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Hydrodynamic accumulation of *Karenia* off the west coast of Florida ☆

Richard P. Stumpf[a,*], R. Wayne Litaker[b], Lyon Lanerolle[c], Patricia A. Tester[b]

[a]*National Ocean Service, NOAA, 1305 East-West Highway, Silver Spring, MD 20910, USA*
[b]*National Ocean Service, NOAA, 101 Pivers Island, Beaufort, NC 28516, USA*
[c]*National Ocean Service, NOAA, 1315 East-West Highway, Silver Spring, MD 20910, USA*

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Abstract

Blooms of the toxic dinoflagellates, *Karenia* spp. occur nearly annually in the eastern Gulf of Mexico with cell abundances typically $>10^5$ cells L^{-1}. Thermal and ocean color satellite imagery shows sea surface temperature patterns indicative of upwelling events and the concentration of chlorophyll at fronts along the west Florida continental shelf. Daily cell counts of *Karenia* show greater increases in cell concentrations at fronts than can be explained by *Karenia*'s maximum specific growth rate. This is observed in satellite images as up to a 10-fold greater increase in chlorophyll biomass over 1–2 d periods than can be explained by *in situ* growth. In this study, we propose a model that explains why surface blooms of *Karenia* may develop even when nutrients on the west Florida shelf are low. In the summer, northward winds produce a net flow east and southeast bringing water and nutrients from the Mississippi River plume onto the west Florida shelf at depths of 20–50 m. This water mass supplies utilizable inorganic and organic forms of nitrogen that promote the growth of *Karenia* to pre-bloom concentrations in sub-surface waters in the mid-shelf region. In the fall, a change to upwelling favorable winds produces onshore transport. This transport, coupled with the swimming behavior of *Karenia*, leads to physical accumulation at frontal regions near the coast, resulting in fall blooms. Strong thermal fronts during the winter provide a mechanism for re-intensification of the blooms, if *Karenia* cells are located north of the fronts. This conceptual model leads to testable hypotheses on bloom development throughout the Gulf of Mexico.
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1. Introduction

1.1. Hydrodynamic accumulation and nutrient sufficiency

Toxic *Karenia* spp. blooms occur frequently along the west coast of Florida during late summer to fall (Tester and Steidinger, 1997; Stumpf et al., 1998). Blooms can extend for hundreds to thousands of

*Corresponding author. Tel.: +1 301 713 3028x173.
E-mail address: Richard.Stumpf@noaa.gov (R.P. Stumpf).

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square kilometers (Steidinger and Joyce, 1973) and can represent a significant portion of the annual primary production in the oligotrophic waters over the west Florida continental shelf (WFS) (Vargo et al., 1987). While blooms can persist for months, high concentrations of cells are temporally and spatially quite variable (Tester and Steidinger, 1997) due to the influence of hydrodynamic concentration, dispersion and transport (Steidinger and Haddad, 1981; Stumpf et al., 1998), as well as *in situ* growth (Steidinger et al., 1998).

A major conundrum concerning the development of *Karenia* blooms is how sufficient nutrients are acquired to support *in situ* population growth to cell densities exceeding $10^5\,L^{-1}$ on the WFS. Investigations by Heil et al. (2001b) and Vargo et al. (2007) have not identified nutrient sources adequate to support *in situ* growth of high density *Karenia* blooms ($>10^5$ cells L^{-1}). The riddle of how such large biomass blooms can initiate and maintain for weeks to months in the low nutrient environment of the WFS may be solved, in part, by examining the contribution of physical forcing in the formation of *Karenia* blooms. Over the last 30 years both simulations and field data have shown that hydrodynamic concentration of phytoplankton is a major force in bloom formation (Pingree et al., 1975; Simpson et al., 1979; Seliger et al., 1981; Steidinger and Haddad, 1981; Pitcher et al. 1998) and the primary cause of high biomass blooms for motile cells like *Karenia* (Murphy et al., 1975; Kamykowski, 1981; Franks, 1992).

1.2. Modeled Karenia vertical migration behavior

A recent modeling effort described specifically how hydrodynamic accumulation can occur on the WFS (Janowitz and Kamykowski, 2006). The mechanism involves a combination of fluid advection and postulated swimming behavior of *Karenia*. The starting conditions assume a two-dimensional barotropic flow under upwelling-favorable winds, with offshore flow at the surface and onshore flow at depth. These conditions set up a nutrient-enriched frontal region onshore of the 10 m isobath on the WFS. Onshore of this front, cells were postulated to swim upwards owing to a positive phototaxis (or negative geotaxis) (Heil, 1986) with subsequent advection offshore in the surface layer. Seaward of the front where nutrients were assumed to be limiting there was a downward migration toward a potential nutrient source at the sediment interface. Once again in the bottom layer, cells would be advected shoreward. Comparison of the results of simulations with and without the offshore bottom nutrient source indicated that the nutrient source strongly enhanced population development near the front. The Janowitz and Kamykowski (2006) model indicated that the combination of two-layer circulation and *Karenia* swimming behavior could increase cell concentrations more than one order of magnitude near the front.

1.3. Hydrodynamic accumulation of Karenia and nutrient sufficiency

Hydrodynamic concentration has profound implications for how the nutrient requirements of a bloom are determined. High biomass blooms produced by *in situ* growth alone would require much greater ambient nutrient concentrations than if cells from a large area were accumulated. Currently, nearshore nutrient sources sufficient to support the *Karenia* bloom densities commonly observed just offshore of the Tampa Bay/Sarasota area (Fig. 1) have not been identified (Vargo et al., 2007). However, a potential offshore nutrient source does exist. An eastward surface flow in the northern Gulf during summer can deliver nutrient-rich water from the Mississippi River plume to the WFS (Fig. 1) (DiMarco et al., 2005; Hamilton and Lee, 2005; Morey et al., 2005). A number of studies have demonstrated that the Mississippi River plume does flow eastward during summer in response to the prevailing winds (e.g., Walker et al., 2005; Gardner et al., 2006). Modeling studies have shown that *Karenia* are capable of vertical migration to depths as great as 90 m to access nutrients (Sinclair and Kamykowski, 2006), indicating that even nutrients from the Mississippi plume regenerated at depth and transported near the bottom would be accessible.

This project used satellite imagery to assess the development of *Karenia* blooms through hydrodynamic concentration of cells from offshore as proposed in Murphy et al. (1975), Haddad (1982) and Vargo et al. (2001), and predicted by the Janowitz-Kamykowski (2006) model. Ocean color satellite imagery from the same time of the day over consecutive days recorded high frequency spatial and temporal changes in the chlorophyll (chl) biomass which correlated well with *Karenia* cell densities at the surface (Stumpf et al., 2003; Tomlinson et al., 2004). Satellite detection was

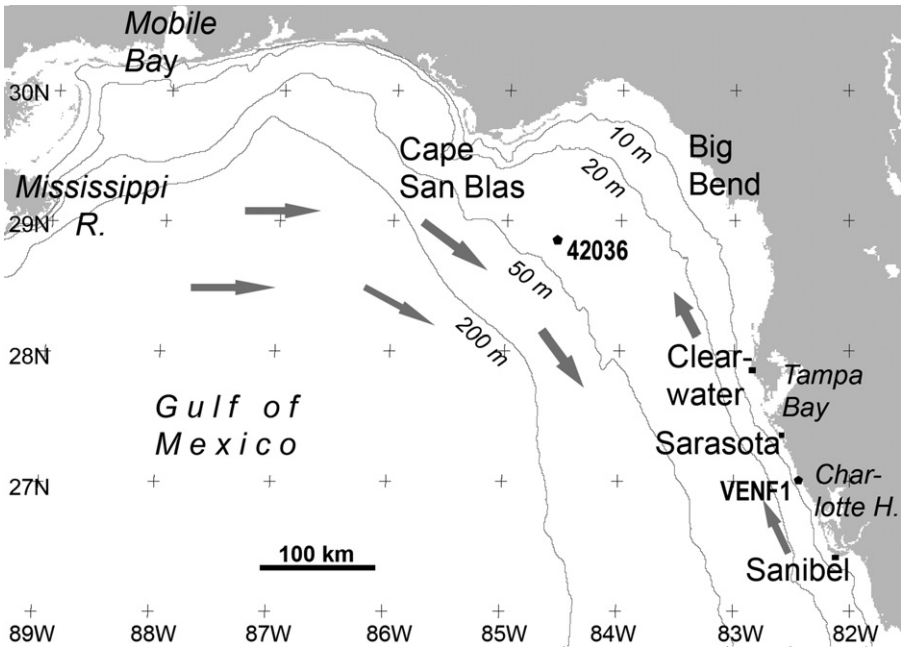

Fig. 1. Northeast Gulf of Mexico. Bathymetric contours shown. Arrows indicate dominant current directions in summer (DiMarco et al., 2005; Liu and Weisberg, 2005; Morey et al., 2005). The two NOAA meteorological stations from which wind data were obtained are marked as 42036 and VENF1.

possible because *Karenia* produces spatially large (from 10^2 to $>10^3\,km^2$), high-density blooms near the surface during the afternoon owing to positive phototaxis (Steidinger, 1975; Heil, 1986; Schofield et al., 2006).

We estimated how quickly blooms formed due to hydrodynamic accumulation and considered the spatial area over which *Karenia* cells were concentrated. We also assessed how upwelling events interacted with frontal regions to cause accumulation of *Karenia* cells. Further, we evaluated whether offshore sources of nutrients were sufficient to support the observed phytoplankton biomass. The results of the analyses indicated the interaction of circulation and an offshore supply of nutrients and cells may account for the development of *Karenia* blooms. This paper also presents a testable hypothesis as to why *Karenia* blooms are observed less frequently off the Texas coast.

2. Materials and methods

2.1. Satellite data

Chl concentrations were obtained from the Sea Viewing Wide Field-of-View Sensor (SeaWiFS) on the OrbView-2 satellite (operated by GeoEye). Version 4.7 of the standard SeaDAS software (NASA, 2007) was used to process the data employing the standard atmospheric correction in conjunction with the Stumpf (2000) chl algorithm specific to the study region. This approach represents a variant of the methods used by O'Reilly et al. (1998). At chl concentrations less than $0.5\,\mu g\,L^{-1}$, the Stumpf (2000) algorithm is equivalent to the global OC4v4 algorithm (O'Reilly et al., 1998). At higher chl concentrations the OC4v4 overestimates chl on the WFS by ~2-fold relative to that estimated by the Stumpf (2000) algorithm. SeaWiFS imagery was projected to a sinusoidal equal area projection with a pixel size of 1.1 km equal to the nominal pixel size of the sensor.

SeaWiFS scans a wide swath, such that at the edges of a scan (or image), the satellite "looks" through far more atmosphere than at near-nadir (the satellite passing directly overhead). This results in greater potential for error in the atmospheric correction when the ocean is viewed at angles far from nadir. When the area of interest is off-nadir, the estimated chl concentration is subject to greater uncertainty, tending to overestimate chl greater than $1–3\,\mu g\,L^{-1}$ as compared to near-nadir scenes collected the day before or after. As nadir occurs at the same time each day, overpasses taken within

20 min of nadir [about 1715–1755 Greenwich Mean Time (GMT) in 2000–2001 drifting to about 1745–1825 GMT in 2005] are most suitable for direct comparison in quantitative analyses. Off-nadir views (>20 min from nadir), were used only if the average chl field showed no bias relative to a nadir view on the preceding or following day.

Sea surface temperature (SST) imagery was obtained from the Advanced Very High Resolution Radiometer, which also has a nominal pixel size of 1 km. This thermal imagery was processed by the US Geological Survey (USGS, 2007) using the standard multi-channel temperature algorithm and a Mercator projection. The SST images were remapped to co-register to the SeaWiFS data in order to identify physical fronts.

2.2. *Karenia spp.*

While we know several species of *Karenia* co-occur in the Gulf of Mexico, the toxic, bloom forming *K. brevis* is by far the most abundant and best characterized. All *Karenia* species will be referred to as *Karenia* in this study. *Karenia* is a relatively large diameter cell (~32 μm) with numerous chloroplasts. It is capable of strong vertical migration with swimming speeds on the order of $1\,m\,h^{-1}$ (Kamykowski and Yamazaki, 1997; McKay et al., 2006). The strong positive phototaxis (Heil, 1986) accounts for why blooms of *Karenia* are observed to concentrate at or near the surface during the day. At night the cells migrate downward from the surface (Schofield et al., 2006). However, when *Karenia* cells become nutrient limited they switch to a positive chemotaxis, readily migrating toward available nutrient sources (Liu et al., 2001b). Despite *Karenia*'s relatively slow growth rate (~0.1–0.35 d^{-1}) (Van Dolah et al., 2007) concentrations of 10^5 cells L^{-1} are not uncommon in WFS waters.

2.3. *Chlorophyll-specific changes in biomass*

In this study the biomass changes in bloom regions from day to day were determined as follows. Once a bloom region was established, those pixels with more than $2.5\,\mu g\,L^{-1}$ chl in the region were flagged. The chl biomass in the bloom was then estimated by multiplying the flagged area (at $1.21\,km^2$ per pixel) by the median chlorophyll concentration for all the flagged pixels. Changes in chl concentrations in the bloom region from day to day were then used to estimate chl-specific rates of change (r) using the following equation:

$$r = (\mathrm{Ln}\,\mathrm{chl}_{n+1} - \mathrm{Ln}\,\mathrm{chl}_n)/D,$$

where chl_n is the estimated amount of chl present in a given surface region at time period n, chl_{n+1} is the total chl present in the corresponding region at the next time period for which data are available, D is the time elapsed in days between observations. These estimated chl-specific rates of change were compared to *Karenia* growth rates measured in the laboratory and in the field. In cases where it was obvious that the entire bloom was moving in a specific direction the bloom location was adjusted to compensate for the movements. Where possible, matching *Karenia* cell counts for the same region were obtained from the Florida Fish and Wildlife Commission, Florida Marine Research Institute (FWRI) data sets.

2.4. *Estimating maximal Karenia growth rates from laboratory and field studies*

Estimates of *Karenia* specific growth rates were compiled from both laboratory and field studies. Growth rates were only included when light levels appeared to be saturating (>65–70 μmol photons $m^{-2}\,s^{-1}$; Magaña and Villareal, 2006) and salinities were >30 psu. The maximal temperature specific growth rates were estimated by drawing a curve inclusive of all the maximal values reported between 15 and 30 °C.

2.5. *Nutrient data*

The nutrient data came from the Northeast Gulf of Mexico (NEGOM) program (Jochens et al., 2002; Texas A&M University, 2007). Nine seasonal cruises were made between 1997 and 2000 using transects perpendicular to the coast. The transects were made from the Mississippi River delta to Tampa Bay, Florida. Water samples were taken at depths of 10–1000 m. Samples were analyzed for nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+) (Grasshoff, 1970; Atlas et al., 1971; Slawyk and MacIsaac, 1972), and urea (Aminot and Kerovel, 1982). The combination of these four nitrogen sources will be subsequently referred to as dissolved nitrogen (DN). Analyses, including chl and accessory algal pigments were also completed during the NEGOM cruises as described by Qian et al. (2003). For our study, we calculated total DN

integrated over depths from 0 to 20 m and from 20 to 50 m. The euphotic zone in the cruise area (excluding the Mississippi River plume) extended to at least 40–100 m (based on 1% light level and attenuation of 0.1–0.04 m^{-1} in Gardner et al., 2006) so we assumed light was not limiting. The partition between surface water (<20 m) and deep water (>20 m) was used to approximate the depth of the shallow-stratified nutrient-limited surface layer that sometimes develops on the WFS. The nutrient data were plotted on maps of the NEGOM cruise area using Grapher v. 6 (Golden Software, Inc.). The size of the bubbles was scaled proportionally to the nutrient concentrations.

2.6. Cell concentrations

Karenia cell concentrations were based on microscopic cell counts in water samples or cell counts made by a Coulter electronic particle counter (Multisizer II, Beckman Coulter). Data came from the FWRI online database (FWRI, 2007) and from the Ecology and Oceanography of Harmful Algal Blooms (ECOHAB) Florida project. *Karenia* cell concentration ranges (Low to High), as defined by FWRI and used in this paper are shown in Table 1. The categories "Low A and Low B" were combined in many of the FMRI reports and listed simply as "Low". Thus, in this manuscript Low A, Low B or simply "Low" references will specifically refer how the data are reported in the particular FMRI report being cited. State and Federal regulations require shellfish beds to close when *Karenia* cell concentrations over the beds exceed 5000 cells L^{-1} (Very Low B). Respiratory irritation and fish kills are most common when concentrations are $>10^5$ cells L^{-1} (Medium or High).

Karenia has ~1 μg chl per 10^5 cells. (Tester et al., 2007). During *Karenia* blooms when cell densities exceed 5000 cells L^{-1}, the coefficient of variation (r^2) between chl and *Karenia* is 0.78 (Tester et al., 2007). Satellite imagery has limited abilities to identify blooms as *Karenia* with concentrations less than $\sim 5 \times 10^4$ cells L^{-1} (Tester and Stumpf, 1998; Tester et al., 2007), which correspond to chl levels <0.5 μg L^{-1}. The background concentration of chl along the inner Florida shelf is generally 0.2–0.5 μg L^{-1}.

Table 1
Concentration ranges for *Karenia brevis* cells as defined by the Fish and Wildlife Commission, State of Florida

Range	Concentration (cells L^{-1})
Not present	No cells
Present	<1001
Very Low A	1001–5000
Very Low B	5000–10^4
Low A	10^4–5×10^4
Low B	5×10^4–10^5
Medium	10^5–10^6
High	>10^6

2.7. Winds and sea surface temperature

Hourly winds and SST came from the National Oceanic and Atmospheric Administration (NOAA) Coastal Meteorological Automated Network (CMAN) station, VENF1, at Venice Pier, and the NOAA buoy, 42036 located at 27.07°N, 82.45°W about 80 km NNW off Tampa Bay (NOAA, 2004). The wind vectors were plotted in the direction toward which the wind is blowing, the oceanographic convention. The oceanographic naming convention will also be used when describing winds, i.e. the terms "northward" and "southward" will indicate that winds were blowing toward the north or south, respectively.

Sea surface temperatures were also extracted from the thermal imagery and checked against the instruments on VENF1 and 42036. Satellite SSTs showed agreement to within 1 °C for the periods of interest.

2.8. Modeling framework

A modeling effort was undertaken to estimate how many of the cells in the bottom waters along the shelf potentially might be concentrated onshore over a period of days by upwelling favorable winds. The numerical model implementation, calibration and application are described fully in Lanerolle et al. (2006). Briefly, the numerical ocean model used in this study was the Regional Ocean Modeling System (ROMS) of Rutgers University (ROMS, 2005; Shchepetkin and McWilliams, 2005). It is a finite difference model and employs an orthogonal, curvilinear grid system in the horizontal plane. In the vertical, the model uses a bottom-terrain following sigma-coordinate system (Song and Haidvogel, 1994).

ROMS can be run in a purely two-dimensional setup only by invoking its barotropic mode that essentially performs computations in the horizontal plane. Therefore for the present application, the computational domain consisted of a quasi-two-dimensional (872 km long by 4 km wide) vertical

slice originating perpendicular to the Sarasota, Florida coast. The model had 400 grid points over 872 km in the cross-shelf direction, 80 vertical levels, and an alongshore component of 7 grid points over a distance of 4 km. The bathymetry along the model domain was formed by interpolating observed sounding data from the slice area (NOAA, 2004) onto the model grid nodes.

The coastal boundary condition was a closed space, land condition. The off-shore boundary condition was a radiation/far-field condition (Marchesiello et al., 2001) whose validity was ensured by making the cross-shore domain length sufficiently long. To insure a two-dimensional simulation, boundaries in the alongshore direction, which are normal to the coast, were prescribed using periodic/cyclic conditions. The bottom stress was prescribed using the quadratic law with a drag coefficient of 0.003. The vertical eddy viscosity model employed was the General Length Scale (GLS) k–ω model available within the ROMS model.

The initial conditions were generated by interpolating (on to the ROMS model grid) T–S fields from the output of the NOAA, National Ocean Service, Gulf of Mexico (NGOM) nowcast/forecast model (currently running in real-time at NOS) corresponding to the required initialization dates. A geostrophic balance procedure was performed to obtain the initial velocities.

The surface meteorological forcing for this application employed winds from the VENF1-CMAN station and the 42036 buoy together with air temperature, air pressure, air relative humidity, shortwave radiation, downward longwave radiation from the 0.1° North American Regional Re-analysis (NARR) model predicted fields. These meteorological variables were combined in a bulk flux formulation in ROMS (Berliand and Berliand, 1952; Liu et al., 1979; Fairall et al., 1996a, b) to generate the surface wind stress and heat fluxes. The time step used for the model computations was 150 s. The movements of the *Karenia* cells were modeled using Lagrangian particles with infinitely small mass and dimensions. No swimming behavior was included in the current iteration of the model.

3. Results

3.1. Upwelling

Events were examined with a combination of the presence of mono-specific *Karenia* blooms and closely spaced (in time) satellite imagery. Changes in *Karenia* cell concentrations during blooms are shown for September 2000 and August 2001. In late September 2000, high cell concentrations near the coast followed upwelling favorable winds (Figs. 2 and 3). During the last 2 weeks of September 2000 (until September 25), a Florida ECOHAB cruise (Leg C) observed concentrations of up to 22,000 cells L^{-1} (Low). During the first week of October, Medium to High concentrations were reported offshore of Tampa Bay and Charlotte Harbor, Florida. For several weeks until 26 September, winds were variable (Fig. 3). Southwestward winds, which are favorable for upwelling, started 27 September and lasted for weeks. From 27 to 29 September, offshore movement of surface water was evident (Fig. 2c, d). The chl field with greater than about 0.5 μg L^{-1} moved offshore and there were indications of filament-like structures consistent with upwelling (Fig. 2d, e). The chl concentration increased by 2–4-fold offshore of Tampa Bay and Charlotte Harbor, with some smaller areas showing increases of up to 10-fold. However, the area off Sarasota Bay showed stable or decreasing chl concentrations (Fig. 2e). The *Karenia* bloom occurred only in the two areas of greatest increase in chl concentrations. No *Karenia* was found in Tampa Bay or Charlotte Harbor before or during the event (Fig. 2a, b) indicating the bloom did not originate there. The prevailing temperature during the August 2001 study was ~28 °C. At these temperatures maximal growth rates based on laboratory studies were approximately 0.35 d^{-1} (Fig. 4).

In August 2001, light upwelling favorable winds began 7 August, following several weeks of moderate northwestward (downwelling favorable) winds (Fig. 3). Medium cell counts were recorded at the coast during the week of 12 August south of Sarasota. Cell counts from transects taken offshore from Sarasota and Tampa Bay the same week, showed only "Present to Very Low" concentrations. Consequently, there were no large concentrations of *Karenia* offshore that could have been moved into the area of interest southwest of Ft. Myers by the southeastward current flow. Southeastward winds persisted until 30 August, with slightly stronger winds 14 August, and again 26–28 August. Satellite imagery indicated southward transport of chl from 16 to 20 August (not shown). The bloom on the coast north of Charlotte Harbor is evident in the satellite imagery (Fig. 5a, d, i). High chl is found in a small area for 23 and 25 August (Fig. 5d). The high

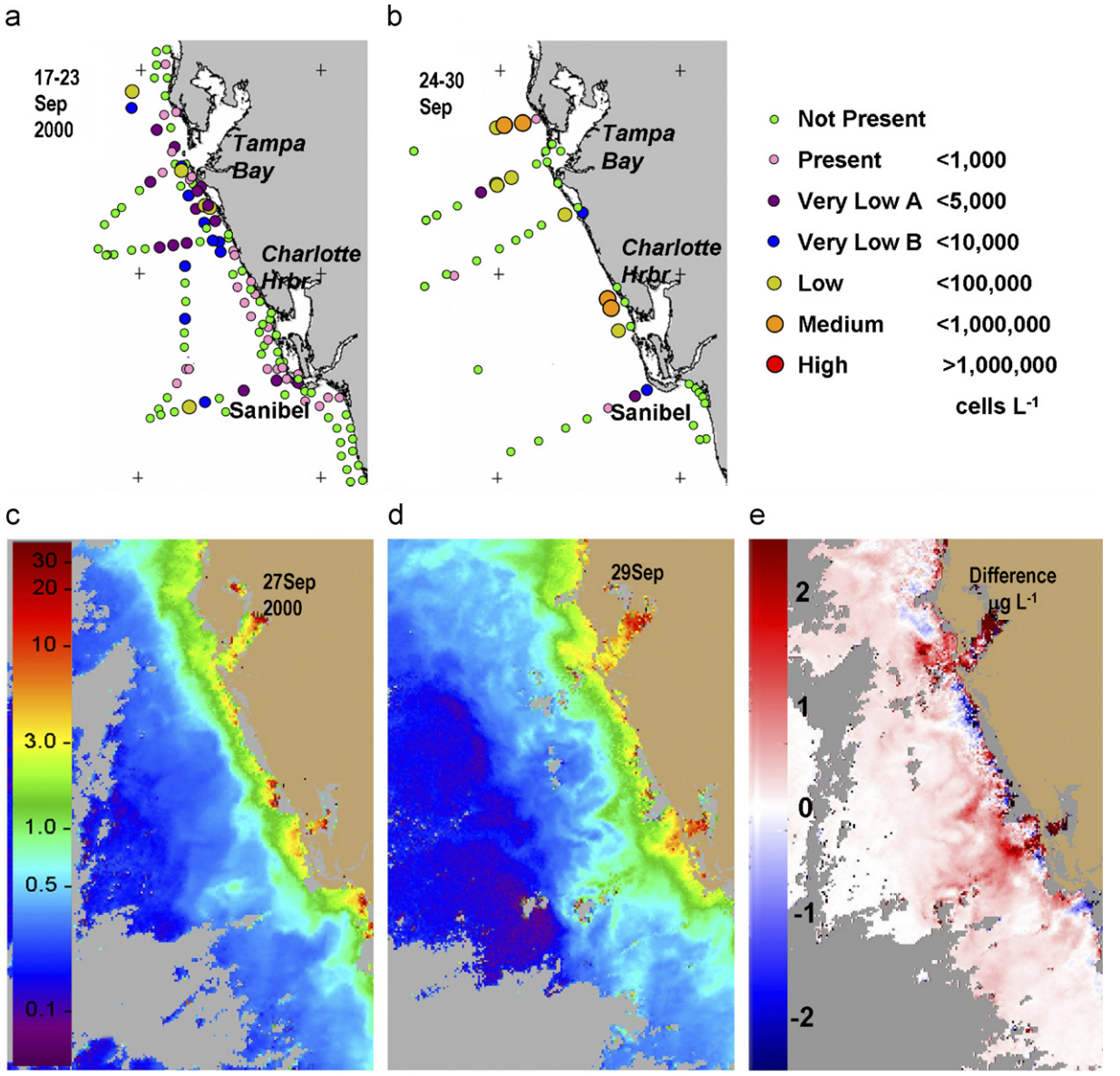

Fig. 2. (a), (b) *Karenia brevis* counts for southwest Florida, 17–23 September and 24–30 September, 2000, respectively (after Fish and Wildlife Research Institute maps, 2007). (c), (d) Satellite chlorophyll imagery in $\mu g\,L^{-1}$ from 27 September and 29 September, 2000, respectively. (e) The linear difference in chlorophyll concentrations in equivalent pixels between 29 September and 27 September. Red indicates an increase in chl (with a maximum change of $2.5\,\mu g\,L^{-1}$), and blue indicates decrease in chl (also a maximum change of $2.5\,\mu g\,L^{-1}$). Gray indicates clouds in the imagery.

chl filament offshore of Ft. Myers (Sanibel) remained fixed (29 August, Fig. 5e). There was no evidence for southward transport of chl between 25 and 29 August. A significant change in chl concentration occurred by 29 August, with large increases in chl by 30 August (Fig. 5f, k). The area with chl concentrations greater than $2.5\,\mu g\,L^{-1}$ chl increased five-fold. If this chl increase was due to *in situ* growth of *Karenia* it would have required a specific growth rate (r) $= 1.7\,d^{-1}$ (Table 2). At the prevailing water temperatures, maximal *Karenia* growth rates are $\sim 0.35\,d^{-1}$ indicating cells accumulated at least three times faster than could be accounted for by growth alone (Fig. 4, Van Dolah et al., 2007).

Between 25 and 30 August, the satellite imagery indicated that features remained in place. Thus, the bloom near Charlotte Harbor area was not

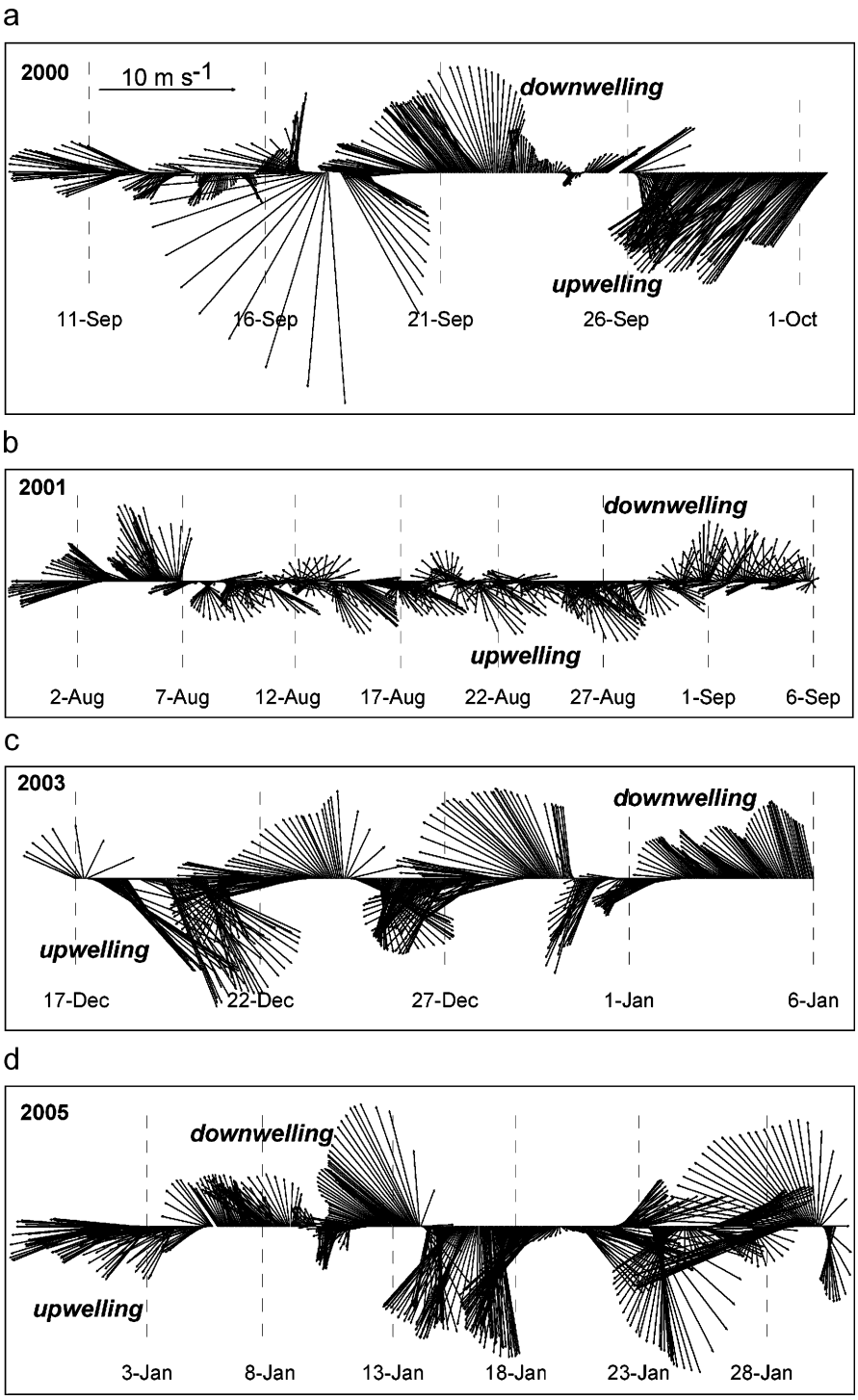

Fig. 3. Winds (oceanographic convention) from stations 42036 and VENF1 (See Fig. 1 for locations). VENF1 was used for the 2001 event. 42036 was used for the 2000, 2003 and 2005 events. For ease of visualization, winds were vector-averaged using a 7-h boxcar filter.

transported to form the bloom offshore of Sanibel (Fig. 5d, e, f, i–k). In contrast, between 30 August and 3 September, the imagery showed that the bloom moved onshore and northward due to a wind reversal (Fig. 3, 5f, g, k, l). These northwestward and downwelling-favorable winds from 1 to 6

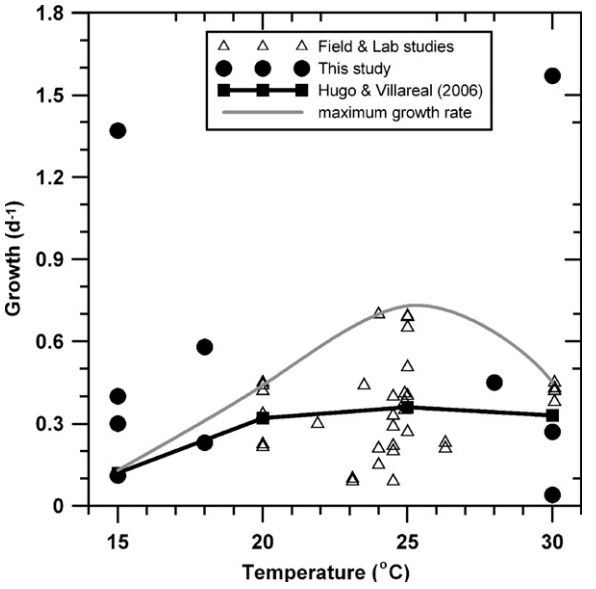

Fig. 4. Light saturated *Karenia brevis* growth rates from laboratory and field studies versus temperature where ambient salinities were between 30 and 36, representative of coastal conditions. The data depicted by connected squares represent maximal growth rates for *Karenia brevis* determined in the laboratory by Magaña and Villareal (2006). Other sources include: Van Dolah and Leighfield, 1999; Loret et al., 2002; Maier Brown et al., 2006; Richardson et al., 2006; Sinclair et al., 2006; Van Dolah et al., 2007. Many of the lower growth rates were from field samples where factors other than temperature or light were likely limiting growth. The upper envelope encompasses the maximal growth values reported at each temperature from the literature. It is not clear whether these relatively high rates are real and represent short-term bursts in growth (Van Dolah et al., 2007) or if they are perhaps due to overestimates similar to those which can occur when determining growth using short-term C_{14} measurements. The bulk of the data indicate that growth rates less than $0.35\,d^{-1}$ are more typical. The open circles indicate the *in situ* growth rates that would be required to account for the chl-specific increases in *Karenia* biomass observed in this study.

September transported the entire feature north. This led to a *Karenia* bloom on the coast from Ft. Myers (Sanibel) to Tampa Bay, as shown by cell counts and satellite imagery (Fig. 5). Along the coast, the area with chl concentrations $>4\,\mu g\,L^{-1}$ increased four-fold. The extensive Medium to High cell concentrations monitored by FWRI are sufficient to account for the observed chl, indicating this was a nearly monospecific *Karenia* bloom.

3.2. Estimated maximal Karenia growth rates from laboratory and field studies

The available data from laboratory and field studies for light-saturated growth rates of *Karenia* versus temperature are shown in Fig. 4. The lower line connecting the data points indicated by squares represent the observed maximal growth rates in the laboratory study done by Magaña and Villareal (2006). This study was specifically designed to determine how varying light and temperature levels affect *Karenia* growth. The upper gray line encompasses the maximum temperature-specific growth rates (d^{-1}) reported in the literature. Some of these estimates represent short-term measures and it is not clear whether they overestimate growth rates or if *Karenia* cells can actually achieve short-term growth rates exceeding $\sim 0.35\,d^{-1}$ observed in the laboratory (Magaña and Villareal, 2006).

All studies indicate a substantial drop in growth rates below 20 °C. The four hydrographic concentration events examined in this study occurred at the extremes of temperature range for *Karenia*: 28 and 30 °C in 2000 and 2001, respectively, and 15 and 18 °C in 2003 and 2005 (Fig. 4). The chl-specific increases calculated from the 2000 and 2001 fall season (>28 °C, filled circles Fig. 4) were generally at or above the maximal growth rates estimated in the laboratory (Fig. 4). During the winter (<18 °C) the chl-specific increases calculated from the satellite images equaled, or in most cases significantly exceeded the maximum temperature-specific growth rates possible given the prevailing temperatures.

3.3. Nutrients

Representative NEGOM cruise data collected between April and November are presented (Fig. 6). The data showed that $NO_3^- + NO_2^-$ (DIN) in surface waters in the northeastern Gulf of Mexico were generally less than 0.5 μM, which agrees well with observations of Vargo et al. (2007). Total dissolved nitrogen (DN, NO_3^-, NO_2^-, NH_4^+ + urea) measurements provided a different picture. DN was lowest in winter and early spring (Fig. 6a). In May, 1999, high DN concentrations appeared to the east of the Mississippi Delta in surface (0–20 m) waters (Fig. 6b), with high subsurface (20–50 m) concentrations further east. Elevated DN, about 0.5–1 μM, was found along the outer WFS in the summer, particularly in the subsurface (Fig. 6c). Other events can introduce nutrient variations as well. For example, an upwelling event in May 1998 produced unusually elevated DN concentrations in the northern Gulf (Nowlin et al., 2000). This high DN persisted into summer of 1998 and resulted in somewhat higher DN than observed in the other

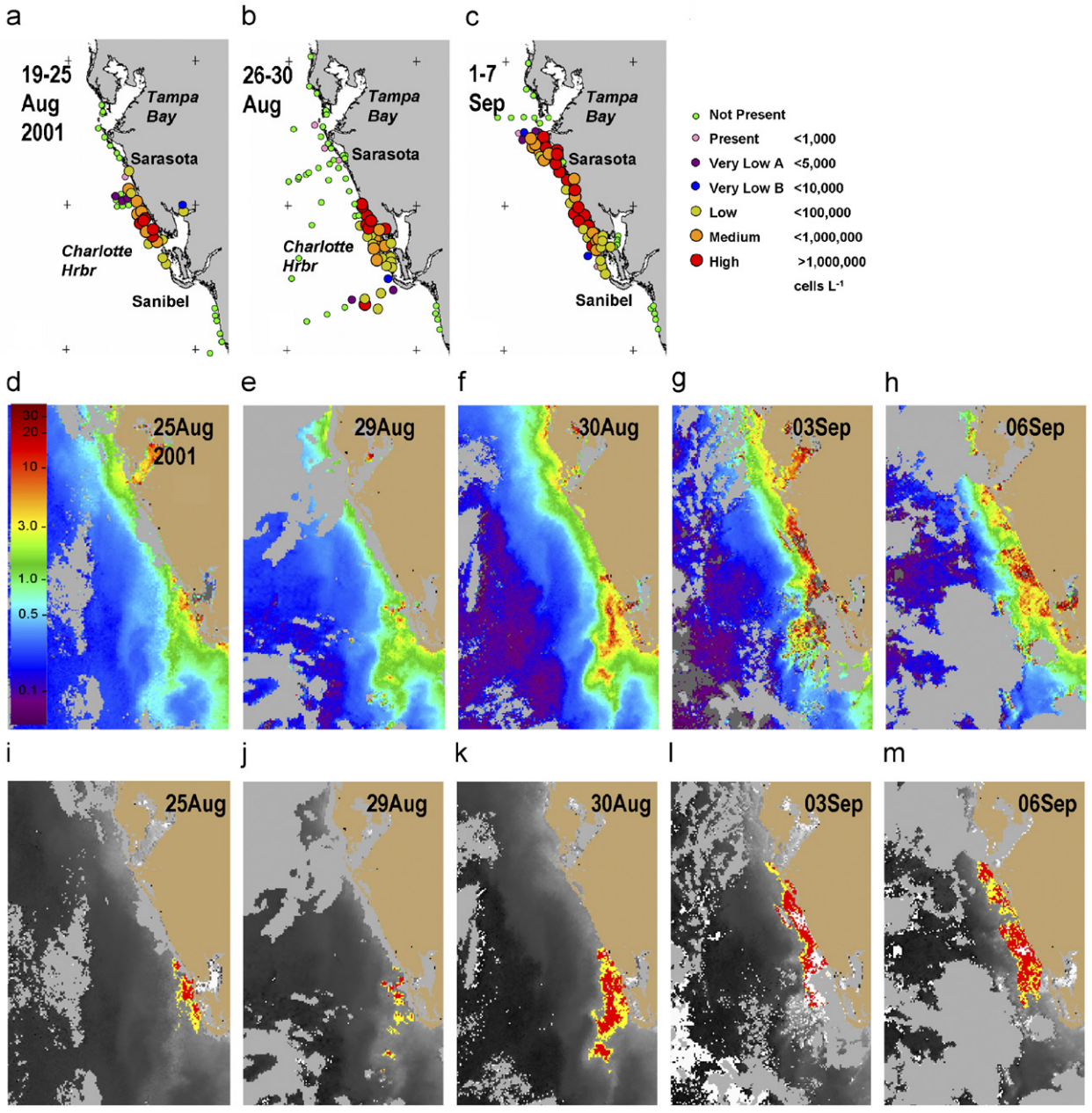

Fig. 5. (a) *Karenia brevis* counts for Clearwater to Sanibel from 19 to 25 August 2001, (b) 26–30 August 2001 and (c) 1–7 September 2001 (after maps from the Fish and Wildlife Research Institute, 2007). Middle row: satellite chlorophyll imagery from (d) 25 August 2001, (e) 29 August 2001, (f) 30 August 2001, (g) 3 September 2001, (h) 25 August 2001. Bottom row: Chl anomalies for (i) 25 August 2001, (j) 29 August 2001, (k) 30 August 2001, (l) 3 September 2001, (m) 25 August 2001. Pixels where chl concentrations exceeding 2.5–4 $\mu g\,L^{-1}$ chl were colored yellow and those $>4\,\mu g\,L^{-1}$ chl are shown in red. For the background image, dark indicates low chl, light indicates higher chl. Gray in all images indicates clouds.

summers (Nowlin et al., 2000). In waters away from the Mississippi River (east of 88°W), the median DN/P ratio was 18:1 for surface (0–20 m) samples, and 16:1 for subsurface (20–50 m) samples, indicating that the system was not phosphate-limited, a result consistent with previous studies (Heil et al., 2001b).

DN concentrations increased with depth throughout the region during the summer (Fig. 7). In areas of deep water, significant increases occurred below

Table 2
Estimated chl-specific changes in *Karenia* bloom densities during the late summer and fall upwelling events

Upwelling conditions		Area of Chl $>2.5\,\mu g\,L^{-1}$ (km^2)	Median Chl conc.	Chl-specific increase (d^{-1})
Coastal 2000	9/27	289	3.16	
	9/29	698	3.25	0.45
Offshore 2001	8/27	276	4.41	
	8/29	1181	5.53	0.86
Coastal 2001	8/29	105	3.63	
	8/30	453	4.06	1.57
	9/3	778	7.05	0.27
	9/6	1341	4.66	0.04

These estimates are based on the interday changes in surface chlorophyll concentrations calculated as described in Section 2.

50 m. A subsurface chl maximum generally occurred between 20 and 50 m along the WFS and was located in the lower portions of the euphotic zone close to the nutricline (e.g. profiles from 29 July to 7 August 2000, Fig. 7).

3.4. Cross-shelf transport of cells

For the upwelling events in September 2000 and August 2001, the cross-shelf transport was examined with the 2-D circulation model (Figs. 8 and 9). The initial conditions of the model allowed particles representative of phytoplankton cells to be released simultaneously at 10 km intervals in the offshore dimension between 30 and 100 km. The movement of the particles under the influence of wind driven currents was then followed for a month. The 20 m isobath was approximately 30 km offshore and the 50 m isobath 100 km offshore. The circulation model caused a few particles to leave the bottom, but most remained there. If *Karenia* started near the bottom, it is reasonable to assume that chemotaxis would cause the cells to prefer to stay near the bottom, so only those particles that remained near the bottom are considered in this simulation.

In 2000, the first transport event occurred on 18–20 September and a subsequent event on 27–30 September (Fig. 8). The winds associated with the first event included the passage of the tropical storm Gordon (17–18 September), followed by winds associated with an atmospheric cold front (19–20 September) (NOAA, 2000; Fig. 3). The southward upwelling-favorable winds produced excursions of the model particles 20–30 km onshore along the bottom. The second event was associated with passage of a front through central Florida on 26 September. In advance of the front, prevailing northward (downwelling) winds persisted from 22 to 25 September. Once this front passed on 26 September, southward winds persisted until 1 October. These winds produced an excursion of about 20 km for particles inshore of 60 km. Frontal passages are common, with progressively stronger fronts through the fall and winter seasons. As noted previously, Low cell counts were reported in the area after the 18–20 September event, and Medium cell counts were reported after 1 October. Cells found near the bottom at 60 km on 16 September would have had a total onshore excursion of 30 km if they remained near the bottom. This indicates that cells over a 30 km swath of shelf could have been brought near the coast.

In September 2001, transport resulted from development of a high-pressure system that set up over the southeastern US during the last 2 weeks of August (NOAA, 2001). This high-pressure system set up a persistent southward wind pattern (Fig. 3b). The result was a steady onshore excursion of model particles along the bottom during this time (Fig. 9). From 12 to 30 August, the model indicates an onshore excursion of about 40 km. The steady (and slow) onshore excursion is consistent with the gradual development of a coastal bloom that is seen from 25 to 30 August 2001 (Fig. 5d–f, i–k).

3.5. Relationship of wind direction and intensity with bloom occurrence

Mean monthly wind vectors were calculated from Tampa, Florida, 1960 to 1998 as reported in Stumpf et al. (1998). The *Karenia* cell count data collected by FWRI from 1954 to 2005 were analyzed month by month. Each bloom event within 10 km of the southwest Florida coast exceeding 100,000 cells L^{-1} was binned by month. Results of this analysis showed that the greatest numbers of blooms were associated with southwestward, upwelling-favorable winds that occurred September to January (Fig. 10). Blooms were less frequent in March through July when the winds were on average weak and unfavorable for upwelling.

3.6. Spatial distribution of blooms

Karenia blooms in the eastern Gulf of Mexico occur most frequently in the Tampa Bay to

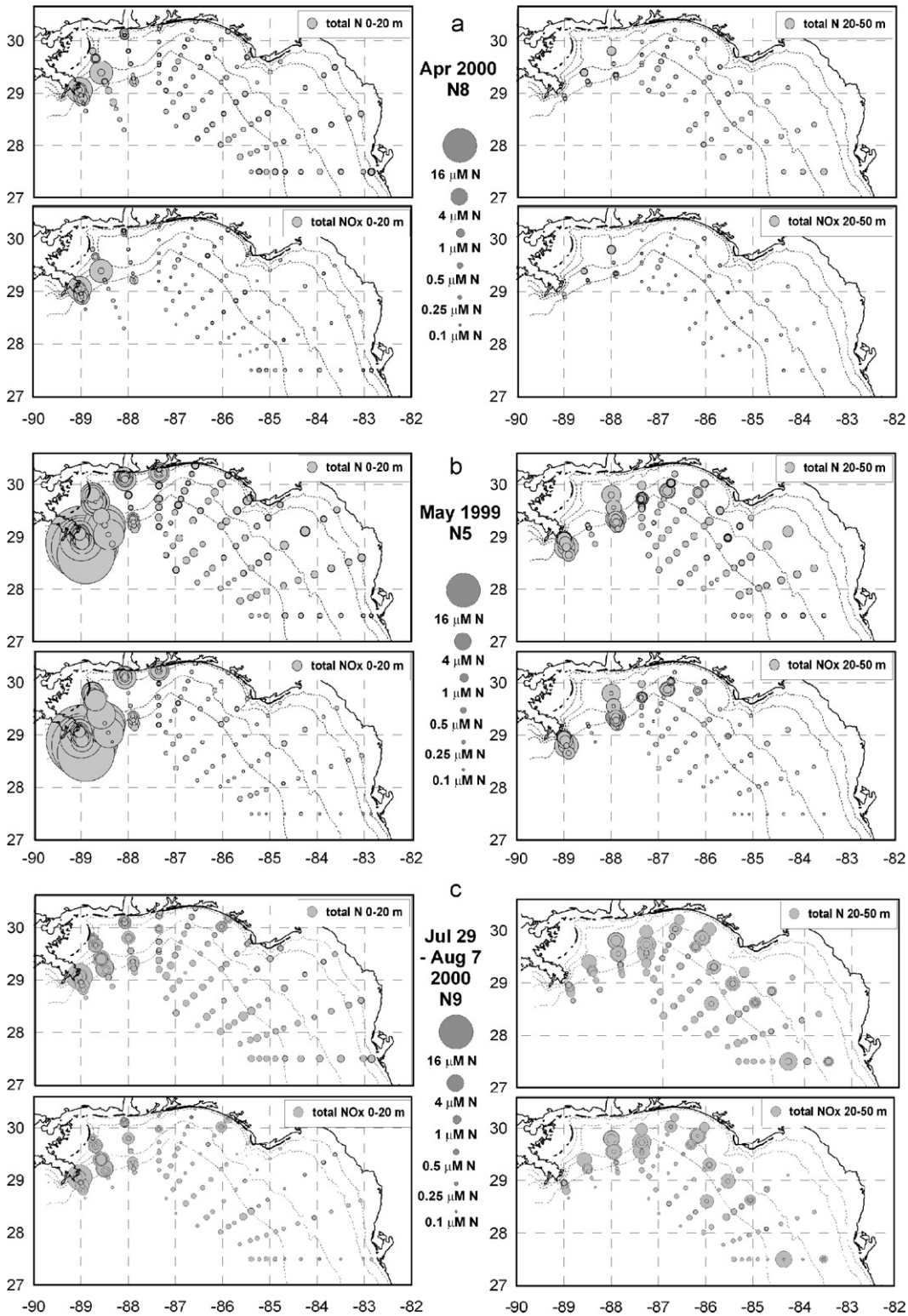

Fig. 6. Dissolved nitrogen from NEGOM cruises. Data were collected at multiple depths. Only the data for 0–20 and 20–50 m were plotted. Multiple data points from each of these layers were plotted as overlapping concentric circles. In each Figure, the top row is total DN (total N determined by summing NO_3^-, NO_2^-, NH_4^+ and urea), the bottom row is the DIN (NO_x). Left column shows data from 0 to 20 m, right column for samples from 20 to 50 m. Bathymetric contours are those shown in Fig. 1 (10, 20, 50, 200 m). (a) The data from April 2000, which represents the low nutrient conditions that prevail from late fall through spring. (b) May 1999, which represents the start of the eastward transport season for the Mississippi plume water. (c) Mid-summer, 2000, peak eastward transport.

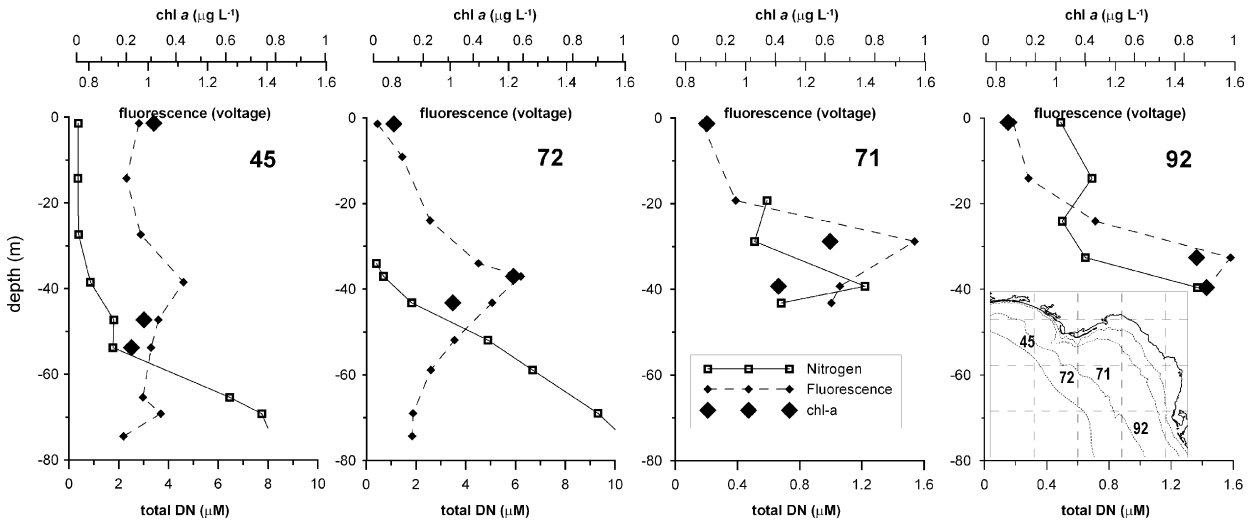

Fig. 7. Depth profiles for chl *a* ($\mu g\,L^{-1}$), relative chlorophyll fluorescence (voltage) and total dissolved nitrogen (NO_3^-, NO_2^-, NH_4^+ + urea) from the N9 NEGOM cruise (29 July–7 August 2000). The relative fluorescence shows the location of the deep chl *a* maximum relative to the nitrocline.

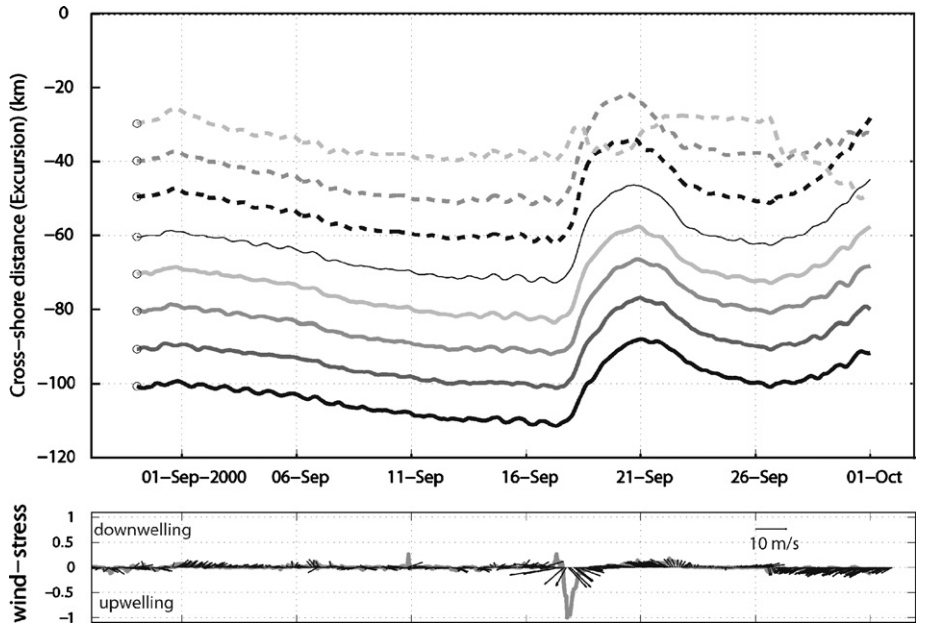

Fig. 8. September 2000 excursion of particles from the 2-D model (top), and winds and along coast wind stress used for the model (bottom). Onshore excursion along the bottom is indicated by the model between September 16 and October 1. Each line traces the movement of a different set of particles through time that were "released" into the model near the bottom at 10 km intervals from shore (starting in water deeper than 20 m). The particles starting at 30 and 40 km offshore drifted upward in the water column, causing the deviation in excursion. For particles remaining near the bottom, 30–40 km of shoreward excursion is indicated between September 16 and October 1.

Charlotte Harbor region (Fig. 11, Fish and Wildlife Research Institute, 2007). Blooms were less frequent in the Big Bend region and occurred with intermediate frequency off Cape San Blas (Figs. 1 and 11). A vast majority of blooms developed within 50 km of shore. Concentrations >5000 cells L^{-1} did not appear in surface waters further offshore, except when blooms that had previously accumulated

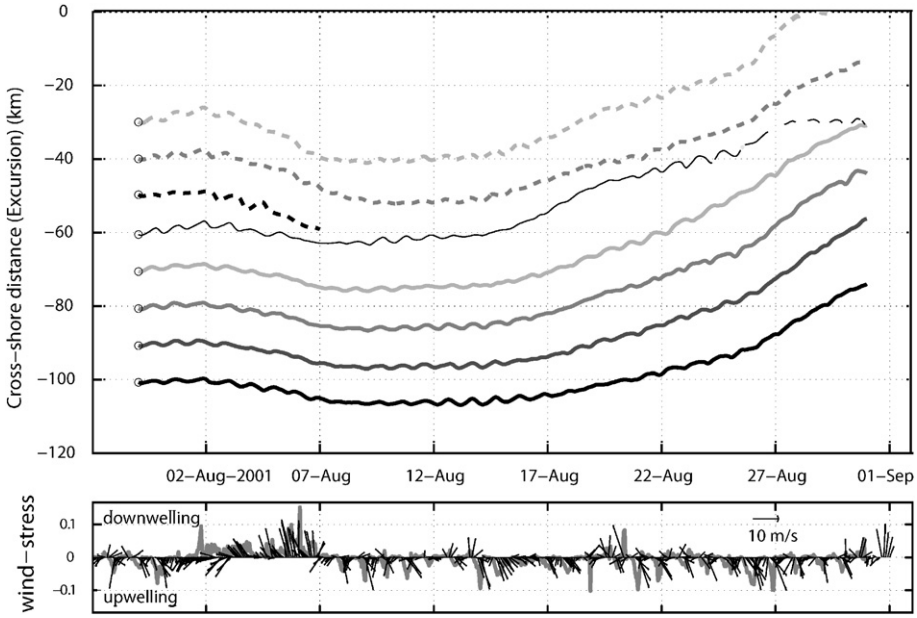

Fig. 9. August 2001 excursion of particles (see Fig. 7 legend for details). The particles released at 30 km that were dispersed more than 10 m above the bottom were excluded. Steady onward transport along the bottom for all other release locations is indicated by the model, with about. Approximately 40 km of onshore excursion occured between August 12 and August 30.

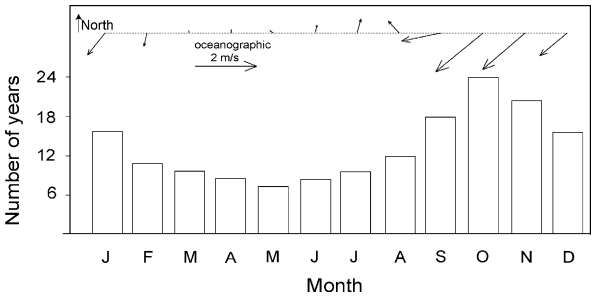

Fig. 10. Relationship between mean monthly wind speed and direction at Tampa (from 1950 to 1998) and the frequency of blooms $>100{,}000\,\text{cells}\,\text{L}^{-1}$ within 10 km of the west coast of Florida (1954 and 2005).

along the coast were transported offshore (e.g. Fig. 7; circled regions labeled 2001 and 2005).

3.7. Accumulation of Karenia along fronts in winter

The effects of frontal intensification on *Karenia* biomass are captured by winter events in 2003 and 2005. In 2003, strong northerlies occurred from 20 to 22 December (Fig. 12c). Southward transport of coastal water was evident from the SST and chl imagery (Fig. 12). This transport of the cool coastal water resulted in a strong thermal front (Fig. 12c). On 22 December the wind shifted to a westward cross-frontal direction and subsequently chl concentrations intensified along a thermal front on 23 December. The patch had chl concentrations above $4\,\mu\text{g}\,\text{L}^{-1}$ which indicated a ten-fold increase in the area of high chl concentrations. This bloom would have required a *Karenia* growth rate of $>1.37\,\text{d}^{-1}$ if the bloom had developed by *in situ* growth alone (Table 3). While cell counts were not collected during this time, Medium cell counts were reported along the coast north of Tampa Bay the following week. The northwestward winds from 2 to 6 January 2004 promoted the transport of these *Karenia* cells onshore causing fish kills and respiratory irritation (FWRI, 2007).

In January 2005, a fontal intensification of *Karenia* cells occurred (Fig. 13). The thermal front itself originated when a plume of cold water moved down the coast in late December 2004. This water mass in addition to being colder, contained high chl, and probably represented a mixed phytoplankton community that included *Karenia* (Fig. 13a). Southwestward winds from 1 to 5 January favored movement of surface water toward the thermal front, which promoted accumulation of *Karenia* cells along the frontal boundary (Fig. 13a–c). On 5 January, the winds switched and blew continuously

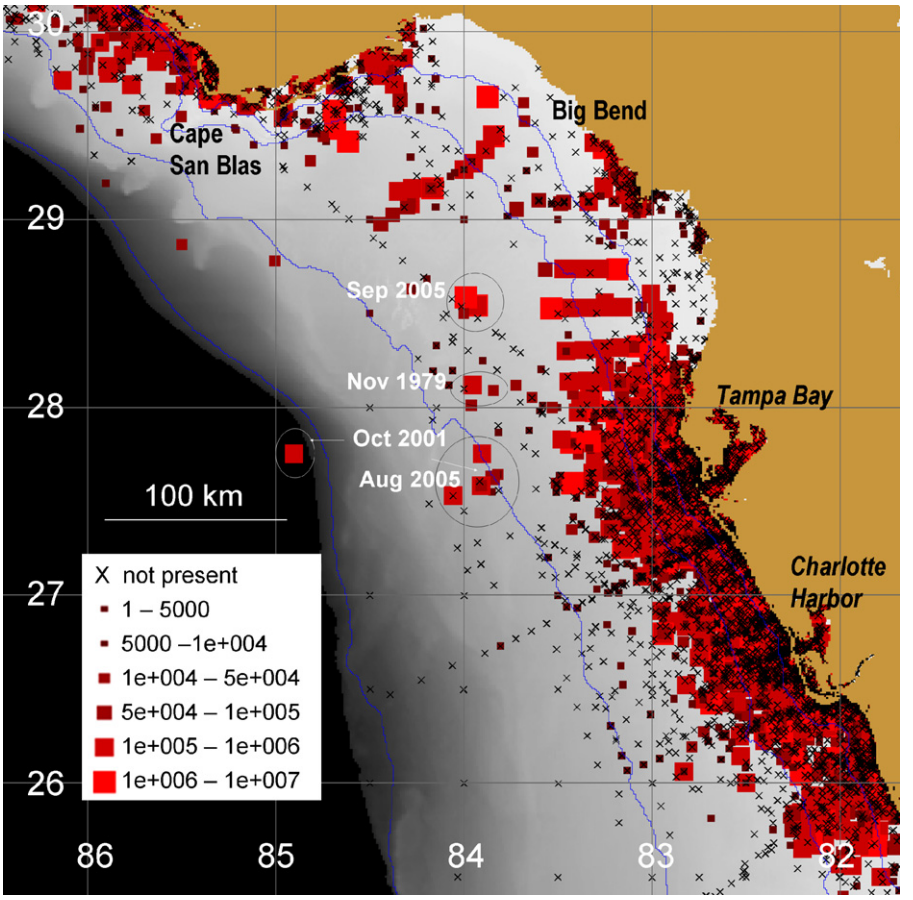

Fig. 11. Cell counts from FWRI database from 1954 until 2005. A vast majority of blooms occur between the shore and the 20 m isobath. Offshore blooms in contrast are rare and result from the transport of previously formed nearshore blooms. This translocation process was observed in detail for the October 2002 and August–September 2005 events circled above.

toward the northwest until 9 January (Fig. 3). These winds parallel to the coast caused downwelling and drove a two-layer, cross-frontal flow (Weisberg et al., 2001). Subsequently, cells entrained in this flow accumulated along the thermal boundary (Fig. 13d–h) (Janowitz and Kamykowski, 2006). The chl intensification observed on 9 January is consistent with conditions set up by northwestward winds, and would account for the extremely high chl ($\geqslant 20\,\mu g\,L^{-1}$) at the frontal region (Figs. 3d and 13h). The intensification between 4 and 6 January near the thermal front would have required a growth rate of $\sim 0.6\,d^{-1}$ in sub-optimal temperatures for a *Karenia* bloom to have developed *in situ* (Table 3; Fig. 4). *Karenia* was found in the coastal plume and Medium to High cell concentrations were found by FWRI in the outer region of the plume on 7 January. This plume subsequently moved south and east, making landfall near Sarasota and initiated a year-long "red tide" event.

Another aspect of the January 2005 study is the dramatic shift in the spatial distribution of chl over the course of days (Fig. 13). These shifts are more consistent with the physical redistribution of cells rather than differential changes in short-term growth and loss rates over relatively large areas (Fig. 13d–h).

4. Discussion

4.1. Climatology of bloom formation

The linkage between the Mississippi River plume water and *Karenia* blooms is likely to be an ancient one (d' Anghiera, 1912). Northward winds produce an eastward flow that delivers nutrients from the Mississippi plume region onto the WFS (DiMarco et al., 2005; Morey et al., 2005) and these nutrients foster the growth of *Karenia* in sub-surface waters. Southward, upwelling favorable, winds (Li and

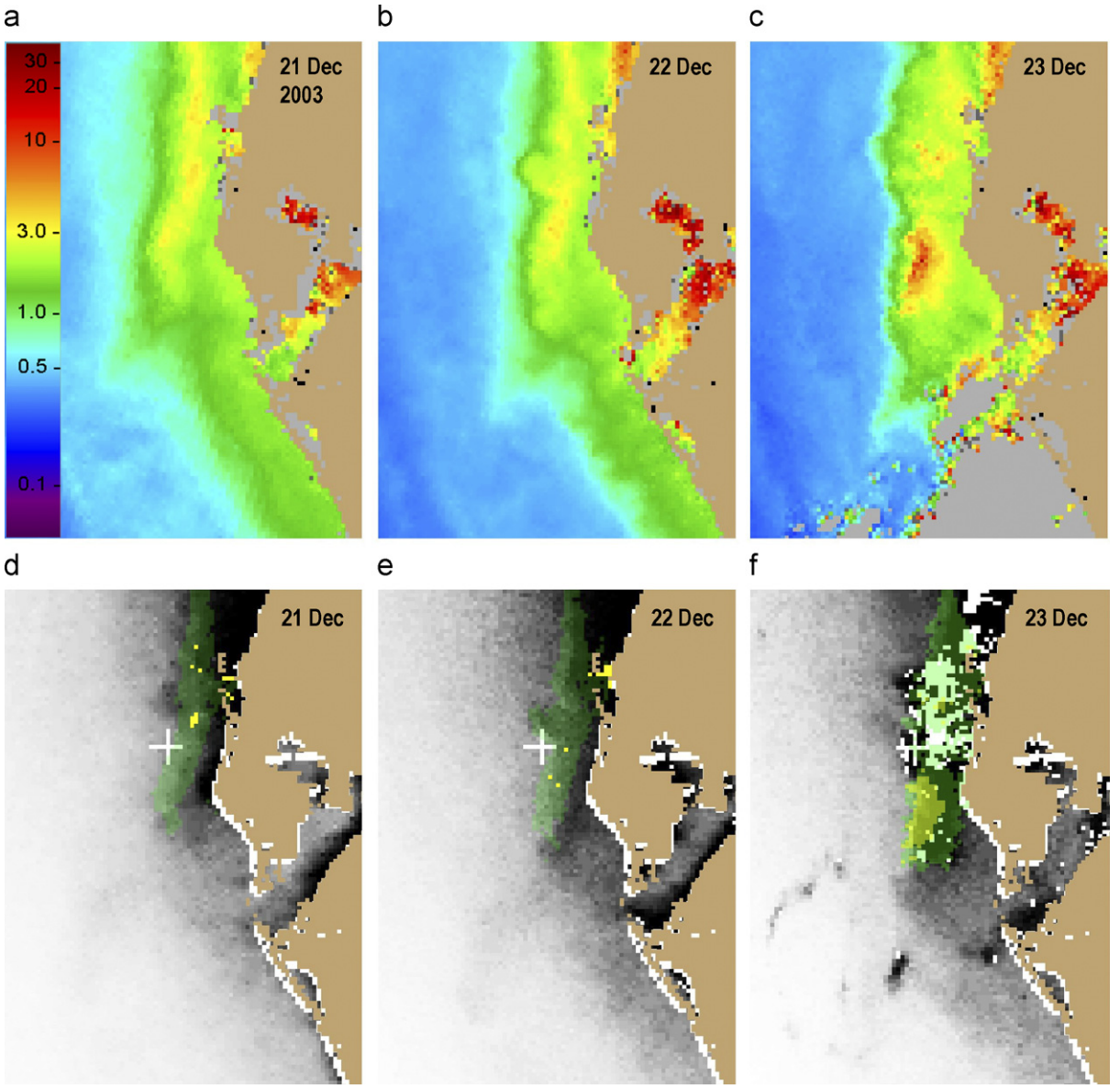

Fig. 12. A. Satellite chlorophyll concentrations for (a) 21 December 2003 (b) 22 December 2003 and (c) 23 December 2003. Bottom panels show relative sea surface temperature for the corresponding period in December 2003. In the SST imagery, dark indicates colder temperatures. Chlorophyll anomalies for (d) 21 December 2003, (e) 22 December 2003 and (f) 23 December 2003 were superimposed on the SST data. Green shading indicates pixels where chl concentrations were $>2.5\,\mu g\,L^{-1}$ and yellow corresponds to pixels with $>4\,\mu g\,L^{-1}$ chl. White pixels in the SST imagery indicate clouds.

Weisberg, 1999; Weisberg et al., 2001) cause a cross-shelf flow that advects and concentrates *Karenia* cells at the coast. This concentration usually occurs at nearshore fronts that may become reinforced at the entrances to major estuaries where density discontinuities are normally present. In instances where these fronts fail to form, the shoreline itself may serve as a functional "frontal" boundary. This interaction between upwelling favorable winds and the concentration of *Karenia* cells at nearshore frontal boundaries helps explain the recurrent annual seasonal pattern in bloom formation (Fig. 10).

4.2. Hydrodynamic accumulation

The satellite data from 2000 and 2001 show the hydrodynamic accumulation of *Karenia* cells in the

Table 3
Estimated chl-specific changes in *Karenia* bloom densities during the hydrodynamic concentration events in 2003 and 2005

Concentration along fronts		Area of Chl > 2.5 μg L^{-1} (km^2)	Median Chl conc.	Chl-specific increase (d^{-1})
Coastal 2003	12/18	247	2.83	
	12/20	448	2.70	0.30
	12/21	1763	2.99	1.37
	12/22	1961	2.91	0.11
	12/23	2928	2.99	0.40
Coastal 2005	01/02	843	6.67	
	01/04	1037	4.66	−0.15
	01/05	386	9.04	−0.33
	01/06	860	7.24	0.58
	01/08	650	4.17	−0.42
	01/09	794	4.29	0.23

These estimates are based on the interday changes in surface chlorophyll concentrations calculated as described in Section 2. Accumulation of cells occurs along the frontal regions that form in winter at the boundary between the cooler inshore water and the warmer offshore water. If only the high chl region shown in Fig. 12c is considered, the estimated chl-specific increase in the *Karenia* bloom from 22 to 23 December 2003 would have been 2.35 d^{-1}.

frontal regions near the coast during upwelling events (Figs. 2, 3 and 5). Chl concentrations primarily due to *Karenia* (Tester et al., 2007) increased by two to three fold over the entire area of the bloom and up to 10 fold in localized areas within 1 d (Table 2, Figs. 2 and 5). The *in situ* growth rates measured in *Karenia* blooms are typically less than 0.3 d^{-1} (Van Dolah and Leighfield, 1999), though in certain instances the growth rates appear to be higher (Fig. 4). Given an ambient growth rate of 0.3 d^{-1}, the accumulation of *Karenia* cells, measured as changes in chl biomass, could exceed *in situ* growth by 1.5–5 fold (Table 2, Fig. 4).

This concentration of *Karenia* cells at these frontal boundaries under upwelling conditions is dependent on both the phototactic and chemotactic behaviors of *Karenia* (Liu et al., 2001a; Janowitz and Kamykowski, 2006). During the day *Karenia* tends to be positively phototactic (Heil, 1986; Schofield et al., 2006). This would lead to the offshore movement of cells in surface waters. But at night, there is a net downward movement of the population that causes the cells to be reentrained in the onshore flow. The closer to shore this occurs, the shallower the water column, and the more efficient the entrainment process. More importantly, as cell move offshore in surface waters they become progressively more nutrient depleted and a chemotactic behavior becomes dominant. The chemotaxis causes cells to migrate downward toward the benthic nutrient supply where they acquire nutrients and become reentrained in the onshore flow (Liu et al., 2001b). This phototrophically and chemotrophically driven swimming behavior, in combination with the dominant two-layer flow, results in the accumulation of *Karenia* cells at the coast. This scenario is consistent with the modeling study by Janowitz and Kamykowski (2006) where two-layer flow was shown to concentrate *Karenia*. It is also consistent with previous observations described in Haddad (1982) and Vargo et al. (2001). The actual physics of how cells are entrained in the frontal region itself still requires further investigation because the hydrodynamics of upwelling frontal zones on shallow continental shelves is less well understood than for deepwater upwelling systems.

Lanerolle et al. (2006) presented both satellite data and modeling results that support the actual transport of a sub-surface chl patch toward the shore at Sarasota in late August 2001. This transport led to the formation of an onshore bloom that developed coincidently with the *Karenia* bloom southwest of Sanibel documented in this study. Both of these blooms were associated with a thermal front that ran from offshore of Sarasota to the southwest of Sanibel. This front was distinguished by warmer water on the southeast side. The co-occurrence of the Sarasota event of Lanerolle et al. (2006) and the Sanibel bloom shown in Fig. 5b indicated that the accumulation of *Karenia* was taking place over a significant section of the WFS.

Once *Karenia* cells are accumulated in nearshore regions, shifts to downwelling favorable winds can bring the accumulated cells in these coastal fronts onshore rapidly. This is most evident in the 30 August to 6 September 2001 imagery (Figs. 3 and 5), where a large coastal bloom was moved onshore and advected northward. The movement of the bloom was reflected in the *Karenia* cell counts as well (Fig. 5b). With a change of the wind direction to downwelling favorable conditions a reversal of flow occurred with shoreward flow at the surface and offshore flow at the bottom. Also, the downwelling currents near the bottom appeared to be significantly weaker than those during upwelling (Weisberg et al., 2001). This would cause cells that come onshore during upwelling to remain onshore.

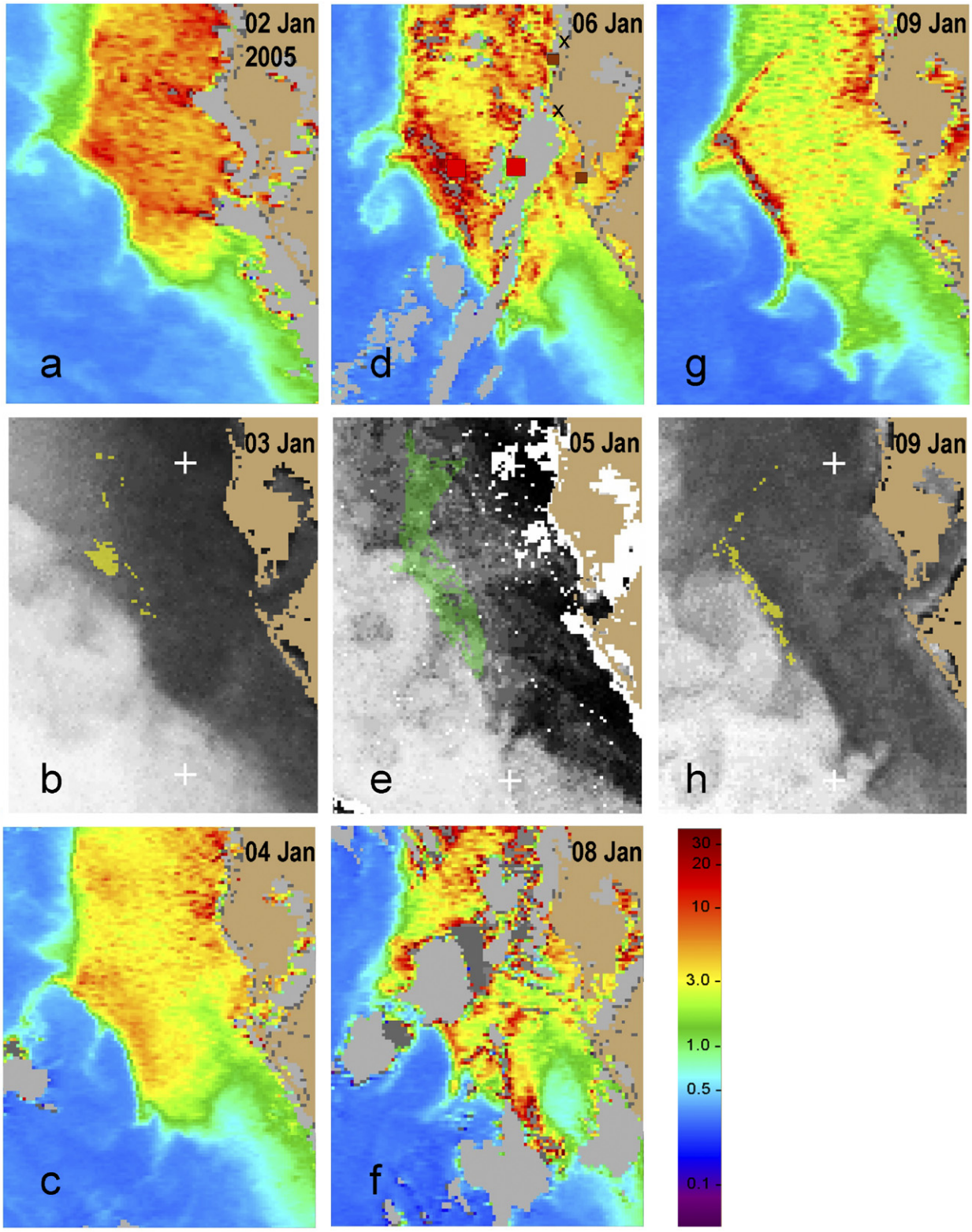

Fig. 13. (a) Satellite chlorophyll concentrations for 2 January 2005. (b) Sea surface temperature (SST) for 3 January 2005 with chlorophyll concentrations $>10\,\mu g\,L^{-1}$ superimposed. (c) Satellite chl imagery for 4 January 2005. (d) Satellite chl imagery for 6 January 2005. (e) SST image for 5 January 2005 with chl concentrations $>4\,\mu g\,L^{-1}$ superimposed. (f) Satellite chlorophyll concentrations for 8 January 2005 and (g) 9 January 2005. (h) SST image for 9 January 2005 with chl concentrations $>10\,\mu g\,L^{-1}$ superimposed. In the SST imagery, dark indicates colder temperatures. White areas near-shore in the 5 January SST image are clouds.

In addition, the high concentrations of cells likely caused light limitation that intensified positive phototactic response at or shoreward of the front. This could result in a net upward movement of the population that enhances retention in the onshore surface flow.

4.3. The nutrient sufficiency conundrum

Nitrogen sources sufficient to support *Karenia* blooms have not been identified previously (Steidinger et al., 1998; Vargo et al., 2002, 2007). The hydrodynamic concentration model supported by the data in this study could help account for the missing nitrogen if the *Karenia* cells arriving at the frontal zones were nutrient sufficient. For this to happen the cells would need access to an offshore source of nutrients prior to onshore transport. Nutrient data from the summer NEGOM cruises (Jochens et al., 2002) indicate that a source of utilizable nitrogen is being supplied subsurface (>20 m) as a result of transport of Mississippi plume water over the WFS (DiMarco et al., 2005; Morey et al., 2005; Figs. 6 and 7). These subsurface waters carry as much or more nitrogen in the form of NH_4^+ and urea as NO_3+NO_2 (Fig. 6). The observed NO_3+NO_2 concentrations reported in the NEGOM data agreed well with those reported for the same region by Vargo et al. (2007). When all available forms of measured nitrogen were combined, the median DN:P ratio was 16:1 (Jochens et al., 2002). This indicated that nutrient conditions were favorable for phytoplankton growth and is consistent with previous reports that suggest this system is not P-limited (Heil et al., 2001b).

Modeling studies have shown that *Karenia* is quite capable of accessing these nutrients via vertical migration to depths of 90 m (Sinclair and Kamykowski, 2006). As noted, when *Karenia* becomes nutrient-limited it migrates toward nutrient sources (Liu et al., 2001a) and is also known to utilize NO_3^-, NO_2^-, NH_4^+ and urea equally well (Bronk et al., 2004). Based on ~10–13 pmol N per cell for nutrient replete cells (Janowitz and Kamykowski, 2006) (Table 4), the prevailing 0.2–1.0 μM of dissolved available nitrogen found below 20 m would support *Karenia* populations of between $\sim 2\times10^4$ and 1×10^5 *Karenia* cells L^{-1} (Fig. 6). Further, these cells are unlikely to be severely light limited because the euphotic zone extends to 40–100 m in offshore waters and *Karenia* has a low light requirement for growth (Fig. 7, Gardner et al., 2006). Laboratory studies have shown that the compensation point for *Karenia* is ~10–30 μmol photons $m^2 s^{-1}$ and that maximal growth requires only about 60–70 μmol photons $m^2 s^{-1}$ (Magaña and Villareal, 2006). *Karenia brevis* actually stops growing when light exceeds 220 μmol photons $m^2 s^{-1}$ (Millie et al., 1995).

Table 4
The CHN analysis of a log phase *Karenia brevis* culture (Wilson Clone)

K. brevis	Mean	SD
Carbon/cell (pmol $cell^{-1}$)	93.64	4.87
Nitrogen/cell (pmol $cell^{-1}$)	9.97	0.66
C:N (mol:mol)	9.41	0.24

The average nitrogen per cell (pmol $cell^{-1}$) measured in this study falls within the range listed in Janowitz and Kamokowski (2006) of 6.3 pmol N $cell^{-1}$ for "nutrient poor and 12.7 pmol N $cell^{-1}$ for nutrient-rich cells.

Dinoflagellates comprise 10–15% of the phytoplankton chl biomass during the summer at chl concentrations of 0.1–0.4 μg L^{-1} on the WFS according to the HPLC data from the NEGOM cruises (Qian et al., 2003). Assuming *Karenia* accounts for 10% of the total chl biomass (a majority of the dinoflagellates), there would be $1–4\times10^3$ *Karenia* cells L^{-1} based on an average chl per cell of 0.009 ng (Tester et al., 2007). As noted above, concentrations of *Karenia* 10^3 cells L^{-1} are not generally observed on the WFS in summer, but this is likely due to sampling bias. The majority of monitoring samples are taken from the low nutrient surface waters whereas the highest concentrations of nutrients occur below 20 m (Fig. 7). Because *Karenia* is chemotrophic (Kamykowski and Yamazaki, 1997), the prevailing nutrient regime would result in a subsurface maximum of *Karenia* cells. Although a majority of these cells are likely to be resident in subsurface waters, a proportion of these cells will be migrating toward the surface in search of light during the day once nutrient requirements are met. This would explain both the presence and low abundance of *Karenia* cells (1–>100 L^{-1}) typically observed by Geesey and Tester (1993) and why the historic FWRI monitoring data base, which is mostly surface cell counts, usually shows cells are Not Present or in Very Low concentrations in samples taken >50 km from the shore (Fig. 11).

The accumulation mechanism proposed in this paper would therefore account for the development

of high density *Karenia* blooms in the absence of sufficient local nutrients to support equivalent *in situ* growth (Heil et al., 2001a; Vargo et al., 2007). Under this scenario, a significant portion of the nutrients initially delivered to a coastal bloom are contained within the cells arriving at a front. The modeling simulations done in this study indicate that a 20–40 km wide parcel of shelf water can be accumulated onshore over a 1–4 d period by upwelling favorable winds (Figs. 3, 8 and 9). Assuming an average 20 m depth, if cells from 20 to 40 km of shelf along 60 km of coastline were concentrated into a typical bloom patch of 5 m depth by 1000 km^2, it would result in at least an order of magnitude increase in ambient cell densities over a few days. It should be emphasized that once entrained and concentrated, the initially nutrient sufficient cells find favorable growth conditions at upwelling fronts (Janowitz and Kamykowski, 2006). Also, once these cells are accumulated, normal grazing and nutrient regeneration processes could help maintain the *Karenia* population for prolonged periods (see Vargo et al., 2007).

4.4. Temporal and spatial variability of blooms

While the model describes the mean conditions that lead to *Karenia* blooms, the actual bloom distributions are highly variable in space and time (Fig. 5). This results from the interaction of *Karenia* swimming behavior and hydrographic variability. The wind patterns and circulation fields change within days and rarely follow the mean conditions for long. In addition to the general southeastward movement of cells toward the coast caused by upwelling favorable winds (see Tester and Steidinger, 1997), there is also an alongshore transport component that can both concentrate and supply cells. The presence of fronts, plumes, and eddies within the generalized flow patterns produce spatial and temporal discontinuities that influence the characteristics and accumulation of *Karenia* cells on a daily basis. These more complex hydrodynamic features likely account for the greatest short-term accumulations of chl in localized regions (Fig. 2). The swimming behavior of *Karenia* can also redistribute some or all of a bloom to a new position in the water column that has different current patterns. This complexity of dispersal and reaggregation has profound implications for the sampling strategies employed in monitoring programs.

4.5. Winter blooms

Unlike fall blooms, which depend only on normal climatological conditions, the winter blooms have additional requirements. During this period, the Mississippi plume is moving westward depriving *Karenia* cells of a readily accessible nutrient supply. In addition, cool 15–18 °C water temperatures limit *Karenia* growth (Fig. 4). Consequently, winter blooms result from reaggregation of cells as evidenced by the data in this study. The process begins when the water in the extremely shallow "Big Bend" region of Florida (Fig. 1) cools more rapidly in the fall and early winter than the area from Tampa Bay south. Strong northerly wind events, such as observed in December 2003 and January 2005 transport the cooler coastal water southward producing a strong thermal front. Because the temperature differential is greater in winter than in the fall, the density fronts are enhanced, making these winter coastal fronts are significantly stronger. During winter more intense atmospheric fronts frequently lead to strong northwestward winds (Figs. 3, 12 and 13). These winds set up cross-shelf surface currents perpendicular to the frontal regions that are accompanied by return flow along the bottom. This two-layer flow perpendicular to the front causes the residual cells in the region to accumulate along the leading edge of that front, as would be predicted by the Janowitz and Kamykowski (2006) model. Based on an average growth rate of 0.1–0.2 d^{-1} at winter temperatures the accumulation of cells measured at frontal zones occurred ~2–5 times faster than could be accounted for by *in situ* growth (Table 3, Fig. 4).

The winter re-development of *Karenia* blooms therefore requires several concurrent conditions in order to form. A bloom must persist through the fall leaving residual cells in the water column, a thermal front is needed, and a significant two-layer flow perpendicular to the front must be initiated by winds blowing in the correct direction. Given the complex nature of this sequence, it would occur less frequently than the more predictable upwelling events during late summer and fall that reliably move cells onshore. Fewer winter re-intensification events are indeed what is observed in the monthly bloom averages shown in Fig. 11.

4.6. Spring diatom blooms not associated with the fall Karenia blooms

Karenia are not the only phytoplankton that blooms along the WFS as a result of annual

patterns of nutrient dynamics and climate forcing. Gilbes et al. (2002) described the development of a spring diatom bloom along the middle WFS. Nutrients were provided in February and March by the peak annual discharge of the north Florida rivers. During late winter and early spring, the mid-shelf had a prevailing southward transport (Liu and Weisberg, 2005) resulting in the development of diatom blooms found up to 200 km south of Cape San Blas (Fig. 1). Gilbes et al. (2002) report that this is a frequent seasonal event. The maximum nutrient load from these rivers, however, is quite small and short in duration, compared to that delivered by the Mississippi River (Gilbes et al., 2002). It is unlikely that these nutrients persist into summer or fall where they could contribute to *Karenia* blooms. Furthermore, the persistent southward current in the spring (Liu and Weisberg, 2005), that initially delivered the nutrients responsible for the diatom bloom, would subsequently disperse the nutrients off the WFS to the south when the river inputs diminish.

4.7. Why are blooms less frequent in Texas and north Florida?

The results of this study also have implications for why *Karenia* blooms are less frequent in northwest Florida and off Texas (Tester et al., 2004). The reason is in large measure due to the orientation of their shorelines in relation to the prevailing winds. Southward winds favor upwelling along a coast with southeast–northwest orientation such as the central coast of Florida. In the northwest region of Florida, known as the Big Bend (Fig. 1), the predominant east–west orientation of the coast and the wide shallow shelf (<20 m) are unfavorable to upwelling. As a result, *Karenia* blooms are infrequent in this region and when they do occur they are less likely to reach the coast (Fig. 11). In contrast, blooms do occur just northwest of Cape San Blas, where the coast has a northwest-southeast orientation more like that of southwest Florida (Figs. 1 and 11).

The situation in Texas more closely resembles that of the Big Bend region of Florida in that the coast is oriented in the wrong direction to foster upwelling. Hypothetically, *Karenia* should be abundant off Texas because it is directly downstream from the Mississippi River plume, as the prevailing subsurface transport in the western Gulf is westward for all but the summer months (Morey et al., 2005). This should supply ample nutrients during periods when water temperatures are still favorable for growth. However, with frequent southward and westward winds, Texas rarely experiences upwelling favorable conditions. The result is that if *Karenia* populations do develop in the nutrient rich subsurface waters, they are seldom transported onshore. This raises the question as to the source of the *Karenia* blooms in Texas (Magaña et al., 2003). Tester et al. (2004) noted a correlation in timing between *Karenia* events in Mexico and Texas and suggested that many of the Texas blooms start in Mexico, rather than offshore of Texas. The southwestern side of the Bay of Campeche should have upwelling favorable conditions during northward and northwestward winds, so that *Karenia* blooms are likely to develop there via the same mechanisms that prevail off Florida (Tester and Steidinger, 1997). For these blooms to reach Texas, a complex set of conditions must occur in sequence: bloom initiation, then development, then establishment of northward currents, and finally onshore transport to the Texas coast. This complex set of preconditions may account for the low frequency of the blooms observed off Texas.

4.8. Cyanobacterial and terrestrial nutrient supply

Walsh and Steidinger (2001) proposed blooms of the nitrogen-fixing cyanobacteria, *Trichodesmium* as a key source of nitrogen for *Karenia* blooms. The *Trichodesmium* blooms are thought to be iron limited and fluxes of African dust were proposed as the source of iron needed to support the growth of *Trichodesmium*. While *Trichodesmium* blooms may account for some of the needed nitrogen to support *Karenia* growth, the dust hypothesis is limited by the poor correlation between the dust record at Miami (Prospero, 1999) and the occurrence of *Karenia* blooms. Of Prospero's (1999) 20-year record, not all of which was included in the Walsh and Steidinger (2001) paper, the association of dust events and *Karenia* blooms was not consistent. Major dust years (monthly mean events $>25\,\mu g\,m^{-3}$), which all occur in mid-summer, co-occurred with subsequent major *Karenia* blooms in 1983, 1986, and 1992. Major dust events of 1984, 1987, and 1993 were associated with negligible blooms, and 1985 had a bloom of short duration. Minor dust years (monthly mean events $<20\,\mu g\,m^{-3}$) co-occurred with negligible blooms in 1975, 1989 and 1990. However, major blooms

occurred in the minor dust years of 1976, 1979, 1980, 1981, 1994, and 1995. These inconsistencies indicate that it is unlikely that a significant, direct short-term linkage exists between iron-induced cyanobacterial nitrogen production and *Karenia* blooms. This lack of a dust linkage, however, does not discount the potential of *Trichodesmium* blooms as an additional source of nitrogen for the maintenance of *Karenia* blooms.

Another hypothesis that has been extensively studied is that local land-based nutrient sources are required to explain the occurrence of *Karenia* blooms on the WFS. However, all evidence to date points to offshore bloom initiation, (e.g. Tester and Steidinger, 1997). Current studies have failed to identify land-based nutrient sources, or benthic regeneration sufficient to account for the large biomass *Karenia* blooms on the WFS (Vargo et al., 2007). If land-based nutrients were responsible for blooms, evidence should exist for bloom initiation occurring within estuaries and this is has not been observed. The role of land-based nutrients in maintaining established *Karenia* blooms remains to be determined.

5. Conclusions

This paper identifies an annual sequence of events to explain high concentrations of *Karenia* cells along the WFS. Blooms are initiated by the transport of nutrients from the northern Gulf of Mexico onto the WFS in the summer by circulation driven by normal summer northward winds. The Mississippi River is a major source of nutrients, particularly to the subsurface waters. Normal northward winds during the summer produce eastward transport of these nutrients along the coast to the WFS, and fall winds produce sub-surface shoreward transport of nutrients and *Karenia* cells. A key part of the model described in this paper is that *Karenia* can use both DIN and DON and uses chemotaxis to tap nutrients down to depths of ~90 m. The available nitrogen concentrations are sufficient to increase *Karenia* from background levels to Low concentrations throughout the summer. Prevailing southward wind events in the fall produce upwelling that promotes both transport and concentration of vertically migrating *Karenia* near the shore. The cells in a band out to 20–40 km offshore can be concentrated onshore within a period of 1–4 d. Spatial variations in upwelling frequency and intensity can account for the observed differences in the bloom frequency along the Gulf coast. The conditions required to produce the *Karenia* blooms are therefore part of the normal seasonal cycle in river inputs, wind patterns and water circulation in the Gulf of Mexico.

5.1. Hypotheses

The hydrodynamic concentration theory presented in this work suggests a number of testable hypotheses. Sampling of subsurface waters should find "Very Low" or "Low" concentrations of *Karenia* offshore just prior to upwelling and bloom occurrence. Chemical analysis of these cells should show that they are nutrient sufficient. The interaction between the inputs of nutrients from the Mississippi River plume, prevailing circulation and transport patterns, and the strength of the upwelling winds should correlate with the severity and occurrence of the *Karenia* blooms off the west coast of Florida. The interaction of offshore bathymetry and the orientation of the shoreline relative to the prevailing currents and wind fields should have a major effect on where and when blooms initiate. Many of the *Karenia* blooms making landfall in Texas originate in Mexican waters. And finally, we would expect that routine, automated monitoring (Kirkpatrick et al., 2000) of frontal regions on the inner WFS would detect accumulations of *Karenia* cells that could be tracked using a combination of *in situ*, meteorological and remotely sensed information.

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