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Plankton community composition, production, and respiration in relation to dissolved inorganic carbon on the West Florida Shelf, April 1996

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Abstract. In April 1996 the Florida Shelf Lagrangian Experiment examined dissolved inorganic carbon (DIC) dynamics on the West Florida Shelf. DIC concentrations increased over 2 weeks at an average rate of 1 μmol kg⁻¹ d⁻¹ in a patch of the intentionally released tracers sulfur hexafluoride (SF₆) and helium 3 (³He). Approximately 20% of the increase was due to air-sea exchange with the remaining 80% attributed to plankton respiration [Wanninkhof et al., 1997]. Here we present particulate matter concentrations, phytoplankton production, and community respiration rates from the tracer patch that suggest that heterotrophs dominated the community after the termination of a spring bloom. During the experiment, chlorophyll a and phaeopigment concentrations declined from > 1.5 to < 0.5 μg L⁻¹, with 75-85% of total chlorophyll a in the < 5μm size fraction. Particulate matter composition, with mean ratios of particulate organic carbon:chlorophyll a > 200 and particulate organic nitrogen:chlorophyll a > 100, suggests that phytoplankton were a minor component of the plankton biomass. Rates of daily gross primary production estimated by the H₂¹⁸O method averaged 69 ± 5 mmol C m⁻² d⁻¹ (n = 3) while dark respiration rates, estimated from dark bottle incubations, were approximately 40 ± 3 mmol C m⁻² d⁻¹. Net community production rates (6 ± 6 mmol C m⁻² d⁻¹) were much lower than respiration rates. Thus respiration rates nearly balanced phytoplankton production. Light respiration rates were estimated from gross production minus net community production (-41 ± 8 mmol C m⁻² d⁻¹) and exceeded dark respiration. Plankton community respiration rates, corrected for autotrophic carbon fixation, were more than sufficient to account for the observed increase of DIC within the tracer patch.

1. Introduction

Plankton communities alter the dissolved inorganic carbon (DIC) content of oceanic surface waters through the processes of photosynthesis and respiration. In surface waters, DIC concentrations decrease if primary production rates exceed the combined influx of carbon from the atmosphere and respiration [Robertson and Watson, 1995]. In the North Atlantic Ocean, for example, DIC concentrations decline when primary productivity increases during the spring bloom [Chipman et al., 1993]. Measurements of air-sea CO₂ exchange in the North Atlantic show that spatial distributions of primary producers correlate significantly with variations in surface pCO₂ at length scales < 100 km [Watson et al., 1991]. Productivity also influences the spatial distribution of DIC in 'high nutrient-low biomass' waters, where CO₂ fugacity decreases after iron enrichment [Cooper et al., 1996; de Baar et al., 1995].

While several studies have examined plankton productivity and DIC in the open ocean, fewer have examined these processes on continental shelves [Frankignoulle et al., 1996]. In comparison to the open sea, continental shelf environments are characterized by high rates of carbon deposition due to enhanced nutrient inputs, high productivity rates, and an influx of organic matter from terrestrial sources [Wollast, 1993]. These processes contribute to coastal waters as a significant heterotrophic environment in the global ocean [Smith and Mackenzie, 1987]. Nevertheless, high rates of photoautotrophic carbon fixation can reduce DIC levels in shelf surface waters. Codispoti et al. (1986) observed that photosynthetic carbon uptake reduced pCO₂ from > 300 to < 125 ppm during a spring bloom in the Bering Sea. In April 1990, DIC concentrations on Georges Bank initially decreased, and then increased, at rates of several μmol C kg⁻¹ d⁻¹ as the spring bloom developed and subsequently declined [Sambrotto and Langdon, 1994]. In contrast to temperate and boreal lati-
tudes, few studies have been made in subtropical or tropical shelf environments where phytoplankton biomass and productivity rates are relatively low.

In April 1996 the Florida Shelf Lagrangian Experiment (FSLE) characterized the dissolved inorganic carbon system on the West Florida Shelf [Wanninkhof et al., 1997]. The main objective of the study was to quantify air-sea gas exchange rates in a subtropical shelf ecosystem. Since carbon dynamics on continental shelves are complicated by advection and mixing of oceanic, coastal, and riverine waters [DeGrandpre et al., 1998], the FSLE was designed as a “patch” study through the release of the intentional tracers sulfur hexafluoride (SF6) and helium 3 (3He). The Lagrangian design of the experiment provided investigators with the opportunity to follow DIC dynamics in a tagged water mass for 2 weeks. During the study, DIC concentrations in the mixed layer increased at an average rate of ~ 1 μmol kg⁻¹ d⁻¹, with 20% of the increase due to the influx of atmospheric CO₂ [Wanninkhof et al., 1997]. The remaining 80% of the increase was attributed to plankton respiration. Here we report pigment concentrations, particulate matter composition, and community production and respiration rates from the tracer patch. The observations support the conclusions of Wanninkhof et al. [1997], since respiration rates by the predominantly heterotrophic plankton community were more than sufficient to account for observed increases in DIC.

The West Florida Shelf is at the eastern boundary of the oligotrophic Gulf of Mexico. Nutrient concentrations are relatively low in surface waters on the Shelf, although nutrient levels are often enhanced following wind events [Fanning et al., 1982]. Circulation on the inner Shelf is primarily driven by winds and tides [Marmorino, 1983; Mitchum and Clarke, 1986]. The experiment was located at 29° N, 84° W, with the tracer released along the 25-m isobath (Figure 1). Long-term acoustic Doppler current profiler (ADCP) records from 24° N, 84° W reveal that net particle displacement in this region of the Shelf is of the order of a few km d⁻¹, with corresponding along-shore trajectories of hundreds of kilometers per month [Weisberg et al., 1996]. These length scales agree with the observed displacement of the tracer patch [Wanninkhof et al., 1997].

Productivity studies indicate that the West Florida Shelf is oligotrophic. Annual productivity estimates range from 30 to 180 g C m⁻² yr⁻¹ [Vargo et al., 1987; El-Sayed, 1972; Wroblewski and O'Brien, 1973] with maximum rates in blooms of the dinoflagellate Gymnodinium breve Davis. However, most of the production measurements have been made during nonbloom periods when G. breve is absent from surface waters or present at background concentrations of < 10³ cells L⁻¹ [Geesey and Tester, 1993]. Shoreward of the 40-m isobath the daily production rates are typically < 500 mg C m⁻² d⁻¹ with surface chlorophyll a concentrations < 1 μg L⁻¹ [Vargo et al., 1987, Table 1]. Chlorophyll a concentrations on the middle to outer Shelf can exceed 1 μg L⁻¹ for several weeks in the spring (Gilbes et al., 1996). This spring bloom on the West Florida Shelf may be initiated by the influx of allochthonous nutrients from riverine sources on the northern Gulf coast, including the Mississippi River and Mobile Bay, or from onshore transport of nutrient-rich, deep water upwelled at the Shelf break. In April 1996 we observed that surface chlorophyll a and phaeopigment concentrations at mid-Shelf declined from initial levels of 1.5 to < 0.5 μg L⁻¹. Our observations therefore likely coincided with the termination of the 1996 spring bloom.

2. Methods

2.1. Particulate Analyses

Particulate matter was analyzed for chlorophyll a, phaeopigment, and particulate organic carbon, nitrogen, and phosphorus. Chlorophyll a concentrations were measured on samples collected at 20 stations from 30-L Niskin bottles mounted on a General Oceanics rosette with a SeaBird 11 conductivity-temperature-depth (CTD). Duplicate aliquots of 200 mL each were filtered onto Whatman glass fiber filters (GF/F) at a vacuum of 50 mm of Hg. The filters were extracted in 10 mL of methanol for 4 hours in the dark at room temperature. Chlorophyll a and phaeopigment concentrations were determined from fluorescence readings before and after acidification on a Turner Designs Model 10 fluorometer following the method of Holm-Hansen and Riemann [1978]. The fluorometer was calibrated with purified chlorophyll a purchased from Sigma Chemical Corporation.

Particulate organic carbon (POC) and particulate organic nitrogen (PON) concentrations were measured at 12 stations (Table 1) from duplicate 200 mL aliquots filtered onto precombusted Whatman GF/F filters (2 hours at 450°C). The filters were stored over a dessicant at -20°C and assayed in the laboratory on a Carlo Erba 1600 carbon nitrogen hydrogen (CHN) analyzer [Sharp, 1974]. Blanks of precombusted filters and standards were analyzed at the beginning and end of each day. Particulate phosphate was measured by the combustion method of Solisrano and Sharp [1980] on duplicate samples filtered onto precombusted Whatman GF/F filters and stored frozen in precombusted, acid-rinsed, glass scintillation vials.
Vertical profiles of scalar irradiance were measured with a LiCor LI-193S 4° sensor lowered from the stern of the ship. A total of seven profiles were taken within 2 hours of local noon while the stern was positioned toward the Sun.

2.2. Gross and Net Production and Respiration Rates

Samples for production and respiration rates were collected from 2, 5, 10, and 20 m at four CTD stations (Table 1). Gross and net production rates are only available from three of the stations since the in situ array was lost on day 11 (productivity 3). Gross primary production rates were measured by the method of Bender and Grande [1987] from samples incubated for 24 hours with H218O [also see Bender et al., 1987]. All seawater samples for production and respiration measurements were collected at 0400 local time (0800 UT) to ensure that phytoplankton were not exposed to direct sunlight before incubation. Two samples from each depth were enriched with 200 µL of 97.2 atom% H218O (Cambridge Isotope Laboratories, Andover, Massachusetts) for 24-hour incubation. The H218O-enriched samples were then suspended from a surface float at their depth of collection. The float was deployed before dawn and tracked by a VHF beacon until it was retrieved at sundown. At dusk the gross production samples were placed in a darkened on-deck incubator cooled with flowing surface seawater and incubated until dawn.

Two samples from the Niskin bottles were collected for initial 18O concentrations. Approximately 50 mL of seawater were dispensed into preevacuated 150 mL glass flasks poisoned with 200 µL of saturated HgCl2. The dissolved 18O2 was extracted following the procedure of Emerson et al. [1991]. The 18O2 samples were analyzed in the laboratory of M. Bender using a Finnigan MAT 252 mass spectrometer. The analytical precision of the gross production measurement on replicate samples was ± 0.07 ‰.

Rates of net community production (NCP) and dark community respiration (DCR) were estimated from changes in O2 concentrations in initial, light, and dark bottles by the Winkler method utilizing a potentiometric endpoint titrator. Seawater samples were drawn from the Go-Flo bottles into quartz 125-mL flasks, flushed with several hundred milliliters of seawater, and then closed with ground glass stoppers. Four initial O2 samples and a total of 16 light and dark bottles were filled with seawater from each of the four sampling depths. The O2 flasks were suspended with the gross production samples at their collection depth in acrylic carousels. Automatic temperature recorders (Onset Computer Corporation, Bourne, Massachusetts) were placed in each carousel to monitor temperature.

After the in situ array was retrieved at dusk, quadruplicate light and dark bottles were fixed with reagents for determining photoperiod (daylight) rates of NCP and DCR. The remaining four light bottles and four dark bottles from each depth were then placed in the on-deck incubator to complete a 24-hour incubation. The O2 samples were titrated after reaching thermal equilibrium with an automated titration system. The titrations were run to a potentiometric endpoint with a Radiomete Automatic Burette (ABU) and a Titration Manager (TIM) 90 controller. The analytical precision in laboratory samples, calculated as standard deviations, is ± 0.04% for iodate standards and ± 0.07% for replicate O2 samples. At sea the analytical precision is ± 0.15% for replicate oxygen samples drawn from the same Go-Flo bottle. Precision for NCP and DCR rates is estimated to be ± 0.2 µmol O2 L⁻1.

Daily oxygen production rates were converted to carbon equivalents by the following equation:

\[ G_c = \{(N_{O2} / 1.4) + ((G_{O2} - N_{O2}) / 1.1)\} \]  

where gross production from 18O incubations (G_{O2}) and NCP (N_{O2}) from the Winkler titrations are expressed as mmol O2 m⁻² t⁻¹ and \( G_c \) is gross carbon production expressed as mmol C m⁻² t⁻¹. A photosynthetic quotient (PQ) of 1.4 was selected to
Figure 2. Surface distributions in the tracer patch 11 days after release for (a) temperature, (b) salinity, and (c) relative chlorophyll *a* fluorescence. The dotted line in the temperature map (a) shows the ship track during the survey. The fluorescence map includes the station positions for productivity and particulate samples (solid diamonds), and additional stations for chlorophyll *a* (open diamonds). The spatial extent of the SF₆ patch is indicated by the 5 parts per trillion by volume (pptv) contour (dashed line).

Pigment profiles at CTD 75 were typical of the vertical distributions of chlorophyll *a* and phaeopigment during the last week of the study. Chlorophyll *a* exceeded phaeopigment at all depths, with maximum chlorophyll *a* and phaeopigment concentrations in the bottom layer. Chlorophyll *a* concentrations increased from ~0.25 µg L⁻¹ in the surface layer to 0.9 µg L⁻¹ below the pycnocline (Figure 4f). The decline in chlorophyll *a* and phaeopigment concentrations during the first few days of the study and the low initial chlorophyll *a*:phaeopigment ratios suggest that the phytoplankton community was in decline soon after the tracer was injected.

Chlorophyll *a* concentrations were measured in three size fractions on April 8 (CTD 43) and April 16 (CTD 93). Size-fractionated samples were collected from five depths...
convert net oxygen production rates to net carbon production, with a PQ of 1.1 to convert oxygen respiration rates to carbon equivalents [Laws, 1991]. Respiration rates in the light (Rd) were estimated by subtracting the NCP rates from the gross 18O production rates following the procedure of Grande et al. [1989].

3. Results

3.1. Pigment and Particulate Distributions

As discussed by Wanninkhof et al. [1997], the surface distribution of SF6 at 3, 7, and 11 days after injection revealed that the tracer field expanded in response to wind and tides (Wanninkhof et al., 1997, Figure 1). Here we present the corresponding surface distributions of temperature, salinity, and chlorophyll fluorescence from the final survey (Figure 2). The surface fields are not truly synoptic since the survey (Figure 2a) required 40 hours to complete. Nevertheless, a weak gradient is consistent in the surface temperature, salinity, and fluorescence distributions at 84°W. Surface temperature increased from 16.5°C at the eastern edge of the patch, near 83.7°W, to a maximum of 17.4°C at 84.2°W (Figure 2a). The thermal gradient was centered between 84.0° and 84.1°W, where surface temperature increased from 16.8° to 17.2°C. Salinity increased from 35.0 at the eastern edge of the patch to 35.6 at the western margin (Figure 2b). A surface gradient was also evident at 84.10°W, where salinity increased from 35.2 to 35.4.

Chlorophyll fluorescence varied by less than twofold across the width of the tracer patch. The tracer patch, as defined by the 5 parts per trillion by volume (pptv) SF6 contour, extended from 83.7° to 84.3°W (Figure 2c). Stations for particulate, nutrient, and productivity samples were concentrated in the center of the patch, where maximum chlorophyll a fluorescence values coincided with the weak surface gradient in temperature and salinity (Figure 2c). Lower fluorescence values were found to the east and west (Figure 2c). Surface samples for total chlorophyll a (chlorophyll + phaeopigment) indicated that total pigment concentrations ranged from a minimum of 0.5 μg L⁻¹ along the western edge of the survey to a maximum of 0.7 μg L⁻¹ near the center. This range of concentrations is comparable to the surface pigment concentrations observed in the tracer patch during the last week of the study (Figure 3a).

Chlorophyll a concentrations decreased in the surface layer during the first week of the experiment. Initial chlorophyll a concentrations varied from 1.0 to 1.5 μg L⁻¹ at the time of the tracer release, with corresponding phaeopigment concentrations at 1.5-2.0 μg L⁻¹ (Figure 3a). Chlorophyll a: phaeopigment ratios were initially < 1 and then increased to > 1 as surface pigment concentrations declined. Five days after the injection, chlorophyll a concentrations in the center of the patch were 0.5-1.0 μg L⁻¹, with phaeopigment concentrations at 0.5-1.5 μg L⁻¹. One week after the injection, the chlorophyll a and phaeopigment concentrations in the surface layer of the tracer patch ranged from 0.25 to 0.45 μg L⁻¹.

Ratios of particulate organic carbon to chlorophyll (Chl) a (POC:Chl a) and particulate organic nitrogen to chlorophyll a (PON:Chl a) suggest that phytoplankton were a minor component of the particulate matter in surface waters. Particulate organic carbon concentrations varied about two-fold, from 8.3 to 17 μmol L⁻¹ (Figure 3b), with corresponding weight-based ratios of POC:Chl a (grams:grams) at 97:1-310:1. For the surface samples listed in Table 1 the mean POC:Chl a ratio was 226:1. Particulate organic nitrogen concentrations varied fourfold, from 1.65-9.72 μmol L⁻¹, with no apparent relationship to the variability in chlorophyll a (Figure 3). As with POC, the weight-based ratios of PON:Chl a were high compared to those in algal cultures, with a mean of 102:1. Particulate organic phosphorus (POP) concentrations exhibited less variability than did PON, ranging from 0.46-0.79 μmol L⁻¹, with a mean weight-based ratio of POP:Chl a of 3.1:1 (grams:grams). As discussed below, this POP:Chl a ratio is comparable to that in oligotrophic waters.

The molar ratios of particulate organic carbon, nitrogen, and phosphorus in the tracer patch did not correspond to Redfield ratios. The mean molar ratio of POC:PON (moles:moles) was 3.36 ± 1.6:1, about half the Redfield ratio of 6.6:1. Molar ratios of POC:PON were 5:1-6:1 on days 5-7, otherwise the ratios (3:1-5:1) were lower than those in phytoplankton cultures. Molar ratios of PON:POC declined from a maximum of 100:1 in the first 2 days of the study, to between 33:1 and 76:1 during the last week. The mean molar ratio of PON:POC was 76 ± 34:1, considerably higher than the Redfield ratio of 16:1. Similarly, molar ratios of POC:POC were higher than the Redfield ratio of 106:1, varying from a minimum of 163:1 to a maximum of 224:1. The mean POC:PON ratio was 180 ± 24:1.

Vertical profiles of properties from the CTD casts show the surface layer deepened by ~5 m during the study. CTD station 17 was completed soon after the tracer injection and ~10 hours before the first productivity station (Table 1). Density and SF6 tracer profiles from CTD 17 show that the mixed layer was 10 m deep, with the pycnocline extending to 15 m (Figure 4a). Although the density and tracer profiles clearly show stratification, dissolved ammonia and nitrate concentrations were similar in the surface and bottom layers. Ammonia (NH₃) varied from 150 to 300 nmol kg⁻¹ between the surface and 25 m, while nitrate (NO₃) concentrations ranged from 150 to 225 nmol kg⁻¹ (Figure 4b). Nitrite concentrations, in contrast, increased with depth from ~150 nmol kg⁻¹ at the surface layer to 300 nmol kg⁻¹ at 25 m.

The vertical pigment distributions show that maximum concentrations were always in the bottom layer. At CTD 17, chlorophyll a concentrations in the surface layer were 0.50 μg L⁻¹, with corresponding phaeopigment concentrations of 1.10 μg L⁻¹ (Figure 4c). In the bottom layer, chlorophyll a concentrations increased to 3.2 μg L⁻¹, with phaeopigment at 6.0 μg L⁻¹.

A final productivity station was occupied at CTD 73 2 weeks after the tracer injection (Table 1). Vertical profiles compiled from data at CTD stations 73-75 were representative of the property distributions observed during the last week of the experiment. By day 14 the mixed layer had deepened to 17 m with maximum SF6 concentrations of 25 pptv in the center of the patch. Concentrations of SF6 in the mixed layer of CTD 73-75 were ~20 pptv, indicating that the stations were near the tracer patch center. In contrast to the initial profiles (e.g., CTD 17), SF6 was present in the bottom layer at 5 pptv (Figure 4d). As seen in the first week of the study, dissolved inorganic nitrogen concentrations were variable throughout the water column. At CTD 74 the NH₄ concentrations ranged from 100 to 250 nmol kg⁻¹ with maximum levels near the pycnocline (Figure 4e). Concentrations of NO₂ in the surface layer had decreased, although maximum concentrations were still in the bottom layer. Nitrite concentra-
between the surface and 25 m. At both stations the > 12-μm size fraction accounted for < 10% of total chlorophyll a in the mixed layer, while the 5- to 12-μm size fraction contained at most 15% of total chlorophyll a. At CTD 43, the > 12-μm size fraction also represented < 10% of total chlorophyll a, and the 5- to 12-μm size fraction contained 13-16%. The highest proportion of the larger size fractions was in the pycnocline. The < 5-μm size fraction, in contrast, represented 75-85% of the total chlorophyll a biomass throughout the water column at both stations. Thus the size fraction data indicate that the phytoplankton community was dominated by picoplankton, or small nanoplankton, throughout the water column, with larger forms accounting for a slightly higher proportion of pigment biomass in the pycnocline. Microscopic observations of whole water samples confirmed that small, 1-μm diameter, unicellular phytoplankton were dominant in the mixed layer. Examination of 4'-6-diamidino-2-phenylindole (DAP)-stained samples from the mixed layer with an epifluorescent microscope revealed that the cells had the typical orange and red fluorescence signature of Synechococcus spp.

3.2. Community Production and Respiration Rates

Seven light casts were completed between days 4 and 14 to estimate vertical extinction coefficients $K_d$ (m$^{-1}$) in the tracer patch. Values for $K_d$ ranged from 0.20 to 0.15 m$^{-1}$ between days 4 and 8 and then decreased to ~ 0.10 m$^{-1}$ for the remainder of the study. The corresponding euphotic zone depths ranged from 20 m to the bottom. Since the depth of the euphotic zone was > 20 m, the euphotic zone always extended below the mixed layer.

Mean gross production rates decreased from a maximum of 4.5 μmol O$_2$ kg$^{-1}$ d$^{-1}$ at the surface to 3.4 μmol O$_2$ kg$^{-1}$ d$^{-1}$ at 20 m (Figure 5). Although in situ light intensities at 20 m were < 15% of surface values, gross production rates from 20 m were ~ 70% of those at the surface. Gross production rates normalized to chlorophyll a yield assimilation indices of 1 μmol O$_2$ μg Chl a$^{-1}$ h$^{-1}$ at the surface, decreasing to 0.2 μmol O$_2$ μg Chl a$^{-1}$ h$^{-1}$ at 20 m. These assimilation indices are comparable to those reported for plankton communities in the oligotrophic central North Pacific Ocean [Williams and Purdie, 1991]. The mean net community production rates (NCP) from 12-hour in situ incubations during the photoperiod decreased from 2 μmol O$_2$ kg$^{-1}$ near the surface to ~ 1 μmol O$_2$ kg$^{-1}$ at the base of the euphotic zone. In general, the NCP from the photoperiod incubations were twice those from 24-hour (day-night) incubations (NCP$_{12}$ versus NCP$_{24}$, Figure 5). At 20 m, gross production was balanced by losses to respiration, resulting in a mean 24-hour NCP rate of ~ 0 μmol C kg$^{-1}$.

A comparison of dark community respiration (DCR) rates from the 12- and 24-hour incubations shows that respiration rates during the photoperiod were approximately twofold higher than at night. The photoperiod respiration rates (DCR$_{12}$) were about −1.4 ± 0.5 μmol O$_2$ kg$^{-1}$ 12 h$^{-1}$, with little variation with depth (Figure 5). At night the mean DCR was −0.8 ± 0.4 μmol O$_2$ kg$^{-1}$ 12 h$^{-1}$. The rate of light respiration ($R_L$), estimated from the difference between gross production and NCP$_{12}$, exceeded the maximum rates of dark respiration. However, there was little variation in $R_L$ throughout the euphotic zone. Oxygen consumption rates were approximately −2.5 μmol O$_2$ kg$^{-1}$ 12 h$^{-1}$ throughout the upper 20 m (Figure 5).

Carbon-based rates of production and respiration integrated through the mixed layer indicate that a large fraction of gross production was consumed by respiration. Daily gross production based on the H$_2$O method varied from 65 to 75 mmol C m$^{-2}$, with a mean of 69 mmol C m$^{-2}$ (G$_{24}$ in Figure 6). Rates of NCP estimated from the Winkler method, in contrast, were 14.7-20.6 mmol C m$^{-2}$ in the photoperiod incubations (N$_{24}$), decreasing to 12.1 to −0.9 mmol C m$^{-2}$ in the 24 hour incubations (N$_{24}$). Absolute rates of dark community respiration were higher than net community production, at −25 ± 7 mmol C m$^{-2}$ during the 12-hour photoperiod and −40 ± 4 mmol C m$^{-2}$ over 24 hours. The difference in dark respiration rates at 12 and 24 hours reflects the reduced rate of dark respiration at night, equivalent to −15 ± 4 mmol C m$^{-2}$. The enhanced dark respiration observed during the photoperiod was exceeded by light respiration (compare $R_{L12}$ and $R_{L}$ in Figure 6). Thus the plankton community in the tracer patch was characterized by rates of gross production that were almost balanced by respiratory losses, resulting in low rates of daily net production.

Ratios of dark respiration:net production are useful in assessing the ability of phytoplankton to meet the respiration demands of the plankton community. The ratios of dark community respiration:net community production (DCR$_{12}$:NCP$_{12}$) during the photoperiod varied from a maximum of 2.25:1 on day 4 to a minimum of 0.9:1 on day 14. The mean ratio of DCR$_{12}$:NCP$_{12}$ for the three experiments was 1.5:1, indicating that the respiration demands of the plankton community exceeded the net production by phytoplankton. When the corresponding respiration and net production rates are compared from the 24-hour incubations, the mean ratio (DCR$_{24}$:NCP$_{24}$) declined to < 0.2:1. The sum of the mean
Figure 4. Vertical property profiles from conductivity-temperature-depth (CTD) station 17 for (a) $\sigma_t$ (solid line) and SF$_6$ (dot), (b) ammonia (NH$_3$), nitrite (NO$_2$) and nitrate (NO$_3$) concentrations, and (c) chlorophyll a (dots) and phaeopigment (triangles). (d-f) Corresponding properties from CTD 74 and 75. Nitrogen data are courtesy of K. Fanning and R. Masserini, University of South Florida. DIN, dissolved inorganic nitrogen.

Figure 5. Production and respiration rates as a function of depth from three productivity stations. The right half contains gross production rates from $^{18}$O incubations ($G_{24}$) and the net community production rates from Winkler potentiometric analyses of 12-hour ($N_{12}$) and 24-hour ($N_{24}$) incubations. The left half contains dark community respiration rates from 12-hour ($R_{12}$) and 24-hour ($R_{24}$) incubations and estimates of light respiration rates ($R_L$). Symbols correspond to mean ± 2 standard deviations.

DCR$_{24}$ and NCP$_{24}$ from the Winkler potentiometric titrations is 43 mmol C m$^{-2}$ 24 h$^{-1}$. This estimate of gross production is 62% of that derived from the $H_2$O$_{18}$ incubations; the difference is due to light respiration.

4. Discussion

Our observations indicate that the FSLE study took place during the transition from a spring bloom to a microheterotroph-dominated community. During this transition, high rates of plankton respiration contributed CO$_2$ to the mixed layer. This interpretation is based on the temporal pattern in chlorophyll a and phaeopigment concentrations, the particulate matter composition, and plankton production and respiration rates.

Between summer and winter the surface chlorophyll a concentrations on the oligotrophic West Florida Shelf are typically < 0.5 $\mu$g L$^{-1}$ [Vargo et al., 1987; Tomas, 1995]. In spring, high pigment concentrations extend south from Cape San Blas with chlorophyll a concentrations on the middle to outer Shelf > 1.0 $\mu$g L$^{-1}$ [Gilbes et al., 1996]. Ocean color imagery from 1979 to 1986 shows that the features develop in February to May. As the features propagate south, total chlo-
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Figure 6. (top) Mean gross productivity rates, as carbon, from 24-hour **N<sub>2</sub>** incubations (**G<sub>24</sub>**) and net community productivity from 12-hour (**N<sub>12</sub>**) and 24-hour (**N<sub>24</sub>**) **O<sub>2</sub>** incubations for days 4, 8, and 14. No productivity rates are available for productivity 3 (day 11) since the in situ bottles were lost. (bottom) Mean dark community respiration rates from 12-hour (**R<sub>12</sub>**) and 24-hour (**R<sub>24</sub>**) **O<sub>2</sub>** incubations, with light respiration rates (**R<sub>L</sub>**). **R<sub>L</sub>** is estimated from the difference between gross productivity (**G<sub>24</sub>**) and 12-hour net community productivity (**N<sub>12</sub>**) rates.

Chlorophyll **a** (chlorophyll **a** plus phaeopigment) concentrations can reach 3-8 µg L<sup>-1</sup>. These relatively high pigment concentrations can persist for a month, as verified by in situ sampling in 1992 and 1993 [Gilbes et al., 1996; Tomas, 1995]. The surface pigment concentrations observed in 1992 and 1993 were similar to the total chlorophyll **a** levels initially present in the tracer patch. Our observations in 1996 suggest that the postbloom transition of surface pigment concentrations is rapid, with chlorophyll **a** and phaeopigment decreasing from > 1.5 to < 0.5 µg L<sup>-1</sup> in less than a week.

Although the factors that trigger the onset of the spring pigment maxima on the West Florida Shelf have not been conclusively identified, phytoplankton growth is likely enhanced by the input of allochthonous nutrients. There are several potential nutrient sources, including (1) the rivers of the northwest Florida coast, (2) the upwelling of dense, nutrient-rich subsurface water along the Shelf break, (3) Loop Current intrusions, or (4) the advection of nutrient-rich Mississippi River water onto the Shelf [Gilbes et al., 1996]. Although the dates of initiation of the 1996 spring bloom are not known, changes in chlorophyll **a**/phaeopigment ratios suggest zooplankton grazing may have contributed to the reduction in pigment concentrations. (There is little interference from chlorophyll **b** in the estimation of phaeopigment in this region. Three years of observations indicate that chlorophyll **b** concentrations are typically < 5% of chlorophyll **a** on the West Florida Shelf (G. Vargo, unpublished data, 1999).) On April 2, chlorophyll **a**/phaeopigment ratios in the tracer patch ranged from 0.6:1 to 0.8:1; the ratio increased to > 1 by April 8. Since phaeopigments are products of microzooplankton and macro-zooplankton grazers [e.g., Buck and Newton, 1995], the low initial ratios suggest that grazing pressure may have contributed to the decrease in phytoplankton biomass observed during the first few days of the study. In summer, chlorophyll **a** concentrations exceed phaeopigment on the West Florida Shelf [Tomas, 1994], so the transition from high chlorophyll levels during the spring bloom to "typical" summer conditions can occur within a week.

The elemental composition of particulate matter indicates that a large fraction of organic matter was associated with the microbial food web (in the sense of Rassoulzadegan [1993]), rather than phytoplankton. In phytoplankton cultures, POC:Chl **a** ratios vary from minimum values of < 20, under optimal growth conditions, to typical values of 100-150 under conditions of high light, low temperatures, or nutrient stress [e.g., Laws et al., 1985; Sakshaug and Holm-Hansen, 1977; Kana and Gilbert, 1987]. Although POC:Chl **a** ratios can exceed 300 under high light levels, the average irradiance in the water column during FSLE was 35% of incident surface irradiance. The POC:Chl **a** ratio in natural phytoplankton populations has been estimated from flow cytometric methods and epifluorescence microscopy [Buck et al., 1996]. These methods have demonstrated that the phytoplankton POC:Chl **a** ratio in the North Atlantic varies as a function of latitude, with ratios > 150 in oligotrophic waters of the subtropical gyre. Although the inherent variability in POC:Chl **a** ratios limits their application as estimators of autotrophic carbon biomass [Banse, 1977; Geider et al., 1997], average ratios of POC:Chl **a** on the West Florida Shelf (> 200) were higher than ratios typically found in phytoplankton and cyanobacteria cultures under nutrient-limited conditions. The POC:Chl **a** ratios in the tracer patch are also higher than those reported by Buck et al. [1996] for the oligotrophic North Atlantic gyre. Thus a large fraction of the nondetrital POC in the tracer patch was probably associated microheterotrophs.

Ratios of PON:Chl **a** support this conclusion. Batch cultures of Skeletonema costatum (Grev.) Cleve and Pavlova lutheri (Droop) Green exhibit PON:Chl **a** ratios of 8-20 in logarithmic to stationary phase cultures under N-, P-, or Fe-limited conditions [Sakshaug and Holm-Hansen, 1977]. Thus average PON:Chl **a** ratios > 100:1 in the tracer patch were nearly five-fold higher than those in phytoplankton cultures. Molar ratios of POC:PON also suggest that the major fraction of particulate organic carbon and nitrogen was associated with microheterotrophs. The average POC:PON ratio of 3.1:1 was less than half the Redfield ratio (C:N = 6.6:1) and within the range observed in cultured marine bacteria [Goldman et al., 1979], as well as heterotrophic organisms in Georgia coastal waters [Hopkinson et al., 1989]. Detrital material, in contrast, is relatively depleted of organic nitrogen [Banse, 1974], with POC:PON ratios > 30:1 [Sambrotto and Logan, 1994].

Composition ratios of POC:POP and PON:POP further support an interpretation that a heterotrophic plankton community contributed to a large proportion of the particulate matter in the surface layer of the tracer patch. Phosphorus-limited bacterioplankton dominate the plankton biomass in the oligotrophic surface waters of the Sargasso Sea, where mean POC:POP ratios are ~ 260:1 [Cotner et al., 1997]. In these waters, PON:POP ratios vary from 24:1 to 75:1, similar to the mean PON:POP ratio of 69:1 on the West Florida Shelf. Bacterioplankton biomass in the surface waters of the oligotrophic Gulf of Mexico is phosphorus-limited [Pomeroy...
et al., 1995], although, to our knowledge, similar studies have not been conducted on the West Florida Shelf. While we lack bacterial densities in the tracer patch, or phosphorus dynamics for the plankton community, we hypothesize that a phosphorus-limited bacterioplankton population dominated plankton biomass following the end of the spring bloom [cf. Ducklow et al., 1986].

Ratios of POP:Chl a in the tracer patch also suggest that P availability limited the biomass of the plankton community. The mean ratio of POP:Chl a in the tracer patch (3:1) is similar to that in phytoplankton cultures under P-limiting conditions [e.g., Saksharg and Holm-Hansen, 1977, Table III]. In natural plankton communities, POP:Chl a ratios typically range from a minimum of 1:1 in eutrophic waters, where chlorophyll a concentrations are high, to maximum values of 5:1 in oligotrophic waters, where phytoplankton biomass is relatively low [Harris, 1986]. Thus the elemental composition of particulate matter suggests that at the termination of the spring bloom the particulate organic matter was predominantly associated with microheterotrophs; furthermore, the plankton community biomass may have been limited by phosphorus availability. The relative abundance of POC, PON, and POP in the tracer patch is similar to that observed in oceanic particulate matter as it sinks from the euphotic zone [Knaer et al., 1979; Bishop et al., 1980]. In the open sea, particulate matter is initially depleted of P, relative to C and N, as organic matter is recycled below the euphotic zone.

Production and respiration rates in the tracer patch support the conclusion that the plankton community biomass was predominantly heterotrophic with a high proportion of gross production consumed by respiration. Although phytoplankton biomass declined during the study, the phytoplankton community was actively photosynthesizing with gross production rates and assimilation ratios similar to those reported for the oligotrophic North Pacific Gyre [Williams and Purdie, 1991]. Ratios of DCR:NCP in the tracer patch were high, at an average value of 1.5:1. In phytoplankton cultures the ratio of respiration:production is typically < 0.4:1 [Langdon, 1993; Grande et al., 1989], and in temperate coastal plankton communities the ratio of DCR:NCP is low when primary production rates are high [Bender et al., 1987; Grande et al., 1991]. On the West Florida Shelf, in contrast, dark respiration reduced gross carbon production by 90% (6 versus 69 mmol C m⁻² d⁻¹). Since gross production was an order of magnitude higher than net production, and photoautotrophs typically have DCR < NCP, the respiration data suggest as well that microheterotrophs dominated the plankton community metabolism.

In photoautotrophic organisms, light respiration reduces gross production through several metabolic pathways. These include (1) photorespiration and associated glycollate metabolism; (2) the Mehler reaction, in which oxygen is produced in photosystem II and consumed in photosystem I; and (3) chlororespiration, in which NAD(P)H is oxidized in chloroplasts [Beardall and Raven, 1990]. In phytoplankton cultures, light respiration (Rₗ) typically equals or exceeds, dark respiration [Falkowsk et al., 1985; Grande et al., 1989; Kana, 1990], and in the tracer patch, Rₗ was higher than dark respiration (Figure 6). The dominant photoautotrophs in the tracer patch were Synechococcus spp., in which light respiration is primarily associated with the Mehler reaction [Kana, 1992]. In Synechococcus cultures, light respiration can exceed dark respiration at saturating light intensities [Grande et al., 1989]. However, while the Mehler reaction consumes oxygen in the light reactions of photosynthesis, carbon substrates are not oxidized. Thus light respiration may have reduced gross photosynthesis rates through the consumption of oxygen but may have released relatively little, if any, CO₂ to the surface waters.

Irrespective of any potential effects of light respiration, dark community respiration rates were more than sufficient to account for the observed increase in DIC in the tracer patch. Wanninkhof et al. [1997] attributed 80% of the observed 1 μmol kg⁻¹ d⁻¹ increase in DIC to respiration. The mean rate of DCRₚ was ~40 mmol C m⁻² d⁻¹, equivalent to an increase of 2 mmol C m⁻³ d⁻¹ (~2 μmol kg⁻¹ d⁻¹) in the 20 m mixed layer. The CO₂ contribution from dark respiration would be reduced by the net production of 6 mmol C m⁻² d⁻¹ (0.3 μmol C m⁻³ d⁻¹), yielding a net increase of ~1.7 mmol C m⁻³ d⁻¹ (1.7 μmol DIC kg⁻¹ d⁻¹). Our estimate of carbon contributed to the water column by the plankton community was therefore nearly 70% higher than the observed increase in DIC. Other factors could account for the discrepancy, including the uncertainty based on a small number of production and respiration measurements. We also have not quantified any contribution to the DIC pool from the metabolism of dissolved organic carbon released during phytoplankton excretion [see Biddanda and Benner, 1997a]. Although we cannot quantify these unknowns, we conclude that plankton community respiration was the primary source of the observed increase in DIC within the tracer patch.

Bacterioplankton are the primary organisms responsible for respiration in the sea [Williams, 1981; Cole et al., 1988], and as discussed above, they may have dominated plankton biomass in the tracer patch. Several carbon sources potentially sustained bacterioplankton respiration on the West Florida Shelf. Riverine dissolved organic matter, principally from the Mississippi River, likely provides a large flux of organic matter to the northern Gulf of Mexico. Since riverine nutrient sources may trigger the onset of the spring pigment maximum on the West Florida Shelf [Gilbes et al., 1996], riverine dissolved organic matter (DOM) may also serve as a source of organic matter to fuel bacterioplankton respiration. Phytoplankton also provided an unknown quantity of organic matter as they were grazed by microheterotrophs. A third potential source are photoautotrophs such as Synechococcus spp., which release ~10% of their carbon production as dissolved organic matter [Biddanda and Benner, 1997a, b]. Thus several sources of DOM on the West Florida Shelf can potentially support bacterioplankton respiration.

In temperate coastal ecosystems, microbial respiration rates reach a maximum 1-2 weeks after the termination of the spring bloom [Blight et al., 1995]. The lag between peak primary productivity and the seasonal maximum in microheterotrophic respiration has been attributed to the rate at which DOM becomes available to bacterioplankton [Azam et al., 1994; Blight et al., 1995]. Sherr and Sherr [1996] propose that the delay in primary production and microheterotrophic respiration in temperate marine ecosystems may be regulated by temperature, seasonal changes in bacterial growth efficiencies, or seasonal changes in the availability of DOM to bacterioplankton. The rapid response of the microheterotrophic community to a decline in phytoplankton biomass on the West Florida Shelf could reflect, in part, the relatively warm


