1981

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Role of Gulf Stream frontal eddies in forming phytoplankton patches on the outer southeastern shelf

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Abstract
Continuous surface mapping of temperature, salinity, and chlorophyll along a 300-km segment of the Gulf Stream cyclonic front defined the spatial scales of a large diatom patch that persisted throughout a 10-day study. The patch was localized in the upwelled cold core of a Gulf Stream frontal eddy centered over the 200-m isobath off Jacksonville, Florida, in April 1979. The 2 µg·liter⁻¹ surface chlorophyll isopleth enclosed an area >1,000 km² with an alongshore dimension of 130 km. Surface chlorophyll exceeded 5 µg·liter⁻¹ within the upwelled cold core of the eddy, 10–100× higher than concentrations in Gulf Stream or resident shelf surface water. Diatoms dominated the patch with the maximum observed abundance >10⁶ cells·liter⁻¹. Several days after the initial shipboard mapping, the size, location, and strong chlorophyll gradients of the patch were confirmed with a surface chlorophyll image generated from an ocean color scanner (OCS) flown aboard a NASA U-2 aircraft. We show that the upwelling associated with eddies forming along the Gulf Stream cyclonic front results in localized zones of high near-surface production and plant biomass that lie adjacent to oligotrophic surface waters of the Gulf Stream.

Seasonal phytoplankton blooms occur on the continental shelf north of Cape Hatteras, N.C. (Riley 1947, 1959; Smayda 1973, 1976; Walsh et al. 1978), but not on the outer southeastern continental shelf (Haines and Dunstan 1975; Bishop et al. 1980). Blooms in the south are short-lived, aperiodic, and are associated with episodic upwelling and intrusions of North Atlantic Central Water (NACW) onto the shelf (Dunstan and Atkinson 1976; Atkinson et al. 1978). Studies have shown that high phytoplankton biomass are generally within nutrient-enriched subsurface layers which underlay a surface mixed layer characterized by low chlorophyll (<0.5 µg·liter⁻¹) and nutrients.

During the seasons (winter and spring) of high temperature contrast between surface Gulf Stream (warm) and shelf (cold) water, satellite thermal images show meanders and other disturbances of the Gulf Stream cyclonic front. A common type of disturbance looks like a “finger” of warm water emanating from the stream which folds back to enclose a core of colder water. From satellite images Vukovich et al. (1979) showed that off the north Florida coast these features have average lengths of 136 km, widths of 36 km, and propagate north along the front with an average speed of 30 km·d⁻¹. Earlier these features were referred to as Gulf Stream spin-off eddies (e.g. Lee 1975) but are now called frontal eddies (Lee et al. 1981). An important point is that these frontal eddies are distinct from the larger cold-core Gulf Stream rings that detach from the stream north of Cape Hatteras and move into the Sargasso Sea. The cold core of a frontal eddy is a result of upwelling of NACW (Lee et al. 1981), not of entrainment of a resident slope.

1 This work was supported by U.S. Department of Energy contracts EY-76-S-09-0036, EY-76-S-09-0889, EY-76-S-05-5163, and by the National Aeronautics and Space Administration. Shiptime was provided under NSF grant OCE76-01142 to G.-A. Paffenholzer.
phytoplankton bloom which occurred within the core of an eddy studied in April 1979. Our data provide evidence that a significant proportion of upwelled nutrients is used by phytoplankton and that resultant phytoplankton blooms probably are important in the food chain dynamics of the outer southeastern shelf.

We thank the captain and crew of the RV Gilliss. Technical assistants were C. Baker, S. Bishop, B. Chandler, W. Hart, E. Hofmann, and S. Lasley. D. Menzel made helpful comments and we especially thank G.-A. Paffenhofer.

Methods

The study area (Fig. 1) was intensively sampled by ship 20–22 April 1979. During the cruise we received satellite-derived Gulf Stream front analyses indicating the presence of an eddy near 29°N on 19 April. The satellite information and our experience in sampling eddies in 1977 and 1978 were used to design the cruise track (Fig. 2). Turning points were determined from shipboard measurements of sea surface temperature, which indicated the position of the Gulf Stream front and the eddy.

For surface mapping, water was pumped from a small sea chest about 2 m below the waterline into a debubbler one deck above the laboratory. Water flowed from the debubbler (ca. 20 liters·min⁻¹) through a Turner Designs model 10 fluorometer, into the salinity chamber of a thermosalinograph, and then into a bucket enclosing the temperature and salinity sensors of a Grundy (Plessy) CTD. The temperature probe of the thermosalinograph was mounted to the sea chest and was, therefore, the sensor closest to source water. Temperatures recorded by the thermosalinograph and the CTD agreed within 0.2°C. The temperature and salinity data presented here are from the CTD, which was calibrated with procedures described by Chandler et al. (Tech. Rep. Ser. No. 78-7, Georgia Mar. Sci. Center). Digitized signals from the fluorometer and CTD were logged every 10 s by a Hewlett-Packard 9825 desktop computer.
Eddies and phytoplankton patches

Discrete water samples, collected every 30–90 min from a valve in line with the instruments, were analyzed for chlorophyll a and pheopigment (Yentsch and Menzel 1963, as modified by Strickland and Parsons 1968). We tried to obtain discrete samples at fluorometer readings within the entire range of observed in vivo fluorescence. In vivo fluorescence was calibrated against extracted chlorophyll a + pheopigment (Strickland and Parsons 1968). The FO:FA ratio of extracted pigment generally exceeded 1.8, indicating a high proportion of chlorophyll a. Except for one 36-h period (28–29 April), we used a single linear regression to relate in vivo fluorescence to extracted pigment (n = 42, r = 0.95, C.V. of the slope = 5.1%, intercept not significantly different from 0.0 and only 2% of a reading indicating 5 µg·liter⁻¹ of Chl a). Other measurements summarized here (nutrients, primary production, and phytoplankton species composition) were made as by Bishop et al. (1980).

Results

Transects across the study area are identified by letter (A–U) going south to north starting at Cape Canaveral, Florida (Fig. 2). Results of the surface survey between 20 and 22 April 1979 are shown. The Gulf Stream surface front is characterized by the strong thermal gradient between 23°C and 26°C. The area of strong upwelling, indicated by waters of <21°C, was situated at 30°N. Upwelling velocities associated with disturbances of the Gulf Stream cyclonic front are of the order of 10⁻² cm·s⁻¹ (Deschamps et al.: Tech. Rep. Ser. No. 79-1, Georgia Mar. Sci. Center). The lobe of 23°C water west and northwest of the 21°C core is warmer Gulf Stream water and is the fingerlike structure referred to earlier. Although the length of the frontal eddy was not determined from shipboard measurements, VHRR satellite imagery showed that the feature was about 200 km long on 20 April. The slightly lower salinity (36.0‰) of the upwelled cold core of the eddy is
consistent with the observed T-S relation of NACW located beneath the surface mixed layer of the Gulf Stream.

The surface manifestation of the phytoplankton patch was centered over the 200-m isobath and extended shoreward as far as the 40-m isobath at the widest point, just north of 30°N. The 2 µg·liter⁻¹ chlorophyll isopleth enclosed an area of about 1,100 km² with an alongshore dimension of almost 130 km (Fig. 2). The northern extension of the 1 µg·liter⁻¹ isopleth was not closed off by the sampling grid, but the area covered would be about 25–50% greater than that covered by the 2 µg·liter⁻¹ isopleth if the trends north of 31°N follow those observed farther south. On the seaward side of the front, the chlorophyll concentration of surface Gulf Stream water was only 2% (ca. 0.1 µg·liter⁻¹) of the peak concentration (>4 µg·liter⁻¹) within the patch. On the shelf side of the patch, surface concentrations were <0.5 µg·liter⁻¹ or about 10% of the maximum values observed within the patch. In the absence of upwelling, surface chlorophyll is often near 0.1 µg·liter⁻¹ across the entire shelf seaward of the 20-m isobath (Bishop et al. 1980).

Figure 3 illustrates surface temperature and chlorophyll structures along six crossings of the Gulf Stream front. Results from those transects which cross latitude lines (and thus isobaths) at an oblique angle are presented as if the transect were parallel to latitude. Surface chlorophyll was dramatically different at the position of the eddy core (zone of upwelling) from that farther south. South of 29°30'N, the cross-shelf dimension of a band of high surface chlorophyll was 1–5 km with peak concentrations near 1 µg·liter⁻¹. The band was widest (ca. 40 km) and peak concentrations were greatest (>4.0 µg·liter⁻¹) where we found the coldest (<21°C) surface temperatures. South of 29°30'N, the chlorophyll band, just shoreward of the Gulf Stream front, was associated with a drop in surface temperature. North of 30°N, the band spread shoreward from the front (transects P and T: Fig. 3).

The vertical section of temperature, nitrate, and chlorophyll shown in Fig. 4 (transect Q in Fig. 2) is typical of those taken through a cold-core frontal eddy in this area (Lee et al. 1981). Doming of isotherms suggests a cyclonic circulation that has, in fact, been observed from ship drift and current meter observations. A current meter mooring at the 75-m isobath at 31°30'N (Fig. 2) showed southward flow in the near-surface layer (17 m) from 15–27 April, accompanied by a decrease of 4.5°C in near-bottom temperature. This is the characteristic current and temperature signature of a Gulf Stream frontal eddy (Lee et al. 1981). Southward currents were greatest (30–40 cm·s⁻¹) on 18 and 25 April. On 27 April, surface currents (17 m) rotated back to the north, signifying the passage of the eddy from the study area. The density structure at transect Q implies northward currents off-
shore of station 70C, with southward currents onshore. The lens of warmer surface water near station 66C is the lobe of southward-flowing Gulf Stream water (Fig. 4), which can also be seen in the surface temperature plot (Fig. 2). The colder water between stations 68C and 70C is recently upwelled. The only significant source of nitrate for the outer southeastern shelf is upwelling and intrusion of NACW (Lee et al. 1981). Since nutrient concentrations are inversely proportional to temperature below 22°C (Atkinson; Tech. Rep. Ser. No. 78-1, Georgia Mar. Sci. Center), the degree of upwelling critically determines near-surface nitrate concentration. Surface temperatures of 21°C imply initial nitrate concentrations within the upwelled water of 5 µg-atoms NO₃-N·liter⁻¹ or less.

Subsurface sampling along transects O and S yielded results similar to those shown in Fig. 4; but since these were the only other subsurface nutrient and chlorophyll samples collected during the initial mapping of the shelf break, the vertical structure south of 30°N is not known. The results from transect Q (Fig. 4) show that the high surface chlorophyll concentrations were located above the dome defined by nitrate isopleths ≥1 µg-atom N·liter⁻¹. Chlorophyll isopleths extended beneath the surface another 20 km shoreward of their surface manifestations and were associated with nutrient-enriched water that intruded onto the shelf.

Beginning on 28 April (6 days after the initial mapping of the shelf break), four transects, 12 h apart, were completed along the original position of transect S (near 30°40'N). From the record of the 17-m current meter at 31°30'N and using an eddy propagation speed of 35 cm·s⁻¹ (Vukovich et al. 1979; Lee et al. 1981), we estimate that these four transects began about 3 days after the frontal eddy mapped on 20–22 April had passed by transect S. On the first transect, surface chlorophyll reached 7.5 µg·liter⁻¹, but it was only about 2 µg·liter⁻¹ 1.5 days later. The band of high surface chlorophyll was still located just shoreward of the cyclonic side of the Gulf Stream front, with a cross-shelf dimension identical to that observed earlier (ca. 20 km). Vertical sampling at selected stations showed...
these high concentrations reached depths of 20-25 m. Wind mixing of subsurface nutrients into the near-surface layer may have led to the high surface chlorophyll concentrations that we observed on the first of the four transects. The transects began 2 days after a severe storm interrupted our sampling of the area. The 2-day storm had sustained winds of 20 m s\(^{-1}\) from the east on 25 April, which decreased and shifted to the south (upwelling-favorable) on 26 April as a cold front and trailing low passed over the area. The storm probably contributed to further upwelling and certainly increased the rate of vertical mixing. Despite high winds and their potential effect on the near-surface layer, 2 days after the storm the chlorophyll band was still centered over the 200-m isobath.

A surface chlorophyll map of the study area was generated by an ocean color scanner (OCS) flown aboard a NASA U-2 aircraft on 28 April (Kim et al. 1980). The aircraft coverage did not define the entire alongshore dimension of the chlorophyll feature, but the image showed surface chlorophyll concentrations exceeding 5 \(\mu g\) liter\(^{-1}\) within a 10-km-wide band extending along the Gulf Stream front for more than 90 km. Shipboard measurements concurrent with the overflight showed that the location of the chlorophyll band was identical to that observed earlier (i.e. centered over the 200-m isobath) and that the image was an accurate representation of near-surface gradients in chlorophyll \(a\) + pheopigment \(a\) (Kim et al. 1980). A false color reproduction of the image is available on request.

On three separate days following initial surface mapping, we determined rates of primary production within the chlorophyll-rich surface band along the original position of transect S (near 30°40'N). Within the upper 10 m of the water column, primary production ranged from 1.2 to 2.4 g C m\(^{-2}\) d\(^{-1}\) with assimilation numbers of 15-19 mg C mg Chl \(a\)\(^{-1}\) h\(^{-1}\). Primary productivity in the water column was as high as 6 g C m\(^{-2}\) d\(^{-1}\) with a euphotic zone depth of 25–40 m. Diatoms dominated the phytoplankton, with maximum observed concentrations of \(7.3 \times 10^6\), \(4.3 \times 10^6\), and \(2.6 \times 10^7\) cells liter\(^{-1}\) for \(Skeletonema\) \(costatum\), \(Nitzschia\) sp., and a small \(Chaetoceros\) sp. The maximum observed concentration of total diatoms at a single station was \(1.8 \times 10^6\) cells liter\(^{-1}\).

Discussion

Our study determined the spatial scales of a diatom patch that formed in response to eddy-forced upwelling at the shelf break of the southeastern shelf. Except during blooms of the blue-green \(Oscillatoria\) sp. (Dunstan and Hosford 1977), previous investigators, with one exception, have not reported high surface chlorophyll or primary production on the outer southeastern shelf. Bishop et al. (1980) observed high surface chlorophyll (>5 \(\mu g\) liter\(^{-1}\)) at a single station near the shelf break during January and presented evidence that upwelling was also responsible for these high concentrations. Our results show that the surface chlorophyll field of the outer shelf is dramatically influenced by upwelling associated with Gulf Stream frontal eddies. The diatom patch that we observed covered > 1,000 km\(^2\) with maximum chlorophyll concentrations 10–100× higher than typical values for surface Gulf Stream water off the southeastern shelf and for the shelf proper in the absence of upwelling (Haines and Dunstan 1975; Dunstan and Atkinson 1976; Atkinson et al. 1978; Bishop et al. 1980; Yoder unpubl.). The patch remained identifiable for the duration of our study (10 days) and remained centered over the 200-m isobath. We are not sure whether the duration of the patch is typical of upwelling associated with Gulf Stream frontal eddies, since the severe storm during our study probably brought additional nutrients into the euphotic zone.

The location of the patch near the Gulf Stream front complicates the interpretation of patch formation and its stability. High surface chlorophyll concentrations on other continental shelves are associated with fronts not related to upwelling (Pingree et al. 1978; Fournier 1978; Iver-
son et al. 1979). However, the mechanisms invoked to explain these associations do not apply to the southeastern shelf. On the continental shelf off England and France (Pingree et al. 1978) and off Nova Scotia (Fournier 1978), an elevated pycnocline near the front decreases the mixing depth of the surface phytoplankton population. As a result, phytoplankton blooms develop in response to relatively high mean levels of irradiance within a nutrient-rich surface layer. This mechanism cannot operate on either side of the Gulf Stream cyclonic front off the southeastern shelf, as both resident shelf and Gulf Stream mixed-layer water have very low concentrations of nitrate and other plant nutrients (e.g. Haines 1974; Dunstan and Atkinson 1976; Bishop et al. 1980). Convergent flow in frontal zones has also been used to explain high surface concentrations of particulate matter, specifically those particles which are positively buoyant (Okubo 1978). This explanation cannot be solely responsible for the presence of the patch we observed. Phytoplankton were dominated by diatoms, which are not positively buoyant (Smayda 1970), and the very high rates of primary production and high assimilation numbers show that the patch was not formed by an accumulation of physiologically inactive cells. The hydrographic data presented in Fig. 4, similar data acquired during other studies of frontal eddies (Lee et al. 1981), phytoplankton species composition, and high phytoplankton assimilation numbers show that the patch we studied formed in response to upwelling—i.e., high rates of vertical advection and diffusion of nutrients into the euphotic zone. This interpretation is also supported by our observation that the highest chlorophyll values were associated with the coldest surface water indicative of the most intense upwelling.

The southeastern continental shelf was originally characterized as relatively unproductive (Haines and Dunstan 1975), with either recycled nutrients (Haines 1974) or outwelling of nearshore nutrients (Turner et al. 1979) supporting most of the outer shelf production. This view was challenged once NACW was identified as an important source of nutrients (e.g. Atkinson et al. 1978; Bishop et al. 1980). Our study supports the latter contention and defines a dimension (eddy scale) apparently important to outer shelf primary production and to the distribution of chlorophyll. Since frontal eddies pass a fixed point on the outer shelf on the average of once every 2 weeks throughout the year, the eddy scale of high surface chlorophyll and primary production on the outer shelf may be the rule rather than the exception.

Phytoplankton response to eddy-forced upwelling in winter and spring may partially explain why fish overwinter and spawn on, or near, the shelf break of the southeastern shelf. This area is one of the major spawning grounds of Atlantic menhaden (Brevoortia tyrannus) (Nelson et al. 1977; Nicholson 1978), bluefish (Pomatomus saltatrix) (Kendall and Walford 1979), and other species (Powles and Stender: Tech. Rep. Ser. II, S.C. Mar. Resour. Center, Charleston; Berrien 1978). Adult menhaden and bluefish from the entire east coast of North America migrate south of Cape Hatteras, N.C., during fall. High primary production associated with eddy-forced upwelling may directly support the adults of those species that can feed directly on phytoplankton (e.g. menhaden), and the larger chain-forming diatoms may be an important source of food for larval stages of all fish species that breed on the outer southeastern shelf.

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