

Introduction to the JGOFS North Atlantic Bloom Experiment

HUGH W. DUCKLOW* and ROGER P. HARRIS†

THIS is the first collection of papers from the Joint Global Ocean Flux Study (JGOFS). Formed as an international program in 1987, JGOFS has four principal elements: modelling and data management, multidisciplinary regional process studies, a global survey of biogeochemical properties and long-term time series observations.

In 1989–1990 JGOFS conducted a pilot process study of the spring phytoplankton bloom, the North Atlantic Bloom Experiment (NABE). JGOFS decided to conduct a large-scale, internationally-coordinated pilot study in the North Atlantic because of its proximity to the founding nations of the project, the size and predictability of the bloom, and its fundamental impact on ocean biogeochemistry (BILLETT *et al.*, 1983; WATSON and WHITFIELD, 1985; PFANNKUCHE, 1993). In 1989, six research vessels from Canada, Germany, The Netherlands, the U.K. and the U.S.A., and over 200 scientists and students from more than a dozen nations participated in NABE. Some of their initial results are reported in this volume.

The spring bloom in the North Atlantic is one of the most conspicuous seasonal events in the world ocean. Coastal Zone Color Scanner (CZCS) imagery shows that the bloom is manifested as a sudden explosion of ocean color that fills the basin north of about 40 degrees latitude in April and May each year (see cover; ESAIAS *et al.*, 1986; U.S. JGOFS, 1989). It must seem surprising to anyone examining these beautiful images to learn that until the early part of this century, there was scant mention of the bloom in the literature at all. As MILLS (1989, p. 121) states:

A phenomenon as striking as the sudden appearance of phytoplankton cells during spring in temperate and high latitudes should have been noted very early, perhaps even incorporated into fishermen's folk-wisdom. Yet there is little mention of phenomena that in modern terms would be called the spring bloom in the scientific literature of the early nineteenth century . . . Plankton blooms, during the first decade of the twentieth century, were reified; the concept became the expression of a new and influential approach to the biology of the seas.

Mills describes how the bloom concept was defined by the Kiel School of oceanography following Victor Hensen's pioneering Plankton Expedition of 1889 (MILLS, 1989). Later the concept was formulated in quantitative terms by RILEY (1942) and SVERDRUP (1953), following on the initial model provided by GRAN and BRAARUD (1935; see PLATT *et al.*, 1991 for a recent discussion). NABE was a centennial celebration of Hensen's expedition (DUCKLOW, 1989).

Figure 1 shows the oceanographic context of NABE. In the eastern North Atlantic,

*Horn Point Environmental Laboratory, University of Maryland CEES, P.O. Box 775, Cambridge, MD 21613 0775, U.S.A.

†Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, U.K.

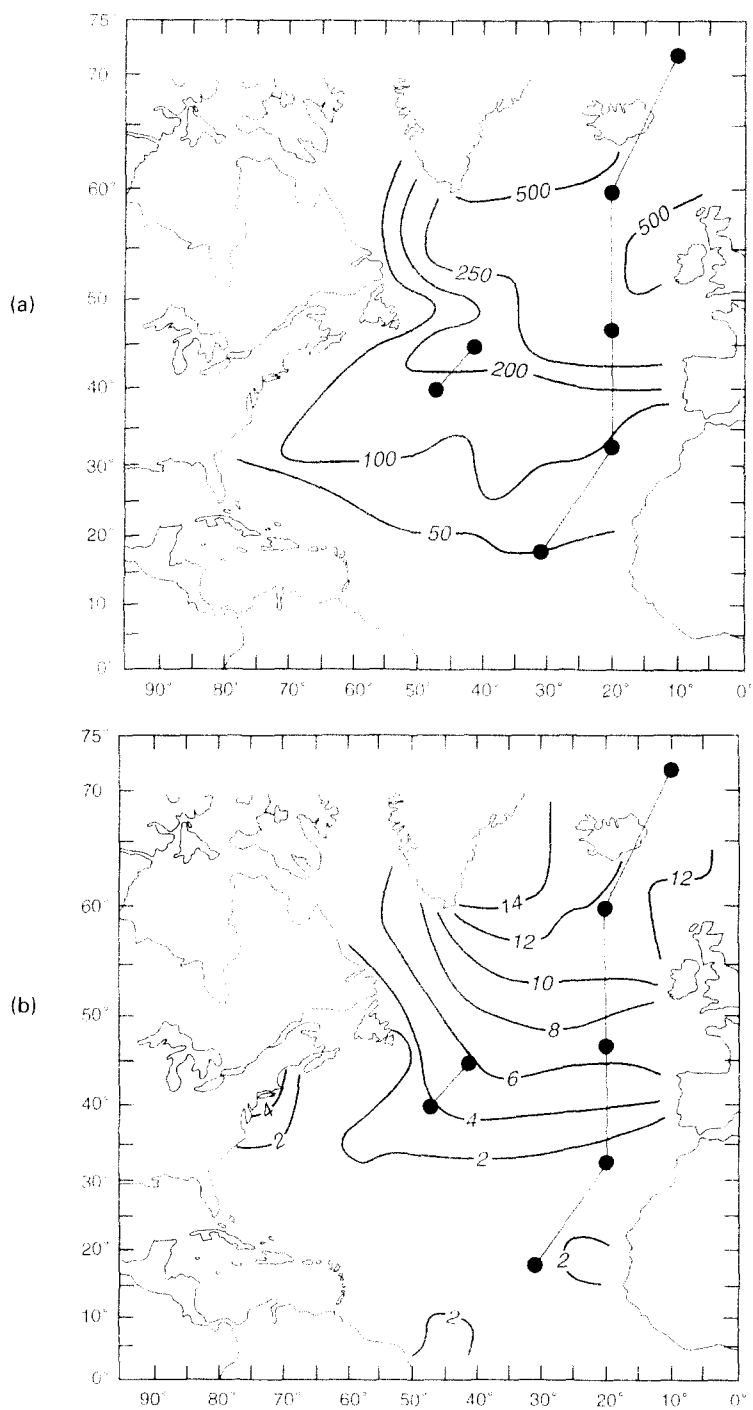


Fig. 1. Maps of the JGOFS-NABE study area in the North Atlantic Ocean. (a) winter mixed layer depths based on the depth of a σ_{θ} 0.125 units greater than the surface value. (b) Estimated winter maximum surface nitrate concentrations ($\mu\text{mol l}^{-1}$). Contour lines after GLOVER and BREWER (1987). The principal NABE stations are also indicated.

Table 1. JGOFS North Atlantic Bloom Experiment. Operations at main stations in 1989

Station	Dates	Nations	Deep traps	Other
18°N, 31°W	23/8–8/4	F.R.G.	—	drifting traps
33°N, 20°W	13/4–25/4	F.R.G.	U.S.A.	drifting traps
	30/8–7/9	NL		NASA overflight
40°N, 47°W	27/4–4/5	CAN	—	drifting traps
45°N, 41°W	8/5–13/5	CAN	—	drifting traps
47°N, 20°W	24/4–9/5	U.S.A.	F.R.G., NL	drifting traps
	5/5–24/5	F.R.G.	U.K., U.S.A.	NASA overflights
	11/5–18/5	U.K.		Geosat altimetry
	18/5–31/5	U.S.A.		
	1/7–8/7	U.K.		
	16/7–26/7	U.K.		
	10/8–25/8	F.R.G.		
	22/8–25/8	NL		
	19/4–20/4	U.S.A.	U.K., F.R.G.	drifting traps
	25/5–5/6	U.K.		NASA overflights
59°N, 20°W	26/5–10/6	F.R.G.		ONR MLML mooring
	6/6–7/6	U.S.A.		
	14/6–21/6	U.K.		
	30/6–5/7	U.S.A.		
	19/7–8/8	F.R.G.		
	3/8–10/8	U.K.		
72°N, 8°W	5/8–17/8	NL		
	16/6–10/7	F.R.G.	F.R.G.	drifting traps

deep convection in late winter supplies the upper ocean with 2–14 μg -atoms (μMol) of nitrate which supports new primary production following restratification in April–May. In the absence of removal by zooplankton, this process culminates in the accumulation of phytoplankton biomass shown on the cover of this volume.

Seven primary locations were occupied during NABE in 1989 (Table 1). Stations at 18 and 72°N were only visited by the *Meteor* (F.R.G.) during the Hensen centennial “Plankton 89 – Benthos 89” expedition. PASSOW and PEINERT (1993) provide a brief overview of conditions at 18°N in their paper on plankton and particulate fluxes. The stations in the western Atlantic were part of the Canadian JGOFS “Western NABE.” HARRISON *et al.* (1993) give an in-depth analysis of upper ocean processes at the 40°W stations. The stations at 47 and 59°N were studied intensively during multiple occupations by Germany, the Netherlands, U.K. and U.S.A. LOCHTE *et al.* (1993) and WEEKS *et al.* (1993) summarize multinational observations on plankton ecology, chemistry and physics at 47 and 59°N, respectively.

NABE investigations took place in a region of the ocean with strong mesoscale eddy structure and horizontal advection. PINGREE (1993) describes drogoue studies of currents in the study region. ROBINSON *et al.* (1993) report an altimetric study that revealed the existence of three anticyclonic eddies and other complex mesoscale and submesoscale variability in the 47°N study area. The structure of chlorophyll fields sensed by airborne LIDAR (YODER *et al.*, 1993; HOGUE and SWIFT, 1993) coincided at the same spatial scales as the physical field, indicating intimate causal connections between the mesoscale circulation and biological dynamics of the bloom. Most of the larger scale variability in the

chlorophyll field was oriented in the north-south direction, as originally hypothesized. Complex hydrographic structures in the southern part of the NABE study region were observed during the *Meteor* occupations at 18°N (PODEWSKI *et al.*, 1993).

Perhaps the most important early scientific contribution of NABE is the development and refinement of analytical techniques for CO₂, and the collection of a large data set on seasonal and spatial trends in surface pCO₂ (WATSON *et al.*, 1991). Less than a decade ago, as JGOFS was first being discussed, BREWER (1986) asked, "What controls the variability of CO₂ in the surface ocean?" After NABE, there can be little argument that in temperate seas, this variability is strongly tied to the dynamics of the bloom. GOYET and BREWER (unpublished), observing that CO₂ was depleted in the upper 150 m at 47°N by 2820 μmol m⁻² during the bloom, suggest the importance of specifying small-scale variations in surface CO₂ which can have a large impact on our estimates of air-sea fluxes. ROBERTSON *et al.* (1993) describe diurnal variations in surface pCO₂ and O₂.

Phytoplankton blooms are driven by an excess of production over consumption and export, leading to accumulations of biogenic material in surface waters. Several papers in this volume report rates of primary production in excess of 80 μmol C m⁻² day⁻¹ (1000 mgC m⁻² day⁻¹ or *ca* 3000 μmol m⁻² over 36 days), a figure agreeing well with the direct observations of CO₂ depletion reported by Goyet and Brewer. CHIPMAN *et al.* (1993) also show that ¹⁴C estimates of primary production in bottles were consistent with direct observations of CO₂ depletion in the mixed layer. MARTIN *et al.* (1993) report on determinations of trace metal contamination in productivity bottles used by NABE investigators. Their findings, in conjunction with the comparisons just described, suggest that when performed carefully with attention to clean technique, the NABE productivity protocols yielded a high-quality data set. MARRA and Ho (1993) present a two-dimensional (Z-t) model that represents the triggering of the bloom following restratification at 47°N. A related approach stressing the importance of diurnal heating is given in TAYLOR and STEPHENS (1993) the models relating to the data of ROBERTSON *et al.* (1993). GARDNER *et al.* (1993) detailed light transmission profiles to demonstrate both diurnal cycles and a longer term increase in small particle stocks, both of which phenomena are closely tied to bloom dynamics.

High rates of new production during blooms are supported by high concentrations of nitrate supplied during winter mixing. KOEVE *et al.* (1993) observed great spatial variability in nitracline depth at 18°N, where nitrate was already depleted in the surface layer. GARSIDE and GARSIDE (1993) present data on the *f*-ratio on 20°W during NABE. Although models predict that under bloom conditions up to 70–80% of the total primary production may be supported by nitrate new production (FASHAM *et al.*, submitted), NABE observations generally indicate lower *f*-ratios of 30–45% (40°W: HARRISON *et al.*, 1993; 59°N: SAMBROTTO *et al.*, 1993; 47°N: MARTIN *et al.*, 1993). These findings suggest that processes supporting regenerated primary production, such as grazing and microbial activity, were already proceeding at comparatively rapid rates during the bloom. Determinations of the size distribution of primary (JOCHAM *et al.*, 1993; JOINT *et al.*, 1993) and new (SAMBROTTO *et al.*, 1993) production indicate that over 50% of the production was by cells less than 5 μm, which tend to be more closely coupled to regenerative processes than larger cells like diatoms and dinoflagellates.

Studies of heterotrophic plankton ecology and rate processes were an important feature of NABE, confirming the hypothesis that supplies of regenerated nutrients are abundant during the bloom. As expected, mesozooplankton (largely copepods) contributed only a

small portion to the plankton biomass, and grazed only a few per cent of the daily production (MORALES *et al.*, 1991; DAM *et al.*, 1993; HARRISON *et al.* 1993). Several papers estimate that the contribution of mesozooplankton fecal pellets to measured vertical export rates ranged from *ca* 10–100%. PASSOW and PEINERT (1993) found that viable diatoms made up about 30% of the vertical flux at 33°N. HEAD and HORNE (1993) speculate that in future studies, analyses of phaeophorbide pigments in sediment traps might characterize the balance between grazing and diatom autolysis as contributors to the export.

Another key finding of NABE was the unexpected importance of microbial activities during the bloom. Simple models of bloom dynamics postulate a period characterized by low grazing and high exports of uningested diatom cells. In contrast, NABE investigators on both sides of the Atlantic observed rapid successions of pigments, phytoplankton and microzooplankton following the onset of the bloom at tropical to subpolar latitudes (BARLOW *et al.*, 1993; SIERACKI *et al.*, 1993). VELDHIJS *et al.* (1993) document postbloom summer phytoplankton community structure and dynamics. A large and diverse fauna consisting of nanoflagellates, ciliates and dinoflagellates (BURKILL *et al.*, 1993; VERITY *et al.*, 1993) consumed up to 100% of the daily production at 41–47°W, and 47–59°N. An interesting speculation arising from NABE is that this intense activity by protozoans not only fuels primary production by ammonium and urea excretion, but also drives the vertical flux through predation by mesozooplankton (WEEKS *et al.*, 1993). Thus although mesozooplankton herbivory was insignificant, these larger animals may have exerted top-down control on the grazer assemblage and contributed to the vertical flux by repackaging smaller grazers into fecal pellets. Such a scenario may explain the high rates of mesozooplankton respiration discussed by LENZ *et al.* (1993). HONJO and MANGANINI (1993) present their observations of fluxes to the deep sea at two NABE stations.

Grazer activity also may have stimulated bacterial production. A bacterial bloom lagging the phytoplankton bloom by 10–20 days was observed at 41–47°W and 47–59°N (LI *et al.*, 1993; DUCKLOW *et al.*, 1993). Because bacterial production averaged 20–30% of primary production, it was unlikely that these levels were supported by exudation from phytoplankton. Grazer-mediated release and particle decay (*cf.* MARTIN *et al.*, 1993) are logical sources of sustenance for the bacteria. The large pool of dissolved organic carbon (DOC) also may have contributed to bacterial production. KIRCHMAN *et al.* (1991) observed that bacteria utilized 25% of surface DOC ($50 \mu\text{mol kg}^{-1}$) in experiments conducted at 47°N. LOCHTE *et al.* (1993) suggest that bacteria using DOC at efficiencies of *ca* 20–30% could explain net consumption of $110 \text{ mMol m}^{-2} \text{ day}^{-1}$ at 47°N. Based on NABE measurements of DOC stocks, PELTZER *et al.* (submitted) and MARTIN and FITZWATER (submitted) suggest upward revisions of the size of the oceanic DOC reservoir to 1680–1800 Gt. Are bacterioplankton the filter through which DOC produced by plankton in the upper ocean passes into the ocean interior? The processes responsible for forming and cycling the oceanic DOC pool are just beginning to be addressed.

NABE continued in 1990 with coordinated studies by the U.K., Germany and The Netherlands. SAVIDGE *et al.* (1992) describe the ambitious attempts by BOFS to conduct Lagrangian observations of the bloom in the eddy field between 46 and 50°N. Lagrangian studies of the survival and evolution of microbial communities in Mediterranean outflow eddies (“Meddies”) studied by the French JGOFS program are presented by SAVENKOFF *et al.* (1993). PFANNKUCHE (1993) presents time series observations of the benthic response to organic matter sedimentation at 47°N between 1985 and 1990.

NABE, the first JGOFS process study and first large-scale multinational study of ocean biogeochemistry, has revealed that the North Atlantic phytoplankton bloom was a complex phenomenon with many unexpected features. Its most surprising attribute was intense nutrient regeneration activity supported by large stocks of microbes, and presumably, high rates of respiration. Yet over the 30–40 day observation period at 47°N, CO₂ was depleted from the mixed layer with great efficiency, at about 75% of the rate of primary production. This apparent paradox calls into question the oft-quoted identification of CO₂ drawdown with new production, and requires new models of bloom dynamics for its resolution. The strong connection between the mesoscale physical and biogeochemical fields demonstrates the need for eddy-resolving coupled circulation/biogeochemical models to help understand oceanic blooms.

REFERENCES

- BARLOW R. G., M. A. GOUGH, R. F. C. MANTOURA and T. W. FILEMAN (1993) Pigment signatures of the phytoplankton composition in the North Eastern Atlantic during the 1990 spring bloom. *Deep-Sea Research II*, **40**, 459–477.
- BENDER M. L., H. W. DUCKLOW, J. KIDDON, J. MARRA and J. H. MARTIN (1992) The carbon balance during the 1989 spring bloom in the North Atlantic Ocean, 47°N, 20°W. *Deep-Sea Research*, **39**, 1707–1725.
- BILLET D. S. M., R. S. LAMPIE, A. L. RICE and R. F. C. MANTOURA (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature*, **302**, 520–522.
- BREWER P. G. (1986) What controls the variability of carbon dioxide in the surface ocean? A plea for complete information. In: *Dynamic processes in the chemistry of the upper ocean*, J. D. BURTON, P. G. BREWER and R. CHESSELET, editors. Plenum, New York, pp. 215–231.
- BURKILE P. H., E. S. EDWARDS, A. W. J. JOHN and M. A. SLEIGH (1993) Microzooplankton and their herbivorous activity in the north eastern Atlantic Ocean. *Deep-Sea Research II*, **40**, 479–493.
- CHIPMAN D. W., J. MARRA and T. TAKAHASHI (1993) Primary production at 47°N, 20°W in the North Atlantic Ocean: a comparison between the ¹⁴C incubation method and mixed layer carbon budget observations. *Deep-Sea Research II*, **40**, 151–169.
- COLEBROOK J. M. (1982) Continuous plankton records: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. *Journal of Plankton Research*, **4**, 435–462.
- DAM H. G., C. A. MILLER and S. H. JONASDOTTIR (1993) The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 197–212.
- DUCKLOW H. W. (1989) Joint Global Ocean Flux Experiment: the North Atlantic Spring Bloom Experiment, 1989. *Oceanography Magazine*, **2**, 4–8.
- DUCKLOW H. W., D. L. KIRCHMAN, H. L. QUINBY, C. A. CARLSON and H. G. DAM (1993) Bacterioplankton carbon cycling during the spring bloom in the eastern North Atlantic Ocean. *Deep-Sea Research II*, **40**, 245–263.
- ESAIAS W. E., G. C. FELDMAN, C. R. McCLAIN and J. A. EIROD (1986) Monthly satellite-derived phytoplankton pigment distribution for the North Atlantic Ocean basin. EOS, 835–837.
- FASHAM M. J. R., J. L. SARMIENTO, R. D. SLATER, H. W. DUCKLOW and R. WILLIAMS (submitted) A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone: a comparison of the model results with observations from Bermuda Station “S” and OWS “India.” *Journal of Geophysical Research*.
- GARDNER W. D., I. D. WALSH and M. J. RICHARDSON (1993) Biophysical forcing of particle distributions during the North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 171–195.
- GARSIDE G. and J. C. GARSIDE (1993) The “f-ratio” on 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 75–90.
- GLOVER D. M. and P. G. BREWER (1988) Estimates of wintertime mixed layer nutrient concentrations in the North Atlantic. *Deep-Sea Research*, **35**, 1525–1546.
- GOYET C. and P. G. BREWER (unpublished) Temporal variations of the properties of the carbonate system in the North Atlantic Ocean at 47°N, 20°W: The CO₂ flux across the air–sea interface.
- GRAN H. H. and T. BRAARUD (1935) A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf

- of Maine including observations on the hydrography, chemistry and turbidity. *Journal of the Biological Board of Canada* **1**, 219–467.
- HARRISON W. G., E. J. H. HEAD, E. P. W. HORNE, B. IRWIN, W. K. W. LI, A. R. LONGHURST, M. PARANJAPÉ and T. PLATT (1993) The Western North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 279–305.
- HEAD E. J. H. and E. P. W. HORNE (1993) Algal pigment transformation and vertical flux in an area of convergence in the North Atlantic. *Deep-Sea Research II*, **40**, 329–346.
- HÖGE F. E. and R. N. SWIFT (1993) The influence of chlorophyll pigment upon upwelling spectral radiances from the North Atlantic Ocean: an active–passive correlation spectroscopy study. *Deep-Sea Research II*, **40**, 265–277.
- HONJO S. and S. J. MANGANINI (1993) Annual biogenic particle fluxes to the interior of the North Atlantic Ocean studied at 34°N, 21°W and 48°N, 21°W. *Deep-Sea Research II*, **40**, 587–607.
- JOCHUM F. J. and B. ZEITSCHSEL (1993) Productivity regime and phytoplankton size structure in the tropical and subtropical North Atlantic in spring 1989. *Deep-Sea Research II*, **40**, 495–519.
- JOINT I. R., A. POMROY, G. SAVIDGE and P. BOYD (1993) Size fractionated primary productivity in the North East Atlantic in Spring 1989. *Deep-Sea Research II*, **40**, 423–440.
- KIRCHMAN D. L., Y. SUZUKI, C. GARSIDE and H. W. DUCKLOW (1991) High turnover rates of dissolved organic carbon during a spring phytoplankton bloom. *Nature*, **352**, 612–614.
- KOEVE W., R. W. EPPLEY, S. PODEWSKI and B. ZEITSCHSEL (1993) An unexpected nitrate distribution in the tropical North Atlantic at 18°N, 30°W—implication for new production. *Deep-Sea Research II*, **40**, 521–536.
- LENZ J., A. MORALES and J. GUNKEL (1993) Mesozooplankton standing stock during the North Atlantic spring bloom study in 1989 and its potential grazing pressure on phytoplankton: a comparison between low, medium and high latitudes. *Deep-Sea Research II*, **40**, 559–572.
- LI W. K. W., P. M. DICKIE, W. G. HARRISON and B. D. IRWIN (1993) Biomass and production of bacteria and phytoplankton during the spring bloom in the western North Atlantic Ocean. *Deep-Sea Research II*, **40**, 307–327.
- LOCHE K., H. W. DUCKLOW, M. J. R. FASHAM and C. STIENEN (1993) Plankton succession and carbon cycling at 47°N, 20°W during the JGOFS North Atlantic bloom experiment. *Deep-Sea Research II*, **40**, 91–114.
- MARRA J. and C. HO (1993) Initiation of the Spring Bloom in the North Atlantic (47°N, 20°W) a numerical simulation. *Deep-Sea Research II*, **40**, 55–73.
- MARTIN J. H. and S. E. FITZWATER (submitted) Dissolved organic carbon in the Atlantic, Southern and Pacific Oceans. *Nature*.
- MARTIN J. H. and S. E. FITZWATER, R. M. GORDON, C. N. HUNTER and S. J. TANNER (1993) Iron, primary production and flux studies during the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 115–134.
- MILLS E. L. (1989) *Biological Oceanography, an early history, 1870–1960*. Ithaca, 378 pp.
- MORALES C. E., A. BEDO, R. P. HARRIS and P. R. G. TRANTER (1991) Grazing of copepod assemblages in the north-east Atlantic: the importance of the small size fraction. *Journal of Plankton Research*, **13**, 455–472.
- PASSOW U. and R. PEINERT (1993) The role of plankton in particle flux: two case studies from the North Atlantic. *Deep-Sea Research II*, **40**, 573–585.
- PELTZER E. T., P. G. BREWER, Y. SUZUKI and Y. SUGIMURA (submitted) Measurement of dissolved organic carbon in seawater by high temperature catalytic oxidation. *Journal of Marine Research*.
- PFANNKUCHE O. (1993) Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station 47°N, 20°W. *Deep-Sea Research II*, **40**, 135–149.
- PINGREE R. D. (1993) Flow of surface waters to the west of the British Isles and in the Bay of Biscay. *Deep-Sea Research II*, **40**, 369–388.
- PLATT T., D. F. BIRD and S. SATHYENDRANATH (1991) Critical depth and marine primary production. *Proceedings of the Royal Society of London*, **B264**, 205–217.
- PODEWSKI S., G. SAURE, R. W. EPPLEY, W. KOEVE, R. PEINERT and B. ZEITSCHSEL (1993) The nose: a characteristic inversion within the salinity maximum water in the tropical North-East Atlantic. *Deep-Sea Research II*, **40**, 537–557.
- RILEY G. A. (1942) The relationship of vertical turbulence and spring diatom flowerings. *Journal of Marine Research*, **5**, 67–87.
- ROBERTSON J. R., A. J. WATSON, C. LANGDON, R. D. LING and J. WOOD (1993) Diurnal variation in surface pCO₂ and O₂ at 60°N, 20°W in the North Atlantic. *Deep-Sea Research II*, **40**, 409–422.
- ROBINSON A. R., D. J. MCGILLICUDDY, J. COLMAN, H. W. DUCKLOW, M. J. R. FASHAM, F. E. HÖGE, W. G. LESLIE, J. J. MCCARTHY, S. PODEWSKI, D. L. PORTER, G. SAURE and J. A. RÖDER (1993) Mesoscale and upper ocean variability during the 1989 JGOFS Bloom Study. *Deep-Sea Research II*, **40**, 9–35.

- SAMBROTTO R. N., J. H. MARTIN, W. W. BROENKOW, C. A. CARLSON and S. E. FITZWATER (1993) Nitrate utilization in surface waters of the Iceland Basin during Spring and Summer of 1989. *Deep-Sea Research II*, **40**, 441–457.
- SAVENKOFF C., D. LEFEVRE, M. DENIS and C. E. LAMBERT (1993) How do microbial communities keep living in the Mediterranean outflow within N.E. Atlantic intermediate waters? *Deep-Sea Research II*, **40**, 627–641.
- SAVIDGE G., D. R. TURNER, P. H. BURKILL, A. J. WATSON, M. V. ANGEL, R. D. PINGREE, H. LEACH and K. J. RICHARDS (1992) The BOFS 1990 spring bloom experiment: temporal evolution and spatial variability of the hydrographic field. *Progress in Oceanography*, **29**, 235–281.
- SIERACKI M. E., P. G. VERITY and D. K. STOECKER (1993) Plankton community response to sequential silicate and nitrate depletion during the 1989 North Atlantic Spring Bloom. *Deep-Sea Research II*, **40**, 213–225.
- SVERDRUP H. U. (1953) On the conditions for the vernal blooming of phytoplankton. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, **18**, 287–295.
- TAYLOR A. H. and J. A. STEPHENS (1993) Diurnal variations of convective mixing and the spring bloom of phytoplankton. *Deep-Sea Research II*, **40**, 389–408.
- U.S. JOINT GLOBAL OCEAN FLUX STUDY OFFICE (1989) Ocean color from space. a folio of Coastal Zone Color Scanner imagery. WHOI, Woods Hole, MA, U.S.A.
- VELDHUIS M. J. W., G. W. KRAAY and W. C. GIESKES (1993) Growth and fluorescence characteristics of ultraplankton on a north–south transect in the eastern North Atlantic. *Deep-Sea Research II*, **40**, 609–626.
- VERITY P. G., D. K. STOECKER, M. E. SIERACKI, P. H. BURKILL, E. S. EDWARDS and C. R. TRONZO (1993) Abundance, biomass, and distribution of heterotrophic dinoflagellates during the North Atlantic Spring Bloom. *Deep-Sea Research II*, **40**, 227–244.
- WATSON A. J., C. ROBINSON, J. E. ROBERTSON, P. J. LEB. WILLIAMS and M. J. R. FASHAM (1991) Spatial variability in the sink for atmospheric carbon dioxide in the North Atlantic. *Nature*, **350**, 50–53.
- WATSON A. J. and M. WHITFIELD (1985) Composition of particles in the global ocean. *Deep-Sea Research*, **32**, 1023–1039.
- WEEKS A., M. H. CONTE, R. P. HARRIS, A. BEDO, I. BELLAN, P. H. BURKILL, E. S. EDWARDS, D. S. HARBOUR, H. KENNEDY, C. LLEWELLYN, R. F. C. MANFOURA, C. E. MORALES, A. J. POMROY and C. M. TURLEY (1993) The physical and chemical environment and changes in community structure associated with bloom evolution. the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 347–368.
- YODER J. A., J. AIKEN, R. N. SWIFT, F. E. HOGE and P. M. STEGEMANN (1993) Spatial variability in near-surface chlorophyll a fluorescence measured by the airborne oceanographic LIDAR (AOL). *Deep-Sea Research II*, **40**, 37–53.