



New evidence for the West Florida Shelf Plume

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Abstract

The occurrence of an episodic chlorophyll plume detected on the West Florida Shelf between 1979 and 1986 was confirmed in March 1995 with shipboard data and in March 1998 with new ocean color data from the SeaWiFS sensor. New evidence is presented to support the hypothesis that diatom blooms off Apalachicola Bay are the precursor of the seasonal West Florida Shelf plume, and that the nutrient requirements for such blooms, especially silicate, can be supported by river discharge. The observations indicate that the impact of rivers is maximal over the middle shelf and decreases over the outer shelf. Salinity and discharge measurements support the concept that the Apalachicola River had a major impact at distances exceeding 100 km from the coast and that it plays an important role in the formation of offshore blooms. Preliminary analyses suggest that successional processes lead to cryptophytes dominating in the offshore blooms.

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1. Introduction

The episodic formation of a high concentration chlorophyll plume on the West Florida Shelf was described for the first time by Gilbes et al. (1996). They used ocean color satellite images collected between January 1979 and June 1986 to establish that this plume occurs mainly during spring, that it persists for 1–6 weeks, and that it extends over 250 km southward along the shelf. The information available at that time (Weisberg et al., 1996) suggested that the plume could be related to a

seasonal southward flow at mid-shelf set up by seasonal steric height differences between the shelf and Gulf of Mexico common waters. Since then, He and Weisberg (2002) confirm that such seasonal currents can be driven by local wind and buoyancy forcing, and Weisberg et al. (2001) show how these spring season features respond to synoptic scale wind forcing.

Although the development of spring phytoplankton blooms in subtropical and temperate regions is well documented (Ridout and Morris, 1988; Hulburt, 1990; Weeks et al., 1993; Napier, 1995), in the West Florida Shelf only the summer-fall blooms of toxic dinoflagellates have received major attention because of their dramatic consequences on the economy and marine ecology of

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the region (Haddad and Carder, 1979; Carder and Steward, 1985; Vargo et al., 1987; Millie et al., 1995; Tester and Steidinger, 1997).

The blooms described by Gilbes et al. (1996) were confirmed by in situ observations made in March 1992. However, the information available at that time was insufficient to explain the origin and dynamics of the plume with certainty. In March 1995, we carried out an oceanographic cruise in the Eastern Gulf of Mexico with the purpose of getting more evidence to test our hypotheses of plume formation. Several stations were occupied from Tampa Bay to the Mobile River and the spatial variability of parameters associated to phytoplankton dynamics was determined. Here, we describe these data, and in addition, show recent images collected with the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite sensor to show the occurrence of the West Florida Shelf plume during March 1998.

2. Methods

A research cruise to the Eastern Gulf of Mexico was carried out by oceanographers of the University of South Florida, University of Maryland, University of Puerto Rico, and the Instituto de Oceanología (Cuba) from 19 to 24 March 1995. Five transects with 14 stations were occupied between Tampa Bay and the Mobile River to determine cross- and along-shelf variability (Fig. 1). Hereafter, TB1, SR1, AR1, DC1, and MR1 are referred to as nearshore stations; TB2, SR2, AR2, and MR2 as middle shelf stations; and TB3, SR3, AR3, AR4, and DC2 as offshore stations. Station DC2 was located on the De Soto Canyon. At each station, water samples were collected with 5 l, teflon-coated Go-Flo bottles at two depths: 1 m (surface) and at the deep in vivo fluorescence maximum (DFM). Profiles of temperature and salinity were obtained using a SEACAT Profiler Model SBE 19-01 (SeaBird Electronics). Chlorophyll fluorescence in surface waters was measured continuously along the ship's track using a flow-through system. These values were converted to Chlorophyll-*a* (Chl-*a*) in $\mu\text{g l}^{-1}$

using discrete samples of extracted Chl-*a* and a linear regression equation ($r^2 = 0.99$).

The Chl-*a* concentration of discrete samples, corrected for Phaeophytin-*a* (Phaeo-*a*), was obtained using the fluorometric method described by Yentsch and Menzel (1963), and measured using a Turner Model 10-AU fluorometer. The concentration of phytoplankton pigments was also determined by high-performance liquid chromatography (HPLC) using the methods described by Van Heukelem et al. (1992) and Van Heukelem et al. (1994). The chromatographic system included a fully automated Hewlett Packard Series II, 1090M integrated HPLC equipped with binary DR5 solvent delivery pump and a built-in diode array detector with 8 μl flow cell. This detector was programmed to collect absorbance spectra of accessory pigments from 350 to 600 nm and to monitor 452 nm for plotting the chromatograms. A Hewlett Packard 1046A time-programmable fluorescence detector was installed after the diode array detector and it was programmed with 416 nm excitation and 670 nm emission to measure the concentration of Chl-*a* (referred here as HPLC Chl-*a*).

Primary productivity measurements were obtained by radioactive ^{14}C -uptake experiments on board the ship following the procedure described by Harding et al. (1986). Concentrations of dissolved organic carbon (DOC) were obtained using high-temperature catalysis in a Shimadzu TOC-5000 instrument.

Dissolved inorganic nutrients were measured by standard automated methods using both Lachat and Technicon auto-analyzers. To obtain the total dissolved nitrogen and total dissolved phosphorus, samples were predigested with persulfate and filtered using a GF/F filter (Valderrama, 1981). Total particulate nitrogen was obtained by high-temperature combustion of the particulates captured on the GF/F filters and using an elemental analyzer Model 440 (Leeman Labs). Total particulate phosphorus was obtained by ignition/acid solubilization using an adapted method of Anderson (1976).

Profiles of upwelling radiance, $L_u(Z, \lambda)$, and downwelling irradiance, $E_d(Z, \lambda)$, were obtained using a submersible profiling spectroradiometer

Model MER 2040 from Biospherical Instrument. Downwelling irradiance above the surface water, $E_s(\lambda)$, was measured with a deck profiling spectroradiometer Model MER 2041 from Biospherical Instrument. The diffuse attenuation coefficient of the photosynthetic available radiation, K_{par} , was calculated as per Smith and Baker (1984).

The cross-shelf and along-shelf differences in phytoplankton pigments, primary production, nutrients, organic carbon, suspended sediments, and K_{par} were examined using statistical analyses. Logarithmic transformations, $\log_{10}(x + 1)$, were carried out to apply parametric procedures (Zar, 1996). Some parameters were compared using regression and correlation tests (Zar, 1996).

Data collected by SeaWiFS during March 1998 were used to derive Chl-*a* using a modified cubic polynomial algorithm (OC2) presented in O'Reilly et al. (1998)

$$\text{Chl-}a = 10^{(0.2974 - 2.2429R + 0.8358R^2 - 0.0077R^3)} - 0.0929$$

where $R = \log_{10}(R_{rs}(490)/R_{rs}(555))$, and R_{rs} is the remote sensing reflectance from the sensor.

3. Results

3.1. Phytoplankton pigments

The surface distribution of Chl-*a* calculated from continuous in vivo fluorescence measurements ($r^2 = 0.99$) and registered along the cruise track is shown in Fig. 1. Very high Chl-*a* concentrations in surface waters were detected at three different locations. On 21 March, values up to $29 \mu\text{g l}^{-1}$ Chl-*a* were recorded south of Apalachicola Bay close to stations AR3 and AR4, defining a phytoplankton bloom. Later, on 23 March up to $20 \mu\text{g l}^{-1}$ Chl-*a* were registered south of the Mobile River, and on 24 March between 7 and $10 \mu\text{g l}^{-1}$ Chl-*a* were detected northwest of Tampa Bay. This last location was sampled for the first time on 19 March and these high Chl-*a* concentrations were not detected at that time. These observations suggest that such high Chl-*a* could be related to the phytoplankton bloom detected farther north 3 days earlier.

Chl-*a* concentrations at two different depths are presented in Fig. 2A. One-way analysis of variance (ANOVA) showed that there are no significant differences between the surface and DFM values ($P > 0.05$; $n = 28$). The nearshore-offshore differences are not significant either ($P > 0.05$; $n = 28$), in spite of offshore stations showing the lowest mean value ($0.78 \mu\text{g l}^{-1}$; $\text{SD} = 0.72$). Differences between transects, however, are highly significant ($P < 0.005$; $n = 28$). The Mobile River transect presented the highest mean value ($2.62 \mu\text{g l}^{-1}$; $\text{SD} = 1.56$) whereas the Tampa Bay and Suwannee River transects presented the lowest mean value ($0.4 \mu\text{g l}^{-1}$; $\text{SD} = 0.2$). The highest variability was shown by the Apalachicola River transect (Fig. 2A). The spatial trends of Phaeo-*a* concentration were very similar to those of Chl-*a* (Fig. 2B).

The concentrations of phytoplankton pigments measured by HPLC are shown in Fig. 3. Some pigments were difficult to quantify due to low concentrations and the low volume of seawater that was filtered for this analysis ($< 2.0 \text{ l}$). The limit of quantification ranged from 0.05 to $0.2 \mu\text{g l}^{-1}$ pigment, and the instrument detection limit (Signal/Noise = 5:1) ranged from 0.025 to $0.1 \mu\text{g l}^{-1}$ pigment (Laurie Van Heukelem, personal communication).

HPLC Chl-*a* concentrations showed similar patterns to those obtained by the standard fluorometric method. A comparison between the fluorometric and HPLC Chl-*a* measurements provided a correlation coefficient of 0.92 at the surface (Fig. 4). At DFM, the correlation coefficient was reduced to 0.68 mainly due to the overestimation of fluorometric Chl-*a* in station AR2 (Fig. 4). Such overestimation was produced by the occurrence of high Chl-*c* (Fig. 3B). The same analysis without AR2 gave a correlation coefficient of 0.79 ($r^2 = 0.62$; $n = 13$). Most stations registered higher fluorometric values, except for AR1 at the surface and DC1 at the DFM. The HPLC Phaeo-*a* concentrations were undetectable at all stations.

At the surface, nearshore stations showed more variety of pigments than the middle and offshore stations (Fig. 3A). Monovinyl Chl-*a* was the most abundant photosynthetic pigment, ranging from

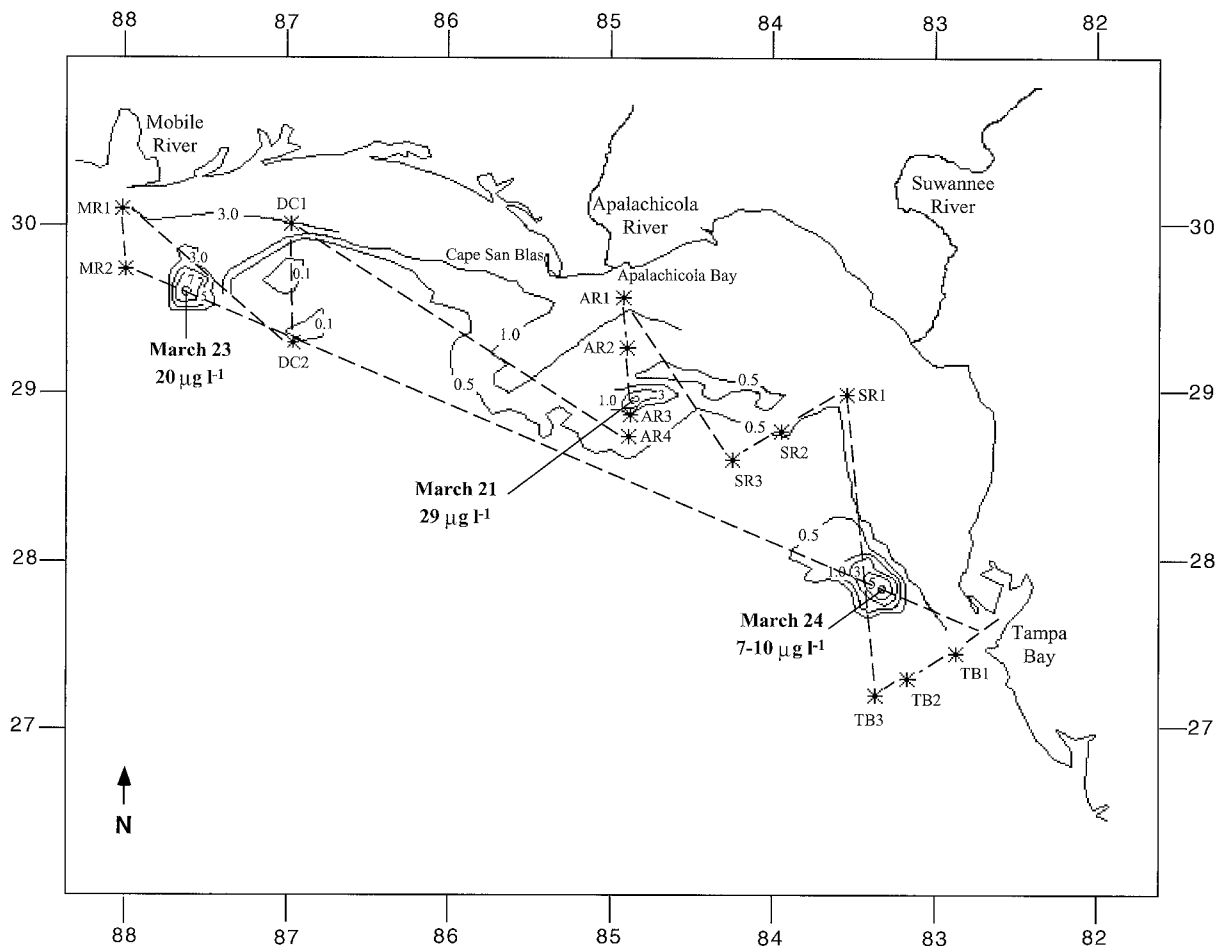


Fig. 1. Chlorophyll-*a* concentrations ($\mu\text{g l}^{-1}$) mapped with along-track fluorometry ($r^2 = 0.99$). Sampling stations are shown with stars and the station number. TB stations were sampled on 19 March, SR stations on 20 March, AR stations on 21 March, DC stations on 22 March, and MR stations on 23 March 1995. Dashed lines indicate the cruise track.

0.04 to $3.6 \mu\text{g l}^{-1}$. Divinyl Chl-*a*, Chl-*b*, and Chl-*c* were detected mainly in the nearshore stations with maximum concentrations of 0.24, 0.34, and $0.70 \mu\text{g l}^{-1}$, respectively. Fucoxanthin was also found mostly in nearshore stations with values up to $1.5 \mu\text{g l}^{-1}$. Among transects, those off the Apalachicola and Mobile rivers registered the highest pigment concentrations.

At the DFM, monovinyl Chl-*a* was the most abundant pigment (0.21 – $1.2 \mu\text{g l}^{-1}$; Fig. 3B). At this depth, more accessory pigments were detected at all stations. Chl-*b* and Chl-*c* reached their highest values in middle and offshore stations.

Fucoxanthin showed its maximum concentrations at stations AR1, AR2, MR1, and MR2 (Fig. 3B). The highest pigment concentrations at the DFM were registered in the Apalachicola River transect.

The relationship between HPLC Chl-*a* and the sum of seven accessory pigments is presented in Fig. 5. The linear regression was highly significant ($P < 0.001$; $n = 28$), showing that Chl-*a* can be used to estimate the overall phytoplankton biomass. This relationship was weak for stations AR2 at DFM and AR3 at the surface (Fig. 5) because of the presence of high concentrations of Chl-*c* and fucoxanthin (Fig. 3B), and Chl-*a* (Fig. 3A),

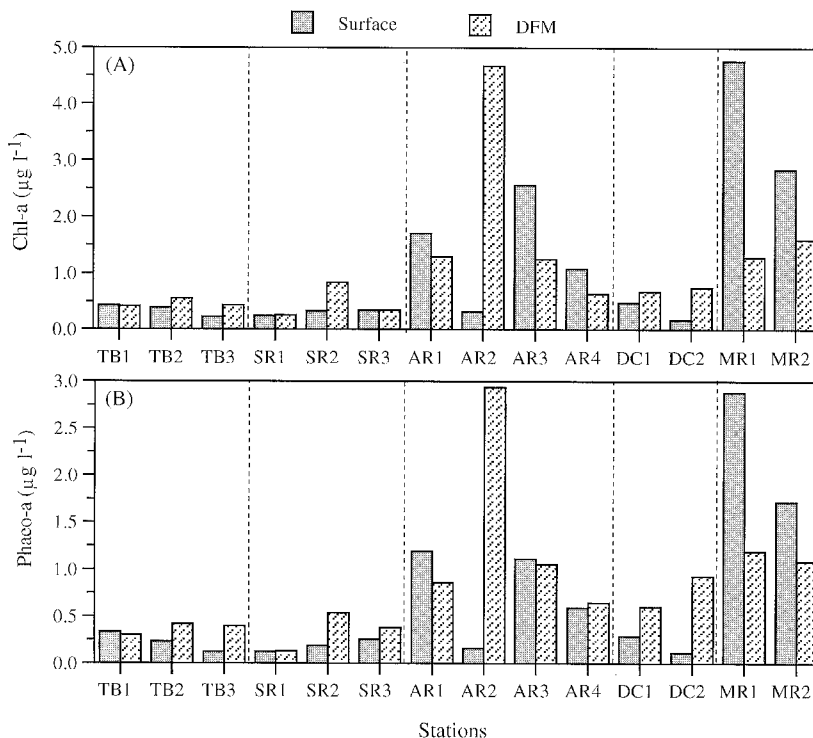


Fig. 2. Concentrations of Chlorophyll-*a* (A) and Phaeopigments (B) at the surface and at the deep fluorescence maximum (DFM). Note different scales on ordinate axes.

respectively. A high concentration of Chl-*a* was also registered in station MR1 at the surface, but the relationship between Chl-*a* and accessory pigments was maintained because of the high concentrations of Chl-*c* and fucoxanthin present at that station (Fig. 3A).

3.2. Primary production

Primary production ranged from 0.25 to 14.8 $\text{g C m}^{-2} \text{d}^{-1}$ along the shelf (Fig. 6A). Most productivity from 4 to 24 h incubations matched very well. However, larger differences were found at stations DC2 and MR2 (Fig. 6A). The differences between nearshore and offshore stations were not significant ($P > 0.05$; $n = 12$), but a very high production was registered at station AR3 because of a phytoplankton bloom (Fig. 1). Among transects, the differences were significant ($P < 0.05$; $n = 12$), and the Apalachicola and

Mobile river transects showed the highest mean production.

The assimilation number (P^B) ranged from 2.32 to 10.33 $\text{mg C mg}^{-1} \text{Chl-}a \text{ h}^{-1}$ at the surface and from 0.05 to 8.94 $\text{mg C mg}^{-1} \text{Chl-}a \text{ h}^{-1}$ at the DFM (Fig. 6B). These depths showed very significant differences in P^B values ($P < 0.01$; $n = 26$). The differences among transects and stations, however, were not significant ($P > 0.05$; $n = 26$). Surface waters showed low P^B at nearshore stations and high P^B at offshore stations, except at the Mobile River transect. At the DFM, the nearshore–offshore gradient of P^B was opposite to the one at the surface.

3.3. Organic carbon

DOC concentrations ranged from 90 to 306 μM at the surface and from 84 to 342 μM at the DFM (Fig. 7A). The differences among depths, stations, and transects were not significant ($P > 0.05$;

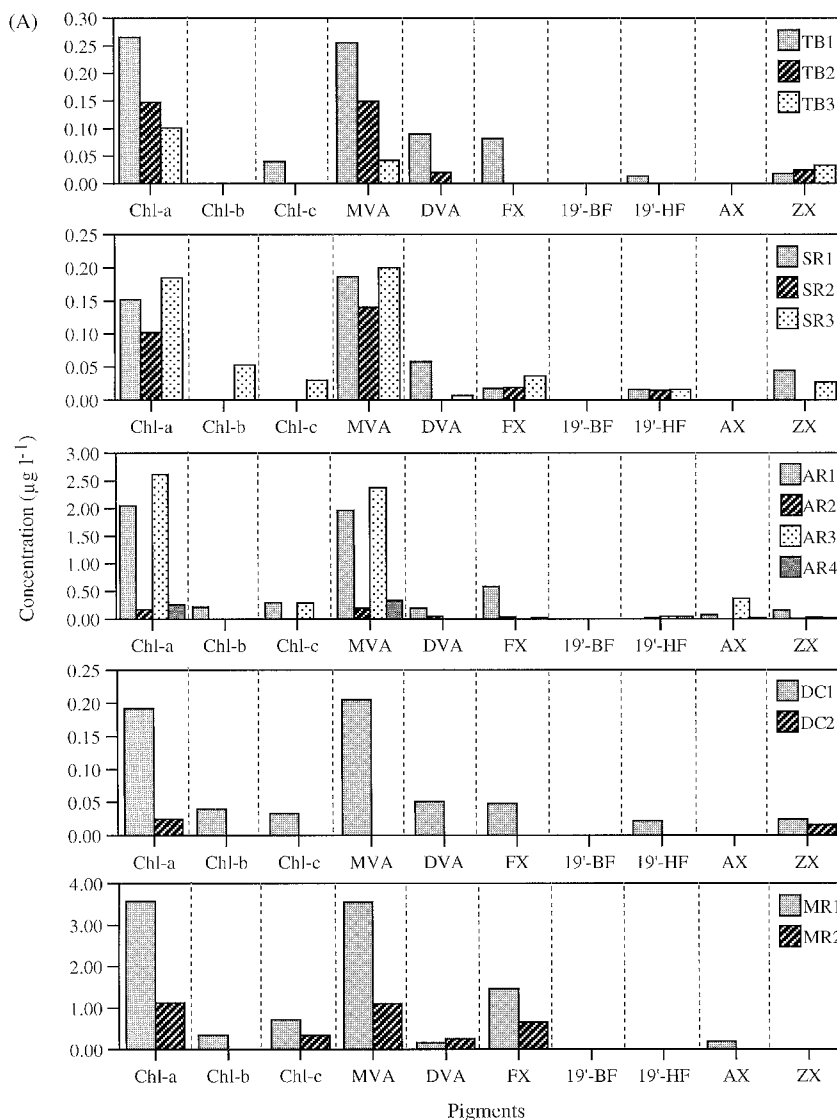


Fig. 3. (A) HPLC concentration of phytoplankton pigments at the surface: Chl-*a*=Chlorophyll-*a*; Chl-*b*=Chlorophyll-*b*; Chl-*c*=Chlorophyll-*c*; MVA=Monovinyl Chlorophyll-*a*; DVA=Divinyl Chlorophyll-*a*; FX=Fucoxanthin; 19'-BF=19' Butanoyloxy Fucoxanthin; 19'-HF=19' Hexanoyloxy Fucoxanthin; AX=Alloxanthin; ZX=Zeaxanthin. Note different scales on ordinate axes. Stations without bars showed pigment concentrations below detection limits. (B) HPLC concentration of phytoplankton pigments at the DFM: Chl-*a*=Chlorophyll-*a*; Chl-*b*=Chlorophyll-*b*; Chl-*c*=Chlorophyll-*c*; MVA=Monovinyl Chlorophyll-*a*; DVA=Divinyl Chlorophyll-*a*; FX=Fucoxanthin; 19'-BF=19' Butanoyloxy Fucoxanthin; 19'-HF=19' Hexanoyloxy Fucoxanthin; AX=Alloxanthin; ZX=Zeaxanthin. Note different scales on ordinate axes. Stations without bars showed pigment concentrations below the detection limits.

$n = 28$). The POC concentrations varied from 8.9 to 50.7 μM at the surface (Fig. 7B). Although the spatial changes of POC did not follow the DOC

trend, both parameters showed higher concentrations in the Apalachicola and Mobile River transects.

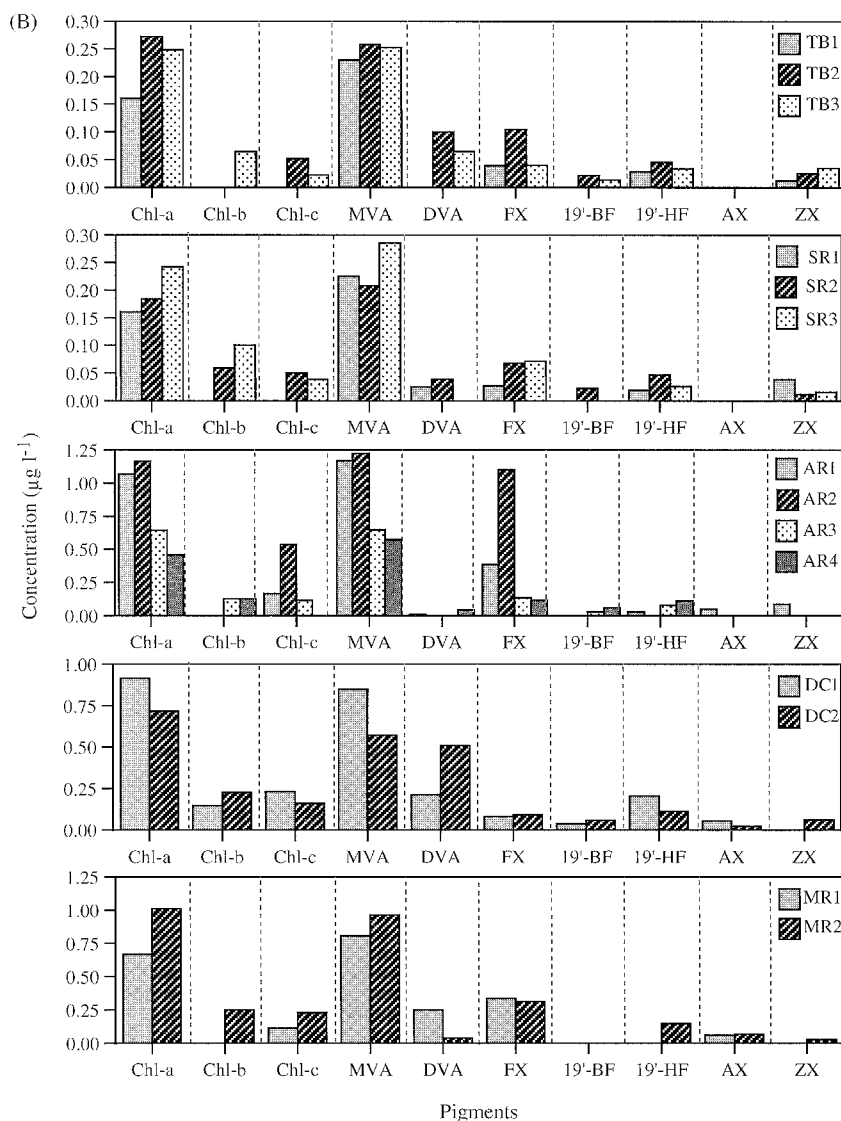


Fig. 3 (continued).

3.4. Nutrients

The overall variability of nutrient concentration between surface and the DFM was not significant ($P > 0.05$; $n = 28$), although some stations (SR3, AR3, DC2, and MR1) showed large variation in $\text{NO}_3 + \text{NO}_2$ and PO_4 concentrations (Fig. 8). The highest variability of nutrients was detected in the Apalachicola transect.

At the surface, the total dissolved nitrogen and dissolved organic nitrogen showed their highest concentrations in nearshore stations. The total particulate nitrogen, however, presented most of its highest values in the middle and offshore stations (TB2, SR2, and AR3). Particulate nitrogen and particulate phosphorus showed their highest concentrations at station AR3 (Fig. 8). Silicate showed detectable

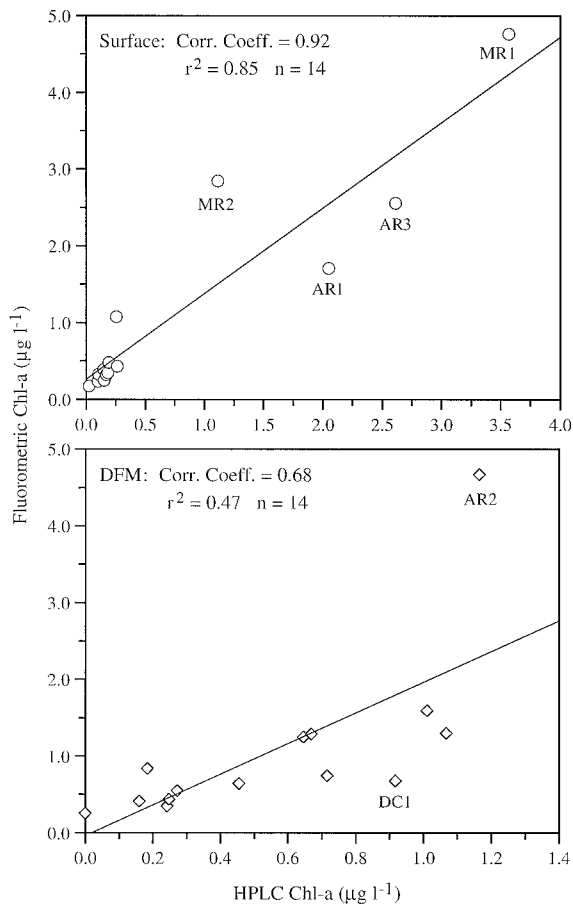


Fig. 4. Comparison between fluorometric and HPLC determinations of Chlorophyll-*a*. Samples of surface and DFM are shown at the top and the bottom, respectively. Note the different scales on graph ordinates.

concentrations at stations AR1, MR1, and MR2 (Fig. 8B).

3.5. Ancillary data

During the first quarter of 1995, the Loop Current intruded into the northern Gulf of Mexico (north of 28°N). The formation of an anticyclonic eddy was observed during the same week of the cruise using Advanced Very High Resolution Radiometer images (Gilbes, 1996). On 22 March a warm (25°C) filament from this new eddy was detected at the De Soto Canyon (station DC2; Fig. 9A). The spatial differences of temperature

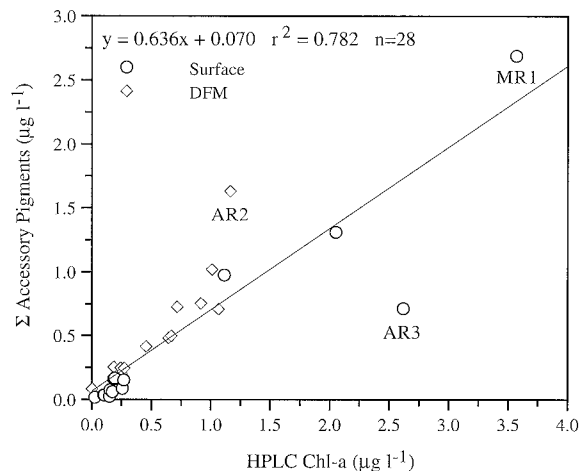


Fig. 5. Relationship between HPLC Chl-*a* and the sum of 7 accessory pigments (Chl-*b*, Chl-*c*, Fucoxanthin, 19' Butanoyloxy Fucoxanthin, 19' Hexanoyloxy Fucoxanthin, Alloxanthin, and Zeaxanthin) as determined by HPLC. Samples of surface and DFM are identified.

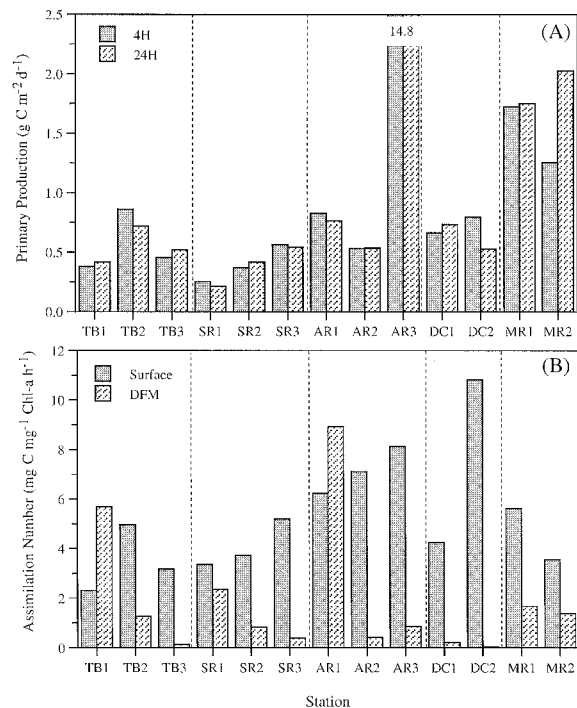


Fig. 6. Primary production: (A) measured with the ¹⁴C method during 4 and 24 h of incubation and the assimilation number; (B) at the surface and at the DFM using the mean of both incubations.

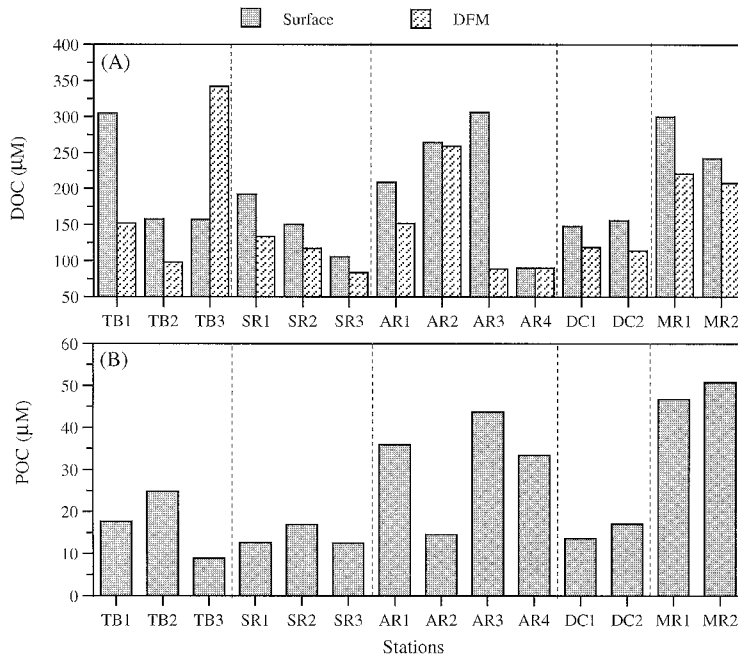


Fig. 7. Concentration of DOC and particulate organic carbon (POC) at the surface and at the DFM. POC was not measured at DFM.

and salinity were significant only among transects ($P < 0.05$; $n = 28$; Fig. 9). However, the lowest temperature and salinity were detected at near-shore stations.

The overall differences in suspended sediment concentration between surface and the DFM were not significant ($P > 0.05$; $n = 24$), although stations AR2 and AR3 showed very large differences between these two depths (Fig. 9C). The surface concentration of suspended sediments decreased from nearshore to offshore stations. Among transects, the differences were significant ($P > 0.05$; $n = 24$), and the Apalachicola and Mobile Rivers showed the highest mean values (Fig. 9C).

The overall differences between K_{par} values at the surface and at the DFM were not significant ($P > 0.05$; $n = 26$; Fig. 9D). However, stations AR2 and MR2 showed large differences between these two depths, which indicates that the water column exhibited large vertical structure in optical properties. The nearshore–offshore gradient ranged from 0.08 to 0.45 m^{-1} , and nearshore stations were statistically different from the offshore stations ($P < 0.05$; $n = 26$; Fig. 9D). The Apalachi-

cola and Mobile River transects showed significant differences ($P < 0.01$; $n = 26$) because of the high values measured in stations AR1, MR1, and MR2.

3.6. SeaWiFS data

The occurrence of the West Florida Shelf plume was also detected with SeaWiFS imagery during March of 1998 (Fig. 10). The plume followed the same spatial pattern presented in historical CZCS images by Gilbes et al. (1996). High Chl-*a* concentrations developed in coastal waters of Apalachicola Bay and persisted for at least 4 weeks. During the second week of March, a plume with Chl-*a* concentrations higher than $0.5 \mu\text{g l}^{-1}$ extended southward along the shelf (Fig. 10). The spatial extent of this plume was reduced by the third week of March, and by the end of the month, Chl-*a* concentrations were lower than $0.5 \mu\text{g l}^{-1}$ in the southern portion of the mid-shelf. However, high Chl-*a* persisted in the northern portion of the shelf. At that time, south of the Mississippi River delta, a large mass of Mississippi River water also moved to the southeast (Fig. 10).

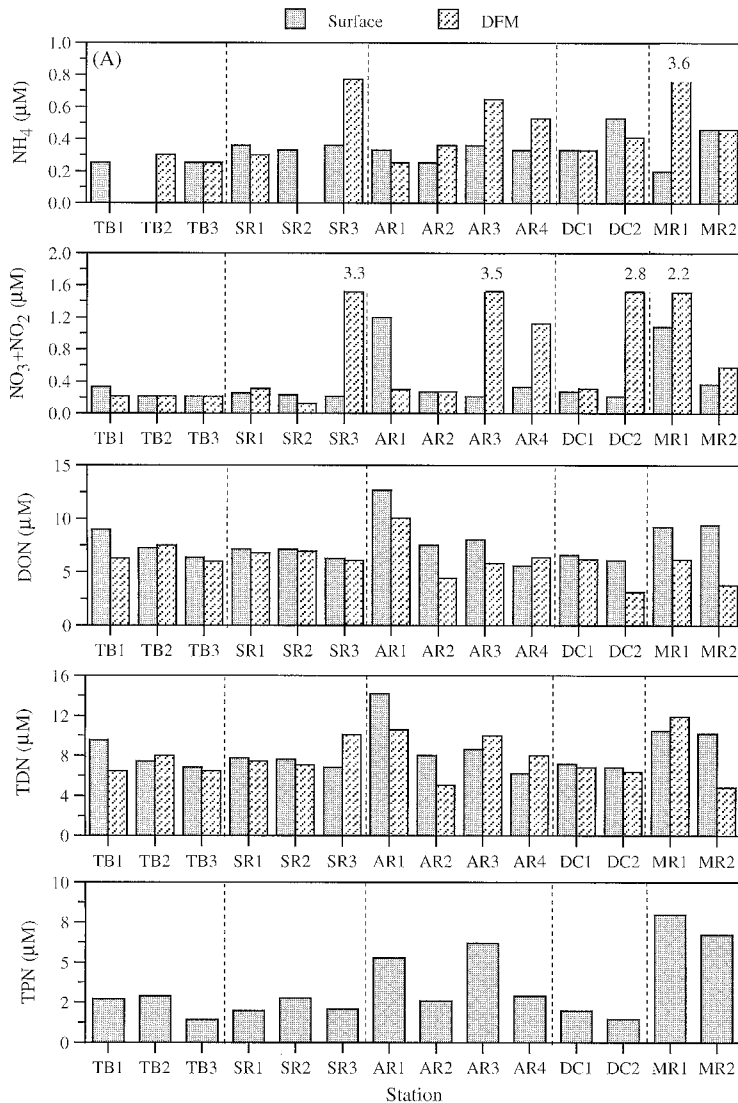


Fig. 8. (A) Concentration of nitrogen nutrients at the surface and at the DFM: DON=dissolved organic nitrogen; TDN=total dissolved nitrogen; TPN=total particulate nitrogen. TPN was not measured at DFM. Note the different scales on ordinates; (B) Concentration of phosphorus nutrients and silicate at the surface and at the DFM: DOP=dissolved organic phosphorus; TDP=total dissolved phosphorus; TPP=total particulate phosphorus. TPP was not measured at DFM. Note the different scales on ordinates.

4. Discussion

The occurrence of intense phytoplankton blooms on the West Florida Shelf was documented using field data collected during March 1995. These observations and recent SeaWiFS data corroborate the extent of the West Florida Shelf

plume described by Gilbes et al. (1996). Continuous in situ fluorescence measurements revealed three regions of very high Chl-*a* concentrations (Fig. 1). The maximum concentrations were registered south of Apalachicola Bay with values up to $29 \mu\text{g l}^{-1}$ Chl-*a*. In situ Chl-*a* concentrations in these blooms were higher than those estimated

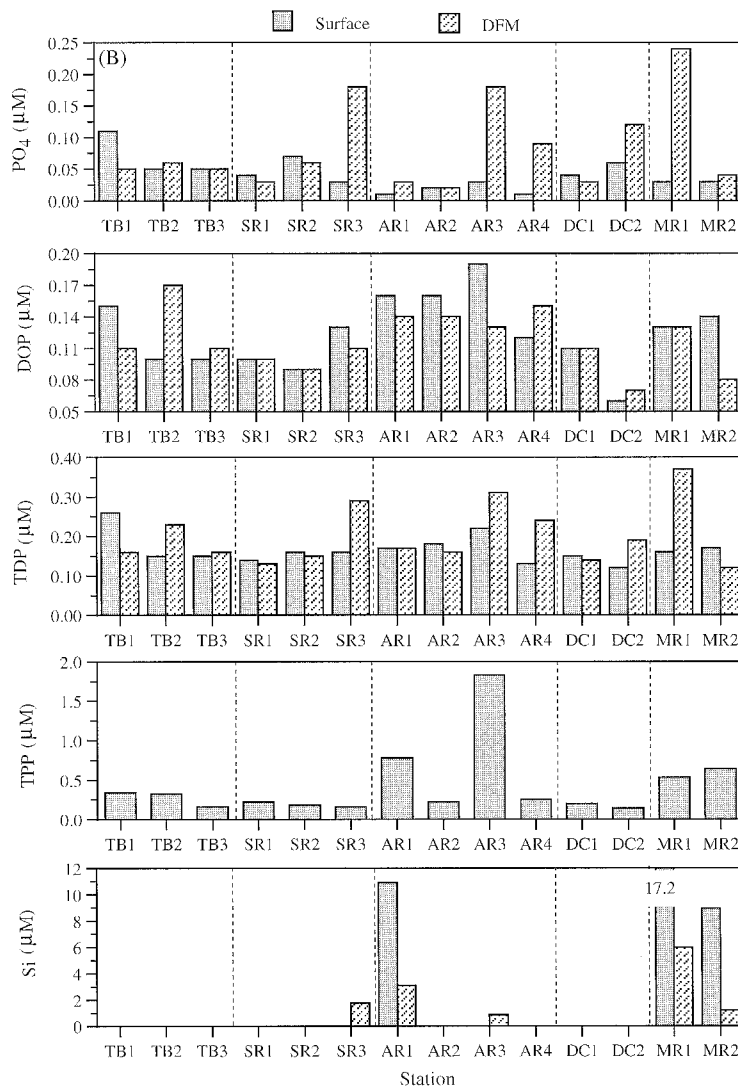


Fig. 8 (continued).

from historical CZCS and recent SeaWiFS imagery. Similar results were obtained during March 1992, which suggests a systematic overestimation in the in situ data in comparison with the satellite data (Gilbes et al., 1996).

Potential problems in the estimation of Chl-*a* using the standard fluorometric method have been identified when compared with concurrent HPLC data (Trees et al., 1985; Gieskes, 1991; Bianchi et al., 1995). In our study, the fluorometric method overestimated Chl-*a* concentrations about 10–30%

over the HPLC method (Fig. 4). This agrees with results reported for other regions (Gieskes, 1991), and has been attributed to the presence of Chl-*c* (Bianchi et al., 1995). Although Chl-*c* was detected in several stations (Fig. 4), we could not establish an overall trend between the Chl-*a* overestimations and the Chl-*c* concentrations. Only in station AR2 at DFM this trend was clear (Figs. 3B and 4).

The standard fluorometric method can also overestimate phaeopigments and underestimate Chl-*a* in presence of Chl-*b* (Gibbs, 1979; Lorenzen,

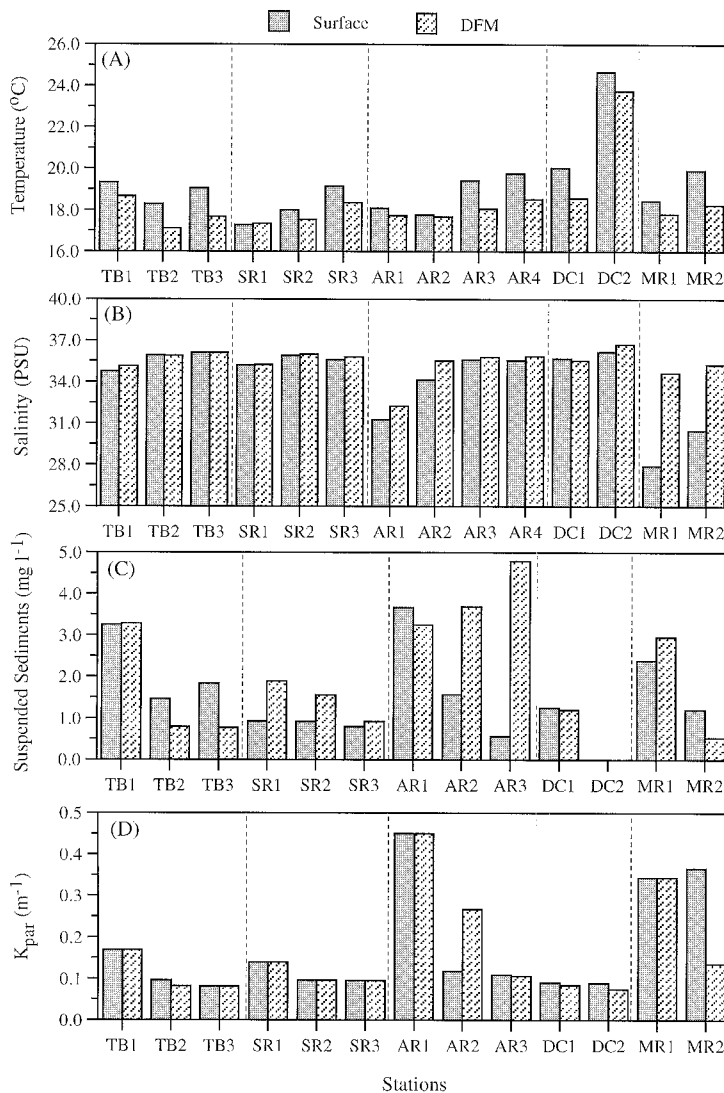


Fig. 9. Temperature (A), salinity (B), suspended sediments (C), and diffuse attenuation coefficient of the photosynthetic available radiation (D) at the surface and at the DFM.

1981; Trees et al., 1985; Welschmeyer, 1994). An underestimate of the fluorometric Chl-*a* concentrations was determined at stations AR1 (surface) and DC1 (DFM). Concurrent high concentrations of Phaeo-*a* (fluorometric method) and Chl-*b* (HPLC method) were also observed at several stations (Figs. 2B and 3), but we could not establish a direct relationship between the error in the estimations and the presence of Chl-*b*.

We documented large spatial variations in biological, chemical, and aquatic optical properties during March 1995 on the West Florida Shelf. Although the complexity of the region cannot be fully understood with only one cruise, our concurrent in situ data allow us to better describe nearshore-offshore and longshore variations of oceanographic parameters that affect the phytoplankton dynamics during a plume formation.

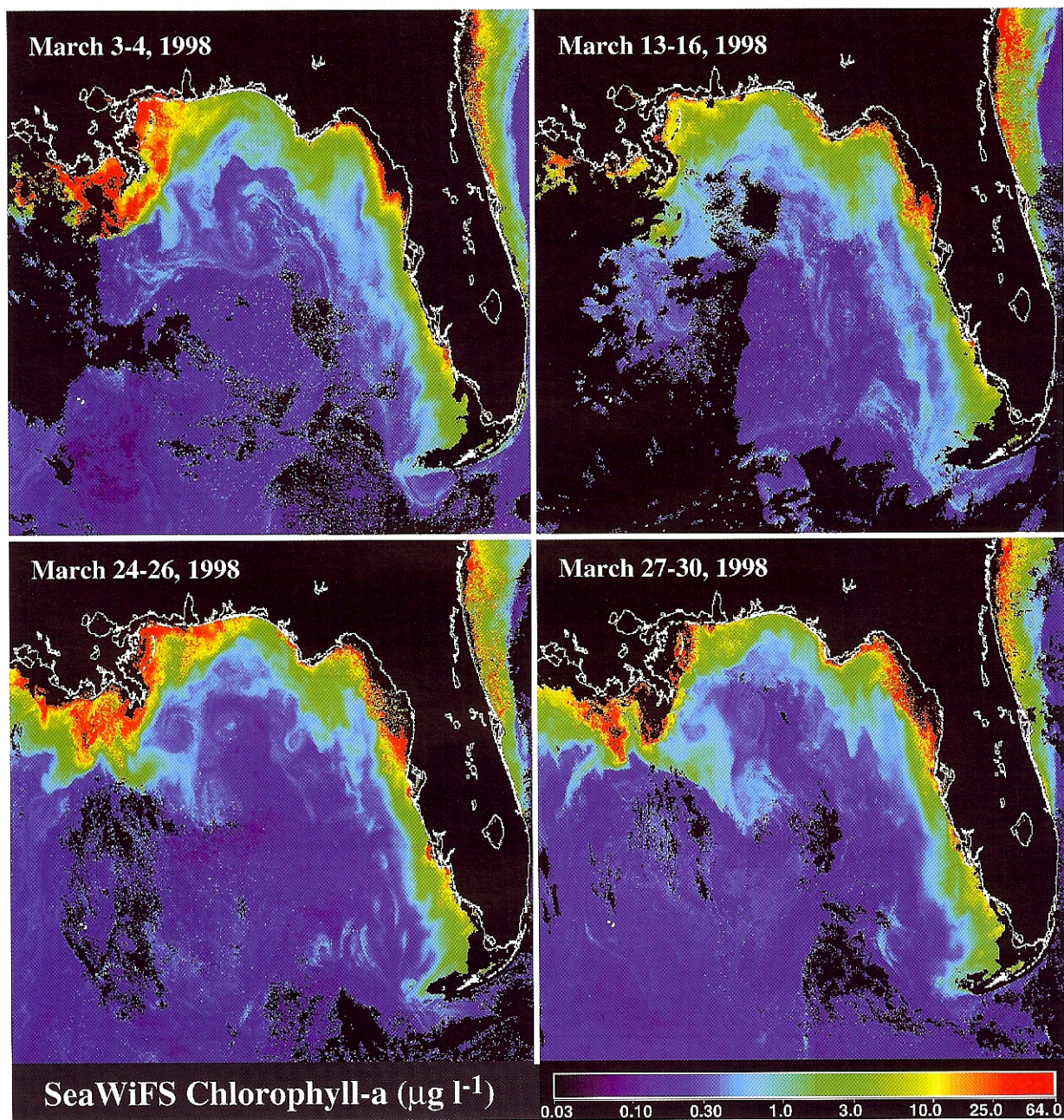


Fig. 10. Daily images of Chlorophyll-*a* concentration ($\mu\text{g l}^{-1}$) in the West Florida Shelf obtained with the SeaWiFS during March 1998. High concentrations are represented with yellow, orange, and red colors. Low concentrations are represented with purple and blue colors. Land, clouds and missing data are black.

4.1. Nearshore–offshore variations

Nearshore stations were characterized by high surface nutrient levels (Fig. 8), low salinities, high suspended sediments, and high diffuse attenuation coefficients (Fig. 9). These conditions resulted from the large river discharge that occurred in the northeast Gulf of Mexico during spring of 1995 (Fig. 11). A high negative correlation between salinity and pigment concentrations ($r^2 > 0.9$; $n = 12$) corroborates that the local river discharge profoundly affects the composition and dynamics of the phytoplankton communities of the inner West Florida Shelf.

High concentrations of dissolved substances in nearshore stations caused a rapid attenuation of blue light and the preferential transmission of

green-to-yellow wavelengths (Fig. 12). According to Kirk (1994), under these conditions, the efficiency of photosynthesis is enhanced by increasing the concentration of accessory pigments that can absorb the usable light. Fucoxanthin, which absorbs green light, was found in highest concentrations at nearshore stations (Fig. 3). Fucoxanthin also denotes the occurrence of diatoms and/or chrysophytes (Jeffrey, 1974; Rowan, 1989), which have been reported along the coastal areas of the northeast Gulf of Mexico (Curl, 1959; Khromov, 1969; Livingston, 1984). This initial formation of diatom blooms off Cape San Blas has been proposed as the precursor of the West Florida plume (Gilbes et al., 1996). Our current study supports this hypothesis and suggests that the nutrient requirements for such

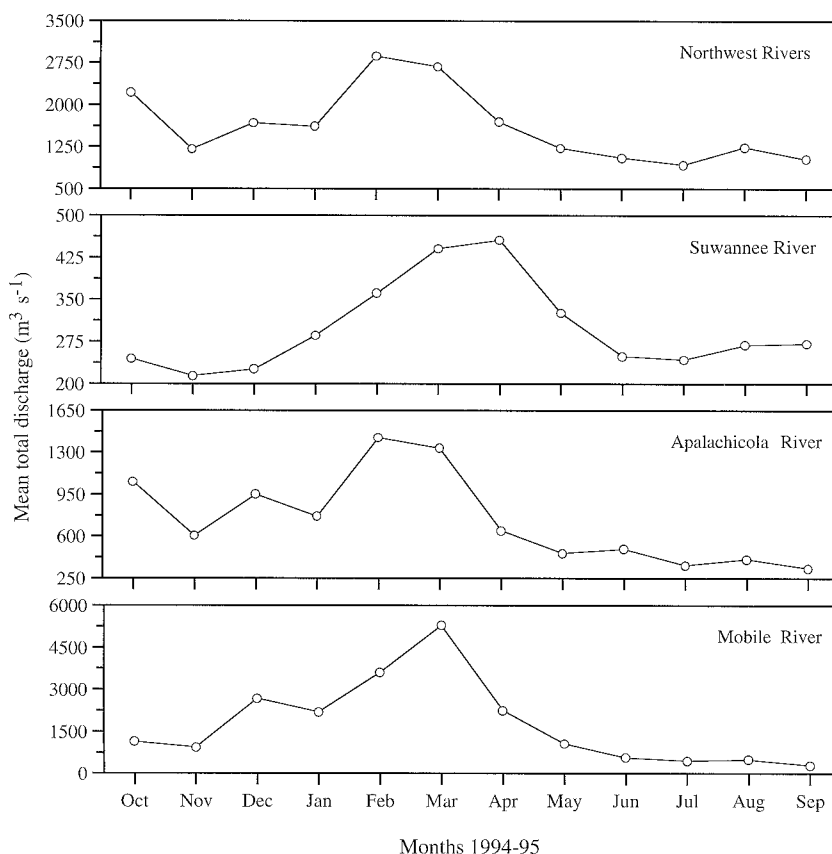


Fig. 11. Total monthly Mean River discharge between October 1994 and September 1995. Note the different scales on graph ordinates. Northwest rivers are described in Gilbes et al. (1996).

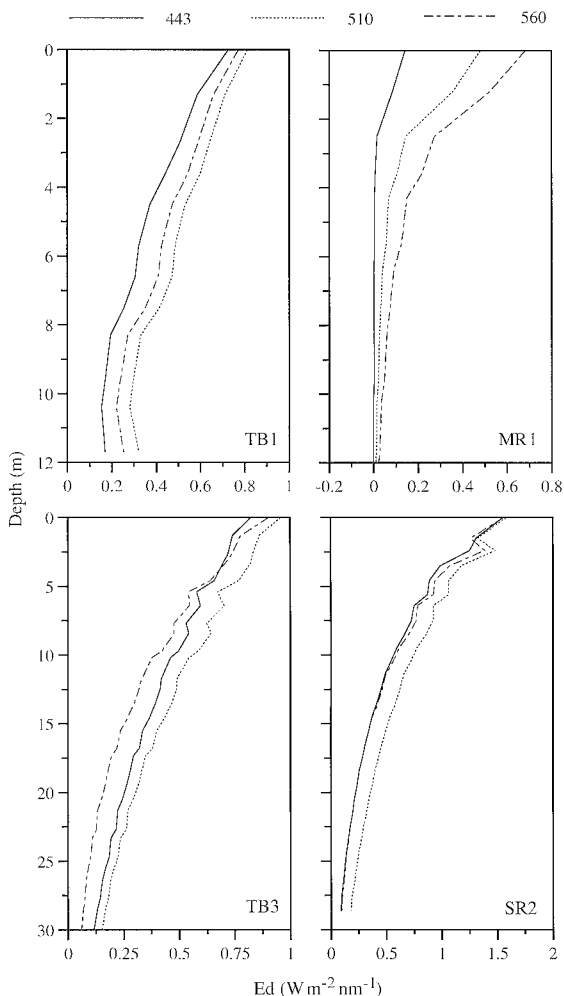


Fig. 12. Profiles of downwelling irradiance (E_d) measured with the MER 2040 at selected stations (see Fig. 1 for locations) and three wavelengths (nm). Note the different scales on graph ordinates.

blooms, especially silicate are satisfied by the large concentrations of river-derived silicate detected off the Apalachicola Bay (AR1; Fig. 8B). These blooms can move southward to offshore waters where successional and biochemical processes take place. After silicate limitation, the diatoms may sink out (e.g. stations AR2 and AR3 in Fig. 9C) and other species dominate the surface waters. Evidence of sinking and possible succession was found in station AR2, where Chl-*a* and fuco-

xanthin showed very high concentrations at the DFM (Figs. 2 and 3B).

In middle-shelf and offshore stations, an increase in salinity was accompanied by a decrease in surface nutrients, suspended sediments, diffuse attenuation coefficient, and surface pigments, showing a decline in the impact of river discharge over the outer shelf. At these stations, a large abundance of accessory pigments was detected at the DFM (Fig. 3B). This might be attributed to physiological adaptations of phytoplankton to the increased quantity of available blue-green light (Fig. 12; Kirk, 1994).

Although an overall gradient of phytoplankton pigment concentration was registered across the shelf, with high values nearshore and low values offshore, stations SR3 and AR3 (offshore stations) showed their maximum concentrations within their respective transects. The differences were attributed to the phytoplankton bloom detected south of Apalachicola Bay (Fig. 1). This bloom was also associated with high values of primary production, DOC and POC at AR3.

Salinity measurements suggest that the origin of this offshore bloom could be related to river discharge as proposed by Gilbes et al. (1996). In the Apalachicola River transect, low surface salinities were detected at nearshore and middle shelf stations (Fig. 9B). In the Suwannee River transect, however, the differences in salinities were not significant. This indicates that the discharge of the Apalachicola River, which was almost three times higher than the discharge of the Suwannee River (Fig. 11), had a major impact over middle shelf stations.

The primary production measurements obtained from 4 h incubations showed a nearshore–offshore trend similar to that of the phytoplankton pigments, except in the Tampa Bay and De Soto Canyon transects, where the production peaks were registered at stations TB2 and DC2 (Fig. 6). The cause of the maximum in production at TB2 is not clear, but high POC and TPN values were also registered. Temperatures at this station were depressed, suggesting that upwelling may have been important here. This area seems to have upwelling regularly over a topographic anomaly off Tampa Bay.

The most anomalous measurement of primary production was obtained at station AR3, where $14.8 \text{ g C m}^{-2} \text{ d}^{-1}$ were estimated. A high production was expected at this station because of the phytoplankton bloom, but this level of production has never been reported in this region (Vargo et al., 1987; Lohrenz et al., 1990; Biggs, 1992). While this value could be considered an overestimation originated by an error in the method, this high productivity coincides with very high surface Chl-*a*, DOC, TPN, TPP, and low suspended sediments.

An initial test showed a non-significant regression between water-column integrated primary production and surface DOC. The regression between surface DOC and surface production was significant ($P < 0.05$; $n = 13$), however. An analysis excluding stations TB1 and SR3, which registered extreme values of DOC, showed even higher significant regression ($P = 0.002$; $n = 11$). These analyses demonstrate that the DOC pool is indeed affected by primary production. At inshore stations, the relationship between DOC and production showed only a weak correlation, suggesting that the main source of dissolved organic material in those stations is mostly terrestrial. This idea is supported by a significant correlation between DOC and salinity in all stations, excluding TB1 and SR3 ($P < 0.05$; $n = 11$). Additional information on the relationship between DOC, PP, and salinity is presented in Del Castillo et al. (2000).

4.2. Longshore variations

An analysis of the HPLC photosynthetic pigment measurements indicated that, in March 1995, the phytoplankton community along the West Florida Shelf was a mixed assemblage. The most abundant pigment was monovinyl Chl-*a*, which is found in most phytoplankton groups (Laurie Van Heukelem, personal communication). Other chlorophylls were also detected at various stations as shown in Fig. 3, indicating the presence of different groups. High concentrations of divinyl Chl-*a*, Chl-*b*, and Chl-*c* in surface waters of nearshore stations and in deep waters of middle and offshore stations may indicate the presence of prochlorophytes (Gieskes, 1991; Goericke and

Repeta, 1992), chlorophytes and/or prasinophytes (Jeffrey, 1980; Rowan, 1989) and bacillariophytes and/or chrysophytes (Millie et al., 1993), respectively.

The along-shelf distribution of carotenoids also confirmed the taxonomic diversity of the phytoplankton community along the West Florida Shelf. The presence of diatoms and/or chrysophytes is inferred by the presence of fucoxanthin (Jeffrey, 1974; Rowan, 1989). Peridinin, a diagnostic pigment of most dinophytes (Jeffrey, 1980; Rowan, 1989; Millie et al., 1993), was detected only at station AR1 ($0.075 \mu\text{g l}^{-1}$). However, it has been reported that some species of dinoflagellates, like *Gymnodinium*, can contain fucoxanthin and its derivatives rather than peridinin (Rowan, 1989). 19'-hexanoyloxy fucoxanthin was detected at some stations (Fig. 3), and this derivative of fucoxanthin is one of the primary light-harvesting pigments of several dinophytes, including *Gymnodinium breve* (Rowan, 1989; Millie et al., 1995). Finally, the occurrence of cryptophytes and/or cyanophytes is indicated by the presence of alloxanthin and zeaxanthin (Rowan, 1989; Millie et al., 1993).

Similar groups have been described for other regions of the Gulf of Mexico by Khromov (1969) and Noh (1991). HPLC data did not allow the distinction of which group was dominating at specific locations because many taxonomic pigments were undetectable. However, three different pieces of evidence help us to identify the possible dominance of cryptophytes in the bloom south of Apalachicola Bay. At AR3, a high concentration of alloxanthin (Fig. 3A), a biomarker of cryptophytes (Millie et al., 1993), was observed. Also, the absorption spectrum of the bloom presented the distinctive absorption peak of phycoerythrin at 545 nm (Gilbes, 1996), which is another marker of cryptophytes (Rowan, 1989). Finally, a taxonomic sample taken from the bloom only showed small ($d < 3 \mu\text{m}$) and unidentifiable phytoplankters. Gieskes and Kraay (1983) found under similar conditions that the appearance of cryptophytes is altered beyond recognition in preservatives, which could explain why we were not able to identify them in the taxonomy samples.

5. Conclusions

During March 1995 and March 1998 the seasonal, spring-time formation of a high chlorophyll plume previously described along the entire West Florida Shelf was confirmed. In situ phytoplankton pigment observations indicate that the phytoplankton community growing during such events is a mixed assemblage. Specific analyses of HPLC data, the absorption spectrum, taxonomic samples, and nutrients suggest that nearshore communities of diatoms are the precursor of the offshore blooms, which after successional processes can be dominated by cryptophytes. Local River discharge affects the composition and dynamics of the phytoplankton communities in the inner Northwest Florida Shelf, but its impact decreases over the outer shelf. The discharge of the Apalachicola River, which is almost three times higher than the discharge of the Suwannee River, has a major impact over offshore locations and, therefore, might play a major role in the formation and development of the West Florida Plume. The seasonal appearance of this plume is still detected by new ocean color sensors like SeaWiFS.

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