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Microzooplankton grazing activity in the temperate and sub-tropical NE Atlantic: summer 1996

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ABSTRACT: The role of microzooplankton herbivory in the fate of phytoplankton production was quantified within 2 biologically contrasting water masses in the NE Atlantic during the summertime. Seawater dilution experiments were conducted to quantify phytoplankton growth and losses due to grazing during 2 Lagrangian surveys, at 60° N and 37° N, in the vicinity of the 20° W meridian. Phytoplankton growth rates were higher during the northerly study at 60° N (mean 1.54 d^{-1}) than at the southerly study, 37° N. Estimates of phytoplankton growth during the southerly study were corrected for photoadaptation, and the mean growth rate was 0.62 d^{-1}. The day-to-day pattern of phytoplankton mortality due to microzooplankton grazing was similar to the growth rates, with higher values recorded in the northerly study (1.25 d^{-1}) and lower values at the southerly site (0.43 d^{-1}). In the northerly waters, microzooplankton consumed up to 77 % d^{-1} of the chlorophyll standing stock, while microzooplankton herbivory at the southerly site accounted for <44 % d^{-1} of the chlorophyll stocks. Microzooplankton grazing represented a carbon flux of between 3 and 37 µg C l^{-1} d^{-1}, with highest values found in the eutrophic northerly waters. The microzooplankton community were numerically dominated by small heterotrophic nanoflagellates (HNAN) (0.7 to 4.2 × 10^5 cells l^{-1}). However in terms of the microzooplankton biomass, heterotrophic dinoflagellates dominated at the northerly site (5.6 µg C l^{-1}) while the HNAN (1.1 µg C l^{-1}) and oligotrich ciliates (0.7 µg C l^{-1}) were more important at the southerly station. Tintinnids and 'other' ciliates contributed less to the total microzooplankton abundance or biomass. We conclude that microzooplankton formed a significant component of the food web in the NE Atlantic and were important controllers of phytoplankton production, particularly in temperate waters, during this investigation period. Our data suggest that microzooplankton grazing did not control the picoplankton production in the oligotrophic sub-tropical NE Atlantic during the summer, and this may be attributable to the dominance of *Prochlorococcus* spp.

KEY WORDS: Microzooplankton grazing · Seawater dilution · Microzooplankton community · Chlorophyll · NE Atlantic

INTRODUCTION

Microzooplankton, defined herein as heterotrophic organisms between 2 and 200 µm in size, form a significant proportion of total zooplankton biomass in many oceanic environments. They are a taxonomically diverse group that includes ciliates, flagellates, dinoflagellates, sarcodines and small metazoans (Capriulo et al. 1991). Estimates of their grazing impact indicate that they can control phytoplankton production (e.g. Gifford 1988, Burkill et al. 1993, Verity et al. 1993) and play a significant role in the fate of bacteria (e.g. Weisse & Scheffel-Möser 1991) and in the regeneration of nutrients (e.g. Goldman et al. 1987). Ciliates and dinoflagellates often form a significant part of the diets of larger zooplankton, such as copepods (Atkinson 1996), and therefore provide an important trophic link

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between small prey and larger predators (Sherr et al. 1986). Microzooplankton are able to select food, based on size and nutritional value (Anderson 1997), which coupled with a rapid population response to changes in food abundance, allow them to play a significant role in structuring plankton communities and determining the fate of phytoplankton production within the euphotic zone and its export from it (Michaels & Silver 1988, Strom & Strom 1996, Wassmann 1998).

The NE Atlantic Ocean is characterised by large seasonal variations in phytoplankton biomass. The most notable event is the spring phytoplankton bloom, which develops near 40° N during April and May and proceeds towards 60 to 70° N by June (Ducklow & Harris 1993, Verity et al. 1993). High concentrations of nitrate supplied during winter mixing combined with thermal stratification and increased light levels enable the spring bloom to develop. Uncoupling between production and consumption leads to accumulation of biogenic material in surface waters as larger phytoplankton cells, particularly diatoms and dinoflagellates, become important (Colebrook 1982, Joint et al. 1993). During the summer, post-bloom phytoplankton are dominated by nanoplankton, which can account for more than 50% of the seasonal primary production (Ducklow & Harris 1993). In contrast, in the sub-tropical region to the south of 40° N, oligotrophic conditions prevail during the summer and low phytoplankton production rates are dominated by picoplankton (0.2 to 2 µm).

The role of microzooplankton herbivory and the fate of phytoplankton production in the NE Atlantic was studied during the Joint Global Ocean Flux Study (JGOFS) North Atlantic Bloom Experiment (NABE) in 1989 and the Office of Naval Research (USA) Marine Light Mixed Layer (MLML) programme in 1991. These studies demonstrated that microzooplankton were important controllers of the fate of phytoplankton production in surface waters between 47 and 60° N, and between 20 and 21° W. Results from experiments using the dilution technique of Landry & Hassett (1982) showed that microzooplankton herbivory accounted for up to 115% of daily phytoplankton production (Burkill et al. 1993, Verity et al. 1993, Gifford et al. 1995). However, these studies focused on the spring and summer phytoplankton communities in northern, eutrophic waters and did not investigate the role of microzooplankton grazing in the southerly, oligotrophic region of the NE Atlantic. The current study compares the role of microzooplankton grazing activity within 2 biologically contrasting water masses in the temperate and sub-tropical NE Atlantic during the summer period. In particular, this study examines the extent to which production from contrasting plankton communities can be fully utilised by microzooplankton consumption. This work forms part of the UK Plankton Reactivity in the Marine Environment (PRIME) programme, which is outlined by Savidge & Williams (2000). A more detailed description of the phytoplankton community is given by Tarran et al. (2001).

MATERIALS AND METHODS

Study location. Experiments to investigate the impact of microzooplankton grazing on phytoplankton stocks in the NE Atlantic were conducted aboard RRS 'Discovery' on Cruise D221 during June/July 1996. The dilution technique (Landry & Hassett 1982) was used to estimate phytoplankton growth and mortality due to microzooplankton herbivory. The cruise formed part of the PRIME Special Topic programme and involved 2 Lagrangian studies in contrasting oceanic sites. The 2 studies were centred in the vicinity of 60° N, 20° W during June and 37° N, 19° W during July. The northerly Lagrangian study formed part of a sulphur hexafluoride (SF_6) tracer-release experiment within a mesoscale eddy (Martin et al. 1998) which enabled an essentially coherent body of water to be sampled over a 9 d period. A detailed description of the SF_6 experiment can be found in Law et al. (2001). Experiments were carried out between 18 and 27 June within the eddy, and on 28 June a comparative experiment was conducted outside the SF_6 tracer patch. During the southerly study, an Argos buoy was drogued at 14 m and followed for 7 d. Samples were taken close to the buoy and 5 grazing experiments were conducted between 11 and 18 July.

Experimental set-up. Seawater was collected predawn from a depth corresponding to the 33% surface irradiance (determined from daily irradiance profiles) using 30 l acid-clean Go-Flo bottles. One exception to this was on 27 June, when experimental water was collected from the 55% surface-irradiance depth. Filtered seawater was prepared by draining water, via silicone tubing, from the Go-Flo bottles into 10 l polycarbonate carboys and then filtered, using a peristaltic pump, through a 0.2 µm Gelman Supor-capsule filter into 2.3 l polycarbonate bottles. Prior to use, capsule filters were soaked overnight in 10% HCl and flushed with 10 l of Nanopure water; the first 10 l of filtrate were discarded to prevent contamination of the experimental water. Unfiltered seawater was gently siphoned directly from the Go-Flo bottles using silicone tubing (fitted with a 200 µm mesh bag to remove mesozooplankton predators) into the 2.3 l incubation bottles. The tubing end with the mesh bag was inserted below the water line in each bottle to ensure negligible bubble formation (which could damage the fragile microzooplankton). Each experiment consisted of a series of 4 dilution lev-

els, set up in triplicate, which were nominally at concentrations of 0.1, 0.4, 0.7 and 1.0 that of the ambient seawater. Although nutrients are often routinely added during dilution experiments (e.g. Landry & Hassett 1982, Landry et al. 1995) to prevent nutrient limitation of phytoplankton growth during the 24 h incubation period, we chose not to do so in our experiments in order to avoid deleterious effects on microzooplankton numbers (Gifford 1988) and on phytoplankton growth (Lessard & Murrell 1998). All tubing, filtration apparatus and polycarbonate containers were cleaned with 10% HCl and thoroughly rinsed with Nanopure water and filtered seawater prior to each experiment. In addition, during set-up, the carboys and experimental bottles were covered with black plastic bags to minimise exposure to artificial light.

From each experimental bottle, sub-samples were taken for the determination of initial chlorophyll concentration. Additionally, a 300 ml sample was taken from each of the undiluted bottles to determine the microzooplankton, including the heterotrophic nanoflagellate (HNAN), community composition. Each bottle was carefully re-filled to the same dilution level and tightly capped to exclude any air bubbles. All bottles were then placed in an on-deck incubator, which was cooled by flowing surface water and covered with a neutral-density screen to mimic *in situ* light conditions, for 24 h. To check that experimental water was incubated under appropriate light conditions, flow cytometric counts were made on undiluted samples at the beginning and end of each experiment to monitor that the chlorophyll content per cell had not altered as a result of photoadaptation (Perry et al. 1981). At the end of each experiment, samples were taken from each bottle for the determination of total chlorophyll. The samples were filtered onto 0.2 µm polycarbonate filters and extracted in 10 ml of 90% acetone at –20°C overnight. Analysis for chlorophyll *a* was made on board ship using a sensitive fluorometer (Aiken 1981) calibrated against HPLC-determined chlorophyll *a*. Chlorophyll concentrations measured in the t_0 (time zero) subsamples were used to determine the actual dilution level (as fraction of undiluted seawater) in each bottle.

To determine the community structure of the microzooplankton in the initial undiluted experimental water, 250 ml subsamples were fixed in acid Lugol's solution (1% final concentration) and stored in the dark until analysis in the laboratory by inverted settlement microscopy (Utermöhl 1958). Losses of oligotrich ciliates may occur during preservation using this method, thereby underestimating ciliate abundance and total microzooplankton biomass (Stoecker et al. 1994a). Small volumes (up to 100 ml) were concentrated by sedimentation for 24 h, and all heterotrophic individuals <200 µm (excluding the heterotrophic nanoflagellates <20 µm) were identified and enumerated at ×300 magnification using an Olympus inverted microscope. As it is not possible to distinguish heterotrophic nanoflagellates (HNAN) from autotrophic forms using ordinary light microscopy, a separate method was used to enumerate the HNAN (see below). The microzooplankton fraction was divided into 4 main categories: dinoflagellates, oligotrich ciliates, tintinnids and 'other' ciliates. Metazoans (copepod nauplii <190 µm in length) and sarcodines (acantharians, radiolarians and foraminiferans) were enumerated, but because of their low abundance and the low sensitivity of this method, these data are not presented. The microzooplankton were sized using image-analysis, whereby heterotrophic cells were traced using a computer programme and, assuming appropriate geometric shapes, volumes were calculated from cell area and maximum length. The biovolume of each cell was then converted into carbon using conversion factors of 0.14 pg C μm^{-3} for dinoflagellates (Lessard 1991) and 0.19 pg C μm^{-3} for ciliates (Putt & Stoecker 1989). All ciliated protozoans were classified as potential herbivores, except for the ciliate *Mesodinium* spp., which was regarded as functionally autotrophic and therefore not quantified. Heterotrophic dinoflagellates were distinguished from autotrophic and mixotrophic taxa by the absence of chlorophyll fluorescence in fresh samples, which were gently concentrated onto a 20 µm mesh, transferred to a counting chamber, and examined by epifluorescence inverted-microscopy at sea. Therefore, only strictly heterotrophic dinoflagellates >20 µm in size were enumerated during this study.

To quantify the <20 µm-sized HNAN (which includes heterotrophic dinoflagellates), initial undiluted water samples of between 30 and 50 ml were fixed with 0.3% (final concentration) glutaraldehyde. The fixed sample was then stained with diamidino-2-phenylindole (DAPI) and proflavine (final concentration 5 µg ml^{-1}), mounted on 0.8 µm black polycarbonate filters (Sieracki et al. 1993, Stoecker et al. 1994b), and kept frozen at –20°C until analysis by epifluorescence microscopy (×900 magnification). Heterotrophic cells, which were distinguished from autotrophic taxa by the absence of chlorophyll autofluorescence, were enumerated and sized using an ocular micrometer. Cell volumes were calculated, assuming a prolate ellipsoid shape, from average dimensions of 30 to 50 cells measured for each morphotype using our image-analysis system. Biovolume was then converted to carbon using a factor of 0.14 pg C μm^{-3} for heterotrophic dinoflagellates (Lessard 1991) and 0.22 pg C μm^{-3} for nanoflagellates (Børsheim & Bratbak 1987). HNAN between 5 and 20 µm were enumerated during the northerly study, and cells between 2 and 20 µm were quantified at the southerly site.

Microzooplankton grazing was determined from measurements of the apparent growth rate of phytoplankton that were made assuming the exponential growth equation of Landry & Hassett (1982):

$$P_t = P_0 e^{(k-cg)t}$$

or

$$\frac{1}{t}\ln\left(\frac{P_t}{P_0}\right) = k - cg$$

where P_0 and P_t are the initial and final concentrations of chlorophyll *a* respectively; k and g are the instantaneous coefficients of phytoplankton growth and grazing mortality respectively; and c is the concentration of the prey and predator populations relative to ambient seawater. Values of growth and mortality were determined from linear regression analysis between the apparent growth rate of chlorophyll *a* and the fraction of undiluted seawater. The proportion of initial chlorophyll standing stock (P_i) turned over, as % d^{-1}, by the microzooplankton was calculated according to:

$$P_i = 1 - e^{-g} \times 100$$

while microzooplankton ingestion rates (*IR*) were estimated from:

$$IR = P_i \times P_0 \times (\text{C:chl } a)$$

RESULTS

Environmental conditions

The northerly study was centred within a mesoscale eddy, which was characterised as a cold-core feature with a strong anticyclonic circulation that extended approximately 40 km across (for a more detailed description see Martin et al. 1998, 2001). The eddy had a shallow mixed layer (average of 20 m), a sea-surface temperature of approximately 10.4°C, and an average chlorophyll *a* concentration of 1.1 µg l^{-1}. Approximately half of the chlorophyll biomass was concentrated in cells >5 µm, and an average of 72% of the daily phytoplankton production was attributed to the >5 µm fraction (Rees et al. 2001) which coincided with a bloom of the coccolithophore *Coccolithus pelagicus*. Most of the daily phytoplankton production was restricted to the surface mixed layer; approximately 12% (SD = 8%) occurred below the mixed layer (Donald et al. 2001). Nanophytoplankton were also abundant, while the contribution of diatoms and autotrophic dinoflagellates to the total phytoplankton standing stock was low (Tarran et al. 2001). Surface concentrations of new nutrients were high, and maximum concentrations, e.g. nitrate (8.3 µmol l^{-1}) and phosphate (0.5 µmol l^{-1}), were recorded in the centre of the eddy (Woodward & Rees 2001). During the initial period of the study, an increase in the surface temperature was mirrored by a decrease in nitrate and phosphate (Woodward & Rees 2001), and bacterial abundance (Zubkov et al. 2001). However, a storm on 24 June resulted in upwelling of cool, nutrient-rich water. Thereafter bacterial concentrations increased at a rate of 8% d^{-1} (Zubkov et al. 2001), while the mesozooplankton biomass (6.7 µg C l^{-1}) showed little change and no diurnal activity (Head et al. 1999). Outside the eddy, the surface mixed layer was deeper and the sea-surface temperature was approximately 1°C warmer. Lower chlorophyll *a* concentrations were mirrored by a reduction in the phytoplankton standing stock, which did not contain *C. pelagicus* and had lower nanophytoplankton concentrations (Tarran et al. 2001).

In contrast to the northerly waters, the southerly site was characterised by oligotrophic conditions, warmer surface temperatures (>20°C), a deeper surface mixed layer (average 25 m) and depleted nutrient levels (e.g. <0.05 µmol l^{-1} nitrate, 0.02 µmol l^{-1} phosphate) (Donald et al. 2001). Chlorophyll concentrations were low (<0.1 µg l^{-1}), and a pronounced deep chlorophyll maximum was observed at around 70 m. Phytoplankton standing stocks were much lower, approximately one-third of the stocks measured in the northerly study, and were dominated by picoplankton (Tarran et al. 2001), which accounted for up to 71% of the total phytoplankton production (Donald et al. 2001). Daily production rates were also lower, but a considerable proportion (average 69%, SD = 14%) occurred below the surface mixed layer. High values of the depth integrated *f*-ratio were recorded due to the deep euphotic zone depth and light penetration of the nitracline, indicating that nitrate was important for phytoplankton production rather than nutrient regeneration, which is more typical of oligotrophic environments (Donald et al. 2001). Mesozooplankton biomass was lower, in comparison with the temperate waters, and a distinct diel cycle was recorded whereby biomass was 2.2 and 1.4 µg C l^{-1} for night and day periods respectively (Head et al. 1999). Weakening of the thermocline during the study and a transition towards higher salinity water on 14 July suggested that the drogued buoy was drifting through different water masses.

Phytoplankton growth and mortality due to grazing

Table 1 summarises the estimates of phytoplankton growth and grazing coefficients from the dilution experiments conducted during the cruise, together with associated environmental variables. Estimates of phytoplankton growth rates (k) were higher in the northerly waters (average 1.54 d^{-1}, SD = 0.18) com-

pared to the southerly site (average 0.93 d^{-1}, SD = 0.22). However, evidence from the flow cytometry counts taken from undiluted samples suggest that photoadaptation occurred in the experiments conducted during the southerly study, while those conducted during the northerly study did not show any evidence of photoadaptation. During the northerly study, the apparent phytoplankton growth showed little change with time, although the highest growth rate, equivalent to 2.5 doublings d^{-1}, was recorded on 23 June, just prior to a storm. After the storm, growth rates corresponded to slightly more than 2 doublings d^{-1}. The experiment conducted outside the eddy showed that phytoplankton growth rates were similar to those within the eddy. In the southerly waters, growth rates were more variable over the 7 d and decreased from 1.14 to 0.70 d^{-1}. However, the flow cytometric data from the southerly study showed an increase in the chlorophyll content per cell (measured as the mean red fluorescence per cell) for the 3 main picoplankton groups, *Synechococcus* spp. *Prochlorococcus* spp. and the picoeukaryotes, due to photoadaptation. This led to an overestimate of the apparent growth rate of phytoplankton. From the flow cytometric counts we determined the total red fluorescence of the picoplankton and used this as a proxy for the picoplankton chlorophyll (µg l^{-1}), which was assumed to be 71% of our initial chlorophyll biomass (Donald et al. 2001). Using this method, we calculated a correction factor for estimating the chlorophyll biomass at the end of our experiments and hence determine that phytoplankton growth was overestimated by approximately 32% during the southerly study. By taking this into account, we predict that growth rates (k_c) would have ranged from 0.43 to 0.79 d^{-1} (Table 1). Rates of phytoplankton loss due to microzooplankton grazing (g) were also higher during the northerly study (avg. 1.25 d^{-1}, SD = 0.22), and there was no significant difference in grazing rates between the centre of the eddy and the area outside. In the southerly waters, grazing averaged 0.43 d^{-1} (SD = 0.1) and followed the same pattern as estimates of growth, whereby rates decreased with time.

Microzooplankton community structure

The microzooplankton communities in the undiluted experimental water also showed distinct differences between the 2 study sites. The total concentration of microzooplankton (including the heterotrophic nanoflagellates) ranged from 88 000 to 380 000 cells l^{-1}, with the HNAN contributing up to 99% of the total abundance. However in terms of biomass, the small flagellates contributed, on average, up to one-third of the total microzooplankton biomass at the northerly site, whilst in the southerly waters the HNAN accounted for almost half the total biomass. HNAN abundance and biomass are displayed in Fig. 1 and show that during the northerly study their numbers and carbon biomass (5 to 20 µm) were highest on 23 June (361 ml^{-1}, 5.18 µg C l^{-1}), before the storm. Outside the eddy, HNAN abundance was lower (102 ml^{-1}), and was similar to the concentrations (2 to 20 µm) recorded at the southerly site (116 ml^{-1}, SD = 21). HNAN biomass in the southerly waters was also low (µg C l^{-1}, SD = 0.1).

The microzooplankton community (determined from the Lugol-fixed samples) was composed principally of dinoflagellates and oligotrich ciliates, with tintinnids and 'other' ciliates present in lower concentrations. Heterotrophic dinoflagellates dominated the assem-

Table 1. Specific growth (k) and grazing (g) coefficients determined from dilution experiments, and summary of environmental conditions. k_c: the growth coefficient corrected for photoadaptation (±95% confidence intervals); r: correlation coefficient of linear regression between apparent phytoplankton growth rate and dilution factor, (*$p < 0.01$, **$p < 0.001$). Initial chlorophyll *a* (chl *a*) was determined fluorometrically for experimental (<200 µm) water; experimental depth is equivalent to the 33% irradiance level except where noted otherwise; T: *in situ* temperature; ML: surface mixed-layer depth; EZ: euphotic-zone depth; –: no evidence of photoadaptation

Date (1996)	Latitude °N	Longitude °W	Growth, k (d^{-1})	Growth, k_c (d^{-1})	Grazing, g (d^{-1})	r	Initial chl *a* (µg l^{-1})	Experimental depth (m)	T (°C)	ML (m)	EZ (m)
22 Jun	59.201	20.122	1.24 (±0.29)	–	0.89 (±0.32)	0.71*	1.20 (±0.1)	15	10.5	20	32
23 Jun	58.968	20.021	1.70 (±0.16)	–	1.31 (±0.19)	0.92**	1.26 (±0.02)	15	10.9	17	32
25 Jun	59.143	20.733	1.61 (±0.25)	–	1.48 (±0.47)	0.95**	0.94 (±0.04)	15	10.7	16	30
27 Jun	58.988	20.668	1.51 (±0.12)	–	1.25 (±0.18)	0.91**	1.08 (±0.11)	5[a]	10.8	28	32
28 Jun	59.093	19.448	1.62 (±0.32)	–	1.34 (±0.35)	0.87**	0.61 (±0.05)	15	11.4	34	60
11 Jul	37.008	19.001	1.09 (±0.14)	0.79	0.57 (±0.19)	0.93**	0.05 (±0.004)	25	20.3	29	108
13 Jul	36.922	19.212	1.14 (±0.21)	0.73	0.54 (±0.24)	0.77*	0.06 (±0.01)	25	20.2	23	120
15 Jul	36.691	19.225	0.80 (±0.07)	0.52	0.36 (±0.09)	0.89**	0.07 (±0.002)	25	20.4	26	106
17 Jul	36.319	19.150	0.70 (±0.07)	0.43	0.26 (±0.02)	0.71*	0.06 (±0.002)	25	20.8	22	108

[a]Equivalent to 55% surface irradiance in this experiment

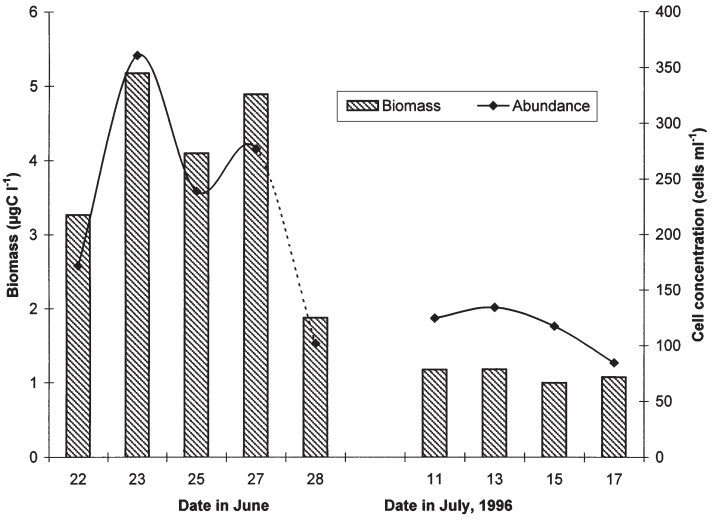

Fig. 1. Average heterotrophic nanoflagellate (HNAN) abundance and biomass concentrations in initial experimental water

blage during the northerly study in terms of abundance and biomass (Fig. 2), whilst oligotrich ciliates were generally more important at the southerly station. Total cell numbers (excluding the HNAN) were similar within the eddy, and averaged 17 330 cells l^{-1}, whilst outside the eddy abundance was lower (12 625 l^{-1}). In the southerly region, abundance of the microzooplankton fraction was lower with an average concentration of 2400 ind. l^{-1}. In terms of their biomass, values recorded within the eddy ranged between 8 and 13 µg C l^{-1}, and followed a similar pattern to the HNAN biomass, with highest values recorded on 23 June. Biomass of the microzooplankton was also lower outside the eddy (5 µg C l^{-1}, SD = 0.5). As observed with the HNAN, low biomass values (1 µg C l^{-1}, SD = 0.4) were associated with the southerly study.

The mean cellular carbon of the microzooplankton, excluding the HNAN (Fig. 3) demonstrates that at the northerly site the dinoflagellates and oligotrichs were of a similar size and suggests that within the eddy the same community was sampled, despite the disruption of the storm. Size differences, inferred by the mean cellular carbon per cell, in the 'other' ciliates and tintinnids may be a reflection of their low abundance and reduced accuracy of the counting method. However, at the southerly site, relatively large dinoflagellates and oligotrichs appear to be replaced by smaller individuals with time, while 'other' ciliates may have increased in size. Despite low tintinnid abundances, those recorded were clearly dominated by larger individuals.

DISCUSSION

This study has illustrated distinct differences in the microzooplankton communities and their herbivorous impact on the phytoplankton stocks associated with the temperate and subtropical regions of the NE Atlantic during the summer. Our findings reflect the contrasting environmental conditions encountered at the northerly and southerly sites.

Conditions during our northerly study indicated that the phytoplankton were in a mid-bloom phase, because of high concentrations of new nutrients and a dominance of coccolithophores (Weeks et al. 1993). It seems likely that Verity et al. (1993) sampled mid- to late-bloom conditions at 47° N during spring 1989, while Burkill et al. (1993) sampled late-bloom conditions at 60° N and post-bloom conditions at 47° N during the summer 1989 (Weeks et al. 1993). The MLML study site was occupied during both the initial phase of the spring bloom (when *Phaeocystis* spp. and small diatoms dominated the phytoplankton) during spring 1991 and the post-bloom phase during summer 1991 (Gifford et al. 1995). Therefore, our northerly study falls within the range of conditions previously described in the temperate NE Atlantic.

The microzooplankton were abundant in the northerly waters and were dominated by HNAN and dinoflagellates; this is in keeping with the community pre-

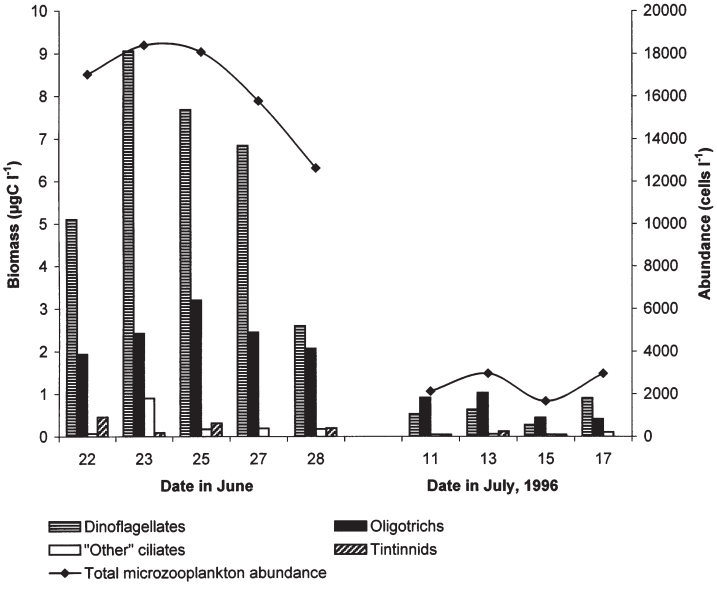

Fig. 2. Mean biomass of 4 main categories of the microzooplankton fraction and total cell concentration, excluding the HNAN, recorded in initial experimental water

Table 2. Comparison of apparent phytoplankton growth (k) and mortality (g) rates and microzooplankton herbivory on daily chlorophyll (Chl) standing stocks measured by dilution technique in this and previous studies. –: not published

Region	Month	Growth k (d^{-1})	Grazing g (d^{-1})	Chl *a* turnover % (d^{-1})	Chl *a* µg l^{-1}	Source
47° N, 18° W	May	0.59–0.97	0.56–0.76	43–53	2.0–4.0	Verity et al. (1993)
60° N, 20° W	Jun	–	0.33	27	0.97	Burkill et al. (1993)
56° N, 20° W	Jun	–	0.60	45	0.44	Burkill et al. (1993)
52° N, 20° W	Jun	0.46–0.5	0.26–0.36	23–30	1.33–1.69	Burkill et al. (1993)
47° N, 20° W	Jul	0.21–0.67	0.36–0.57	29–43	1.27–1.46	Burkill et al. (1993)
60° N, 20° W	Jun	1.24–1.7	0.89–1.48	59–77	0.94–1.26	This study
59° N, 19° W	Jun	1.62	1.34	74	0.61	This study
37° N, 19° W	Jul	0.7–1.14	0.26–0.57	23–43	0.05–0.07	This study
59° N, 21° W	May	0.13–0.87	0.83–1.01	56–64[a]	0.59–2.89	Gifford et al. (1995)
59° N, 21° W	Aug	0.3–0.45	0.11–0.24	10–21	1.19–1.8	Gifford et al. (1995)
Sargasso Sea	Mar–Oct	0.08–0.75	0.28–0.71	25–56[b]	0.04–1.05	Lessard & Murrell (1998)
Gulf of Mexico	May	0.46	0.15	14[c]	0.21	Strom & Strom (1996)

[a]>20 µm chlorophyll
[b]Oligotrophic and nutrient-limiting
[c]Oligotrophic waters

viously recorded in the temperate NE Atlantic during the spring (Verity et al. 1993) and summer (Burkill et al. 1993, Sleigh et al. 1996) periods. However, in contrast to the findings of our study, aloricate ciliates dominated at 60° N during the summer of 1989 (Burkill et al. 1993) and 59° N during the spring and summer periods in 1991 (Gifford et al. 1995). Nevertheless, variations in the fixation methods used could account for the discrepancy between these data through the potential losses of ciliates (Stoecker et al. 1994a). In the southerly waters, microzooplankton abundance was on average 85% lower than in northerly waters, and HNAN and oligotrich ciliates were the major herbivores. This is typical of oligotrophic communities (Strom & Strom 1996, Stelfox et al. 1999), as the dominant picoplankton groups may be too small for efficient grazing by some dinoflagellates. This shift in the microzooplankton community structure appeared to be clearly associated with a shift in the phytoplankton community from nanoflagellates and a bloom of coccolithophores in the northerly waters to a dominance of picoplankton in the southerly waters.

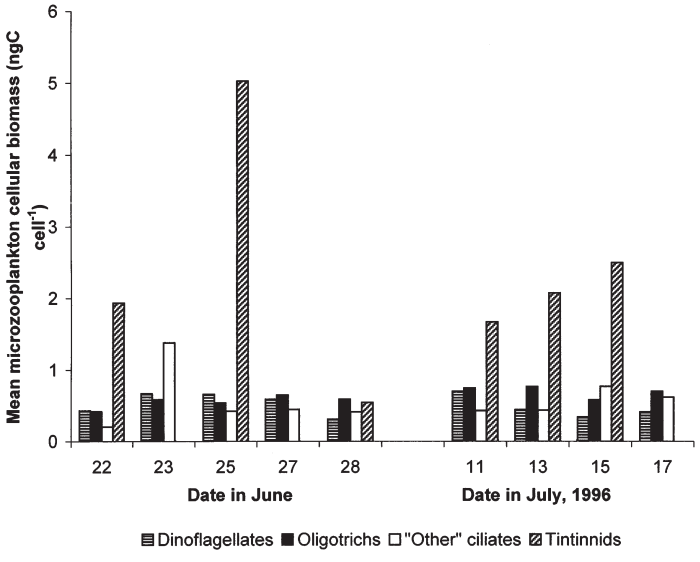

Fig. 3. Size composition of 4 main categories of the microzooplankton fraction, excluding the HNAN, expressed as carbon biomass per individual grazer, recorded in initial replicate experimental water samples

Growth rates of phytoplankton, estimated from our experiments, were generally higher than those previously recorded for the NE Atlantic and other sub-tropical regions (Table 2). Estimates of the apparent growth of phytoplankton in the northerly waters (>1 d^{-1}) were almost double those recorded at 47° N during the 1989 spring bloom (Verity et al. 1993) and at 59° N in 1991 (Gifford et al. 1995). We attribute this to the fast growth response of *Coccolithus pelagicus*, which were smaller in cell size than previously found in other populations and suggests that they were rapidly dividing (D. Harbour pers. comm.). At the southerly station, our phytoplankton growth estimates appeared at first sight to be considerably higher than growth rates recorded in oligotrophic conditions in the Sargasso Sea (Lessard & Murrell 1998) and the Gulf of Mexico (Strom & Strom 1996). In fact, our lowest growth rates seemed similar to the highest rates recorded in the Sargasso Sea (Lessard & Murrell 1998). However, since our

initial growth rates were overestimated by approximately 32% due to photoadaptation (Perry et al. 1981), the corrected values (Table 1) were in fact similar to rates previously recorded in the oligotrophic Sargasso Sea (Lessard & Murrell 1998) and Gulf of Mexico (Strom & Strom 1996).

Our estimates of microzooplankton specific grazing rates during the northerly study, inferred by *g*, were also higher than those in comparable studies. Our lowest estimates exceeded the highest grazing rates reported between 47 and 60° N during spring and summer 1989 (Burkill et al. 1993, Verity et al. 1993) and were similar to the highest rates recorded in 1991 by Gifford et al. (1995). It is possible that grazing rates may have been overestimated if the microzooplankton were rapidly dividing in response to the high concentration and growth rates of coccolithophores and nanoflagellates. In this situation, microzooplankton population densities would increase at a faster rate in the undiluted samples, where phytoplankton concentration was higher (Landry et al. 1995). We did not quantify the microzooplankton community structure in each dilution sample, nor at the end of each experiment, and therefore cannot comment on changes in predator densities and how these may have affected our grazing rates. However, it may be difficult to determine small changes in predator concentrations because of the error of the counting method (Gifford 1988). For example, the average coefficient of variation for cell counts on initial undiluted water samples from this study are 15% for all microzooplankton, 24% for heterotrophic dinoflagellates and 16% for oligotrich ciliates. Verity et al. (1993) measured changes in the relative densities of the microzooplankton during 24 h incubations at 47° N during May 1989 and reported that growth rates of ciliates and dinoflagellates were highly variable (e.g. dinoflagellates −0.2 to +0.3, ciliates −1.7 to +0.4 d^{-1}). They concluded that growth of ciliates and dinoflagellates were coupled with mortality of HNAN, suggesting that changes in the relative densities of microzooplankton were complicated by trophic interactions between microbial predators. Whilst nutrient limitation in our experimental incubations may have led to an overestimation of grazing and underestimation of growth (Gifford 1988), there was no evidence of negative growth in the undiluted treatments. Since grazing did not exceed growth in any of our experiments it seems unlikely that nutrient limitation occurred.

The vigorous grazing activity of the microzooplankton, measured during our northerly study, accounted for a turnover of 71% d^{-1} (SD = 7%) of the chlorophyll standing stock (Table 3). This represented a flux of between 18 and 37 µg C l^{-1} d^{-1} which, when compared to the daily rates of primary production (24.3 to 50.5 µg C l^{-1} d^{-1}; Rees et al. 2001), indicated that microzooplankton grazed between 65 and 167% of the daily phytoplankton production.

During the southerly study, microzooplankton specific grazing rates were similar to estimates from the oligotrophic Sargasso Sea (Lessard & Murrell 1998), but slightly higher than values recorded in the Gulf of Mexico (Strom & Strom 1996). Grazing steadily decreased over the 7 d period, which coincided with an increase in *Prochlorococcus* spp. abundance (Tarran et al. 2001). Whilst it is likely that the HNAN are the most important grazers of picoplankton in this and other regions, a recent study by Christaki et al. (1999) suggested that *Prochlorococcus* spp. are less actively grazed by ciliates than *Synechococcus* spp. A significant linear relationship ($p < 0.05$) showed that as the prochlorophyte population increased, the proportion of apparent phytoplankton growth lost to microzooplankton grazing decreased (Fig. 4) and may explain the observed decrease in grazing activity during the southerly study.

Table 3. Estimates of chlorophyll turnover (P_i), carbon flux through ingestion rates (*IR*) and proportion of daily primary production consumed by the microzooplankton (P_c). ΔPC: daily photosynthetic rate from ^{14}C productivity measurements (Donald et al. 2001, Rees et al. 2001). IR calculated assuming C:chlorophyll *a* of 40 at 60° N and 180 at 37° N (chlorophyll *a* from Table 1)

Date (1996)	Latitude °N	Longitude °W	P_i (% d^{-1})	*IR* (µg C l^{-1} d^{-1})	$P_c = \frac{IR}{\Delta PC}$ (% d^{-1})
22 Jun	59.201	20.122	59	28.4	
23 Jun	58.968	20.021	73	36.9	167
24 Jun	59.143	20.733	77	28.9	79
27 Jun	58.988	20.668	71	30.9	80
28 Jun	59.093	19.448	74	18.0	65
11 Jul	37.008	19.001	44	3.8	143
13 Jul	36.922	19.212	42	4.3	228
15 Jul	36.691	19.225	30	3.9	101
17 Jul	36.319	19.150	23	2.6	35

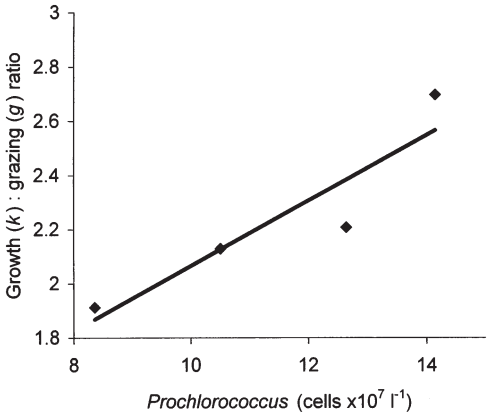

Fig. 4. Relationship between *Prochlorococcus* spp. cell concentration and the proportion of daily phytoplankton growth lost to grazing (*k*:*g*). Equation of the regression line is $y = 0.1209x + 0.8565$, $r^2 = 0.85$, n = 4

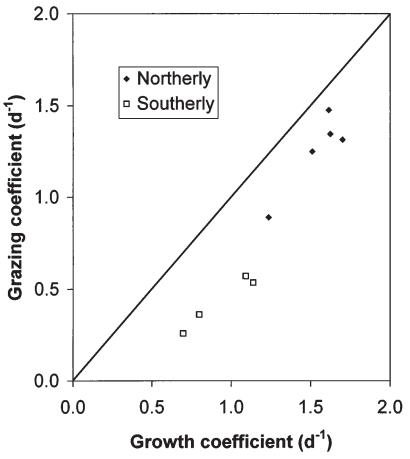

Fig. 5. Ratio between daily apparent phytoplankton growth and mortality (as grazing coefficient) rates, measured at northerly and southerly sites

Grazing in the southerly waters accounted for 35% d^{-1} (SD = 9%) of the phytoplankton stocks and a flux of 3 to 4 µg C l^{-1} d^{-1}. Comparison of the grazing rates with parallel measurements of ^{14}C primary production (1.9 to 7.4 µg C l^{-1} d^{-1}, Donald et al. 2001) suggests that microzooplankton grazing exceeded phytoplankton production (>200%) in the southerly waters, in contrast to the estimates of phytoplankton growth and mortality from the dilution experiments. Estimates of this kind are strongly influenced by carbon to chlorophyll *a* ratios. We used a factor of 40 for the experiments conducted in the northerly study (Verity et al. 1993) and 180 for the southerly study (Buck et al. 1996). However, a C:chlorophyll *a* value of 180 may not be representative of our southerly site. C:chlorophyll *a* ratios are sensitive to depth and latitude, and considering that the experiments were sampled from the 33% surface irradiance level, we quantified phytoplankton growth in water at or below the surface mixed layer. Applying a lower C:chlorophyll *a* conversion value of 100 suggests that on average 70% (range between 19 and 128%) of the daily primary production was grazed by the microzooplankton, which is in better agreement with our estimates of lower trophic coupling between growth and grazing in the southerly than northerly waters estimated from the dilution experiments.

Fig. 5 demonstrates the uncoupling between production and consumption during this study and shows that a higher ratio, attributed to excess growth, was observed in the southerly region. In the northerly study, microzooplankton grazing (*g*) accounted for between 71 and 91% of the apparent phytoplankton growth estimates (*k*), but this decreased with decreasing latitude, suggesting that in the southerly waters the microzooplankton were less efficient at controlling phytoplankton growth (average 46%, SD = 6%). Despite corrections for photoadaptation in the southerly waters, grazing efficiency remained low and accounted for <73% of the daily phytoplankton growth rates (k_c). This is surprising, as one might expect tighter trophic coupling between microzooplankton and the small phytoplankton forms typical of oligotrophic conditions. Several other studies from oligotrophic areas (Landry et al. 1997, Latasa et al. 1997) have demonstrated a balance between phytoplankton growth and loss through grazing. Excess growth often occurs in areas dominated by larger phytoplankton, especially diatoms, which have particularly high growth rates (Strom & Welschmeyer 1991, Latasa et al. 1997). However, Ferrier & Rassoulzadegan (1991) reported that protozoan grazing may actually enhance *in situ* picoplankton specific-growth rates by more than a factor of 2 through the regeneration of nutrients.

We compared our estimates of net phytoplankton growth (μ, as doublings d^{-1}) with estimates of phytoplankton growth derived from parallel ^{14}C primary-production incubations (Donald et al. 2001, Rees et al. 2001) (as described by Harrison et al. 1982), and the results are presented in Table 4. The data show that in the northerly waters, net phytoplankton growth from the dilution experiments is similar but slightly lower than that estimated from primary production. This is not surprising, as the measurements of ^{14}C-derived phytoplankton production fall between the gross and net production (Donald et al. 2001). In contrast, our initial estimates of net phytoplankton growth (*k*-*g*), at the southerly site, were considerably higher than those estimated using the primary-productivity method. However, corrections for photoadaptation showed that in fact net phytoplankton growth rates (k_c-*g*) at the

Table 4. Comparison of net phytoplankton growth rates (μ doublings d^{-1}) from dilution experiments and ^{14}C productivity measurements (data from Donald et al. 2001, Rees et al. 2001). (k-g and k_c-g data from Table 1). PC: phytoplankton carbon; ΔPC: daily photosynthetic rate. PC calculated assuming C:chlorophyll *a* of 40 at 60° N and 180 and 37° N (chlorophyll *a* data from Table 1). –: no evidence of photoadaptation, therefore not determined

Date	Latitude	Longitude	$\mu = \frac{(k-g)}{\ln 2}$	$\mu = \frac{(k_c-g)}{\ln 2}$	$\mu = \log_2\left(\frac{PC+\Delta PC}{PC}\right)$
(1996)	°N	°W	(doublings d^{-1})	(doublings d^{-1})	(doublings d^{-1})
22 Jun	59.201	20.122	0.50	–	0.54
23 Jun	58.968	20.021	0.56	–	0.43
24 Jun	59.143	20.733	0.20	–	0.60
27 Jun	58.988	20.668	0.38	–	0.57
28 Jun	59.093	19.448	0.40	–	0.64
11 Jul	37.008	19.001	0.75	0.31	0.39
13 Jul	36.922	19.212	0.87	0.29	0.36
15 Jul	36.691	19.225	0.63	0.23	0.39
17 Jul	36.319	19.150	0.63	0.25	0.50

southerly study were comparable with the estimates of ^{14}C-derived phytoplankton growth rates from the parallel primary-production experiments.

The vigorous grazing activity of the microzooplankton during this study suggests strong coupling between phytoplankton production and consumption, particularly at the northerly study. This would indicate that the grazing activity of mesozooplankton on phytoplankton production would, in comparison, be minimal. Head et al. (1999) demonstrated that mesozooplankton herbivory accounted for only 2% of the daily phytoplankton stocks at the northerly site and 6% at the southerly site. This reflects the tighter trophic coupling in northerly waters compared to the southerly waters, where uncoupling between phytoplankton growth and microzooplankton grazing was emphasised by higher mesozooplankton grazing of the phytoplankton stock. The low grazing impact of the mesozooplankton, particularly in the northern waters, suggests that phytoplankton consumption alone would not meet the nutritional requirements of the larger grazers for growth or egg production (Head et al. 1999, Irigoien et al. 2000). Therefore, while the mesozooplankton will consume a small proportion of the phytoplankton stocks and hence contribute to export flux from the euphotic zone, they will also graze on the microzooplankton and detritus and thus export organic material via a multiple-step process. These findings are similar to those reported for the temperate northeast Atlantic during spring (Gifford et al. 1995) and summer (Morales et al. 1991, Burkill et al. 1993).

We therefore conclude that microzooplankton were important grazers of phytoplankton in the northern, temperate waters of the NE Atlantic during the summer, which suggests strong coupling between production and consumption. Our findings support those previously reported for this region (Burkill et al. 1993, Verity et al. 1993, Weeks et al. 1993, Gifford et al. 1995). During the southerly study, we observed high phytoplankton growth rates which were not matched by phytoplankton mortality, suggesting that microzooplankton were not controlling phytoplankton production. However, because of lower incubation light levels, photoadaptation, caused an overestimation of apparent phytoplankton growth rates in our experiments. Despite making corrections for this our data still suggest trophic uncoupling between microzooplankton and phytoplankton at or below the surface mixed layer during our southerly study. This coincided with an increase in *Prochlorococcus* spp. abundance, and infers that microzooplankton were not capable of controlling the production of prochlorophytes in the oligotrophic sub-tropical NE Atlantic during the summer.

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