ELSEVIER

In Collaboration with
the Netherlands Institute for Sea Research

Journal of Sea Research 50 (2003) 1–9

JOURNAL OF SEA RESEARCH

www.elsevier.com/locate/seares

Grazing loss-rates in pico- and nanoplankton in the Faroe-Shetland Channel and their different relations with prey density

Bouwe Kuipers*, Harry Witte, Govert van Noort, Santiago Gonzalez

Department of Biological Oceanography, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg (Texel), The Netherlands

Received 6 June 2002; accepted 27 January 2003

Abstract

In a number of dilution experiments performed in different surface water masses of the Faroe-Shetland Channel loss-rates due to grazing were determined for heterotrophic bacteria and three size categories of small phytoplankton between 1 and 10 μm. The prey abundance and loss-rates varied considerably among stations; grazing on picoplankton was strongly correlated with prey abundance while no correlation between grazing and abundance was detectable for the larger prey. Grazing control, assumed to be exerted by unicellular grazers in general, seems thus to be restricted to the smaller microbial components of the food web. The absence of density-dependent grazing of nanophytoplankton (2–5 μm) and larger algae suggests that the microzooplankton, dominated by ciliates, are not as tightly linked to their prey populations as heterotrophic nanoflagellates.

Keywords: Microbial food web; Grazing control; Picoplankton; Nanophytoplankton

1. Introduction

During the two last decades there has been a change in the traditional view that pico- and nanophytoplankton dominate in the central oceans because they are typically adapted to oligotrophic conditions, whereas larger phytoplankton (especially diatoms) are more successful in shelf seas and coastal waters under conditions of lower light, higher turbulence and higher and more fluctuating nutrient levels. As argued in Riegman et al. (1993), Armstrong (1994) and Riegman and Kuipers (1994), physiological diversity cannot explain the observed differences in the dominating phytoplankton groups without the involvement of other control mechanisms, because cells with the highest affinities for nutrients and the highest maximum growth rates - basically the picoplankton - would dominate throughout the world's oceans and coastal seas. Size differential grazing control of the plankton has been suggested by Riegman et al. (1993) as the most likely mechanism preventing the domination of pico- and nanoplankton in coastal waters. At present, all pelagic ecosystem models include, apart from the relatively slow phytoplankton, zooplankton and nekton, a 'microbial loop module' where the heterotrophic bacteria, picophytoplankton and protist grazers are always functioning and recycling nutrients at high rates typical of such small organisms (Thingstad, 1992; Baretta et al., 1995; Baretta-Bekker et al., 1995). Although the size differential grazing concept

* Corresponding author.
E-mail address: bouwe@nioz.nl (B. Kuipers).

1385-1101/03/$ - see front matter © 2003 Elsevier B.V. All rights reserved.
doi:10.1016/S1385-1101(03)00043-1

has been widely accepted (Franks, 2001), the underlying evidence is observations of size-differential responses in the plankton to input of the limiting nutrients or light (Chisholm, 1992; Riegman et al., 1993; Kiørboe, 1993; Coale et al., 1996) and model simulations (Armstrong, 1994; Riegman and Kuipers, 1994) rather than measurements of grazing itself. Only Riegman et al. (1993) demonstrated that by daily dilution of incubated coastal water, collected during the exponential phase of the phytoplankton spring bloom, the grazing pressure on the smaller algae could be released with the result that in a few days the pico- and nanophytoplankton became dominant instead of the diatoms. The present paper presents a set of size differential grazing experiments in different surface water masses in the Faroe-Shetland Channel and compares loss-rates due to grazing with the abundance of different plankton size categories in order to identify the cell-size above which prey populations are no longer controlled by grazing.

2. Materials and methods

Three transects across the Faroe-Shetland Channel (Fig. 1) were sampled from RV 'Pelagia' in June 1999. Sampling stations were situated in the slope current of relatively warm North Atlantic water flowing to the north along the Shetlands (NAW), in the transition area in the centre of the channel ('Ecotone'), and in the Modified North Atlantic Water to the Faroe-side where Atlantic surface water from the north of the Faroes mixes into the channel (MNAW). Detailed information on the hydrography can be found in Hansen et al.

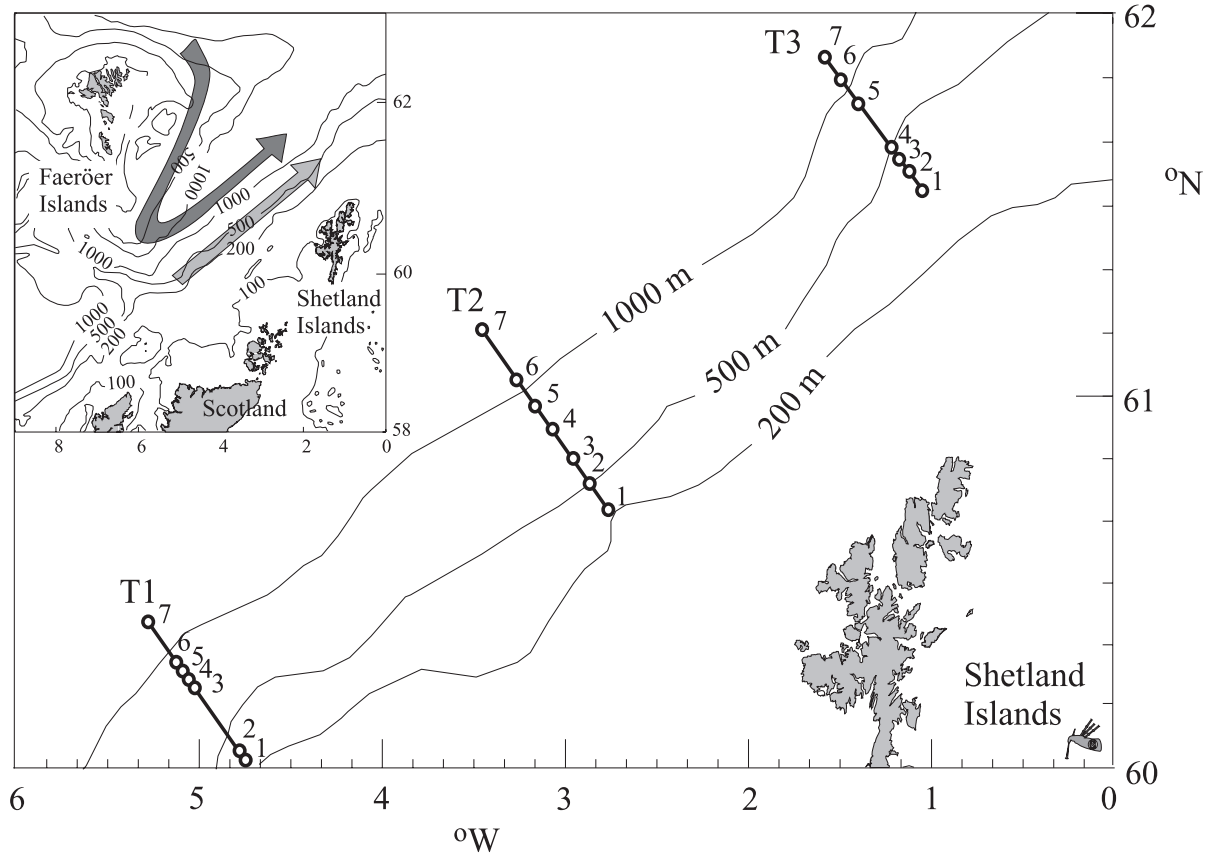

Fig. 1. Map of the Faroe-Shetland Channel research area with transects and stations.

(1999) and Sherwin et al. (1999), and on the nutrient- and phytoplankton distributions in Riegman and Kraay (2001). Water samples were collected at 7 stations on each transect with a CTD-Rosette sampler (Seabird) with 22 NOEX (Technicap-CAP D'AIL, France) 10-l bottles and equipped with sensors for oxygen, PAR and fluorescence (Chelsea). Samples were taken at different depths in the euphotic zone and the deeper water layers for various measurements and analyses for other parts of the program (Riegman and Kraay, 2001). From all depths, 5-ml samples were preserved with glutaraldehyde (2% final concentration), stained with Acridine Orange and filtered onto black 0.22-μm Poretics polycarbonate filters (25 mm diameter) for the enumeration of heterotrophic bacteria by epifluorescence microscopy. Samples of 30 ml were preserved and filtered likewise, but stained with DAPI for the enumeration of heterotrophic nanoflagellates (HNF). All filters were mounted on slides embedded in immersion-oil and stored frozen at −20 °C. For the enumeration of bacteria a minimum of 10 fields of 40 × 40 μm, or at least 200 cells per sample were counted with an epifluorescence microscope (Zeiss Axioplan) at 1250× magnification (Hobbie et al., 1977). For the HNF 75 of 100 × 100 μm fields were always counted.

Series of dilutions according to Landry and Hassett (1982) were prepared to measure the loss rates in different plankton size categories using water from 15 m depth, i.e. in the middle of the 20–30 m deep mixed surface layer as indicated by the CTD-profiles. Three 24-h grazing experiments were performed in each of the water types (NAW, 'Ecotone' and MNAW). The grazing measurements started in the morning with the collection of 10 l of water from 15-m depth. Five litres were filtered through a Gelman MicroCulture Capsule (0.2-μm) to produce particle-free water for the series of dilutions. Polycarbonate incubation bottles of 300 ml were filled with the appropriate volumes of 0.2-μm filtered water and unfiltered water was added to obtain dilutions of 100, 70, 40, 20 and 10% of raw seawater (all dilutions in triplicate). Samples of 5 ml were taken from the 15 dilution bottles for flow cytometry (Coulter XL-MCL) at the start of the incubation (T_0) and finally the bottles were attached to a slowly rotating incubation wheel (1 rpm) and sampled again after 24 h (T_{24}). The incubation temperature was adjusted to the water temperature at 15-m depth given by the CTD (between 10 and 12 °C). The PAR-meter registered light intensities from 10–100 μE m^{-2} s^{-1} at 15-m depth and therefore the incubation light regime (daylight TL-tubes) was adjusted to 50 μE m^{-2} s^{-1} on average

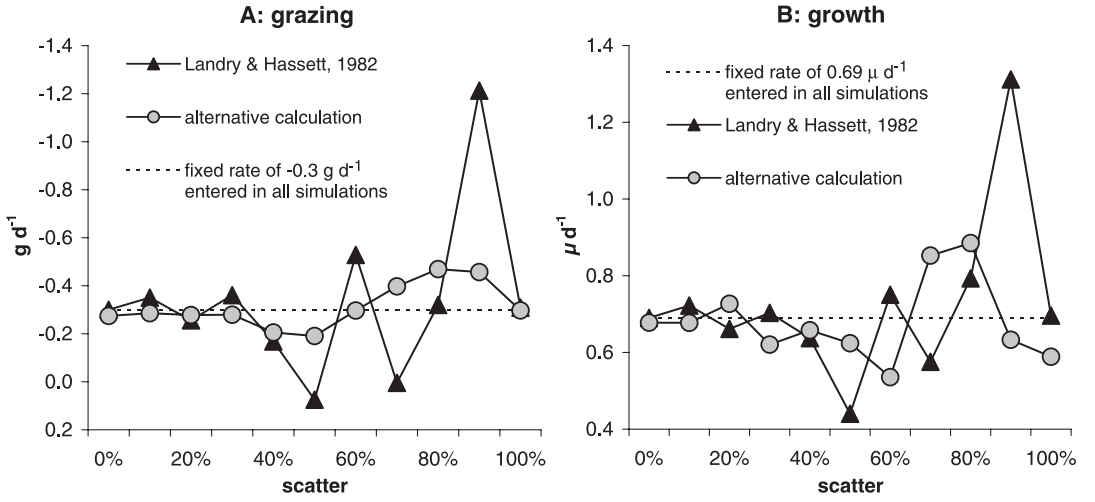

Fig. 2. Results of a simulated grazing experiment (series of dilutions: 100, 70, 40, 20 and 10% where N_0(100%) is set at 1000, μ d^{-1} at 0.69 and g d^{-1} at −0.3), in which g (A) and μ (B) were calculated according to Landry and Hassett (1982) and in the alternative way as described in Materials and Methods. The rates were calculated for simulated sets of N_0 and N_{24} which were given stepwise increasing random scatter (N plus or minus random figures from 10% to maximally 100% of N). Especially the alternatively calculated grazing rate (plot A) reflected the given g of −0.3 much closer, even at unrealistically high 'counting errors', than grazing rate calculated according to Landry and Hassett (1982).

form front to back of the wheel from 08:00 to 20:00 h. For measurements of the loss-rates due to grazing in heterotrophic bacteria, separate dilution experiments (in triplicate) were prepared with seawater, to which approx. 4×10^4 ml^{-1} of fluorescently labelled bacteria (FLB) were added before the dilution procedure began. These FLB-incubations were treated identically to the other incubations and sampled at T_0 and T_{24} and the numbers of FLB were counted with the flow cytometer. The FLB were prepared according to Sherr and Sherr (1993) prior to the cruise from a 0.6-μm filtered natural bacterial community of Atlantic Surface Water collected west of Ireland and stored frozen in ampoules at −20 °C until use. As a check for a possible loss of fluorescence, FLB (10^5 ml^{-1}) were repeatedly incubated in 0.2 μm filtered seawater on an incubation wheel at room temperature for 24 h. Counting by epifluorescence microscopy at T_0 and T_{24} did not show any significant loss in the number of FLB in the 0.2 μm filtered seawater.

Phytoplankton loss-rates due to grazing were measured on 3 different size-clusters as determined by flow cytometry. These clusters were autotrophic cells in the size categories 1–2 μm (low fluorescence per cell and an abundance of $5–25 \times 10^3$ ml^{-1}), 2–5 μm (intermediate fluorescence, abundance of $3–35 \times 10^3$ ml^{-1}) and, 5–10 μm (highly fluorescent, abundance of $1–10 \times 10^3$ ml^{-1}). The phytoplankton composition in the Faroe-Shetland Channel was studied in detail by Riegman and Kraay (2001), who carried out pigment analysis by Chemtax-HPLC at all sampling stations and 6 depths. According to these authors, *Prymnesiophyceae* and *Prasinophyceae* were ubiquitously present in the area and accounted for up

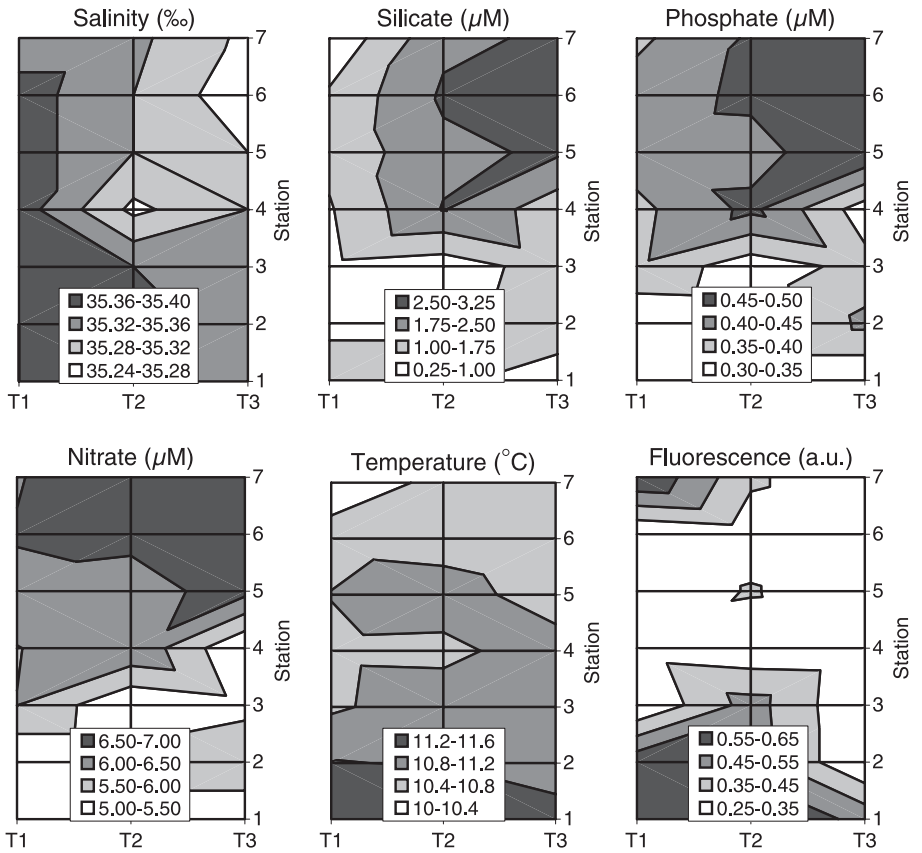

Fig. 3. Distribution pattern of the major nutrients, temperature, salinity and fluorescence based on measurements at 15 m depth at all sampling stations in the Faroe-Shetland Channel (3 transects of 7 stations). Actual positions of the stations are given in Fig. 1; all data in Table 1.

to 50% and 10% of the total Chl-a, respectively. Diatoms, *Cryptophyceae* and *Chrysophyceae* accounted for about 10% of total Chl-a each, but their abundance was variable. Finally, *Cyanophyceae* (<5% of total Chl-a), *Chlorophyceae* (<2%) and *Dinophyceae* (<2%) were, in terms of biomass, less important and were not always present. A comparison between the contribution of different size categories of algae to the total Chl-a determined by the HPLC analysis and the flow cytometer counts indicated that the cluster of 1–2 μm consisted mainly of *Prasinophyceae* and cyanobacteria, the cluster of 2–5 μm of *Prasinophyceae*, *Chrysophyceae* and *Cryptophyceae*, and the cluster of 5–10 μm entirely of *Prymnesiophyceae* (nanophytoplankton such as *Emiliania* and *Chrysochromulina*).

The calculation of the grazing loss-rates in the three phytoplankton size categories and the bacteria was done slightly differently from Landry and Hassett (1982). In the original concept, loss rates are calculated from the apparent growth rates μ_{app} d^{-1} ($= \ln(N_t / N_0)/t \times 24$, with t in hours) in each of the 15 incubation bottles. When flow cytometry is applied to estimate N_0 and N_t for any selected size cluster of natural phytoplankton, a much larger error than in the counting of a monoculture is unavoidable. In the apparent growth rates both errors accumulate, and the μ_{app} in triplicate bottles of the same dilution, incubated under identical conditions, often show a considerable variance. In contrast, the linear regression of N_0 on dilution used in the present experiments as a standard check on the accuracy of the dilution procedure always gave extremely good linear fits (in most cases $R^2 > 0.95$). Because N_t has principally a non-linear relation with dilution, the robustness of the N_t estimates was always checked by fitting power functions, which were significant in all cases with most $R^2 > 0.7$. Therefore, it was decided to use these functions to calculate average μ_{app}-values for the different dilutions, and to use these average μ_{app} in the Landry and Hassett plots providing μ d^{-1} and g d^{-1}, instead of the individual apparent growth rates. As a check, N_0 and N_t of simulated dilution series with a fixed μ of 0.69 d^{-1} and g of -0.3 d^{-1} were given a stepwise increasing random error, after which μ and g were estimated according to Landry and Hassett (1982), and according to the suggested alternative method which basically removes the counting variance in N_0 and N_t by averaging before

Table 1
Nutrient concentrations, temperature, fluorescence (arbitrary units) and salinity at all stations

Trans/Stat	PO4(μM)	NH4(μM)	NO2(μM)	NO3(μM)	SiO4(μM)	Nx/P	Temp (°C)	Fluoresc.	Salinity
T1St7	0.389	0.236	0.185	6.468	0.359	17.690	9.990	0.840	35.330
T1St6	0.423	0.237	0.127	6.527	1.112	16.296	10.680	0.090	35.380
T1St5	0.426	0.248	0.119	6.407	1.192	15.898	10.810	0.090	35.380
T1St4	0.387	0.316	0.138	5.978	0.934	16.633	10.720	0.300	35.380
T1St3	0.393	0.366	0.126	6.007	0.802	16.548	10.740	0.200	35.370
T1St2	0.303	0.165	0.115	4.501	0.705	15.796	11.210	0.620	35.400
T1St1	0.315	0.190	0.099	5.136	1.690	17.234	11.230	0.550	35.400
T2St7	0.457	0.191	0.139	6.896	2.338	15.823	10.560	0.370	35.330
T2St6	0.461	0.259	0.090	6.587	2.604	15.042	10.610	0.290	35.320
T2St5	0.430	0.298	0.119	6.357	2.337	15.763	10.950	0.360	35.320
T2St4	0.462	0.296	0.108	6.428	2.534	14.782	10.640	0.270	35.270
T2St3	0.319	0.188	0.124	5.043	0.579	16.771	11.020	0.490	35.360
T2St2	0.309	0.275	0.082	4.951	0.700	17.205	11.180	0.500	35.370
T2St1	0.259	0.335	0.103	3.792	1.103	16.354	11.520	0.720	35.380
T3St7	0.476	0.413	0.117	6.667	2.620	15.128	10.620	0.130	35.270
T3St6	0.479	0.462	0.104	6.534	2.408	14.833	10.440	0.080	35.250
T3St5	0.496	0.561	0.089	6.653	2.609	14.731	10.580	0.220	35.280
T3St4	0.323	0.447	0.091	4.870	1.287	16.721	11.000	0.260	35.320
T3St3	0.368	0.556	0.108	5.315	1.363	16.268	11.110	0.150	35.340
T3St2	0.413	0.815	0.123	5.998	1.331	16.806	10.940	0.170	35.340
T3St1	0.260	0.424	0.064	3.649	0.718	15.904	11.410	0.520	35.340

The data refer to measurements at 15 m depth. The grazing study was restricted to stations 2, 4 and 7.

μ and g are calculated from the linear regression of their (logarithmic) ratio on dilution. As shown in Fig. 2, μ and g calculated according to the alternative method agreed closely with the entered μ and g (of 0.69 d^{-1} and -0.3 d^{-1}, respectively), even at degrees of scattering in N_0 and N_t where the Landry and Hassett method of calculation gave erratic results. Hence, we decided to calculate all estimates of μ and g for phytoplankton and FLB from the relations of N_0 and N_t with dilution instead of from the individual bottles.

3. Results

Fig. 3 gives distribution patterns of temperature, salinity, fluorescence and the major nutrients over the research area at 15-m depth (for the actual data on the nine incubation stations see Table 1). The patterns of Fig. 3, though based on a limited number of CTD-stations and therefore very general, reflect the different surface water masses and their movements in the Faroe-Shetland Channel as given in Hansen et al. (1999) and Sherwin et al. (1999). Warmer and more saline North Atlantic Water (NAW) with lower nutrient concentrations flows along the Scottish and West Shetland Continental Slope to the north. On the Faroe side of the Channel there is a northern inflow of less saline water with higher nutrient concentrations, the Modified North Atlantic Water (MNAW). The MNAW is colder than the NAW (which is a shorter branch of the 'Warm Gulf Current'), but, as shown in Fig. 3, the temperature differences are less pronounced than the differences in salinity and inorganic nutrients. The transition area between NAW and MNAW in the central part of the Channel, represented by the 'Ecotone' stations, is recognisable as the zone with the steepest gradients in the nutrient concentrations (Fig. 3).

Fig. 4 gives the results of the grazing experiments at the stations 2 (NAW), 4 ('Ecotone') and 7 (MNAW) of each transect (T1,T2 and T3) together with the prey abundance. The latter were determined for the autotrophic prey categories as the average n ml^{-1} (by flow cytometry) in the three undiluted incubation bottles at the start of the experiments and, for the bacteria as the total bacterial counts at 15-m depth at the stations. Fig. 4 suggests that there

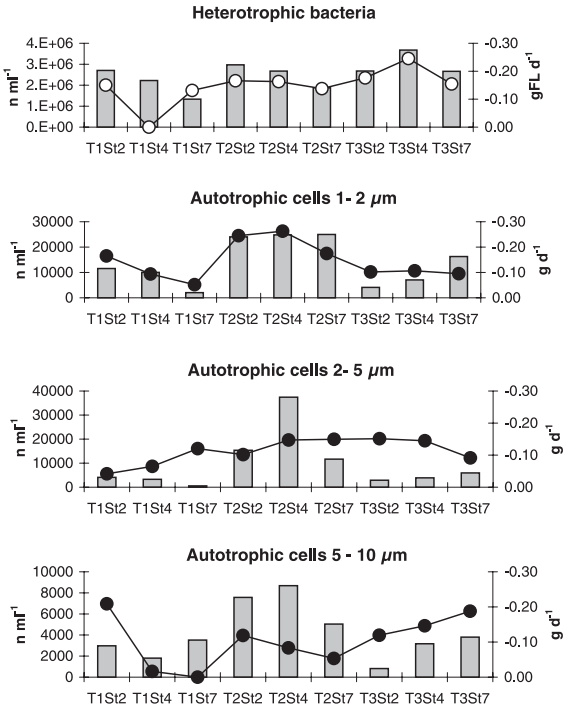

Fig. 4. Results of the grazing dilution experiments at the different stations (open circles represent FLB grazing rates, solid circles grazing rates for the algae) for the different prey-size categories indicated, together with the abundances (n ml^{-1}) of the respective prey in the natural water (shaded bars).

is a positive relation between loss-rates due to grazing and prey abundance in the picoplankton whereas there is no such relation for the larger algae. Regressions (least squares) of the grazing loss-rates on prey abundance for the four different prey categories confirm this: exponential correlations for bacteria and picophytoplankton were highly significant. In contrast, no correlations were found for the algal size groups 2–5 μ and 5–10 μ (Fig. 5).

Although the results for the picoplankton may suggest that the loss-rates due to grazing depend on prey abundance alone, the number of grazers and their grazing activity are the decisive factors. The observed differences between grazing on picoplankton and grazing on the rest of the phytoplankton community can only be explained if in contrast to the rest, the number and the feeding-activity of consumers of picoplankton follow the changes in the abundance of their prey closely. This basic assumption of the size differential grazing control concept could

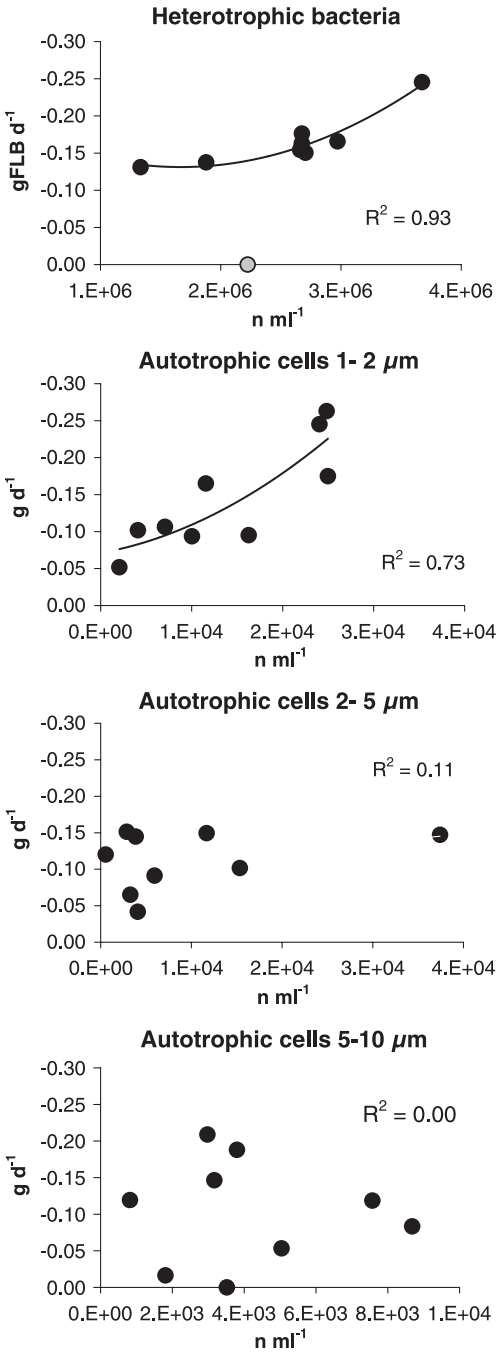

Fig. 5. Dependence of grazing rates on prey abundance measured at all stations for the indicated prey categories, with fitted relations (least squares) and correlation coefficients R^2.

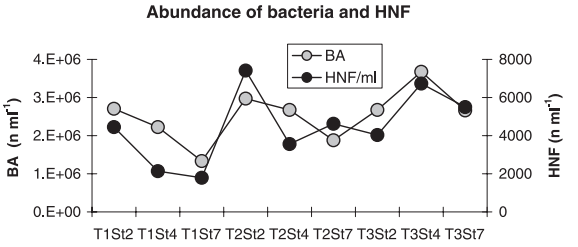

Fig. 6. Fluctuation in abundance of heterotrophic bacteria and heterotrophic nanoflagellates (HNF) at 15 m depth as counted by epifluorescence microscopy for the different sampling stations.

only be checked for the heterotrophic nanoflagellates (HNF), which are the prime grazers of the bacteria. Fig. 6 gives the abundance of HNF and heterotrophic bacteria at all incubation stations at 15-m depth and indicates that the abundance of both, bacteria and HNF, covaried indeed. Since it is impossible to determine in microzooplankton samples the number of grazers feeding on a given size category of phytoplankton, we can only assume that the actual grazers of the smallest autotrophic cells show a numerical response similar to the HNF. A plot of the correlation coefficients (R^2) of the relations between prey abundance and loss-rate due to grazing for the four different prey categories on the average prey size (Fig. 7) indicates that in summer grazing control was most likely restricted to only the picoplankton (cells smaller than 2-µm).

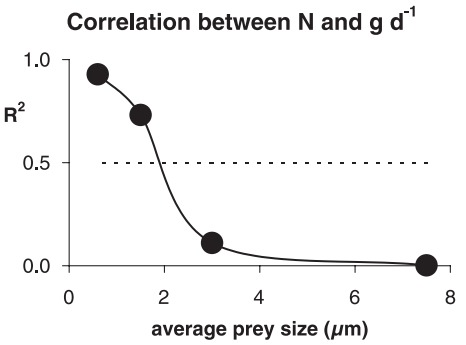

Fig. 7. Relation between the correlation coefficient R^2 from the grazing rate/abundance plots shown in Fig. 5 and the average size of the respective prey categories indicating that grazing control is basically restricted to the picoplankton (95% significance level of R^2 at n = 9 is 4.99, indicated by the stippled line).

4. Discussion

According to the present observations there is a close relation between loss-rate due to grazing and abundance of the prey only for heterotrophic bacteria and picoautotrophs (*Prasinophyceae* and cyanobacteria). The conclusion that such a relationship points to a tight grazing control seems in contradiction with the large variation in the observed prey abundance, which ranges from 1.5 to 4.0 $\times$ 10^6 cells ml^{-1} for the bacteria and from 2000 to 25 000 cells ml^{-1} for the picoalgae. The observations, however, refer to different stations in the Faroe-Shetland Channel, where abiotic conditions vary considerably (Fig. 3 and Table 1). Most striking in this respect are the differences in phytoplankton abundance (all sizes) between Transect 1 and Transect 2 where the algae were most abundant. Riegman and Kraay (2001) measured overall primary production on this cruise and suggested that in the colder and nutrient-rich water flowing into the Faroe-Shetland Channel from the north (see Fig. 3) a phytoplankton bloom developed gradually. The salinity-plot in Fig. 3 shows that at the time of sampling Transect 1 was in a different water mass, not influenced by this northern inflow. The fluorescence plot in Fig. 3 does not indicate such a bloom in the MNAW. However, a comparison with the silicate plot (Fig. 3) strongly suggests that, because the higher fluorescence signal from the CTD fluorometer coincided with low silicate concentrations, this fluorescence signal is dominated by relatively large diatoms, despite the fact that they occurred only in low numbers (Riegman and Kraay, 2001). Thus, the large variation in the abundance of the three small phytoplankton size categories in Fig. 3 reflects most likely quite a large variation in growth conditions at the different stations.

In a grazing controlled population, loss-rates due to grazing (g) should, during given phases of the predator/prey-cycle, exceed gross growth-rates (μ) of the prey. Since it is impossible to directly measure μ for given size categories or species of plankton in the field, only a tentative estimate can be given on the basis of the Clorophyll concentration as a measure of phytoplankton carbon biomass, and in situ primary production as a measure of gross carbon biomass increase per day. Both parameters measured by Riegman and Kraay (2001) indicate that - when a Chl-a/C-ratio of 50 is applied - gross growth rate for the phytoplankton community as a whole varied between 0.3 and 1.0 d^{-1}, whereas the present loss-rates due to grazing hardly exceeded 0.2 d^{-1}. However, other Chl-a/C-ratios lead to widely different values for μ and it is at present impossible, also because phytoplankton loss-rates due to lysis are unknown and grazing loss-rates may be underestimated, to compare g and μ on the basis of the available data. However, the fact that loss-rates in the picophytoplankton covary with their abundance (Fig. 5) may indicate that grazing is density dependent, which is a basic requirement for grazing control. Excluding one FLB-experiment which apparently failed (the Ecotone station of Transect 1), the other 8 measured FLB loss-rates show an exponential relation with the bacterial abundance in the original water, suggesting that grazing control in bacteria is even stronger than in picophytoplankton. The fact that bacterial abundance varied less between stations than the abundance of the picoalgae (Fig. 4) supports this view. We could find no relation between prey density and loss-rate due to grazing in the algae of 2–5 μm and 5–10 μm in diameter and it is hardly conceivable, therefore, that grazing regulated the abundance of the nanophytoplankton. This does not fit into the generally accepted size differential grazing control concept (Riegman et al., 1993; Riegman and Kuipers, 1994; Armstrong, 1994; Franks, 2001). According to that view, grazers gradually increase in size and decrease in growth-rate with increasing size of the prey until the point where the grazer-type shifts from the dividing protists to the sexually reproducing mesozooplankton for which a numerical response takes many days. This fundamental difference is generally regarded as the reason why, during the exponential phase of plankton blooms, pico- and nanophytoplankton stay under control of their protist grazers while net-phytoplankton can exhibit uncontrolled biomass increases. According to Riegman and Kraay (2001), the 2–5 μm phytoplankton in the Faroe-Shetland Channel consisted mainly of *Prasinophyceae* and *Chrysophyceae*, which are too small as food for copepods but too large for heterotrophic nanoflagellates. Microzooplankton, mainly ciliates ranging in size between 10 to 100 μm, were most likely the grazers of this category. Perhaps, the larger of these protist grazers could not exhibit the fast numerical response needed to dampen the changes in nanophytoplankton abundance, because their maximum division rates were lower than those of

their prey. In the Faroe-Shetland Channel, the regulation of abundance by a tight grazing control seemed to be restricted to only the microbial food web, or to prey below 2-μm in size.

Acknowledgements

We wish to thank the officers and crew of RV 'Pelagia' and the NIOZ technicians for their support during the cruise, Gijs Kraay and Marcel Veldhuis for their flow cytometry expertise and Gerhard Herndl for his help in improving the manuscript.

References

Armstrong, R.A., 1994. Grazing limitation and nutrient limitation in marine ecosystems: Steady state solutions of an ecosystem model with multiple food chains. Limnol. Oceanogr. 39, 597–608.

Baretta, J.W., Ebenhöh, W., Ruardij, P., 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model. Neth. J. Sea Res. 33, 233–264.

Baretta-Bekker, J.G., Baretta, J.W., Koch Rasmussen, E., 1995. The microbial food web in the European Regional Seas Ecosystem Model. Neth. J. Sea Res. 33, 363–379.

Chisholm, S.W., 1992. Phytoplankton size. In: Falkowski, P.G., Woodhead, A. (Eds.), Primary Production and Biochemical Cycles in the Sea. Plenum, New York, pp. 213–238.

Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, R.M., Tanner, S., Chavez, F.P., Ferioli, L., Sakamoto, C., Rogers, P., Millero, F., Steinberg, P., Nightingale, P., Cooper, D., Cochlan, W.P., Kudela, R., 1996. A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the Equatorial Pacific Ocean. Nature 383, 495–501.

Franks, P.J.S., 2001. Phytoplankton blooms in a fluctuating environment: the role of plankton response time scales and grazing. J. Plankton Res. 23, 1433–1441.

Hansen, B., Larsen, K.H.M., Østerhus, S., Turrell, B., Jónsson, S., 1999. The Atlantic Water inflow to the Nordic Seas. Internat. WOCE Newslett. 35, 33–35.

Hobbie, J.E., Daley, R.J., Jasper, S., 1977. Use of Nucleopore filters for counting bacteria by fluorescence microscopy. Appl. Environ. Microbiol. 33, 1225–1228.

Kiørboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Adv. Mar., 1–72.

Landry, M.R., Hassett, R.P., 1982. Estimating the grazing impact of marine micro-zooplankton. Mar. Biol. 67, 283–288.

Riegman, R., Kraay, G.W., 2001. Phytoplankton community structure derived from HPLC analysis of pigments in the Faroe-Shetland Channel during summer 1999: the distribution of taxonomical groups in relation to physical/chemical conditions in the photic zone. J. Plankton Res. 23, 191–205.

Riegman, R., Kuipers, B.R., 1994. Resource competition and selective grazing of plankton in a multispecies pelagic food web model. Mar. Ecol. 15, 153–164.

Riegman, R., Kuipers, B.R., Noordeloos, A.A.M., Witte, H.J., 1993. Size-differential control of phytoplankton and the structure of plankton communities. Neth. J. Sea Res. 31, 255–265.

Sherr, E.B., Sherr, B.F., 1993. Protistan grazing rates via uptake of fluorescently labeled prey. In: Kemp, P.F., Sherr, B.F., Sherr, E.B., Cole, J.J. (Eds.), Handbook of Methods in Aquatic Microbial Ecology. Lewis Publishers, Boca Raton, pp. 695–703.

Sherwin, T.J., Turrell, W.R., Jeans, D.R.G., Dye, S., 1999. Eddies and a mesoscale deflection of the slope current in the Faroe-Shetland Channel. Deep-Sea Res. I 46, 415–438.

Thingstad, T.F., 1992. Modelling the microbial food web structure in pelagic ecosystems. Arch. Hydrobiol. Beih. Ergebn. Limnol. 37, 111–119.