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# Phytoplankton species composition and abundance in a Gulf Stream warm core ring. I. Changes over a five month period

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## ABSTRACT

During the spring and summer of 1982, Gulf Stream warm core ring (WCR) 82B was sampled during four cruises from April to August to investigate the changes in the phytoplankton flora with time. Discrete water samples from 28 stations were collected for identification and enumeration of phytoplankton.

The spring increase in WCR 82B occurred from late April to mid-May and was multiphasic; early periods were dominated by the diatoms *Minidiscus trioculatus* (4–5  $\mu\text{m}$  diam.) and a small *Thalassiosira*, possibly *T. bulbosa*, while later periods were dominated by a small (2–3  $\mu\text{m}$ ) biflagellate. In June, another diatom concentration was detected at ring center, but this one was dominated by *Chaetoceros* cf. *vixibilis* and *Leptocylindrus danicus*. After interactions with and overwashes by the Gulf Stream and Slope Water in July, diatom numbers in the surface waters of the ring in August were greatly reduced relative to June, and no single species dominated.

Changes in phytoplankton abundance in the ring core occurred on different time sequences from changes in the surrounding Slope Water or in the source water, the Sargasso Sea. The dominant taxa in the ring changed rapidly, on time scales of 1.5 months or less (intercruise time period). Successional changes were more important in altering the phytoplankton composition during the first two cruises, while sequential changes characterized the end of the study period. The ring center showed dramatic differences from its source water just 2 months after ring formation but remained distinct from the Slope Water for 4–5 months.

## 1. Introduction

As the Gulf Stream breaks away from the east coast of the United States and flows eastward across the North Atlantic Ocean, meanders develop in the current, fold back on themselves, and occasionally pinch off to form isolated, rotating bodies of water known as rings (Joyce and Wiebe, 1983). If the rings form south of the Gulf Stream, they rotate cyclonically and have a central core of cool, low salinity Slope Water; hence the name cold core rings (CCR) is used. If the rings form north of the Gulf Stream, they rotate anticyclonically and the central core consists of warm, saline Sargasso Sea water; these are called warm core rings (WCR). In either case, the higher-speed

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current bordering the ring is a Gulf Stream remnant. Gulf Stream rings, and their counterparts in other major current systems in the ocean, are effective transporters of energy, heat, salt, nutrients, pollution, and organisms (Robinson, 1983) and serve to "mix" the waters through which they move (Olson *et al.*, 1985; Yentsch and Phinney, 1985). The temperature and salinity anomalies within a ring can extend to the sea floor at 4000 to 5000 m (The Ring Group, 1981; Joyce, 1984), and the passage of a ring can affect bottom currents (Weatherly and Kelley, 1985; Mulhearn *et al.*, 1986). Warm core rings entrain Shelf, Slope, and Gulf Stream waters, and this entrainment can affect processes outside the ring, such as larval fish survival in the New England fisheries (Flierl and Wroblewski, 1985), as well as physical, chemical, and biological distributions within the ring (Brown *et al.*, 1983; Joyce *et al.*, 1983, 1984; Joyce and Stalcup, 1984; Nelson *et al.*, 1985).

In 1981, a large, multidisciplinary project involving 25 principal investigators from 13 research and academic institutions was initiated to investigate the biological, chemical, and physical processes occurring in warm core rings (The Warm Core Rings Executive Committee, 1982; Joyce and Wiebe, 1983). With regard to the phytoplankton, the original hypothesis at that time proposed that the species composition of a WCR would gradually change from a Sargasso Sea flora to an assemblage resembling that found in the Slope Water surrounding the ring.

The phytoplankton assemblages of WCRs 81D and 82H have been studied during the fall of subsequent years. Ring 82H was sampled as it pinched off from the Gulf Stream in October 1982; 81D was three months old when it was visited in October 1981. Although the age of the ring is a critical factor in determining the proportion of Slope Water species in the ring (Fryxell *et al.*, 1985), it is not as important in other respects. For example, these two rings not only shared many of the same dominant taxa, they also shared similar concentrations of cells (Gould *et al.*, 1986). Stations from one ring frequently grouped with stations from the other ring when clustering techniques or principal component analyses were employed (Fryxell *et al.*, 1985; Gould *et al.*, 1986). Also, dinoflagellates were abundant at the Slope Water and ring edge stations, while diatoms and coccolithophorids responded rapidly to storm-induced mixing and thrived at ring center (Fryxell *et al.*, 1984, 1985; Gould *et al.*, 1986; Herzig, 1988). Taxonomic studies of the diatom genera *Thalassiosira* and *Nitzschia* have been carried out (Fryxell *et al.*, 1984; Herzig and Fryxell, 1986; Kaczmarzka and Fryxell, 1986) and certain species of these genera show promise as indicators of water masses and nutrient dynamics in the northwest Atlantic (Fryxell *et al.*, 1984; Herzig, 1988; Kaczmarzka *et al.*, 1986).

Changes in phytoplankton biomass (as measured by chlorophyll *a* concentration) in WCR 82B have been examined by several investigators during the five month period from April to August, 1982. Three distinct phases in the evolution of the chlorophyll structure were observed. Smith and Baker (1985) sampled rapidly along transects in an asterisk pattern to gain wide spatial coverage of the ring, while Hitchcock *et al.*

(1985) devoted more time to studies at ring center. First, a period of deep convective overturn during the winter and lasting until May resulted in uniformly low chlorophyll concentrations to a depth of 400 m. Following this was a stratification phase in May and June; subsurface (20–30 m) pigment maxima were now apparent with relatively high concentrations at ring center (also see Nelson *et al.*, 1985). During the final period (July and August) the ring repeatedly interacted with the Gulf Stream and experienced overwashes of low pigment water from outside the ring.

During the spring and summer of 1982, one WCR, 82B (the second warm core ring formed in 1982), was tracked by satellite (Evans *et al.*, 1985) and sampled periodically on three multiple-ship cruises throughout a five month period to investigate the changes in the ring flora with time. The objectives of this research are to: (1) determine the changes in phytoplankton species composition and abundance at ring, Sargasso Sea, and Slope Water stations over a five month period; (2) compare the ring flora to the Sargasso Sea and the Slope Water floras, and; (3) provide a synthesis of evolution of WCR 82B. The present study provides a unique opportunity to follow sequential changes in the phytoplankton population of an evolving, semi-enclosed parcel of water during a dynamic period in its lifetime.

## 2. Methods

*a. Data collection.* Samples were collected during four cruises to WCR 82B from April to August, 1982. All cruises originated from and returned to Woods Hole Oceanographic Institution (WHOI), Woods Hole, Massachusetts. R/V *Knorr* Cruise 93 (19 April–6 May) visited 82B during a period when deep convective overturn was still evident, with homogeneous temperature and salinity to a depth of 400 m at ring center. Additional samples were provided by P. Glibert from a ship-of-opportunity cruise in late May (*Knorr* Cruise 94). *Knorr* Cruise 95 (12 June–29 June) occupied stations during the summer stratification period, when a sharp thermocline was present at 25–35 m. *Knorr* Cruise 97 (7 August–24 August) followed a period of interaction between the Gulf Stream and the ring in late July. See Figure 1 and Table 1 for station locations. Only water samples are discussed in this paper (see Gould, 1988, for discussion of net samples). In Table 1, the first number of "Event" is the month, the next two are the day, and the last two (to the right of the decimal) represent the sequential operation number for that day. For example, 426.01 was the first operation on 26 April.

The ring center position was estimated from drifter trajectories and satellite imagery and a polar coordinate scheme ( $r, \theta$ ) was used to indicate the station positions relative to a translating ring center (Hooker and Olson, 1984). Stations from the ring center, ring edge, Slope Water, Gulf Stream, and Sargasso Sea were occupied. Also, two transects in an "X" pattern were taken across the ring in June to provide horizontal coverage (see Gould and Fryxell, 1988, this issue).

Discrete water samples were collected at 28 stations, from generally six or nine

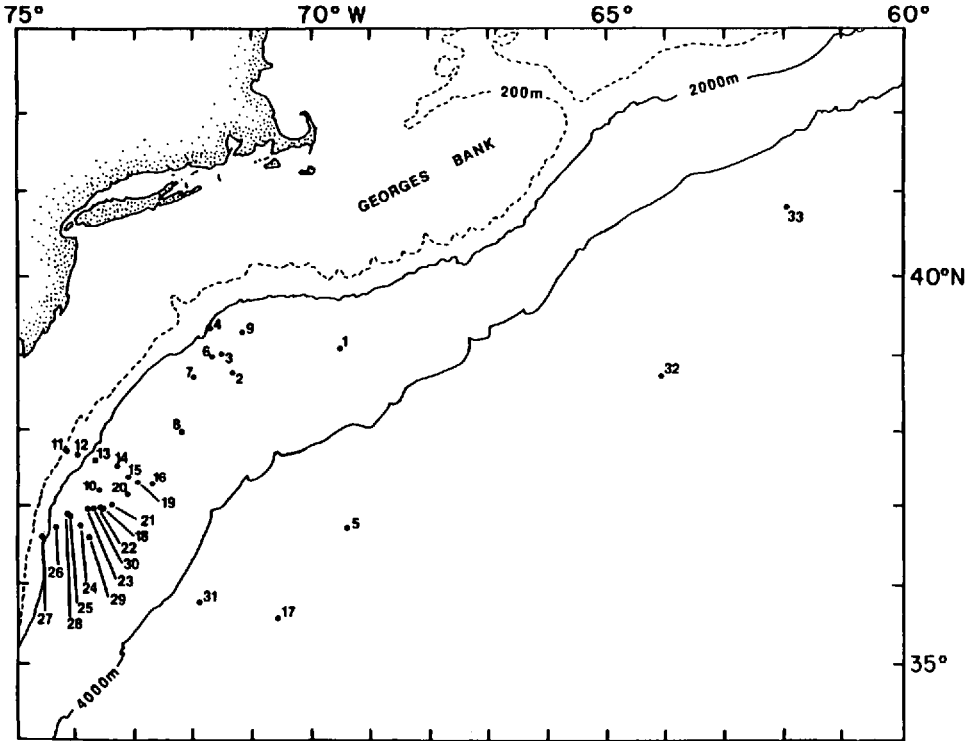


Figure 1. Station locations. Station numbers correspond to locations in Table 1.

Table 1. Locations of sample sites in and around Warm Core Ring 82B. Station numbers correspond to numbers on Figure 1.  $r$  = station distance (in km) from ring center,  $\theta$  is the clockwise angle from north around the ring, WS = water sample, Net = standard phytoplankton net tow, MOC = MOCNESS tow, SL = Slope Water, RC = ring center, HVR = high velocity region, SS = Sargasso Sea, T1 = first June transect, T2 = second June transect, GS = Gulf Stream.

Station	Event	Lat. (N)	Long. (W)	$r$	$\theta$	WS	Net	MOC	Location
1	420.08	39° 5.0'	69° 29.0'	158.9	84.1°			X	SL
2	422.09	38° 47.2'	71° 20.8'	17.0	158.1°			X	RC
3	426.01	39° 0.1'	71° 29.8'	13.6	44.8°	X			RC
	426.03	38° 59.9'	71° 30.0'	13.8	47.1°		X		
	426.06	39° 0.2'	71° 29.7'	14.9	48.0°	X			
	426.10	38° 54.2'	71° 21.8'	23.6	92.4°			X	
4	429.01	39° 20.0'	71° 56.2'	50.0	343.2°	X			HVR
	429.11	39° 22.6'	71° 41.2'	53.6	9.5°		X		
	429.17	39° 22.7'	71° 31.7'	57.7	23.0°			X	
5	501.01	36° 41.7'	69° 25.3'	313.0	141.4°		X		SS
	501.02	36° 42.5'	69° 24.7'	312.2	141.2°	X			
	501.13	36° 45.5'	69° 18.4'	311.6	139.7°			X	

Table 1. (Continued)

Station	Event	Lat. (N)	Long. (W)	<i>r</i>	$\theta$	WS	Net	MOC	Location
6	503.08	38° 55.4'	71° 39.6'	9.2	332.9°			X	RC
	504.01	38° 57.3'	71° 39.8'	14.6	340.9°	X			
	504.04	38° 57.7'	71° 39.5'	15.5	343.6°		X		
7	519.01	38° 44.2'	71° 57.7'	40.0		X			HVR
8	603.01	37° 55.8'	72° 13.5'	51.2		X			HVR
9	613.05	39° 18.5'	71° 14.5'	284.4	41.0°	X			SL
	613.11	39° 23.0'	71° 9.6'	298.7	40.9°			X	
	613.13	39° 24.0'	71° 9.1'	301.4	40.8°		X		
10	615.01	37° 10.5'	73° 36.9'	17.1	240.0°			X	RC
11	616.02	37° 43.6'	74° 8.2'	84.0	319.4°	X			T1
12	616.04	37° 41.7'	73° 58.2'	72.6	327.1°	X			T1
13	616.06	37° 38.1'	73° 38.7'	56.9	350.3°	X			T1
14	616.08	37° 33.9'	73° 20.3'	53.0	20.3°	X			T1
	616.10	37° 32.1'	73° 15.9'	53.5	28.2°		X		
15	617.01	37° 24.4'	73° 7.0'	53.2	49.3°	X			T1
16	617.03	37° 19.6'	72° 44.1'	79.4	70.7°	X			T1
17	618.03	35° 40.1'	70° 30.1'	317.3	119.4°		X		SS
	618.08	35° 33.3'	70° 33.1'	320.9	121.4°	X			
	618.11	35° 30.8'	70° 33.3'	323.8	122.0°			X	
18	620.12	36° 54.4'	73° 33.8'	20.3	122.0°			X	RC
19	623.01	37° 20.7'	72° 57.1'	96.5	61.5°	X			T2
20	623.03	37° 8.2'	73° 9.2'	71.6	70.9°	X			T2
21	623.06	36° 59.7'	73° 24.3'	47.3	79.7°	X			T2
22	625.01	36° 56.9'	73° 35.4'	29.3	75.3°	X			T2
23	625.03	36° 54.9'	73° 47.7'	10.6	66.9°	X			RC
24	625.07	36° 42.3'	73° 53.1'	18.2	177.1°		X		RC
25	624.07	36° 50.1'	74° 5.2'	16.0	245.4°	X			RC
26	624.04	36° 42.9'	74° 24.4'	46.9	244.1°		X		T2
	624.03	36° 42.2'	74° 24.2'	47.4	242.5°	X			
27	624.01	36° 36.0'	74° 36.5'	68.8	240.6°	X			T2
28	626.21	36° 52.9'	74° 7.1'	22.9	281.1°			X	RC
29	809.07	36° 37.4'	73° 49.1'	18.5	230.4°	X			RC
	809.09	36° 35.7'	73° 41.1'	16.1	191.0°			X	
	809.10	36° 34.9'	73° 47.0'	21.3	214.4°		X		
30	811.04	36° 55.4'	73° 42.0'	16.3	294.4°		X		RC
	811.06	36° 55.1'	73° 41.3'	15.2	292.7°			X	
	812.03	36° 58.1'	73° 40.9'	18.4	290.4°	X			
31	813.02	35° 44.2'	71° 51.9'	202.7	133.6°	X			SS
	813.03	35° 44.0'	71° 51.9'	203.4	133.7°			X	
	813.05	35° 40.7'	71° 54.9'	205.3	135.9°		X		
32	815.01	38° 32.0'	64° 4.5'	888.0	79.1°		X		GS
	815.06	38° 54.7'	63° 56.0'	915.5	76.6°	X			
33	818.02	40° 50.0'	61° 49.5'	1194.4	67.6°			X	SL
	818.04	40° 50.2'	61° 49.6'	1197.5	67.5°	X			
	818.05	40° 50.2'	61° 49.6'	1198.1	67.5°		X		

depths, using a 12-bottle Neil Brown CTD rosette system. If nine depths were taken, they corresponded to the 100, 60, 36, 22, 8, 3, 1, 0.3, and 0.1% incident light levels, as determined by an irradiance profile prior to the CTD cast. If fewer depths were taken, as along the two June transects (6), they corresponded to hydrographic features of interest (such as temperature, salinity, or oxygen anomalies) in the upper 110 m, as determined on the downward portion of the CTD cast. One station had only two depths (603.01), two other stations had three depths (519.01 and 815.06), and one station had 12 depths (429.01). Two 30 l Niskin "Go-Flo" bottles were tripped at each depth and drained with a section of tygon tubing into 90 l polypropylene vats to give a homogeneous sample from which all the investigators could subsample. Aliquots (500 ml) from the vats were preserved with hexamine buffered formalin to a final concentration of 1% (Thronsdon, 1978) and transported back to the lab at Texas A&M University for examination.

Examination of whole water samples generally provides a better estimate of patterns of nanoplankton abundance than netplankton abundance, because the small cells are more abundant and therefore more likely to be observed in settled water samples. At most oceanic stations the larger cells are rare and require concentration by net before reliable numbers of cells can be observed. See Gould (1988) for a more detailed discussion of the netplankton in WCR 82B.

*b. Data analysis.* The unconcentrated water samples were settled and cells enumerated using the Utermohl technique for the inverted microscope (Hasle, 1978a, b), with 50 or 100 ml settled as needed. A Zeiss ICM-405 microscope was used with phase contrast or brightfield illumination, at 160 $\times$  or 400 $\times$ , as needed. Three hundred consecutive cells were counted to attain a 95% probability of finding an organism present at the 1% relative abundance level in the population, assuming the cells are randomly distributed in the chamber (Shaw, 1964). Empty cells were distinguished and tabulated separately from cells containing cytoplasm. Two settled chambers were examined for each sample; in one chamber, cells were identified to species when possible, and in the other only to group (i.e., diatom, dinoflagellate, coccolithophorid, or other). These two counts (from a single sample) were averaged for each of the four phytoplankton categories for use as group counts. The location of specimens difficult to identify during the counting procedure was noted, and these cells were later examined at 1000 $\times$ . The species cited in the text are listed in the Appendix with their respective authorities.

The taxa observed were assigned to one of four major phytoplankton groups: diatoms, dinoflagellates, coccolithophorids, or other algae. The "other" category contains all cells not contained in the first three categories. Included are silicoflagellates, chlorophytes, prymnesiophytes, cryptophytes, chrysophytes, prasinophytes, and cyanophytes. Most of these taxa could not be distinguished below the class level in water mounts under the light microscope. The "others" were the numerically dominant

group, accounting for approximately 67% (mean) of the total phytoplankton cell numbers. By far, the dominant component in the "other" group in all samples was a coccoid, unicellular monad (without flagella in the preserved samples) approximately 1–3  $\mu\text{m}$  in diameter. Fluorescent microscopy on board ship and later pigment analysis and transmission electron microscopy (Herzig, unpublished observations) showed the presence of at least two major algal groups in the monad category, a cyanophyte, possibly *Synechococcus*, and a chlorophyte similar in appearance to *Chlorella*.

The quantitative estimates of the abundant components of the phytoplankton (abundant enough to be seen without prior concentration by net or filter) were compared to assess variation with depth, variation between stations, and variations at a single location over time. The principal component analysis (PCA) was done with the Statistical Analysis System (SAS) and is based on the correlation matrix.

The continuous CTD data (temperature, salinity, oxygen) were collected by T. Joyce.

### 3. Results

The diatoms increased in abundance at ring center during the course of the April/May cruise (Fig. 2). The largest increases occurred in the surface waters between 26 April and 4 May. Although the ring was only two months old, it already showed dramatic differences from its source water, the Sargasso Sea; diatom numbers at ring center were an order of magnitude greater than Sargasso Sea numbers.

Coccolithophorids did not show the same dramatic increases as the diatoms at ring center, although there was some growth during the course of the cruise (Fig. 2). Maximum numbers of this group were found at the ring edge, and the abundances at ring center were approximately 25% of those in the Sargasso Sea.

In April, dinoflagellates were in low abundance at all stations and did not show increases in numbers until mid-May to early-June at the ring edge (Fig. 3).

The other algae showed a two to three fold increase at ring center over the eight day period from 26 April to 4 May, but the direction of that change was already indicated between the morning and afternoon stations on 26 April (Fig. 3).

In each group plot, large relative differences in abundance were noted between the morning and afternoon stations on 26 April. The temperature and salinity data from the CTD did not indicate a major water mass change, but a drop in salinity of 0.05 suggests small scale advective patchiness; a streamer from the ring edge may have penetrated to the center. Species composition data support this explanation (see Gould and Fryxell, part II, 1988, this issue).

The other algae were the numerically dominant group at all stations during this cruise, and the dinoflagellates were generally the least abundant, but there were shifts in dominance between the diatoms and coccolithophorids at the various stations (Figs. 2, 3). At the morning station on 26 April, coccolithophorids greatly exceeded the



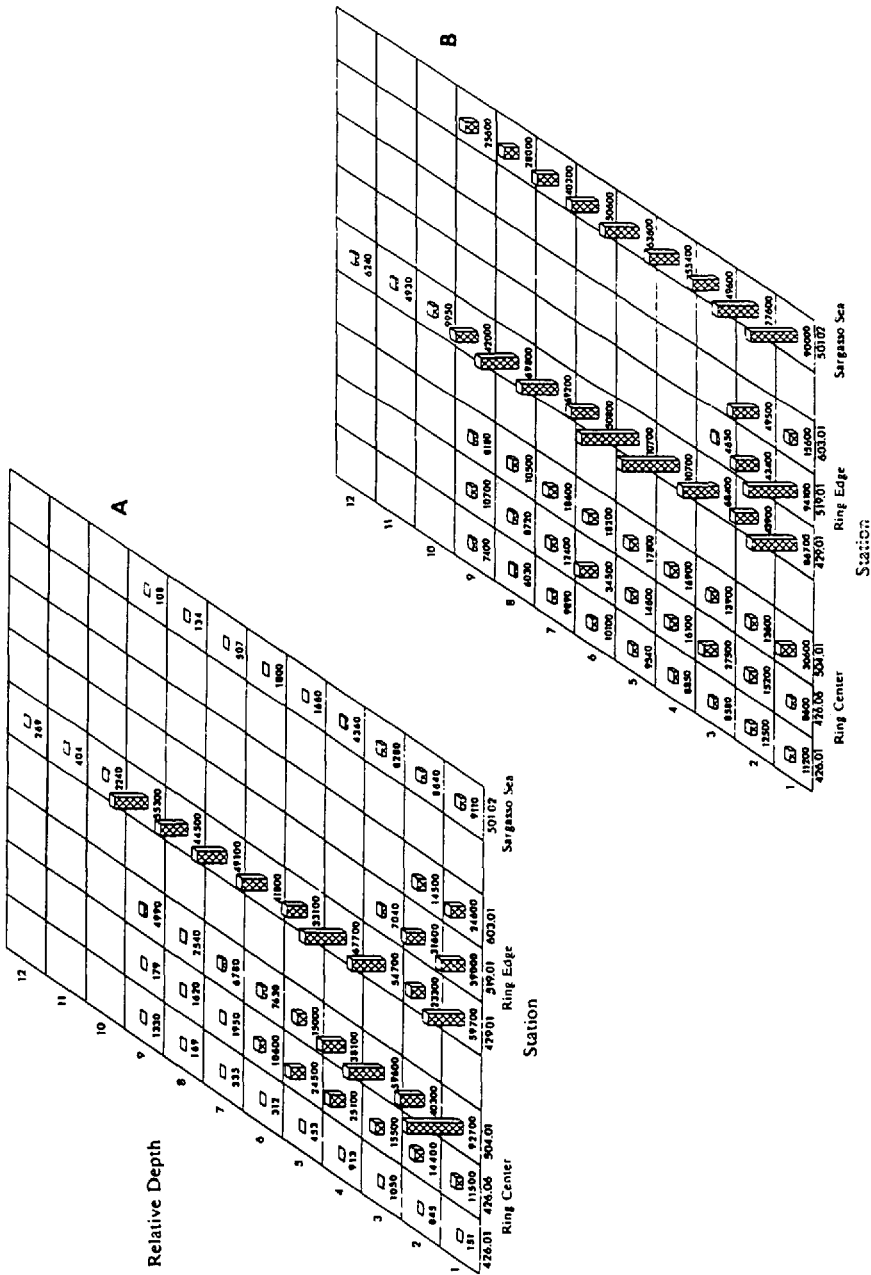


Figure 2. Vertical distribution of diatoms and coccolithophorids, April/May. (A) Diatoms. (B) Coccolithophorids. Abundances in cells l<sup>-1</sup>. Note the different abundance scales.

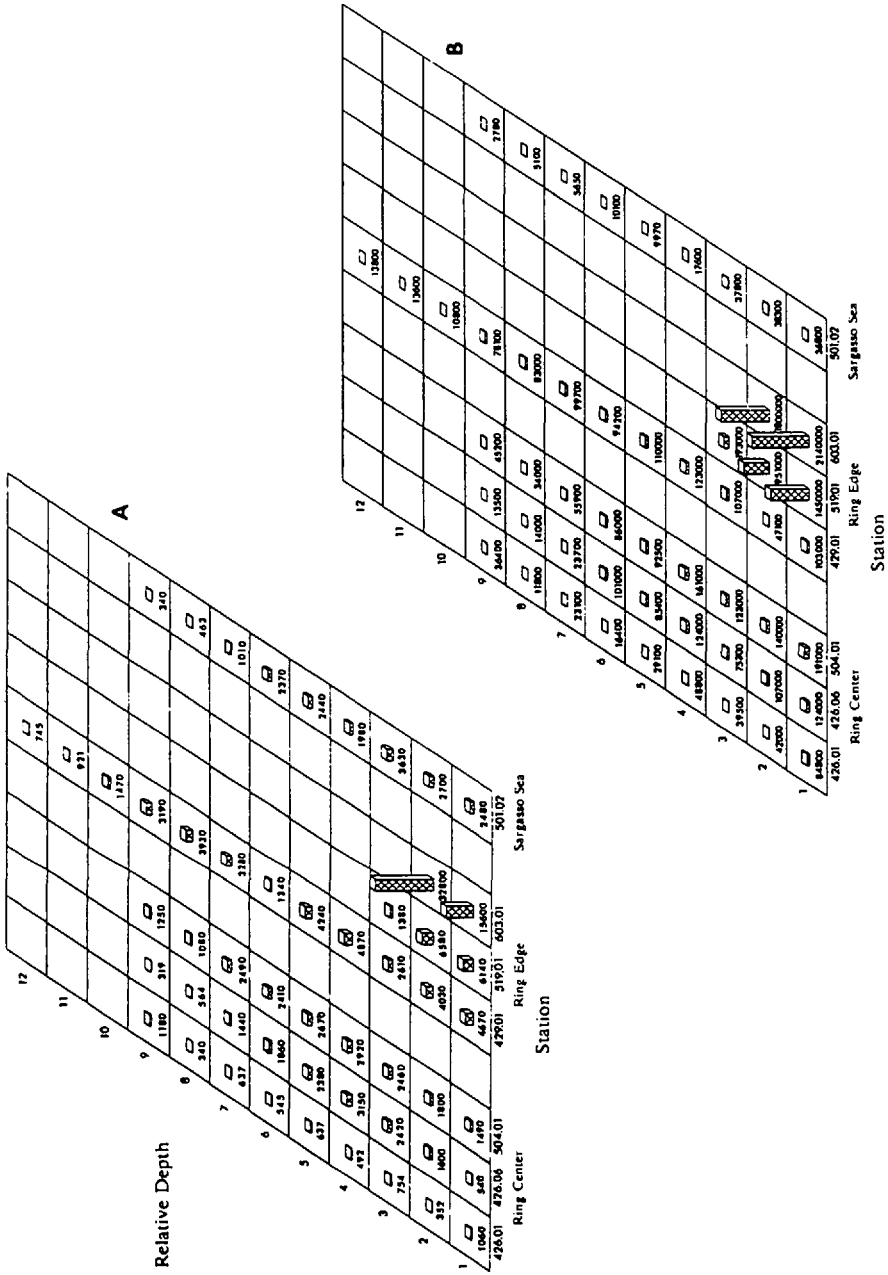


Figure 3. Vertical distribution of dinoflagellates and other algae, April/May. (A) Dinoflagellates. (B) Other algae. Abundances in cells l<sup>-1</sup>. Note the different abundance scales.

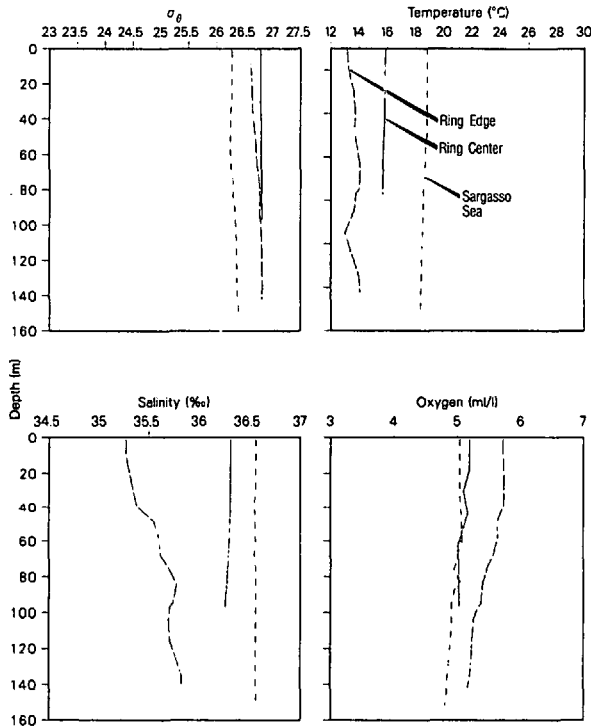


Figure 4. Vertical distribution of density, temperature, salinity, and oxygen, April/May. Ring center, 426.01 (—); ring edge, 429.01 (—); and Sargasso Sea, 501.02 (-----).

diatoms, which were as low in abundance as the dinoflagellates. At the afternoon station, diatoms were as abundant or more abundant than the coccolithophorids in the upper 40 m (relative depths 1–5), and the relative maxima of these two groups were staggered in the water column. The processes that caused this staggered distribution are not clear, however, as the physical characteristics of the water column were nearly uniform with depth (Fig. 4). At the high velocity region on 29 April, coccolithophorids exceeded diatoms, and their depth distributions were nearly identical. Coccolithophorids were also very abundant at the Sargasso Sea station on 1 May and at the ring edge station on 19 May, but at ring center on 4 May diatoms dominated in the upper 20 m (relative depths 0–4).

Mean abundances for centric diatoms, pennate diatoms, dinoflagellates, coccolithophorids, and other algae are listed by location and cruise in Table 2. In April, the pennates were always the lowest in number (of the 5 categories), and frequently none at all were counted. Except for the morning ring center station on 26 April (426.01) the centrics exceeded the numbers of dinoflagellates in the ring, especially in the surface waters. At that station, dinoflagellates equalled or exceeded the centrics at all depths. At the afternoon station on 26 April and the ring edge station on 29 April,

Table 2. Mean phytoplankton group abundances, by cruise and location. Values are in cells  $l^{-1}$ .

For the June ring samples, subscripts "s" and "d" represent surface (thermocline samples and shallower) and deep (below thermocline), respectively. Values in parentheses are the coefficients of variation, expressed as percentages [ $CV = (s/\bar{x}) \cdot 100$ ]. SS = Sargasso Sea, SH = Shelf Water, SL = Slope Water. Stations included in April/May calculations: ring—426.01, 426.06, 429.02, 504.01; SS—501.02. Stations included in June calculations: ring—616.04, 616.06, 616.08, 617.01, 623.06, 624.03, 624.07, 625.01, 625.03; SS—618.08; SH and SL—613.05, 623.01, 623.03, 624.01. Stations included in August calculations: ring—809.07, 812.03; SS—813.02; SH and SL—818.04.

	Ring ( $n = 39$ )	April/May SS ( $n = 9$ )	SH and SL
centrics	19300 (117.4%)	4150 (109.6%)	
pennates	498 (170.1%)	304 (91.1%)	
dinoflagellates	1910 (83.4%)	2040 (66.2%)	
coccolithophorids	26600 (112.0%)	54500 (54.6%)	
other algae	68100 (60.9%)	19500 (92.7%)	
		June	
	Ring ( $n_s = 26, n_d = 27$ )	SS ( $n = 6$ )	SH and SL ( $n = 27$ )
centrics <sub>s</sub>	13400 (98.3%)	340 (89.4%)	559 (110.4%)
centrics <sub>d</sub>	301 (209.6%)		
pennates <sub>s</sub>	2760 (111.5%)	449 (49.4%)	228 (174.1%)
pennates <sub>d</sub>	65 (383.1%)		
dinoflagellates <sub>s</sub>	7840 (69.8%)	3490 (51.3%)	3280 (87.5%)
dinoflagellates <sub>d</sub>	3420 (180.7%)		
coccolithophorids <sub>s</sub>	6230 (61.7%)	4530 (56.2%)	15700 (116.4%)
coccolithophorids <sub>d</sub>	6540 (83.6%)		
other algae <sub>s</sub>	20000 (67.8%)	35400 (45.8%)	48600 (104.4%)
other algae <sub>d</sub>	76800 (122.3%)		
		August	
	Ring ( $n = 18$ )	SS ( $n = 9$ )	SH and SL ( $n = 6$ )
centrics	931 (111.3%)	130 (141.5%)	164 (62.2%)
pennates	1240 (77.9%)	465 (74.4%)	307 (58.3%)
dinoflagellates	6670 (132.9%)	5500 (63.5%)	4490 (43.5%)
coccolithophorids	7860 (64.6%)	7130 (67.3%)	5080 (61.2%)
other algae	57800 (111.4%)	21000 (60.4%)	53800 (44.5%)

dinoflagellate numbers exceeded centrics only in the deepest one or two samples. In the Sargasso Sea, however, dinoflagellates exceeded centrics in all samples below 34 m (deepest 5 samples).

The density, temperature, salinity, and oxygen profiles all indicated a well-mixed water column in terms of the physical properties, but there were differences between the ring center, ring edge, and Sargasso Sea stations in terms of absolute values (Fig. 4). For the ring center stations, only data from event 426.01 were plotted because

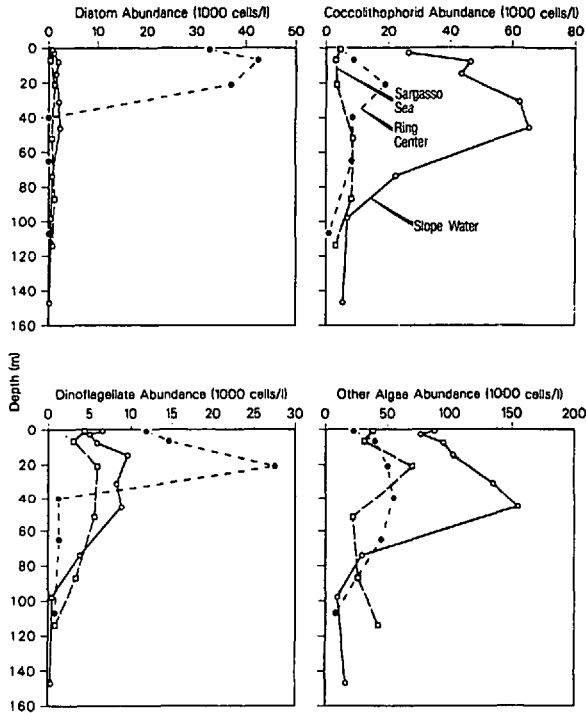


Figure 5. Vertical distribution of diatoms, coccolithophorids, dinoflagellates, and other algae, June. Slope Water, 613.05 (○); Sargasso Sea, 618.08 (□); and ring center, 625.03 (●). Note the different abundance scales.

the other curves were similar. The ring center stations had intermediate values of temperature, salinity, and oxygen, and were highest in density.

Ring center, Slope Water, and Sargasso Sea stations from June are compared in Figure 5. Large differences are apparent between the ring and its source water, and between the ring and the water in which it is embedded. Diatoms and dinoflagellates were most abundant in the upper 25 m at ring center and other algae and coccolithophorids were most abundant at the Slope station. The Sargasso Sea station generally had the lowest absolute numbers in all phytoplankton groups.

Examination of the mean phytoplankton group abundances for this cruise revealed similarities and contrasts to the April cruise (Table 2). Pennates still generally exhibited the lowest abundances, but now dinoflagellates were much more abundant in most samples. Centrics reached high numbers in the surface waters toward the ring center. In the ring, large abundance differences are evident between the samples taken in and above the thermocline and those collected below it, for the centrics, pennates, dinoflagellates, and other algae. Coccolithophorid numbers decreased greatly in the ring and Sargasso Sea since April.

Stratification was apparent by June (Fig. 6). The mixed layer at the Slope station

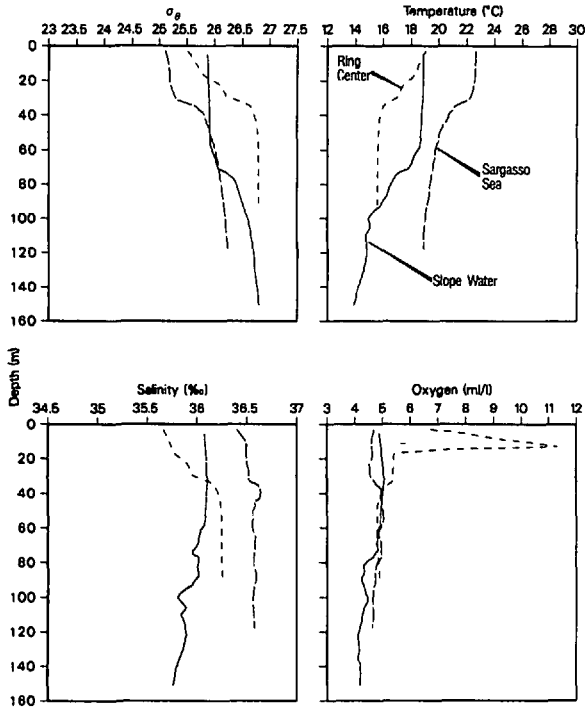


Figure 6. Vertical distribution of density, temperature, salinity, and oxygen, June. Slope Water, 613.05 (—); Sargasso Sea, 618.08 (---); and ring center, 625.03 (.....).

extended to about 60 m, but it extended only to about 30 m in the Sargasso Sea. The ring center station had a surface mixed layer of only 10 m; a sharp pycnocline was present to 35 m. There was a very sharp subsurface oxygen peak around 15 m, however.

In August, diatoms were greatly reduced in number relative to the earlier cruises (Fig. 7), except for the first ring center station in April, which also had low diatom abundances. However, ring center numbers still remained higher than those in the Slope Water, Sargasso Sea, or Gulf Stream, until the overwash on 10 August. Coccolithophorids, dinoflagellates, and other algae had slightly higher numbers at the first ring center station on 9 August relative to the Slope Water, Sargasso Sea, or Gulf Stream stations (Figs. 7, 8). However, abundances of all groups were generally very similar at all four locations.

Large changes in distribution and abundance are evident between 9 and 12 August. For each day, the depth distribution was similar for each group. For example, on 12 August, the diatoms, coccolithophorids, dinoflagellates, and others all had relative abundance maxima at 15–20 m (relative depths 3 and 4) and again at 80 m (relative depth 8). However, these patterns were drastically different from those observed three days earlier on the 9th. In fact, coccolithophorids showed nearly opposite patterns.

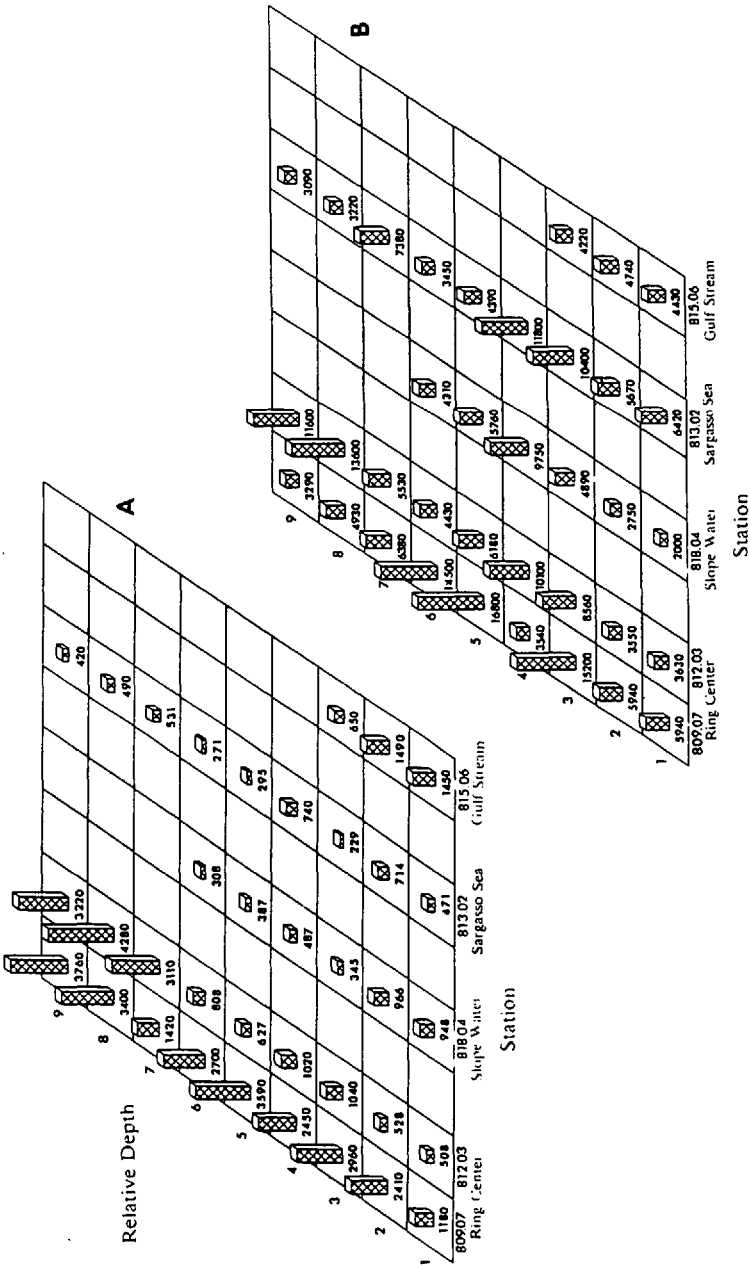


Figure 7. Vertical distribution of diatoms and coccolithophorids, August. A. Diatoms. B. Coccolithophorids. Abundances in cells  $l^{-1}$ . Note the different abundance scales.

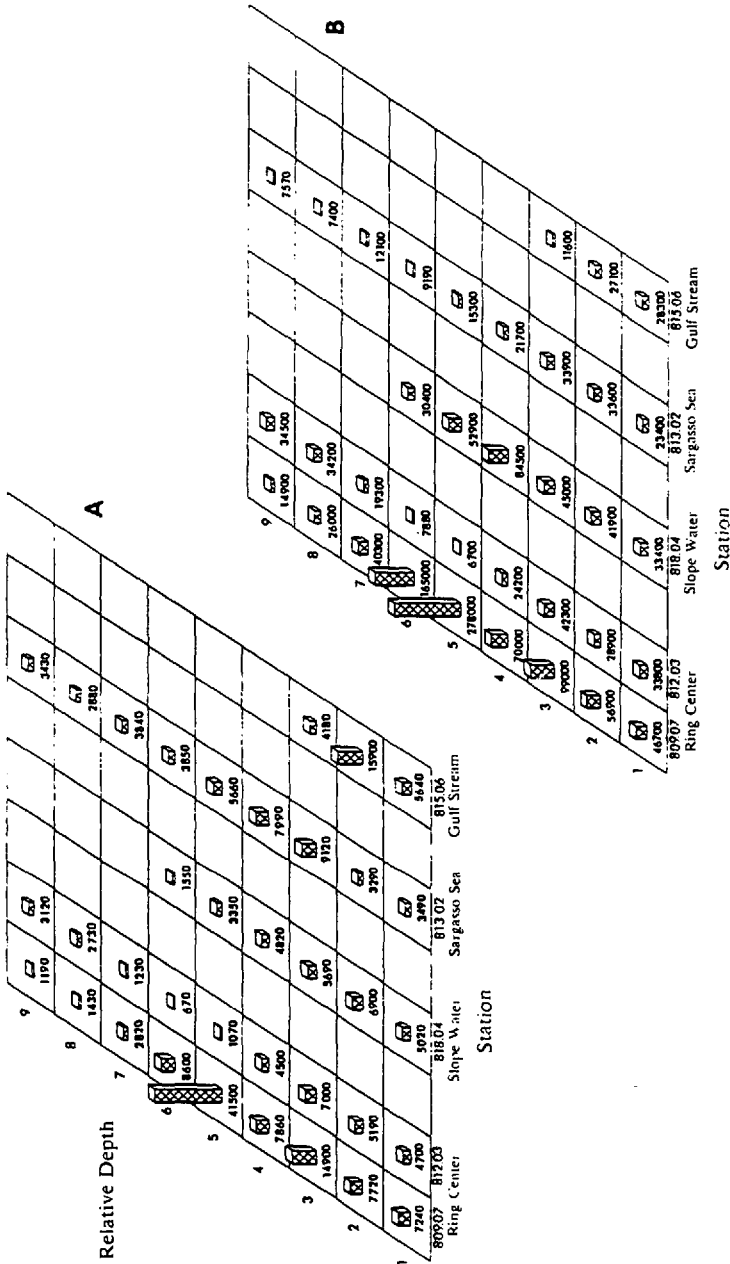


Figure 8. Vertical distribution of dinoflagellates and other algae, August. (A) Dinoflagellates. (B) Other algae. Abundances in cells l<sup>-1</sup>. Note the different abundance scales.



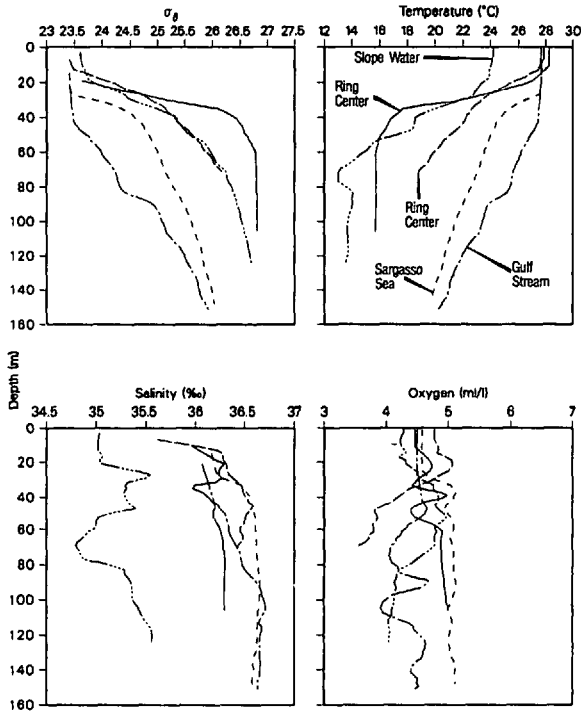


Figure 9. Vertical distribution of density, temperature, salinity, and oxygen, August. Ring center, 809.07 (—); and 812.03 (···); Sargasso Sea, 813.02 (-·-·-); Gulf Stream, 815.06 (— — —); and Slope Water, 818.04 (-----).

These differences were related to the heterogeneous nature of the surface layer of the ring in August.

Trends in the mean group abundances showed changes from the June cruise (Table 2). After the other algae, coccolithophorids had the greatest mean abundances of the four remaining phytoplankton divisions, but dinoflagellates were nearly as abundant. Within the diatom division, pennates nearly always exceeded centrics in the ring, for the first time during the study.

The plots of the physical properties (density, temperature, salinity, oxygen) for each of the August stations are shown in Figure 9. The heterogeneous nature of the ring water and Slope Water is obvious. The two ring center stations and the Slope station had shallower pycnoclines than the Gulf Stream and Sargasso Sea stations. The Slope station was the coolest and freshest of the five stations. The oxygen maxima at 20 and 40 m at ring center on 9 August corresponded to abundance maxima of all four of the phytoplankton groups.

The profiles of phytoplankton in the Slope Water stations in June and August were very different from each other (Fig. 10). All four phytoplankton groups were in greater

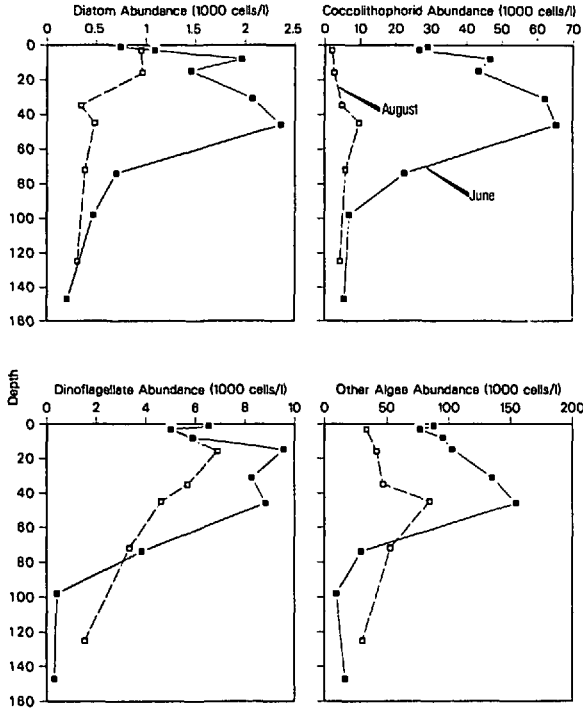


Figure 10. Comparisons of the vertical distribution of diatoms, coccolithophorids, dinoflagellates, and other algae in the Slope Water over time. June, 613.05 (■); August, 818.04 (□). Note the different abundance scales.

abundance in June than in August in the upper 70 m. Except for the diatoms, however, the shapes of the curves were similar for each group at both stations.

A comparison of the Sargasso Sea stations in April/May, June, and August shows high numbers of diatoms and coccolithophorids at the surface during the first cruise (Fig. 11). In June and August these two groups were in lower numbers and were distributed fairly uniformly with depth. Dinoflagellates, in contrast, steadily increased in abundance from April to August and maintained a maximum at 20 m. Other algae were always present in high numbers in the Sargasso Sea, but they were particularly abundant in June. The May and August profiles showed similar abundances and depth distributions.

Some of the most abundant taxa are listed by location for each cruise in Tables 3–5. The most abundant taxa were determined by taking the mean of all species observed during a given cruise and ranking them. Eight taxa, several of which represent coarse taxonomic groupings, were abundant at most locations during all three cruises: monad, Gymnodiniaceae, yellow cell (often called olive-green cell), undetermined dinoflagellate, eukaryotic cell, undetermined flagellate, *Emiliania huxleyi*, and *Caneosphaera*

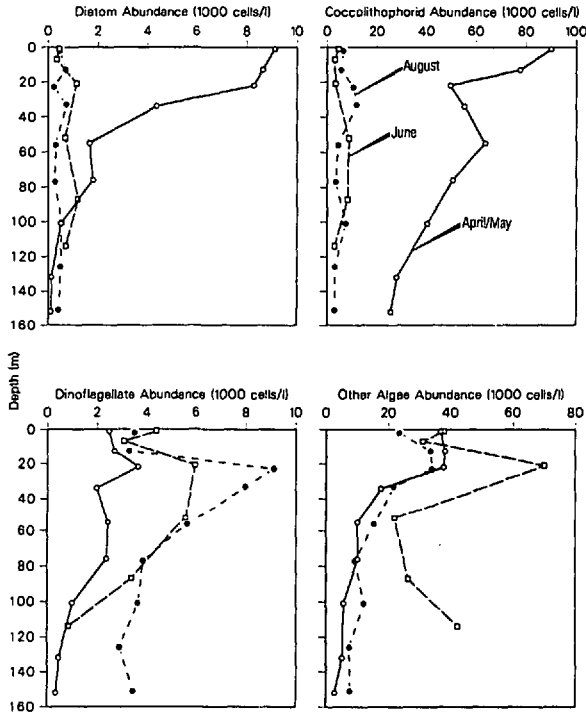


Figure 11. Comparisons of the vertical distribution of diatoms, coccolithophorids, dinoflagellates, and other algae in the Sargasso Sea over time. April/May, 501.02 (○); June, 618.08 (□); and August, 813.02 (●). Note the different abundance scales.

Table 3. Twenty most abundant taxa by location, April/May. The list excludes the 8 taxa abundant in all samples (see text) and taxa of uncertain taxonomic placement. SS = Sargasso Sea. Stations included for each location are as in Table 2. Taxa with "?" after the specific epithet were not positively identified. Abundances are in cells  $l^{-1}$ .

Ring	Mean abundance	SS	Mean abundance
<i>Minidiscus trioculatus</i>	8250	<i>Phaeocystis</i> spp.	4830
<i>Thalassiosira bulbosa</i> ?	2140	<i>Gephyrocapsa ericsonii</i> ?	2530
<i>Gephyrocapsa ericsonii</i> ?	754	<i>Minidiscus trioculatus</i>	1610
<i>Protoperdinium bipes</i>	165	<i>Chaetoceros</i> spp.	868
<i>Leptocylindrus danicus</i>	133	<i>Syracosphaera pulchra</i>	504
<i>Rhizosolenia delicatula</i>	116	<i>Chaetoceros breve</i>	319
<i>Thoracosphaera heimii</i>	112	<i>Bacteriastrum</i> spp.	312
<i>Prorocentrum</i> spp.	110	<i>Laminolithus marsilii</i>	262
		<i>Gonyaulax</i> sp. "A"	248
		<i>Calyptrolithophora gracillima</i>	245

Table 4. Twenty most abundant taxa by location, June. The list excludes the 8 taxa abundant in all samples (see text) and taxa of uncertain taxonomic placement. SS = Sargasso Sea, SH = Shelf Water, SL = Slope Water. Stations included for each location are as in Table 2. Taxa with "?" after the specific epithet were not positively identified. Abundances are in cells  $l^{-1}$ .

Ring	Mean abundance	SS	Mean abundance
<i>Chaetoceros</i> cf. <i>vixvisibilis</i>	3320	<i>Gonyaulax</i> sp. "A"	1700
<i>Leptocylindrus danicus</i>	2850	<i>Phaeocystis</i> spp.	445
<i>Gonyaulax</i> sp. "A"	1580	<i>Oxytoxum variabile</i>	306
<i>Prorocentrum</i> spp.	1270	<i>Gephyrocapsa ericsonii</i> ?	191
<i>Calyptrorphaera catillifera</i>	1170	<i>Anthosphaera oryza</i>	162
<i>Gephyrocapsa ericsonii</i> ?	432	<i>Oxytoxum scolopax</i>	158
<i>Nitzschia pseudodelicatissima</i>	327	<i>Nitzschia bicapitata</i>	146
<i>Periphyllorpha mirabilis</i>	308	<i>Leptocylindrus danicus</i>	119
<i>Nitzschia closterium</i>	304	<i>Thoracosphaera heimii</i>	100
<i>Syracosphaera pulchra</i>	175	<i>Oxytoxum globosum</i>	88
<i>Thalassiothrix mediterranea</i>	172	<i>Nitzschia pseudodelicatissima</i>	68
<i>Triadinium sphaericum</i>	169		
		Mean abundance	
	SH and SL		
	<i>Gephyrocapsa ericsonii</i> ?	2280	
	<i>Gonyaulax</i> sp. "A"	975	
	<i>Prorocentrum</i> spp.	430	
	<i>Calyptrorphaera catillifera</i>	415	
	<i>Phaeocystis</i> spp.	348	
	<i>Periphyllorpha mirabilis</i>	240	
	<i>Leptocylindrus danicus</i>	213	
	<i>Anthosphaera oryza</i>	159	
	<i>Minidiscus trioculatus</i>	125	
	<i>Gephyrocapsa oceanica</i>	98	
	<i>Solenicola setigera</i>	95	

*molischii*. The category "Gymnodiniaceae," for example, included all the unarmored dinoflagellates that we could not identify to genus. These taxa are not included in Tables 3–5.

In April, most of the abundant taxa were small, making identifications to species difficult. *Minidiscus trioculatus* and a small *Thalassiosira*, possibly *T. bulbosa*, were observed with the scanning electron microscope. Pennate diatoms, and members of the genus *Nitzschia* in particular, are also difficult to identify in water mounts. *Gonyaulax* sp. "A" is, to our knowledge, an undescribed species. It is a lightly thecate dinoflagellate about 8–15  $\mu\text{m}$  in length, with a wide girdle and distinct apical pore.

*Minidiscus trioculatus* was present at concentrations of 2,700–6,000 cells  $l^{-1}$  in the surface waters at the first ring center station in April, but increased greatly in numbers during the course of the cruise. By 4 May it had attained densities of 33,000–67,000

Table 5. Twenty most abundant taxa by location, August. The list excludes the 8 taxa abundant in all samples (see text) and taxa of uncertain taxonomic placement. SS = Sargasso Sea, SH = Shelf Water, SL = Slope Water. Stations included for each location are as in Table 2. Taxa with "?" after the specific epithet were not positively identified. Abundances are in cells  $l^{-1}$ .

Ring	Mean abundance	SS	Mean abundance
<i>Gonyaulax</i> sp. "A"	2050	<i>Gonyaulax</i> sp. "A"	2700
<i>Ophiaster hydroideus</i>	751	<i>Umbellosphaera irregularis</i>	688
cryptophytes	740	<i>Anthosphaera oryza</i>	326
<i>Anthosphaera oryza</i>	379	<i>Helladosphaera cornifera</i>	300
<i>Minidiscus trioculatus</i>	357	<i>Oxytoxum variabile</i>	284
<i>Calciosolenia murrayi</i>	329	cryptophytes	283
<i>Glenodinium danicum</i>	324	<i>Syracosphaera pulchra</i>	214
<i>Oxytoxum variabile</i>	268	<i>Discosphaera tubifera</i>	196
<i>Thalassionema nitzschioides</i>	220	<i>Calyptrosphaera catillifera</i>	186
<i>Nitzschia</i> spp.	218	<i>Gyrodinium</i> spp.	176
<i>Nitzschia bicapitata</i>	207		
<i>Calyptrosphaera catillifera</i>	200		
		Mean abundance	
	SH and SL		
	<i>Gonyaulax</i> sp. "A"	1740	
	<i>Gephyrocapsa ericsonii</i> ?	672	
	<i>Ophiaster hydroideus</i>	462	
	<i>Anthosphaera oryza</i>	368	
	<i>Oxytoxum variabile</i>	254	
	chrysophytes	217	
	cryptophytes	190	
	<i>Gyrodinium</i> spp.	188	
	<i>Dinobryon</i> spp.	139	
	<i>Nitzschia</i> spp.	112	
	<i>Calciosolenia murrayi</i>	106	
	<i>Glenodinium danicum</i>	105	

cells  $l^{-1}$ . It was also observed at the ring edge and Sargasso Sea stations, but in lower numbers (only 3,200–5,200 cells  $l^{-1}$  in the Sargasso Sea). In June, *Minidiscus trioculatus* was only observed at the Slope Water station, but in August it was present at all stations at concentrations of several hundred cells  $l^{-1}$ .

Small (2–3  $\mu$ m diameter) biflagellates were extremely abundant in the ring edge samples from mid-May and early-June. Abundances of 450,000 to 1,600,000 cells  $l^{-1}$  were observed. In mid-June, flagellates were seen in maximum concentrations at the Slope Water station and in the Shelf Water entrainment feature along transect two, but only in concentrations of 3000–7000 cells  $l^{-1}$ . Flagellates were observed at all August stations in slightly greater abundances than in June.

The diatoms *Chaetoceros* cf. *vixvisibilis* and *Leptocylindrus danicus* showed

similar abundance changes over time. Both species were observed at scattered locations in low abundances in April, but in June they were both concentrated in the surface water at ring center (see Gould and Fryxell, 1988, this issue). By August, *C. cf. vixvisibilis* was not seen in any of the samples, and *L. danicus* was observed in low concentrations (100–500 cells  $l^{-1}$ ) at the first ring center station and in two of the deep samples from the Sargasso Sea.

The changes in the dominant taxa listed in Tables 3–5 can be summarized as follows. Of the eight taxa listed as abundant in the ring in April (Table 3), only two were also abundant at that time in the Sargasso Sea. Only three taxa that were abundant in the ring in April remained abundant in the ring in June. Four taxa out of the twelve listed as abundant in the ring in June (Table 4) were also abundant in the Sargasso Sea in June, while six were also abundant in the Shelf and Slope Water. Of those taxa abundant in the ring in June, only two remained abundant in August. Five taxa out of twelve abundant in the ring in August (Table 5) were also abundant in the Sargasso Sea at that time, but eight of the twelve were also abundant in the Shelf and Slope Water. It is apparent that the abundant taxa in the ring were very different from the abundant taxa in the source water, the Sargasso Sea, even in April, just two months after ring formation; there were large, rapid shifts in the dominant taxa in the ring between cruises, and; the dominant taxa were similar in all three regions in August.

The ratios of empty cells to full cells in each sample were calculated for the diatoms. In April, the ratio in the ring generally fell in the 0–0.1 range (mean = 0.04). The ratio in the Sargasso Sea was slightly larger (mean = 0.15). Below 100 m, however, the ratio increased, both in the ring and in the Sargasso Sea, to anywhere from 0.2 to 0.8. Few total cells were seen in the deeper samples, so although percentages were high, absolute numbers were low.

In June, there was a tendency for higher ratios in the ring than in April (mean = 0.31). More samples were in the 0.1–0.3 range now, even at depths less than 50 m. In the deep samples, more empty diatom cells than full cells were occasionally encountered.

At the ring center stations in August, empty diatom cells were frequently observed (mean empty:full ratio was 0.41). On the 9th, the four deepest samples (50–100 m) had an empty:full ratio of at least 0.75; on the 12th, 6 of the 9 sample depths had values from 0.3–0.9. The Slope Water station, however, had a mean ratio of only 0.08 and the Sargasso Sea 0.24. Thus, there was an increase in the percentage of empty diatom valves in the ring as it aged, suggesting a generally declining population, or possibly grazing pressure.

The most frequently observed taxa (present in at least 10% of the samples) were determined for each cruise. In April, 41 species met this criterion. In June and August, there were 64 and 66 species, respectively. This yielded a combined total of 100 different taxa for the 3 cruises (some species were frequent in more than one cruise). When these 100 species were used as variables and PCA was performed using

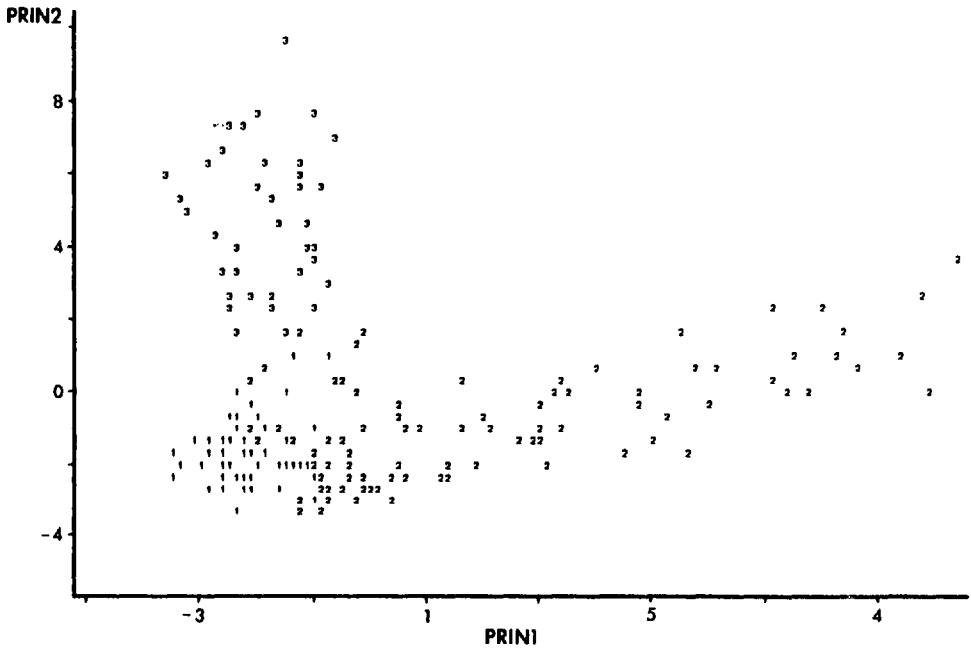


Figure 12. Principal component analysis using the 100 most frequently observed taxa as variables, on the pooled natural-log abundance data from all three cruises. Symbols represent cruises: 1 — April/May; 2 — June; 3 — August.

natural-log transformed abundance values (to reduce the effect of extreme values), samples from the three cruises separated quite clearly (Fig. 12), indicating that there were dramatic changes in the phytoplankton species composition between the cruises (on time scales of 1.5 months or less). The floristic changes occurred more rapidly and more sporadically than initially expected.

#### 4. Discussion

*a. WCR 82B evolution.* Over the course of the April cruise, all four phytoplankton groups (diatoms, dinoflagellates, coccolithophorids, and other algae) showed increases in abundance, but the small diatoms exhibited the most dramatic growth with as much as a thousandfold increase in cell numbers at the surface over the eight day period from 26 April to 4 May. The growth of phytoplankton in the surface layers at ring center is consistent with the observed increases in particulate nitrogen, nitrate uptake rate, and carbon fixation rate. The nitrogen uptake increased by a factor of five at the surface between 23 April and 4 May (McCarthy and Nevins, 1986), while the carbon-specific growth rate increased from  $0.50 \text{ day}^{-1}$  to  $0.90 \text{ day}^{-1}$  (Hitchcock *et al.*, 1985). All but a few percent of the primary production occurred shallower than 50 m in April (Bishop *et al.*, 1986).

The increase in cell numbers occurred before warming was observed in the water, by either satellite or shipboard observations (Brown *et al.*, 1985). Deep convective mixing may have ceased before thermal stratification was apparent, however, thereby enabling phytoplankton growth in the surface layers. Bishop *et al.* (1986) used CTD, XBT, chlorophyll, and nutrient profiles to argue that convective mixing was occurring to depths as great as 400 m in the late-April to early-May period, but mixed layers as shallow as 20 m were also observed, during periods of quiescence. McCarthy and Nevins (1986) suggested that the reduced winds during the periods of quiescence resulted in a reduction of deep mixing, confining the phytoplankton to the upper few tens of meters.

The large differences in phytoplankton abundance and distribution that were observed at the morning and afternoon ring center stations on 26 April could be due to several factors. Although many of the same taxa were observed on both occasions, several new taxa were observed in the afternoon, taxa that were also observed at the ring edge station. Thus, the differences might have been due to a combination of advection from the ring edge and *in situ* growth. However, the patterns could also have resulted from patchiness. Anomalously high chlorophyll, particulate carbon, and particulate nitrogen values were also observed at that afternoon station (Hitchcock *et al.*, 1985; McCarthy and Nevins, 1986).

At least two, and possibly three phases of the spring phytoplankton increase occurred in WCR 82B during the period from 15 April to 3 June. The first phase peaked on 20 April and was only observed by satellite (Brown *et al.*, 1985); no quantitative water samples were available for cell counts and species identifications. That phase was erased by deep convective mixing associated with a storm on 26–28 April. Satellite imagery showed the initiation of a second phase (or possibly a continuation of the first phase) on 1 May that lasted at least until 7 May when satellite coverage ended.

In late April and early May, the species that contributed the most to the second bloom phase, in terms of cell numbers, were the small diatoms *Minidiscus trioculatus* and *Thalassiosira* sp., possibly *T. bulbosa*. It is difficult to say what the source was for these species, because quantitative Slope water samples were not available for the April cruise. However, *M. trioculatus* was observed in the Sargasso Sea (although in much lower abundances) and at the ring edge, and *T. bulbosa* was observed at only the ring edge station (recall that the high velocity region near the ring edge is considered to be a Gulf Stream remnant that encircles the ring). So the spring bloom in the ring was possibly due to species that were originally present at ring formation, in either the Sargasso Sea or Gulf Stream water.

$\text{NO}_3^-$ ,  $\text{PO}_4^{-3}$  and  $\text{Si(OH)}_4$  concentrations were still high in the ring at the end of the first cruise (5.1, 0.25, and  $2.5 \mu\text{m kg}^{-1}$ , respectively, at station 504.01; Fox *et al.*, 1984), but  $\text{NO}_3^-$  and  $\text{PO}_4^{-3}$  were both undetectable ( $\text{NO}_3^-$  detection limit was  $0.1 \mu\text{m kg}^{-1}$  and  $\text{PO}_4^{-3}$  limit was  $0.05 \mu\text{m kg}^{-1}$ ) in the upper 20 m by 19 May (P. Glibert and



D. Kester, personal communication), so further phytoplankton growth must have occurred after the first cruise left the area. Samples obtained from a ship-of-opportunity cruise from mid May to early June (courtesy of P. Glibert) showed small biflagellates in great abundance, suggesting that this group might have been responsible for a third bloom phase in the ring. *Minidiscus trioculatus* remained abundant but was present in lower numbers than in early May. Several newly observed species, *Leptocylindrus danicus*, *Dinophysis tripos*, and *Rhizosolenia* spp., were increasing in numbers and became abundant in the ring in June.

The species that bloomed in April/May were evidently opportunistic species that were able to take advantage of favorable nutrient and light regimes. As McCarthy and Nevins (1986) point out, the  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  concentrations in the ring in April/May were higher than concentrations oceanic phytoplankton are typically exposed to in the Sargasso Sea (maximum surface values of 1.8 and  $0.16 \mu\text{M kg}^{-1}$ ; Menzel and Ryther, 1960). These high nutrient concentrations in the ring surface waters were originally achieved through deep convective mixing and were replenished during the cruise by an upward flux from storms and from the relaxation of the depressed density surfaces. The high  $f$  values (0.62–0.66; fraction of nitrogen taken up as  $\text{NO}_3^-$ ) indicate that the cells were able to take advantage of this nitrogen source (McCarthy and Nevins, 1986).

From February to April, particle production exceeded particle consumption by zooplankton in the euphotic zone of the ring (upper 50 m, to 3%  $I_0$ ), but particle concentration remained constant (Bishop *et al.*, 1986). Thus, another removal process must have been operating. Bishop *et al.* (1986) estimate that approximately 67% of the primary produced carbon was exported by mixing to the thermocline waters deeper than 50 m. In April, grazing by zooplankton  $>64 \mu\text{m}$  consumed only about 50% of the daily phytoplankton production, and Bishop *et al.* (1986) suggest that mixing removed the remaining 50% of the production ( $46 \text{ mmole C m}^{-2} \text{ d}^{-1}$ ), because they observed no biomass accumulation in the upper 50 m of the ring. However, the phytoplankton abundance profiles at ring center did show increases over the course of the cruise, with systematic increases apparent for diatoms and other algae (Figs. 2, 3). The cells that were accumulating were so small, though, that carbon biomass measurements and flux calculations were not affected. We estimate a carbon accumulation rate of  $0.10 \text{ mmole C m}^{-2} \text{ d}^{-1}$  for diatoms and  $0.14 \text{ mmole C m}^{-2} \text{ d}^{-1}$  for other algae in the upper 50 m of the ring between 26 April and 4 May. These estimates are based on changes in integrated cell numbers, cell diameters of  $4 \mu\text{m}$  and  $2 \mu\text{m}$  for the small diatoms and monads, respectively, and carbon estimates from cell volume using the modified Strathmann equations given in Smayda (1978). The total accumulation rate of  $0.24 \text{ mmole C m}^{-2} \text{ d}^{-1}$  is small compared to the total production, however, so the estimated delivery rate of carbon to the mixed layer,  $46 \text{ mmole C m}^{-2} \text{ d}^{-1}$ , and the six day estimated time for removal of suspended particulate matter from the thermocline after stratification (Bishop *et al.*, 1986) are probably accurate.

Of the 50% of the production that was grazed in April, only 5% was accounted for by animals  $<333 \mu\text{m}$  (Bishop *et al.*, 1986). However, as mentioned earlier, the most abundant phytoplankton particles at that time were in the 2–6  $\mu\text{m}$  size range. For some reason the small zooplankton had low grazing rates (or were not abundant) and the larger ones evidently had difficulty filtering these small cells.

McCarthy and Nevins (1986) state that the high  $f$  values observed in the ring in April indicate that the heterotrophic plankton in the euphotic zone were unable to consume and recycle the primary production as efficiently as in a coastal upwelling case (typically, large centric diatoms dominate in upwelling regions). They suggest mixing or sinking of phytoplankton resulted in a less efficient coupling between the trophic levels. We offer an alternative, and possibly complementary explanation, that the large zooplankton that were doing most of the grazing simply were not efficiently filtering the small phytoplankton cells that were abundant. The inability to graze and the reduction in deep mixing were probably responsible for the spring bloom in WCR 82B.

During the first cruise, numbers of centric diatoms generally exceeded numbers of dinoflagellates in the ring (especially in the surface layers), and very few pennate diatoms were observed. The ratios of empty to full cells were  $<0.10$ , indicating a healthy, growing population. Ratios of empty cells increased below 100 m.

By June, thermal stratification was apparent in the ring; a 10 m mixed layer overlaid a well-developed thermocline that extended to 40 m. The thermal barrier reduced downward mixing and particle supply to the thermocline, and zooplankton shoaled to the upper 50 m. An estimated 140% of the primary production in June ( $>100\%$  consumption indicates the magnitude of the error associated with the grazing rates) was consumed by zooplankton grazing (Bishop *et al.*, 1986). The relatively constant phytoplankton biomass and primary productivity (Hitchcock *et al.*, 1985) suggest that phytoplankton production and consumption were in balance in WCR 82B in June.

Dinoflagellates were more abundant in June than they had been in April and they generally exceeded numbers of centric diatoms, except in the surface water at ring center. Pennates were still in low abundance relative to the centrics and dinoflagellates. There was a tendency for higher ratios of empty to full diatoms compared to April, with more samples in the 0.1–0.3 range, even at depths less than 50 m.

Thus, species composition and abundances reveal that the ring remained distinct from the Slope Water in June, four months after formation. However, some Slope species had penetrated into the ring as early as April (Gould, 1988) and had influenced the ring to the extent that it was distinct from the Sargasso Sea as rapidly as two months after formation. The ring achieved and maintained its own identity regarding the presence and abundance of phytoplankton species.

Between the second and third cruises, the ring underwent numerous interactions with and overwashes by the Gulf Stream and Slope Water. As it translated to the southwest, the ring became trapped near Cape Hatteras at the vertex formed by the

shelf break and the north wall of the Gulf Stream. The salinity values ranged from 33.2–36.3‰ in the upper 50 m of the ring in August, indicating the heterogeneous nature of the surface layer during that cruise. Silicate profiles confirmed the presence of Shelf, Slope, and Gulf Stream water (Fox and Kester, 1986).

Diatoms were generally reduced in numbers in the ring during the August cruise. The effect of the Gulf Stream overwash on 10 August was apparent and caused a reduction in cell numbers in the upper 50 m. The group abundances at the stations after 9 August were very similar and did not vary much by location or depth.

No single diatom species dominated in August, but *Minidiscus trioculatus* and *Leptocylindrus danicus*, bloom diatoms from April and June, respectively, were still observed in the ring in low numbers. Several *Nitzschia* spp. were also common in the ring. *Gonyaulax* sp. "A" and Gymnodiniaceae were the most abundant dinoflagellate taxa in the ring in August, and the coccolithophorid *Emiliania huxleyi* remained relatively abundant.

The ratio of empty to full diatom cells increased after June, with many samples falling in the 0.3–0.9 range. Dinoflagellates were generally more abundant than either the centrics or pennates in the ring, and pennates exceeded centrics for the first time during the study. The ring followed the three stages of succession outlined by Margalef (1958): (1) small cells with a large surface:volume ratio, capable of rapid increases in numbers (including diatoms and chlorophytes); followed by (2) a mixed community of diatoms with larger cells, smaller surface:volume ratios, and lower growth rates; and finally (3) large numbers of dinoflagellates. Margalef believed the phenomenon to be independent of proximity to the coast, temperature, or season.

Analysis of the water bottle samples revealed large differences in species composition and abundance between each of the cruises. Thus, changes in the ring occurred within 1.5 month intervals.

The question of whether the changes in the ring flora were due to species succession or sequence is an appropriate one here. Species succession is defined as the series of changes that occur in a local community in a single water mass, due to either physical, chemical, or biological factors. Sequence changes, on the other hand, are the result of introduction of species through water mass transport. The original hypothesis was that the rings remain as relatively intact, isolated bodies of water that translate through the Slope Water, and that most species changes would be the result of succession. This theory was rapidly dispelled when sampling and satellite imagery revealed Shelf and Slope water penetration even to the ring core.

We believe that during the first two cruises (April–June) changes due to succession were more important than changes due to sequence. The dominant species in April/May (*Minidiscus trioculatus* and *Thalassiosira bulbosa*?) were probably present at ring formation; they became abundant when light increased, mixing decreased, and grazing rate was low. The dominant species in June (*Chaetoceros* cf.

*vixvisibilis* and *Leptocylindrus danicus*) were also present in the ring in April, but in much lower numbers. If a change in conditions in the ring water enabled them to become abundant, perhaps these species were good competitors in stratified, low-nutrient environments (i.e., able to take up nutrients efficiently when they are in low concentrations). However, of the 12 taxa listed as abundant in the ring in June (Table 3), 6 were also abundant in the Shelf/Slope Water at that time, so Shelf/Slope input was also very evident as well by June. Changes by August were more related to sequence. Numerous overwashes of Slope and Gulf Stream water in July, and mixing, resulted in similar phytoplankton assemblages and abundances at all sampling locations.

Differences in species composition and abundance were very evident from April to August in 82B, differences that were not observed between two rings sampled in the same season (Gould *et al.*, 1986). Therefore, we believe there is a strong seasonal effect. Gould *et al.* (1986) observed similar species and abundances in two rings that were sampled in the autumn of subsequent years. Seasonal and climatological factors are probably more important when the ring is young and away from the influence of the Gulf Stream. As the ring ages it moves closer to the shelf break and Gulf Stream. At some point (possibly 4 or 5 months after formation) Slope Water and Gulf Stream interactions dominate the phytoplankton changes, and these are relatively independent of season.

*b. The importance of warm core rings.* With regard to the phytoplankton, warm core rings are important in that they inject Sargasso Sea species into the Slope Water. Over long time periods this might result in an evolutionary pressure to adapt to a wider range of temperature and nutrient regimes. Over shorter time scales we can view the rings as ecological experiments to determine how long it takes Slope Water species to penetrate the ring and how long Sargasso Sea species can persist. The rings also represent seasonal biomass minima (April) and maxima (June) relative to the Slope Water (Brown *et al.*, 1985; Smith and Baker, 1985); thus, time scales and possibly amounts of deposition of organic carbon, silica, and calcium carbonate to the sediments may be altered.

Hitchcock *et al.* (1985) estimated similar productivity for WCR 82B and the Slope Water over a six month period, indicating that temporally and spatially integrated carbon production at the lowest trophic level may not be altered by the introduction of warm core rings into the Slope Water. Higher trophic levels may be affected to a greater degree, however. Davis and Wiebe (1985) postulate that the invasion of opportunistic Slope Water zooplankton species into the ring not only causes a rapid increase of macrozooplankton biomass in the ring to levels approaching those in the Slope Water, but it also alters the trophic structure in such a way that net production in higher trophic levels is increased. Yentsch and Phinney (1985) suggest that one of the

more important effects of rings is the breakdown of stratification in the water through which the rings translate. The turbulence generated mixes nutrient-rich deep water to the surface. Indeed, Olson (1986) observed distinct increases in remotely sensed pigment concentration to the northeast in the ring's wake, relative to concentrations in the water ahead of the ring. Higher concentrations of suspended particulate matter have also been detected in the offshore flow behind a ring (Bishop and Joyce, 1986). Hitchcock *et al.* (1985) estimated that the total primary production in the Slope Water was unaffected by the presence of warm core rings, because Slope Water and ring production were similar when integrated over a six month period. However, when both ring production and ring-generated production are considered in the estimate, primary production in the Slope Water may be greater with rings than without.

## 5. Conclusions

1. Two or three phases of phytoplankton increase were observed in WCR 82B in the spring. *Minidiscus trioculatus* and a small *Thalassiosira* dominated from late April to early May, while a small biflagellate dominated in mid May.

2. Another diatom concentration was observed in the ring in June, but this one was dominated by *Chaetoceros cf. vixvisibilis* and *Leptocylindrus danicus*.

3. After Slope Water and Gulf Stream interactions in July, diatom numbers in the surface waters of the ring were greatly reduced in August relative to June, and no single species dominated in the ring.

4. Changes in phytoplankton abundance in the ring core occurred independently of changes in either the surrounding Slope Water or in the source water, the Sargasso Sea.

5. Shifts in the dominant taxa in the ring occurred rapidly, on intercruise time scales of 1.5 months, or less.

6. The ring showed dramatic differences from its source water just two months after ring formation but remained distinct from the Slope Water for 4–5 months.

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## APPENDIX

Table A-1. Species cited in text and authorities.

## Bacillariophyceae

- Chaetoceros breve* Schutt  
*Chaetoceros vixvisibilis* Schiller  
*Leptocylindrus danicus* Cleve  
*Minidiscus trioculatus* (F.J.R. Taylor) Hasle  
*Nitzschia bicapitata* Cleve  
*Nitzschia closterium* (Ehrenberg) Smith  
*Nitzschia pseudodelicatissima* Hasle  
*Rhizosolenia delicatula* Cleve  
*Thalassionema nitzschioides* Grunow  
*Thalassiosira bulbosa* Syvertsen  
*Thalassiothrix mediterranea* Pavillard

## Dinophyceae

- Dinophysis tripos* Gourret  
*Glenodinium danicum* Paulsen  
*Oxytoxum globosum* Schiller  
*Oxytoxum scolopax* Stein  
*Oxytoxum variabile* Schiller  
*Protoperidinium bipes* (Paulsen) Balech  
*Thoracosphaera heimii* (Lohmann) Kamptner  
*Triadinium sphaericum* (Murray & Whitting) Dodge

## Prymnesiophyceae

- Anthosphaera oryza* (Schlauder) Gaarder  
*Calyptrolithophora gracillima* (Kamptner) Heimdahl  
*Caneosphaera molischii* (Schiller) Gaarder  
*Calciosolenia murrayi* Gran  
*Calyptrosphaera catillifera* (Kamptner) Gaarder  
*Discosphaera tubifera* (Murray & Blackman) Ostenfeld  
*Emiliania huxleyi* (Lohmann) Hay  
*Gephyrocapsa ericsonii* McIntyre & Be  
*Gephyrocapsa oceanica* Kamptner  
*Helladosphaera cornifera* (Schiller) Kamptner  
*Laminolithus marsilii* (Borsetti & Cati) Heimdahl  
*Ophiaster hydroideus* (Lohmann) Lohmann  
*Periphyllophora mirabilis* (Schiller) Deflandre  
*Syracosphaera pulchra* Lohmann  
*Umbellosphaera irregularis* Paasche

## Other Algae

- Solenicola setigera* Pavillard

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