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# Microzooplankton dynamics during the development of the spring bloom in the north-east Atlantic

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Microzooplankton community composition, abundance, biomass and grazing impact were assessed, along with measurements of ciliate growth and mortality, during the onset of the spring bloom in the north-east Atlantic. The study was undertaken as part of the UK Biogeochemical Ocean Flux Study during 1 May to 15 June 1990. The microzooplankton community was composed of protozoans and metazoan developmental stages with respective mixed-layer depth integrated biomass values ranging from 127 to 638 and 74 to 394 mg C $m^{-2}$. High numbers of aloricate ciliates (up to 35,000 cells $l^{-1}$) dominated the microzooplankton community during early May prior to the onset of the spring bloom. Ciliate abundance then declined rapidly during mid-May with community growth rates ranging from $-0.71$ to 0.23 $d^{-1}$. High abundances of metazoplankton (up to 400 $l^{-1}$) were also recorded at this time and may have contributed to the decline in ciliate numbers. In late May and early June the protozoan community comprised a more even mix of dinoflagellates, tintinnids and aloricate ciliates. Phytoplankton mortality rates, measured using a dilution technique, ranged from 0.2 to 0.5 $d^{-1}$. The microzooplankton consumed 8 to 44 $\mu$g C $l^{-1}$ $d^{-1}$, equivalent to between 16 and 40% of the chlorophyll biomass and 38 and 154% of primary production. These high rates of herbivory reflect the predominance of small ($<5\,\mu$m in length) phytoplankton cells present throughout the first half of the study and support previous studies demonstrating the microzooplankton to be the main grazers of phytoplankton in the north-east Atlantic. However, there is also evidence that a disparity between predator and prey may have prevented a response by the microzooplankton to rapid increases in phytoplankton biomass and production during the spring bloom.

## INTRODUCTION

It is now well established that the microzooplankton form a significant proportion of the total zooplankton biomass in both coastal and oceanic environments and play an important role in carbon and energy flow through pelagic ecosystems (Calbet & Landry, 2004). In particular, microzooplankton have been shown to consume a large fraction of primary production in the sea and they often exert a higher grazing pressure on phytoplankton than the mesozooplankton (e.g. Paranjape et al., 1987; Landry et al., 1997; Fileman & Burkill, 2001; Strom et al., 2001; Verity et al., 2002). The microzooplankton, as defined by Dussart (1965), comprise protozoa and metazoa $<200\,\mu$m in length. This is a useful practical definition in so far as it relates to pre-screening protocols often used in experimental techniques such as dilution assays (Landry & Hassett, 1982). However, it is the protozoan component of the microzooplankton, mainly composed of ciliates and dinoflagellates (and referred to hereafter as the protozooplankton), which is responsible for most herbivorous activity. The small size and high growth rates of these herbivorous protozooplankton enable them to respond rapidly to changes in pico- and nanophytoplankton, thereby maintaining close coupling between production and consumption in the euphotic zone. In addition to their role as herbivores, these protozoa may feed on heterotrophic cells (Jeong, 1999), are a source of food for organisms in higher trophic levels (Stoecker & Capuzzo, 1990; Fessenden & Cowles, 1994) and are important remineralizers of organic material and nutrients (Goldman & Caron, 1985; Goldman et al., 1987).

The North Atlantic Ocean is characterized by large seasonal variations in phytoplankton biomass, the most prominent of these seasonal events being the spring bloom. These blooms have been witnessed by satellite imagery (Esaias et al., 1986) and have been described as 'the largest biological signal on the planet' (Lewis, 1989). It has been suggested that a large part of the phytoplankton may sink directly out of surface waters at the end of the spring bloom (Billet et al., 1983); however, the magnitude of this vertical flux of biological material is thought to depend upon the composition of the phytoplankton assemblage (Michaels & Silver, 1988). The bloom has traditionally been described as being numerically dominated by large diatoms (Robinson, 1965; Colebrook, 1982) although more recent evidence suggests that the bloom can sometimes be dominated by small cells in the pico- and nanoplankton size-classes (Murphy & Haugen, 1985; Sieracki et al., 1993). Microzooplankton grazing is often important when these small phytoplankton dominate productivity resulting in the loss of fixed carbon through respiration and excretion; significant vertical flux of carbon out of the euphotic zone is therefore unlikely under these conditions (Longhurst & Harrison, 1989).

Several studies have examined the fate of phytoplankton with respect to microzooplankton herbivory during various phases of the phytoplankton bloom in the north-east Atlantic. Verity et al. (1993a) examined microzooplankton grazing at 46°N during mid- to late bloom conditions in May 1989, whilst in June/July of the same year, Burkill et al. (1993) sampled late bloom and post-bloom conditions between 60° and 47°N respectively. Gifford et al. (1995), reported on microzooplankton grazing during declining spring bloom and post-bloom periods in the high latitude North Atlantic. More recently Stelfox-Widdicombe et al. (2000) examined microzooplankton herbivory during a mid-bloom phase at similar high latitude. These studies have all documented abundant and dynamic microzooplankton populations, dominated by protozoa, during and following the spring bloom with grazing impacts of 37 to >100% of primary production daily. However, none of these studies document information on microzoooplankton dynamics during the onset of the spring phytoplankton bloom in the North Atlantic.

The aim of the present study was to examine the dynamics of the microzooplankton community in open ocean waters of the north-east Atlantic during the development of the spring bloom from well-mixed winter to stratified summer conditions. The composition, abundance, biomass and grazing impact of the microzooplankton community were assessed along with measurements of ciliate growth and mortality due to predation. Spring bloom conditions were encountered during the study but the phytoplankton community was dominated by small (<5 $\mu$m) diatom cells (Savidge et al., 1995) rather than the larger diatoms which are more characteristic of spring bloom conditions in the region (Colebrook, 1982; Lochte et al., 1993). The diatom bloom also took place over a relatively short time-scale. Insights could therefore be made into the factors controlling the development of the microzooplankton community and its significance to carbon flow through the pelagic food web under these somewhat 'atypical' circumstances. The study was undertaken as part of the Biogeochemical Ocean Flux Study (BOFS), the UK contribution to the Joint Global Ocean Flux Study programme. Concurrent investigations of the abundance, biomass and distribution of nanoflagellates, heterotrophic dinoflagellates and plastidic microzooplankton have been described elsewhere (Verity et al., 1993b; Stoecker et al., 1994).

## MATERIALS AND METHODS

### *Study site and sampling protocol*

The study was undertaken between 1 and 20 May and 28 May and 15 June 1990 in the vicinity of 47–50°N 15–20°W as part of two consecutive research cruises on the RRS 'Charles Darwin' (Figure 1). The two cruises employed a Lagrangian approach to track a single body of water over a two month period. To achieve this a drifting buoy, attached to a sub-surface drogue at 20 m, was released on 26 April at 49°N 19°W. A large scale SeaSoar survey of the region, undertaken from the RRS 'Discovery' between 19–25 April, identified that this site was within an anticyclonic eddy and that there was no evidence by that date of a seasonal thermocline or

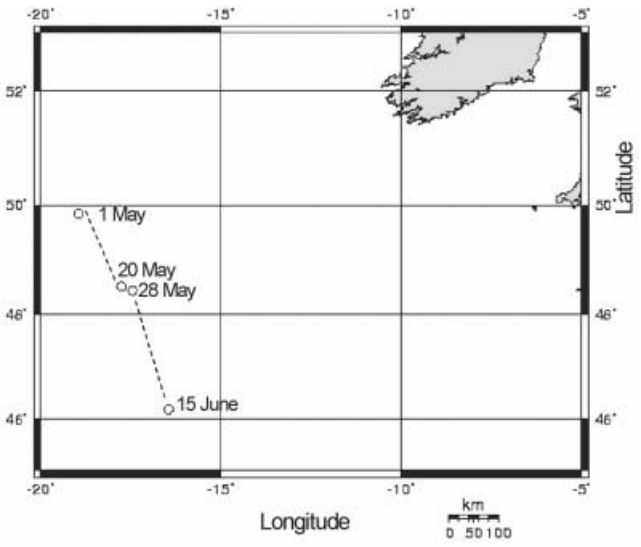


**Figure 1.** Location of the study area in the north-east Atlantic. Sampling was conducted between 1 May and 15 June 1990. Dashed line represents approximate cruise track.

phytoplankton bloom development (Savidge et al., 1992). Samples for microzooplankton state and rate variables were collected adjacent to the drogue. Between the two cruises, when the RRS 'Charles Darwin' was 'off station' (20–28 May), sampling was carried out on 23 May by the RRS 'Discovery' (Savidge et al., 1992). Full details of the cruises, the drogue, its movement and the hydrographic environment are reported by Savidge et al. (1992).

### *Microzooplankton abundance, biomass and community composition*

To determine the vertical structure of the microzooplankton community, water samples were collected from seven depths within the top 100 m of the water column on seven occasions during the sampling period (Table 1). On each occasion water was collected from each depth using a 10 litre Niskin water sampling bottle during a dawn conductivity–temperature–depth cast and a 1-l water sample was preserved in 1% final concentration acid–Lugol's iodine solution then stored cool and in the dark. Sub-samples of 110 ml were concentrated by sedimentation and observed at ×300 magnification with an Olympus IMT-2 inverted microscope using phase contrast optics (Utermöhl, 1958). All ciliates were enumerated and identified along with heterotrophic dinoflagellates >20 $\mu$m in length. The latter were distinguished from autotrophic dinoflagellates by reference to known heterotrophic species reported by Lessard & Swift (1986) and Lebour (1925). Where this was not possible, live cells of representative dinoflagellate taxa from selected Niskin bottles were videoed under epifluorescent illumination for the presence of chlorophyll-*a* autofluorescence. By contrast all ciliates were assumed to be heterotrophic. Each organism was categorized into one of five groups: heterotrophic dinoflagellates (>20 $\mu$m), aloricate choreotrich ciliates, tintinnid ciliates, other ciliates and other microzooplankton (which included sarcodines and metazooplankton <200 $\mu$m in size). For protozoans, the volume of each cell was calculated from cell area, measured using



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**Table 1.** *Station positions, sea-surface temperature and depths from which samples were collected for analysis and experimentation undertaken during May and June 1990 in the north-east Atlantic.*

| Date | Latitude °N | Longitude °W | Sea-surface temperature °C | Vertical distribution of microzooplankton biomass | Microzooplankton herbivory | Ciliate growth and mortality |
|---|---|---|---|---|---|---|
| May 1 | 49 51 38 | 018 53 15 | 12.3 | 10, 20, 30, 40, 50, 75, 100 | 10 | |
| 3 | 49 56 27 | 018 32 17 | 12.3 | | 25 | 25 |
| 4 | 49 50 49 | 018 31 40 | 12.5 | | 10 | |
| 5 | 49 46 36 | 018 32 47 | 12.3 | | 25 | |
| 7 | 49 34 50 | 018 35 22 | 12.7 | | 10 | 10 |
| 8 | 49 32 03 | 018 37 49 | 12.7 | | 10 | |
| 9 | 49 31 30 | 018 35 12 | 12.7 | 10, 20, 30, 40, 50, 75, 100 | 10 | |
| 11 | 49 23 10 | 018 21 09 | 12.9 | | 25 | 25 |
| 13 | 49 12 25 | 017 52 23 | 12.7 | | 25 | |
| 15 | 49 09 58 | 017 17 52 | 13.4 | | 10 | 10 |
| 17 | 48 54 59 | 017 03 21 | 13.4 | | 10 | |
| 19 | 48 33 23 | 017 19 32 | 13.8 | 10, 20, 30, 40, 50, 75, 100 | 25 | 25 |
| 23 | 48 29 09 | 017 46 09 | 14.0 | 10, 20, 30, 40, 50, 75, 100 | | |
| 28 | 48 26 52 | 017 28 13 | 14.3 | 10, 20, 30, 40, 50, 75, 100 | 25 | |
| 30 | 48 24 77 | 017 18 54 | 14.9 | | 25 | |
| June 1 | 48 17 98 | 017 04 24 | 14.5 | | 10 | |
| 3 | 47 54 68 | 016 46 05 | 15.2 | | 10 | |
| 5 | 47 37 82 | 016 2612 | 14.7 | 10, 20, 30, 40, 50, 75, 100 | 25 | |
| 8 | 47 19 67 | 015 46 90 | 14.7 | | 25 | |
| 11 | 46 55 18 | 015 25 80 | 15.3 | | 10 | |
| 13 | 46 17 90 | 016 02 69 | 15.6 | | 10 | |
| 15 | 46 08 19 | 016 28 50 | 15.6 | 10, 20, 30, 40, 50, 75, 100 | 10 | |

a Kontron image analyser, assuming an ellipsoid or semi-ellipsoid shape. The carbon content of each protozoan cell was then determined using the carbon to volume conversion equations in Menden-Deuer & Lessard (2000) for ciliates and heterotrophic dinoflagellates, and 0.10 pg $\mu m^{-3}$ for sarcodines (Michaels et al., 1995). Carbon biomass was calculated for metazoans using a conversion factor of 60 ng C individual$^{-1}$ (Verity et al., 1993a).

### *Microzooplankton herbivory*

Microzooplankton herbivory was determined using the dilution technique first described by Landry & Hassett (1982). Herbivory experiments were performed on 21 occasions during the study period (Table 1). For each experiment 60 l of water were collected pre-dawn in acid-cleaned 30-l Go-Flo bottles from a depth of either 10 or 25 m. Water was carefully pre-screened through a 200 $\mu$m mesh bag to exclude any larger predators. Dilution series were prepared with 0, 30, 60 and 90% filtered seawater (Gelman capsule filter, 0.2 $\mu$m pore size) from the same collection in triplicate 2-l acid-cleaned transparent polycarbonate bottles. For all experiments, bottles were incubated for 24 h in a laboratory incubator at ambient temperature with a day/night light cycle, and on one occasion, using an *in situ* rig positioned at the depth from which the sample was collected.

Chlorophyll-*a* concentration was determined in three sub-samples taken from each bottle initially ($T_0$) and after 24 h ($T_{24}$) incubation. The phytoplankton in these sub-samples were concentrated onto 0.2 $\mu$m polycarbonate filters after which their chlorophyll-*a* was extracted with 90% acetone and measured using a highly sensitive fluorometer (Aiken, 1981). Changes in chlorophyll-*a* concentration were used to calculate the apparent growth rate of phytoplankton according to the exponential growth rate equation of Landry & Hassett (1982):

$$\frac{1}{t} \ln\left(\frac{P_t}{P_0}\right) = k - c \cdot g \quad (1)$$

where $P_0$ and $P_t$ are the initial and final chlorophyll concentrations respectively, $k$ and $g$ are the instantaneous coefficients of phytoplankton growth and grazing mortality respectively, and $c$ is the relative concentration of the prey and predator population. Growth and mortality estimates of phytoplankton were calculated by linear regression of the daily net phytoplankton growth rate against the fraction of unfiltered seawater (*c*). The proportion of phytoplankton standing stocks turned over daily by the microzooplankton was calculated as:

$$1 - e^{-g} \times 100 \quad (2)$$

Estimates of the grazing coefficient '*g*' were converted to carbon using a carbon:chlorophyll conversion factor of 47 as estimated by the model of Fasham et al. (1999).

The concentrations of nitrate and phosphate were also determined in 50 ml sub-samples taken at $T_0$ and $T_{24}$ using standard autoanalyser techniques (Chemlab) based on the methods of Strickland & Parsons (1972).

Microzooplankton abundance and carbon biomass were determined in 20–50 ml sub-samples taken at $T_0$ only (from 18 out of 21 experiments). The number of cells counted in each sub-sample was >200. Samples were analysed as already outlined except that protozooplankton cell volumes were not measured; instead the taxon specific cell volumes measured from water-column samples were used.



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*Ciliate growth and mortality*

Ciliate growth rates were determined from changes in ciliate abundance in natural communities which had been screened to remove metazoan predators. Ciliate mortality rates due to predation were then calculated by comparing growth rates in screened and unscreened samples (Verity, 1986; McManus, 1993). Experiments were undertaken on five occasions during the first half of the study period (Table 1). For each experiment, three replicate 30 l Go-Flo water bottle samples were collected pre-dawn and each gently decanted into a 30-l plastic tank containing a 150 $\mu$m nylon mesh bag of similar size to the tank. For each replicate, two 2-l transparent polycarbonate bottles were filled with water by submerging and sealing each bottle underwater; this procedure ensured minimum disturbance to the sample and prevented air bubbles remaining in the bottles. The remaining water was then screened by slowly removing the mesh bag from each tank and a further two polycarbonate bottles filled. One of each pair of screened and unscreened bottles was immediately processed by preserving 500 ml in 0.4% final concentration Lugol's iodine solution and stored cool and in the dark. The remaining bottle from each pair was then incubated for 24 h on ship under ambient conditions and processed as above. For the experiment undertaken on 7 May, an extra screened and unscreened bottle was filled and incubated *in situ* at the depth of sampling for 24 h prior to processing. Ciliate counts were undertaken on 50 ml sub-samples, concentrated as described above, and observed at ×400 magnification using a Nikon Diaphot inverted microscope. Counts of metazoan zooplankton (<150 $\mu$m) were also undertaken on the same sub-samples. Ciliate growth rates were calculated from changes in total ciliate abundance (excluding the functional autotroph, *Myrionecta rubra* (Lohman)), assuming exponential growth, as follows:

$$k = (1/t)\ \mathrm{Log_e}(N_t/N_0) \quad (3)$$

where $k$=intrinsic rate of increase ($d^{-1}$), N=cell abundance in screened samples, t=incubation time ($d^{-1}$). Rates of ciliate mortality were calculated as follows:

$$g = k - (1/t)\ \mathrm{Log_e}(N_t/N_0) \quad (4)$$

where $g$=mortality due to predation ($d^{-1}$), N=cell abundance in unscreened samples.

## RESULTS

*Physical, chemical and biological character of the study area*

The general characteristics of a spring bloom were observed during the study period despite the area being characterized by a complex hydrographic pattern, including eddies, discontinuities and warm and cold intrusions (Savidge et al., 1992). During early May low cloud and misty conditions prevailed, resulting in low irradiance. From 12 May onwards less cloudy conditions were encountered leading to increased irradiances. Mean sea-surface temperature increased gradually from 12 to 16°C and was accompanied by an increase in stratification. A seasonal thermocline became detectable around 16 May and progressively developed at a depth of 20–35 m (Savidge et al., 1992). Nitrate concentrations in the surface mixed layer decreased slowly but steadily from 7 $\mu$M $l^{-1}$ on 1 May to 3 $\mu$M $l^{-1}$ on 14 May (Savidge et al., 1995). This decreasing trend was consistent with changes in chlorophyll-*a* concentrations which, at a depth of 5 m, increased from 1.2 $\mu$g $l^{-1}$ on 1 May to 3.7 $\mu$g $l^{-1}$ at the peak of the bloom on 14–17 May (Barlow et al., 1993). The dominant phytoplankton species was identified as the small (5 $\mu$m in length) diatom *Nanoneis haslae* (Norris) (Savidge et al., 1995). Following this there was a subsequent decline in chlorophyll-*a* concentration by 19 May. At the same time nitrate concentrations decreased from 3 $\mu$M $l^{-1}$ to <0.5 $\mu$M $l^{-1}$.

A rapid uptake of silicate between 13 and 17 May indicated that diatoms dominated the major growth of the phytoplankton (Savidge et al., 1992); this was confirmed by taxonomic observations (Savidge et al., 1995). However, the phytoplankton was dominated by nanoplankton and not microplankton as had been hypothesized for the spring bloom period. Size-fractionated chlorophyll-*a* measurements showed a dominance of the 1–5 $\mu$m size phytoplankton with the picoplankton averaging <10% of the phytoplankton. Water column integrated primary production steadily increased reaching a peak of 1914 mg C $m^{-2}$ $d^{-1}$ on 17 May (Savidge et al., 1995). In June, the post-bloom phase, the phytoplankton population was dominated by prymnesiophytes (Barlow et al., 1993) and was characterized by decreasing chlorophyll-*a* concentrations (Savidge et al., 1995).

*Microzooplankton abundance, biomass and community composition*

The biomass of the protozooplankton within the surface 100 m, as determined on seven occasions throughout the study, revealed significant changes in the vertical distribution and depth-integrated biomass of the protozooplankton with time. On most occasions protozooplankton biomass was higher in surface waters (10–20 m) (Figure 2). This was most pronounced on 9 May when biomass levels were in excess of 22 $\mu$g C $l^{-1}$ at 10 m and decreased to 1 $\mu$g C $l^{-1}$ at 100 m depth. Later in May protozooplankton biomass in surface waters decreased to as low as 2 $\mu$g C $l^{-1}$, increasing in June from 6 to 13 $\mu$g C $l^{-1}$. Differences were observed in the composition of the protozooplankton community with depth, particularly in June. The ratio of heterotrophic dinoflagellate biomass to ciliate biomass was lower in the mixed layer than in deeper waters. Within the mixed layer the average ratio of heterotrophic dinoflagellate biomass to ciliate biomass gradually increased from 0.2 in early May to 1.7 in June whereas this increase was more pronounced below the mixed layer ranging from 0.8 in May to 7.4 in June. Aloricate taxa dominated ciliate biomass at all depths during early May and late June whereas tintinnids contributed most to ciliate biomass in surface waters in late May and early June.

Depth integrated biomass was calculated assuming a constant mixed layer depth of 35 m (Fasham et al., 1999). During early May depth-integrated protozooplankton biomass increased from 430 to 638 mg C $m^{-2}$; however, a much lower value of 127 mg C $m^{-2}$ was recorded on 19 May following a decrease in chlorophyll concentration (Figure 2). Between 23 May and the end of the study on 15 June depth-integrated protozooplankton biomass values



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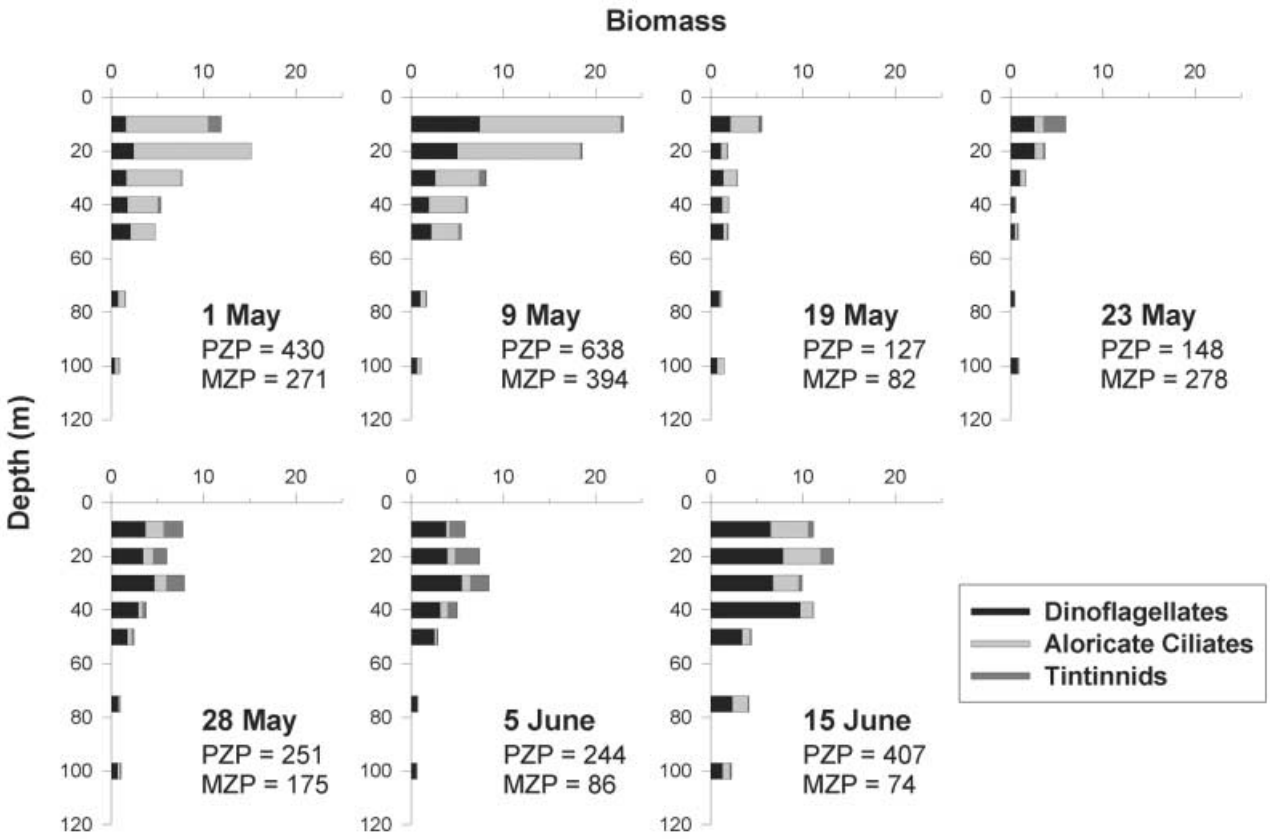


**Figure 2.** Vertical distribution of biomass of three categories of protozooplankton ($\mu g\,C\,l^{-1}$) between 10 and 100 m in the north-east Atlantic during May and June 1990. PZP, mixed layer depth integrated protozooplankton biomass ($mg\,C\,m^{-2}$); MZP, mixed layer depth integrated metazooplankton biomass ($<200\,\mu m$) ($mg\,C\,m^{-2}$). Planktonic sarcodine biomass was very low and is excluded from this figure. Mixed layer depth, 35 m.

increased from 148 to 407 $mg\,C\,m^{-2}$. Metazooplankton ($<200\,\mu m$) were more abundant in surface waters than at depth. Depth-integrated biomass of this group ranged between 74 and 394 $mg\,C\,m^{-2}$ and was highest in May. It should be noted, however, that the methods used to estimate metazooplankton abundance and biomass in this study are limited due to small sample volumes and the use of a single factor to convert nauplii abundance to carbon biomass.

More detailed data on the temporal changes in the abundance, biomass and community composition of the microzooplankton community within the mixed layer were derived from analysis of undiluted samples from herbivory experiments. Protozooplankton were very abundant in early May with concentrations in excess of 36,000 cells $l^{-1}$ (Table 2). Within three days, abundance had declined by more than 80% to around 7000 cells $l^{-1}$. Protozooplankton abundance increased until 9 May and then decreased again towards the end of May. In early June protozooplankton concentrations were again higher at 25–27,000 cells $l^{-1}$ decreasing to 5–9000 cells $l^{-1}$ by mid June. Nauplii abundance generally appeared to be higher during May when abundance ranged between 48 and 400 individuals $l^{-1}$.

The trend in protozooplankton biomass generally reflected that of abundance with an overall decrease from 10 $\mu g\,C\,l^{-1}$ on 1 May to 1 $\mu g\,C\,l^{-1}$ on 19 May (Figure 3 and Table 2). However, on 8 and 9 May biomass reached maximum values of between 11 and 12 $\mu g\,C\,l^{-1}$ due to a higher proportion of larger aloricate ciliates. During June, protozooplankton biomass was less variable ranging from 2 to 6 $\mu g\,C\,l^{-1}$. Nauplii biomass ranged from 3 to 24 $\mu g\,C\,l^{-1}$ (average 12 $\mu g\,C\,l^{-1}$) during May and was lower in June averaging 4 $\mu g\,C\,l^{-1}$. On all but four occasions, the biomass of nauplii exceeded that of the protozooplankton.

Aloricate choreotrich ciliates dominated the protozooplankton biomass during May although there was a shift in the size of this community. Small choreotrichs $<20\,\mu m$ in length and primarily of the genus *Strombidium* (Claparède & Lachmann) dominated in early May with abundance up to 28,000 cells $l^{-1}$. There then followed a dramatic decrease in the abundance of small choreotrichs followed by an increase in the proportion of larger choreotrichs, typically *Strombidium* spp. and *Strobilidium* spp. (Schewiakoff), when chlorophyll concentrations were increasing. Tintinnids dominated the ciliate community in early June with abundances up to 23,000 cells $l^{-1}$ when they comprised up to 80% of the total protozooplankton biomass. During May the most abundant tintinnids were *Dictyocysta* spp. (Ehrenberg) and *Salpingella* spp. (Jörgensen) while in June one species of *Salpingella* dominated the tintinnid community. Throughout the study heterotrophic dinoflagellates comprised members of the Gymnodiniales and Peridiniales. In May Gymnodiniales, in particular a *Gyrodinium* sp. (Kofoid & Swezy) ($\sim 30\,\mu m$ in length), were most abundant whereas during June *Protoperidinium* spp. (Bergh) were also abundant.



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**Table 2.** *Temporal changes in the total abundance (cells $l^{-1}$) and biomass ($\mu g\,C\,l^{-1}$) of microzooplankton in undiluted treatments for 18 out of the 21 herbivory experiments undertaken in the north-east Atlantic in May and June 1990. Due to their low abundance, planktonic sarcodines have been excluded.*

| | May 1990 | | | | | | | | | | | June 1990 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 3 | 4 | 5 | 8 | 9 | 11 | 13 | 15 | 19 | 30 | 1 | 3 | 5 | 8 | 11 | 13 | 15 |
| PROTOZOOPLANKTON | | | | | | | | | | | | | | | | | | |
| Abundance (cells $l^{-1}$) | | | | | | | | | | | | | | | | | | |
| Choreotrich ciliates | | | | | | | | | | | | | | | | | | |
| —aloricate | 35048 | 17280 | 5800 | 9500 | 14700 | 14360 | 2714 | 4600 | 2233 | 2450 | 2500 | 4500 | 3600 | 2700 | 3900 | 3850 | 5800 | 3650 |
| —loricate (tintinnids) | 0 | 470 | 0 | 300 | 0 | 40 | 280 | 100 | 0 | 0 | 3850 | 19800 | 22650 | 7000 | 7100 | 850 | 150 | 300 |
| Other ciliates | 476 | 400 | 0 | 1100 | 50 | 80 | 8 | 150 | 17 | 100 | 150 | 100 | 0 | 0 | 0 | 300 | 50 | 350 |
| Heterotrophic dinoflagellates $>20\,\mu m$ | 1048 | 2951 | 1300 | 2350 | 1100 | 1240 | 3857 | 950 | 717 | 700 | 1100 | 800 | 800 | 850 | 3300 | 600 | 3000 | 4050 |
| Total | 36572 | 21101 | 7100 | 13250 | 15850 | 15720 | 6859 | 5800 | 2967 | 3250 | 7600 | 25200 | 27050 | 10550 | 14300 | 5600 | 9000 | 8350 |
| Biomass ($\mu g\,C\,l^{-1}$) | | | | | | | | | | | | | | | | | | |
| Choreotrich ciliates | | | | | | | | | | | | | | | | | | |
| —aloricate | 9.24 | 5.61 | 1.63 | 3.31 | 11.06 | 12.18 | 1.32 | 2.43 | 1.34 | 0.84 | 0.94 | 0.93 | 0.74 | 0.86 | 0.73 | 2.47 | 2.42 | 0.83 |
| —loricate (tintinnids) | 0 | 0.50 | 0.22 | 0.98 | 0 | 0.01 | 1.07 | 0.20 | 0 | 0 | 0.85 | 2.24 | 5.14 | 1.59 | 1.61 | 0.31 | 0.05 | 0.08 |
| Other ciliates | 0.03 | 0.04 | 0.05 | 0.07 | 0 | 0.01 | 0.45 | 0.38 | 0.01 | 0.01 | 0.01 | 0.01 | 0 | 0 | 0 | 1.32 | 0 | 0.03 |
| Heterotrophic dinoflagellates $>20\,\mu m$ | 0.34 | 1.81 | 0.67 | 1.38 | 0.38 | 0.26 | 1.27 | 0.42 | 1.00 | 0.32 | 0.59 | 0.34 | 0.50 | 1.14 | 2.24 | 0.52 | 1.76 | 1.21 |
| Total | 9.61 | 7.97 | 2.57 | 5.76 | 11.44 | 12.46 | 4.11 | 3.25 | 2.34 | 1.16 | 2.38 | 3.51 | 6.38 | 3.58 | 4.58 | 3.29 | 4.23 | 2.11 |
| METAZOOPLANKTON | | | | | | | | | | | | | | | | | | |
| Nauplii abundance (ind $l^{-1}$) | 233 | 200 | 100 | 100 | 400 | 150 | 48 | 250 | 167 | 300 | 150 | 100 | 0 | 0 | 100 | 100 | 100 | 100 |
| Nauplii biomass ($\mu g\,C\,l^{-1}$) | 14 | 12 | 6 | 6 | 24 | 9 | 3 | 15 | 10 | 18 | 9 | 6 | 0 | 0 | 6 | 6 | 6 | 6 |

No data are available for experiments conducted on 7, 17 and 28 May. Sample depths were 10 and 25 m. See Table 1 for details.

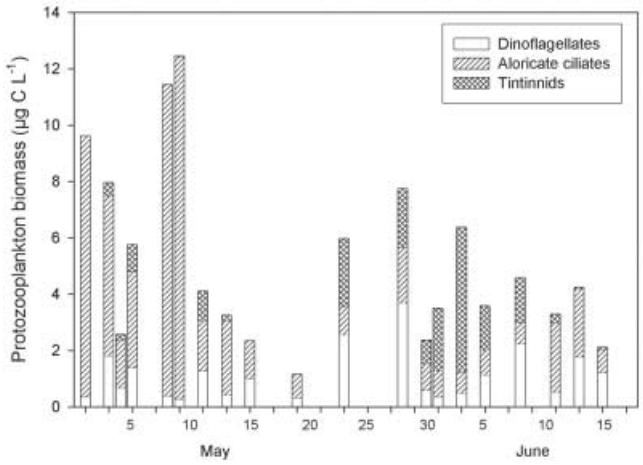


**Figure 3.** Changes in initial biomass of three categories of protozooplankton in undiluted experimental bottles for 18 out of the 21 herbivory experiments conducted in May and June 1990. Sample depths were 10 and 25 m, see Table 1 for details. Data for 23, 28 May from 10 m vertical profile samples.

Heterotrophic dinoflagellates were more important in mid-June when they comprised >40% of the protozooplankton abundance. Abundance of planktonic sarcodines was very low (<100 cells $l^{-1}$); they were only found in samples collected on 13 and 15 June.

It was possible, using data from vertical profiles and herbivory experiment samples, to explore relationships between protozooplankton biomass and both metazooplankton biomass and chlorophyll-*a* concentration (data from the British Oceanographic Data Centre). Interestingly, between 1 and 9 May, metazooplankton biomass (<200 $\mu$m) was positively correlated with protozooplankton biomass (y=0.67x+1.8; $r^2$=0.85; N=18; $P<0.001$). However, no significant relationships were observed between these two microzooplankton groups during the remainder of the study, or between protozooplankton biomass and total chlorophyll-*a* concentration (vertical profile data only) throughout the whole study.

### *Microzooplankton grazing and phytoplankton growth*

A linear relationship between phytoplankton growth and dilution factor was recorded in all of the experiments conducted during the study although due to higher variability between some samples this relationship was only significant in 16 out of the 21 experiments. The results of all herbivory experiments are summarized in Table 3. The phytoplankton growth coefficient '*k*' ranged from 0 to 0.7 $d^{-1}$ while the grazing coefficient '*g*' ranged from 0.2 to 0.5 $d^{-1}$. Growth and grazing coefficients were variable and there were no clear trends in the data. Substantial decreases in microzooplankton abundance, combined with less variability in grazing rate, resulted in a significant linear increase in average microzooplankton cell clearance rates during May (y=0.15x+0.068; $r^2$=0.88; N=17; $P<0.001$). On occasions when measured, concentrations of nitrate and phosphate within undiluted experimental bottles did not become depleted during the incubation period.

**Table 3.** *Environmental chemical conditions and phytoplankton specific growth rate (*k*) and grazing mortality (*g*) (with standard error, N=3) determined from herbivory experiments undertaken in the north-east Atlantic in May and June 1990.*

| Date | Chl-*a* ($\mu$g $L^{-1}$) | $NO_3-T_0$ ($\mu$M) | $NO_3-T_{24}$ ($\mu$M) | $PO_4-T_0$ ($\mu$M) | $PO_4-T_{24}$ ($\mu$M) | *k* ($d^{-1}$) | *g* ($d^{-1}$) | $r^2$ | % Turnover |
|---|---|---|---|---|---|---|---|---|---|
| 1 May | 1.47 | — | — | — | — | 0.32 (0.08) | −0.45 (0.11) | 0.70** | 36 |
| 3 May | 1.30 | 6.3 | — | — | — | 0.13 | −0.30 | 0.44 n.s. | |
| 4 May | 1.30 | — | — | — | — | 0.57 (0.02) | −0.28 (0.03) | 0.92**** | 25 |
| 5 May | 1.24 | 6.31 | 6.01 | 0.51 | 0.44 | 0.20 (0.03) | −0.48 (0.05) | 0.58* | 38 |
| 7 May | 2.13 | 4.91 | 4.58 | — | — | 0.22 (0.00) | −0.34 (0.03) | 0.86**** | 29 |
| 8 May | 1.32 | 4.36 | — | 0.41 | — | 0.18 (0.06) | −0.29 (0.10) | 0.58* | 25 |
| 9 May *in situ* | 1.89 | 4.26 | 4.29 | 0.37 | 0.36 | 0.35 (0.06) | −0.46 (0.09) | 0.93**** | 37 |
| 9 May | 1.89 | 4.26 | 4.29 | — | — | 0.49 (0.11) | −0.46 (0.15) | 0.77*** | 37 |
| 11 May | 1.15 | 6.52 | 6.42 | 0.61 | 0.55 | 0.28 (0.07) | −0.37 (0.11) | 0.56* | 31 |
| 13 May | 2.10 | 3.77 | 3.01 | 0.44 | 0.39 | 0.22 (0.03) | −0.34 (0.04) | 0.85**** | 29 |
| 15 May | 3.70 | — | 2.77 | — | — | 0.05 | −0.06 | 0.06 n.s. | |
| 17 May | 3.50 | — | — | — | — | 0.34 | −0.18 | 0.24 n.s. | |
| 19 May | 1.80 | — | — | — | — | 0.01 (0.004) | −0.25 (0.06) | 0.67* | 22 |
| 28 May | 1.31 | — | — | — | — | 0.65 (0.07) | −0.37 (0.06) | 0.67* | 32 |
| 30 May | 1.80 | — | — | — | — | 0.04 | −0.26 | 0.37 n.s. | |
| 1 June | 2.36 | 0.51 | 0.49 | 0.15 | 0.16 | 0.40 (0.06) | −0.50 (0.08) | 0.71** | 39 |
| 3 June | 1.42 | — | — | — | — | 0.28 | −0.11 | 0.21 n.s. | |
| 5 June | 1.30 | 2.57 | 2.57 | 0.28 | 0.24 | 0.22 (0.05) | −0.27 (0.07) | 0.65* | 23 |
| 8 June | 1.20 | 0.63 | 0.65 | 0.16 | 0.12 | 0.12 (0.02) | −0.20 (0.03) | 0.78*** | 18 |
| 11 June | 1.20 | 0.26 | 0.06 | 0.11 | 0.08 | 0.08 (0.02) | −0.18 (0.03) | 0.75*** | 16 |
| 13 June | 0.50 | 0.41 | 0.34 | 0.12 | 0.13 | 0.54 (0.06) | −0.50 (0.09) | 0.75*** | 40 |
| 15 June | 0.50 | — | — | — | — | 0.19 (0.09) | −0.42 (0.14) | 0.50* | 34 |

Chl-*a*, initial chlorophyll concentration; $NO_3$, dissolved nitrate concentration at $T_0$ or $T_{24}$; $PO_4$, dissolved phosphate concentration at $T_0$ or $T_{24}$; *k*, instantaneous growth coefficient; *g*, instantaneous grazing coefficient; $r^2$, correlation coefficient of regression analysis; n.s., not significant, *, $P<0.05$, **, $P<0.01$, ***, $P<0.005$, ****, $P<0.001$; % turnover, daily turnover of chlorophyll biomass; —, no measurements made.



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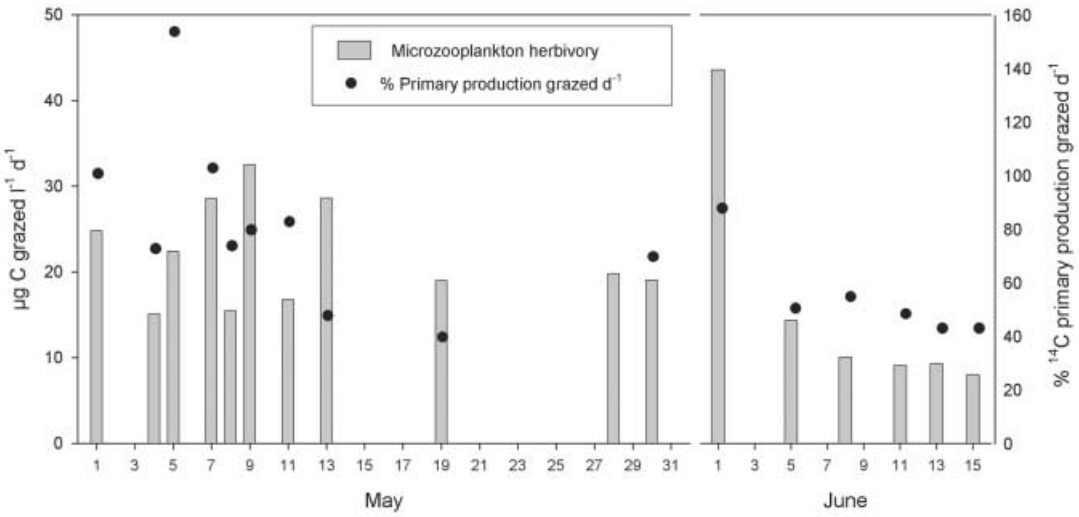


**Figure 4.** Microzooplankton herbivory and the % $^{14}$C primary production (as estimated by Savidge et al., 1995) grazed daily in the mixed layer of the north-east Atlantic during May and June 1990. Sample depths were 10 and 25 m, see Table 1 for details.

The daily turnover of chlorophyll biomass ranged from 22 to 38% in May and from 16 to 40% in June (Table 3) and microzooplankton herbivory was positively correlated with 200 $\mu$m pre-screened chlorophyll-*a* concentration during the entire study ($y=10.9x-2.7$; $r^2=0.75$; $N=17$; $P<0.001$). Using this data the grazing impact on phytoplankton carbon biomass and production was calculated assuming a carbon to chlorophyll ratio of 47 (Fasham et al., 1999) and using $^{14}$C primary production determined concurrently from the same locations and depths by Savidge et al. (1995). Microzooplankton herbivory removed between 8 and 44 $\mu g\,C\,l^{-1}d^{-1}$ throughout the study. This corresponded to an average of 95% of the $^{14}$C primary production in the mixed layer between 1 and 12 of May, and 44% of $^{14}$C primary production between 13 and 19 of May (Figure 4). During the period 28 May to 15 June an average of 52% of $^{14}$C primary production was grazed by the microzooplankton.

### *Ciliate growth and mortality*

No significant differences (*t*-tests, $P \geqslant 0.23$) were detected between initial ciliate abundance in screened and unscreened samples across all five growth and mortality experiments indicating that fractionation through 150 $\mu$m mesh had not reduced ciliate numbers prior to incubation. However, concurrent counts of metazooplankton (<150 $\mu$m) revealed relatively high numbers of juveniles (mean 11–222 nauplii $l^{-1}$ and 2–25 copepodites $l^{-1}$) in screened samples. No significant differences (*t*-tests, $P \geqslant 0.85$) were recorded between growth rates measured in samples incubated on ship or *in situ* for either screened or unscreened samples.

Mean total ciliate community growth in screened samples varied from $-0.71\,d^{-1}$ on 11 May to $0.23\,d^{-1}$ on 19 May with negative rates recorded in all but one of the five experiments (Table 4); however, only the rates measured on the 7 and 11 May were significantly different from zero. On the one occasion when a positive community growth was recorded, the ciliate community was dominated by three aloricate taxa with growth rates ranging from 0.14 to $1.14\,d^{-1}$. The latter value, recorded for a taxon resembling *Lohmaniella* (Leegaard), was significantly different from zero. With the exception of the experiment undertaken on 19 May, growth rates in unscreened samples were generally similar to those in screened samples. Consequently, significant mortality due to predation by larger metazoans was recorded only on 19 May (Table 4).

**Table 4.** *Mean growth (*k*) and mortality (*g*) rates (with standard deviation, N=3) of the ciliate community determined from growth rate experiments undertaken in the north-east Atlantic during May 1990.*

| Date | Ciliate taxa | $k$ ($d^{-1}$) | $g$ ($d^{-1}$) |
|---|---|---|---|
| 3 May | All ciliates | −0.55 (0.40) | 0.12 (0.31) |
| 7 May | All ciliates | −0.48 (0.39)* | 0.18 (0.51) |
| | | −0.47 (0.28)*$^{in\ situ}$ | 0.13 (0.37)$^{in\ situ}$ |
| 11 May | All ciliates | −0.71 (0.30)* | −0.05 (0.12) |
| 15 May | All ciliates | −0.07 (0.45) | 0.49 (0.15) |
| 19 May | All ciliates | 0.23 (0.07) | 0.54 (0.08)** |
| | *Strombidium* sp. 1 | 0.14 (0.16) | 0.28 (0.32) |
| | *Strombidium* sp. 2 | 0.16 (0.34) | 0.98 (0.86) |
| | Unknown sp. | 1.14 (0.22)* | 1.07 (0.74)* |

*Strombidium* sp. 1, 20×14 $\mu$m in size; *Strombidium* sp. 2, 30×25 $\mu$m in size; Unknown sp., 20×20 $\mu$m in size (possibly *Lohmaniella* sp.).
*, $P<0.05$, **, $P<0.01$.

## DISCUSSION

The composition of the microzooplankton community observed in this study was typical for the North Atlantic with protozoa dominating the assemblage and mostly comprising aloricate ciliates and heterotrophic dinoflagellates (e.g. Gifford et al., 1995; Sleigh et al., 1996). As with other studies in the region and elsewhere (e.g. Burkill et al., 1993; Nielsen & Hansen 1995; Stelfox et al., 1999), highest concentrations of these protozooplankton were



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found in the surface waters with all major groups represented throughout the water column. By contrast, considerable temporal variability was observed in protozooplankton abundance, biomass, and community structure during the study period. The initial high biomass community was dominated by aloricate ciliates, evolving into a lower biomass community comprising a more even mix of tintinnids, aloricate ciliates and dinoflagellates. It should be noted that sampling within the mixed layer was limited to only one depth on several occasions throughout the study. Our interpretation of temporal changes is therefore subject to some uncertainty given the heterogeneous distribution of protozooplankton (Montagnes et al., 1999). It is also possible that the changes observed over time do not represent a temporal progression within a single water body. Savidge et al. (1992) suggested that the reference drogue only remained within the anticyclonic eddy until 13 May, after which it became entrained in a discontinuity zone between warmer and cooler water-bodies before finally moving into a cold water intrusion on 19 May. However, the same authors found no evidence in the physical data from the surface layer to indicate any major changes in the water masses adjacent to the drogue; a conclusion supported by temporal patterns of biological variables recorded adjacent to the drogue (Verity et al., 1993b).

Previous studies conducted in the same region in spring 1989 have recorded lower ciliate and heterotrophic dinoflagellate abundances than in the present study at a time when the microphytoplankton community was dominated by a mixture of diatoms and dinoflagellates (Verity et al., 1993b; Stoecker et al., 1994). These inter-annual differences in the structure of the protozooplankton communities in the north-east Atlantic, therefore, seem to reflect the differences in the phytoplankton community encountered between the two years and may be a common feature of this region (Verity et al., 1993b).

A distinctive feature of the present study was the very high initial abundance of choreotrich ciliates (>35,000 cells $l^{-1}$ on 1 May), most of which were $<20\,\mu$m in length (almost 28,000 cells $l^{-1}$). Our data are comparable with observations of nanociliate abundance in estuarine waters (Sherr et al., 1986) and temperate nearshore environments (Tamigneaux et al., 1997) but are higher than values we have encountered in the literature for oceanic waters. This high concentration of small ciliates clearly indicates a period of substantial ciliate growth, fuelled by a significant food resource, prior to the start of the study. Choreotrich ciliates are known to consume both nano- and pico-sized cells (Rassoulzadegan et al., 1988) although nano-sized ciliates are most likely to consume picoplankton (Sherr et al., 1986; Lynn et al., 1991; Pérez et al., 2000). Therefore, this period of ciliate growth may have been supported by a range of autotrophic or heterotrophic prey including flagellates, cyanobacteria or bacteria. Rates of primary production and chlorophyll-*a* concentrations at the beginning of May were substantially higher than typical background winter values indicating that some phytoplankton growth had already commenced (Savidge et al., 1995). There is no evidence of higher bacterial abundance at this time (Fasham et al., 1999) although cyanobacterial abundance was twice as high between 1–12 May as during 13–19 May (Stoecker et al., 1994). An autotrophic food resource may therefore have been available. Whatever the food resource, the high abundance of small ciliates, coupled with concurrent ammonium-uptake rates (Bury et al., 2001), suggests the presence of a microbial dominated system supported by the rapid recycling of nitrogen prior to the onset of the spring bloom. Substantial rates of primary production associated with nano-sized phytoplankton and supported by regenerated nutrients have been previously recorded in the same area prior to the development of the main phase of the spring bloom during 1989 (Joint et al., 1993). Results from a modelling study also suggest that pre-bloom phytoflagellates and picophytoplankton populations may be a regular feature of the development of phytoplankton communities in the North Atlantic (Taylor et al., 1993).

Another interesting feature of the present study, and a natural consequence of the high ciliate abundances discussed above, was the marked decline in ciliate abundance recorded during May. This population decline was coincident with negative ciliate growth rates observed during early to mid-May in samples incubated for 24 h after screening to remove metazoan predators. These negative rates may be a consequence of food limitation caused by high ciliate grazing pressure; however, predation by metazoans cannot be excluded as a cause given the relatively high number of copepod developmental stages which passed through the mesh used to screen samples. Copepod nauplii were abundant during the study with mean abundances of 11–222 $l^{-1}$ in the ciliate growth rate experimental samples. They are also known to be efficient grazers on auto- and heterotrophic cells as small as 4–5 $\mu$m, including ciliates (Stoecker & Egloff, 1987; Berggreen et al., 1988; Paffenhöfer, 1998). Assuming a maximum filtration rate of 7–12 $ml^{-1}ind^{-1}d^{-1}$, calculated for *Calanus finmarchicus* nauplii feeding on ciliates (Irigoien et al., 2003), they would clear between 8 and >100% of the water column daily. Such predation may therefore have been a significant factor in the decline of the ciliate population. By contrast, significant predation on ciliates by larger metazoans was only recorded on one occasion suggesting that the larger zooplankton were less important as grazers of protozoans; an observation in part supported by concurrent low rates (<10% primary production) of mesozooplankton herbivory (Morales et al., 1993).

It should be noted that the reductions in ciliate numbers recorded in the incubated samples were greater than those observed in the water column between sampling events. This may be a consequence of the difficulty of sampling the same ciliate population during the study. In addition, ciliate populations are known to be highly heterogeneous over small spatial scales (Montagnes et al., 1999) which may have contributed to differential ciliate dynamics in field and incubated populations. It is also possible that methodological factors may also have contributed to ciliate mortality. Alteration of phytoplankton prey growth rates due to incubation under artificial irradiance (discussed with respect to dilution experiments below) may have indirectly effected ciliate growth. There were, however, no differences in ciliate growth recorded between samples incubated on ship and *in situ*. Fractionation and enclosure within incubation bottles can contribute towards mortality (Venrick et al., 1977). These latter effects could not be assessed via controls so cannot be discounted



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as a cause of ciliate mortality despite the careful measures taken to reduce such factors. Indeed ciliate growth rates measured in screened samples should be considered to be minimum estimates (Leakey et al., 1994). A significant, positive growth rate was, however, recorded for one species after the ciliate community had declined to lower levels in mid-May demonstrating active growth within incubation bottles. The range of values ($-0.71$ to $1.14\ d^{-1}$) recorded in this study also falls within the range observed for natural populations of ciliates from other temperate marine environments (Leakey et al., 1994; Nielsen & Kiørboe, 1994) including the North Atlantic (Verity et al., 1993a).

Estimates of phytoplankton specific growth rate ($k$) and grazing mortality ($g$) determined from the herbivory experiments during May ranged from 0 to 0.7 $d^{-1}$ and 0.2 to 0.5 $d^{-1}$, respectively. These values are within the ranges reported for oceanic areas (e.g. Strom & Strom 1996; Verity et al., 1996) although the former are lower than those reported for the north-east Atlantic spring bloom in May 1989 (Verity et al., 1993a). Before discussing the implications of these data, it is important to assess their accuracy by considering the methodological limitations associated with the dilution technique as applied in this study.

With regard to estimates of phytoplankton specific growth rate, it is possible that values determined in the present study may have been underestimated. Firstly, it is clear that the phytoplankton growth coefficient was lower than the grazing coefficient in most experiments. This suggests that growth rates were at times underestimated as illustrated by the observed increase in phytoplankton biomass recorded *in situ* during mid-May at a time of modest grazing mortality. Secondly, the growth rates measured in the herbivory experiments were on all but two occasions lower than estimates of growth determined from concurrent $^{14}C$ primary production experiments (Savidge et al., 1995). Nutrient limitation in experimental incubations can limit phytoplankton growth and, in situations where nutrients become differentially depleted between dilution treatments, this can lead to an overestimation of grazing and an underestimation of growth (Gifford, 1988); however, no nutrient (nitrate and phosphate) depletion was observed for those experiments where nutrient measurements were made. Alternatively, shipboard incubations may have been biased if light levels were not realistic. The shipboard incubator used in the present study had a programmable lighting regime but with fixed lighting levels; therefore it was not possible to accurately match the significant changes in ambient irradiance which occurred during the study period. This may have led to a reduction in phytoplankton growth rate, especially if photo-inhibition had taken place. Fortunately, while irradiance may have influenced phytoplankton growth rate estimates, it is less likely to have influenced estimates of grazing mortality via differential effects on phytoplankton growth in different dilution treatments. Overall, it would seem likely that phytoplankton growth rates have been underestimated in this study and that the $^{14}C$ primary production values of Savidge at al. (1995) should be considered a more accurate measure of primary production.

With regard to estimates of grazing mortality, it is possible that values determined in the present study may have been under- or overestimated due to a non-linear response of grazing pressure to dilution factor. There is no evidence in the present study to suggest that high food concentrations may have saturated protozooplankton grazing kinetics leading to an underestimate of grazing rates (Gallegos, 1989). Indeed, the decline in ciliates recorded in both field and experimental samples suggests that they may have been food limited during early May. By contrast, dilution may have led to starvation induced grazer mortality leading to an overestimate of grazing rates (Dolan & McKeon, 2004); perhaps, in the case of ciliates, further stressing a population which was already food limited. Although this is possible, apparent protozooplankton clearance rates, calculated for each experiment from abundance and grazing mortality data, were relatively modest, ranging between 0.5 and 3 $\mu l\ cell^{-1}\ h^{-1}$ (Dolan & McKeon, 2004). In addition, it has been proposed that overestimated grazing rates determined by the dilution technique are more likely to occur in oligotrophic environments characterized by chlorophyll concentrations which are generally lower than those recorded in the present study (Dolan & McKeon, 2004).

The above assessment of grazing mortality estimates is, however, complicated by the relatively high abundance of metazooplankton ($<200\ \mu m$) within experimental treatments. If metazooplankton were feeding on autotrophic cells then they, like the protozooplankton, may have exhibited a non-linear response of grazing pressure to dilution factor thus contributing to under- or overestimated microzooplankton grazing rates. On the other hand, if they were feeding on heterotrophic cells (as also suggested by the decline in ciliates recorded in both field and experimental samples during early May) then dilution may have released the protozooplankton from predation pressure leading to enhanced protozooplankton growth and grazing in diluted treatments. Unfortunately it is not possible to draw conclusions on the significance of such complex, counteracting effects from the data available.

Microzooplankton were active grazers of the phytoplankton population during this study consuming between 16 and 40% of chlorophyll standing stock and between 38 and 154% of daily primary production. These values fall within the range recorded for other oceanic areas where typically microzooplankton removed an average of 59 to 70% of primary production (Calbet & Landry, 2004). Concurrent rates of mesozooplankton herbivory were low, equivalent to $<10\%$ of primary production (Morales et al., 1993). It would therefore appear that microzooplankton were the most important herbivores reflecting the predominance of nanophytoplankton observed throughout much of the study period. Interestingly, similar values of microzooplankton grazing impact (37–100% of the daily primary production grazed) were recorded during the 1989 spring bloom in the north-east Atlantic at a time when the phytoplankton community was dominated by larger diatom cells than in the present study (Verity et al., 1993a). Such comparisons are highly dependent on the choice of carbon:chlorophyll ratio; however, the value of 47 used in this study is similar to the ratio of 40 used by Verity et al. (1993a). Although protozoa dominated the microzooplankton assemblage in the present study, metazooplankton ($<200\ \mu m$), as outlined above, were also abundant and potentially

capable of clearing >100% of the water column daily on several occasions. The contribution of the metazoa to the total microzooplankton herbivorous activity could therefore have been significant.

During the study there were no clear temporal trends in microzooplankton grazing coefficients, despite considerable change in the biomass and composition of the phytoplankton and protozooplankton communities. Similarly, the amount of phytoplankton carbon biomass grazed did not show any distinctive trends although values tended to be lower towards the end of the study reflecting lower protozooplankton abundance and biomass. Phytoplankton biomass and production increased during the study with maximum values recorded on 17 May (Savidge et al., 1992). These increases did not appear to elicit a similar response in the microzooplankton grazing impact on $^{14}C$ primary production recorded between 5 to 19 May. The spring bloom therefore appears to have been uncoupled from the protozooplankton community in mid-May, although it should be cautioned that grazing data were unavailable from 14 to 18 May when maximum phytoplankton values were recorded. The phytoplankton community during mid-May was dominated by the nanoplankton and, in particular, by the small diatom *Nannoeis haslae*. It may well be that the morphology of *N. haslae* may have offered some protection from microzooplankton grazers or that the nutritional content of the diatom was unsuitable for the resident grazer community. Changes in microzooplankton composition or cell morphology would therefore have been required for the community to adjust to the available prey (Strom, 2002). In their modelling study of ecosystem carbon flow in the north-east Atlantic, using BOFS data collected in 1990, Fasham et al. (1999) found that modelled microzooplankton herbivory was up to four times greater than the water column integrated values; the latter calculated for the mixed layer depth using the herbivory rates reported in the present study. The inability of microzooplankton to fully exploit the nanophytoplankton may therefore help explain this disparity.

In summarizing their concomitant studies on phytoplankton processes, Savidge et al. (1995) describe three phases in the sequence of changes in the phytoplankton community from May through to mid-June: (1) from 1 to 12 May a period of low irradiance, chlorophyll-*a* concentration and primary production with the phytoplankton dominated by the $<5\,\mu$m size fraction; (2) from 13 to 19 May a period of increased irradiance and rapid increase in both chlorophyll-*a* concentration and primary productivity; and (3) from 28 May to 15 June a period of decreasing chlorophyll-*a* concentration and primary productivity dominated by the $>5\,\mu$m fraction. Given the relationship between microzooplankton and their phytoplankton prey, it is useful to employ the same temporal framework when summarizing the changes in the microzooplankton community which occurred during the present study:

(i) Early May was characterized by high protozooplankton abundance which subsequently declined reflecting rapid decreases in the number of small ciliates. Food limitation may have been responsible for this decline in ciliate numbers but predation by copepod developmental stages is also likely given the high numbers of nauplii present at this time. Microzooplankton grazing activity remained relatively constant, removing on average 95% of primary production, despite prominent changes in the ciliate community. This suggests that small ciliates may have exerted minimal grazing impact on the phytoplankton with larger ciliates dinoflagellates or smaller metazoans being the main herbivores.

(ii) Mid-May was characterized by further reductions in both protozooplankton abundance and biomass due largely to a continued decline in the numbers of ciliates. Microzooplankton herbivory remained relatively constant but removed a lower average of 44% of primary production. It is possible that microzooplankton were unable to respond to the increased availability of small diatoms responsible for the rapid increase in phytoplankton biomass and production observed at this time.

(iii) Late May and early June were characterized by relatively stable microzooplankton abundance and biomass comprising a mix of dinoflagellates, tintinnids and aloricate ciliates. Microzooplankton herbivory tended to decline towards the end of this period, removing an average of 52% of primary production, and reflecting decreases in both the phytoplankton and protozooplankton communities.

The above synthesis of microzooplankton dynamics is somewhat speculative due to the uncertainties associated with possible changes in the water mass sampled during the study as described by Savidge et al. (1992). However, overall the study reveals the presence of a microzooplankton community in this region of the north-east Atlantic which was (a) initially in decline following a period of ciliate growth which took place before the study was conducted, and (b) the major consumer of phytoplankton although probably uncoupled from the spring bloom.

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