The JGOFS North Atlantic Bloom Experiment
An Overview

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The North Atlantic Bloom Experiment (NABE) of JGOFS presents a unique opportunity and challenge to the data management community because of the diversity and large size of biogeochemical data sets collected (Figure 1). NABE was a pilot study for JGOFS and has also served as a pilot study within the US NODC for management and archiving of the data sets. Here I present an overview to some of the scientific results of NABE, which will be published as an introduction to a special volume of NABE results in Deep-Sea Research later this year. An overview of NABE data management is given elsewhere in the present report.

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 observatories. In 1989-90 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, 1992). In 1989, six research vessels from Canada, Germany, The Netherlands, the United Kingdom and the USA 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 which fills the basin north of about 40 degrees latitude in April and May each year (see cover; ESAI A S et al., 1986; US 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 2 shows the oceanographic context of NABE. In the eastern North Atlantic, deep convection in late winter supplies the upper ocean with 2-14 [mu]g-atoms ([mu]Mol) 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. Seven primary locations were occupied during NABE in 1989 (Table 1). Stations at 18 at 72 North were only visited by the METEOR (FRG) during the Hensen centennial "Plankton 89 - Benthos 89" expedition. Passow and Peinert (1992) provide a brief overview of conditions at 18 North 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. (1992) is an in-depth analysis of upper ocean processes at the 40 West stations. The stations at 47 and 59 North were studied intensively during multiple occupations by Germany, The Netherlands, UK and USA. Lochte et al. (1992) and Weeks et al. (1992) summarize multinational observations on plankton ecology, chemistry and physics at 47N and 59N, respectively.

NABE investigations took place in a region of the ocean with strong mesoscale eddy structure and horizontal advection. Pingree (1992) describes drogue studies of currents in the study region. Robinson et al. (1992) report an altimetric study which revealed the existence of three anticyclonic eddies and other complex mesoscale and submesoscale variability in the 47N study area Figure 3). The structure of chlorophyll fields sensed by airborne LIDAR (Yoder et al., 1992; Hoge and Swift, 1992) coincided at the same spatial scales as the physical field, indicating intimate causal connections between the mesoscale circulation and biological dynamics of the bloom (Figure 4). 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 North (Podewski et al., 1992).

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. Chipman et al (1992; Figure 5) and Goyet and
Brewer (1992) observed that CO2 was depleted in the upper 150 m at 47N by 2820 [mu]mol m-2 during the bloom, and point to the importance of specifying small-scale variations in surface CO2 which can have a large impact on our estimates of air-sea fluxes.

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 [mu]mol C m-2 d-1 (1000 gC m-2 d-1 or ca 3000 [mu] mol m-2 over 36 d; Figure 6), a figure agreeing well with the direct observations of CO2 depletion reported by Goyet and Brewer. Chipman et al (1992) also show that 14C estimates of primary production in bottles were consistent with direct observations of CO2 depletion in the mixed layer (Figure 7). Martin et al. (1992) 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 using moderate clean technique, the NABE productivity protocols yielded a high-quality data set (Figure 8). Marra and Ho present a 2-dimensional (Z-t) model which represents the triggering of the bloom following restratification at 47N. A related approach stressing the importance of diurnal heating is given in Taylor et al., (1992). Gardner et al. (1992) used a transmissometer to demonstrate both diurnal cycles and a longer term increase in small particle stocks, both of which phenomena were closely tied to bloom dynamics (Figure 9).

High rates of new production during blooms are supported by high concentrations of nitrate supplied during winter mixing. Koeve et al., (1992) observed great spatial variability in nitracline depth at 18 North, where nitrate was already depleted in the surface layer. 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., 1990), NABE observations generally indicated lower f-ratios of 30-45% (40W: Harrison et al., 1992; 59N: Sambrotto et al., 1992; 47N: Martin et al., 1992). 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 (Jochem et al., 1992; Joint et al., 1992) and new (Sambrotto et al., 1992) production indicated that over 50% of the production was by cells less than 5 [mu]m, 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 which confirmed the hypothesis that supplies of regenerated nutrients were abundant during the bloom. As expected, mesozooplankton (largely copepods) contributed just a small portion to the plankton biomass, and grazed only a few per cent of the daily production (Figure 10; Morales et al., 1991; Dam et al., 1992; Harrison et al., 1992). Several papers estimate that the contribution of mesozooplankton fecal pellets to measured vertical export rates, ranged from ca 10-100%. Passow and Peinert (1992) found that viable diatoms made up about
30% of the vertical flux at 33N. Head and Horne (1992) 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 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 (Figure 11) and microzooplankton following the onset of the bloom at tropical to subpolar latitudes (Barlow et al., 1992; Sieracki et al., 1992). Veldhuis et al., (1992) document postbloom summer phytoplankton community structure and dynamics. A large and diverse fauna consisting of nanoflagellates, ciliates and dinoflagellates (Burkill et al., 1992; Verity et al., 1992) consumed up to 100% of the daily production at 41- 47W, and 47-59N. 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., 1992). 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., (1992). Honjo and Manganani (1992) present their observations of fluxes to the deep sea at two NABE stations.

Grazer activity may also have stimulated bacterial production. A bacterial bloom lagging the phytoplankton bloom by 10-20 days was observed at 41-47W and 47-59N (Li et al., 1992; Ducklow et al., 1992). 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., 1992) are logical sources of sustenance for the bacteria. The large pool of dissolved organic carbon (DOC) may also have contributed to bacterial production. Kirchman et al., (1991) observed that bacteria utilized 25% of surface DOC (50 [mu]mol kg-1) in experiments conducted at 47N. Lochte et al. (1992) suggest that bacteria using DOC at efficiencies of ca. 20-30% could explain net consumption of 110 mMol m-2 d-1 at 47N. Based on NABE measurements of DOC stocks, Peltzer et al (1992) and Martin and Fitzwater (1992) 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 UK, Germany and The Netherlands. Savidge et al., (1992) described the ambitious attempts by BOFS to conduct Lagrangian observations of the bloom in the eddy field between 46 and 50 North. 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., (1992). Pfannkuche (1992) presents time series
observations of the benthic response to organic matter sedimentation at 47 North between 1985-1990.

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 47N, 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 demonstrate the need for eddy-resolving coupled circulation/biogeochemical models to help understand oceanic blooms.

Acknowledgments

This article was written in association with the co-editor of the NABE Special Volume, Roger Harris (Plymouth, UK). I am grateful to the authors of papers in that volume for use of their data and figures presented in this report.

References


Pfannkuche, O. Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station 47N/20W. *Deep-Sea Res.* (Special NABE Volume, in press).


Savenkoff, C., Lefevre, D., Denis, M. and Lambert, C.E. How do microbial communities keep living in the Mediterranean outflow within N.E. Atlantic intermediate waters?


Yoder, J. A., J. Aiken, R. N. Swift,, F. E. Hoge, and P.M. Stegeman, 1992. Spatial variability in near-surface chlorophyll a fluorescence measured by the air-

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

<table>
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<th>Station</th>
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<th>Other</th>
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Figure 1. Data collected during the USA cruise at 47 North, May 18-31, 1989, courtesy of R. Williams, Scripps (NO3); H. Ducklow, HPEL (PON, bacteria); D. Repeta, WHOI (phytoplankton); H. Dam, HPEL (mesozooplankton); P. Verity, Skidaway (microzooplankton); J. Martin, Moss Landing (primary production and export); and J. McCarthy (N-15 uptake).
47 NORTH 20 WEST  C-14 PRIMARY PROD.  
May 18–31, 1989  and LIGHT

N–15 NITROGEN UPTAKE

BACTERIAL PRODUCTION

MICROZOOPLANKTON HERBIVORY

MESOZOOPLANKTON HERBIVORY

PON EXPORT (50 METERS)
Figure 2. Maps of the JGOFS-NABE study area in the North Atlantic Ocean showing A (above): winter mixed layer depths based on the depth of a sigma-t 0.125 units greater than the surface value. B (next page: estimated winter maximum surface nitrate concentrations ([μmol l⁻¹]). Contour lines after Glover and Brewer (1987). The principal NABE stations are also indicated.
Figure 3. Map of mesoscale eddy field deduced from Geosat altimetric observations (Robinson et al., 1992).
Figure 4. Alongtrack temperature and lidar-induced chlorophyll-fluorescence (LICF) in the JGOFS study area (Yoder et al., 1992).
Figure 5. Drawdown of pCO$_2$ at 47 North, April 25 - May 31, 1989, drawn from data provided by T. Takahashi, J. Goddard and D. Chipman (Lamont-Doherty).
Primary Production 4/25 - 5/31 at 47 North

Figure 6. Primary production rates at 47 North, courtesy J. Marra (Lamont) and J. Martin (Moss Landing).
Figure 7. Comparison of primary production estimates from in situ C14 incubations and observed CO2 drawdown in the mixed layer at 47 North, April 25 - May 8, 1989 (Chipman et al., 1992).
Figure 8. Concentration of trace metal contaminants in water samples (open boxes) and primary production incubations (shaded boxes) by different NABE nations (numbers) in 1989. All levels except perhaps Zn in some incubations are below toxic concentration (Martin et al., 1992).
Figure 9. Comparison of changes in particle concentration from transmissometry and CO2 utilization at 47 North (Gardner et al., 1992).
Primary production and its removal by mesozooplankton (Dam et al., 1992).

Figure 10.
Figure 11. Succession of phytoplankton groups at 47 North. Data after D. Repeta (WHOI), following interpretation of J. Marra (Lamont) and M. Sieracki (Bigelow Lab.).