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The role of mesoscale hydrography on microbial dynamics in the northeast Atlantic: Results of a spring bloom experiment

by B. Karrasch[1], H.-G. Hoppe[2], S. Ullrich[2] and S. Podewski[2]

ABSTRACT

During RV *Meteor* cruise No. 10 from May to June 1989 (JGOFS pilot study) bacterial and picocyanobacterial abundance, biomass, and bacterial production were estimated at two drift stations close to 47N, 20W and 58N, 20W in the northeast Atlantic. At 47N two different mesoscale hydrographic structures were sampled which divided the drift experiment into a cyclonic and an anticyclonic circulation phase. Transition from one phase to the next was clearly reflected by changes of the biological structure in the upper water column. Phytoplankton stocks maintained during the cyclonic phase were about 1.8 times higher than those of the anticyclonic phase (1552 mg C m^{-2} and 880 mg C m^{-2}, resp., integrated over the mixed layer, Deckers, 1991). Integrated stocks of bacteria showed an opposite pattern of distribution. Picocyanobacterial biomass (PCB) was 3.4 times higher during the anticyclonic phase than during the cyclonic phase (96 mg C m^{-2} and 28 mg C m^{-2}, resp.), and the respective factor for total bacterial biomass (TBB) was 3.7 (830 mg C m^{-2} and 225 mg C m^{-2}, resp.). Our analysis indicates that the combined bacterial biomass dominated within the mixed layer during the anticyclonic phase, while the cyclonic phase was clearly dominated by eucaryotic phytoplankton. Additional evidence for a shift of biology toward the microbial food web was indicated by a strong increase of bacteria during the anticyclonic phase. Thus, simultaneously and side by side, an autotrophic and a heterotrophic system were supported by the prevailing hydrographic conditions. At 58N within an anticyclonic mesoscale hydrographic structure the phytoplankton bloom was at a developing stage, characterized by low biomass (730 mg C m^{-2} in the mixed layer, Deckers, 1991) but relatively high primary production. In contrast, bacterial stocks were quite high, but bacterial production was low in comparison to the anticyclonic phase at 47N (90 mg C m^{-2} d^{-1} and 153 mg C m^{-2} d^{-1}, resp., integrated from 0–300 m). It was calculated that bacterial gross production averaged 42% (47N, anticyclonic phase) and 25% (58N) of primary production. These results suggest that within a specific type of hydrographic structure either a heterotrophic or an autotrophic system can be established, depending on the stage of bloom development. In conclusion: Depending on their origin and age, mesoscale hydrographic structures can be correlated with different stages of biological development. This leads to the mesoscale patchiness of biological measurements, which is a characteristic feature of the northeast Atlantic.

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1. Introduction

The general picture of the vernal phytoplankton bloom development in the ocean is that of a successive process of bloom initiation, culmination and decline. The latter period is connected with a shift in dominance from autotrophic to heterotrophic communities of organisms. In terms of its spatial dimension the spring bloom may stretch nearly homogenously over many degrees of longitude, depending on the stability of the water column and nutrient and light availability. This ideal picture does not seem to hold true for oceanic regions of unsteady hydrography due to mesoscale variability, such as the northeast Atlantic. However, space and time scales of former biological investigations frequently were not adjusted to resolve mesoscale hydrographic features in the open ocean. Thus, the influence of hydrography on biology could be hardly detected (Angel and Fasham, 1983). In recent years multinational interdisciplinary programmes (e.g. JGOFS) were initiated and increasing information on the impact of mesoscale hydrographic variability on the dynamics of biological processes in the open ocean is now becoming available.

The analysis of near-surface drifters and Geosat altimeter data has shown that mesoscale variability and high eddy energy in the central North Atlantic is concentrated along the North Atlantic Current (NAC), the Azores Current and the North Equatorial Current (Beckmann *et al.,* 1994; Brügge, 1995). Along these mean zonal flow bands baroclinic instability seems to be the main mechanism of eddy generation, resulting in a meandering of the currents and a subsequent shedding of mesoscale eddies from the main stream (Mittelstaedt, 1987; Onken and Klein, 1991; Beckmann *et al.,* 1994). The expression "mesoscale" or "eddy variability" is often defined rather broadly, including eddies, fronts, meanders, rings and planetary waves (Le Traon, 1992). Mesoscale eddies are mainly in quasigeostrophic balance and have lifetimes of weeks or up to three years, and spatial scales ranging from tens to hundreds of kilometers (Angel and Fasham, 1983; Le Traon, 1992).

Cold (cyclonic) and warm-core (anticyclonic) rings have been observed frequently in the western part of the North Atlantic and investigations have been carried out especially in the rings of the Gulf Stream (e.g. Ortner *et al.,* 1979; The Ring Group, 1981; Wiebe, 1982; Robinson, 1983; Hitchcock *et al.,* 1985; Fryxell *et al.,* 1985; Peele *et al.,* 1985; Hanson *et al.,* 1986) which are generally detached from the main stream east of 70W (e.g. Richardson, 1980). The Ring Group presented the first interdisciplinary investigation of the physics, chemistry, and biology of cold-core Gulf Stream rings and identified some of the main processes and phenomena associated with them. The cold core of such rings is characterized by low temperatures and low salinities indicating their subarctic origin, high nutrient concentrations and high biological activity. They have considerable importance for the transport of nutrients and biota. For example, the input of living organic material into the northern Sargasso Sea by cold-core rings accounts for about 5×10^{11} g C a^{-1}. Many organisms

adapted to cold water have been found in cold-core rings but nowhere else in the Sargasso Sea (The Ring Group, 1981).

In contrast, mesoscale eddies have seldom been studied in the eastern part of the North Atlantic (Le Groupe Tourbillon, 1983; Kupfermann *et al.,* 1986; Mittelstaedt, 1987; Schauer, 1989; Krauss *et al.,* 1990) and these investigations were mostly restricted to physical properties. The first report of horizontal and vertical distribution of nutrients, phytoplankton, and bacterioplankton in a cyclonic cold-core eddy in the northeast Atlantic was given by Lochte and Pfannkuche (1987). It was found that the cold core was different from ambient northeast Atlantic water in terms of nutrient chemistry, phytoplankton species, distribution and abundance, bacterial numbers and cell size, and in the processes determining the phyto- and bacterioplankton abundance. Highest concentrations of chlorophyll *a,* total phytoplankton biomass, dinoflagellates, and bacteria were observed in the surface water of the eddy center.

In the present paper we describe in detail the magnitude and succession of bacterial standing stocks and bacterial production as a function of different mesoscale hydrographic regimes (cyclonic and anticyclonic eddy-like features) observed during two drift experiments in the vicinity of 47N, 20W and 58N, 20W. These studies were carried out within the framework of the JGOFS "North Atlantic Bloom Experiment" in May/June 1989. A first overview of plankton succession and carbon cycling during this experiment was published by Lochte *et al.* (1993) who combined results from different cruises of the international study. Additional information on mesoscale hydrographic variability in the southern area of investigation—derived from GEOSAT altimetric data and CTD casts—was provided by Robinson *et al.* (1993). The results of the present work demonstrate the variability of the link between autotrophic and heterotrophic biological processes triggered by the observed hydrographic conditions.

2. Methods

a. Study area. The main study sites of the North Atlantic Bloom Experiment (NABE) as part of the JGOFS project were located in the northeast Atlantic along 20W. The international approach concentrated on drift stations at 47N and 58N and sections in between (Fig. 1a, b; Fig. 2a, b). The northern study area was situated in the vicinity of the subarctic front connected with the northernmost permanent current branch of the NAC. The subarctic front is known to be one of the major sources of eddy production (Viehoff and Fischer, 1988). The southern area was embedded in the transition zone between the NAC regime and the subtropical gyre circulation (Krauss, 1986; Dickson *et al.,* 1988; Brügge, 1995). Branches of the NAC occurred as transient features within this transition zone showing high variability both in strength and position (Sy, 1988; Arhan, 1990; Sy *et al.,* 1992). Schauer (1989) and Sy *et al.* (1992) reported the occurrence of two cyclonic structures at 47N, 20W

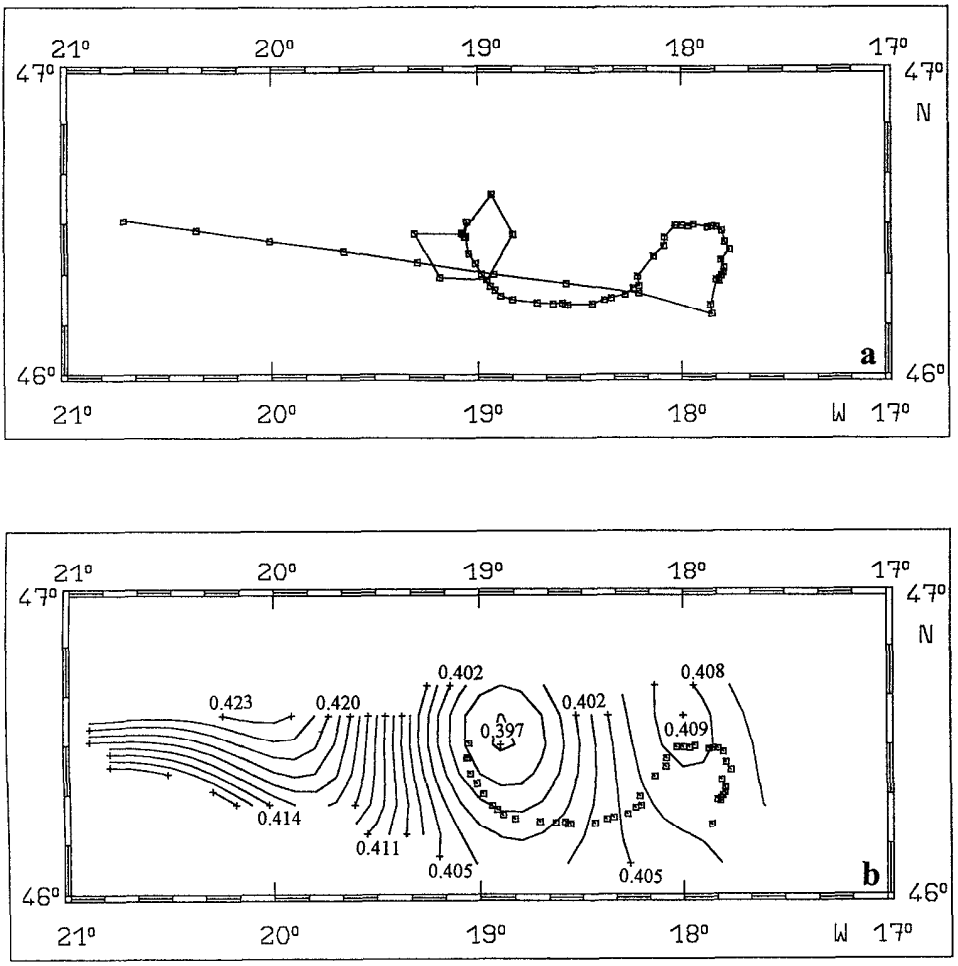

Figure 1. (a) Positions of the CTD casts at 47N taken from 7–22 May 1989. (b) Objectively analyzed dynamic height at 80 dbar relative to 485 dbar in dyn m. The sequence of open squares represents the drifter trajectory from the center of the small cyclonic eddy into the mesoscale anticyclonic structure.

possibly meanders or detached eddies from a NAC branch. Earlier investigations revealed the existence of mesoscale cyclonic and anticyclonic eddies as a characteristic feature of the northeast Atlantic (Dietrich and Ulrich, 1968; Le Groupe Tourbillon, 1983; Kupfermann *et al.,* 1986; Mittelstaedt, 1987; Schauer, 1989; Krauss *et al.,* 1990).

In late winter the upper water column is influenced by deep winter mixing resulting in a supply of new nutrients to the surface layer (Glover and Brewer, 1988). During April/May the subsequent warming, light increase and stratification of the

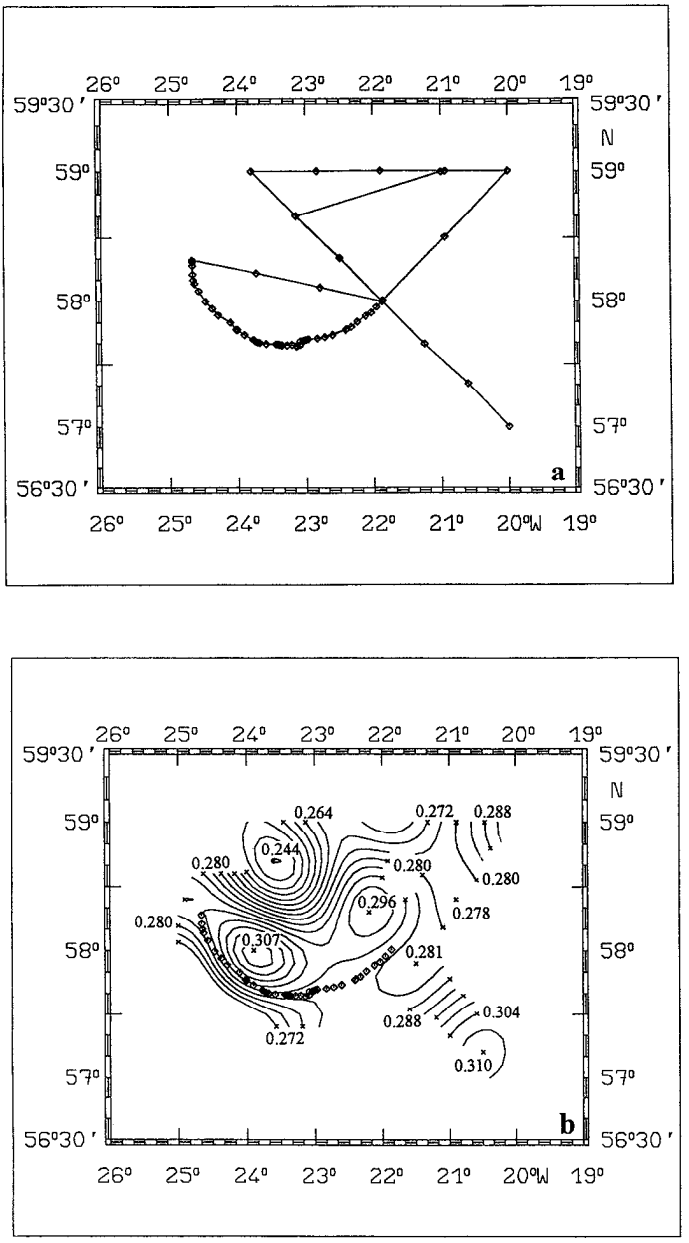

Figure 2. (a) Positions of the CTD casts at 58N taken from 26 May–10 June 1989. The two pre-survey sections were investigated from 57N, 20W to 59N, 23.8W (southeast-northwest) and from 59N, 23.8W to 59N, 20W (west-east). (b) Objectively analyzed dynamic height at 100 dbar relative to 485 dbar in dyn m. The sequence of open squares represents the drifter trajectory within the mesoscale anticyclonic structure.

upper water column triggers an extensive phytoplankton bloom which—derived from Coastal Zone Color Scanner (CZCS) imagery—is one of the most conspicuous seasonal events on a global scale (e.g. Esaias *et al.,* 1986).

b. Sampling and measurements. From May 9th to June 8th 1989, samples were collected at two drift stations in the vicinity of 47N, 20W and 58N, 20W following a drifting rig equipped with two "Kiel sediment traps" (approximate target of 2–2.5 m^2 per trap) at 80 and 300 m (47N) and 100 and 300 m (58N) in combination with temperature/fluorescence probes at several depths. These deployment depths of the traps were chosen to resolve the particle flux within the euphotic zone below the mixed layer and in the upper mesopelagic zone which is the main zone of particle degradation. No additional sails were used within this arrangement. The arrays were connected to an ARGOS buoy at the sea surface (Zeitzschel *et al.,* 1990). The southern drift area (May 9th to 21st) stretched from 46°30′N, 19°03′W to 46°14′N, 17°49′W (Fig. 1a,b). The northern drift study (May 29th to June 8th) extended from 58°N, 21°50′W to 58°18′N, 24°40′W (Fig. 2a,b).

Water samples for the time series observations were taken close to the buoys trajectories with a rosette of 24 × 10 − liter Niskin bottles combined with a Neil Brown CTD-unit. CTD profiles were taken down to 500 dbar. Calibration procedures were described by Podewski *et al.* (1993). The horizontal fields presented in this paper were calculated with the objective mapping procedure of Hiller and Käse (1983) using a spatial correlation scale of 60 km and an error variance of 25% of the total variance. Sampling strategy was deduced from *in situ* fluorescence profiles (0–150 m).

We followed core measurement protocols specified by JGOFS (JGOFS, 1990b) for acridine orange direct counts of bacteria (AODC) and measurements of bacterial production derived from ^{3}H-thymidine incorporation. Samples for AODC were preserved with 1% formalin, then immediately filtered onto Irgalan Black stained Nuclepore filters (0.2 μm pore size) and stored frozen until examination. Bacterial biomass was calculated from cell size measurements for each sample by using a nonlinear equation derived from Simon and Azam (1989): cell carbon = cell volume$^{0.59}$ × 88.6 × 1.04878. Picocyanobacteria were counted directly after preservation with formalin (1%) and filtration onto Irgalan Black stained 0.2 μm Nuclepore filters. Cell numbers of picocyanobacteria were converted into carbon biomass using a factor of 0.19 pg C cell^{-1}. This factor was calculated by assuming a cell density of 1.1 g ml^{-1}, dry wt 30% of wet wt, a carbon content of 50% dry wt and a measured average cell volume of 1.15 μm^3, which was determined from 10 different stations.

Samples for bacterial production measurements were processed immediately after collection. A sample volume of 10 ml was inoculated with 5 nM ^{3}H-thymidine (TdR) and incubated for 2 h in plastic vials (3 parallels and one formalin-treated (1%) control) using dark laboratory incubators at *in situ* temperatures. Incubations were

terminated by adding 1% formalin, after which samples were collected on 0.2 μm Nuclepore filters by vacuum filtration, rinsed several times with seawater and extracted with ice-cold 5% trichloroacetic acid (TCA). Bacterial carbon biomass production was estimated by using a TdR conversion factor of 2×10^{18} cells $mole^{-1}$ (JGOFS, 1990a). Due to additional investigations carried out during this cruise (Karrasch, 1992; Hoppe *et al.,* 1993) we were not able to measure bacterial production rates at each station.

Integrated particulate organic carbon (POC), chlorophyll *a* (chl *a*) (estimated by members of the Dept. of Planktology, IfM, Kiel), ^{14}C primary production (pp) (Stienen, 1990), and phytoplankton biomass (PPC) (Deckers, 1991; according to the procedure given by Utermöhl (1958) using conversion factors from Edler (1979)) were used in this paper to complete the list of variables necessary for system calculations.

c. Definition of layers. For the interpretation and presentation of our data we divided the water column into two layers. The upper layer was defined by the mixed layer and ranged from the surface to the main seasonal thermocline (47N: cyclonic drift phase 0–30 m; anticyclonic drift phase 0–50 m; 58N: 0–30 m). The lower layer extended approximately to the depth where the compensation point was reached, according to sampling strategies of phytoplanktologists (47N: cyclonic drift phase 30–80 m; anticyclonic drift phase 50–80 m; 58N: 30–80 m). Additionally we integrated the measured rates for bacterial production down to 300 m. Integrated values and their standard deviations were calculated for the different biological parameters measured in the defined layers.

3. Results

Integrated bacteriological and planktological data presented in the following sections for the defined layers are compiled in Table 1. Data obtained during the transition from the cyclonic to the anticyclonic circulation phase (May 15th to 16th, see below) at 47N were excluded from the calculations because several measurements indicated that the transition zone was characterized by the occurrence of special biological processes within the euphotic zone most probably caused by eddy-eddy interaction processes which differed strongly from those within the adjacent mesoscale hydrographic structures.

a. Study site 47N, 20W

i. Hydrography and nutrients. In situ observations and remote sensing revealed that at least three mesoscale cyclonic eddies of different spatial dimensions were present in the investigation area (Robinson *et al.,* 1993). Based on the dynamic height field at 80 dbar relative to 485 dbar derived from *Meteor* CTD casts (Fig. 1a) the drifter track

Table 1. Carbon stocks (mg C m^{-2}) and production (mg C m^{-2} d^{-1}) in the mixed layer (0–30 m at 47N cyclonic drift phase and at 58N; 0–50 m at 47N anticyclonic drift phase) and lower layer (30–80 m at 47N cyclonic drift phase and at 58N; 50–80 m at 47N anticyclonic drift phase). POC = particulate organic carbon, PPC = phytoplankton carbon, TBB = total bacterial biomass, TCB = total picocyanobacterial biomass, PP = primary production, BP = bacterial production, [ ] = mean content per 1 m^3 for the defined layer (mg C m^{-3}, mg C m^{-3} d^{-1}, resp.), n.s. = no samples.

		47N		
Stocks		Cyclonic	Anticyclonic	58N
POC m.l.	*	8499 ± 977 [283.3]	10527 ± 519 [220.3]	8631 ± 2233 [287.7]
POC l.l.	*	7904 ± 1072 [142.8]	3401 ± 756 [98.8]	7713 ± 2873 [154.3]
PPC m.l.	#	1552 ± 634 [51.7]	880 ± 167 [17.6]	730 ± 422 [24.3]
PPC l.l.	#	1944 ± 1154 [38.9]	230 ± 85 [7.7]	880 ± 420 [17.6]
TCB m.l.		28 ± 7 [0.9]	96 ± 34 [1.9]	33 ± 10 [1.1]
TCB l.l.		16 ± 7 [0.3]	9 ± 7 [0.3]	25 ± 14 [0.5]
TBB m.l.		225 ± 66 [7.5]	830 ± 212 [16.6]	448 ± 148 [14.9]
TBB l.l.		260 ± 91 [5.2]	282 ± 71 [9.4]	402 ± 148 [8.0]
Production				
PP	†	742 ± 192 [23.2]	657 ± 169 [13.1]	655 ± 123 [21.8]
BP m.l.		n.s.	89 ± 60 [1.8]	30 ± 24 [1.0]
BP l.l.		n.s.	24 ± 24 [0.8]	17 ± 9 [0.3]
BP (0–300 m)		n.s.	153 ± 112 [0.5]	90 ± 56 [0.3]

*Calculated from data of Dep. of Planktology (IfM, Kiel).
#Calculated from data of Deckers (1991).
†Calculated from data of Stienen (1990).

could be divided into two major phases: (i) from May 9th to 14th the rig moved east from the center of the so-called small cyclonic eddy to its periphery. During May 15th to 16th the drifter crossed a north-south front and (ii) then drifted within an anticyclonic hydrographic structure until the end of the experiment on May 21st (Fig. 1b, see also Robinson *et al.,* 1993). Due to the sparse data resolution there is no evidence that the anticyclonic cell of circulation was closed. The transition from

the cyclonic into the anticyclonic feature coincided with the deepening of the main seasonal thermocline from about 30 to 50 m.

Surface temperatures ranged from 13.0 to 14.2°C, salinities ranged from 35.61 to 35.65. At the beginning of the drift experiment relatively high concentrations of phosphate and nitrate (0.1–0.3 μmol PO_4 dm^{-3}; 2.0–5.0 μmol NO_3 dm^{-3}) were measured within the mixed layer while silicate concentrations were low (nondetectable – 0.9 μmol SiO_4 dm^{-3}). During the second drift phase PO_4 and NO_3 concentrations decreased considerably (0.06 and 0.4 μmol dm^{-3}, resp.). SiO_4 concentrations were also low during this period (0.1–0.5 μmol dm^{-3}) but above detection limit (Wenck, pers. comm.).

ii. Phytoplankton characteristics. The different hydrographic conditions were reflected by distinct differences occurring in biological measurements. According to Deckers (1991) the phytoplankton community was dominated by diatoms (e.g. *Nitzschia seriata, Chaetoceros decipiens, Rhizosolenia* sp.) during the first phase of the experiment when nutrients were present at higher concentrations, while the amount of dinoflagellates (e.g. different *Ceratium* species, *Gonyaulax furca, Exuviella marina, Gymnodinium* sp., *Peridinium* sp.) increased during the second phase when nutrient concentrations showed lower values. Either few or no coccolithophorides and silicoflagellates were observed.

Averaged integrated values (0–80 m) for POC, chl *a*, primary production, and PPC (Meyerhöfer and Stienen, 1990; Stienen, 1990; Deckers, 1991) were higher during the first part of the drift experiment (16.4 g POC m^{-2}, 0.13 g chl *a* m^{-2}, 0.74 g C m^{-2} d^{-1}, 3.5 g PPC m^{-2}) than during the second part (13.9 g POC m^{-2}, 0.07 g chl *a* m^{-2}, 0.66 g C m^{-2} d^{-1}, 1.1 g PPC m^{-2}, Table 1). In any case, minimum integrated values were determined for the front transition (data not shown).

iii. Picocyanobacterial abundance and biomass. At the beginning of the drift experiment (1st to 7th drift day) only small cell numbers (3.9–7.5 × 10^9 cells m^{-3}) and low biomass (0.74–1.4 mg C m^{-3}) were determined for the mixed layer (data averaged over mixed layer depth, Fig. 3a,b). After the front crossing, cell numbers and biomass sharply increased to 7.4–15.1 × 10^9 cells m^{-3} and 1.4–2.9 mg C m^{-3}, respectively. Highest abundance and biomass of picocyanobacteria were always found in the mixed layer.

iv. Bacterial abundance and biomass. The distribution of bacterial abundance and biomass (Fig. 4a,b) corresponded to the distribution patterns of picocyanobacteria. During the cyclonic drift phase, bacterial numbers and biomass averaged over the mixed layer ranged between 0.4–0.9 × 10^{12} cells m^{-3} and 5.4–11.5 mg C m^{-3}, respectively. Below the mixed layer down to 80 m averaged integrated values reached approximately half of the surface concentrations. As for the picocyanobacteria,

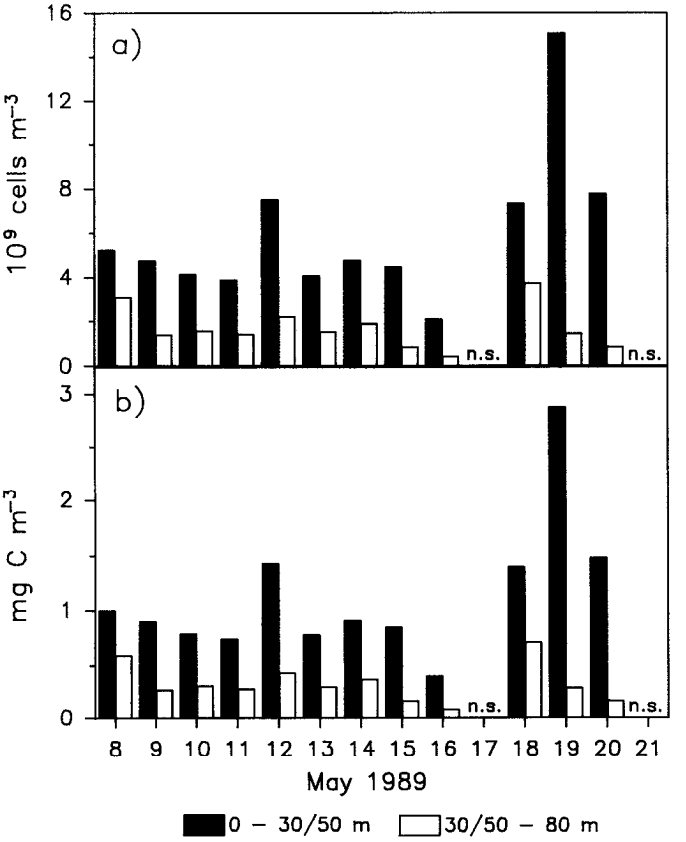

Figure 3. Picocyanobacterial abundance (a) and biomass (b) during the drift experiment at 47N. Integrated data averaged over mixed and lower layer depth (n.s. = no samples).

bacterial standing stocks showed their lowest values during the front crossing ($0.2 \cdot 10^{12}$ cells m^{-3}; 1.7 mg C m^{-3}). Higher bacterial abundance ($0.7–1.3 \times 10^{12}$ cells m^{-3}; 12.1–24.2 mg C m^{-3}) was recorded during the second drift phase (Fig. 4a,b). Averaged integrated bacterial stocks (0–80 m, Table 1) indicated that significant differences occurred between the cyclonic (484.6 mg C m^{-2}) and anticyclonic drift phase (1111.1 mg C m^{-2}).

v. Bacterial production. Bacterial production was measured from May 18th to 20th when the drifting buoy was located within the anticyclonic hydrographic structure. During this period integrated bacterial production rates averaged over the mixed layer (0–50 m) reached 3.5 mg C m^{-3} d^{-1} and decreased during the following two days to 0.7 mg C m^{-3} d^{-1} (Fig. 5). A corresponding trend could not be observed in bacterial abundance and biomass distribution during this period. Bacterial produc-

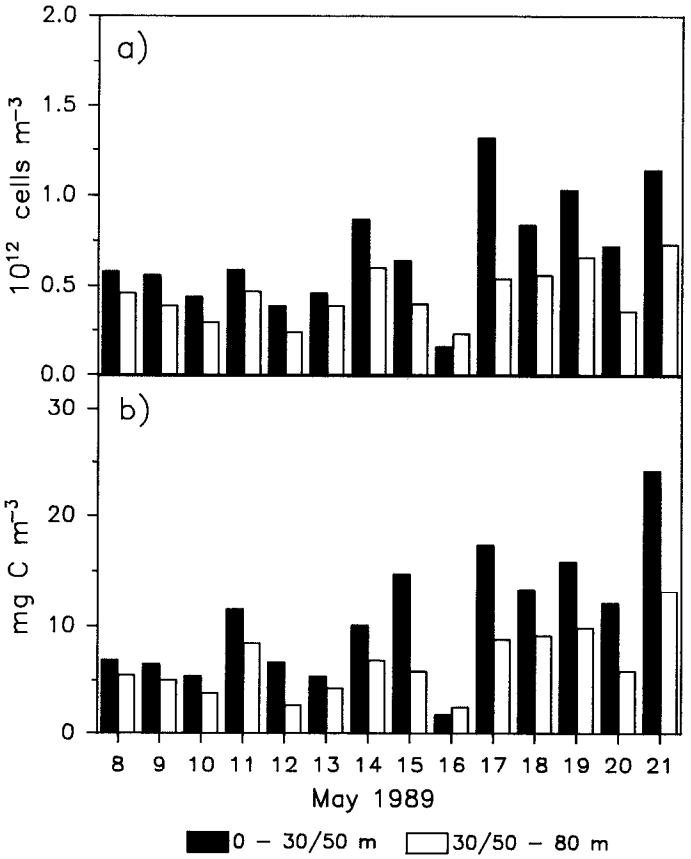

Figure 4. Bacterial abundance (a) and biomass (b) during the drift experiment at 47N. Integrated data averaged over mixed and lower layer depth.

tion clearly decreased beneath the mixed layer. Integrated rates averaged over the lower layer ranged from 1.9 mg to 0.1 mg C m^{-3} d^{-1} during the same period (Fig. 5).

b. Study site 58N, 20W

i. Hydrography and nutrients. During a CTD-fluorescence pre-survey (Fig. 2a) several mesoscale cyclonic and anticyclonic features were detected. The corresponding dynamic height field at 100 dbar relative to 485 dbar is presented in Figure 2b. At the northwestern part of the pre-survey grid a strong frontal region occurred. The isotherme 8°C and the isohaline 35.15 rose from about 600 to 100 dbar within 50 km distance along the southeast-northwest CTD section. At the sea surface a temperature decrease of approximately 1°C on minimum values around 8.2°C north of the front was measured, while salinity dropped by 0.1 on 35.17. No nutrient measurements took place during the pre-survey.

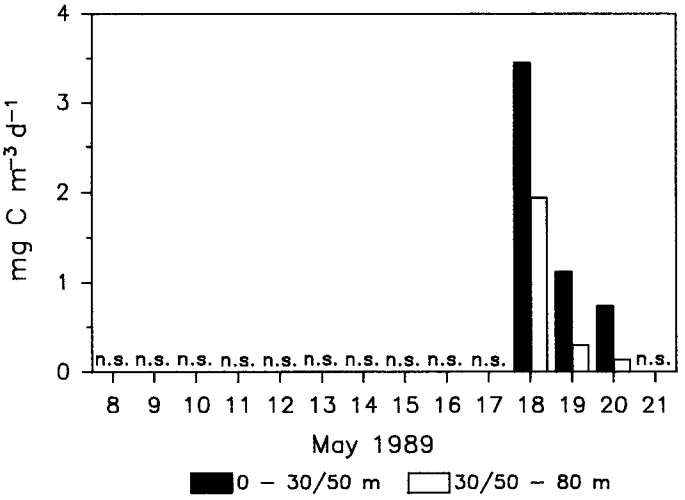

Figure 5. Bacterial production during the drift experiment at 47N. Integrated data averaged over mixed and lower layer depth (n.s. = no samples).

Some days before the drift experiment started, a storm event mixed the upper water column. Due to the relative calm weather conditions the stratification re-established during the drift experiment. The anticyclonic track of the drifter rig and the dynamic height field at 100 dbar relative to 485 dbar (Fig. 2a,b) indicated that the drifting buoy was caught within an anticyclonic hydrographic structure during the whole study period. The surface temperature rose from 9.2°C to 10.4°C, and the mean salinity varied between 35.23 and 35.26. The subsequent warming of the surface water caused the development of a relatively strong seasonal thermocline between 10 and 30 m depth. In this drift area higher nutrient concentrations were measured within the euphotic and subeuphotic zone than at 47N. At the beginning of the experiment SiO_4 ranged from 1.7–4.2 μmol dm^{-3}, PO_4 from 0.6–0.8 μmol dm^{-3}, and NO_3 from 9.2–11.5 μmol dm^{-3} within the mixed layer (Wenck, pers. comm.). Toward the end of the drift experiment nutrient concentrations decreased slightly (1.3 μmol dm^{-3} SiO_4, 0.5 μmol PO_4, and 7.4 μmol dm^{-3} NO_3).

ii. Phytoplankton characteristics. The *in vivo* chlorophyll profiles taken during the pre-survey indicated strong biological variability on the mesoscale. The highest *in vivo* chlorophyll values >2 mg m^{-3} within the mixed layer which were measured at pre-survey stations in the southeast and northeast correlated with relatively high temperatures within anticyclonic circulation cells (Peinert and Podewski, 1993).

During the drift experiment the composition of the phytoplankton community was similar to the one found at 47N. Only some warm water species were missing. Phytoplankton biomass was dominated by diatoms. *Rhizosolenia alata* was the most

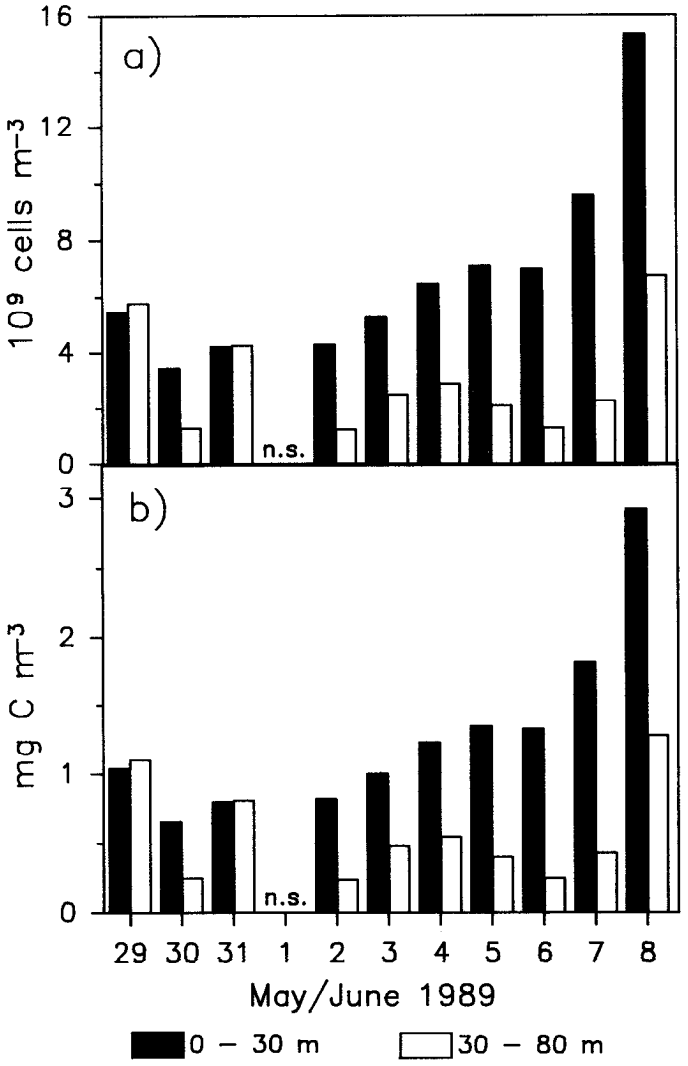

Figure 6. Picocyanobacterial abundance (a) and biomass (b) during the drift experiment at 58N. Integrated data averaged over mixed and lower layer depth (n.s. = no samples).

abundant species. Dinoflagellates were dominated by *Ceratium* sp. Compared to 47N, coccolithophorides were highly abundant (Deckers, 1991).

According to the more homogeneous hydrographic conditions during this drift station the planktological data showed less variability than at 47N (Deckers, 1991; Meyerhöfer and Stienen, 1990; Stienen, 1990). Mean integrated values (0–80 m) of 16.3 g POC m^{-2}, 0.08 g chl *a* m^{-2}, 0.66 g C m^{-2} d^{-1} (primary production), and 1.6 g PPC m^{-2} were calculated (Table 1). Compared to the planktological data from the

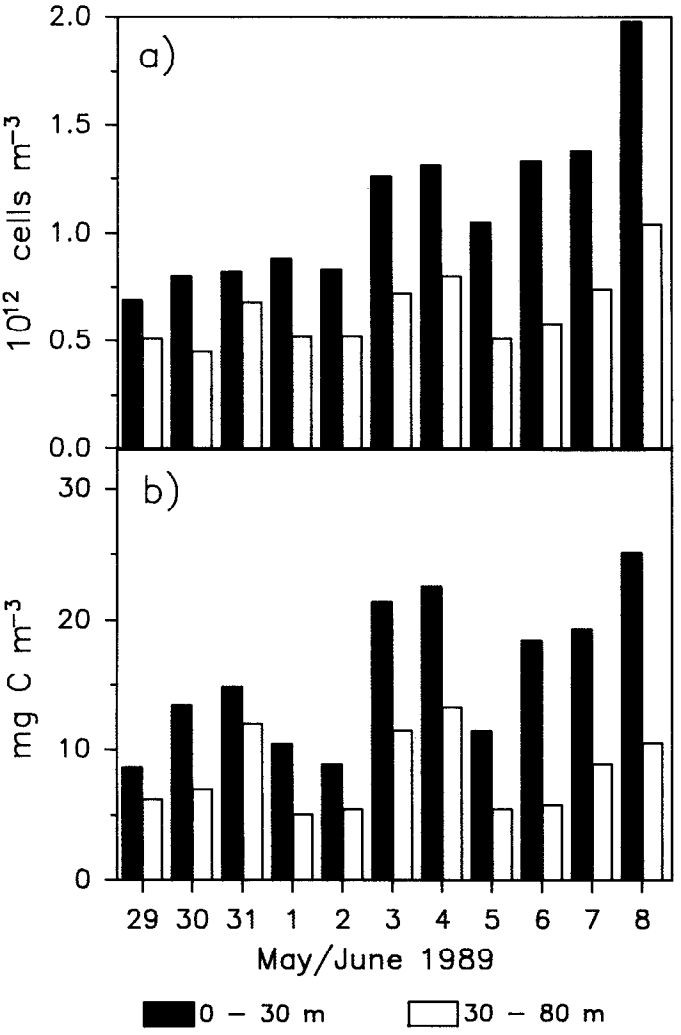

Figure 7. Bacterial abundance (a) and biomass (b) during the drift experiment at 58N. Integrated data averaged over mixed and lower layer depth.

first drift phase at 47N all planktological variables showed lower values with the exception of POC. Compared to the second drift phase at 47N chl *a* standing stocks were almost similar, but POC and PPC standing stocks were higher and primary productivity was slightly lower (Table 1).

iii. Picocyanobacterial abundance and biomass. During the first 5 days of the drift experiment abundance and biomass of picocyanobacteria in the mixed layer oscillated around $4.0 \cdot 10^9$ cells m^{-3}, and 0.8 mg C m^{-3}, respectively (averaged integrated

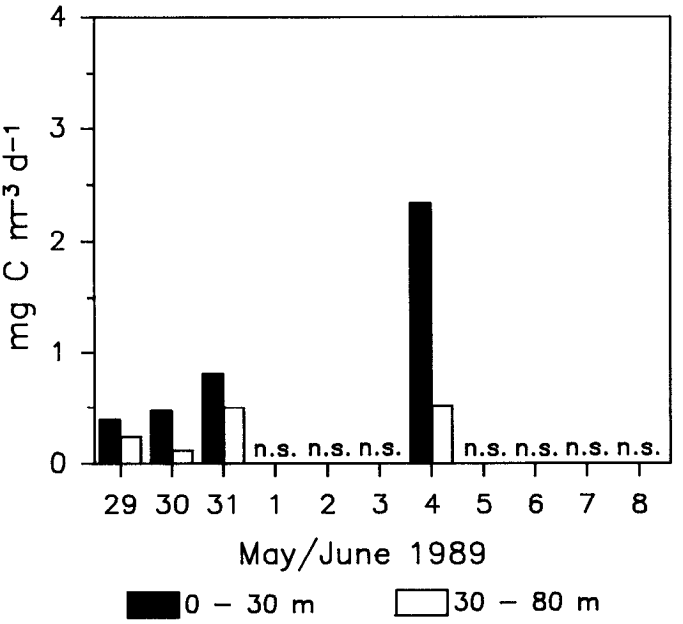

Figure 8. Bacterial production during the drift experiment at 58N. Integrated data averaged over mixed and lower layer depth (n.s. = no samples).

data, Fig. 6a,b). After the fifth drift day abundance more or less continuously increased to 15.35×10^9 cells m^{-3} and 2.9 mg C m^{-3}. At the beginning of the drift experiment abundance and biomass were nearly constant in the lower layer (30–80 m) with the exception of one station. After 2nd June an increase in cell numbers and biomass occurred in the mixed layer, which was not reflected by a similar development in the lower layer.

iv. Bacterial abundance and biomass. Bacterial cell numbers and biomass (Fig. 7a,b) showed almost the same pattern of distribution in the mixed layer as the picocyanobacteria. Initially, cell numbers of about $0.7–0.9 \times 10^{12}$ cells m^{-3} and biomass of about 8.6–14.9 mg C m^{-3} were measured. Subsequently bacterial abundance and biomass increased to maximum values of 2.0×10^{12} cells m^{-3} and 25.1 mg C m^{-3} at the end of the drift experiment (averaged integrated values). In the lower layer (30–80 m) cell numbers and biomass reached only half of the mixed layer concentrations.

v. Bacterial production. Bacterial production measurements were conducted during the first three days and on the seventh drift day (Fig. 8). At the beginning of the investigation mixed layer production rates showed very low averaged integrated values of about 0.4–0.8 mg C m^{-3} d^{-1}. Four days before the drift experiment was

finished bacterial production rates had increased to 2.3 mg C m^{-3} d^{-1}. Beneath this zone (30–80 m) the determined production rates reached distinctly lower values between 0.1 and 0.5 mg C m^{-3} d^{-1}. Integrated production rates for the mixed layer (0–30 m) covered a range of 11.8–70.1 mg C m^{-3} d^{-1} and within the lower layer (30–80 m) of 5.9–25.9 mg C m^{-2} d^{-1}. On average 30.1 mg C m^{-2} d^{-1} and 17.2 mg C m^{-2} d^{-1} were calculated for the mixed layer and the lower layer, respectively (Table 1).

4. Discussion

The hydrographic results have shown that our biological investigations in the northeast Atlantic took place in areas of relatively strong mesoscale hydrographic variability not only detectable at the northern study site in the vicinity of the subarctic front, but also at 47N. The drift experiment at 47N did not represent a time series study due to the different hydrographic structures passed. As a result, our observations reflected partly seasonal and partly spatial variations. At 58N throughout the drift study an anticyclonic circulation phase was met which implied a less complex hydrographic situation during this drift experiment. Therefore, we concluded that our data could be interpreted and presented from 47N as two and from 58N as one temporal sequence.

Generally, observed abundance and stocks of bacteria and picocyanobacteria as well as bacterial net production rates were within the ranges reported for comparable offshore regions (Sieracki *et al.,* 1985; Iturriaga and Marra, 1988; Ducklow *et al.,* 1993; Weeks *et al.,* 1993). Ducklow *et al.* (1993) conducted their investigations during April 24th–May 31th (47N) and June 28th–July 6th (59N) adjacent to our investigation areas. Bacterial production rates reported by them were significantly higher than ours, which could be partly attributed to the different conversion factors used by Ducklow *et al.* (1993) (2.65×10^{18} cells $mole^{-1}$ TdR; $2 \cdot 10^{14}$ g C bacteria $cell^{-1}$) and most probably also to spatial and temporal variabilities of the water columns sampled (Joint *et al.,* 1993; Robinson *et al.,* 1993). Results from one intercomparison and one intercalibration experiment for TdR incorporation rates (JGOFS, 1990a), which were carried out together with Ducklow and Stirling at 47N (May 18th) and with Ietswaart at 59N (August 6th), indicated no significant differences in the determination of bacterial thymidine incorporation rates into DNA (JGOFS, 1990a).

a. Influence of mesoscale hydrographic variability. According to Krauss and Böning (1987) "dispersion by eddies can modify the large-scale distribution of passive scalars considerably." This certainly also holds true for chemical and biological constituents of the water as hypothesized by Mittelstaedt (1987): "They (rings or eddies) transport momentum, heat, physical and chemical water properties and small organisms over long distances from their origin." Angel and Fasham (1983) already

discovered that the interior waters of rings may exhibit ecosystems distinct from ambient waters.

The influence of different mesoscale hydrographic structures on the biology of pelagic systems was clearly visible at 47N. Within the small cyclonic eddy, picocyanobacterial and bacterial standing stocks in the mixed layer remained relatively low but they increased immediately after the drifter rig entered the anticyclonic hydrographic structure. This was accompanied by an increase in bacterial abundance and biomass in the subeuphotic layer down to 500 m (data not shown). The integrated bacterial biomass of the mixed layer, as compared to the integrated phytoplankton standing stocks (Deckers, 1991), showed that the biomass of phytoplankton was about 7 times that of the bacteria on average during the first drift phase. This relation changed drastically during the second drift phase where bacterial carbon almost kept balance with phytoplankton carbon (Table 1). An additional hint concerning the influence of water mass change was visible in the increase of the amount of zooplankton as well as community respiration after the front crossing within the upper 80 m reflecting different zooplankton communities (Martens, 1992). However, we were not able to ascertain whether bacterial and picocyanobacterial standing stocks measured within the two mesoscale features reflected their original biological state, or whether they developed within these structures on their way to the present position. In detail it has been shown that the composition of water masses within an eddy is not unique and does not fully reflect its origin. On its trajectory all kinds of water passed by may become entrapped by an eddy, especially at depth (Mittelstaedt, 1987). Thus the biological development of the eddies cannot be precisely predicted. During this study the simultaneous occurrence of elevated bacterial and picocyanobacterial biomass and relatively low phytoplankton biomass within the anticyclonic feature indicated a pelagic system with a well-developed 'microbial loop' (Fuhrman *et al.,* 1989) dominated by heterotrophic processes. This system existed side by side with a structure dominated by autotrophic organisms (small cyclonic eddy).

During the present study the small cyclonic eddy was characterized by a shallow mixed layer and pronounced seasonal thermocline, which was also observed by Lochte and Pfannkuche (1987) in a cyclonic cold eddy at 48N, 22W in May 1985. Nevertheless, biological patterns were different. We found considerably lower stocks of chl *a* (about ⅓), phytoplankton carbon and bacterial biomass, and the gradients of these variables between the mixed layer and the waters beneath were by far not as steep as reported by Lochte and Pfannkuche (1987). This could be due to different ages of the eddies under observation. While the eddy studied by Lochte and Pfannkuche was young (approximately 3 to 4 weeks), the relatively low phytoplankton biomass which developed during the culminating phase in the eddy described here may indicate a higher age of the latter. Differences in the depth distribution could have also been due to differences in the seasonal stratification caused by varying weather conditions in both years.

At 58N the strong frontal region in the northwestern part of the survey in conjunction with mesoscale eddy-like features indicated that the study site was situated in the vicinity of the subarctic front. The mixed layer temperatures around 8.2°C observed north of the front correlated quite well with values measured by Leach (1990) in June/July 1983 and 1986 along two sections from the Azores to Greenland, but salinities were slightly higher (about 35.17) indicating that modified North Atlantic Waters were present within our investigation area (Dickson *et al.,* 1988). Strong mesoscale hydrographic variability in this area of investigation seemed to be correlated with mesoscale biological variability indicated by chl *a* and temperature profiles along the pre-survey sections (Peinert and Podewski, 1993) unfortunately not resolved by other biological measurements than *in vivo* chlorophyll, nor by any chemical measurements. A similar relationship between high chl *a* and warmer temperature was described by Joint *et al.* (1993) although the authors did not discuss the influence of mesoscale hydrographic variability in detail.

b. Combined hydrographic and regional effects. At least three different stages of the bloom development can be distinguished in the two investigation areas derived from nutrient availability and phytoplankton data (Joint *et al.,* 1993; Lochte *et al.,* 1993). At 47N the spring bloom was in a culminating phase within the small cyclonic eddy and in a declining phase within the anticyclonic feature, where nutrients were almost depleted. The opposite stage of development was encountered at 58N, where the spring bloom was in a building-up phase with high amounts of nutrients still unconsumed.

The different stages of bloom development at 47N and 58N were reflected by different proportions of phytoplankton to bacterial stocks and production rates. Highest integrated stocks of carbon (POC, PPC) as well as highest primary production rates were determined for the cyclonic drift phase at 47N (Table 1). At 58N comparable POC-concentrations and primary production rates were estimated, but PPC reached only half of the concentration measured at 47N. This observation suggests, as stated above, a culminating bloom stage at 47N and a building-up phase of the spring bloom at 58N. Opposite distribution patterns were observed for microbial variables. Highest stocks of carbon per m^3 (POC, PPC) corresponded to a lower microbial biomass and vice versa.

Bacterial production rates also indicated that the spring bloom was in a declining phase at 47N and a building-up phase at 58N. Averaged bacterial net production in the mixed layer reached 1.8 mg C m^{-3} d^{-1} (anticyclonic phase) at 47N and 1.0 mg C m^{-3} d^{-1} at 58N which accounted to about 13.7 and 4.6% of the primary production, respectively. High bacterial production rates as well as high standing stocks of picocyanobacteria and bacteria in contrast to a relatively low phytoplankton stock suggest a great importance of the bacterioplankton for the carbon flow and a decline of the bloom at 47N (anticyclonic phase). Our results confirm observations of

Williams (1981) and Fasham *et al.* (1990) who suggested a relationship between high levels of bacterial production and the decline of the spring bloom. For 58N a weaker coupling between primary production and bacterial consumption and a lower efficiency of recycling of carbon could be stated. This example shows that similar mesoscale hydrographic structures in the northeast Atlantic can be dominated by different trophic regimes, and that there is a general spatial trend of the spring bloom development, despite regional patchiness due to mesoscale hydrographic variability.

c. Vertical distribution. The vertical distribution of all microbiological variables at 47N shows a strong dependence on autotrophic processes in the mixed layer. Microbial productivity in the mixed layer is generally assumed to be fuelled by fluxes of dissolved organic matter derived from several sources including extracellular release from living phytoplankton (e.g. Williams, 1990), sloppy feeding, excretion by grazers (e.g. Jumars *et al.,* 1989) and lysis of biogenic particles and cells (e.g. Sharp, 1977). These materials enter the DOC pool, which has been shown to be far from inert, since 20–40% of it was consumed by bacteria within periods of 3–11 days (Kirchman *et al.,* 1991). During the investigation period, the averaged bacterial net production in the mixed layer covered a range of 1–1.8 mg C m^{-3} d^{-1}. Below the mixed layer down to 300 m microbial stocks and bacterial production (<0.07 mg C m^{-3} d^{-1} at 47N; <0.11 mg C m^{-3} d^{-1} at 58N) decreased significantly. In this zone the carbon supply of bacteria is primarily based on incomplete zooplankton feeding and on the transformation of slow sinking POM and DOM via microbial extracellular enzymes (Hoppe, 1983), which is a major regulating factor for the flux of organic matter (OM) into the ocean's mesopelagic zone (Hoppe *et al.,* 1993).

A comparison of gross bacterial production (integrated 0–300 m, assuming a growth efficiency of 50%, Cole *et al.,* 1982) with gross primary production (respiratory losses of 10%, Stienen, pers. comm.) reveals that a flux equivalent to 42% of primary production was channelled through bacteria at 47N and 25% at 58N, respectively. This calculation demonstrates that the different stages of phytoplankton development at these positions were clearly reflected by bacterial decomposition patterns at depth. On the other hand, more than a ten-fold lower sedimentation rate of PPC was estimated for 47N compared to 58N (0.1% and 1.4%, respectively, Deckers, 1991). Nevertheless a larger share of carbon flow through bacteria in the upper water column (0–300 m) was estimated for 47N. This suggests a higher availability of labile carbon for bacterial energy requirements at 47N, which is not reflected by sedimentation rates obtained from sediment traps.

5. Conclusions

On a spatial scale, upward or downward transport of water within and between mesoscale hydrographic structures in combination with advective processes positively or negatively affect plankton development. As a result, the spring bloom in the

North Atlantic does not follow precisely the ideal picture of the spring development but rather forms a patchwork representing different bloom stages within mesoscale features.

This investigation has shown that different stages of the phytoplankton bloom—developing, culminating and declining systems—occur in the North Atlantic side by side and in the same period of time. In conjunction with the phytoplankton development microbial structures in the upper water column also change drastically. Mesoscale hydrographic variability seems to be responsible for this phenomenon. However, hydrographic structures, such as cyclonic and anticyclonic eddies, are not characterized by specific plankton bloom stages. Many factors, such as their origin, physical specifics, and history must be considered in order to explain and to understand their biological constitution at the moment of observation (Le Groupe Tourbillon, 1983). Hydrographic observations revealed that rings or eddies can have a lifetime of anywhere from weeks to months (Robinson, 1983) or even up to three years (Angel and Fasham, 1983). Thus, time scales of observation by drift experiments are often not long enough to trace whole cycles of plankton development and decay within one and the same hydrographic structure. Light intensity, as it advances from south to north during the spring season, also plays an important role. Theoretical considerations indicate that there should be a more or less narrow belt proceeding from south to north, in which the bloom occurs simultaneously. This is the zone where light reaches its optimal intensity for plankton growth for the first time in the year, and where nutrients are still abundant. However, this expected uniformity can be disturbed by water bodies which approach from the south and may have already gone through several bloom cycles followed by depletion of nutrients.

Based on the observed co-occurrence of autotrophic and heterotrophic systems in the northeast Atlantic it can be assumed that export of C and N by sedimentation from the productive zone to depth may also be variable in space and time (Newton *et al.,* 1994) and may cause local and/or seasonal signals of bentho/pelagic coupling (Graf, 1992; Poremba, 1994). In detail, this variability not only depends on hydrographic phenomena but also on microbial activity. As it could be shown in this investigation, bacterial production together with respiration losses amounted to more than 40% of primary production at the southern station and more than 25% at 58N. This calculation is consistent with results of sediment traps during the JGOFS campaign which suggest "the major part of POC is consumed or dissolved in the mesopelagic zone" (Lochte *et al.,* 1993; Martin *et al.,* 1993). Because organic materials incorporated in bacteria are more or less prevented from sinking to depth (except those incorporated into bacteria which are attached to sedimenting particles), the total amount of potential sedimentation is considerably reduced by bacterial activity. In this way bacteria counteract the "biological pump." Indeed, without the action of bacteria coupled with small bacteria grazers, most organic particles would sediment to depth (except for some losses by exudation, autolysis and

sloppy feeding). The degree of retention and, in turn, sedimentation is regulated by bacterial immobilization of organic matter in the mixed layer and in the mesopelagic zone beneath.

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