k_{Fe} of ~0.03 nmol Fe kg^{-1} for flagellates and ~0.12 nmol Fe kg^{-1} for netplankton diatoms [*Leonard et al.*, 1999], the k_{Fe} for *Trichodesmium* might be ~1.0 nmol Fe kg^{-1}. Laboratory measurements of nitrogen fixation per unit biomass of these cyanophytes, in response to Fe enrichments, indeed suggest a k_{Fe} of ~1.0 nmol Fe kg^{-1} [*Rueter et al.*, 1990].

At background levels of dissolved iron of <0.1 nmol Fe kg^{-1} on the West Florida shelf during the dust-free periods of May and October the cyanophytes would thus be under severe Fe limitation. In contrast, during Saharan dust events, maximal N fixation should ensue if rainfall and phosphorus stocks are also sufficient. We first examine the timing of Saharan dust events at Miami or Barbados during 1980, 1976, 1967, and 1966 in relation to phytoplankton cell counts, as an initial test of our proposed food web link between Fe-starved cyanophytes and N-starved dinoflagellates in coastal waters off western Florida. Finally, we consider interannual variation of helicopter sightings of the cyanophytes, of July–December abundances of *G. breve*, and of July stocks of Barbados dust over different record lengths during 1957–1998.

2.2. Plankton Time Series

The most extensive set of plankton data consists of microscopic enumeration of *G. breve* and *T. erythraeum* populations obtained by both the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission (FWCC) at 25–30 stations (all nearshore symbols of Figure 1) within 9 km of the west Florida coast, from off Cedar Key

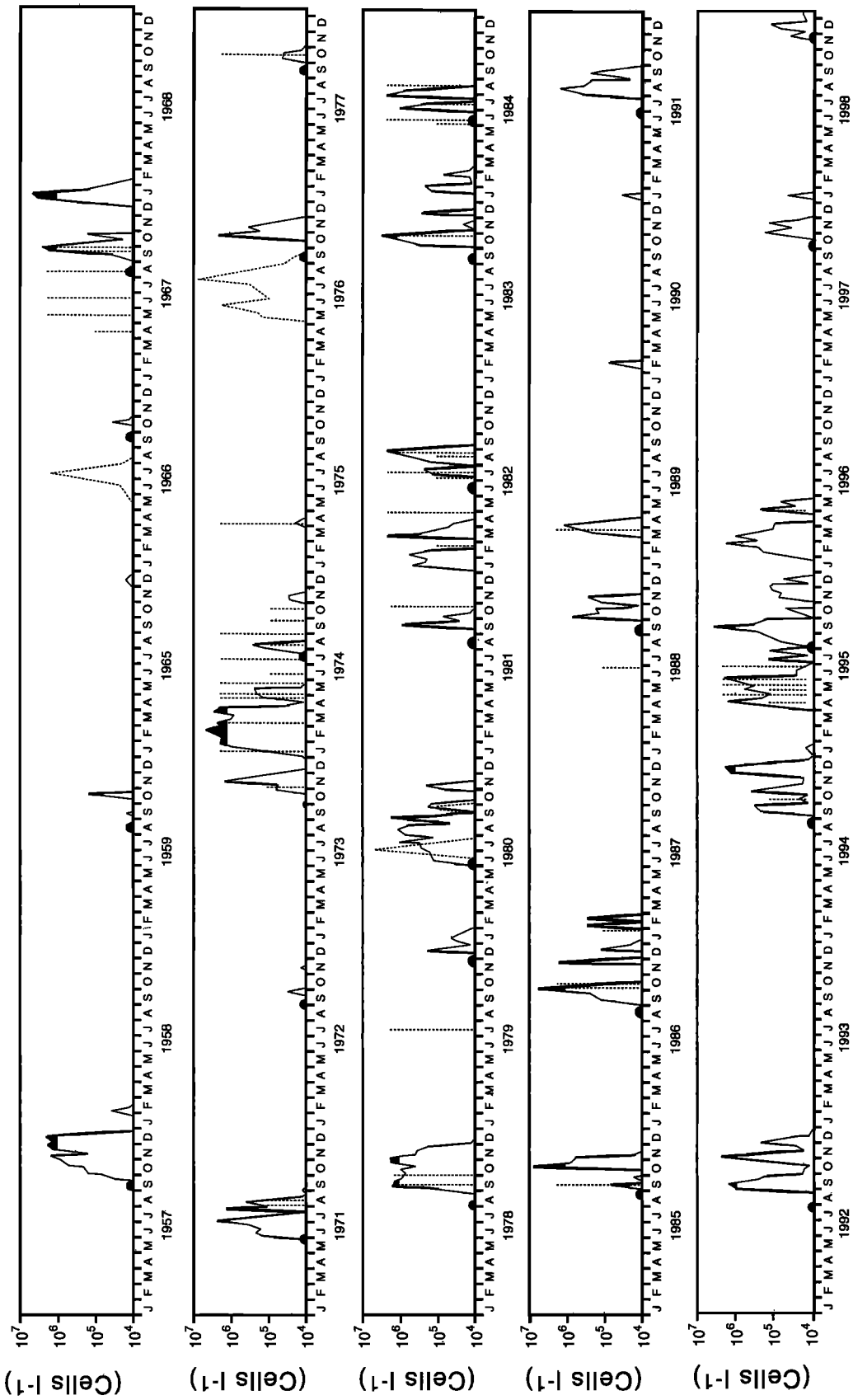

Figure 3. Alongshore weekly means of the daily integrals of *T. erythraeum* (dashed line) and *G. breve* (solid line) surface abundances (10^4–10^6 cells L^{-1}) within 9 km of the west Florida coast from off Cedar Key to near Cape Romano during 1957–1998. Computed initiation of a red tide is denoted by a solid hemisphere, while larger blooms ($>1 \times 10^6$ cells L^{-1}) of *G. breve* are indicated by the shaded portion of the integral.

(29°09′N) to near Cape Romano (25°54′N), during 1957–1998. The USFWS and FWCC assessments of red tides were based on live counts of *G. breve* under ×45–54 magnification of ~6 mL aliquots [*Dragovich et al.*, 1961; *Steidinger and Williams*, 1970].

When cyanophyte counts of trichome abundances were unavailable but aircraft/helicopter surveys provided qualitative assessments of their heavy and light abundances, we assigned respective stocks of 1×10^5 and 2×10^6 cells L^{-1} (Figure 3) on the basis of concurrent shipboard and aerial data. An adaptive sampling mode was used by FWCC in which daily observations were made when and where red tides stranded once dead fish washed ashore to suggest the presence of brevetoxins. To deal with such patchiness of both samples and red tides, we simply sum the alongshore abundances of *G. breve* cells each day, presenting the weekly mean of these integrals in Figure 3.

During 1976, surface samples at longer 2 week intervals were taken along cross-self sections of six stations out to the 40 m isobath (pentagons of Figure 1). Live counts were then made of *G. breve*, other dinoflagellates, *Trichodesmium*, diatoms, microflagellates, and ciliates in relation to temperature, salinity, chlorophyll stocks, and inorganic suspended matter. In the Hourglass study of 1966–1967 [*Steidinger and Williams*, 1970] the same live counts were made at even greater monthly intervals over three depths of two sets of stations at the ~40, ~25, and ~5 m isobaths (open triangles of Figure 1), with additional determination of the abundance of copepod nauplii. The data of this time series are presented as the means over the water column of the paired stations at these isobaths, except for the cyanophyte stocks, which are means of just the surface data.

Finally, during 1972–1974 at coarse approximately bimonthly intervals, estimates of total zooplankton abundance over the same inner-shelf region were obtained [*Houde and Chitty*, 1976] from Bongo net hauls at ~20 stations between the 50 m isobath and the coast, from off Clearwater (28°N) to near Naples (26°N). Another time series of net-caught zooplankton biomass at monthly intervals is available from one station above the 30 m isobath of the Florida Middle Ground (plus of Figure 1) during 1969–1970 [*Austin and Jones*, 1974]. During FWCC cruises in March, August, and October 1992 the feeding preferences of the dominant copepods were studied [*Kleppel et al.*, 1996]. At very high spatial resolution a combined optical and net sampling system also provided an assessment of zooplankton abundances during September 1998 within a 90 km section taken off Sarasota between the 10 and 50 m isobaths [*Sutton et al.*, 2001].

2.3. Simple Growth Model

A Lagrangian formulation of the population dynamics of both *T. erythraeum* (P_1) and of *G. breve* (P_2) is described by

$$\partial P_i/\partial t = g_i P_i - \psi_i P_i - \gamma_i P_i - \partial/\partial z w_i P_i, \qquad (1)$$

where the respective loss terms are respiration (and equivalent DON excretion in the case of the cyanophytes), grazing, and sinking instead of lateral mixing [*Kierstead and Slobodkin*, 1953]. The first term is gross photosynthesis (and nitrogen fixation of the cyanophytes), while uptake of DON and DOP by the dinoflagellates, like that of PO_4 by the diazotrophs, is a function of net photosynthesis to maintain Redfield ratios [*Walsh*, 1996].

Since *Trichodesmium* spp. [*Villareal and Carpenter*, 1990] and *G. breve* (Figure 4) exhibit upward movements, the sinking loss of the last term of (1) is considered negligible. The respective gross growth rates $g_{1,2}$ are 0.70 and 0.25 d^{-1} and the respiration rates $\Psi_{1,2}$ are 0.35 and 0.05 d^{-1}; only the results are shown when the grazing rates $\gamma_{1,2}$ are zero. During the 1980 analysis we predict the stocks of the two phytoplankton groups forward in time; for the 1957–1998 time series we predict backward to estimate the date of initiation of red tides (solid hemispheres of Figure 3).

3. Results

3.1. Daily Time Series: 1980

A mean *Trichodesmium* population of 25,000 trichomes L^{-1}, or an abundance of 2.5×10^6 cells L^{-1} (assuming [*Carpenter and Romans*, 1991] 100 cells trichome^{-1}), was observed within surface waters of 3 FWCC red tide stations off Charlotte County (open circles of Figure 1) on July 7, 1980, at optimal temperatures of >29°C. An earlier Saharan dust event of ≥5 $\mu g\ m^{-3}$ of mineral aerosols was found on June 21–30, 1980 [*Carder et al.*, 1991], similar to those measured at Miami in 1982–1983 [*Prospero et al.*, 1987]. This cyanophyte stock is equivalent to a pigment biomass of ~3.0 μg chl L^{-1} (Figure 5) at their cellular amounts of 1.2×10^{-6} μg chl cell^{-1} [*Borstad*, 1982].

These light-adapted phytoplankton have a C/chl ratio of ~200 [*Carpenter and Roenneberg*, 1995] and a molar C/N ratio of ~6 [*McCarthy and Carpenter*, 1979; *Carpenter et al.*, 1987], such that their PON/chl ratio is ~2.8, compared to that of 0.4 assumed for *G. breve*. An iron requirement of ~18 nmol Fe kg^{-1}, from a PON/chl ratio of 2.8 and N/Fe ratio of 465, could have then been met during shoreward transit from mainly offshore iron stocks like those either measured in 1999 [*Lenes et al.*, 2001] or computed during 1982–1983. In a Redfieldian world [*Walsh*, 1996] the >0.60 μmol PO_4 + DOP kg^{-1} on the West Florida shelf in June 1999 would also yield at least 3.3 μg chl L^{-1} of *Trichodesmium*, without having to invoke vertical migration [*Karl et al.*, 1992] during onshore transport.

The maximal gross growth rate may be only ~0.70 d^{-1} for *Trichodesmium* [*Carpenter and Roenneberg*, 1995], compared to ~1.4 d^{-1} for microflagellates and diatoms in prior models of the Gulf of Mexico and the Carribean Sea [*Walsh et al.*, 1989, 1999]. These cyanophytes and the slower growing dinoflagellates would thus be at a competitive disadvantage if the other phytoplankton groups had access to either N_2 or DON. Moreover, their 50% respiration/excretion losses of C/N suggest that the net population growth rate of cyanophyte particulate matter might instead be ~0.35 d^{-1} under no limitation and negligible grazing losses.

Such computed exponential increments of *T. erythraeum* stock do fit the biomass observations (solid and open circles, respectively, of Figure 5) off Charlotte County during the longer Saharan dust event (>5.0 $\mu g\ m^{-3}$ of aerosols) sampled at Miami on June 21–30, 1980. Our simple growth model suggests that these diazotroph population changes might be attributed to local unlimited growth in response to iron fertilization. Note that a progressive vector diagram of near-surface wind velocities at the Tampa airport (as well as at Sarasota and Fort Myers, Florida; not shown) shows steady southwesterly winds prevailed during this second dust event (Figure 6).

The nearshore time series (Figure 5) thus presumably sampled the history of successive offshore surface Lagrangian populations, as they were advected onshore past the sampling sites

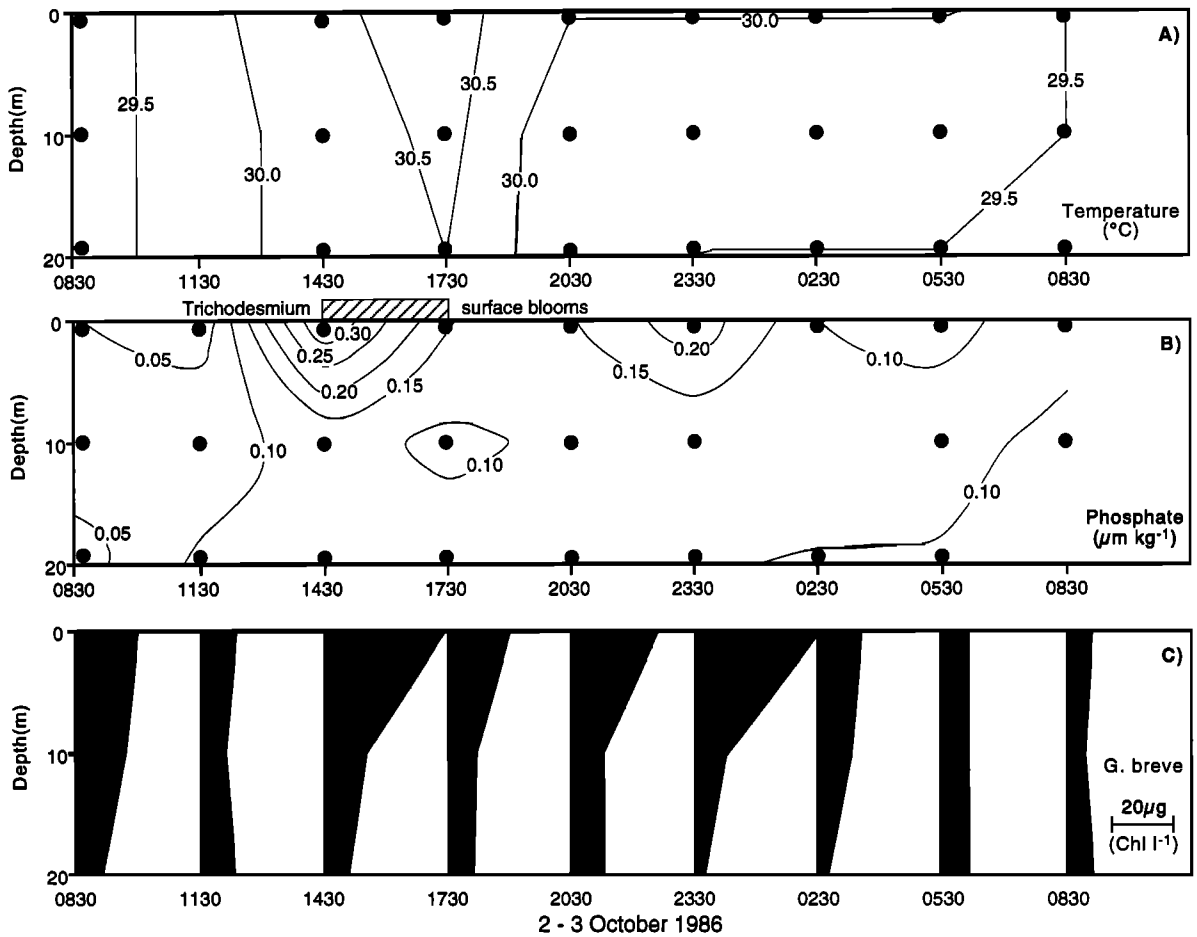

Figure 4. The vertical distributions of (a) temperature (°C), (b) phosphate (μmol kg^{-1}), and (c) estimated biomass (μg chl L^{-1}) of *G. breve* during October 2–3, 1986, above the 20 m isobath of the West Florida shelf.

under such wind forcing [*Yang and Weisberg*, 1999; *Yang et al.*, 1999]. The decline in cyanophyte biomass after July 7, 1980, under renewed onshore winds may be due to cessation of Saharan iron supply rather than to phosphorus limitation. Circulation models suggest that the *Trichodesmium* populations would then have been retained within the nearshore waters, receiving summer estuarine influxes of phosphorus.

With a mean *Trichodesmium* biomass of just 1.1 μg chl L^{-1} over June 20 to July 14, 1980 (Figure 5), a 50% daily loss of their nitrogen fixation as excretion (0.35 d^{-1} $\times$ 1.1 μg chl L^{-1} $\times$ 2.8 μmol PON μg chl^{-1}), i.e., ~1.1 μmol DON kg^{-1} d^{-1}, would yield a cumulative release of 27.0 μmol DON kg^{-1} over the nearshore water column during the 25 day period. Full utilization of the cyanophyte-released DON by a red tide within the upper 5 m, where 10% of the iron of Saharan dust was previously assumed to dissolve, would then lead to a *G. breve* accumulation there of 67.5 μg chl L^{-1} on July 14 if all of the other dinoflagellates were either selectively grazed [*Kleppel et al.*, 1996] or poisoned [*Freeberg et al.*, 1979] and no ammonifying bacteria were present.

The mean *G. breve* stock of 1.9 $\times$ 10^6 cells L^{-1} on July 21 1980 (Figure 5), is equal to 19 μg chl L^{-1} at cellular amounts of 1.0 $\times$ 10^{-5} μg chl cell^{-1} for both cultures [*Shanley and Vargo*, 1993] and field populations in October 1976 (Figure 7). Thus ~72% of the computed release of DON in our simple model could have been diverted to the microbial web and other phytoplankton; alternatively, nitrogen fixation may not have been at the maximal rate during the last week of July 7–14, 1980. In any case, a maximal net growth rate of ~0.20 d^{-1}, at the same optimal temperatures as for *Trichodesmium* [*Steidinger et al.*, 1998], by *G. breve* provides another exponential fit to most of the red tide observations during June–July 1980 (solid and open squares of Figure 5), suggesting that their nitrogen supplies were then adequate.

Like the cyanophytes [*Guo and Tester*, 1994], red tides are thought to be unpalatable to most grazers, such that only respiration losses may usually apply to this toxic group in (1), unless no other phytoplankton are present [*Turner and Tester*, 1997]. In contrast, their dinoflagellate competitors are readily eaten by copepod herbivores on the West Florida shelf, where summer–fall diets of the macrozooplankton contain greater percentages of dinoflagellates than those in the sea, implying selective feeding [*Kleppel et al.*, 1996]. We shall find that these nontoxic, faster growing dinoflagellates, with a net growth rate of ~0.60 d^{-1} at 25°C, actually precede *G. breve* in response to release of DON by the cyanophytes (Figures 7 and 9).

The simple model yields computed stocks of 1.0 $\times$ 10^6 cells L^{-1} on July 25, 1.0 $\times$ 10^5 cells L^{-1} on July 14, 1.0 $\times$ 10^4 cells L^{-1} on July 2, and 1.0 $\times$ 10^3 cells L^{-1} on June 21, i.e., background levels of 0.01 μg chl L^{-1} of *G. breve* when the major dust event began (Figure 5). At this time, *T. erythraeum* presumably initiated exponential growth and released DON, as

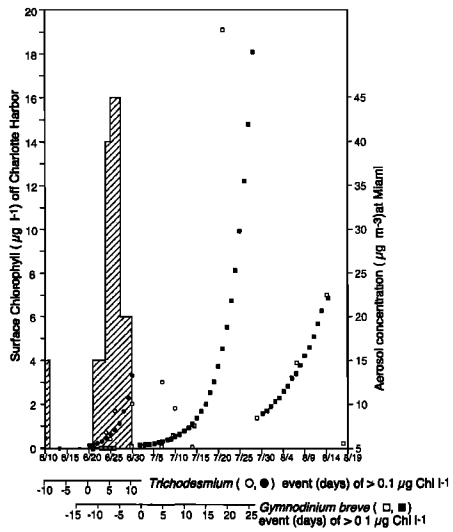

Figure 5. Mean observed (open symbols) and computed (solid symbols) daily biomasses (μg chl L^{-1}) at the surface of the nitrogen fixer *T. erythraeum* (open and solid circles) and the toxic dinoflagellate *G. breve* (open and solid squares) within ~5 km of the west coast of Florida at three sampling sites off Charlotte/Lee Counties (~26°40′N–26°55′N) in relation to Saharan dust (striped columns) events (>5.0 μg m^{-3} of mineral aerosols) observed during June 10 and 21–30, 1980, at Miami (25°45′N). Cell counts were converted to biomass, assuming 1.2×10^{-6} μg chl $cell^{-1}$ for the former and 1.0×10^{-5} μg chl $cell^{-1}$ for the latter.

observed in 1999 [*Lenes et al.*, 2001], while herbivores grazed on the other dinoflagellates. Macrozooplankton biomass on the West Florida shelf during June–November is usually tenfold that of February–March [*Austin and Jones*, 1974; *Houde and Chitty*, 1976], such that increased and selective grazing pressure on nontoxic dinoflagellates would allow slow summer accumulation of *G. breve* in both the "real world" and our model. During August 1969 on the Florida Middle Ground (plus of Figure 1), however, zooplankton abundance was low, tenfold less than that found at some stations there in August 1973, such that no red tide occurred in 1969, compared to those found in 1973 and 1980 (Figure 3).

Upwelling favorable winds on July 19–21, 1980 (Figure 6), would have advected the coastal populations offshore in the surface Ekman layer [*Yang and Weisberg*, 1999; *Yang et al.*, 1999], leading to an export of the nearshore red tide, as seen by concurrent Coastal Zone Color Scanner (CZCS) imagery (F. Muller-Karger, personal communication, 2000). When onshore wind forcing resumed on July 25, 1980 (Figure 6), the nearshore time series recorded another population increment of *G. breve* (Figure 5), but a smaller net growth rate of 0.10 d^{-1} for these dinoflagellates now fits the August observations, suggesting nitrogen limitation once more.

Since *G. breve* has the ability [*Vargo and Shanley*, 1985; *Vargo and Howard-Shamblott*, 1990] to utilize DOP efficiently like *Trichodesmium* [*Yentsch et al.*, 1972], the stocks of just organic phosphorus (~40% of DOP + PO_4) in coastal waters off central Florida are sufficient to meet the daily demands of *G. breve* at population levels of up to ~6.5 μg chl L^{-1} [*Steidinger et al.*, 1998]. Indeed, during an October 1986 red tide of a mean ~13 μg chl L^{-1} of *G. breve* above the 20 m isobath (Figure 4c), as much as 0.30 μmol PO_4 kg^{-1} were still found (Figure 4b) 30 km off the Florida coast (solid diamond of Figure 1) at undetectable amounts of nitrate and ~10 μg chl L^{-1} of the co-occurring nitrogen fixers. Note, again, the large red tide along the central west coast of Florida during 1986, as well as in 1980 (Figure 3).

3.2. Biweekly Time Series: 1976

How often do such cyanophyte blooms precede ones of toxic dinoflagellates at midshelf, where the phosphorus supplies may not support large biomass of both phytoplankton groups as in coastal waters? During 1976, surface samples at longer 2 week intervals of cross-self sections, taken out to the 40 m isobath, again indicated that populations of *T. erythraeum* occurred earlier than those of *G. breve* (Figure 7a), as in 1980 (Figure 5).

Although Saharan dust samples were not collected at Miami before June during 1976, the winter–spring amounts of mineral aerosols in January–May of other years sum [*Prospero*, 1999b] to only 15% of the annual dust loading (Figure 8a). Thus little iron was evidently available to the first spring population of *T. erythraeum*, such that only a small red tide of *G. breve* was found nearshore during May 1976, in response to the seasonal onset of downwelling favorable winds from the south (Figure 7b), i.e., onshore surface flows during the previous April.

No increment of other dinoflagellate abundance (Figure 7c) was associated with the first cyanophyte bloom in 1976 as well. Note that during the massive amounts of *Trichodesmium* off St. Petersburg Beach in May 2000, no red tide co-occurred, at a time when the dissolved iron stocks on the outer West Florida shelf were ≤0.2 nmol Fe kg^{-1} [*Lenes et al.*, 2001].

Since rainfall peaks during summer on the southwest coast of Florida (Figure 7b and 8b), wet deposition of mineral aerosols would also be favored after June 1976. A July combination of greater dust loading, larger rain fall, and mainly onshore surface flows led to both a second summer population of *T. erythraeum* by early August 1976 (Figure 7a) and a tenfold increment of other dinoflagellates (Figure 7c), preceding the fall red tide of *G. breve*. As in 1980 (Figure 5), a daily threshold of ~5 μg m^{-3} of mineral dust at Miami (Figure 7a), or ~12.5 μg m^{-3} at Barbados closer to the Saharan source, seems to provide sufficient iron for cyanophyte-induced red tides of *G. breve*. On the basis of the regression of offshore iron stocks on the West Florida shelf and monthly total dust at Miami during June–October 1999, 5 μg dust m^{-3} ≃0.5 nmol Fe kg^{-1}, which approximates our estimate of k_{Fe} for *Trichodesmium*.

Note that a short July upwelling event fostered a brief surface diatom bloom, curtailed by either inadequate supplies of nitrate, e.g., Figure 2c, and/or selective grazing again by herbivores. During a spring bloom of diatoms from estuarine nutrient sources on the West Florida shelf in March 1992 [*Gilbes et al.*, 1996] this siliceous group constituted ~20–60% of the diets of the dominant copepods, compared to ~10–30% of the available food [*Kleppel et al.*, 1996]. During October 1992 the copepods then selected other dinoflagellates at midshelf during a red tide of *G. breve* along the coast (Figure 3), with, again, a diet of ~35–65% dinoflagellates, compared to a food choice of ~25–30%.

When upwelling favorable winds from the north provided offshore flows in the surface Ekman layer over the rest of August and most of September 1976, however, the populations of both N_2-fixing cyanophytes and nontoxic/toxic DON-utilizing dinoflagellates dispersed to low background levels (Figure 7). A diatom bloom did not occur then, suggesting that the selective grazing pressure, which allows *G. breve* to out-

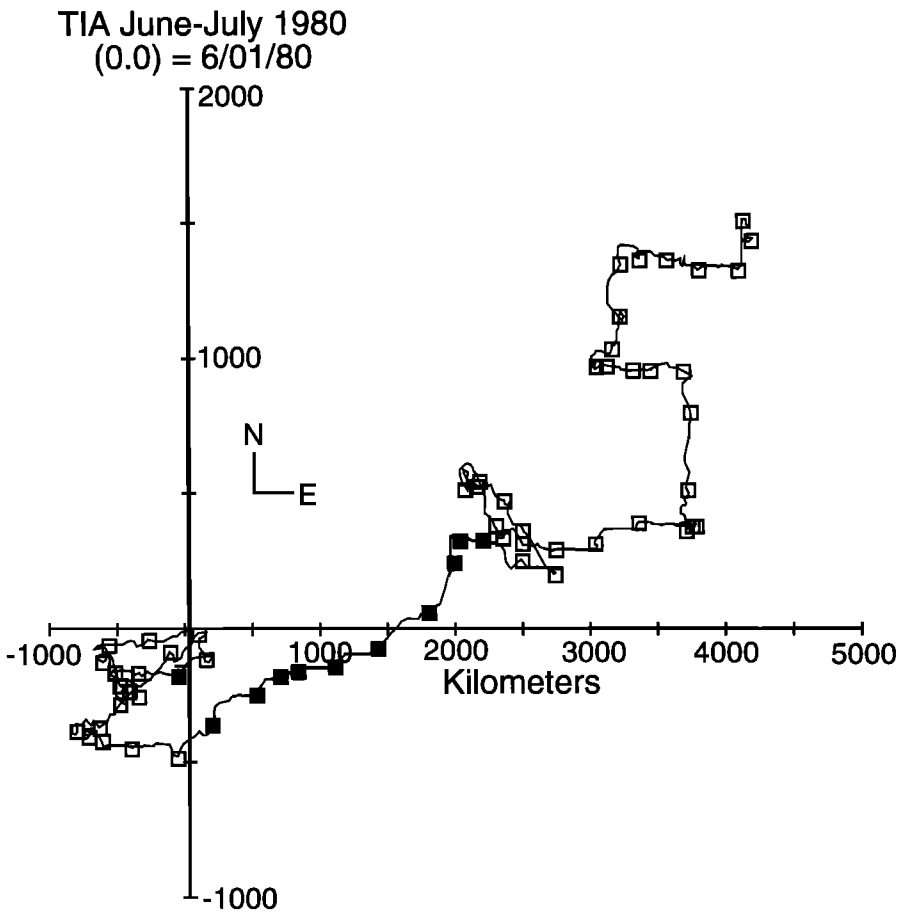

Figure 6. Progressive vector diagram, plotted head to tail, of the hourly near-surface winds (m s^{-1}) at Tampa International Airport (27°58′N) during June–July 1980. The duration of the summer dust events in 1980 are denoted by the solid squares beginning on June 10 and on June 21–30.

compete other faster growing dinoflagellates, must have removed siliceous rivals as well. With return of onshore flows in early October 1976 a red tide of *G. breve* was finally found both above the 15 m isobath (Figure 7a) and along the coast (Figure 3) until northeasterly winds purged the littoral zone once more.

The sum of July rainfall at Fort Myers was similar in 1976 and 1980 (15.5 versus 17.8 cm $month^{-1}$), as were the means of Miami dust [*Prospero*, 1999b] that month (15 versus 18 $\mu g\ m^{-3}$, i.e., equivalent to ~38.7 and 45.0 $\mu g\ m^{-3}$ off Barbados) and the subsequent weekly maxima of red tides (Figure 3) along the coast (3.2×10^6 versus 1.8×10^6 cells l^{-1}). However, are these just anomalous years, or do the first and second time series represent the normal sequence of red tide initiation, stranding, and dispersal?

3.3. Monthly Time Series: 1966–1967

Dust data were not collected in Miami during 1966–1967; we thus use the Barbados data set [*Prospero and Nees*, 1986] as a proxy (Figures 9a and 9c). During June 1967 dust events the presence of *T. erythraeum* was qualitatively noted at the Hourglass stations (Figure 9c). Cell counts in the previous year (Figure 9a) suggested that the population levels of the cyanophytes could have been the same as those in 1976 (Figure 7) and 1980 (Figure 5). The abundances of copepod nauplii were more than tenfold larger in 1967 (Figure 9d) than in 1966 (Figure 9b), indicating greater reproductive success of the adults in the second year. Furthermore, the stocks of other dinoflagellates were tenfold less in July 1967, and large red tides of *G. breve* ensued during October both in offshore waters (Figures 9c) and along the coast (Figure 3).

In contrast, after a smaller June 1966 pulse of dust, high stocks of *T. erythraeum* were associated only with a bloom of other dinoflagellates (Figure 9b), but not of *G. breve* (Figure 9a). The copepod nauplii were then $<10^2\ L^{-1}$ and thus also not plotted in Figure 9b, while a small red tide was found in October 1966 (Figure 3). The equivalent June dust loadings in the eastern Gulf of Mexico would have been monthly means of ~3.3 $\mu g\ m^{-3}$ in 1966 and of ~6.9 $\mu g\ m^{-3}$ in 1967. Clearly, more iron of perhaps ~0.7 nmol Fe kg^{-1} was available to the cyanophytes during 1967 than in 1966 (~0.3 nmol Fe kg^{-1}).

Similar to the small red tide in April 1976, the small one in 1966 may have been both indirectly iron-limited and directly grazer-controlled, as suggested by the differences in copepod abundances during the 2 years of Hourglass observations. For example, off Sarasota, Florida, in the same shelf region during September 1998 the maximum estimate of grazing demands by crustaceans between the 10 and 50 m isobaths would have consumed ~14% of the primary production [*Sutton et al.*, 2001], perhaps allowing the faster growing other dinoflagellates to bloom, as in 1967 and 1976 (Figures 7 and 9). Again, a small red tide was observed in 1998 (Figure 3). Finally,

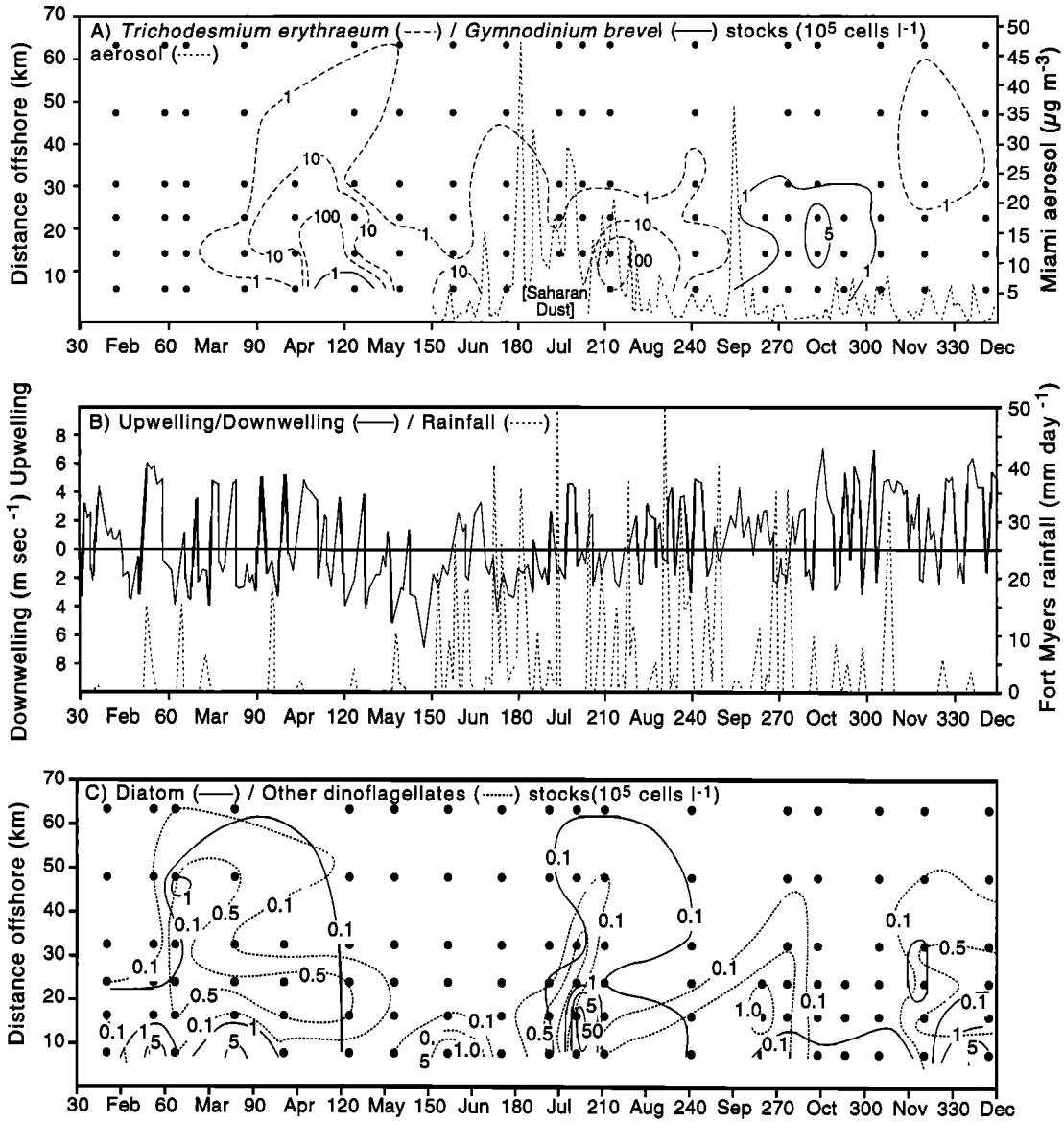

Figure 7. The monthly surface abundances (10^5 cells L^{-1}) of *T. erythraeum* (dashed line) and *G. breve* (solid line) along offshore sections of six stations (solid circles) from Tampa and Sarasota Bays (~27°20′–27°40′N) to the 40 m isobath during 1976 in relation to the daily sampling of (a) Saharan dust (μg m^{-3}) at Miami (dotted line) and (b) both rainfall (dotted line) accumulation (mm) and upwelling/downwelling favorable winds (m s^{-1}) at Fort Myers Page Field (26°35′N) and (c) the monthly abundances (10^5 cells L^{-1}) of the sums of both other unarmored and armored dinoflagellates and of centric and pennate diatoms.

during May 1972 and 1974 the nearshore zooplankton populations were fivefold to tenfold less than those of 1973 [*Houde and Chitty*, 1976], and once more, small red tides were found in the fall of 1972 and 1974, compared to 1973.

3.4. Annual Time Series: 1957–1998

During the past 42 years, 28 red tides of $>1 \times 10^4$ cells L^{-1} of the alongshore integral of *G. breve* populations were found during mainly summer–fall at stations along the central west Florida coast (Figure 1). At population levels of $>5 \times 10^3$ cells L^{-1} the shellfish beds are closed. The winter occurrences of *G. breve* in 1968, 1974, 1982, 1984, 1989, 1995, and 1996 are considered persistent fall blooms of the preceding year (Figure 3), trapped near the coast by circulation patterns of alternating southerly and northerly flows, as observed in 1996 [*Yang et al.*, 1999]. In contrast, during other years of 1972, 1976, 1980, 1987, and 1994 the fall blooms were instead exported to the east coast of Florida [*Murphy et al.*, 1975; *Tester et al.*, 1991], as in 1999. The nonevents of no red tides found during 1960–1964 and 1969–1970 are not shown in Figure 3.

As sighted by aircraft, helicopters, and ships after 1957, the cyanophytes co-occurred along the coast each year (Figure 3) during at least 87% of the 16 larger red tides, i.e., when the alongshore weekly integral of *G. breve* abundance exceeded a value of 1×10^6 cells L^{-1} over the 42 year record. During the most recent red tide of $>3 \times 10^6$ cells L^{-1} in October 2000, large populations of *Trichodesmium* co-occurred as well (C. Heil, personal communication, 2000).

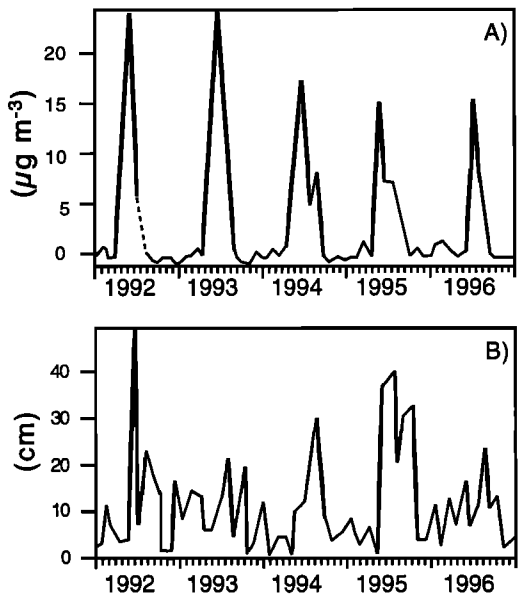

Figure 8. The monthly values of (a) Saharan dust at Miami (μg m^{-3}) and (b) rainfall (cm) at Venice during 1992–1996.

On the basis of the initial growth rate of the 1980 red tide (Figure 5), 20 of these 28 red tides first formed during ~June–August, when 71% of the annual Saharan dust loading arrives at Miami [*Prospero*, 1999b] and 47% of the annual rainfall occurs at Tampa and Fort Myers. Furthermore, 15 of the 16 larger red tides were initiated during these months (Figure 3). Were other red tides undetected by the FWCC adaptive sampling network within ~10 km of the west coast of Florida?

Over a 5 year period of 1992–1996, red tides did not strand within this region during 1993 and 1996; they may have been offshore and thus not sampled. Of these years, however, July rainfall at Venice (between Fort Myers and Tampa) was ~10 cm month^{-1} in 1993 and 1996 (Figure 8b), when Saharan dust was >15 μg m^{-3} at Miami (Figure 8a). Under the same dust loading and rain accumulations of >20 cm month^{-1}, red tides instead formed during both 1994 and 1995 (Figure 3). Thus sufficient rainfall, as well as Saharan dust, must be present for wet deposition of particulate iron [*Prospero et al.*, 1987], but considering the poor correlation between past precipitation events and red tides [*Feinstein*, 1956], other biotic factors must also be important.

4. Discussion

A scatter diagram (Figure 10) of July dust at Barbados in relation to cumulative stocks of *G. breve* along the central west Florida coast (Figure 3) during July–December each year exhibits threshold phenomena, as suggested for the initiation of red tides of *Gymnodinium catenatum* within Australian waters [*Hallegraeff et al.*, 1995]. Below a monthly mean of 12.5 μg m^{-3} of Barbados July dust, i.e., ~5 μg m^{-3} of equivalent Miami dust, or 0.5 nmol Fe kg^{-1} found on the outer part of the west Florida shelf, for example, few red tides are observed off the Florida coast.

Over the full Barbados range of 4.1–42.5 μg m^{-3} of July dust, however, red tides are still not found near the coast during some years, such that Saharan iron loading and rainfall are necessary but not sufficient initial conditions. Seeding of *T. erythraeum* on the West Florida shelf is associated with Loop Current intrusions, carrying populations from upstream regions via the Brazil and Yucatan Currents, i.e., from the South Atlantic [*Calef and Grice*, 1966] and Carribean Sea [*Hulburt*, 1968]. On average, the Loop Current is within the DeSoto Canyon region at ~30°N about 5–10% of the time [*Vukovich and Hamilton*, 1989], i.e., 1 month of the year, when wet deposition of Saharan dust loadings must also occur to yield the red tides found there.

For example, during 1964, no red tide was found at the standard monitoring stations (Figure 1) by either USFWS [*Dragovich and Kelly*, 1966] or FWCC [*Steidinger et al.*, 1967]. Yet that year a large bloom occurred within Apalachee Bay, as during 1974 and 1982. These rare events represent 7% of the 42 year record (Figure 3), i.e., the same frequency as the Loop Current in the northern Gulf of Mexico. Another red tide just occurred there in 1999, when AVHRR, Sea-viewing Wide Field-of-View Sensor (SeaWiFS), and TOPEX imagery all showed deep penetration of the Loop Current; this red tide was also associated with local stocks of *Trichodesmium* (G. Kirkpatrick, personal communication, 2000).

At the edge of shelf south of Tampa Bay the Loop Current is instead present 30–35% of the time at 27°N [*Vukovich and Hamilton*, 1989], providing cyanophyte seed populations more frequently. Recall that 16 large red tides, or 38% of the total 42 year record (Figure 3), were instead observed off central Florida. In addition to cyanophyte precursors of a red tide, the other biotic factor is selective grazing on their competitors.

During at least 1966, 1969, 1972, 1974, and 1998, when red tides were absent or minimal within this nearshore sampling region (Figure 1), low grazing stress may have allowed other dinoflagellates to compete successfully against *G. breve* for the DON of cyanophyte origin. Once a red tide is initiated and moved onshore to the sampling sites (Figure 3), however, the amount of dust (iron) loading in July then appears to determine how large a yield of toxic dinoflagellates may prevail from July to December (Figure 10) within phosphorus replete waters.

We made no detailed statistical analyses since past attempts to correlate red tides with abiotic factors were fruitless exercises. Little correlation of *G. breve* variance was found with hurricanes and/or rainfall [*Feinstein*, 1956], salinity [*Chew*, 1956], inorganic nutrients [*Rounsefell and Dragovich*, 1966] and estuarine iron stocks [*Ingle and Martin*, 1971; *Kim and Martin*, 1974], without consideration of biotic factors.

We are content to conclude from these four sets of time series in 1980, 1976, 1966–1967, and 1957–1998 that the likelihood of a large, long red tide at the shoreline emerges from a sequence of conditional probabilities of (1) summer Saharan dust events, (2) sufficient rainfall, (3) dissolution of aeolian iron, (4) seed stocks of both *T. erythraeum* and *G. breve*, (5) release of DON to all dinoflagellate competitors, (6) selective grazing stress on other dinoflagellates as well as diatoms, and (7) onshore flows to complete landfall.

The origin of small red tides is more enigmatic, reflecting possible additional sediment and estuarine sources of DON. During the small red tide of December 1998 (Figure 3) the δ^{15}PON of ~5 μg chl L^{-1} of *G. breve* at the 15 m isobath was +4.8‰, compared to either +0.3‰ for *Trichodesmium*-dominated populations, fixing atmospheric nitrogen at the shelf break, or +7.3‰ for diatoms above the 30–40 m isobaths, after depletion of nitrate supply from a Loop Current intrusion. The intermediate isotopic value of the red tide may

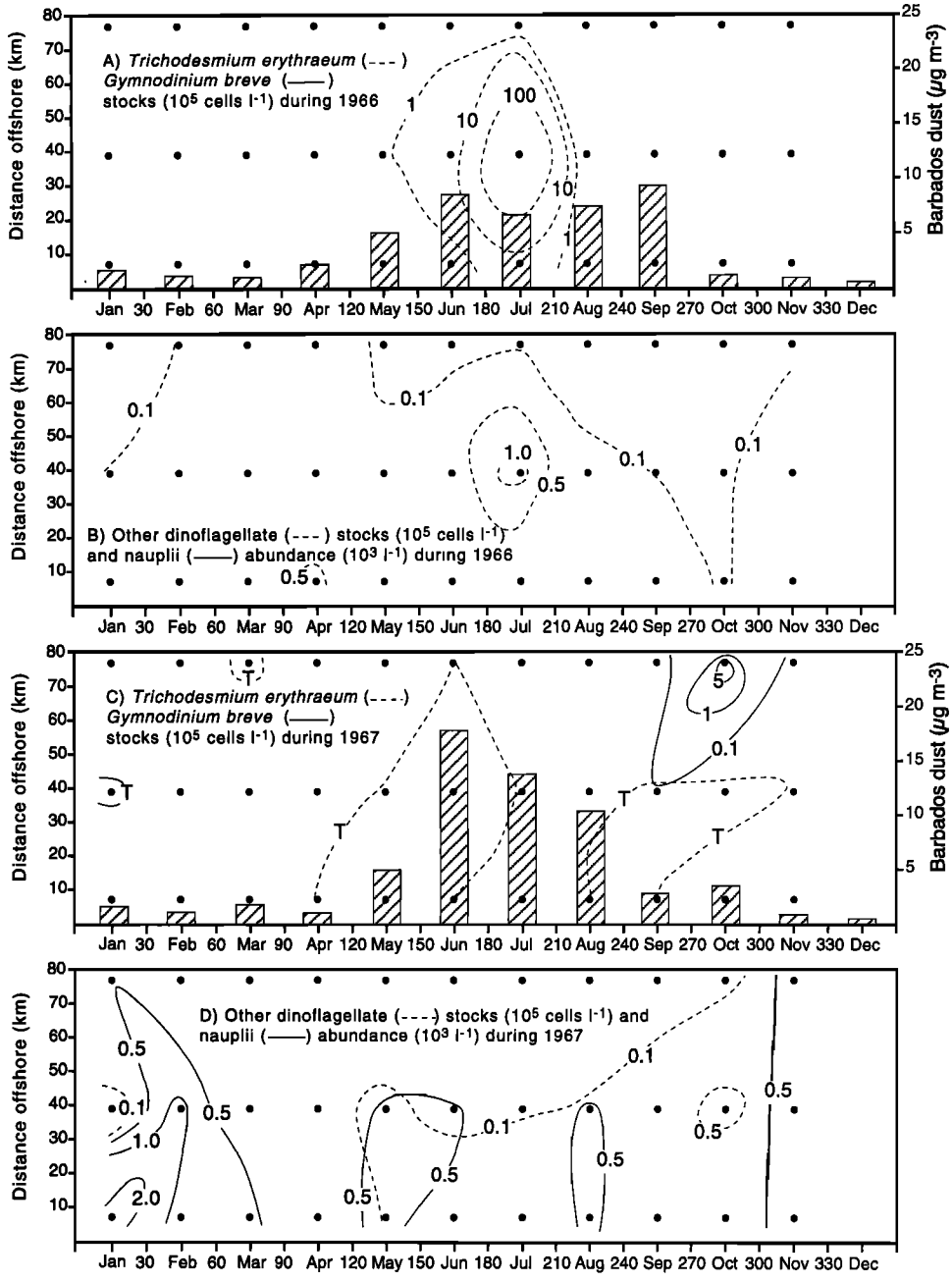

Figure 9. The monthly surface abundances (10^5 cells L^{-1}), or presence *T* and absence, of *T. erythraeum* (dashed line) in relation to both the mean stocks over the water column (10^5 cells L^{-1}) of *G. breve* (solid line) at paired stations on the ~5, 25, and 40 m isobaths (solid circles) and the monthly dust (μg m^{-3}) sampled at Barbados (striped columns) during (a) 1966 and (c) 1967. At these same stations the means over the water column of the sum (10^5 cells L^{-1}) of other unarmored and armored dinoflagellates (dashed line) and of copepod nauplii (10^3 L^{-1} of the solid line) are also shown for (b) 1966 and (d) 1967.

reflect a ^{15}N-enriched DON substrate, compared to a *Trichodesmium* source, produced presumably by bacterial processing.

We are aware of no δ^{15}PON data for bacteria growing on DON, but like phytoplankton, they prefer the lighter isotope of ^{14}N such that their nitrification leads to larger δ^{15}N of the ammonium substrate [*Mariotti et al.*, 1984; *Horrigan et al.*, 1990], while denitrification also yields larger values of the remaining NO_3 [*Cline and Kaplan*, 1975]. During catabolism of phytoplankton (PON → DON → NH_4 → NO_3 → N_2) the bacteria may behave like zooplankton [see *Checkley and Entzeroth*, 1985] by recycling DON to ^{14}N-enriched NH_4 but leaving behind some ^{15}N-enriched DON, i.e., perhaps the urea favored by red tides on the West Florida shelf.

Unfortunately, the reprocessed DON of *Trichodesmium* origin may not have a unique isotopic signal since estuarine detritus also has a δ^{15}PON of +1.1 to +2.9‰ [*Walsh*, 1994]. If the estuarine δ^{15}DON has the same value as the detritus and is palatable to bacteria [*Gardner et al.*, 1996], *G. breve* may utilize this humic source of organic nitrogen as well [*Carlsson and*

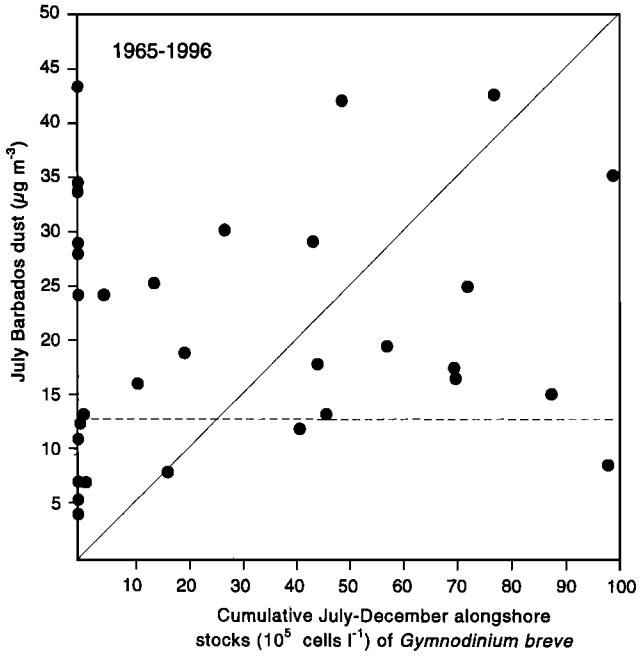

Figure 10. The Saharan dust ($\mu g\ m^{-3}$) sampled at Barbados during July 1965–1996 in relation to cumulative stocks of *G. breve* (10^5 cells L^{-1}) found along the central west Florida coast during July–December of the same years.

Graneli, 1993], yielding a similar $^{15}N/^{14}N$ ratio for their red tides. Moreover, within other subtropical habitats, pristine beds of sea grasses and mangroves have δ^{15}PON of +1.6 to +2.5‰ [*O'Donohue et al.*, 1998; *Corbett et al.*, 1999] derived from nitrogen fixation by symbiont bacteria in sediments such that these macrophytes may provide yet another source of labile DON for *G. breve* of intermediate δ^{15}PON.

We are now coupling more complex versions of (1) to physical circulation models at 1–10 km resolution of the West Florida shelf with Princeton Ocean Model (POM) to explore the seasonal onshore transport of both *T. erythraeum* and *G. breve* [*Walsh et al.*, 2001], as well as their retention and fate along the coast during upwelling and downwelling events. Similarly, the biotic details [*Penta*, 2000] of the toxic consequences, of the bio-optical signals, and of the biogeochemical implications of such a coastal food web response to iron alleviation of nitrogen limitation are now the respective subjects of our National Oceanic and Atmospheric Administration (NOAA)-Environmental Prediction Agency (EPA) ECOHAB:Florida, Office of Naval Research (ONR) Hyperspectral Coastal Ocean Dynamics Experiment (HyCODE), and NASA Synthesis, Modeling, and Prediction (SMP) field projects on the West Florida shelf.

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K. A. Steidinger, Florida Marine Research Institute, Florida Fish and Wildlife Conservation Commission, 100 Eighth Avenue S.E., St. Petersburg, FL 33701.

J. J. Walsh, College of Marine Science, University of South Florida, 140 Seventh Avenue South, St. Petersburg, FL 33701. (walsh@seas.marine.usf.edu)

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