area and volume compressibility. The undulations of quasi-spherical vesicles of different sizes can then be analyzed (Fig. 4). On the basis of these curves, we estimate the effective rigidity of these vesicles as $\kappa/k_BT \approx 3.0 \pm 0.3$. The compressibility constants A and B are subject to much larger errors (however, the relative effect of these terms is quite small for almost all modes). Also it seems that the assumed law for the spectrum of large-scale undulations is consistent with the results of our simulations: the data show the expected scaling behavior emerging from finite-size effects as the system size is increased (Fig. 4). However, one would have to perform much longer simulations with larger systems to measure the exponent characterizing this law and show that there are no nontrivial renormalization effects [a similar remark applies also in our opinion to experimental systems (17)].

This analysis of the fluctuations of fluid vesicles shows that one can use the present model to study the large-scale universal properties of different types of membranes. It would be interesting, for instance, to search for a "crumpling" transition that has been observed in recent simulations of fluid-like membranes (12), a result that seems to contradict other simulations (11) or our intuition based on analytical calculations (18).

Studies of the large-scale behavior of fluid or solid-like vesicles are among the many possible phenomena that can be considered within the framework of the present model or its generalizations. For instance, we have constructed and have begun to study a structure consisting of a polymerized network attached below a fluid vesicle. Such a composite membrane can be a model for the membranes of red blood cells, in which amphiphilic fluid bilayers are coupled to spectrin cytoskeletons (20). Even more interesting should be studies of phenomena that involve changes in membrane topology, such as exo- and endocytosis (21). Another simple but spectacular example of topology changes is the recently observed behavior of fluid vesicles made of chiral phospholipids. When such vesicles are cooled below the fluid-solid transition, they break and form helical ribbons (22). We believe that the numerical studies of such phenomena could shed light on the general principles of self-assembly in membranes and other molecular systems.

REFERENCES AND NOTES

1. D. R. Nelson, T. Piran, S. Weinberg, Eds., *Statistical Mechanics of Membranes and Surfaces* (World Scientific, Singapore, 1989).
2. For recent reviews, see S. Leibler, *Phys. Rep.* **184**, 265 (1989); R. Lipowsky, *Nature* **349**, 475 (1991).
3. J. Meunier, D. Langevin, N. Boccara, Eds., *Physics of Amphiphilic Layers* (Springer-Verlag, Berlin, 1987); D. Beysens and G. Forgacs, Eds., *Dynamical Phenomena at Interfaces, Surfaces and Membranes*, Proceedings of Les Houches Workshop (Springer-Verlag, Berlin, in press).
4. S. Leibler, *Nature* **348**, 586 (1990).
5. W. Helfrich, *Z. Naturforsch. Teil C* **28**, 693 (1973).
6. D. R. Nelson and L. Peliti, *J. Phys. (Paris)* **48**, 1085 (1987).
7. F. David, E. Guitter, L. Peliti, *ibid.*, p. 2059.
8. D. A. Huse and S. Leibler, *ibid.* **49**, 605 (1988).
9. D. R. Nelson, in *Random Fluctuations and Pattern Growth*, H. E. Stanley and N. Ostrowsky, Eds. (Kluwer Academic, Dordrecht, 1988), pp. 193–217.
10. Y. Kantor and D. R. Nelson, *Phys. Rev. A* **38**, 4020 (1987); F. F. Abraham *et al.*, *Phys. Rev. Lett.* **62**, 1757 (1989); F. F. Abraham and D. R. Nelson, *Science* **249**, 393 (1990); R. Lipowsky and M. Girardet, *Phys. Rev. Lett.* **65**, 2893 (1990).
11. J.-S. Ho and A. Baumgärtner, *Europhys. Lett.* **12**, 295 (1990); *Phys. Rev. A* **41**, 5745 (1990).
12. S. M. Catterall, *Phys. Lett. B* **220**, 207 (1989); C. F. Baillie *et al.*, *Nucl. Phys. B* **311**, 469 (1990); R. L. Renken and J. B. Kogut, *ibid.* **354**, 328 (1991).
13. Y. Kantor, M. Kardar, D. R. Nelson, *Phys. Rev. Lett.* **57**, 791 (1986).
14. B. Smit *et al.*, *Nature* **348**, 624 (1990).
15. J. N. Israelachvili, *Intermolecular and Surface Forces* (Academic Press, New York, 1985).
16. G. Cicotti, D. Frenkel, I. R. McDonald, *Molecular Dynamics and Monte Carlo Methods: Statistical Mechanics of Liquids and Solids* (North Holland, New York, 1987).
17. M. B. Schneider *et al.*, *J. Phys. (Paris)* **45**, 1457 (1984); H. Engelhardt *et al.*, *ibid.* **46**, L395 (1985); I. Bivas *et al.*, *ibid.* **48**, 855 (1987); J. F. Faucon *et al.*, *ibid.* **50**, 2389 (1989).
18. This q^4 law is a simple consequence of the fact that the effective elastic free energy density of the undulating membrane is dominated by the curvature energy term proportional to H^2, where H is the local mean curvature. In harmonic approximation H behaves like the Laplacian operator, thus for small q vectors, like q^2. If one takes into account anharmonic terms, this simple law is modified by logarithmic corrections [W. Helfrich, *J. Phys. (Paris)* **46**, 1263 (1985); L. Peliti and S. Leibler, *Phys. Rev. Lett.* **54**, 1690 (1985)].
19. S. Milner and S. A. Safran, *Phys. Rev. A* **36**, 4371 (1987).
20. B. T. Stokke *et al.*, *Eur. Biophys. J.* **13**, 203 (1986); *ibid.*, p. 219.
21. B. Alberts *et al.*, *Molecular Biology of the Cell* (Garland, New York, 1989).
22. W. Helfrich and J. Prost, *Phys. Rev. A* **38**, 3065 (1988).
23. D. J. Evans and S. Murad, *Mol. Phys.* **34**, 327 (1977).

6 June 1991; accepted 8 August 1991

Major Role of the Cyanobacterium *Trichodesmium* in Nutrient Cycling in the North Atlantic Ocean

EDWARD J. CARPENTER* AND KRISTEN ROMANS

The diazotrophic cyanobacterium *Trichodesmium* is a large (about 0.5 by 3 millimeters) phytoplankter that is common in tropical open-ocean waters. Measurements of abundance, plus a review of earlier observations, indicate that it, rather than the picophytoplankton, is the most important primary producer (about 165 milligrams of carbon per square meter per day) in the tropical North Atlantic Ocean. Furthermore, nitrogen fixation by *Trichodesmium* introduces the largest fraction of new nitrogen to the euphotic zone, approximately 30 milligrams of nitrogen per square meter per day, a value exceeding the estimated flux of nitrate across the thermocline. Inclusion of this organism, plus the abundant diazotrophic endosymbiont *Richelia intracellularis* that is present in some large diatoms, in biogeochemical studies of carbon and nitrogen may help explain the disparity between various methods of measuring productivity in the oligotrophic ocean. Carbon and nitrogen fixation by these large phytoplankters also introduces a new paradigm in the biogeochemistry of these elements in the sea.

IT IS NOW COMMONLY ACCEPTED THAT picophytoplankton (<2 μm) are the major primary producers and constitute the largest fraction of the standing crop of phytoplankton in oligotrophic marine waters; this implies that large phytoplankton play a minor role in carbon and nitrogen cycling (1–4). However, because of sampling inadequacies, the very large (~1 to 3 mm) phytoplankton such as the diazotrophic (nitrogen fixing) cyanobacterium *Trichodesmium* have been underrepresented in 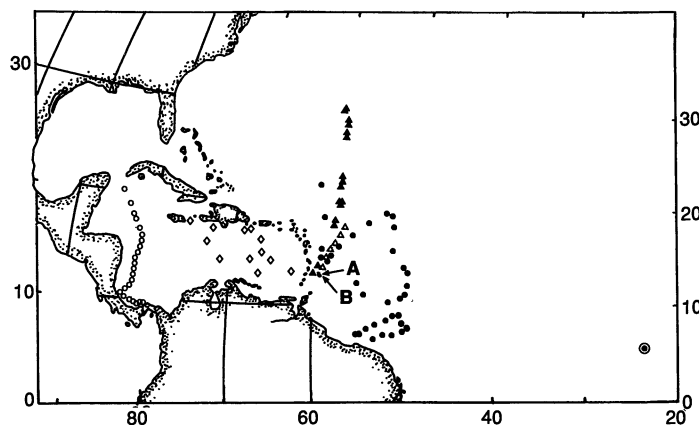most oceanic biomass and C and N flux measurements. A reevaluation of past studies on phytoplankton species distribution, and recent measurements, indicate that *Trichodesmium* is usually the most important phytoplankter as regards standing crop and productivity, and, through N_2 fixation, is the major source of new N to the euphotic zone of the tropical North Atlantic Ocean.

In the equatorial Atlantic Ocean, the less than 1-μm size class has been reported to contain an average of 44 to 71% of the total chlorophyll a (chl a) (2, 4), and to be responsible for 60% of the primary productivity (4). Similar observations have been made for the tropical Pacific Ocean (3). The discovery of this prokaryotic (5, 6) and eukaryotic (7) picoplanktonic flora has led to a new paradigm for biogeochemical cycling in marine surface wa-

E. J. Carpenter, Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794–5000. K. Romans, SEA Education Association, Woods Hole, MA 02543.

*To whom correspondence should be addressed.

Fig. 1. Location of sampling stations. Data sources: R.V. *Westward*, October–November 1990 (▲); Calef and Grice (21) (●); Hulburt (19) (△); Carpenter and Price (15) (◇); Hulburt (17) (○); Kovaleva (22) (⊙); Sander and Steven (20) (▵); Steven and Glombitza (18) (B).

column, 12 stations), and this was 61% of the total chl *a* (15). In contrast, in a study (2) encompassing the equatorial Atlantic Ocean (107 stations), the standing crop of the picoplankton ranged from about 50 to 100 μg of chl *a* m^{-3} for the <1-μm size fraction in NO$_3$-depleted surface water (the 1- to 3-μm fraction did not exceed 5 to 10% of the total chl *a* in the upper 50-m mixed layer).

Trichodesmium is a colonial cyanobacterium (~0.5 mm by 3 mm) which obtains virtually all of its N through N$_2$ fixation (14, 24). It is common in oligotrophic marine waters warmer than 20°C and reaches maximal growth between 25° and 30°C. It does not grow well in upwelling systems, but has its highest growth rates in stratified seas where solar insolation is high and wind stress is low (25). Data from the Sargasso and Caribbean seas indicate that, because of the presence of gas vesicles that make it buoyant, virtually all the *Trichodesmium* biomass is concentrated in the upper 50 m, with a maximum typically found at about 15 m (15). In contrast, the picophytoplankton density maximum is usually deeper in the euphotic zone, at the 0.5 to 1% light level (50 to 100 m) in the North Atlantic (7).

Rates of C and N fixation by *Trichodesmium* measured in the central or northern Sargasso Sea (>30°N) often yield slow particulate nitrogen (PN) or particulate carbon (PC) doubling times, especially when measured at relatively low water temperatures (20° to 24°C) (23, 25). However, usual *Trichodesmium* PC and PN turnover times have been found to be rapid, ranging from 1 to 20 days in tropical and subtropical waters, which were typically 25°C or warmer (Table 2). If *Trichodesmium* colony doubling time is 10 days, then 200 ng of N and 1100 ng of C are required per colony per day (PN and PC per colony = 2 μg N, 11 μg C) (23). For a water column 50 m deep, with 1000 to 5000 colonies m^{-3}, the mean rate of N$_2$ fixation would thus range from 10 to 50 mg N m^{-2} d^{-1}, and C fixation from 55 to 275 mg C m^{-2} d^{-1}. In contrast, input of new N by NO$_3$ flux across the thermocline in the equatorial Atlantic Ocean and western Sargasso Sea has been estimated to be 15.5 and 0.3 to 1.6 mg N m^{-2} d^{-1}, respectively (27, 28), and total phytoplankton C fixation averaged 250 mg C m^{-2} d^{-1} (29). With a mean *Trichodesmium* density of 3000 colonies m^{-3} in this region, this organism may supply 30 mg N and 165 mg C m^{-2} d^{-1}, more than doubling the known input of new N and increasing the estimate of total fixed C significantly. Furthermore, in tropical and subtropical seas, N$_2$ fixation by the cyanobacterial endosymbiont *Richelia intracellularis* within the large chain-forming diatoms *Rhizosolenia* and *Hemiaulus* may equal or exceed rates of C and N$_2$ fixation per square meter calculated for *Trichodesmium* (30).

Trichodesmium and other planktonic diazo-

ters in which the bulk of C and N is cycled through the smallest size class of plankton. However, most sampling for biomass and productivity in these studies involved measurements on small volumes (~200 to 300 ml), which often missed the large colonial phytoplankters such as *Trichodesmium* (8). Investigators in the early 1900s (9–12) noted the abundance of *Trichodesmium* in tropical waters, but all stated that their collection and enumeration techniques underestimated its density.

Quantitative data (13–22) on phytoplankton distribution from the tropical North Atlantic Ocean indicate that the standing crop of *Trichodesmium* equals or exceeds that of the picoplankton (Fig. 1 and Table 1). The range of *Trichodesmium* density in seven studies (about 200 observations) south of 30°N was from 835 colonies per cubic meter in the western Caribbean Sea to 5500 colonies per cubic meter in the North Equatorial Current. To confirm these observations, a research

cruise was conducted in autumn 1990 on a north-south transect covering about 1600 nautical miles at 58° to 60°W in the tropical North Atlantic (Figs. 1 and 2). The mean concentration of *Trichodesmium* in the transect was 1415 colonies per cubic meter (SE = 142, *n* = 34) with a maximum of 3500 m^{-3}. Chlorophyll *a* biomass of *Trichodesmium* averaged 76.3 μg m^{-3}. Thus, the data collected on this transect confirm the extent and high concentrations of *Trichodesmium* observed previously in more localized studies.

With a typical range in concentration of 1000 to 5000 colonies per cubic meter, and a mean chl *a* concentration of 50 ng per colony (23), *Trichodesmium* standing crop usually ranged from about 50 to 250 μg of chl *a* m^{-3} in near surface waters. For the upper 50 m, this totals 2.5 to 12.5 mg of chl *a* m^{-2}. These calculations are similar to measurements for the Caribbean Sea in which *Trichodesmium* chl *a* averaged 15.9 mg m^{-2} (50-m deep water

Table 1. Observations of *Trichodesmium* density between about 30°N and the equator. If concentrations were reported as trichomes or cells, for conversion to colonies it was assumed, on the basis of previous measurements (23), that there were 200 trichomes per colony and 120 cells per trichome. Locations of studies south of 30°N are shown in Fig. 1.

Density colonies per cubic meter	Location	Observations	Season
		North of 30°N	
10.5	Bermuda	7 dates	July–October (13)
50	West Sargasso Sea	11 stations	Autumn (14)
200	West Sargasso Sea	16 stations	August–September (15)
4737	Georgia shelf	20 to 34 stations	4 seasons (16)
		South of 30°N	
835	West Gulf Mexico	26 stations	Autumn (17)
2000	Caribbean Sea	12 stations	Winter and summer (15)
1825	Barbados	65 samples†	3 years, all seasons (18)
5500*	North Equatorial Current	6 stations	February (19)
2700‡	Barbados	46 samples†	2 years, all seasons (20)
1185§	NE S. America	34 stations	Spring (21)
2500	6°N, 24°W	6 profiles†	January (22)

Trichodesmium was not seen north of 17°N; only 50-ml samples were collected. †One station. ‡Trichomes were 20% of total (20, table 7). §Calculated from Calef and Grice (21, figure 1).

Fig. 2. Concentration of *Trichodesmium* colonies (□) and surface water temperature (▲) in October and November 1990 transect on R.V. *Westward*. When replicate samples were collected at one sample location, the calculated mean and standard deviation is shown. *Trichodesmium* was enumerated in surface water collections taken with an 8-liter sampler, and from one to three collections were made at random times daily.
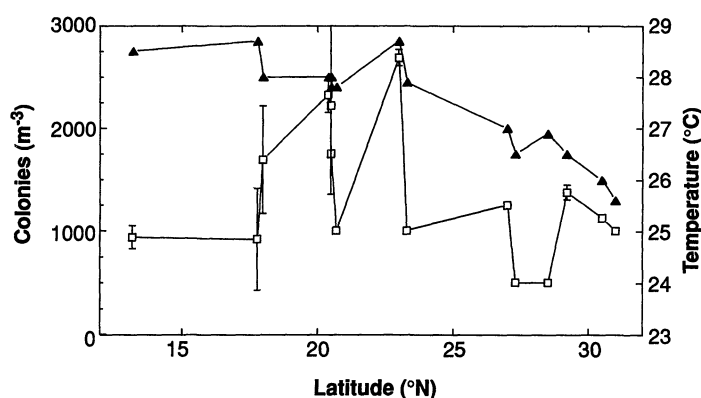
Table 2. Turnover times of *Trichodesmium* PN or PC in tropical and subtropical Atlantic Ocean waters.

Location	Date	Turn-over (days)	Base	Temperature (°C)
W. Sargasso (32)	August	4*	PC	28
Caribbean (38)	April	18	PC	
Caribbean (15)	August	11.6	PC	26–27
Caribbean (15)	August	44.8	PN	26–27
Caribbean (26)	March	1.13	PN	27
Bahamas (26)	Oct–Nov	1.8	PN	
Sargasso (26)	Oct–Nov	1.48	PN	
Caribbean†	Feb	1.8–2.2	PC	26.5

*Bloom, light-saturated.   †Data from Carpenter (39).

trophs in tropical waters play a central role in fixation of C, and the introduction of new N, by N_2 fixation, to the euphotic zone. On a global basis, N_2 fixation in the pelagic region of the sea, estimated to be 4.7×10^{12} g (31) annually, under nonbloom conditions, is low as a source of new N compared to NO_3 fluxes from deep water. The amount of N fixed annually in *Trichodesmium* blooms is poorly known, but it appears to be at least 5.4×10^{12} y^{-1} (32), which more than doubles the current estimate. The inclusion of N_2 fixed by the *Richelia*-diatom symbiosis will further raise the value, increasing the importance of this source of new N. Thus, although N_2 fixation may be low relative to NO_3 input on a global basis, it appears to be significant in warm tropical seas.

Euphotic zone cycling of C and N from these relatively large phytoplankters must be different from that of picoplankton. Much of the energy fixed by the picophytoplankters is passed among the very smallest of plankton, and relatively little appears to reach the higher trophic levels of larger herbivores and predators (27). However, attachment of picoplankters to

sinking detrital material can represent a significant mechanism by which these cells can reach the deep sea (33). Although the fate of C and N fixed by *Trichodesmium* must be better quantified, it is known that copepods, other mesozooplankters, and some fish species feed directly on it (25), thus facilitating transfer to higher trophic levels and ultimately deposition to bottom sediments.

Thus, our recent measurements indicate *Trichodesmium* is a major source of both C and N in the euphotic zone of the tropical North Atlantic Ocean, and possibly in other tropical seas. For example, in the Indian Ocean near Madagascar, mean annual density of *Trichodesmium* was 16,500 colonies m^{-3} (34), a value far exceeding our North Atlantic Ocean measurements. *Trichodesmium* has recently been shown to be significant in introducing new N to the euphotic zone in the tropical Pacific Ocean (35). The large size of *Trichodesmium* and the *Richelia*-diatom symbiosis, high biomass, and productivity rates indicate a paradigm in which the largest, rather than the smallest, phytoplankters most effectively mediate the cycling of C and N, and N_2 fixation is the primary source of new N to the euphotic zone in these stratified seas. Furthermore, inclusion of these cyanobacteria in productivity estimates can help in resolving the disparity between high primary productivity rate measurements, based on seasonal water mass O_2 changes, and the lower values obtained from discrete water samples (36). Because it appears that planktonic diazotrophs in tropical seas can be significant contributors to global fixation and sequestration of carbon, their activity should be included in biogeochemical models.

REFERENCES AND NOTES

1. G. E. Fogg, *Proc. R. Soc. London Ser. B* **228**, 1 (1986).
2. A. Herbland, A. leBoutellier, P. Raimbault, *Deep-Sea Res.* **32**, 819 (1985).
3. W. K. Li et al., *Science* **219**, 292 (1983).
4. T. Platt et al., *Nature* **301**, 702 (1983).
5. P. W. Johnson and J. McN. Sieburth, *Limnol. Oceanogr.* **24**, 928 (1979).

6. J. B. Waterbury et al., *Nature* **277**, 293 (1979).
7. L. S. Murphy and E. M. Haugen, *Limnol. Oceanogr.* **30**, 47 (1985).
8. T. R. Parsons, Y. Maita, C. Lalli, *A Manual of Chemical and Biological Methods for Seawater Analysis* (Pergamon, New York, 1984), pp. 115–120; J. D. H. Strickland and T. R. Parsons, *A Practical Handbook of Seawater Analysis* (Fisheries Research Board of Canada, Ottawa, 1972), pp. 267–278. Underestimates also occur because productivity samples are often pre-screened to remove mesozooplankton (and thus also large phytoplankters) or because the buoyant *Trichodesmium* rose to the top of the seawater sampler, while the water sample was drawn from the bottom. Because of gas vesicles, buoyant *Trichodesmium* colonies will not be concentrated by centrifuge or settling chambers unless vesicles are discharged with an acidified preservative.
9. N. Wille, *Die Schizophyceen der Plankton-Expedition, Ergnebnisse der Plankton-Expedition der Humbolt-Stiftung* (Lipsius & Tischer, Kiel, Germany, 1904).
10. E. Hentschel, *Wiss. Ergnebnisse Dtsch. Atl. Exped.* **10**, 1 (1932).
11. _____, *ibid.* **11**, 1 (1936).
12. H. Lohmann, *Arch. Biontol.* **4**, 1 (1920).
13. R. C. Dugdale, D. W. Menzel, J. H. Ryther, *Deep-Sea Res.* **7**, 298 (1961).
14. E. J. Carpenter and J. J. McCarthy, *Limnol. Oceanogr.* **20**, 389 (1975).
15. _____ and C. C. Price, *ibid.* **22**, 60 (1977).
16. W. M. Dunstan and J. Hosford, *Bull. Mar. Sci.* **27**, 824 (1977).
17. E. M. Hulburt, *ibid.* **18**, 388 (1968).
18. D. M. Steven and R. Glombitza, *Nature* **237**, 105 (1972).
19. E. M. Hulburt, *Limnol. Oceanogr.* **7**, 307 (1962).
20. F. Sander and D. M. Steven, *Bull. Mar. Sci.* **23**, 771 (1973).
21. G. W. Calef and G. D. Grice, *Ecology* **47**, 855 (1966).
22. T. M. Kovaleva, *Hydrobiol. J.* **12**, 1 (1976).
23. J. J. McCarthy and E. J. Carpenter, *J. Phycol.* **15**, 75 (1979).
24. P. M. Gilbert and S. Banahan, *Eos* **69**, 1089 (1988).
25. E. J. Carpenter, *Mar. Biol. Lett.* **4**, 69 (1983).
26. _____, M. I. Scranton, P. C. Novelli, A. Michaels, *J. Plankton Res.* **9**, 1047 (1987); E. J. Carpenter, unpublished data.
27. R. W. Eppley and B. J. Peterson, *Nature* **282**, 677 (1979).
28. A. Knap et al., *ibid.* **320**, 158 (1986).
29. E. Bauerfeind, thesis, Christian Albrechts Universitat, Kiel, Germany (1983).
30. T. A. Villareal, in *Marine Pelagic Cyanobacteria: Trichodesmium and Other Diazotrophs*, E. J. Carpenter, D. G. Capone, J. Rueter, Eds. (Kluwer Academic, Dordrecht the Netherlands, in press).
31. D. G. Capone and E. J. Carpenter, *Science* **217**, 1140 (1982).
32. E. J. Carpenter and D. G. Capone, in (30).
33. M. W. Silver, M. M. Gowing, P. J. Davoll, in *Photosynthetic Picoplankton*, T. Platt and W. K. W. Li, Eds. (Department of Fisheries and Oceans, Ottawa, Canada, 1986), pp. 311–341.
34. A. Sournia, *Intl. Rev. Ges. Hydrobiol.* **53**, 1 (1968). Calculations made assuming 200 trichomes per colony.
35. D. M. Karl, R. Letelier, D. V. Hebel, D. F. Bird, C. D. Winn, in (30); C. Dupouy, in (30).
36. W. J. Jenkins, *Nature* **300**, 246 (1982); E. Schulenberger and J. L. Reid, *Deep-Sea Res.* **33**, 267 (1981).
37. M. R. Lewis, O. Ulloa, T. Platt, *Limnol. Oceanogr.* **33**, 92 (1988).
38. W. K. W. Li, H. E. Glover, I. Morris, *Limnol. Oceanogr.* **25**, 447 (1980).
39. Samples were collected February 1991 at 18°N, 65°W and assayed by methods described by Carpenter et al. (26).
40. We thank W. C. Dennison, J. Chang, J. O'Neil, and G. Weidner for advice; T. Villareal for looking up station locations in WHOI archives for (21); B. Bergman and U. Stockholm, for sabbatical facilities; the NSF and ONR for support of this research; and the SEA Educational Association, Woods Hole, MA, for ship time. MSRC, SUNY Stony Brook contribution 820.

28 June 1991; accepted 19 September 1991